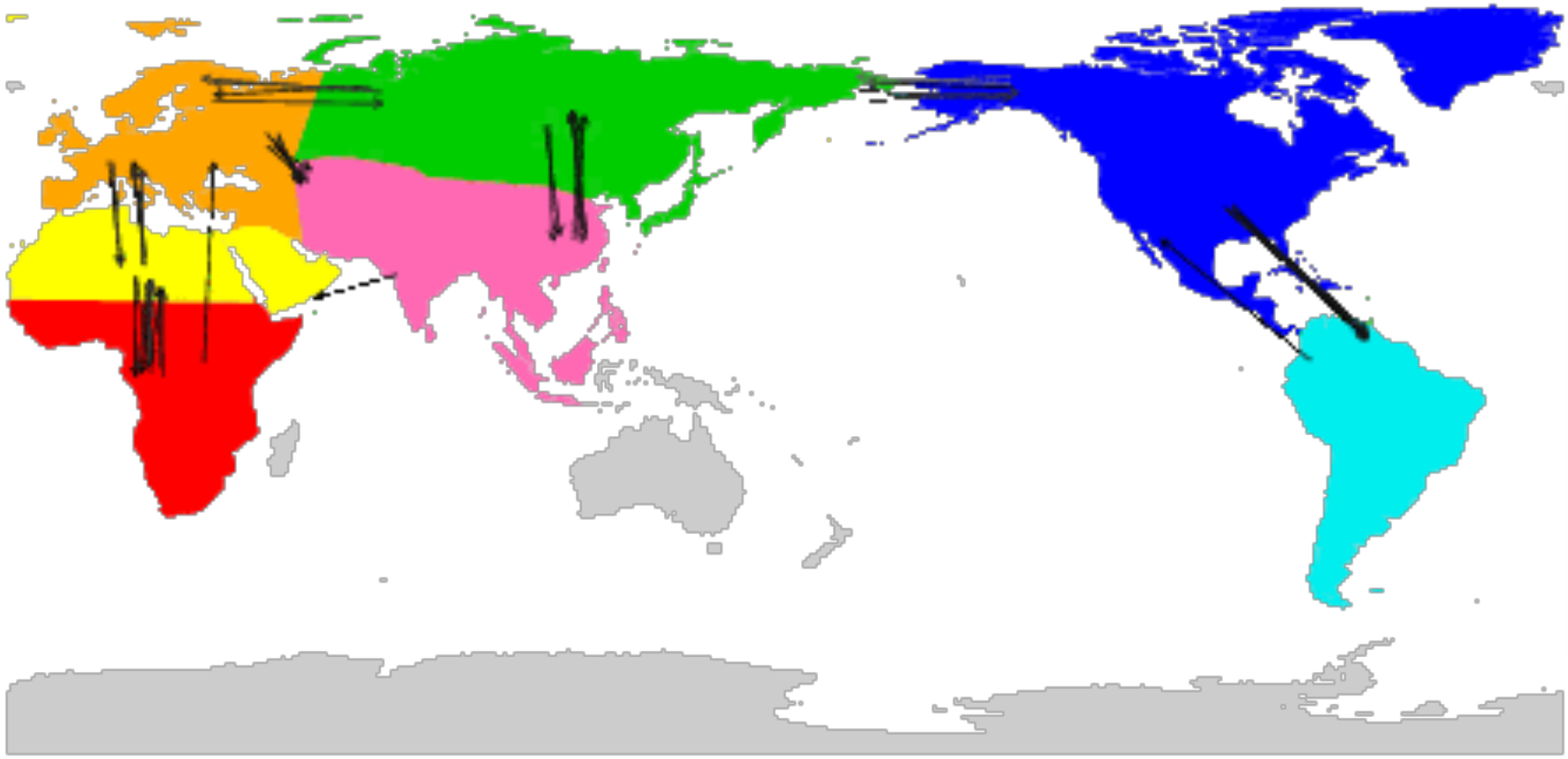
Phylogenetic biogeography of fossil Canidae:

combining models of imperfect detection, databased fossils as taphonomic controls, and Biogeographical Stochastic Mapping



possible histories (DEC+*j*+*w* model)

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Division of Ecology, Evolution, and Genetics
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The Australian National University
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23 June, 2017, 4 p.m.
Session: Biogeography / phylogeography
Evolution 2017, Room A106

Thanks for support from:

Collaborator: Laura K. Säilä

Dept. of Geosciences and Geography

University of Helsinki, Finland

http://www.mv.helsinki.fi/home/lsaila/

Acknowledgements

Questions/comments/ collaborations at:

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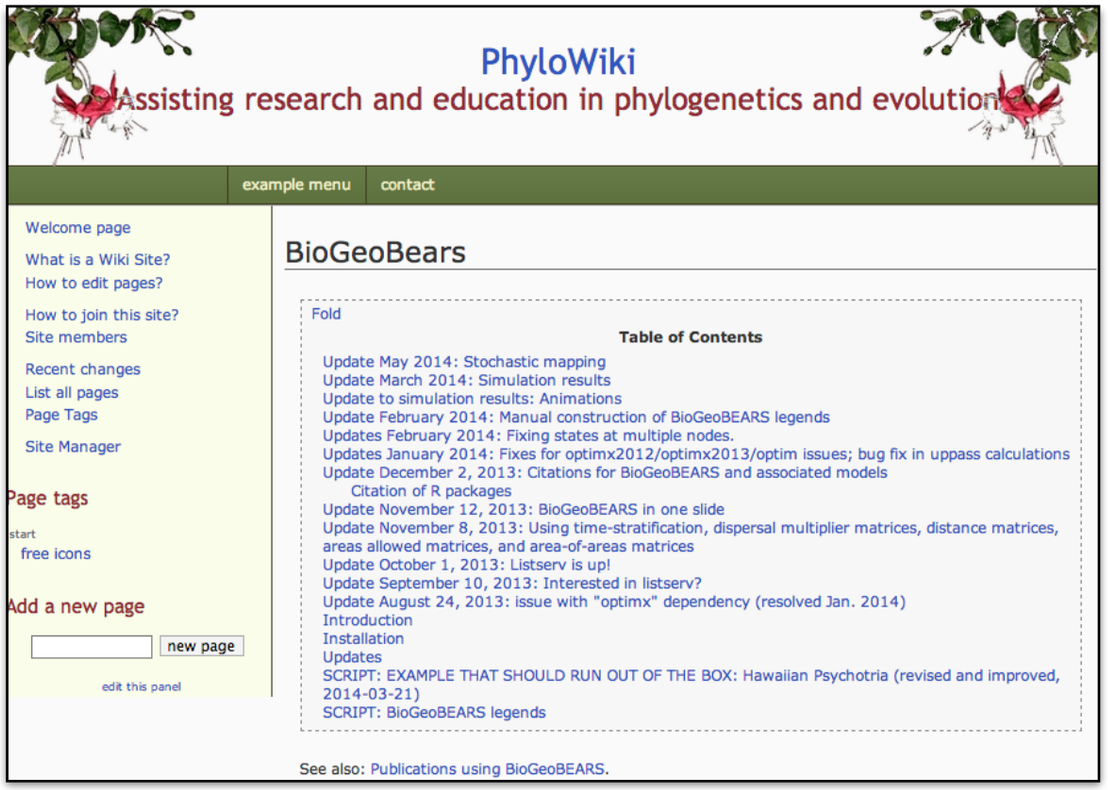
Craig Moritz
NIMBioS
Brian O'Meara
Jeremy Beaulieu
Katie Massana
Michael Landis

Ph.D. committee
John Huelsenbeck
Tony Barnosky
David Jablonski
Roger Byrne



TRY BioGeoBEARS AT:

http://phylo.wikidot.com/biogeobears

Funding: NIMBioS
NSF "Bivalves in Time and Space"
UC Berkeley Wang Fellowship
UC Berkeley Tien Fellowship
Google Summer of Code
NIMBioS, ARC DECRA

Family Canidae

~35 living species

~120+ fossil species

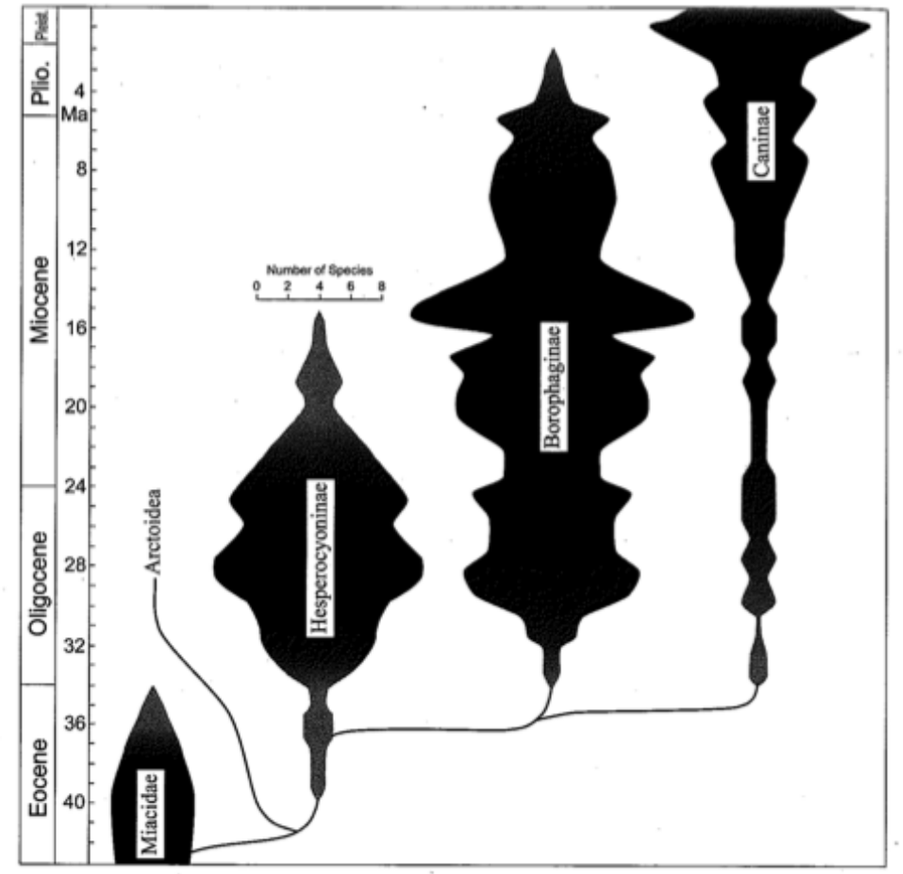
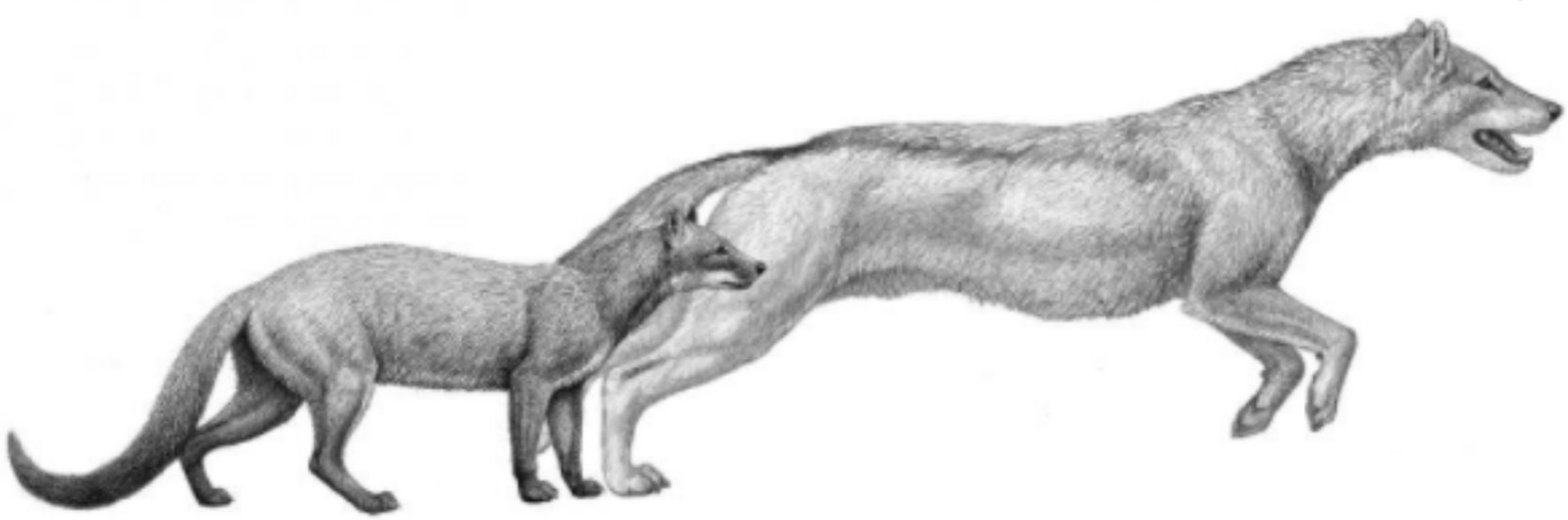


FIGURE 6.6
Diversity of species through time in the three subfamilies of Canidae

(Wang & Tedford 2008)



Hesperocyon and Sunkahetanka, two species of early dog. They were quite small and more closely resembled a mongoose. (Illustration by Mauricio Anton)

Source: http://www.forbes.com/sites/shaenamontanari/2015/08/18/old-dogs-learned-new-tricks-for-hunting-as-climate-changed/

Fossil Canidae

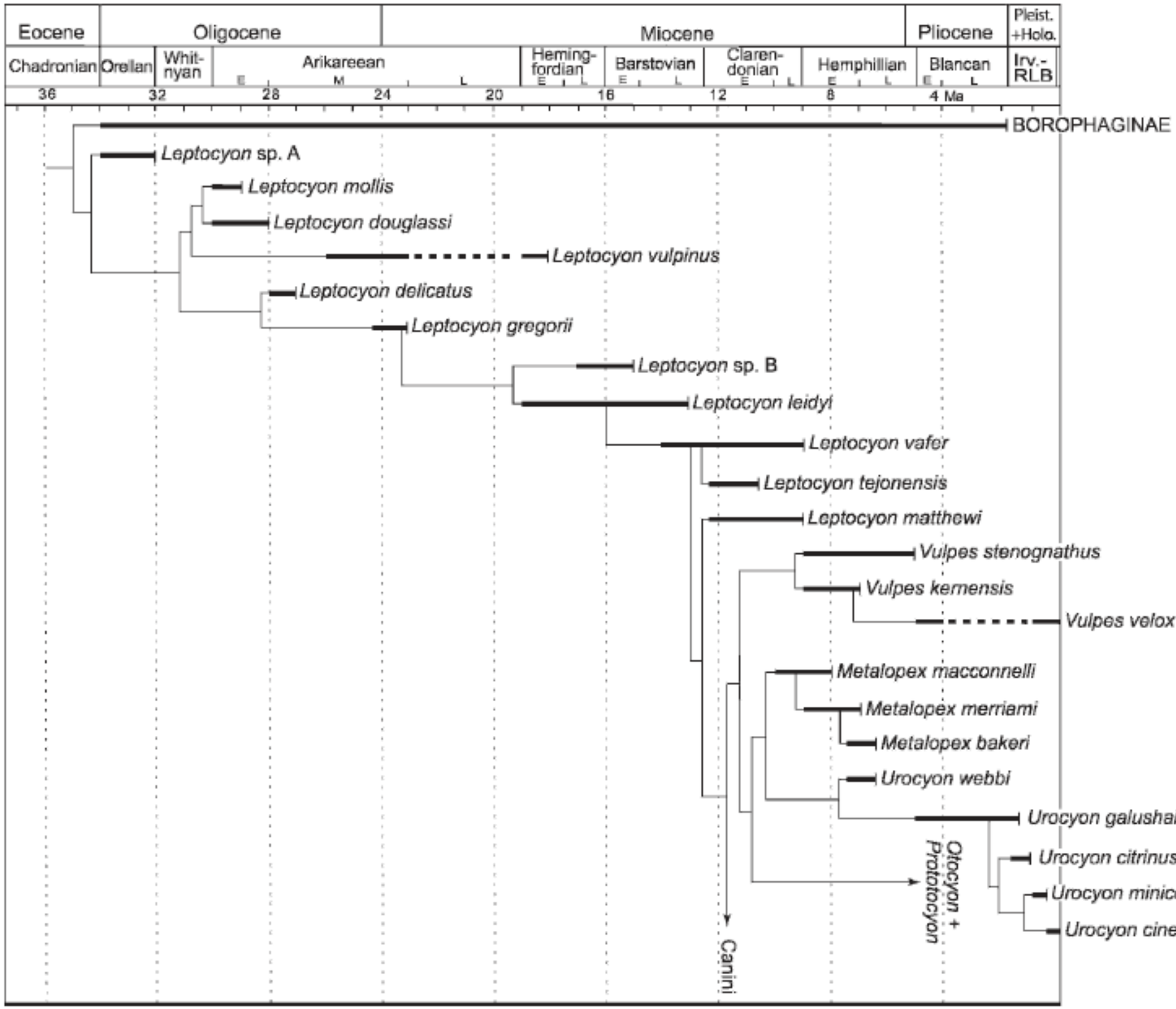


Fig. 66. Stratigraphic ranges and postulated phyletic relationships for taxa of the subfamily Caninae discussed in this report. The relationship is largely based on the preferred cladogram in figure 65, modified by speculations about cladogenetic or anagenetic events. These speculations are based on morphologic features too subtle to be coded in the data matrix but which, nonetheless, offer clues about possible relationships.

Parsimony + expert time-scaling of Caninae subtree: Tedford et al. 2008

Fossil Canidae

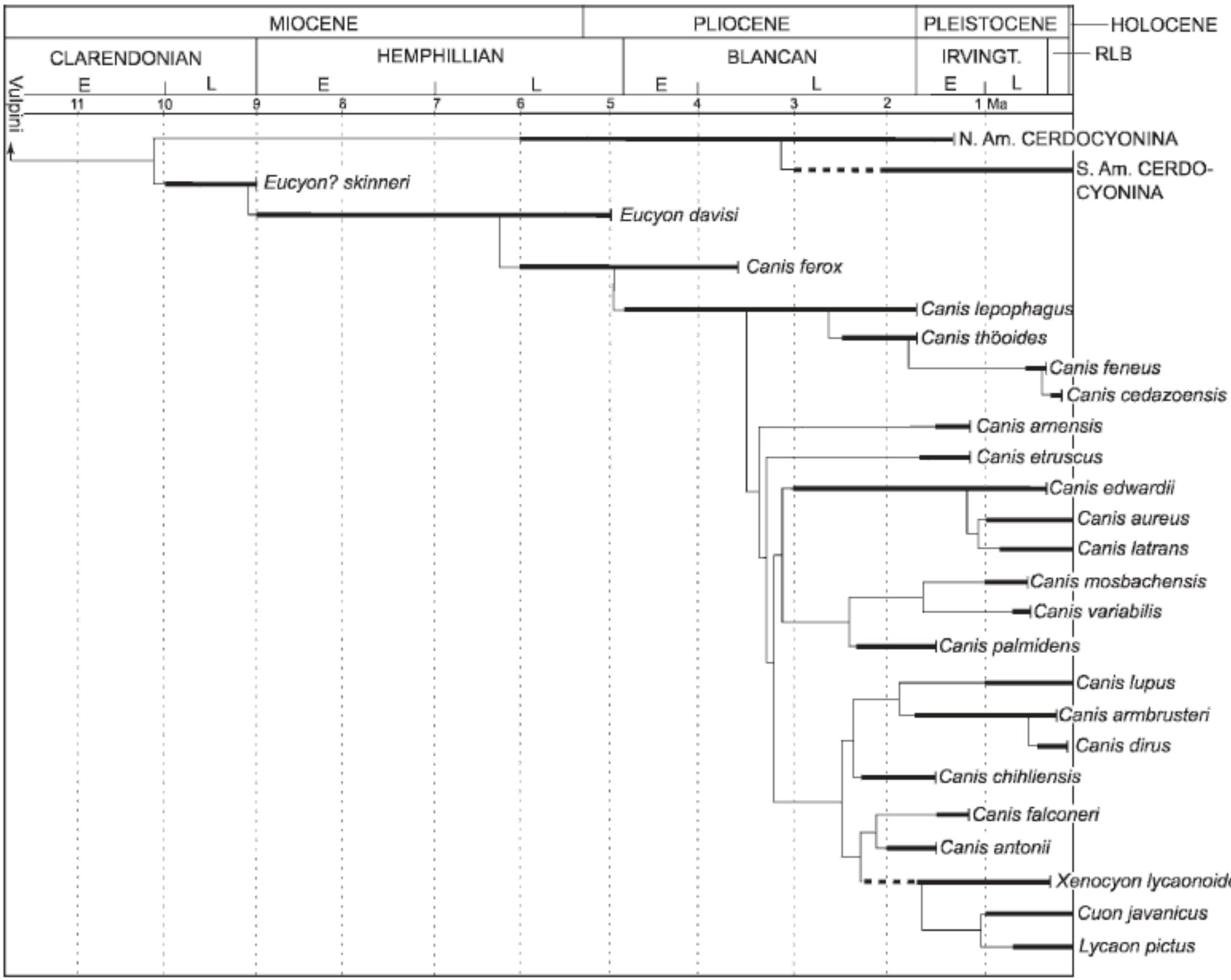
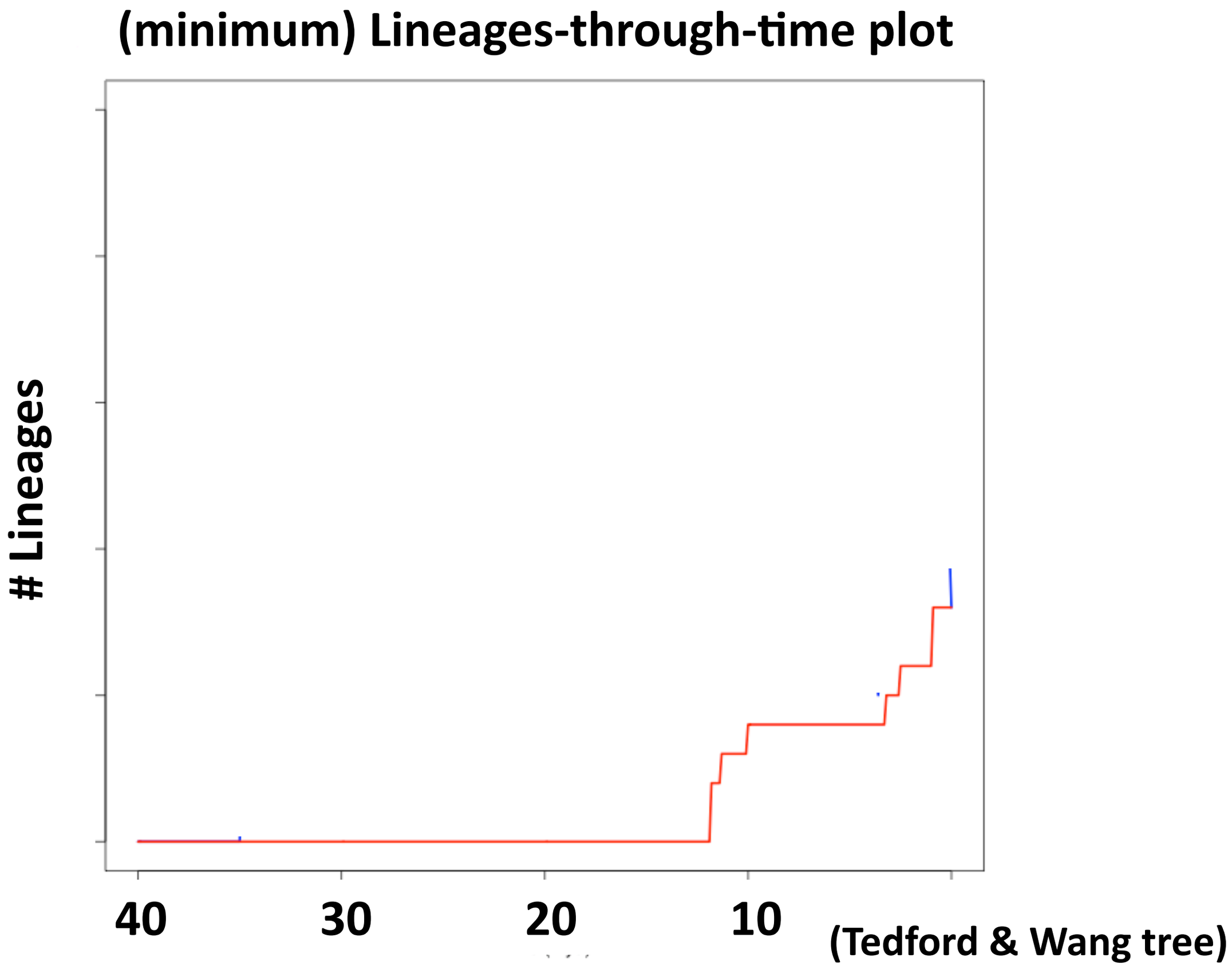


