On the Origin of Morphospecies

Using Bayesian Phylogenetics to Quantify the Mode of Ancestor Descendant Relationships in Paleozoic Invertebrates

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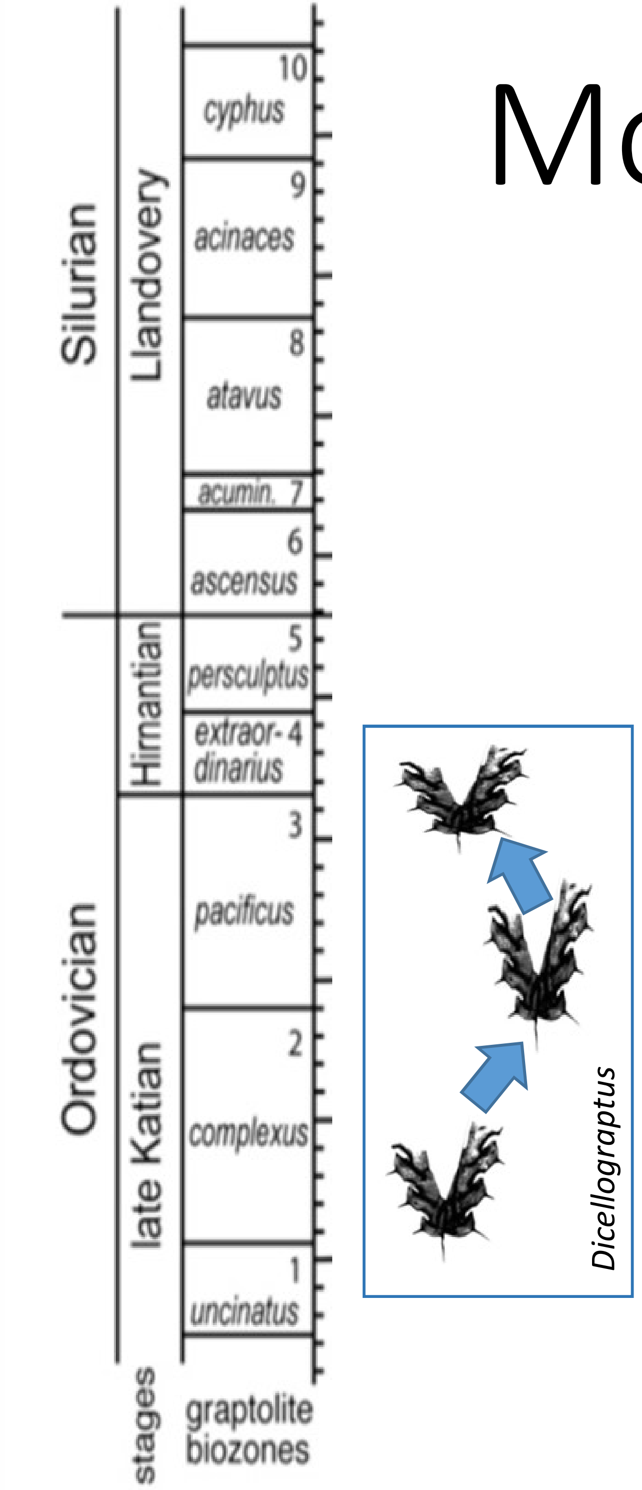
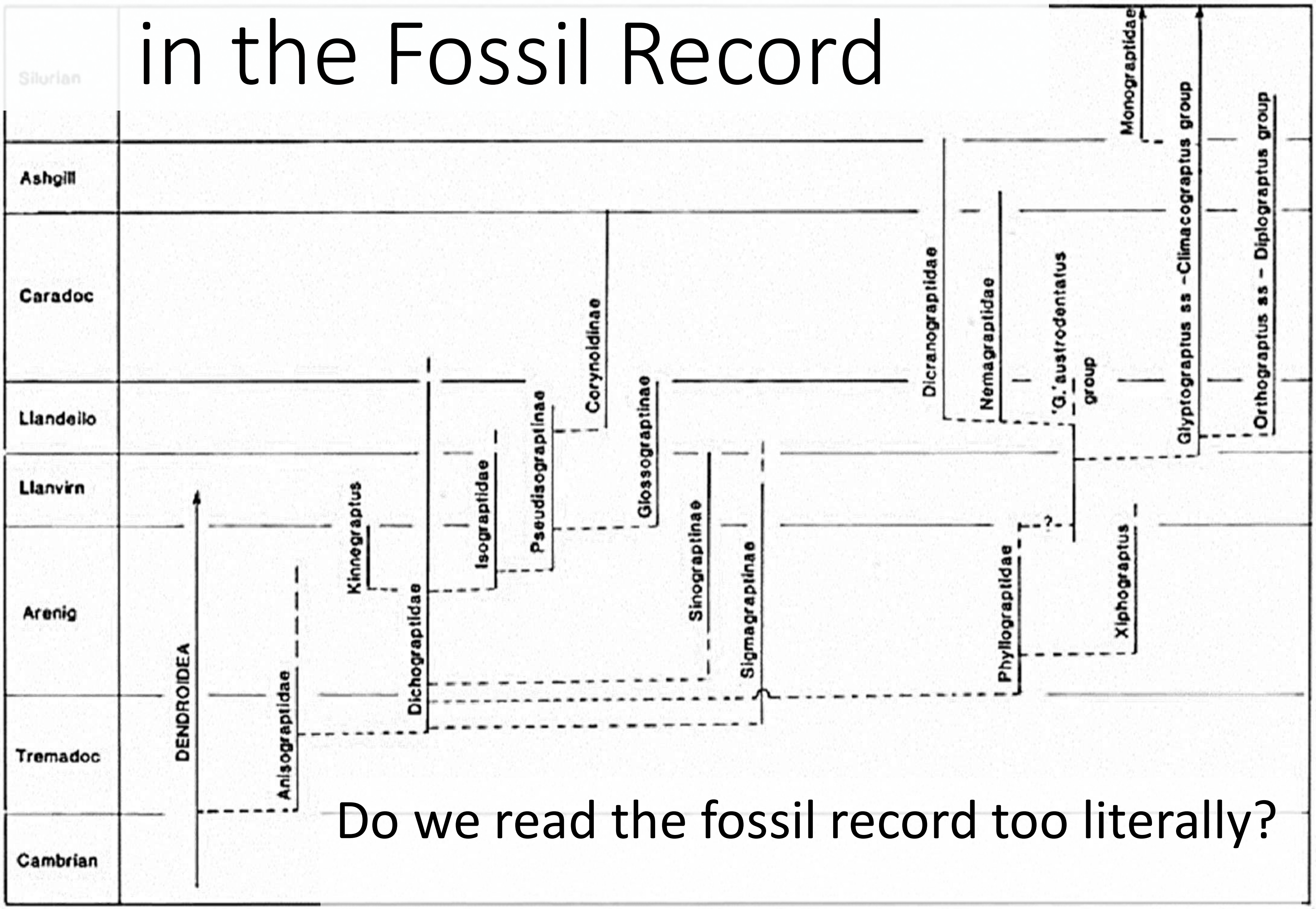
Morphotaxa in the Fossil Record



- Often, we find specimens with similar morphology, but from different localities and stratigraphic height
- We use those features to define morphotaxa that persist over geologic time

The Question of Ancestors in the Fossil Record



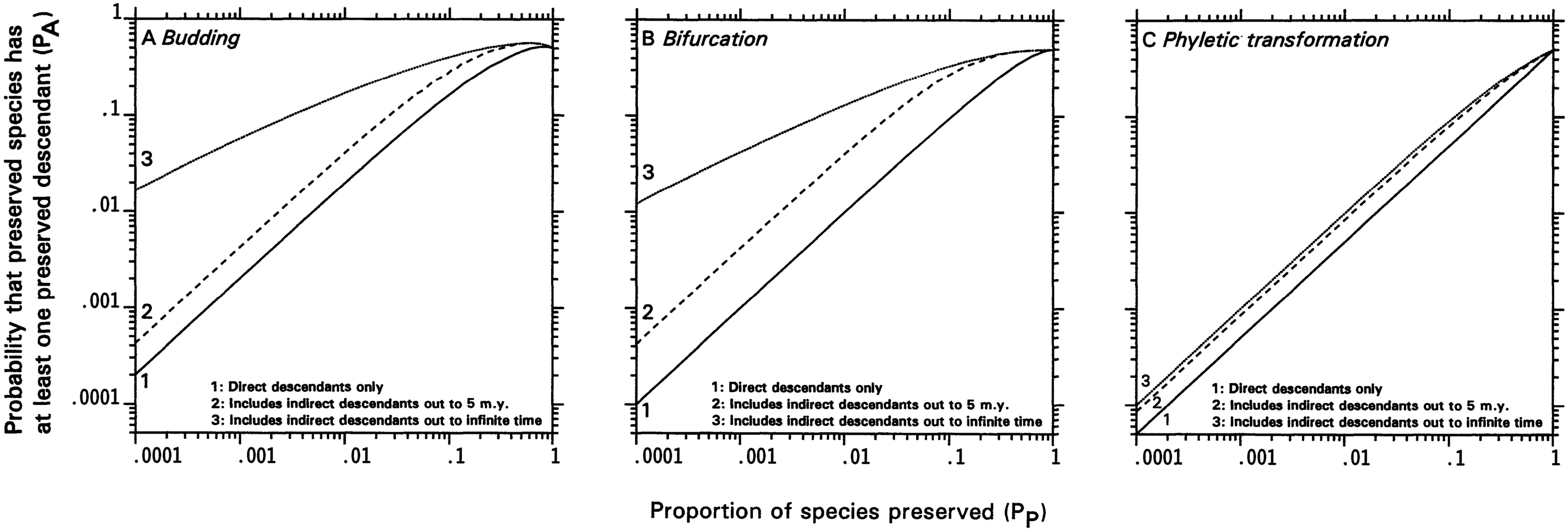
Fortey and Cooper 1986

Do we read the fossil record too literally?

