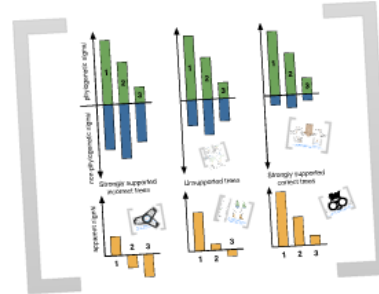


With challenging phylogenetic problems, the difficulty is to make the haystack bigger without enlarging the haystack!

more sequences
are not enough



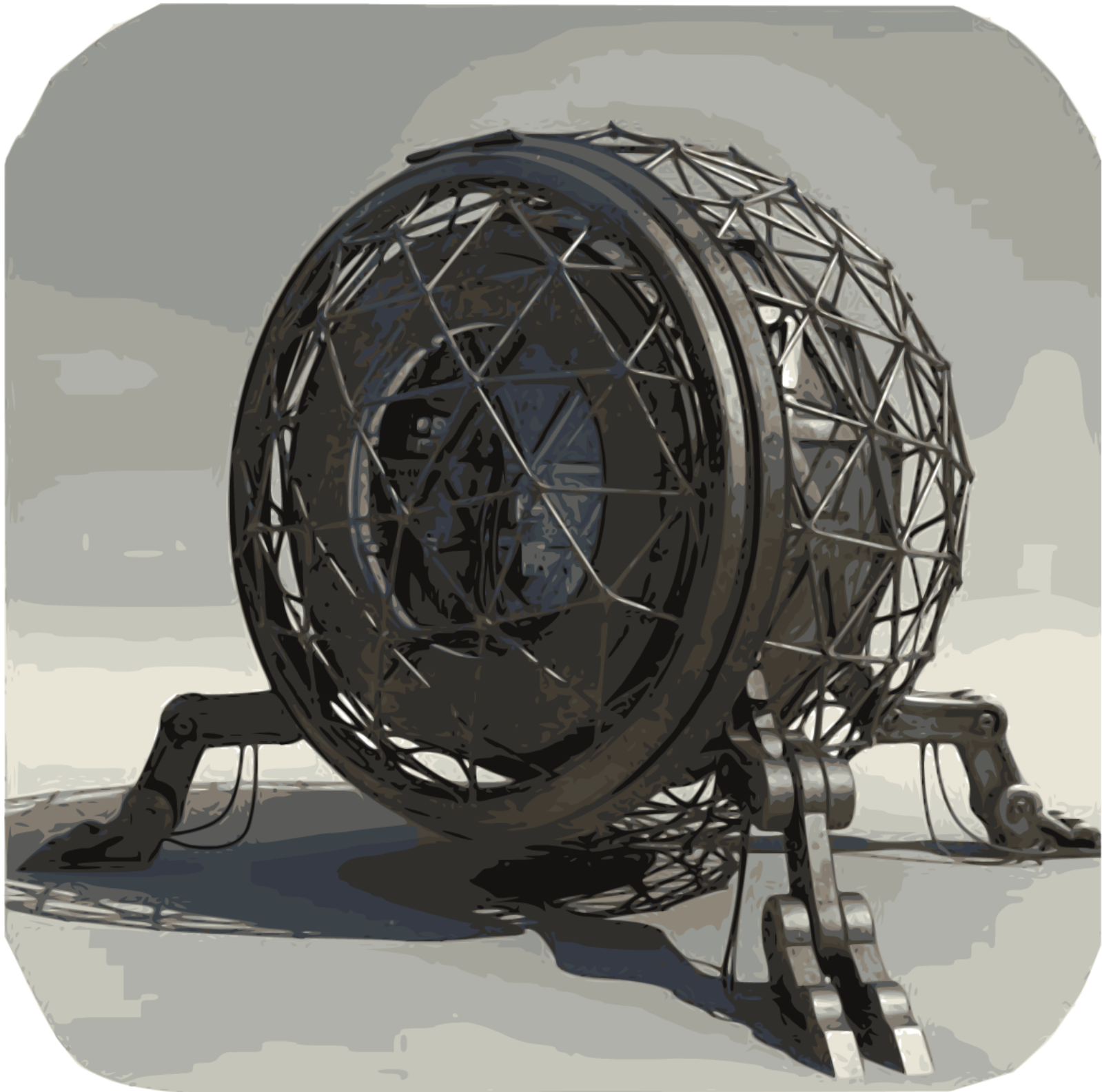
phylogenetic vs.
non-phylogenetic signal

Latimeria chalumnae

The coelacanth is a large marine fish with fleshy fins that resembles the limbs of terrestrial vertebrates.

Comparing Genomes from Molecules
for Molecules and Molecules

phylogenomics can resolve
the evolution of animals



Computers as Genomic Time Machines for Meeting our Ancestors

Ediacaran (635-542)

What did the first
animal look like?



Dickinsonia (4 cm)

Cambrian (542-488)

Can we resolve the
Cambrian explosion?



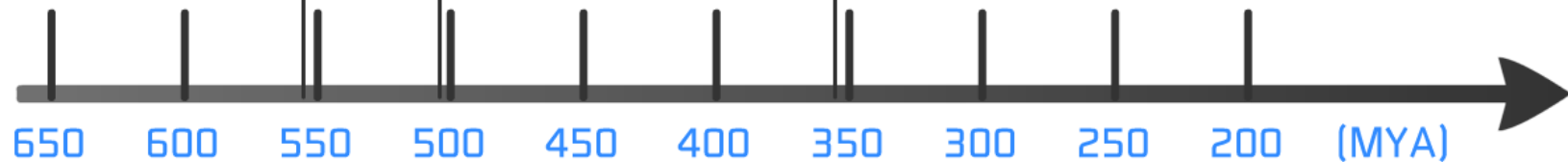
Anomalocaris (60-80 cm)

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What was the fish that
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Acanthostega (50-55 cm)



Prof. Denis Baurain — ULg
Bioforum — April 18th, 2013

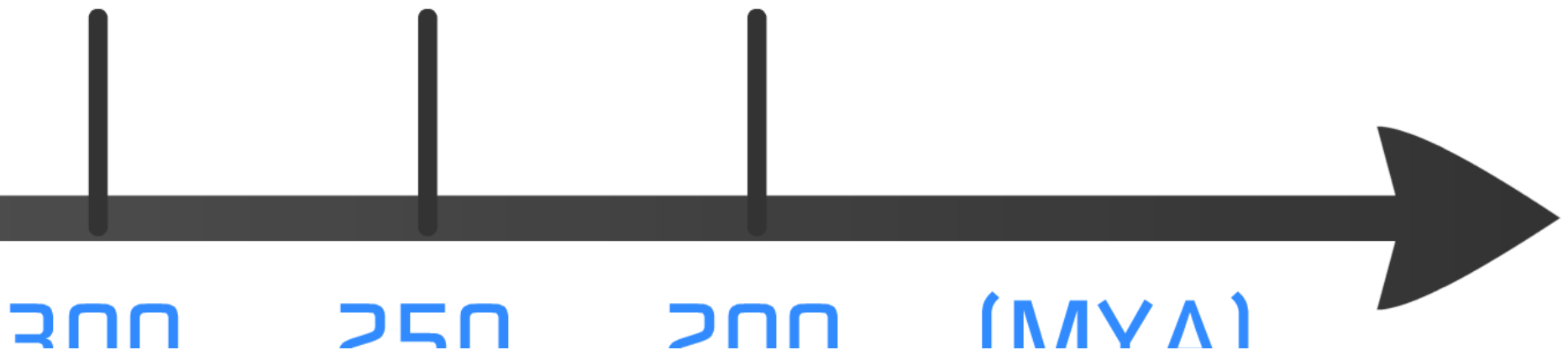
ve the explosion?



Devonian (416-359)

What was the fish that first walked on land?

Anthostega (50-55 cm)

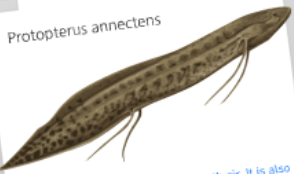


Latimeria chalumnae



Until its rediscovery, the coelacanth was thought to have been extinct since the Late Cretaceous period (70 MYA).

Protopterus annectens



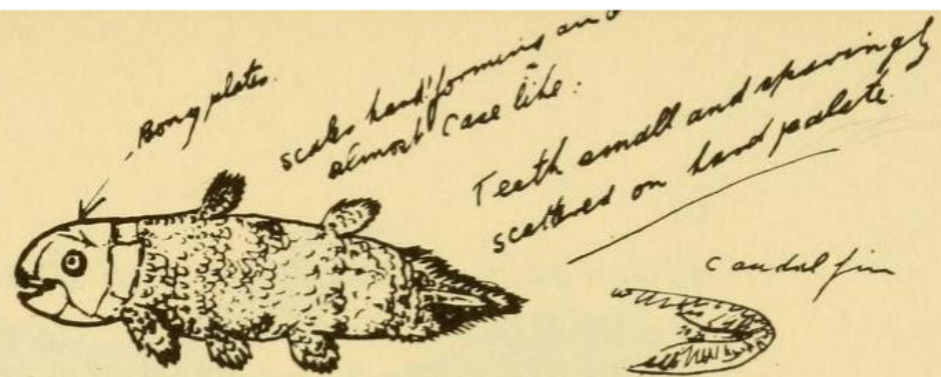
The lungfish has lungs and can breath air. It is also a lobe-finned fish, yet living in freshwater.



The coelacanth is a large marine fish with fleshy fins that resembles the limbs of terrestrial vertebrates.



Miss M. Courtenay-Latimer



Colour dark grey black. (uniform)

Length. 4 1/2 ft.

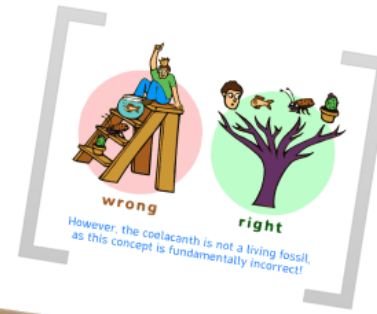
depth of body 18 inches

depth of tail 12 inches.

Length of fins. spinous dorsal. 8"
Soft dorsal 9"
Pectorals = 12"
Pelvics = 5"
ANAL = 12"

Miss Latimer's sketch and notes

It was named after its discoverer, who was the curator of a small museum in South Africa.



Until its rediscovery, the coelacanth was thought to have been extinct since the Late Cretaceous period (70 MYA).



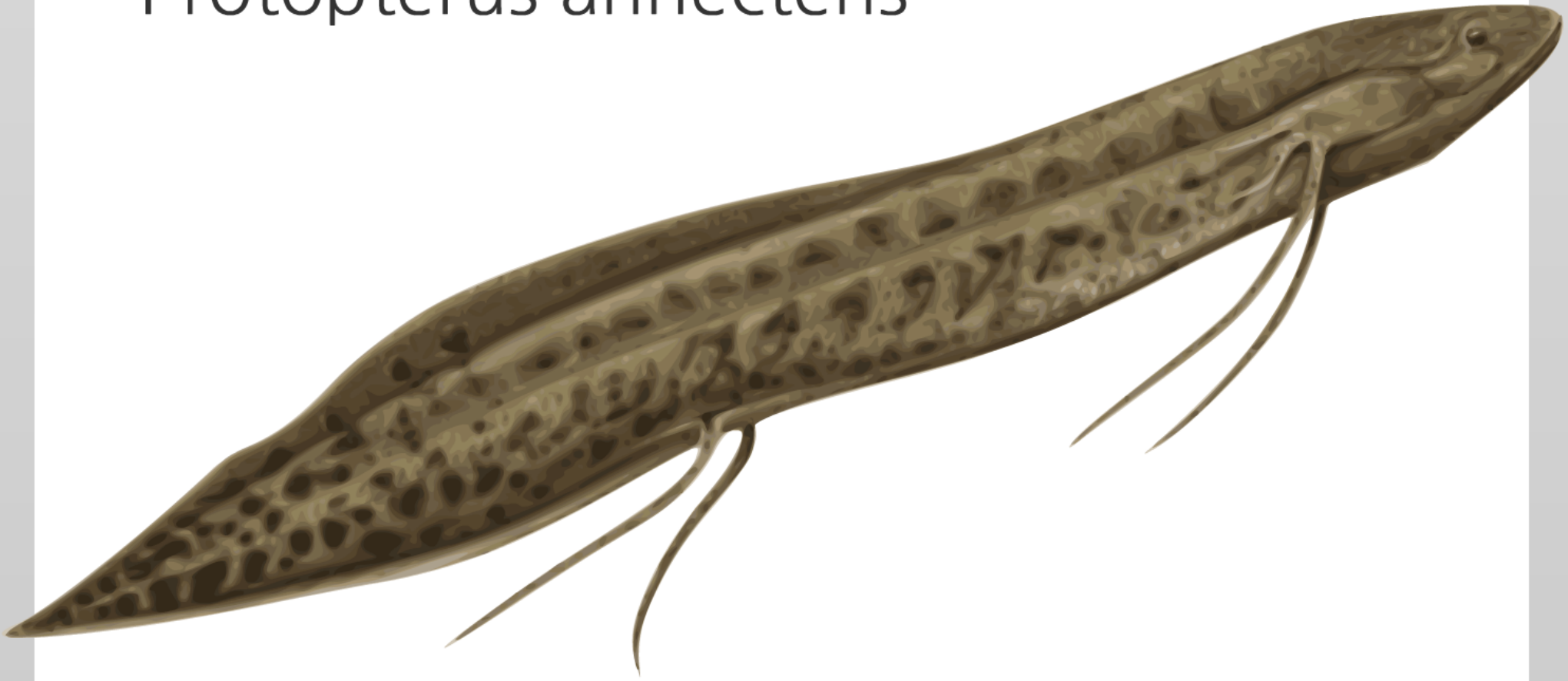
wrong



right

However, the coelacanth is not a living fossil,
as this concept is fundamentally incorrect!

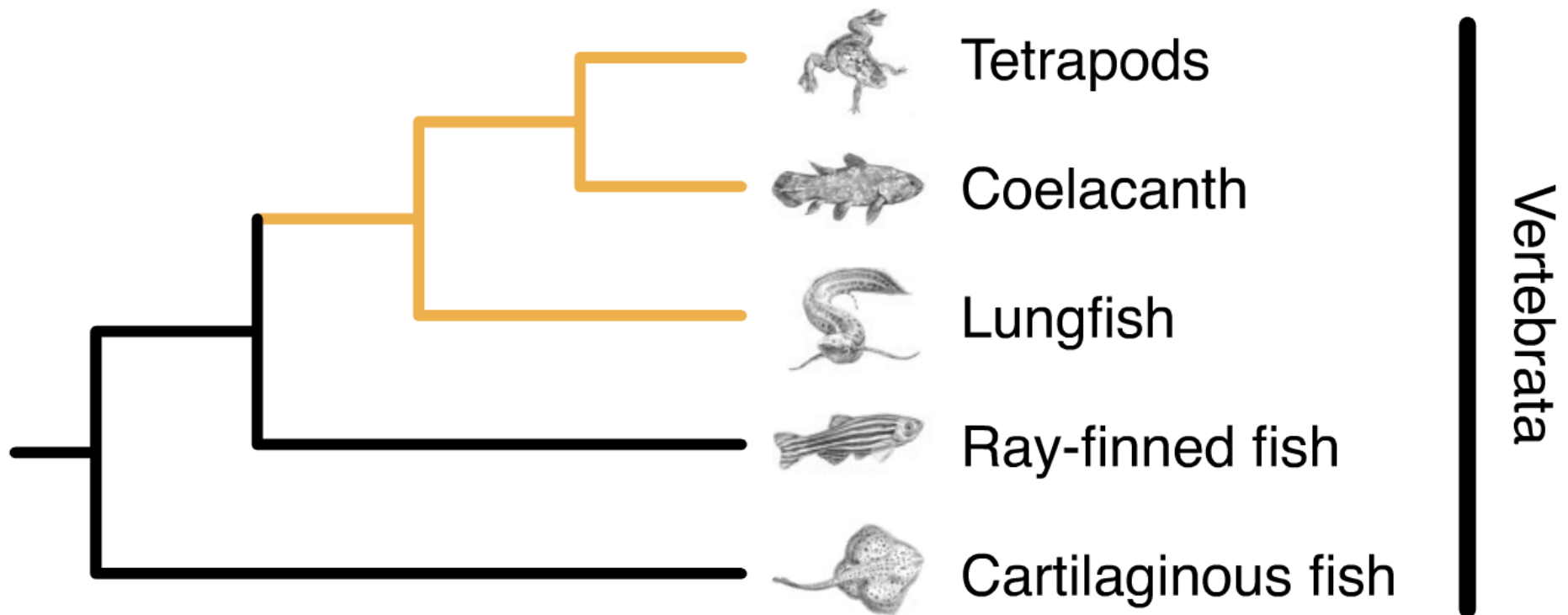
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The coelacanth as the closest relative of tetrapods

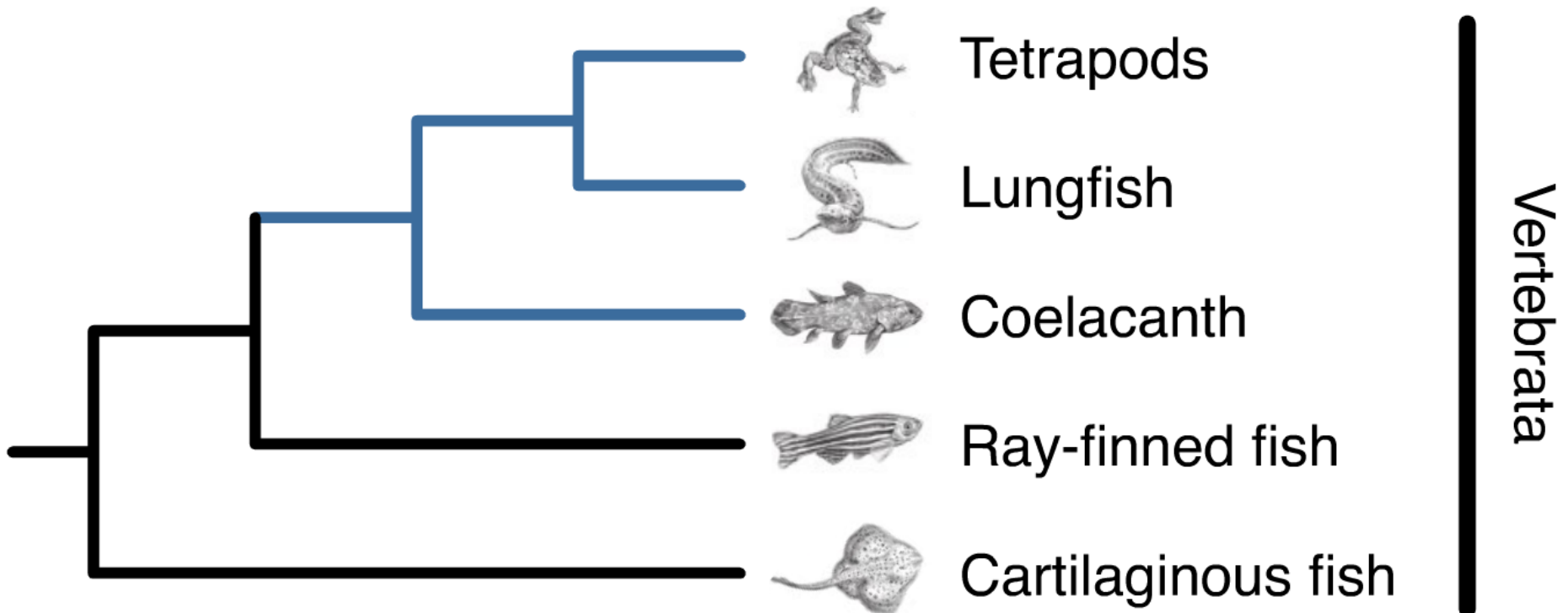
Gorr et al. (1991) – haemoglobins a & b (nucl.)



The lungfish as the closest relative of tetrapods

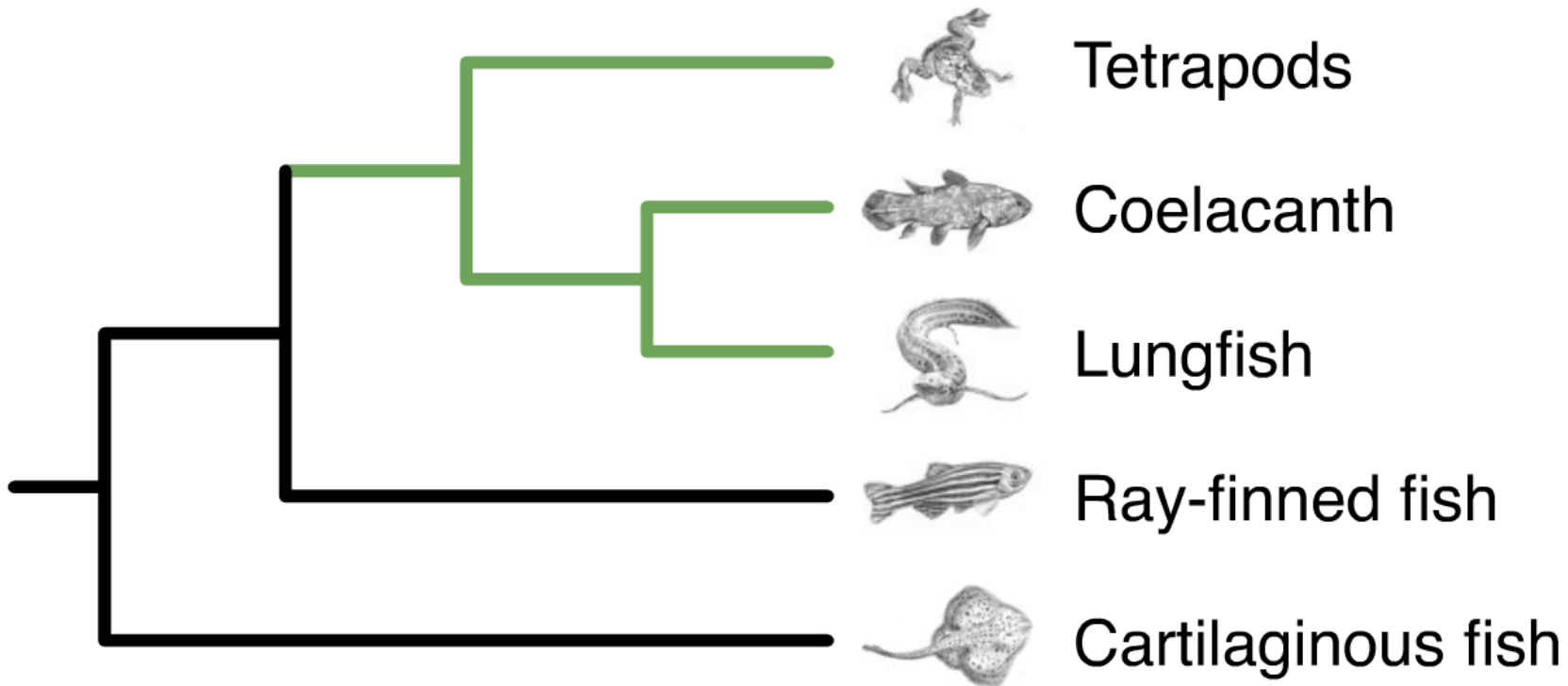
e.g., Meyer & Dolven (1992) – 12S rRNA & cob (mitochondr.)

Brinkmann et al. (2004) – RAS1 & 2 (nucl.)



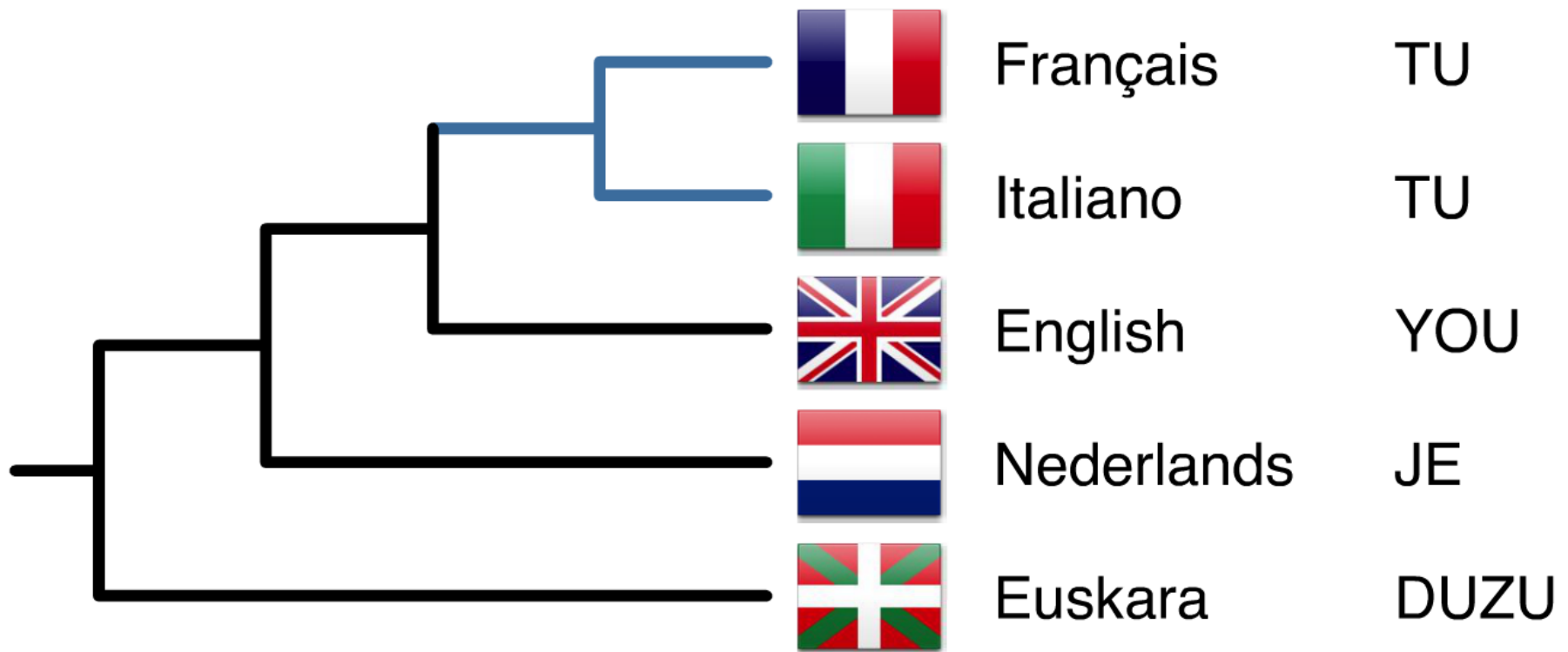
Both the coelacanth and the lungfish!

e.g., Yokobori et al. (1994) – *cox1* (mitochondr.)
Zardoya & Meyer (1996) – 28S rRNA (nucl.)



Potential relationships among European languages

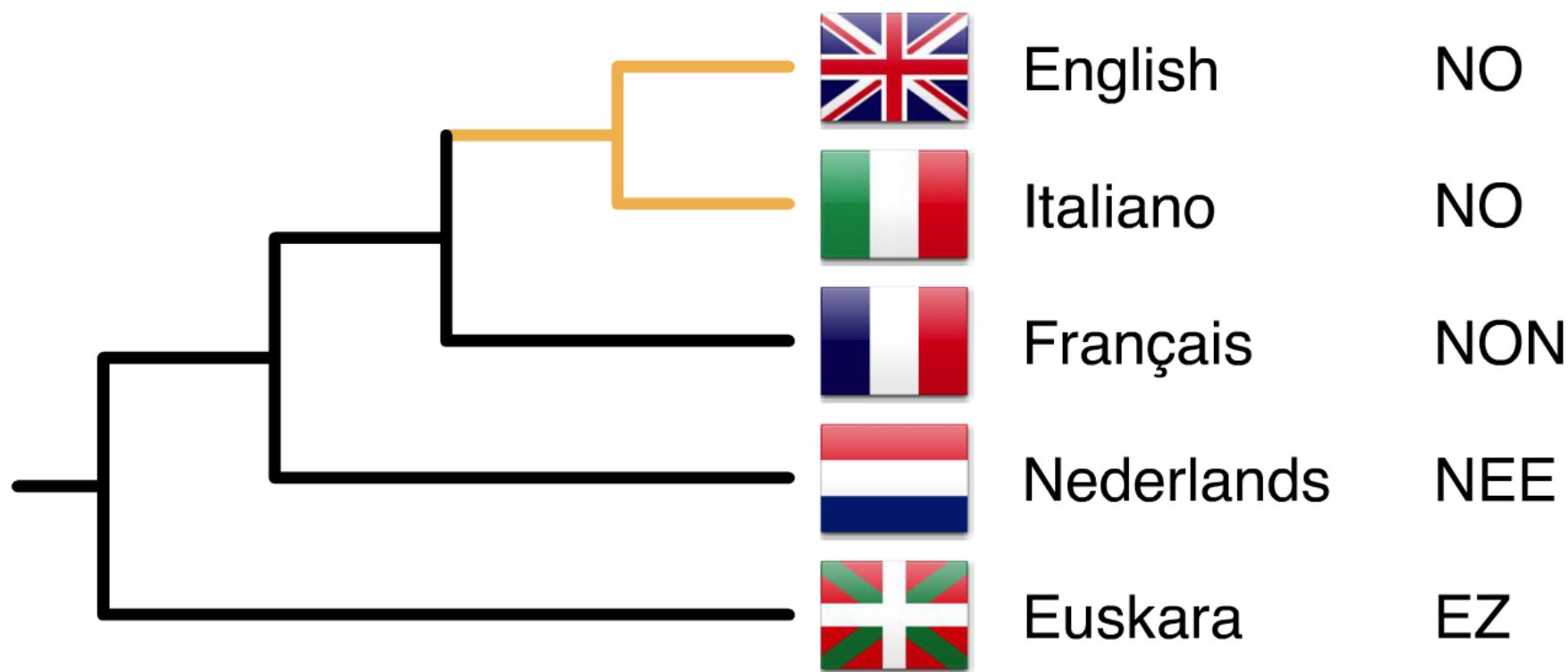
based on the naive analysis of 1 word



The Basque language is our outgroup here.

