The place of *Drosophila* among the metazoans

Peter Holland

Zoology, Oxford

What are metazoans?

- Metazoa = the ‘true’ animals
- Metazoa = the Animal Kingdom
- Metazoa = multicellular animals

- (There are no unicellular animals)

The taxonomic view

Kingdom Metazoa

Phylum Arthropoda

Class Insecta

Order Diptera

Family Drosophilidae

Genus *Drosophila*

species *melanogaster*

The taxonomic view

Kingdom Metazoa

Phylum Arthropoda

Class Insecta

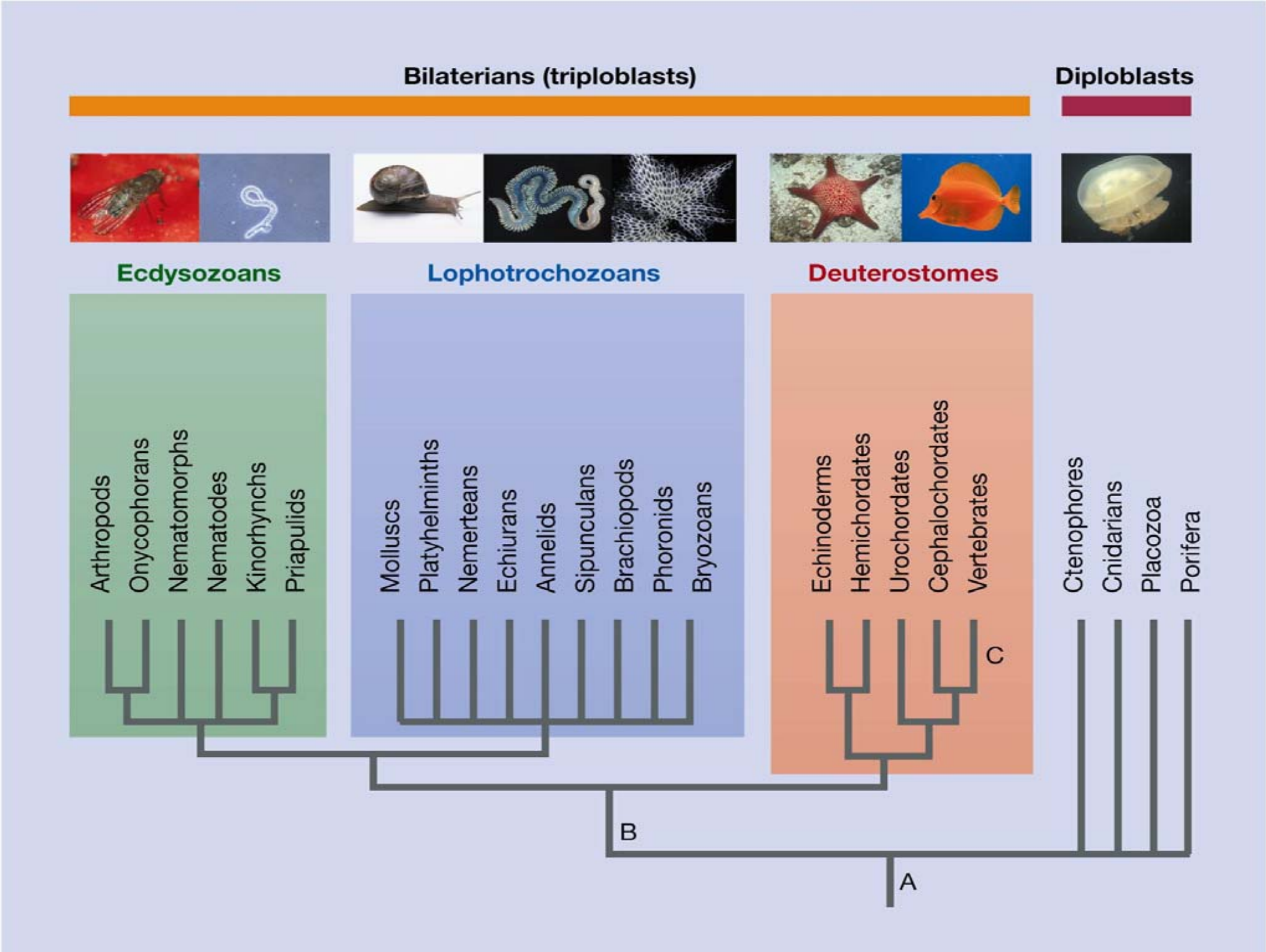
Not perfect if you wish to do any comparative biology, because taxonomy does not always reflect phylogeny

Family Drosophilidae

Genus *Drosophila*

species *melanogaster*

The phylogenetic view



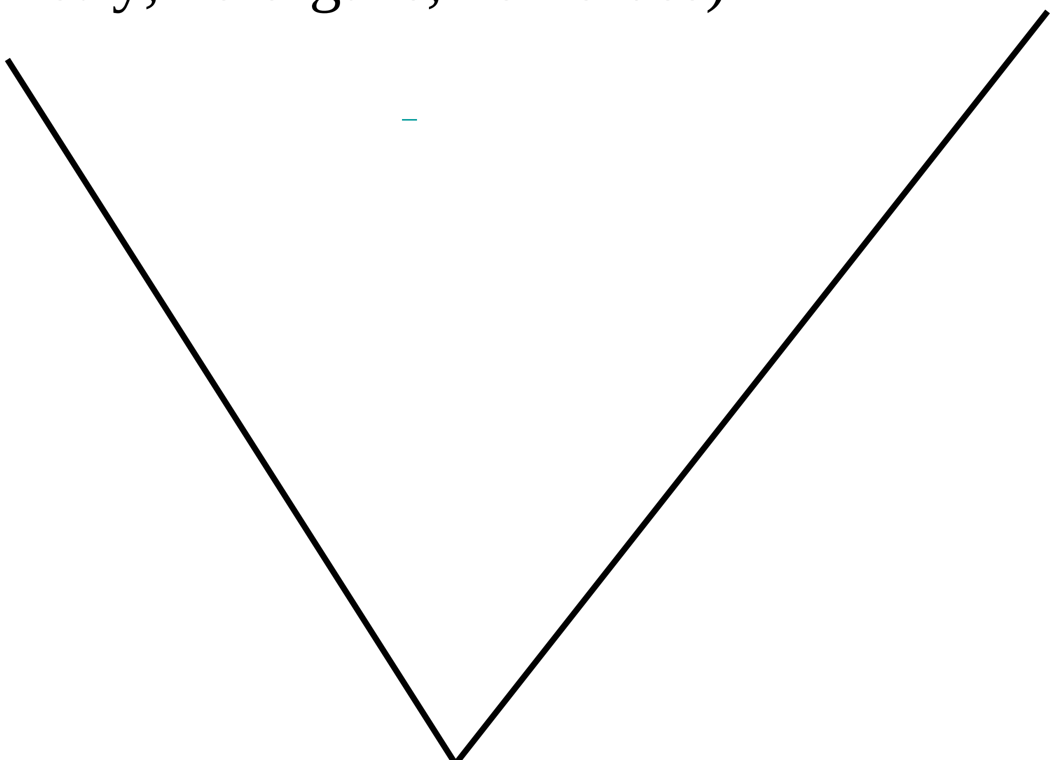
Kingdom Metazoa

Holland, P.W.H. (1999) The future of evolutionary developmental biology. **Nature** 402, C41-C44. *('Impacts of foreseeable science' Supplement)*

At the base of the Metazoa

‘Eumetazoa’
(all the rest of the animals - symmetry, organs)

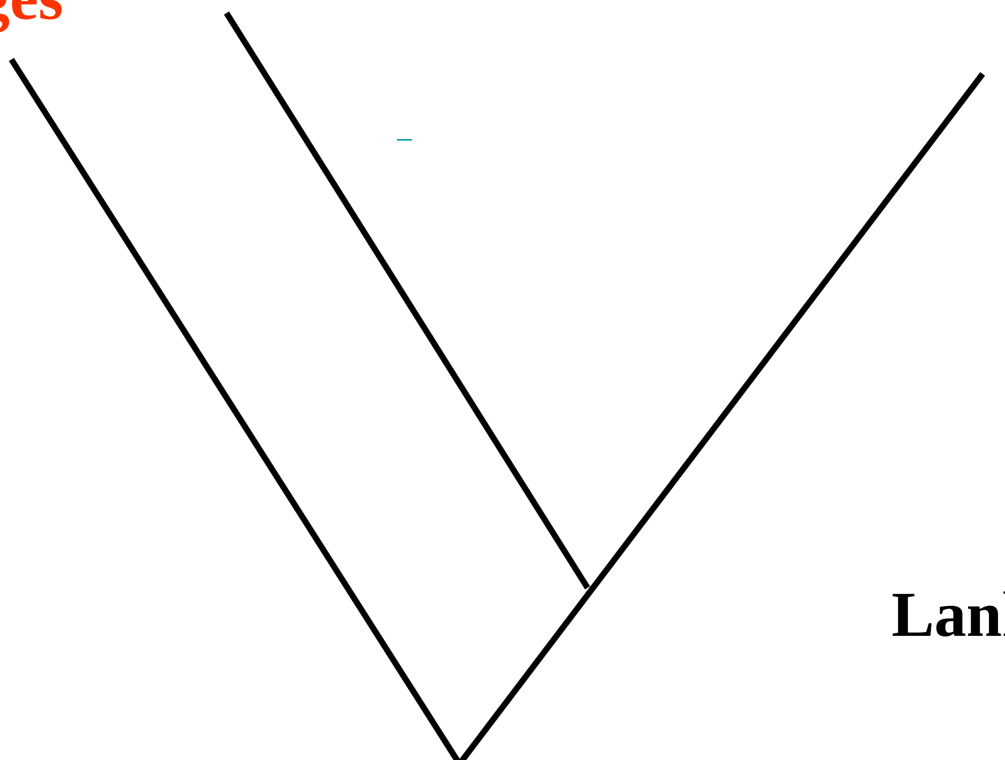
Sponges
(no symmetry, no organs, no nerves)



Diploblasts
(e.g. *Hydra, Nematostella*)
Only 2 germ layers
Radial Symmetry

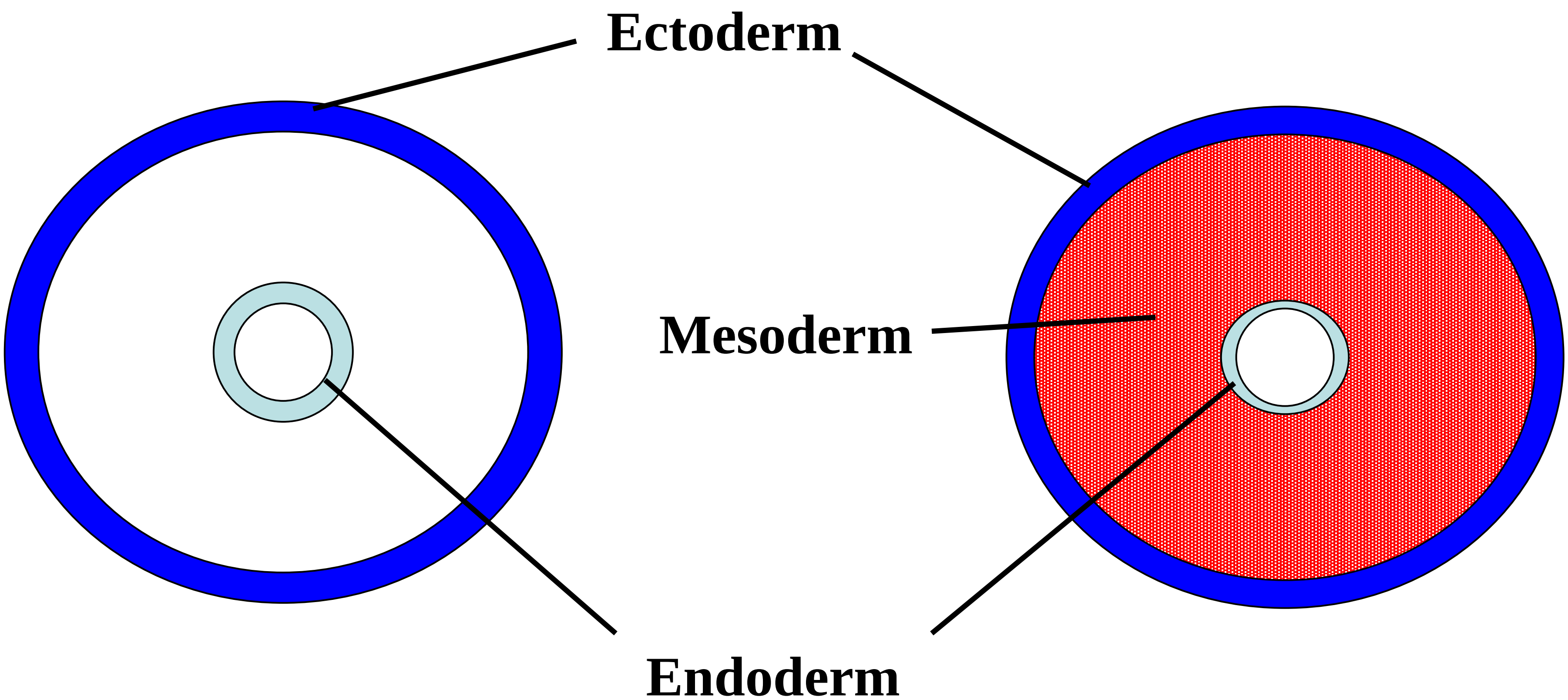
Triploblasts or Bilateria
(the rest!)
3 germ layers
Bilateral Symmetry

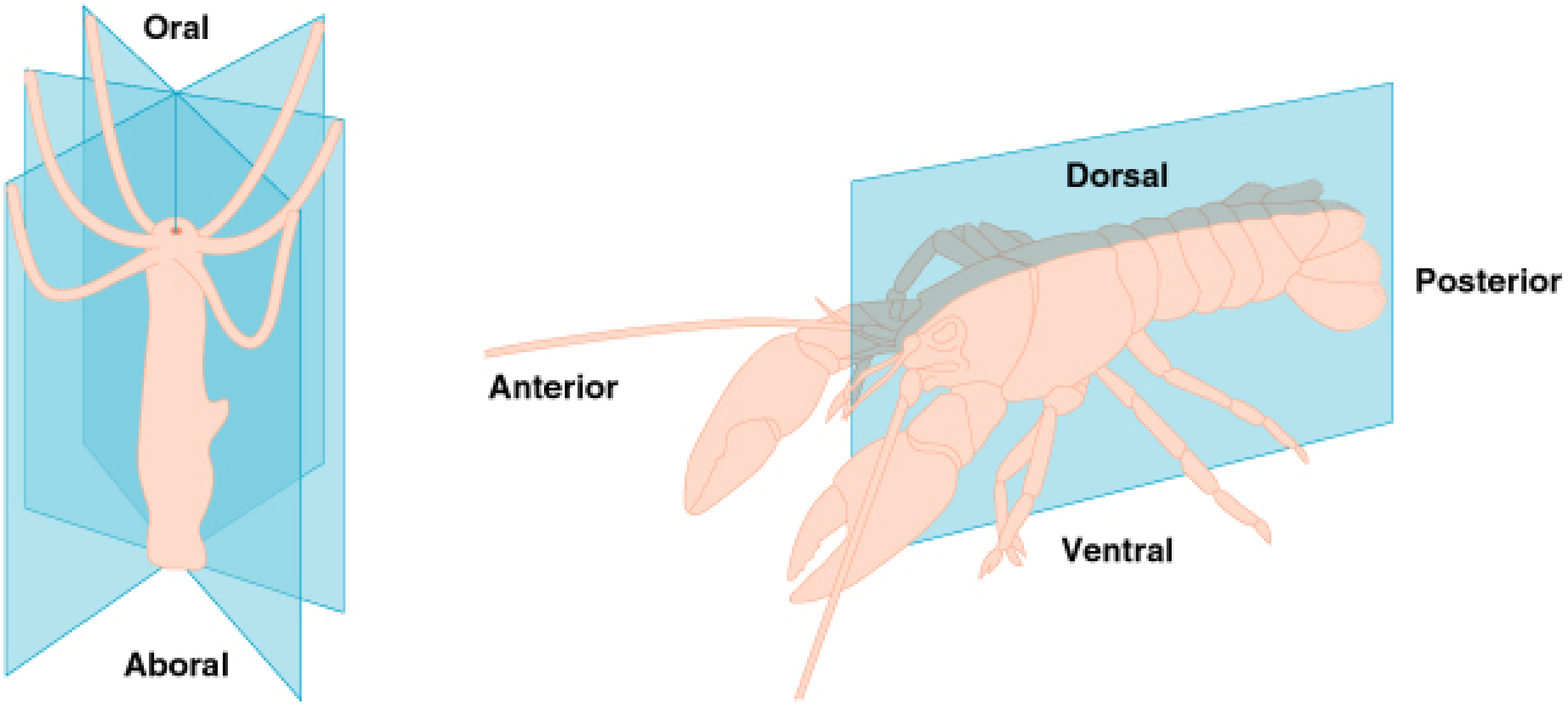
Sponges



Lankester (1873)

