Not The Fly On The Wall:

can systematists cope with uncertainty?

Joe Felsenstein

Systematics Association: Huxley Lecture, 2008

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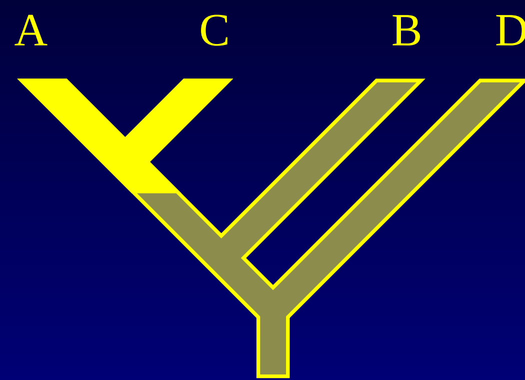
All these are “Fly On The Wall” questions about what actually happened, as opposed to questions about parameters of processes.

Can we describe uncertainty in morphology or behavior?

- Currently, most people using morphological or behavioral characters use parsimony methods
- They also code the characters discretely, which leads to the "character coding problem"
- They have no statistical model and little way of knowing how uncertain are their inferences (except for some bootstrapping or jackknifing which assumes characters change independently)
- Is discrete coding necessary? No.
- Are there statistical models for these discrete phenotypes? Yes.

Current methods for statistical treatment of 0/1 characters

Pagel (1994) and Lewis (2001) treat such data with



$$0 \underset{\beta\,dt}{\overset{\alpha\,dt}{\rightleftarrows}} 1$$

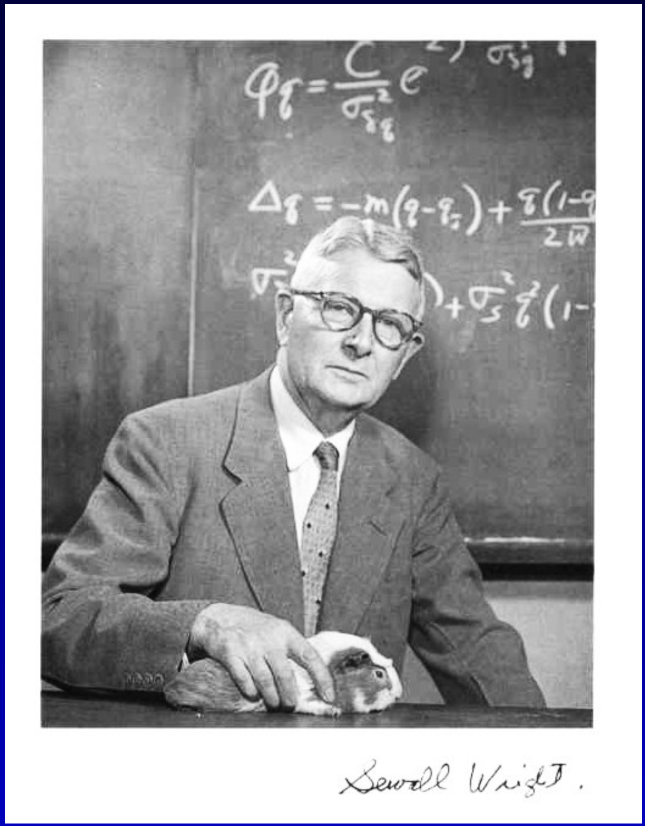
Pagel allows inference of whether change is correlated, on a known tree.

Lewis infers the tree, but does not allow for correlations among characters.

Neither takes into account contributions to a 0/1 character from multiple underlying loci.

