

Phylogenetics

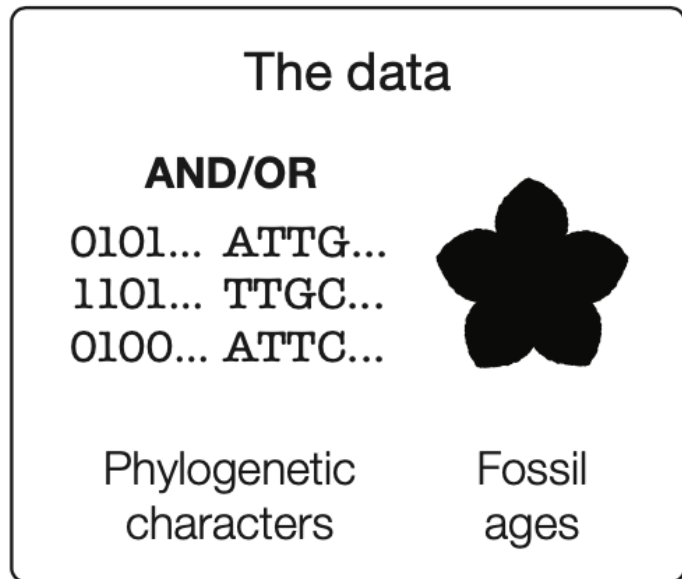
Morphological Substitution models

Rachel Warnock, Tim Brandler, Laura Mulvey

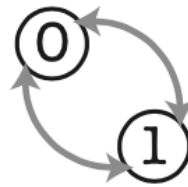
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June 13 2023