Diploblast **Triploblast**





(a) Radial symmetry

(b) Bilateral symmetry

http://www.zo.utexas.edu/faculty/sjasper/images/32.4.jpg

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(e.g. *Hydra, Nematostella*)
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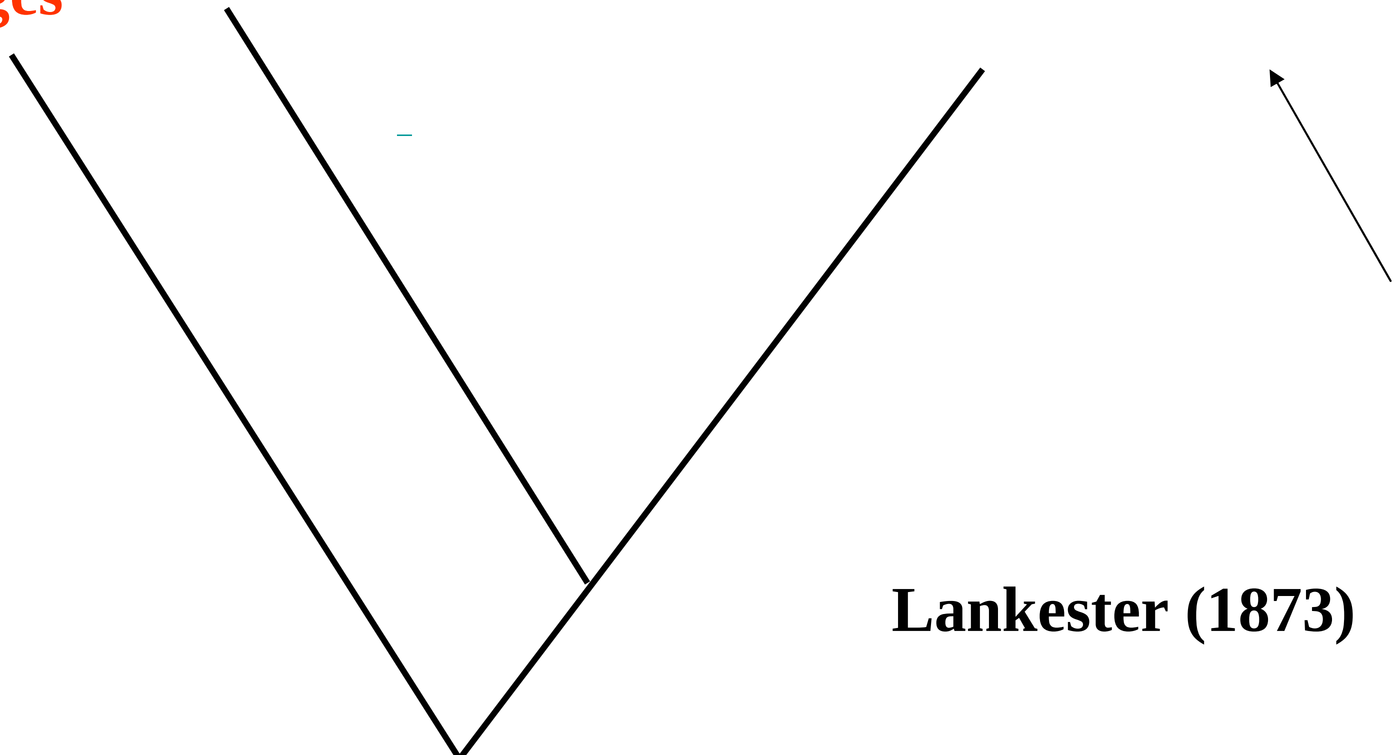


Lankester (1873)

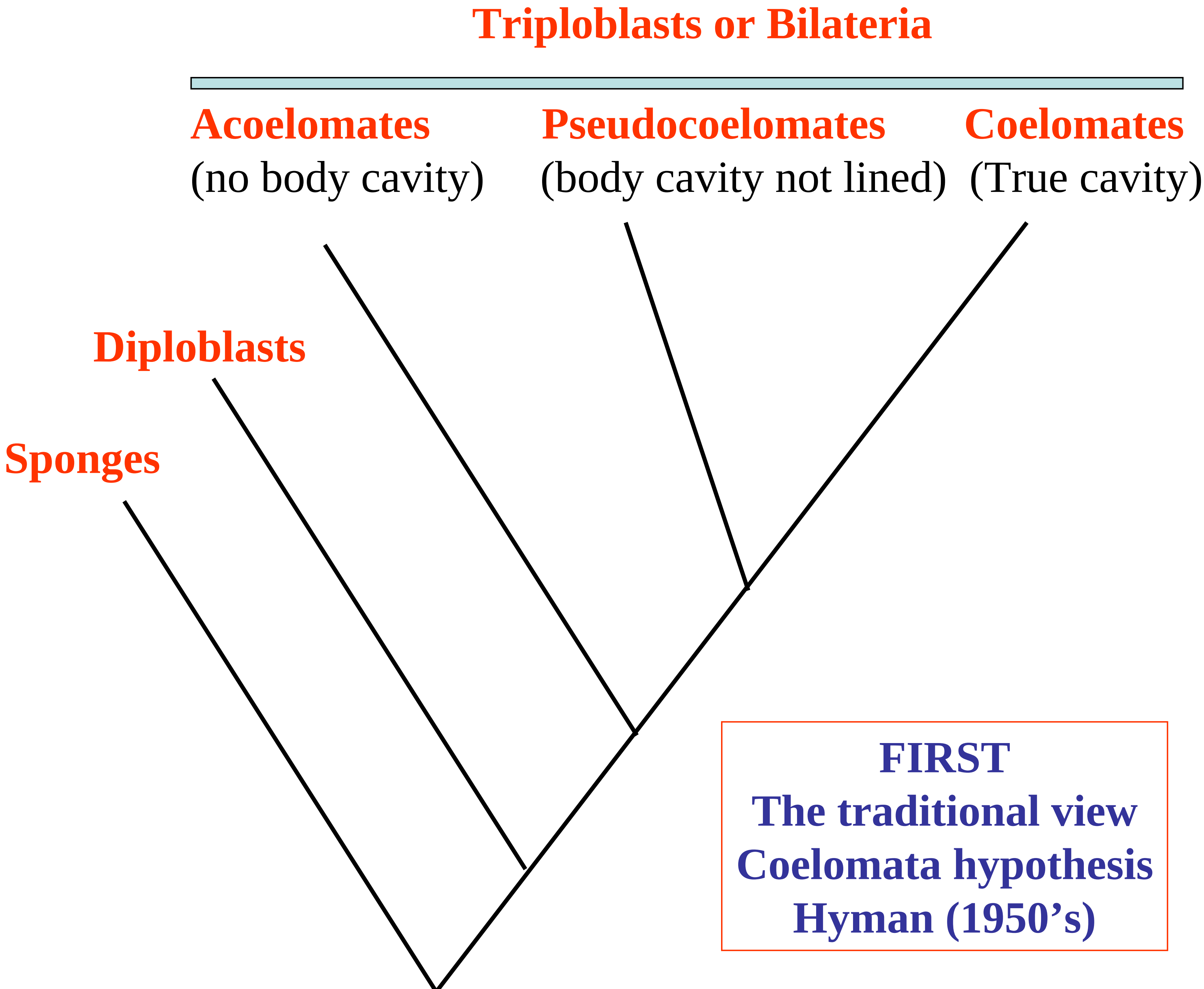
And now for the controversial part…

What is the phylogeny within the Bilateria?

The traditional view = Coelomata hypothesis

or

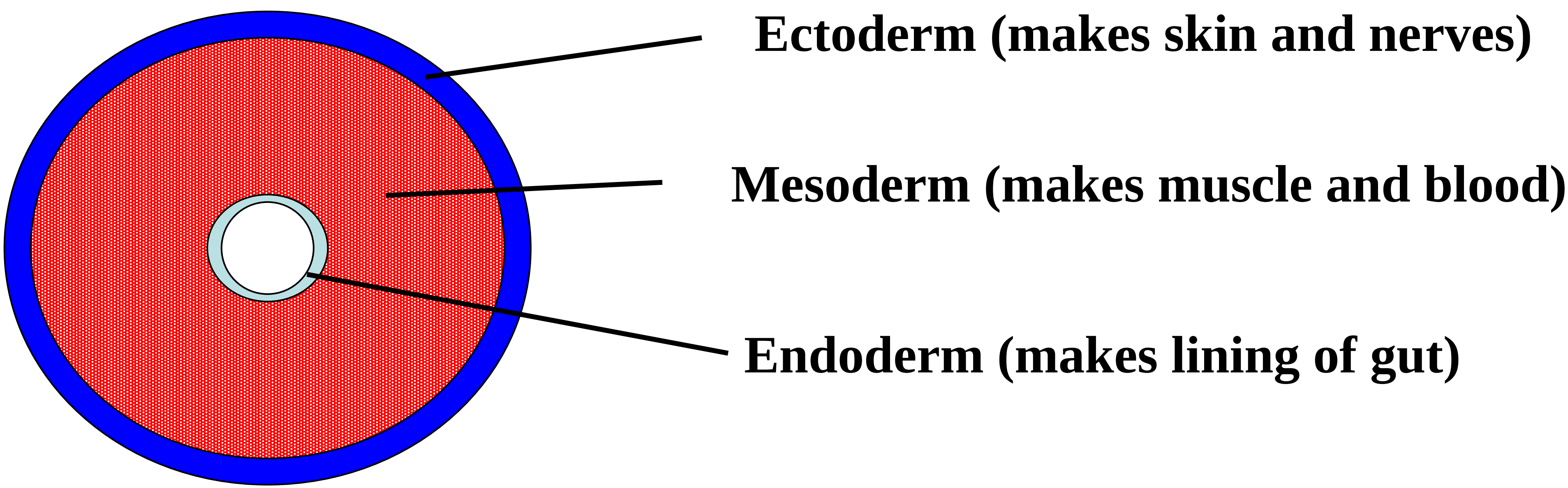
The alternative view = Ecdysozoa hypothesis



FIRST
The traditional view
Coelomata hypothesis
Hyman (1950's)

Triploblasts or Bilateria

Acoelomates	**Pseudocoelomates**	**Coelomates**
(no body cavity)	(body cavity not lined)	(True cavity)



Triploblasts or Bilateria

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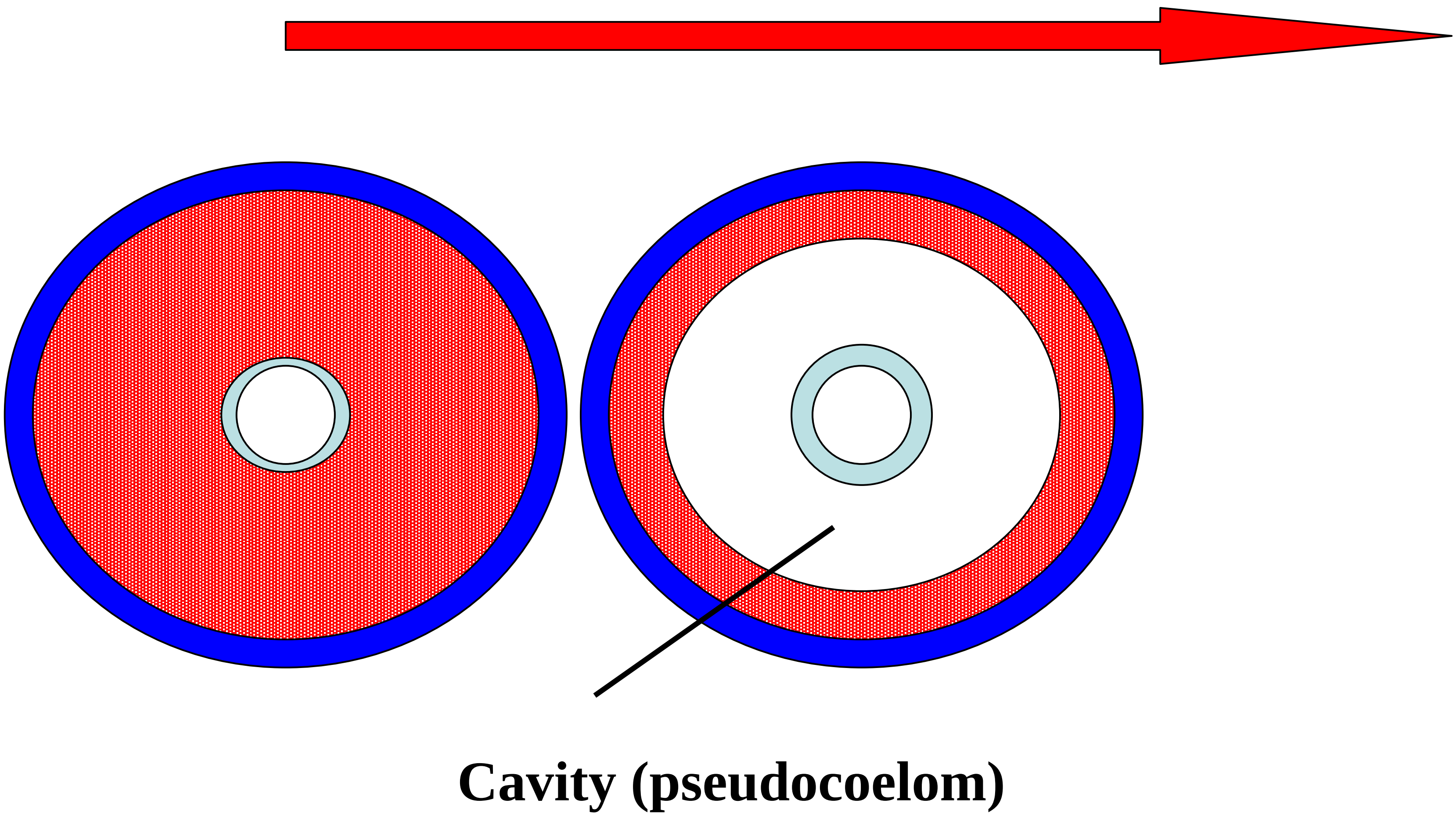
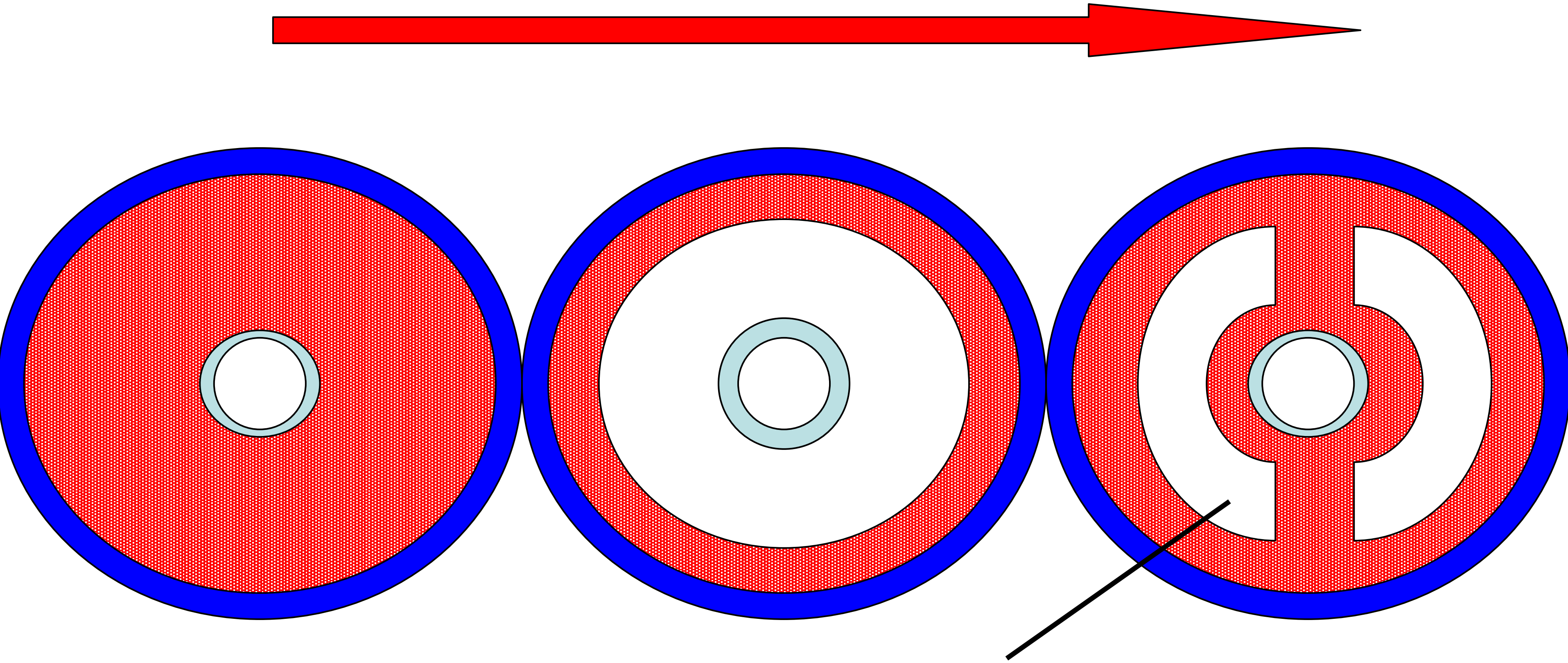


Triploblasts or Bilateria

Acoelomates (no body cavity)

Pseudocoelomates (body cavity not lined)

Coelomates (True cavity)