A New Era of Ancestors on Trees

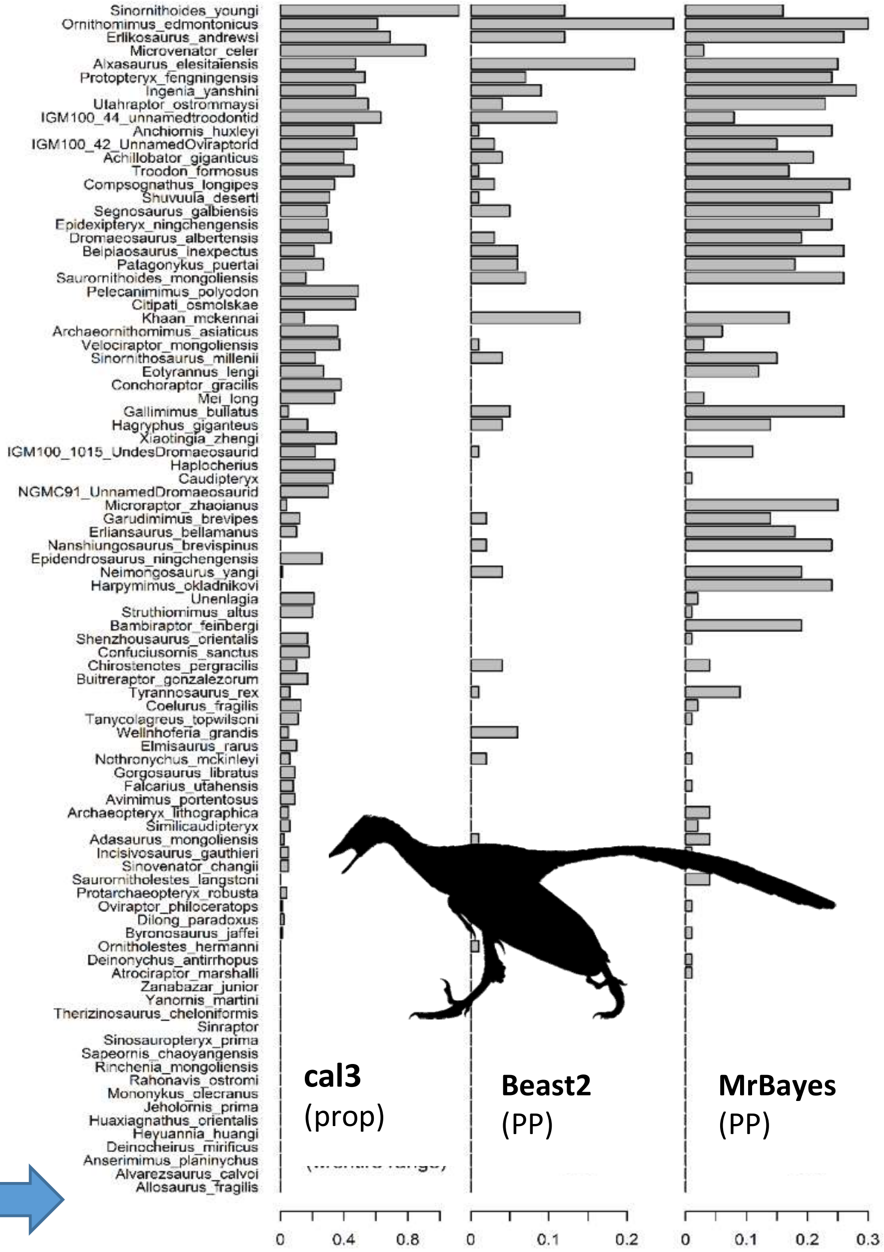
- We expect to sample ancestors *(especially indirect ancestors)* from first principles

Foote, 1996

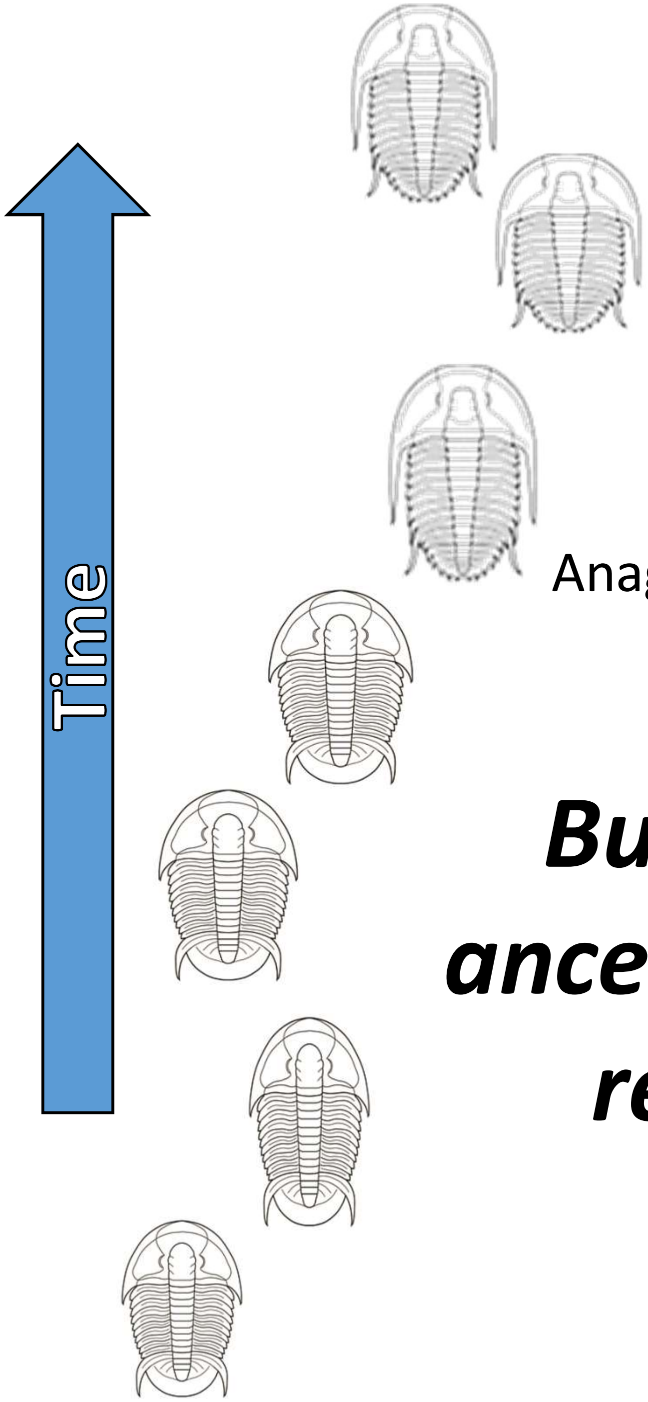


A New Era of Ancestors on Trees

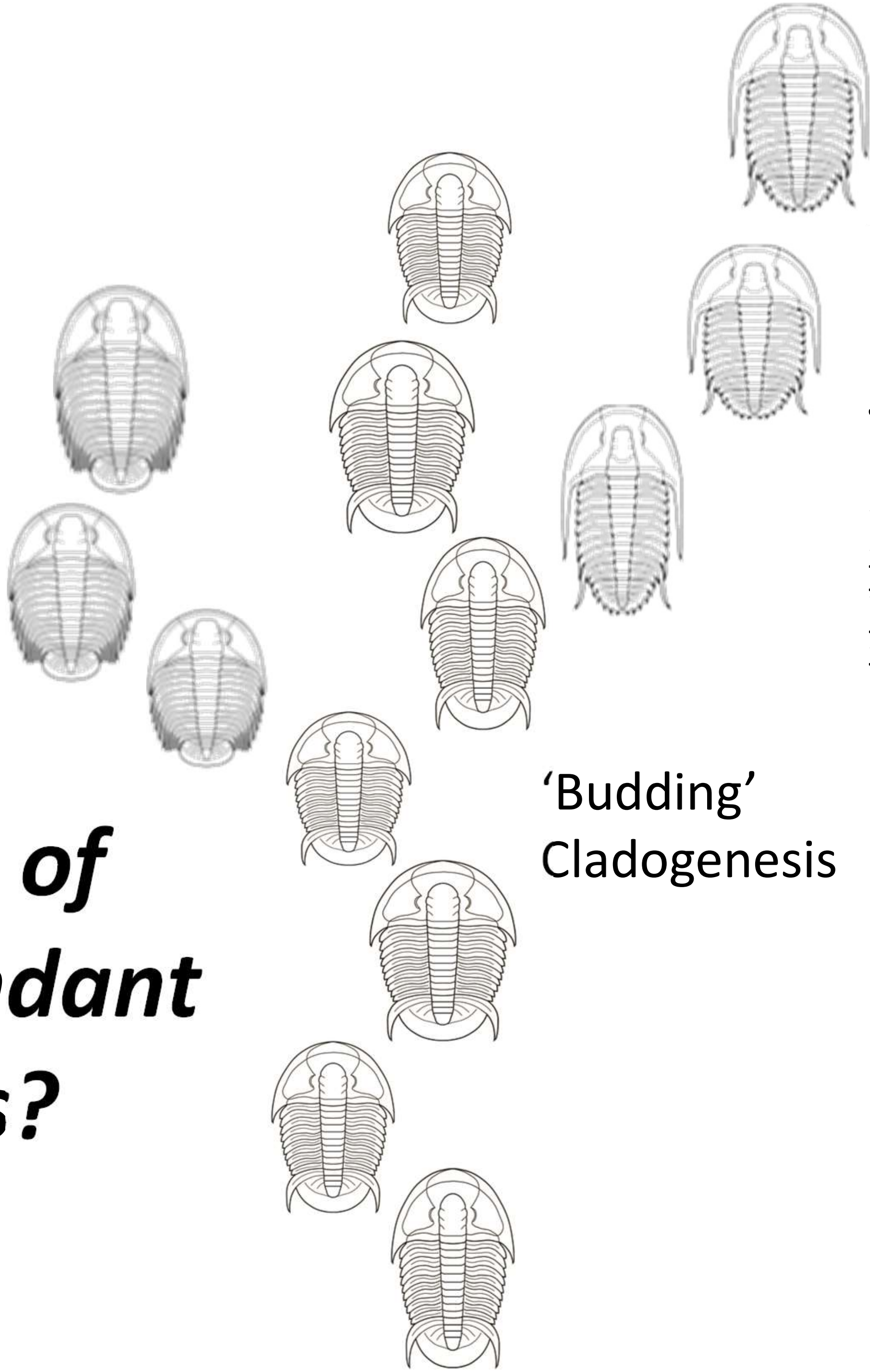
- We expect to sample ancestors *(especially indirect ancestors)* from first principles
- Bayesian tip-dating and other methods let us quantify support for ancestor-descendant relationships
- Different methods seem to assign similar support



Bapst, Wright, Matzke & Lloyd, 2016. Biol. Lett.



Anagenesis



‘Budding’
Cladogenesis

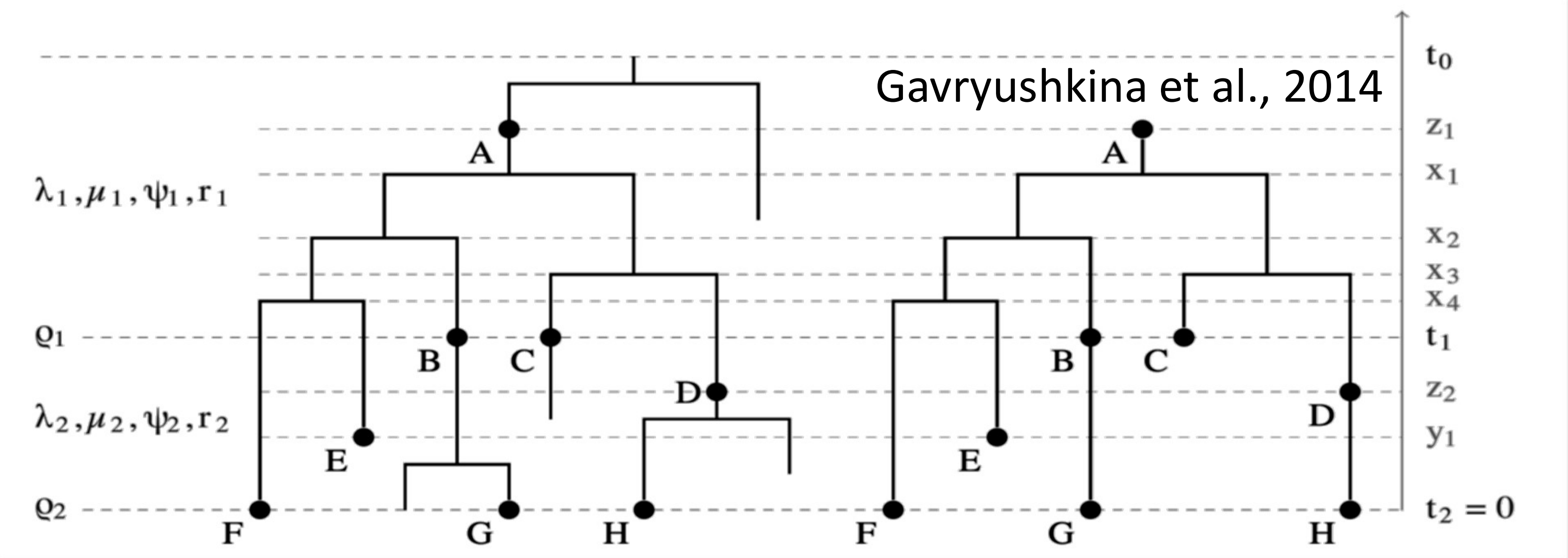
Asaphid trilobite images from Gon, 2009

But what sort of ancestor-descendant relationships?