Potential relationships among European languages

based on the naive analysis of 1 word

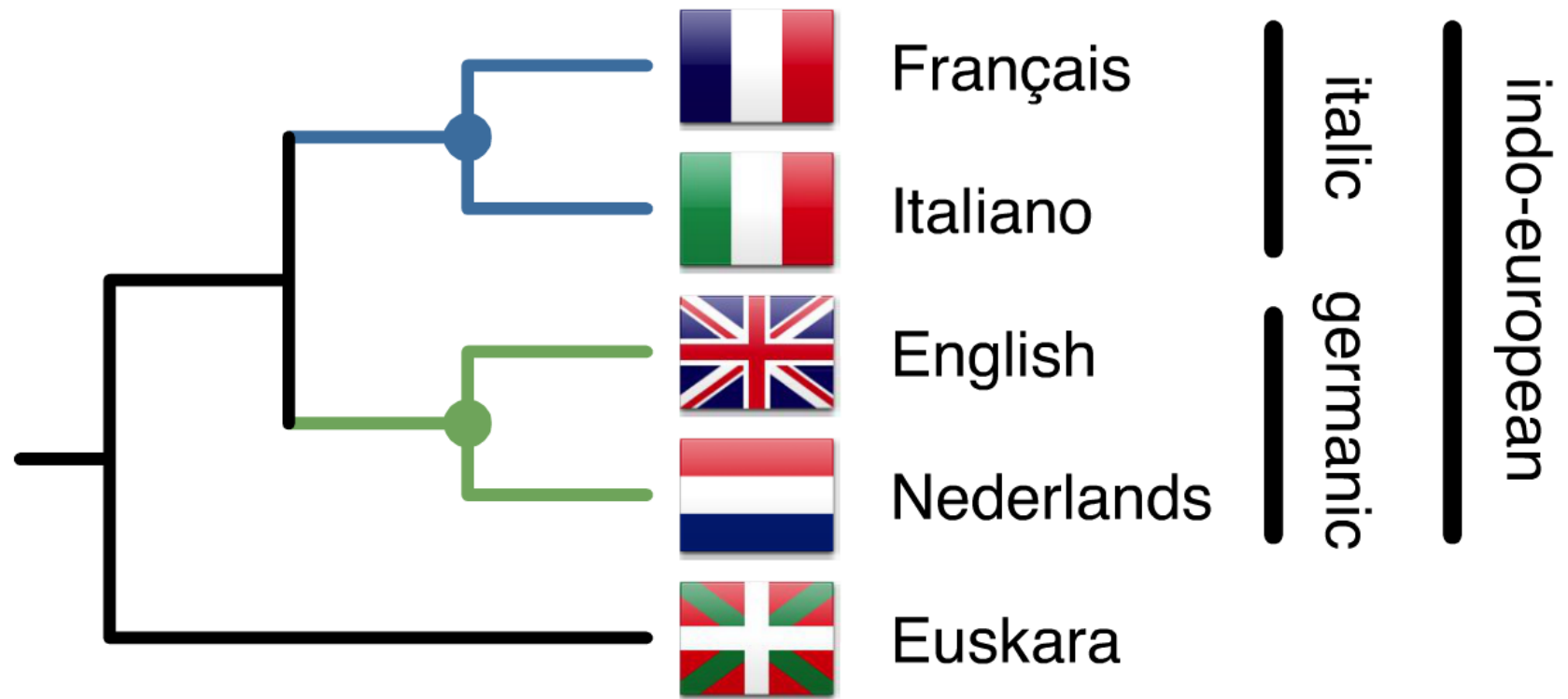


Examining only one or two words exposes us to the stochastic error because of the lack of information.

	français	italiano	english	nederlands	euskara
1	un	uno	one	een	bat
2	deux	due	two	twee	bi
3	trois	tre	three	drie	hiru
4	je	io	I	ik	I
5	tu	tu	you	je	duzu
6	qui ?	chi?	who?	wie?	nor?
7	oui	si	yes	ja	bai
8	non	no	no	nee	ez
9	mère	madre	mother	moeder	ama
10	père	padre	father	vader	aita
11	dent	dente	tooth	tand	hortz
12	coeur	cuore	heart	hart	bihotza
13	pied	piede	foot	voet	oinez
14	souris	topolino	mouse	muis	saguaren

Known relationships among European languages

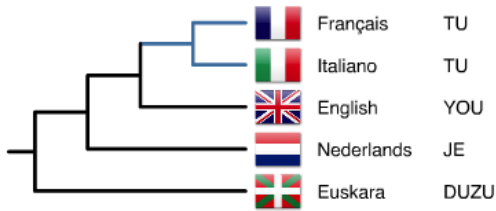
strongly supported by the naive analysis of 14 words



We now have robust statistical support
and phylogenetic resolution!

Potential relationships among European languages

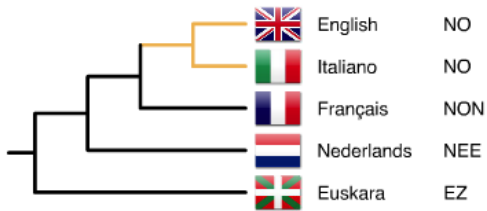
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Potential relationships among European languages

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Similarly, phylogenomics is phylogenetics applied to many genes at once.

African coelacanth



- blood DNA + muscle RNA library
- assembly with ALLPATHS-LG and Trinity
- annotation with the Ensembl pipeline

genome size: 2.85 Gbp (2.18 Gbp)

- 3 RNA libraries (brain, gonad/kidney, gut/liver)
- assembly with Trinity
- no annotation



West African lungfish

genome size: est. 50-100 Gbp

NGS (Illumina) sequencing was used to sequence the two lobe-finned fishes.

collection of proteomes

- 13 tetrapods (Ensembl)
- 2 ray-finned fishes (Ensembl)
- 2 lobe-finned fishes
 - coelacanth (Broad Institute)
 - lungfish (RNA-seq contigs)



319,459 proteins

after filtration

all-vs-all comparison

51,026,866,611
pairwise similarities



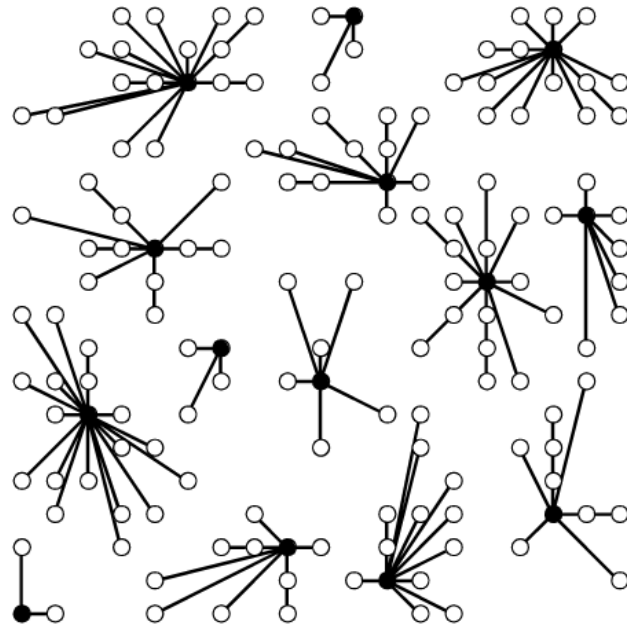
overnight on a
desktop workstation

100x faster than BLAST
using USEARCH

- 2 ray-finned fishes (Ensembl)
- 2 lobe-finned fishes
 - coelacanth (Broad Institute)
 - lungfish (RNA-seq contigs)

319,459 proteins
after filtration

clustering



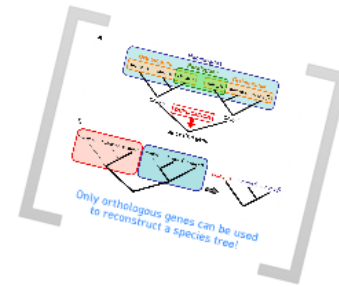
OrthoMCL
(1 hour)

7,764 groups

with both the lungfish
and the coelacanth

addition of transcriptomes

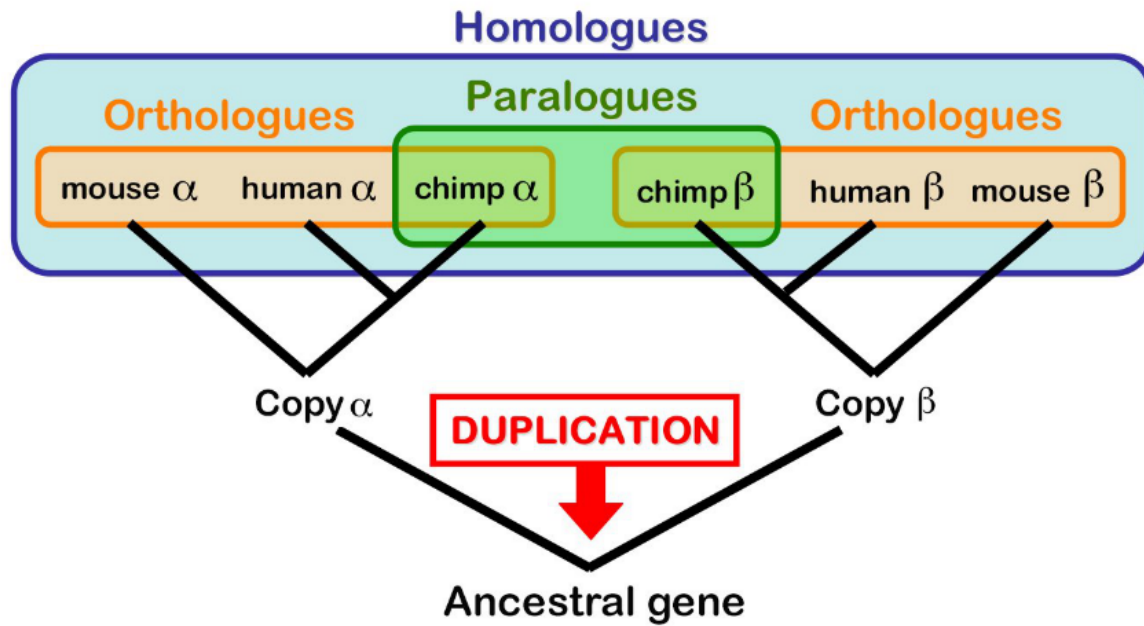
- 1 tetrapod
- 1 ray-finned fish
- 3 cartilaginous fishes



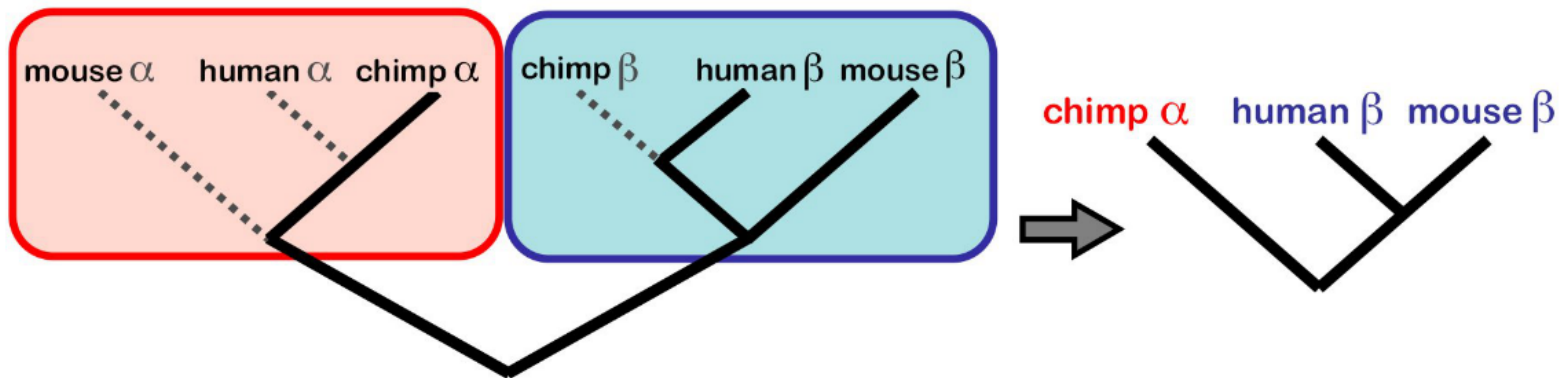
from RNA-seq contigs
using HaMStR (1 week)

**373 single-copy
alignments**

A



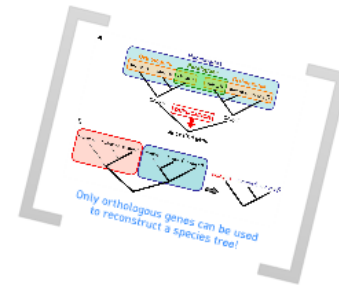
B



Only orthologous genes can be used to reconstruct a species tree!

addition of transcriptomes

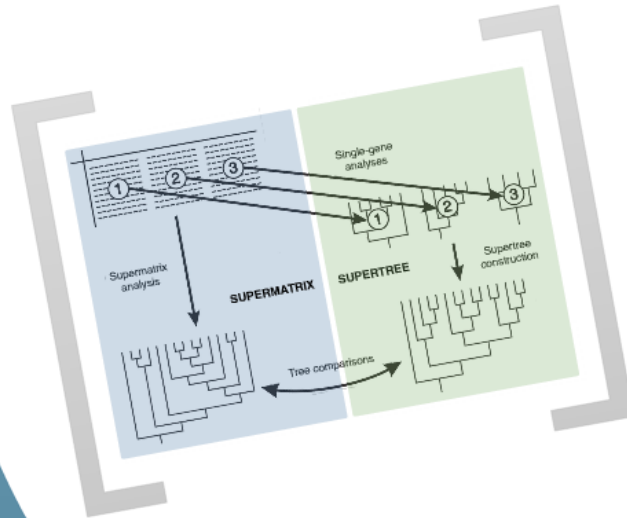
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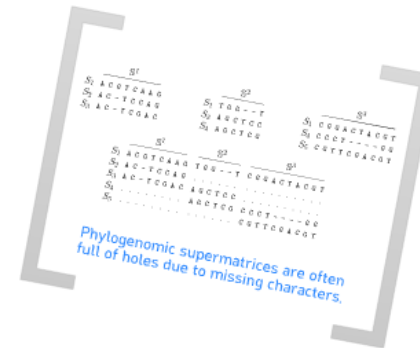
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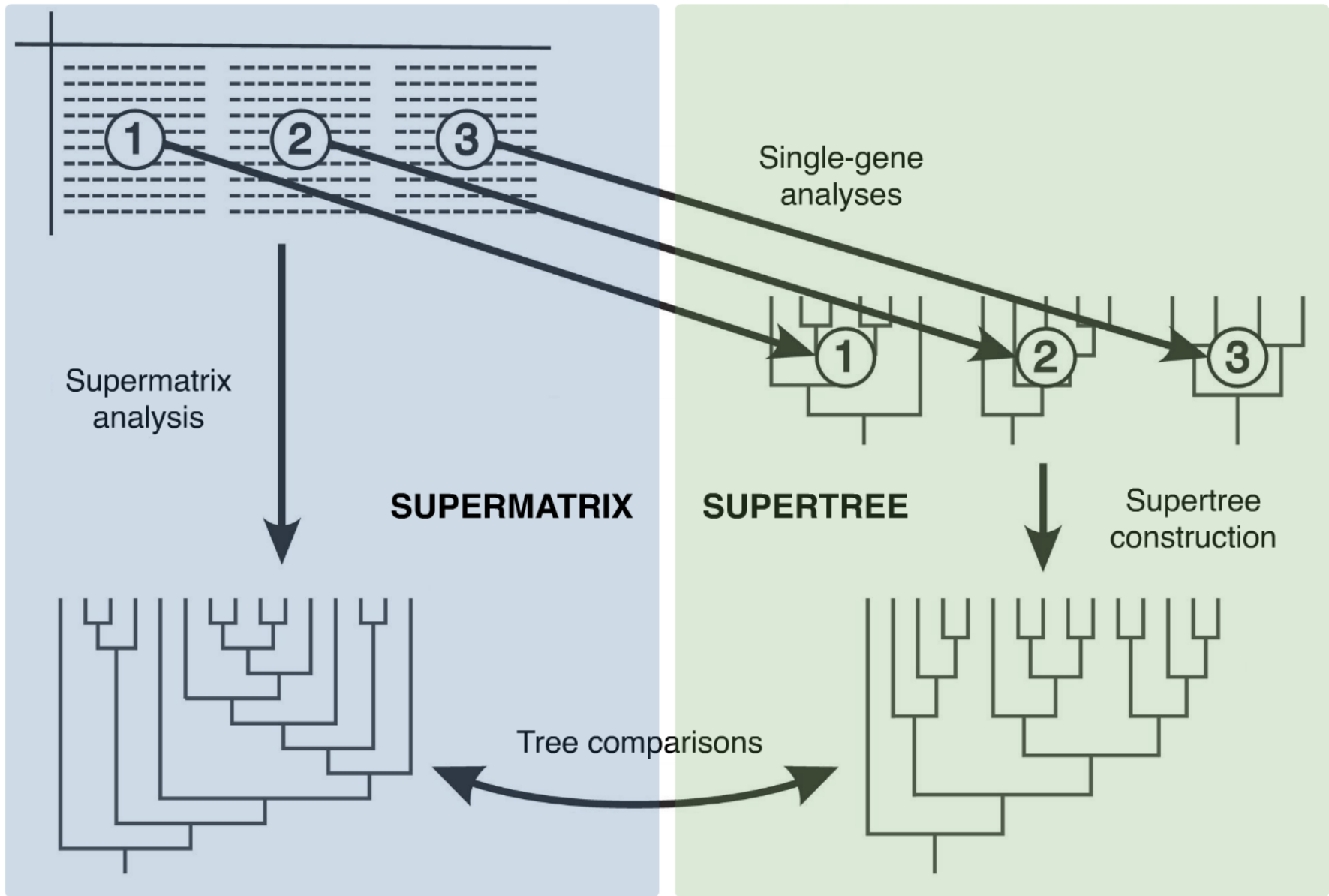
dataset assembly



supermatrix made
with SCaFoS (1 hour)



22 species x 251 genes
(100,583 aligned AA)

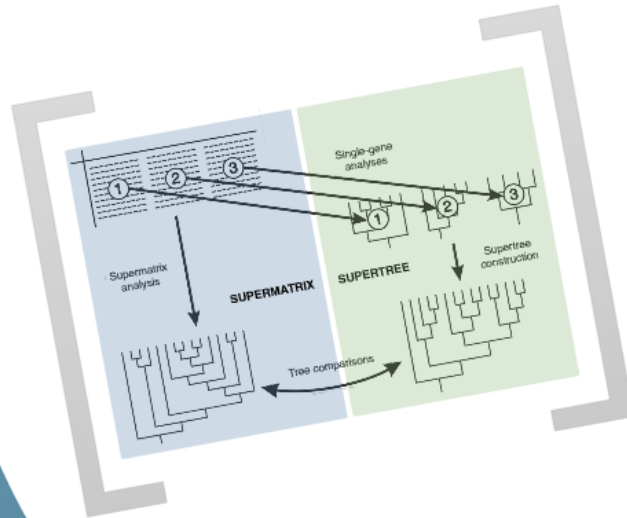


	<u>S¹</u>		<u>S²</u>		<u>S³</u>
<i>S</i> ₁	A C G T C A A G		T G G - - T		C G G A C T A C G T
<i>S</i> ₂	A C - T C C A G		A G C T C C		C C C T - - - G G
<i>S</i> ₃	A C - T C G A C		A G C T C G		C G T T C G A C G T

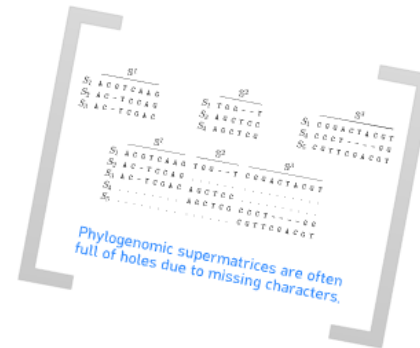
	<u>S¹</u>	<u>S²</u>	<u>S³</u>
<i>S</i> ₁	A C G T C A A G	T G G - - T	C G G A C T A C G T
<i>S</i> ₂	A C - T C C A G
<i>S</i> ₃	A C - T C G A C	A G C T C C
<i>S</i> ₄	A G C T C G	C C C T - - - G G
<i>S</i> ₅	C G T T C G A C G T

Phylogenomic supermatrices are often full of holes due to missing characters.

dataset assembly



supermatrix made with SCaFoS (1 hour)



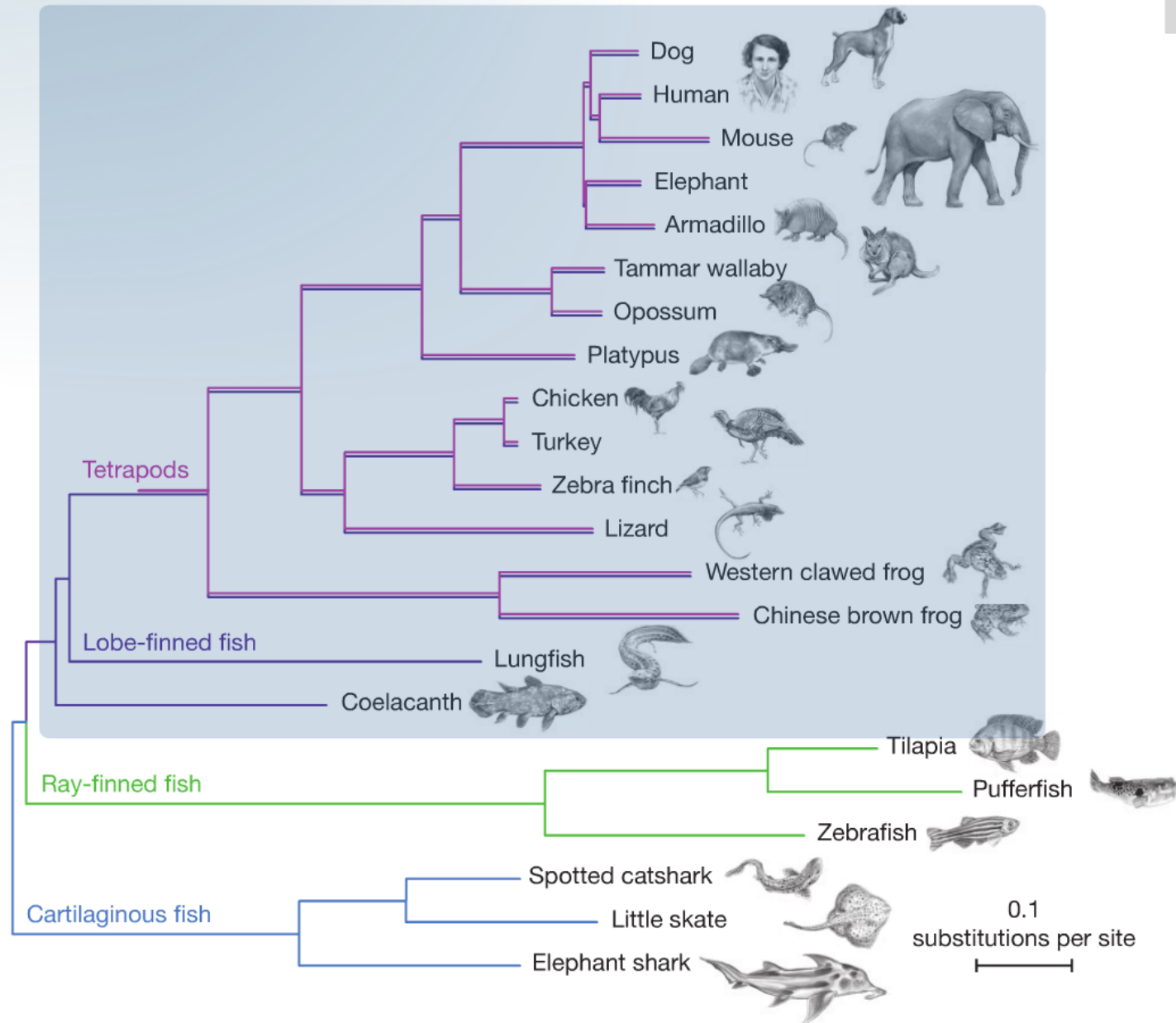
22 species x 251 genes
(100,583 aligned AA)

using PhyloBayes
(CATGTR model)



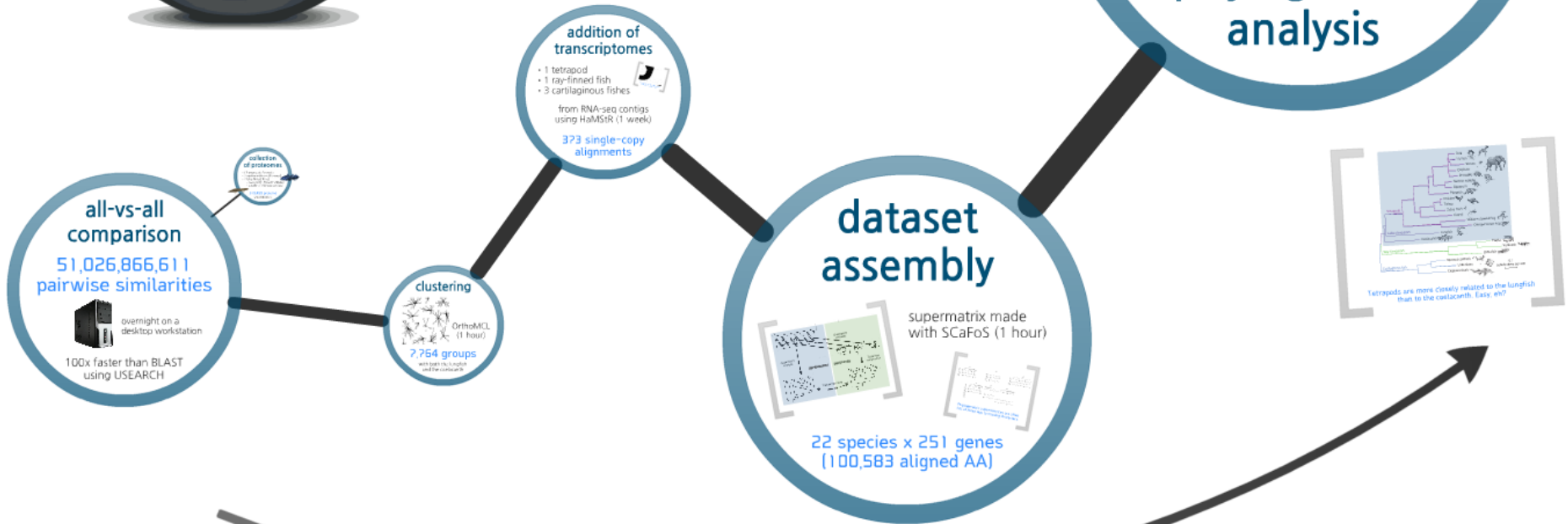
3 months on a
grid computer

**phylogenetic
analysis**



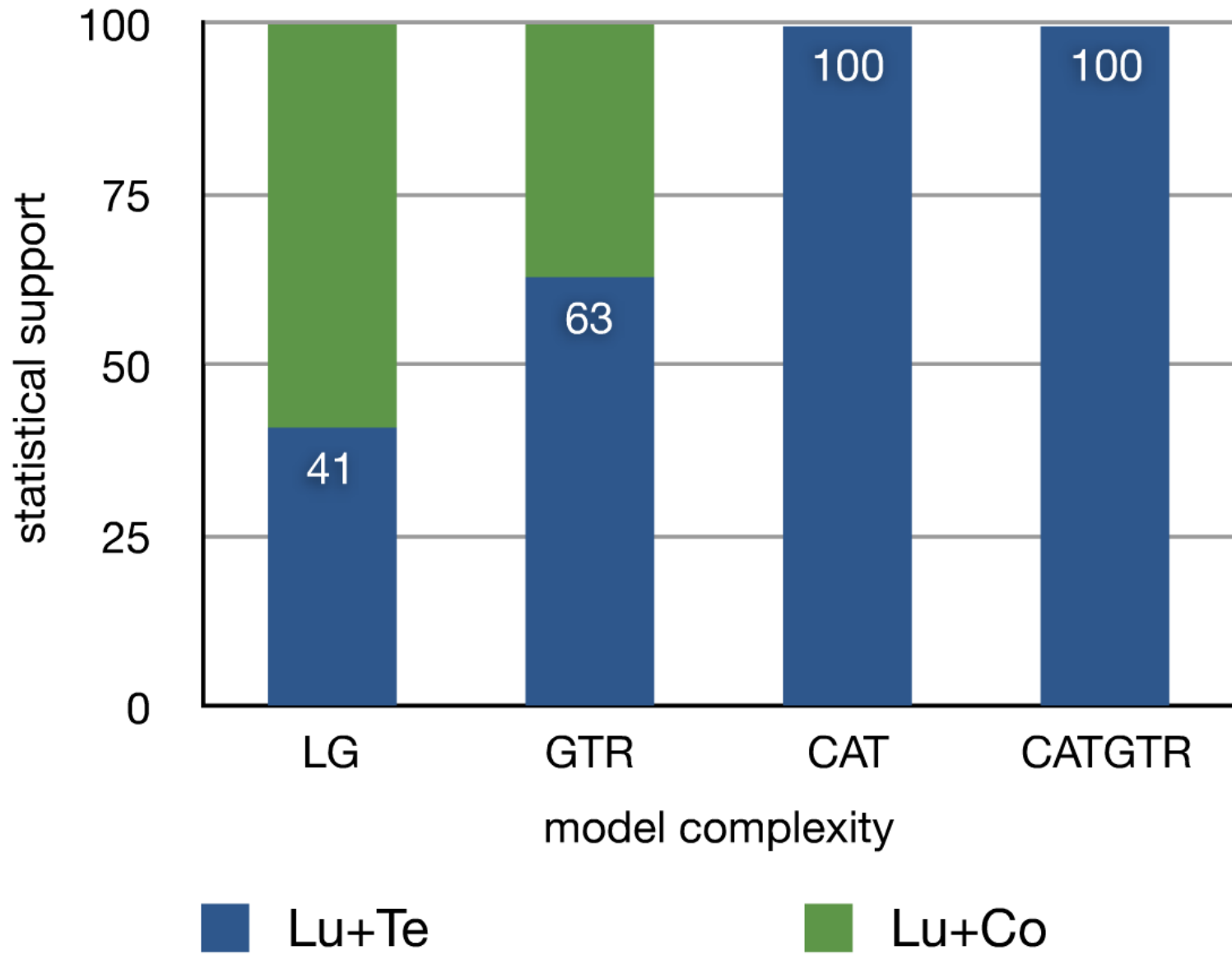
Tetrapods are more closely related to the lungfish than to the coelacanth. Easy, eh?

