Ctenophora **Urochordata** **Nemertea**

Echinodermata **Platyhelminthes**

Kamptozoa **Nematomorpha**

Brachiopoda **Porifera** **Phoronida**

Acoela **Arthropoda**

Annelida **Mollusca** **Bryozoa**

Onychophora **Acanthocephala**

Cnidaria **Tardigrada**

Nematoda **Hemichordata**

Ctenophora Urochordata Nemertea Platyhelminthes Echinodermata

How are phyla related?

Sipuncula Kamptozoa Nematomorpha

When did they appear?

Phoronida Brachiopoda Porifera

How has diversity changed?

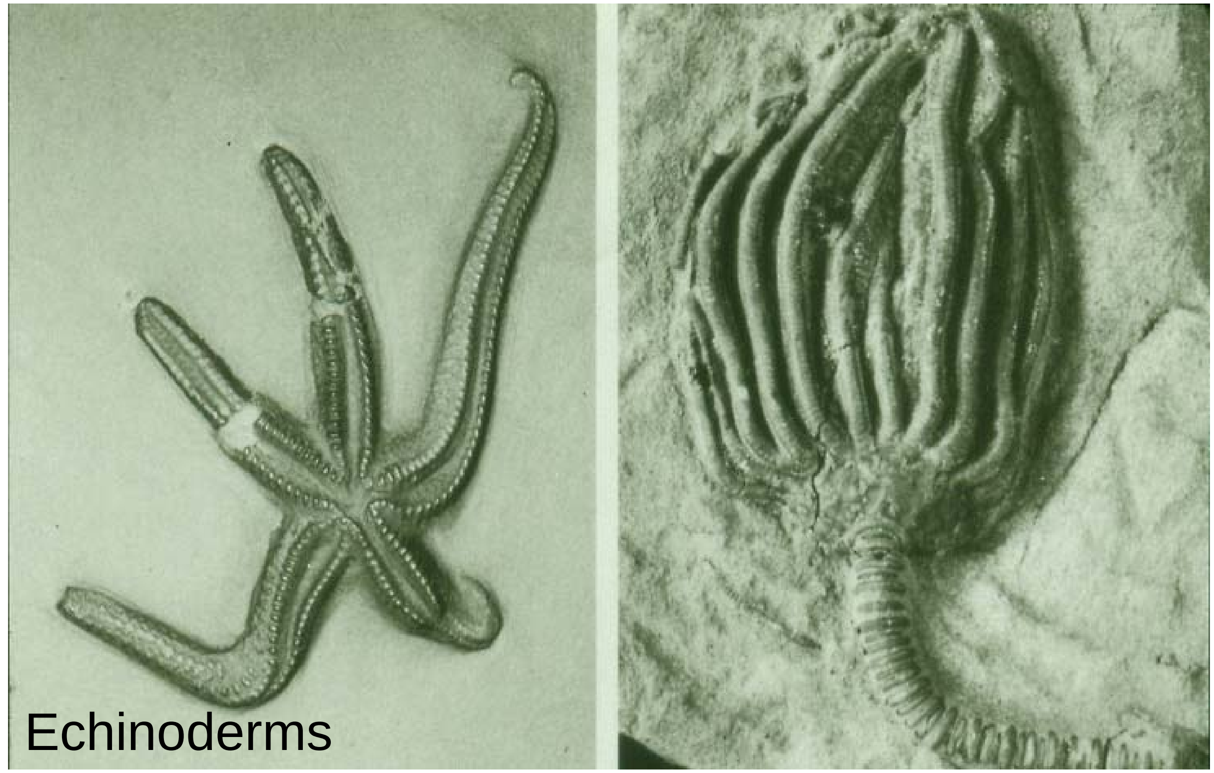
Arthropoda Annelida Bryozoa Mollusca

What mechanisms underlie diversification?

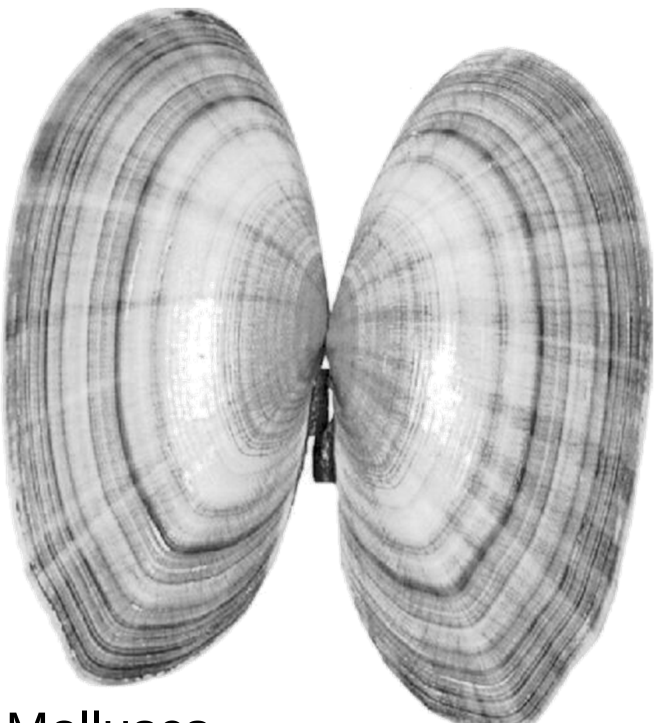
Acanthocephala Cnidaria Hemichordata Nematoda Rotifera

Variable preservation among taxa

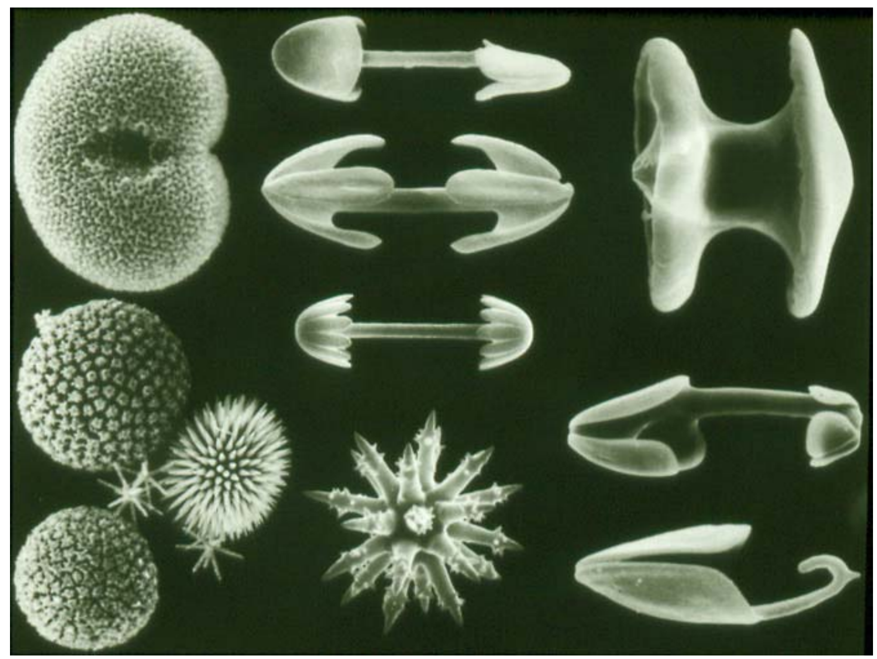
Which phyla are more likely to leave informative records?



