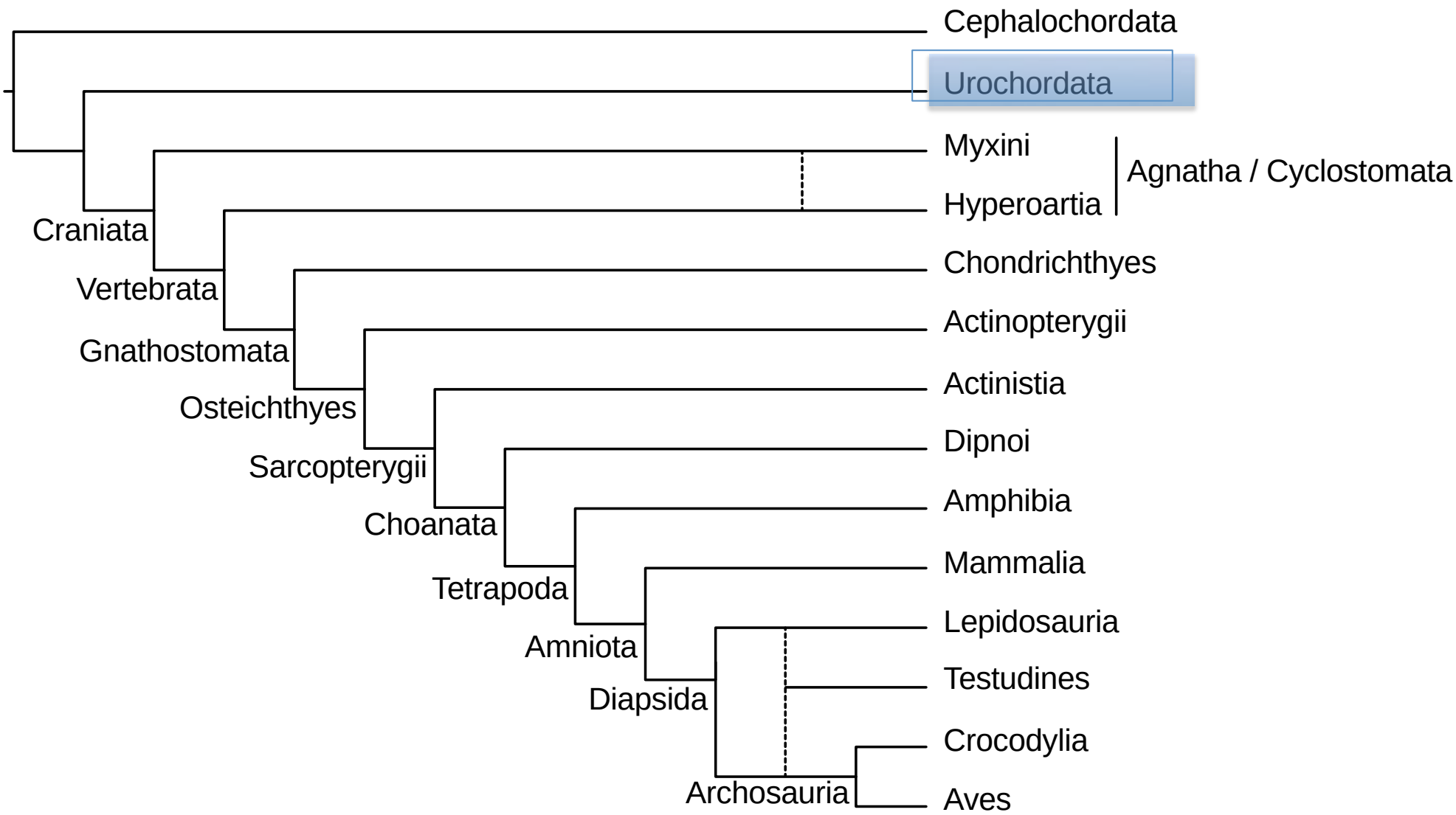
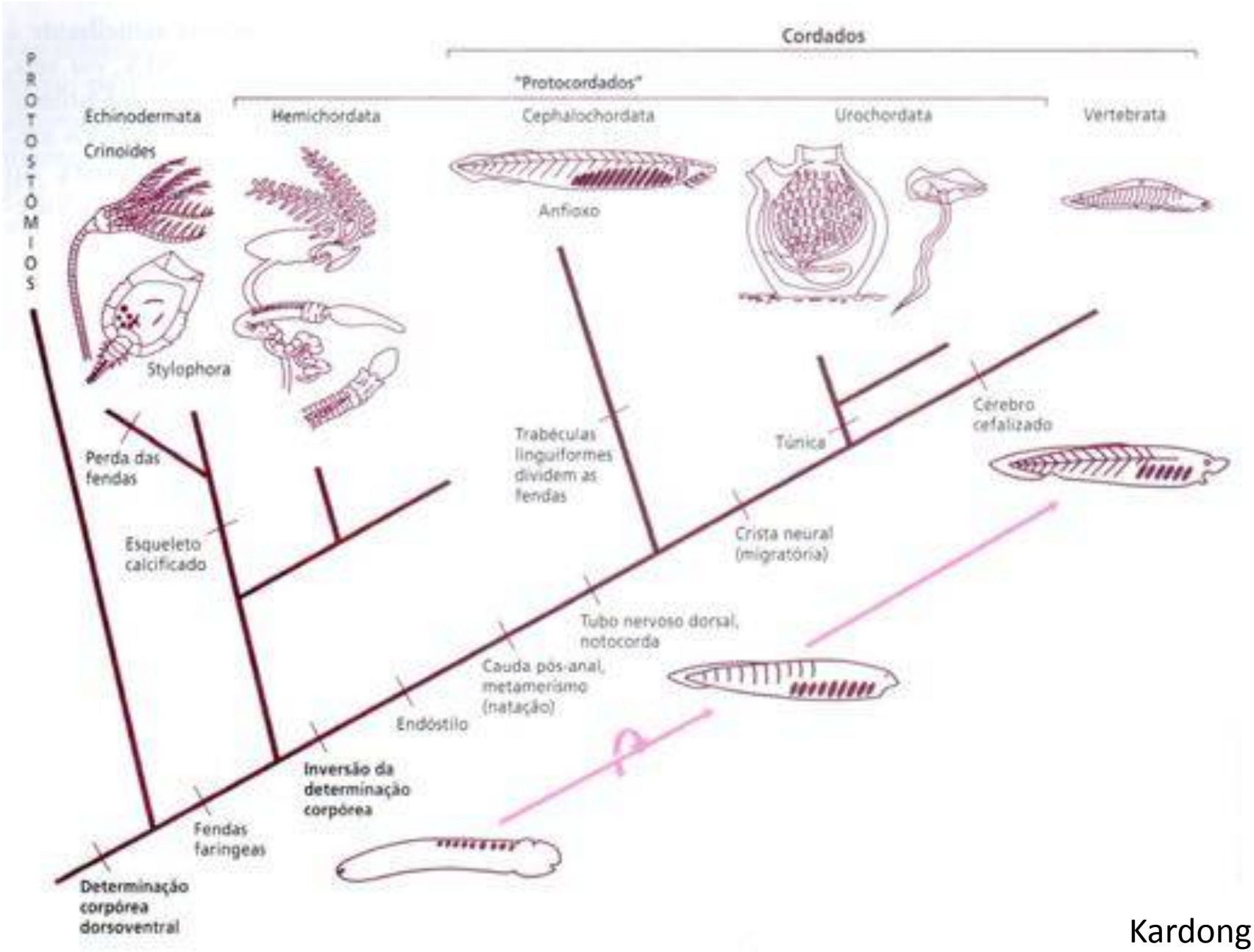
Filogenia de Chordata

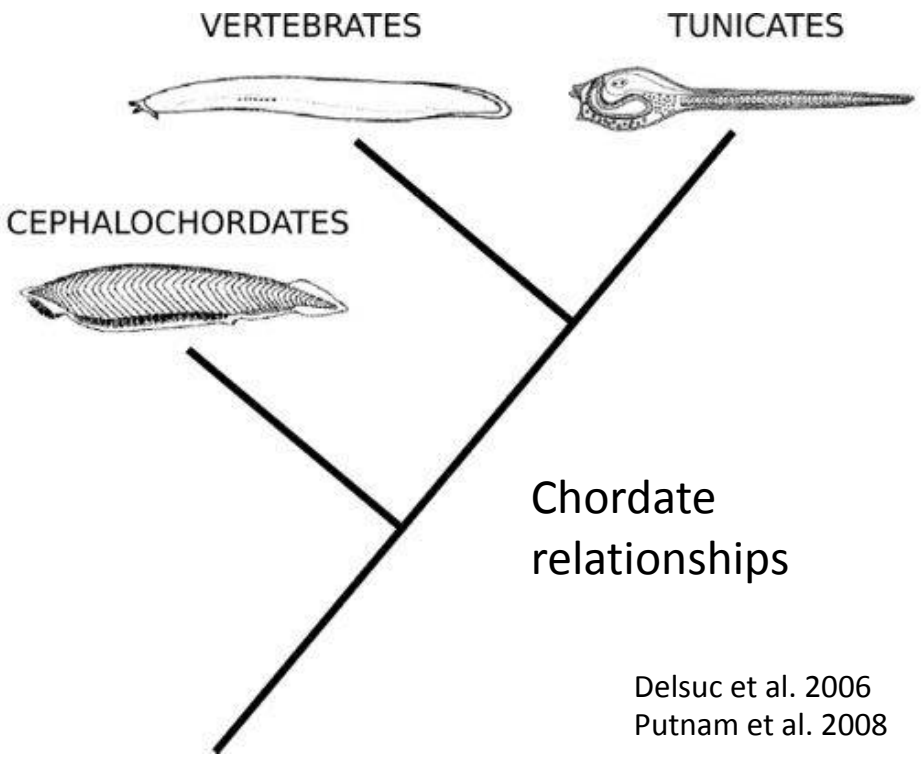


Construindo um cordado



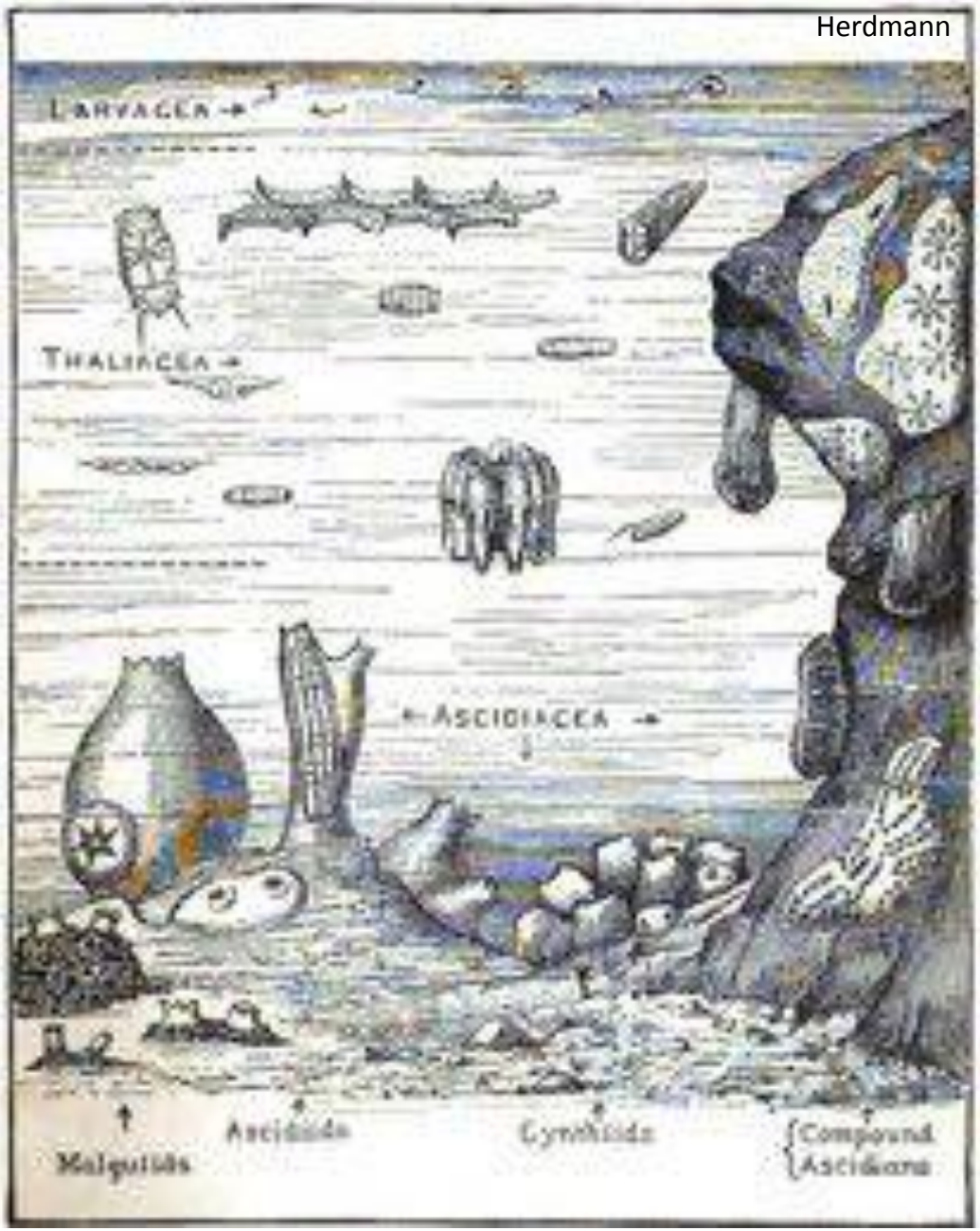
Kardong

The Tunicates



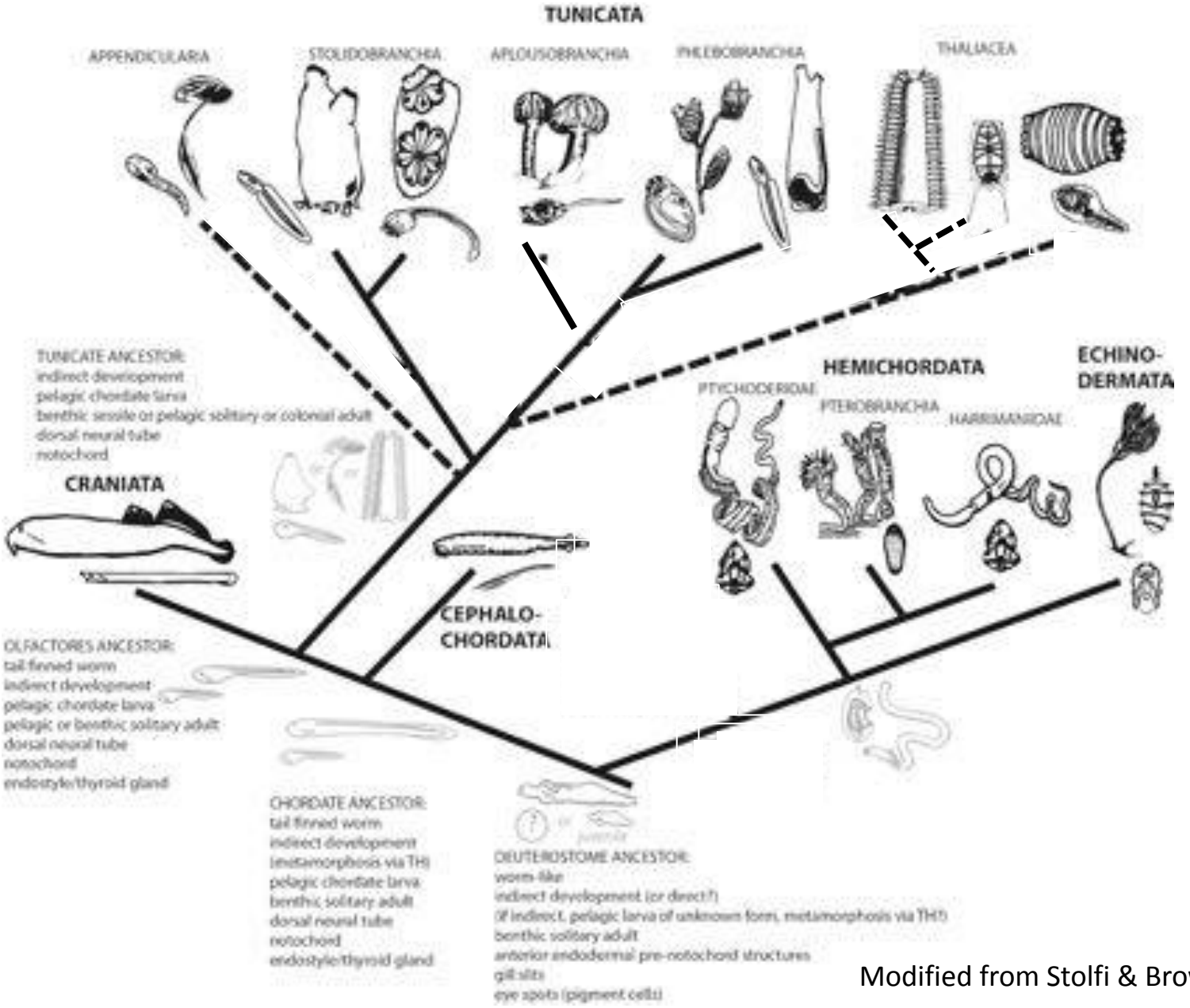
Chordate relationships

Delsuc et al. 2006
Putnam et al. 2008



Tunicata

- Cordados invertebrados (de nosso próprio filo!)



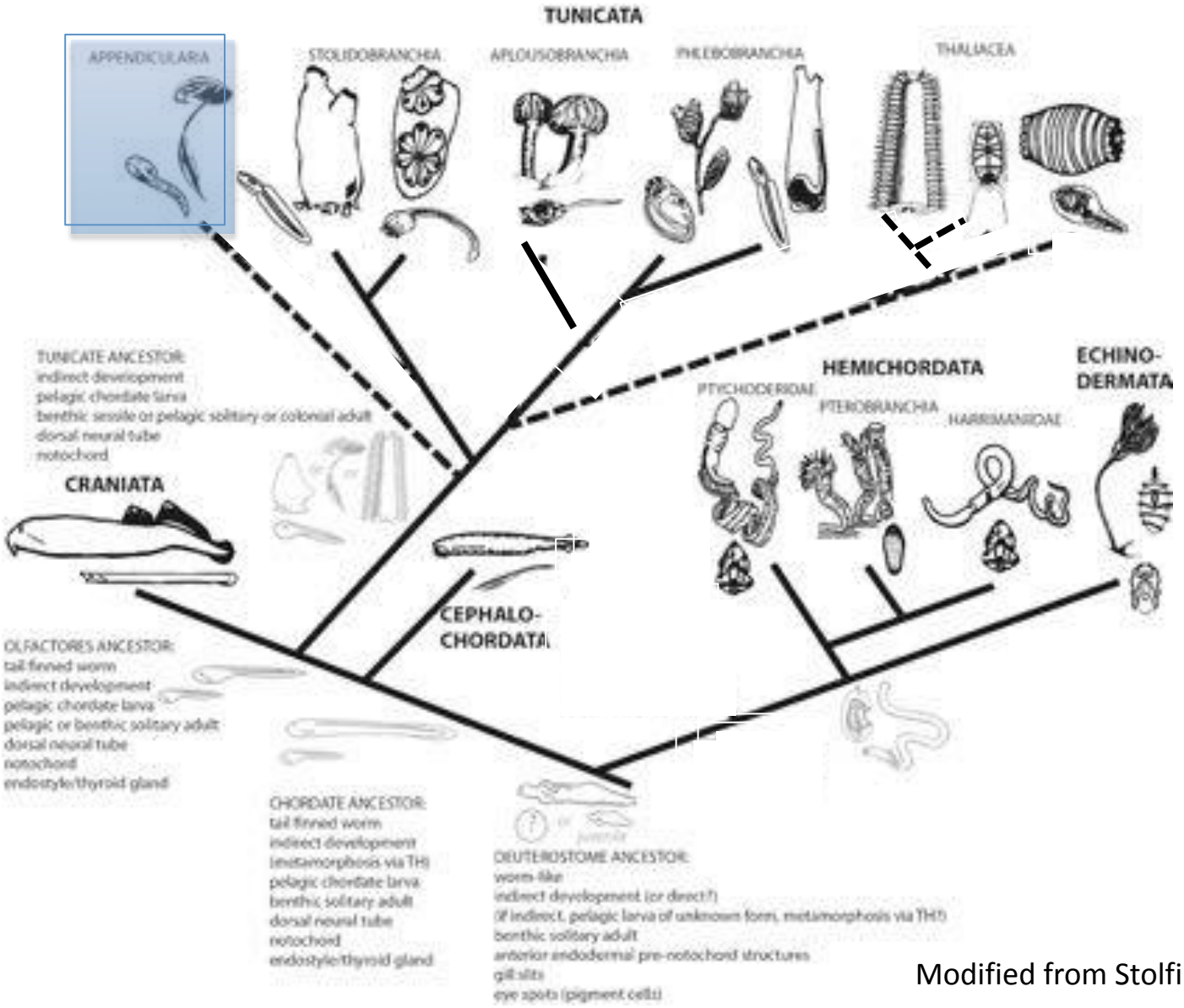
Modified from Stolfi & Brown, 2015

Tunicados

- Pertencem ao filo chordata (juntos conosco)
- São os invertebrados mais próximos aos vertebrados
- Possuem uma túnica de celulose, sintetizada por uma celulose-sintase adquirida através da transferência genética horizontal (Matthysse et al. 2003)
- Nomes comuns: “esguichadores marinhos”, “mija-mija”, “Maria mijona”, ou “mijão”.

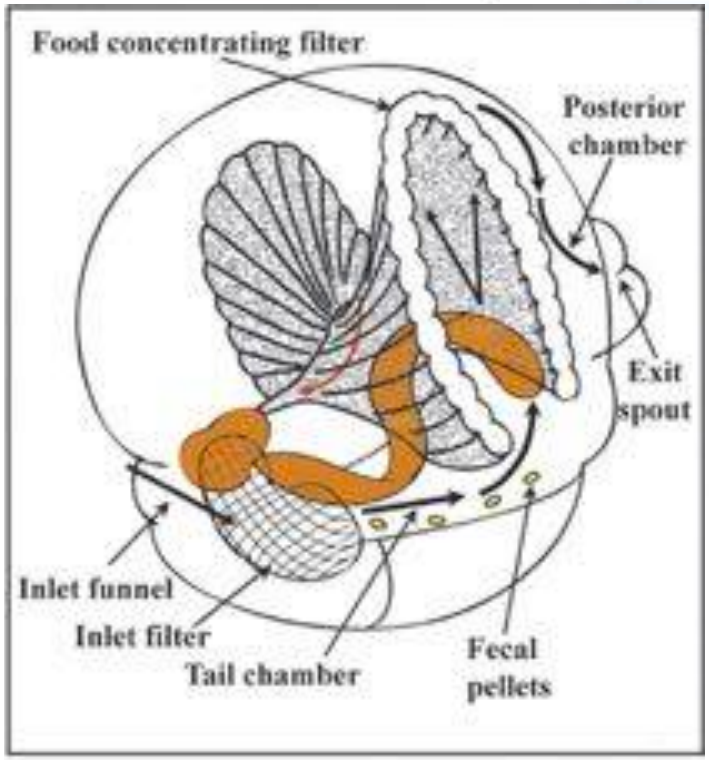
Tunicata

- Cordados invertebrados (de nosso próprio filo!)

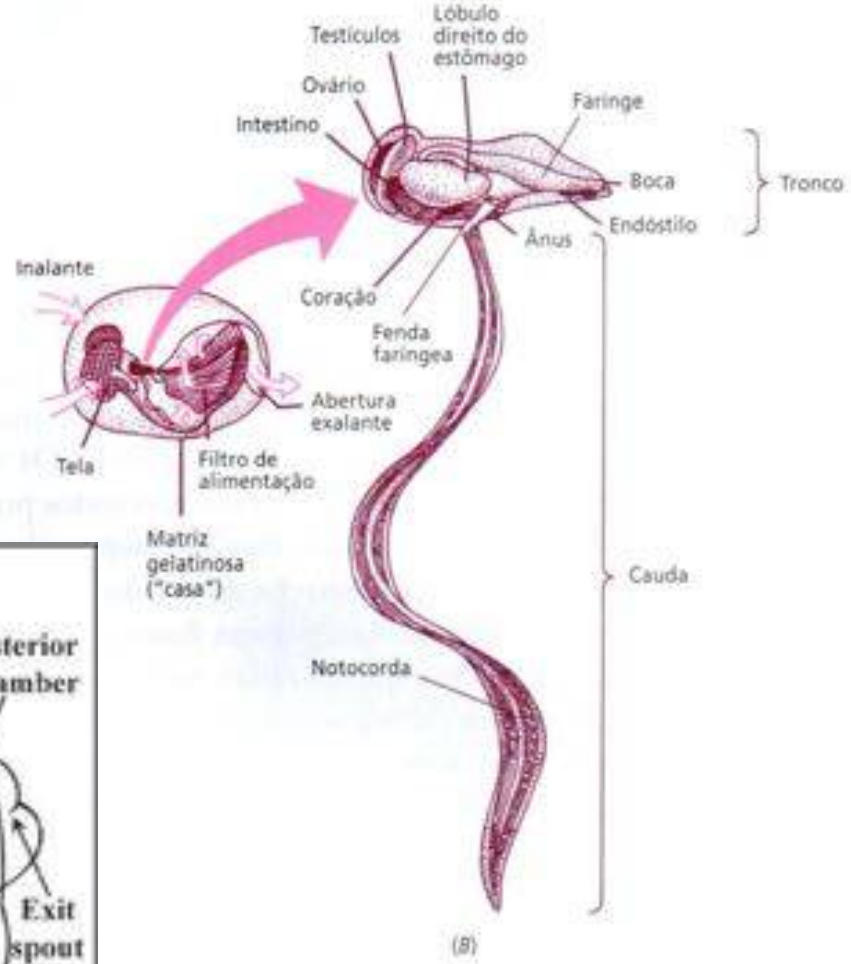


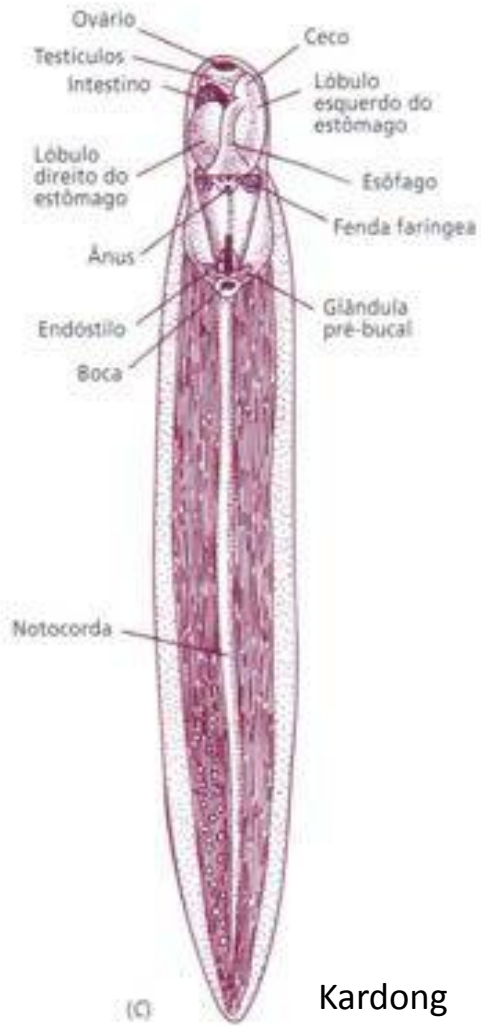
Modified from Stolfi & Brown, 2015

Appendicularia (larvaceos): neotenia?



Stolfi & Brown, 2015

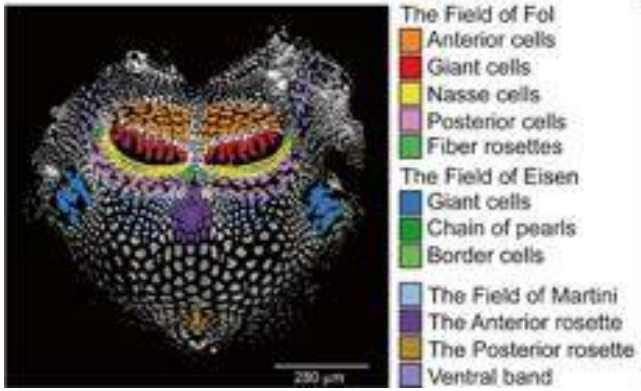


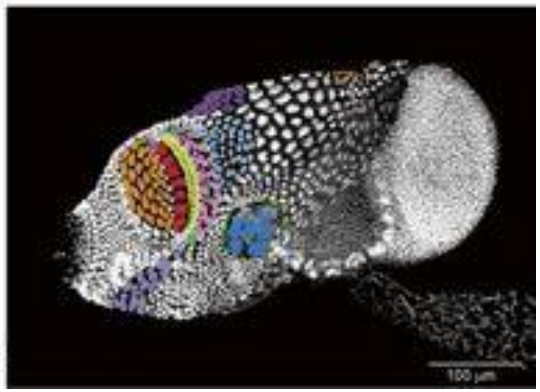


Kardong

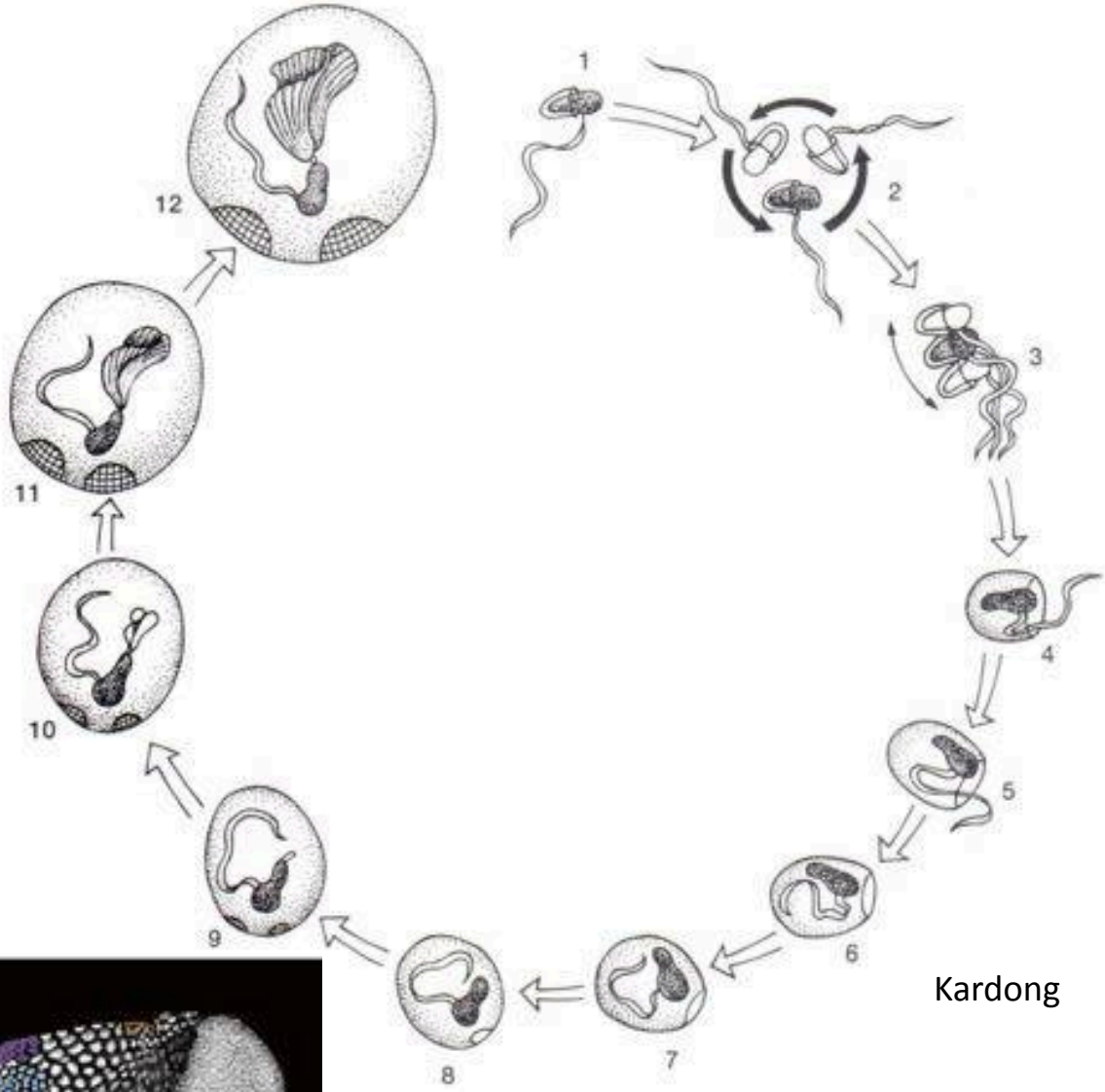
http://planktonchronicles.org/en/episode/larvaceans-their-houses-are-nets/

Appendicularia: construindo a casa





Stolfi & Brown

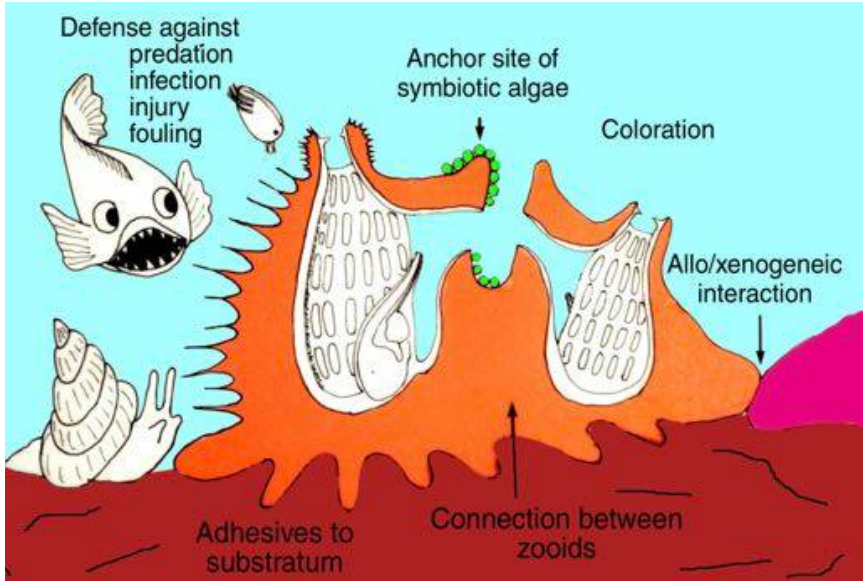


Kardong

Sinapomorfia dos tunicados: A tunica

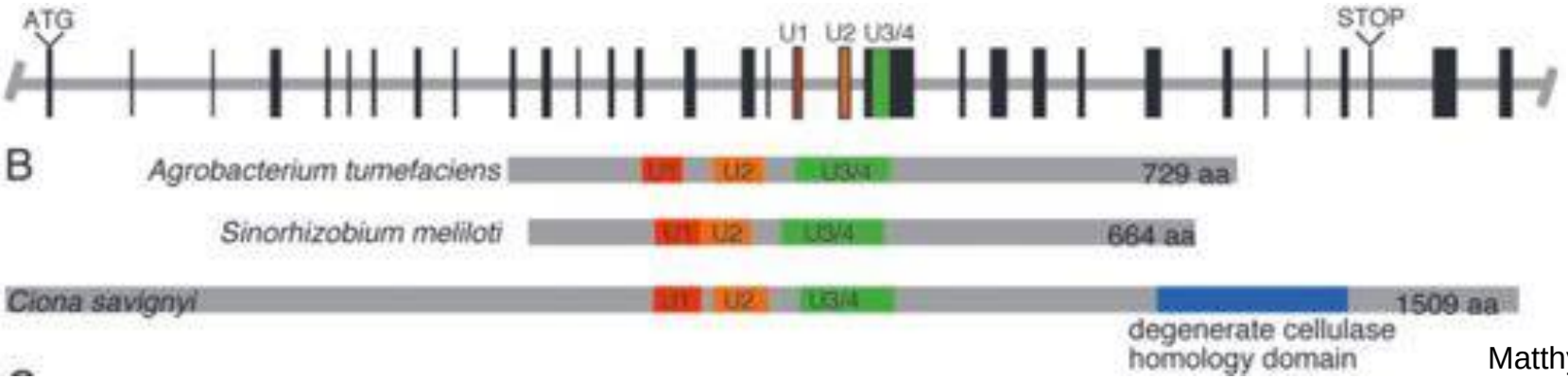
Características da túnica

-Defesa
-Evita adheção de outros organismos
-Pigmentada
-Espículas calcáreas dentro da túnica



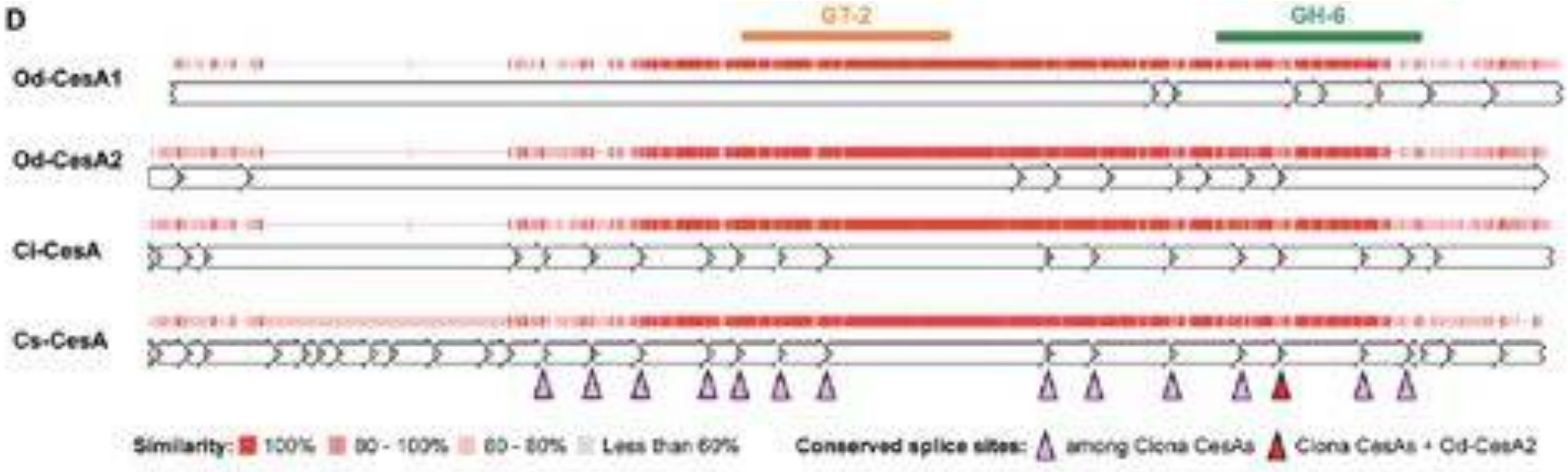
Creditos: E. Hirose

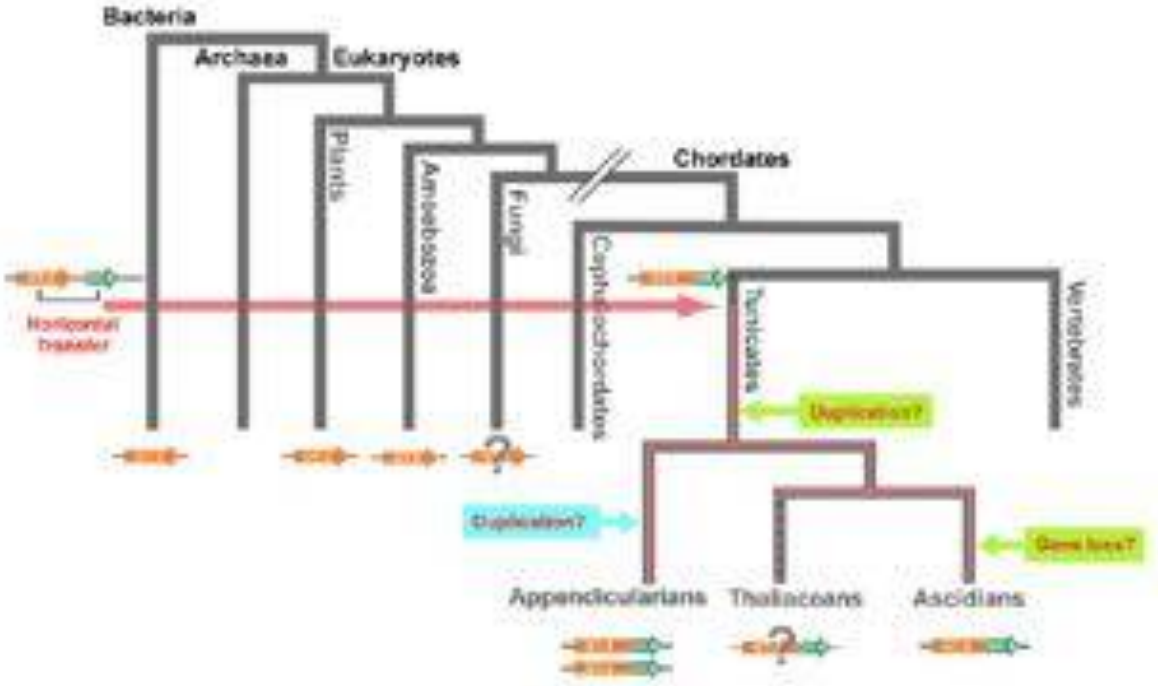
A célulo sintetasa:

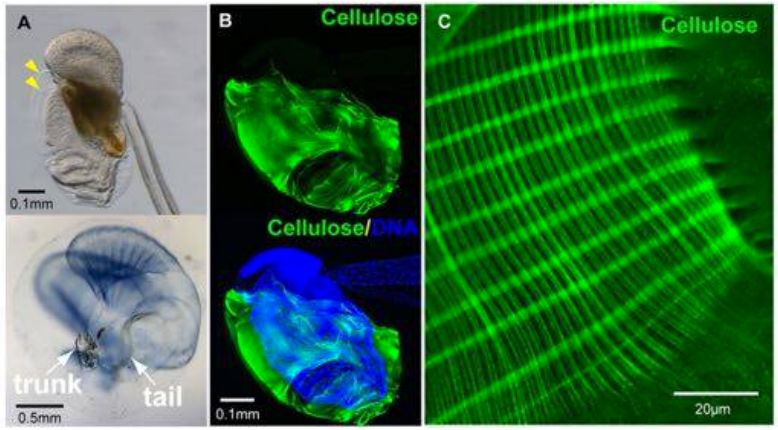


Matthysse, 2004

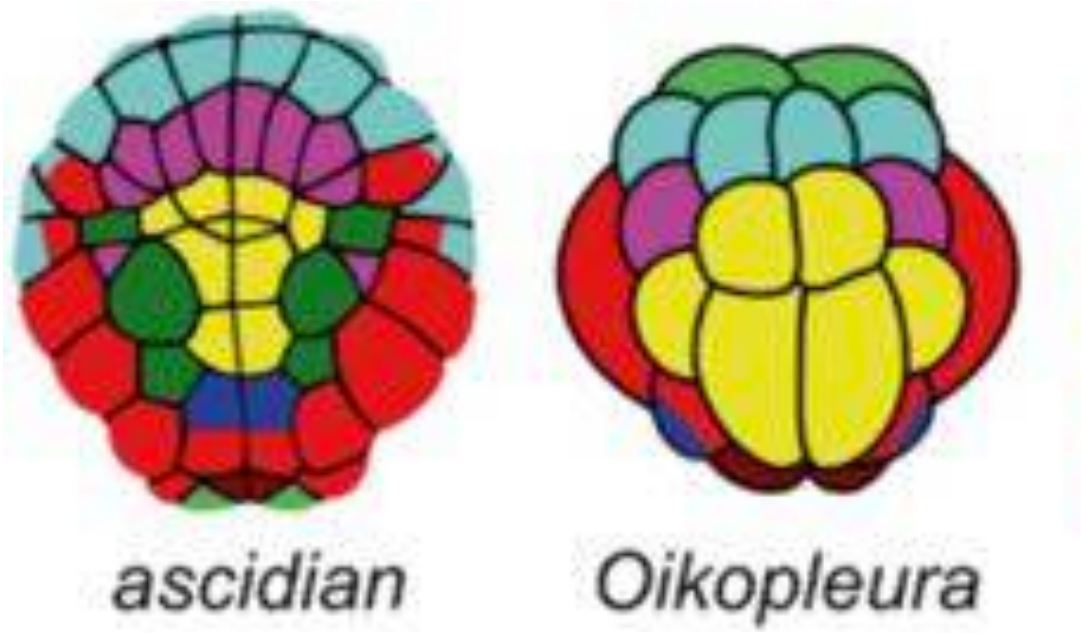
Celulo sintetasa em Oikopleura





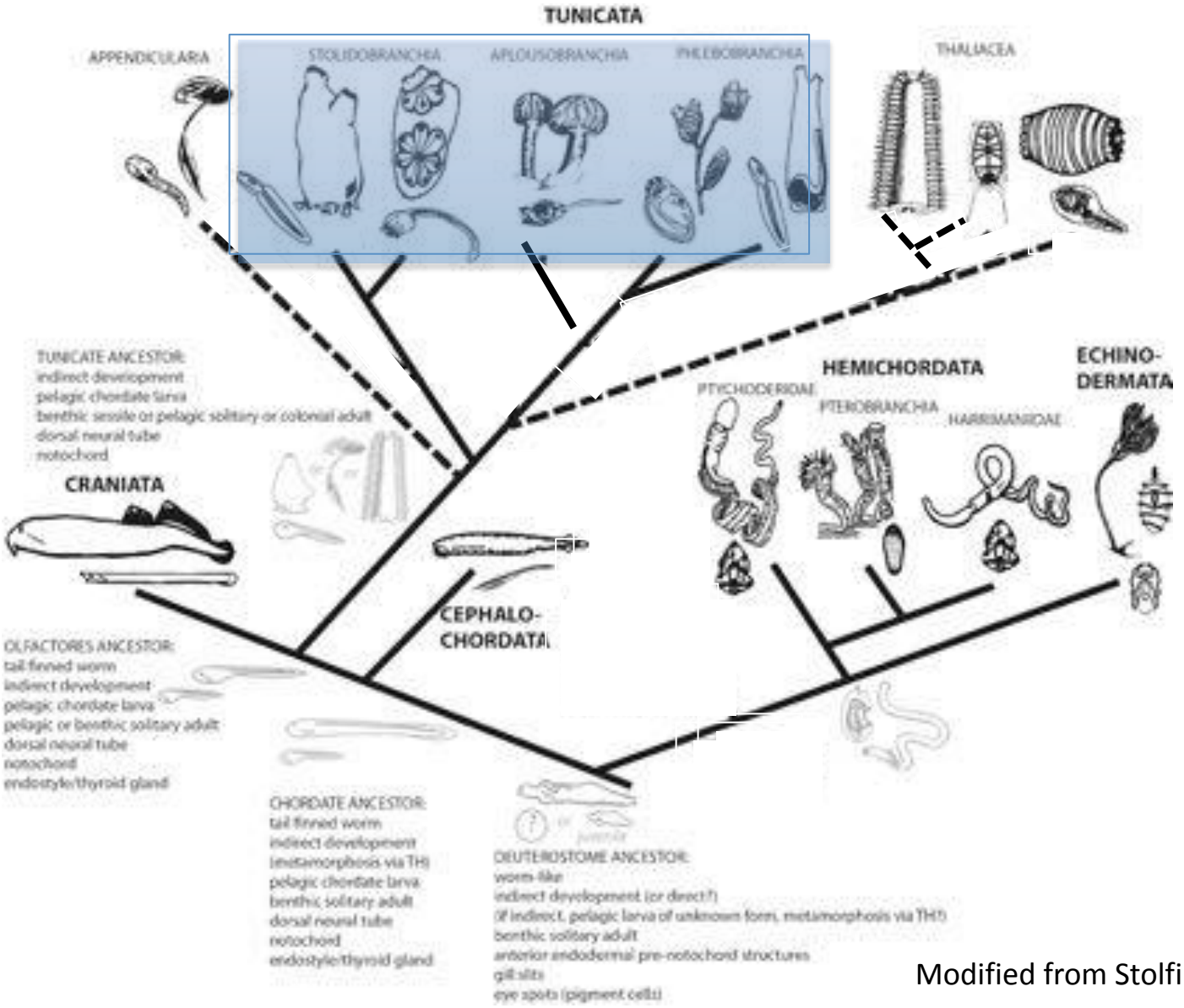


Appendicularia: reduction in cell numbers during development



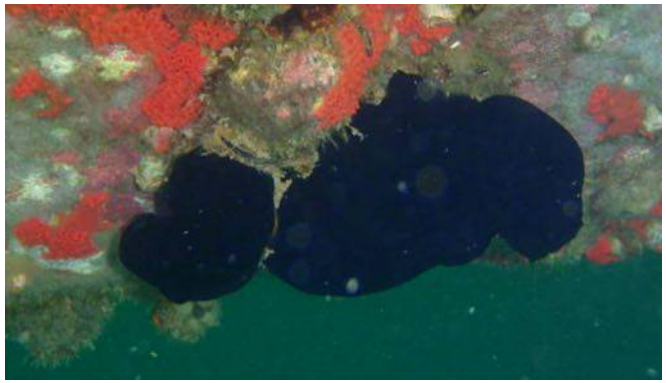
Tunicata

- Cordados invertebrados (de nosso próprio filo!)



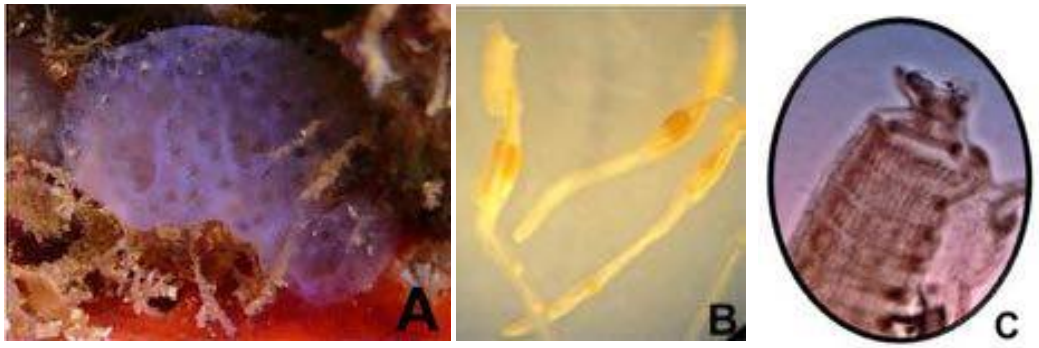
Modified from Stolfi & Brown, 2015

Ascidiaceae: ascidias

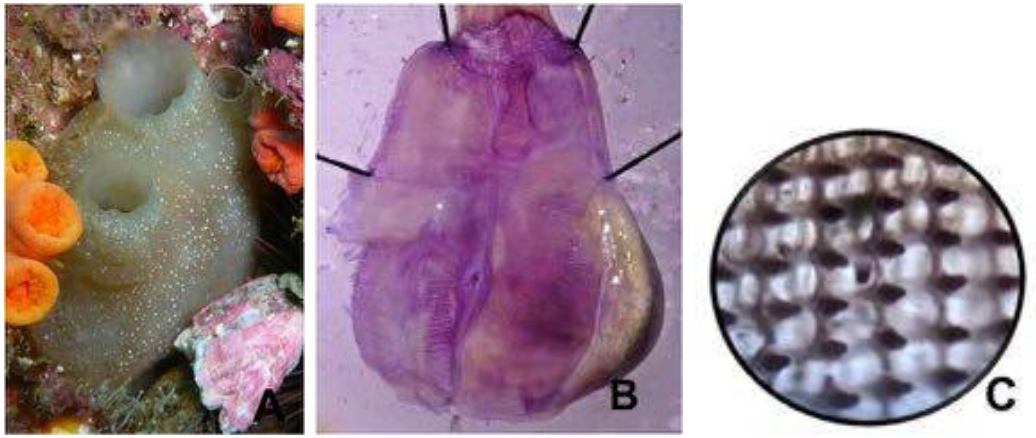


Ordens de Ascidiacea

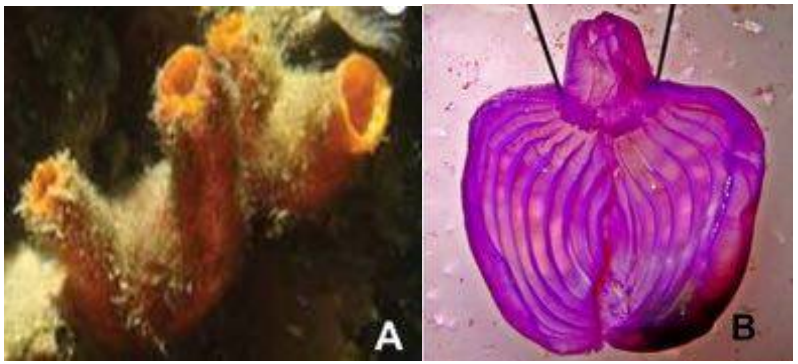
Aplousobranchia



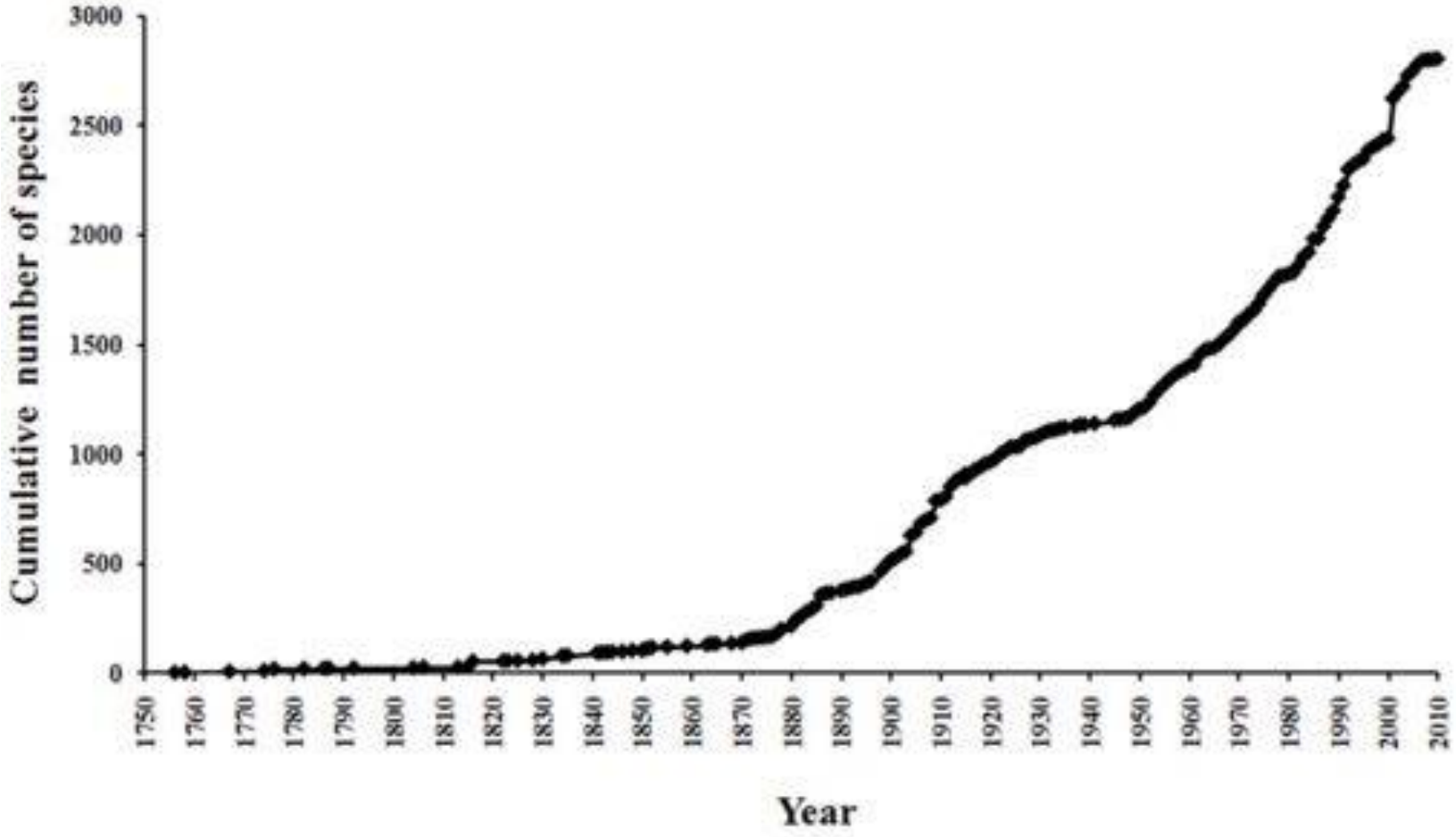
Phlebobranchia



Stolidobranchia



Diversidade de ascidias



Schenkar & Swalla (2011)

Diversidade de ascidias

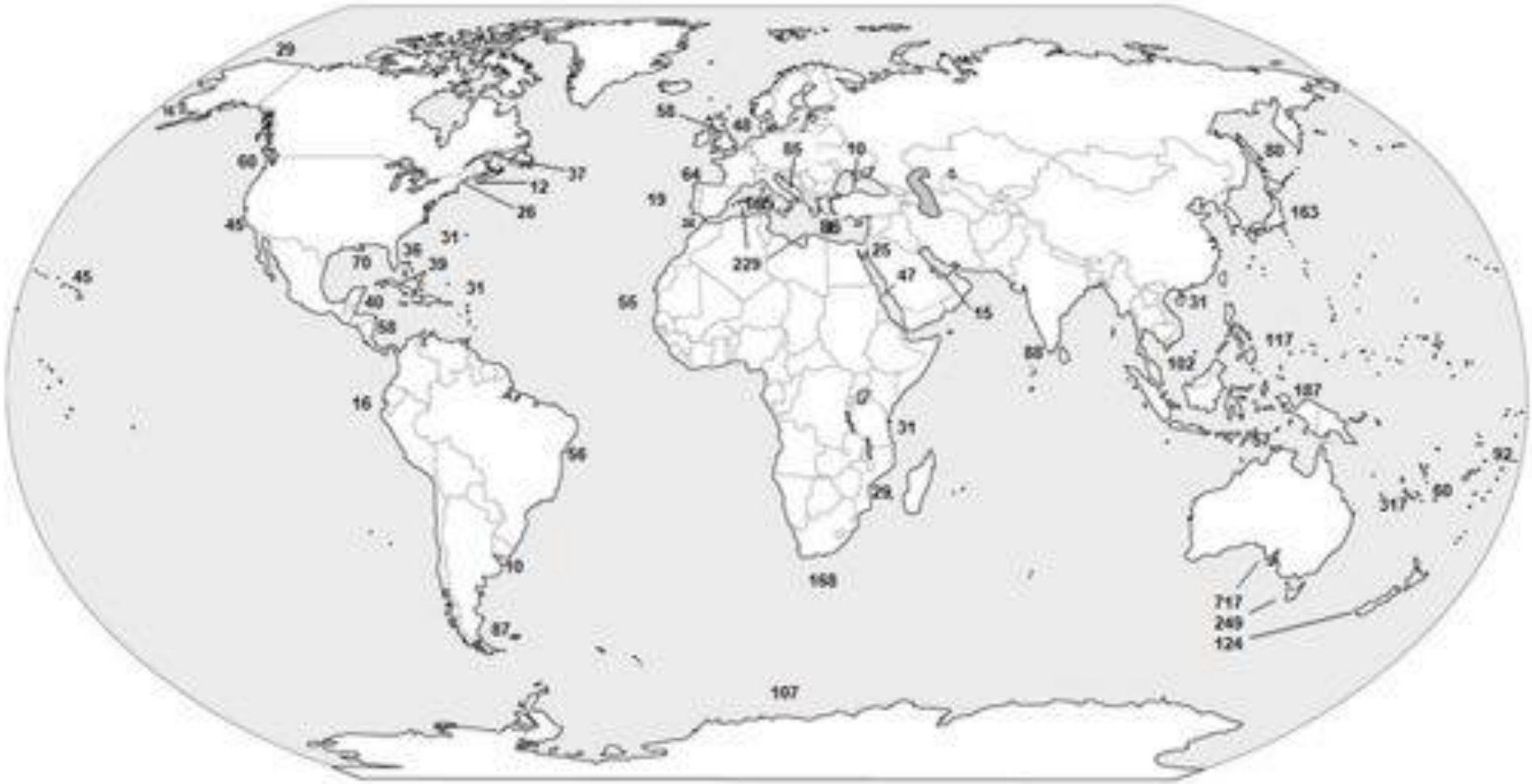
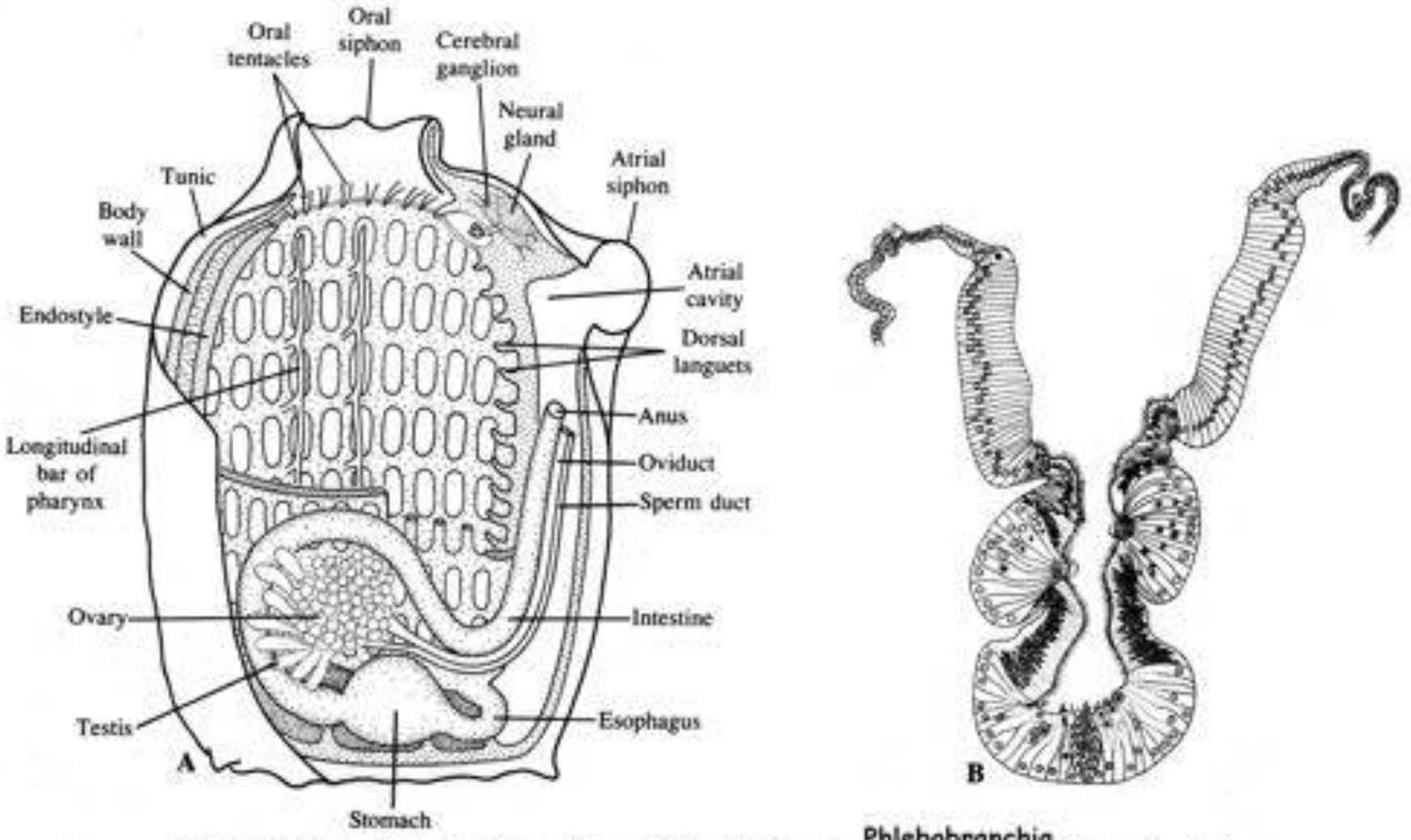


Figure 4. Ascidian global distribution (abyssal species not included).
doi:10.1371/journal.pone.0020657.g004

Schenkar & Swalla (2011)

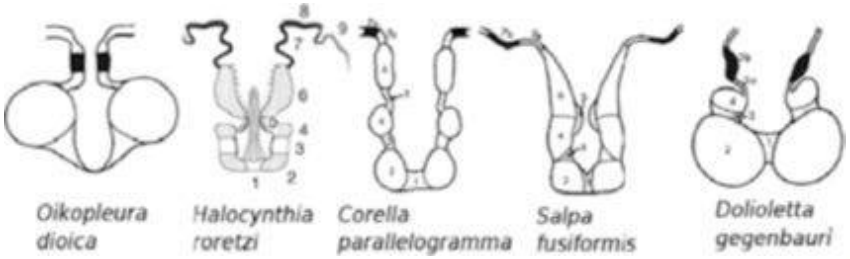
Ascidiacea: Anatomia do adulto

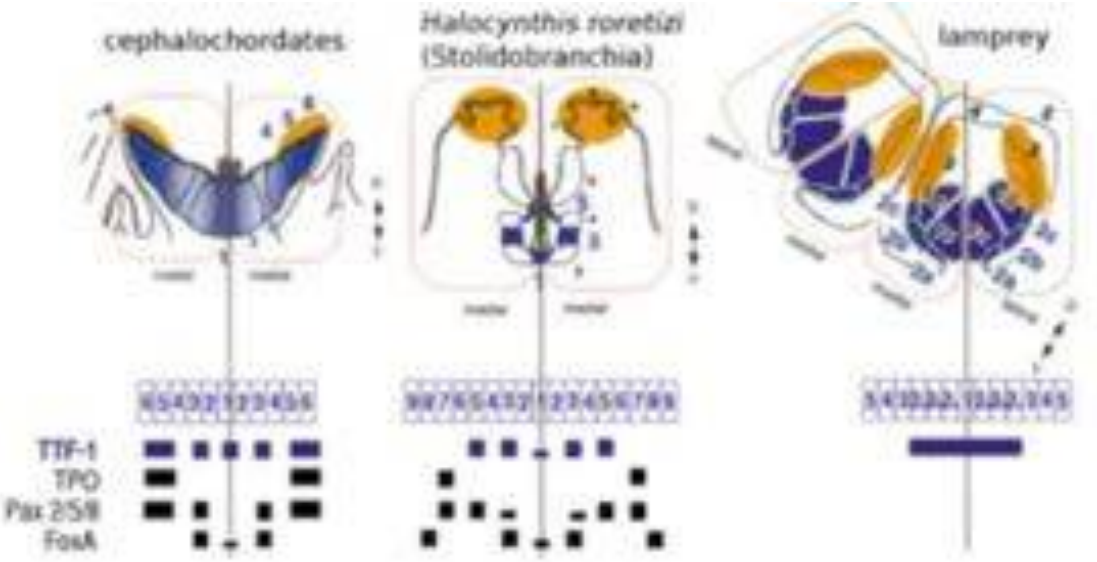


Phlebobranchia

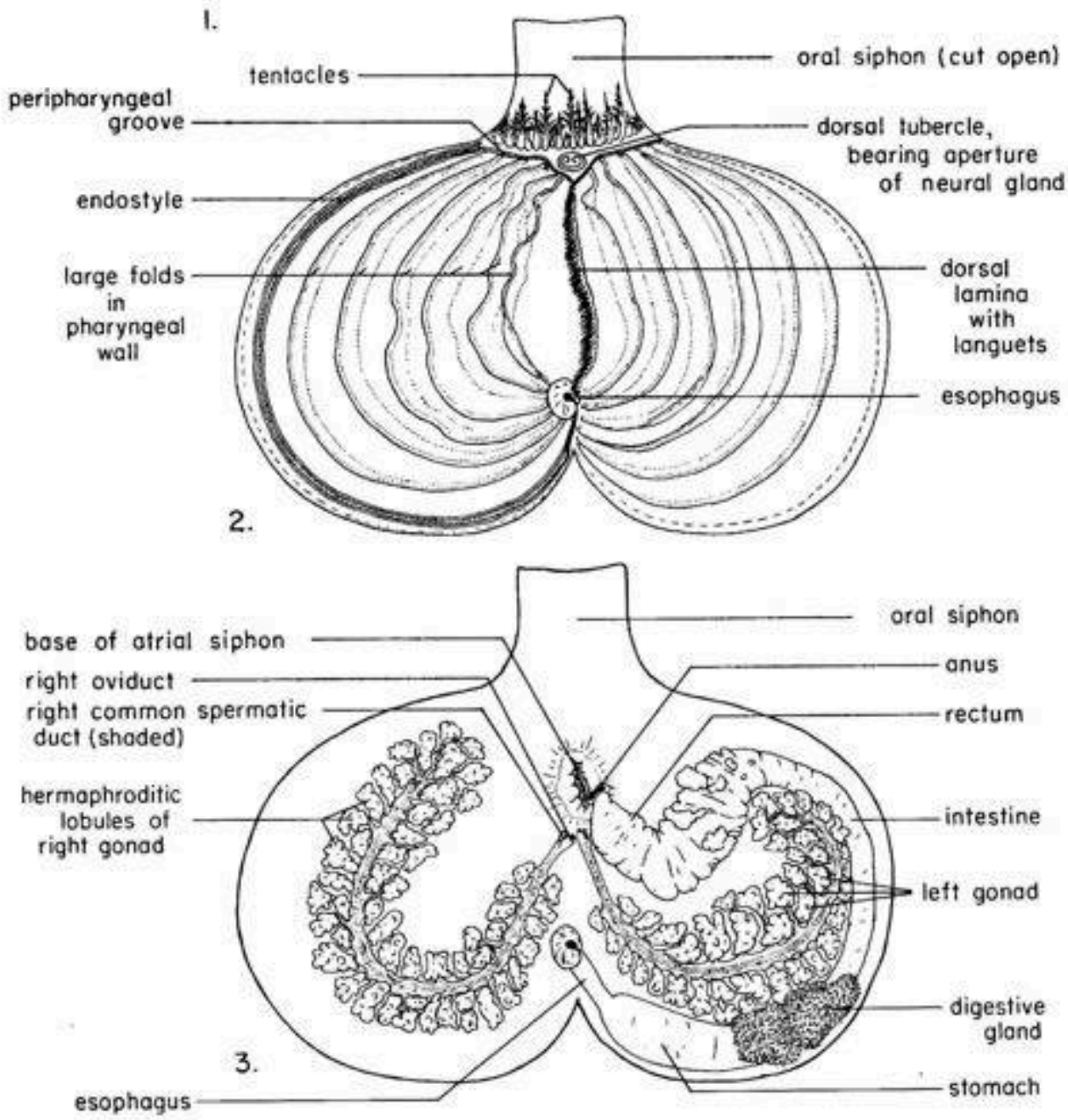
FIGURE 24.6 A. Diagram of a solitary ascidian of the order ~~Stolidobranchia~~. The tunic, body wall, and most of the wall of the pharynx have been removed on the observer's side. Only two of the longitudinal bars of the pharynx are shown. (Mostly after Monniot and Monniot, Oceanography and Marine Biology, An Annual Review, *16*.) B. *Molgula manhattensis*, endostyle, transverse section. There are nine distict histological regions. (Godeaux and Firket, Annales des Sciences Naturelles, Zoologie, series 12, *10*.) From Kozloff EN 1990. Invertebrates. Saunders Publishing, p. 802

Endostilo (glándula thyroidea)

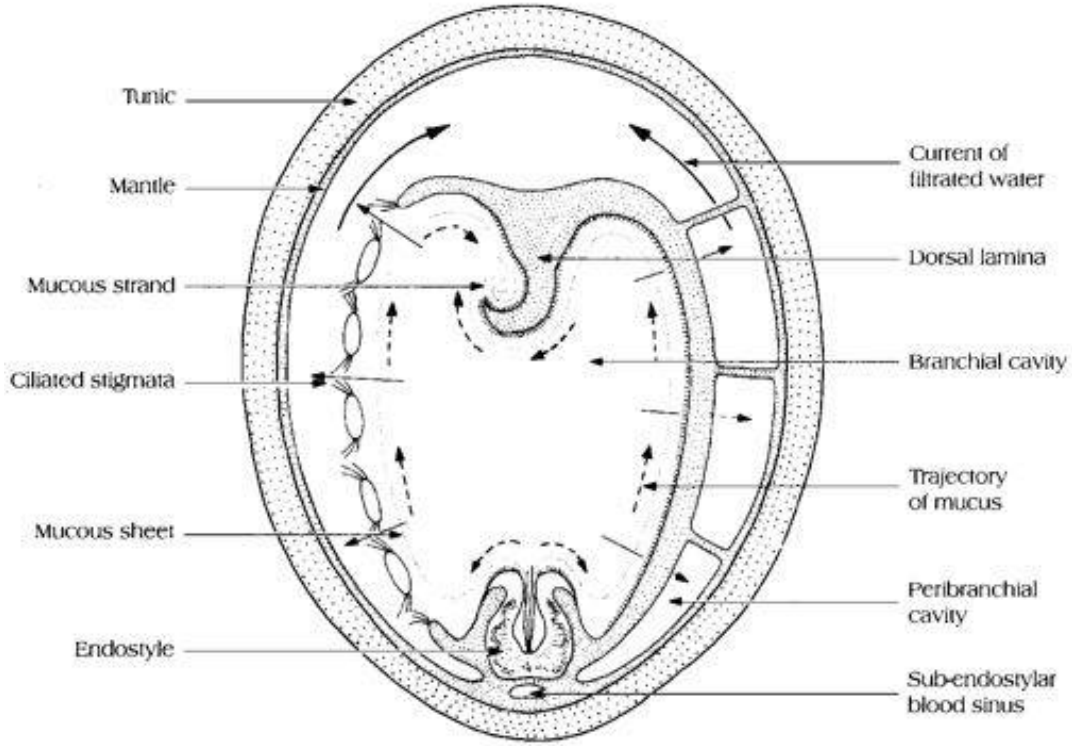




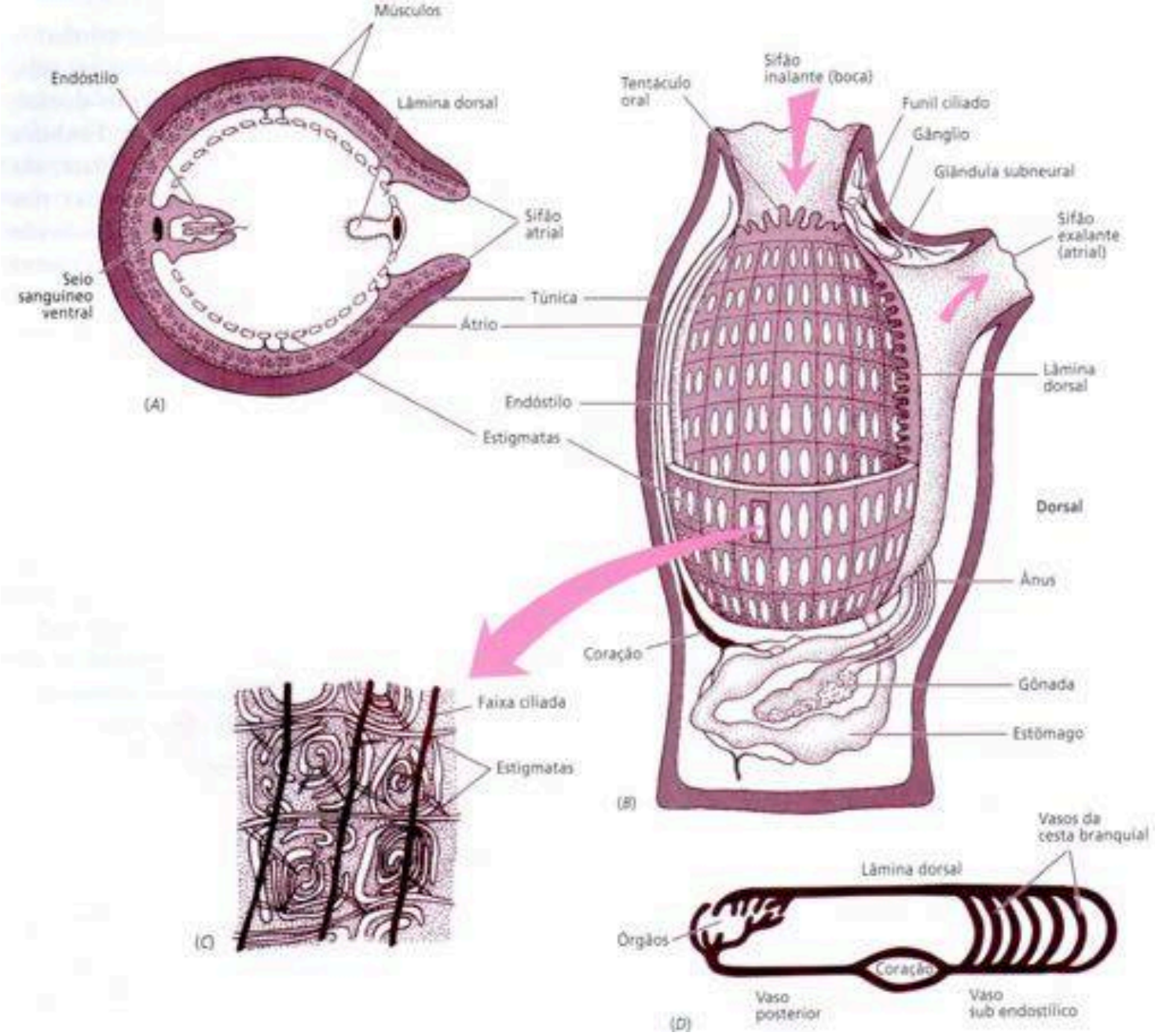
Ascidiacea: Anatomia do adulto



Alimentação



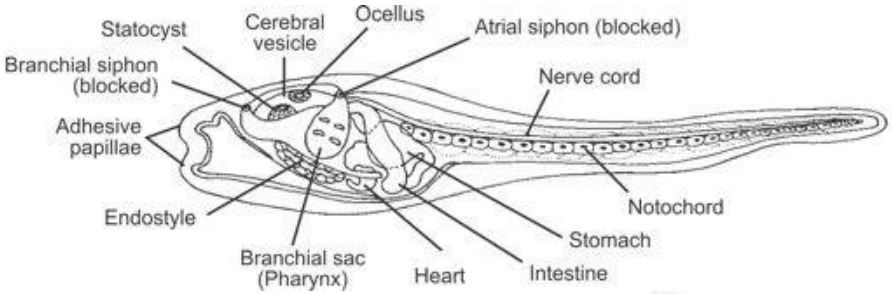
Circulação

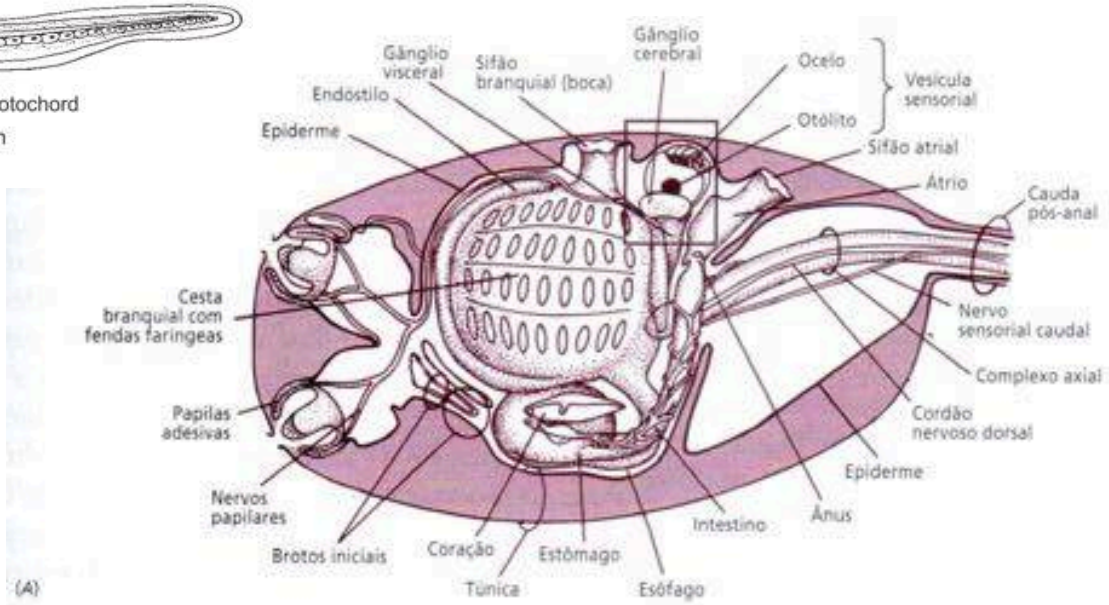

Músculos
Endóstilo
Lâmina dorsal
Sifão atrial
Seio sanguíneo ventral
(A)
Tentáculo oral
Sifão inalante (boca)
Funil ciliado
Gânglio
Glândula subneural
Sifão exalante (atrial)
Túnica
Átrio
Lâmina dorsal
Endóstilo
Estigmatas
Dorsal
Ânus
Coração
Gônada
Estômago
(B)
Faixa ciliada
Estigmatas
(C)
Vasos da cesta branquial
Lâmina dorsal
Órgãos
Coração
Vaso posterior
Vaso sub endostílico
(D)