Our genomic time machine!

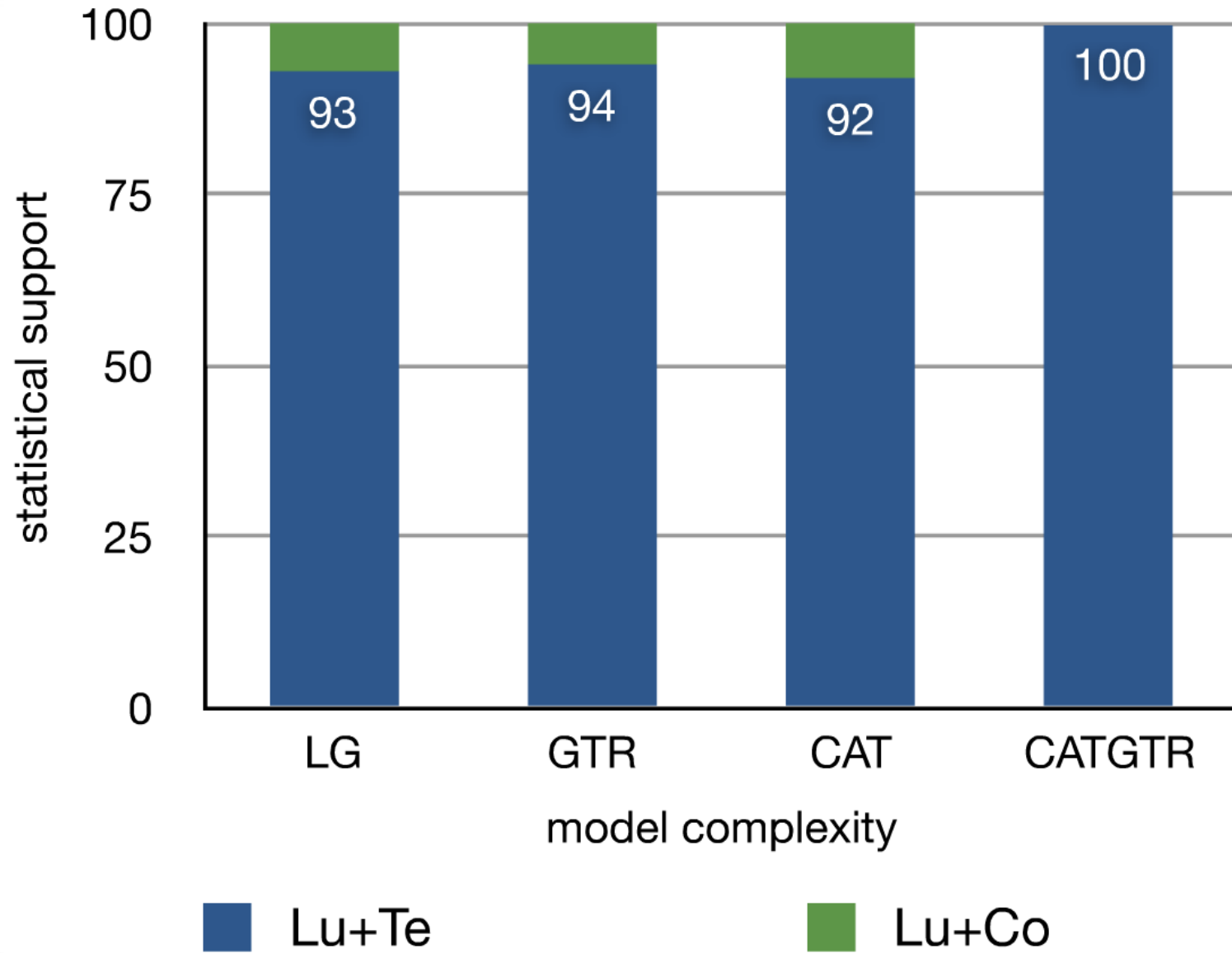


phylogenomic protocol

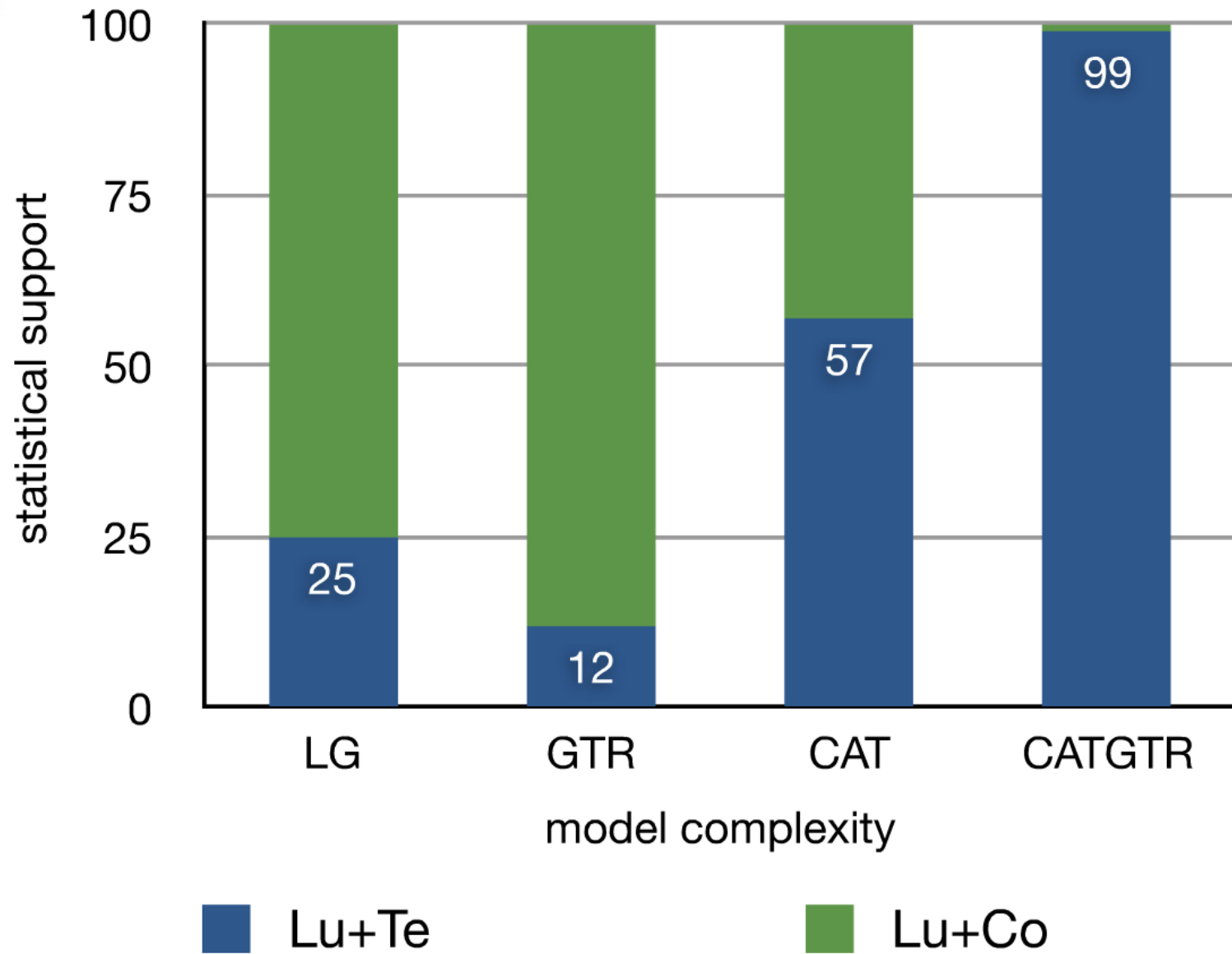
all species

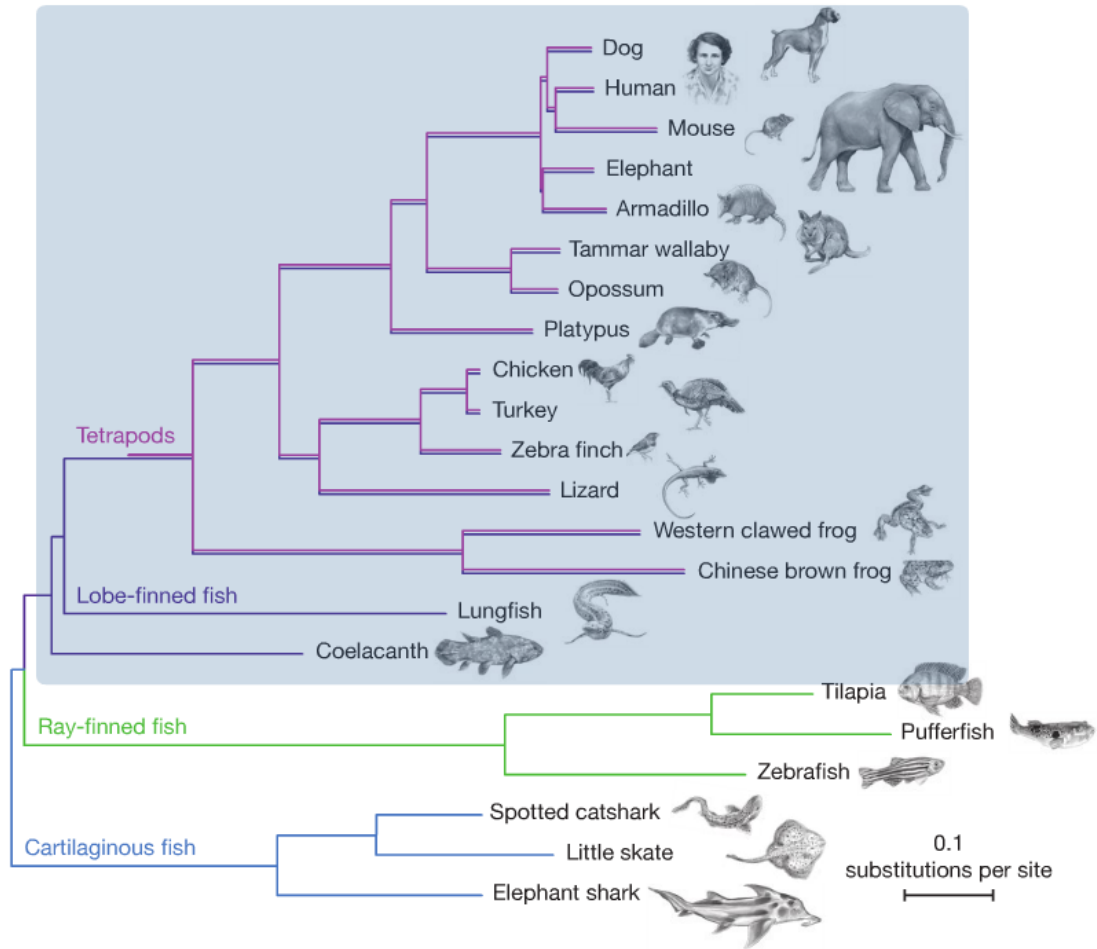
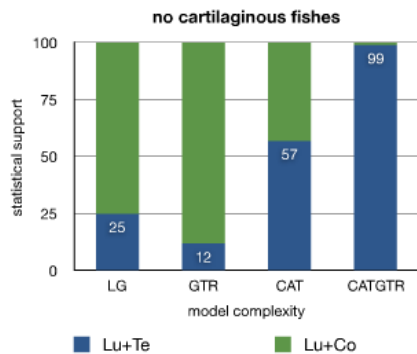
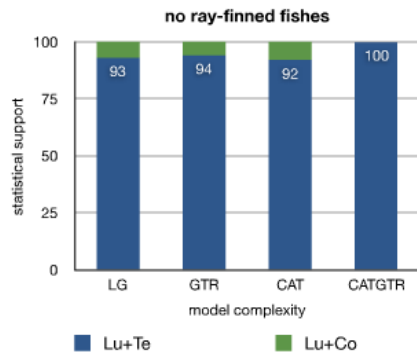
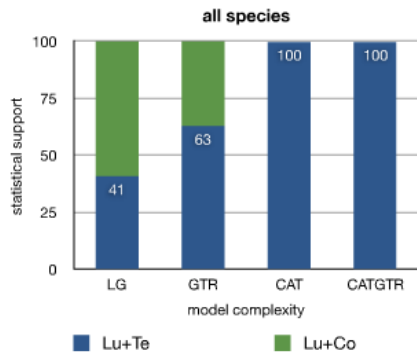


no ray-finned fishes



no cartilaginous fishes

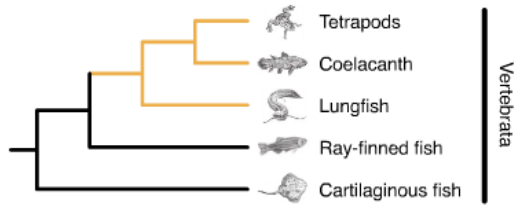




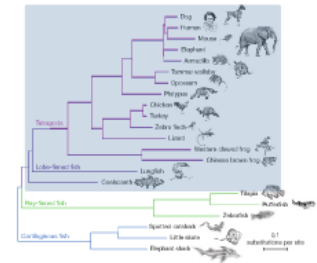
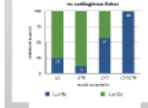
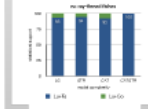
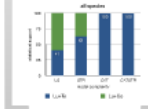
Why do we have such an unstable phylogeny?

The coelacanth as the closest relative of tetrapods

Gorr et al. (1991) – haemoglobins a & b (nucl.)

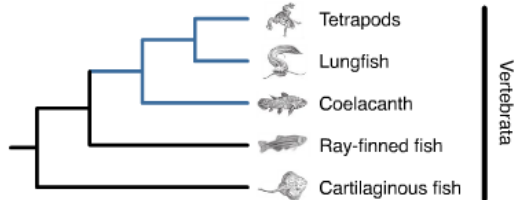


Similarly, phylogenomics is phylogenetics applied to many genes at once.



The lungfish as the closest relative of tetrapods

e.g., Meyer & Dolven (1992) – 12S rRNA & cob (mitochondr.)
Brinkmann et al. (2004) – RAS1 & 2 (nucl.)

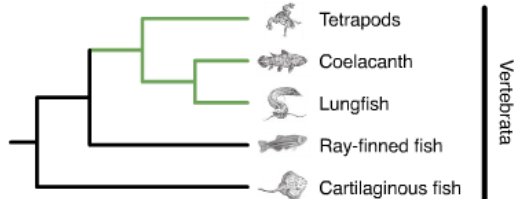


Phylogenomics is useful but can suffer from artifacts!

Let's look at their causes!

Both the coelacanth and the lungfish!

e.g., Yokobori et al. (1994) – cox1 (mitochondr.)
Zardoya & Meyer (1996) – 28S rRNA (nucl.)



African coelacanth



genome size: 2.86 Gbp [2.18 Gbp]

- blood DNA + muscle RNA library
- assembly with ALLPATHS-LG and Trinity
- annotation with the Ensembl pipeline

- 3 RNA libraries (brain, gonad/kidney, gut/liver)
- assembly with Trinity
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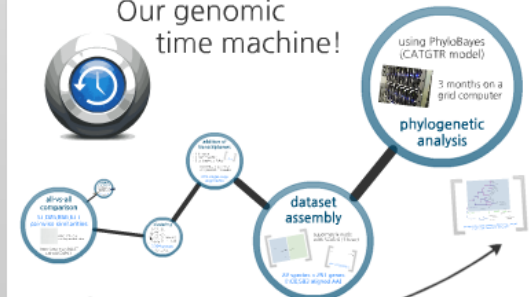


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NGS (Illumina) sequencing was used to sequence the two lobe-finned fishes.

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Computers as Genomic Time Machines for Meeting our Ancestors

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What did the first
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Can we resolve the
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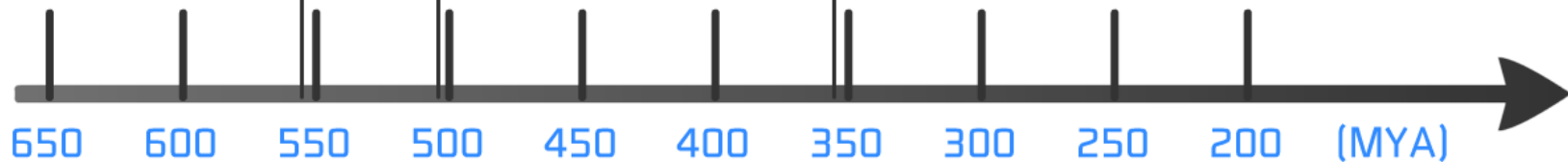
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Prof. Denis Baurain — ULg
Bioforum — April 18th, 2013

FIRST
look like?

Cambrian (542-488)

Can we resolve the
Cambrian explosion?



Devonian

What

first walko

Ediacaran (635-542 MYA)



Only odd soft animals live the sea.

Cambrian (542-488 MYA)

Many animals now thrive in the sea!

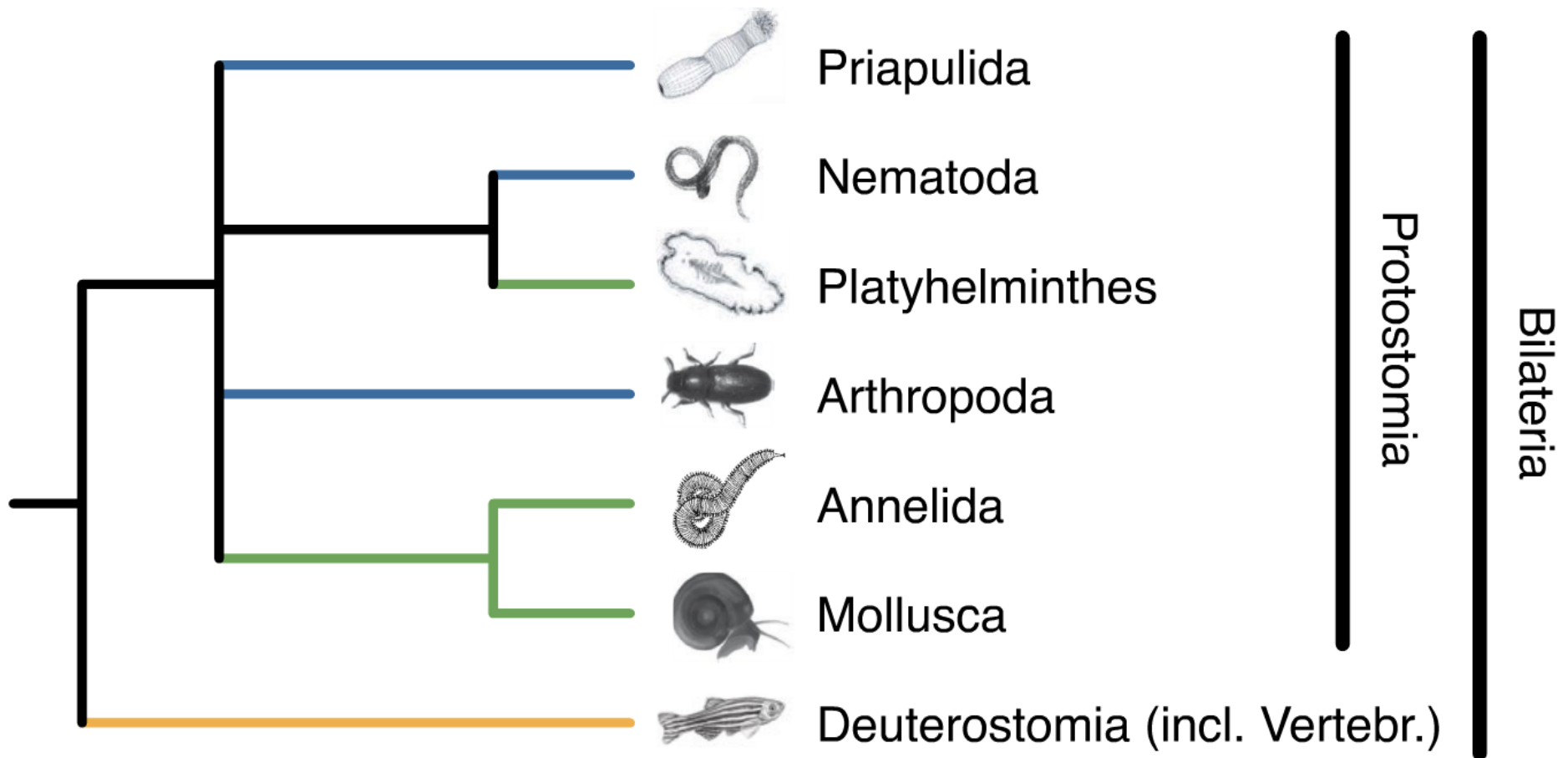




Looking back at the past, it seems like all bilaterian lineages have appeared at once!

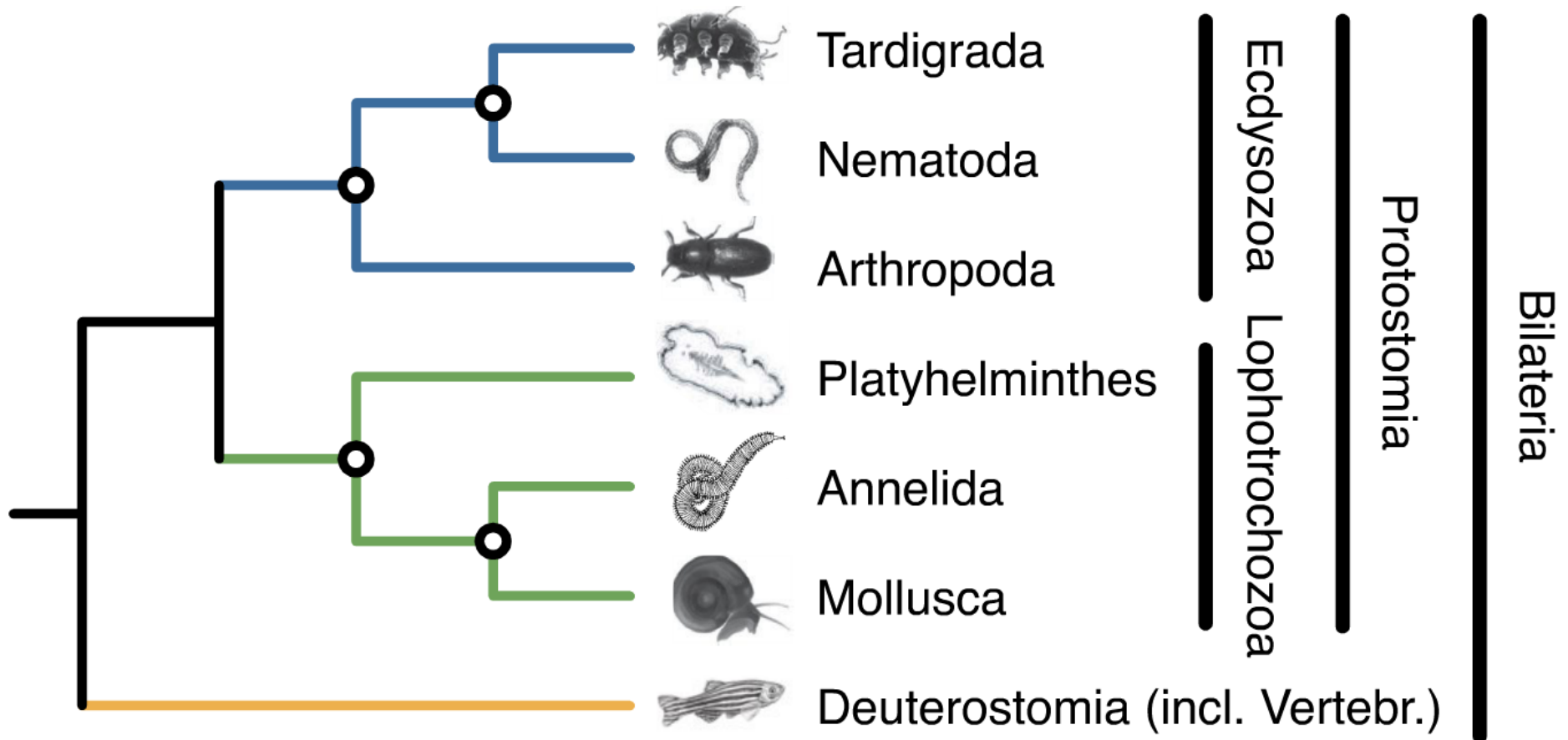
The « Cambrian explosion » – nothing to see!