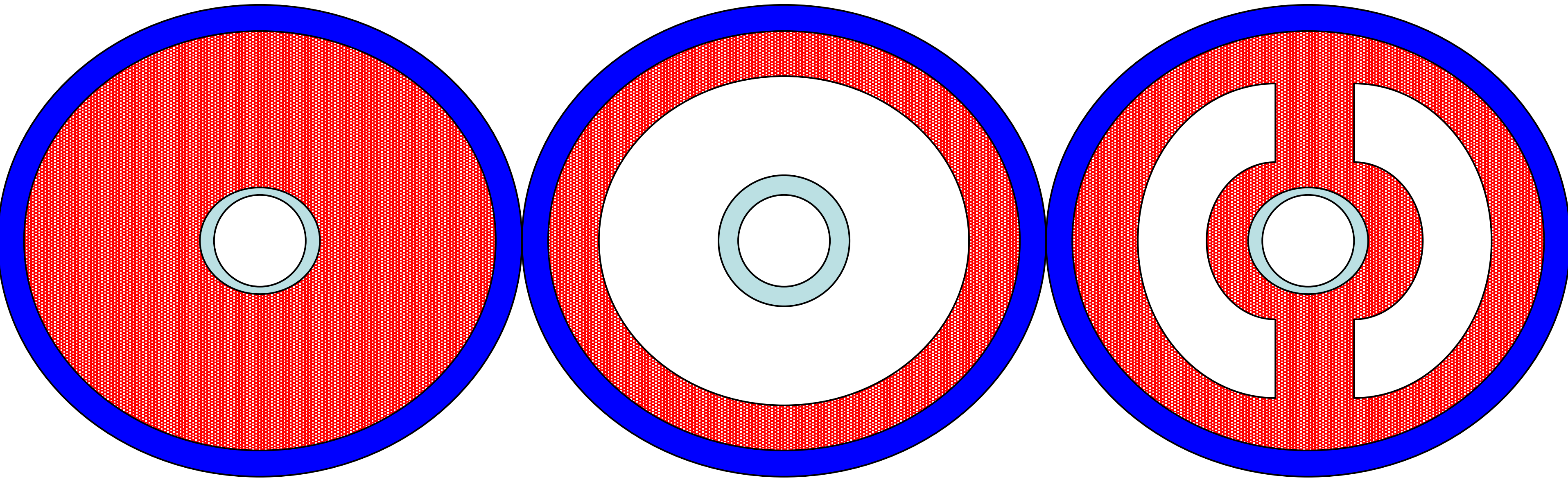
Cavity lined by an epithelial cell layer within mesoderm (coelom)

Triploblasts or Bilateria

Acoelomates (no body cavity)

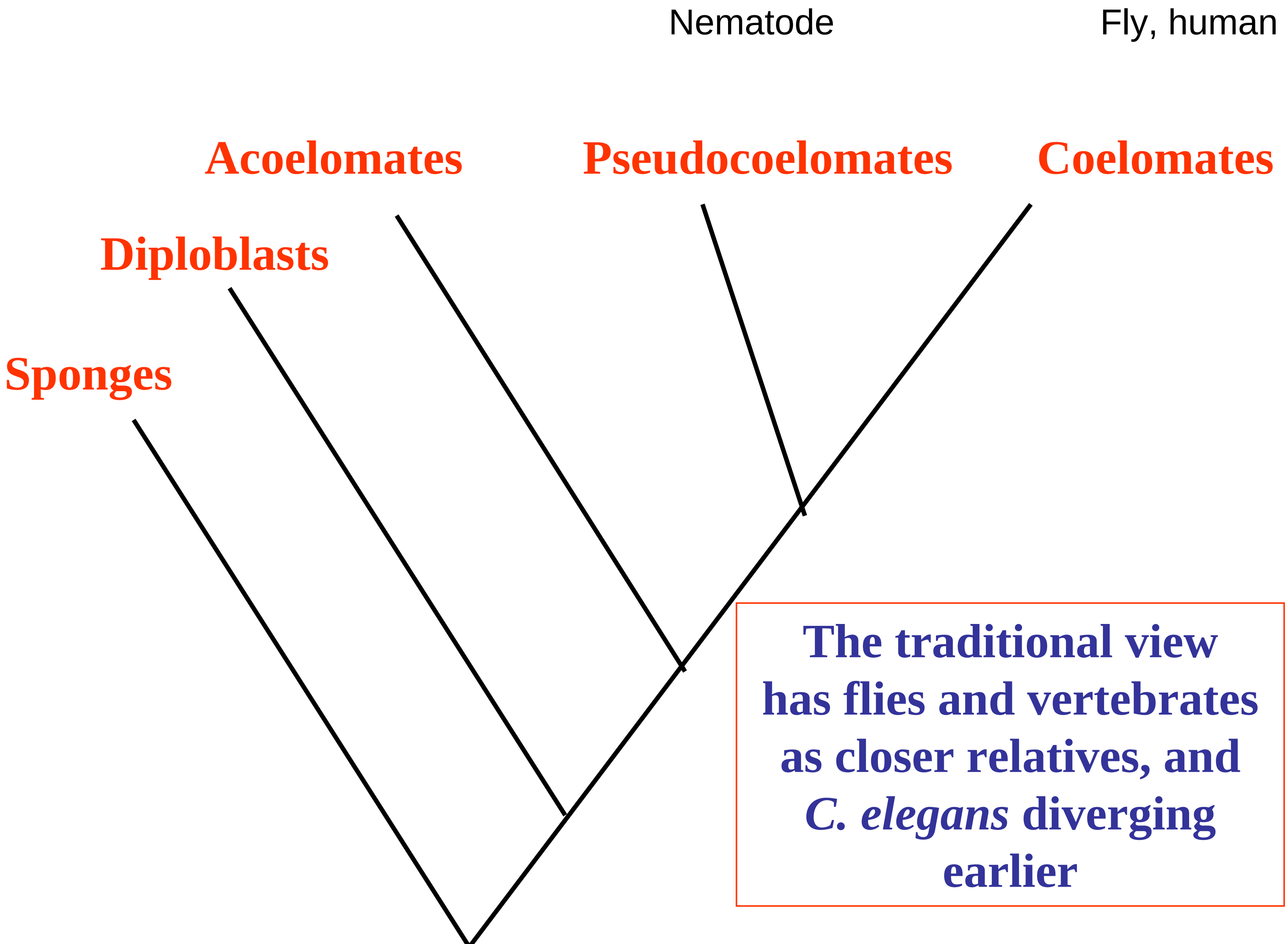
Pseudocoelomates (body cavity not lined)

Coelomates (True cavity)

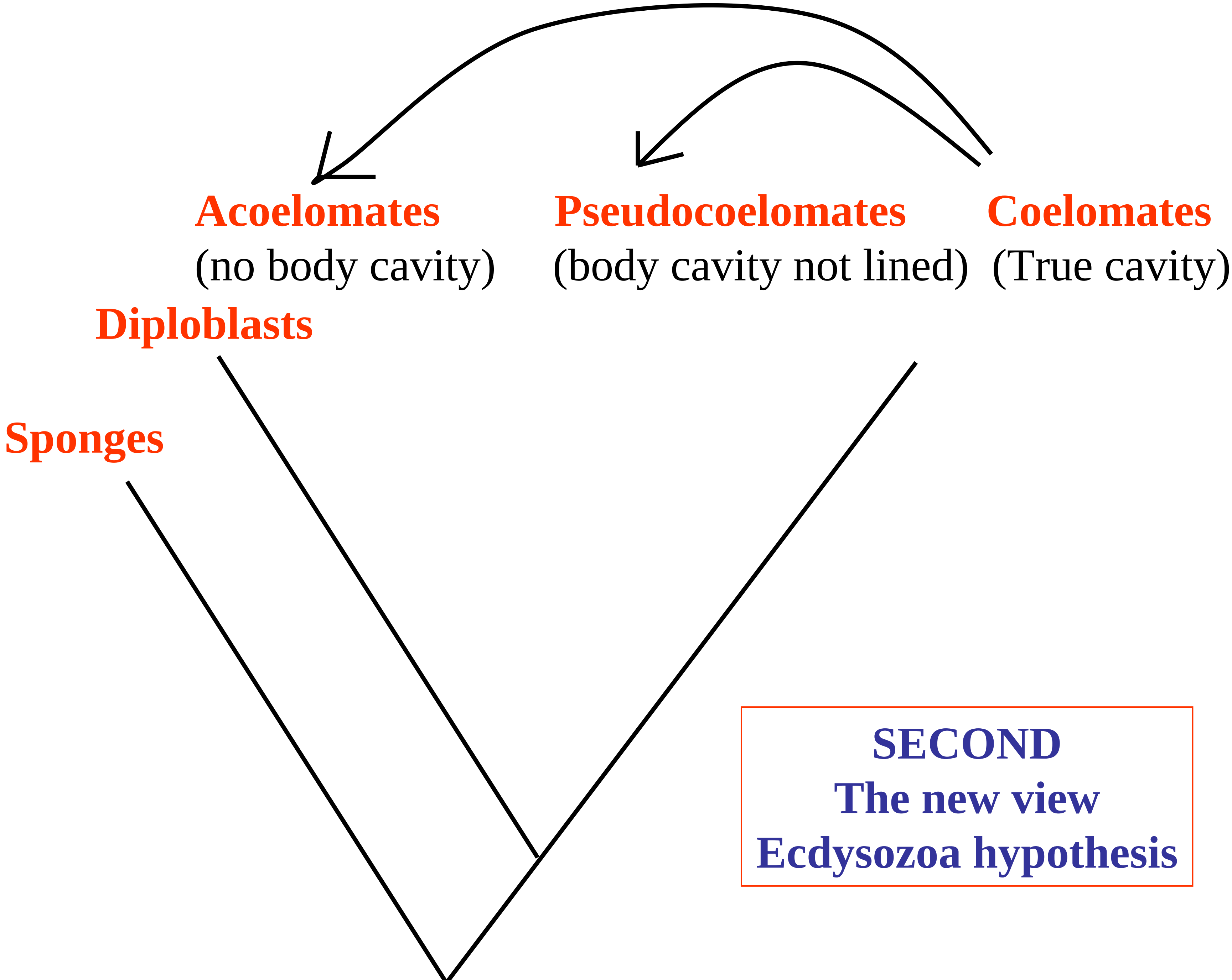


Nematode

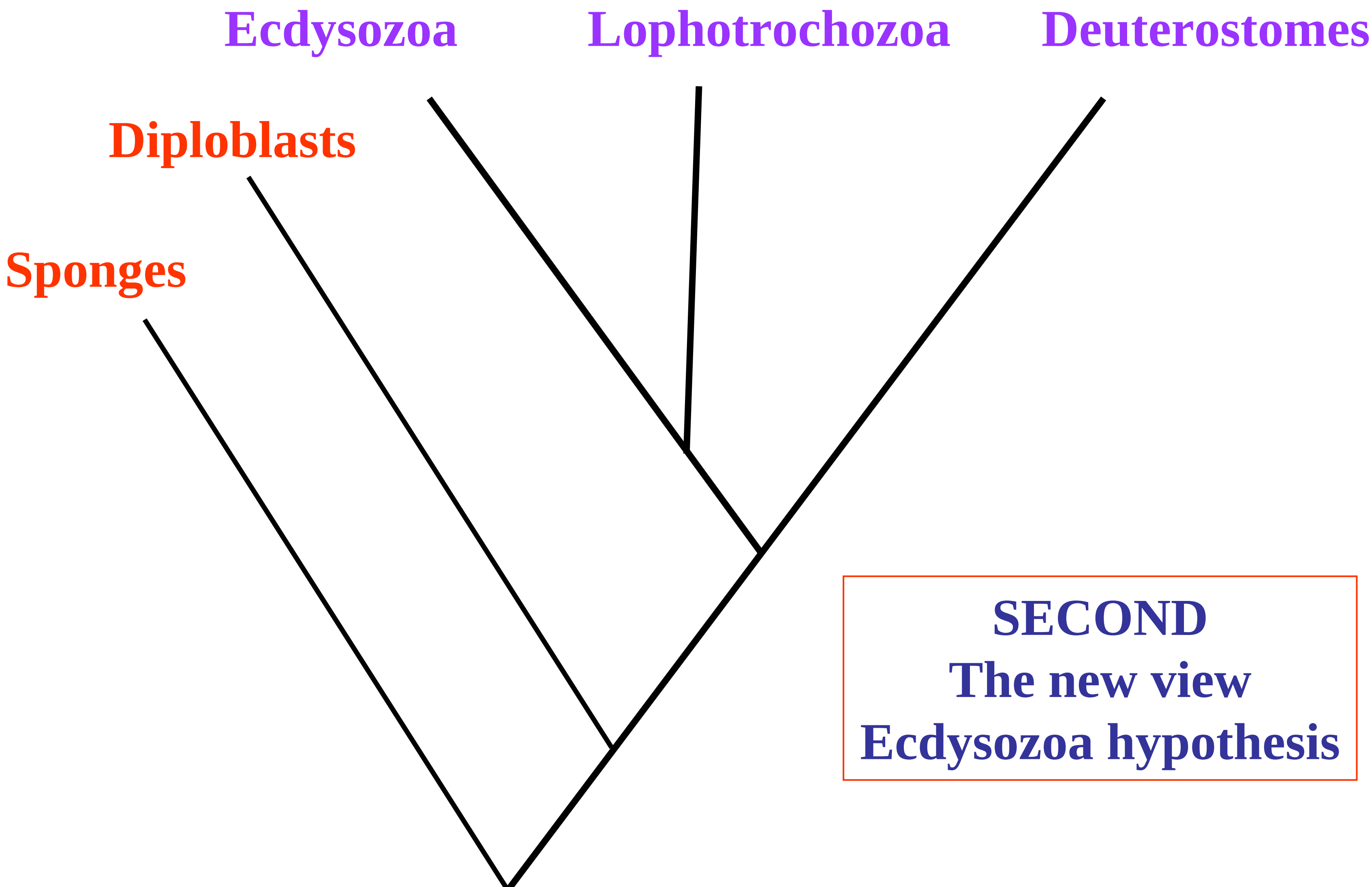
Fly
Human



The traditional view has flies and vertebrates as closer relatives, and *C. elegans* diverging earlier


Acoelomates
(no body cavity)
Pseudocoelomates
(body cavity not lined)
Coelomates
(True cavity)
Diploblasts
Sponges
SECOND
The new view
Ecdysozoa hypothesis

A complete shake-up of the Bilateria phylogeny



SECOND
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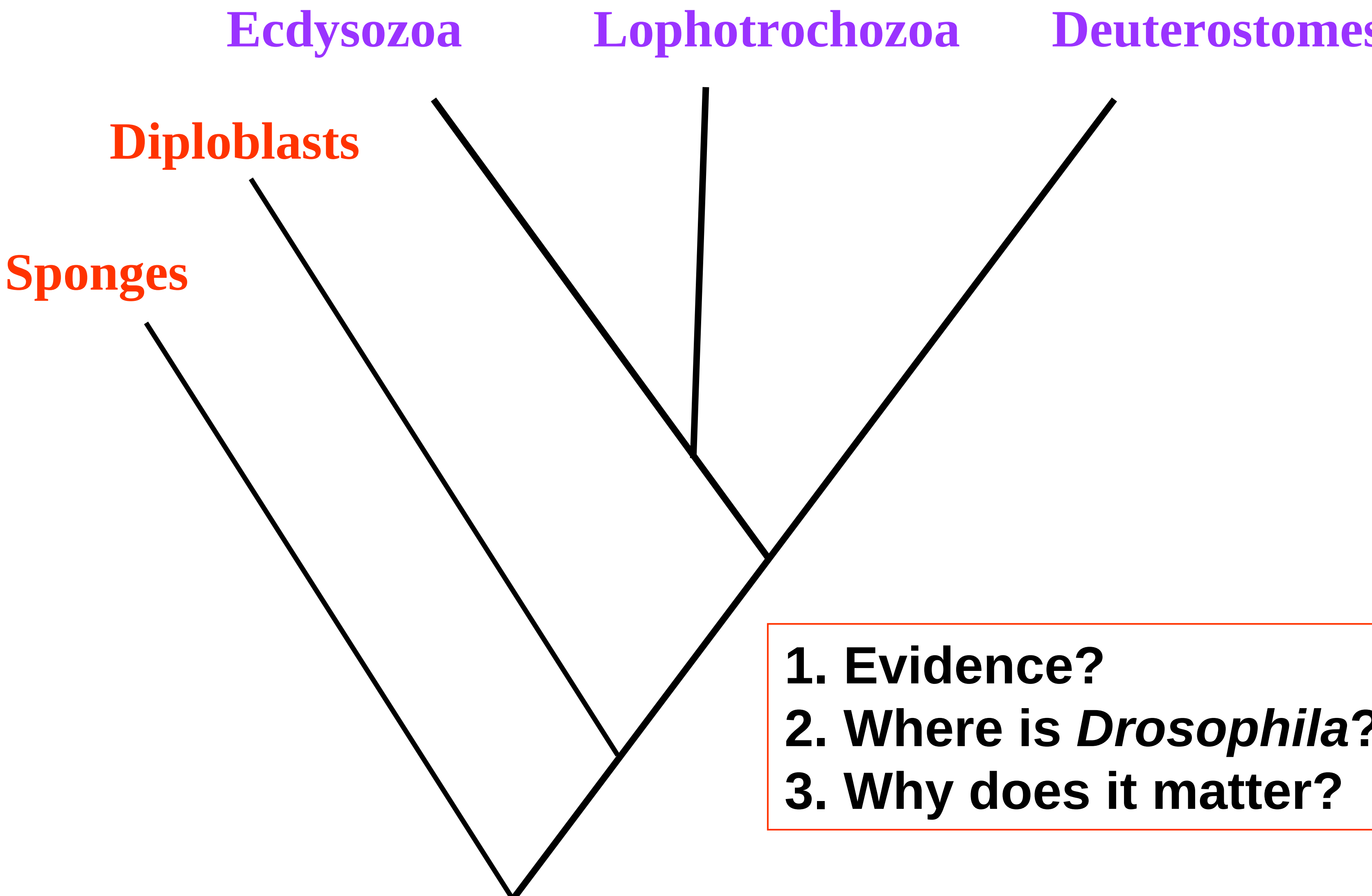