Echinoderms

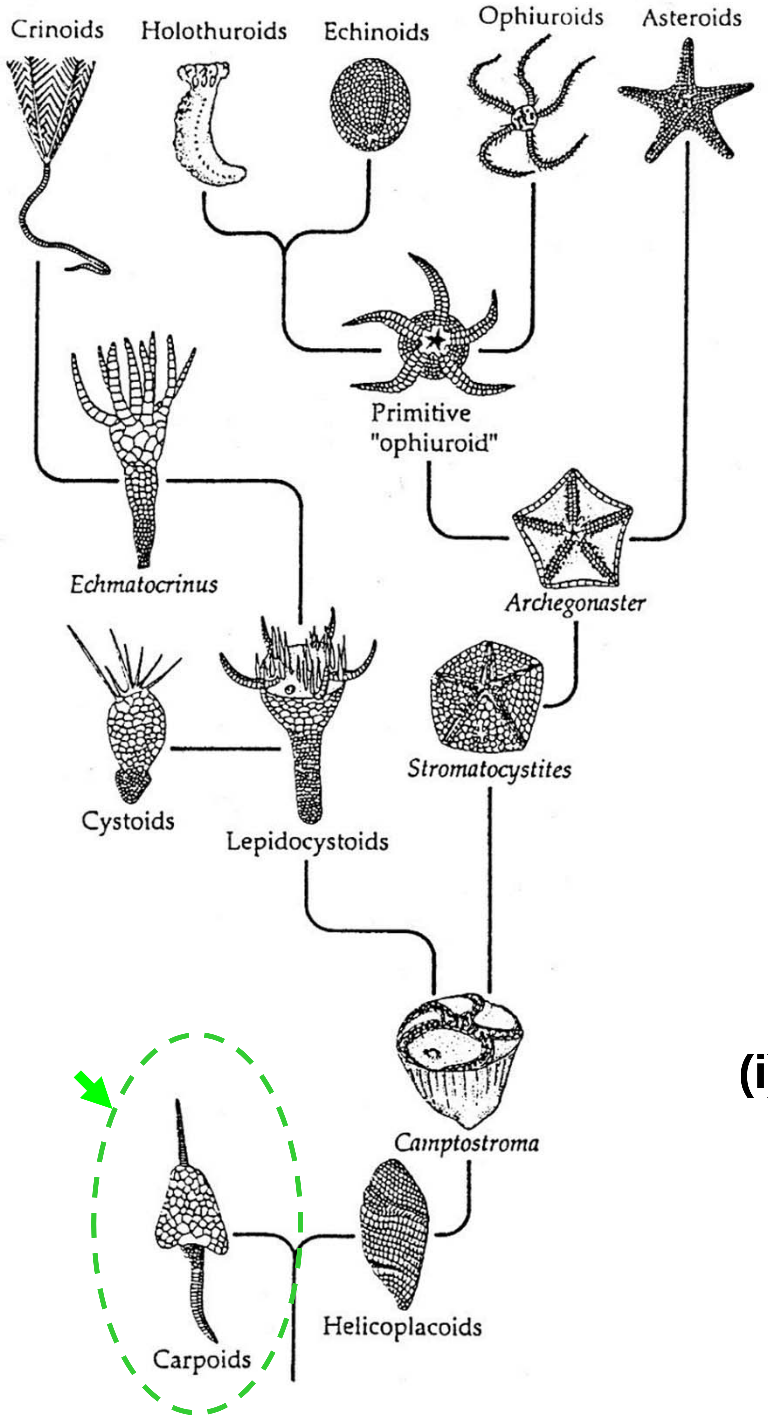


Molluscs

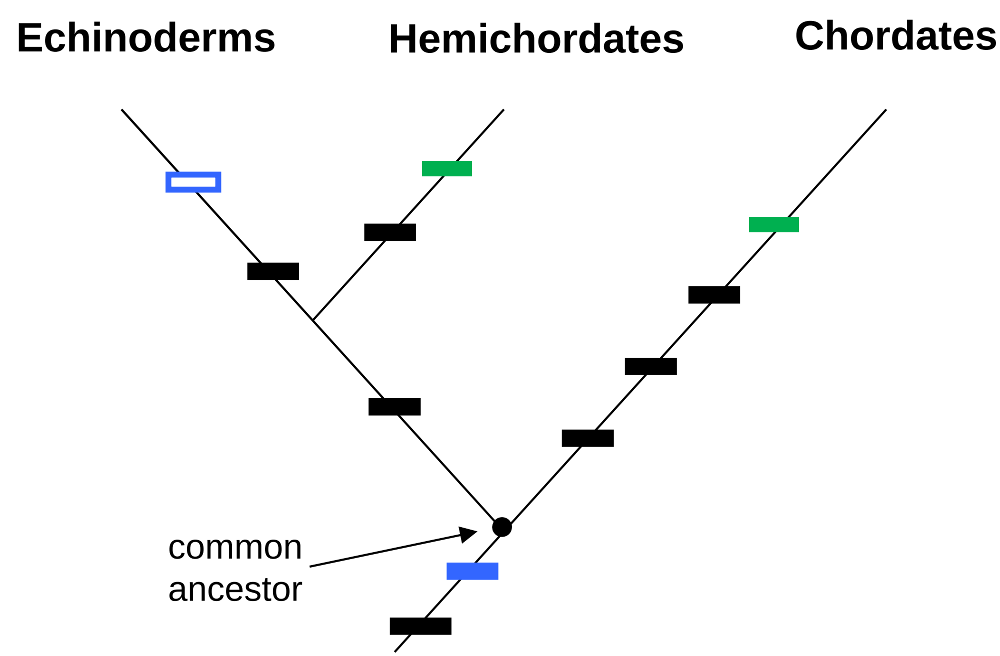


Sponges

1. Analysis of fossil taxa
eg. Echinoderm classes

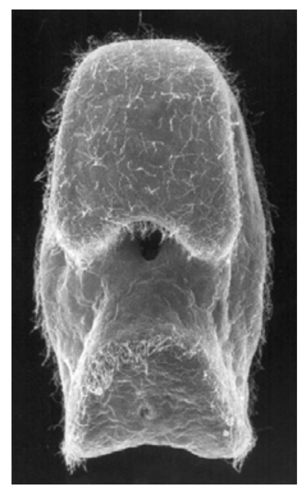


2a. Cladistics: phenotypes of extant taxa
eg. Deuterostomes

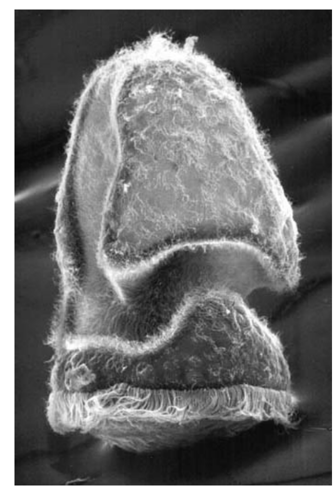


b. Cladistics: phenotypes of larval forms

(i) "dipleurula" type larva

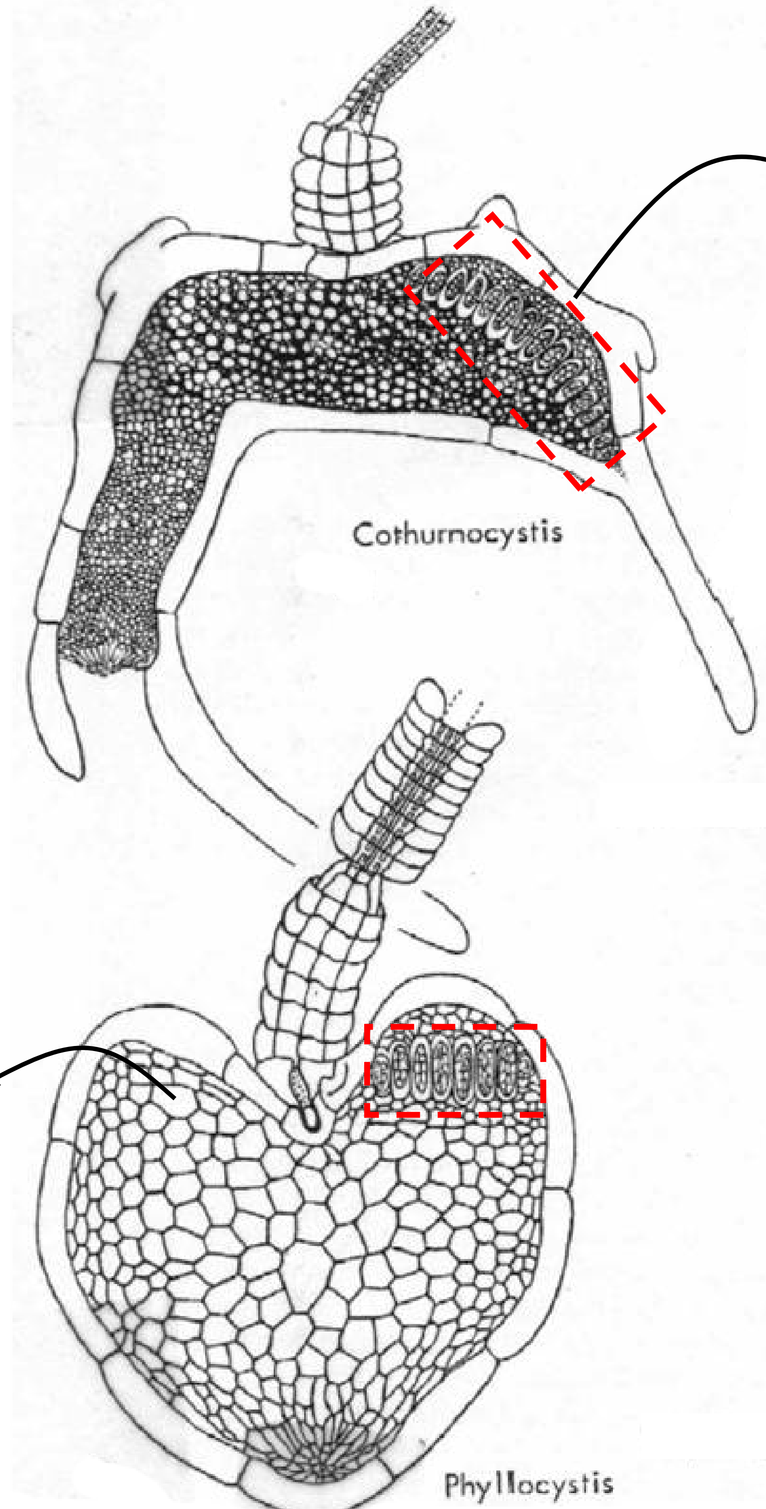


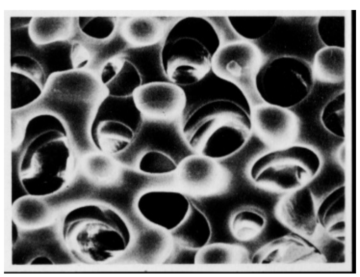
holothuroid echinoderm auricularia



hemichordate tornaria

Carpoids



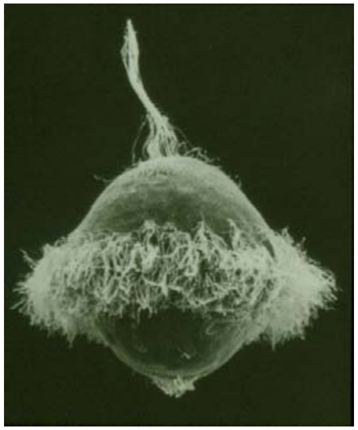


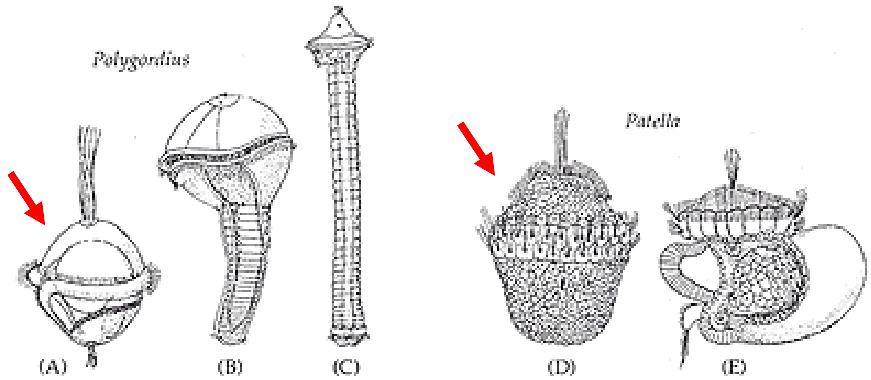
stereom

pharyngeal slits?

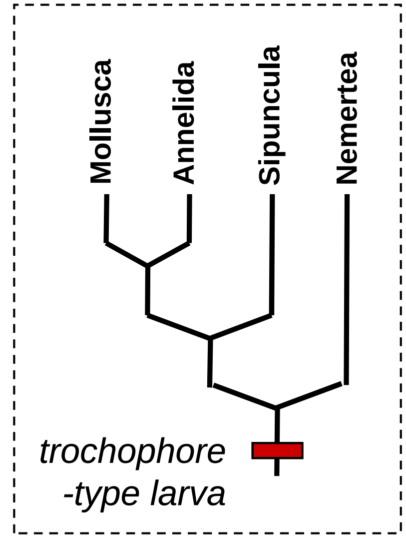
Are larval forms always reliable cladistic characters?