The threshold model

A relevant model was invented in 1934 by



Sewall Wright (1889-1988)
shown here in the late 1950's

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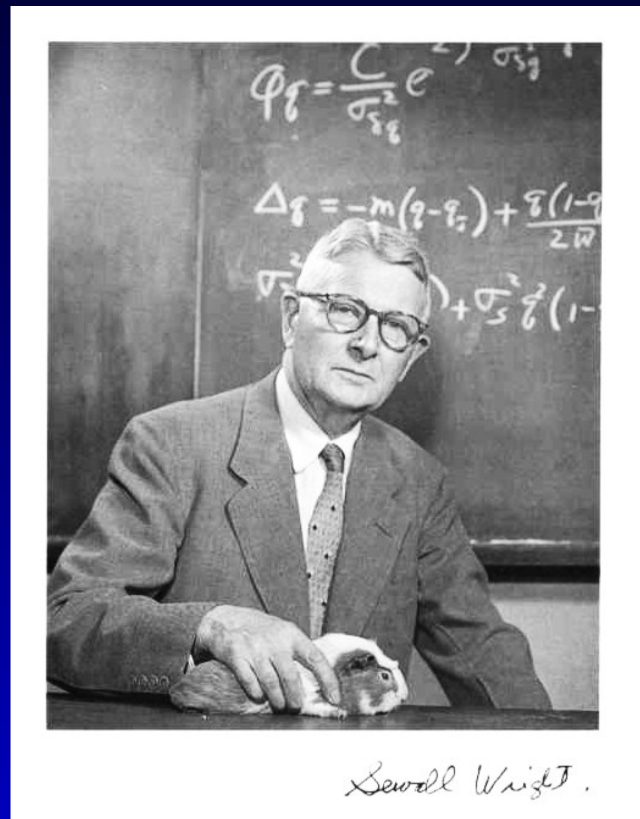
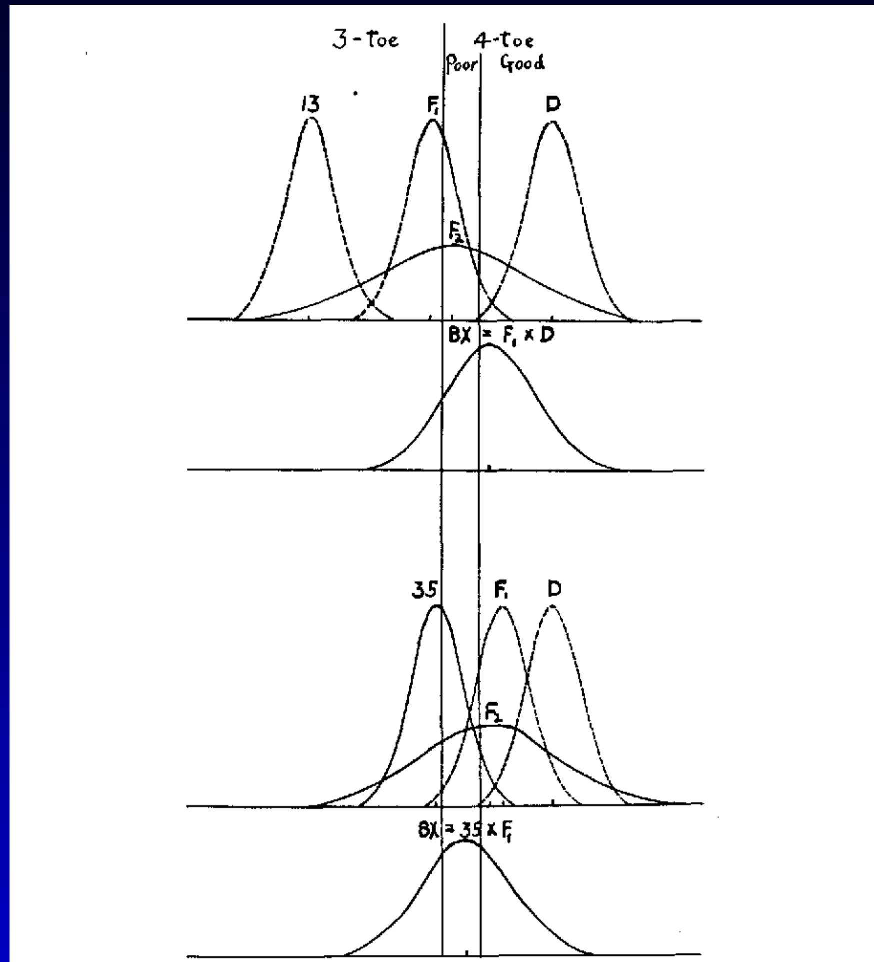


Sewall Wright (1889-1988)
shown here in the late 1950's

(The story goes that he then absent-mindedly started to erase the board with the guinea pig)

The threshold model, applied



Sewall Wright (1934), guinea pig digit number

(from Wright’s follow-up 1934 second paper)

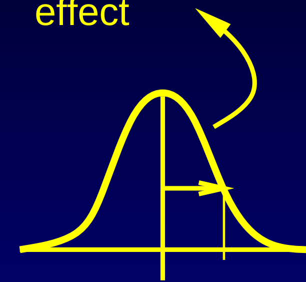
Brownian motion models for continuous characters

- Continuous characters change by natural selection, genetic drift, mutation and other population-genetic forces such as migration.
- The first three of these can be modelled by Brownian motion, with correlations among the changes in different characters.
- The correlations come from
  - Genetic covariation (which includes developmental and functional correlation, and the effects of pleotropic mutations)
  - “Selective correlation” (Olaf Tedin, 1925; Stebbins, 1950) which is the covariation of selection pressures

The model is far from exact but is very tractable and a good starting point for attempts to make it more realistic.