How often do we infer sampled ancestors in real fossil records? Which mode of differentiation is most common among persistent morphotaxa?

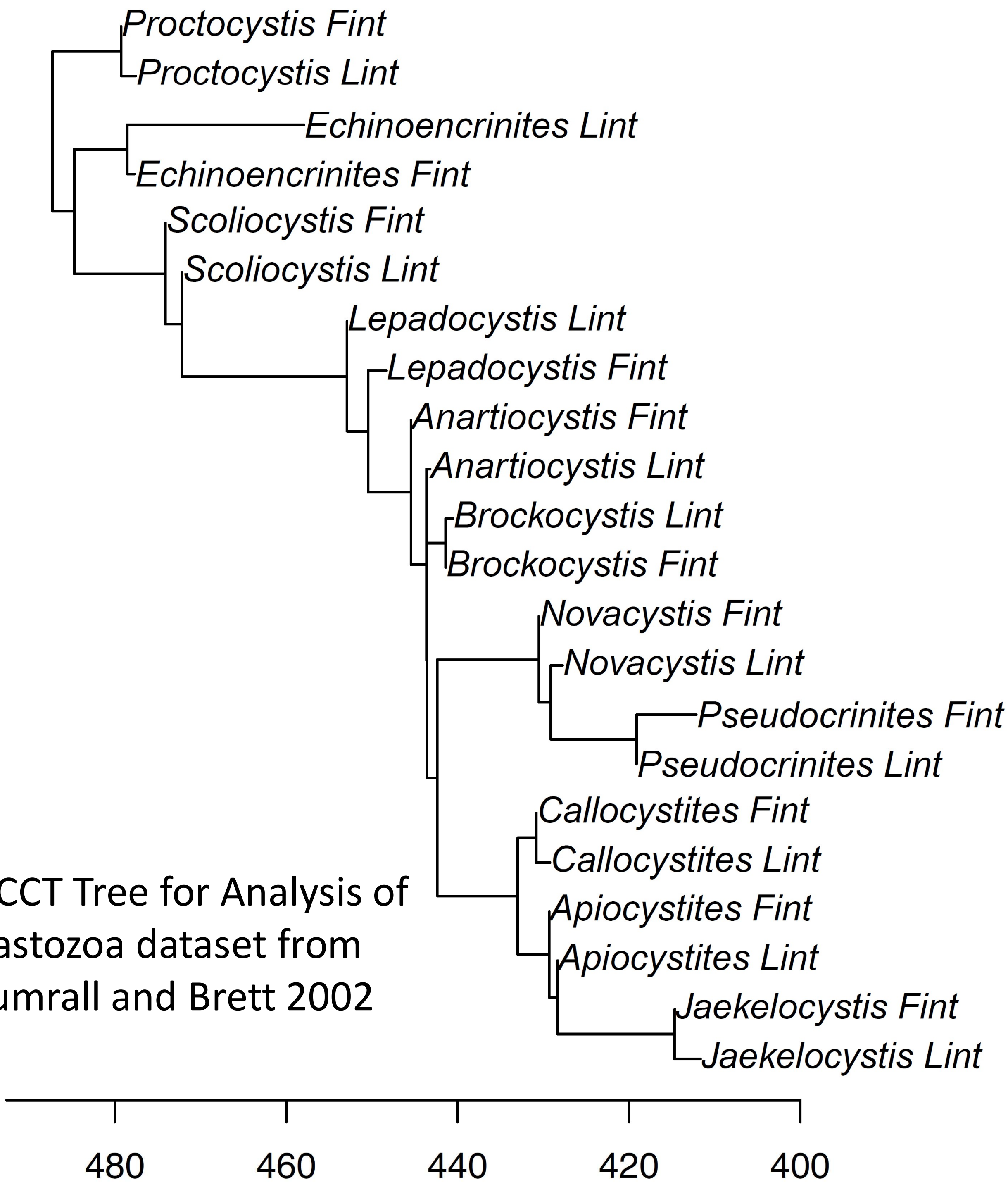
- Implications for our understanding of speciation, trait evolution, extent that taxonomic turnover could be inflated by pseudo-extinction
- Apply tip-dating to morphological matrices from the well-sampled marine invertebrate record
  - More than 35 pre-existing datasets; 26 examined today
  - Predominantly Paleozoic groups, such as brachiopods, graptolites, trilobites, crinoids, other echinoderms
  - Varying matrix size, taxonomic level (species vs genera), sampling schema (e.g. clade-focused vs interval focused)

Sampled-Ancestor Tip-Dating with the Fossilized Birth-Death Model in MrBayes

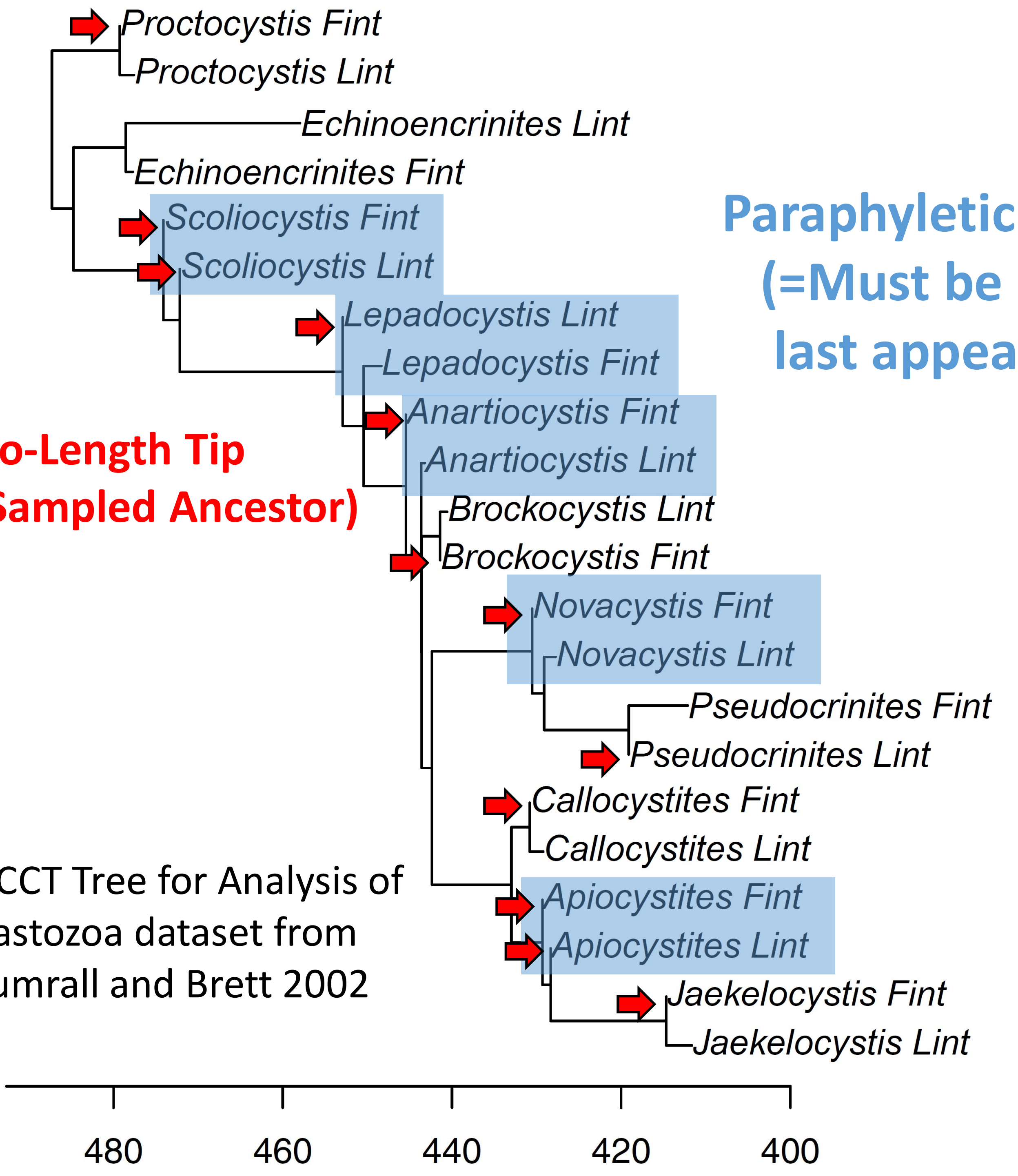


Gavryushkina et al., 2014

- Currently available tip-dating methods limited to considering taxon units as point occurrences in time
- To consider relationships among persistent morphotaxa, we treat first & last appearances as two separate taxon units, with identical morphological characters but different time of appearance
    - Functions for automating this are in R package `paleotree`