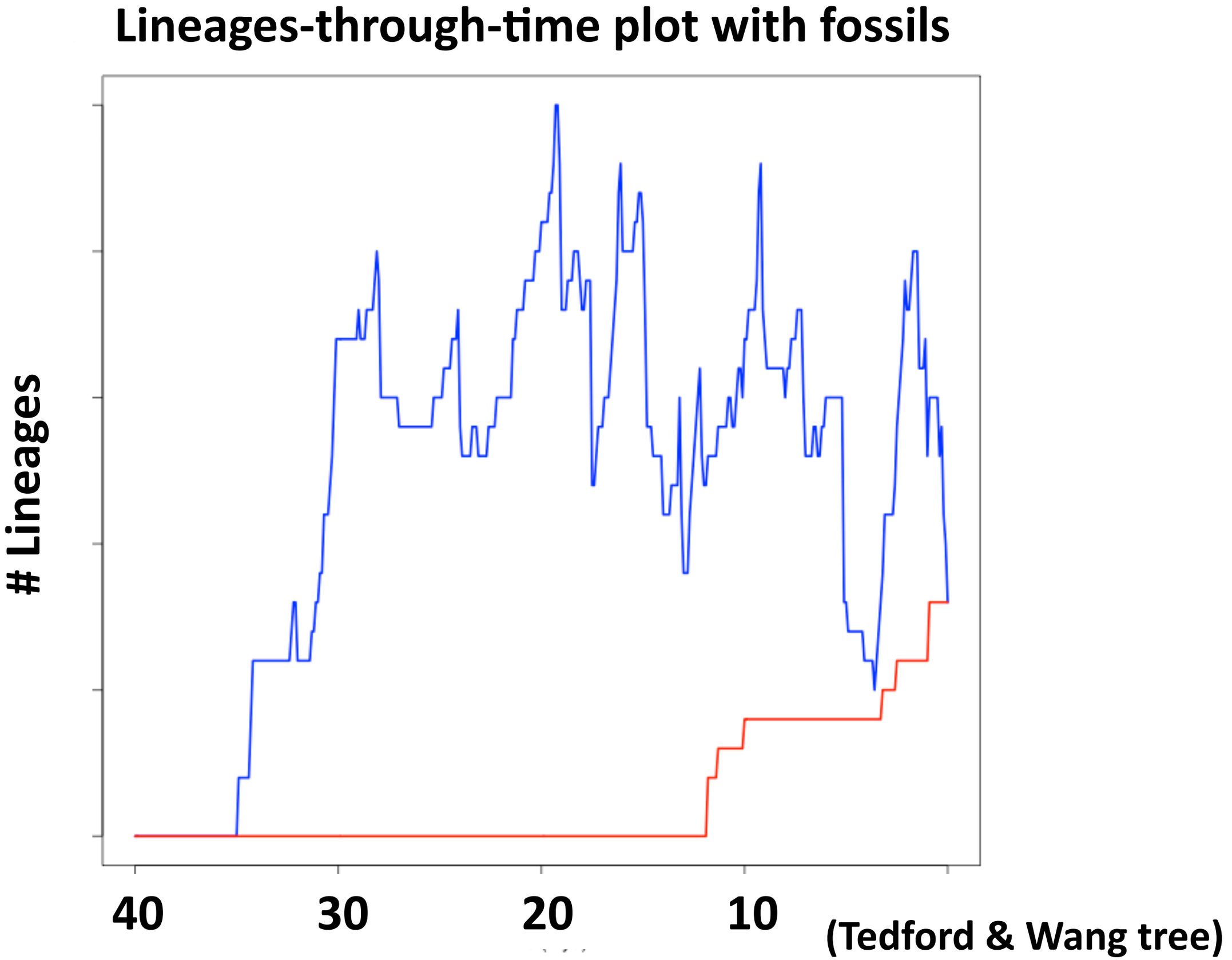
Fig. 66. *Continued.* Taxa that are too poorly known to be included in the phylogenetic analysis are also plotted on this chart. Chronologic framework is based on Tedford et al. (2004). Geographic range changes of Cerdocyonina are shown that schematically reflect dispersal to South America and extinction in North America.

Parsimony + expert time-scaling of Caninae subtree: Tedford et al. 2008

Family Canidae

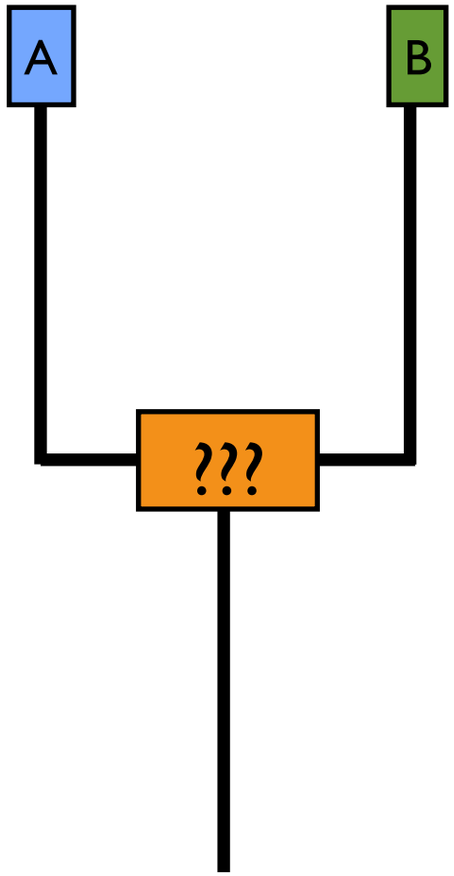


Family Canidae



Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

Strategy #1. Constraints on node ranges



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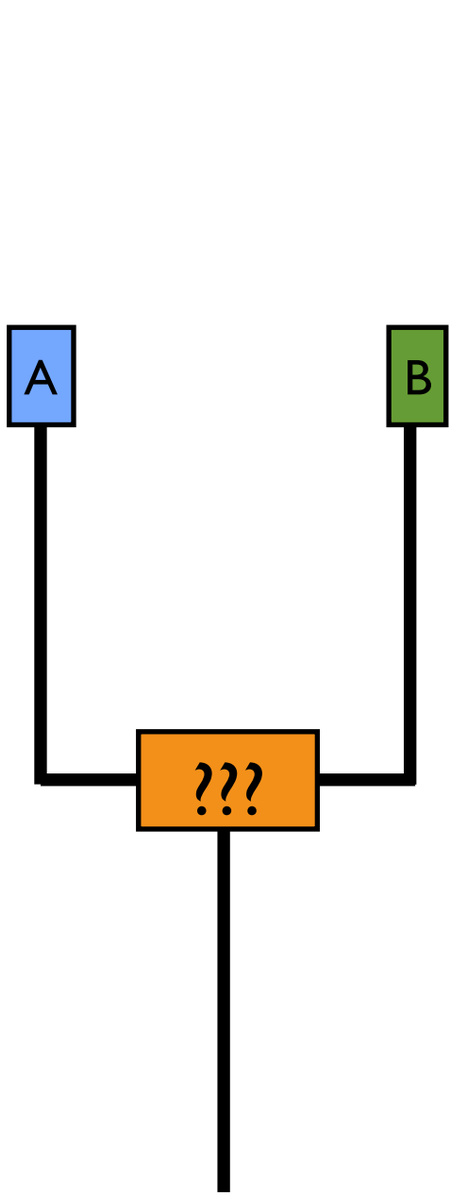

Range:

Tip likelihoods:

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

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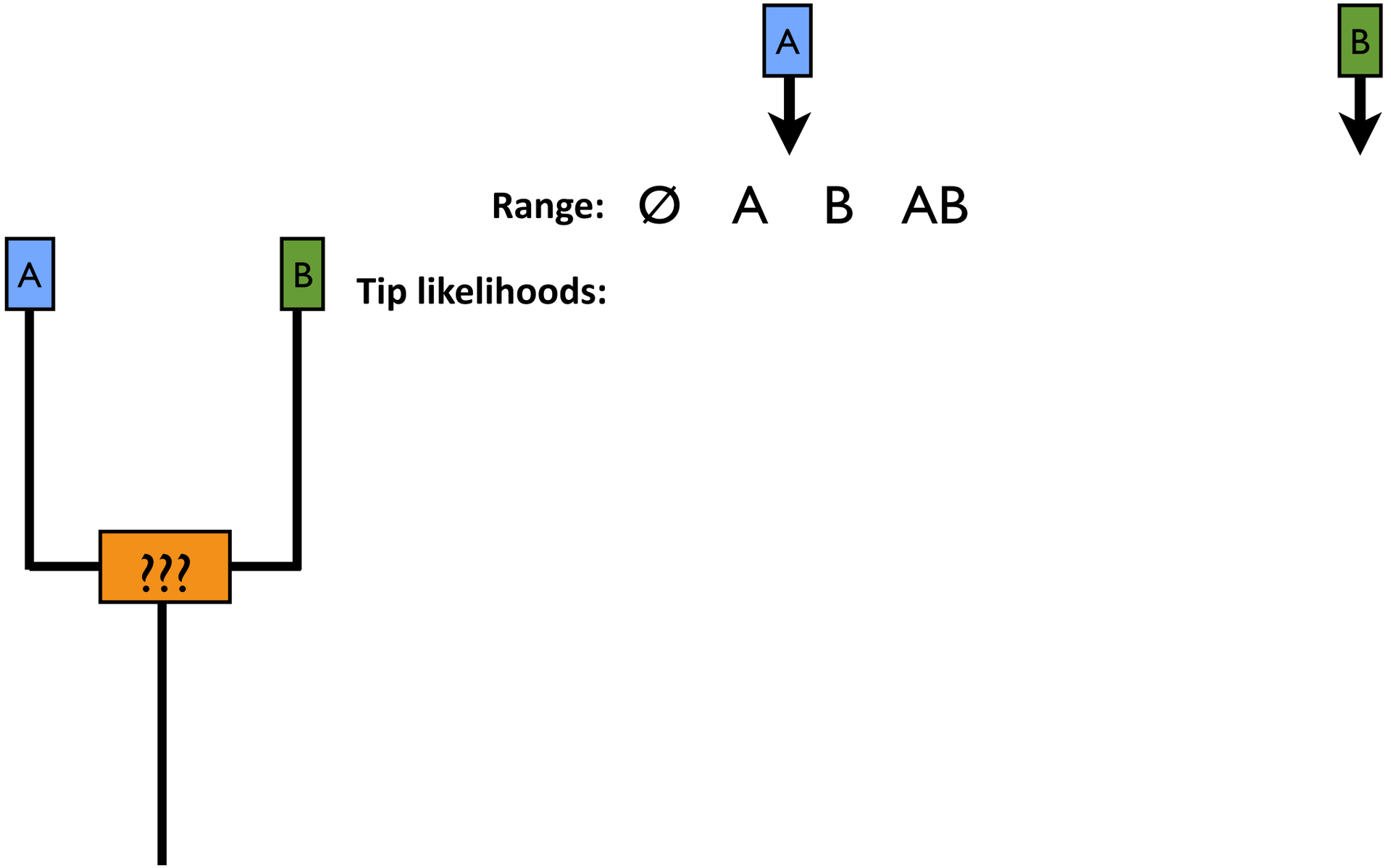

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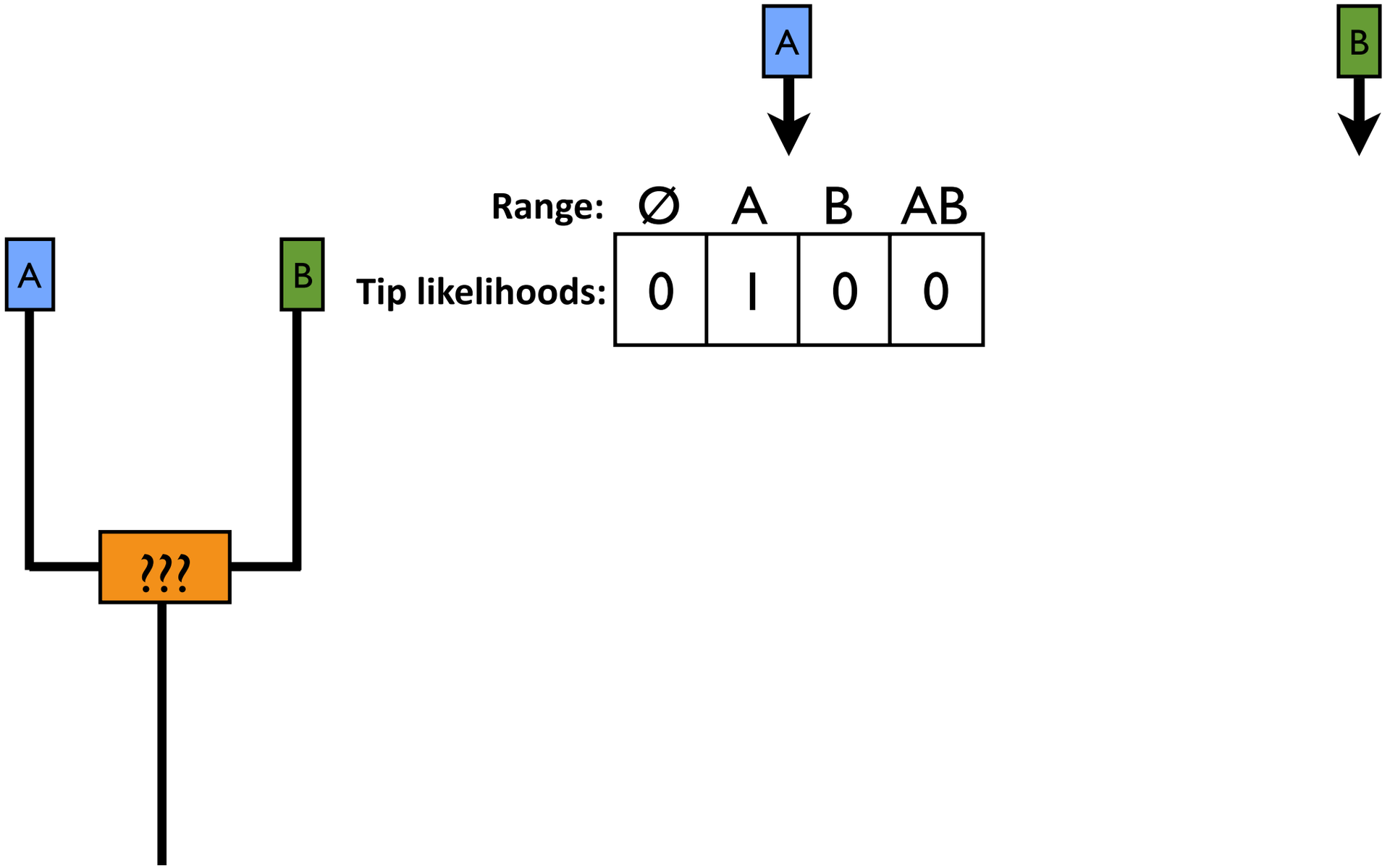

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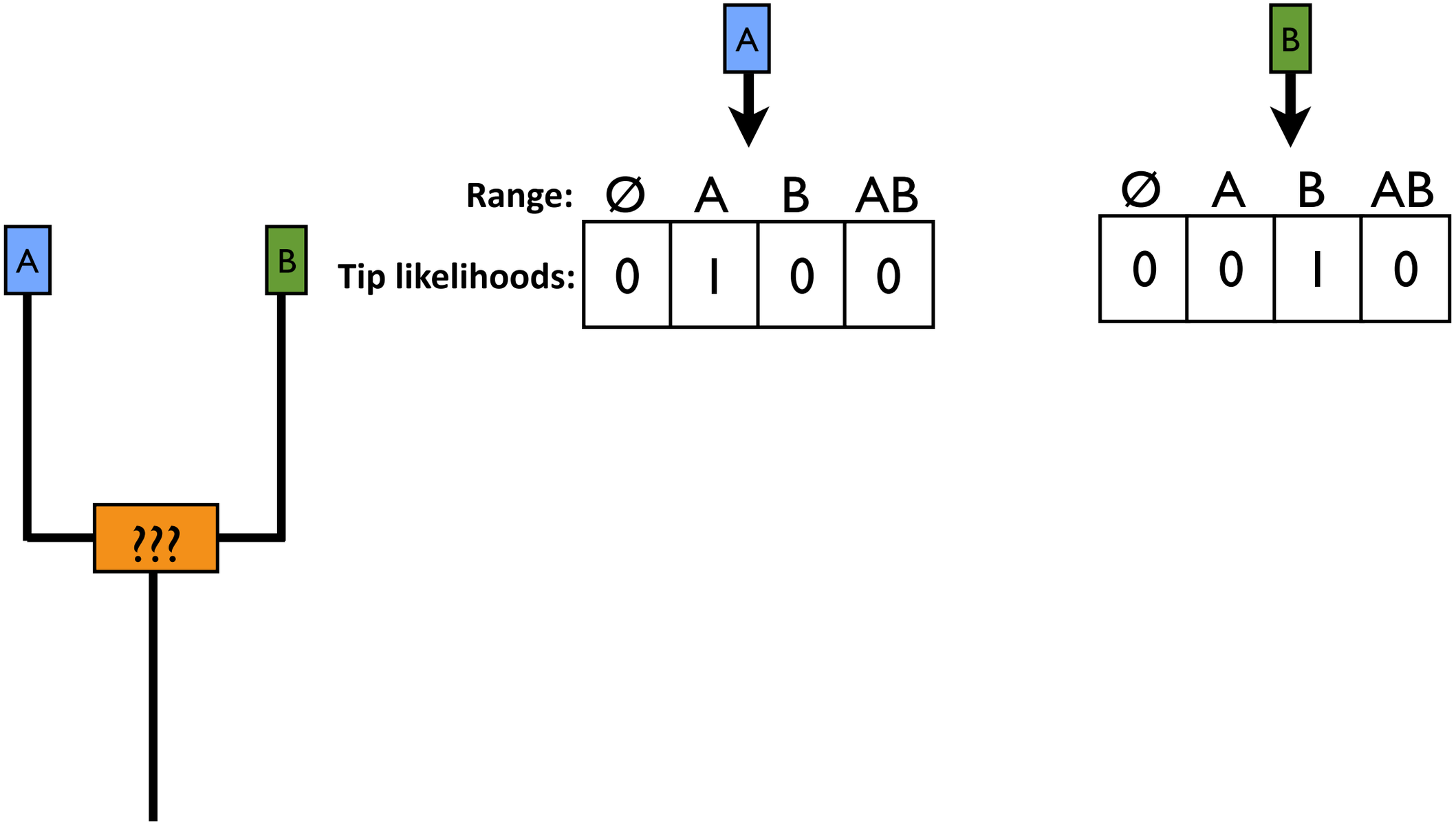

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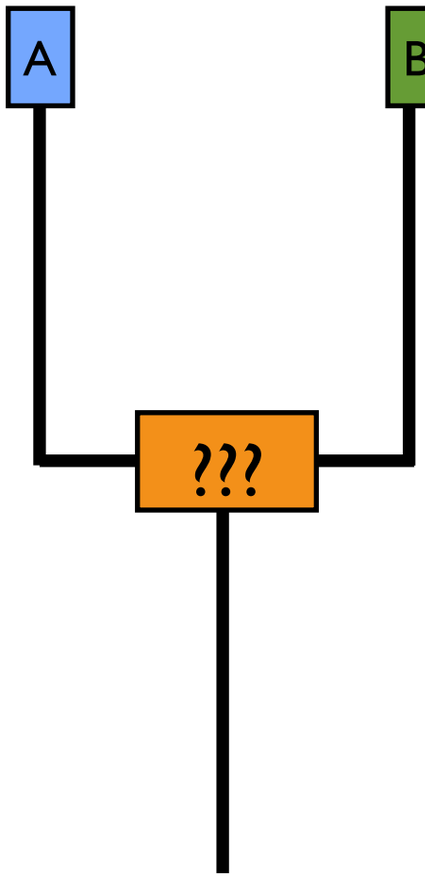