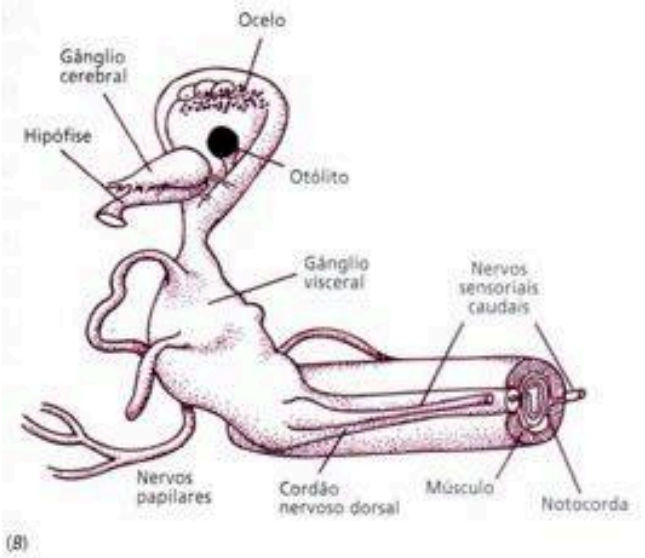
Circulação em *Symplegma brakenhielmi*

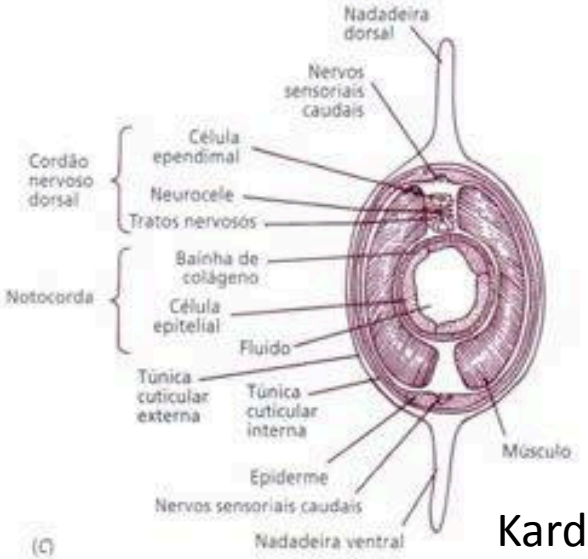
Cortesia de Stefania Gutierrez

Ascidiacea: Anatomia da larva



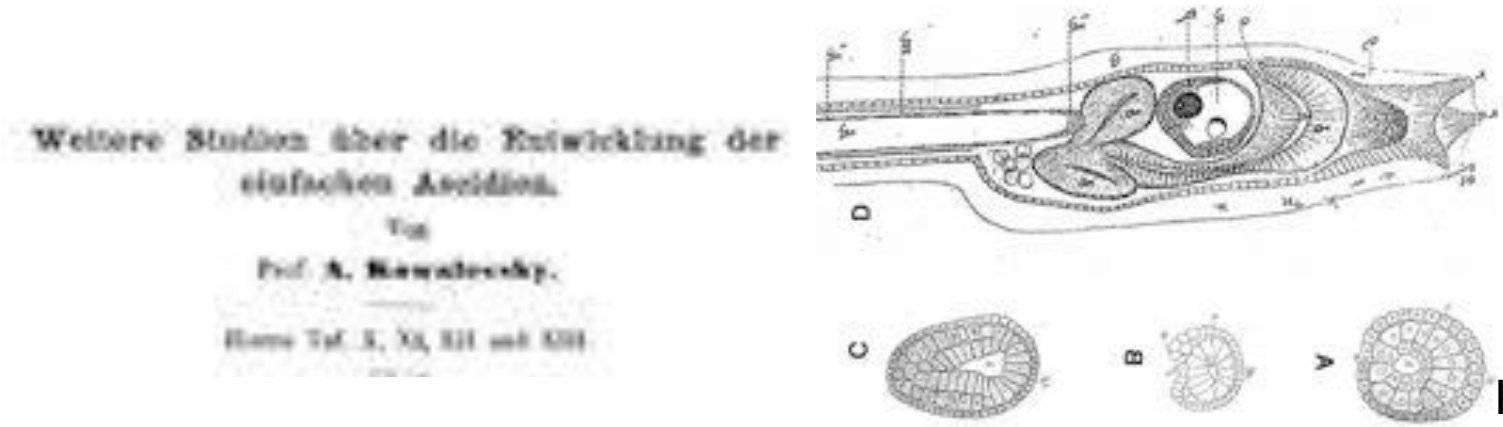




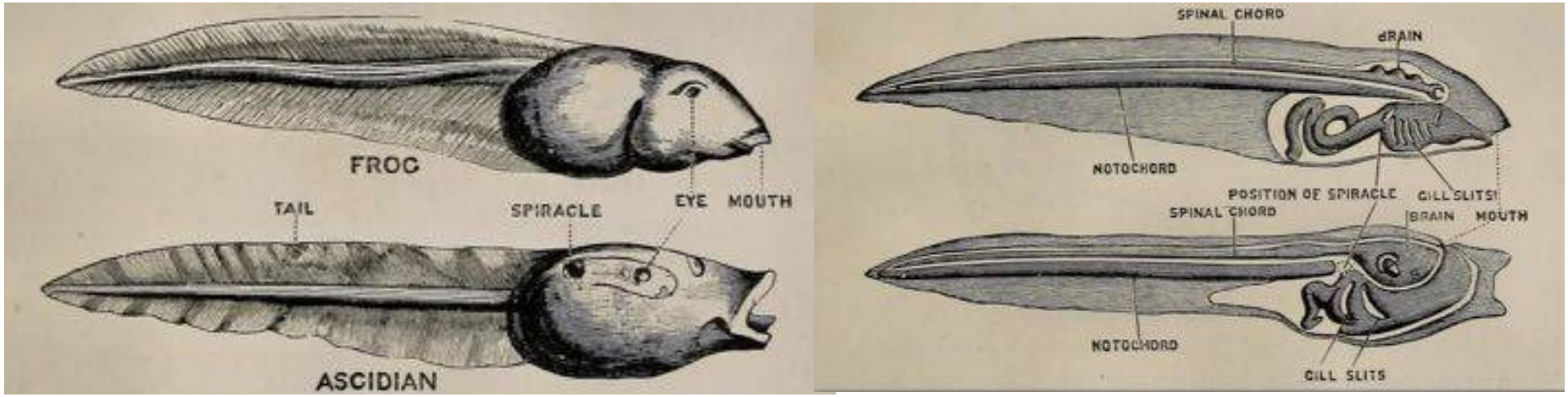


Kardong

A larva das ascídias: um corpo tipicamente cordado

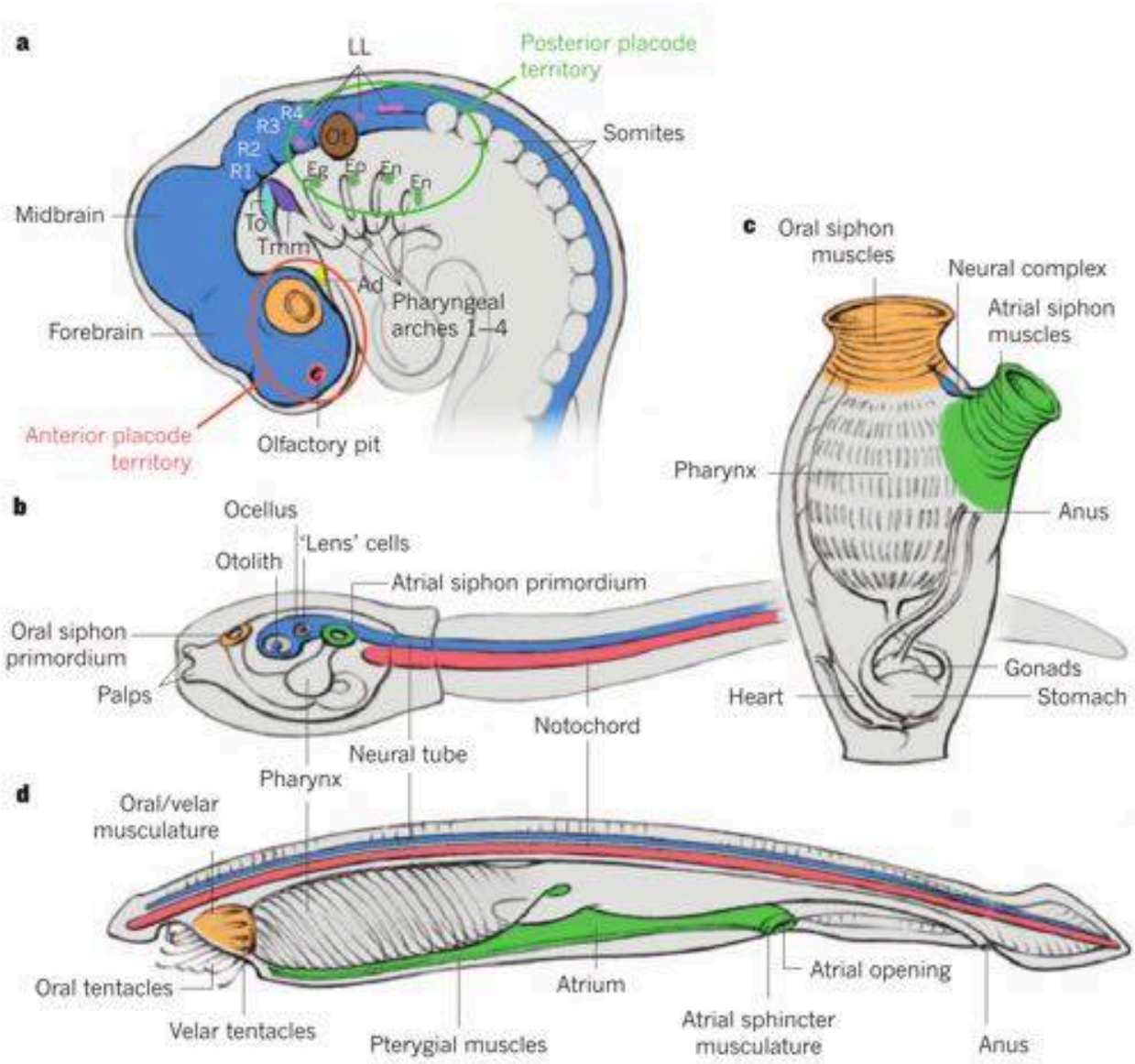


Kowalevski,1866



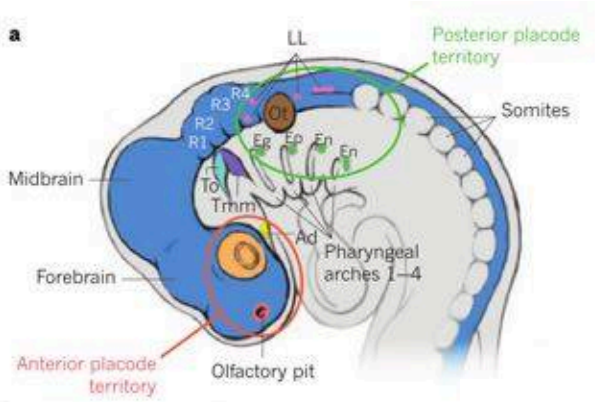
British Museum ,1901

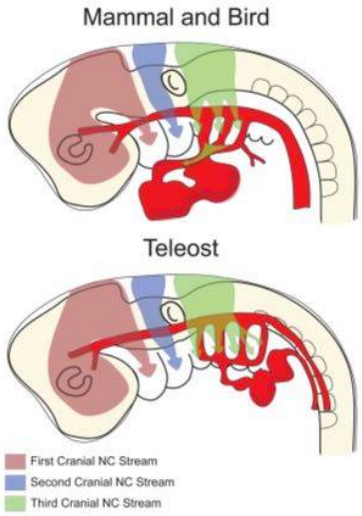
Placodes and branchiomeric muscles within chordates

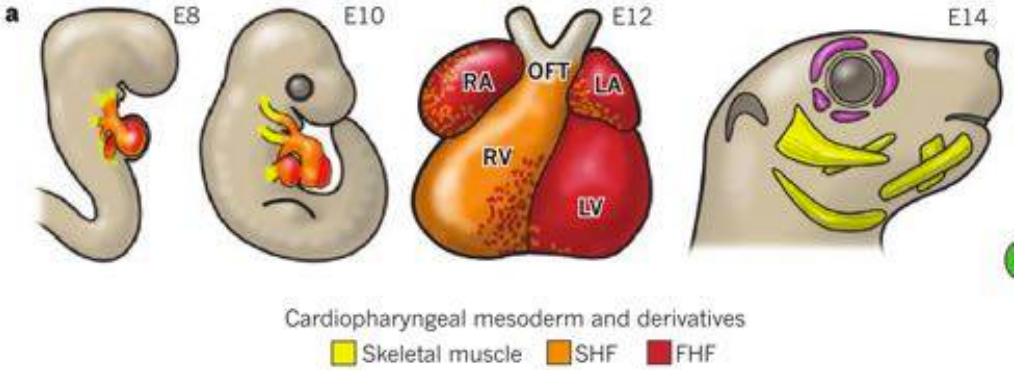


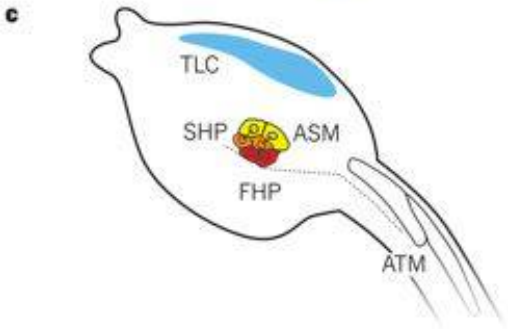
Diogo et al 2015

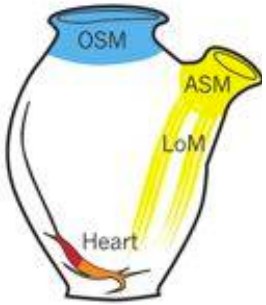
A new heart for a new head: modular muscle innovations from heart cardiopharyngeal precursors

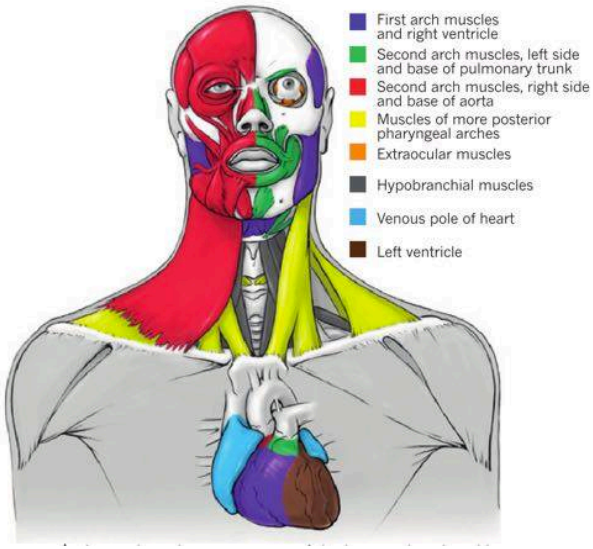






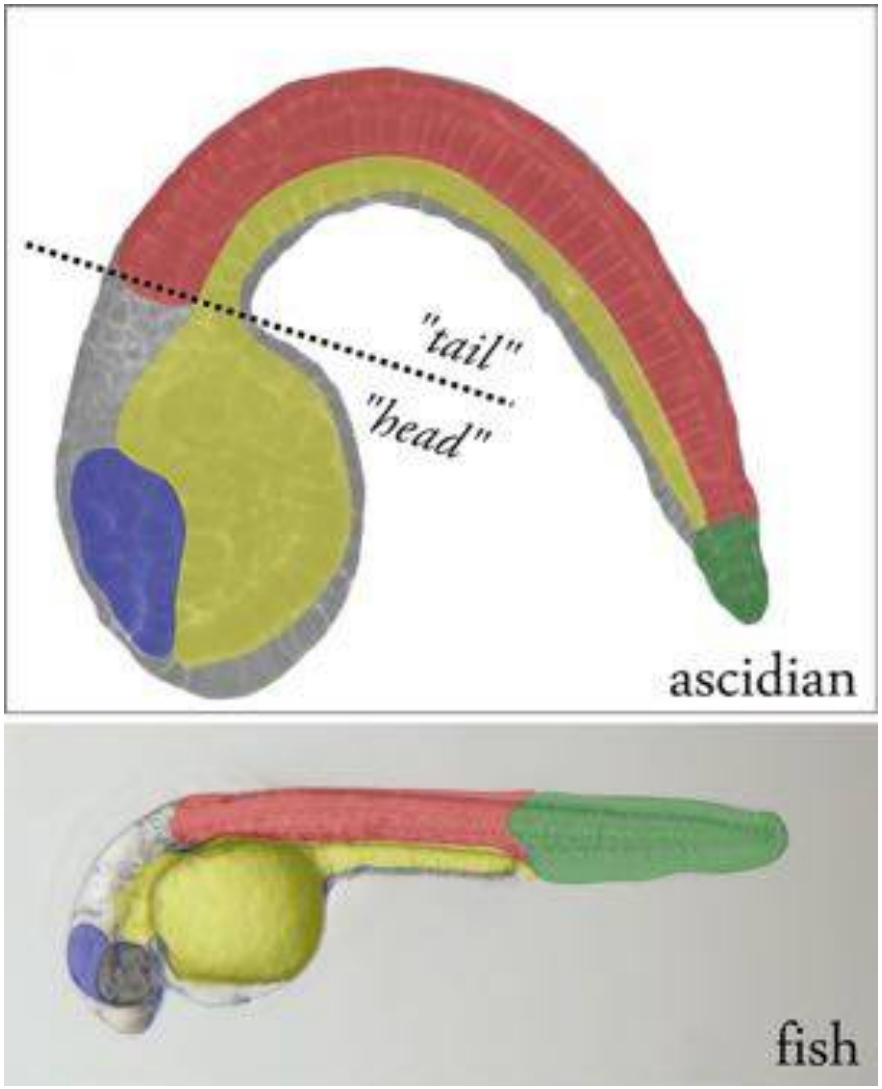




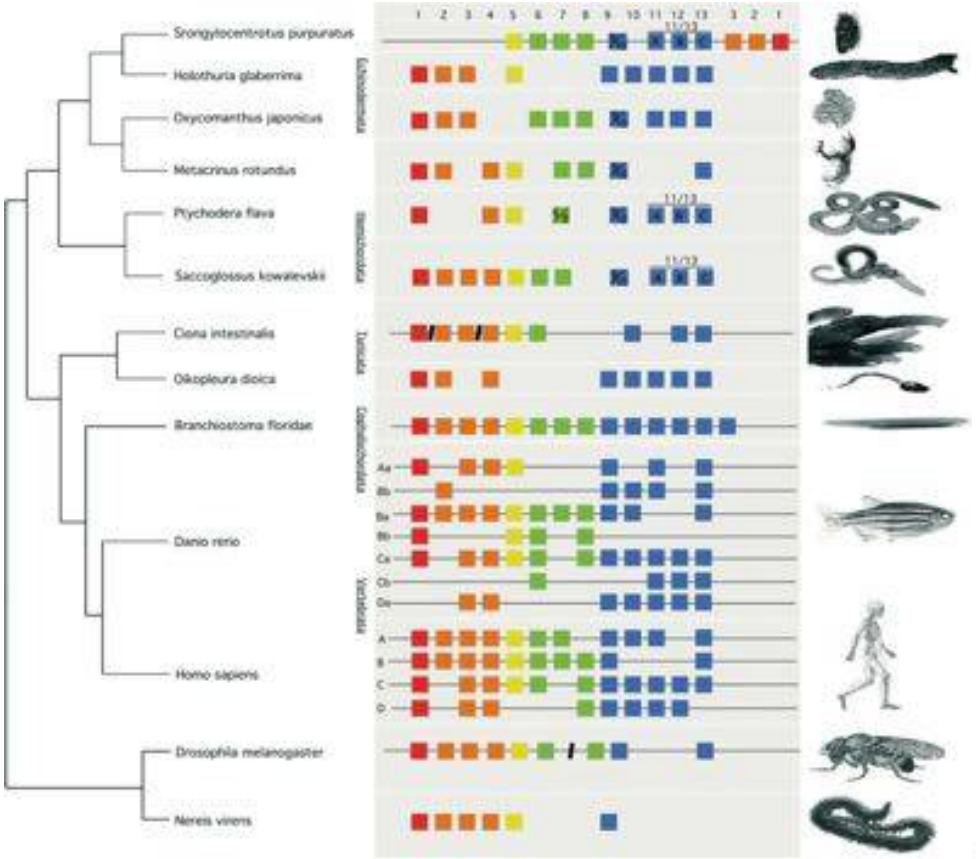


Diogo 2015

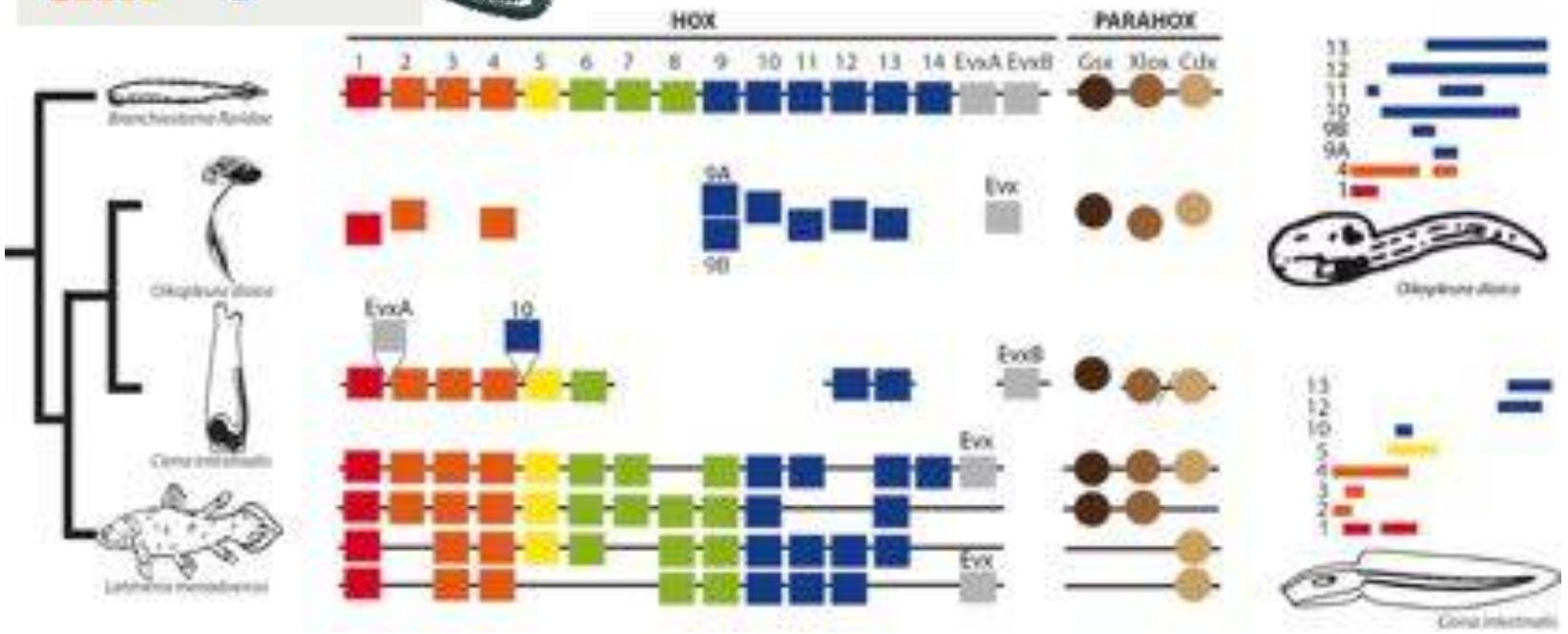
Comparison of ascidian and vertebrate embryo anatomies



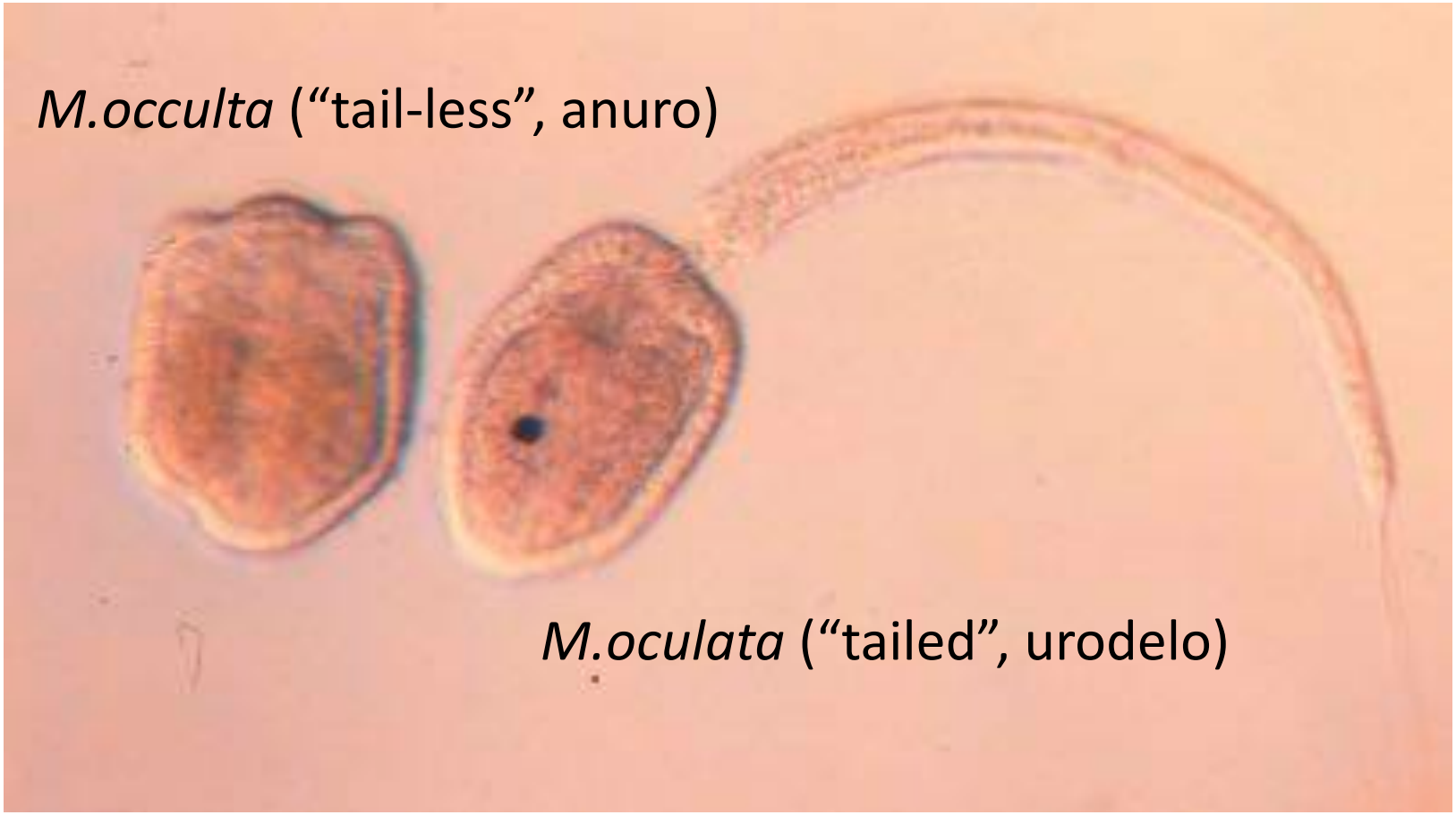
Stolfi & Brown, 2015


Strongylocentrotus purpuratus
Holothuria glaberrima
Oxycomanthus japonicus
Metacrinus rotundus
Ptychodera flava
Saccoglossus kowalevski
Ciona intestinalis
Oikopleura dioica
Branchiostoma floridae
Danio rerio
Homo sapiens
Drosophila melanogaster
Nereis virens

Genes Hox

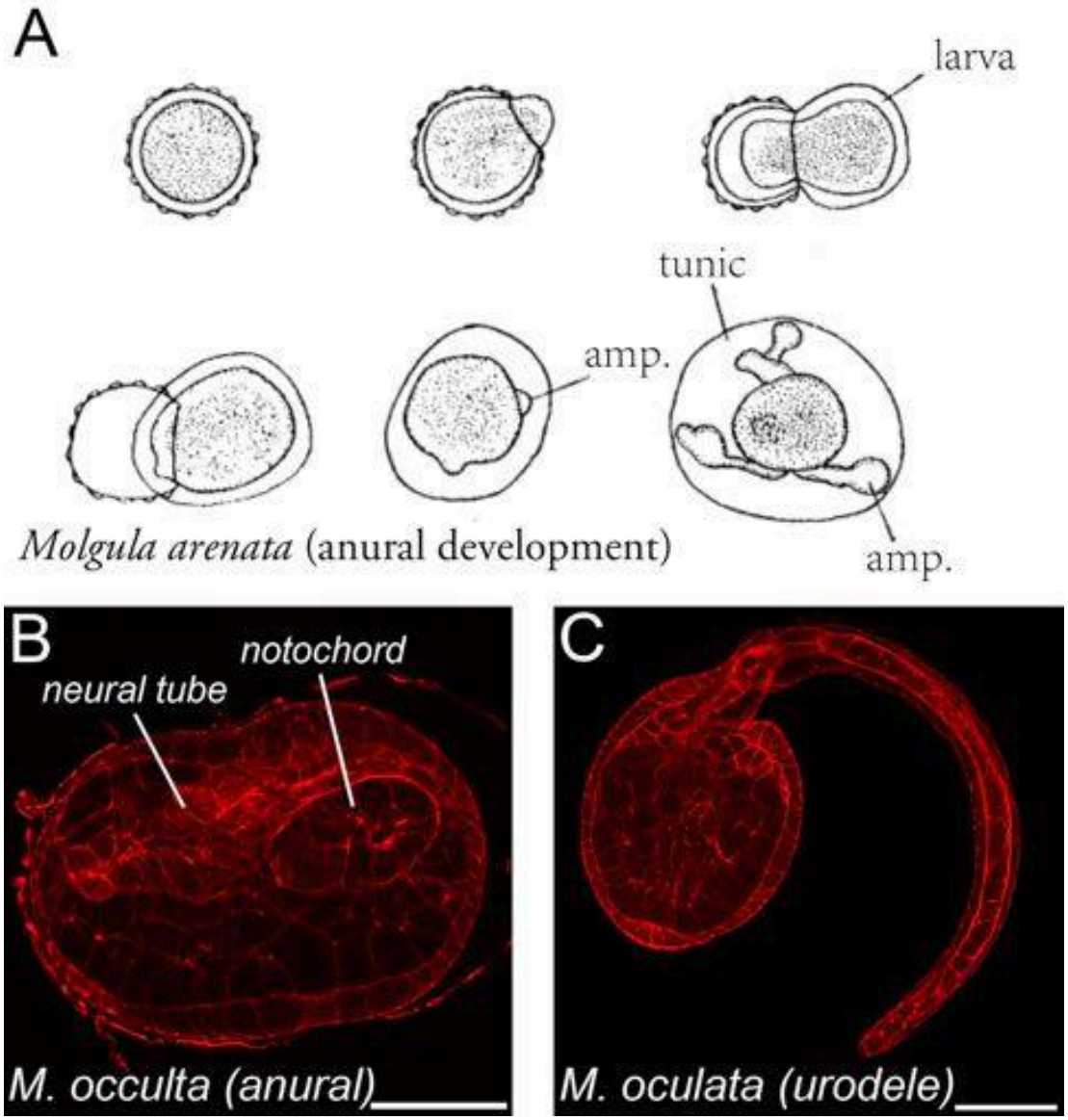

HOX
PARAHOX
1 2 3 4 5 6 7 8 9 10 11 12 13 14 EvxA EvxB
Gsx Xlox Cdx
9A
9B
Evx
EvxA
10
EvxB
Evx
Evx

Não todas as larvas tem cauda! Desenvolvimento anuro em *Molgula*



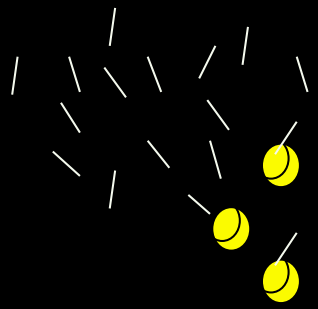
Swalla

Anural development

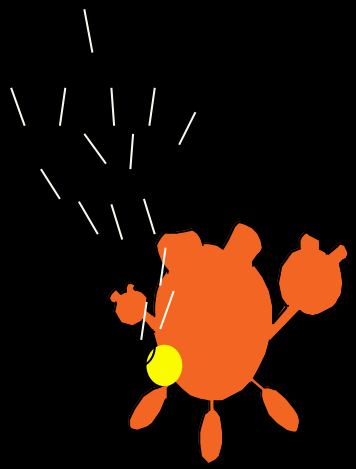


Stolfi

Life cycle



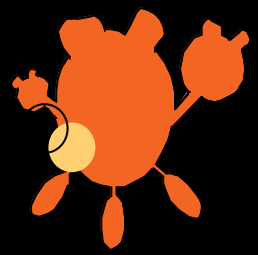
Solitary species:
External fertilization



Colonial species:
Internal fertilization and brooding

Life cycle

Solitary species:
External fertilization



Colonial species:
Internal fertilization and brooding

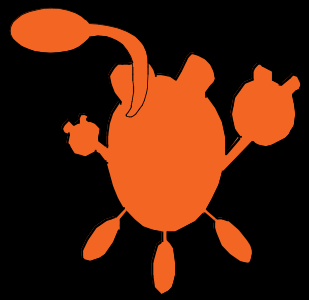
Life cycle

Solitary species:
External fertilization

Colonial species:
Internal fertilization and brooding

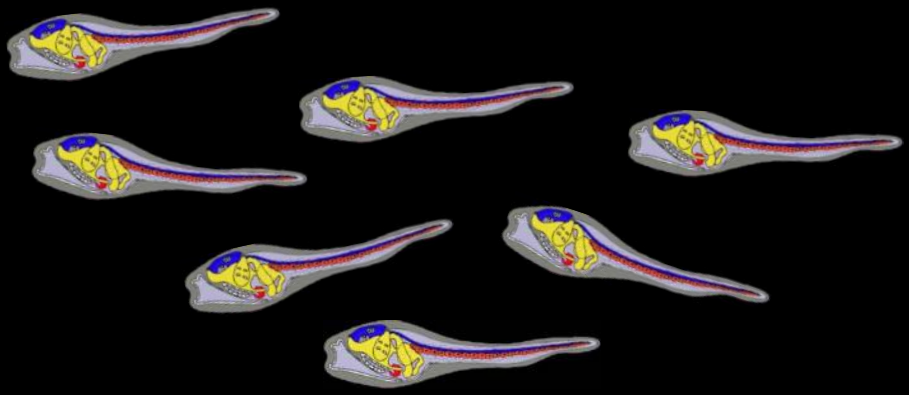
Life cycle

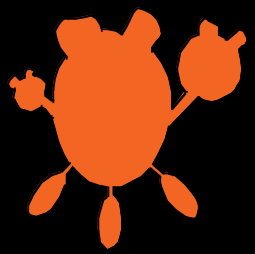
Solitary species:
External fertilization



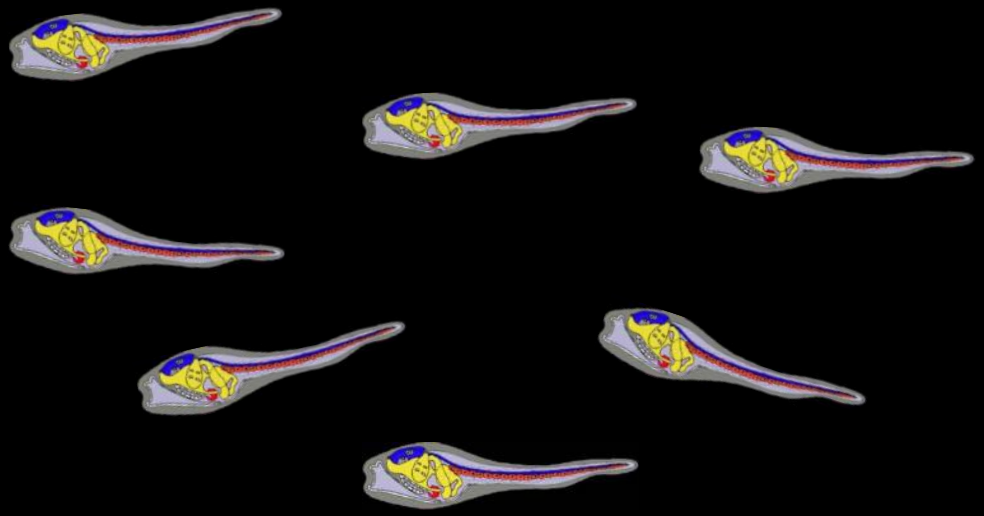
Colonial species:
Internal fertilization and brooding