Rokas et al. (2005) – 50 nuclear genes



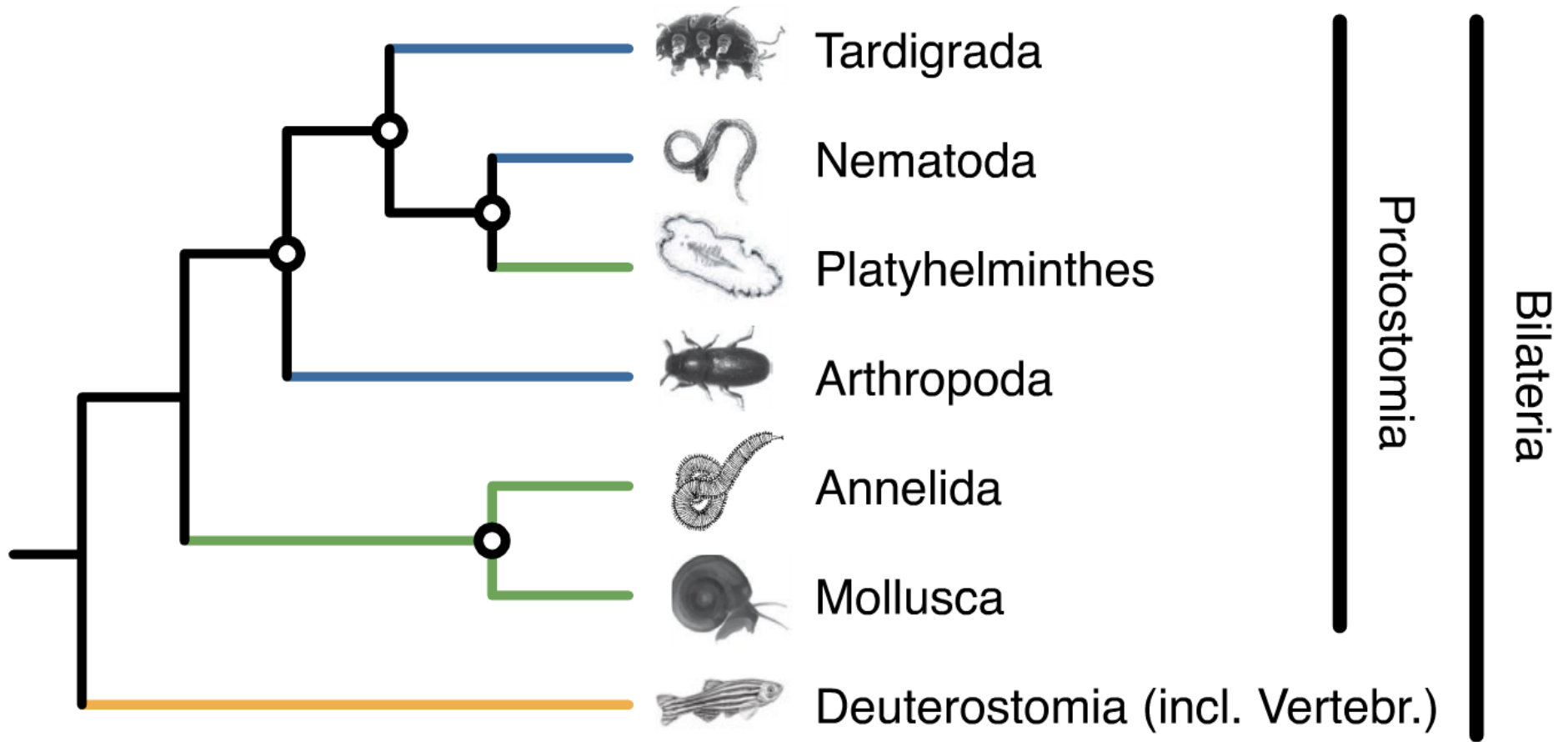
The « new animal phylogeny »

Aguinaldo et al. (1997) – 18S rRNA
Philippe et al. (2005) – 71 nuclear genes



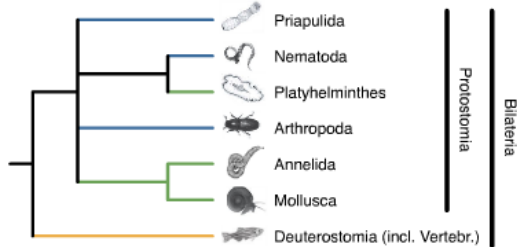
Example of alternative phylogeny

Philippe et al. (2005) – 146 nuclear genes



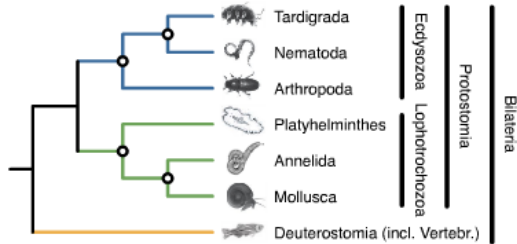
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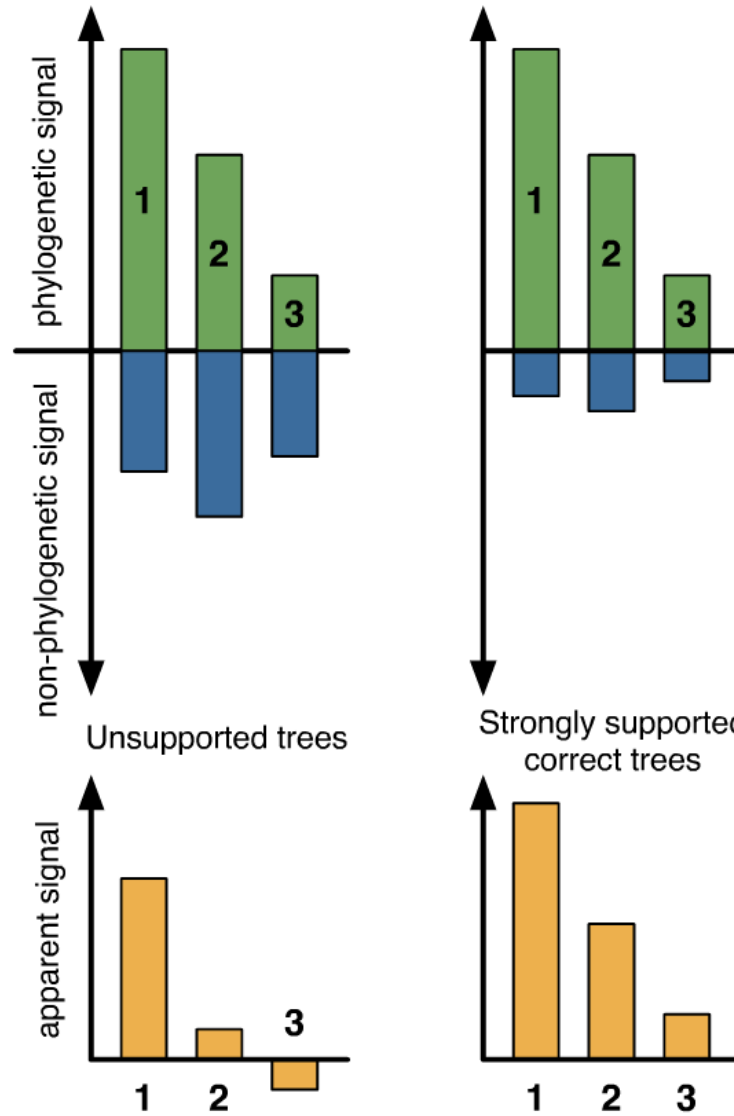
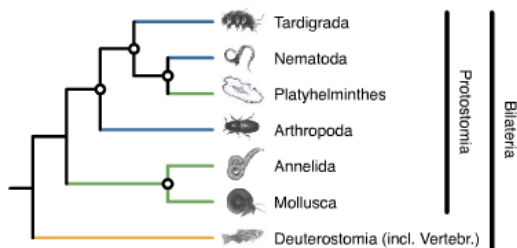
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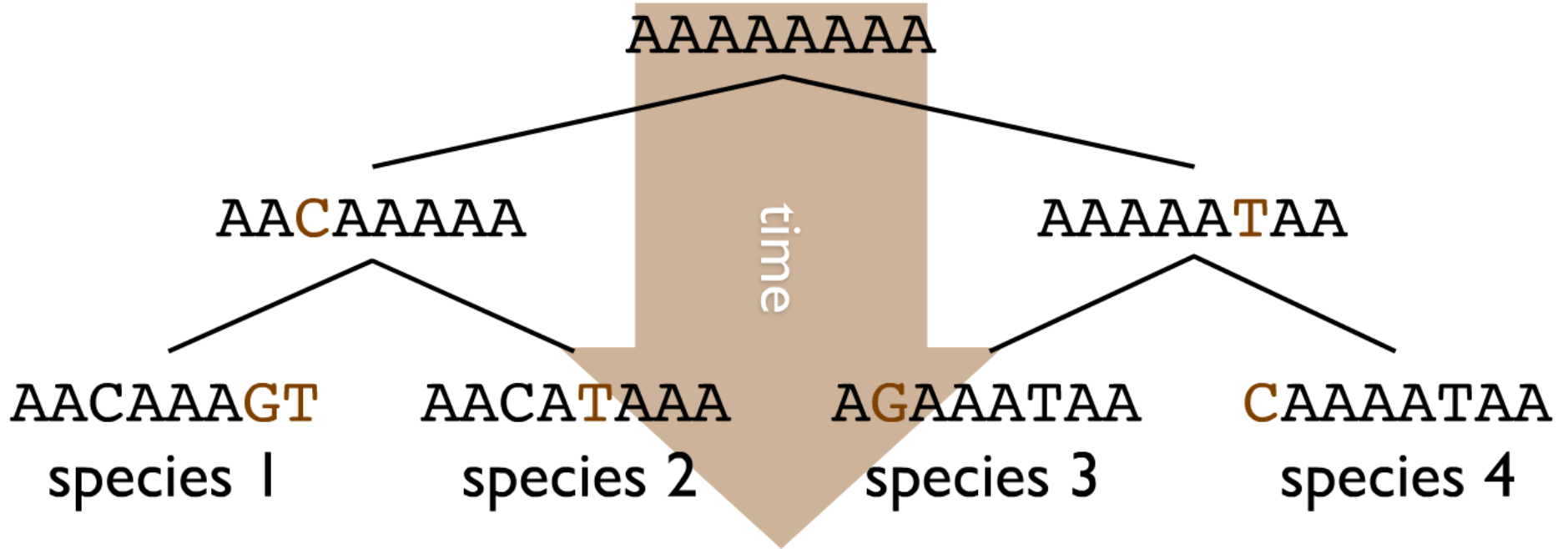


Example of alternative phylogeny

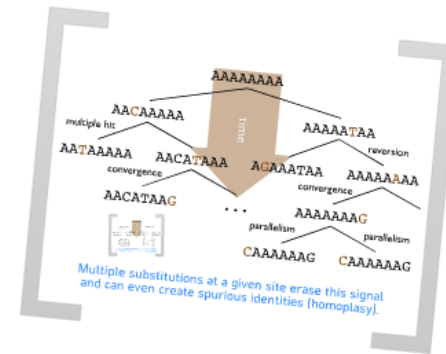
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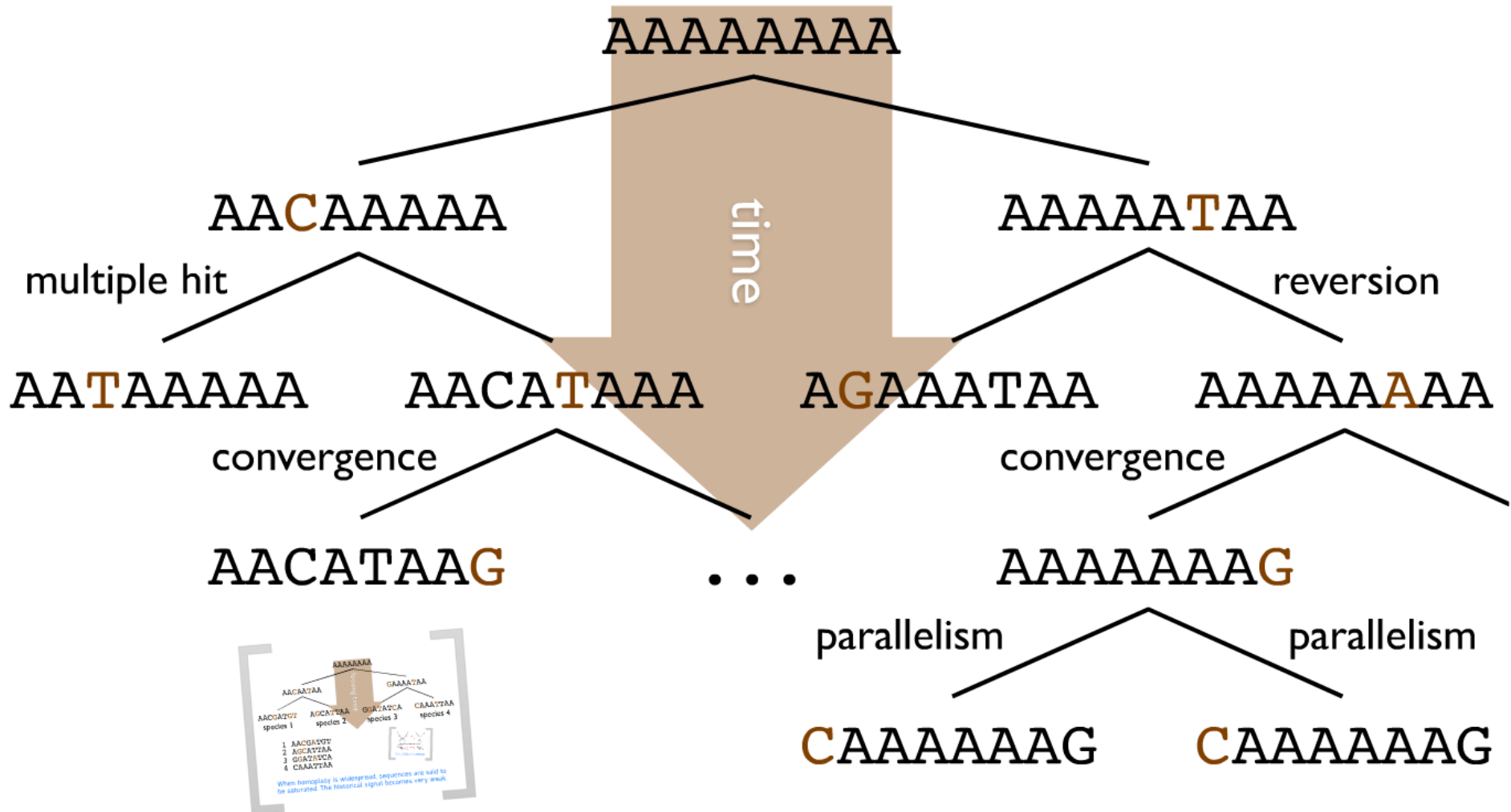
Working hypothesis: the lack of resolution stems from an excess of non-phylogenetic signal.



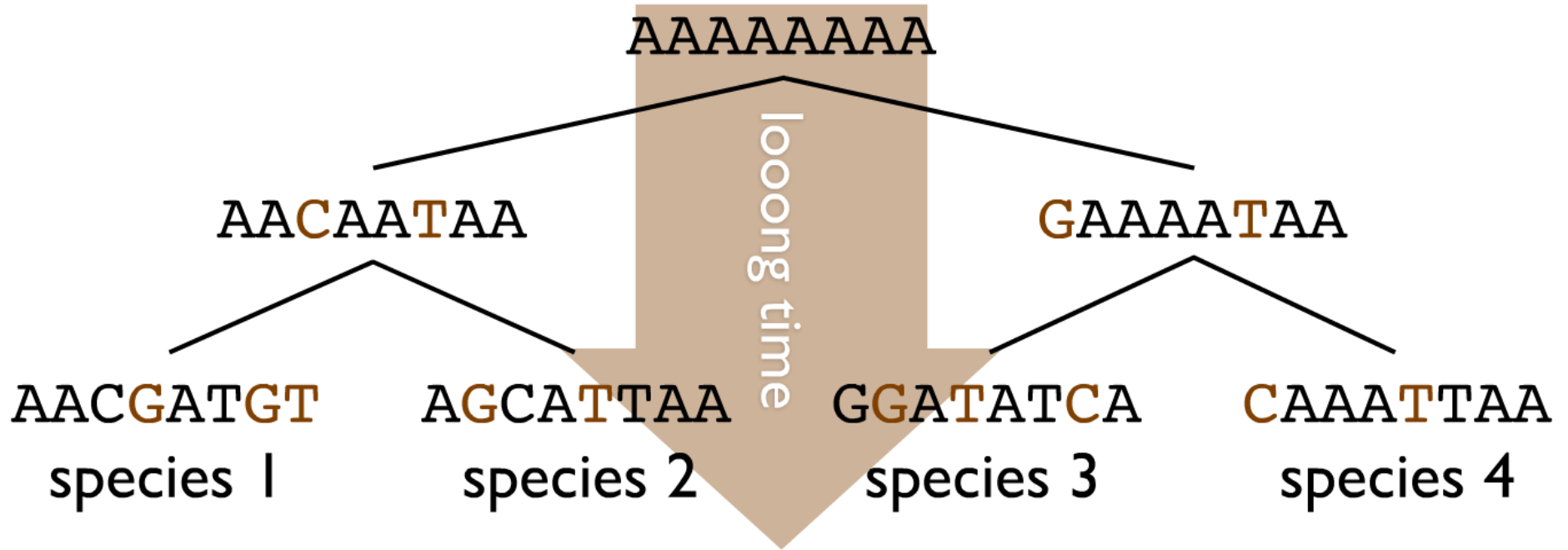
- 1 AACCAAAGT
- 2 AACATAAAA
- 3 AGAAAATAA
- 4 CAAAATAA



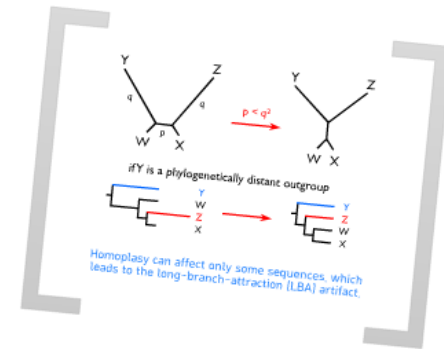
The phylogenetic signal lies in the substitutions inherited from the common ancestors of the sequences.



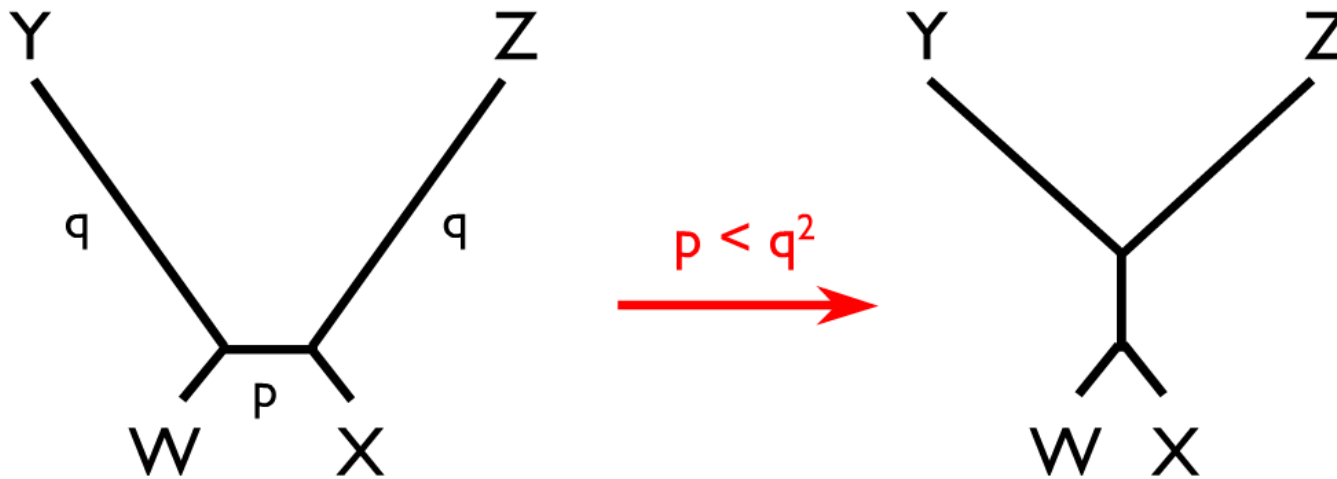
Multiple substitutions at a given site erase this signal and can even create spurious identities (homoplasy).



- 1 AACGATGT
- 2 AGCATTAA
- 3 GGATATCA
- 4 CAAATTAA



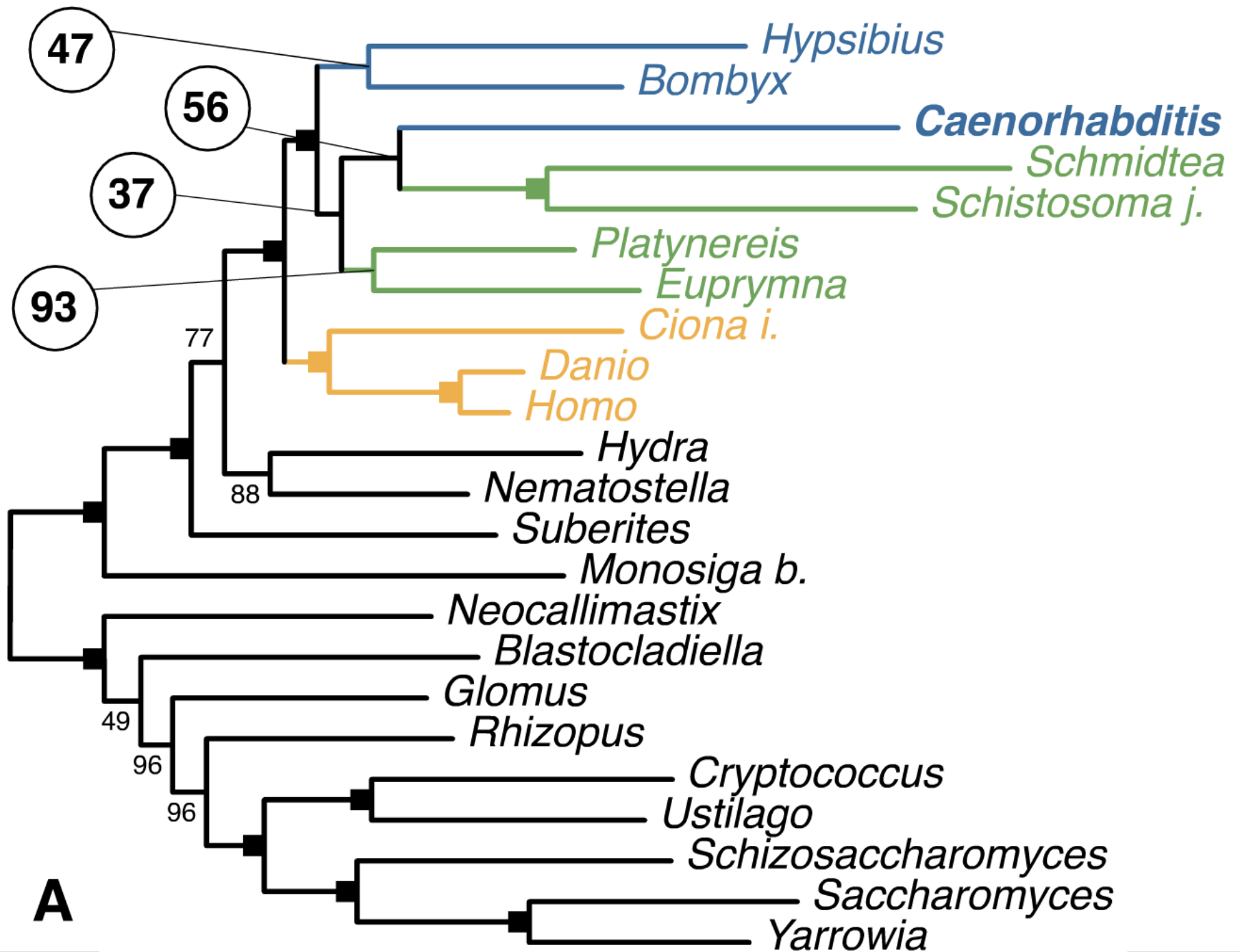
When homoplasy is widespread, sequences are said to be saturated. The historical signal becomes very weak.



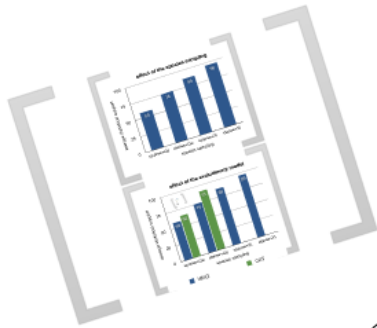
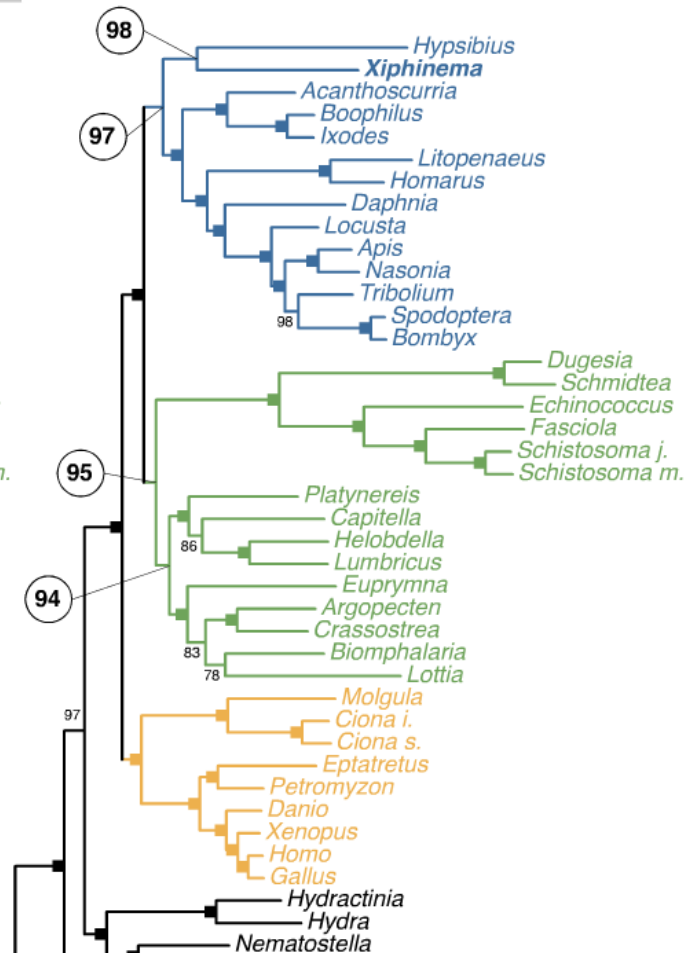
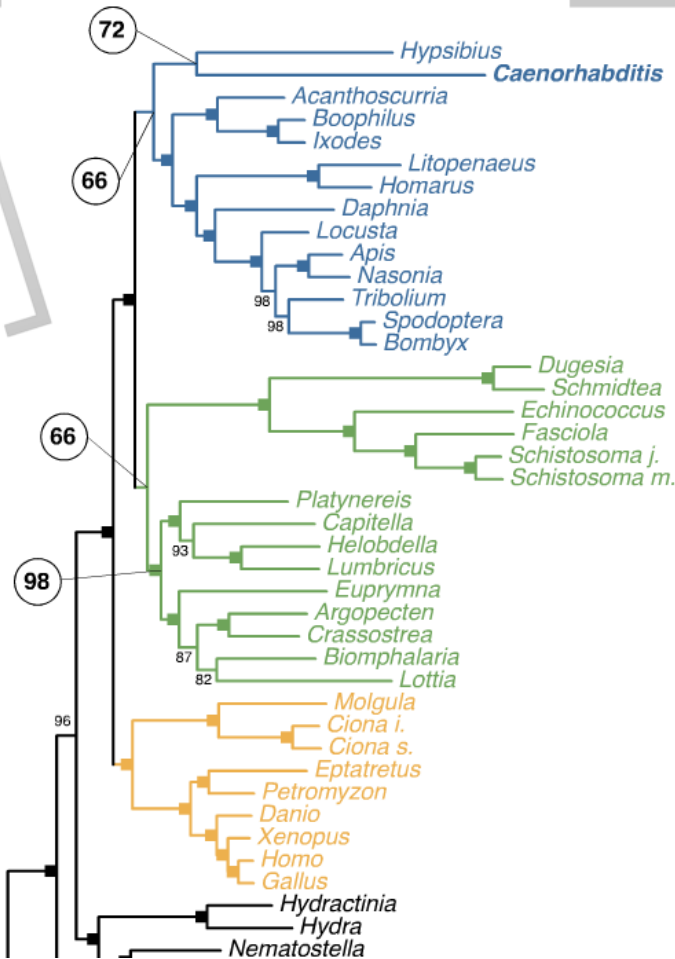
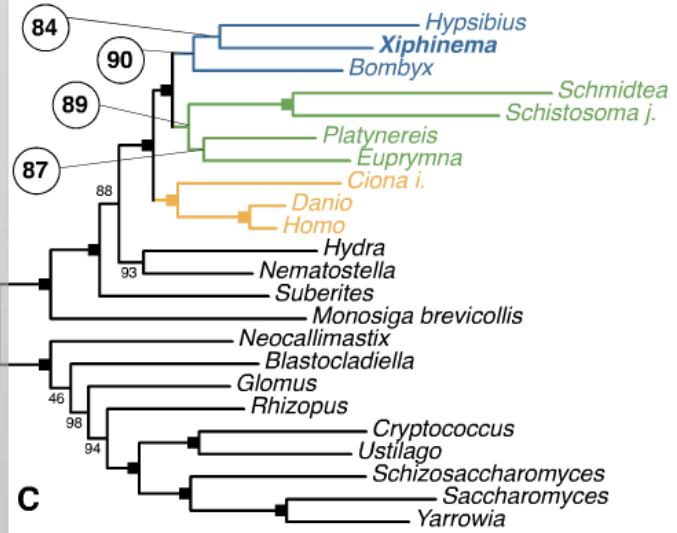
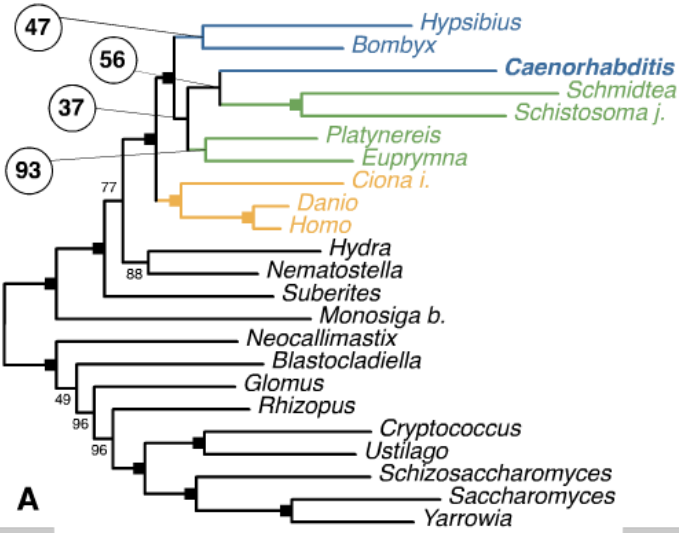
if Y is a phylogenetically distant outgroup



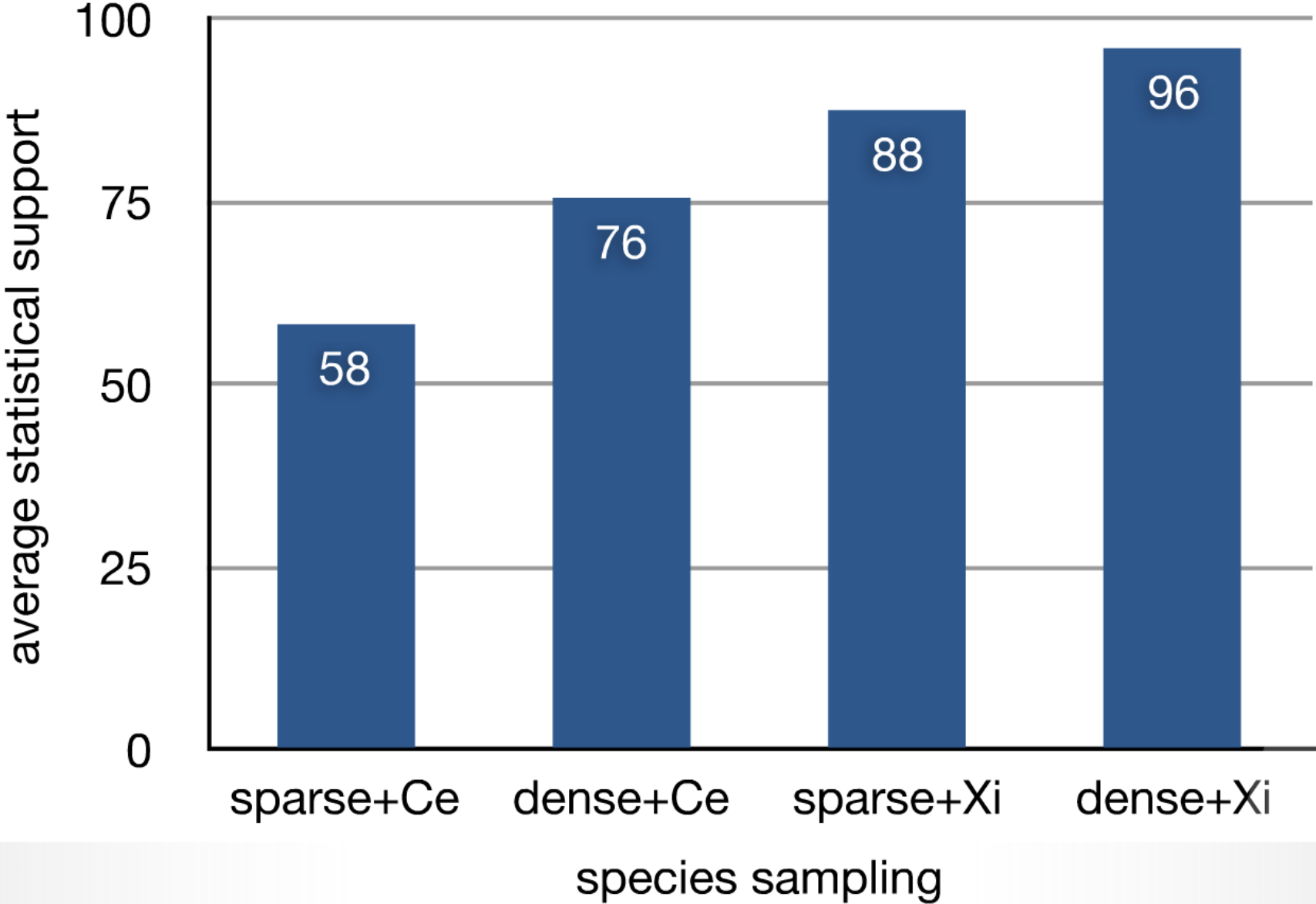
Homoplasy can affect only some sequences, which leads to the long-branch-attraction (LBA) artifact.