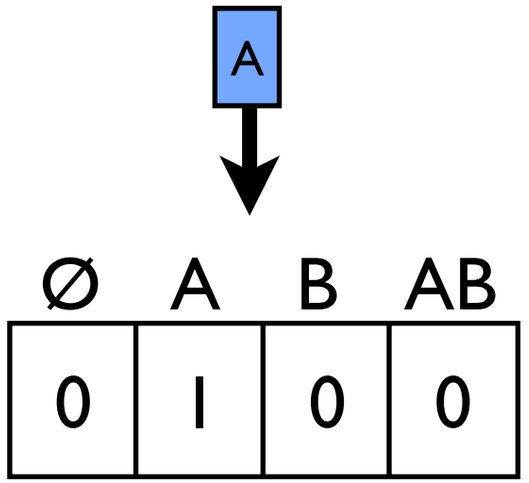

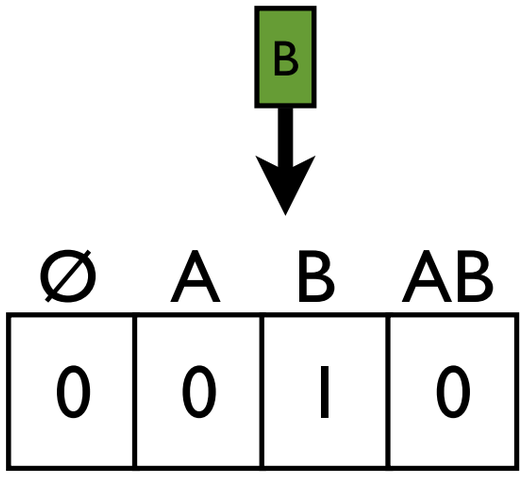

If *d*=0.2, *e*=0.1, *j*=0.15, then, likelihoods at ancestral node::

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

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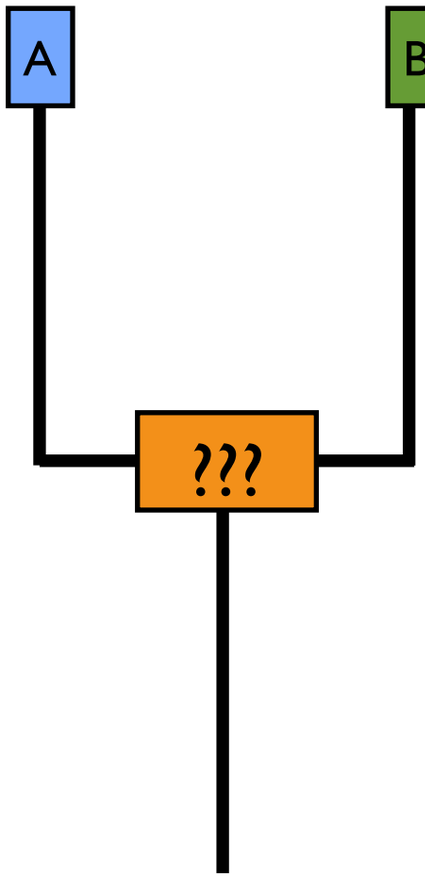

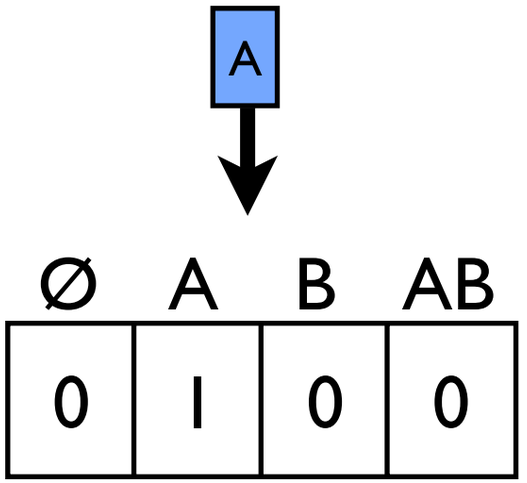

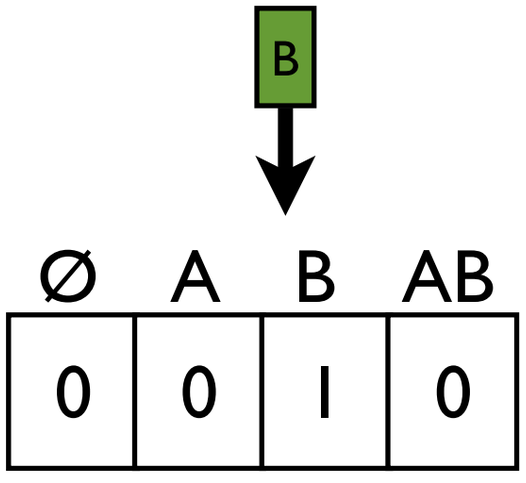

If *d*=0.2, *e*=0.1, *j*=0.15, then, likelihoods at ancestral node::

∅	A	B	AB
0	0.072	0.072	0.113

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

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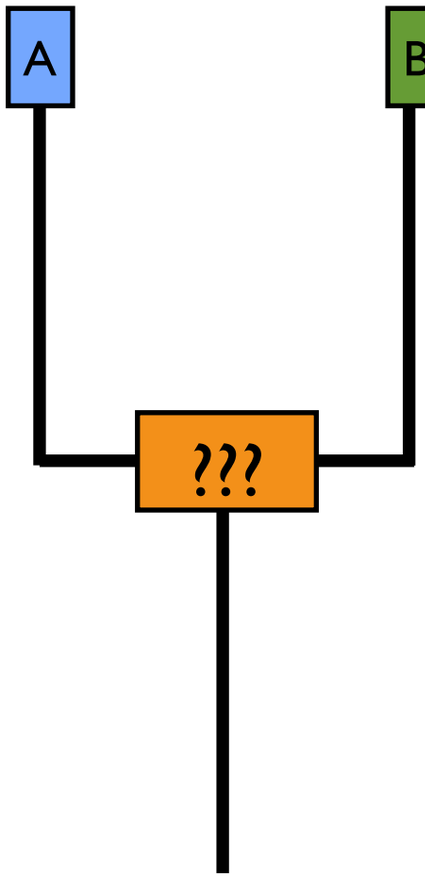

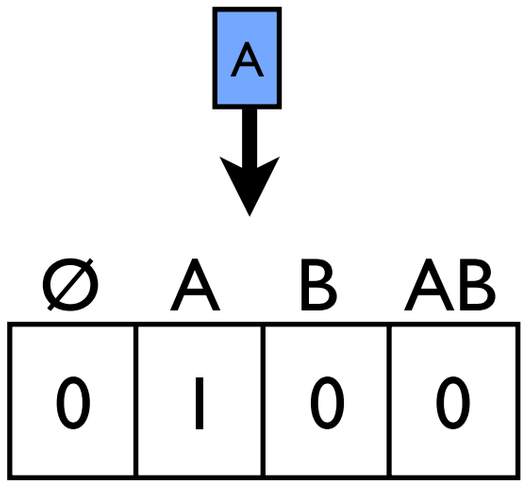

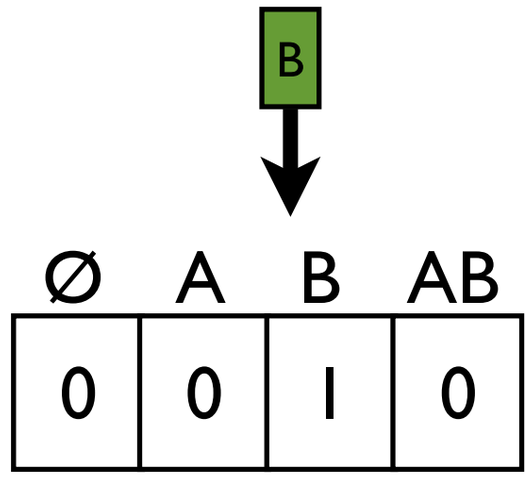

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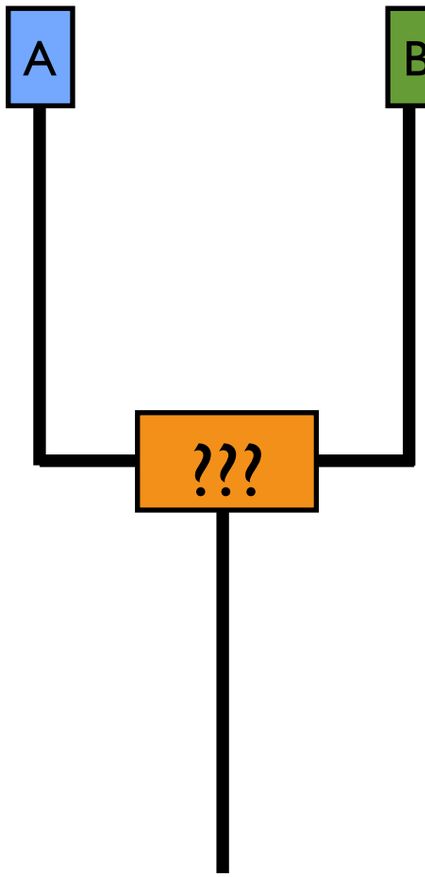
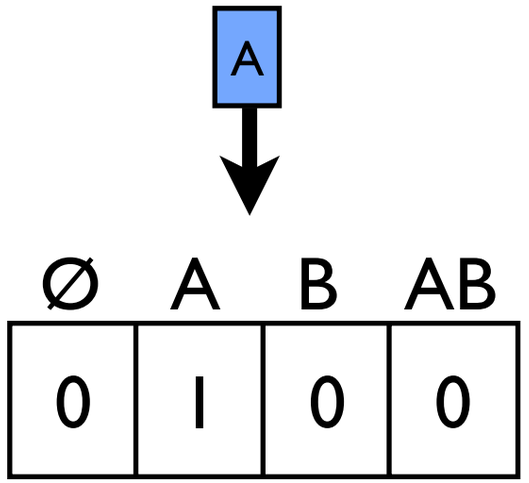
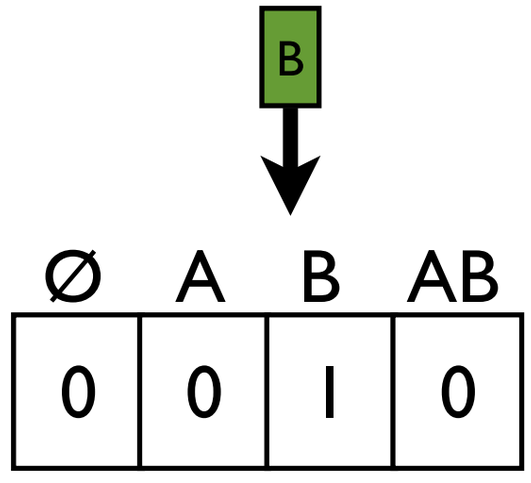
If you "know" / hypothesize the ancestor lived in "B" only:

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

Strategy #1. Constraints on node ranges







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0	0	1	0

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

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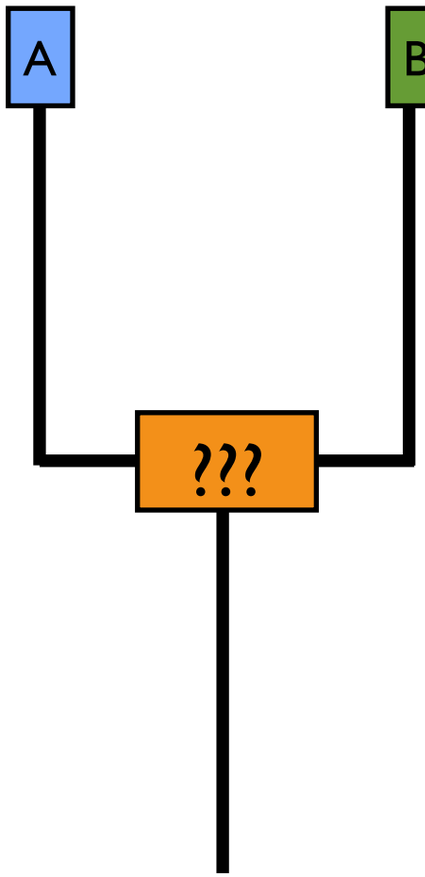

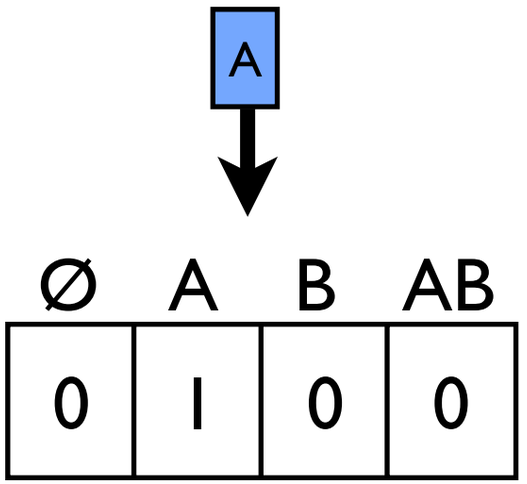

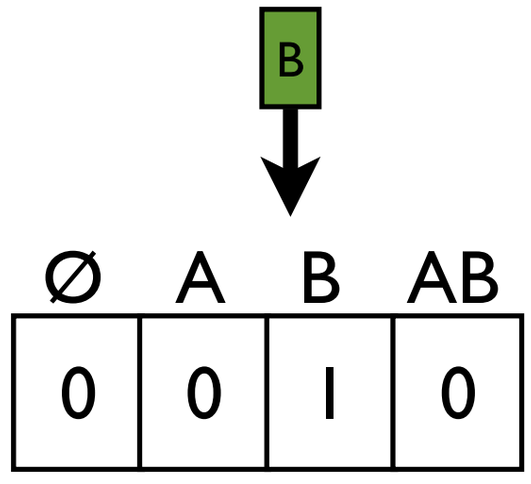

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equals:

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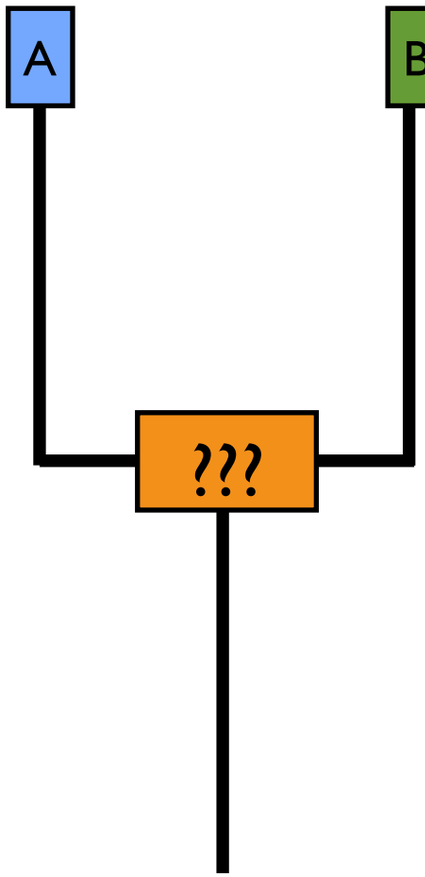
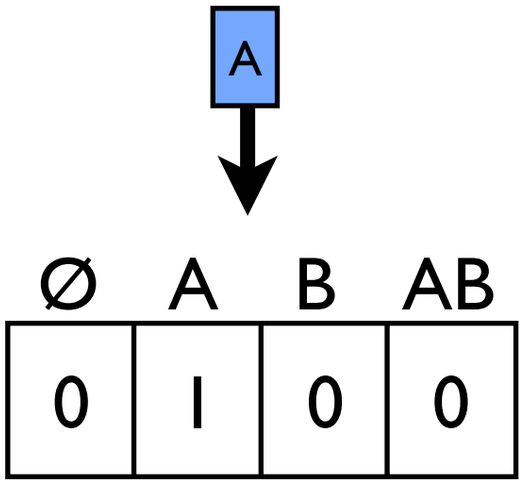
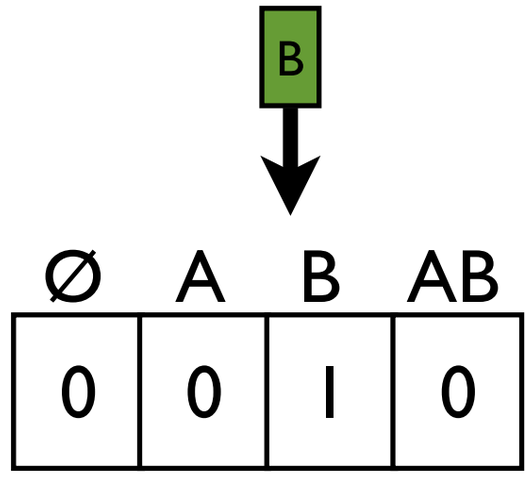
Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

Strategy #1. Constraints on node ranges



If you "know" / hypothesize the ancestor lived in *at least* B:





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Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

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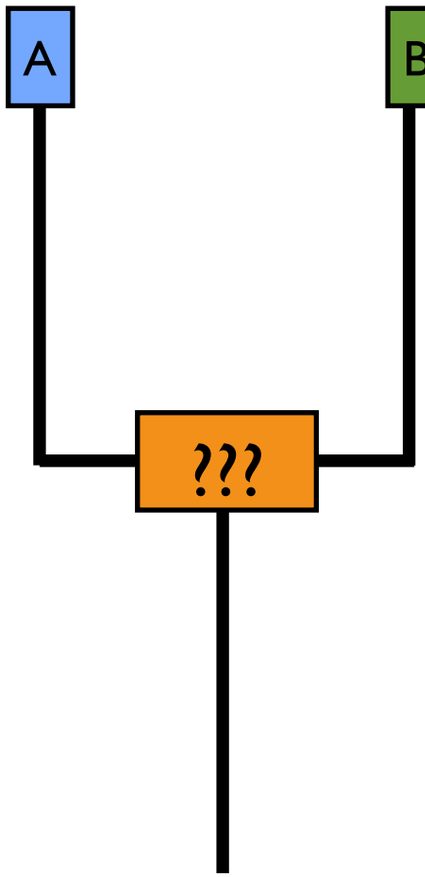

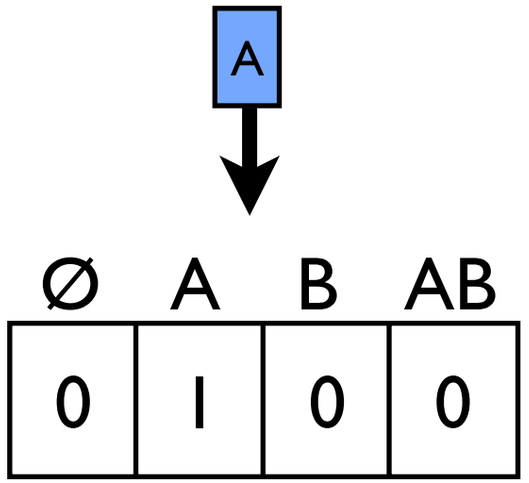

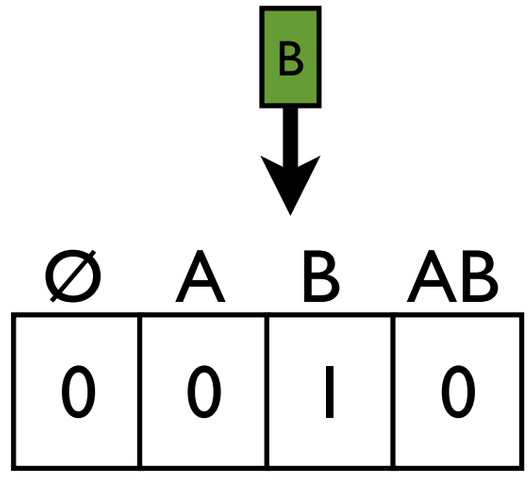

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Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

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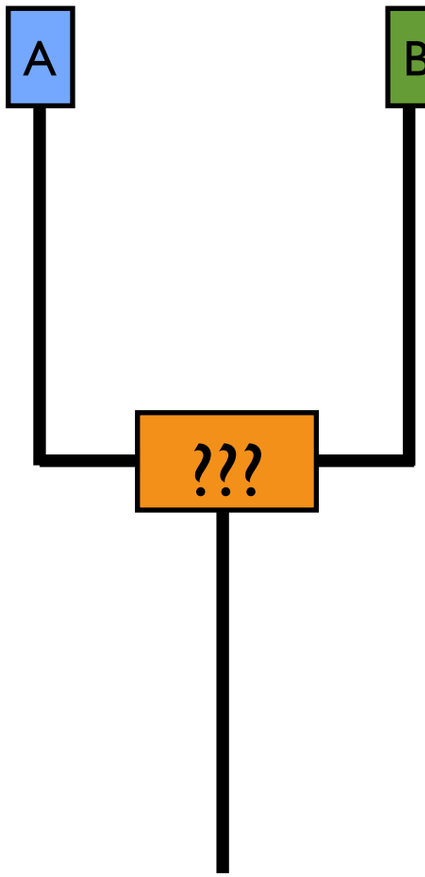

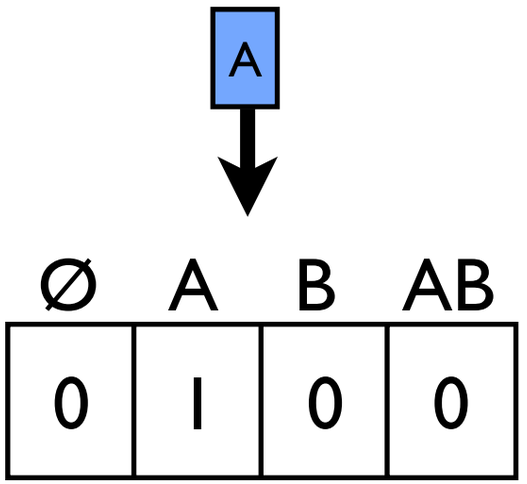

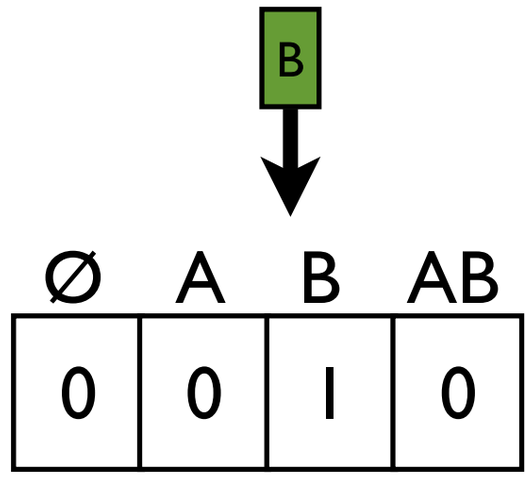

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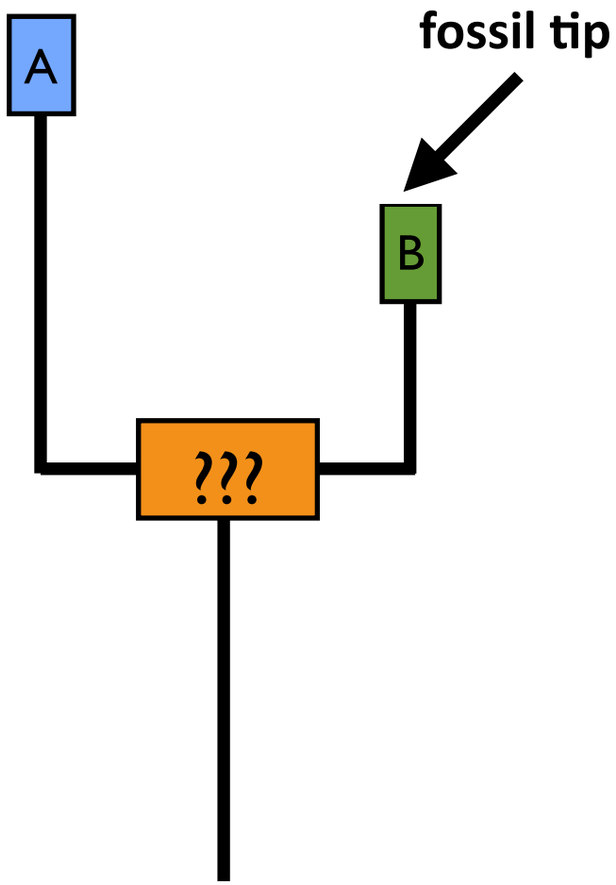
0	0	0.072	0.113

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

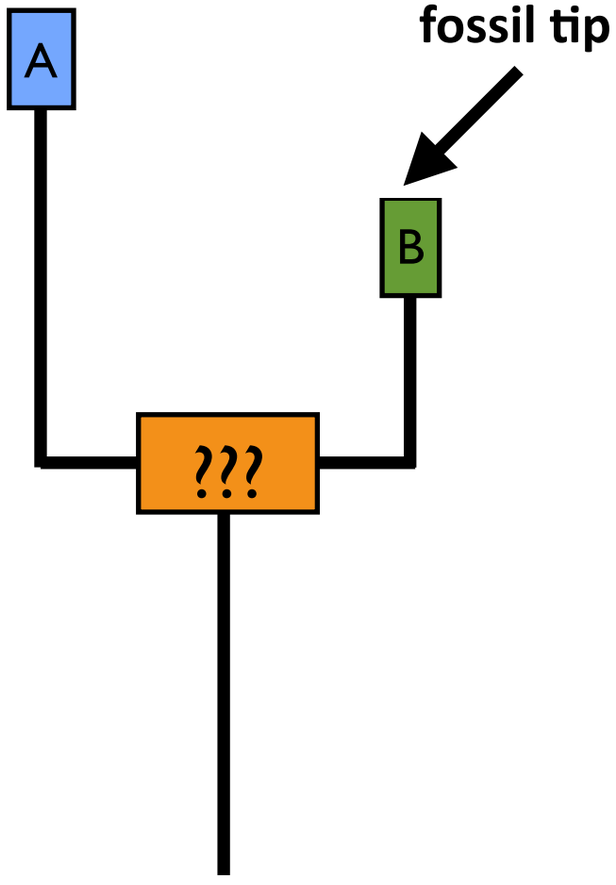
Strategy #2. Including fossils as terminal taxa



Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

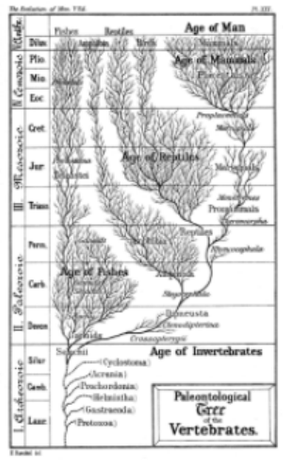
Strategy #2. Including fossils as terminal taxa

See *Biology Letters* Special Issue, "Putting Fossils in Trees," with David Bapst, Graeme Lloyd, April Wright



THE ROYAL SOCIETY

Putting fossils in trees: combining morphology, time, and molecules to estimate phylogenies and divergence times



Articles from across the tree of life as well as issues concerning data quality and methodological choices have been compiled as part of this Special Feature. The papers included span a breadth of topics relating to placing fossils in trees and using them in time-scaling but with particular emphasis on, or comparison to, the suite of new "tip-dating" approaches.