Life cycle

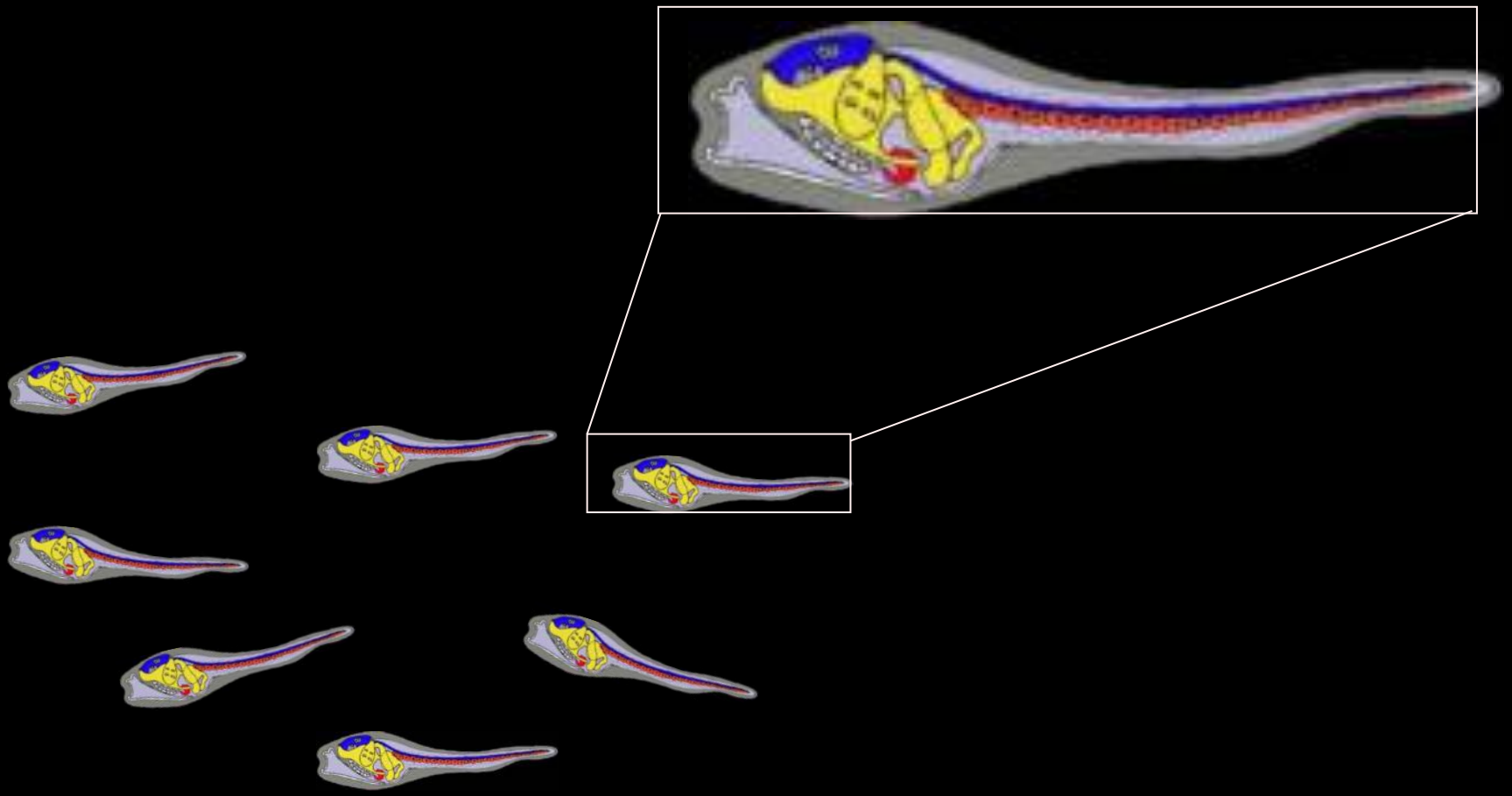




Life cycle

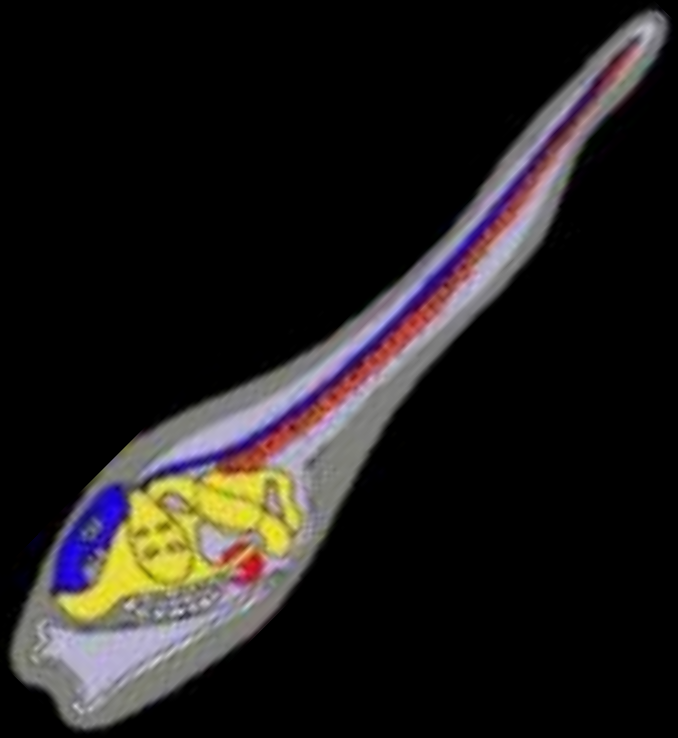


Life cycle



Animation credits: Eva Ma

Life cycle



Animation credits: Eva Ma and Dawn Vaughn

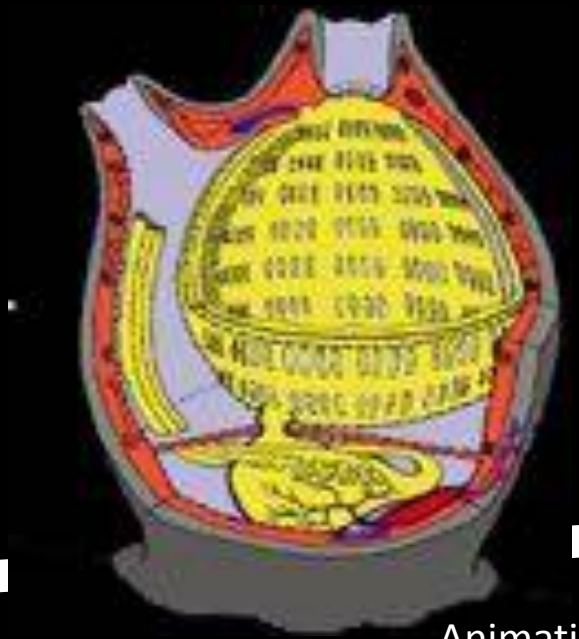
Life cycle

Animation credits: Eva Ma and Dawn Vaughn

Life cycle

Animation credits: Eva Ma and Dawn Vaughn

Life cycle

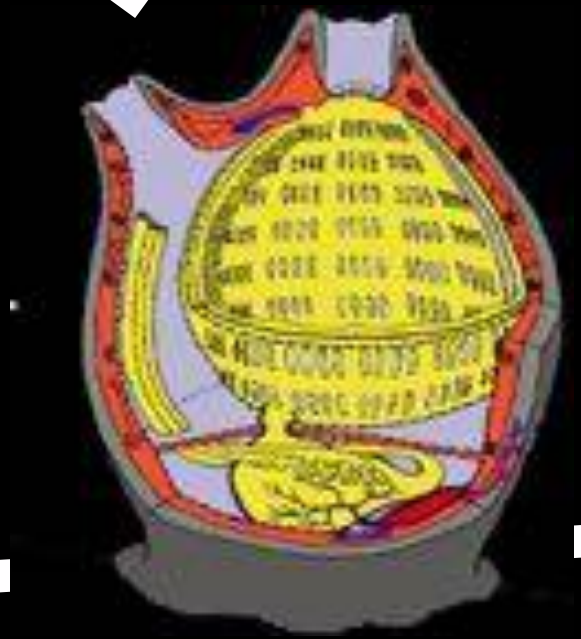


Animation credits: Eva Ma and Dawn Vaughn

Life cycle

Solitary species:
Sexual reproduction only

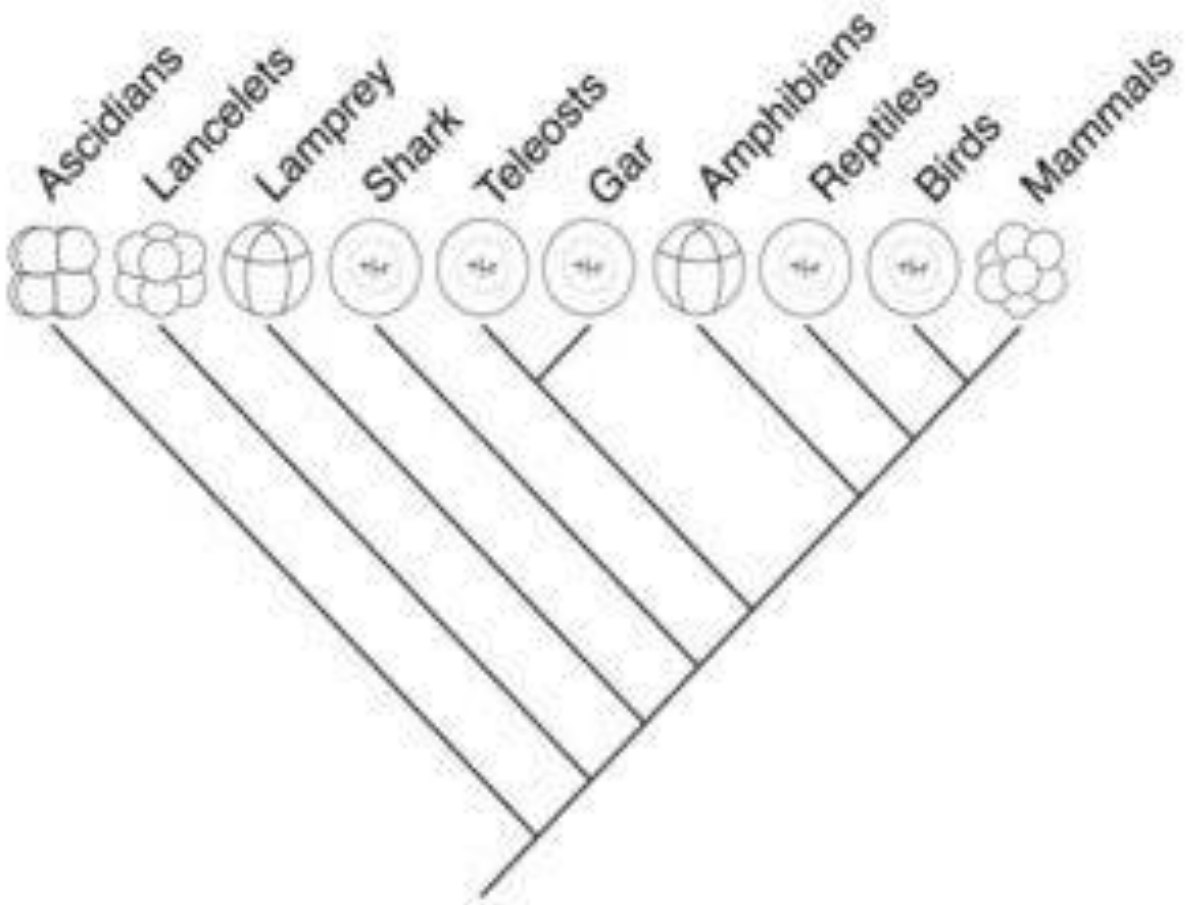
Colonial species: Sexual and asexual reproduction



Animation credits: Eva Ma

Ascidiacea: diversificação de uma vida séssil

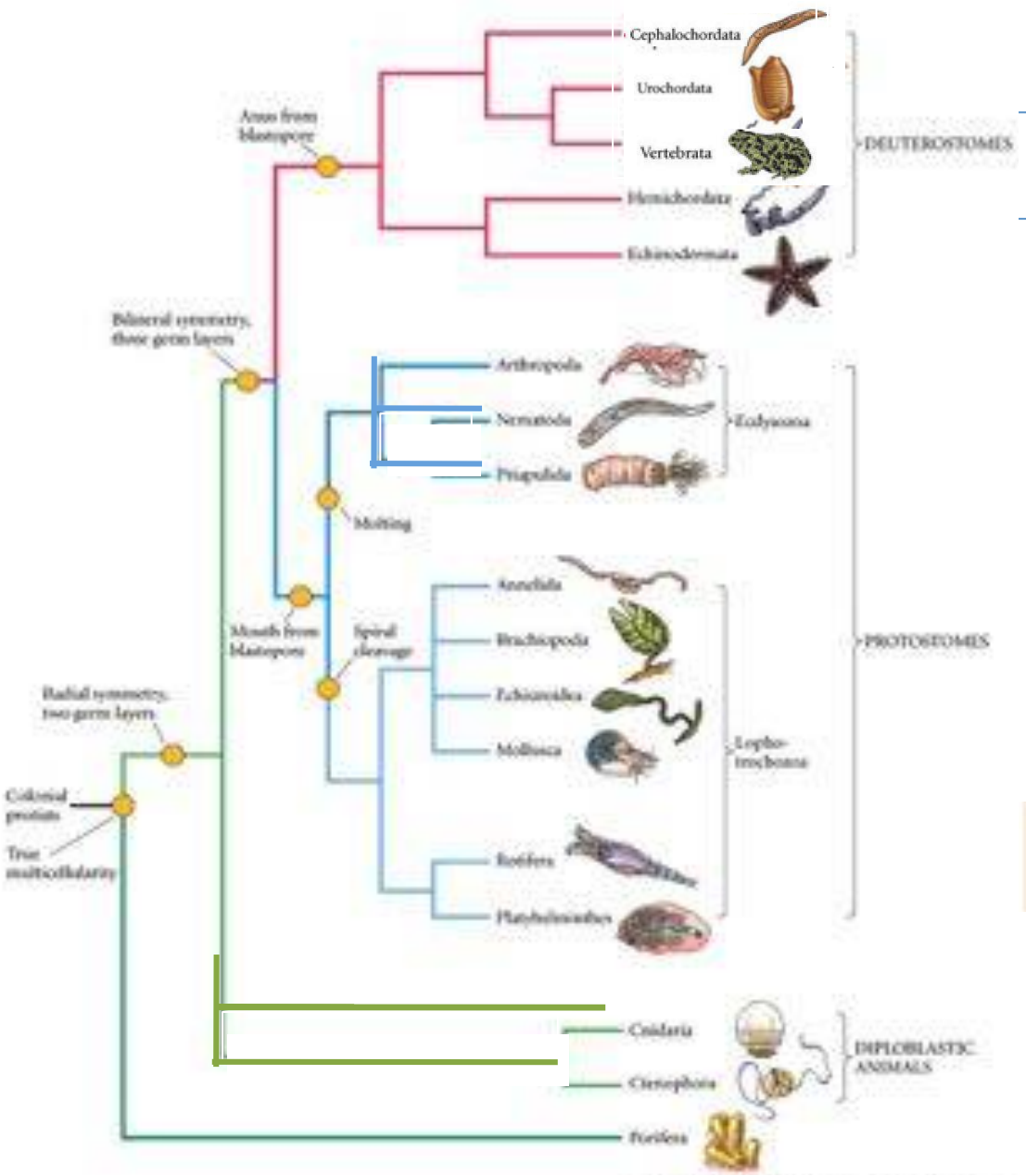
Evolutionary patterns: Deuterostome cleavage patterns



Ancestral mode of cleavage was likely holoblastic

(Chea, et al., 2005)

Deuterostome embryos:



4. Rotational cleavage
Mammals, nematodes

2. Discoidal cleavage
Fish, reptiles, birds

B. **Mesolecithal**

Displaced radial cleavage
Amphibians

3. Bilateral cleavage
Tunicates

A. **Isolecithal**

1. Radial cleavage
Echinoderms, amphioxus

Superficial cleavage
Most insects

4. Rotational cleavage
Mammals, nematodes

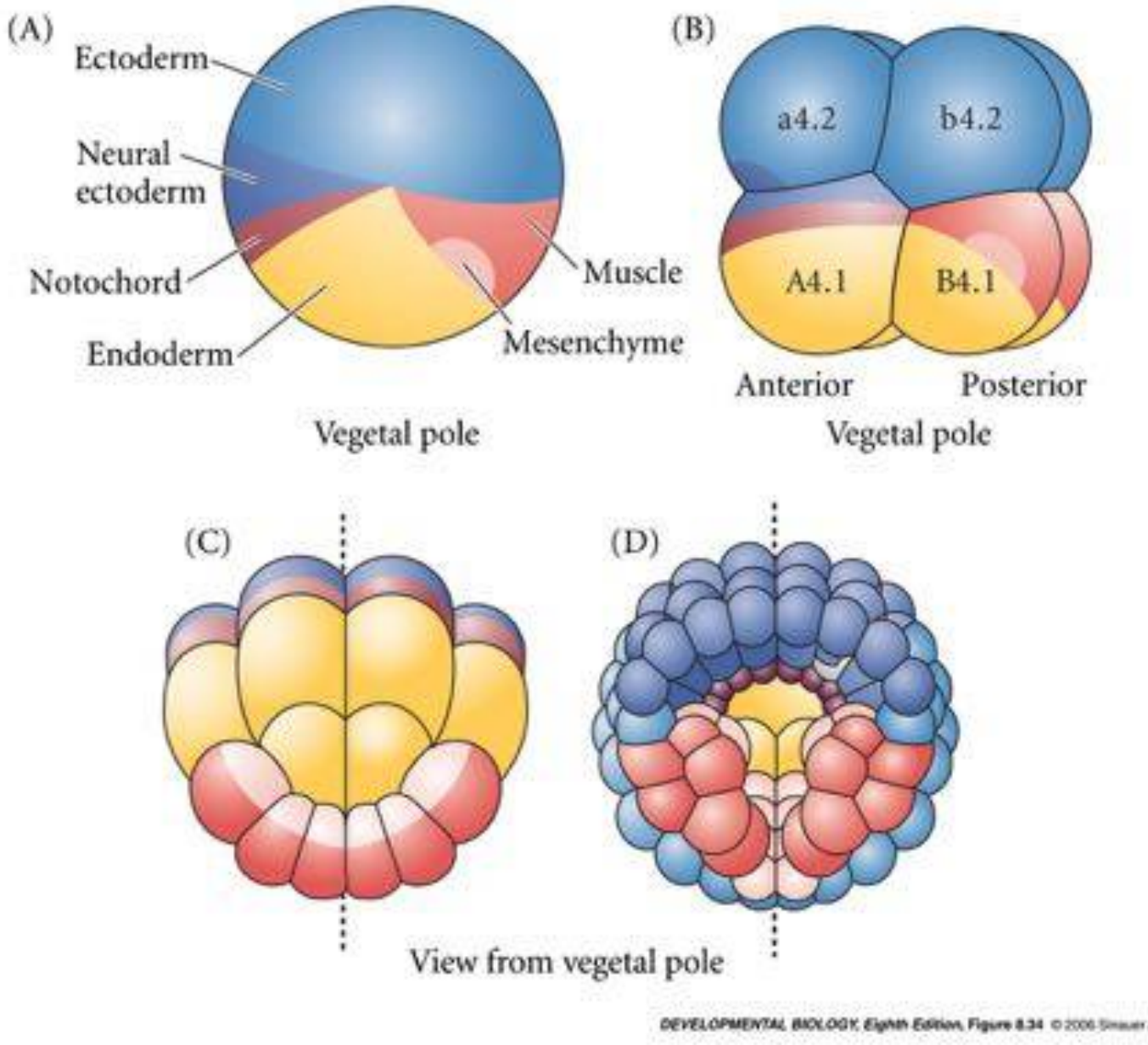
A. **Telolecithal**

1. Bilateral cleavage
Cephalopod molluscs

2. Spiral cleavage
Annelids, molluscs, flatworms

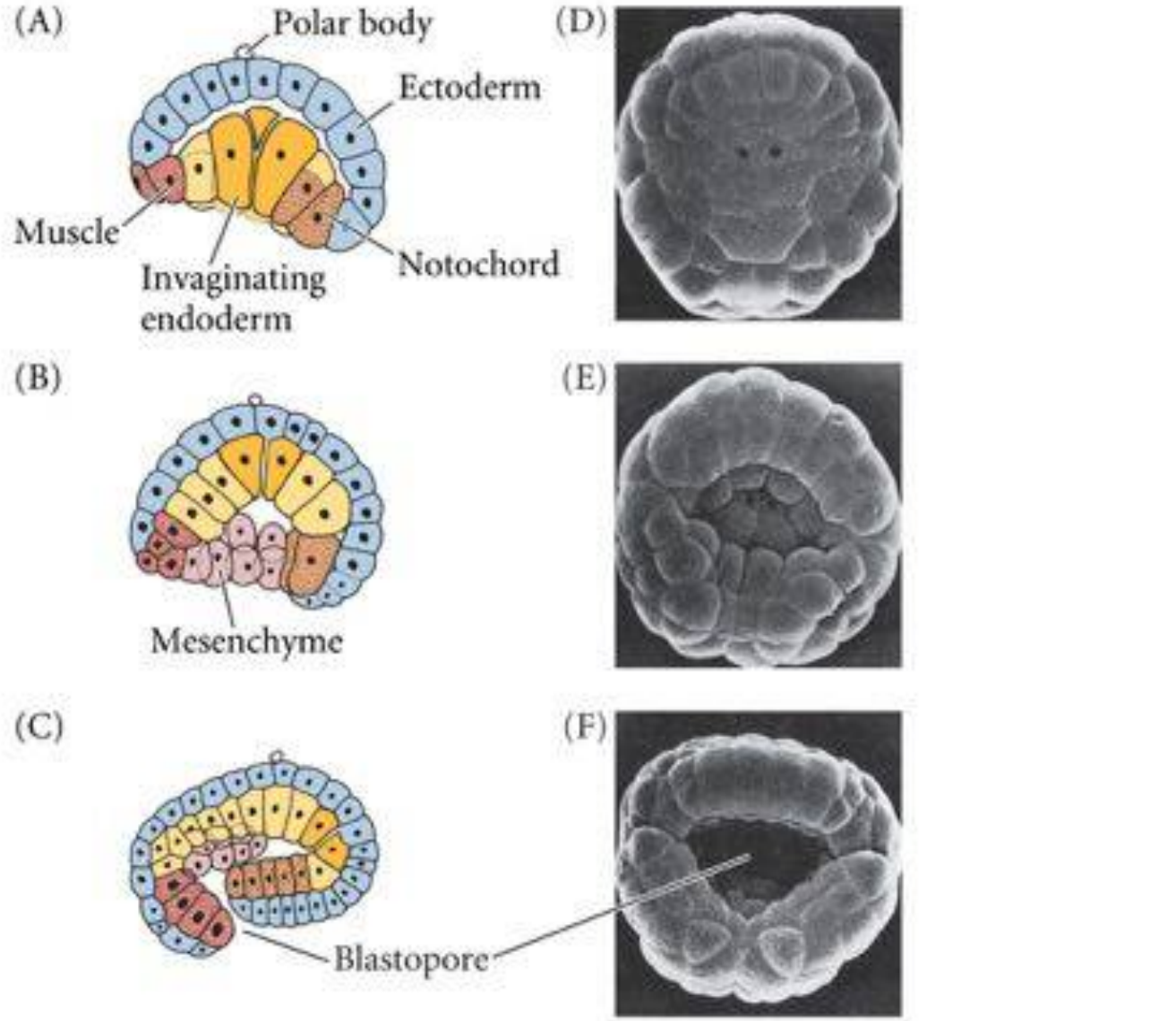
Isolecitos
Mesolecitos
Telolecitos
Centrolecitos

Bilateral symmetry in the egg of the ascidian tunicate *Styela partita*



DEVELOPMENTAL BIOLOGY, Eighth Edition, Figure 8.34 © 2006 Sinauer Associates, Inc.

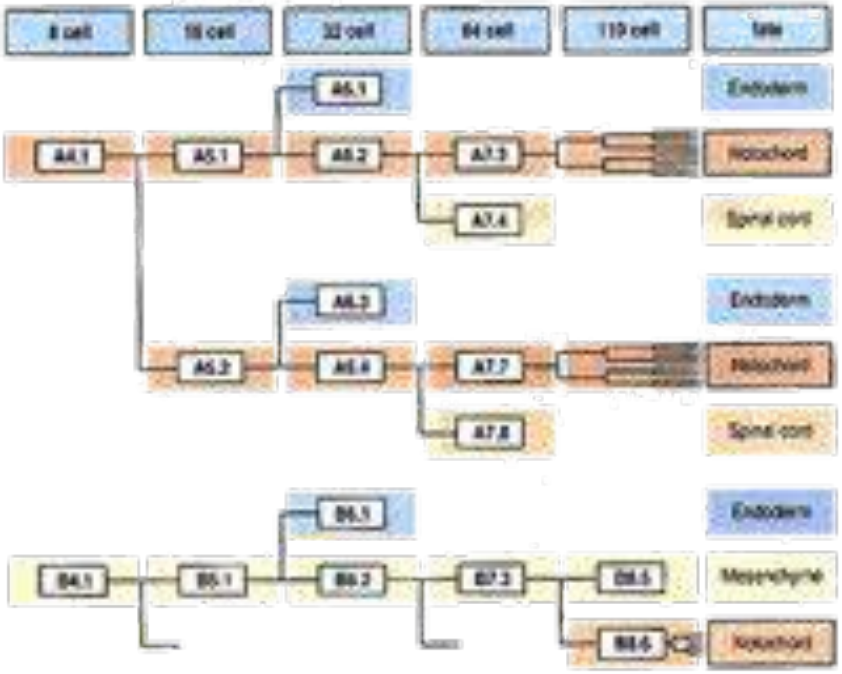
Gastrulation in the tunicate

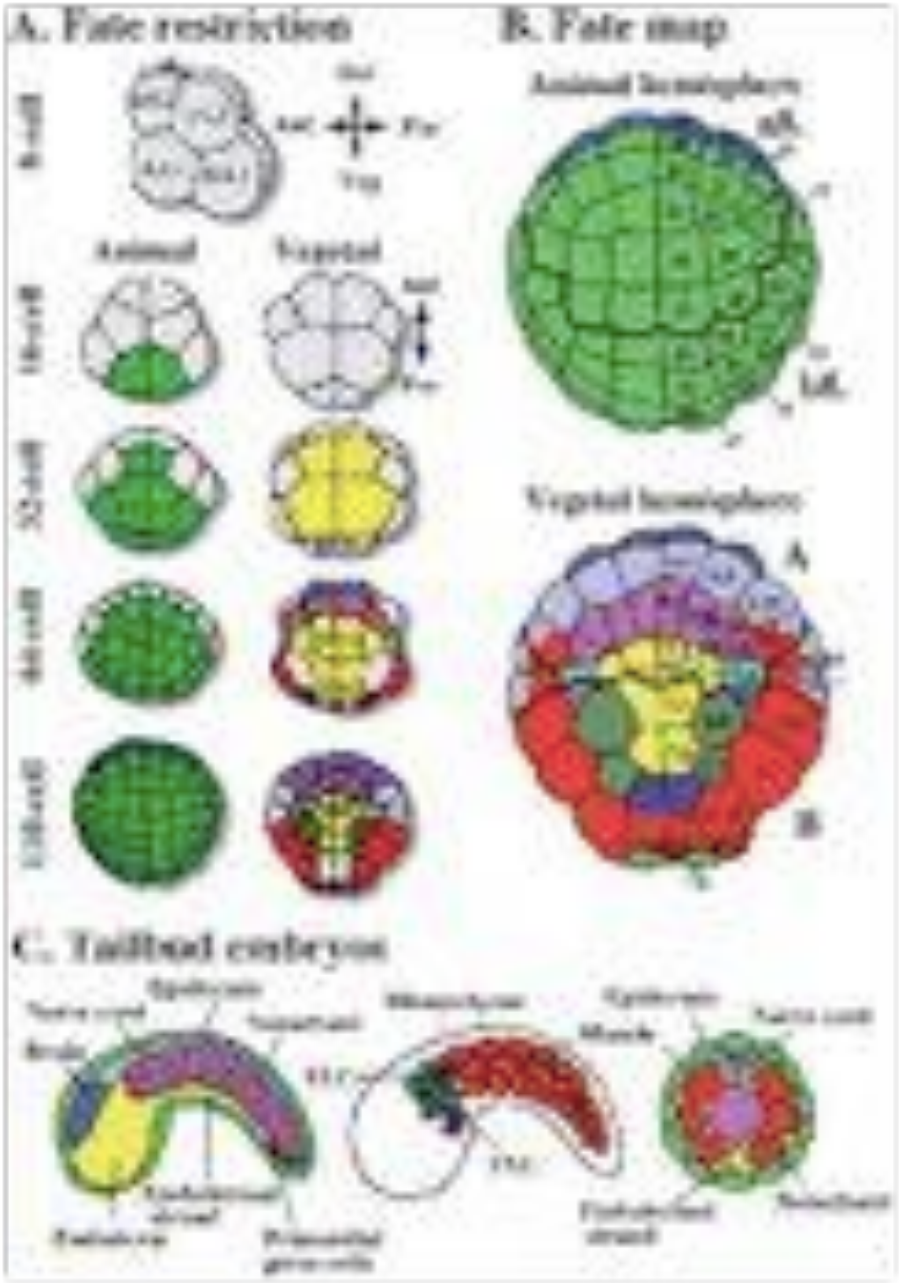


DEVELOPMENTAL BIOLOGY, Eighth Edition, Figure 8.40 © 2006 Sinauer Associates, Inc.

Desenvolvimento invariante

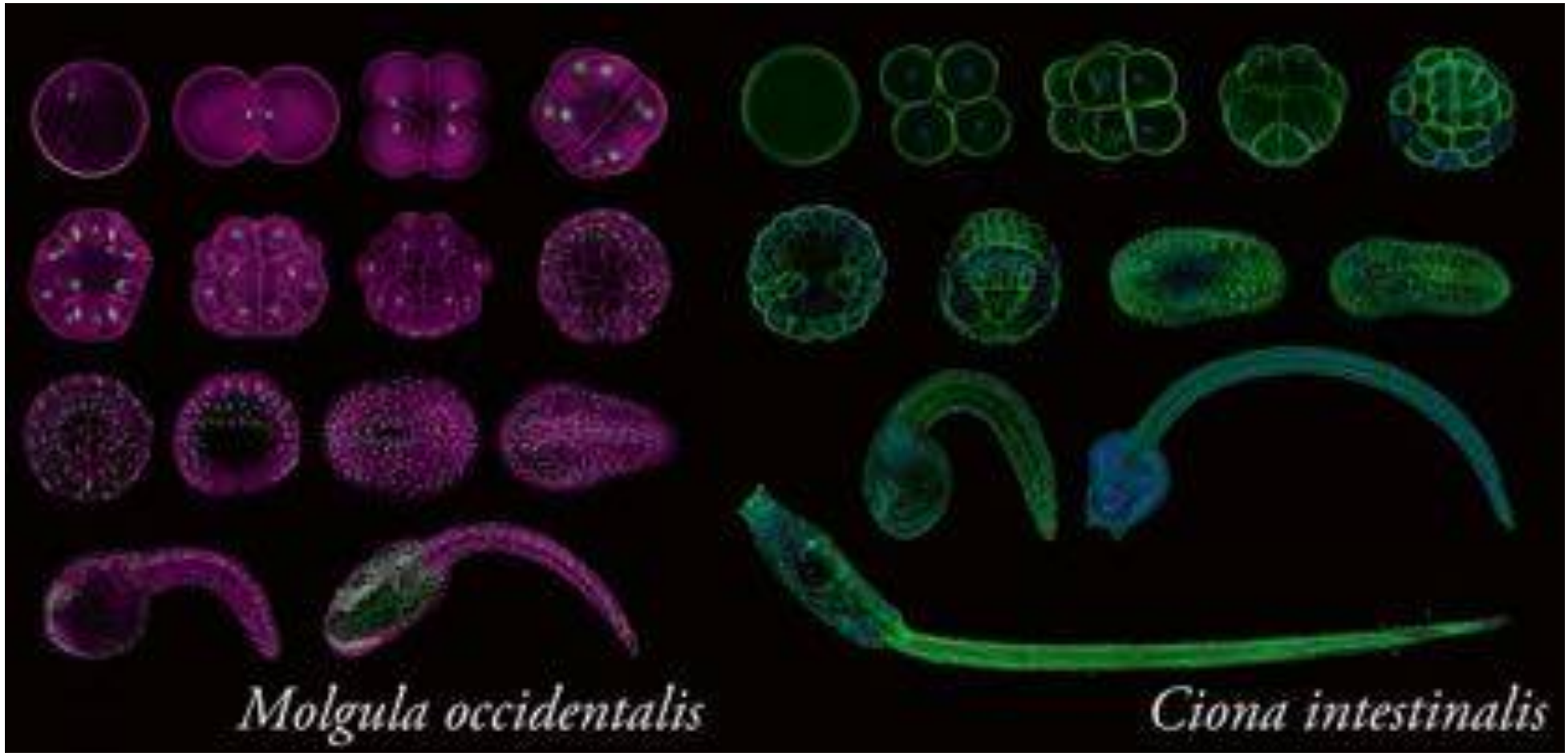
- Todos os embriões se desenvolvem de maneira idêntica
- Cada divisão celular ocorre da mesma maneira no mesmo momento em todos os indivíduos
- Cada célula tem uma identidade única e invariante



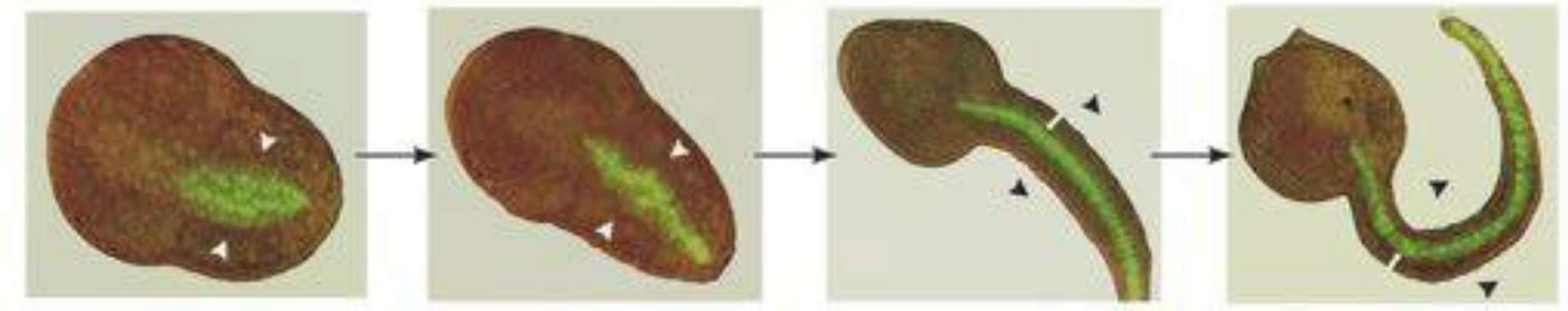


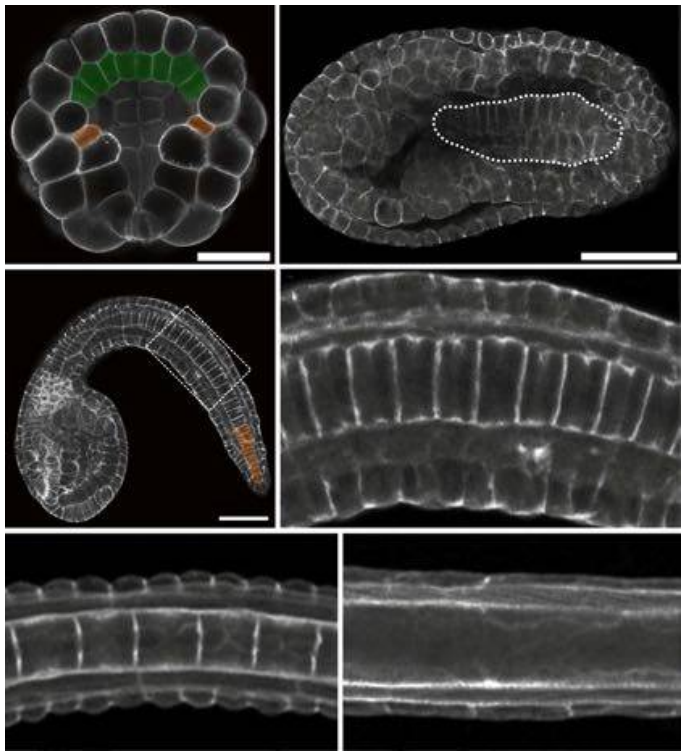
Hirano e Nishida 1997; Nishida 1987, 2005

Desenvolvimento invariante



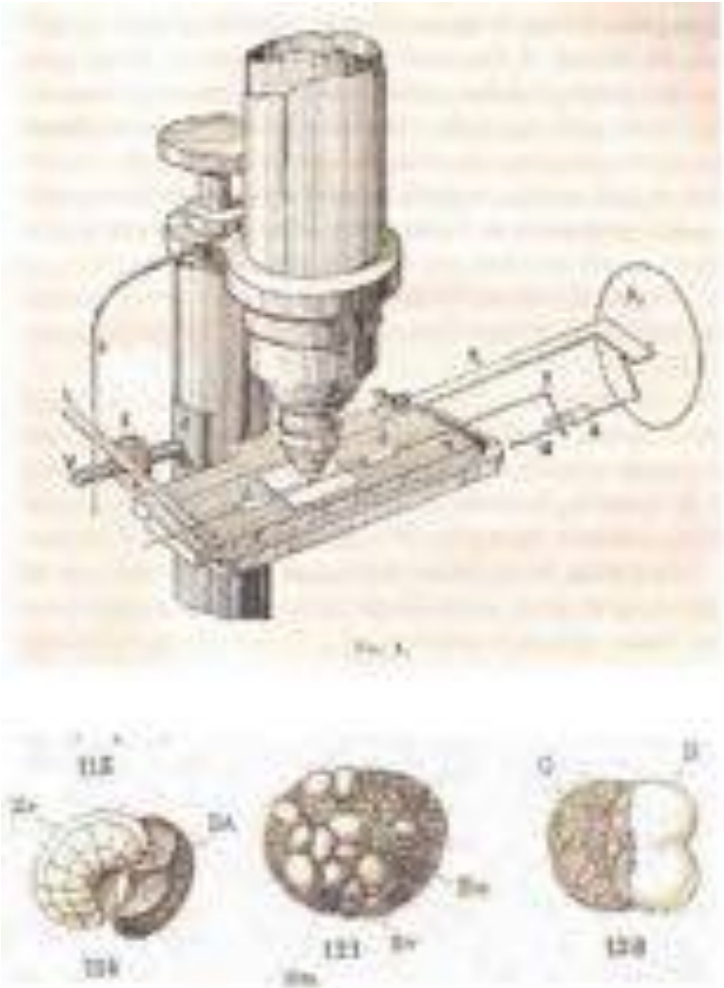
Notocorda se forma por movimentos de convergencia e extensão



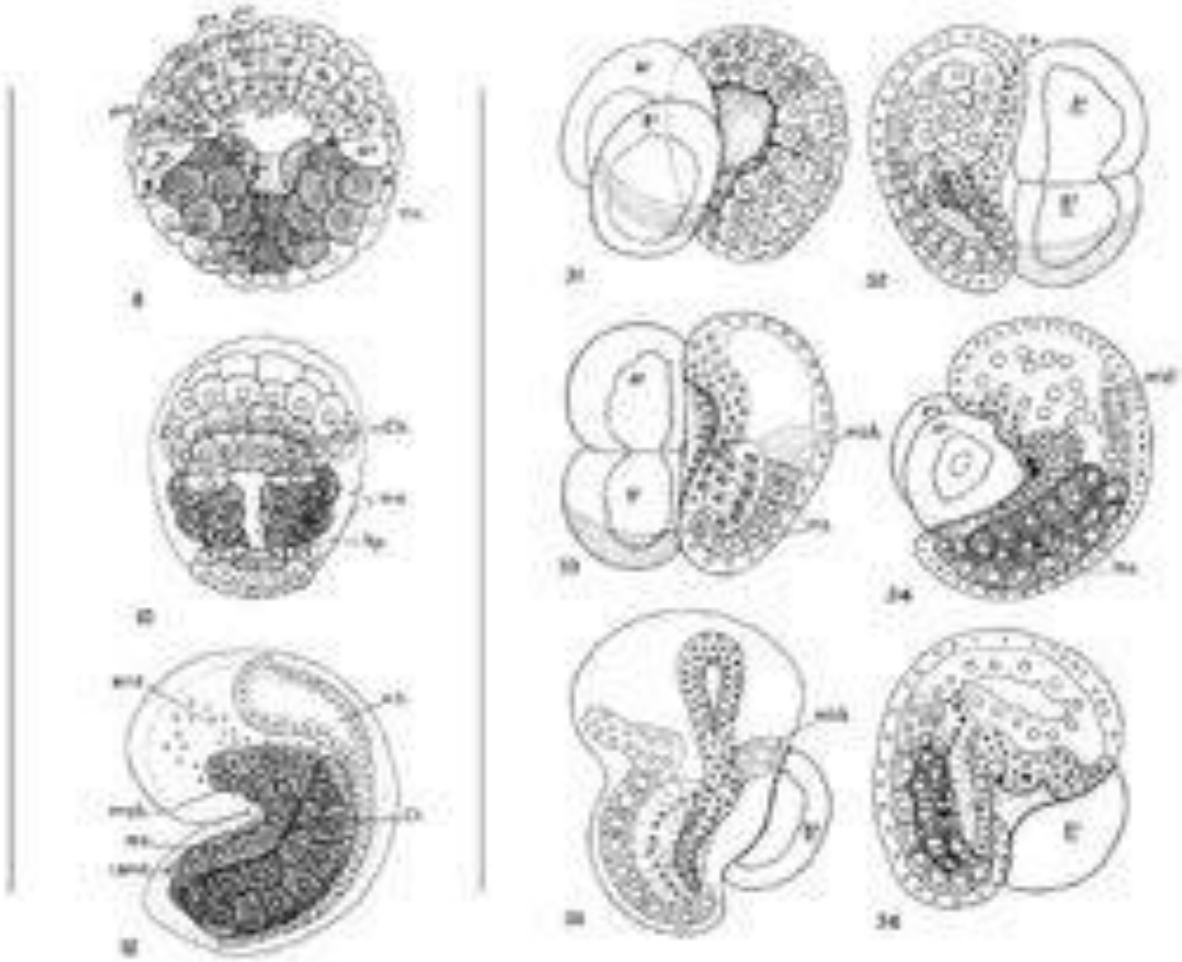


DEVELOPMENTAL BIOLOGY, Eighth Edition, Figure 8.41 © 2006 Sinauer Associates, Inc.