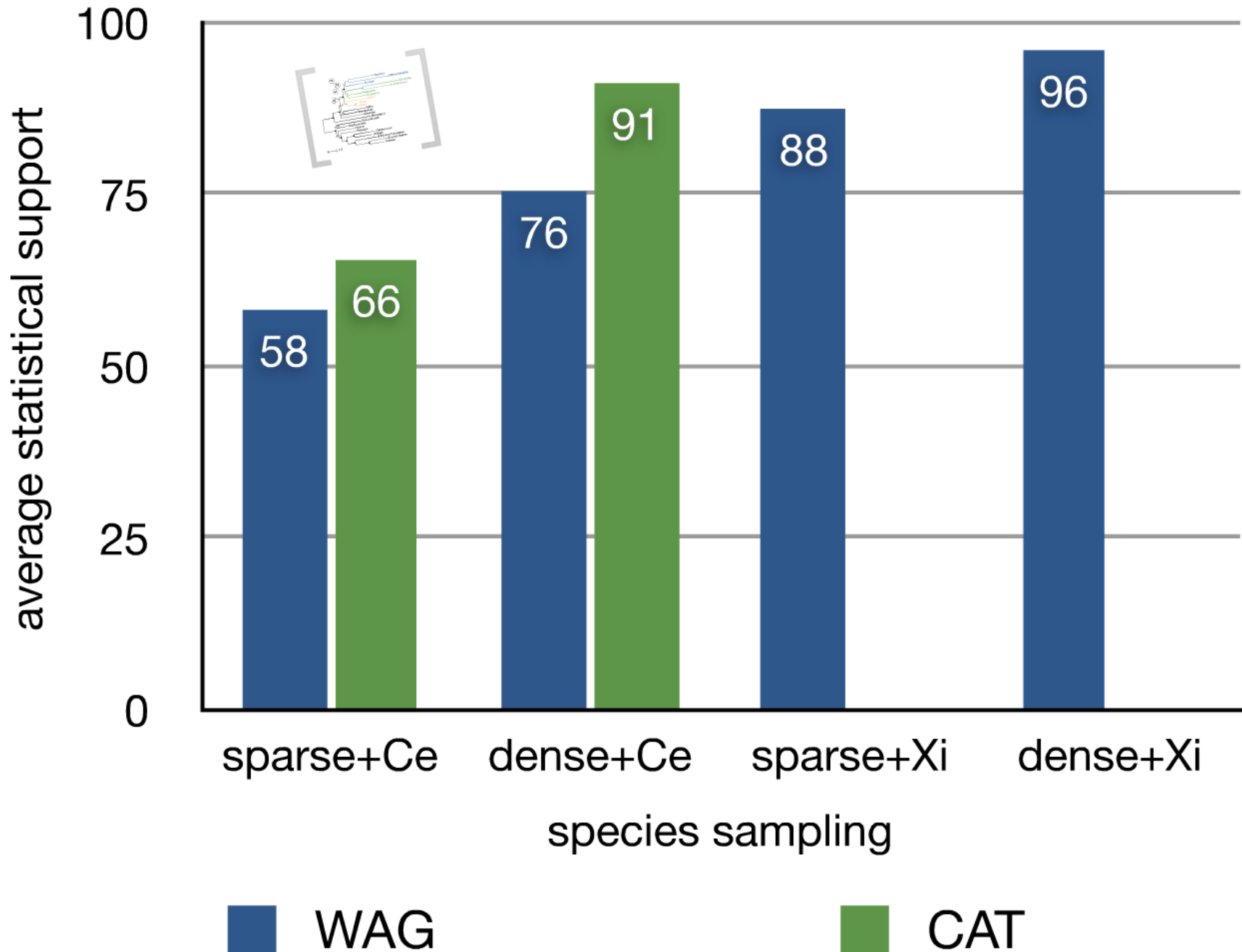
A

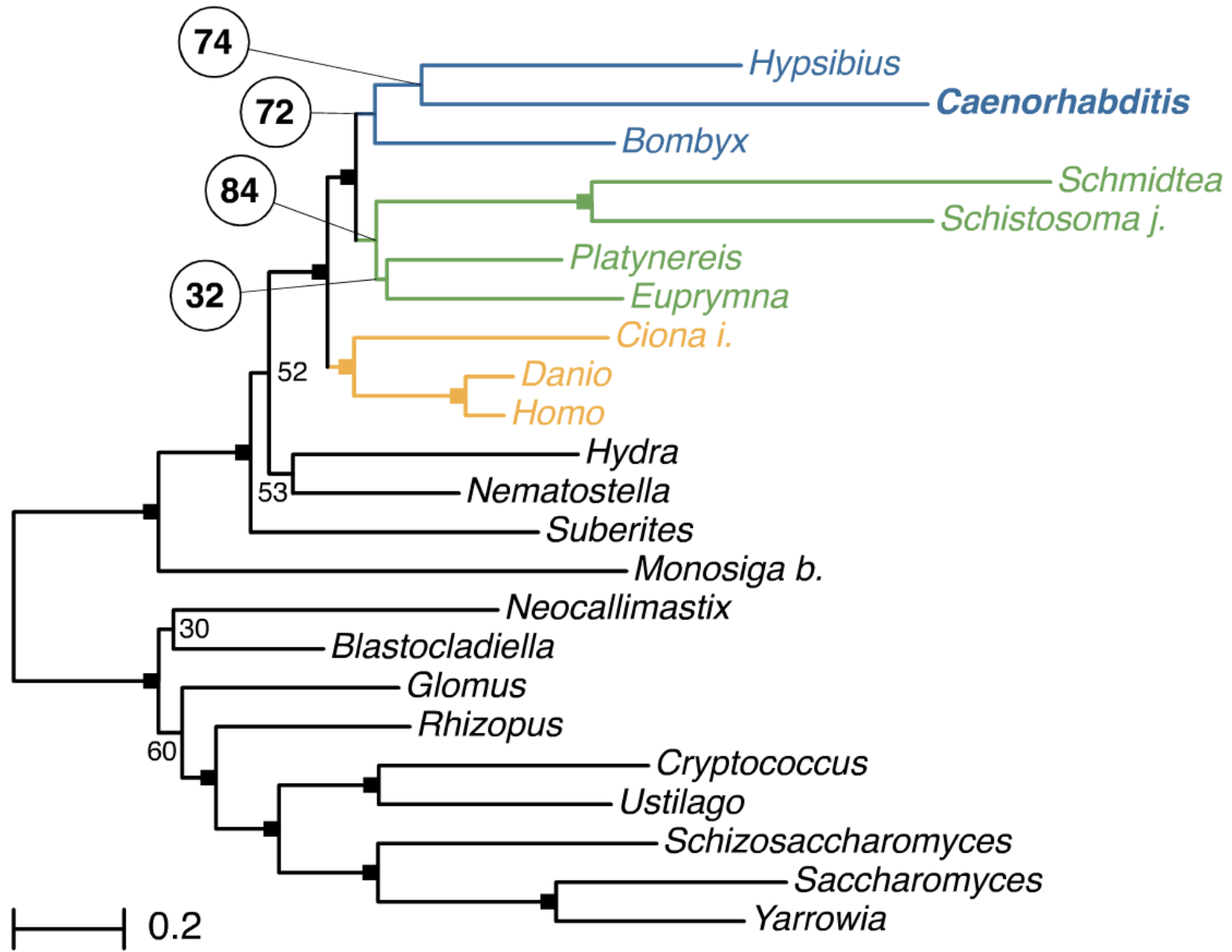


effect of the species sampling

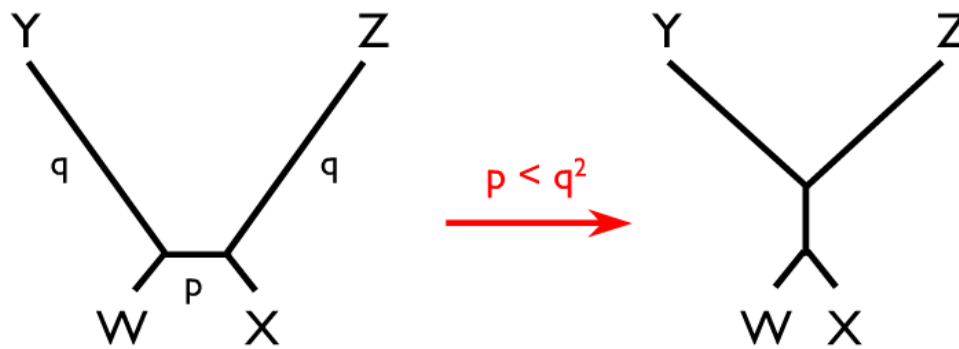


effect of the evolutionary model



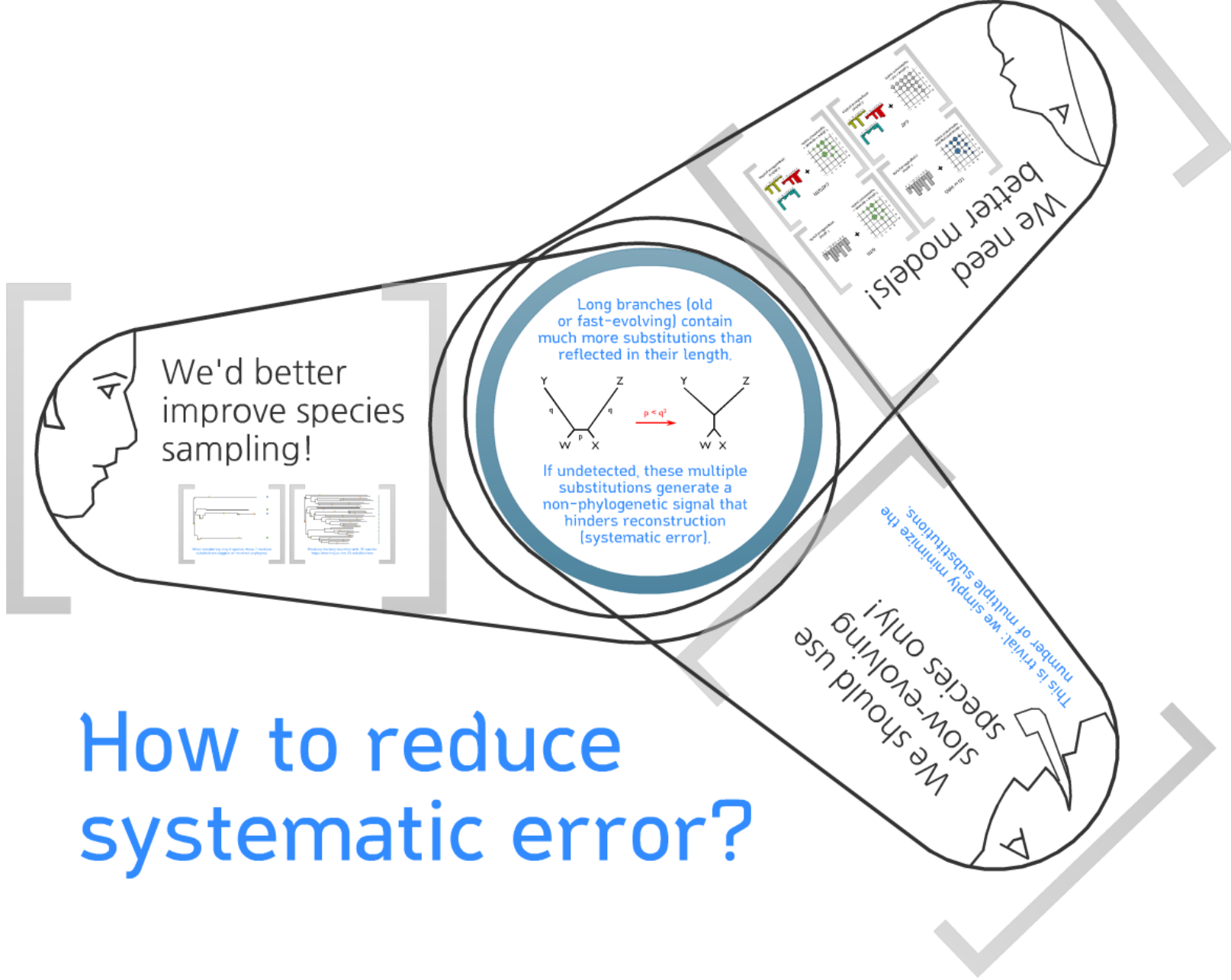


Long branches (old or fast-evolving) contain much more substitutions than reflected in their length.



If undetected, these multiple substitutions generate a non-phylogenetic signal that hinders reconstruction (systematic error).


How to reduce systematic error?



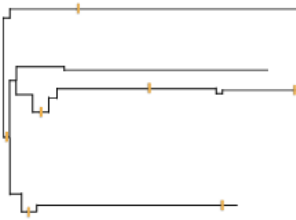


We should use
slow-evolving
species only!

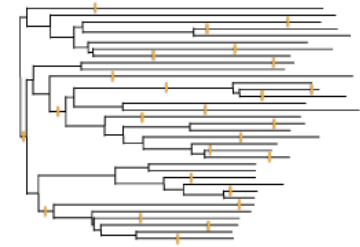
This is trivial: we simply minimize the
number of multiple substitutions.



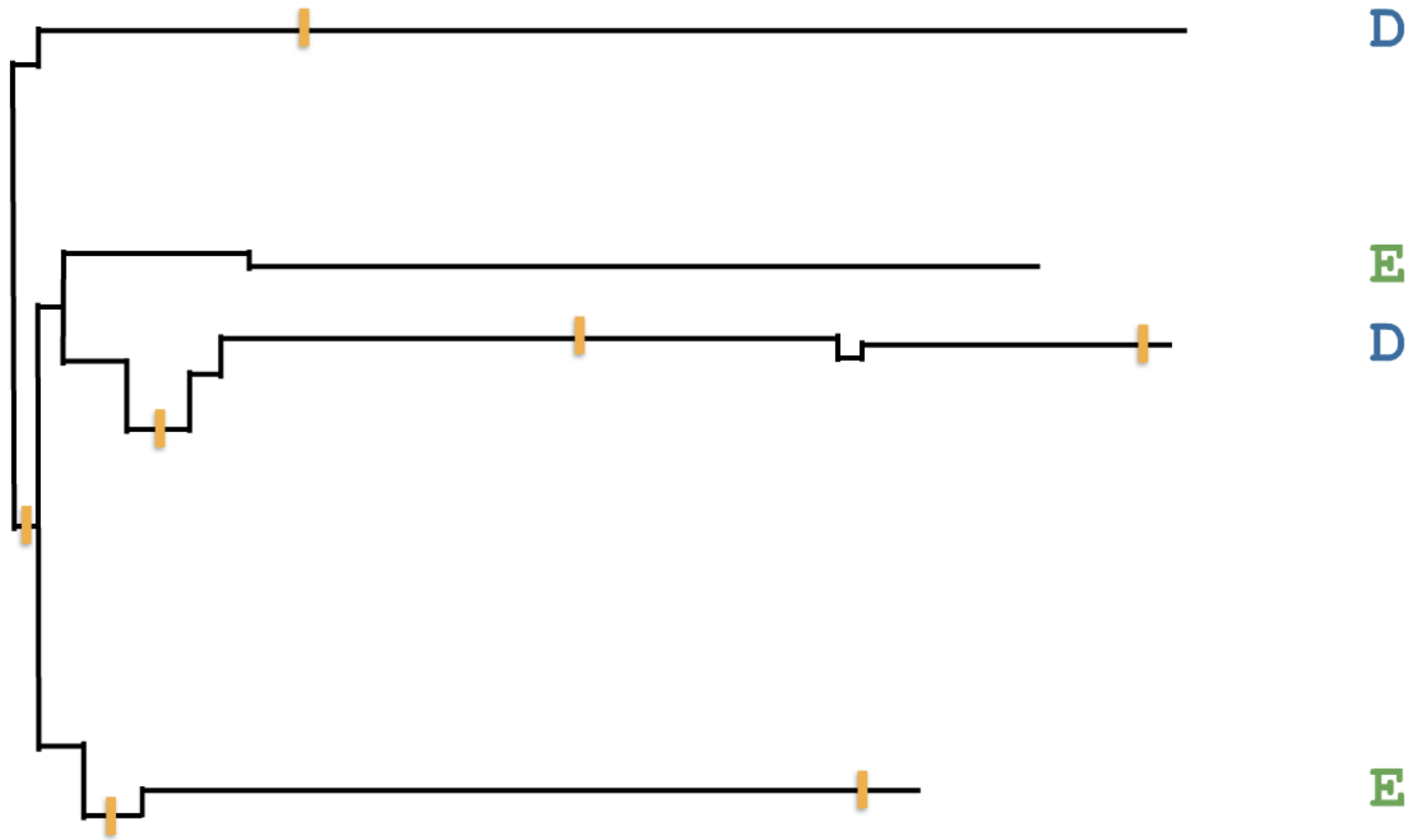
We'd better improve species sampling!



When considering only 4 species, these 7 multiple substitutions suggest an incorrect phylogeny.

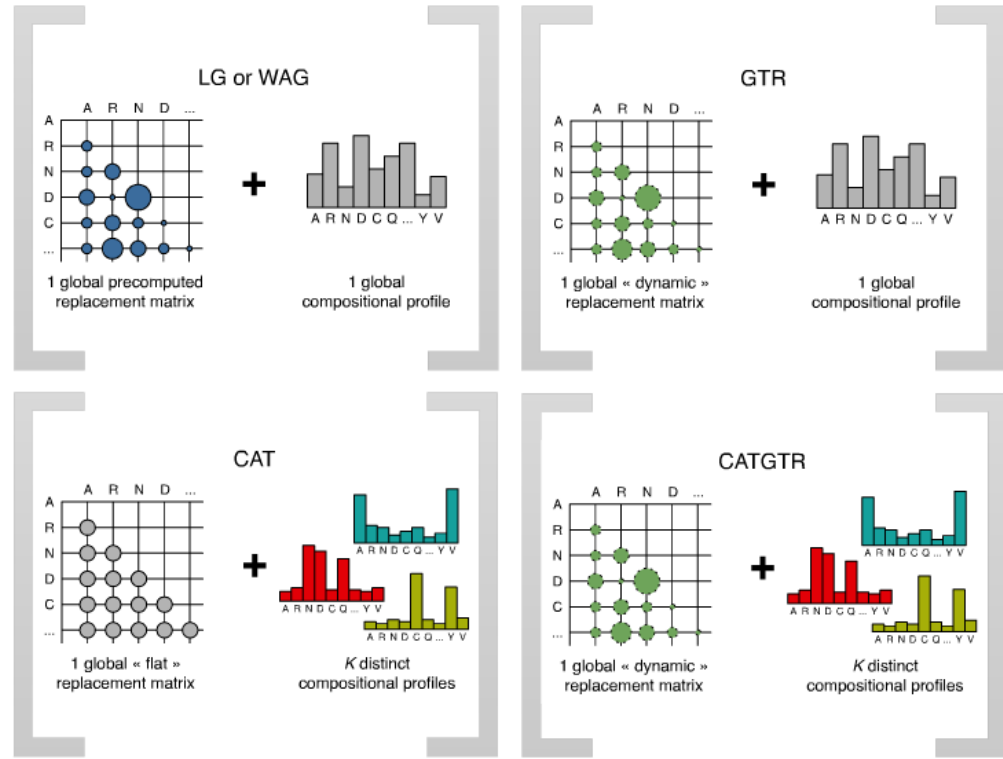


Breaking the long branches with 35 species helps detecting all the 25 substitutions.

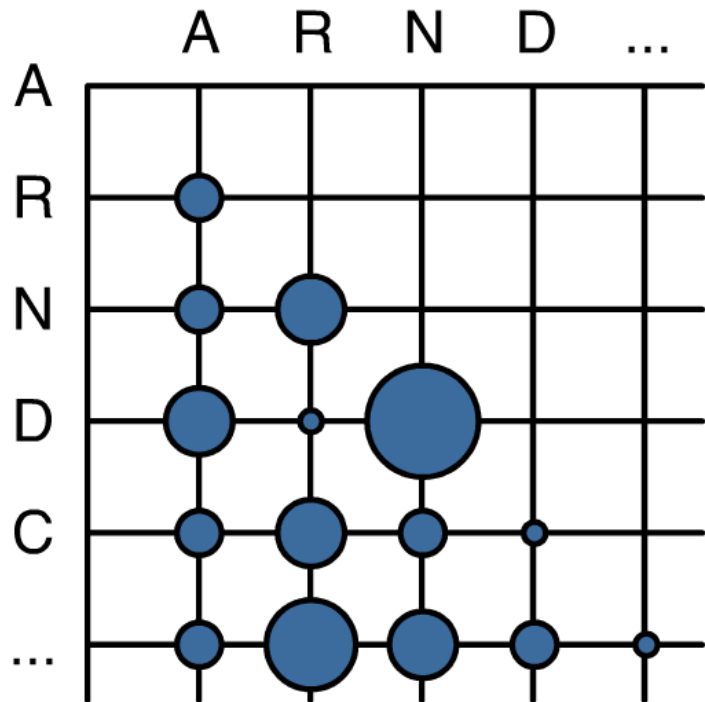


When considering only 4 species, these 7 multiple substitutions suggest an incorrect phylogeny.

We need better models!