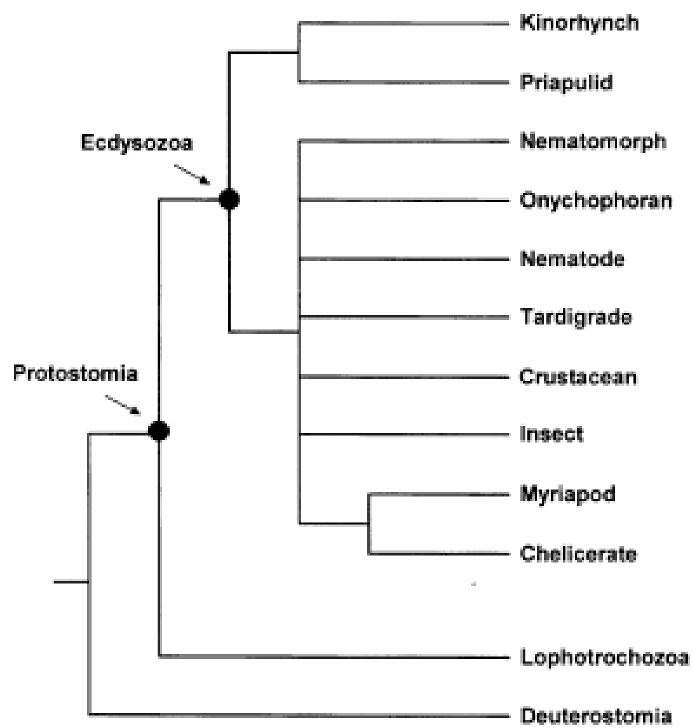
1. **Evidence?**
2. **Where is *Drosophila*?**
3. **Why does it matter?**

Evidence 1: 18S rDNA
(after removal of long branch taxa)

Table 1 Substitution rates of 18S rDNA sequences

Phylum	Genus	Substitutions per site
	Lophotrochozoa	
Chaetognatha	*Sagitta*	0.143 ± 0.111
Sipuncula	*Phascolosoma*	0.079 ± 0.007
Pogonophora	*Siboglinum*	0.070 ± 0.008
Platyhelminthes	*Bdelloura*	0.147 ± 0.012
	Fasciolopsis	0.083 ± 0.009
	Stenostomum	**0.063 ± 0.063**
Nemertea	*Lineus*	0.061 ± 0.007
Echiura	*Ochetostoma*	0.058 ± 0.007
Vestimentifera	*Ridgeia*	0.055 ± 0.007
Mollusca	*Lymnaea*	0.060 ± 0.006
	***Placopecten* (bivalve)**	**0.042 ± 0.007**
	***Acanthopleura* (polyplacophoran)**	**0.040 ± 0.006**
Aschelminthes:		
Acanthocephala	*Moniliformis*	0.111 ± 0.009
Gastrotricha	*Lepidodermella*	0.070 ± 0.007
Rotifera	***Brachionus***	**0.058 ± 0.007**
Lophophorates:		
Phoronida	*Phoronis*	0.053 ± 0.007
Ectoprocta	*Plumatella*	0.049 ± 0.006
Brachiopoda	*Glottidia*	0.044 ± 0.006
	Terebratalia	**0.044 ± 0.006**
Annelida	*Eisenia*	0.057 ± 0.007
	Lanice	0.056 ± 0.006
	***Enchytreus* (oligochaete)**	**0.052 ± 0.006**
	***Stylaria* (oligochaete)**	**0.042 ± 0.006**
	***Glycera* (polychaete)**	**0.033 ± 0.005**
	Arthropods and relatives	
Nematoda	*Strongyloides*	0.192 ± 0.014
	Caenorhabditis	0.187 ± 0.013
	Trichuris	0.141 ± 0.012
	Trichinella	**0.110 ± 0.010**
Onychophora	***Euperipatoides***	**0.090 ± 0.009**
Tardigrada	*Milnesium*	0.079 ± 0.008
	Macrobiotus	**0.079 ± 0.009**
Kinorhyncha	***Pycnophyes***	**0.075 ± 0.007**
Nematomorpha	***Gordius***	**0.068 ± 0.007**
Arthropoda	*Artemia*	0.068 ± 0.007
	***Panulirus* (crustacean)**	**0.065 ± 0.008**
	Drosophila	0.121 ± 0.011
	Crossodonthina	0.056 ± 0.007
	***Tenebrio* (insect)**	**0.048 ± 0.006**
	***Scolopendra* (myriapod)**	**0.043 ± 0.006**
	Androctonus	0.046 ± 0.006
	***Eurypelma* (chelicerate)**	**0.038 ± 0.005**
Priapula	***Priapulus***	**0.040 ± 0.005**
	Outgroups	
Chordata	*Lampetra*	0.065 ± 0.007
	Branchiostoma	0.059 ± 0.006
Echinodermata	*Strongylocentrotus*	0.043 ± 0.006
	Antedon	**0.040 ± 0.005**
Ctenophora	*Mnemiopsis*	0.130 ± 0.111
Cnidaria	*Anemonia*	0.101 ± 0.009
	Tripedalia	**0.100 ± 0.009**

Distances are calculated by paralinear/LogDet distances and the ± s.d. estimated from bootstrap replicates. The number of substitutions per position from the last common ancestor of protostomes was calculated with respect to three slowly evolving reference taxa. Distances to protostome taxa were calculated using *Tripedalia* and *Antedon* as outgroup taxa and either *Glycera* or *Priapulus*, depending upon which ingroup taxon was being examined. Distances to outgroup taxa were calculated using *Glycera*, *Priapulus* and *Acanthopleura* as reference taxa.



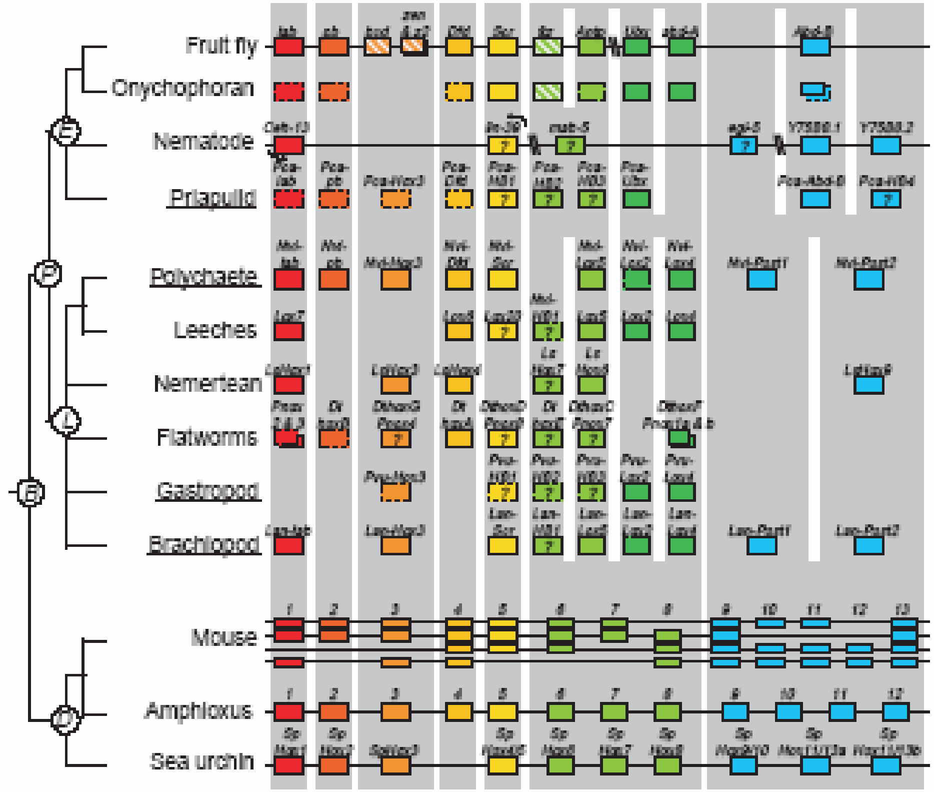
Evidence for a clade of nematodes, arthropods and other moulting animals

Anna Marie A. Aguinaldo*, James M. Turbeville†, Lawrence S. Linford*, Maria C. Rivera*, James R. Garey‡, Rudolf A. Raff§ & James A. Lake*

Nature 387, 489-493.

Evidence 2: Hox gene clusters

(diagnostic gene duplications inside the cluster)

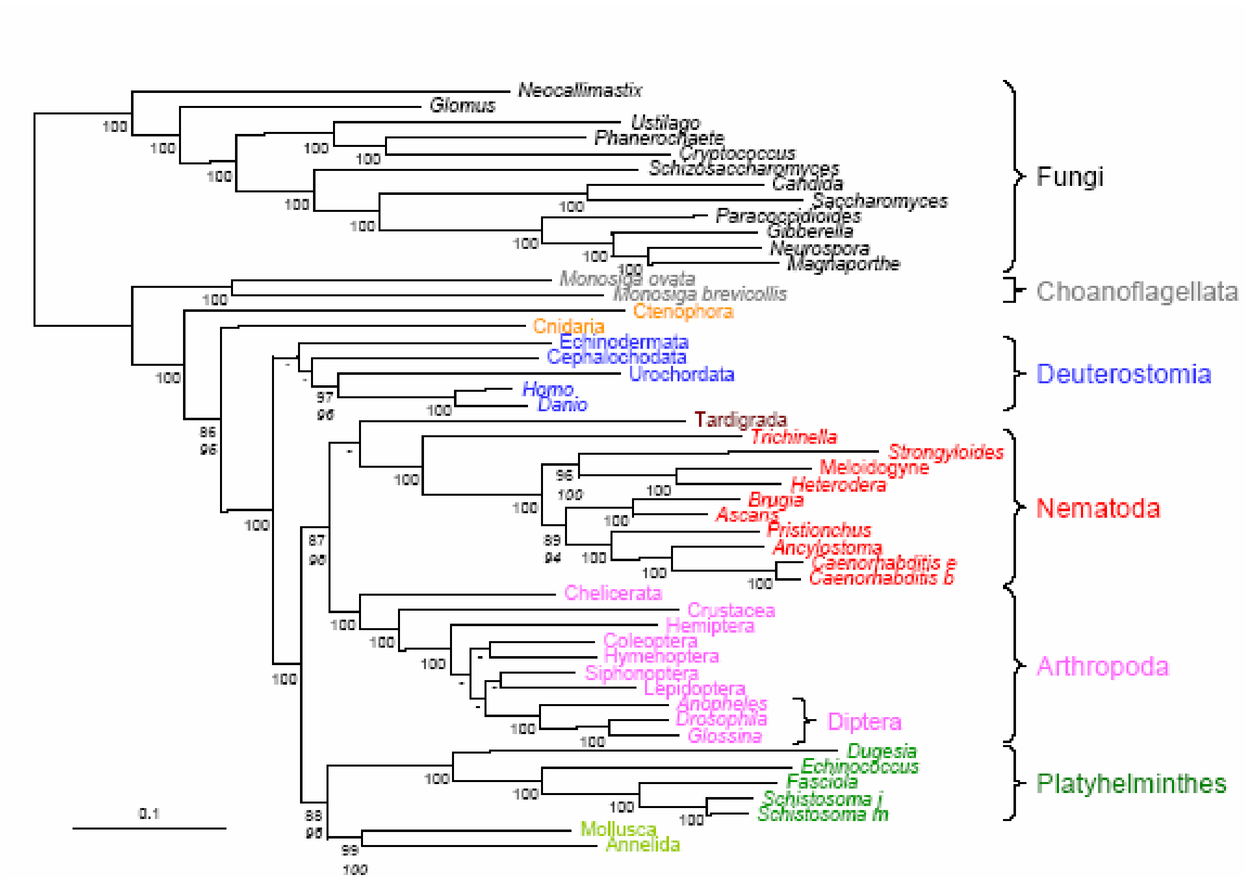


Hox genes in brachiopods and priapulids and protostome evolution

Renaud de Rosa*†, Jennifer K. Grenier*‡, Tatiana Andreeva§, Charles E. Cook‖, André Adoutte†, Michael Akam‖, Sean B. Carroll‡ & Guillaume Balavoine‖¶

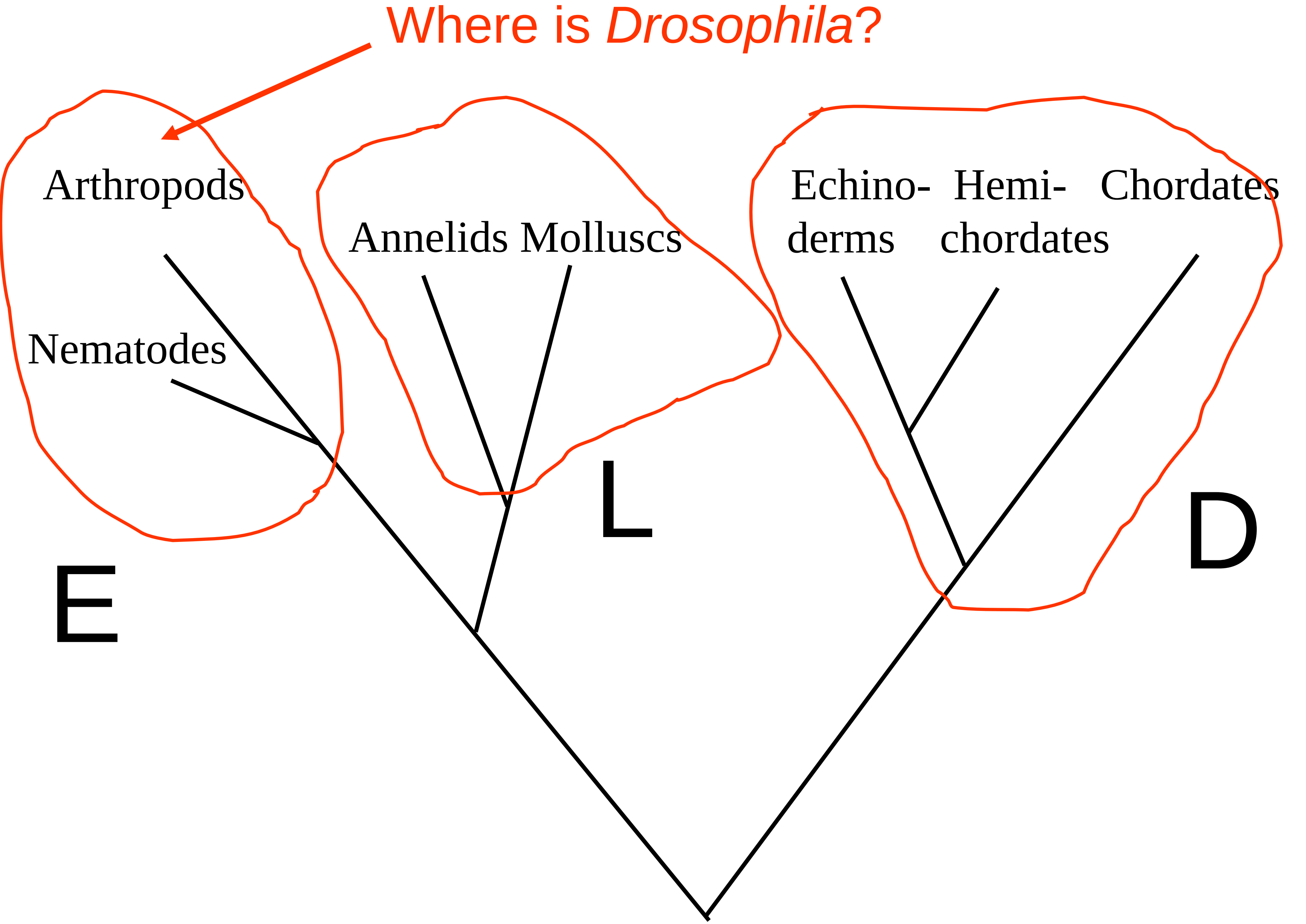
Nature 399, 772-776

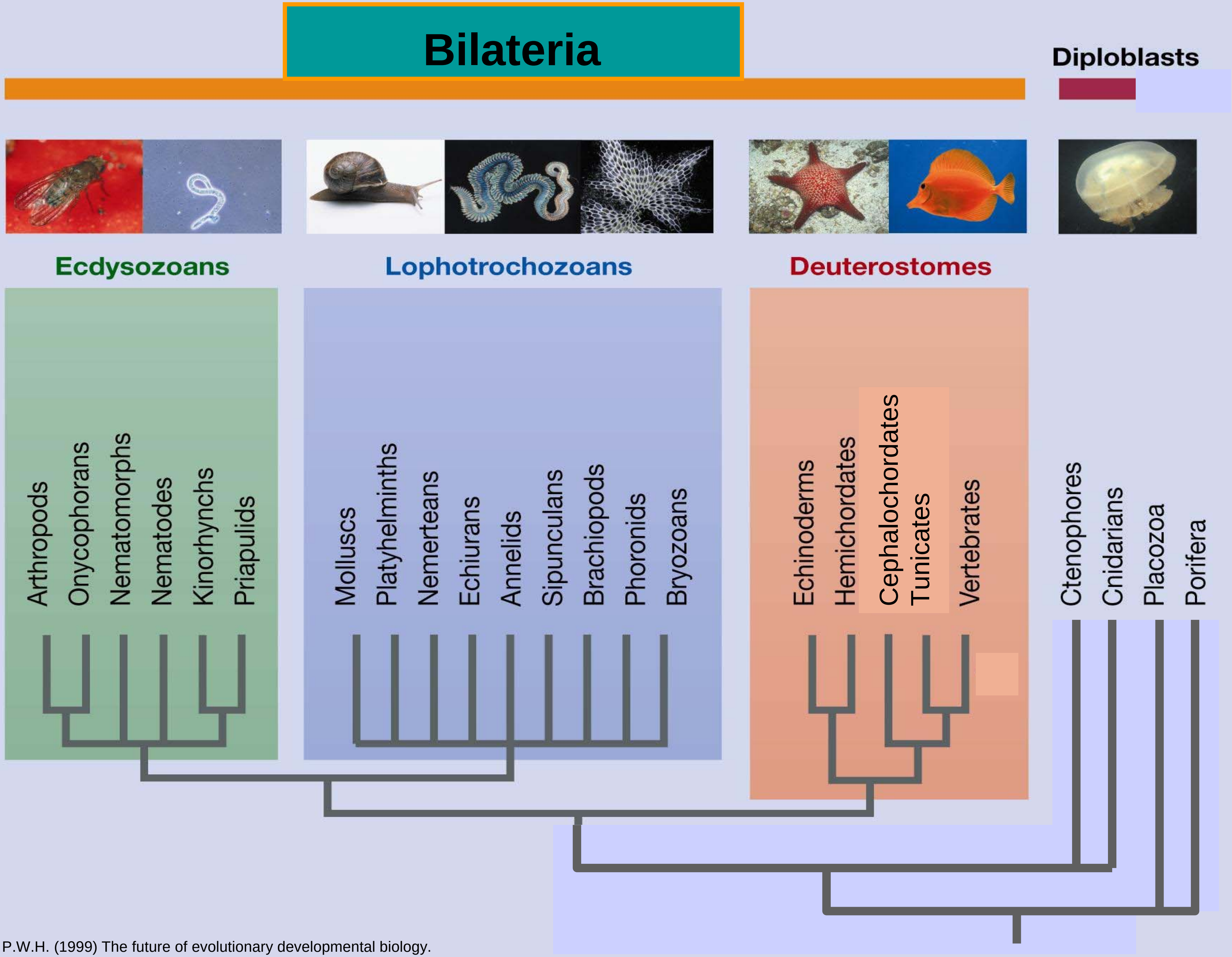
Evidence 3: EST-driven multigene phylogeny