(ii) Trochophore-type larva: molluscs, annelids, sipunculans, nemerteans

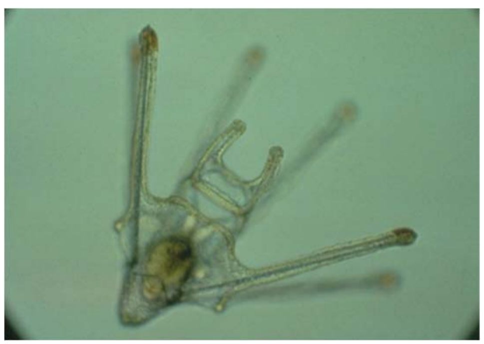




polychaete annelids | gastropod molluscs

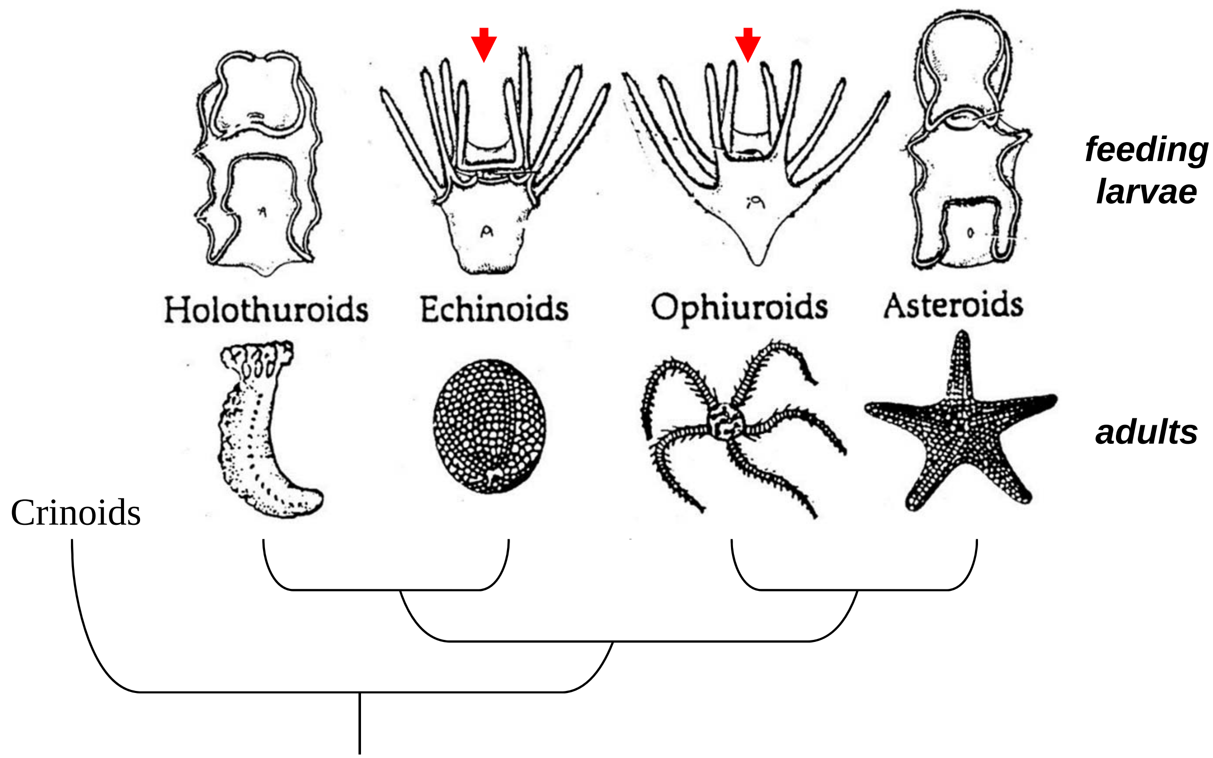


(iii) "Pluteus" larva: echinoid and ophiuroid echinoderms



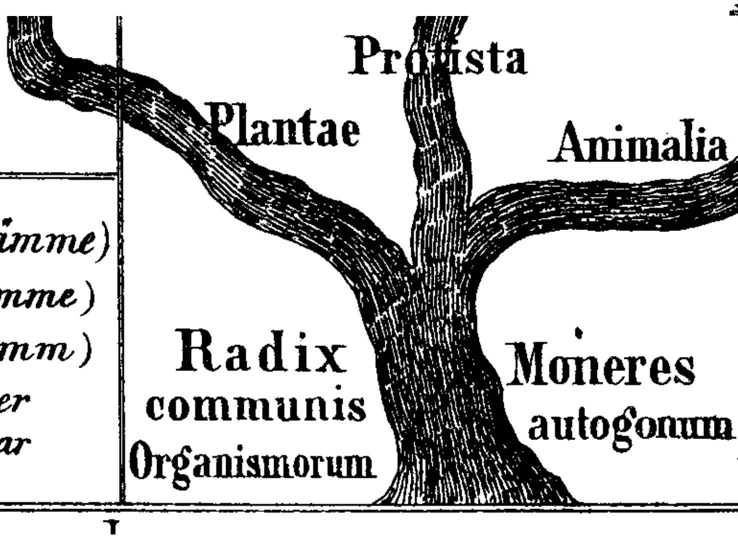
Echinopluteus

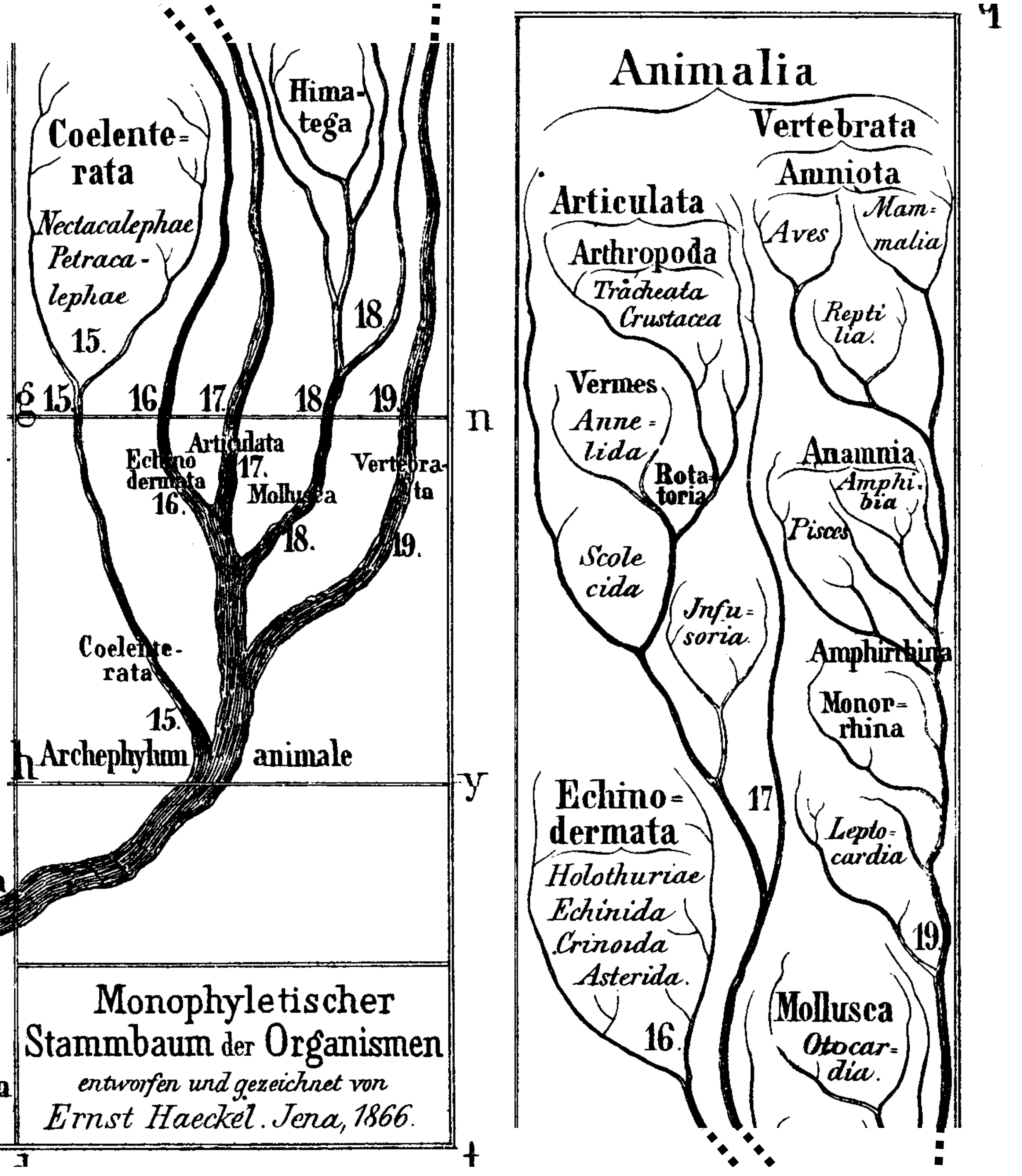
Ophiopluteus

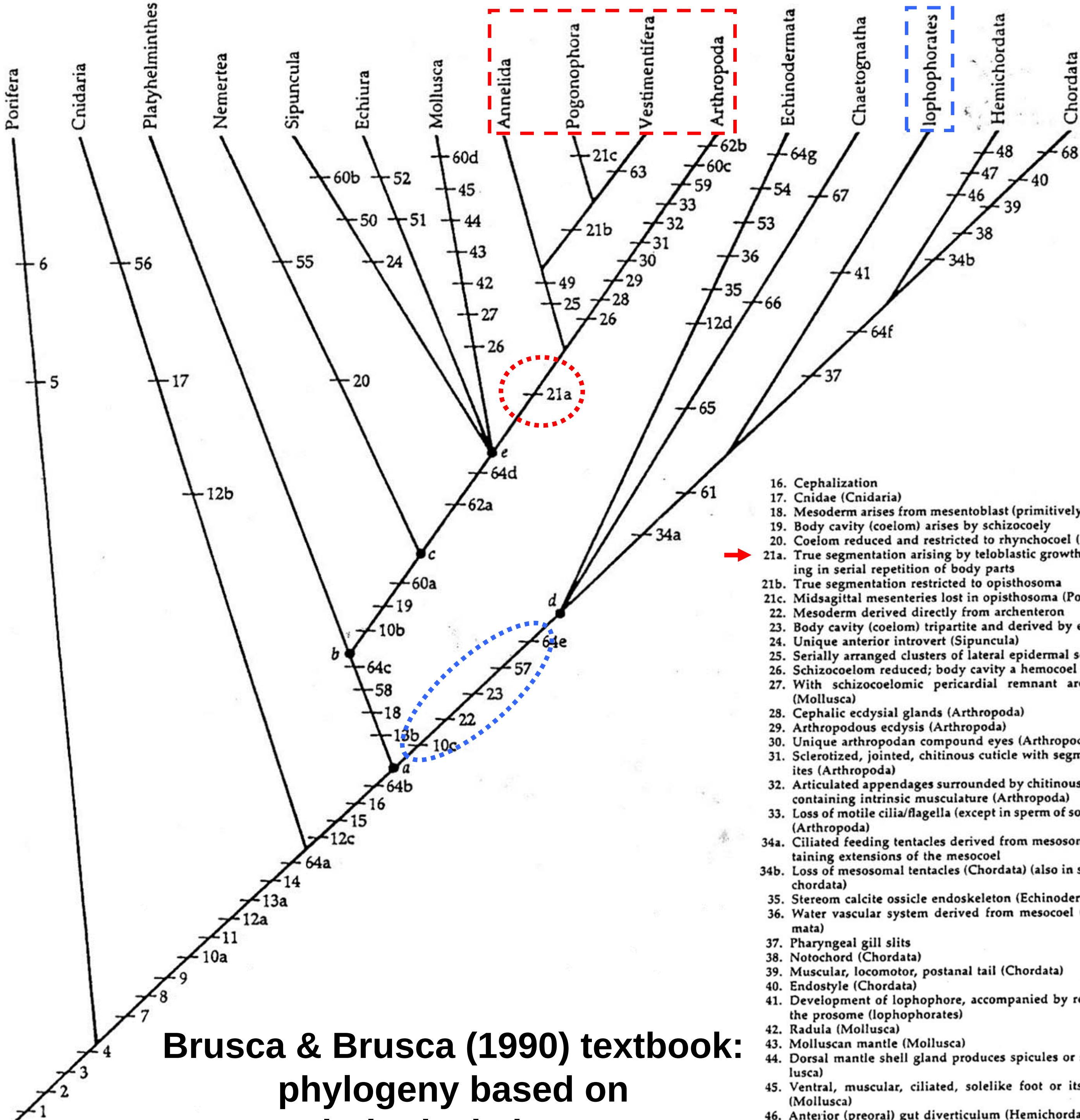


Haeckel E (1866). *'Monophyletischer Stambaum der Organismen' from 'Generelle Morphologie der Organismen'*

Showing the three main branches Plantae, Protista, Animalia.





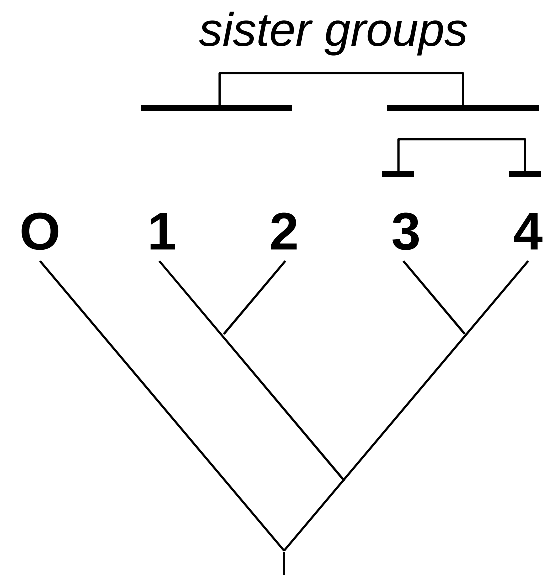


Brusca & Brusca (1990) textbook: phylogeny based on morphological characters

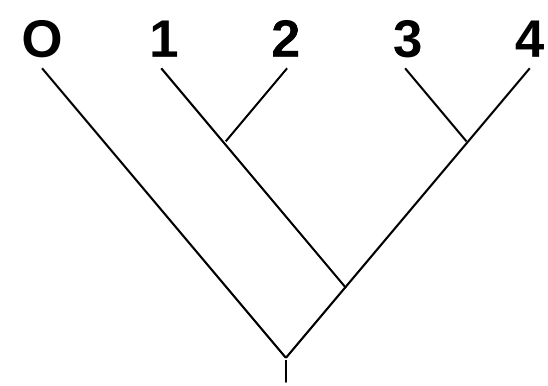
1. Multicellularity, with a high degree of division of labor
2. Acetylcholine/cholinesterase system
3. Collagen
4. Septate/tight junctions between cells
5. Aquiferous system (Porifera)
6. Unique poriferan ontogeny of layered construction (Porifera)
7. Gap junctions between cells
8. Striated myofibrils
9. Loss of flagellated collar cells
10a. Gastrovascular cavity (i.e., incomplete gut) with mouth arising from blastopore
10b. Complete gut with mouth arising from blastopore
10c. Complete gut with mouth not arising from blastopore
11. Gastrulation (origin of true germ layers and diploblastic construction)
12a. Symmetrical body plan
12b. Fundamentally radially symmetrical (Cnidaria)
12c. Fundamentally bilaterally symmetrical
12d. Secondarily pentaradially symmetrical (Echinodermata)
13a. Typical radial cleavage
13b. Typical spiral cleavage
14. Basement membrane (= basal lamina) beneath epidermis
15. Multiciliate/multiflagellate cells
16. Cephalization
17. Cnidae (Cnidaria)
18. Mesoderm arises from mesentoblast (primitively the 4d cell)
19. Body cavity (coelom) arises by schizocoely
20. Coelom reduced and restricted to rhynchocoel (Nemertea)
21a. True segmentation arising by teloblastic growth and resulting in serial repetition of body parts
21b. True segmentation restricted to opisthosoma
21c. Midsagittal mesenteries lost in opisthosoma (Pogonophora)
22. Mesoderm derived directly from archenteron
23. Body cavity (coelom) tripartite and derived by enterocoely
24. Unique anterior introvert (Sipuncula)
25. Serially arranged clusters of lateral epidermal setae
26. Schizocoelom reduced; body cavity a hemocoel
27. With schizocoelomic pericardial remnant around heart (Mollusca)
28. Cephalic ecdysial glands (Arthropoda)
29. Arthropodous ecdysis (Arthropoda)
30. Unique arthropodan compound eyes (Arthropoda)
31. Sclerotized, jointed, chitinous cuticle with segmental sclerites (Arthropoda)
32. Articulated appendages surrounded by chitinous cuticle and containing intrinsic musculature (Arthropoda)
33. Loss of motile cilia/flagella (except in sperm of some species) (Arthropoda)
34a. Ciliated feeding tentacles derived from mesosome and containing extensions of the mesocoel
34b. Loss of mesosomal tentacles (Chordata) (also in some Hemichordata)