Bayesian Phylogenetic Analysis Components from last week



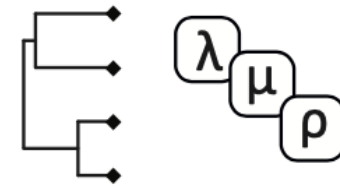
Tripartite model components



Substitution
model

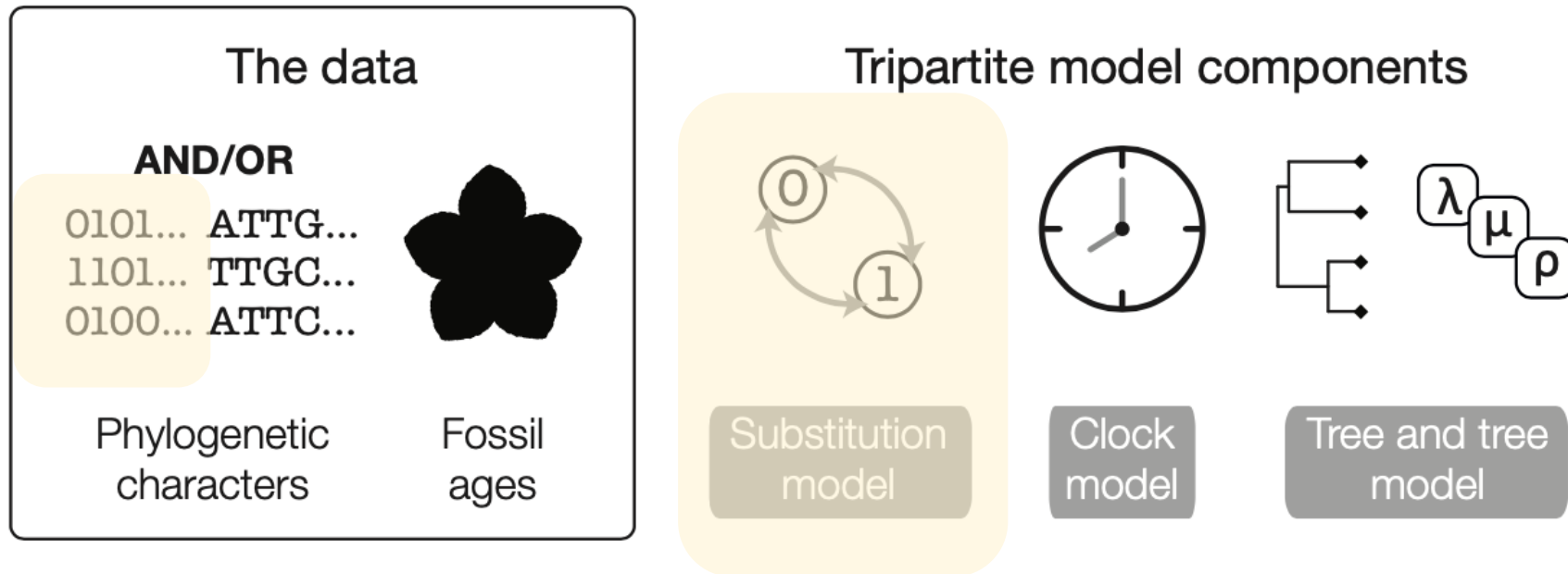


Clock
model



Tree and tree
model

Bayesian Phylogenetic Analysis Components from last week



Molecular Substitution models

JC substitution model

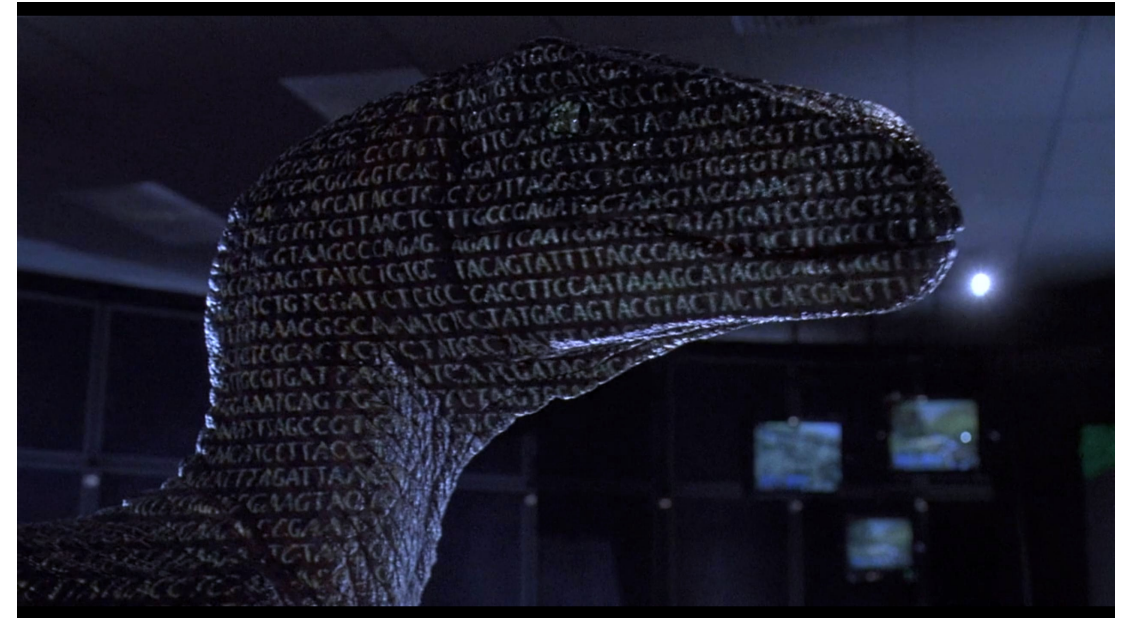
$$Q = \begin{pmatrix} -\mu_A & \mu_{AG} & \mu_{AC} & \mu_{AT} \\ \mu_{GA} & -\mu_G & \mu_{GC} & \mu_{GT} \\ \mu_{CA} & \mu_{CG} & -\mu_C & \mu_{CT} \\ \mu_{TA} & \mu_{TG} & \mu_{TC} & -\mu_T \end{pmatrix}$$

GTR substitution model

$$Q = \begin{pmatrix} * & \mu_{AG}\pi_G & \mu_{AC}\pi_C & \mu_{AT}\pi_T \\ \mu_{GA}\pi_A & * & \mu_{GC}\pi_C & \mu_{GT}\pi_T \\ \mu_{CA}\pi_A & \mu_{CG}\pi_G & * & \mu_{CT}\pi_T \\ \mu_{TA}\pi_A & \mu_{TG}\pi_G & \mu_{TC}\pi_C & * \end{pmatrix}$$