Keywords: Evolution, Palaeontology, Taxonomy and systematics, Bioinformatics

Showing 1 - 9 of 9 items in this collection

Editor's note on 'Putting fossils in trees' special issue

Journal: Biology Letters

Date: Mar 22 2017

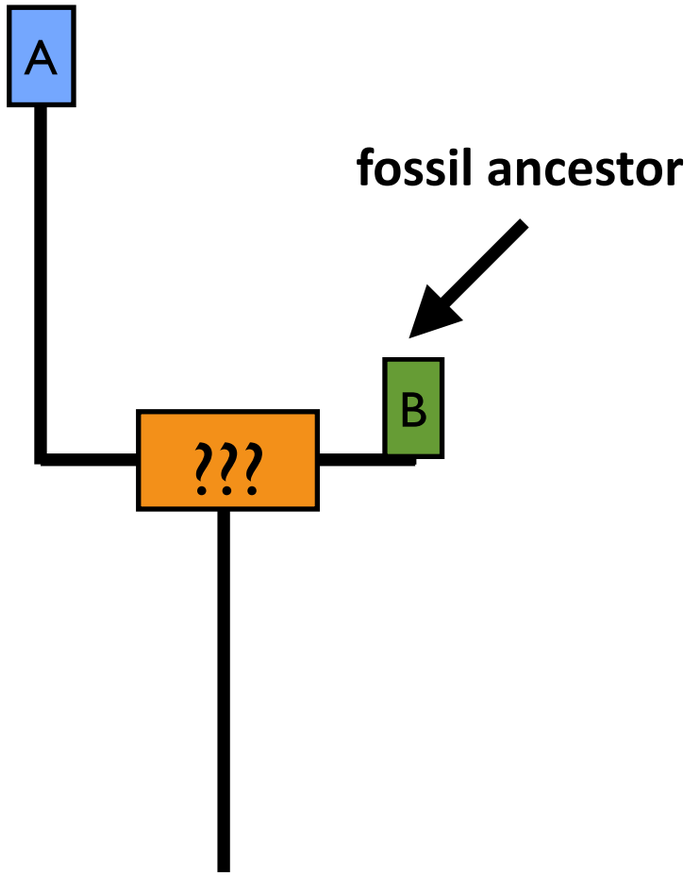
Time-calibrated models support congruency between Cretaceous continental rifting and titanosaurian evolutionary history

Journal: Biology Letters

Date: Apr 05 2016

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

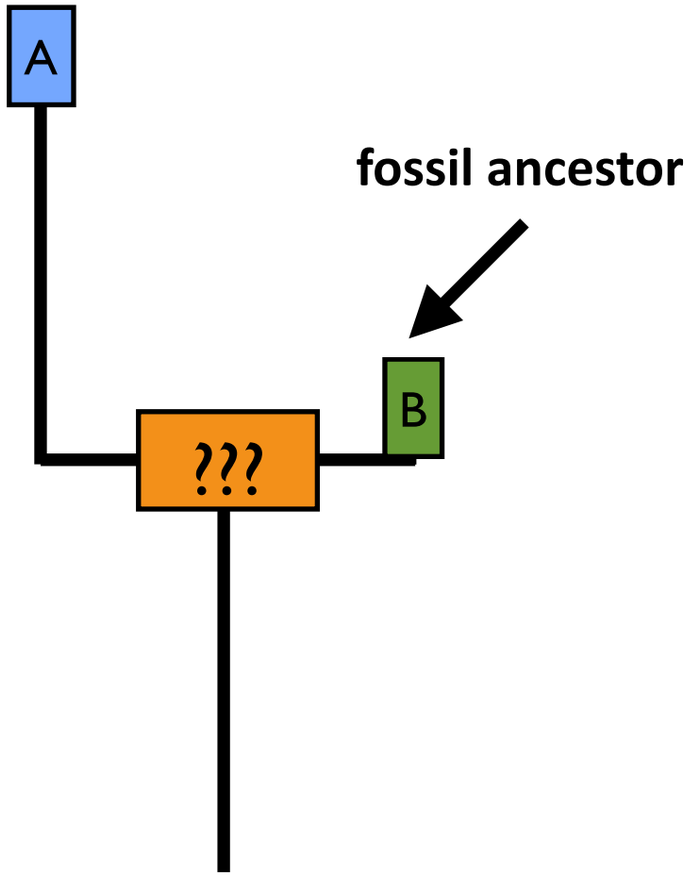
Strategy #3. Including fossils as <u>direct ancestors</u>



Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

Strategy #3. Including fossils as <u>direct ancestors</u>

In *BioGeoBEARS*:



Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

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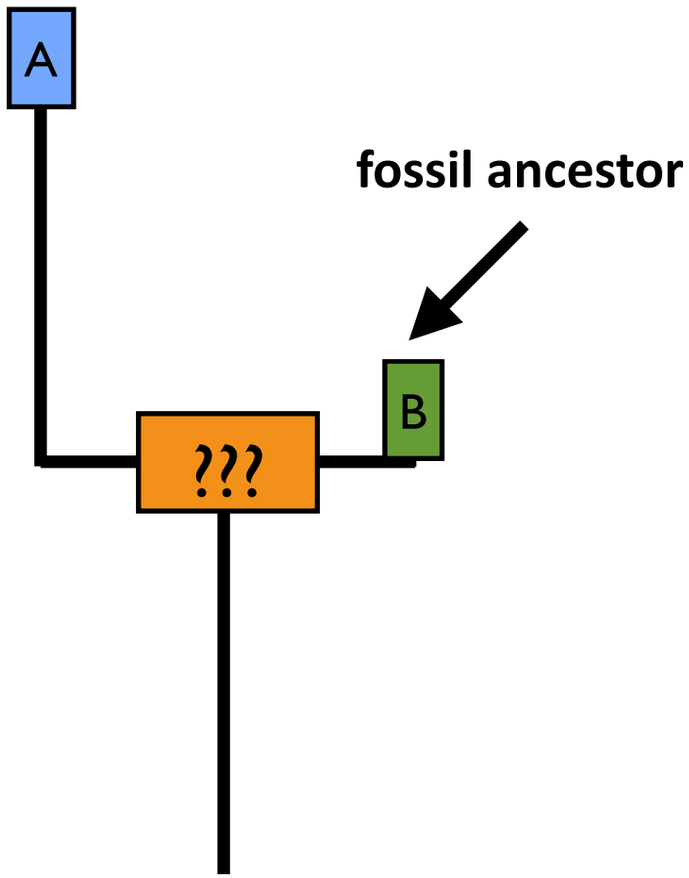
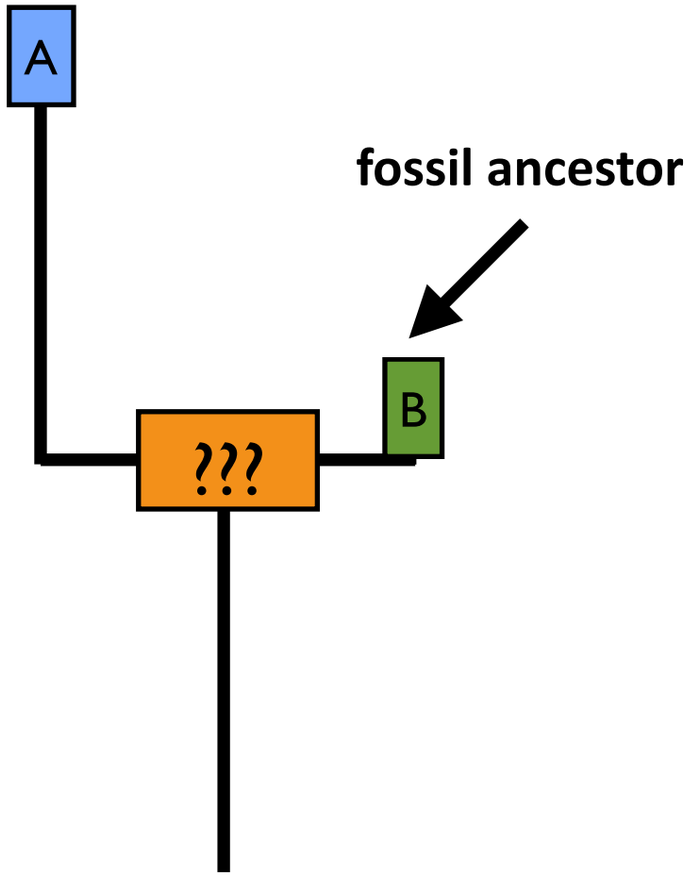


In *BioGeoBEARS*:

- **fossil ancestors are identified as "hooks"**

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

Strategy #3. Including fossils as <u>direct ancestors</u>

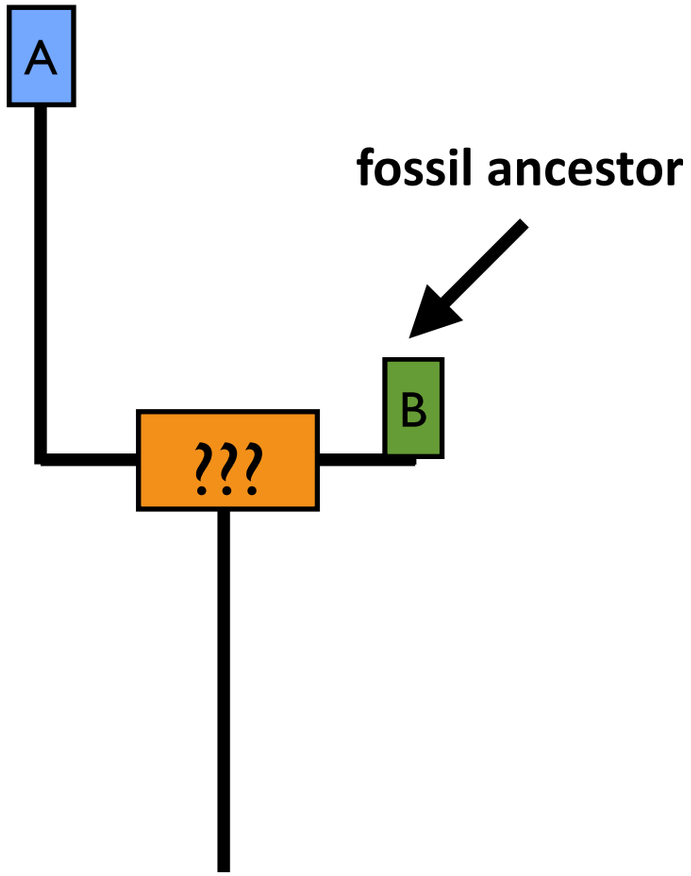


In *BioGeoBEARS*:

- **fossil ancestors are identified as "hooks"**
- **"hook" = branch lengths < 0.000001 (or, user-specified)**

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

Strategy #3. Including fossils as <u>direct ancestors</u>

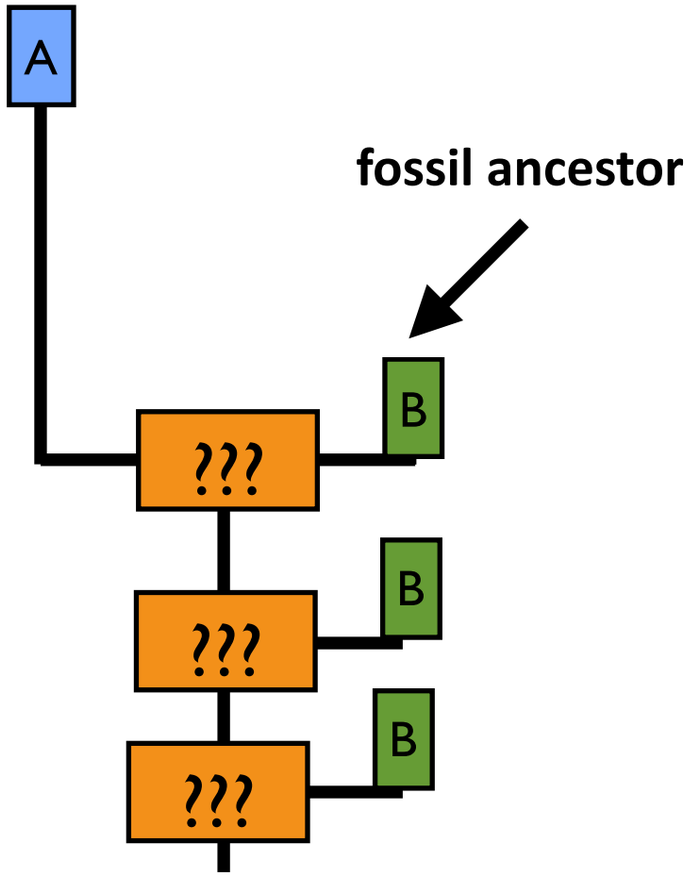


In *BioGeoBEARS*:

- fossil ancestors are identified as "hooks"
- "hook" = branch lengths < 0.000001 (or, user-specified)
- no cladogenesis process applied as these nodes are not real speciation events

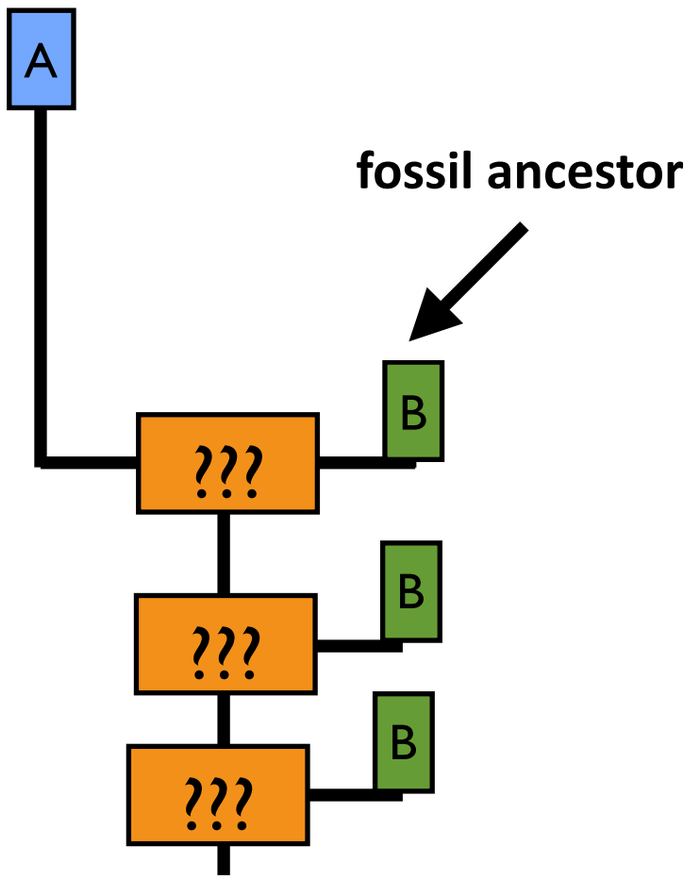
Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

Strategy #4. Fossil species with time-ranges?



Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

Strategy #4. Fossil species with time-ranges?

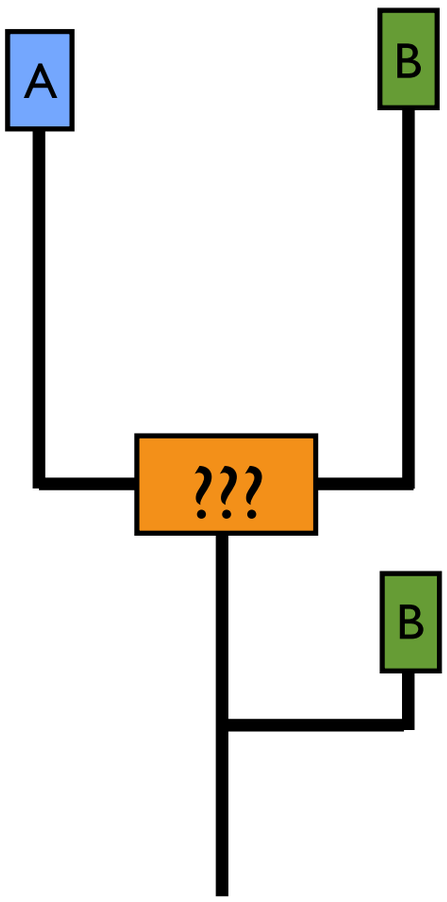


In *BioGeoBEARS*:

- add "hooks" at the midpoint of each geologic unit
- (or a timepoint selected from a uniform prior)

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

Strategy #5. What about fossils without characters?



random placement within node/stem/date constraints

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

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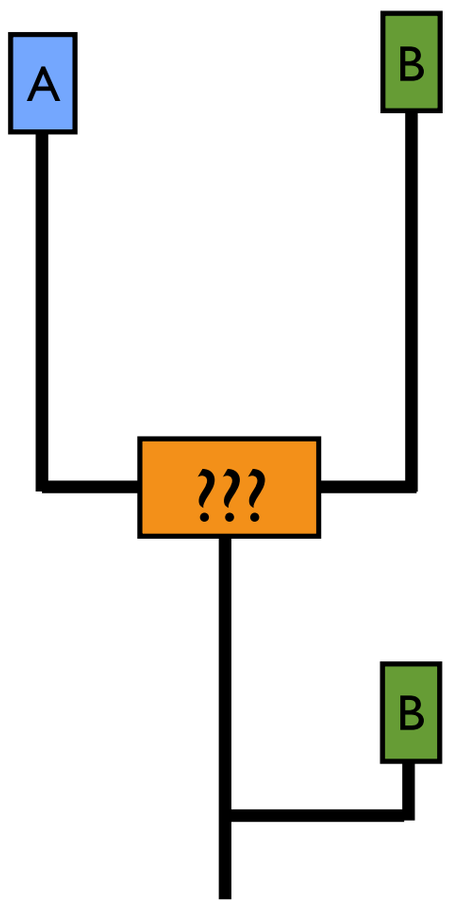

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Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

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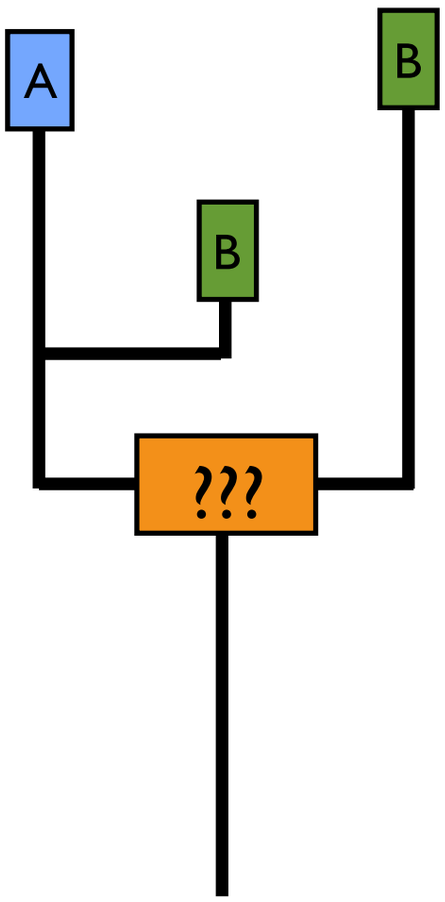

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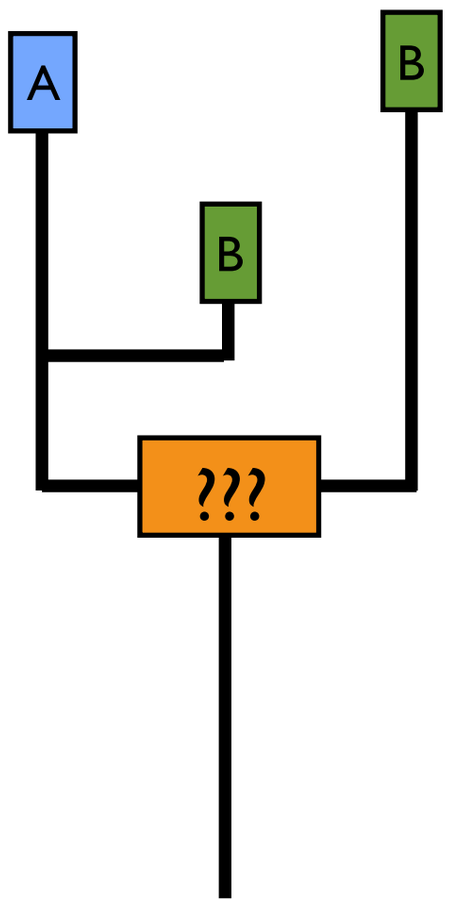
Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

Strategy #5. What about fossils without characters?