35. Stereom calcite ossicle endoskeleton (Echinodermata)
36. Water vascular system derived from mesocoel (Echinodermata)
37. Pharyngeal gill slits
38. Notochord (Chordata)
39. Muscular, locomotor, postanal tail (Chordata)
40. Endostyle (Chordata)
41. Development of lophophore, accompanied by reduction of the prosome (lophophorates)
42. Radula (Mollusca)
43. Molluscan mantle (Mollusca)
44. Dorsal mantle shell gland produces spicules or shell (Mollusca)
45. Ventral, muscular, ciliated, solelike foot or its precursor (Mollusca)
46. Anterior (preoral) gut diverticulum (Hemichordata)
47. Tripartite body arranged as unique proboscis/collar/trunk (Hemichordata)
48. Unique hemichordate kidney "glomerulus" (Hemichordata)
49. Unique annelidan head of presegmental prostomium and peristomium
50. Compensation system (Sipuncula)
51. Unique preoral proboscis (Echiura)
52. Anal vesicles, with excretory funnels (Echiura)
53. Hemal system (Echinodermata)
54. Use of external ciliary grooves for suspension feeding (Echinodermata)
55. Unique proboscis apparatus (Nemertea)
56. Planula larva (Cnidaria)
57. Sheets of subepidermal muscles derived, at least in part, from archenteric mesoderm
58. Sheets of subepidermal muscles derived, at least in part, from 4d mesoderm
59. Muscles concentrated into isolated bands attached to internally directed skeletal apodemes (Arthropoda)
60a. Mesoderm (from mesentoblast) gives rise in part to closed circulatory system of vessels only
60b. Complete loss of closed circulatory system (Sipuncula)
60c. Reduction to open circulatory system with dorsal ostiate heart (Arthropoda)
60d. Reduction to open circulatory system with dorsal chambered heart (Mollusca)
61. Circulatory system derived, at least in part, from archenteric mesoderm (varies among taxa)
62a. Trochophore larva
62b. Trochophore lost (Arthropoda)
63. Vestimentum ("wings") (Vestimentifera)
64. Synaptic nervous system
64a. Nervous system arranged in noncentralized, netlike fashion
64b. Nervous system with anterior concentration of neurons (cerebral ganglion) and tending toward presence of longitudinal cords
64c. Cerebral ganglion issues pairs of longitudinal cords connected by transverse commissures (ladder-like), with tendency to emphasize ventral or ventrolateral cords (reduced to a single ventral cord in some taxa)
64d. With circumenteric nerve ring attached to one or more ventral nerve cords
64e. Longitudinal cords not ladder-like in arrangement and not emphasized ventrally
64f. Dorsal hollow nerve cord
64g. Nervous system pentaradially arranged, loss of cerebral ganglion (Echinodermata)
65. Unique chaetognathan fins (Chaetognatha)
66. Unique chaetognathan buccal apparatus (Chaetognatha)
67. Unique chaetognathan ciliary loop (Chaetognatha)
68. Tadpole larva (Chordata)

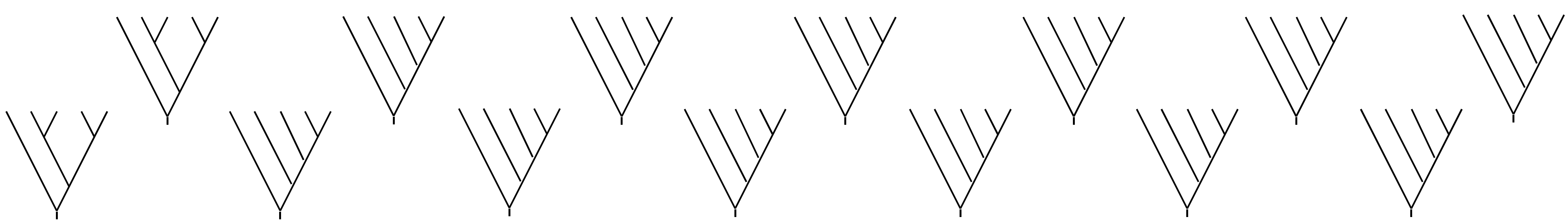
2b. Cladistics: molecular characters

DNA base	1	2	3	4	5	6	7	8	9	10	11	12
sp “O”	A	C	G	C	G	G	T	C	A	T	T	A
sp 1	.	G	.	.	.	.	.	.	.	.	.	T
sp 2	.	G	.	.	A	.	.	.	.	.	.	T
sp 3	.	.	.	.	T	.	C	.	.	A	.	T
sp 4	.	.	.	.	T	.	C	.	.	.	.	T