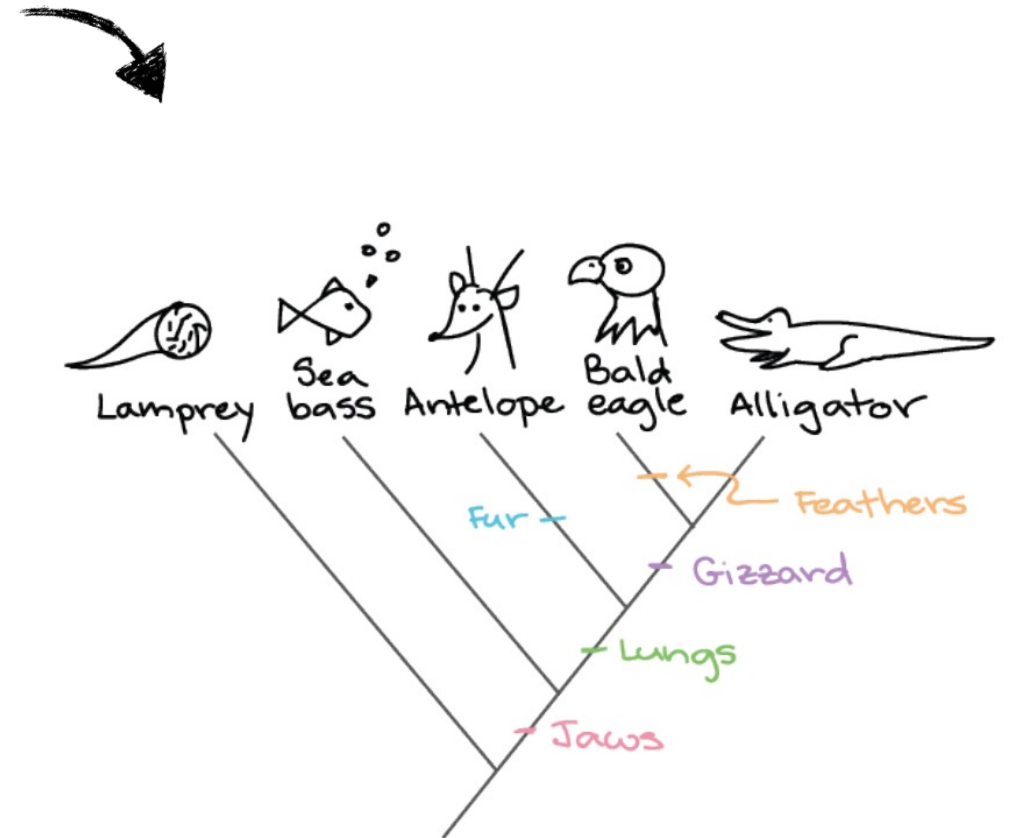
μ = substitution rate

π = stationary frequency



Morphological data

	Lungs	Jaws	Feathers	Gizzards	Fur
taxa A	0	0	0	0	0
taxa B	1	1	0	0	1
taxa C	1	1	1	1	0
taxa D	1	1	0	1	0
taxa E	0	1	0	0	0



Issues with Morphological data



Conodonts

taxa 1	0	1	0	1	2	1
taxa 2	1	2	1	0	1	0
taxa 3	0	0	1	0	0	1
taxa 4	1	1	0	1	0	1

Often used to indicate presence absence data

Issues with Morphological data



Conodonts

taxa 1	0	1	0	1	2	1
taxa 2	1	2	1	0	1	0
taxa 3	0	0	1	0	0	1
taxa 4	1	1	0	1	0	1

Multistate characters can be used to represent types of a trait

Issues with Morphological data



Conodonts

taxa 1	0	1	0	1	2	1
taxa 2	1	2	1	0	1	0
taxa 3	0	0	1	0	0	1
taxa 4	1	1	0	1	0	1

Trait 1

0

≠

1

Trait 2

0

≠

1

Generalising morphological data is much more difficult than molecular



Differences between molecular and morphological data to consider when modelling

Molecular data has a similar biological meaning throughout the alignment.

A T in one part of the alignment represents the same biological unit as a T somewhere else in the alignment.

This is not the same for morphological data.

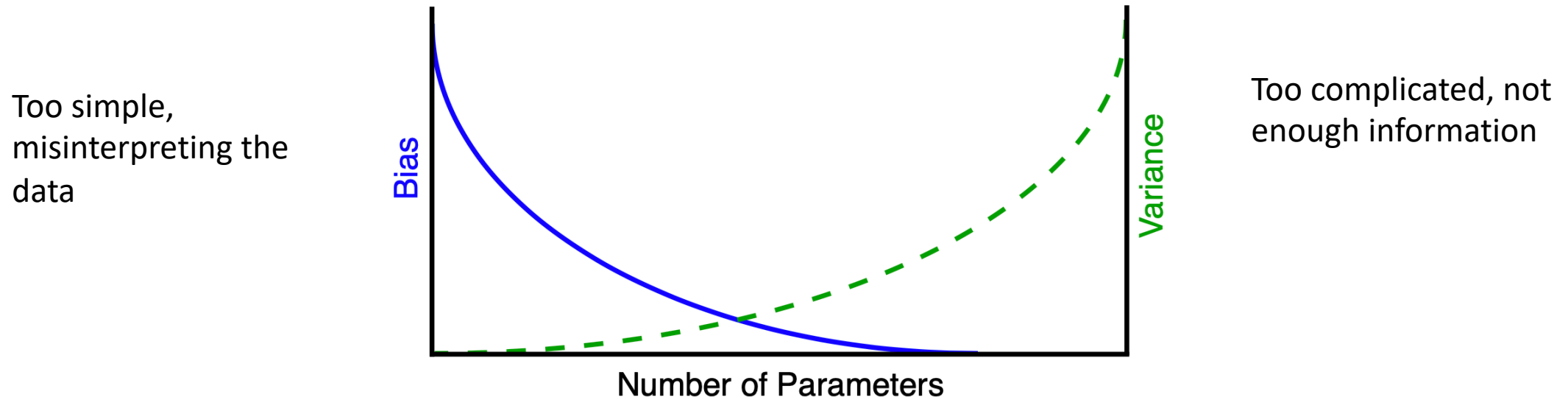
Becomes more **difficult to generalise** morphological data in any biologically meaningful way

What does a good model look like?

To do statistical inference we need a model

What model should that be?

Our goal should be to have a model that is **complex enough** to capture the “important” variation in the data, but **not be more complex** than it needs to be

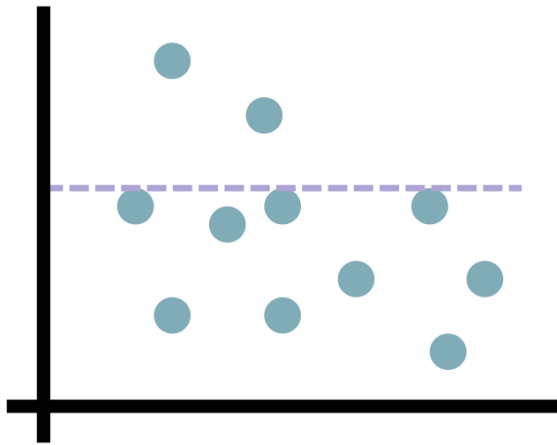


What does a good model look like?