Desenvolvimento em mosaico ou determinativo (Experimentos clásicos)

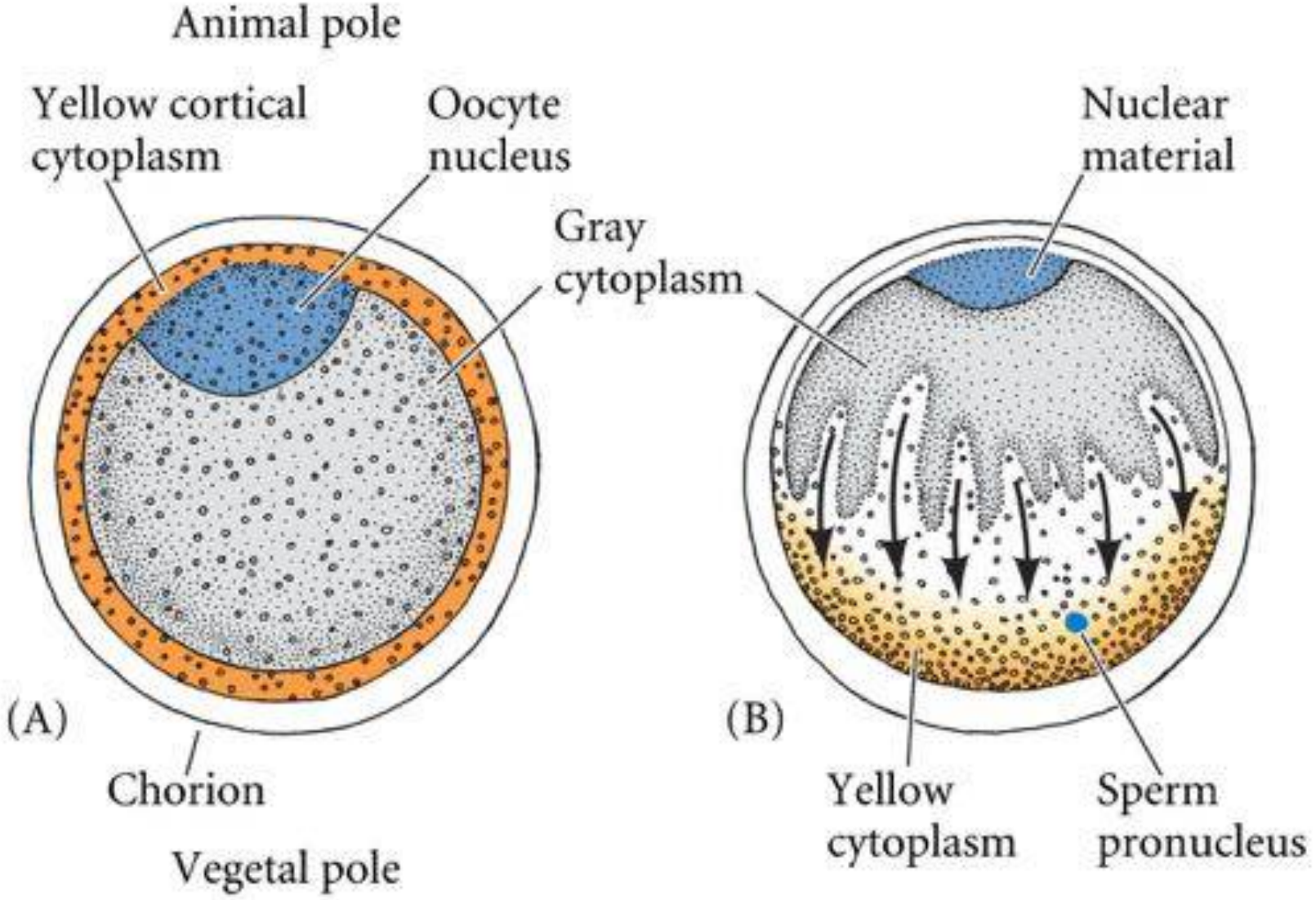


Chabry 1887



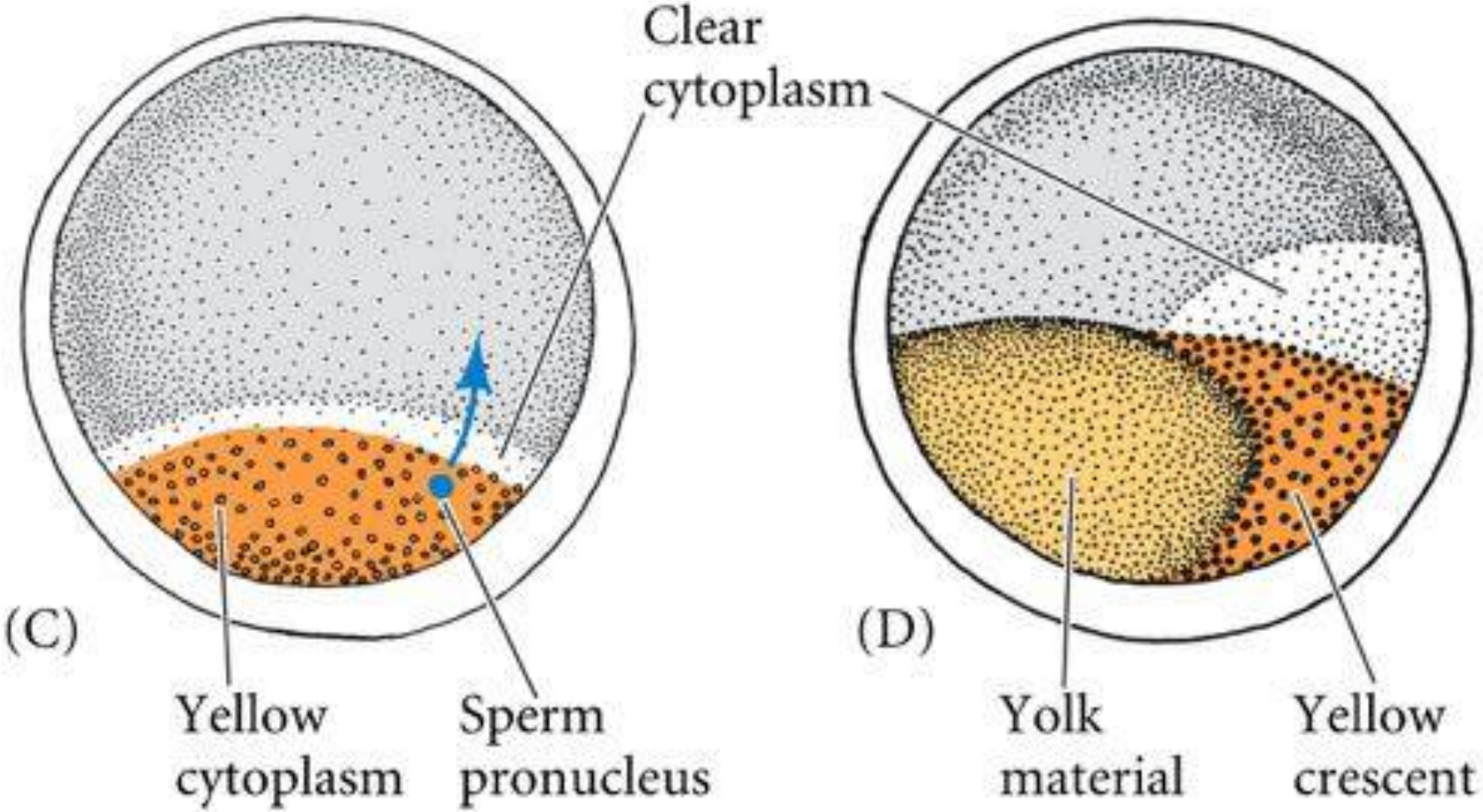
Conklin 1905

Cytoplasmic rearrangement in the fertilized egg of *Styela partita*



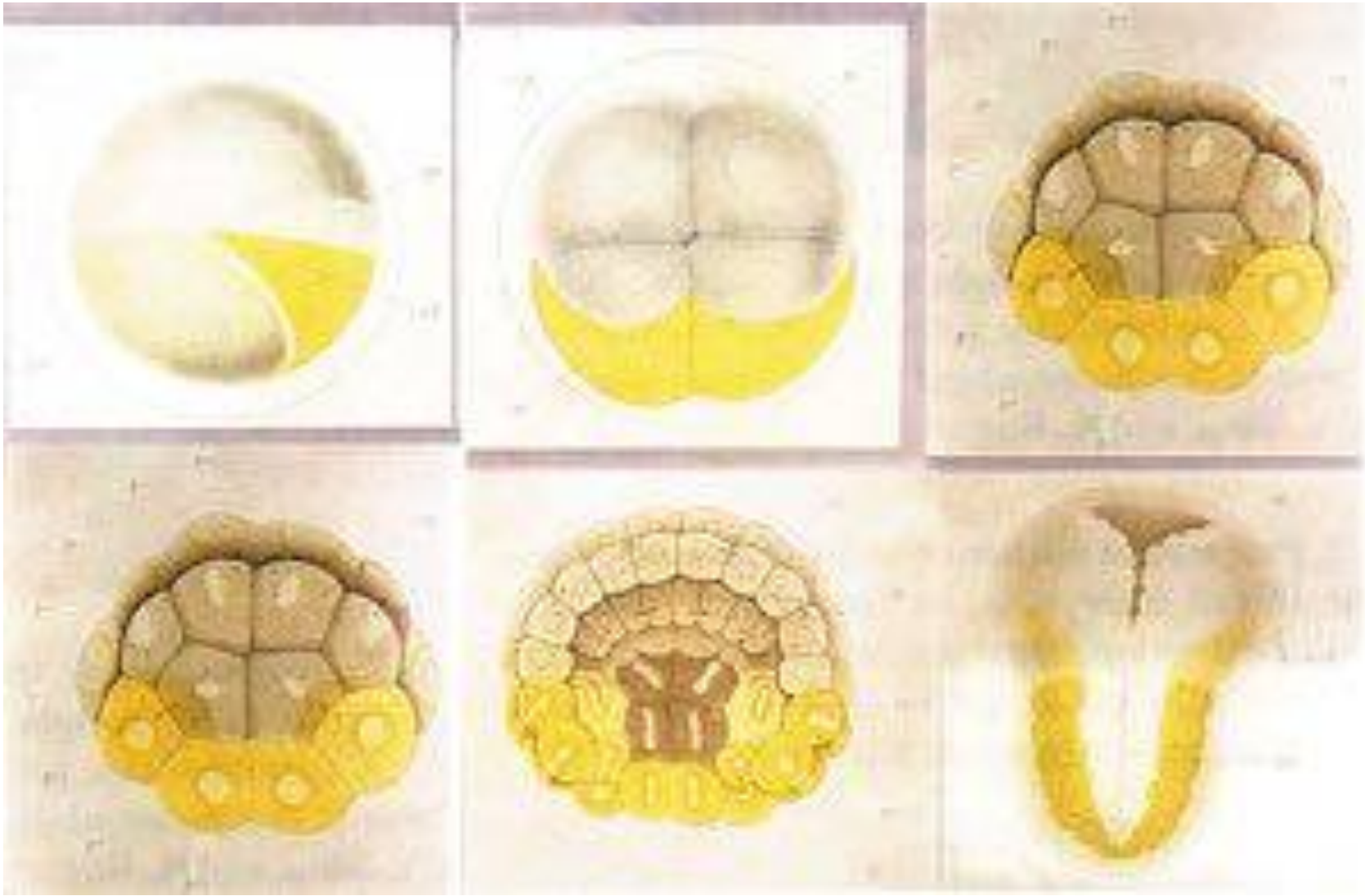
DEVELOPMENTAL BIOLOGY, Eighth Edition, Figure 8.35 (Part 1) © 2006 Sinauer Associates, Inc.

Cytoplasmic rearrangement in the fertilized egg of *Styela partita*



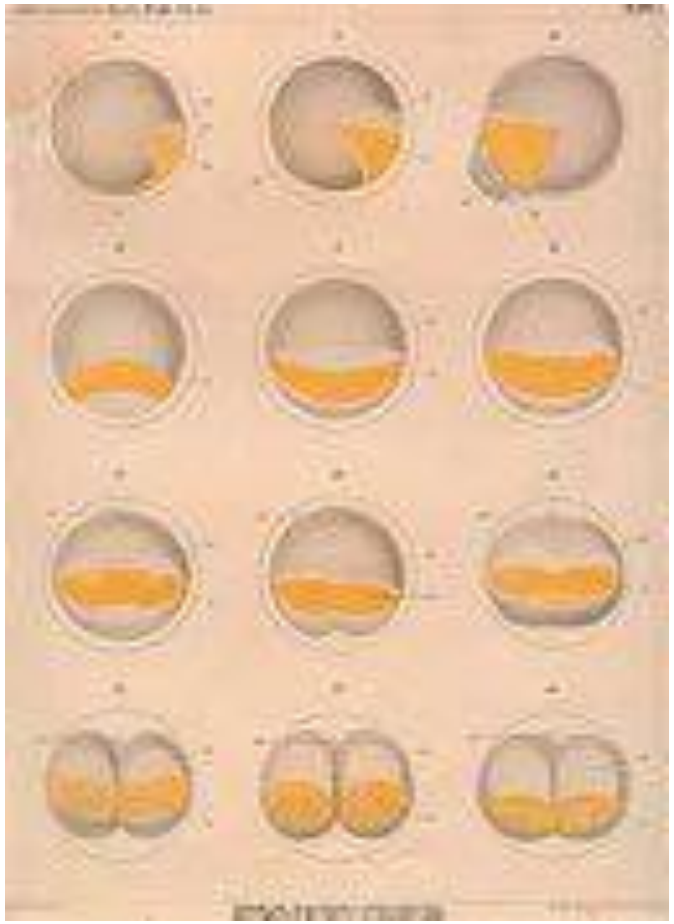
DEVELOPMENTAL BIOLOGY, Eighth Edition, Figure 8.35 (Part 2) © 2006 Sinauer Associates, Inc.

Ascidian embryology: a long history

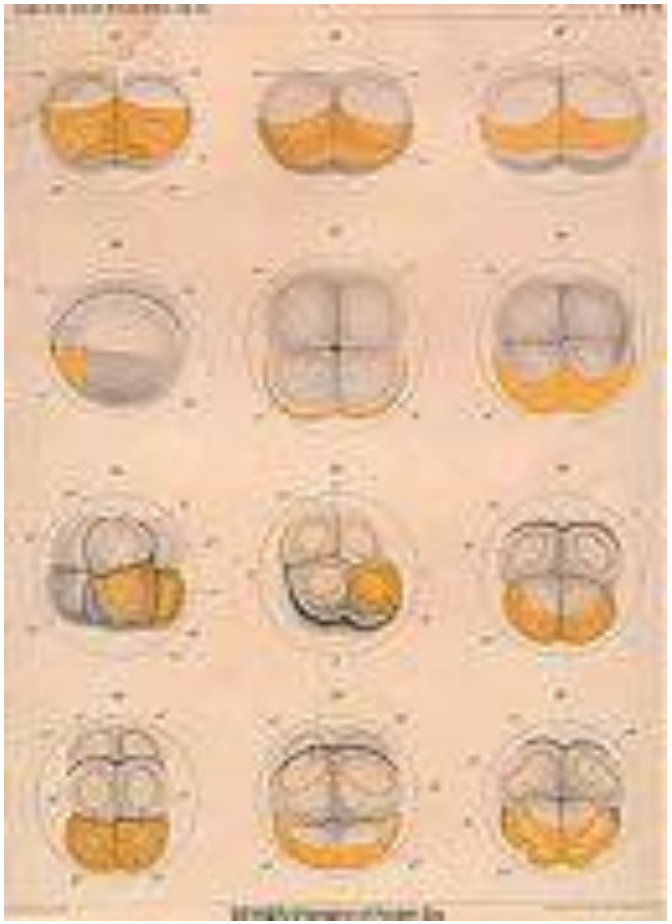


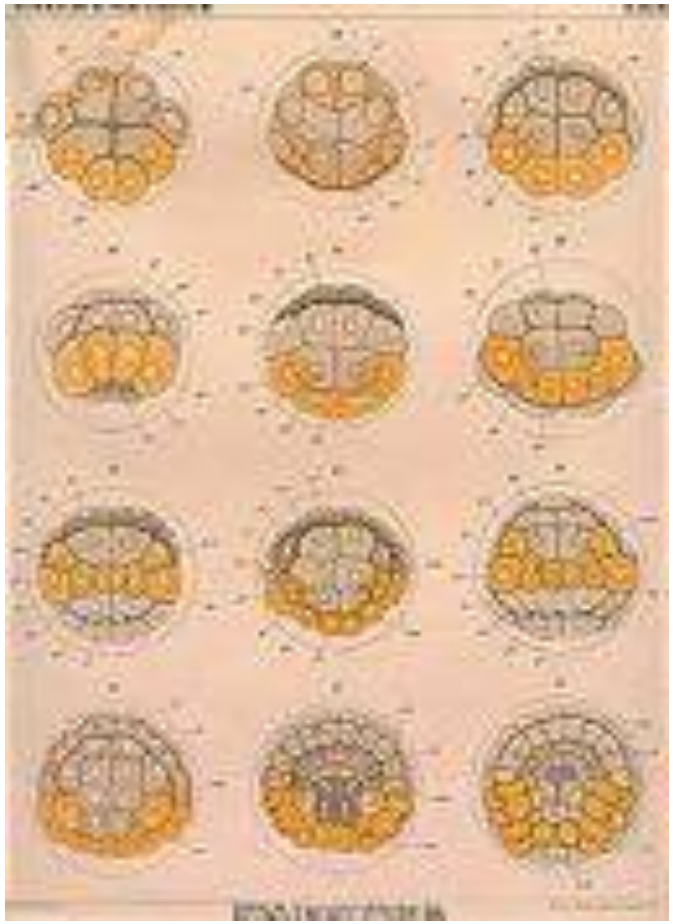
Styela partita Conklin 1905

Ascidian Development (Conklin 1905)

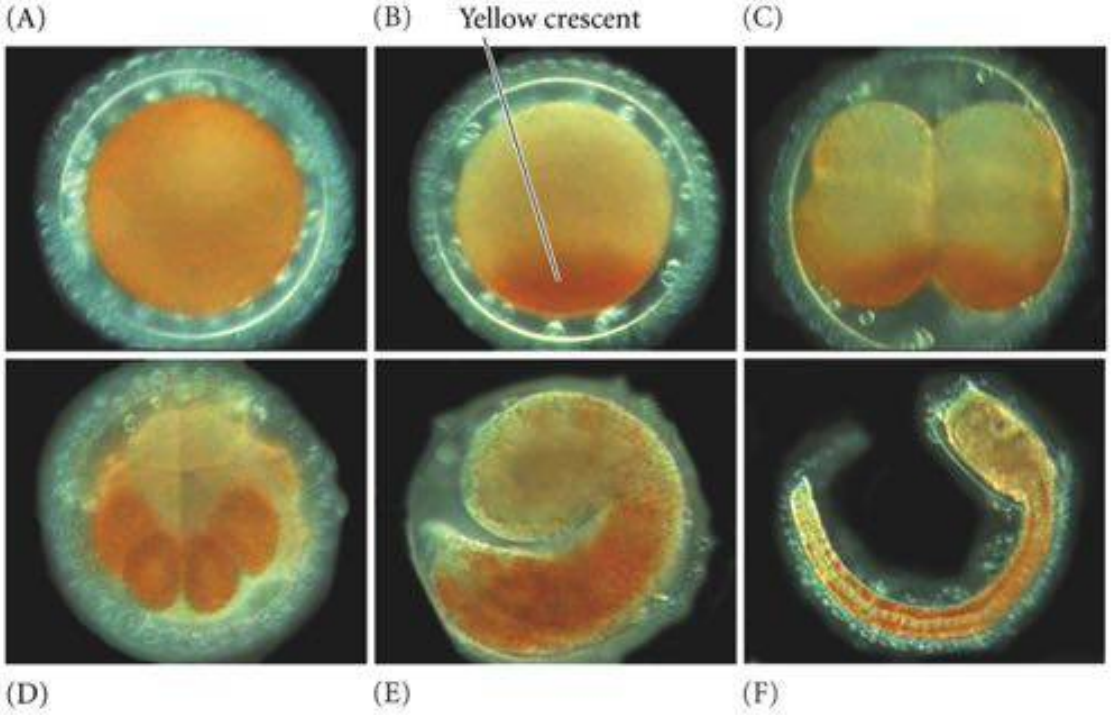


Ascidian Development (Conklin 1905) cont.