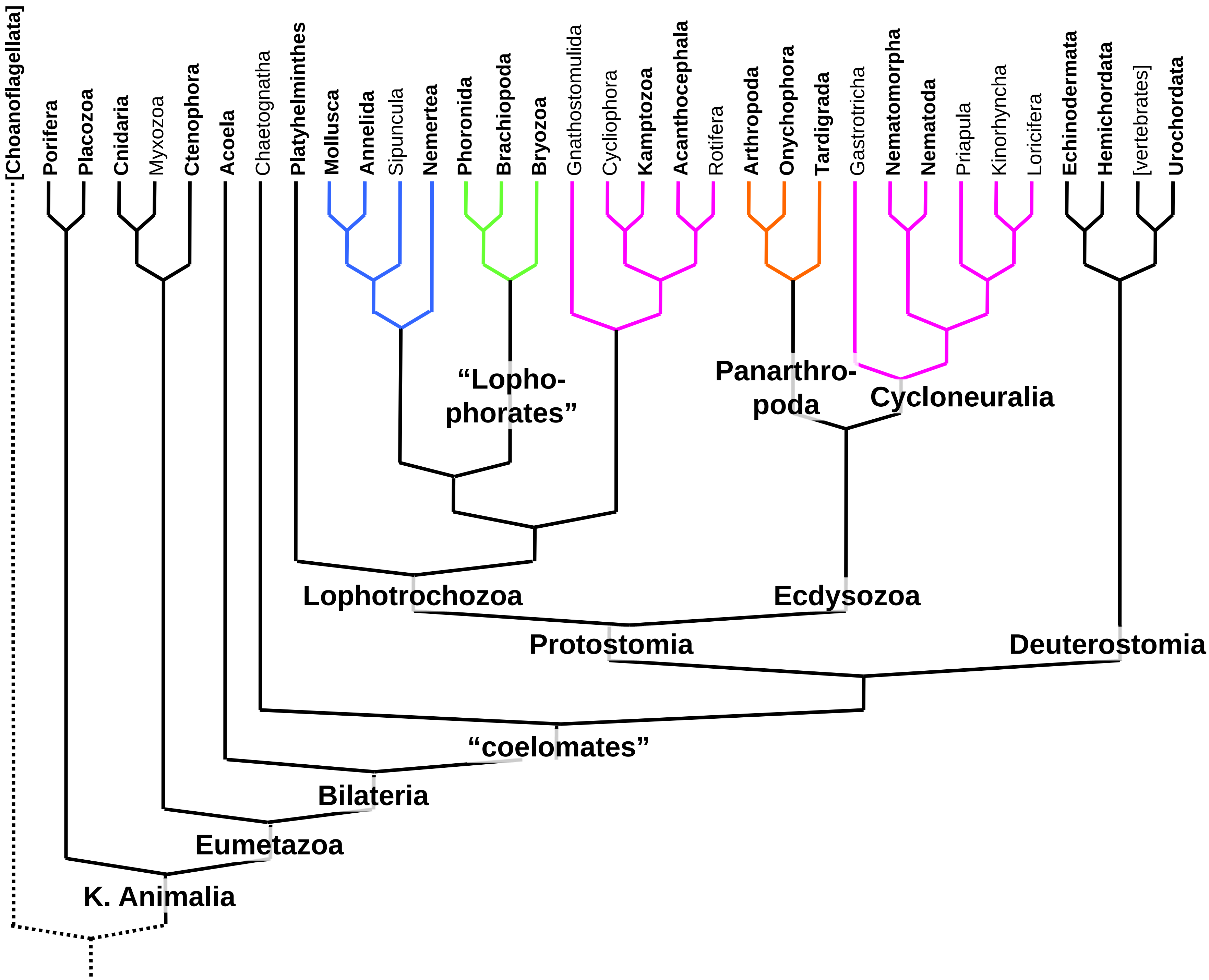


sp “O”	A	C	G	C	G	G	T	C	A	T	T	A
sp 1	.	G	.	.	.	.	.	.	.	.	.	T
sp 2	.	G	.	.	T	.	.	.	.	.	.	T
sp 3	.	.	.	.	T	.	C	.	.	A	.	T
sp 4	.	.	.	.	T	.	C	.	.	.	.	T





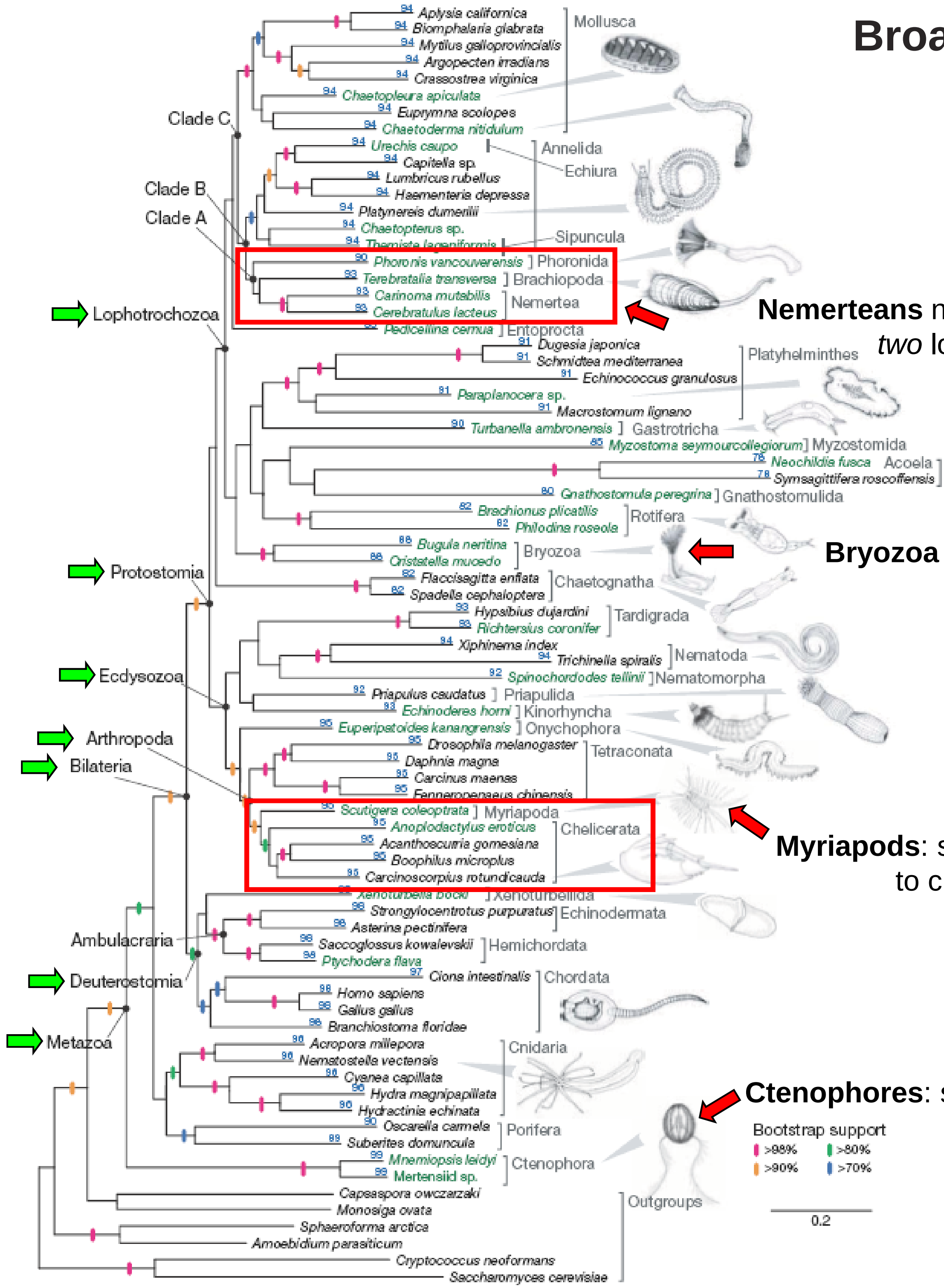
Our phylogenetic roadmap: a consensus view



Broad phylogenomic sampling improves resolution of the animal tree of life

Dunn et al. 2008

(+17 coauthors!)

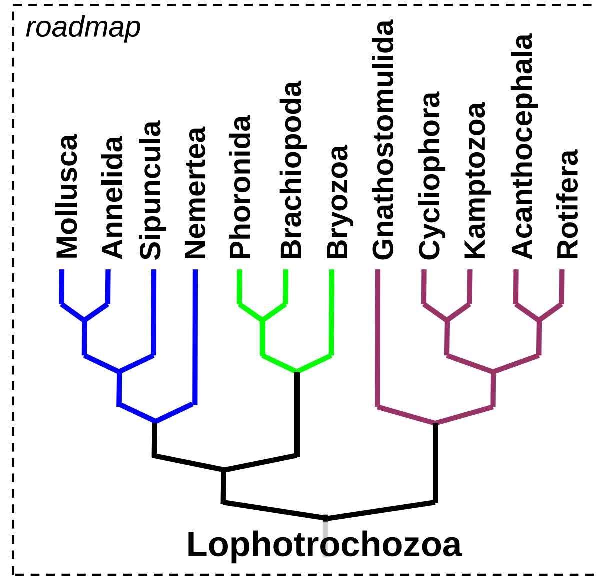


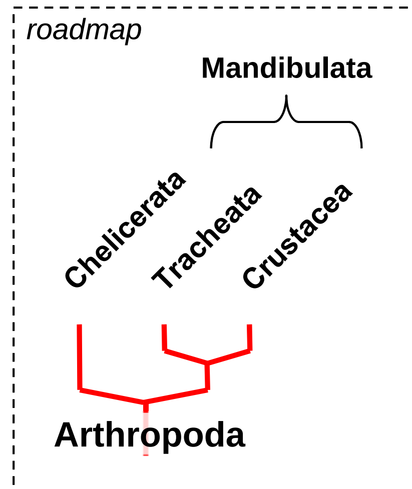
Nemerteans nested in clade with *two* lophophorate phyla?

Bryozoa sister group to former pseudocoelomates?

Myriapods: sister group to chelicerates?

Ctenophores: sister group to rest of animals?