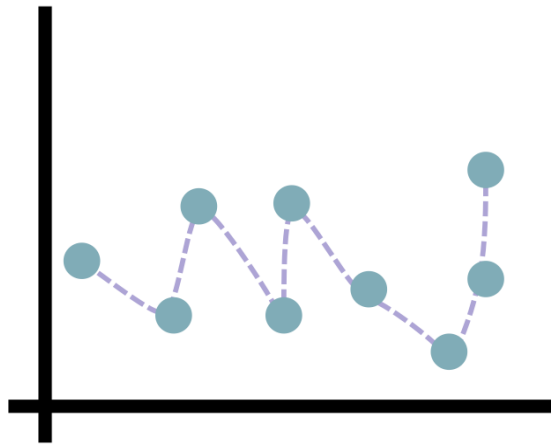
To do statistical inference we need a model

What model should that be?

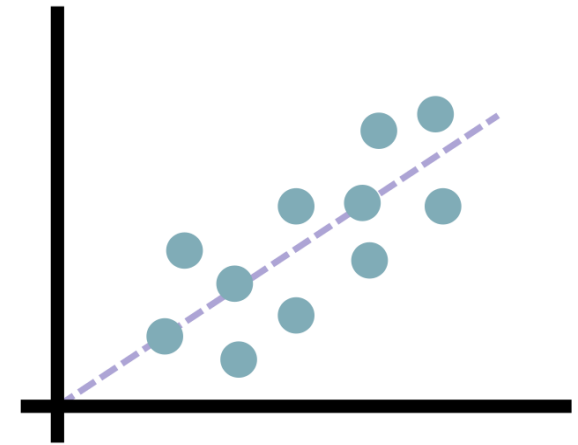
Our goal should be to have a model that is **complex enough** to capture the “important” variation in the data, but **not be more complex** than it needs to be



Underfitting



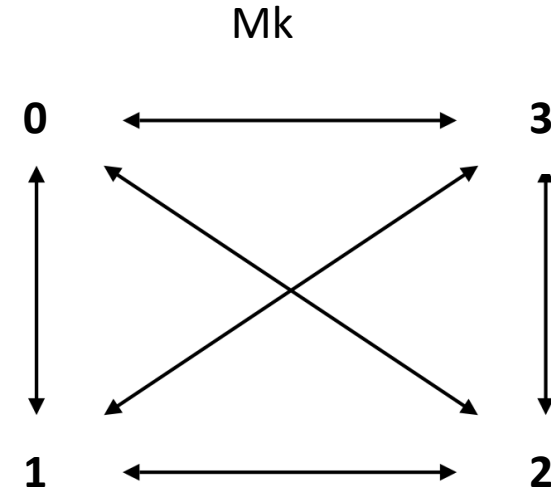
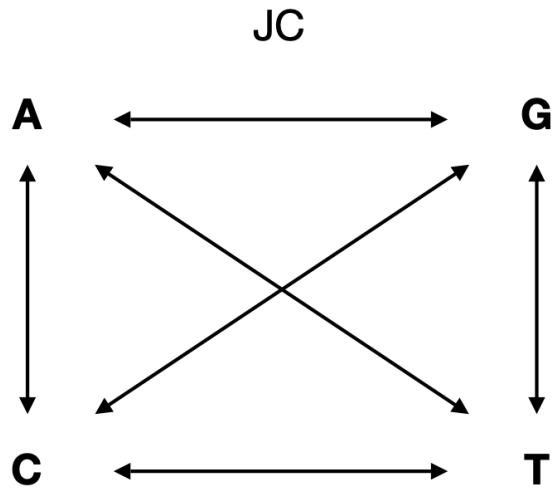
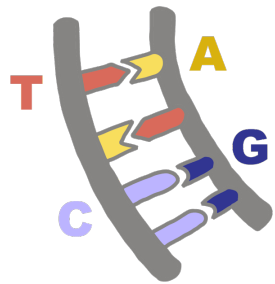
Overfitting



Proper fit

What assumptions might you want to incorporate into a model of morphological character evolution?

Substitution models for morphological data

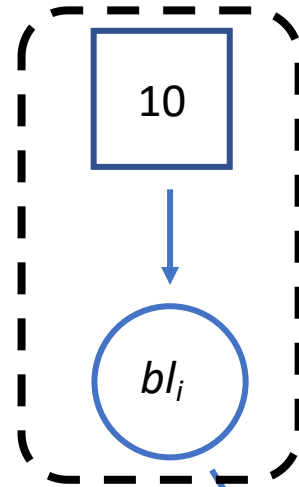


*4 state here as an example, can be any number from 2!