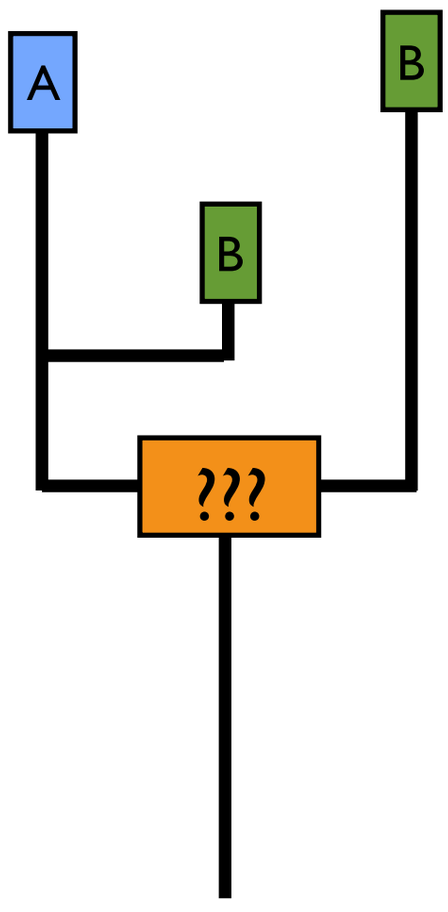


random placement within node/stem/date constraints

- Repeat random placement e.g. 100 times, or randomly place on 100 posterior trees
- Not as desirable as placing fossils according to a birth/death/sampling prior in BEAST, but more flexible

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

<u>Big issue</u>: are fossil ranges equal to real ranges?

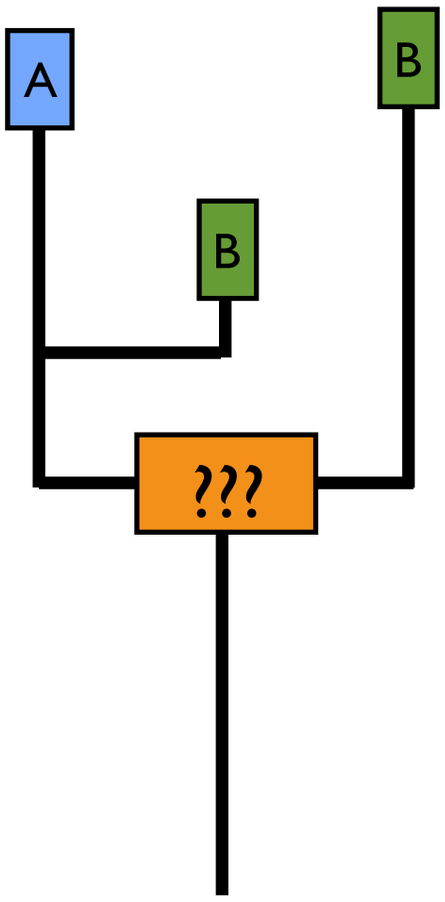


If a fossil is found in area "B"

- **sometimes, you can assume "B" is the complete range (maybe)**
- **But perhaps the real range was AB**
- **(In some cases, this could even be an issue with living taxa)**

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

<u>Big issue</u>: are fossil ranges equal to real ranges?



Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

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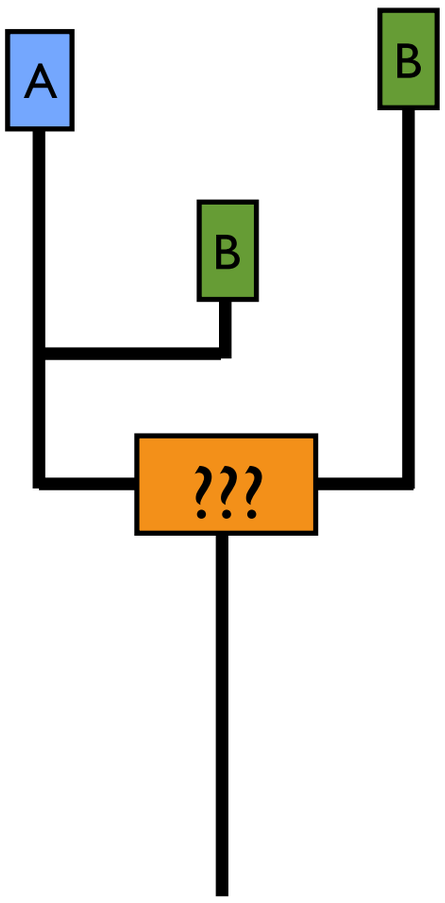

Incomplete ranges strategy #1:

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

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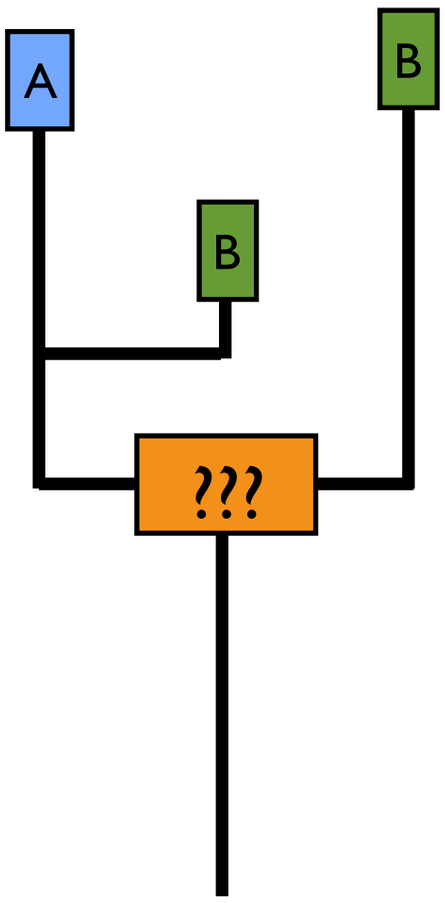


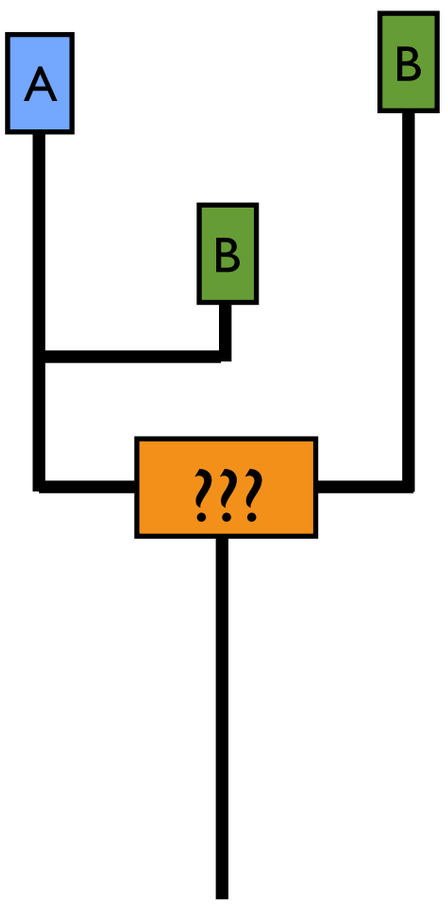
Incomplete ranges strategy #1:

Code with question marks:

A	B
?	I

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

<u>Big issue</u>: are fossil ranges equal to real ranges?



Incomplete ranges strategy #1:

Code with question marks:

A	B
?	I

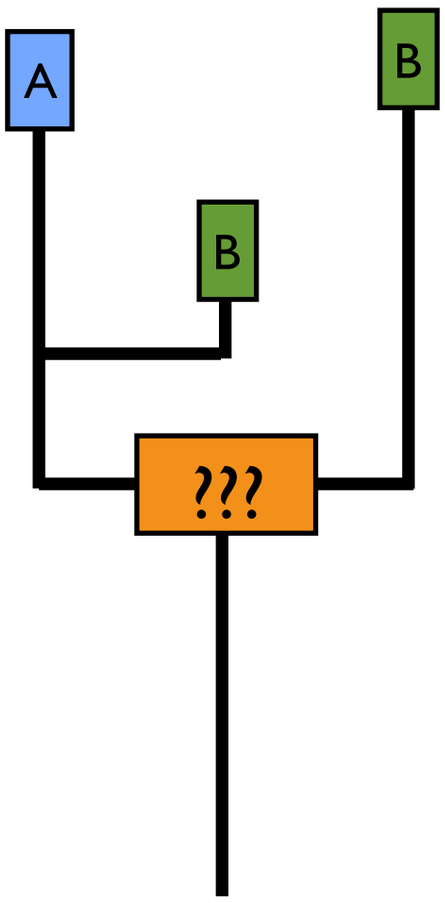
Tip likelihoods:

Ø	A	B	AB
0	0	I	I

My experience: leads to very widespread ancestors, weird parameters

Putting fossils into model-based biogeography: strategies available in *BioGeoBEARS*

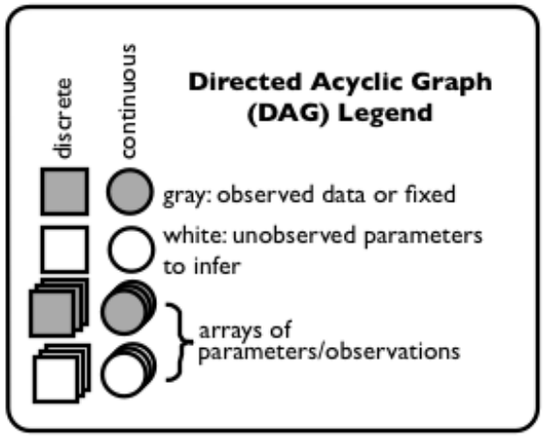
<u>Big issue</u>: are fossil ranges equal to real ranges?



Incomplete ranges strategy #2:

Have a *model* for imperfect detection

BioGeoBEARS model for imperfect detection



model of historical biogeography (e.g. DEC)

inferred history

present distributions

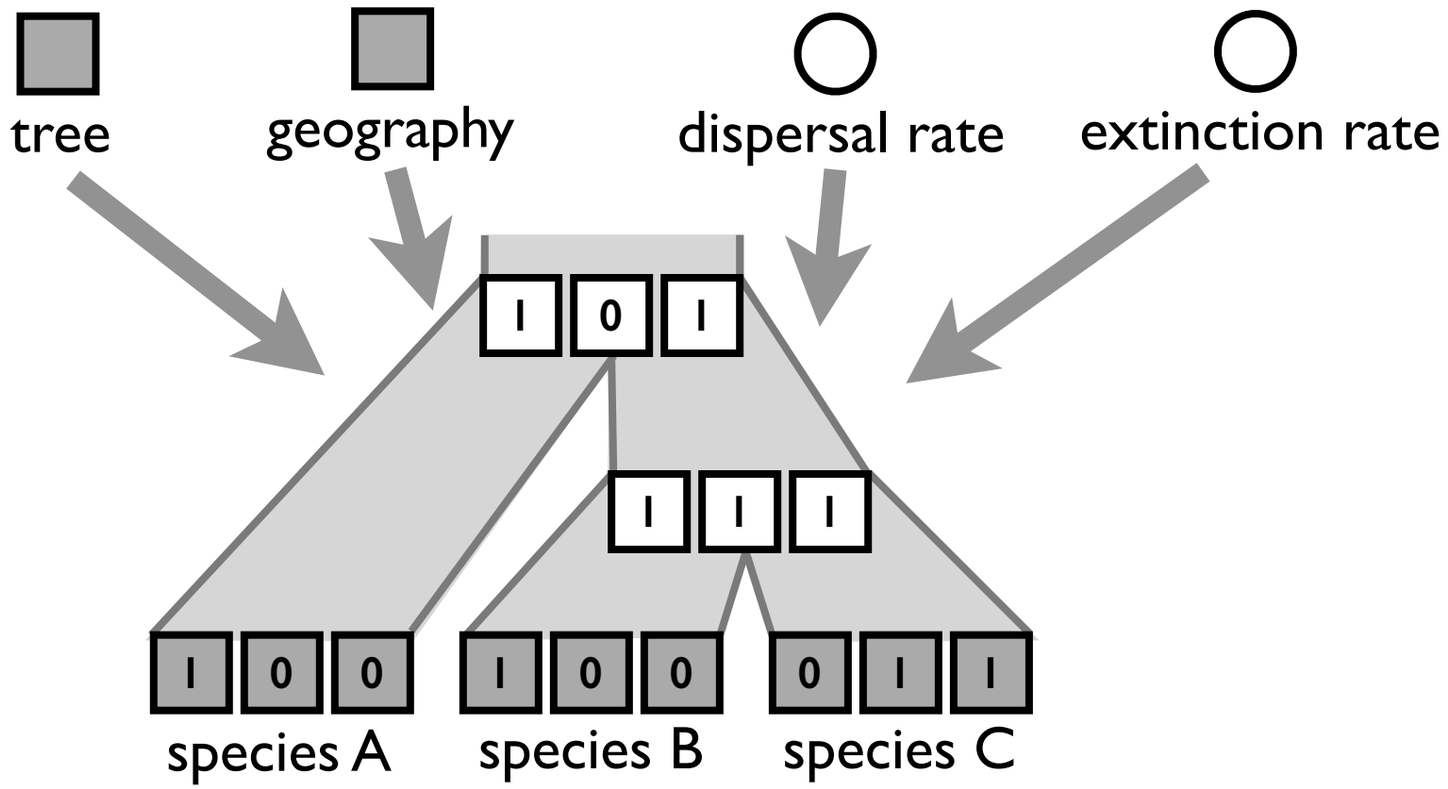
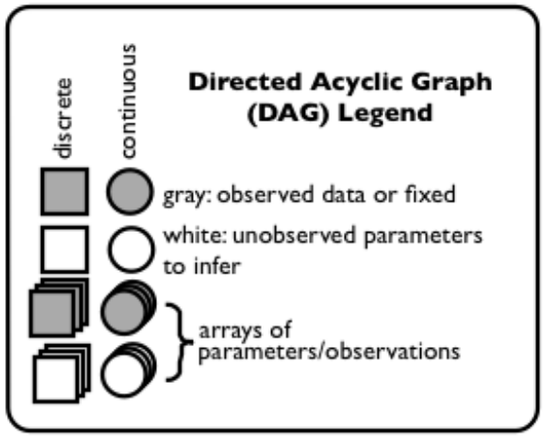


Figure 1A. Traditional inference procedure in likelihood analyses of historical biogeography on a phylogeny.

BioGeoBEARS model for imperfect detection



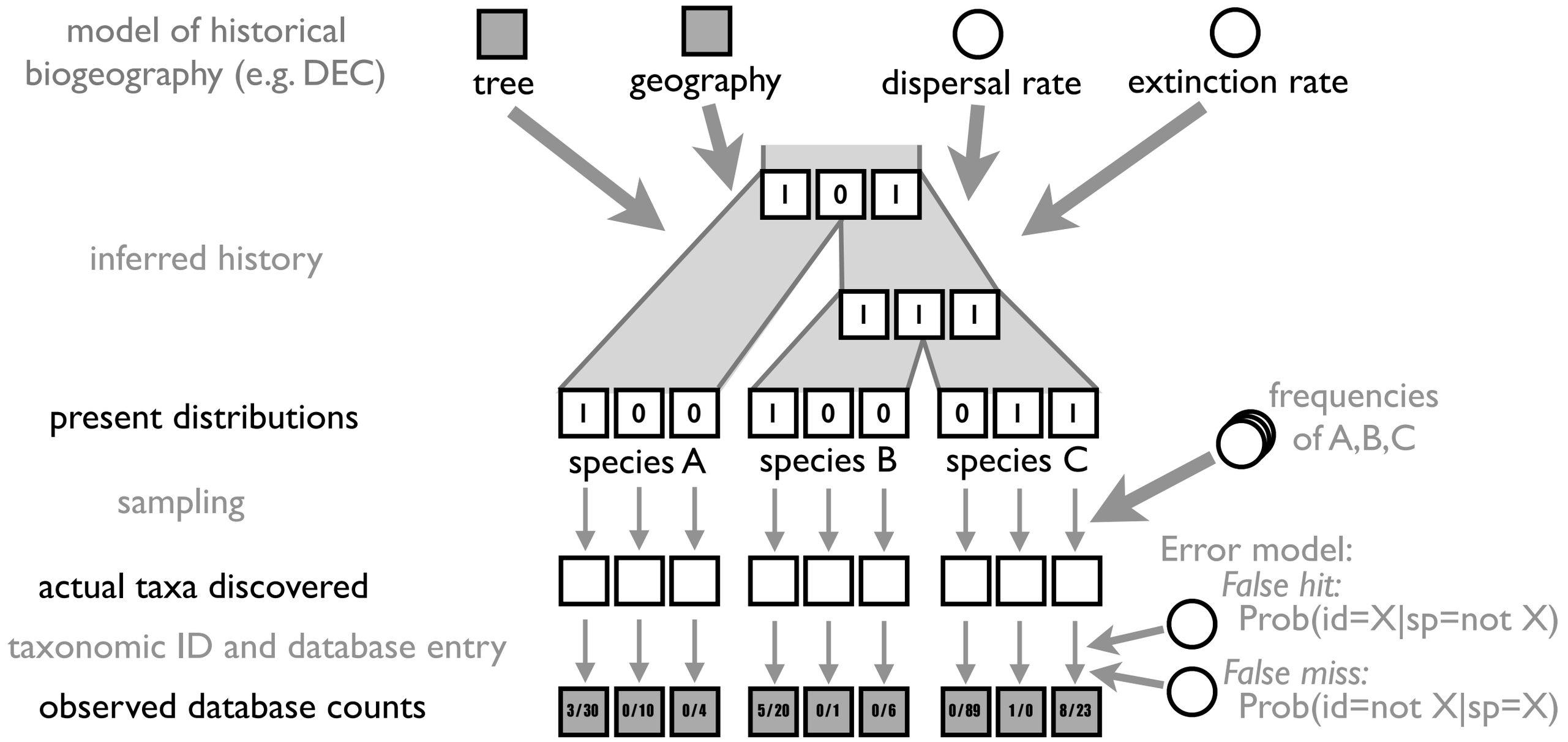
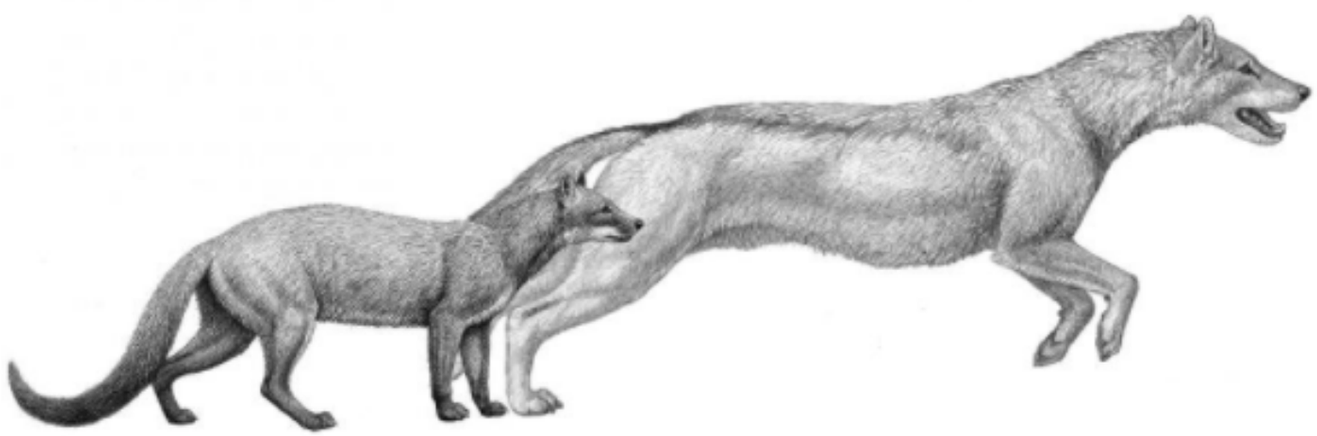


Figure 1B. DAG (Directed Acyclic Graph) for the model of imperfect detection implemented in *BioGeoBEARS*.

Imperfect detection: Let's try it!