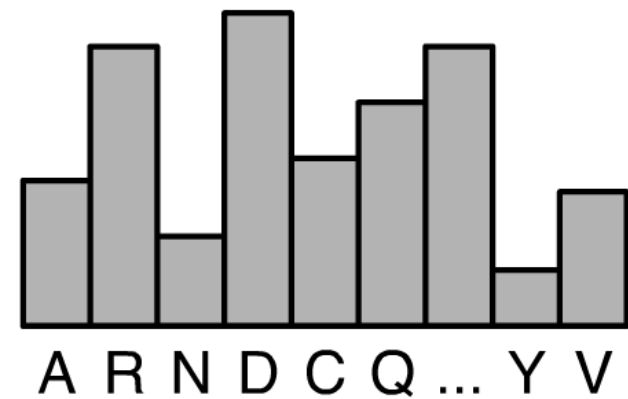


LG or WAG



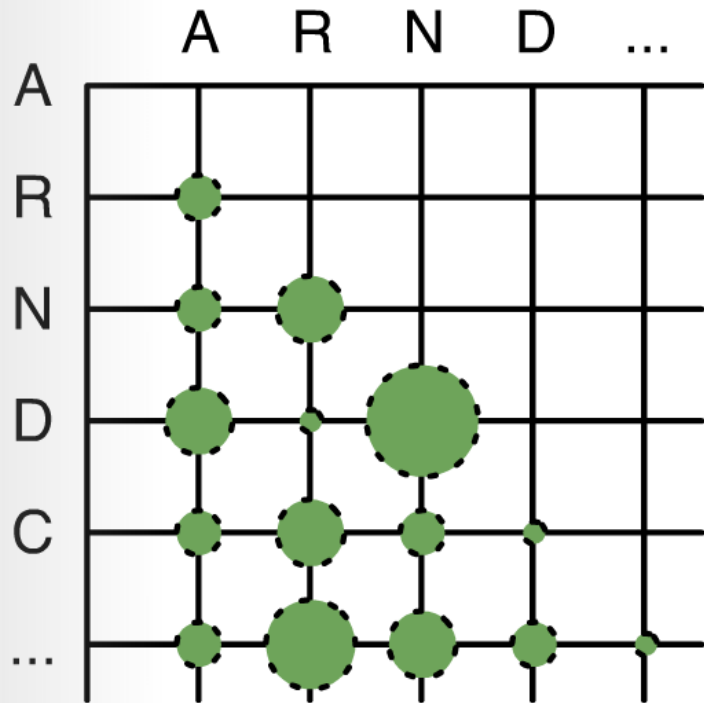
1 global precomputed
replacement matrix

+



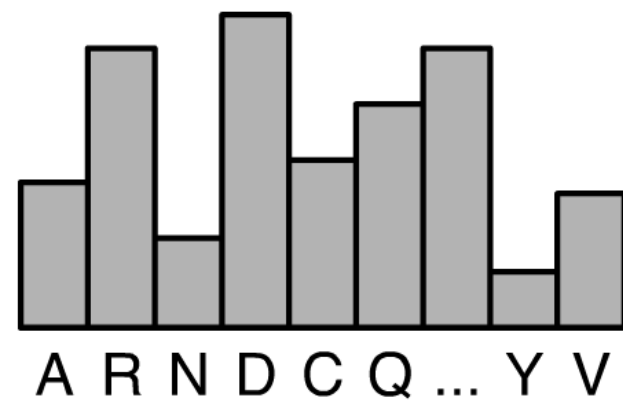
1 global
compositional profile

GTR



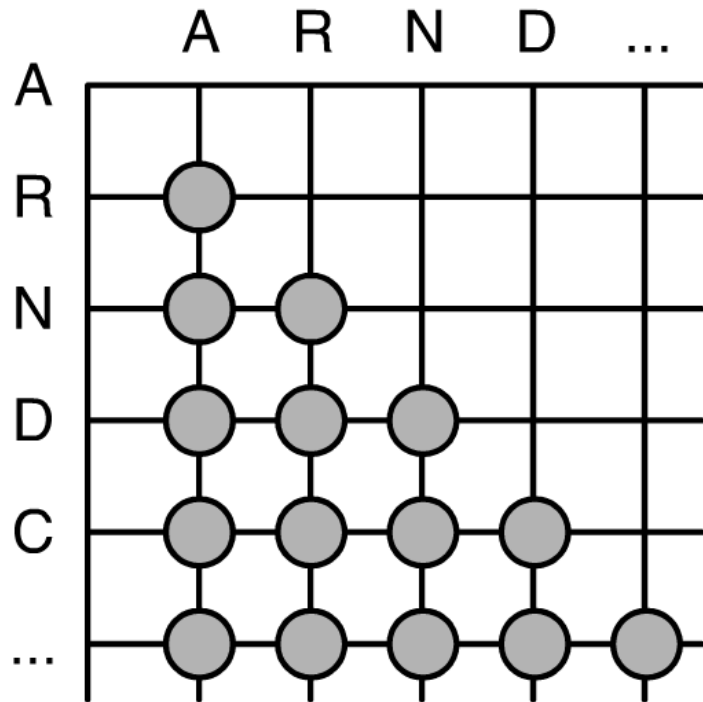
1 global « dynamic »
replacement matrix

+



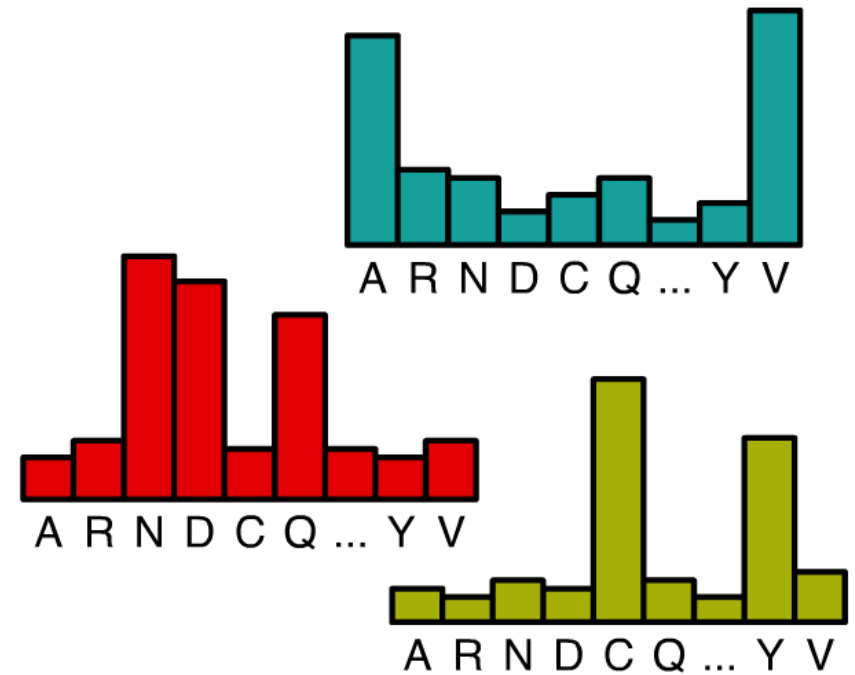
1 global
compositional profile

CAT



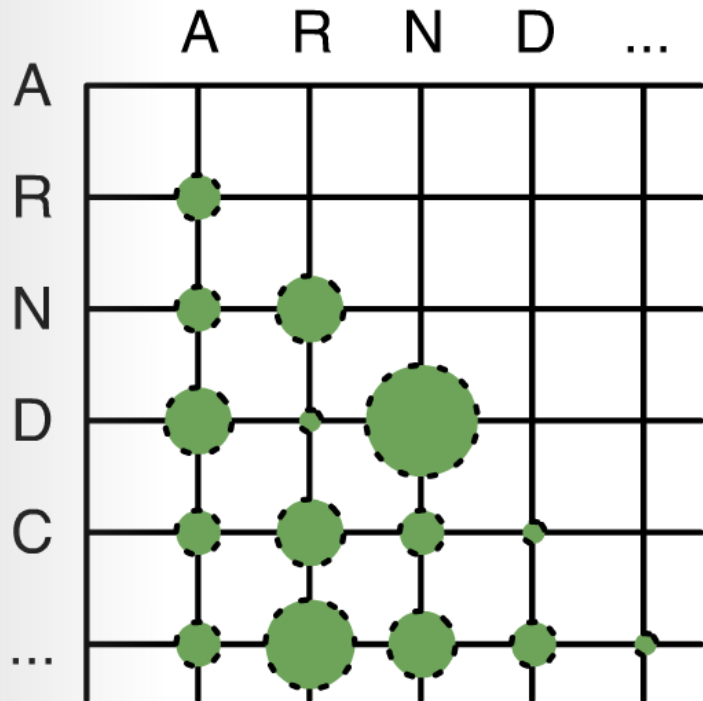
1 global « flat »
replacement matrix

+



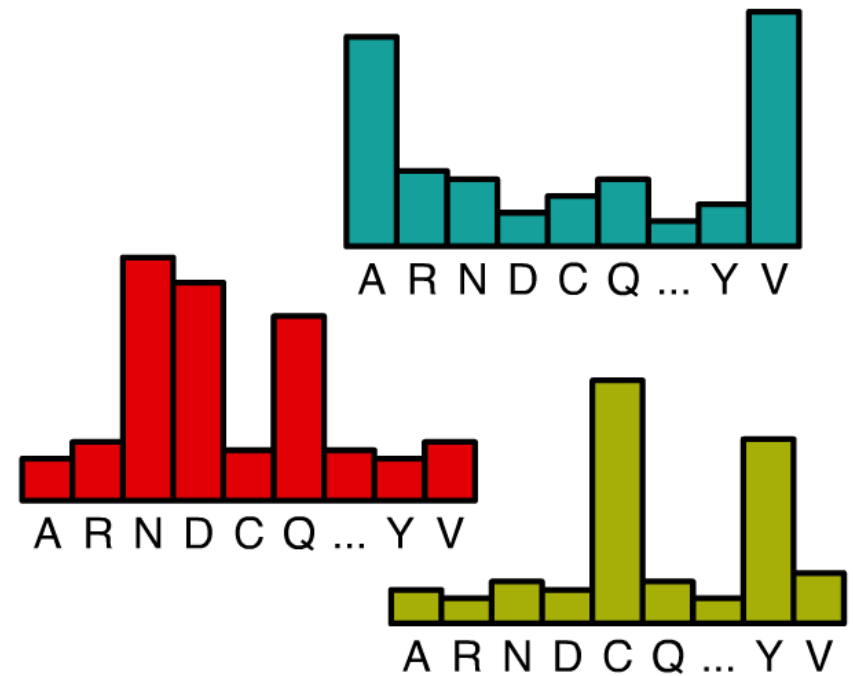
K distinct
compositional profiles

CATGTR

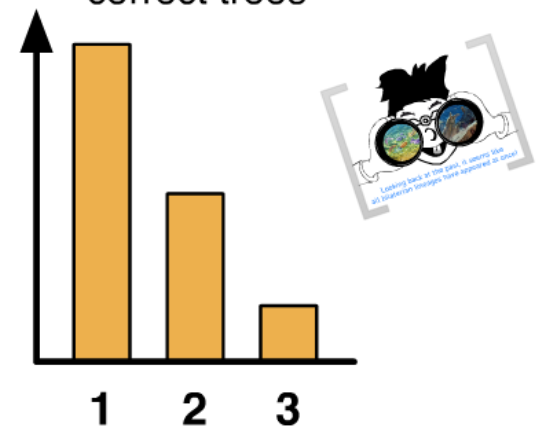
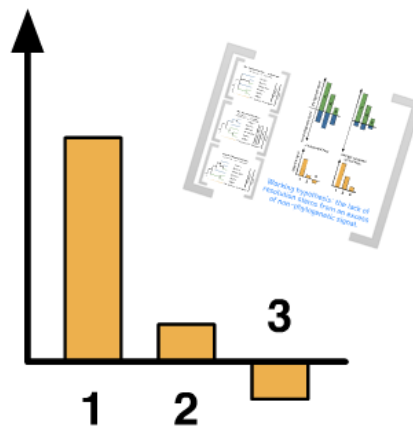
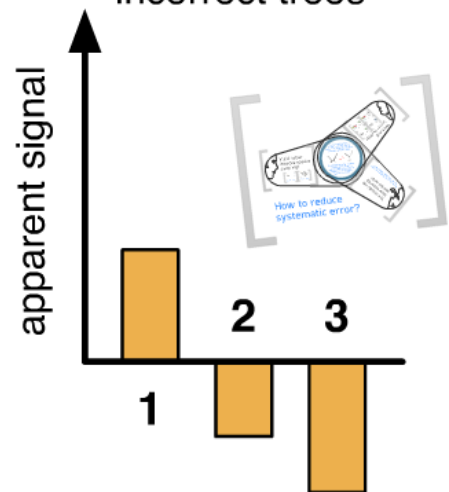
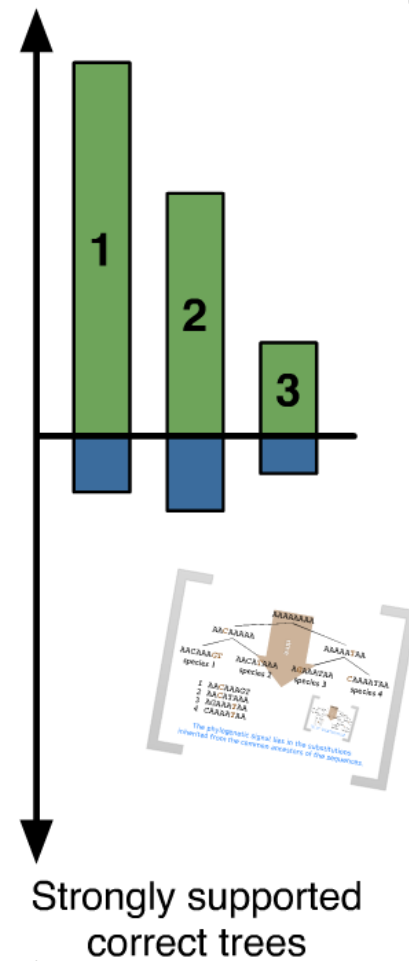
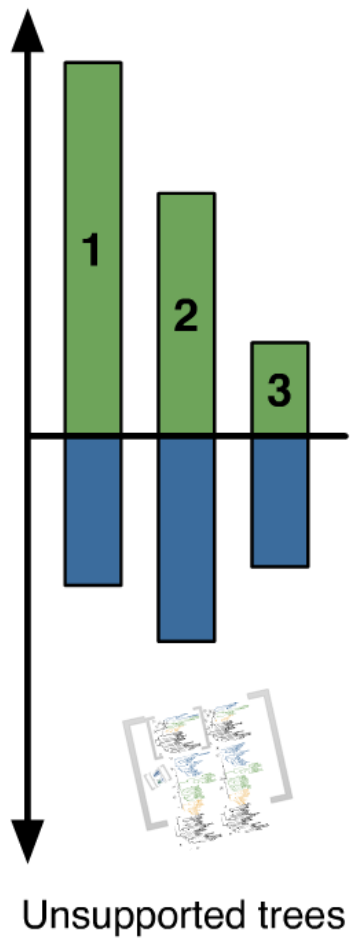
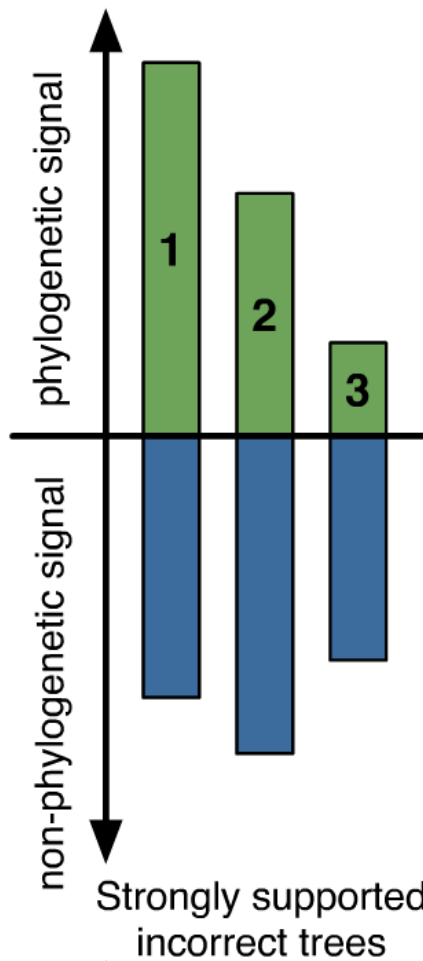


1 global « dynamic »
replacement matrix

+



K distinct
compositional profiles



Computers as Genomic Time Machines for Meeting our Ancestors

Ediacaran (635-542)

What did the first
animal look like?



Dickinsonia (4 cm)

Cambrian (542-488)

Can we resolve the
Cambrian explosion?



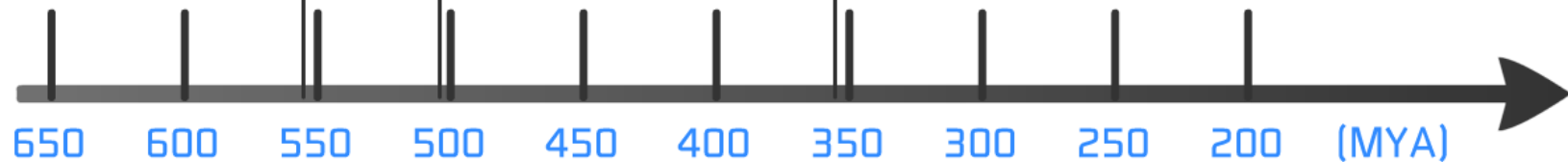
Anomalocaris (60-80 cm)

Devonian (416-359)

What was the fish that
first walked on land?



Acanthostega (50-55 cm)



Prof. Denis Baurain — ULg
Bioforum — April 18th, 2013

Ediacaran (635-542)

What did the first animal look like?



Cambrian (541-485)

Can we

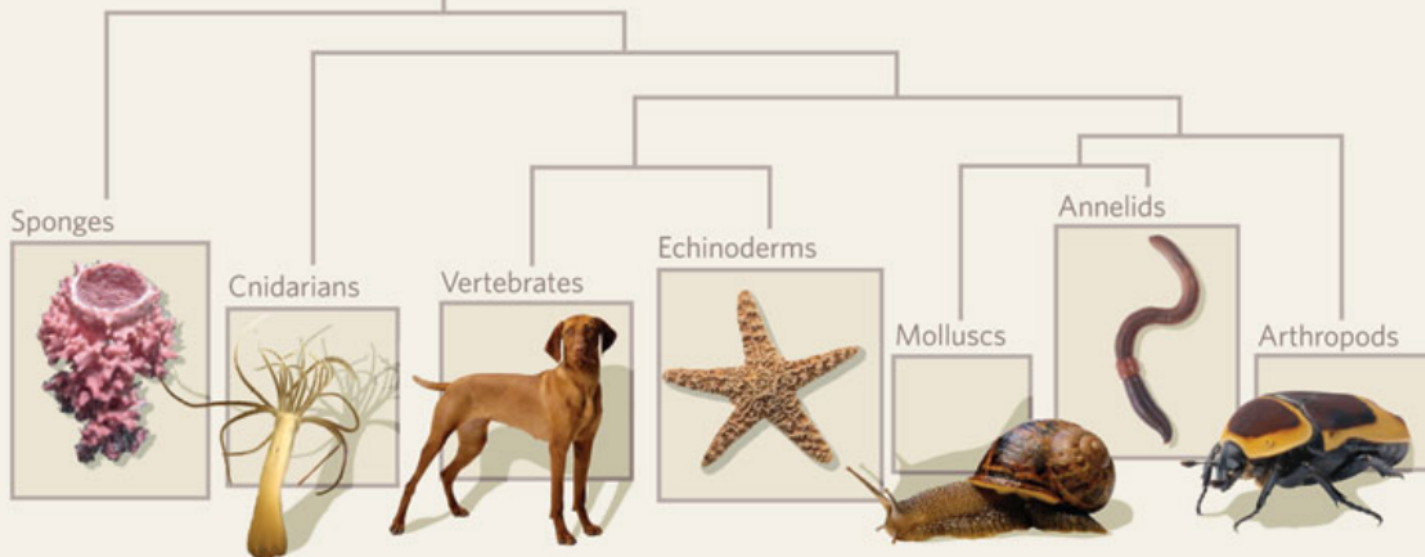
Camb

All tooled up

The animal ancestor, or urmetazoan, had a toolkit of genes that evolved to give the diversity of animal forms seen today.



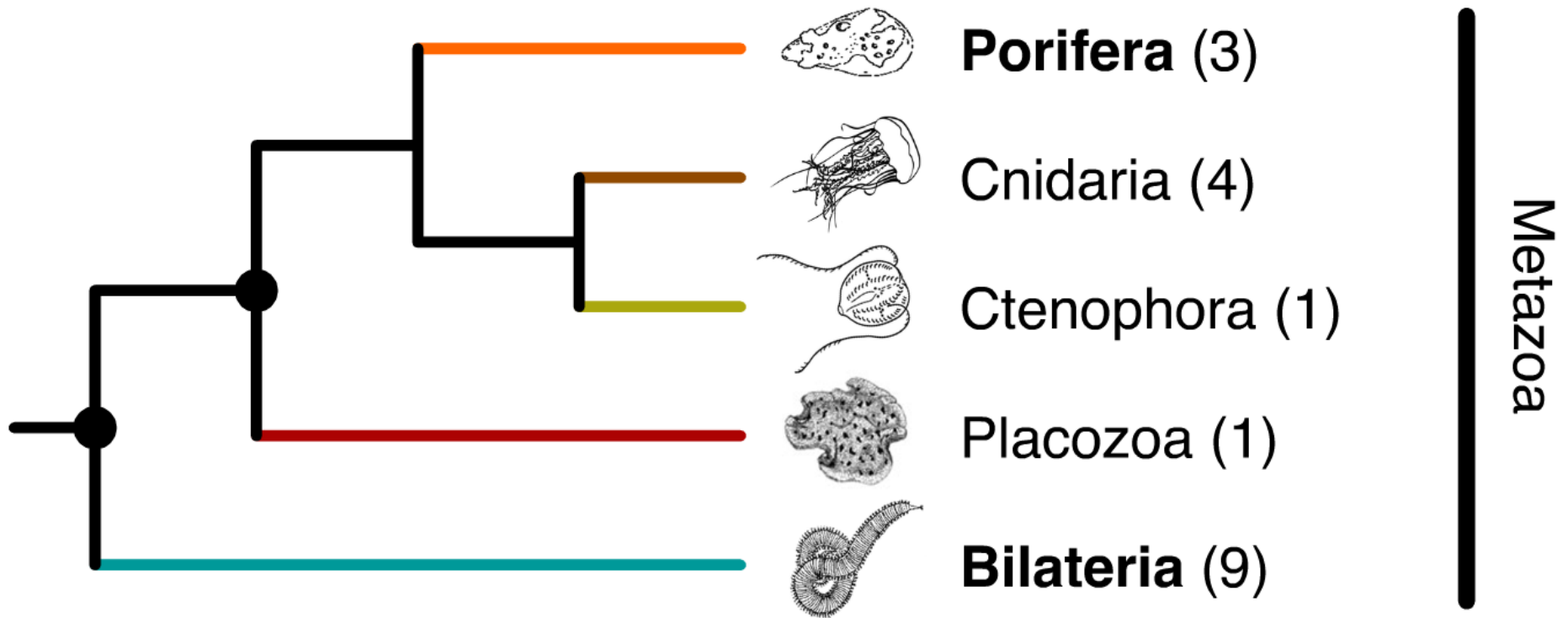
- Body-plan genes
- Specialized cell types
- Cells 'glued' together
- Communication system



The common ancestor of all animals is called the Urmethazoan. What did it look like?

Schierwater et al. (2009)

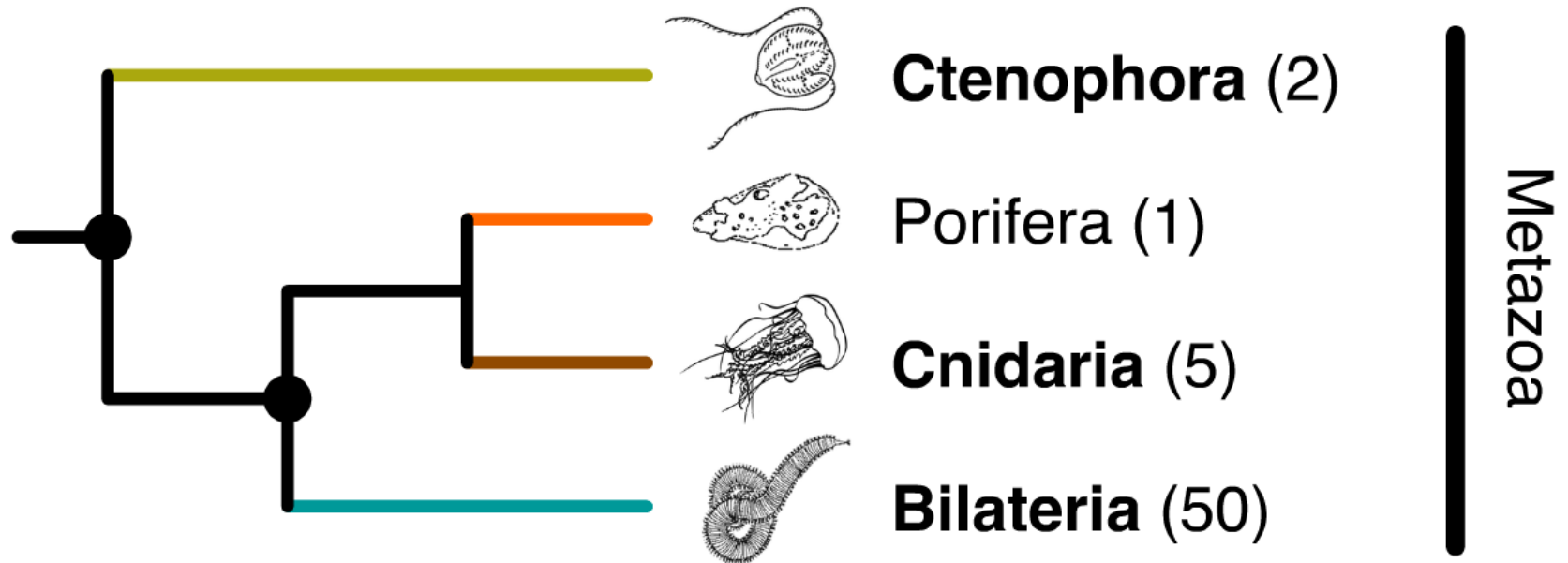
15 mitochondrial and 34 nuclear genes
GTR and WAG models



It was already very complex! All lineages are thus evolutionarily simplified except bilaterians.

Dunn et al. (2008)

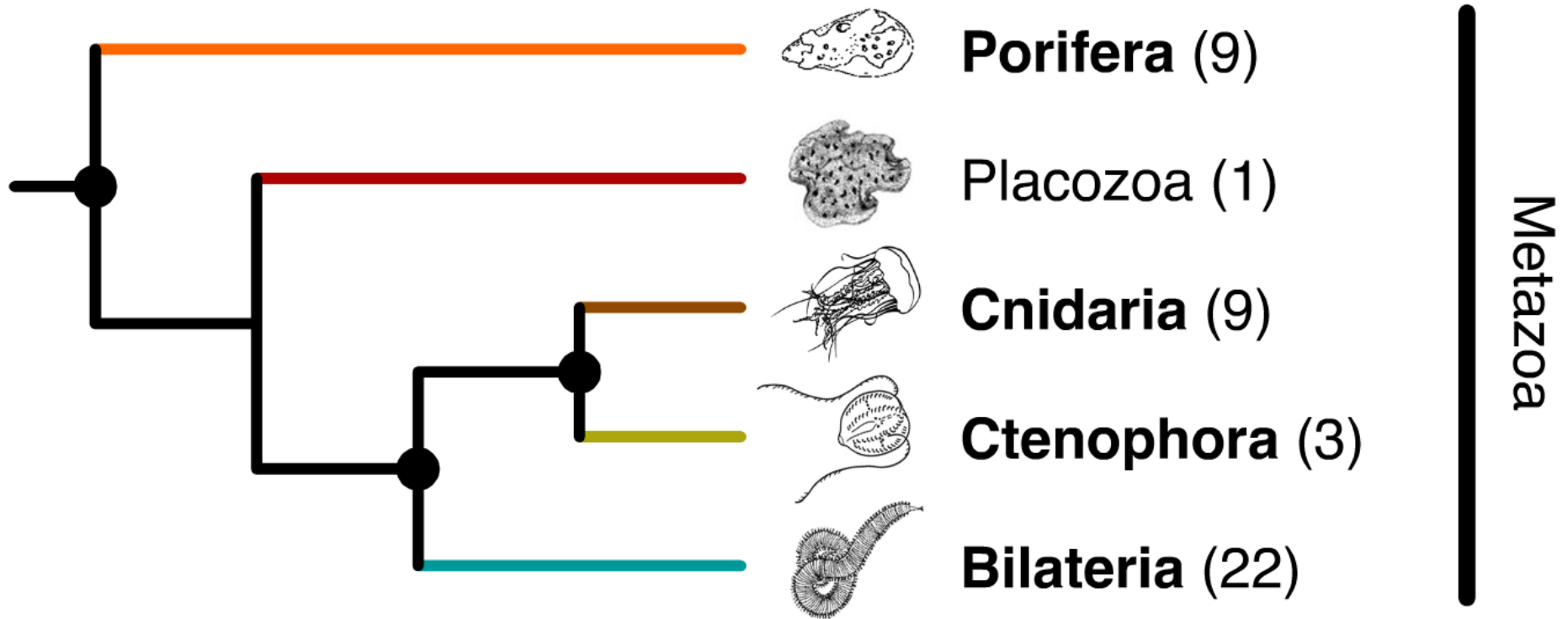
6 mitochondrial and 144 nuclear genes
WAG and CAT models



It featured several complex characters (e.g., neurons)! Or these have evolved convergently...

Philippe et al. (2009)

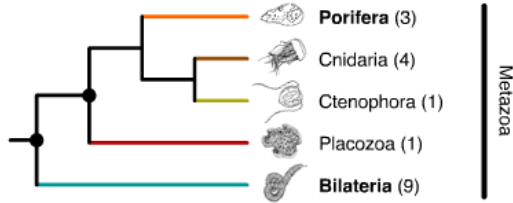
128 nuclear genes
CAT model



It might have been quite simple. Hey! Which one of these 3 strongly supported trees is correct?

Schierwater et al. (2009)

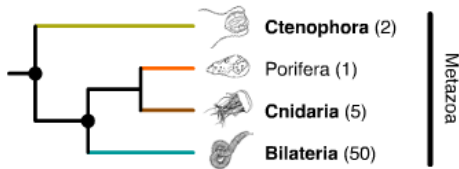
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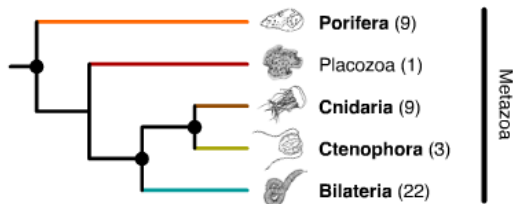
6 mitochondrial and 144 nuclear genes
WAG and CAT models



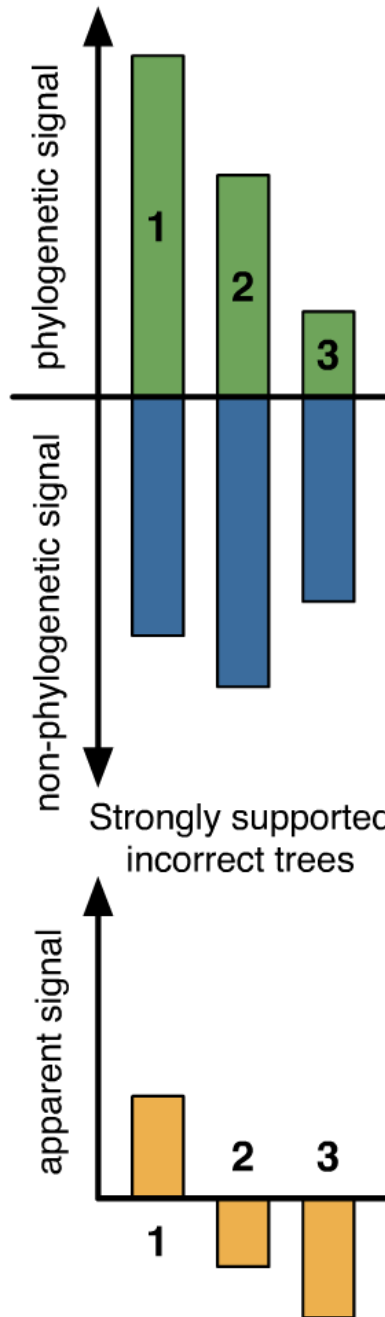
It featured several complex characters (e.g., neurons)! Or these have evolved convergently...

Philippe et al. (2009)

128 nuclear genes
CAT model



It might have been quite simple. Hey! Which one of these 3 strongly supported trees is correct?



For nodes with a scarce phylogenetic signal, even small amounts of non-phylogenetic signal may dominate and yield an incorrect tree.

Ironically, these nodes are those for which phylogenomics would be the most useful!

Diagram showing sources of artifacts: systematic error, missing data, and non-orthology. The text 'Let's look at 3 more sources of artifacts!' is written next to the diagram. Below the diagram, the text reads: 'What are the causes of the non-phylogenetic signal in the studies of Dunn et al. (2008) and Schierwater et al. (2009)?'

systematic error

Failure to reduce systematic error with the dataset of Philippe et al. (2009) also yields artifactual trees.

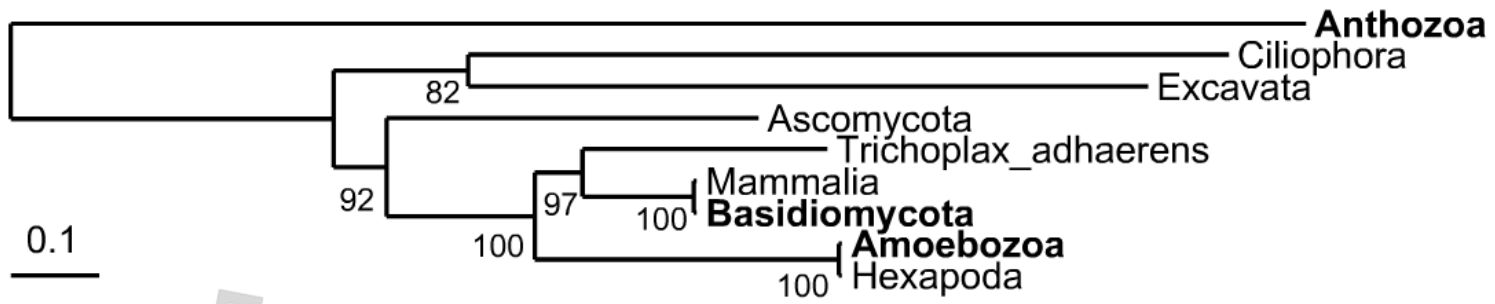
missing data

non-orthology

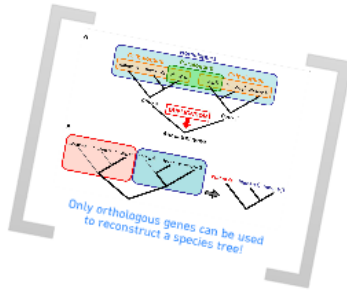
Let's look at 3 more sources of artifacts!