The Genome of the Ctenophore *Mnemiopsis leidyi* and Its Implications for Cell Type Evolution **Science (2013)**

Joseph F. Ryan, Kevin Pang, Christine E. Schnitzler, Anh-Dao Nguyen, R. Travis Moreland, David K. Simmons, Bernard J. Koch, Warren R. Francis, Paul Havlak, NISC Comparative Sequencing Program, Stephen A. Smith, Nicholas H. Putnam, Steven H. D. Haddock, Casey W. Dunn, Tyra G. Wolfsberg, James C. Mullikin, Mark Q. Martindale, Andreas D. Baxevanis*

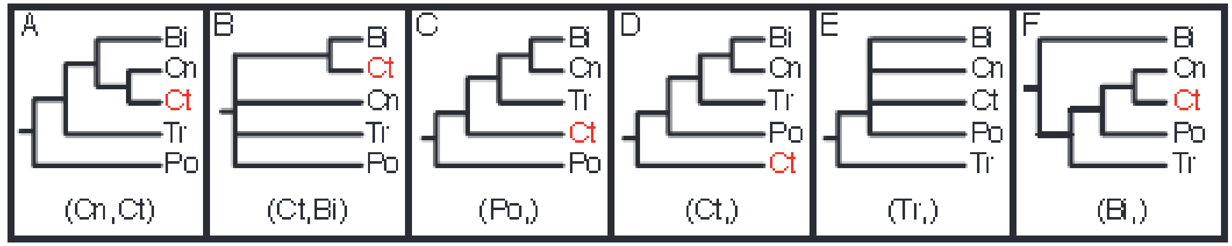
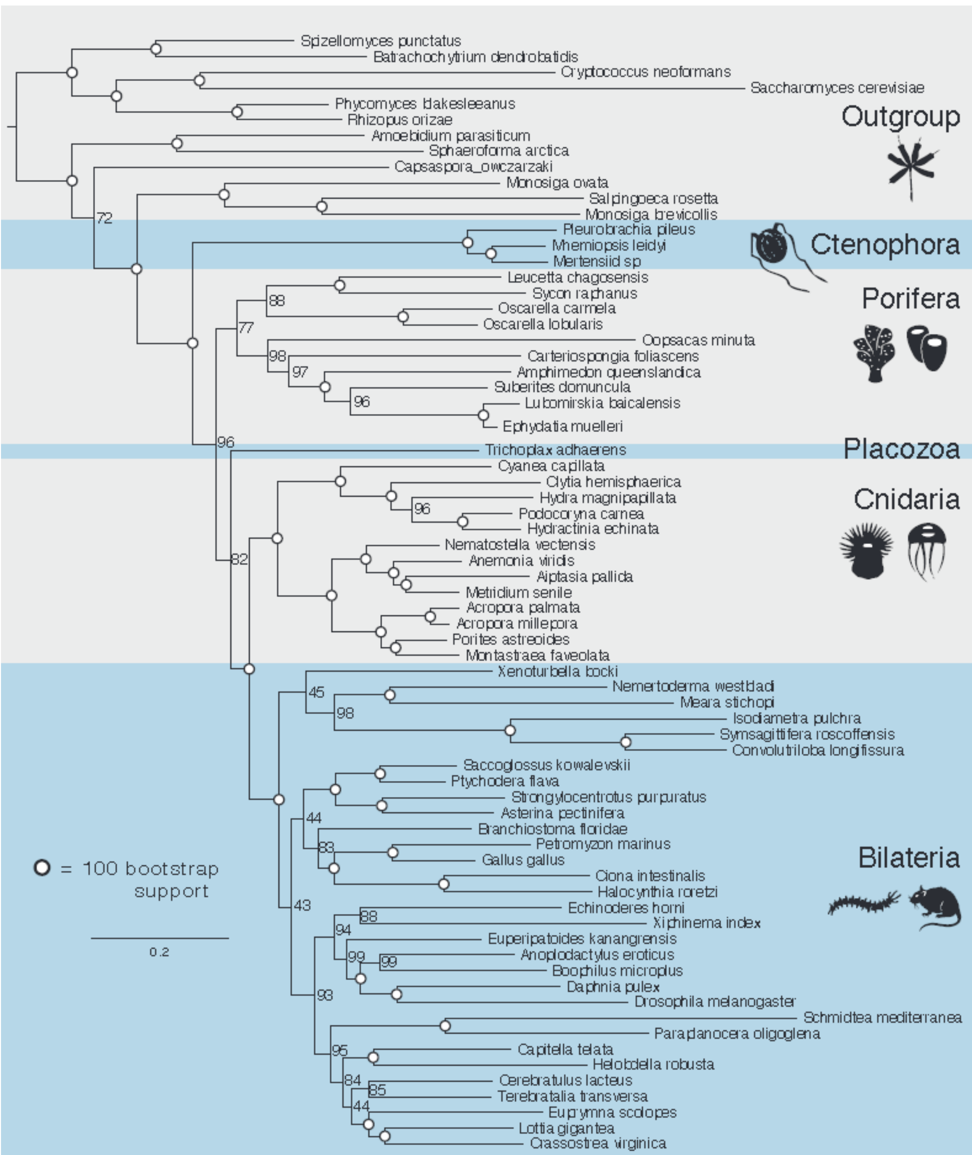
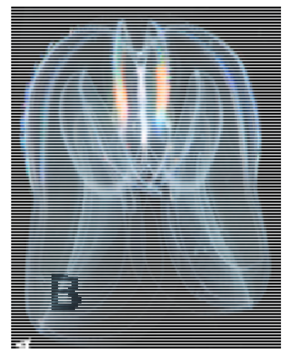
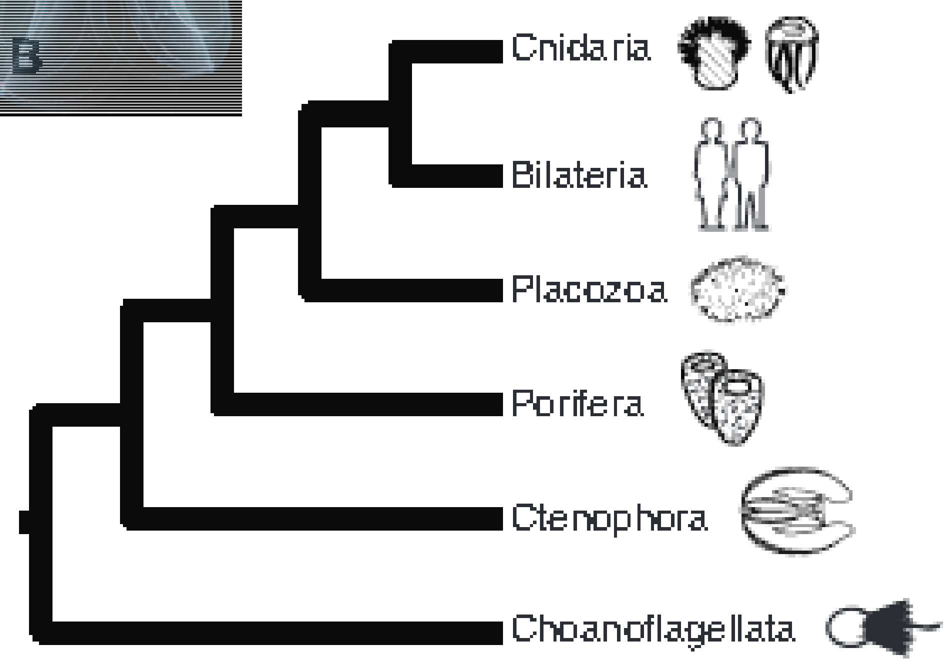


Fig. 2. Previously proposed relationships of the five deep clades of animals. The label at the bottom of each pane corresponds to the header of Table 1. (A) Coelenterata hypothesis. (B) Ctenophora as sister to Bilateria. (C) Porifera as sister group to the rest of Metazoa. (D) Ctenophora as sister group to the rest of Metazoa. (E) Placozoa as sister group to the rest of Metazoa. (F) Diploblastica hypothesis. We see no support in any of our analyses for the hypotheses in (A), (E), and (F) and very little support for (B) (see Table 1). Ct, Ctenophora; Po, Porifera; Tr, Placozoa; Cn, Cnidaria; Bi, Bilateria.





The phylogenetic position of the ctenophore *Mnemiopsis leidyi* and its implications regarding the origin of mesodermal cell types. (A) Adult *M. leidyi*. **(B)** Summary of the relationships of the five main branches of animals and the outgroup Choanoflagellata.



muscles? nerves? epithelia? axes?

Ctenophora Urochordata Nemertea

Echinodermata Platyhelminthes

How are phyla related?

Kamptozoa Nematomorpha Sipuncula

When did they appear?

Brachiopoda Porifera Phoronida

How has diversity changed?

Acoela Arthropoda

Annelida Mollusca Bryozoa

What mechanisms underlie diversification?