Family Canidae

Fossilized Birth-Death analysis in *Beast2* (using *BEASTmasteR*)
~35 living species - DNA from Prevosti 2009, GenBank
~120+ fossil species - morphology from Slater 2015, Prevosti 2009
- "Taphonomic control": background database of large mammal occurrences: NEOMAP and NOW databases
- Caninae occurrence database: assembled by Laura Säilä

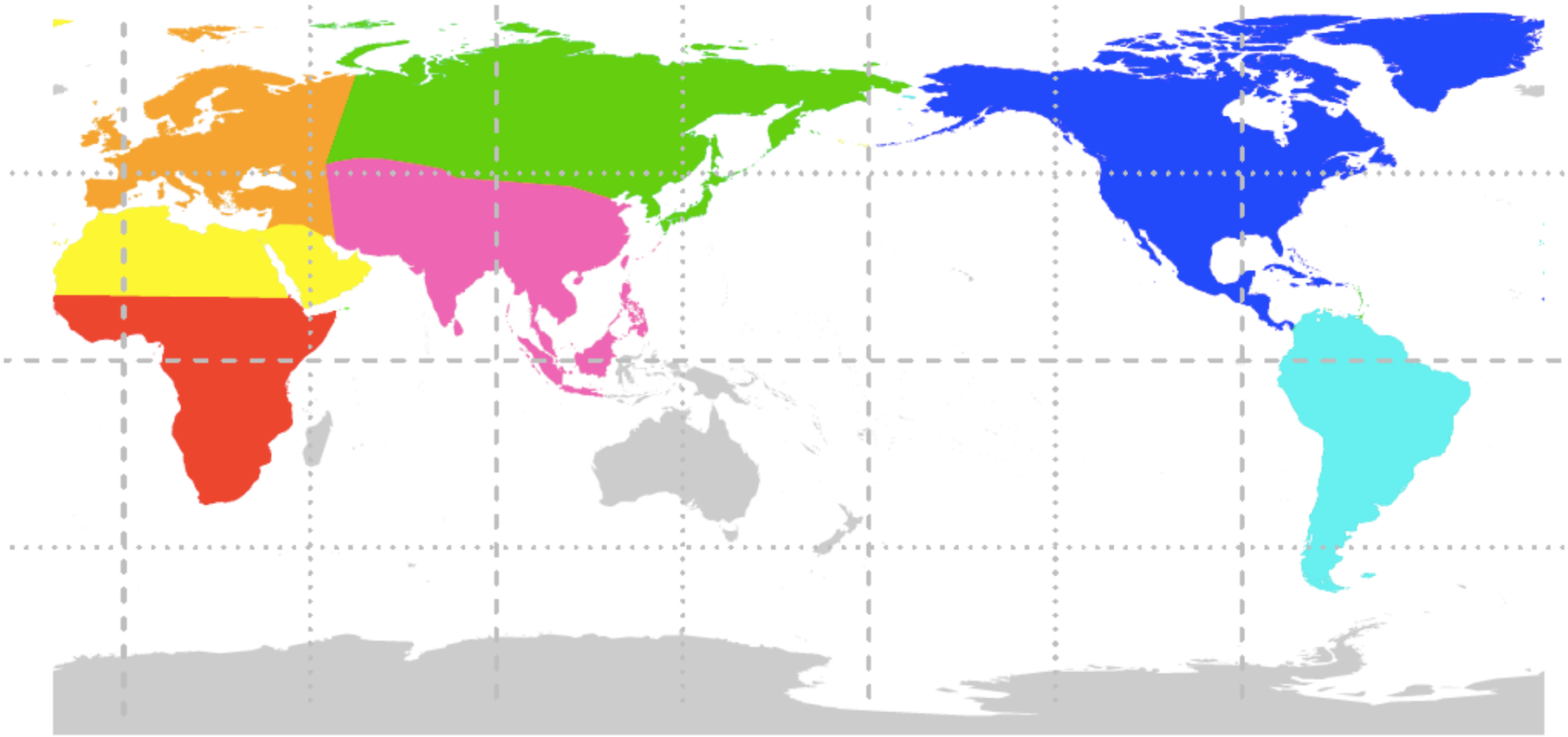


Hesperocyon and Sunkahetanka, two species of early dog. They were quite small and more closely resembled a mongoose. (Illustration by Mauricio Anton)

Source: http://www.forbes.com/sites/shaenamontanari/2015/08/18/old-dogs-learned-new-tricks-for-hunting-as-climate-changed/

Imperfect detection: Let's try it!

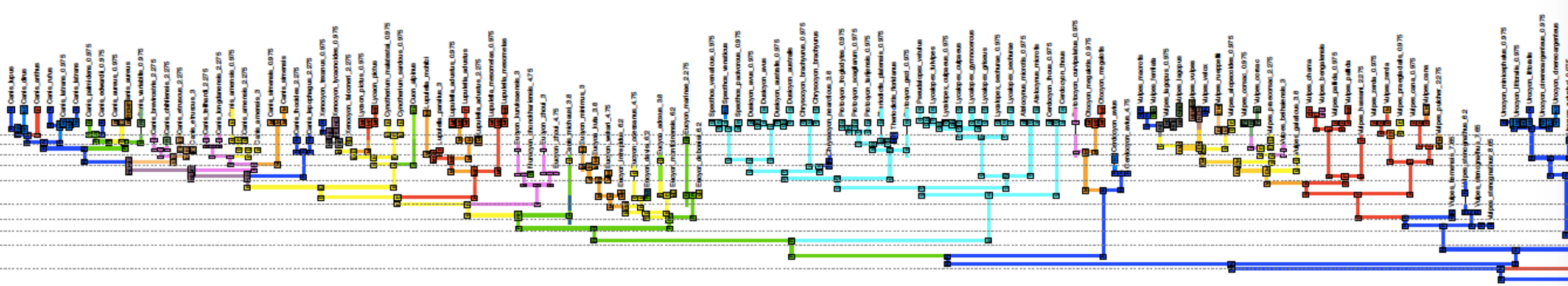
7 discrete regions:



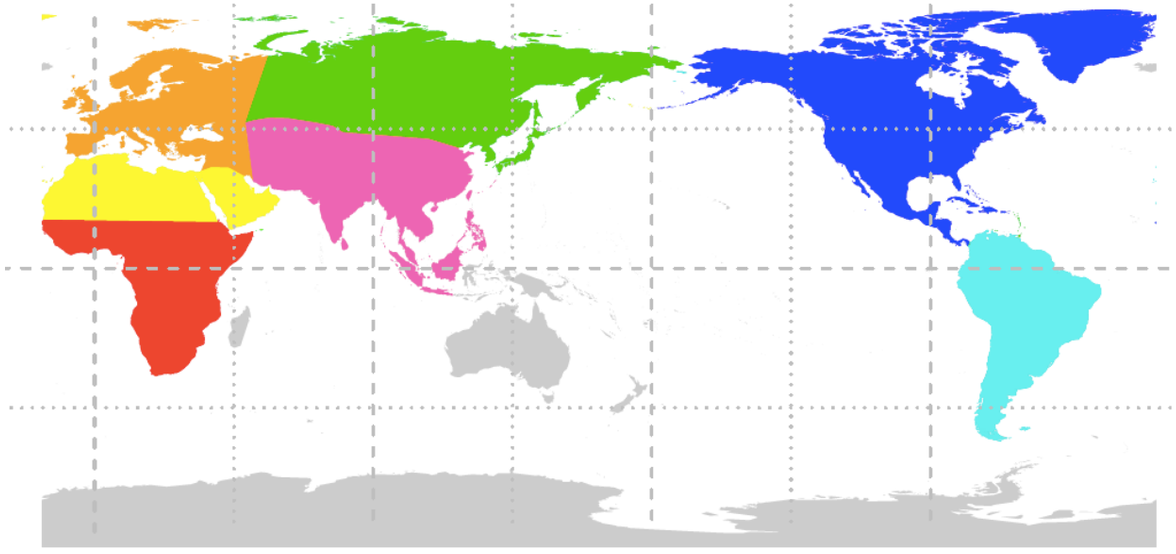
- Time-stratification: 11 time bins
  - Panamanian isthmus, Beringia, Sahara Desert
- +*w* parameter to scale dispersal multipliers*
- Biogeographical Stochastic Mapping*

* = see Dupin, Matzke et al. 2016, *J. Biogeog*

Biogeographical Stochastic Map* #1

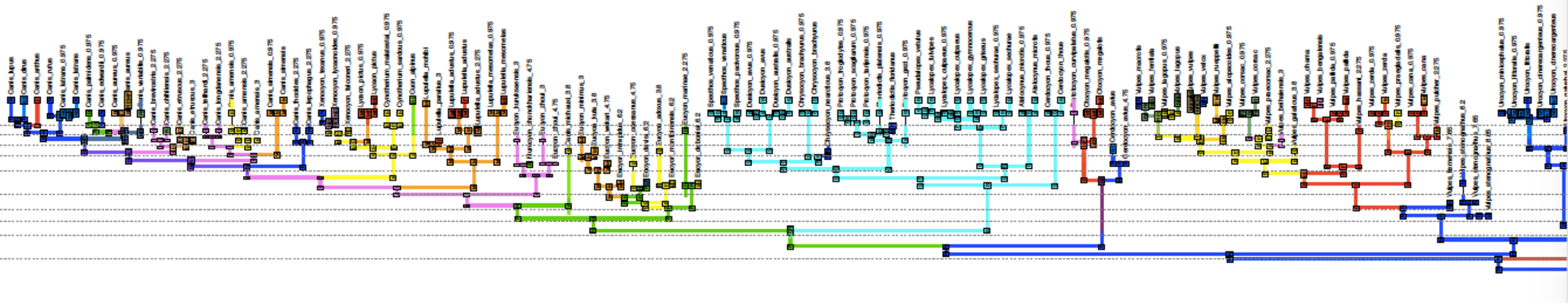


Area colors:

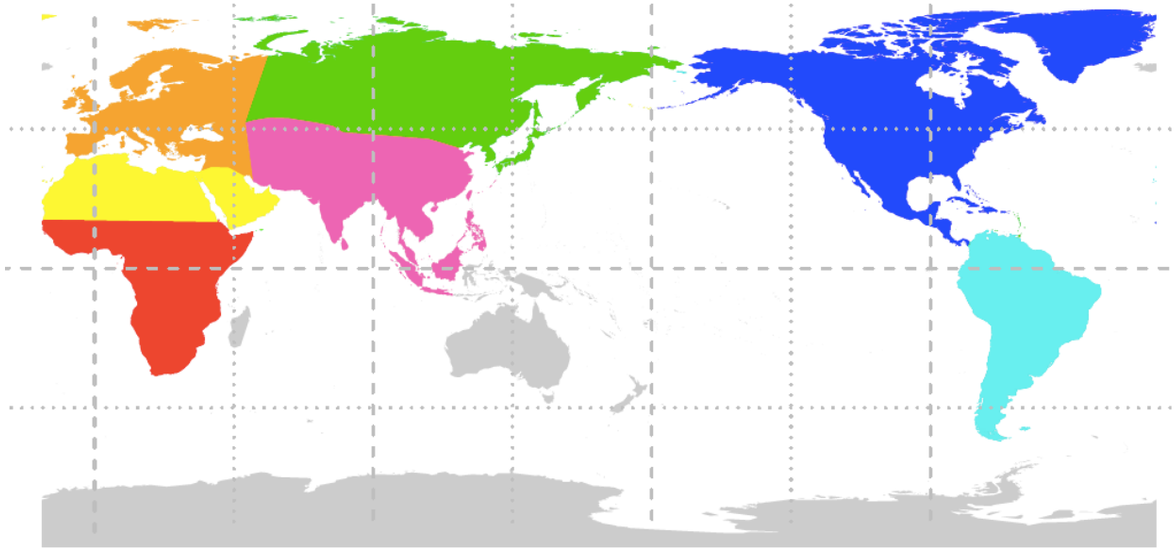


*** = see Dupin, Matzke et al. 2016, *J. Biogeog***

Biogeographical Stochastic Map* #2

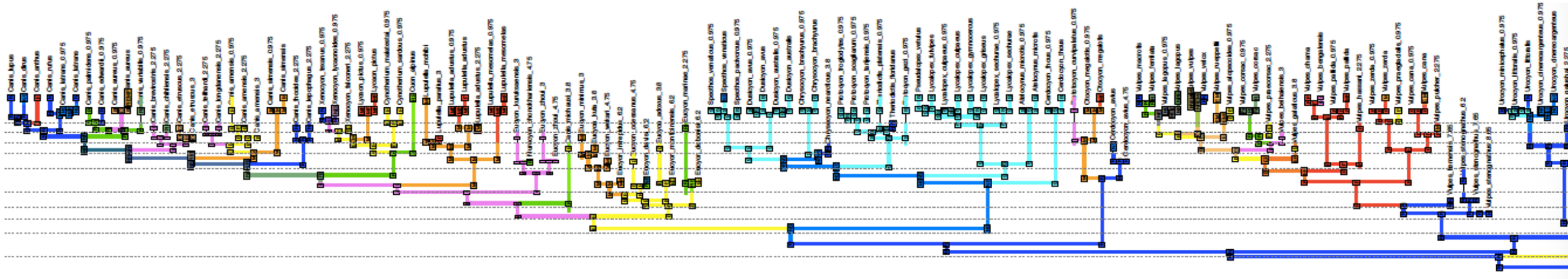


Area colors:

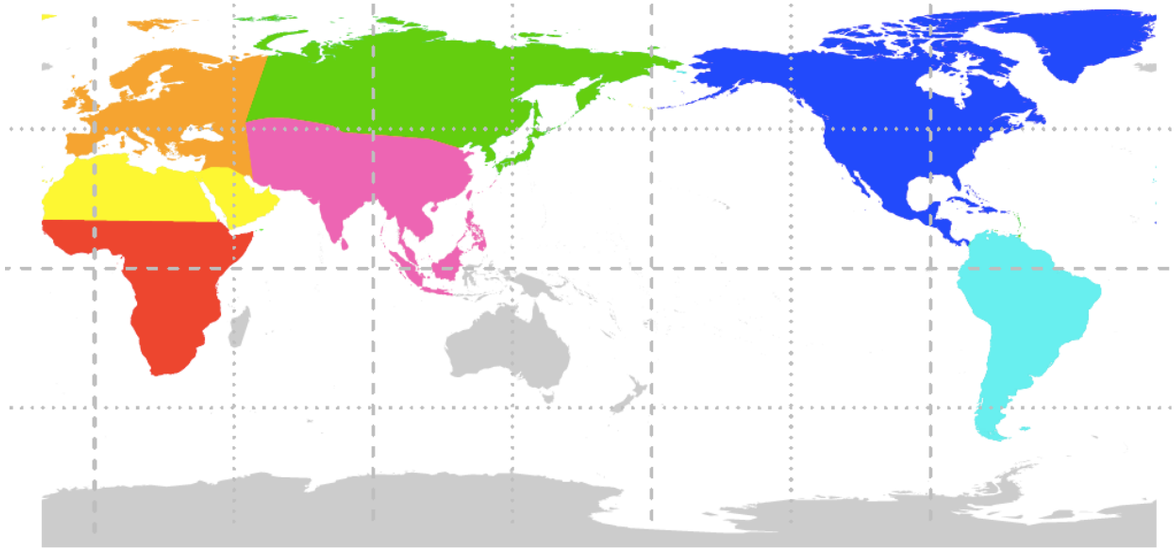


*** = see Dupin, Matzke et al. 2016, *J. Biogeog***

Biogeographical Stochastic Map* #3

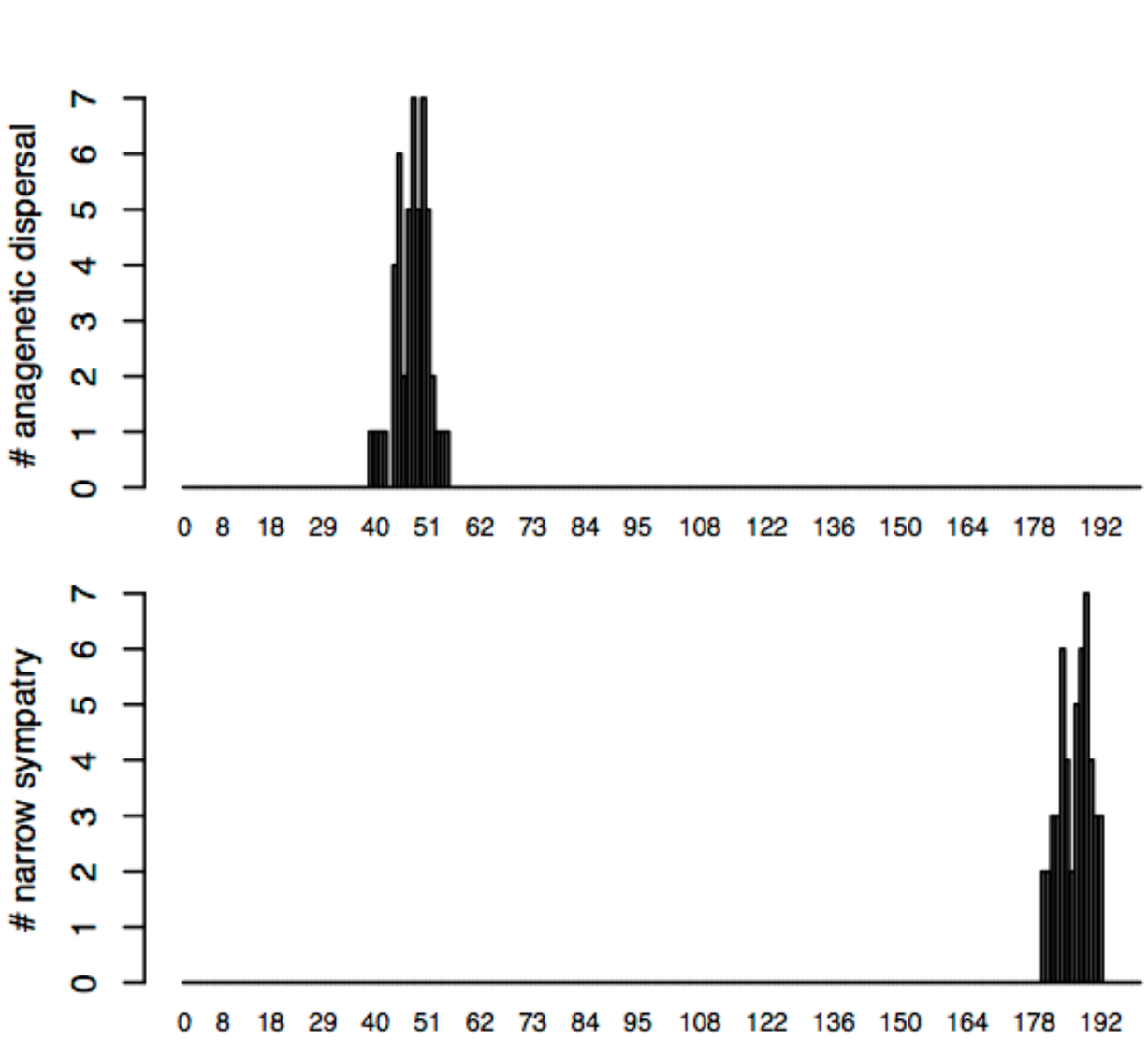


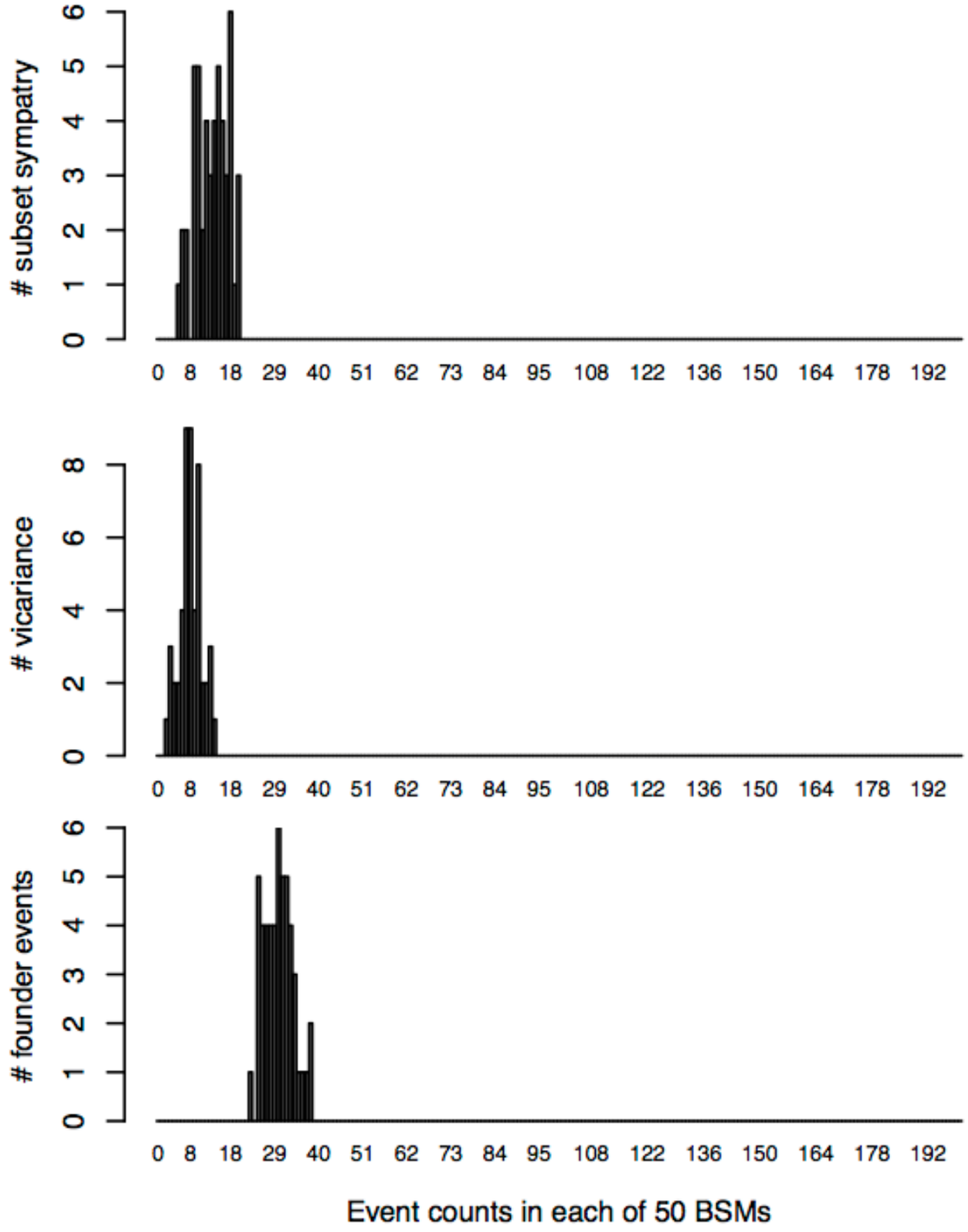
Area colors:



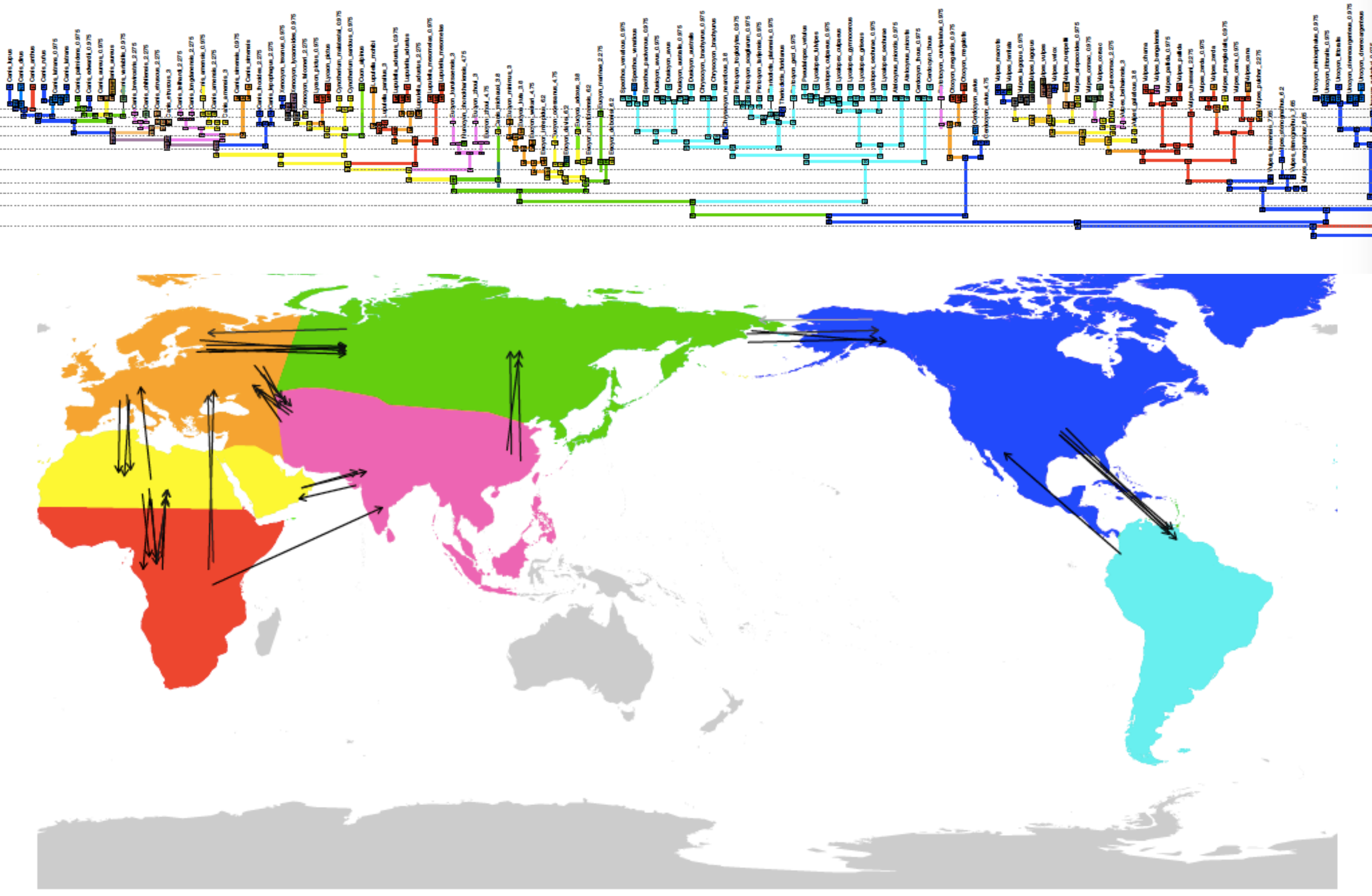
*** = see Dupin, Matzke et al. 2016, *J. Biogeog***

Biogeographical Stochastic Maps: Event counts





Mapping the stochastic maps



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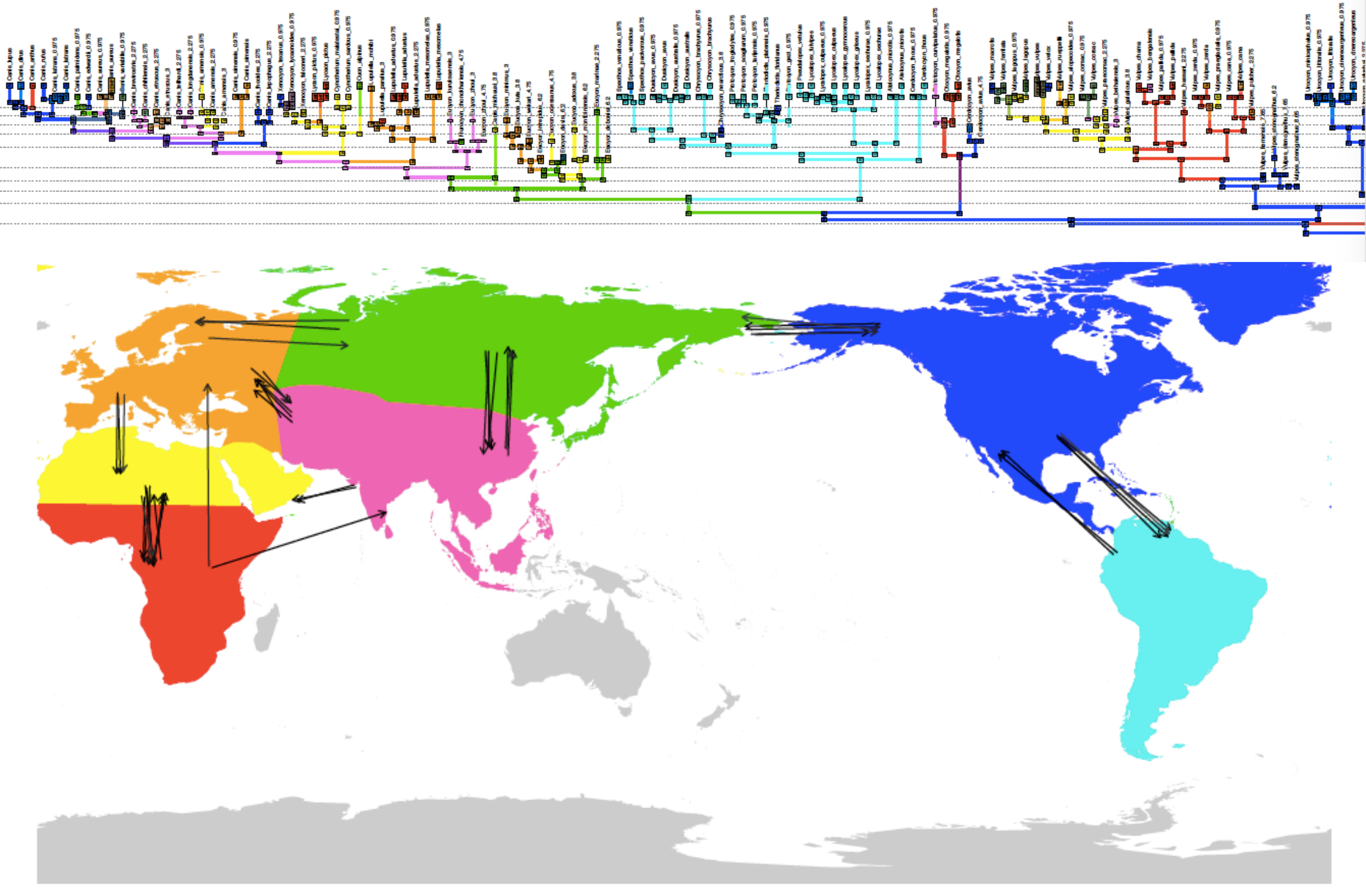
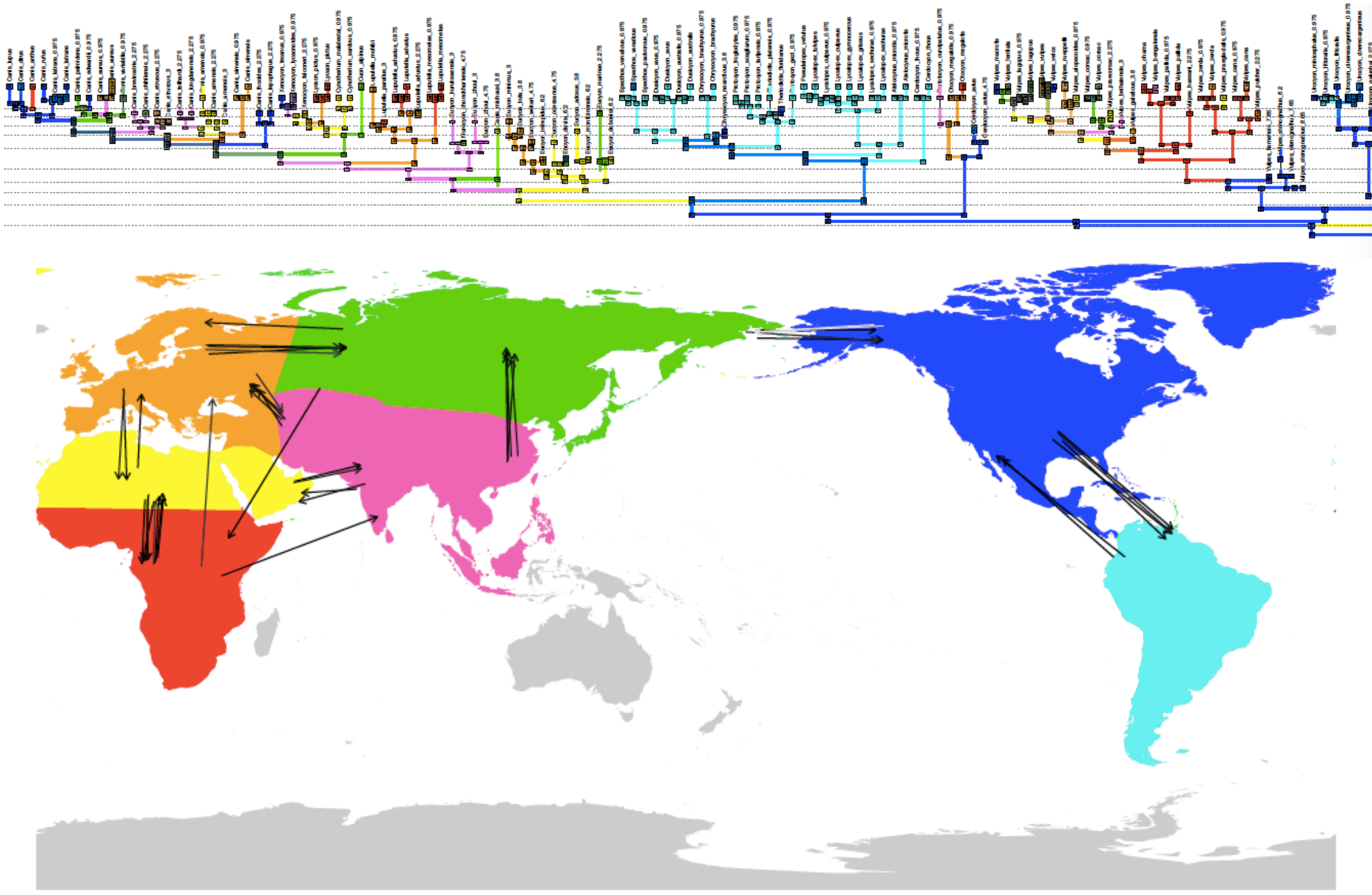
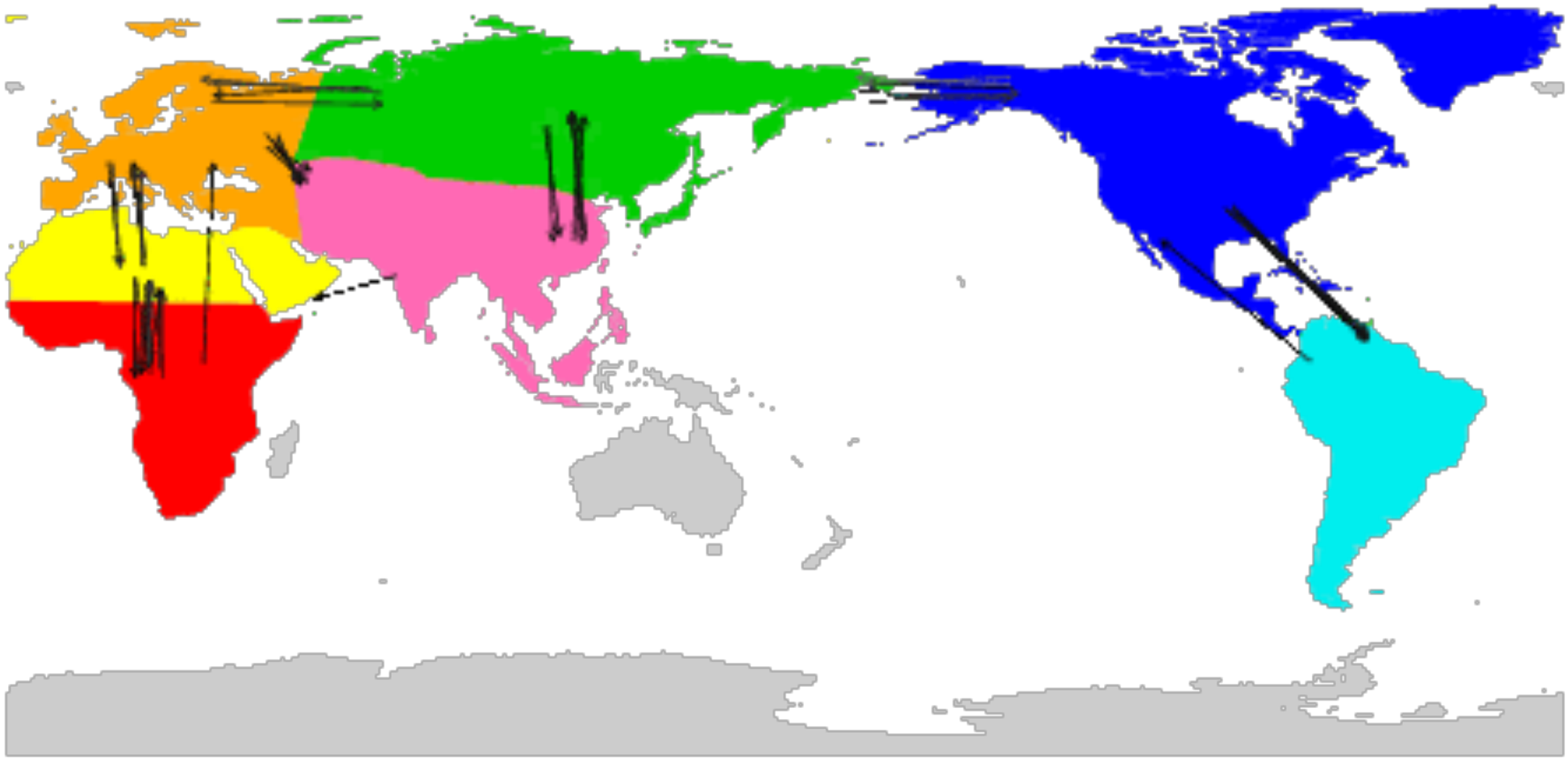


Mapping the stochastic maps



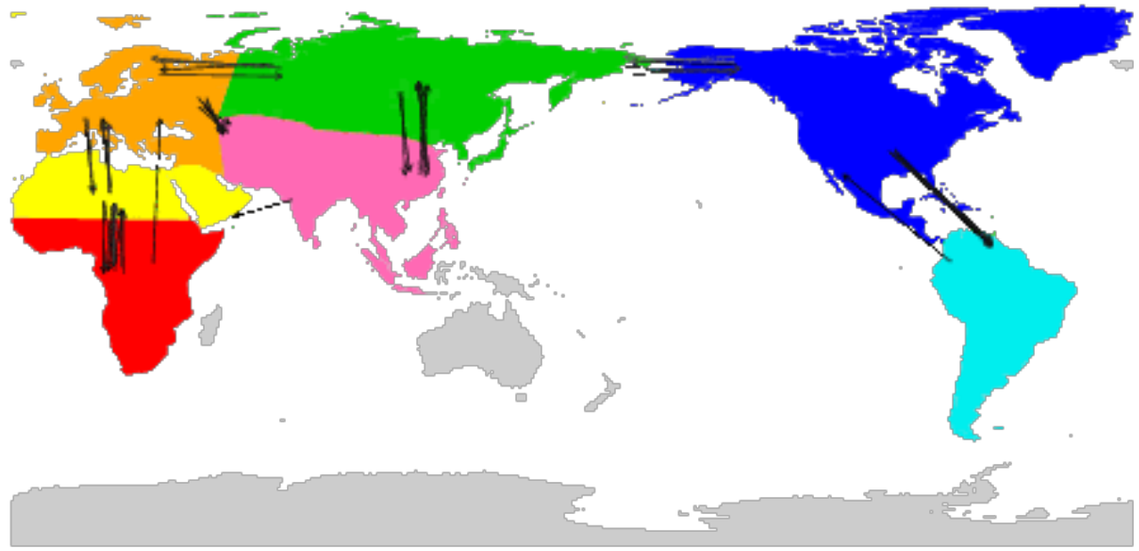
Animation



Conclusions

Not perfect, but useful

A "perfect" model would jointly sample everything



And use the biogeographical sampling model to influence the rate of fossil detection

Funded future work: New Zealand Marsden grant, with Alexei Drummond, Tanya Stadler, et al.

Can we statistically compare how the DEC and DEC+J models fit the data?

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<u>Validation #1</u> of comparing DEC, DEC+J likelihoods:

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likelihood=
Prob(data|model)

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If we add up the probabilities of all possible datasets, under one model, the sum should equal 1

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If we add up the probabilities of all possible datasets, under one model, the sum should equal 1

<u>Let's do the experiment</u>:

2-species tree, 3 areas

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3 areas = 2^3 ranges = 8 possible ranges per species

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That means 8x8=64 possible data patterns

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2-species tree, 3 areas

3 areas = 2^3 ranges = 8 possible ranges per species

That means 8x8=64 possible data patterns

Calculate likelihoods for:
DEC, *d*=0.2, *e*=0.1
DEC+J, *d*=0.2, *e*=0.1, *j*=0.15

Validation #1 of comparing DEC, DEC+J likelihoods:

likelihood= Prob(data|model)

If we add up the probabilities of all possible datasets, under one model, the sum should equal 1

#	sp1	sp2	DEC LnL	DEC like	DEC+J LnL	DEC+J like
1	_000	_000	-3.6198	0.027	-3.6307	0.026
2	000	100	-2.6187	0.073	-2.6286	0.072
3	000	010	-2.6187	0.073	-2.6286	0.072
4	000	001	-2.6187	0.073	-2.6286	0.072
5	000	110	-3.0451	0.048	-3.043	0.048
6	000	011	-3.0451	0.048	-3.043	0.048
7	000	101	-3.0451	0.048	-3.043	0.048
8	000	111	-2.837	0.059	-2.8313	0.059
9	100	000	-2.6187	0.073	-2.6286	0.072
10	100	100	-0.8903	0.411	-1.3316	0.264
11	100	010	-2.3853	0.092	-1.8164	0.163
12	100	001	-2.3853	0.092	-1.8164	0.163
13	100	110	-1.8506	0.157	-1.9656	0.14
14	100	011	-2.6711	0.069	-2.261	0.104
15	100	101	-1.8506	0.157	-1.9656	0.14
16	100	111	-1.8572	0.156	-1.8514	0.157
17	010	000	-2.6187	0.073	-2.6286	0.072
18	010	100	-2.3853	0.092	-1.8164	0.163
19	010	010	-0.8903	0.411	-1.3316	0.264
20	010	001	-2.3853	0.092	-1.8164	0.163
21	010	110	-1.8506	0.157	-1.9656	0.14
22	010	011	-1.8506	0.157	-1.9656	0.14
23	010	101	-2.6711	0.069	-2.261	0.104
24	010	111	-1.8572	0.156	-1.8514	0.157
25	001	000	-2.6187	0.073	-2.6286	0.072
26	001	100	-2.3853	0.092	-1.8164	0.163
27	001	010	-2.3853	0.092	-1.8164	0.163
28	001	001	-0.8903	0.411	-1.3316	0.264
29	001	110	-2.6711	0.069	-2.261	0.104
30	001	011	-1.8506	0.157	-1.9656	0.14
31	001	101	-1.8506	0.157	-1.9656	0.14
32	001	111	-1.8572	0.156	-1.8514	0.157
33	110	000	-3.0451	0.048	-3.043	0.048
34	110	100	-1.8506	0.157	-1.9656	0.14
35	110	010	-1.8506	0.157	-1.9656	0.14
36	110	001	-2.6711	0.069	-2.261	0.104
37	110	110	-2.4889	0.083	-2.5834	0.076
38	110	011	-2.795	0.061	-2.7243	0.066
39	110	101	-2.795	0.061	-2.7243	0.066
40	110	111	-2.6314	0.072	-2.6234	0.073
41	011	000	-3.0451	0.048	-3.043	0.048
42	011	100	-2.6711	0.069	-2.261	0.104
43	011	010	-1.8506	0.157	-1.9656	0.14
44	011	001	-1.8506	0.157	-1.9656	0.14
45	011	110	-2.795	0.061	-2.7243	0.066
46	011	011	-2.4889	0.083	-2.5834	0.076
47	011	101	-2.795	0.061	-2.7243	0.066
48	011	111	-2.6314	0.072	-2.6234	0.073
49	101	000	-3.0451	0.048	-3.043	0.048
50	101	100	-1.8506	0.157	-1.9656	0.14
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52	101	001	-1.8506	0.157	-1.9656	0.14
53	101	110	-2.795	0.061	-2.7243	0.066
54	101	011	-2.795	0.061	-2.7243	0.066
55	101	101	-2.4889	0.083	-2.5834	0.076
56	101	111	-2.6314	0.072	-2.6234	0.073
57	111	000	-2.837	0.059	-2.8313	0.059
58	111	100	-1.8572	0.156	-1.8514	0.157
59	111	010	-1.8572	0.156	-1.8514	0.157
60	111	001	-1.8572	0.156	-1.8514	0.157
61	111	110	-2.6314	0.072	-2.6234	0.073
62	111	011	-2.6314	0.072	-2.6234	0.073
63	111	101	-2.6314	0.072	-2.6234	0.073
64	111	111	-2.7457	0.064	-2.7373	0.065

Validation #1 of comparing DEC, DEC+J likelihoods:

likelihood= Prob(data|model)

If we add up the probabilities of all possible datasets, under one model, the sum should equal 1