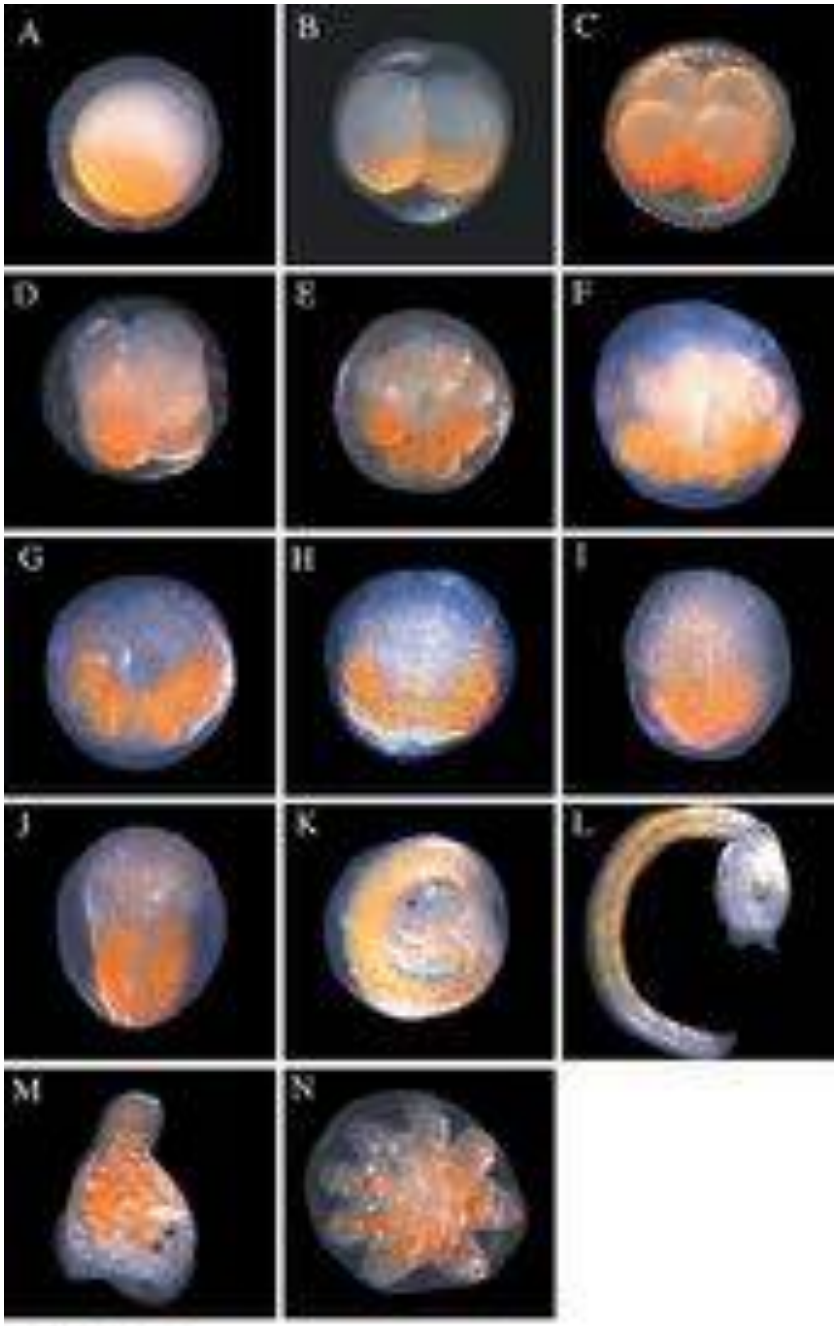




Cytoplasmic segregation in the egg of styelids

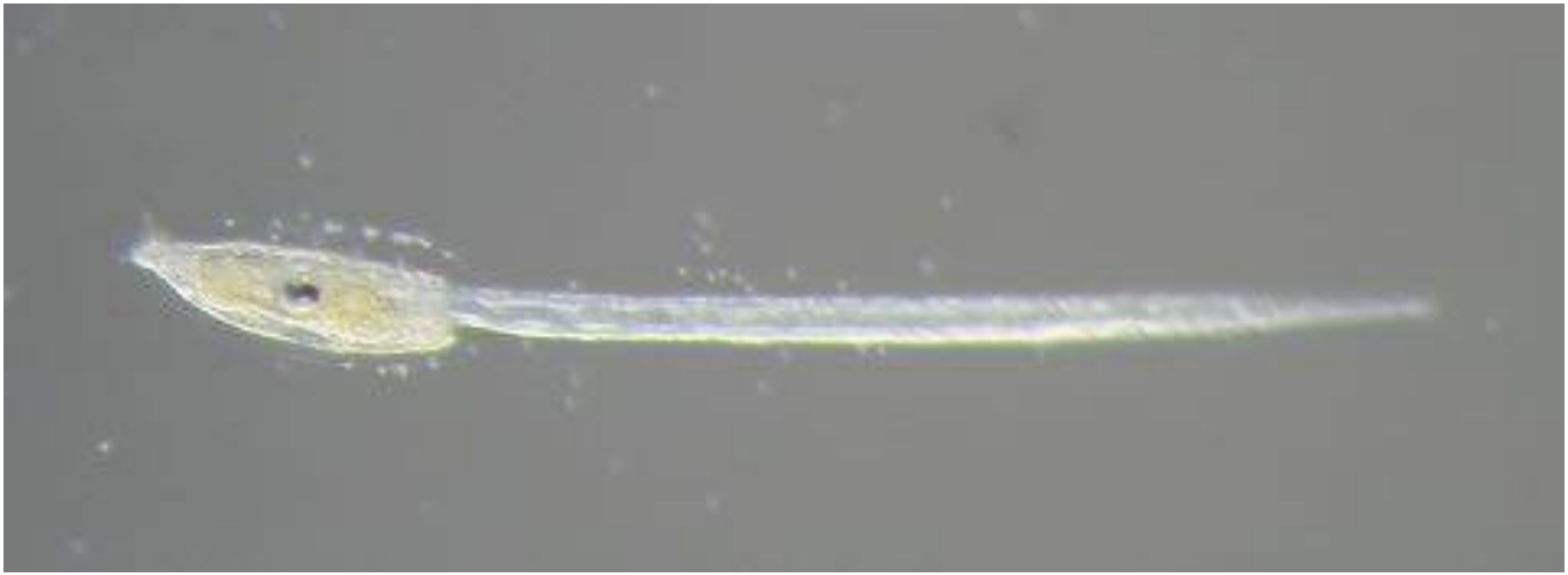


Styela partita



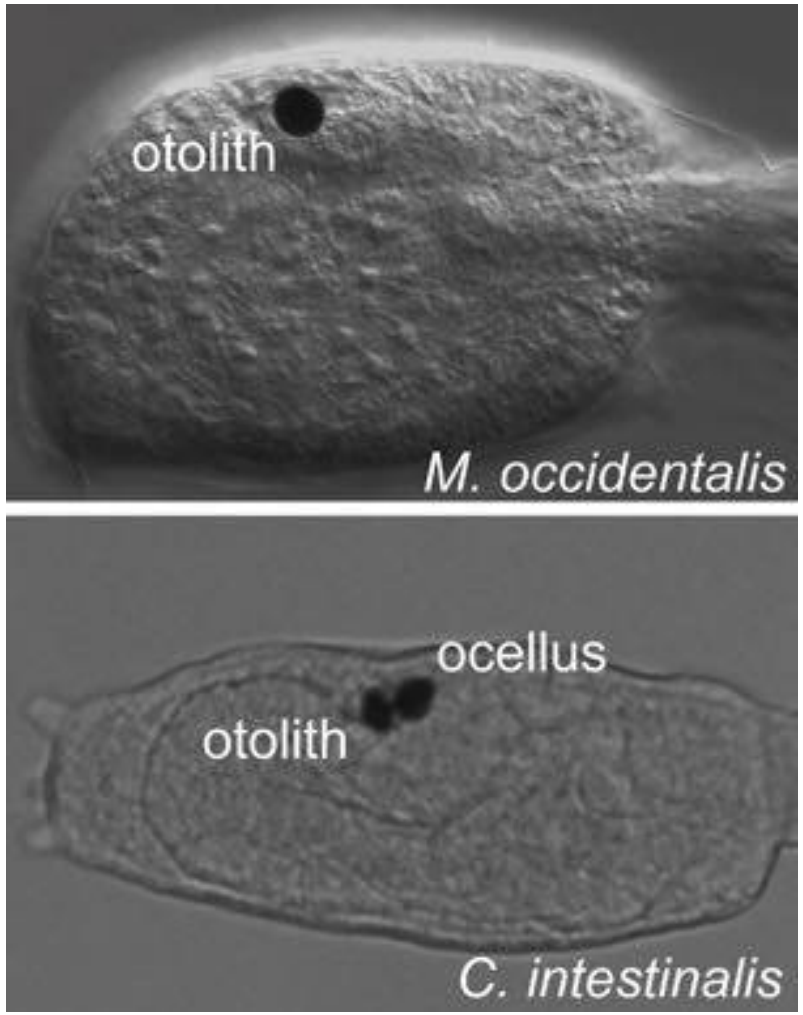
Boltenia villosa

A larva de ascídia

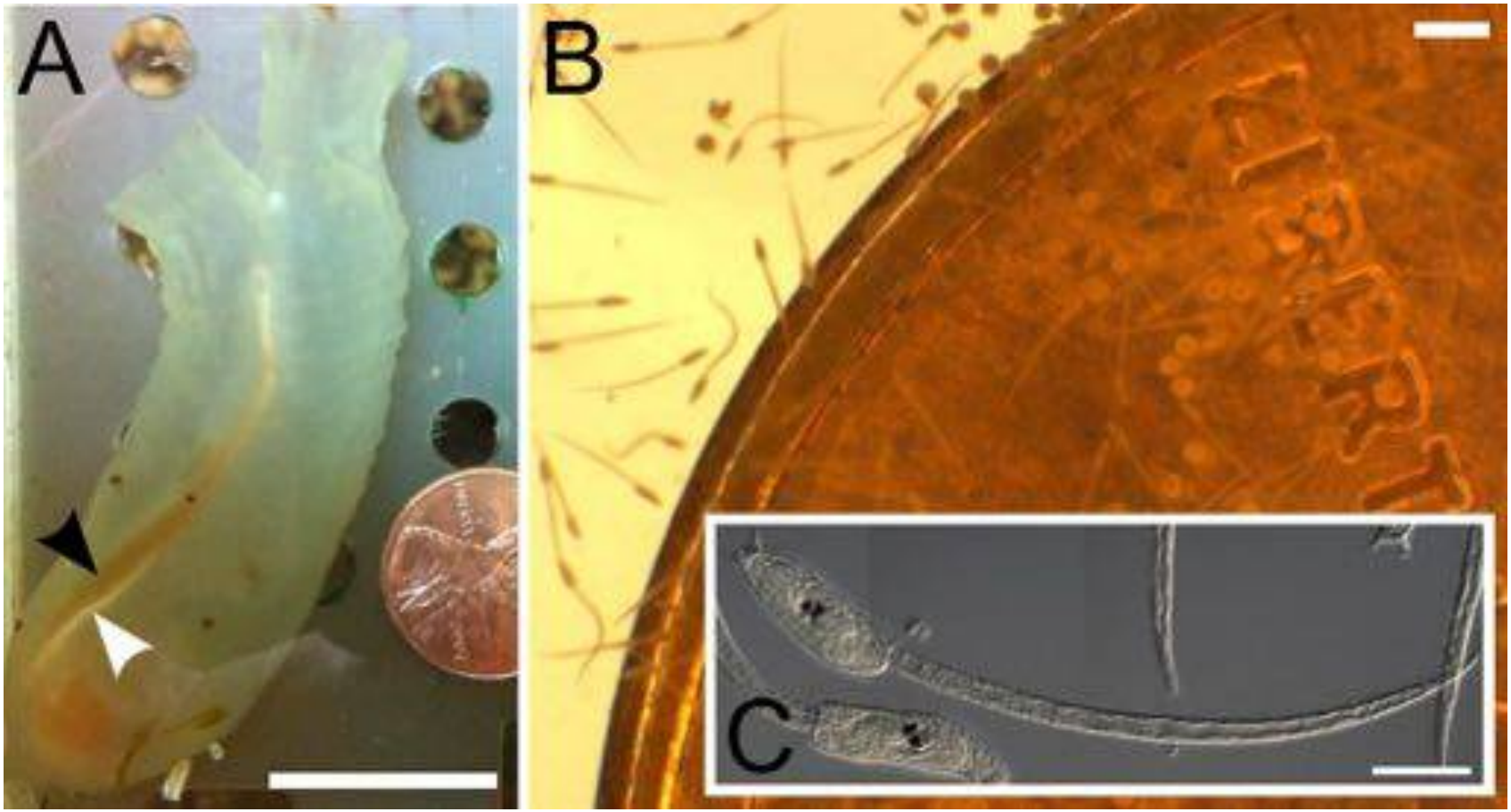


Four-dimensional Ascidian Body Atlas
Hotta et al. 2007

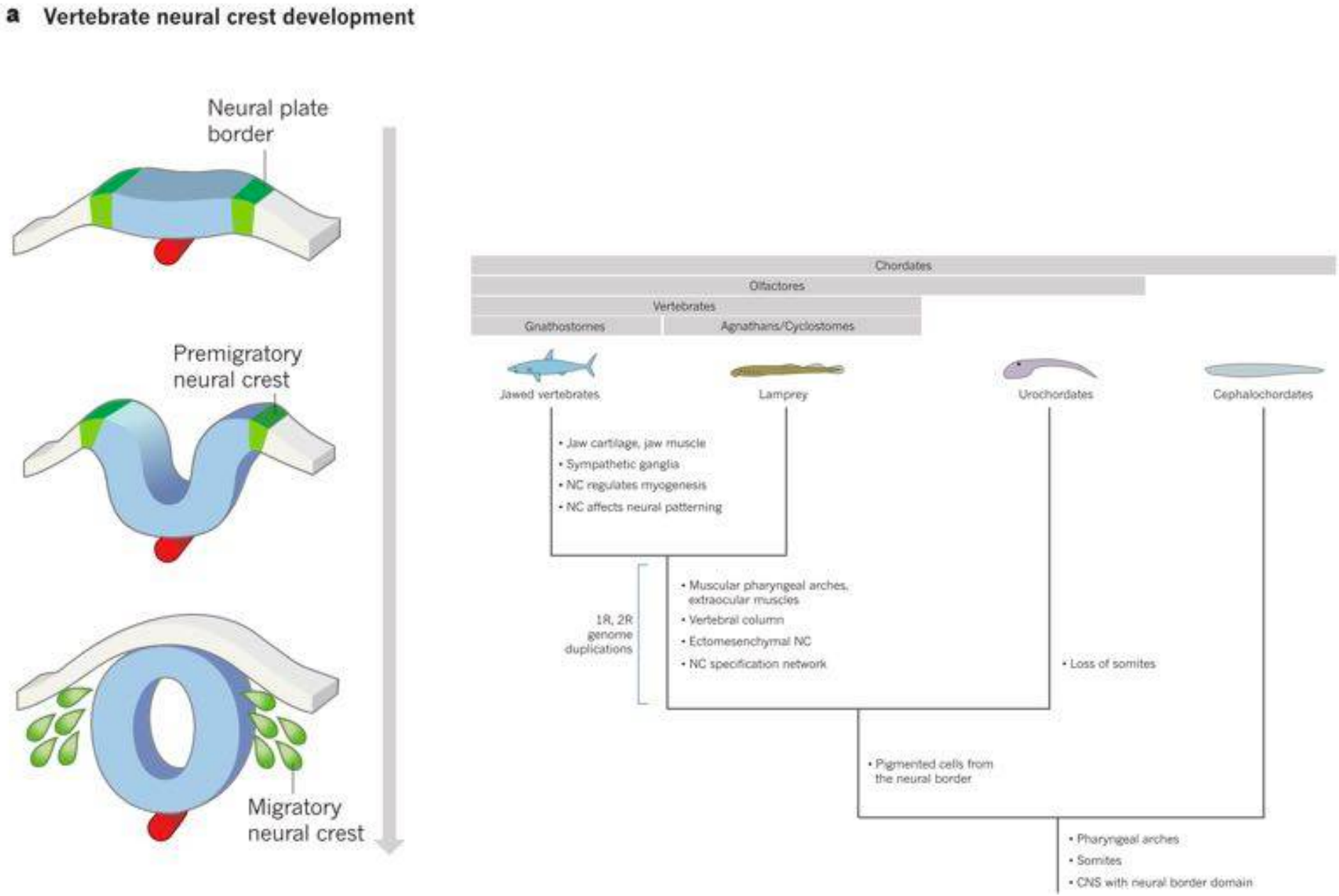
Vesículas sensoriais nas larvas



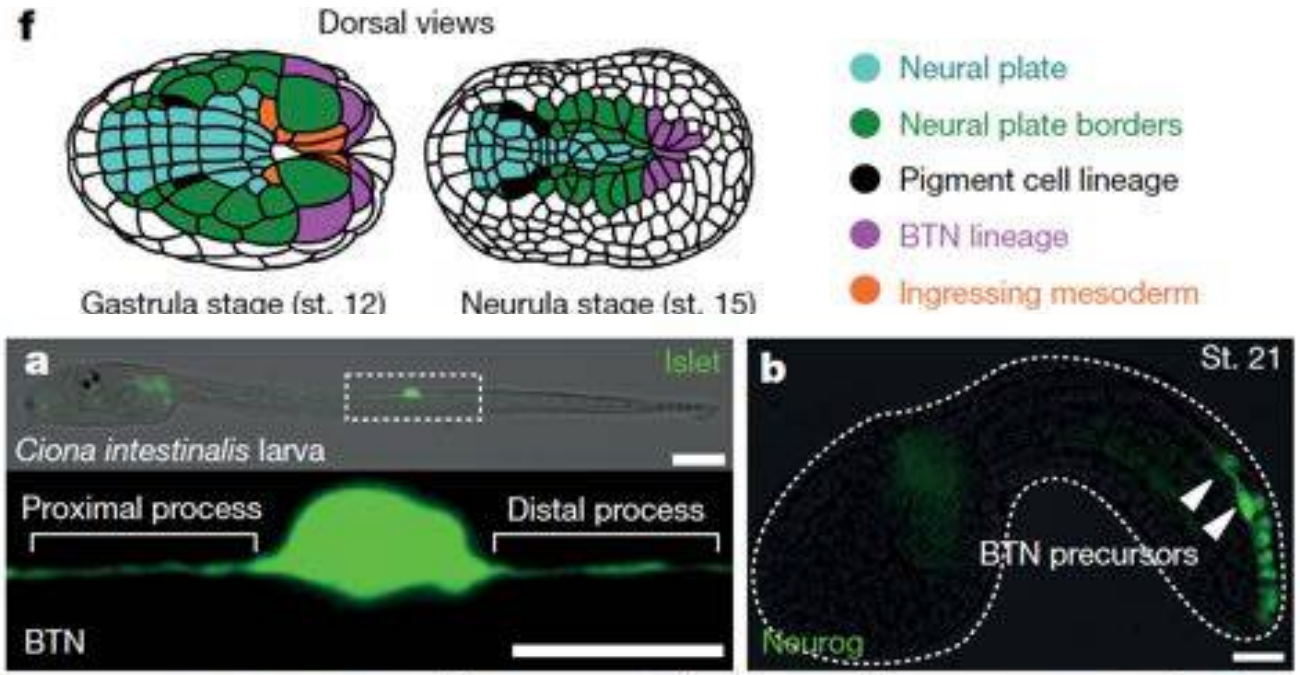
Larva de *Ciona intestinalis*



A cresta neural

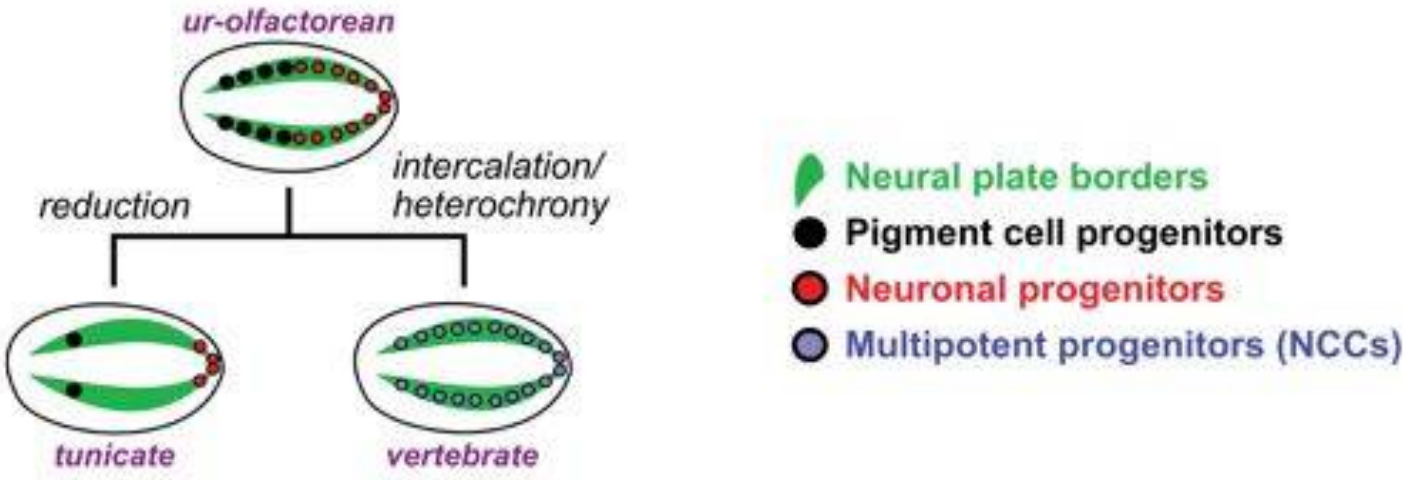


Neural crest like cells in ascidians

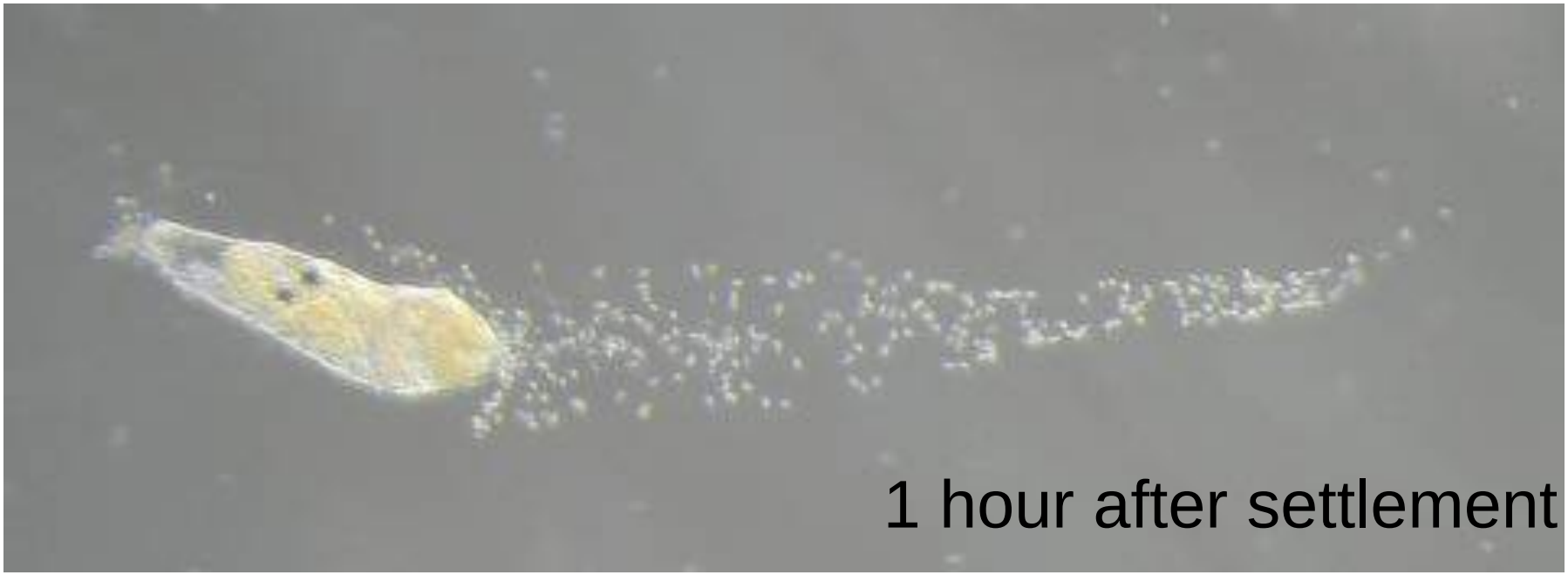


Stolfi et al., 2015

Modelo da evolução da cresta neural em vertebrados:



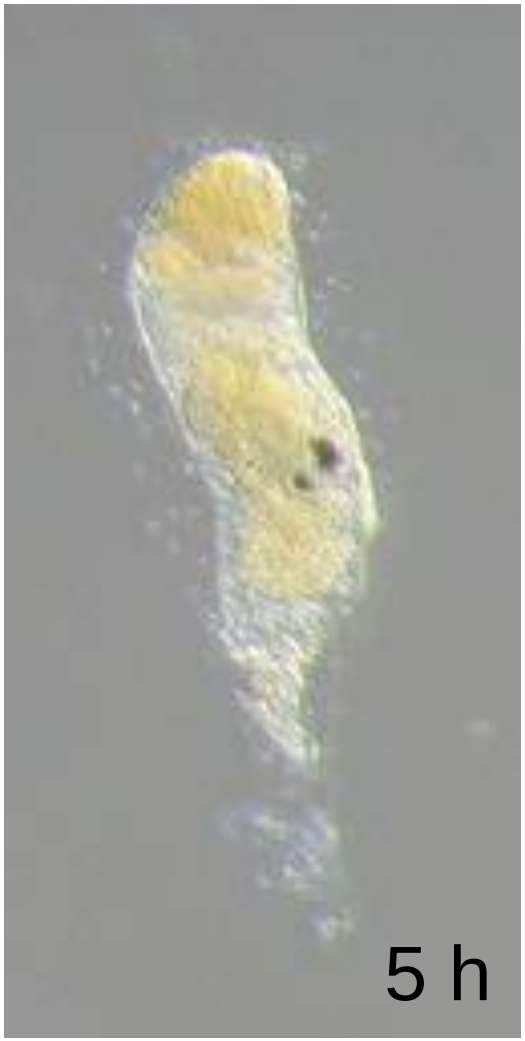
Metamorphosis



Four-dimensional Ascidian Body Atlas
Hotta et al. 2007

Metamorphosis

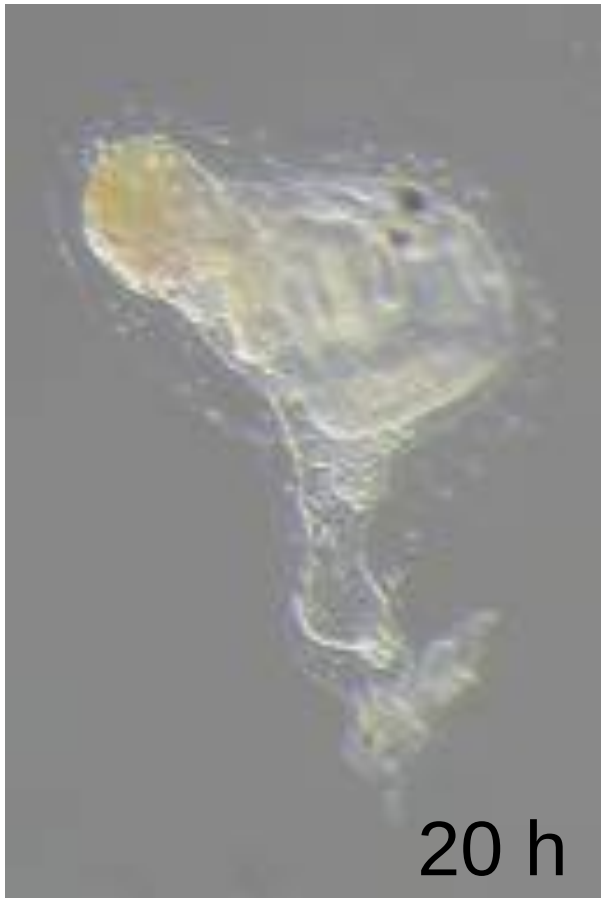
Metamorphosis



Metamorphosis

Metamorphosis

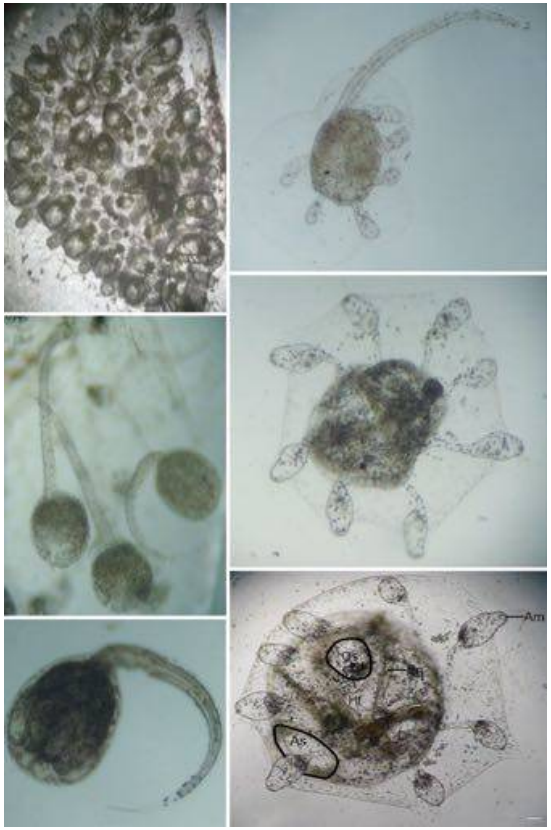
Metamorphosis

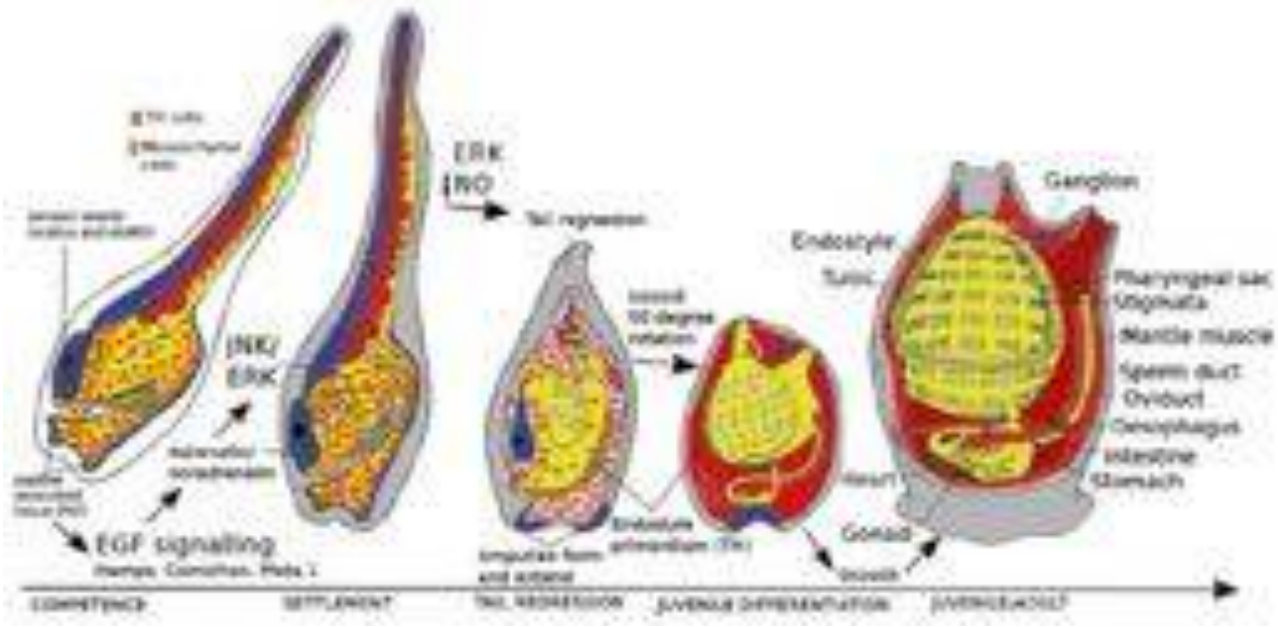


Metamorphosis

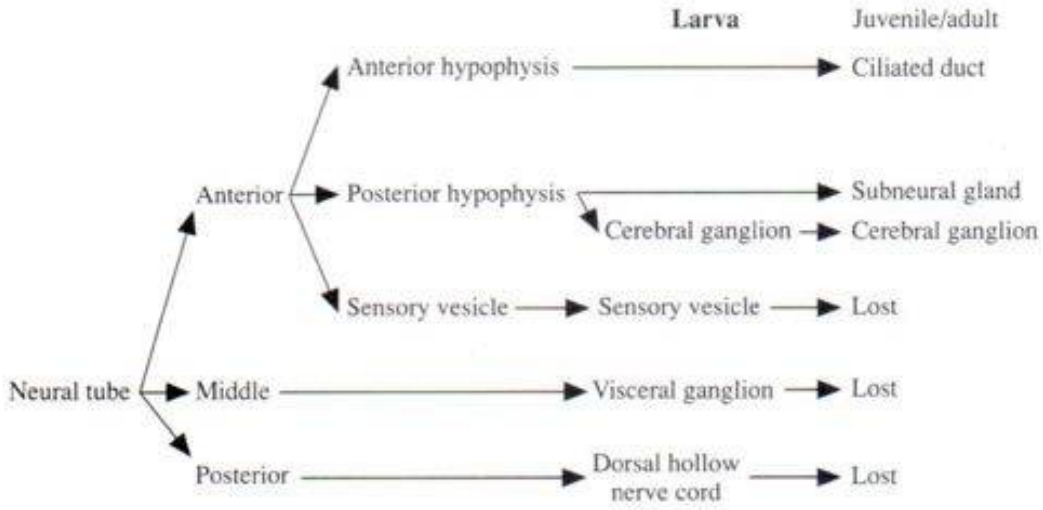
The juvenile

Metamorfose



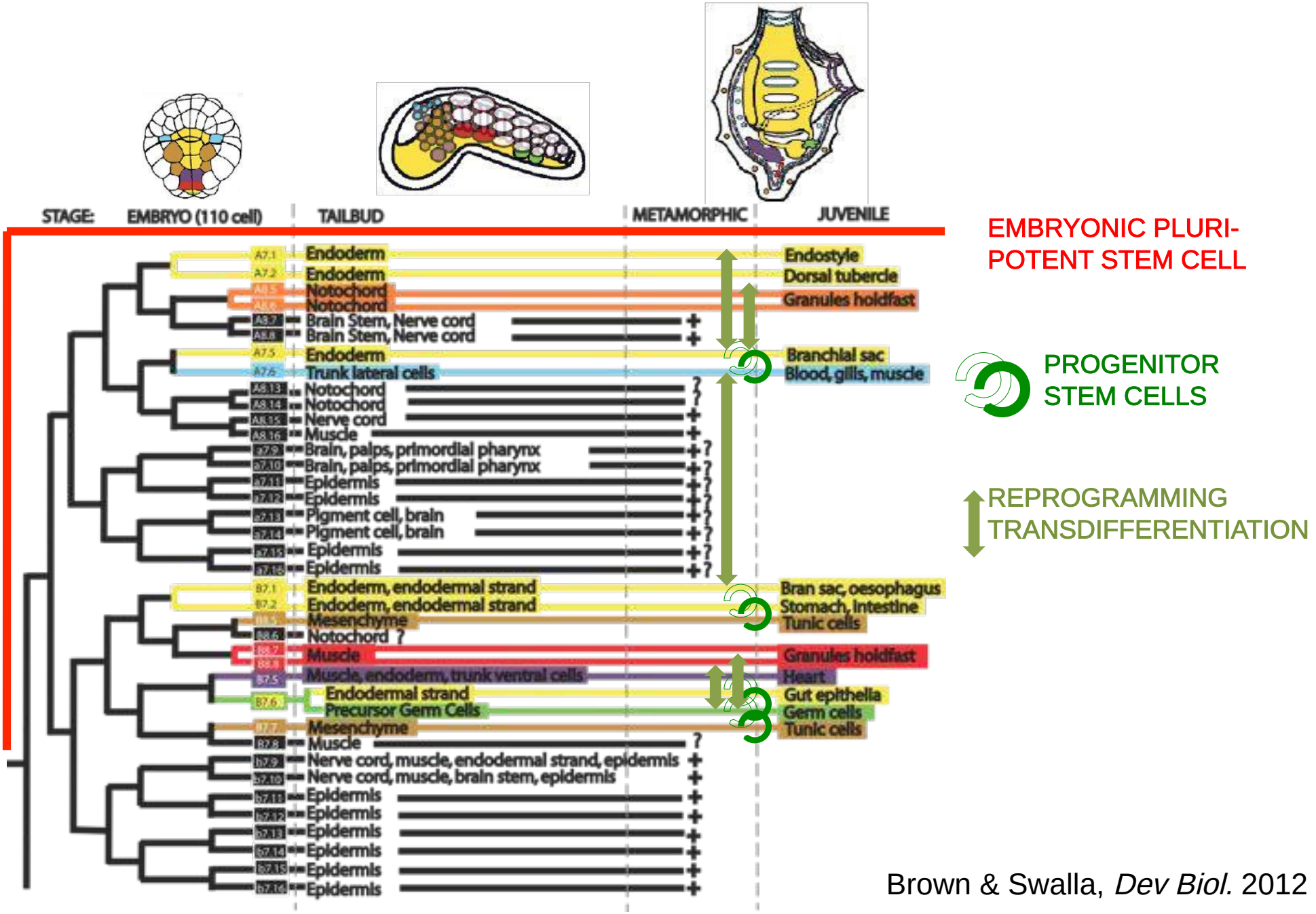


Stolfi & Brown, 2015



Kardong

Plasticidad en los linajes celulares de las ascidias



Brown & Swalla, *Dev Biol.* 2012

Modos de vida nas ascidians

Colonial ascidian development

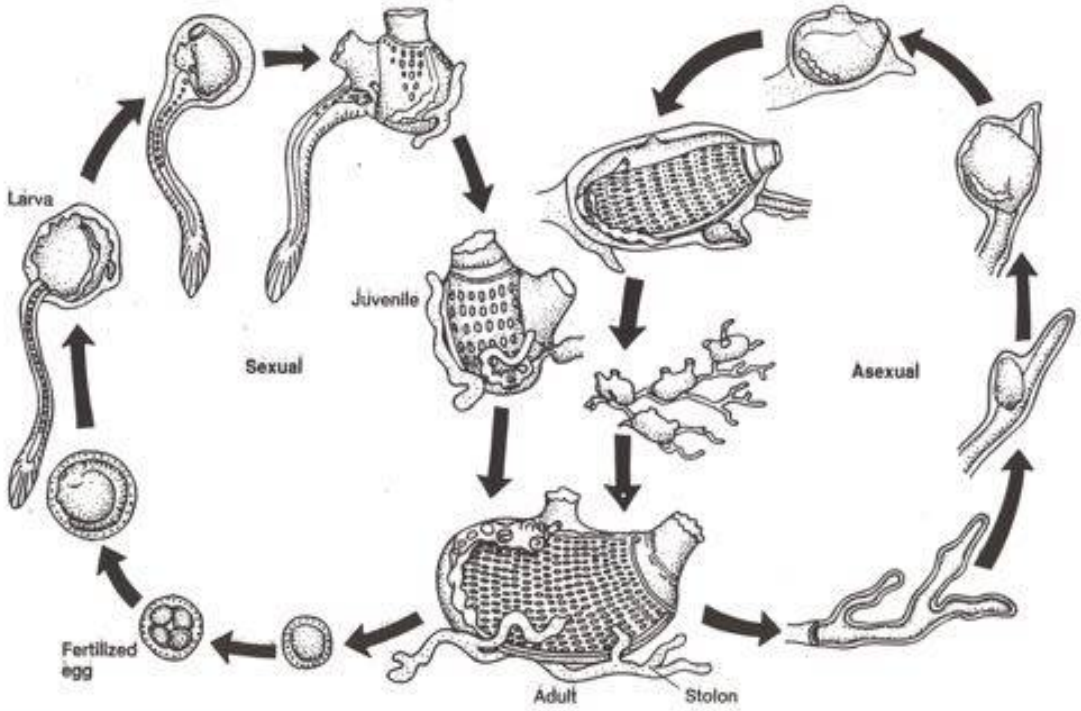
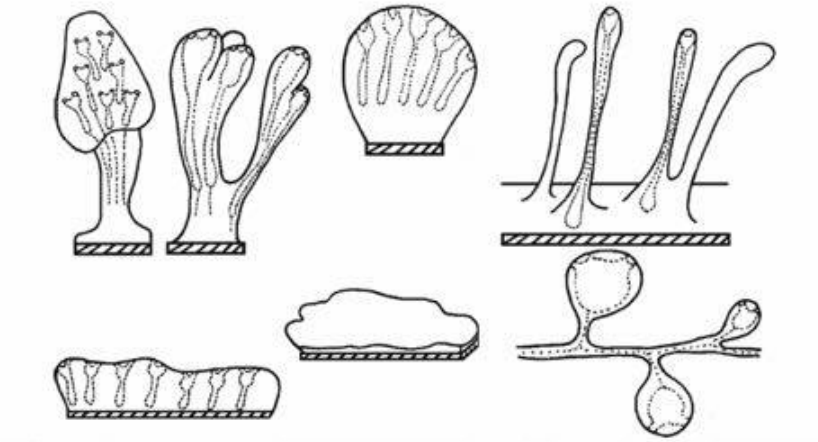
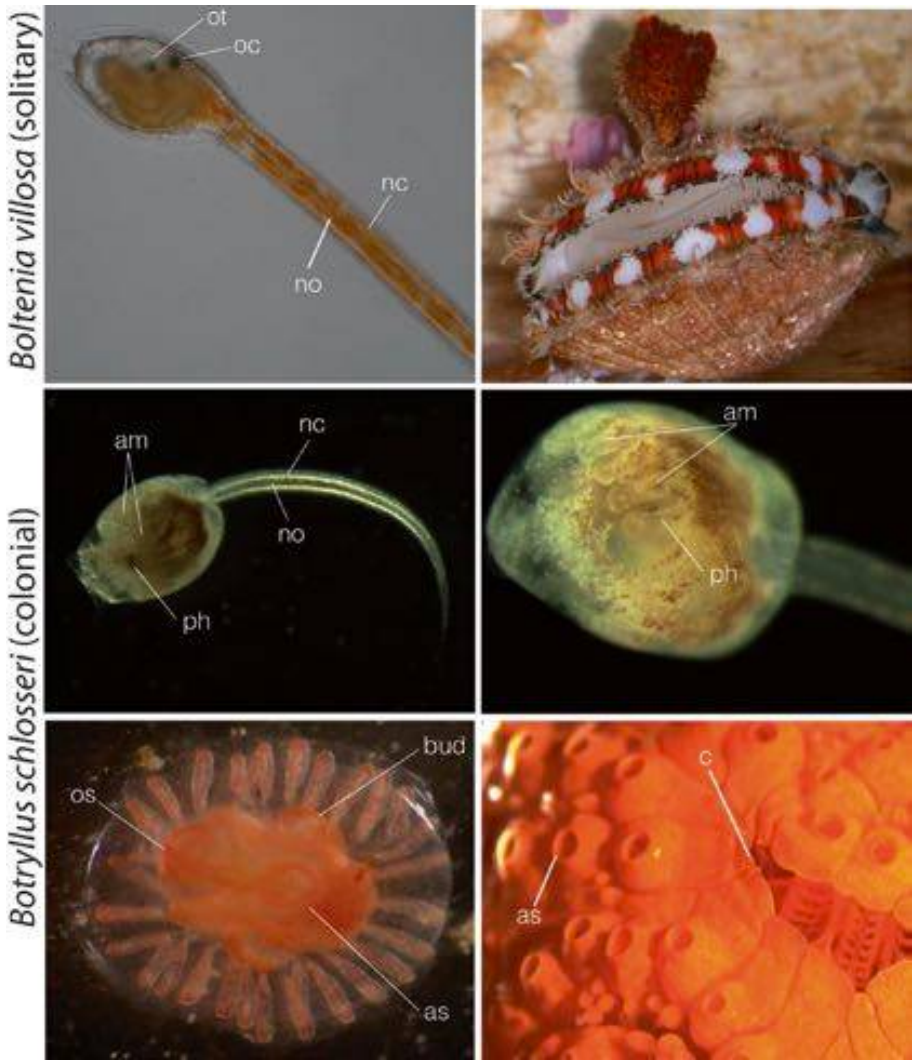


FIGURE 2.18 **Urochordate-ascidian life cycle.** The life cycle of colonial ascidians includes a sexual (left) and an asexual (right) phase. In the sexual phase, the tunicate larva develops from a fertilized egg. This larva is planktonic and persists for a few hours or few days at most. It soon settles on a solid substrate and undergoes metamorphosis into a sessile juvenile that grows into adulthood. The

Kardong, 2006




Boltenia villosa (solitary)
ot
oc
nc
no
Botryllus schlosseri (colonial)
am
nc
no
ph
am
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bud
os
as
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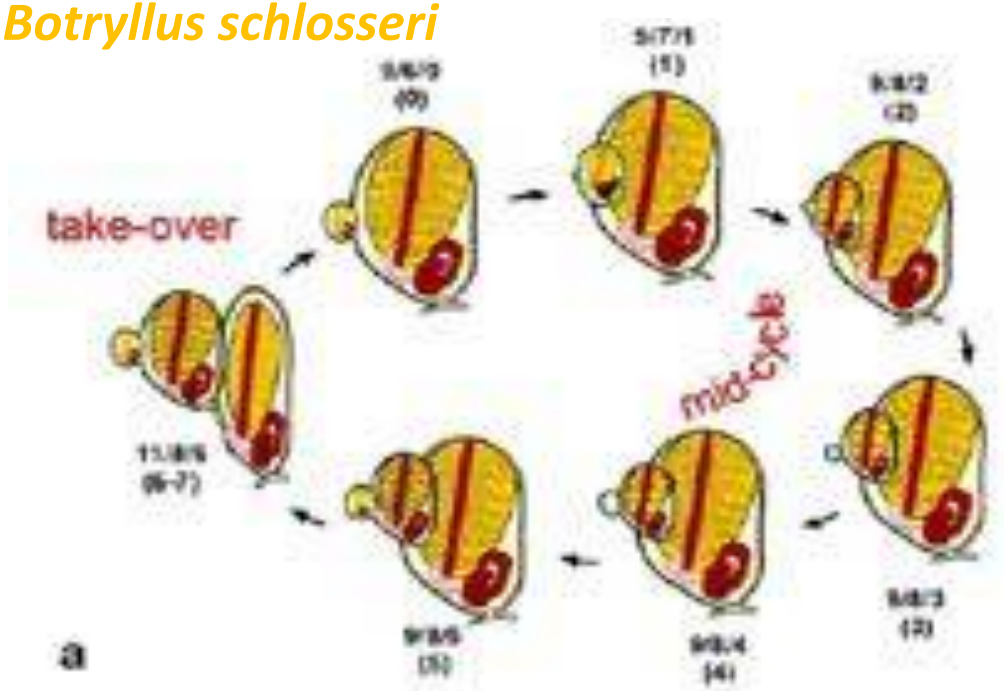
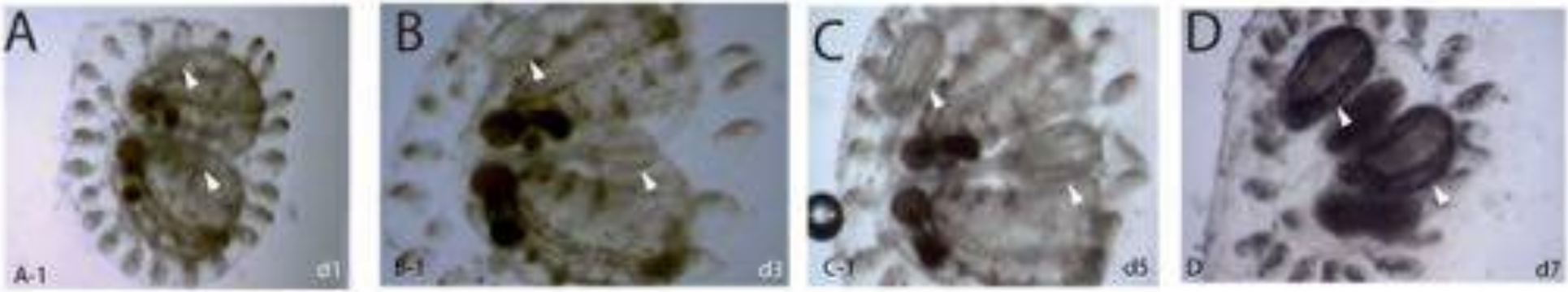
as

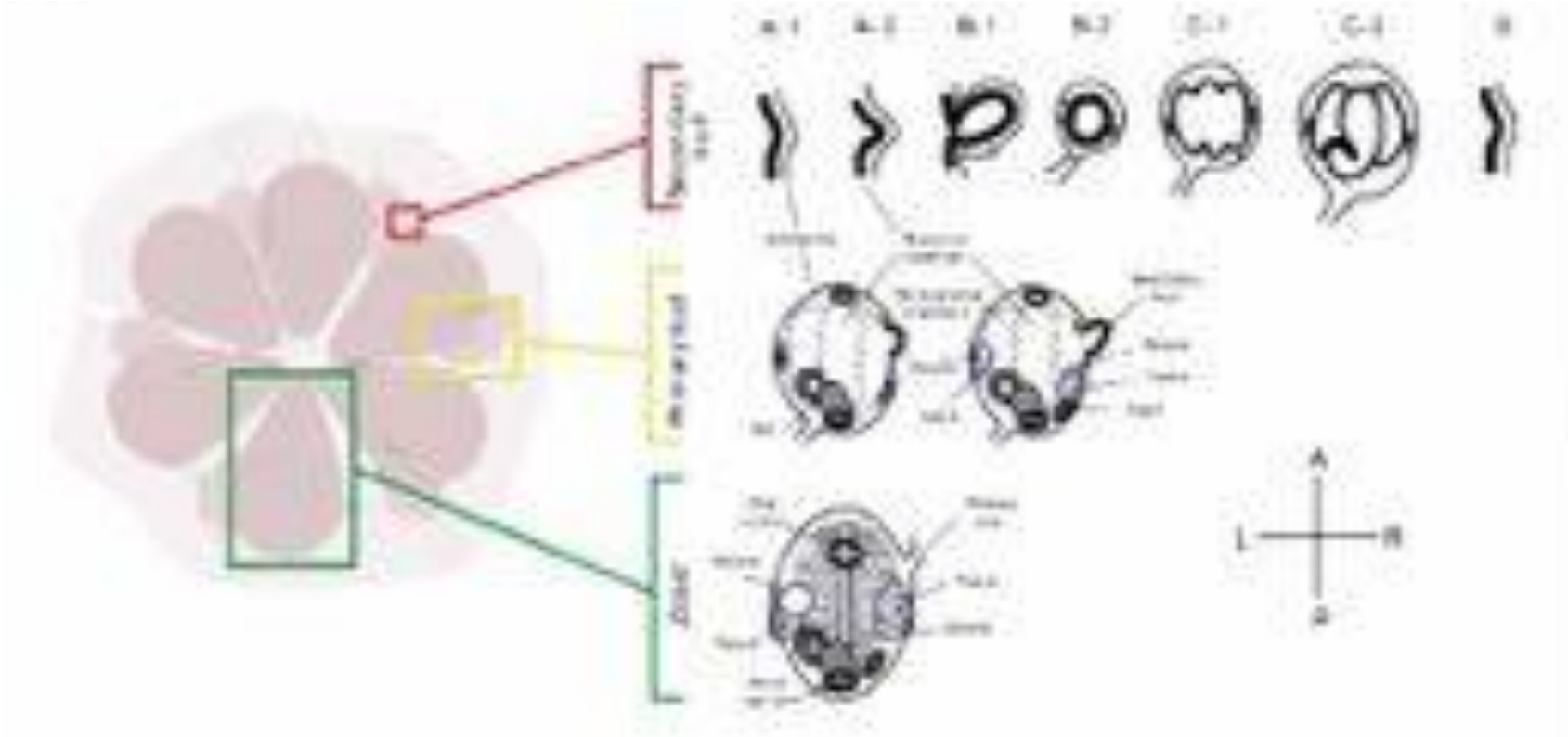
Colonial ascidian model species: *Botryllus*