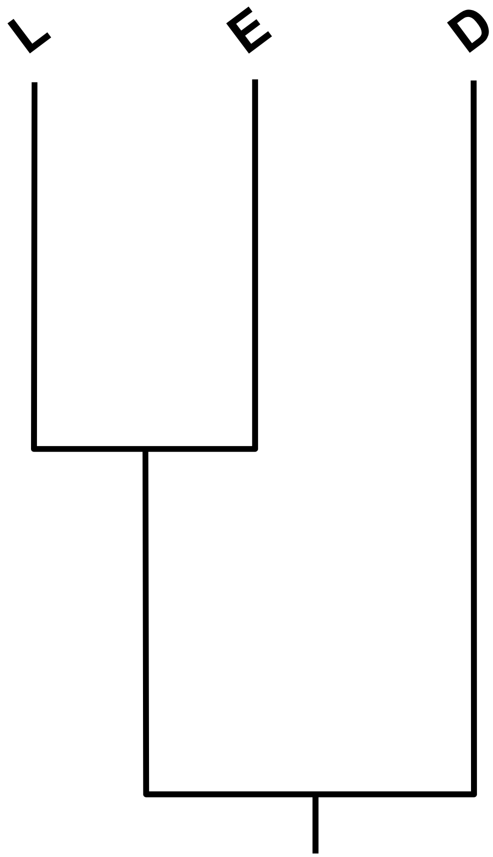
Onychophora Acanthocephala

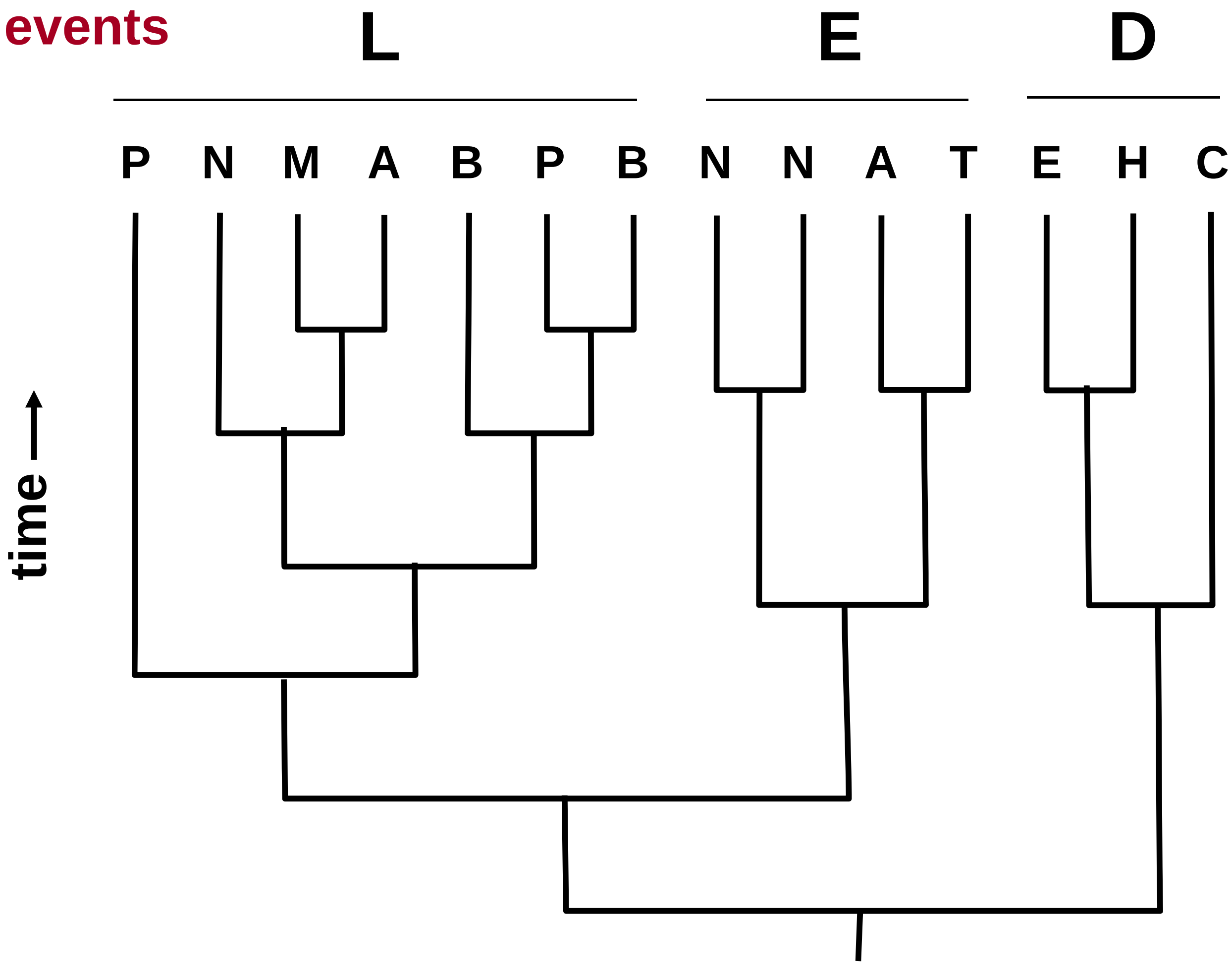
Cnidaria Tardigrada

Nematoda Hemichordata

Pattern of evolutionary relationships

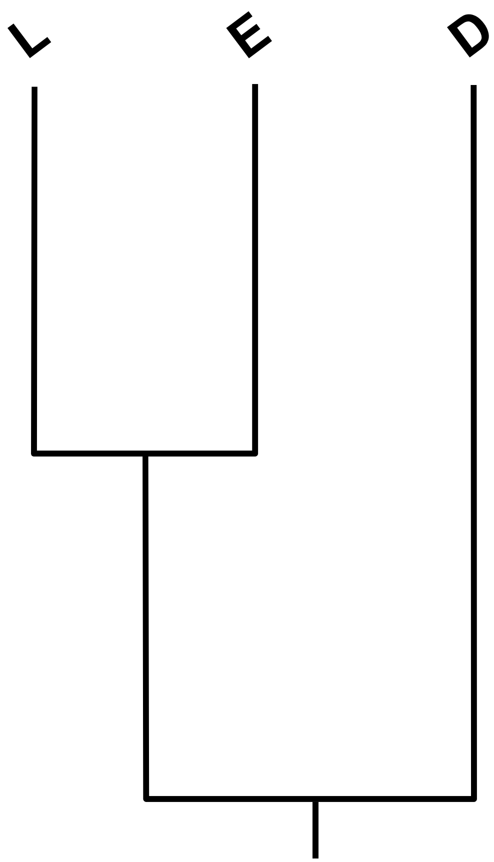
cladogram: relative order of events

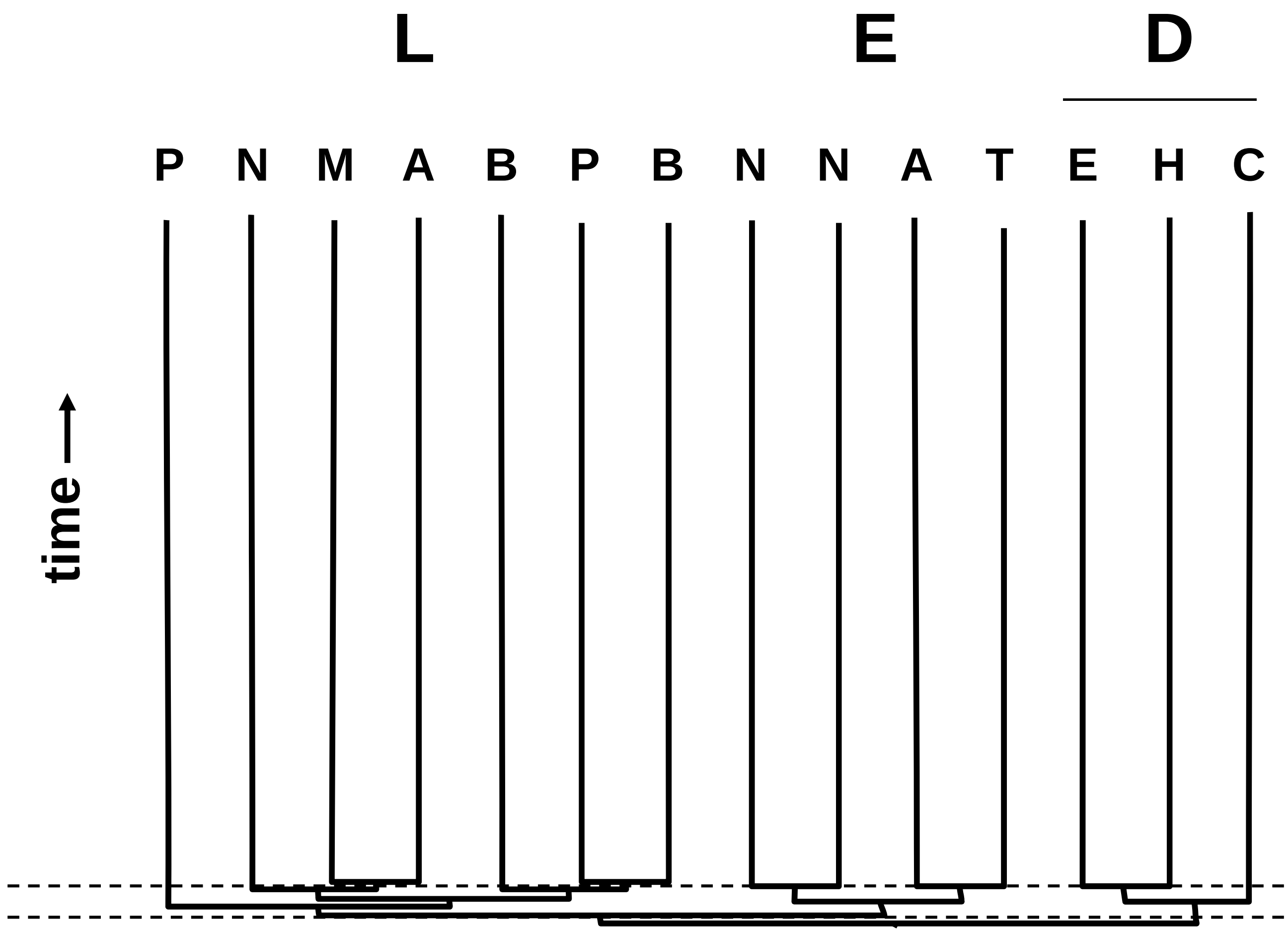




Timing of evolutionary divergences?

absolute timing of events?





The major Pre-Cambrian and Cambrian *Lagerstätten*

Pre-Cambrian		
Bitter Springs	1000–850 Ma	South Australia
Ediacara Hills	630-542 Ma	South Australia
Doushantuo Formation	600–555 Ma	Guizhou Province, China
Cambrian		
Maotianshan Shales (Chengjiang)	525 Ma	Yunnan Province, China
Sirius Passet	518 Ma	Greenland
Emu Bay shale	517 Ma	South Australia
Kaili Formation	513–501 Ma	Guizhou province, south-west China
Wheeler Shale (House Range)	507 Ma	Western Utah, US
Burgess Shale	505 Ma	British Columbia, Canada
Kinnekulle Orsten and Alum Shale	500 Ma	Sweden
Öland Orste and Alum Shale	500 Ma	Sweden

Pre-Cambrian seas?

The Ediacaran (named after the hills in Australia, the site of a major pre-Cambrian fossil deposit) featured soft-bodied life - no bones, shells, teeth or other hard parts. Most of the life forms bear no resemblance to modern day animals, and may have become the eventually extinguished prey of more modern forms. The world's first ever burrowing animals evolved in the Ediacaran but left only trace fossils (burrows).

Enigmatic Ediacaran biota (630-542 mya)

Dickinsonia costata, an iconic Ediacaran organism, displays the characteristic quilted appearance of Ediacaran enigmata

Spriggina superficially resembled a segmented animal but the apparent segments are isomers (alternating on left and right sides).

Charniodiscus, probably a stationary filter feeder, was a frond anchored by a holdfast to a sandy sea bed.

Kimberella may have had a predatory or grazing lifestyle.

Archaeonassa-type trace fossils

Charnia, the first accepted complex Precambrian organism, once interpreted as a relative of the sea pens.

The major Pre-Cambrian and Cambrian *Lagerstätten*

Pre-Cambrian		
Bitter Springs	1000–850 Ma	South Australia
Ediacara Hills	630-542 Ma	South Australia
Doushantuo Formation	600–555 Ma	Guizhou Province, China
Cambrian		
Maotianshan Shales (Chengjiang)	525 Ma	Yunnan Province, China
Sirius Passet	518 Ma	Greenland
Emu Bay shale	517 Ma	South Australia
Kaili Formation	513–501 Ma	Guizhou province, south-west China
Wheeler Shale (House Range)	507 Ma	Western Utah, US
Burgess Shale	505 Ma	British Columbia, Canada
Kinnekulle Orsten and Alum Shale	500 Ma	Sweden
Öland Orste and Alum Shale	500 Ma	Sweden

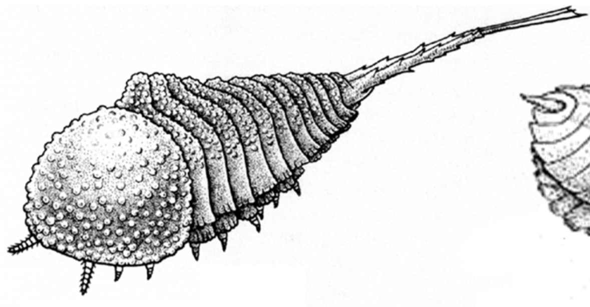
Cambrian seas?