#	sp1	sp2	DEC LnL	DEC like	DEC+J LnL	DEC+J like
1	_000	_000	-3.6198	0.027	-3.6307	0.026
2	000	100	-2.6187	0.073	-2.6286	0.072
3	000	010	-2.6187	0.073	-2.6286	0.072
4	000	001	-2.6187	0.073	-2.6286	0.072
5	000	110	-3.0451	0.048	-3.043	0.048
6	000	011	-3.0451	0.048	-3.043	0.048
7	000	101	-3.0451	0.048	-3.043	0.048
8	000	111	-2.837	0.059	-2.8313	0.059
9	100	000	-2.6187	0.073	-2.6286	0.072
10	100	100	-0.8903	0.411	-1.3316	0.264
11	100	010	-2.3853	0.092	-1.8164	0.163
12	100	001	-2.3853	0.092	-1.8164	0.163
13	100	110	-1.8506	0.157	-1.9656	0.14
14	100	011	-2.6711	0.069	-2.261	0.104
15	100	101	-1.8506	0.157	-1.9656	0.14
16	100	111	-1.8572	0.156	-1.8514	0.157
17	010	000	-2.6187	0.073	-2.6286	0.072
18	010	100	-2.3853	0.092	-1.8164	0.163
19	010	010	-0.8903	0.411	-1.3316	0.264
20	010	001	-2.3853	0.092	-1.8164	0.163
21	010	110	-1.8506	0.157	-1.9656	0.14
22	010	011	-1.8506	0.157	-1.9656	0.14
23	010	101	-2.6711	0.069	-2.261	0.104
24	010	111	-1.8572	0.156	-1.8514	0.157
25	001	000	-2.6187	0.073	-2.6286	0.072
26	001	100	-2.3853	0.092	-1.8164	0.163
27	001	010	-2.3853	0.092	-1.8164	0.163
28	001	001	-0.8903	0.411	-1.3316	0.264
29	001	110	-2.6711	0.069	-2.261	0.104
30	001	011	-1.8506	0.157	-1.9656	0.14
31	001	101	-1.8506	0.157	-1.9656	0.14
32	001	111	-1.8572	0.156	-1.8514	0.157
33	110	000	-3.0451	0.048	-3.043	0.048
34	110	100	-1.8506	0.157	-1.9656	0.14
35	110	010	-1.8506	0.157	-1.9656	0.14
36	110	001	-2.6711	0.069	-2.261	0.104
37	110	110	-2.4889	0.083	-2.5834	0.076
38	110	011	-2.795	0.061	-2.7243	0.066
39	110	101	-2.795	0.061	-2.7243	0.066
40	110	111	-2.6314	0.072	-2.6234	0.073
41	011	000	-3.0451	0.048	-3.043	0.048
42	011	100	-2.6711	0.069	-2.261	0.104
43	011	010	-1.8506	0.157	-1.9656	0.14
44	011	001	-1.8506	0.157	-1.9656	0.14
45	011	110	-2.795	0.061	-2.7243	0.066
46	011	011	-2.4889	0.083	-2.5834	0.076
47	011	101	-2.795	0.061	-2.7243	0.066
48	011	111	-2.6314	0.072	-2.6234	0.073
49	101	000	-3.0451	0.048	-3.043	0.048
50	101	100	-1.8506	0.157	-1.9656	0.14
51	101	010	-2.6711	0.069	-2.261	0.104
52	101	001	-1.8506	0.157	-1.9656	0.14
53	101	110	-2.795	0.061	-2.7243	0.066
54	101	011	-2.795	0.061	-2.7243	0.066
55	101	101	-2.4889	0.083	-2.5834	0.076
56	101	111	-2.6314	0.072	-2.6234	0.073
57	111	000	-2.837	0.059	-2.8313	0.059
58	111	100	-1.8572	0.156	-1.8514	0.157
59	111	010	-1.8572	0.156	-1.8514	0.157
60	111	001	-1.8572	0.156	-1.8514	0.157
61	111	110	-2.6314	0.072	-2.6234	0.073
62	111	011	-2.6314	0.072	-2.6234	0.073
63	111	101	-2.6314	0.072	-2.6234	0.073
64	111	111	-2.7457	0.064	-2.7373	0.065

sum of 64 DEC likes=7.0

Validation #1 of comparing DEC, DEC+J likelihoods:

likelihood= Prob(data|model)

If we add up the probabilities of all possible datasets, under one model, the sum should equal 1

#	sp1	sp2	DEC LnL	DEC like	DEC+J LnL	DEC+J like
1	_000	_000	-3.6198	0.027	-3.6307	0.026
2	000	100	-2.6187	0.073	-2.6286	0.072
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4	000	001	-2.6187	0.073	-2.6286	0.072
5	000	110	-3.0451	0.048	-3.043	0.048
6	000	011	-3.0451	0.048	-3.043	0.048
7	000	101	-3.0451	0.048	-3.043	0.048
8	000	111	-2.837	0.059	-2.8313	0.059
9	100	000	-2.6187	0.073	-2.6286	0.072
10	100	100	-0.8903	0.411	-1.3316	0.264
11	100	010	-2.3853	0.092	-1.8164	0.163
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13	100	110	-1.8506	0.157	-1.9656	0.14
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16	100	111	-1.8572	0.156	-1.8514	0.157
17	010	000	-2.6187	0.073	-2.6286	0.072
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23	010	101	-2.6711	0.069	-2.261	0.104
24	010	111	-1.8572	0.156	-1.8514	0.157
25	001	000	-2.6187	0.073	-2.6286	0.072
26	001	100	-2.3853	0.092	-1.8164	0.163
27	001	010	-2.3853	0.092	-1.8164	0.163
28	001	001	-0.8903	0.411	-1.3316	0.264
29	001	110	-2.6711	0.069	-2.261	0.104
30	001	011	-1.8506	0.157	-1.9656	0.14
31	001	101	-1.8506	0.157	-1.9656	0.14
32	001	111	-1.8572	0.156	-1.8514	0.157
33	110	000	-3.0451	0.048	-3.043	0.048
34	110	100	-1.8506	0.157	-1.9656	0.14
35	110	010	-1.8506	0.157	-1.9656	0.14
36	110	001	-2.6711	0.069	-2.261	0.104
37	110	110	-2.4889	0.083	-2.5834	0.076
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39	110	101	-2.795	0.061	-2.7243	0.066
40	110	111	-2.6314	0.072	-2.6234	0.073
41	011	000	-3.0451	0.048	-3.043	0.048
42	011	100	-2.6711	0.069	-2.261	0.104
43	011	010	-1.8506	0.157	-1.9656	0.14
44	011	001	-1.8506	0.157	-1.9656	0.14
45	011	110	-2.795	0.061	-2.7243	0.066
46	011	011	-2.4889	0.083	-2.5834	0.076
47	011	101	-2.795	0.061	-2.7243	0.066
48	011	111	-2.6314	0.072	-2.6234	0.073
49	101	000	-3.0451	0.048	-3.043	0.048
50	101	100	-1.8506	0.157	-1.9656	0.14
51	101	010	-2.6711	0.069	-2.261	0.104
52	101	001	-1.8506	0.157	-1.9656	0.14
53	101	110	-2.795	0.061	-2.7243	0.066
54	101	011	-2.795	0.061	-2.7243	0.066
55	101	101	-2.4889	0.083	-2.5834	0.076
56	101	111	-2.6314	0.072	-2.6234	0.073
57	111	000	-2.837	0.059	-2.8313	0.059
58	111	100	-1.8572	0.156	-1.8514	0.157
59	111	010	-1.8572	0.156	-1.8514	0.157
60	111	001	-1.8572	0.156	-1.8514	0.157
61	111	110	-2.6314	0.072	-2.6234	0.073
62	111	011	-2.6314	0.072	-2.6234	0.073
63	111	101	-2.6314	0.072	-2.6234	0.073
64	111	111	-2.7457	0.064	-2.7373	0.065

sum of 64 DEC likes=7.0

sum of 64 DEC+J likes=7.0

Validation #1 of comparing DEC, DEC+J likelihoods:

likelihood= Prob(data|model)

If we add up the probabilities of all possible datasets, under one model, the sum should equal 1

#	sp1	sp2	DEC LnL	DEC like	DEC+J LnL	DEC+J like
1	_000	_000	-3.6198	0.027	-3.6307	0.026
2	000	100	-2.6187	0.073	-2.6286	0.072
3	000	010	-2.6187	0.073	-2.6286	0.072
4	000	001	-2.6187	0.073	-2.6286	0.072
5	000	110	-3.0451	0.048	-3.043	0.048
6	000	011	-3.0451	0.048	-3.043	0.048
7	000	101	-3.0451	0.048	-3.043	0.048
8	000	111	-2.837	0.059	-2.8313	0.059
9	100	000	-2.6187	0.073	-2.6286	0.072
10	100	100	-0.8903	0.411	-1.3316	0.264
11	100	010	-2.3853	0.092	-1.8164	0.163
12	100	001	-2.3853	0.092	-1.8164	0.163
13	100	110	-1.8506	0.157	-1.9656	0.14
14	100	011	-2.6711	0.069	-2.261	0.104
15	100	101	-1.8506	0.157	-1.9656	0.14
16	100	111	-1.8572	0.156	-1.8514	0.157
17	010	000	-2.6187	0.073	-2.6286	0.072
18	010	100	-2.3853	0.092	-1.8164	0.163
19	010	010	-0.8903	0.411	-1.3316	0.264
20	010	001	-2.3853	0.092	-1.8164	0.163
21	010	110	-1.8506	0.157	-1.9656	0.14
22	010	011	-1.8506	0.157	-1.9656	0.14
23	010	101	-2.6711	0.069	-2.261	0.104
24	010	111	-1.8572	0.156	-1.8514	0.157
25	001	000	-2.6187	0.073	-2.6286	0.072
26	001	100	-2.3853	0.092	-1.8164	0.163
27	001	010	-2.3853	0.092	-1.8164	0.163
28	001	001	-0.8903	0.411	-1.3316	0.264
29	001	110	-2.6711	0.069	-2.261	0.104
30	001	011	-1.8506	0.157	-1.9656	0.14
31	001	101	-1.8506	0.157	-1.9656	0.14
32	001	111	-1.8572	0.156	-1.8514	0.157
33	110	000	-3.0451	0.048	-3.043	0.048
34	110	100	-1.8506	0.157	-1.9656	0.14
35	110	010	-1.8506	0.157	-1.9656	0.14
36	110	001	-2.6711	0.069	-2.261	0.104
37	110	110	-2.4889	0.083	-2.5834	0.076
38	110	011	-2.795	0.061	-2.7243	0.066
39	110	101	-2.795	0.061	-2.7243	0.066
40	110	111	-2.6314	0.072	-2.6234	0.073
41	011	000	-3.0451	0.048	-3.043	0.048
42	011	100	-2.6711	0.069	-2.261	0.104
43	011	010	-1.8506	0.157	-1.9656	0.14
44	011	001	-1.8506	0.157	-1.9656	0.14
45	011	110	-2.795	0.061	-2.7243	0.066
46	011	011	-2.4889	0.083	-2.5834	0.076
47	011	101	-2.795	0.061	-2.7243	0.066
48	011	111	-2.6314	0.072	-2.6234	0.073
49	101	000	-3.0451	0.048	-3.043	0.048
50	101	100	-1.8506	0.157	-1.9656	0.14
51	101	010	-2.6711	0.069	-2.261	0.104
52	101	001	-1.8506	0.157	-1.9656	0.14
53	101	110	-2.795	0.061	-2.7243	0.066
54	101	011	-2.795	0.061	-2.7243	0.066
55	101	101	-2.4889	0.083	-2.5834	0.076
56	101	111	-2.6314	0.072	-2.6234	0.073
57	111	000	-2.837	0.059	-2.8313	0.059
58	111	100	-1.8572	0.156	-1.8514	0.157
59	111	010	-1.8572	0.156	-1.8514	0.157
60	111	001	-1.8572	0.156	-1.8514	0.157
61	111	110	-2.6314	0.072	-2.6234	0.073
62	111	011	-2.6314	0.072	-2.6234	0.073
63	111	101	-2.6314	0.072	-2.6234	0.073
64	111	111	-2.7457	0.064	-2.7373	0.065

sum of 64 DEC likes=7.0

sum of 64 DEC+J likes=7.0

Why 7?

Validation #1 of comparing DEC, DEC+J likelihoods:

likelihood= Prob(data|model)

If we add up the probabilities of all possible datasets, under one model, the sum should equal 1

#	sp1	sp2	DEC LnL	DEC like	DEC+J LnL	DEC+J like
1	_000	_000	-3.6198	0.027	-3.6307	0.026
2	000	100	-2.6187	0.073	-2.6286	0.072
3	000	010	-2.6187	0.073	-2.6286	0.072
4	000	001	-2.6187	0.073	-2.6286	0.072
5	000	110	-3.0451	0.048	-3.043	0.048
6	000	011	-3.0451	0.048	-3.043	0.048
7	000	101	-3.0451	0.048	-3.043	0.048
8	000	111	-2.837	0.059	-2.8313	0.059
9	100	000	-2.6187	0.073	-2.6286	0.072
10	100	100	-0.8903	0.411	-1.3316	0.264
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13	100	110	-1.8506	0.157	-1.9656	0.14
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26	001	100	-2.3853	0.092	-1.8164	0.163
27	001	010	-2.3853	0.092	-1.8164	0.163
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63	111	101	-2.6314	0.072	-2.6234	0.073
64	111	111	-2.7457	0.064	-2.7373	0.065

sum of 64 DEC likes=7.0

sum of 64 DEC+J likes=7.0

Why 7?

8 states, 1 is null range

Validation #1 of comparing DEC, DEC+J likelihoods:

likelihood= Prob(data|model)

If we add up the probabilities of all possible datasets, under one model, the sum should equal 1

#	sp1	sp2	DEC LnL	DEC like	DEC+J LnL	DEC+J like
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31	001	101	-1.8506	0.157	-1.9656	0.14
32	001	111	-1.8572	0.156	-1.8514	0.157
33	110	000	-3.0451	0.048	-3.043	0.048
34	110	100	-1.8506	0.157	-1.9656	0.14
35	110	010	-1.8506	0.157	-1.9656	0.14
36	110	001	-2.6711	0.069	-2.261	0.104
37	110	110	-2.4889	0.083	-2.5834	0.076
38	110	011	-2.795	0.061	-2.7243	0.066
39	110	101	-2.795	0.061	-2.7243	0.066
40	110	111	-2.6314	0.072	-2.6234	0.073
41	011	000	-3.0451	0.048	-3.043	0.048
42	011	100	-2.6711	0.069	-2.261	0.104
43	011	010	-1.8506	0.157	-1.9656	0.14
44	011	001	-1.8506	0.157	-1.9656	0.14
45	011	110	-2.795	0.061	-2.7243	0.066
46	011	011	-2.4889	0.083	-2.5834	0.076
47	011	101	-2.795	0.061	-2.7243	0.066
48	011	111	-2.6314	0.072	-2.6234	0.073
49	101	000	-3.0451	0.048	-3.043	0.048
50	101	100	-1.8506	0.157	-1.9656	0.14
51	101	010	-2.6711	0.069	-2.261	0.104
52	101	001	-1.8506	0.157	-1.9656	0.14
53	101	110	-2.795	0.061	-2.7243	0.066
54	101	011	-2.795	0.061	-2.7243	0.066
55	101	101	-2.4889	0.083	-2.5834	0.076
56	101	111	-2.6314	0.072	-2.6234	0.073
57	111	000	-2.837	0.059	-2.8313	0.059
58	111	100	-1.8572	0.156	-1.8514	0.157
59	111	010	-1.8572	0.156	-1.8514	0.157
60	111	001	-1.8572	0.156	-1.8514	0.157
61	111	110	-2.6314	0.072	-2.6234	0.073
62	111	011	-2.6314	0.072	-2.6234	0.073
63	111	101	-2.6314	0.072	-2.6234	0.073
64	111	111	-2.7457	0.064	-2.7373	0.065

sum of 64 DEC likes=7.0

sum of 64 DEC+J likes=7.0

Why 7?

8 states, 1 is null range

To get 1, times "base frequencies" of 1/7

<u>Validation #2</u> of comparing DEC, DEC+J likelihoods:

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To simplify to DEC/DEC+J:

Yule process (pure birth)

Set extinction to 0, condition on survival=false

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To simplify to DEC/DEC+J:

But with Yule rate divided into cladogenetic events (rate * probability)

Yule process (pure birth)

Set extinction to 0, condition on survival=false

DEC, DEC+J (BioGeoBEARS) vs. ClaSSE (diversitree)

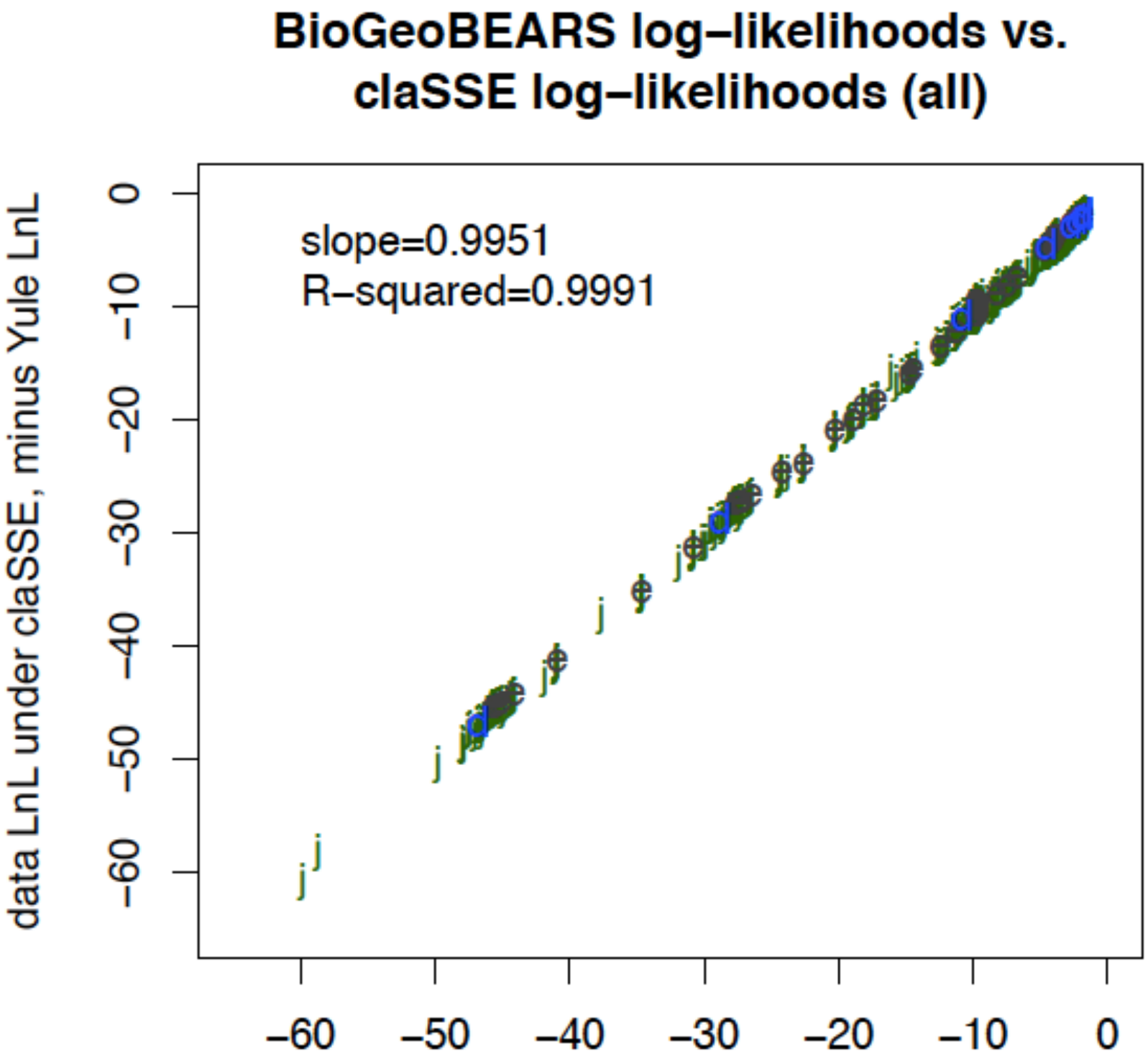
To make ClaSSE & DEC equivalent:

DEC or DEC+J equals ClaSSE, *if*:

- *d* and *e* control ClaSSE character change rates
- all extinction rates set to zero
- speciation rate for each cladogenesis = (Yule rate) times weight/sum(weights)
- subtract equilibrium probabilities at the root

Note: Slide from Evolution 2015, Brazil

DEC, DEC+J (BioGeoBEARS) vs. ClaSSE (diversitree)



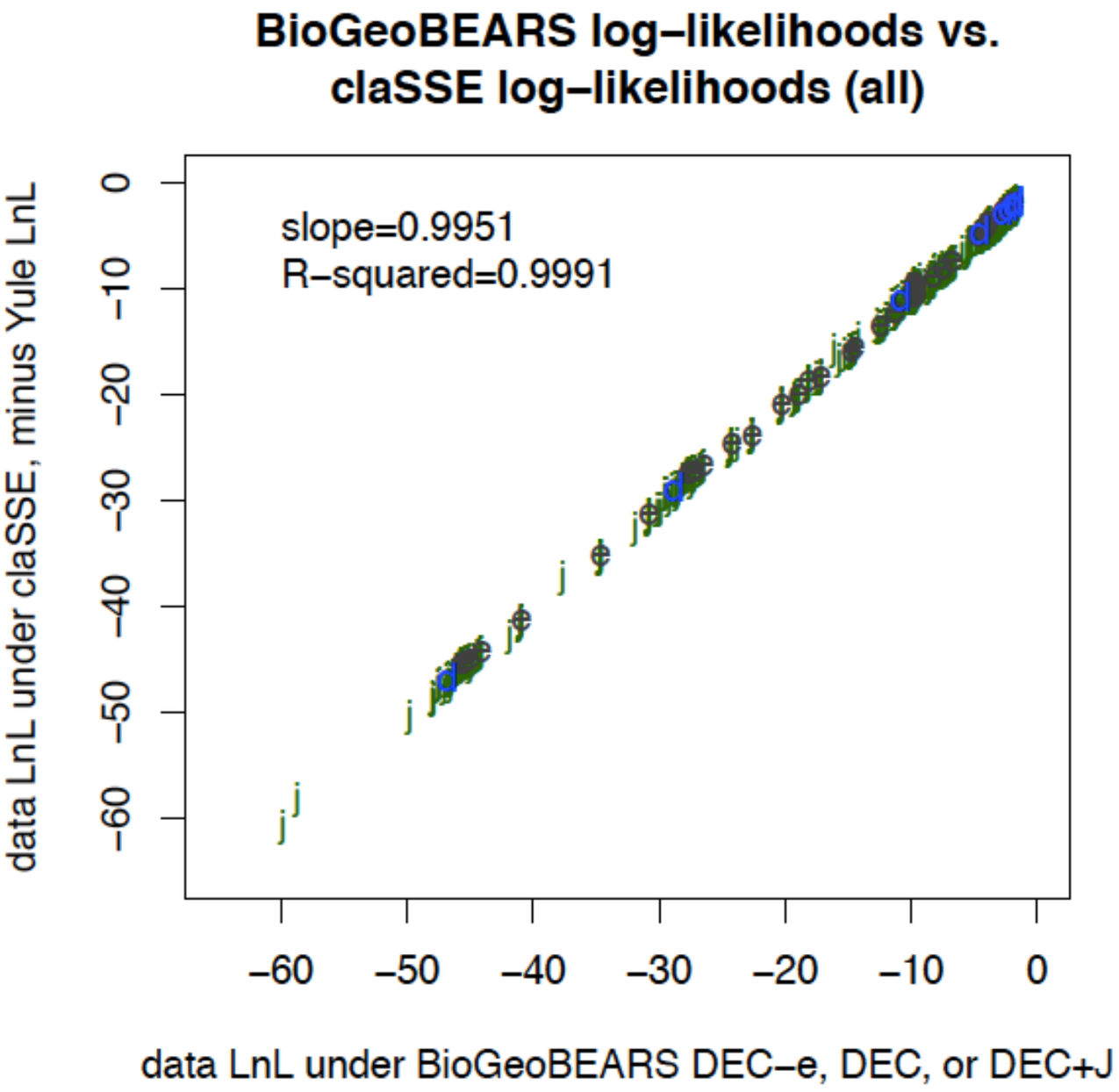
LnLs for:

DEC-e = d

DEC = e

DEC+J = j

Note: Slide from Evolution 2015, Brazil



Summary:

Saying DEC and DEC+J are not statistically comparable…

…is identical to saying two submodels of ClaSSE are not comparable

…or that two valid conditional probabilities of the same data are not comparable

For these scripts, google "BioGeoBEARS validation":

http://phylo.wikidot.com/biogeobears-validation