Asexual reproduction and blastogenesis

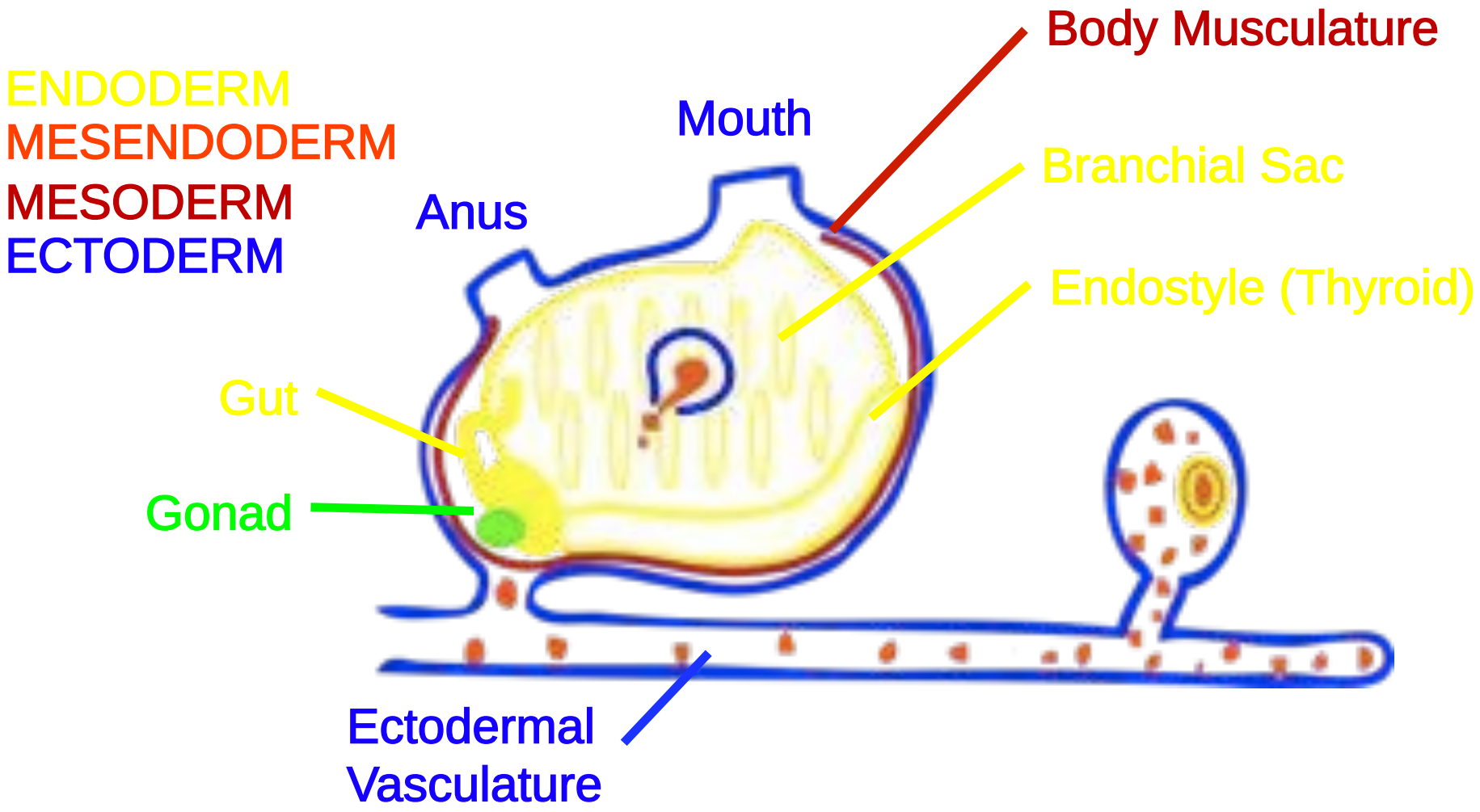
Botryllus schlosseri



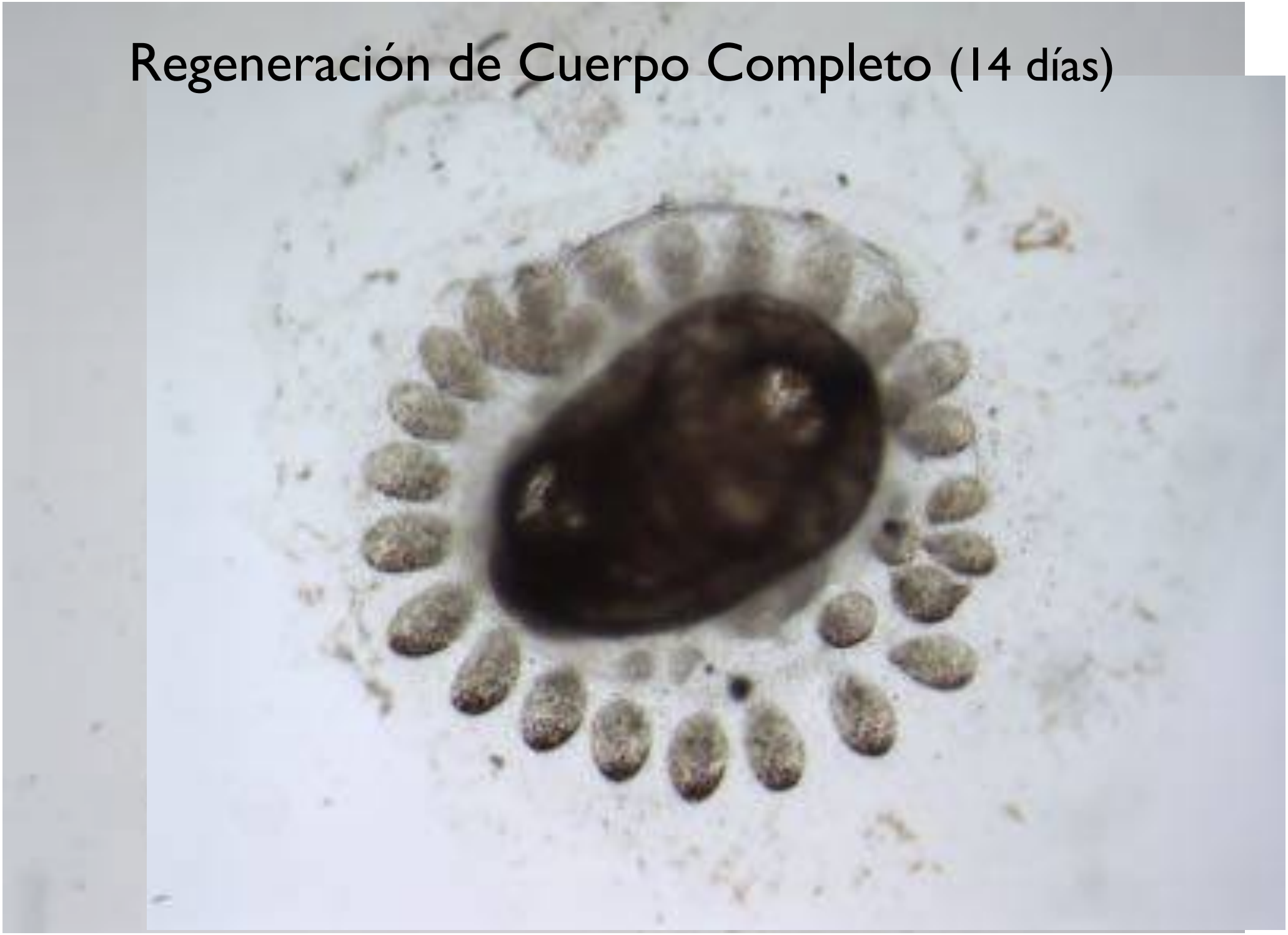

A
A-1
d1
B
B-1
d3
C
C-1
d5
D
D
d7



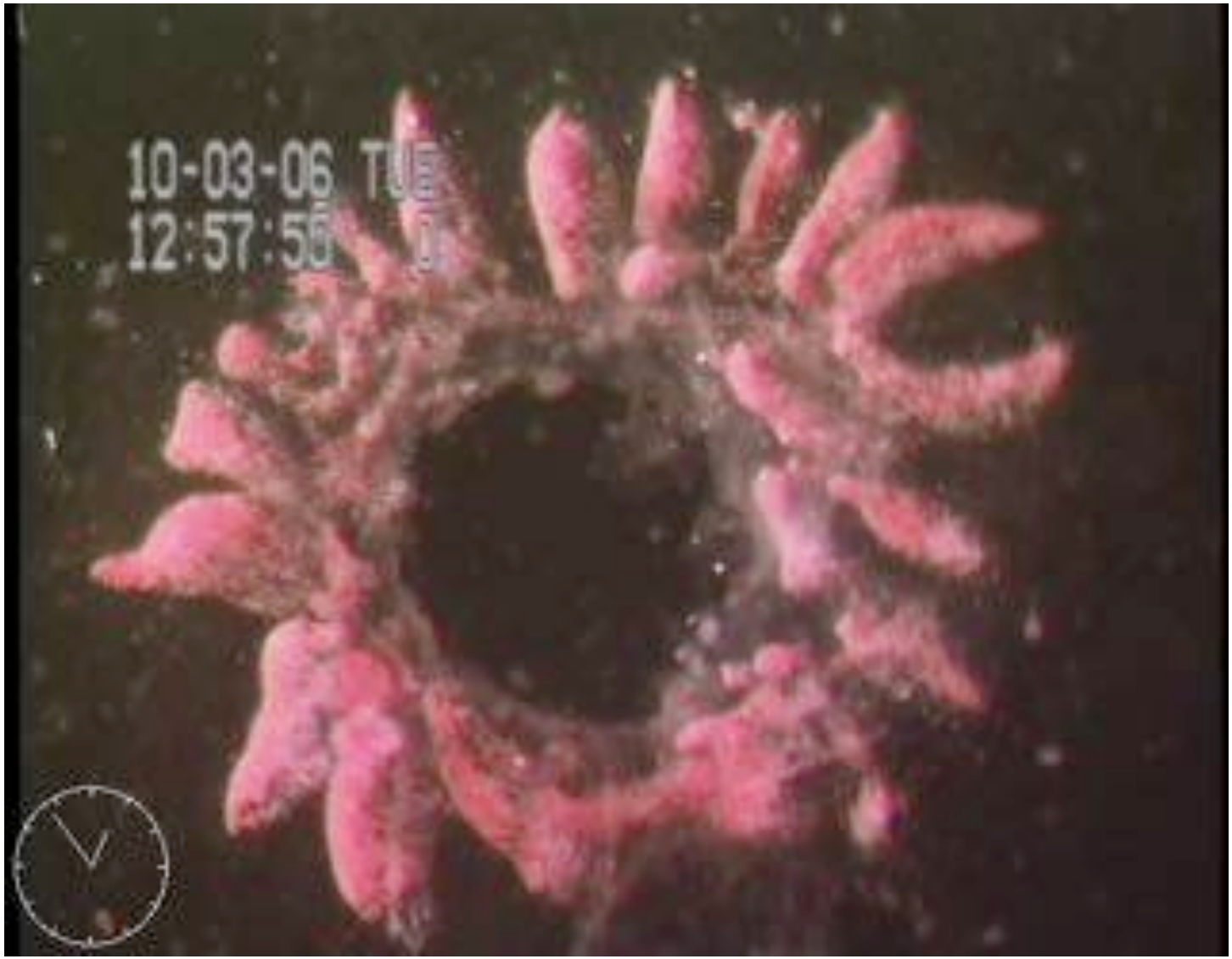
Camadas germinativas:



Regeneración de Cuerpo Completo (14 días)

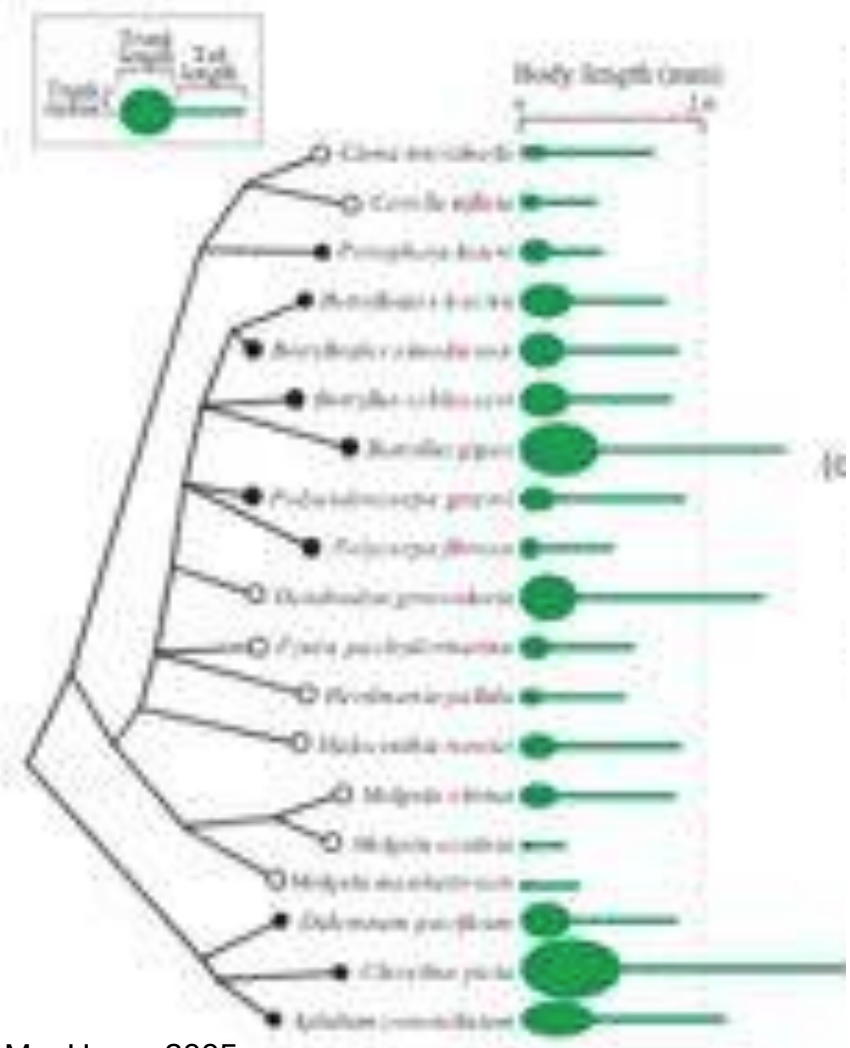


Regeneración de Cuerpo Completo (14 días)

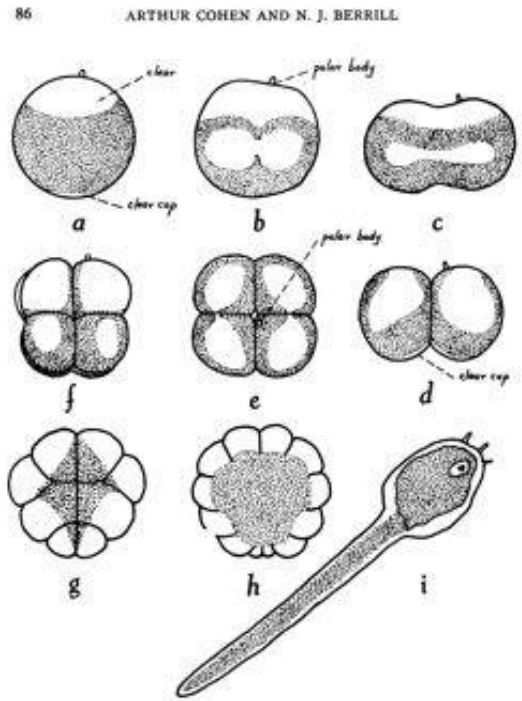


Brown, FD, Keeling, E, et al., 2009

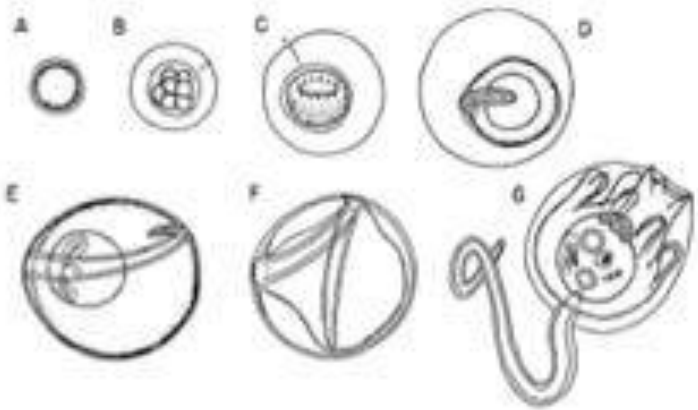
1. Comparison of solitary and colonial ascidian larvae:



Mc. Henry 2005

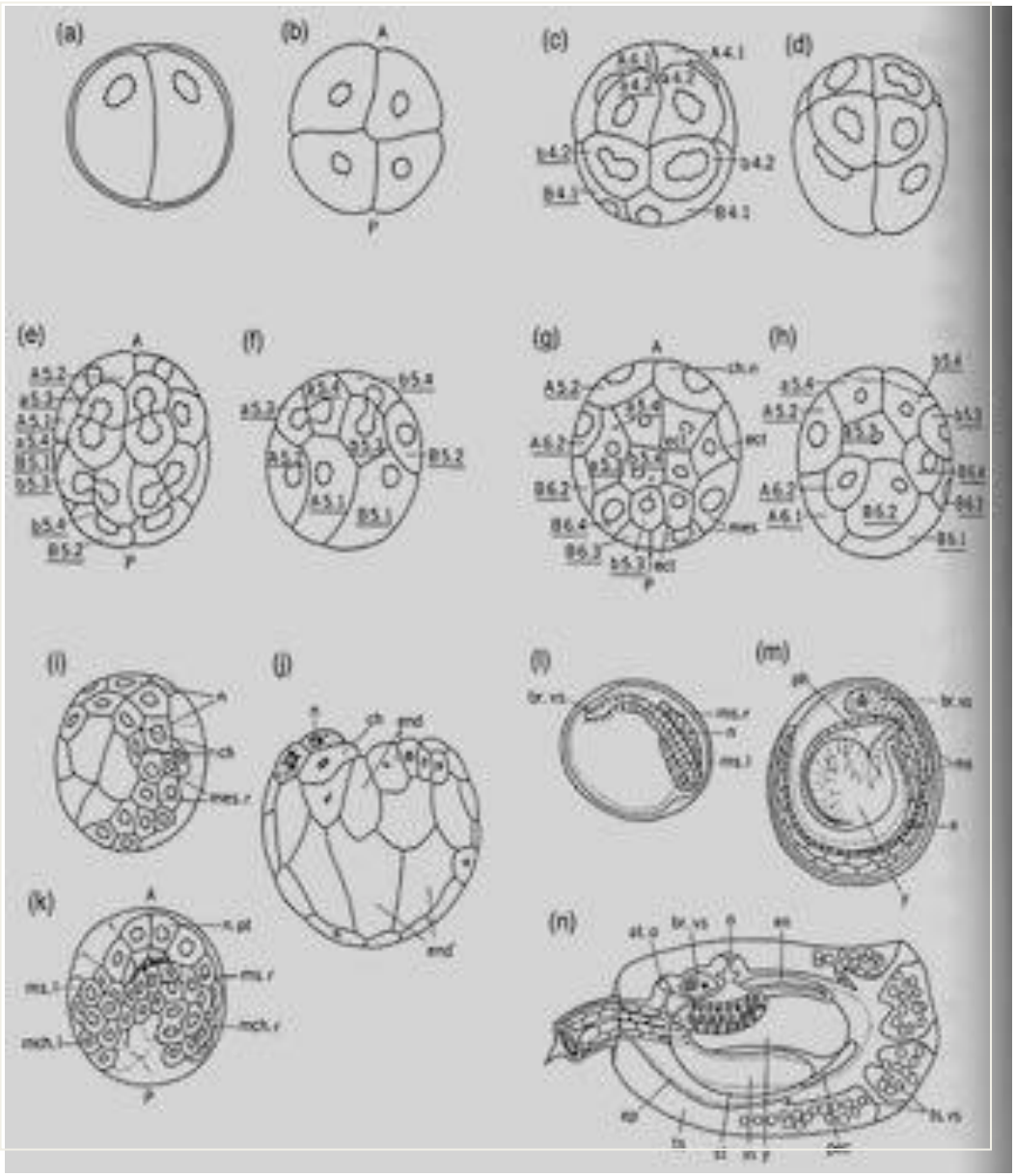


Ascidiella aspersa (Cohen and Berrill 1936)



Botrylloides violaceus (Berrill 1947)

Colonial Ascidian Development



Aplidium constellatum

- Big yolky eggs
- Slow development: takes weeks instead of hours

From Scott, 1946

Slide courtesy: G. and C. Lambert

Developmental acceleration and retardation

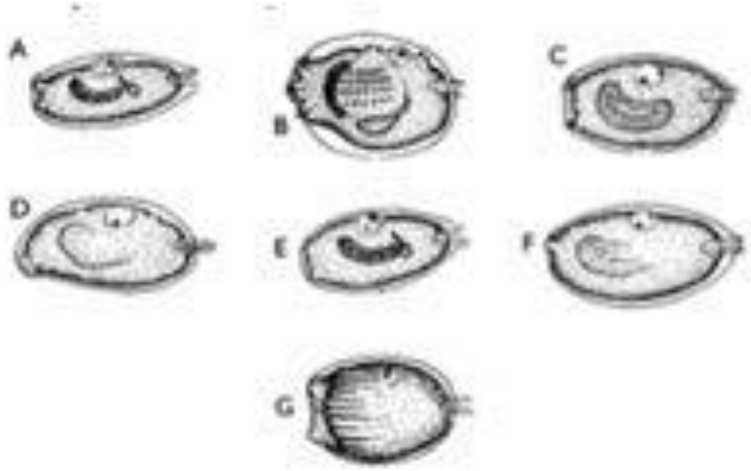


Fig. 6. Larvae of solitary ascidians (tails not shown). (A) **Ciona intestinalis** (B) **Perophora** listeri. (C) **Pyura** microcosmus. (D) **Molgula** citrina. (E) **Ascidia** mentula. (F) **Styela** partita. (G) **Dendrodoa** grossularia. Species or genera found locally in bold. Figures not to scale. (From Millar, 1971, Fig. 5)

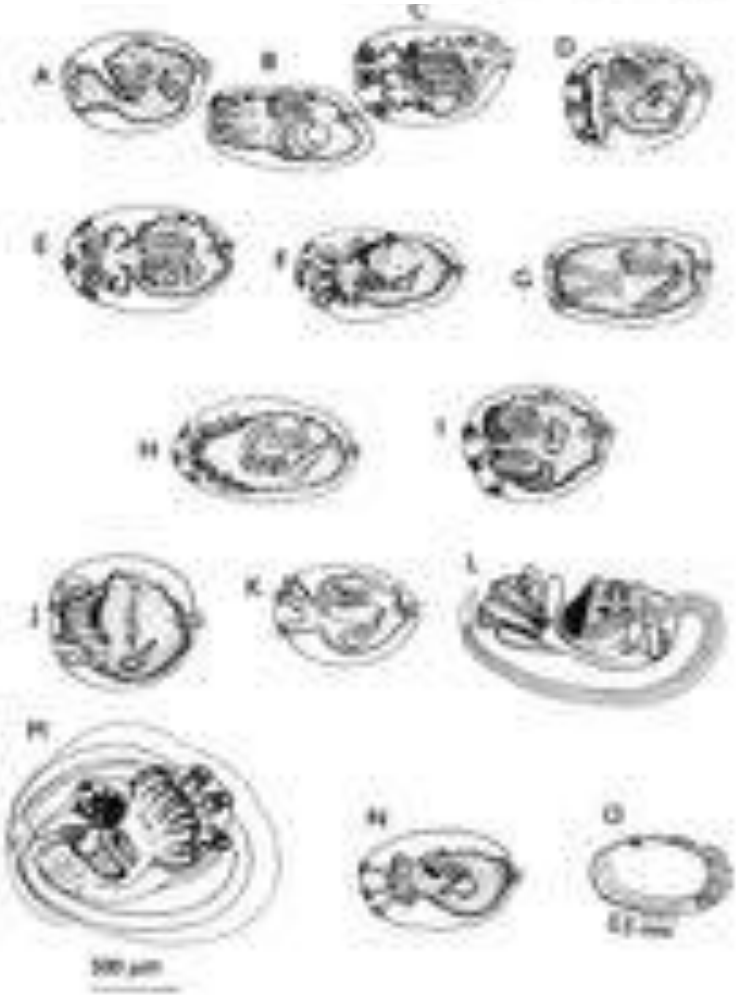
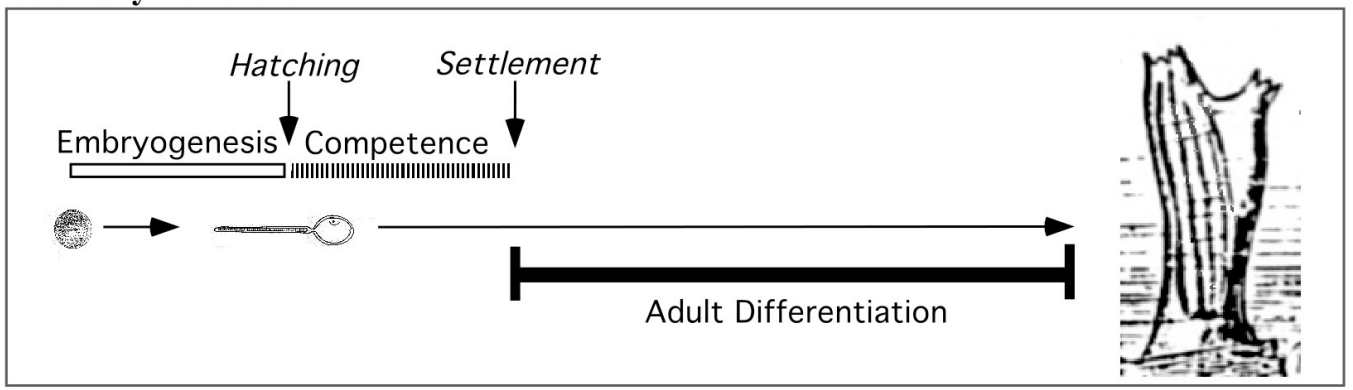


Fig. 7. Larvae of compound ascidians. (A) **Clavelina** lepadiformis. (B) **Pycnoclavella stanleyi**. (C) **Distaplia** rosea. (D) **Cystodytes** dellechiajei. (E) **Eudistoma** durum. (F) **Synoicum** georgianum. (G) **Euherdmania claviformis**. (H) **Aplidium** meridionale. (I) **Diplosoma listerianum**. (J) **Botrylloides** leachii. (K) Social aplidioides. (L) **Archidistoma** aggregatum. (M) **Didemnum albidum**. (N) **Didemnum** helgolandicum. (O) **Rhizonella nubra**. Species or genera found locally are in bold. Figures A–L, N are not to scale. (A–K, N from Millar, 1971, Fig. 5.1, from Berrill, 1948, Fig. 2; M from Maria, 1996, Fig. 4A, O from Abbott and Trason, 1968, Fig. 1C)

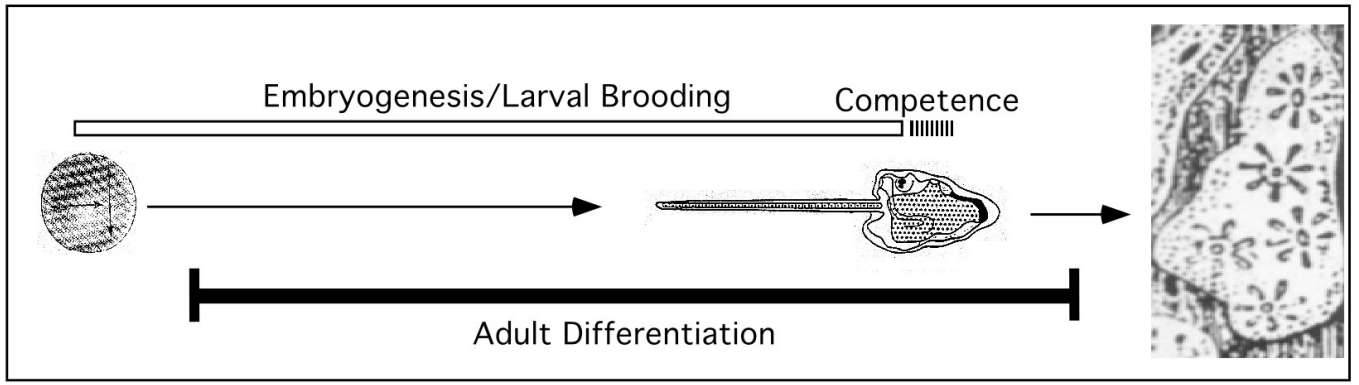
Sadro 2001

Modularity in ascidian development

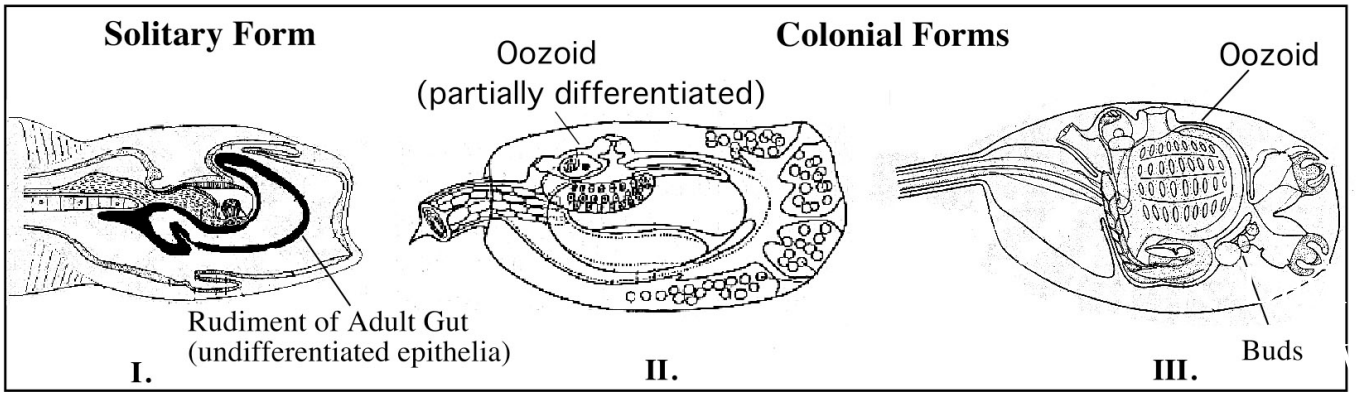
A. Solitary Ascidians

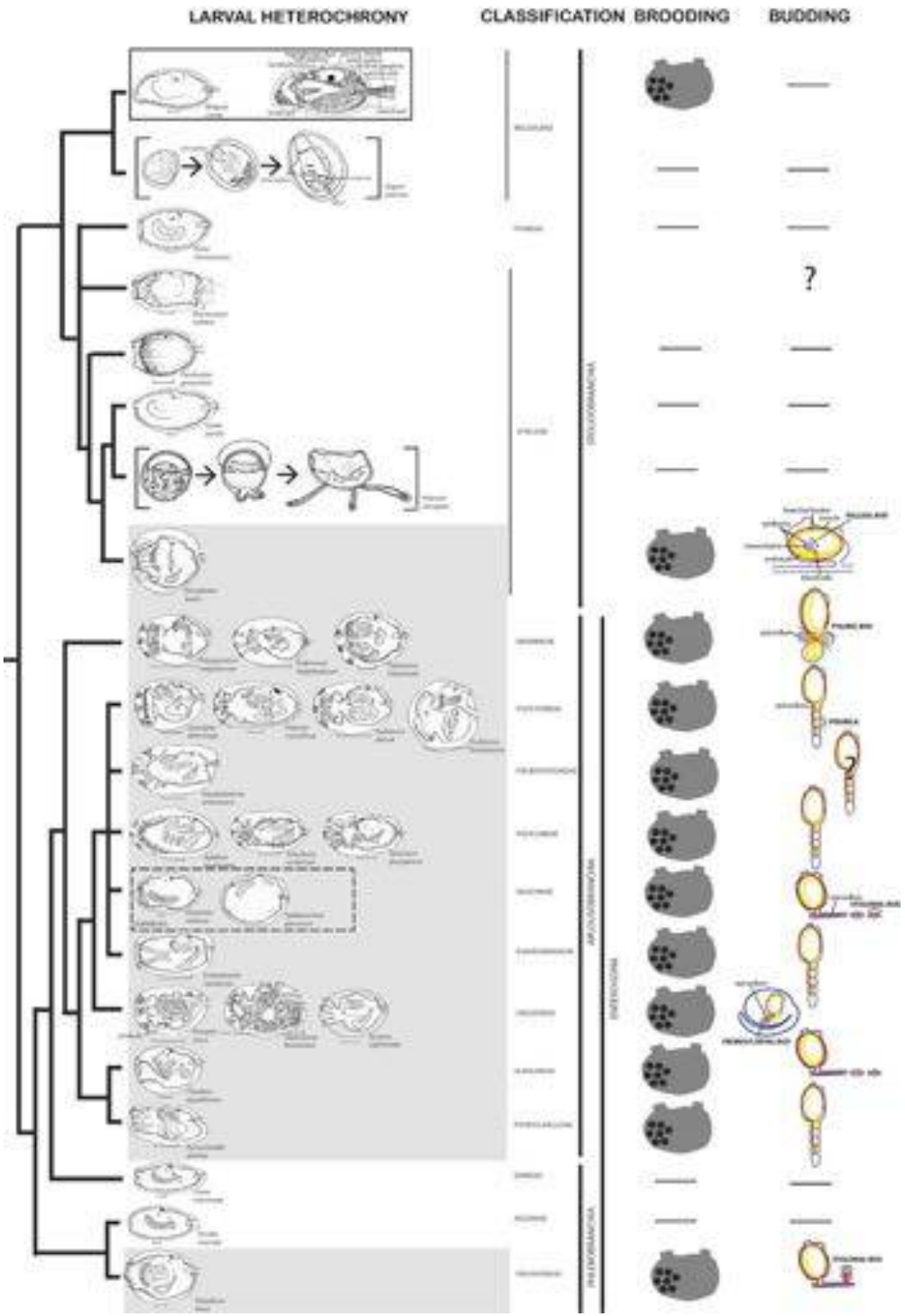


B. Colonial Ascidians

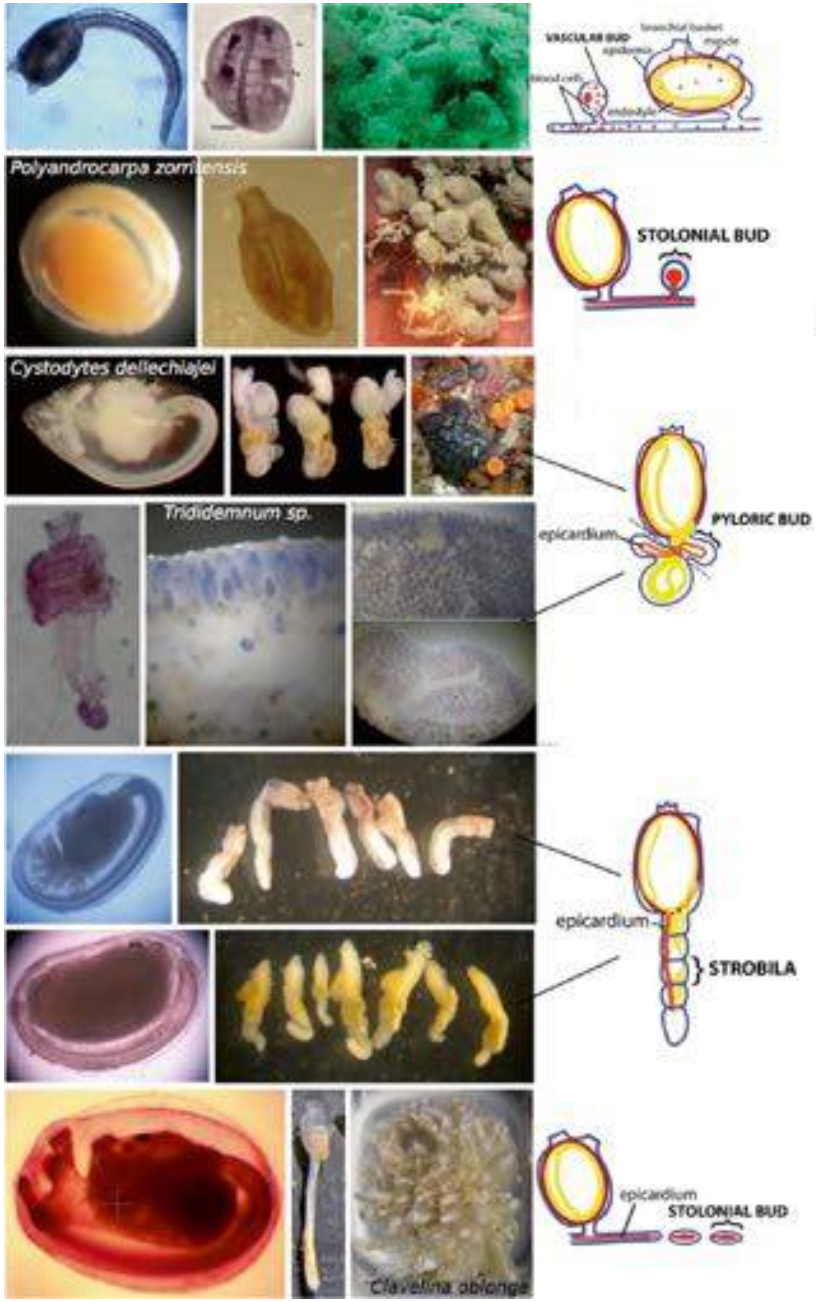


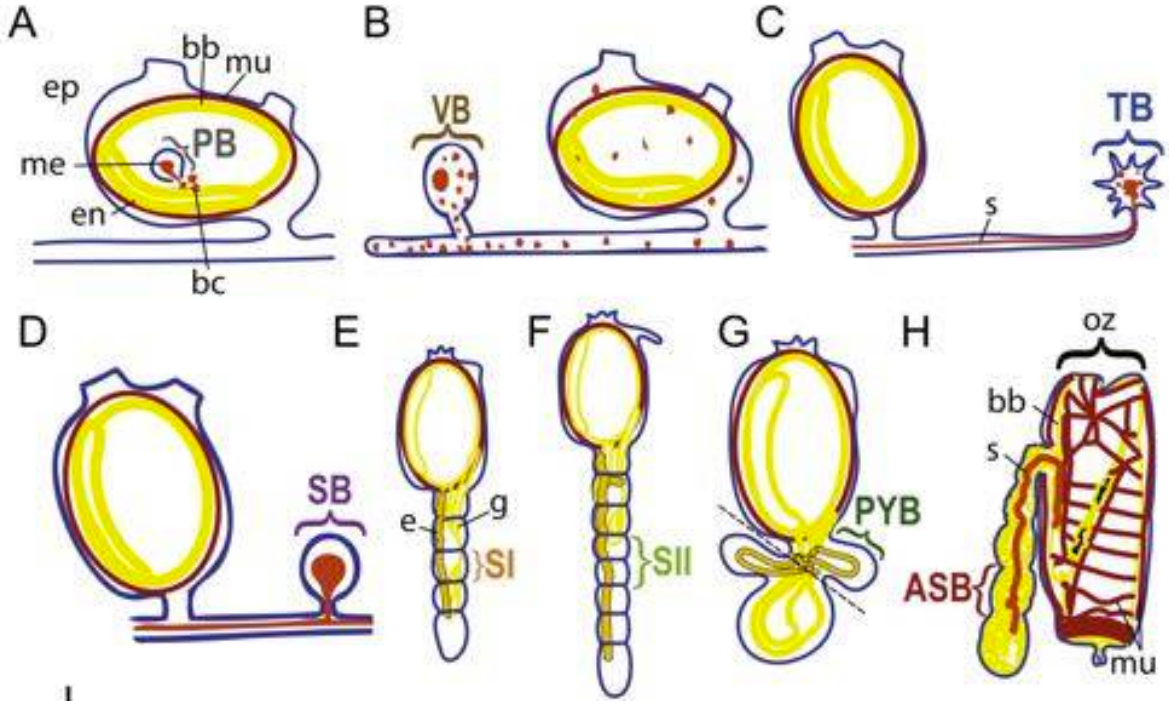
C. Adult Differentiation within the Larval Head/Trunk




LARVAL HETEROCHRONY
CLASSIFICATION
BROODING
BUDDING
?

Tipos de gemación en ascidias



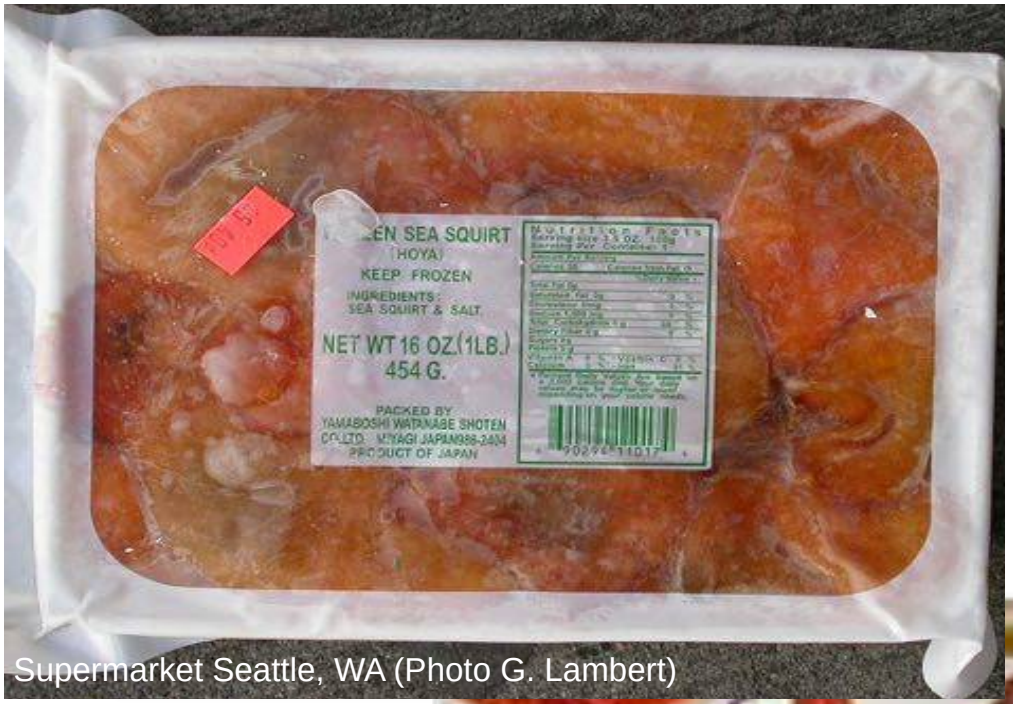


Brown & Swalla, *Dev Biol.* 2012

Interés comercial

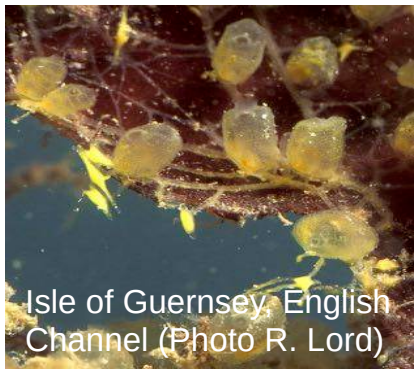
- Alimentação: preservada em MISO ou salgada (vinagre e molho de soya)
- Produção papel (material forte, alto módulo de elasticidade: alto ‘Young modulus’)
- Neve marinha (ciclo de carbono e alimentação de animais bénticos; alimentação para anguila em cultivo)

¿Y se comen?