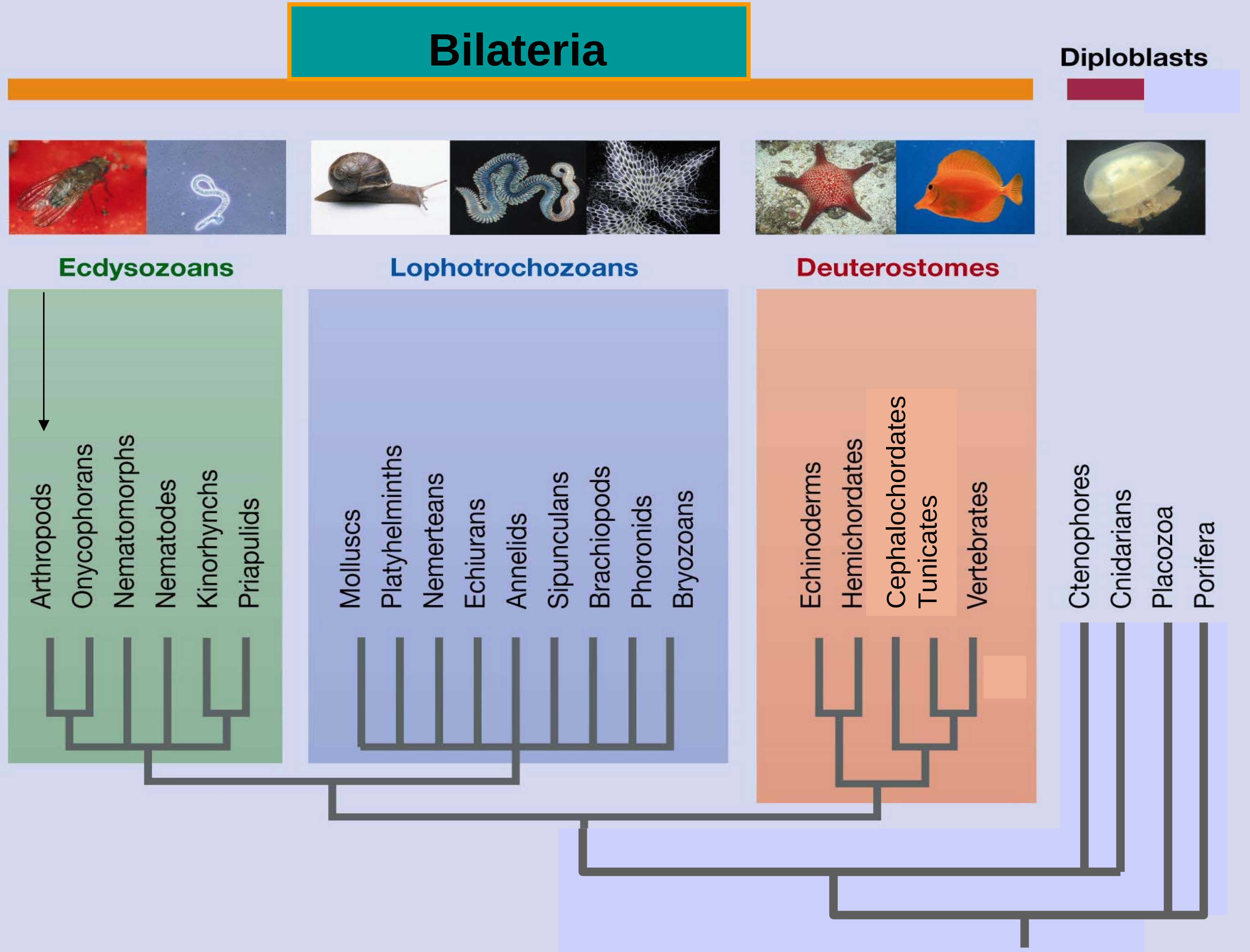
Maximum likelihood tree inferred from the separate analysis of 71 genes that evolve slowly in nematodes and platyhelminthes (20,705 amino-acid positions).

Hervé Philippe, Nicolas Lartillot and Henner Brinkmann (2005)
Molec Biol. Evol 22(5):1246-1253


Where is *Drosophila*?
Arthropods
Nematodes
Annelids
Molluscs
Echino- derms
Hemi- chordates
Chordates
E
L
D



Holland, P.W.H. (1999) The future of evolutionary developmental biology.
Nature 402, C41-C44. *('Impacts of foreseeable science' Supplement)*


Bilateria
Diploblasts
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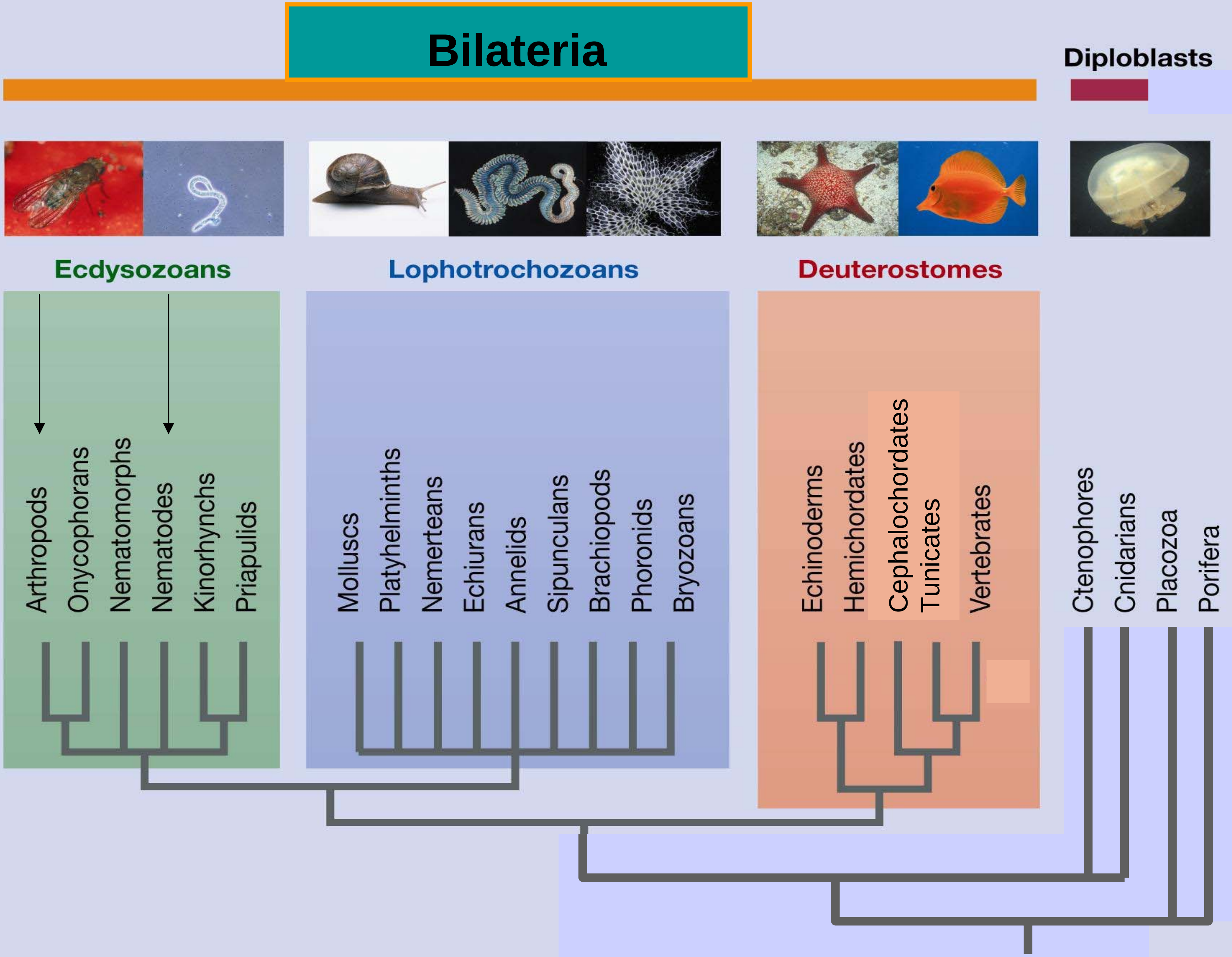
Lophotrochozoans
Deuterostomes
Arthropods
Onycophorans
Nematomorphs
Nematodes
Kinorhynchs
Priapulids
Molluscs
Platyhelminths
Nemerteans
Echiurans
Annelids
Sipunculans
Brachiopods
Phoronids
Bryozoans
Echinoderms
Hemichordates
Cephalochordates
Tunicates
Vertebrates
Ctenophores
Cnidarians
Placozoa
Porifera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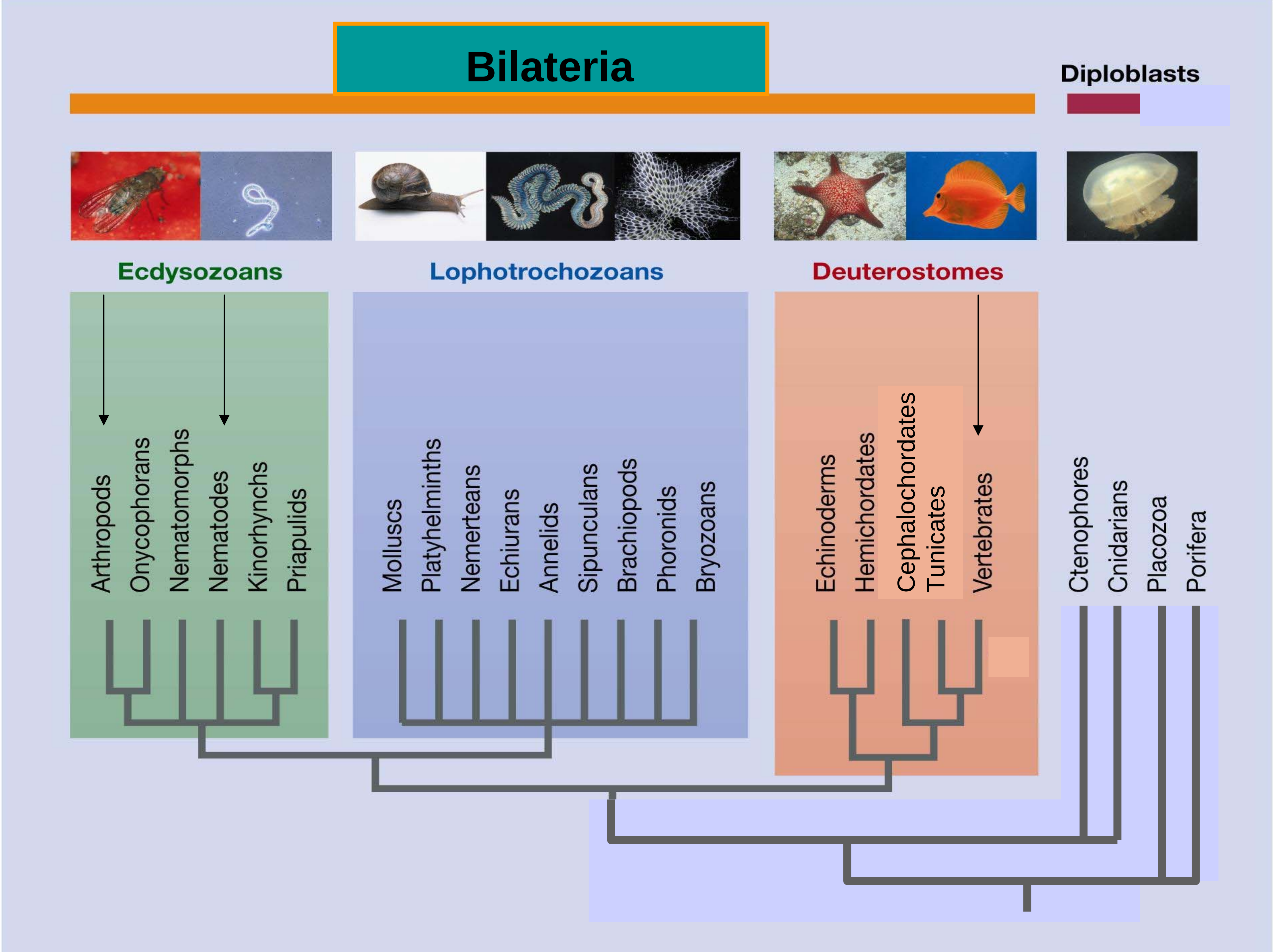
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Why does it matter?

The topology argument: for all comparative biology we need to know the relationships between the species being studied

The character state argument: looking at the whole picture helps us to assess whether characters (e.g. developmental pathways) are 'homologous'

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The character state argument: looking at the whole picture helps us to assess whether characters (e.g. developmental pathways) are 'homologous'

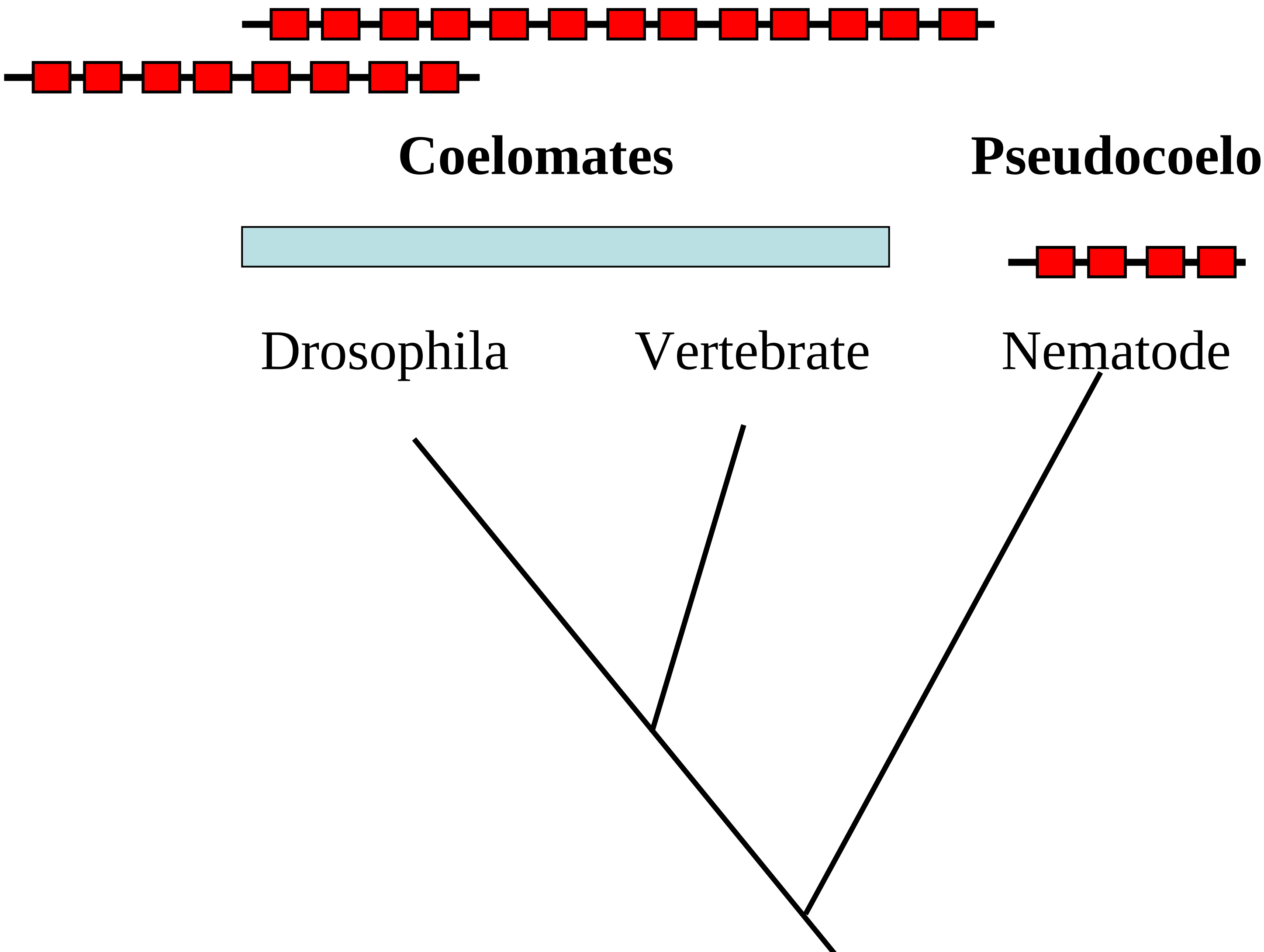
COELOMATA hypothesis has nematodes as primitive, flies and vertebrates as advanced

while

ECDYSOZOA hypothesis sees all three as advanced, and flies/nematodes as relatives!