What are the causes of the non-phylogenetic signal in the studies of Dunn et al. (2008) and Schierwater et al. (2009)?

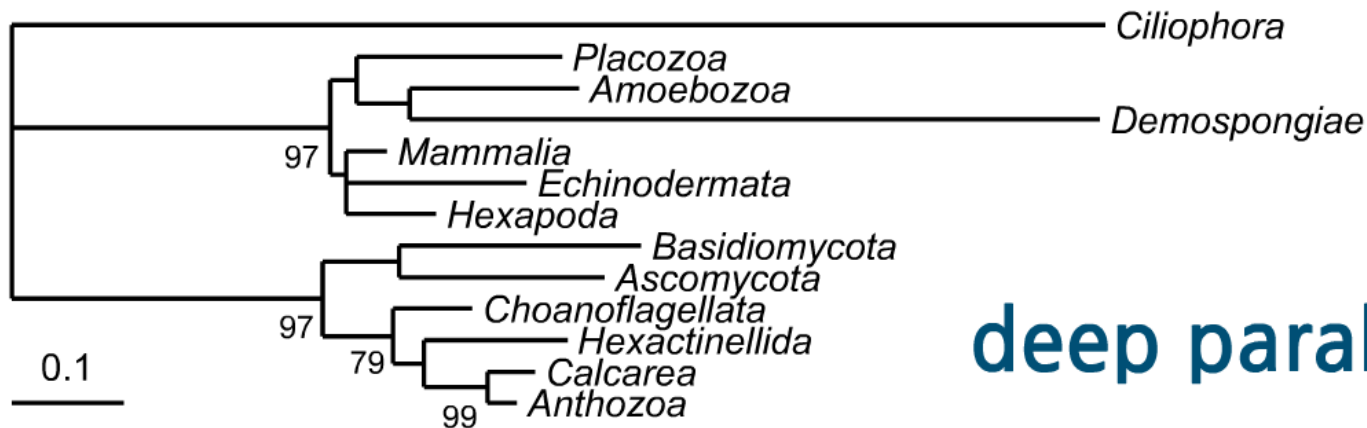
contaminations (xenology)



RP3 gene in Schierwater et al. (2009)

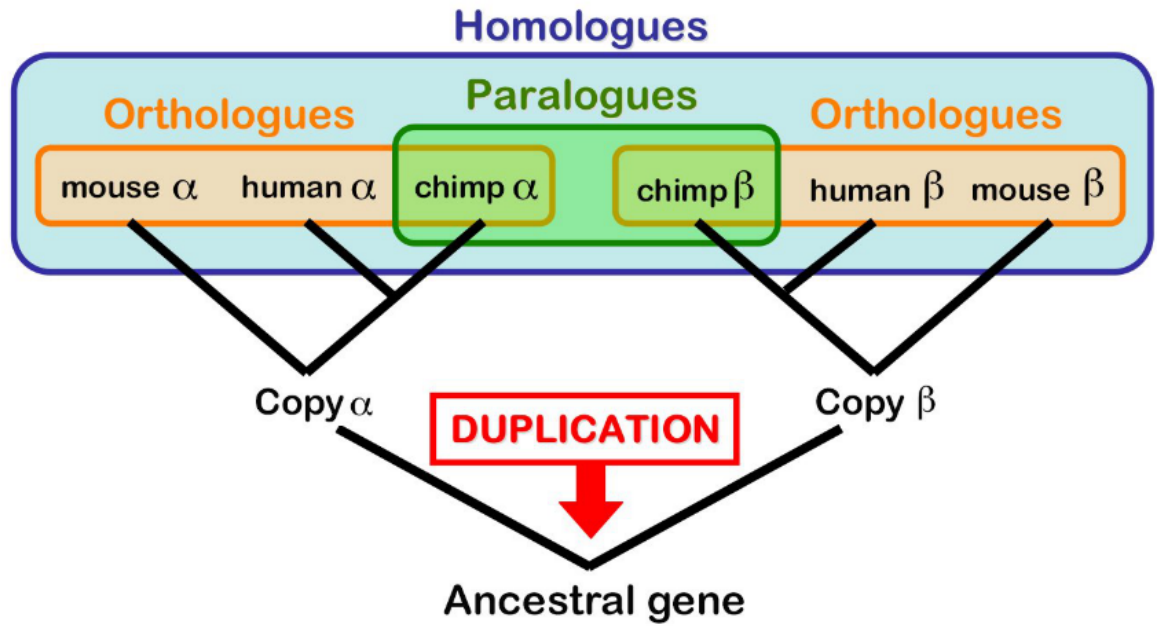


CDC gene in Schierwater et al. (2009)

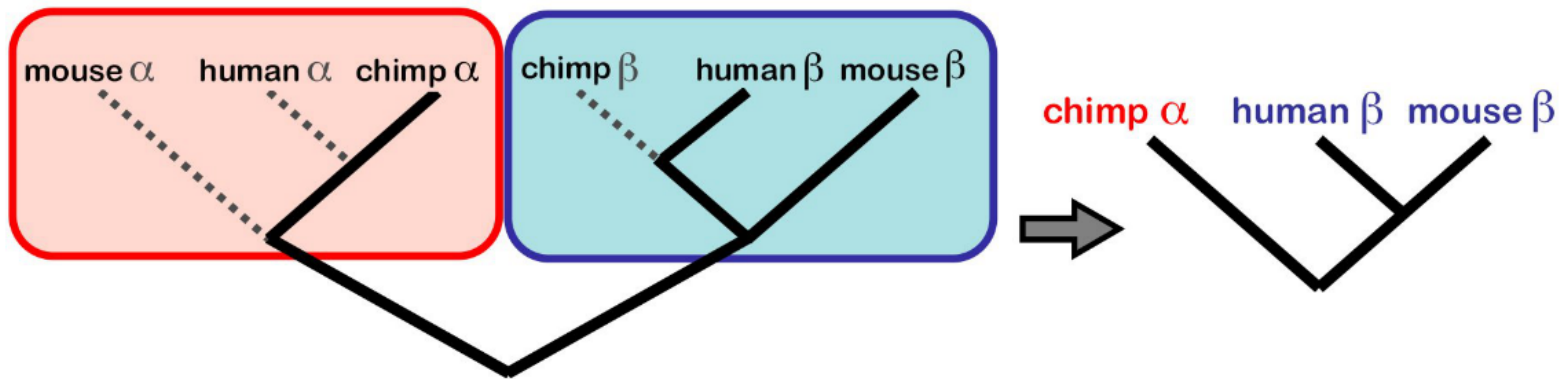


deep paralogy

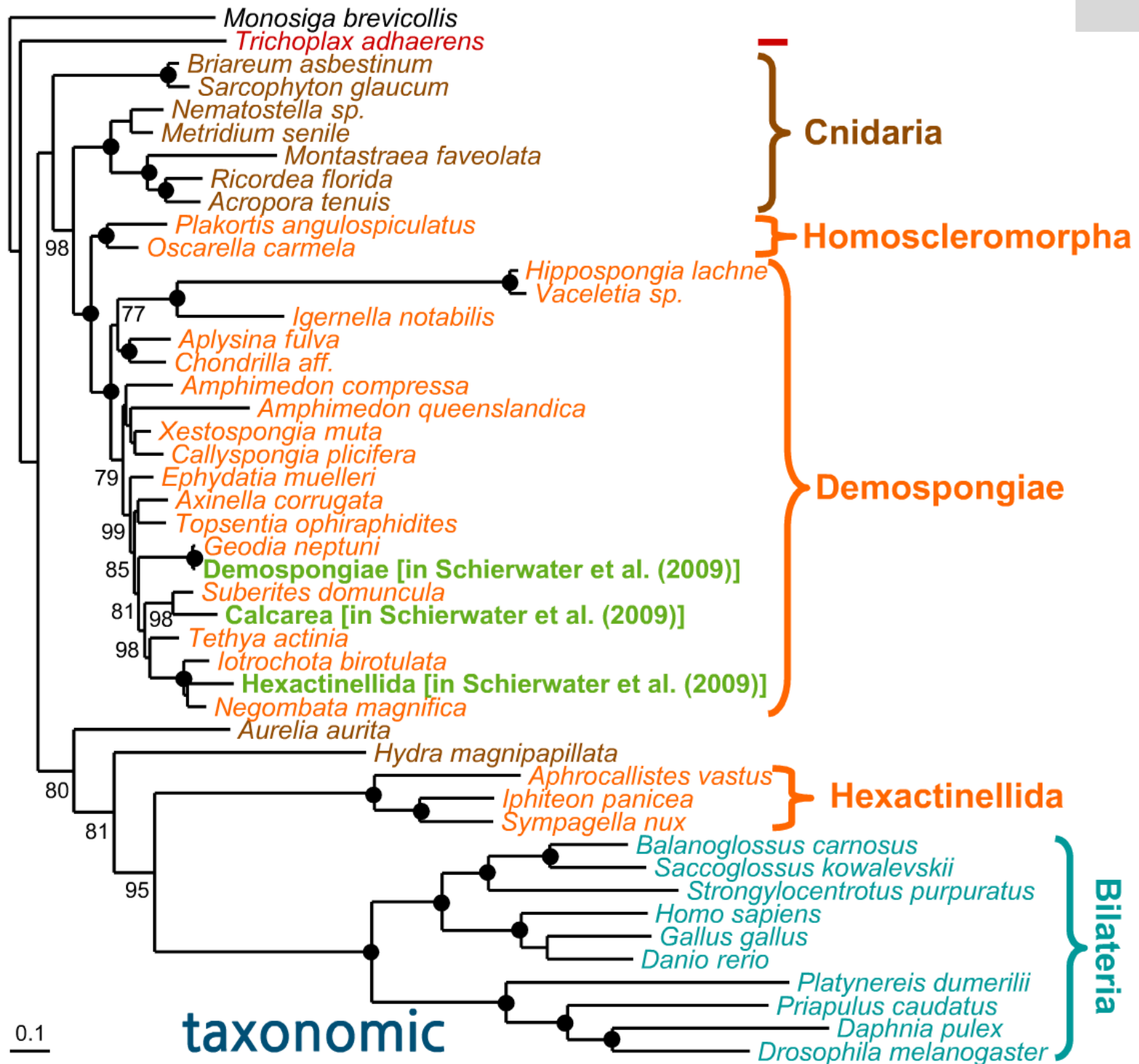
A



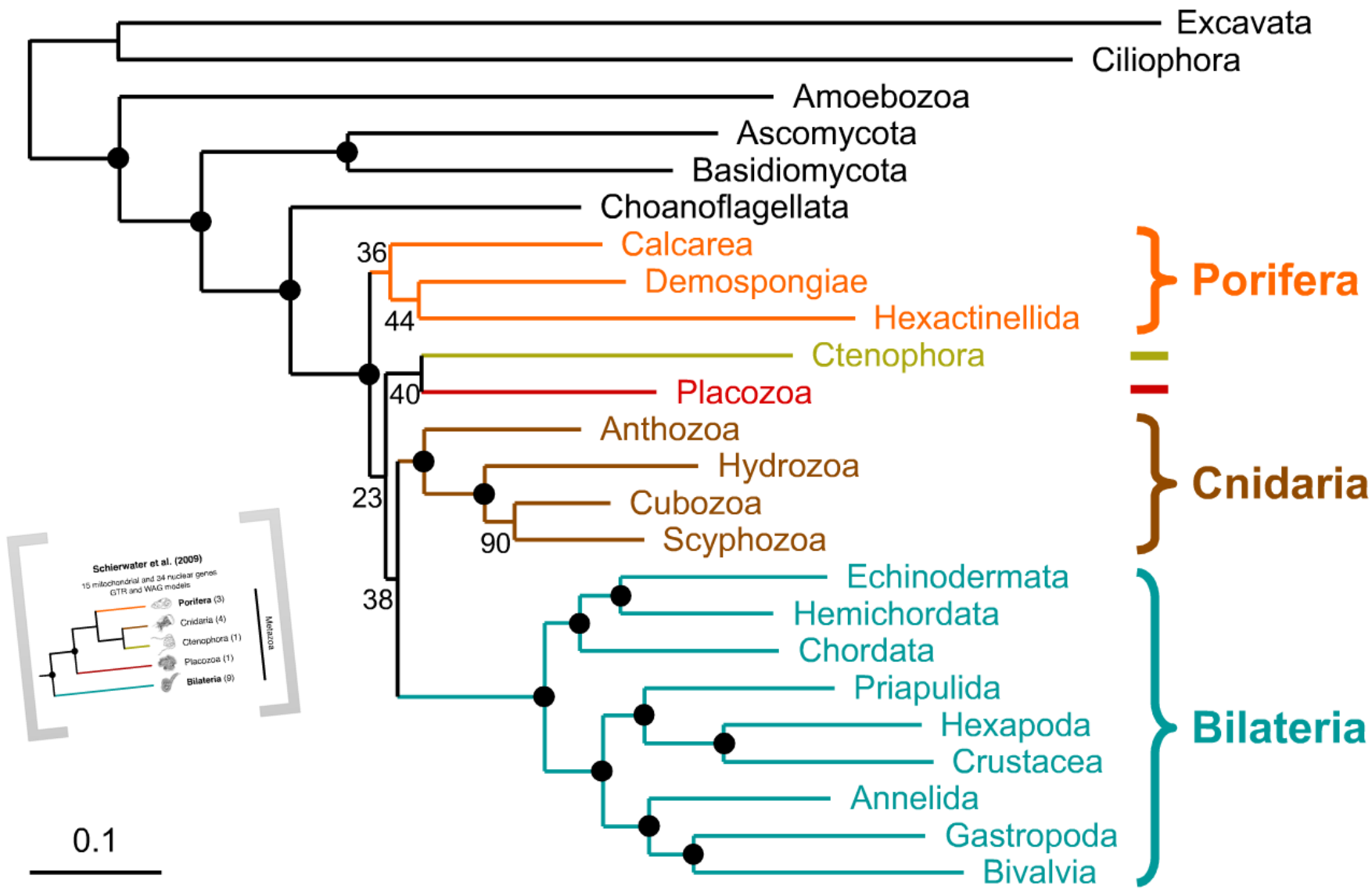
B



Only orthologous genes can be used to reconstruct a species tree!



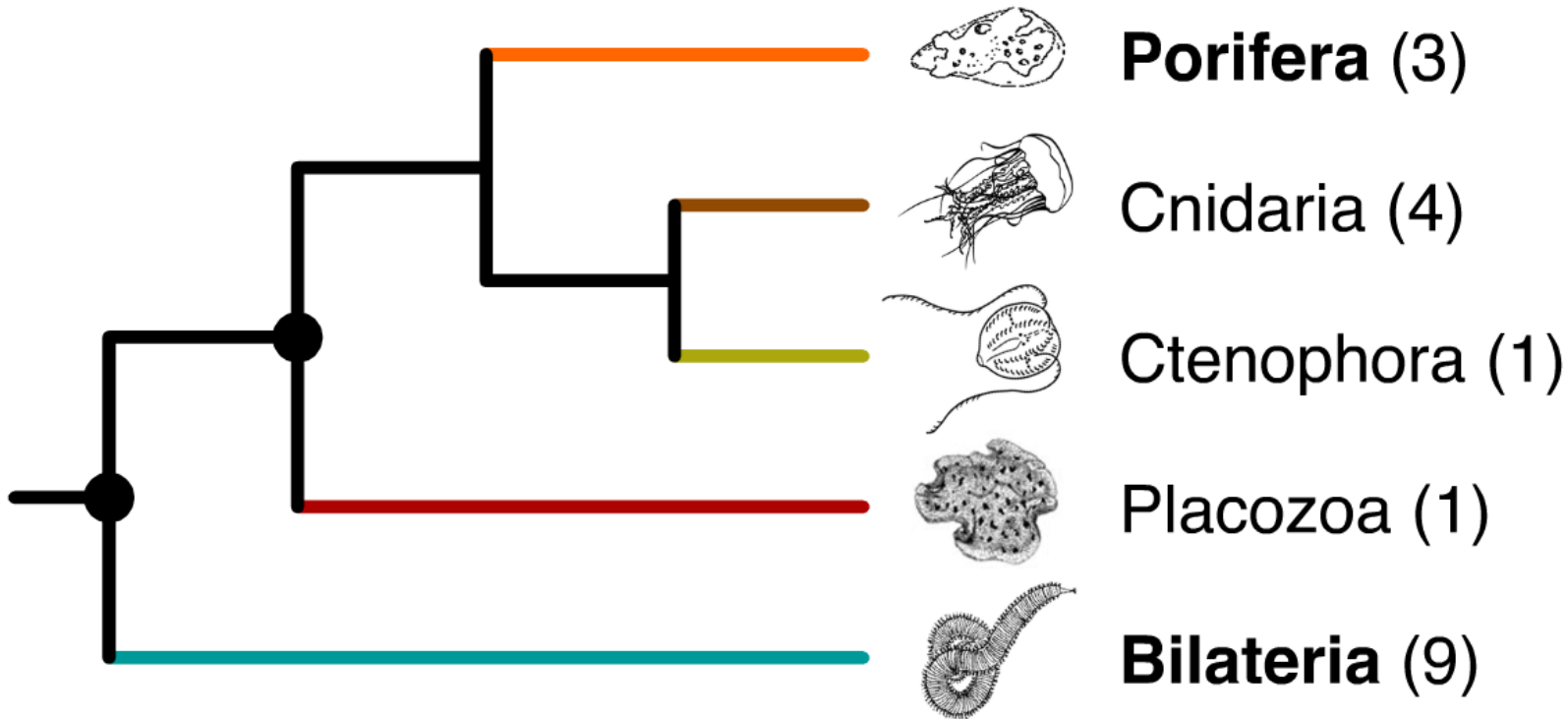
taxonomic
misidentification



Purging the dataset of Schierwater et al. (2009) of its errors yields a very different tree.

Schierwater et al. (2009)

15 mitochondrial and 34 nuclear genes
GTR and WAG models



Metazoa

systematic error

Failure to reduce systematic error with the dataset of Philippe et al. (2009) also yields artifactual trees.

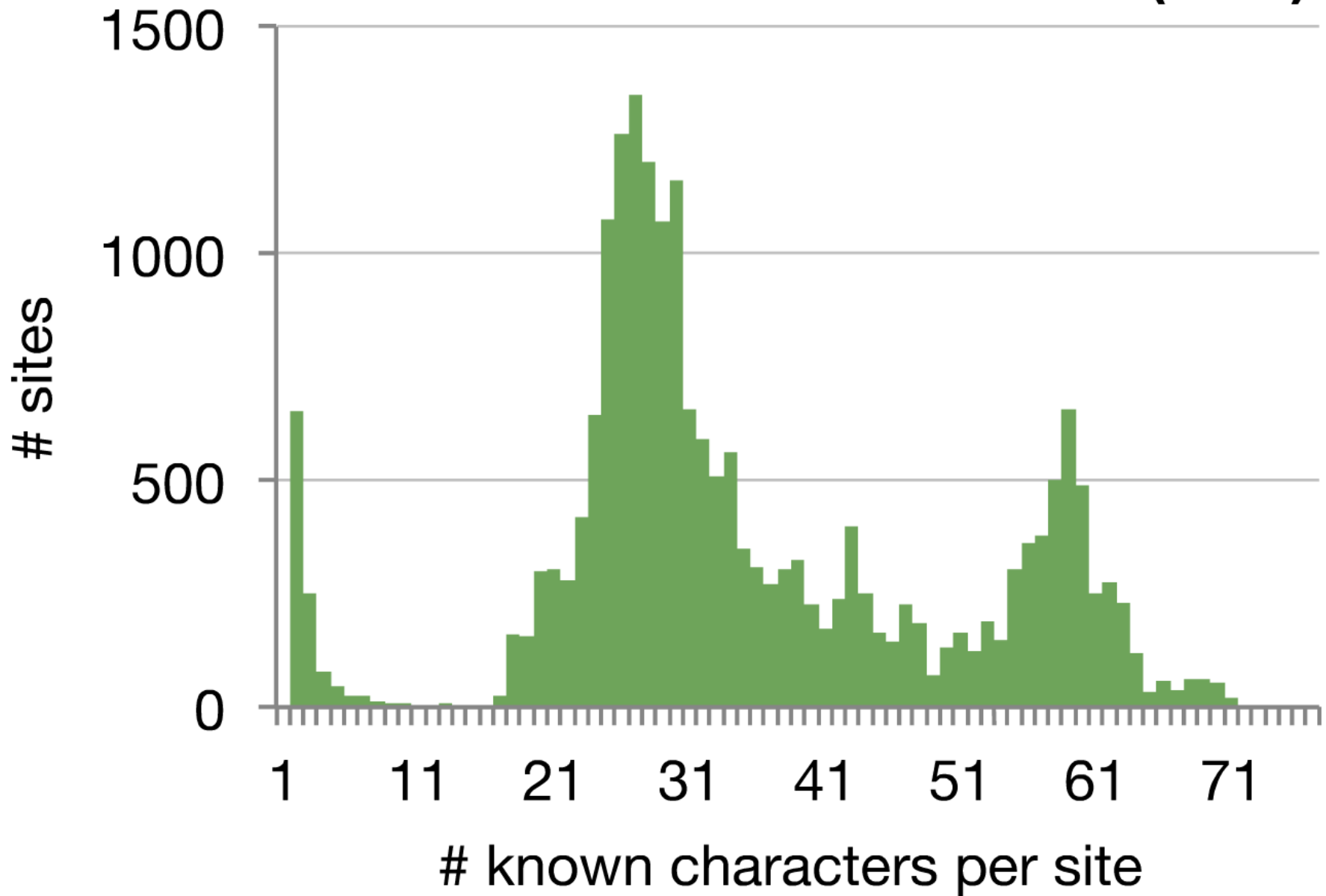
missing data

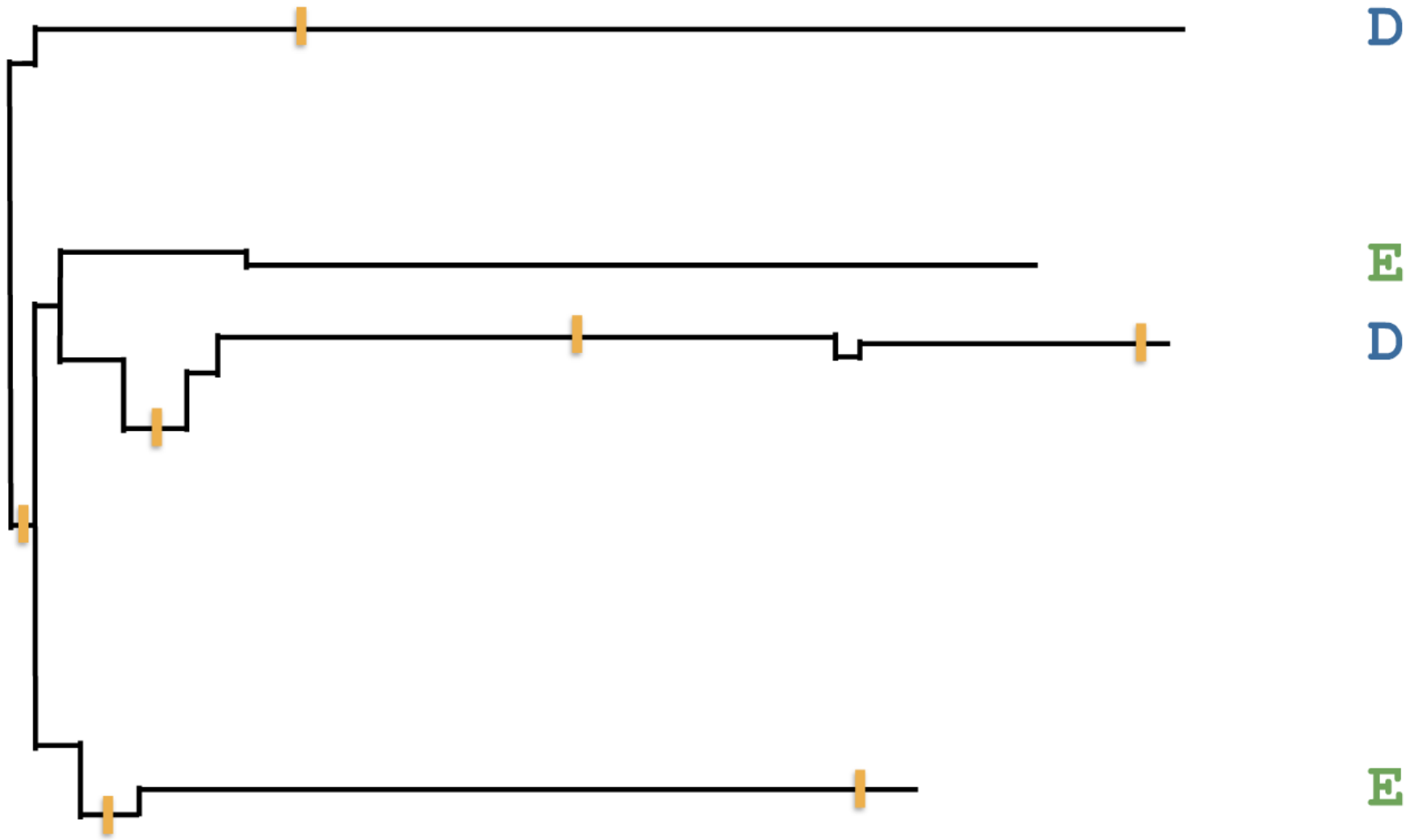
non-orthology

Let's look at 3 more sources of artifacts!

What are the causes of the non-phylogenetic signal in the studies of Dunn et al. (2008) and Schierwater et al. (2009)?

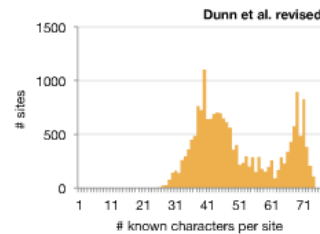
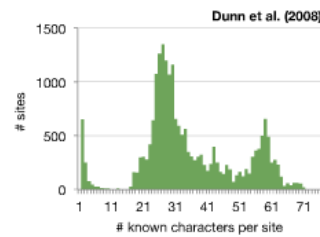
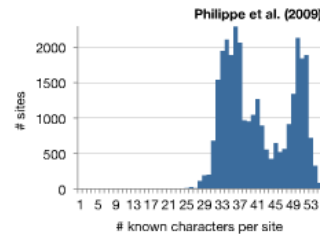
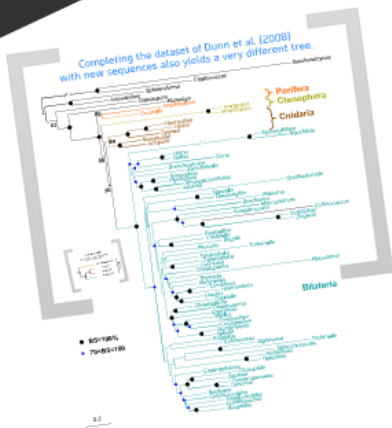
Dunn et al. (2008)



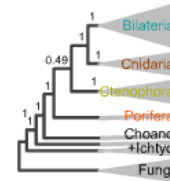


Missing data exacerbate the systematic error by reducing the number of species effectively available.

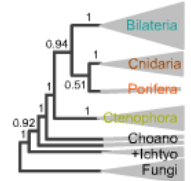
missing data



Dunn et al. with completed outgroup



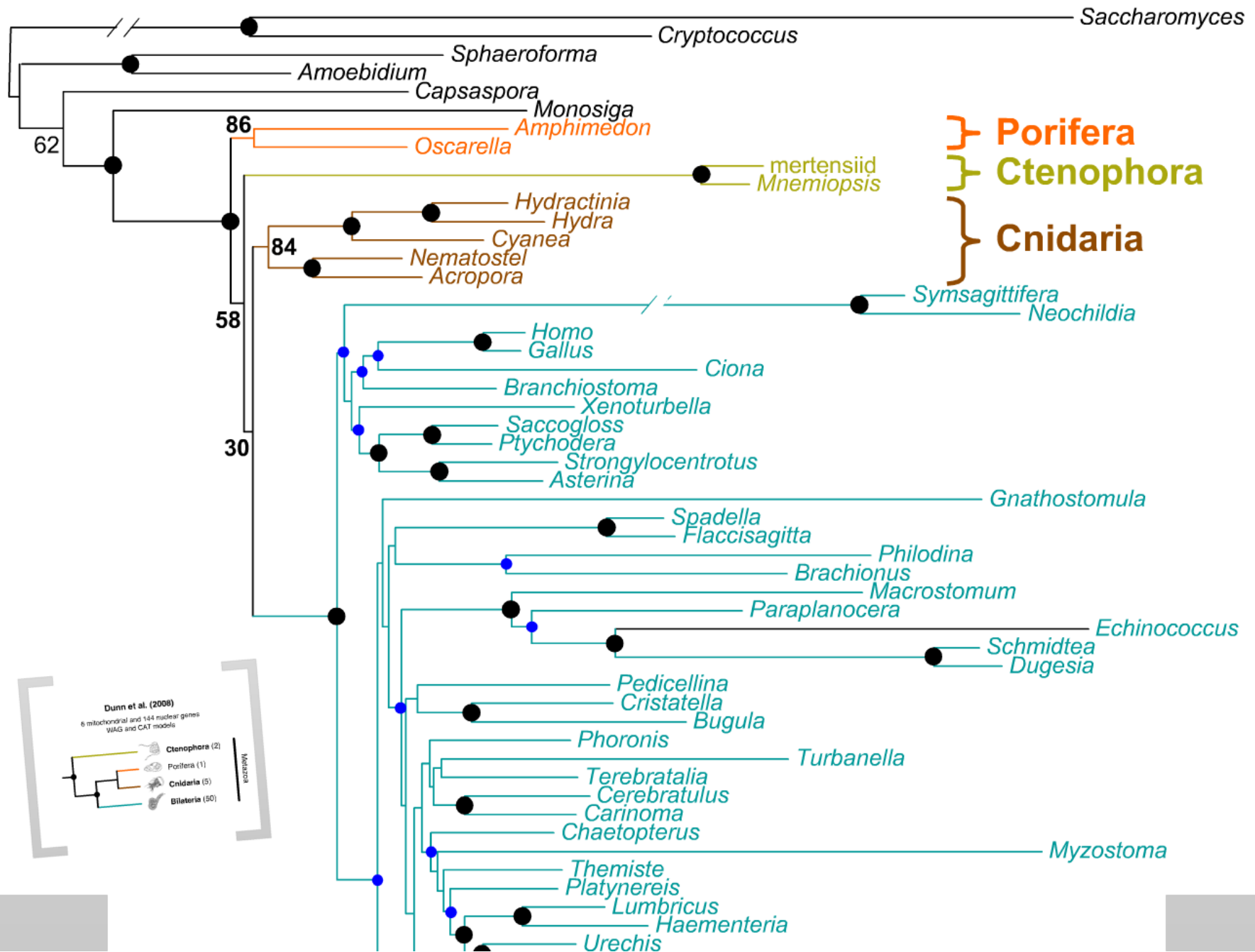
Dunn et al. (2008)



Actually, it is enough to complete the 4 close outgroup sequences (choanoflagellates) to change the tree.