Supermarket Seattle, WA (Photo G. Lambert)

Invasiones e impacto



Ascidias Invasoras

Didemnum vexillum

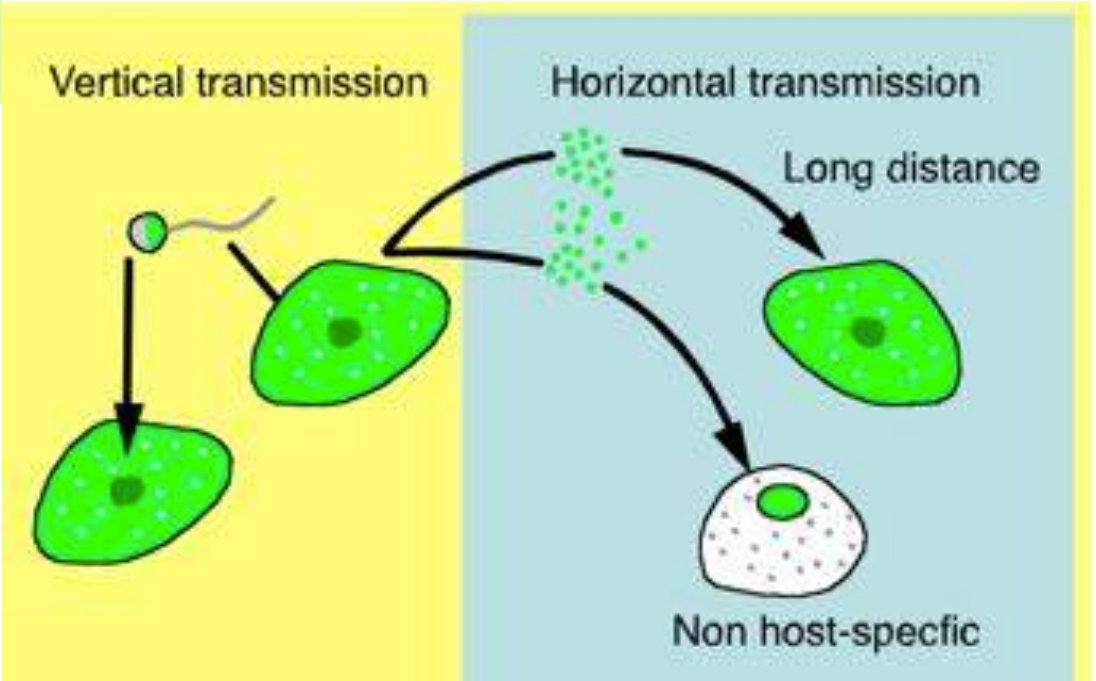
Didemnum perlucidum

Kenya (Photo T. McClanahan)

Ashley Coutts, Cawthron Inst., Nelson, New Zealand

Ascidias Cenaim, Ecuador

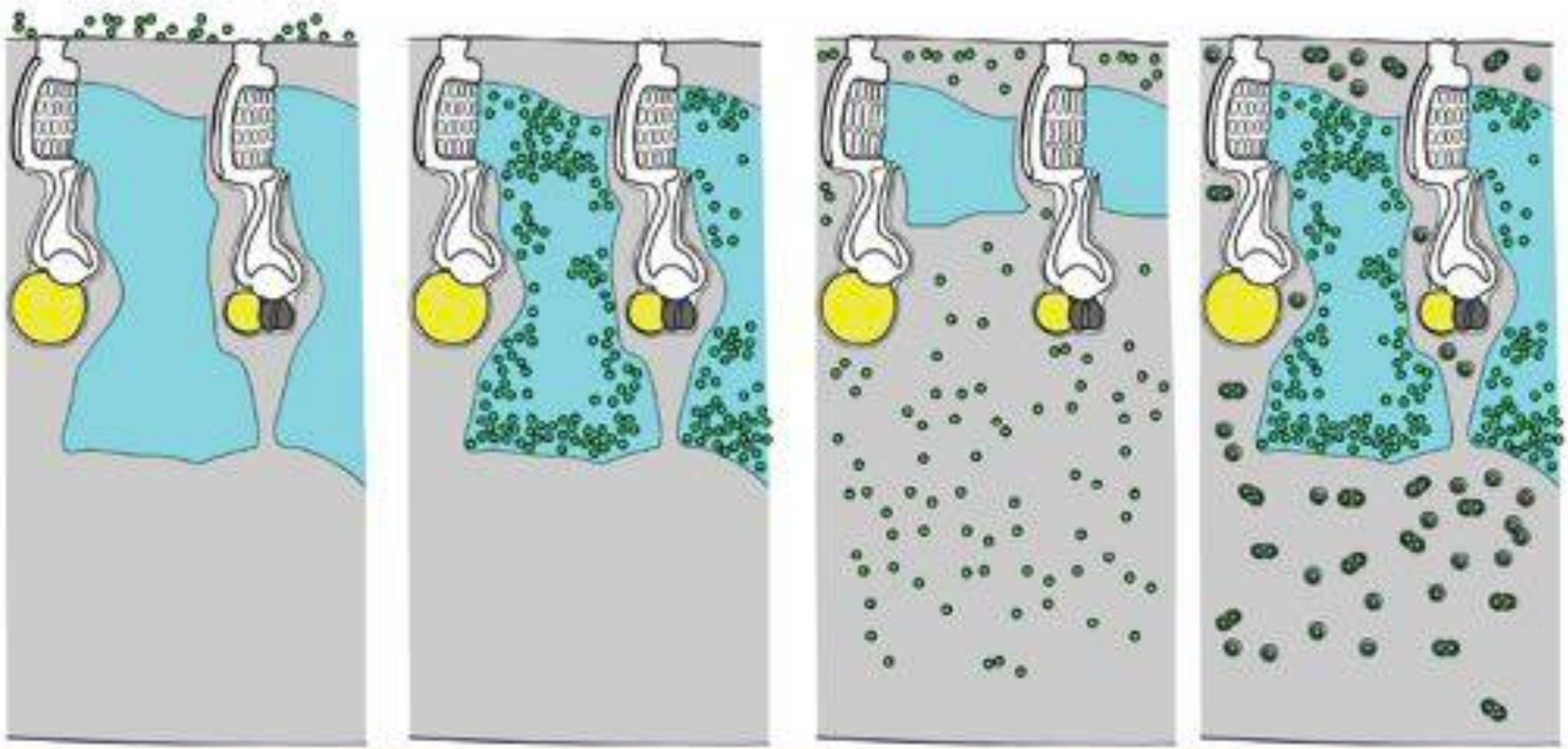
Photosymbiosis in ascidians



It is the only example of strict photosymbiosis in the chordates

Slide courtesy: L. Hirose

Distribution pattern of photosymbionts in the host colonies

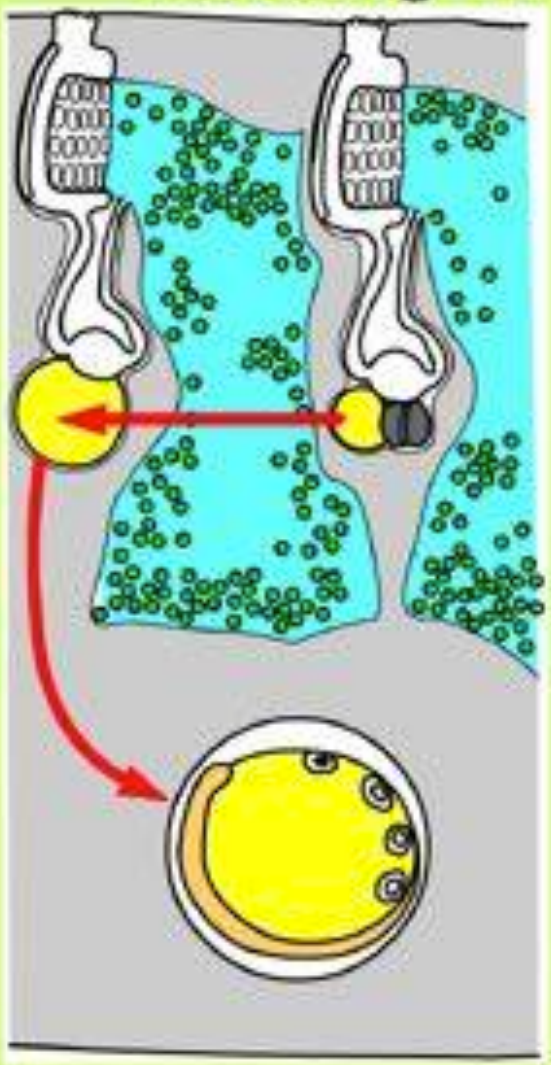


Colony Surface	Common cloacal cavity	Tunic	Cloacal cavity + Tunic (intracellular)
Didemnum candidum	*Didemnum molle* *Trididemnum cyclops,* *T. paracyclops* *Lissoclinum bistratum,* *L. patella* *Diplosoma spp.*	*Trididemnum miniatum* *T. clinides,* *T. nubilum,* *T. solidum*	*Lissoclinum punctatum*

Slide courtesy: L. Hirose

Slide courtesy: L. Hirose

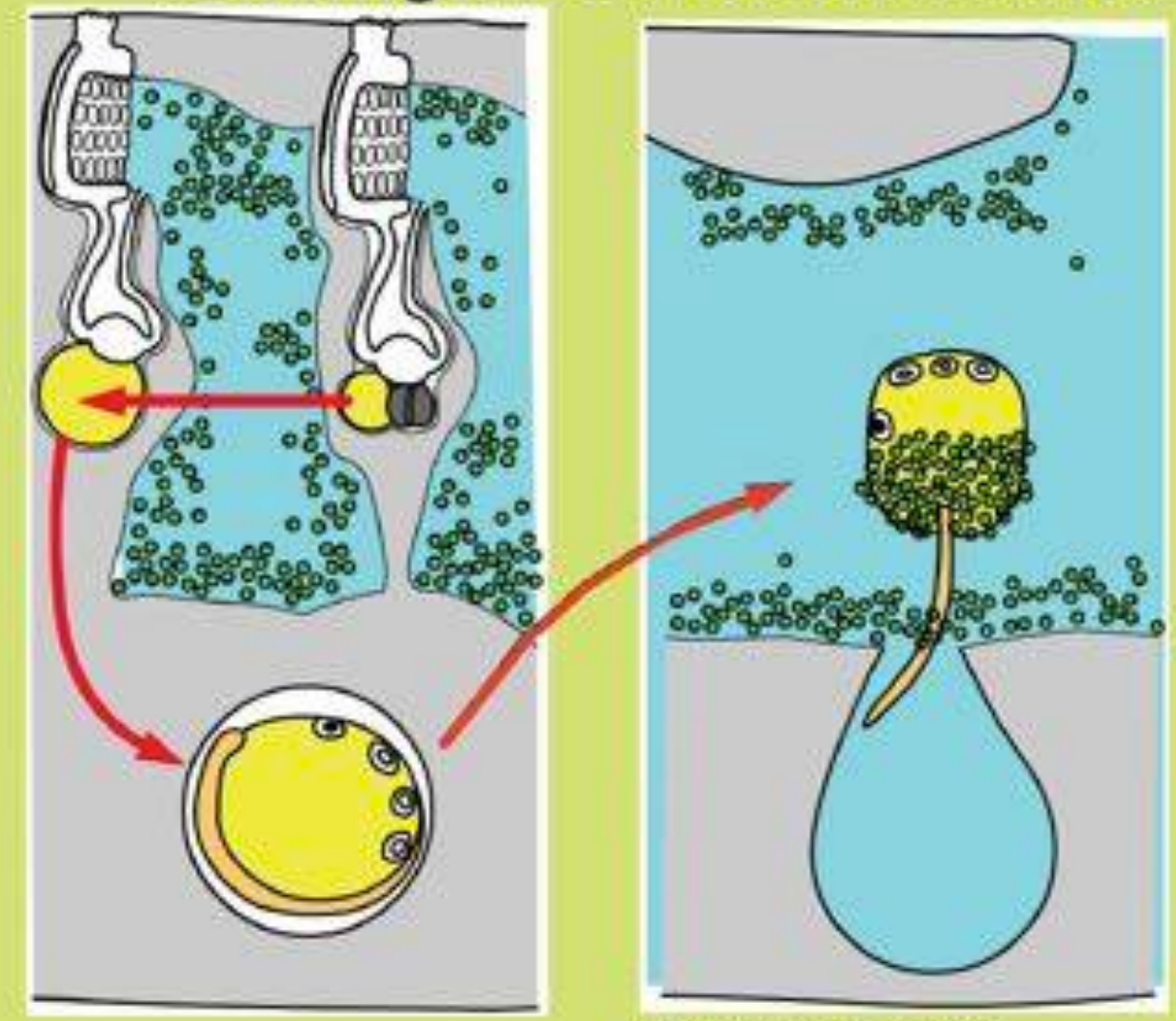
Two modes of the transmission in the hosts bearing *Prochloron* in cloacal cavity.



Slide courtesy: L. Hirose

Slide courtesy: L. Hirose

Two modes of the transmission in the hosts bearing *Prochloron* in cloacal cavity.

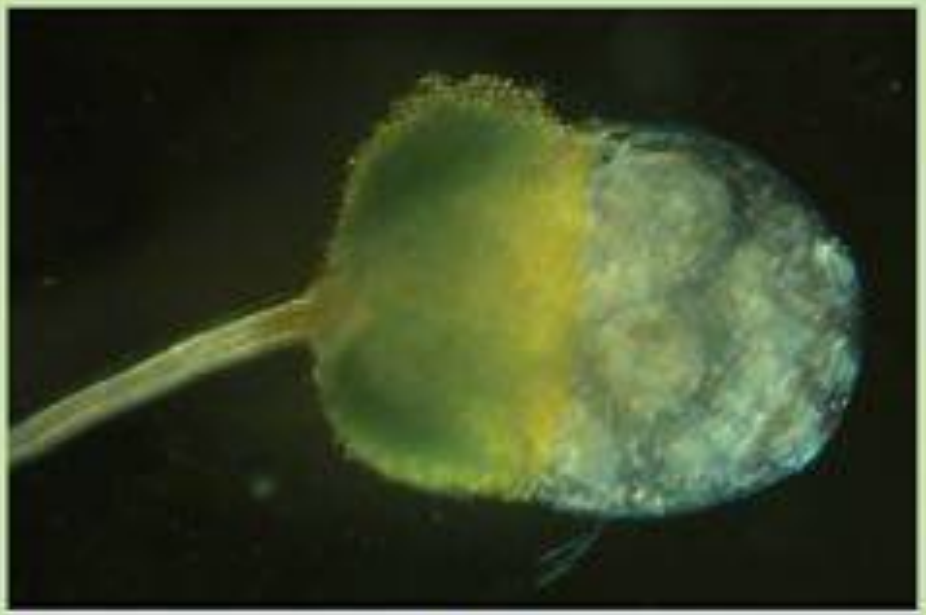


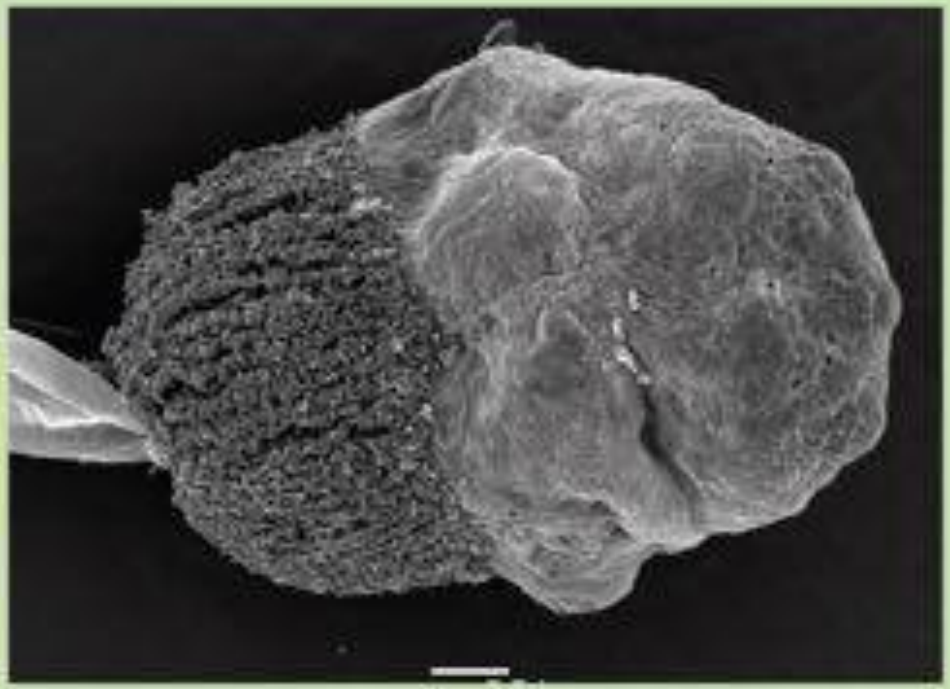
Didemnum molle
Lissoclinum bistratum
Tridemnum cyclops

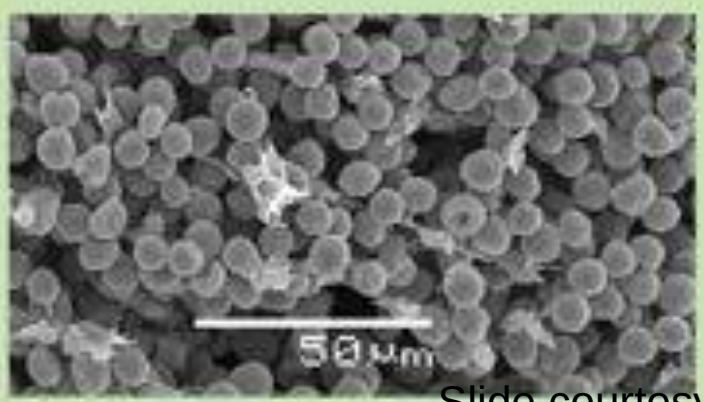
Slide courtesy: L. Hirose

Slide courtesy: L. Hirose

Larva of *Lissoclinum timorense:* Posterior half of the trunk is densely covered with *Prochloron* cells.



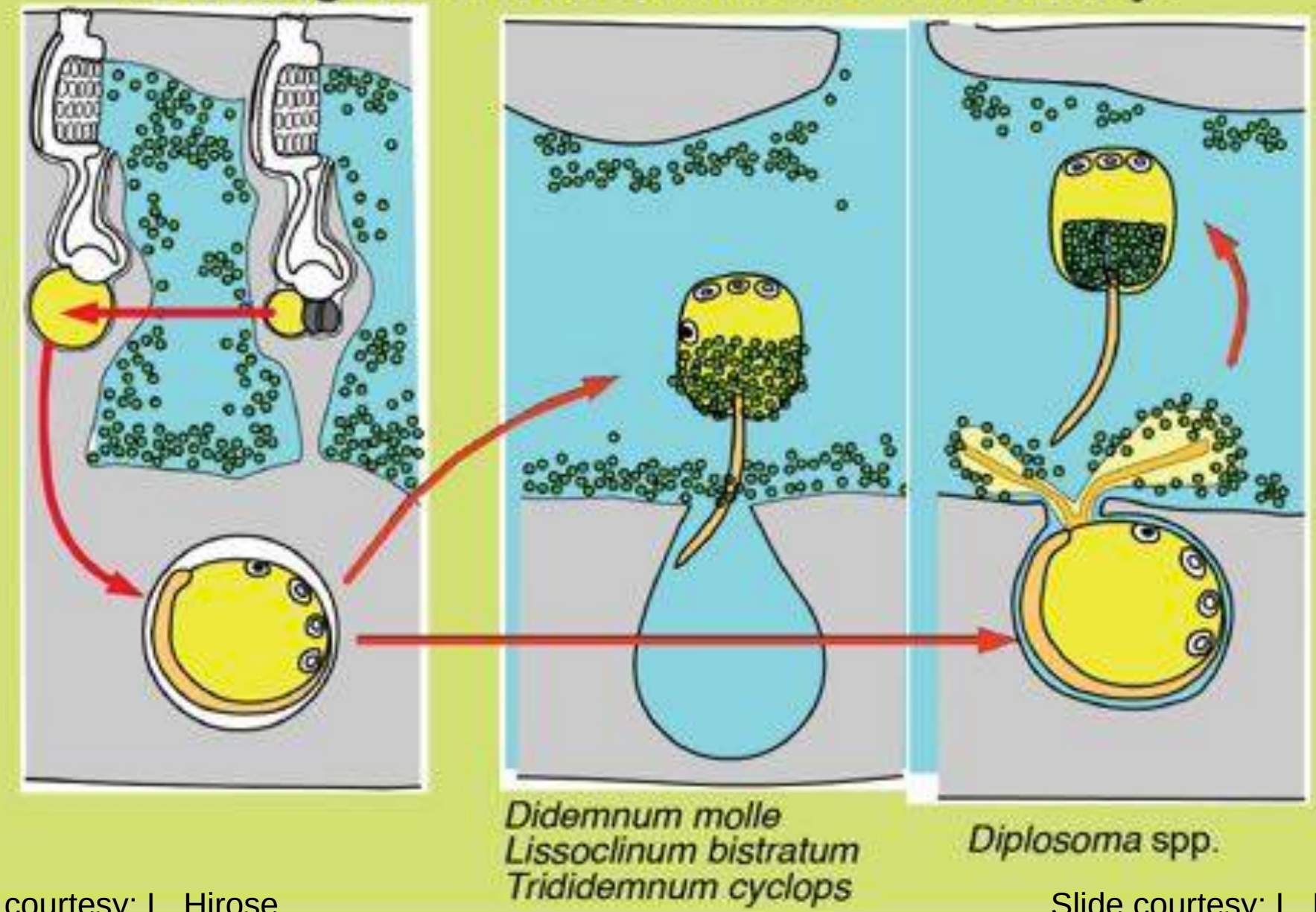




Slide courtesy: L. Hirose

Slide courtesy: L. Hirose

Two modes of the transmission in the hosts bearing *Prochloron* in cloacal cavity.



Slide courtesy: L. Hirose

Slide courtesy: L. Hirose

Diplosoma embryo has a special organ to catch *Prochloron* cells in the cloacal cavity.

The organ is packed in the pouch in the larval trunk.

↑ Embryo of *D. simile*

→ Larva of *D. simile*

Slide courtesy: L. Hirose

Slide courtesy: L. Hirose

Trididemnum miniatum

Didemnum poecilomorpha

Trididemnum paracyclops

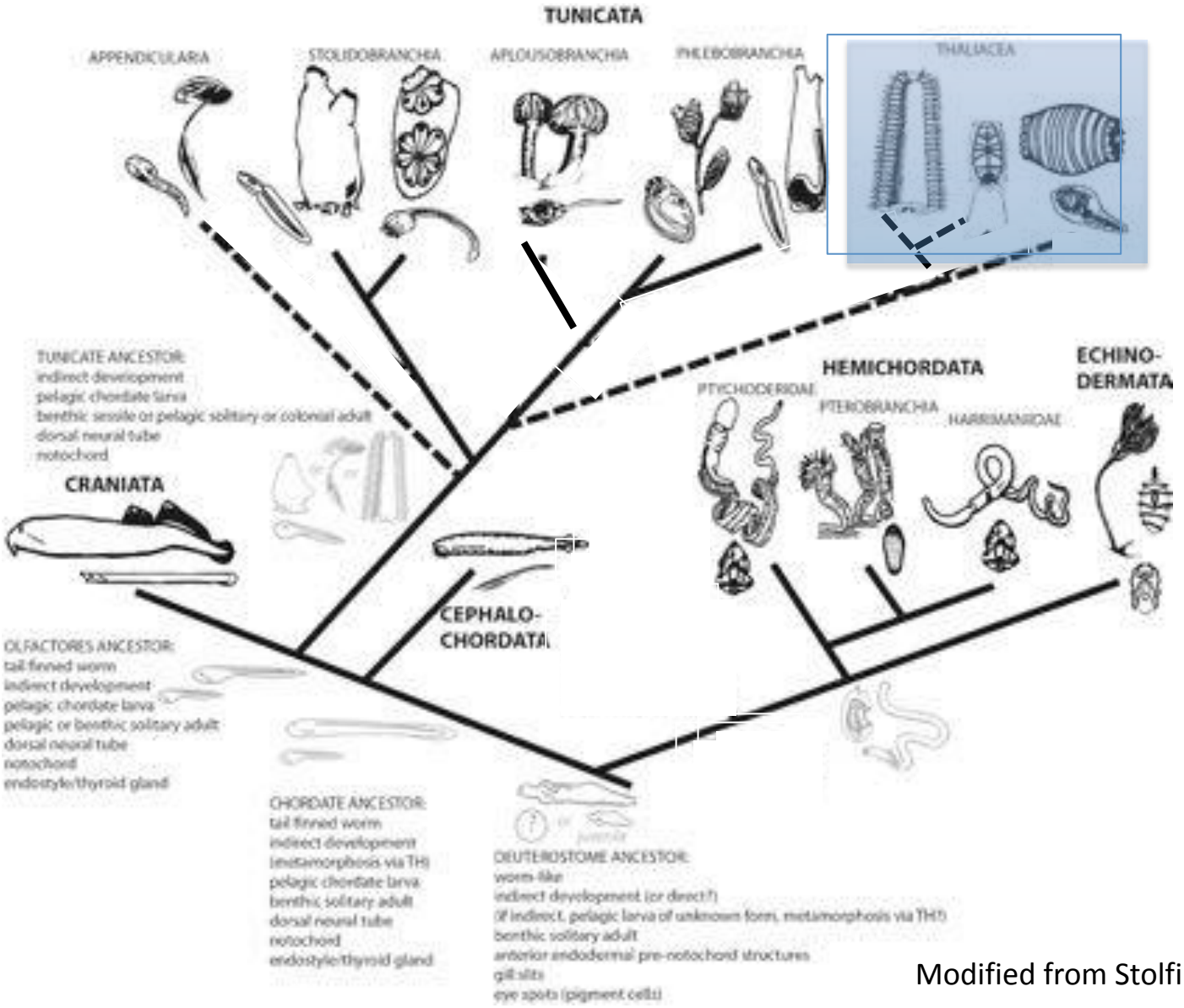
Lissoclinum timorense

Didemnum molle

Diplosoma simile

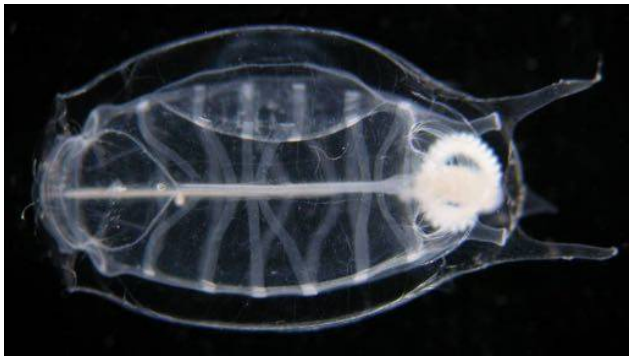
Tunicata

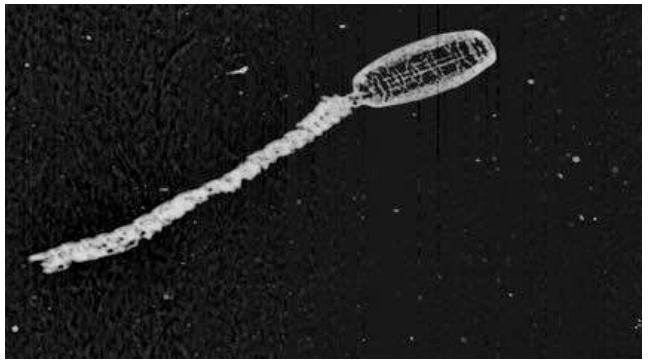
- Cordados invertebrados (de nosso próprio filo!)

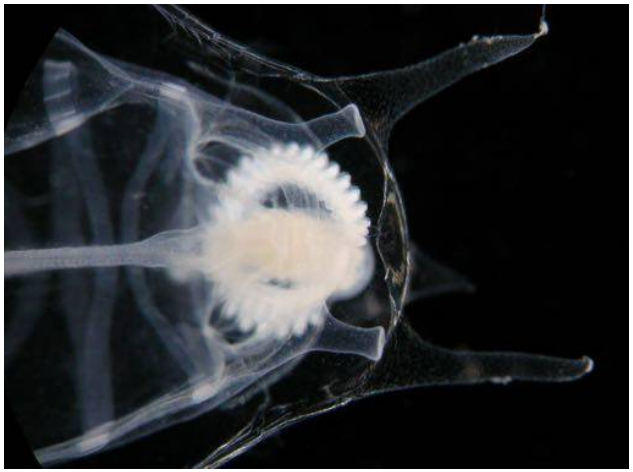


Modified from Stolfi & Brown, 2015

Thaliacea: salpas, doliolidos, e pirosomas







Thaliacea: doliolidos

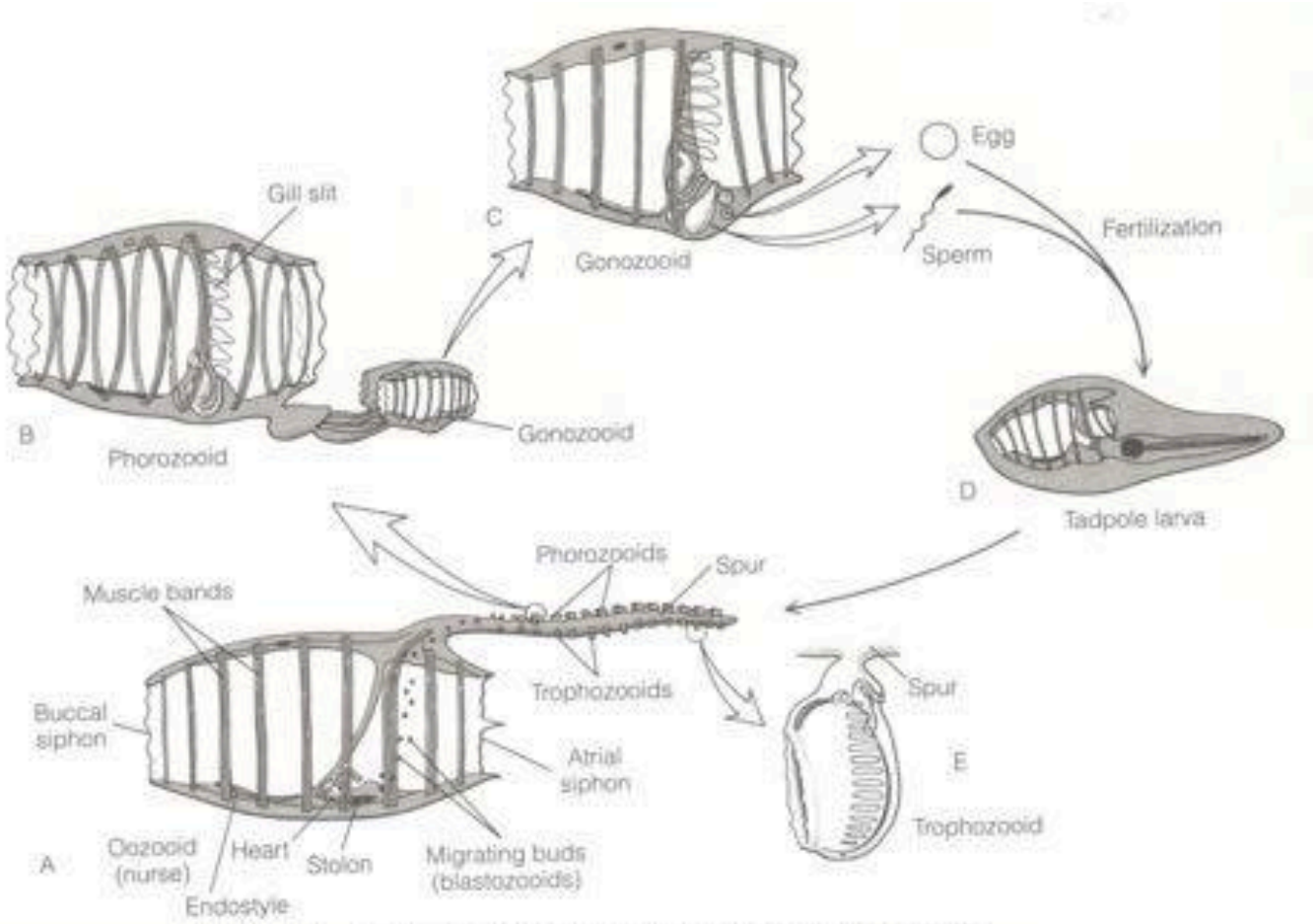


FIGURE 29-28 Tunicata: Doliolida. **A,** The doliolid nurse (oozooid) is a colony of polymorphic zooids. The nurse herself developed from a fertilized egg and subsequent tadpole larva **(D)**, but the other members of the colony arose by budding from the nurse's stolon. The undifferentiated buds migrate from the stolon of the nurse and then lodge in her trailing spur, which may reach 50 cm or more in length. Once attached to the spur, the buds differentiate into trophozooids **(E)**, which are specialized for feeding the colony (the nurse's digestive system degenerates), or phorozooids **(B)**, which eventually break free of the spur and jet away under their own power. Buds attached to the phorozooids differentiate into the sexually reproductive gonozooids **(C)**. Fertilization is probably internal in the gonozooids, but a free-swimming tadpole **(D)** is released to metamorphose into a young nurse in the plankton, thus completing the life cycle.

Thaliacea: salpas

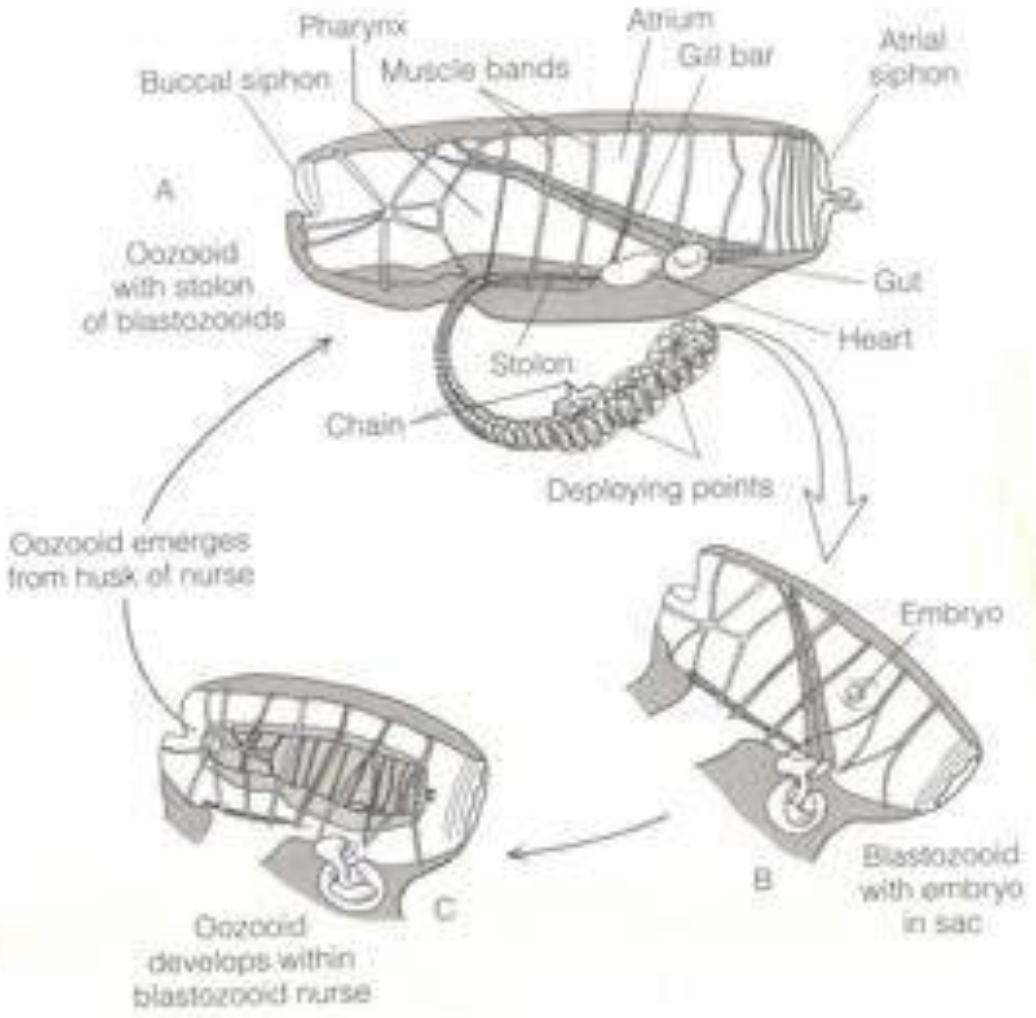


FIGURE 29-29 Tunicata: Salpida. Salp organization and life cycle. **A**, An oozooid of *Cyclosalpa* trailing its stolon of differentiating buds and blastozooids. The stolon breaks at predetermined points and deploys clusters, or chains, of blastozooids, which swim away from the oozooid and other members of the parent colony. Each blastozooid (**B**) bears a single egg that is fertilized internally and develops in a special brood sac, complete with a placental connection to the circulatory system of the blastozooid. The growing embryo eventually occupies the entire volume of the blastozooid-nurse's body (**C**) and then breaks free as a young oozooid, thus completing the life cycle.

http://planktonchronicles.org/en/episode/salps-exploding-populations/

Thaliacea: pirosomas

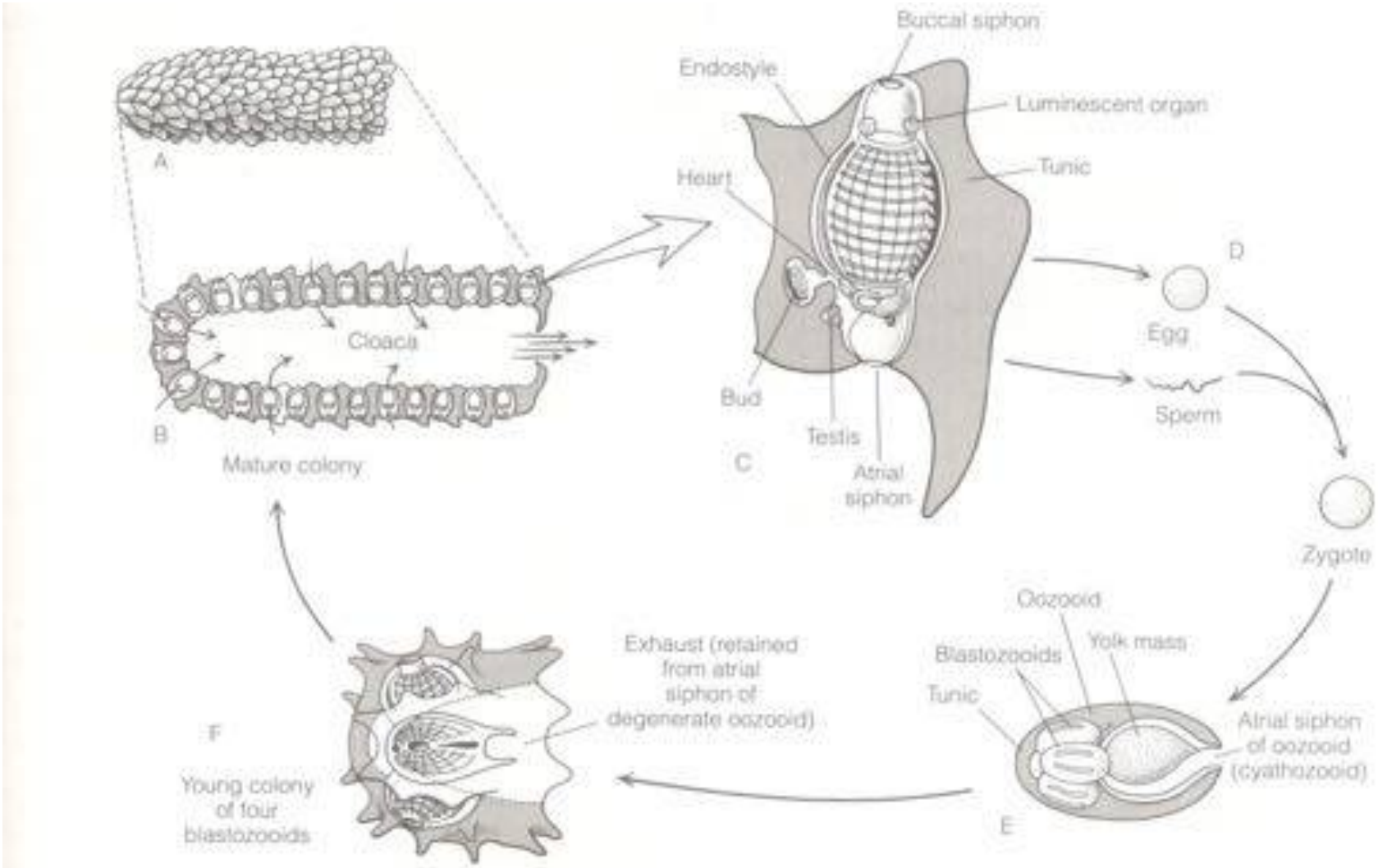


FIGURE 29-27 Tunicata: Pyrosomida. **A**, Adult colony of *Pyrosoma atlanticum*. **B**, Longitudinal section of **A** showing zooids, the common cloaca, and the exhaust aperture. Arrows indicate the path of water flow through the colony. **C**, Enlargement of one zooid from **B**. **D**, Spawned gametes. **E**, Lecithotrophic oozooid (cyathozooid) and its four precocious buds (blastozooids). **F**, Young colony composed of four zooids.

https://www.youtube.com/watch?v=u6SuJ6l_AJA

Ruppert