Some of the diversity of the Burgess Shale biota is depicted in the drawing above by Sam Gon III and John Whorrall. Trilobites such as *Olenoides serratus* (1) were a minority among a diversity of arthropods such as *Sidneyia* (9), *Waptia* (17), *Helmetia* (13), *Sanctacaris* (18), *Tegopelte* (15), *Naraoia* (16), *Leanchoilia* (10), *Canadaspis* (12), *Odaraia* (19), *Marrella* (11), and *Burgessia* (14), as well as oddities such as *Opabinia* (24), *Wiwaxia* (26), *Hallucigenia* (20), and the giant predator, *Anomalocaris* (28).

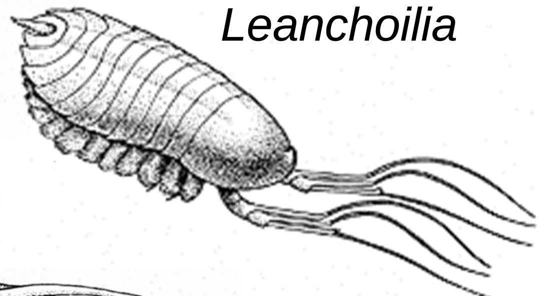
Problematic taxa of the Burgess Shale (525-505 mya)

Wonderful Life, Gould (1990)

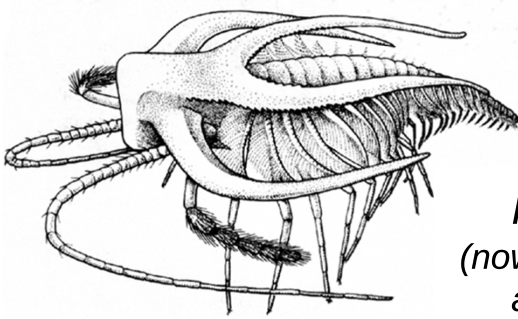
Unique arthropod subphyla?



Habelia

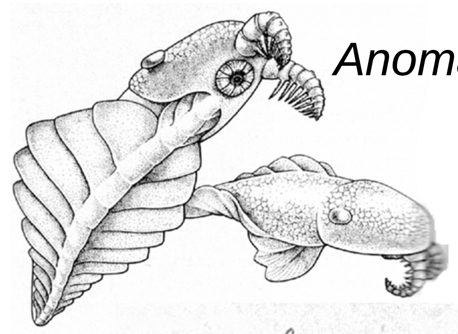


Leanchoilia

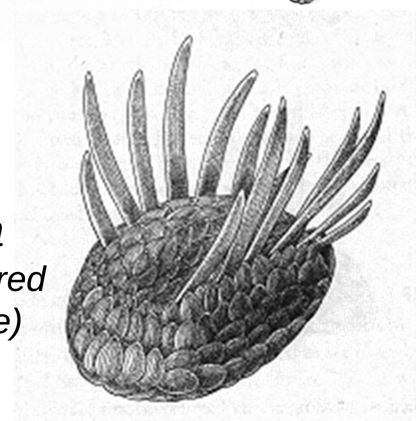


Marella
(now considered a trilobite)

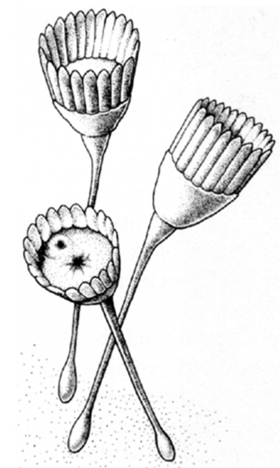
Unique phyla?



Anomalocaris

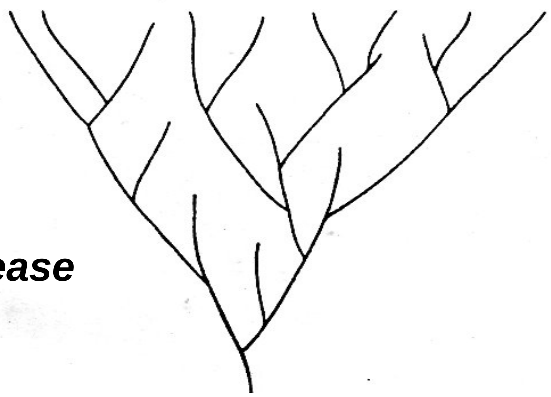


Wiwaxia
(now considered a polychaete)

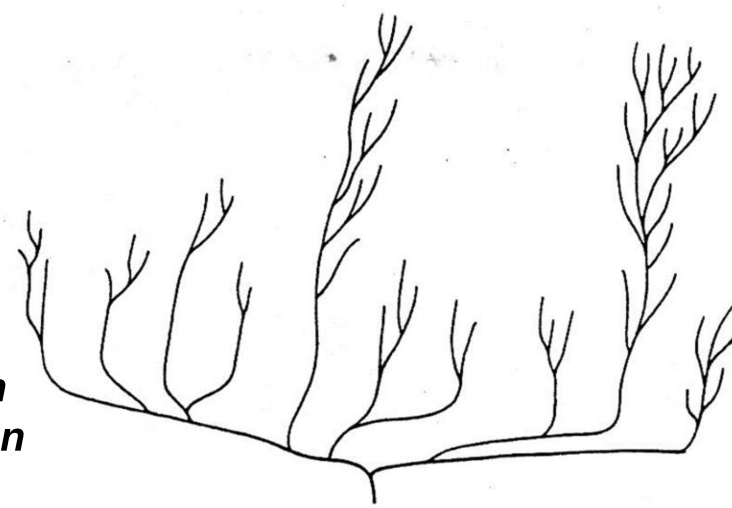


Dinomischus

Two models of the history of diversity

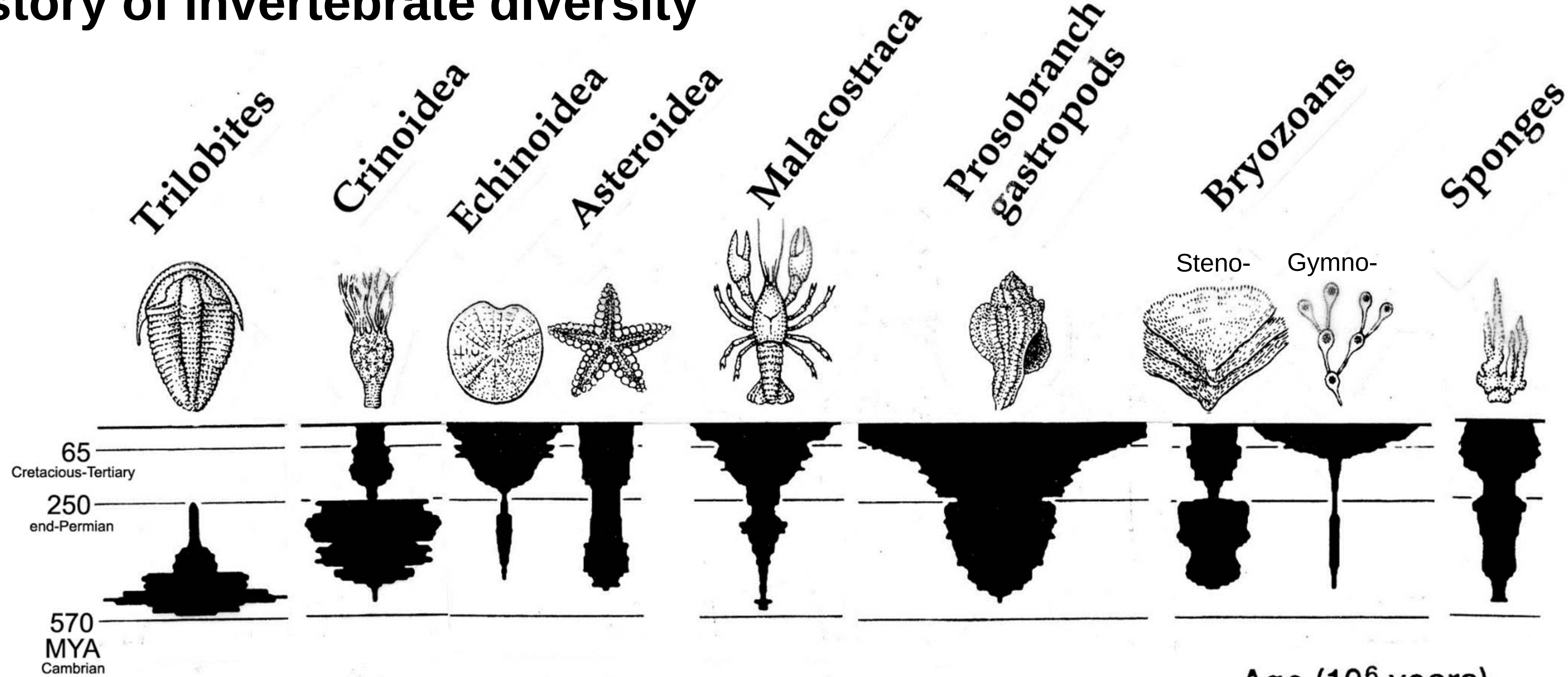


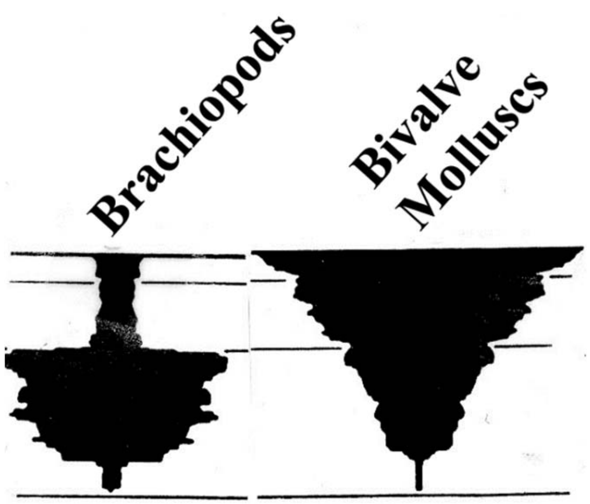
Regular increase



Decimation and radiation

History of invertebrate diversity





Mass extinctions of marine families