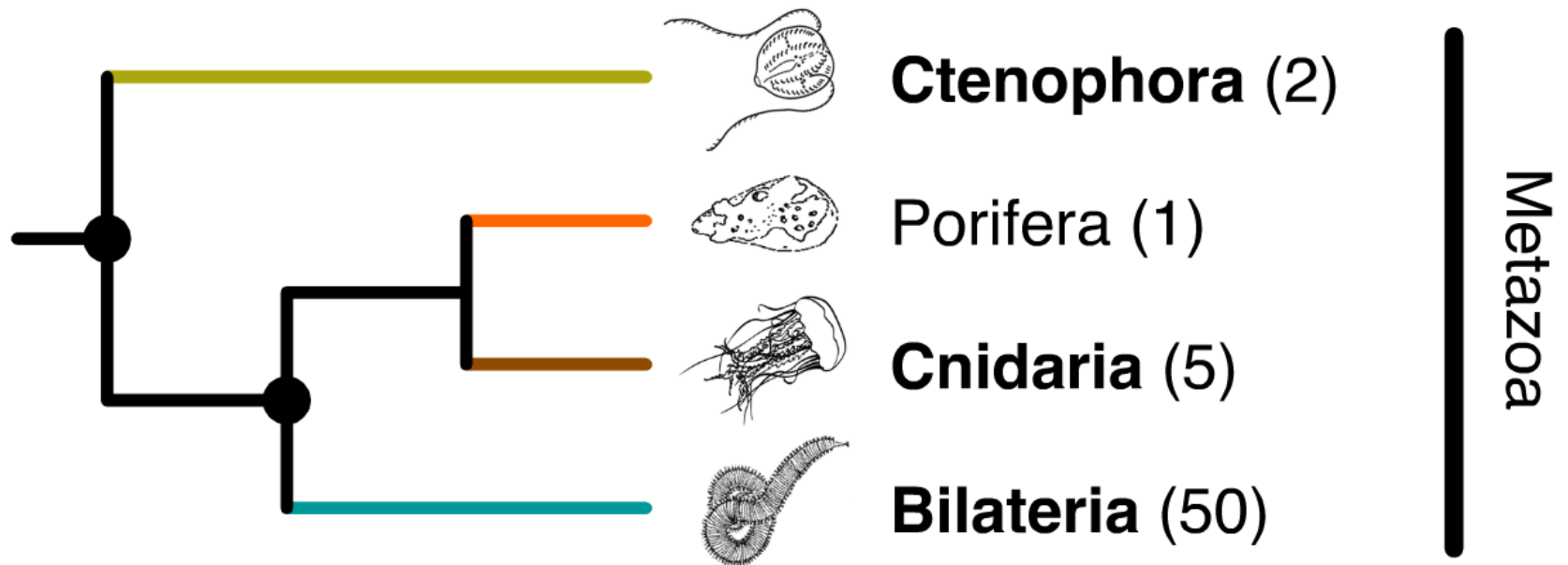


Completing the dataset of Dunn et al. (2008) with new sequences also yields a very different tree.

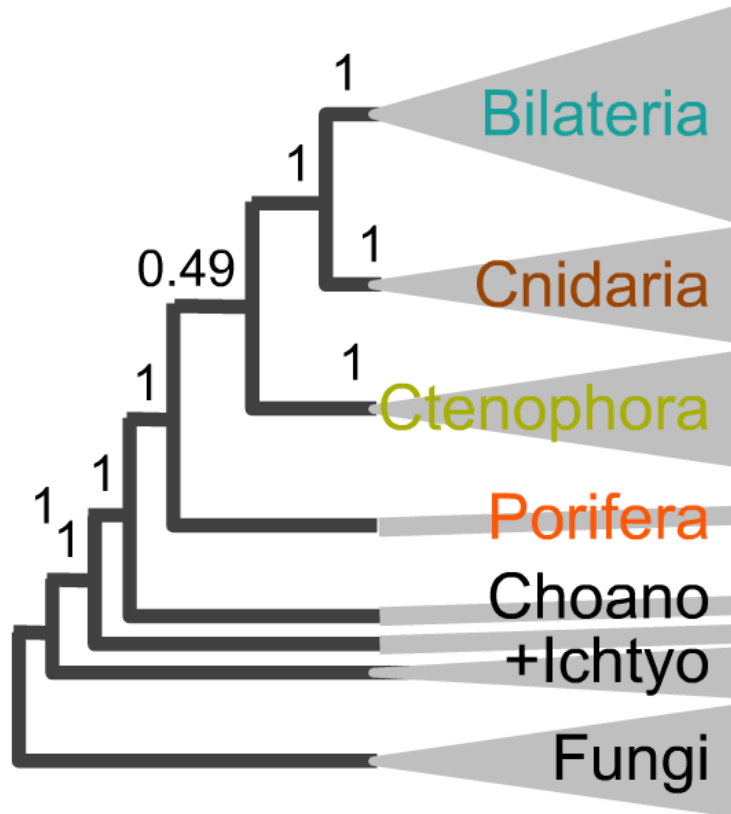


Dunn et al. (2008)

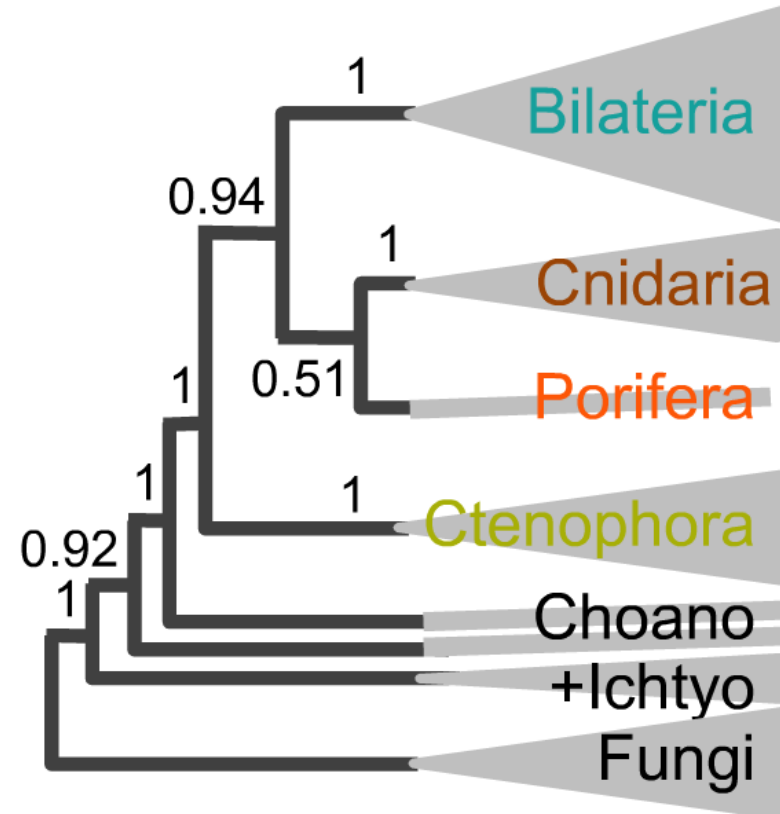
6 mitochondrial and 144 nuclear genes
WAG and CAT models



**Dunn et al. with
completed outgroup**



Dunn et al. (2008)



Actually, it is enough to complete the 4 close outgroup sequences (choanoflagellates) to change the tree.

systematic error

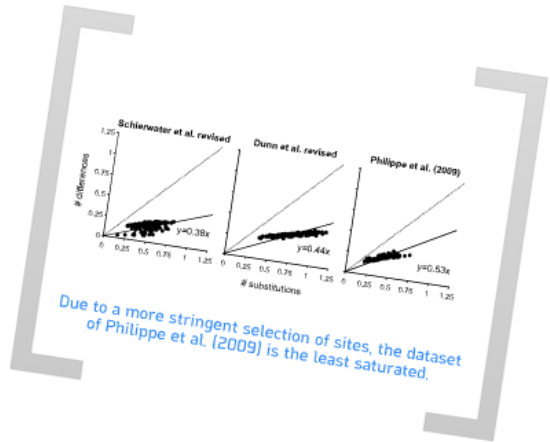
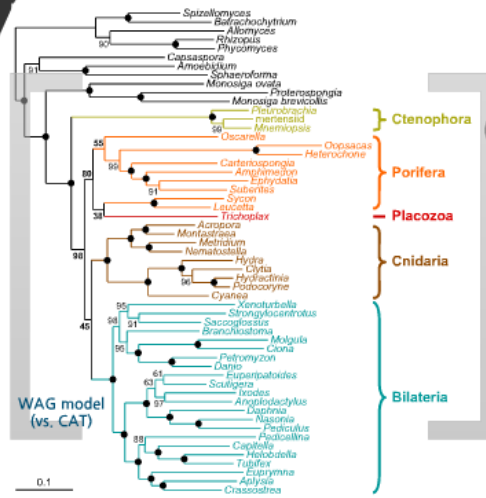
Failure to reduce systematic error with the dataset of Philippe et al. (2009) also yields artifactual trees.

missing data

non-orthology

Let's look at 3 more sources of artifacts!

What are the causes of the non-phylogenetic signal in the studies of Dunn et al. (2008) and Schierwater et al. (2009)?

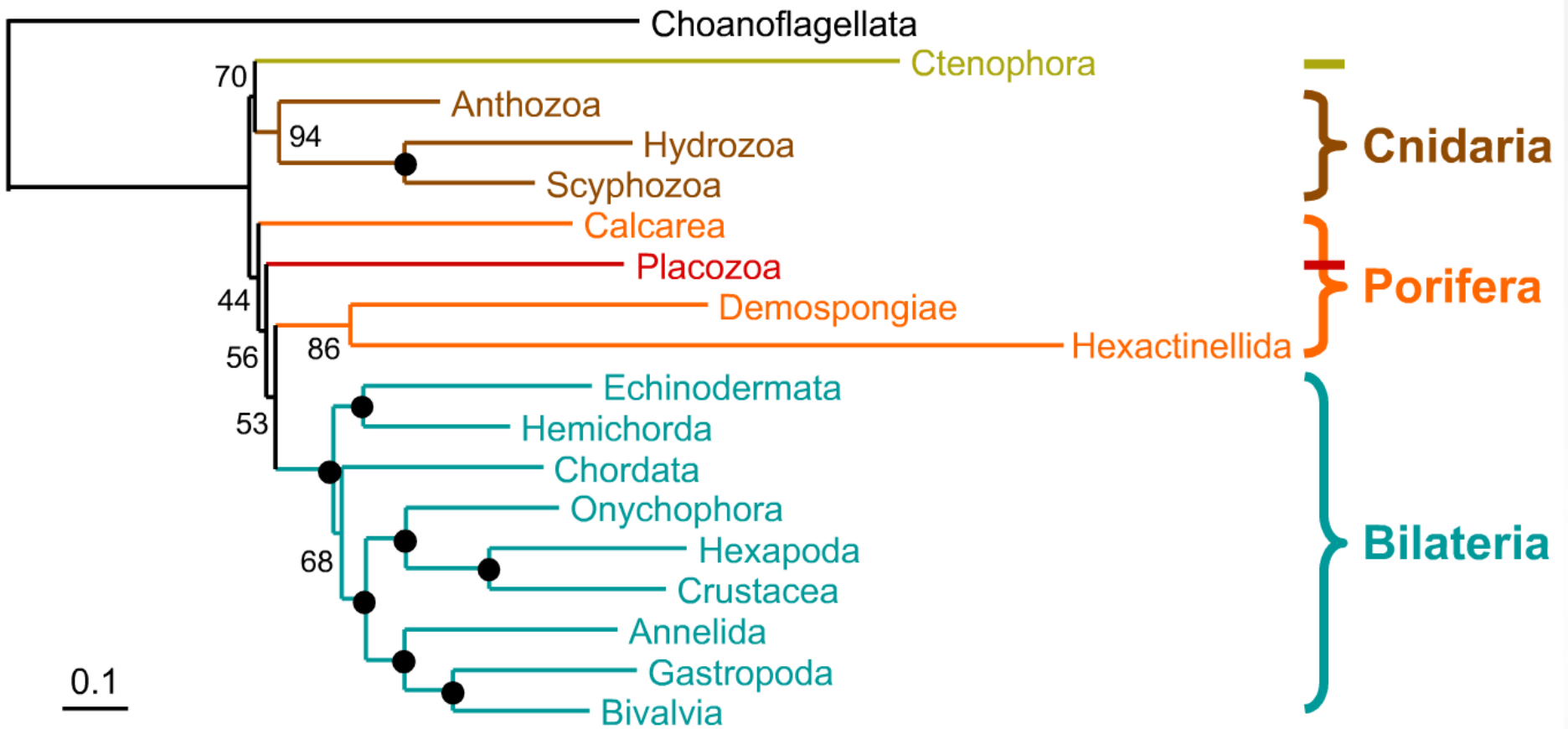


Due to a more stringent selection of sites, the dataset of Philippe et al. (2009) is the least saturated.

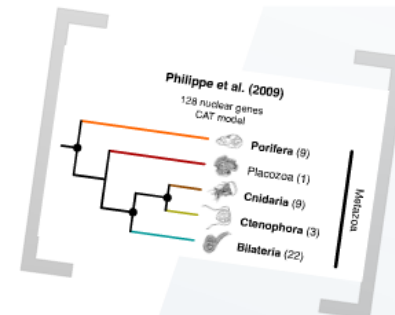


systematic error

Failure to reduce systematic error with the dataset of Philippe et al. (2009) also yields artifactual trees.

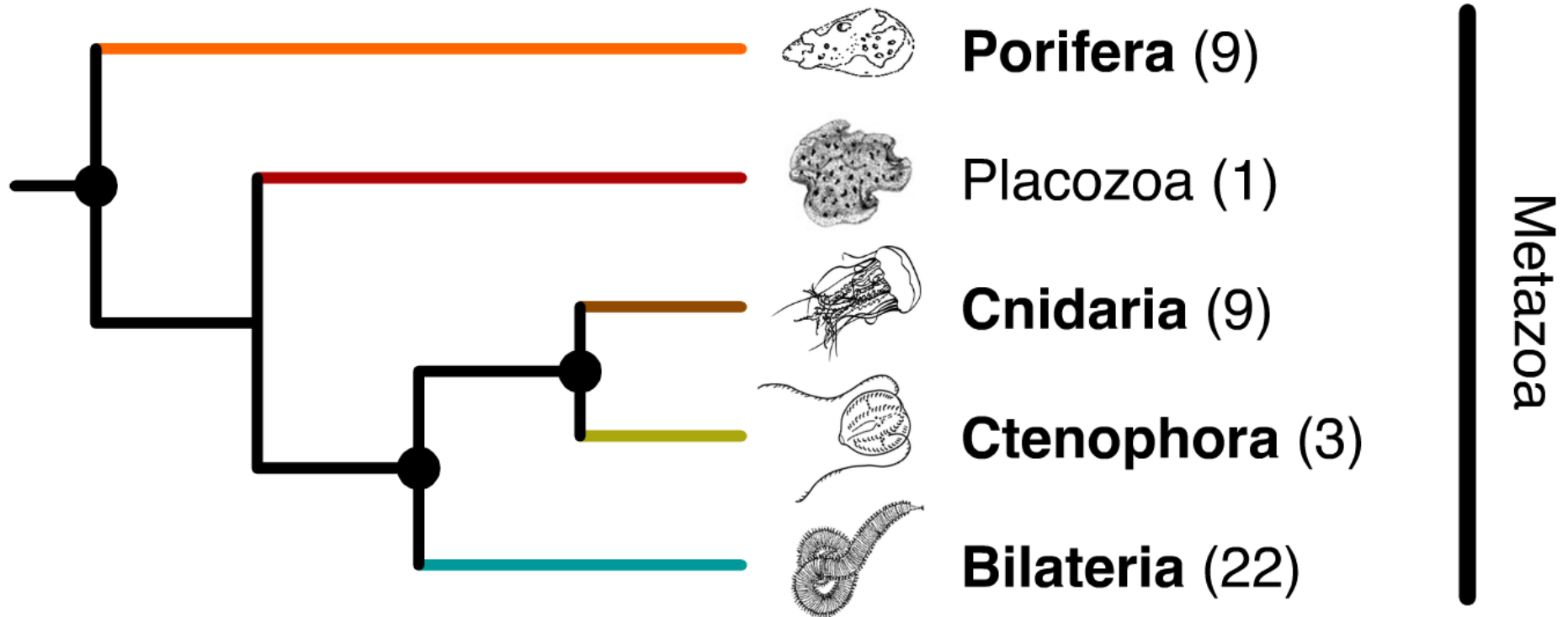


reduced taxon sampling

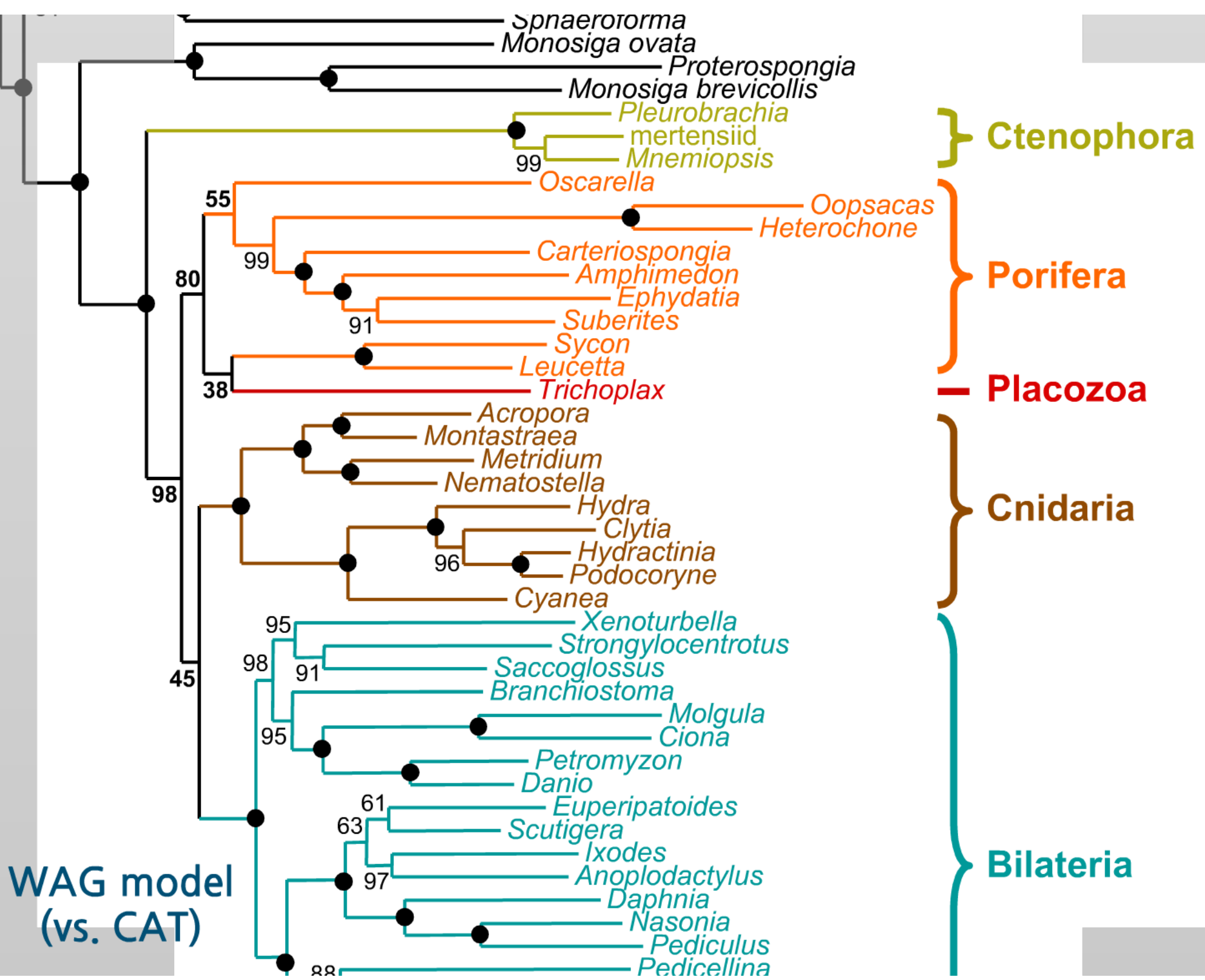


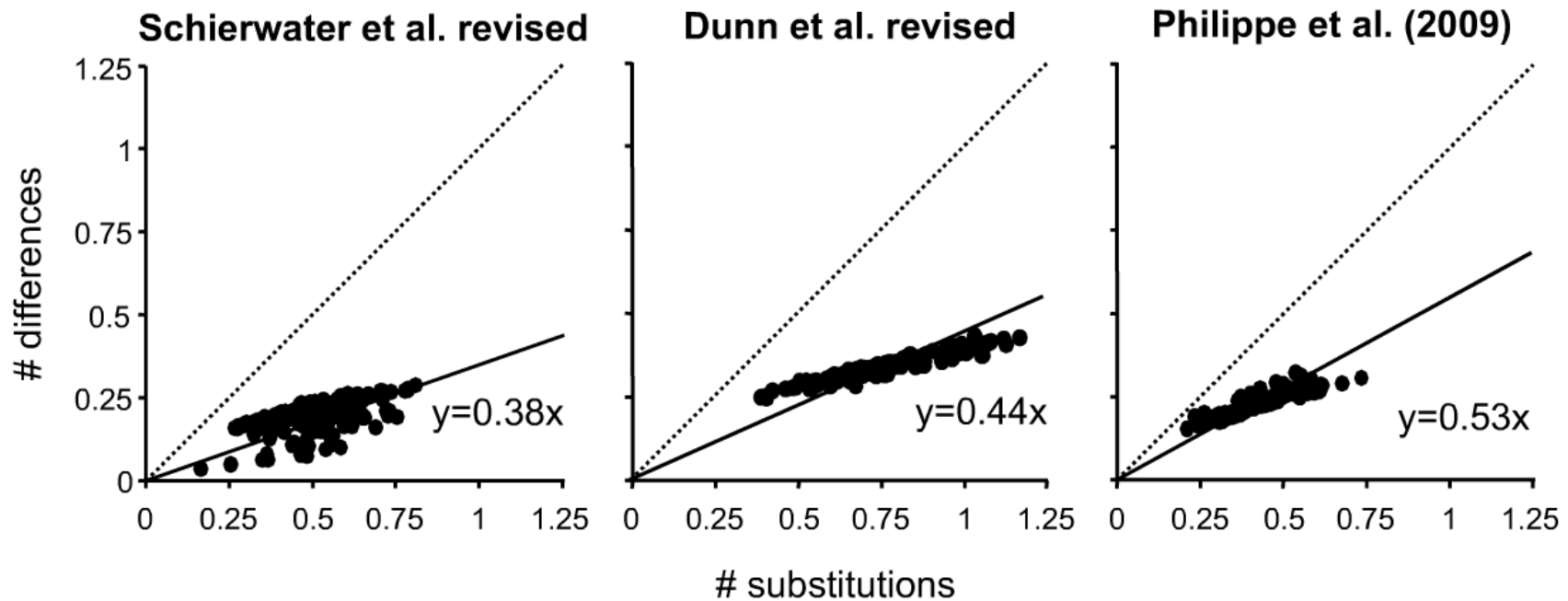
Philippe et al. (2009)

128 nuclear genes
CAT model

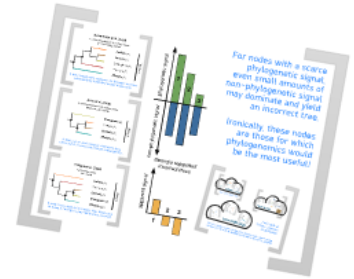
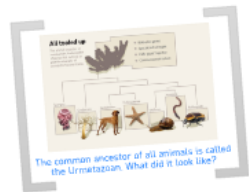


WAG model
(vs. CAT)

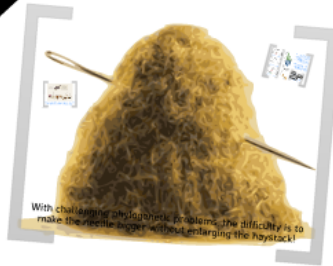
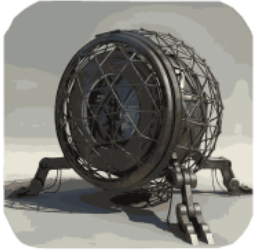




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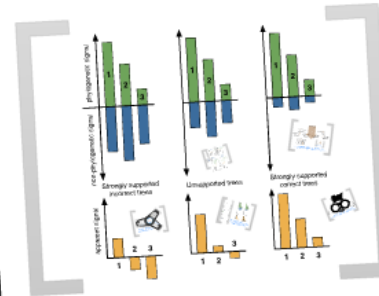


With challenging phylogenetic problems, the difficulty is to make the needle bigger without enlarging the haystack!



With challenging phylogenetic problems, the difficulty is to make the needle bigger - *without* enlarging the haystack!

more sequences
are not enough

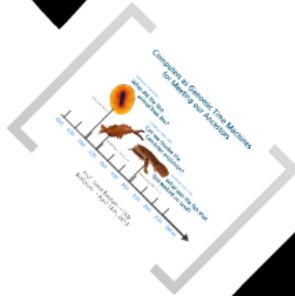


phylogenetic vs.
non-phylogenetic signal



The coelacanth is a large marine fish with fleshy fins that resembles the limbs of terrestrial vertebrates.

phylogenomics can resolve
the evolution of animals



acknowledgment

Université 
de Montréal

- Herve Philippe
- Henner Brinkmann
- Beatrice Roure

Starting grant SFRD-12/04 (FSR)


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Université
de Liège



references



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The African coelacanth genome provides insights into tetrapod evolution.
Nature 496, 311-316.

Roure B, Baurain D, Philippe H (2013)

Impact of missing data on phylogenies inferred from empirical phylogenomic data sets.
Mol Biol Evol 30, 197-214.

Philippe H, Brinkmann H, Lavrov DV, Littlewood DT, Manuel M, Wreheide G, Baurain D (2011)

Resolving difficult phylogenetic questions: why more sequences are not enough.
PLoS Biol 9, e1000602.

Baurain D, Philippe H (2010)

Current approaches to phylogenomic reconstruction.
In Evolutionary Genomics and Systems Biology, ed Caetano-Anolles G (Wiley-Blackwell, Hoboken, N.J.), pp 17-41.

Baurain D, Brinkmann H, Philippe H (2007)

Lack of resolution in the animal phylogeny: closely spaced cladogeneses or undetected systematic errors?
Mol Biol Evol 24, 6-9.

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THIS WEEK

EDITORIALS

Look after the pennies

Government decisions about where to spend and where to cut should be based on evidence, not ideology.

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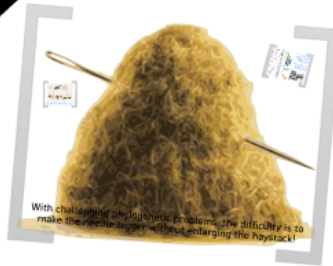

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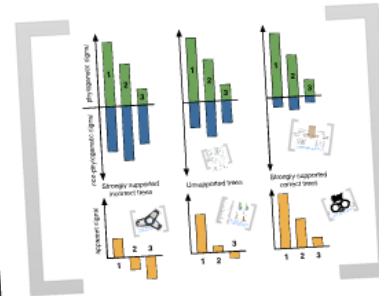
1. **Structural and molecular interrogation of intact biological systems**
Nature | 10 April 2013
2. **Towards practical, high-capacity, low-maintenance information storage in synthesized DNA**
Nature | 23 January 2013
3. **Funding: Australia's grant system wastes time**
Nature | 20 March 2013
4. **Live imaging of stem cell and progeny behaviour in physiological hair-follicle regeneration**
Nature | 01 July 2012
5. **High-level semi-synthetic production of the potent antimalarial artemisinin**
Nature | 10 April 2013

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With challenging phylogenetic problems, the difficulty is to make the needle bigger - *without* enlarging the haystack!

more sequences
are not enough



phylogenetic vs.
non-phylogenetic signal



Latimeria chalumnae

The coelacanth is a large marine fish with fleshy fins that resembles the limbs of terrestrial vertebrates.

phylogenomics can resolve
the evolution of animals