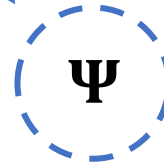
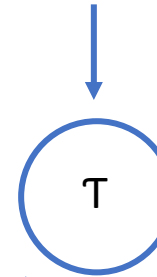
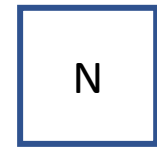
Line width represents the relative rate of change between different steps.

Mk Model

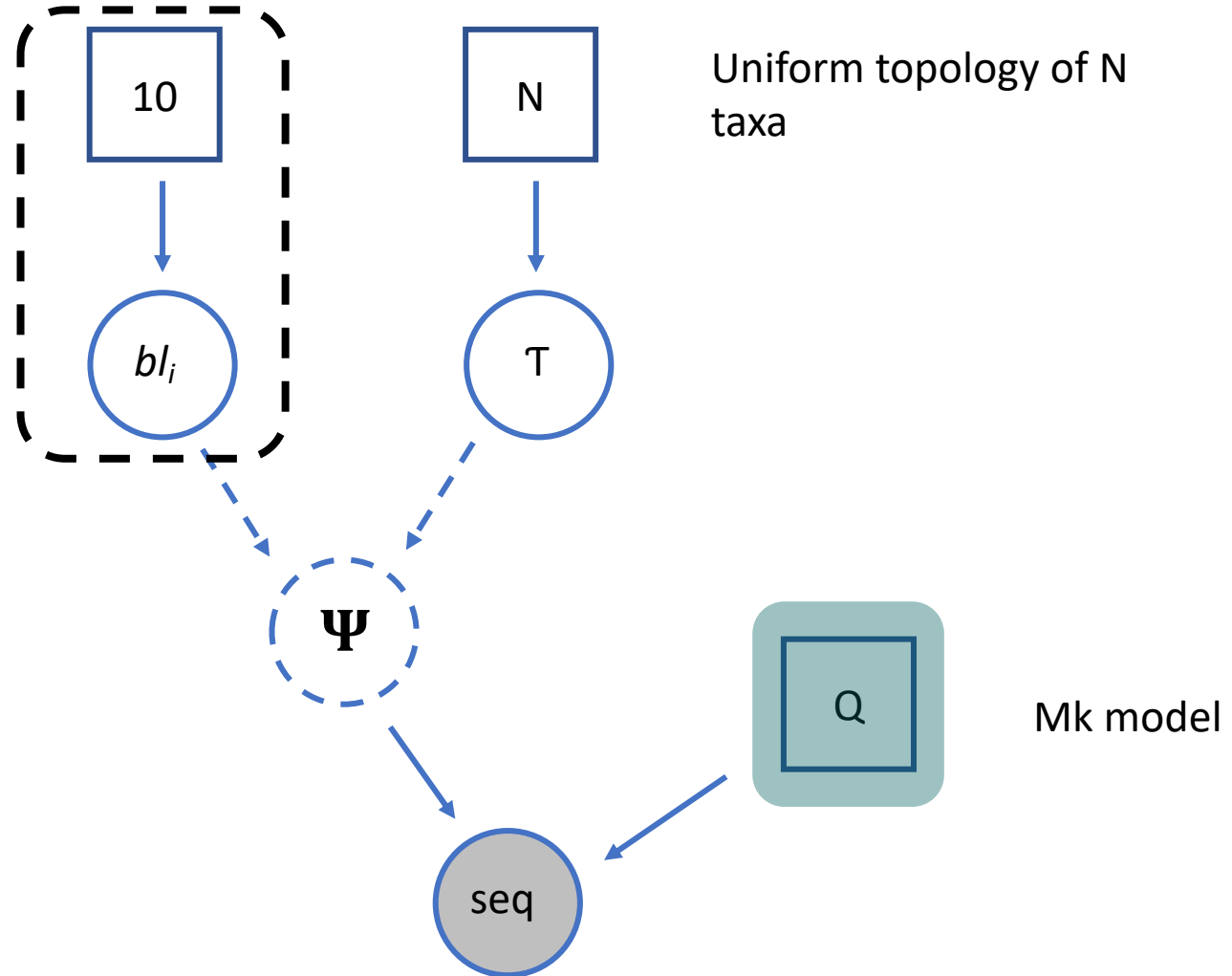
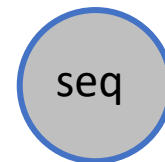
Exponential rate parameter of 10 on branch lengths.