MCCT Tree for Analysis of Blastozoa dataset from Sumrall and Brett 2002

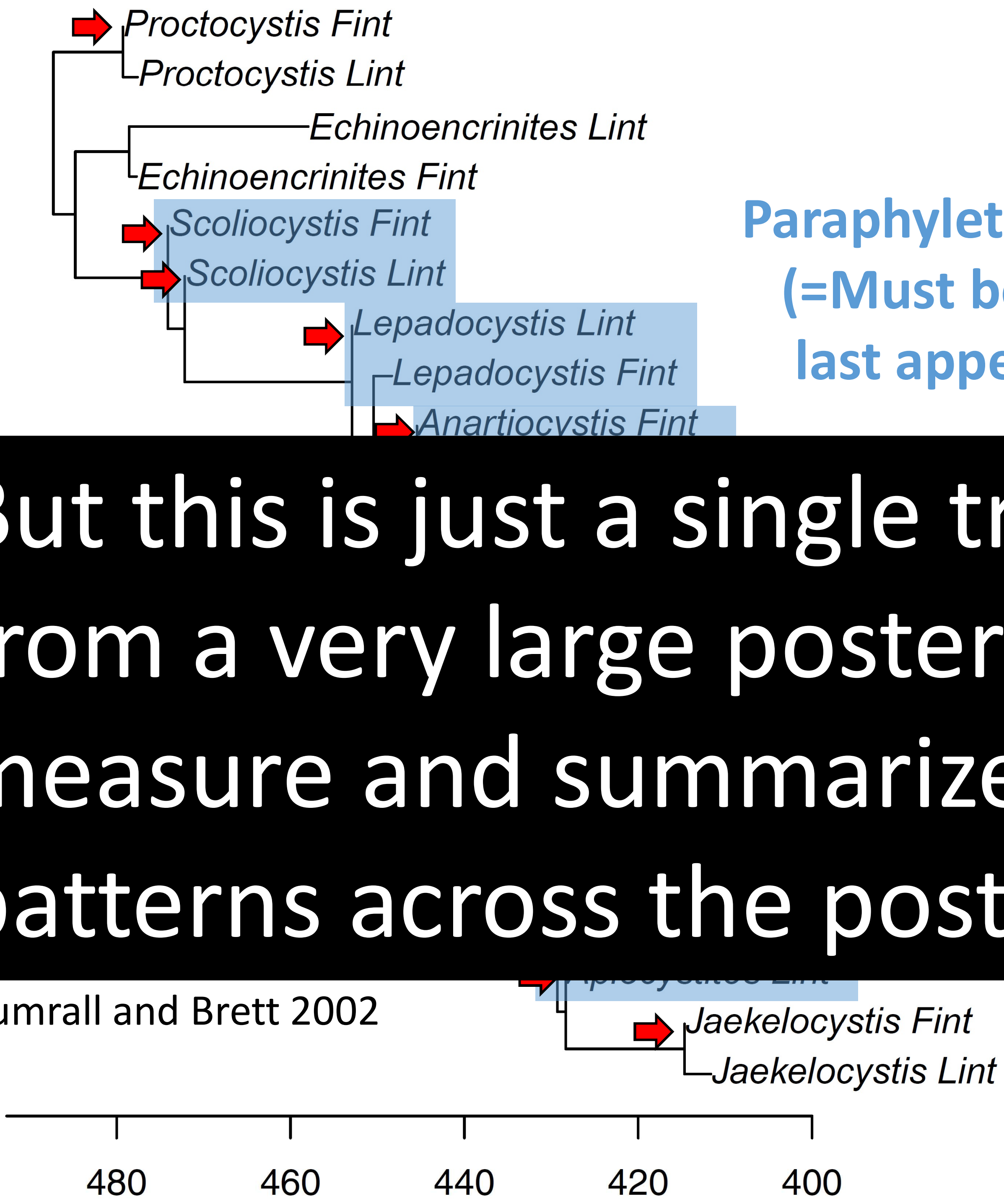


Zero-Length Tip
(=Sampled Ancestor)

Paraphyletic taxon
(=Must be budding, unless
last appearance is an SA)

MCCT Tree for Analysis of Blastozoa dataset from Sumrall and Brett 2002

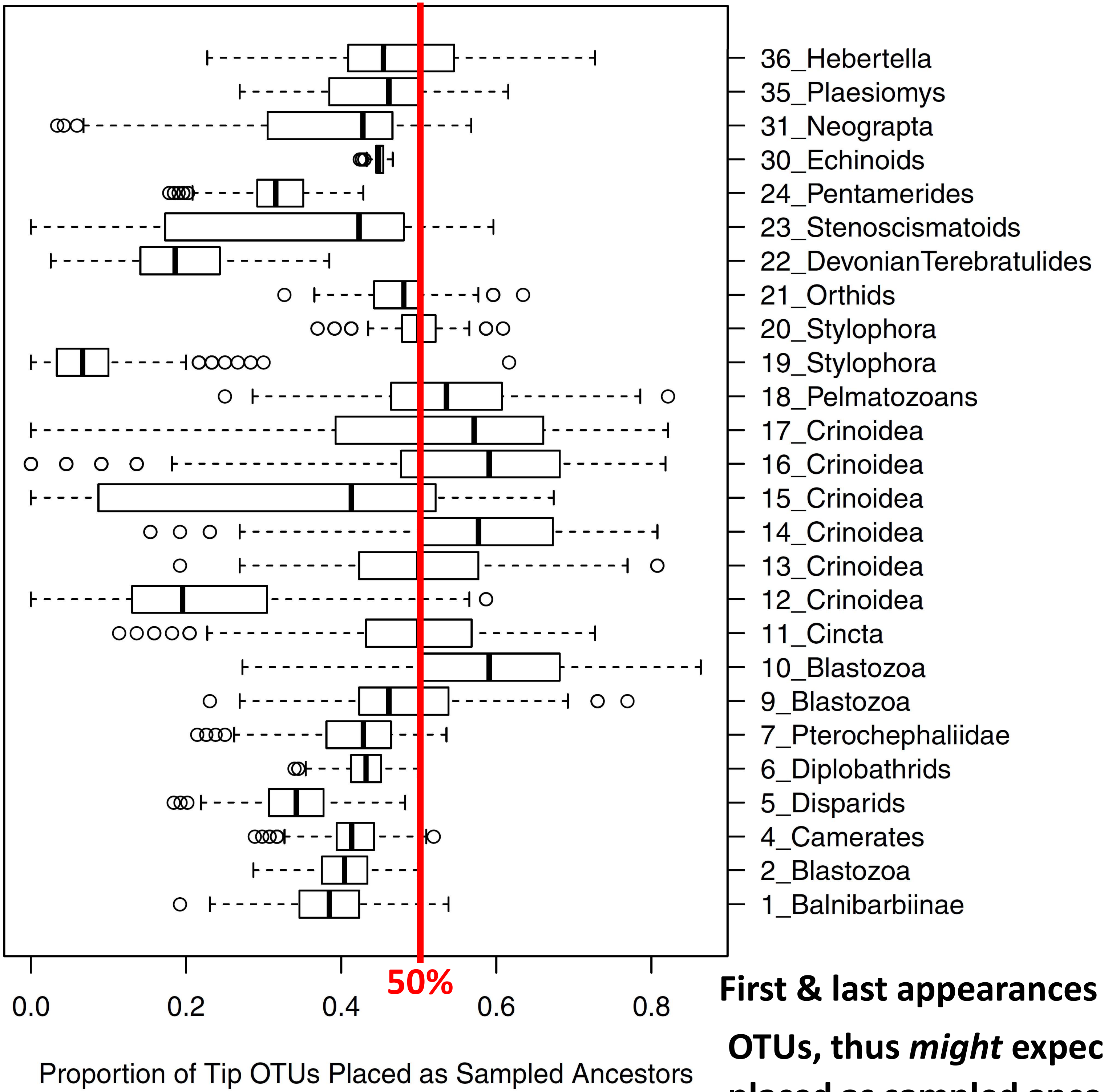
Of 11 original OTUs, five are paraphyletic, three of which must be budding, and two might be examples of pseudo-extinction



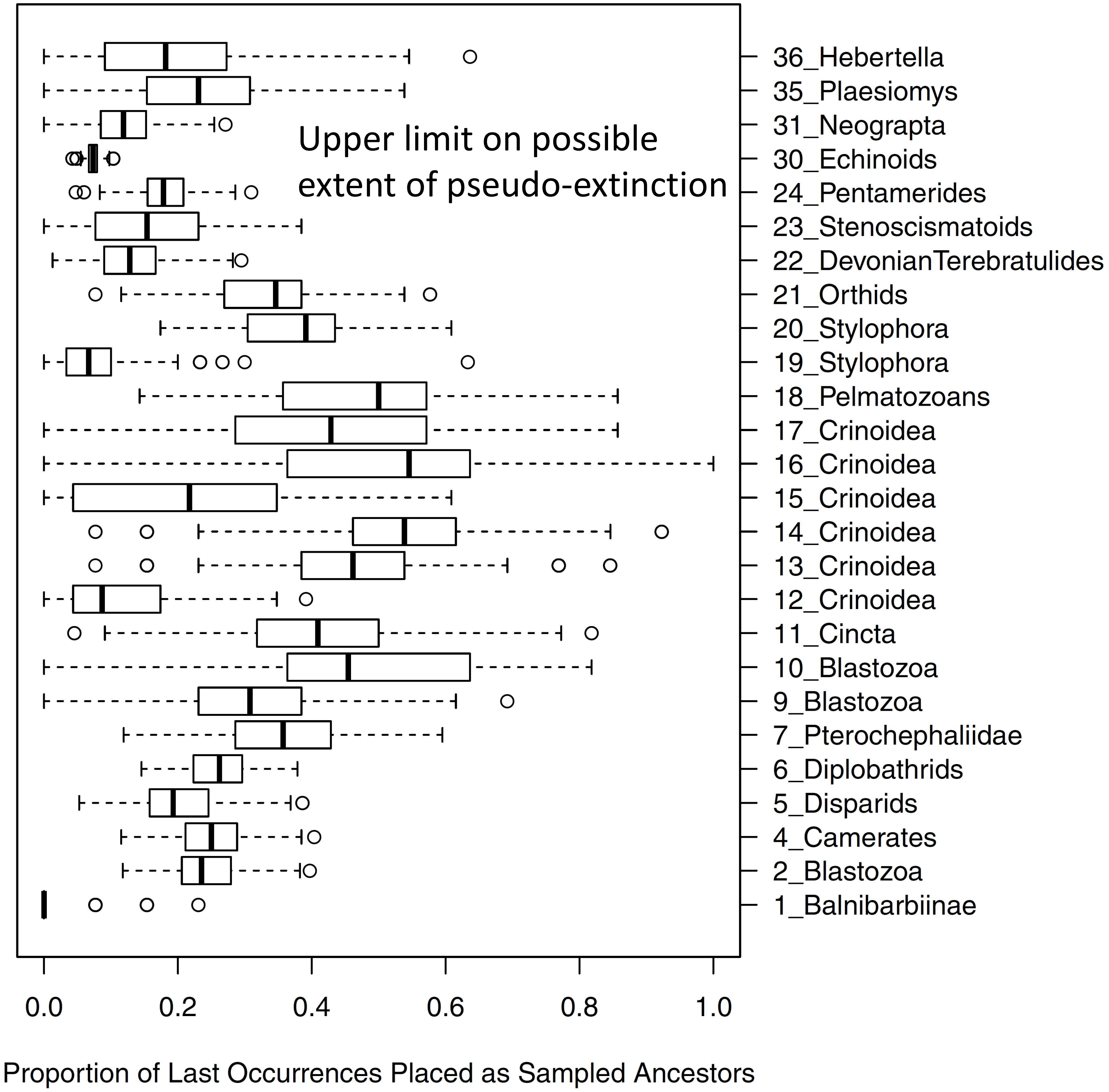
Paraphyletic taxon
(=Must be budding, unless last appearance is an SA)