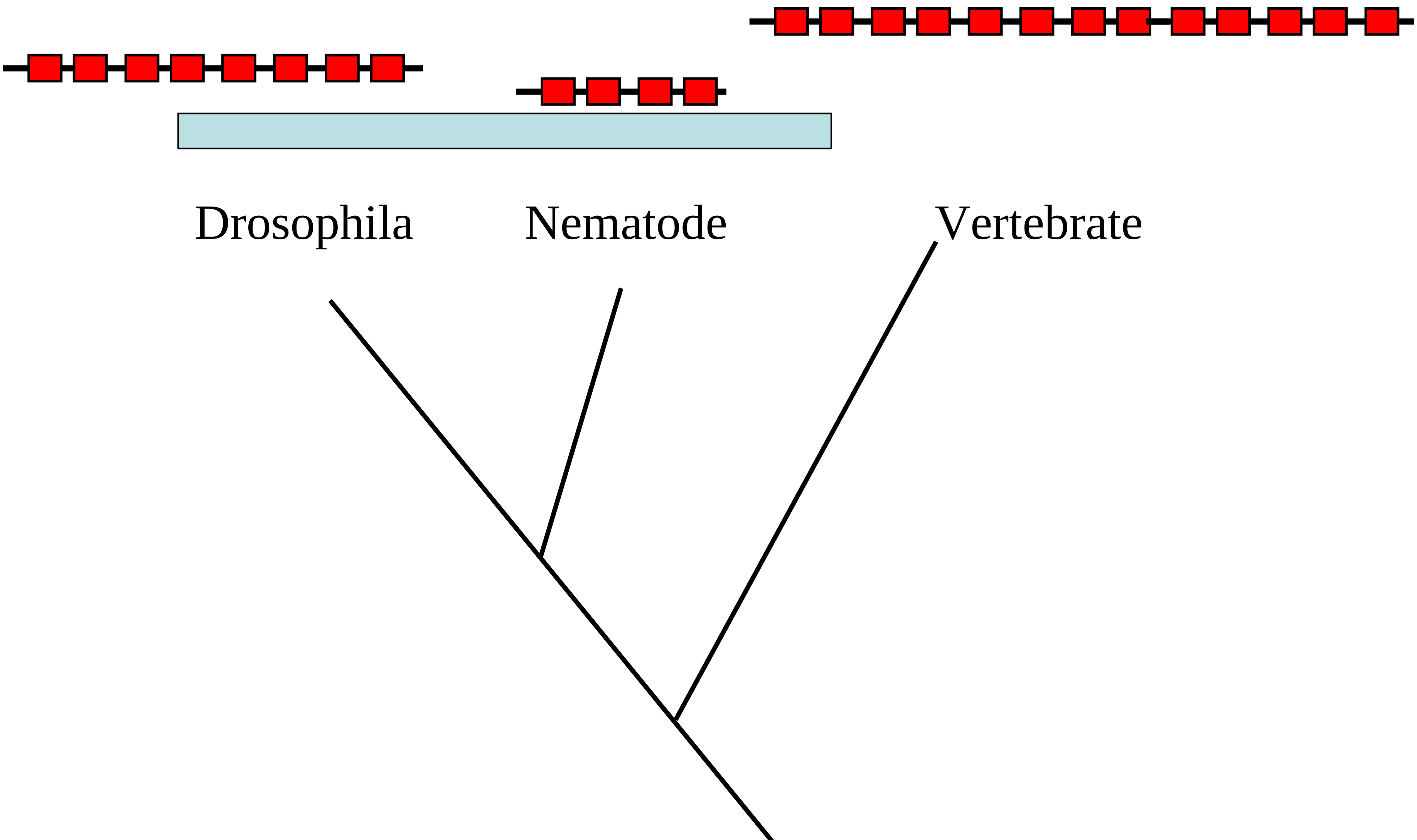
Example 1: Hox clusters

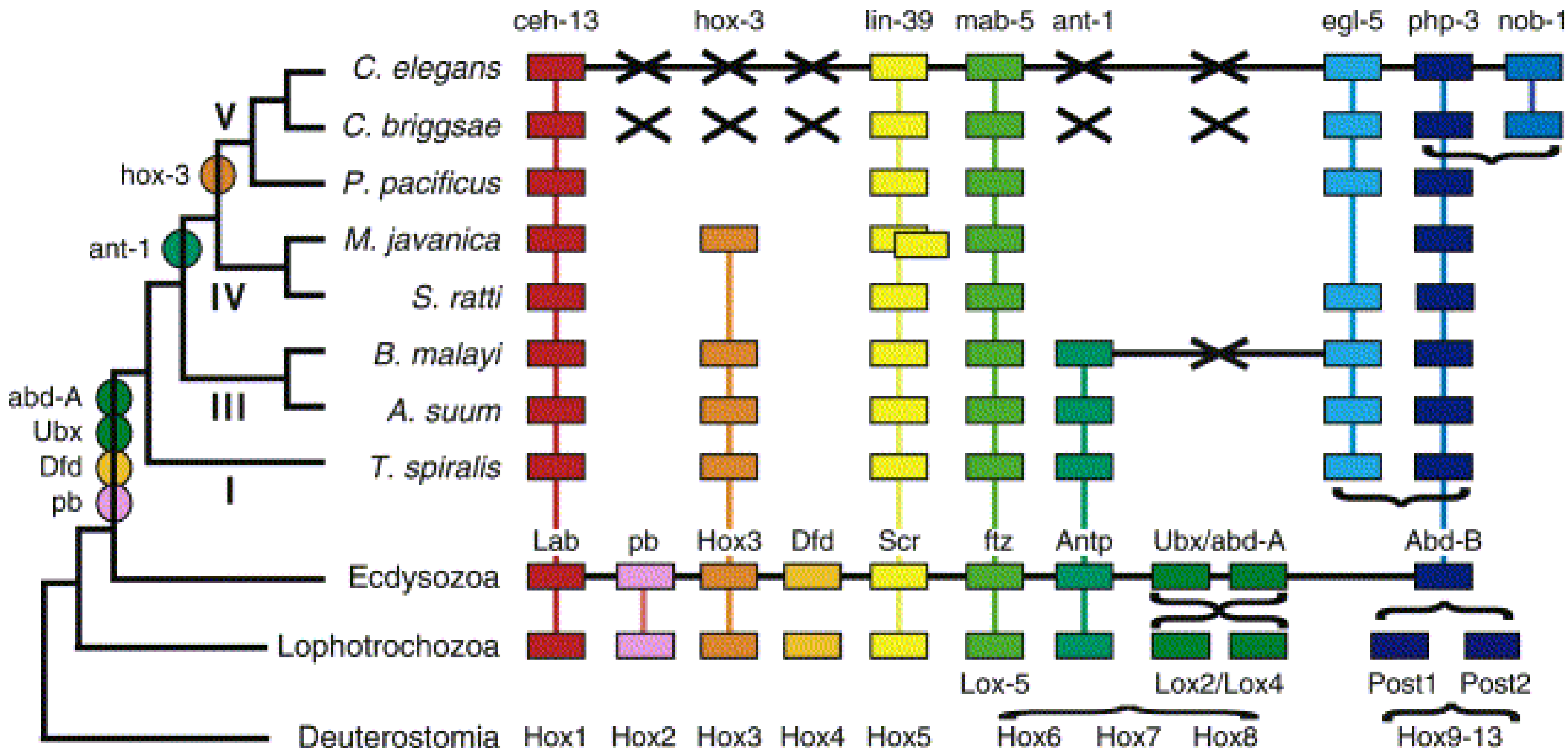
Coelomata view



Example 1: Hox clusters

Ecdysozoa view

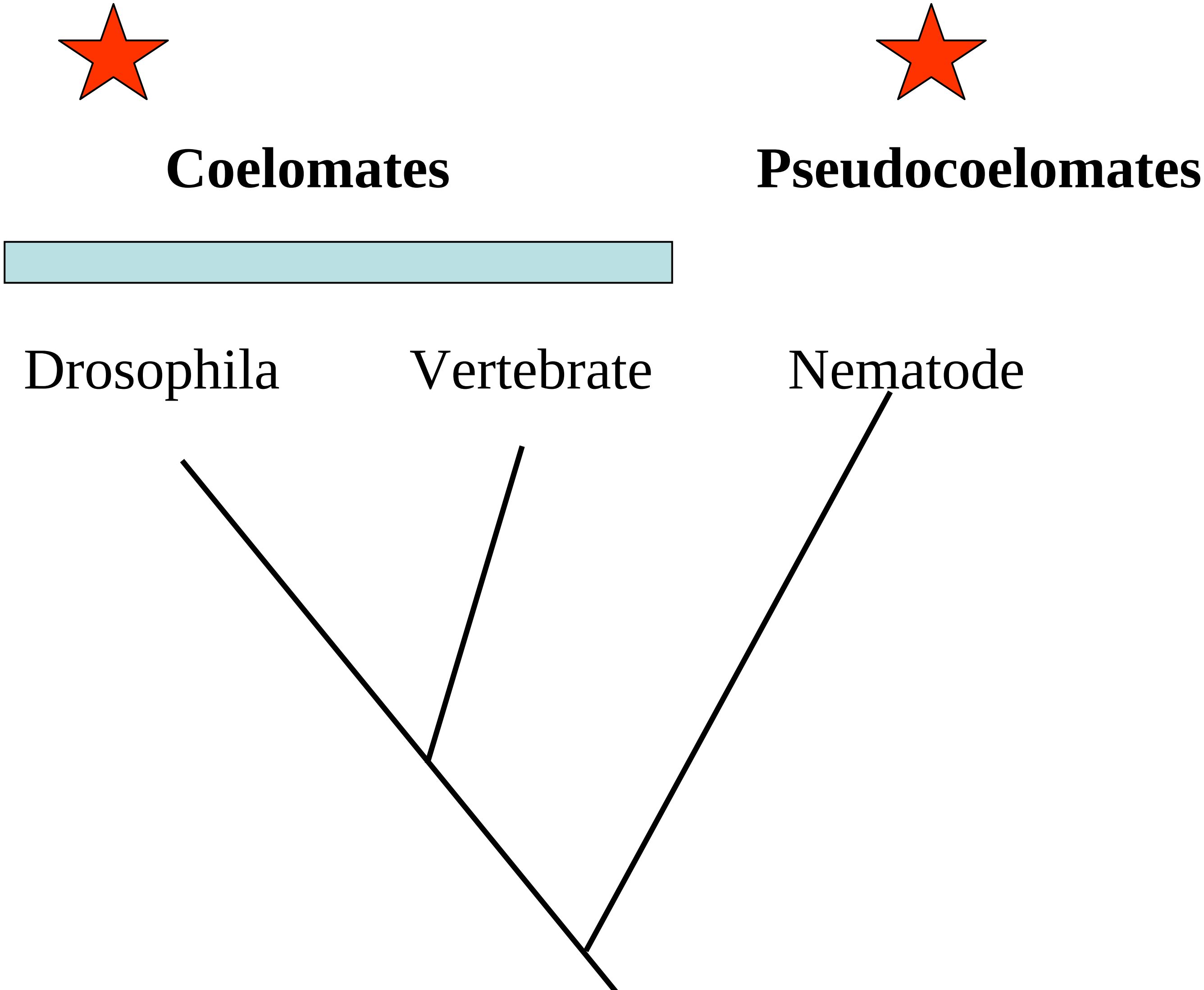




Hox Gene Loss during Dynamic Evolution of the Nematode Cluster
Aboobaker and Blaxter (2003)
Current Biology 13, 37-40

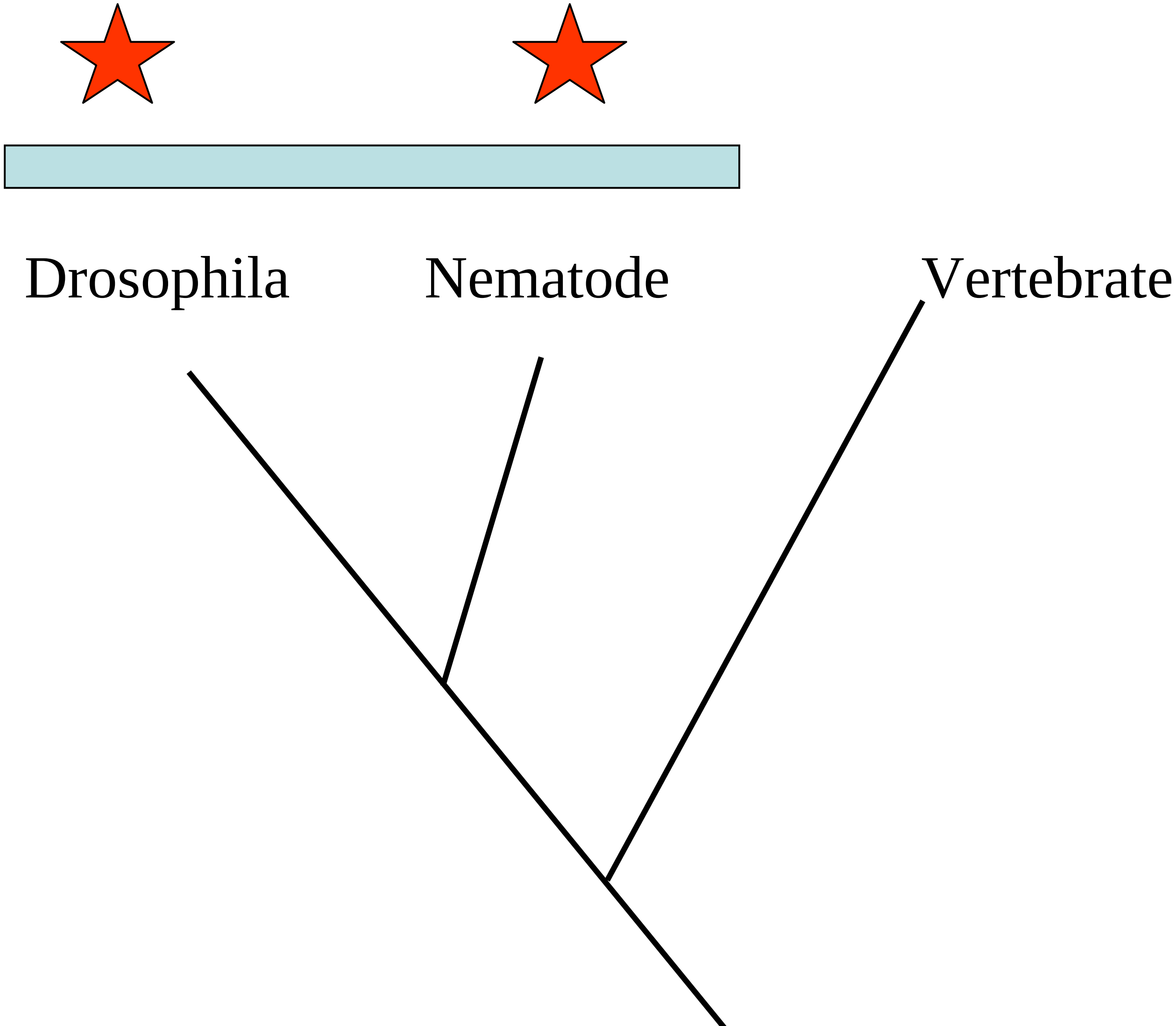
Example 2: Commonalities

Coelomata view



Example 2: Commonalities

Ecdysozoa view



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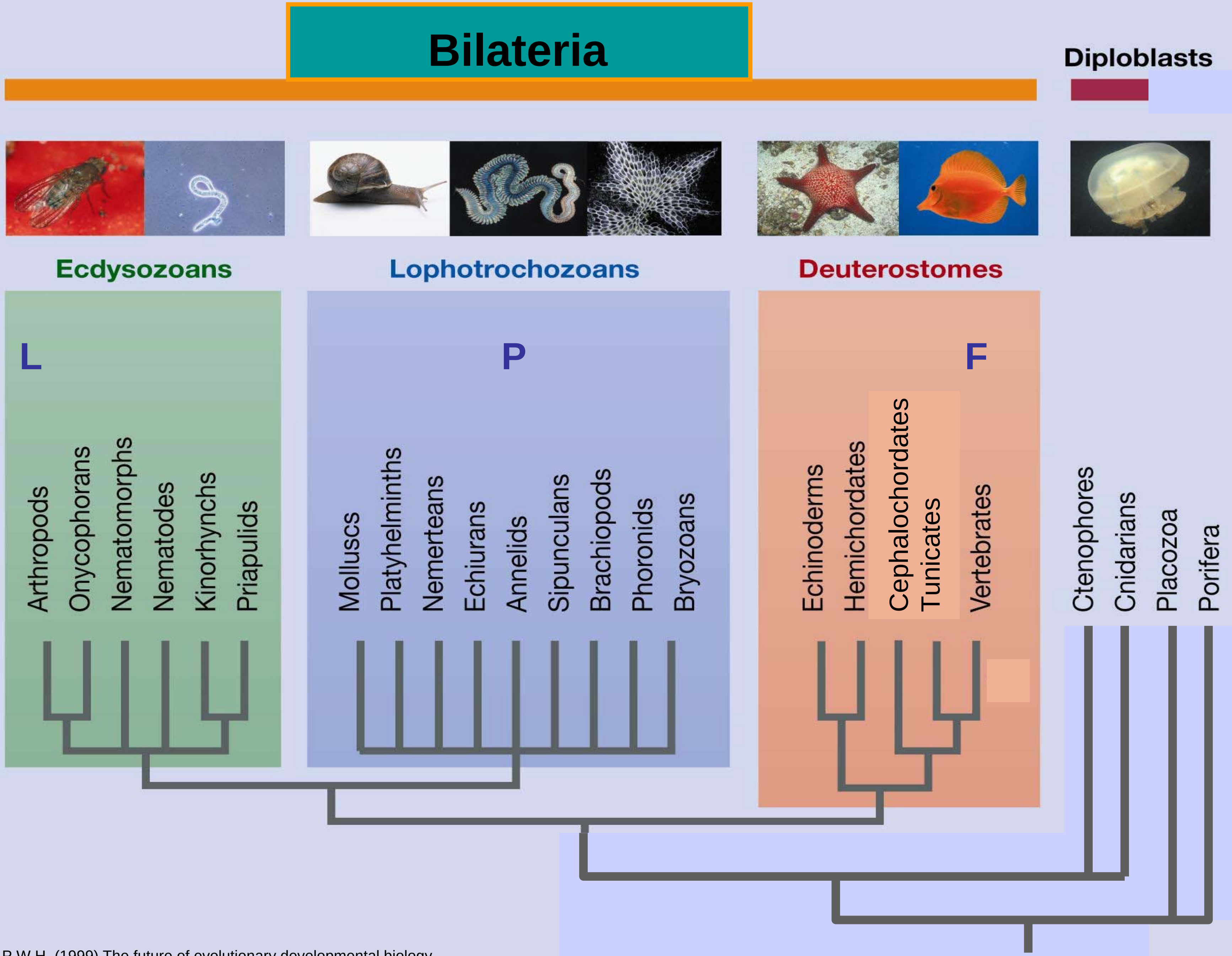
The character state argument: looking at the whole picture helps us to assess whether characters (e.g. developmental pathways) are ‘homologous’