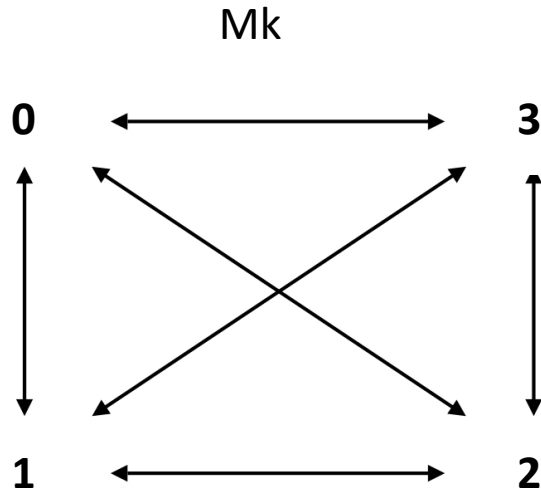
Uniform topology of N taxa



Mk model



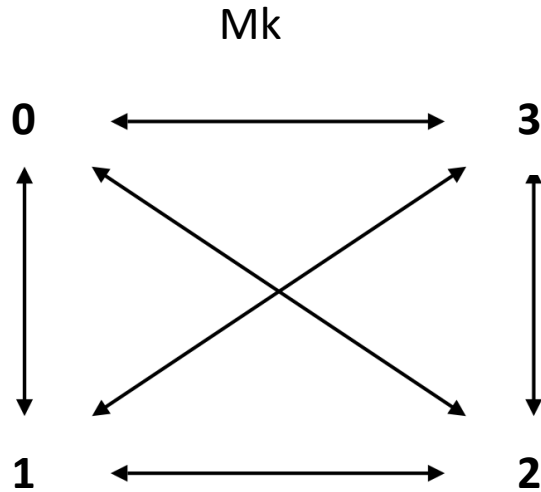
Substitution models for morphological data



$$Q = \begin{pmatrix} -\mu_0 & \mu_{01} & \mu_{02} & \mu_{03} \\ \mu_{10} & -\mu_1 & \mu_{12} & \mu_{13} \\ \mu_{20} & \mu_{21} & -\mu_2 & \mu_{23} \\ \mu_{30} & \mu_{31} & \mu_{32} & -\mu_3 \end{pmatrix},$$

*4 state here as an example, can be any number from 2!

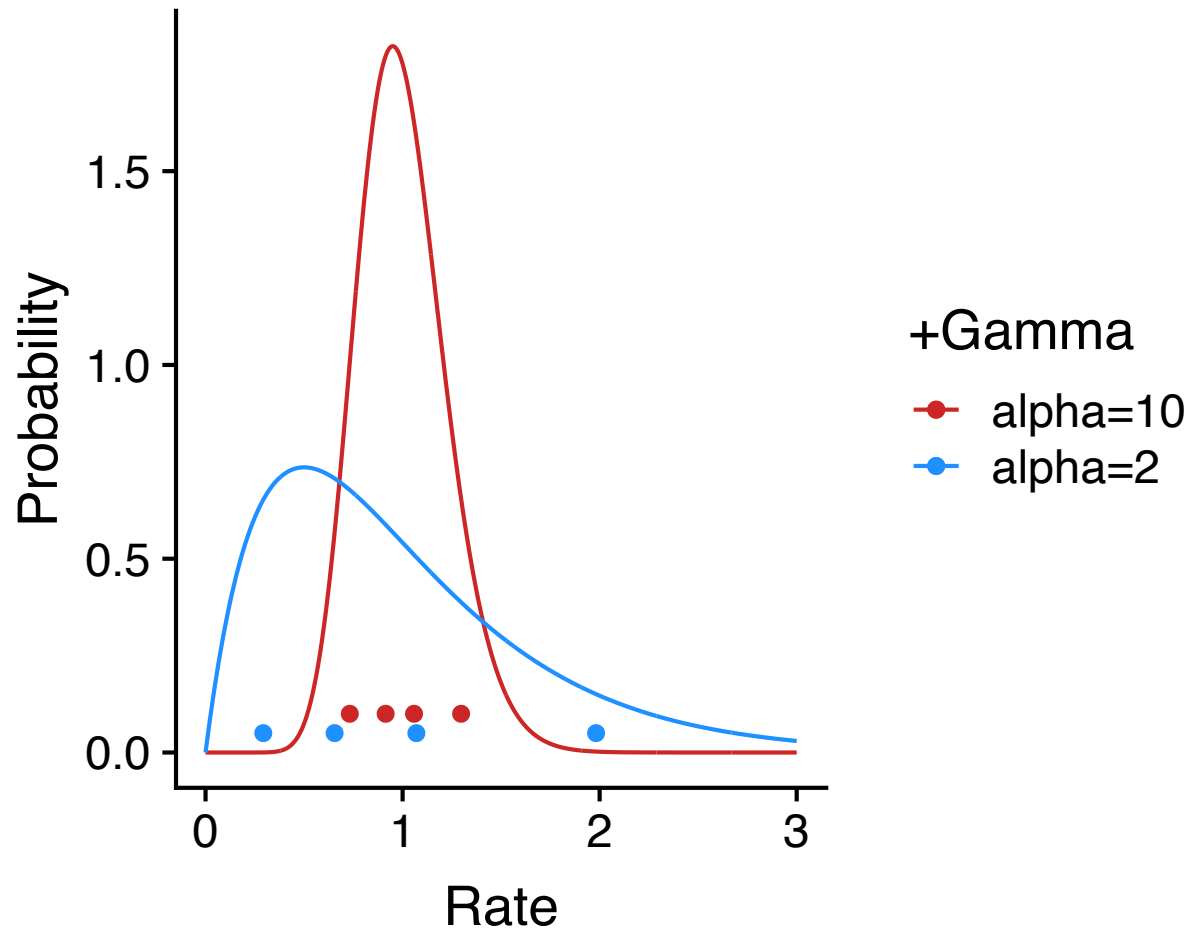
Substitution models for morphological data



We can **add extensions** to the standard Mk model in a number of ways

*4 state here as an example, can be any number from 2!