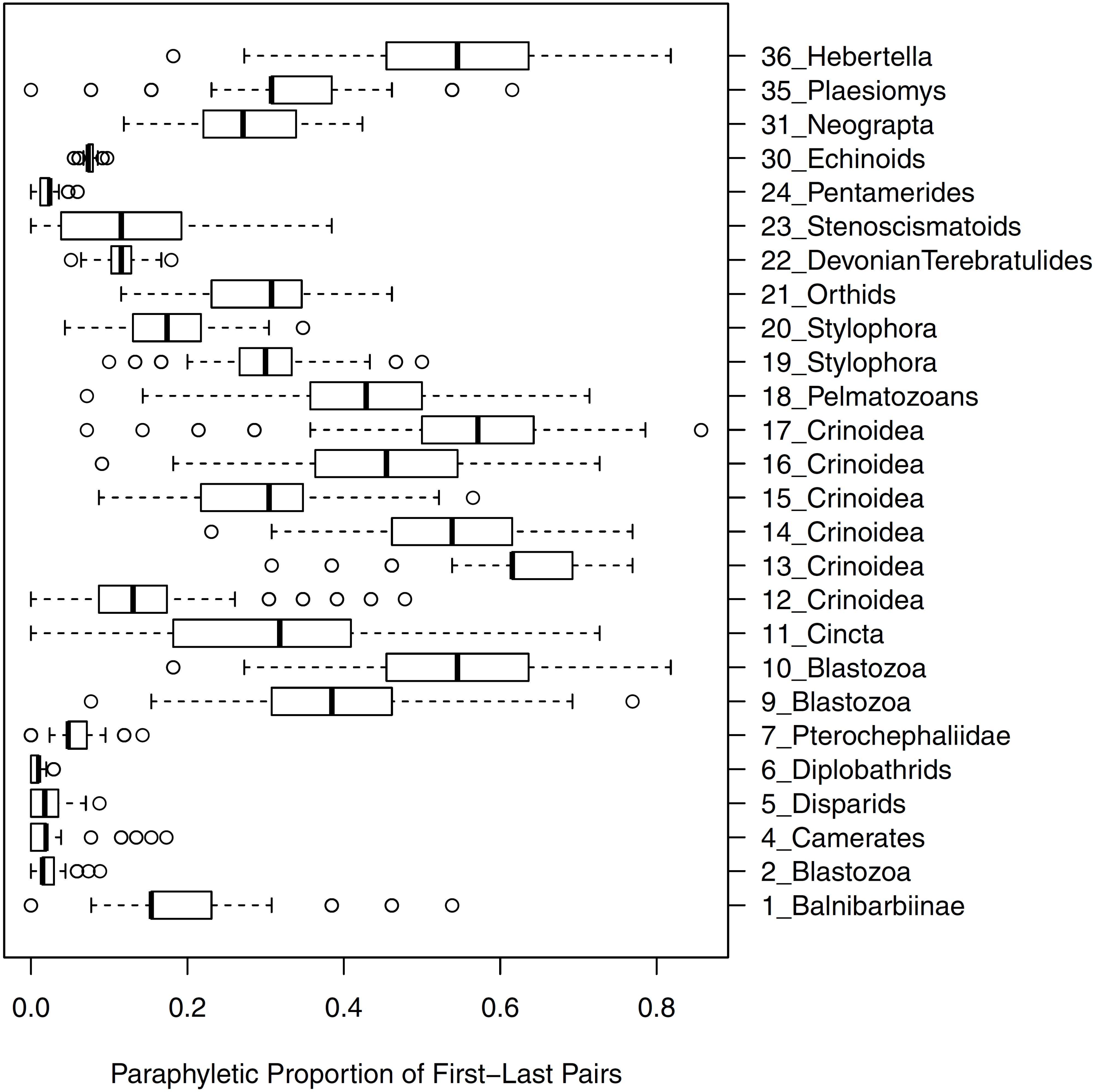
But this is just a single tree pulled from a very large posterior – need to measure and summarize these patterns across the posteriors

Sumrall and Brett 2002



First & last appearances are separate OTUs, thus *might* expect 50% to be placed as sampled ancestors


Upper limit on possible
extent of pseudo-extinction
36_Hebertella
35_Plaesiomys
31_Neograpta
30_Echinoids
24_Pentamerides
23_Stenoscismatoids
22_DevonianTerebratulides
21_Orthids
20_Stylophora
19_Stylophora
18_Pelmatozoans
17_Crinoidea
16_Crinoidea
15_Crinoidea
14_Crinoidea
13_Crinoidea
12_Crinoidea
11_Cincta
10_Blastozoa
9_Blastozoa
7_Pterochephaliidae
6_Diplobathrids
5_Disparids
4_Camerates
2_Blastozoa
1_Balnibarbiinae
0.0
0.2
0.4
0.6
0.8
1.0
Proportion of Last Occurrences Placed as Sampled Ancestors


36_Hebertella
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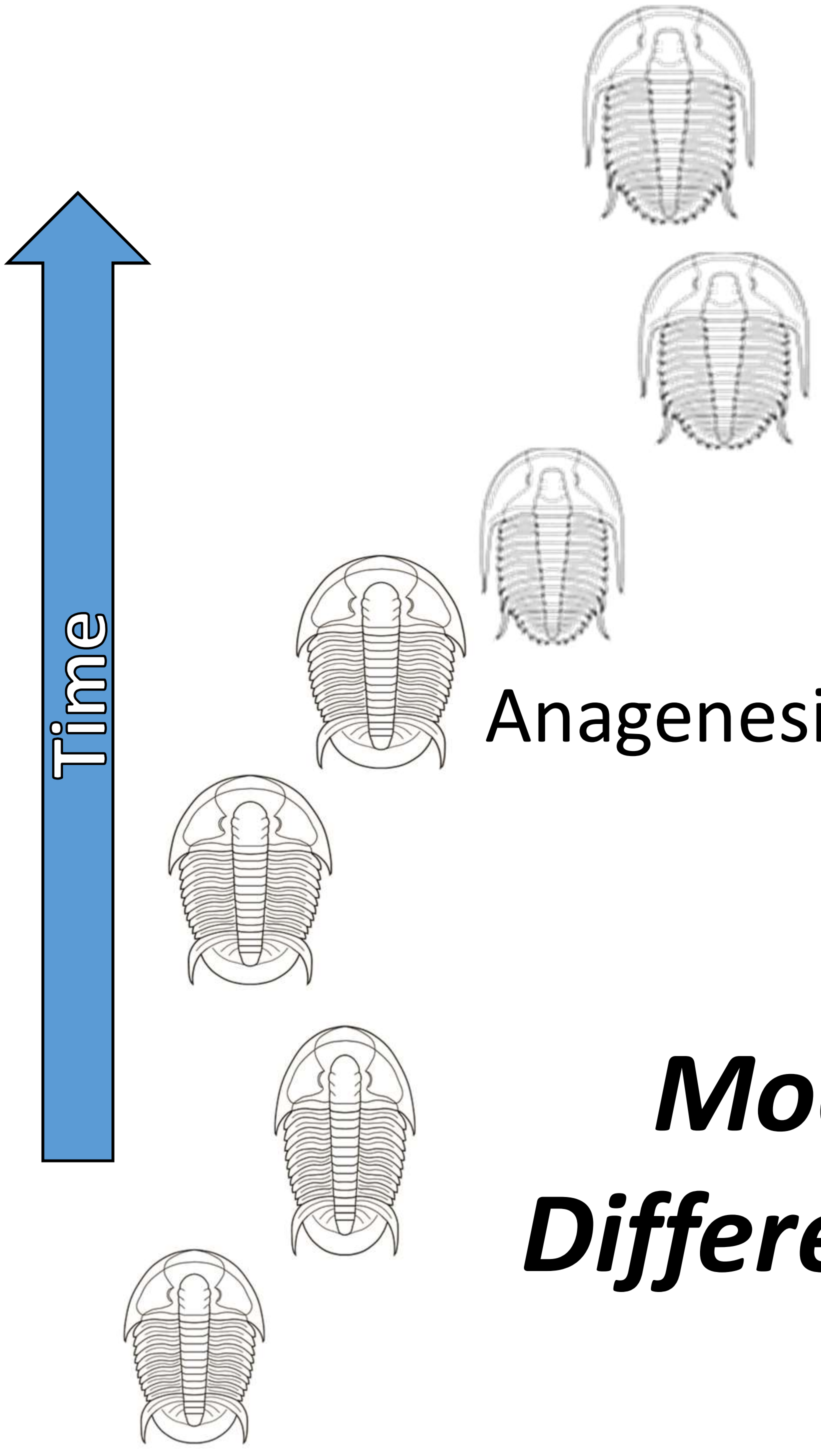
17_Crinoidea
16_Crinoidea
15_Crinoidea
14_Crinoidea
13_Crinoidea
12_Crinoidea
11_Cincta
10_Blastozoa
9_Blastozoa
7_Pterochephaliidae
6_Diplobathrids
5_Disparids
4_Camerates
2_Blastozoa
1_Balnibarbiinae
0.0
0.2
0.4
0.6
0.8
Paraphyletic Proportion of First–Last Pairs

The Pattern of Ancestor-Descendant Relationships

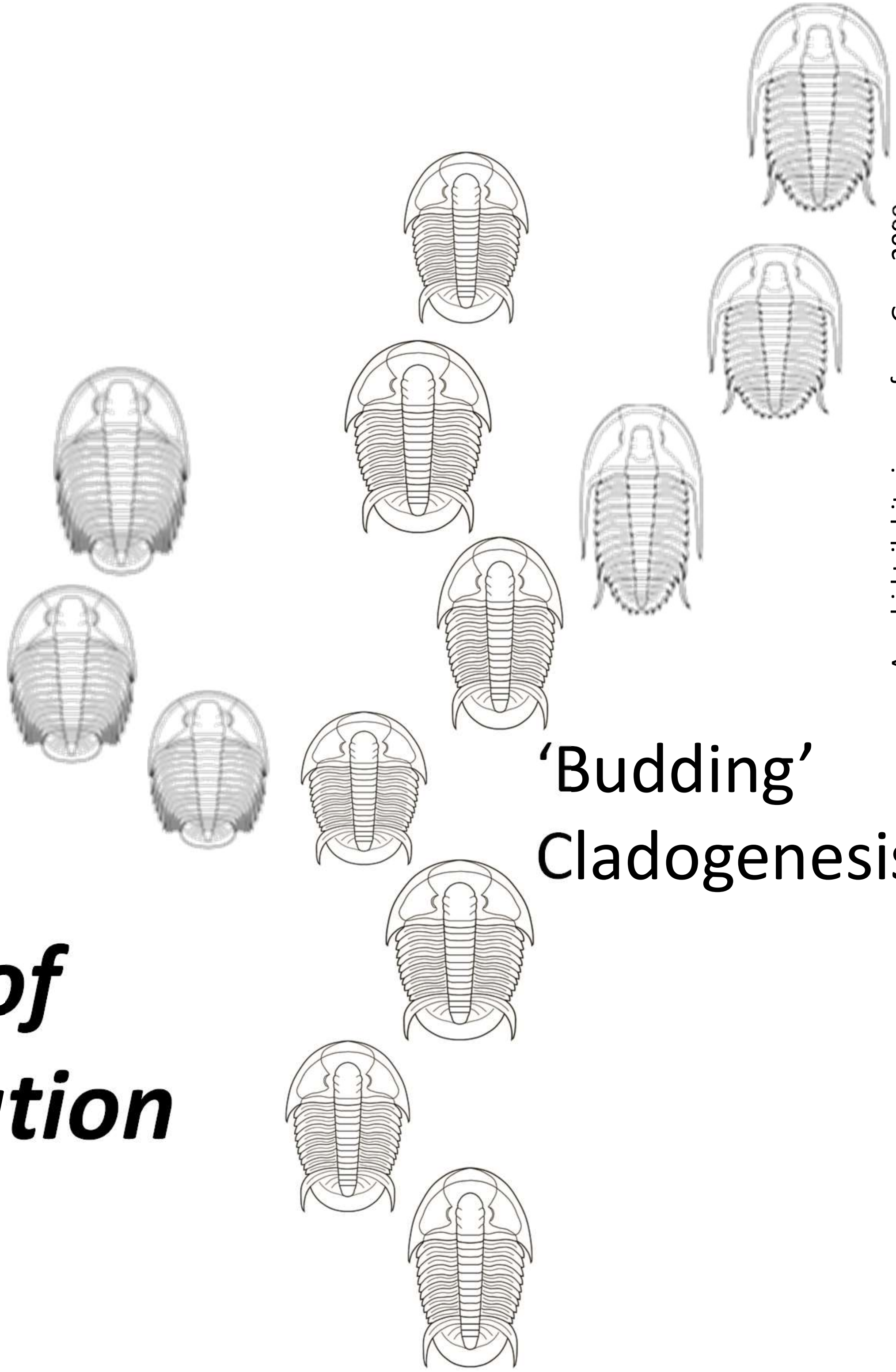
- Treating fossil morphotaxa as more than single OTUs sheds light on patterns of ancestor-descendant relationships
- Ancestor-descendant relationships considerably across different datasets
  - Effects of taxonomic practices? Sampling? Biological differences?