Example 1: limbs

Dlx/dll gene involved in limb development in flies and vertebrates

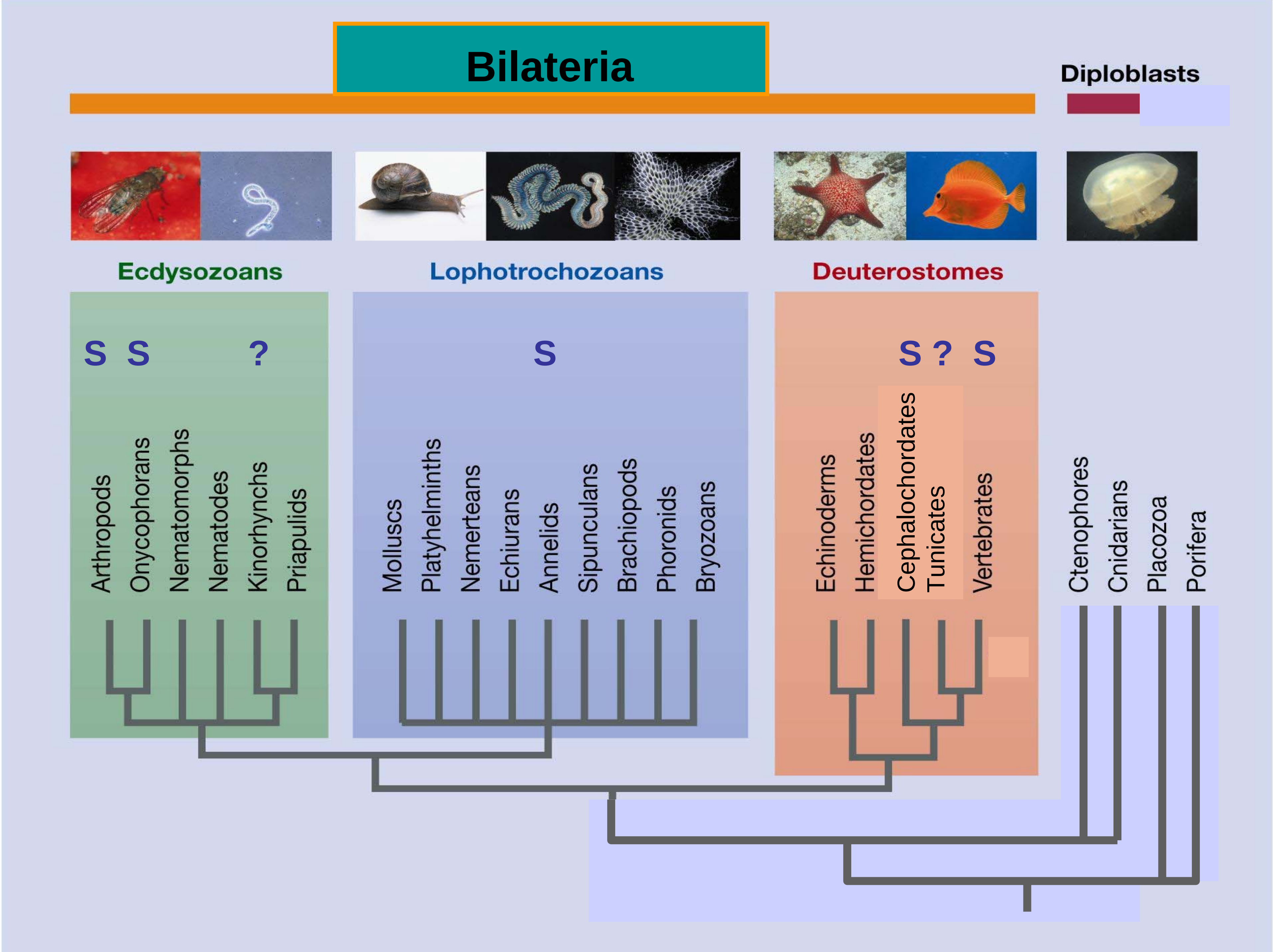
Could this be homologous?



Holland, P.W.H. (1999) The future of evolutionary developmental biology.
Nature 402, C41-C44. *('Impacts of foreseeable science' Supplement)*

Example 2: segmentation

Could this be homologous?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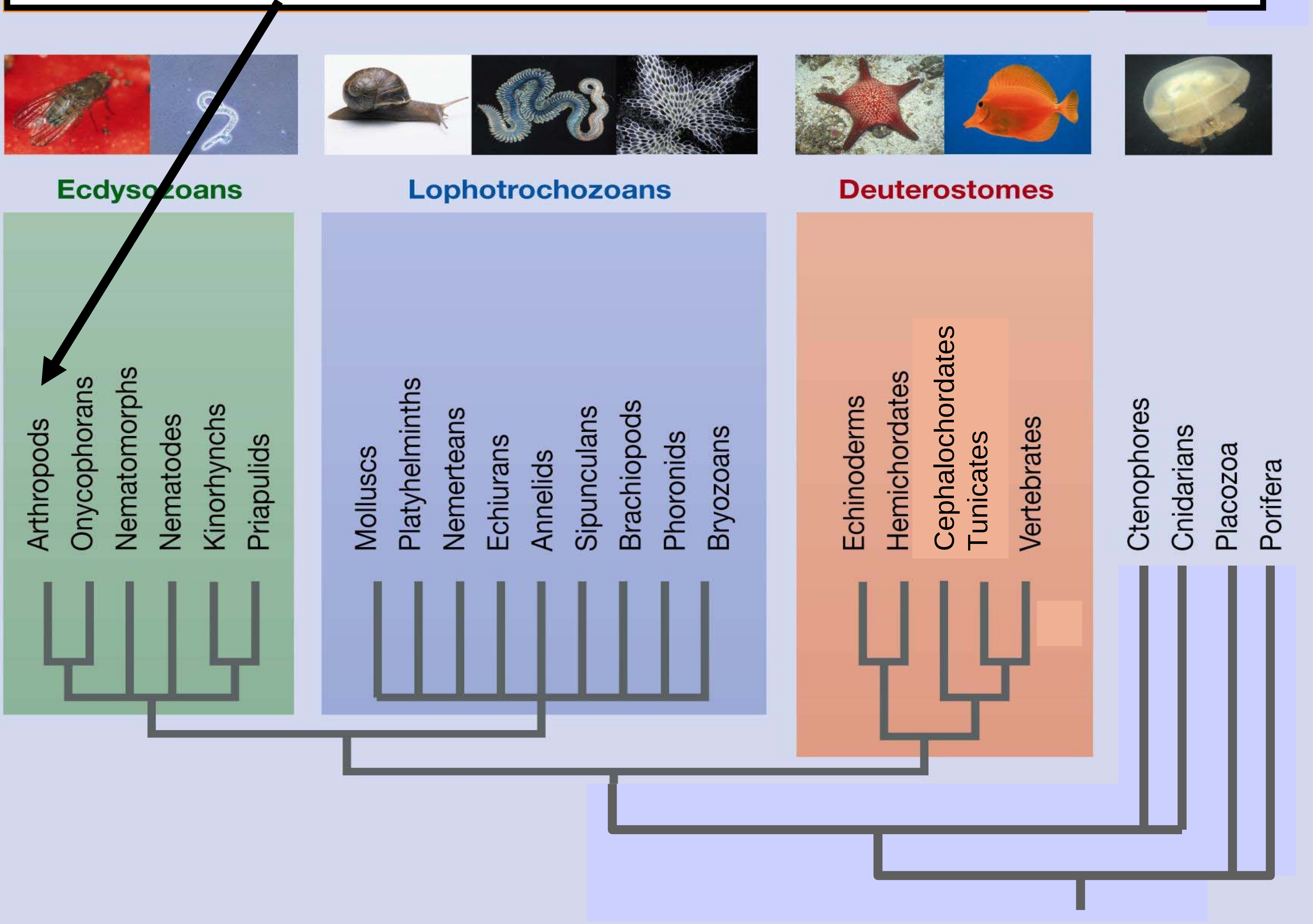
Now let's zoom in to look at Arthropoda



Phylum Arthropoda

Pictures from here removed for copyright reasons.

e.g. spider | shrimp, Daphnia | millipede | Drosophila

Chelicerata | Crustacea | Myriapoda | Insecta

Moulted exoskeleton
Jointed limbs
Ventral nerve cord
Haemolymph

Four Classes

Phylum Arthropoda

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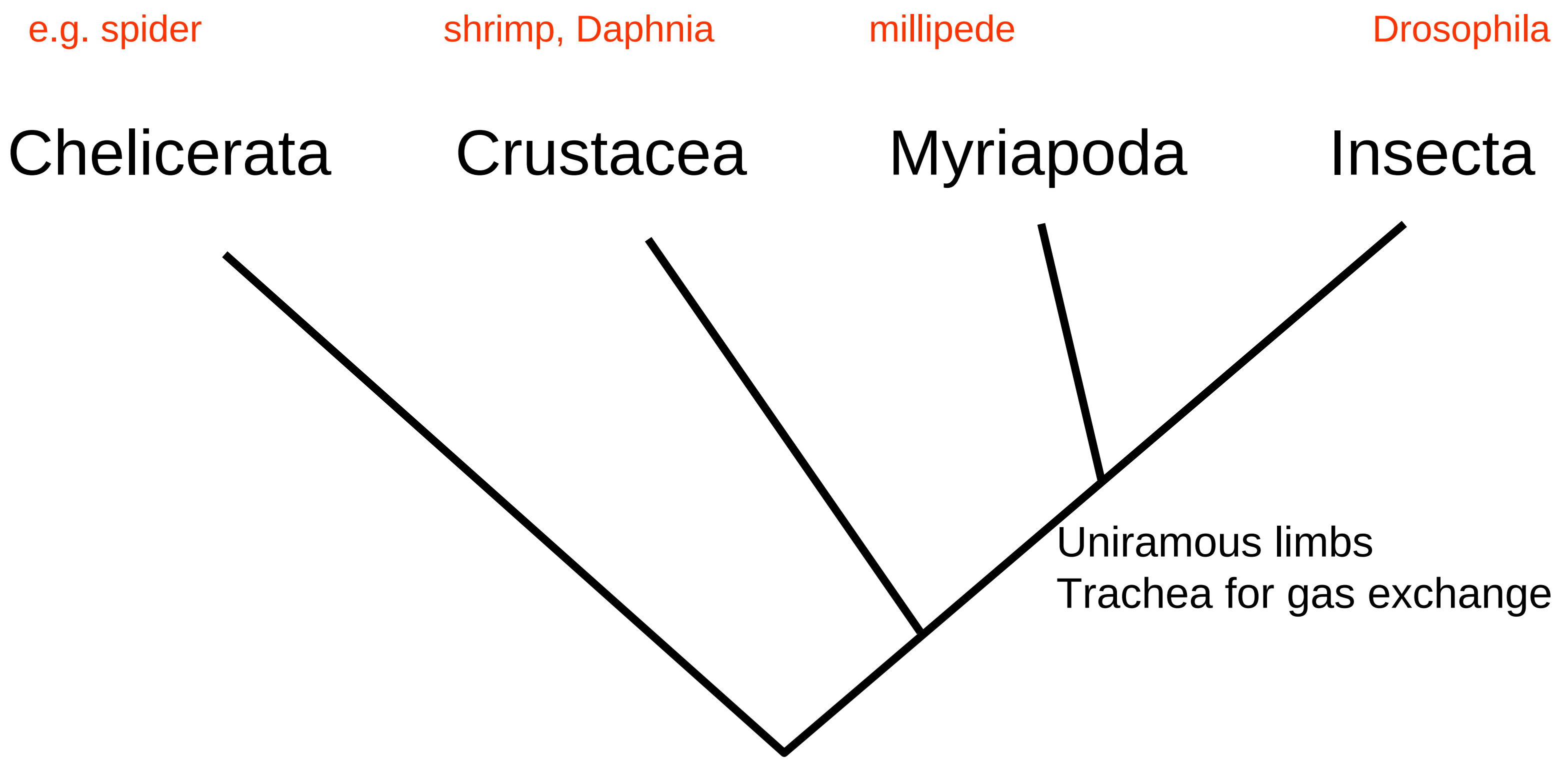


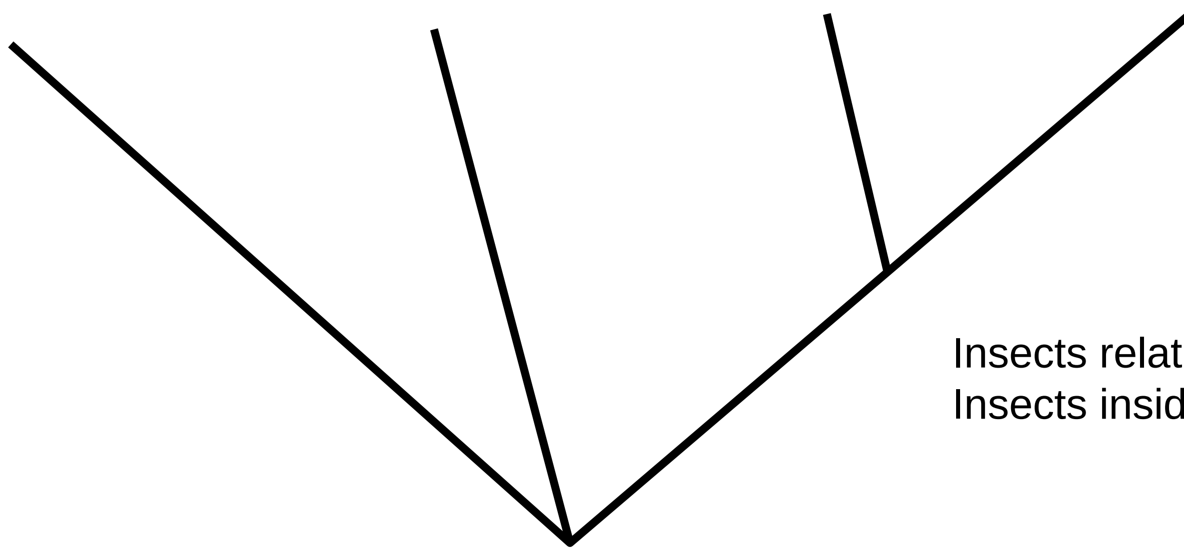
Traditional phylogeny

Phylum Arthropoda

Pictures from here removed for copyright reasons.

e.g. spider shrimp, Daphnia millipede Drosophila

Chelicerata Myriapoda Crustacea Insecta



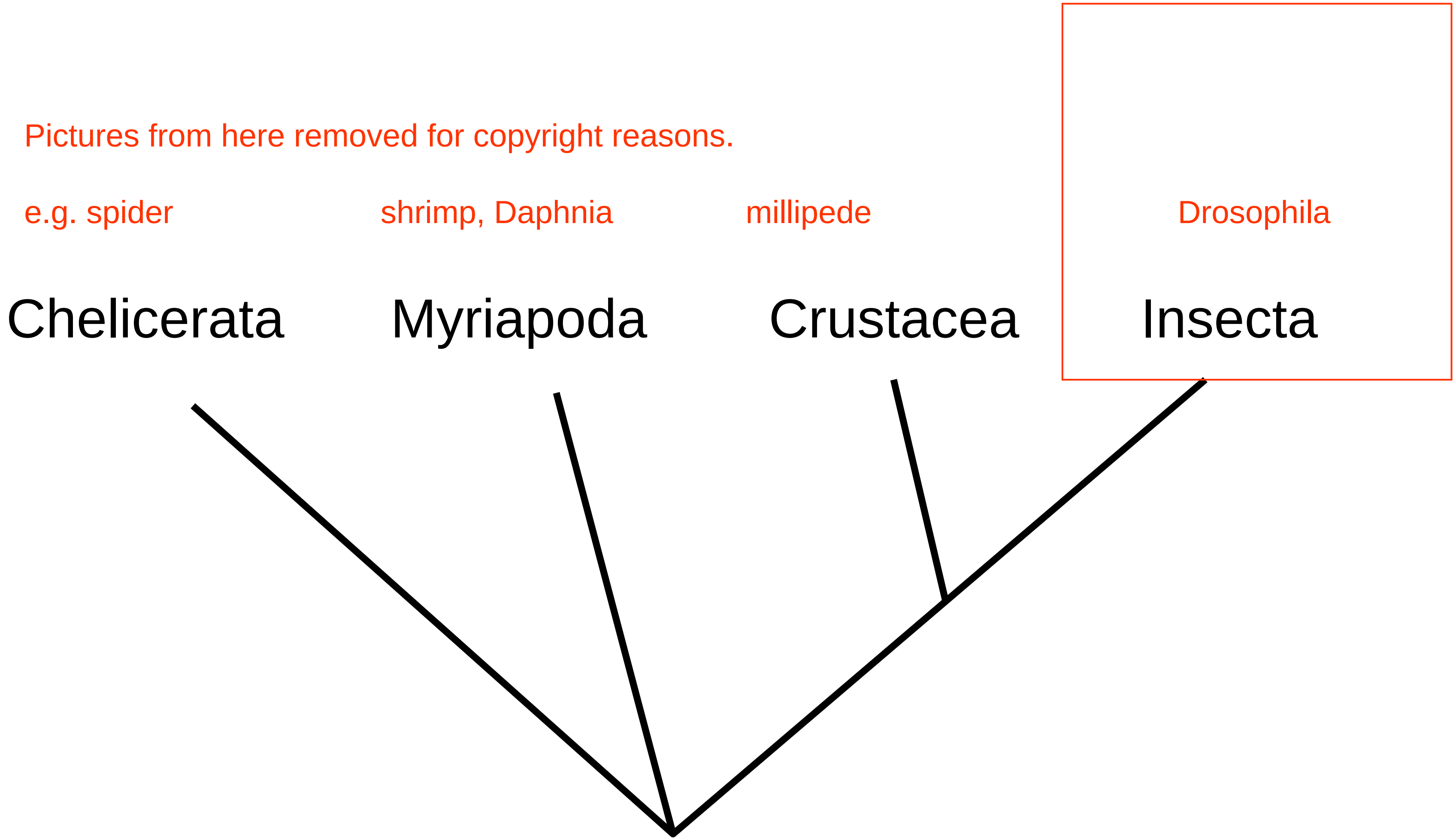
Insects related to Crustacea
Insects inside Crustacea?