Across Site Rate Variation (+G)



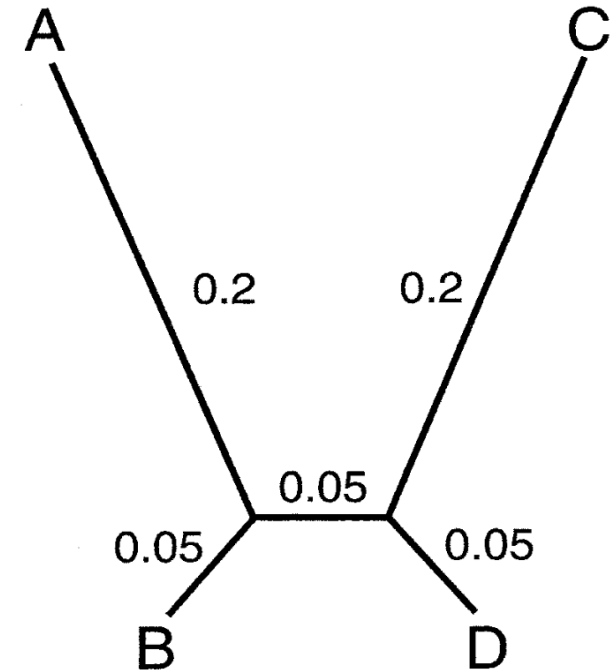
alpha = 10, the rates are similar

alpha = 2 the rates differ

This approach allows **faster evolving sites to evolve according to higher rates** and visa versa

Ascertainment Bias (V)

Conditions on the fact that all sites are variable



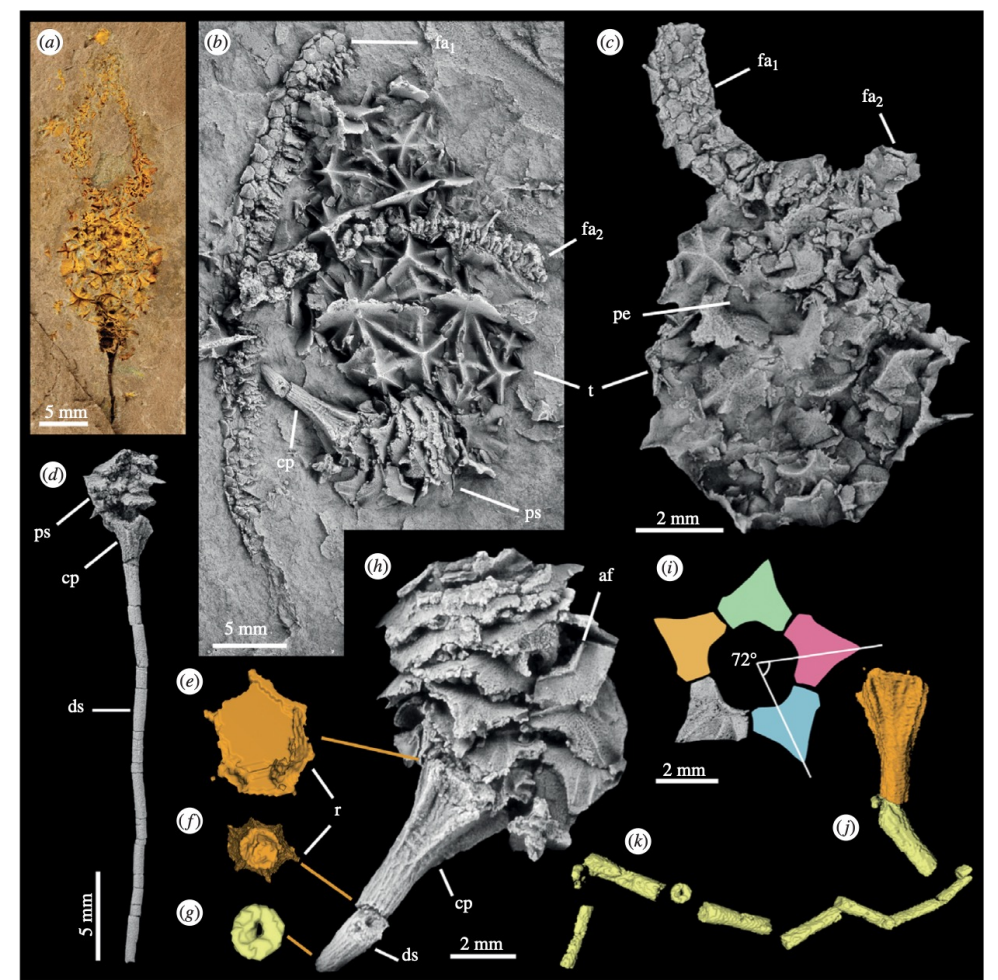
	True branch length	Mk (uncorrected)	Mkv (corrected)
Percent correct	—	74.0	99.8
Branch A	0.2	241,750 ($\pm 349,100$)	0.206 (± 0.060)
Branch B	0.05	0.43210 (± 0.13756)	0.050 (± 0.018)
Branch X	0.05	54.646 ($\pm 1,725.3$)	0.052 (± 0.023)
Branch C	0.2	143,950 ($\pm 228,910$)	0.206 (± 0.059)
Branch D	0.05	0.022 (± 0.054)	0.051 (± 0.019)