Thanks for listening! Questions?

Modes of Differentiation

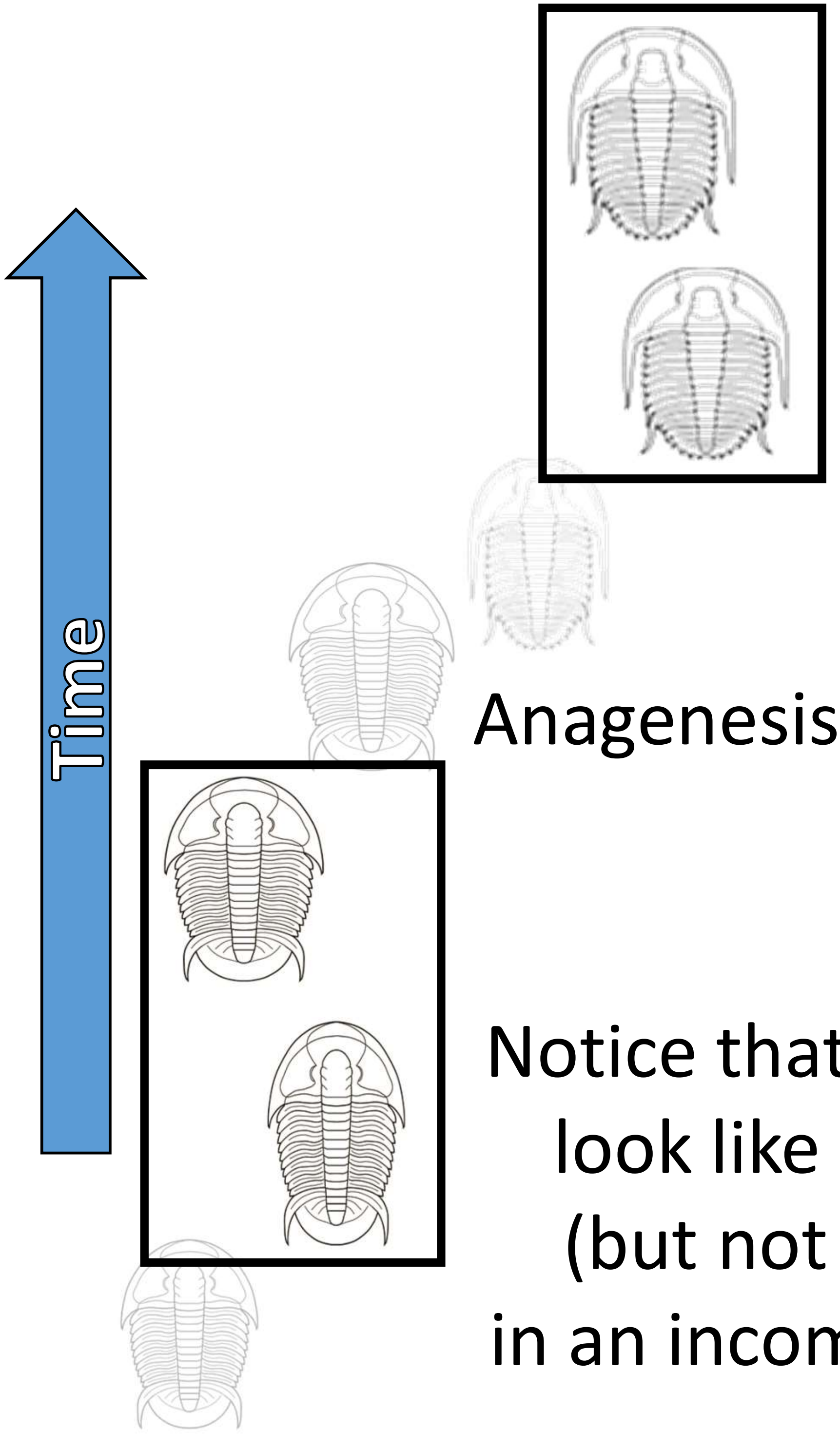


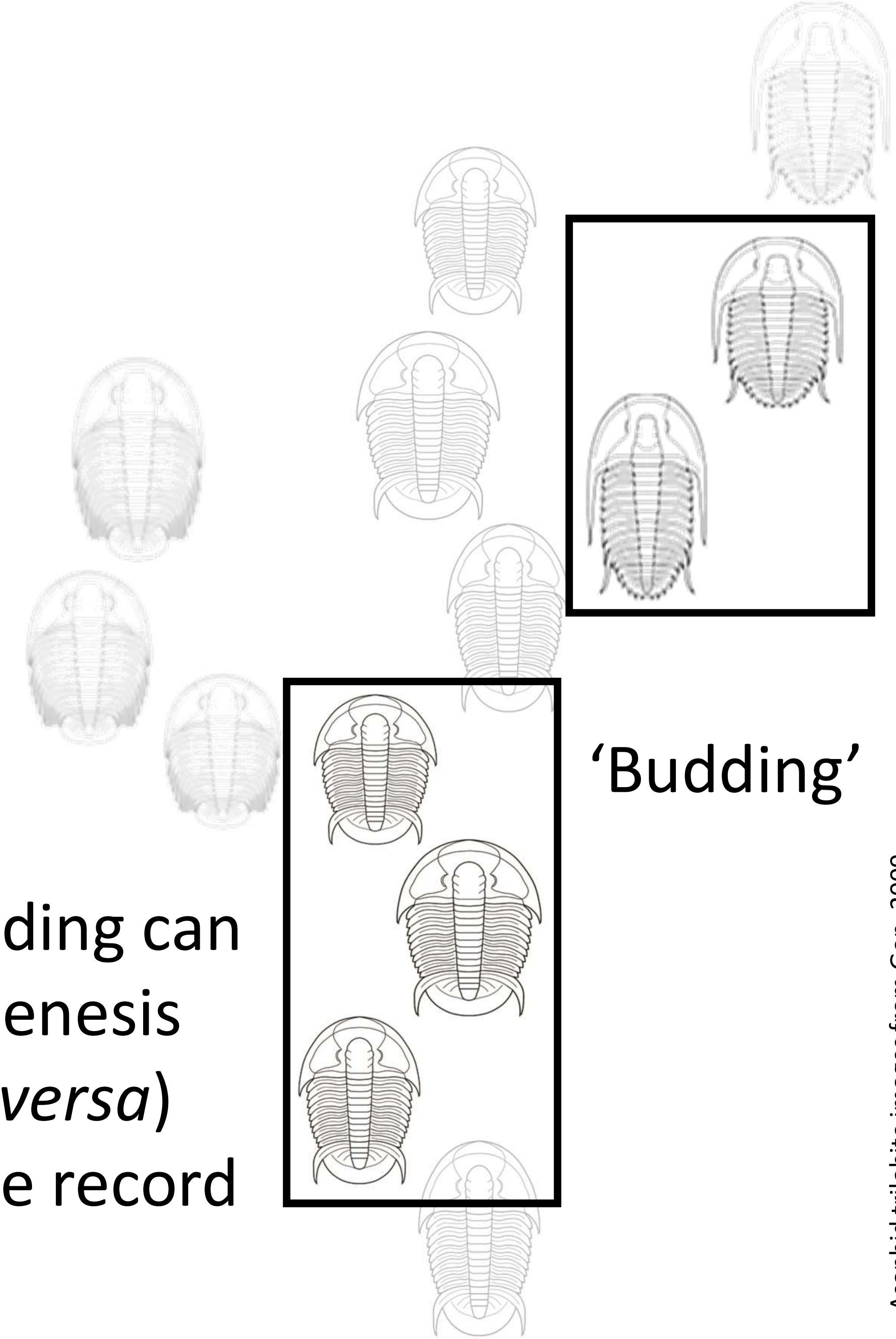
Anagenesis



‘Budding’ Cladogenesis

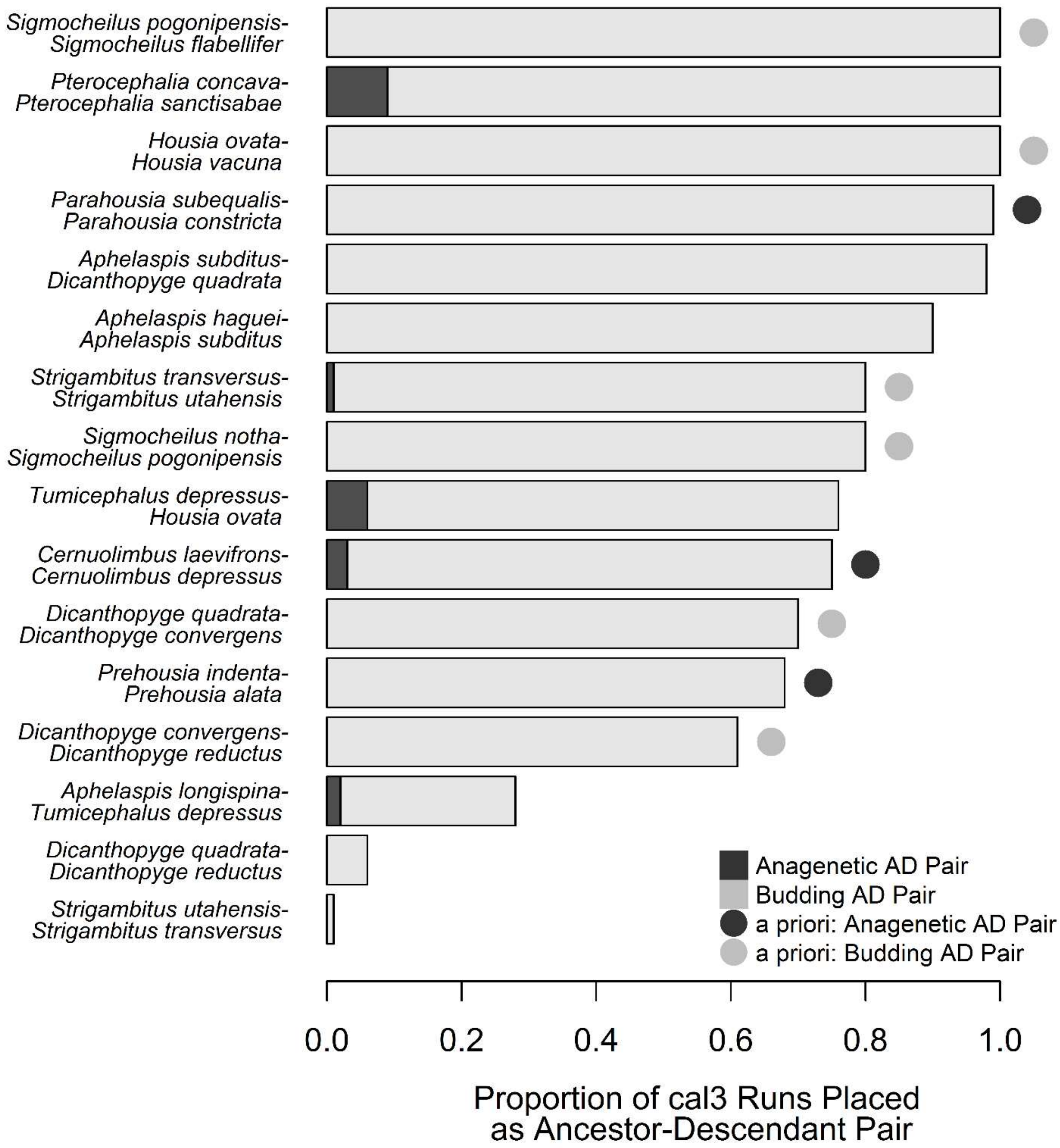
Asaphid trilobite images from Gon, 2009





Notice that budding can look like anagenesis (but not *vice versa*) in an incomplete record