Revised (molecular) phylogeny

Now let's zoom inside Insecta

Pictures from here removed for copyright reasons.

e.g. spider   shrimp, Daphnia   millipede   Drosophila



Class Insecta

Pictures from here removed for copyright reasons.

e.g. bristletail | pea aphid | Drosophila

Wingless insects | Hemimetabola | Holometabola

Three pairs legs
Three tagma (head, thorax, abdomen)
Waxy cuticle

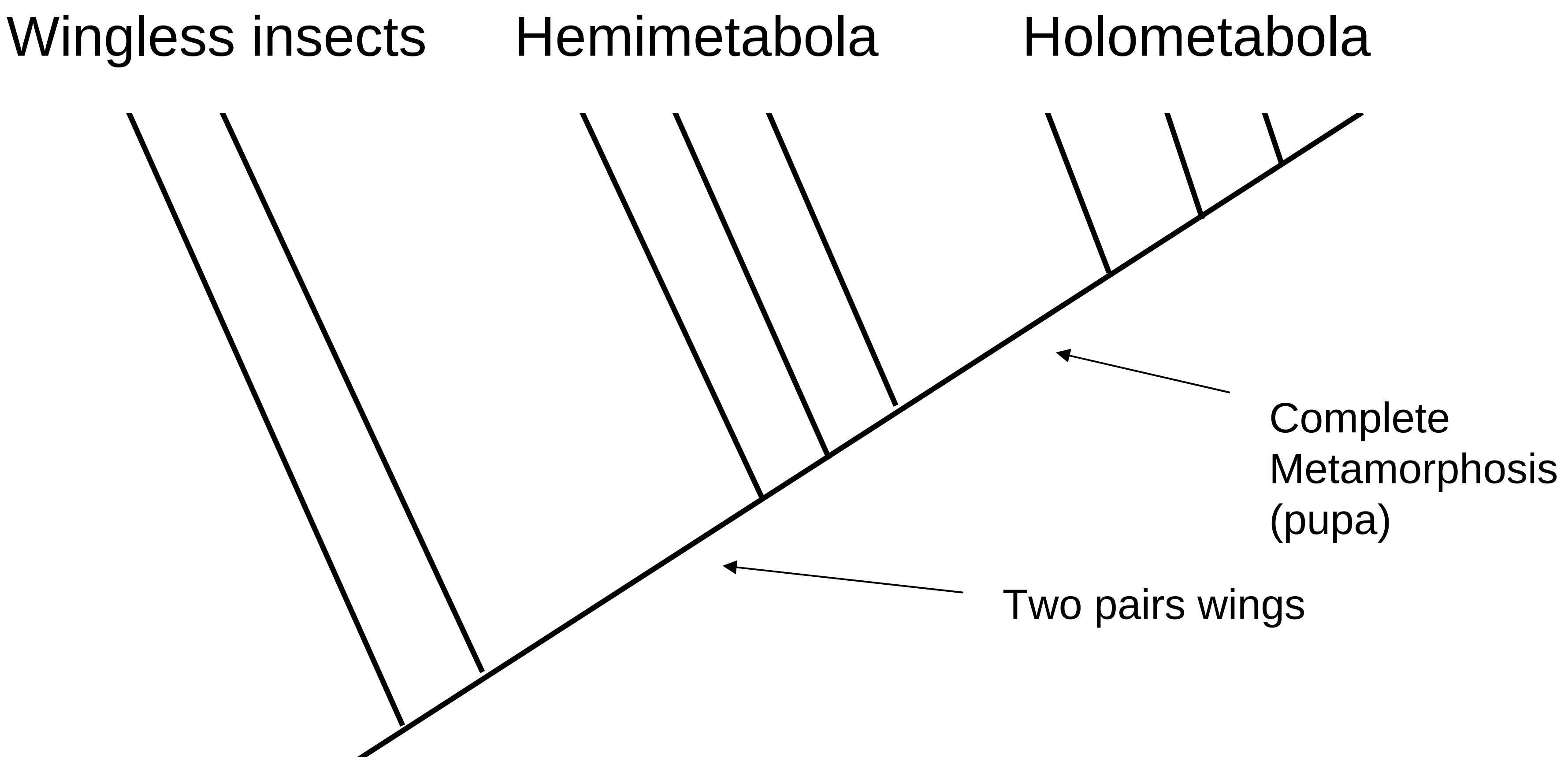
Class Insecta

Pictures from here removed for copyright reasons.

e.g. bristletail

pea aphid

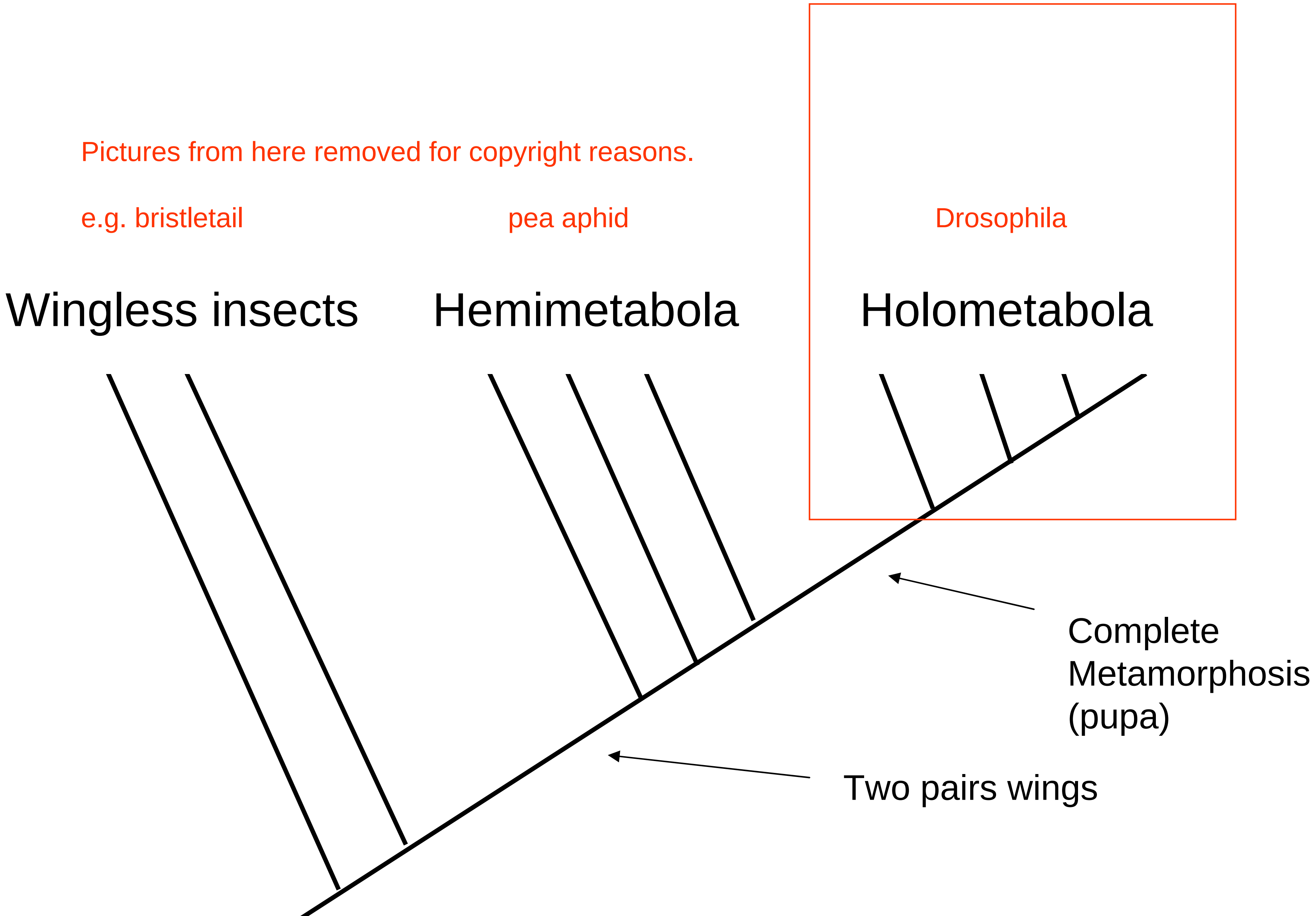
Drosophila



Now zoom into Holometabola

Pictures from here removed for copyright reasons.

e.g. bristletail pea aphid Drosophila

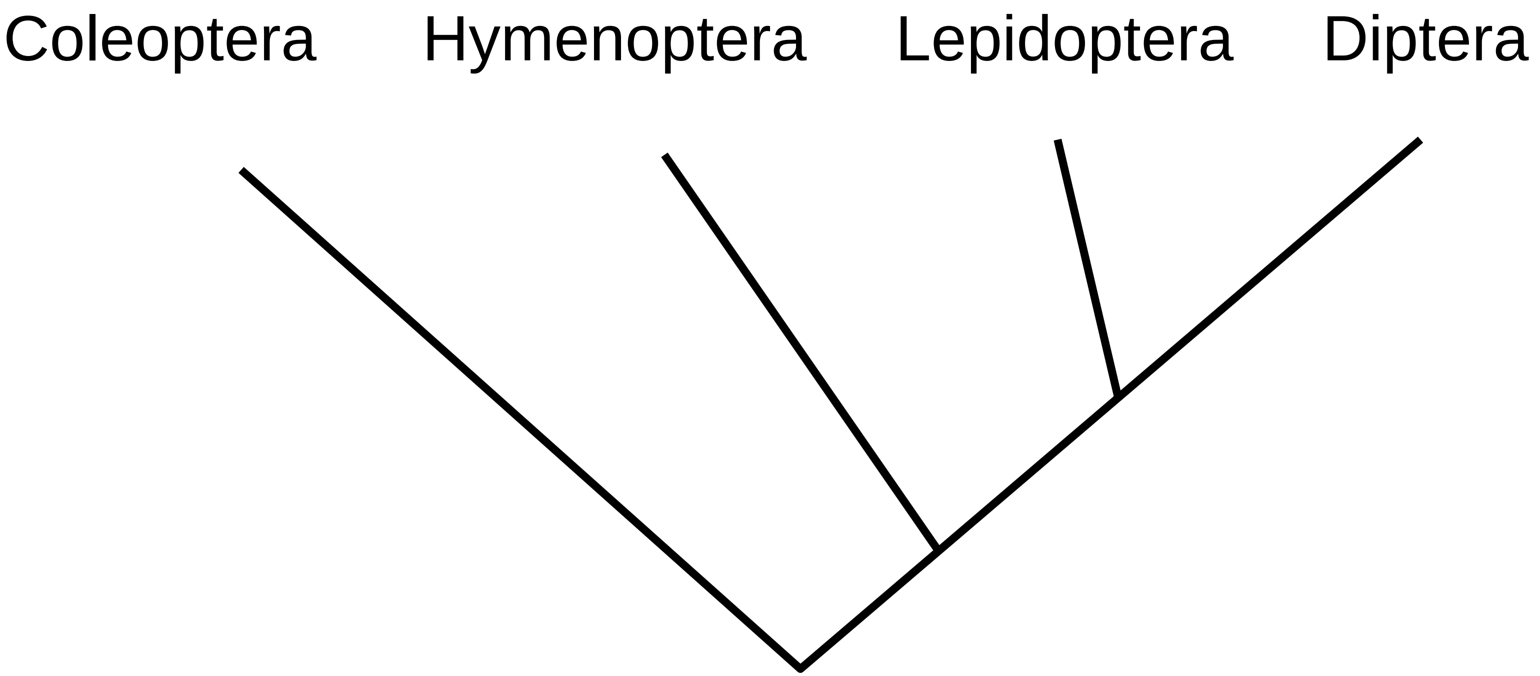


Holometabola

Many insect orders; but the ‘big four’ are these:

Pictures from here removed for copyright reasons.

e.g. Beetle bee butterfly Drosophila



Holometabola

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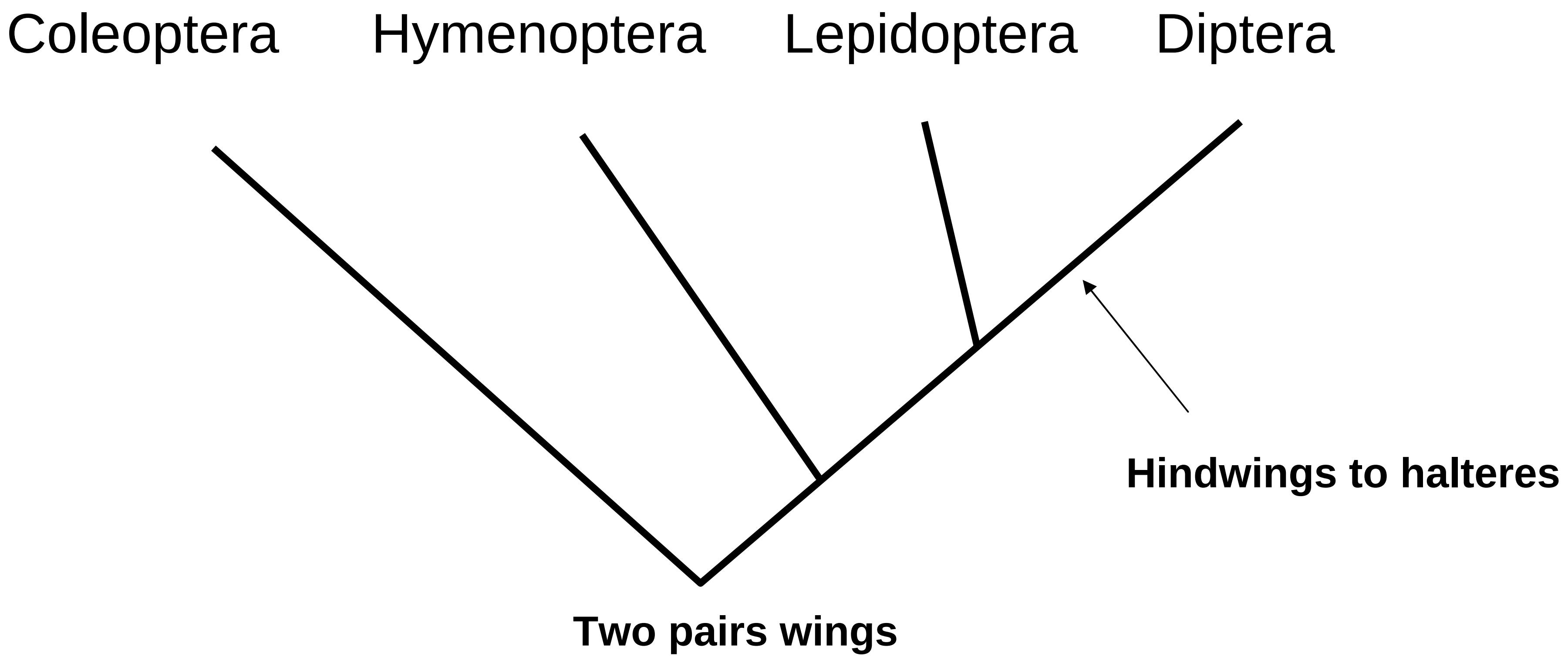

Conclusions

Dobzhansky *"Nothing in biology makes sense except in the light of evolution"*

- *Drosophila* is a metazoan (animal)
- *Drosophila* is a bilaterian
- *Drosophila* is an ecdysozoan – like nematodes!
- *Drosophila* is an arthropod
- *Drosophila* is an insect – insects close to crustaceans

- Phylogeny essential for all comparative biology
- Phylogeny helpful in assessing claims of homology
- Now know overall phylogeny of the Metazoa
- Helps us understand biology of *Drosophila*
- Helps us make sensible comparisons between animals