Partitioning the data

Researchers have argued that it is reasonable
partition a morphological matrix by the number
of character states

Taxa A	0	1	0	0	2	3
Taxa B	2	0	1	1	0	2
Taxa C	1	1	2	1	3	1

001510010?00-100--00000000000
 000500010?200100--00100100000
 002500010?200100--0?100100000
 00?5?0010?200100?-0???010110
 0015000101201000430100011111
 0015000101201010440111011111
 ??050?????201000440?11011111
 01050?010-210000?501??010110
 00020001002101003-1110010110
 0002000100211001441121011111
 000201111-210010?-??11011121
 ?103?0?11?1001104-0000010000
 1005002110100010--0?00110?20
 1005002000101010540?00110020

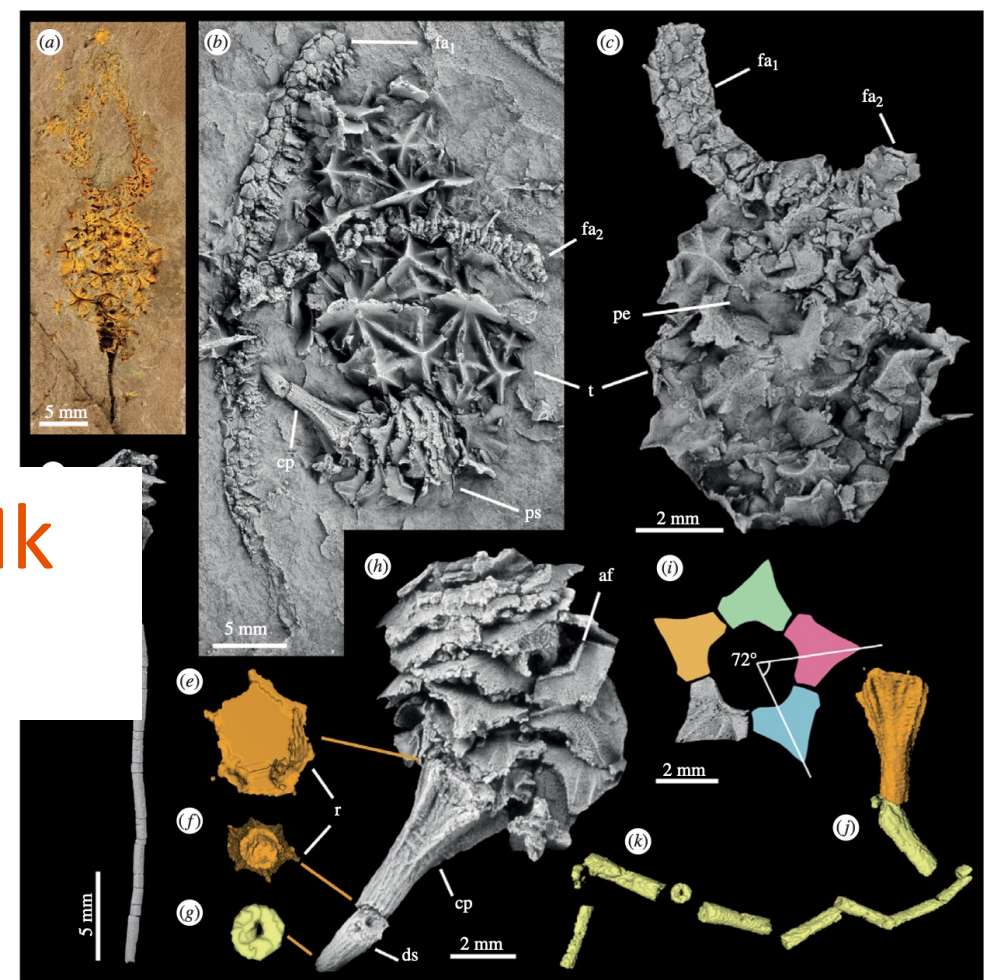


*Cambrian stalked echinoderms show
 unexpected plasticity of arm construction
 Zamora & Smith. 2012 Proc B*

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001510010?00-100--00000000000
000500010?200100--0010010000
002500010?200100--0?10010000
00?5?0010?200100?-0???010110
(
Can you draw the Q-matrix for an Mk
model for this data set?
01050?010-210000?501??010110
00020001002101003-1110010110
0002000100211001441121011111
000201111-210010?-??11011121
?103?0?11?1001104-0000010000
1005002110100010--0?00110?20
1005002000101010540?00110020

```



Cambrian stalked echinoderms show unexpected plasticity of arm construction
Zamora & Smith. 2012 Proc B

Exercise