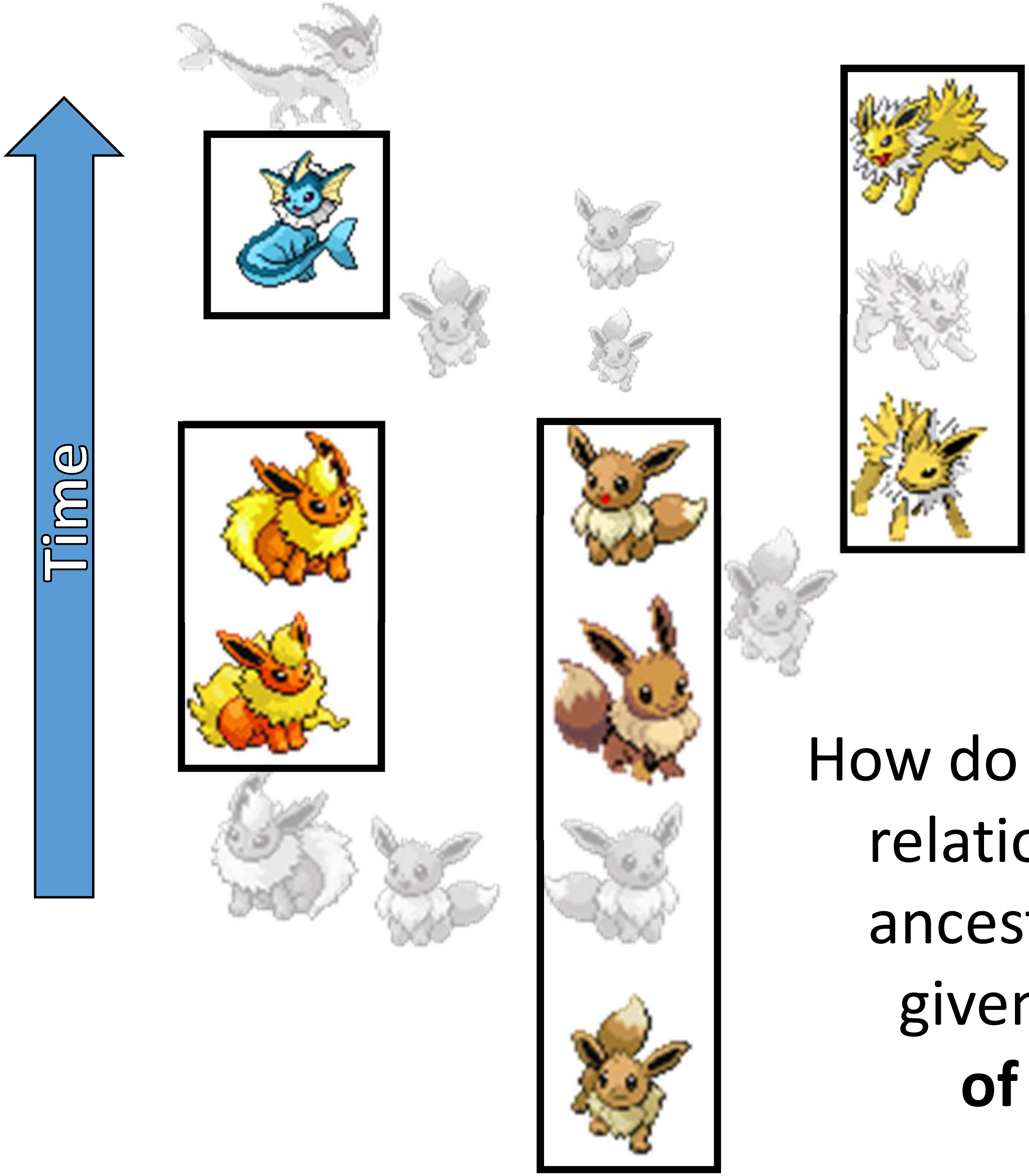
Asaphid trilobite images from Gon, 2009



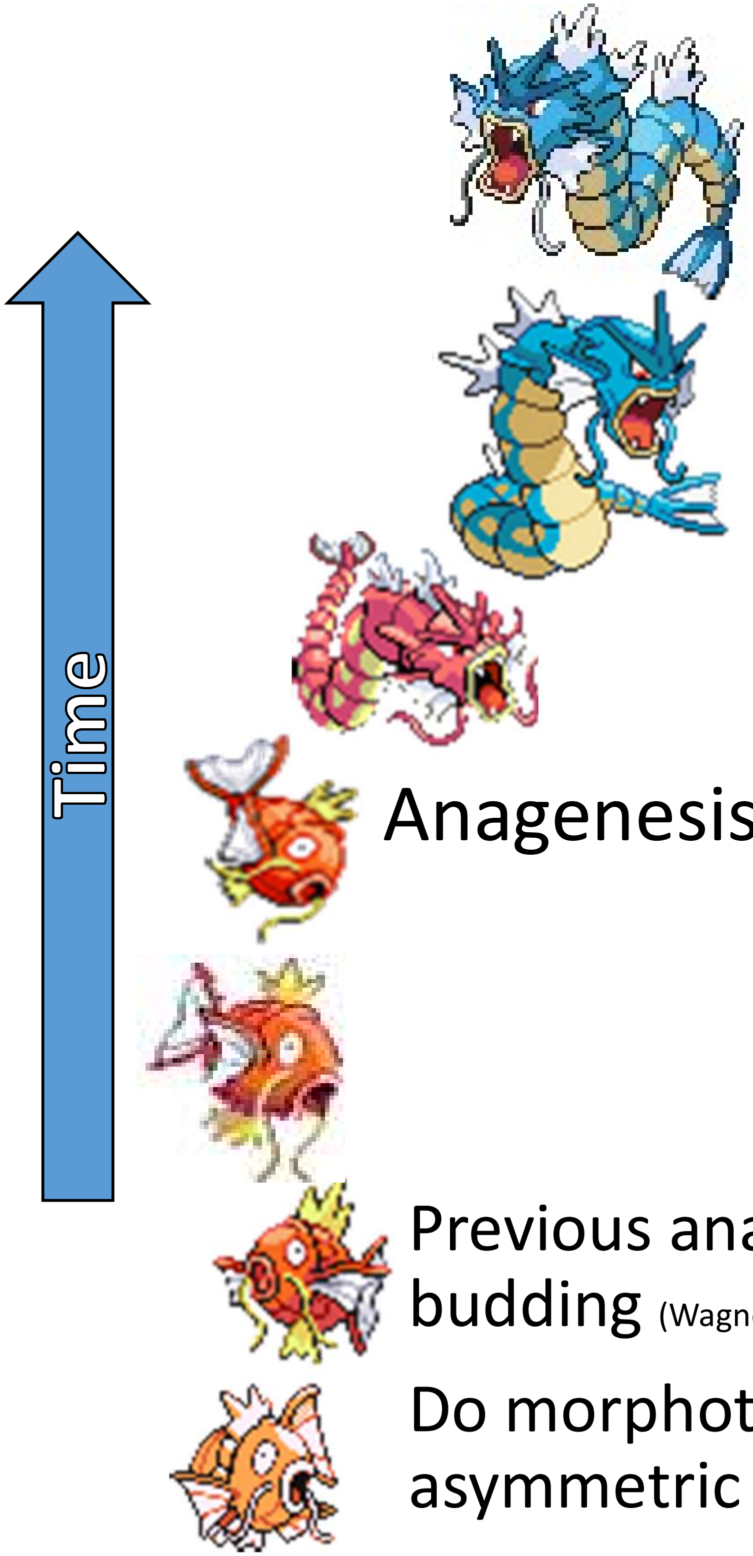
- Each pair is a stacked barplot
- Dots indicate putative pairs
- Evidence for all *a priori* AD pairs, & a few extra
- cal3 finds very little support for anagenesis
  - Given biases, perhaps entirely budding?

Bapst & Hopkins 2017

The problem is, very rarely can we read the fossil record as literally as this



How do we infer the relationships among ancestors & their descendants, given **the incompleteness of the fossil record**?

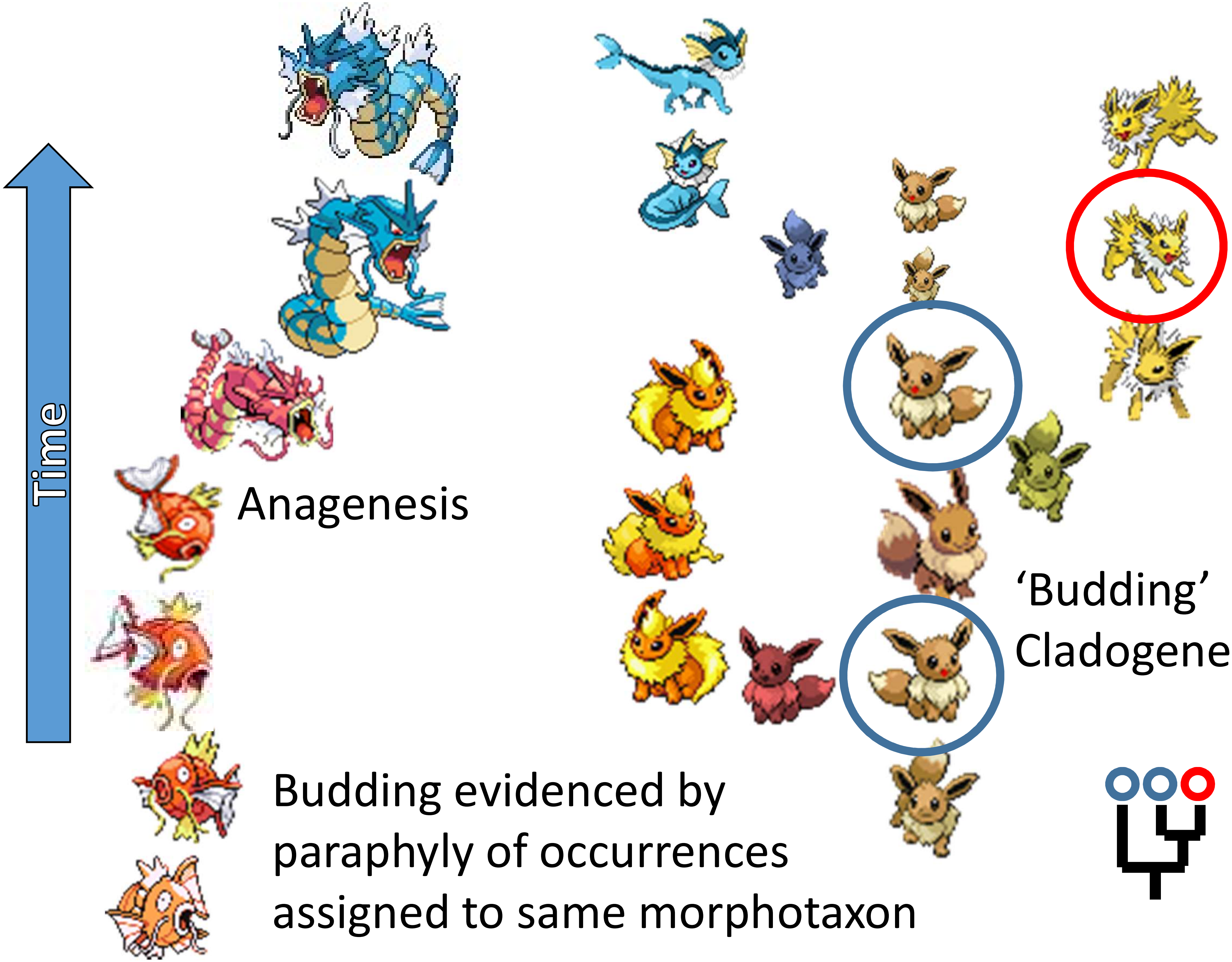


Anagenesis

‘Budding’ Cladogenesis

Previous analyses find support for budding (Wagner & Erwin, 1995; Bapst & Hopkins, 2017)

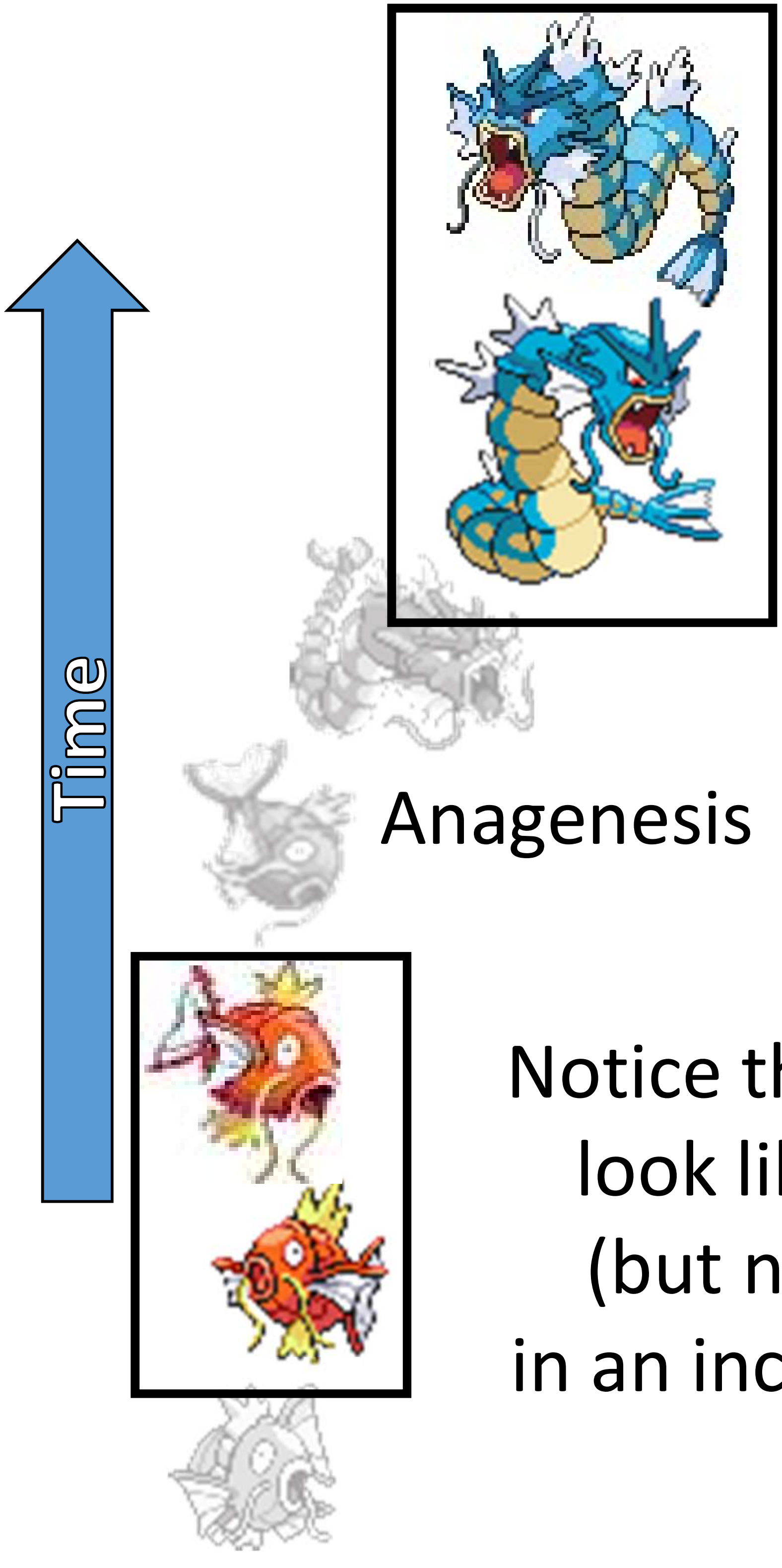
Do morphotypes mainly arise from asymmetric cladogenetic change?



Anagenesis

‘Budding’ Cladogenesis

Budding evidenced by paraphyly of occurrences assigned to same morphotaxon



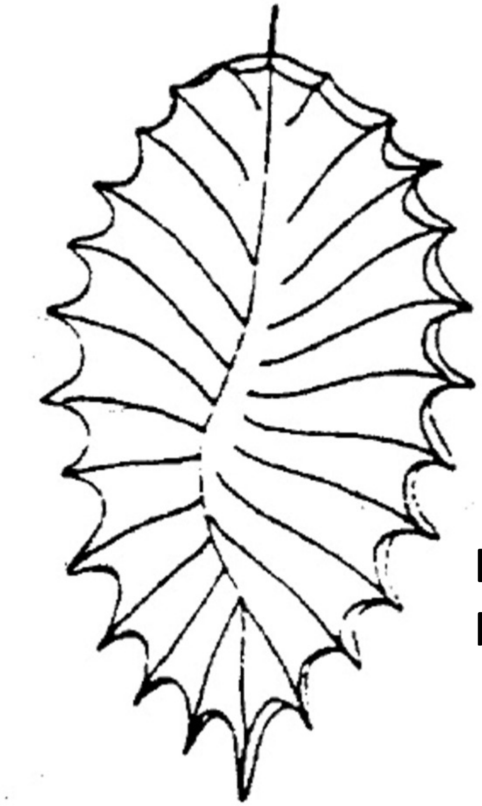
Time

Anagenesis

Notice that budding can
look like anagenesis
(but not *vice versa*)
in an incomplete record

‘Budding’

Gaps in Densely-Sampled Fossil Records



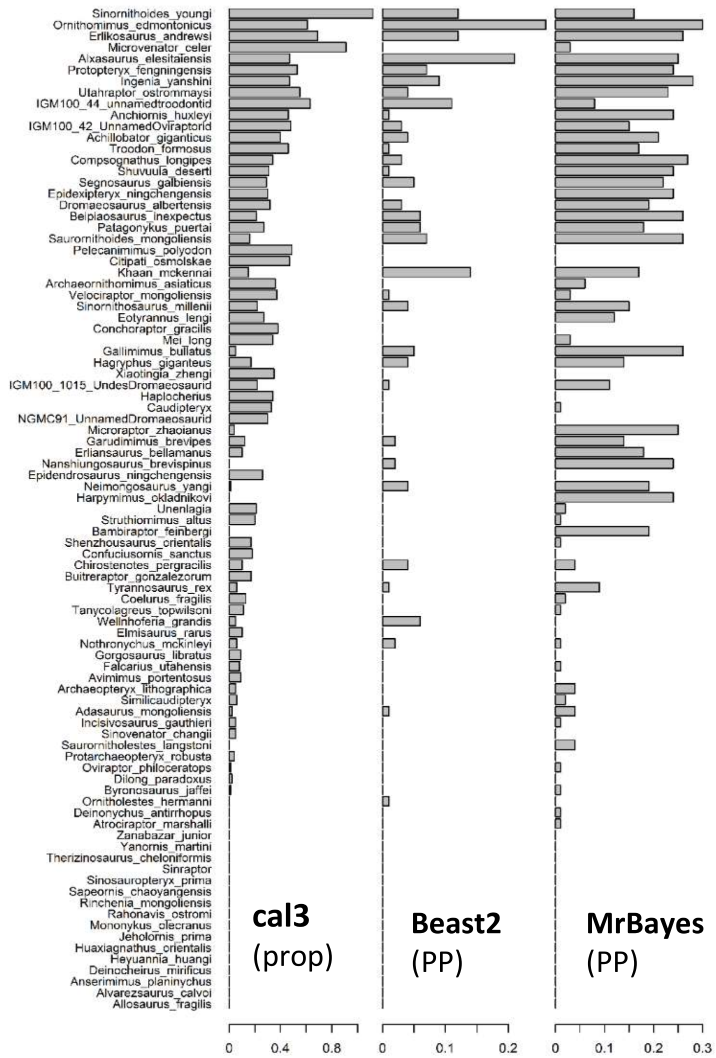
Bergstromgraptus
Middle Darrwillian

Sinoretiograptus
Latest Katian

- Closest relatives separated by a 15 to 20 million year gap in this lineage:
- Were the intermediates living *somewhere else*? Open ocean?

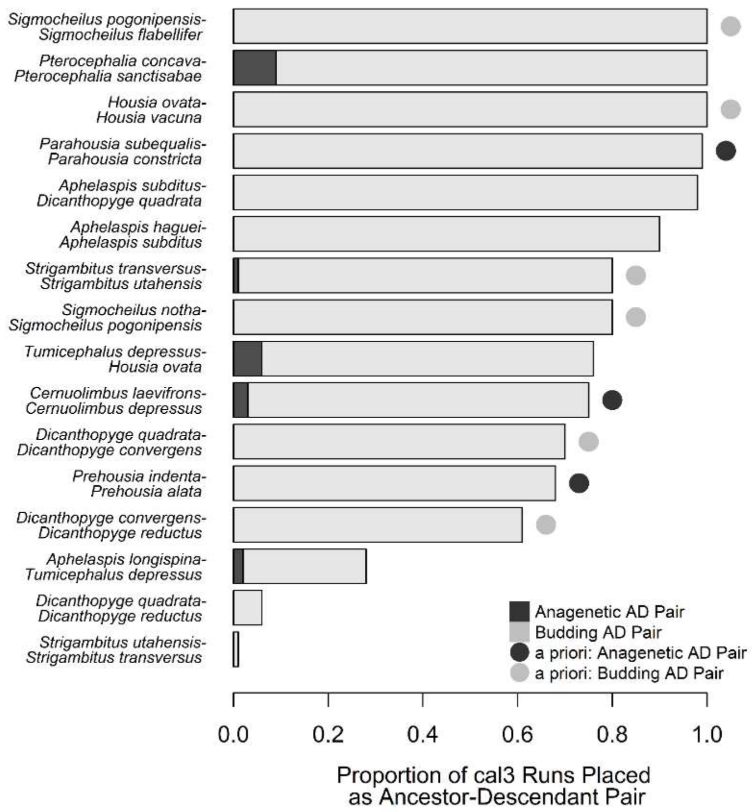
Maletz and Zhang, 2003; Vandenberg, 2003; C.E. Mitchell

In The Age Of Ancestor Inference…



Bapst, Wright, Matzke & Lloyd, 2016. Biol. Lett.

(cal3 is an off-brand tip-dating lite)



Bapst & Hopkins, 2017, Paleobio.

- Different methods agree on placing ancestors [dinosaurs]
- Quantitative inferences agree with previous putative pairs of ancestor-descendants [trilobites]