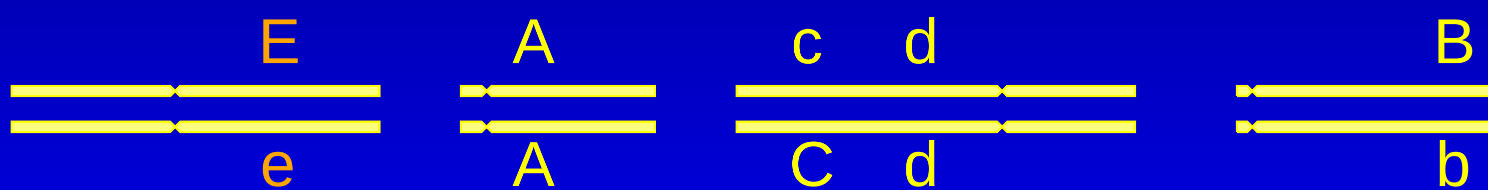
We use the standard quantitative genetic model

$$P = \left\{\begin{matrix} AA & 2 \\ Aa & 4 \\ aa & 7 \end{matrix}\right\} + \left\{\begin{matrix} BB & 0.6 \\ Bb & 0.1 \\ bb & -0.2 \end{matrix}\right\} + \left\{\begin{matrix} CC & -1 \\ Cc & 6 \\ cc & 6 \end{matrix}\right\} + \left\{\begin{matrix} DD & 0.3 \\ Dd & 0.3 \\ dd & 0.7 \end{matrix}\right\} + \left\{\begin{matrix} EE & -0.4 \\ Ee & 0.3 \\ ee & -0.3 \end{matrix}\right\} + \text{environmental effect}$$



AA	**Bb**	**Cc**	**dd**	**Ee**
Aa	**bb**	**cc**	**DD**	**ee**
aa	**bb**	**CC**	**DD**	**Ee**
aa	**bb**	**Cc**	**DD**	**EE**
Aa	**Bb**	**Cc**	**DD**	**Ee**

$$0.3 + 2 + 6 + 0.7 + 0.1 + 0.9$$



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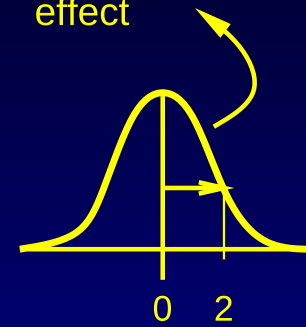

AA	**Bb**	**Cc**	**dd**	**Ee**
Aa	**bb**	**cc**	**DD**	**ee**
aa	**bb**	**CC**	**DD**	**Ee**
aa	**bb**	**Cc**	**DD**	**EE**
Aa	**Bb**	**Cc**	**DD**	**Ee**

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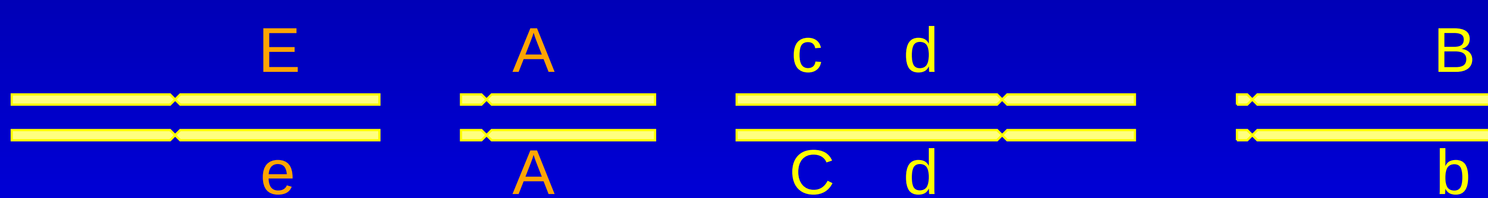

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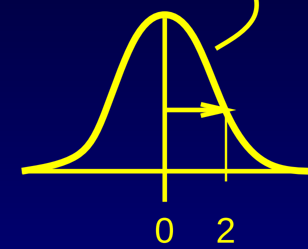

AA	Bb	Cc	dd	Ee
Aa	bb	cc	DD	ee
aa	bb	CC	DD	Ee
aa	bb	Cc	DD	EE
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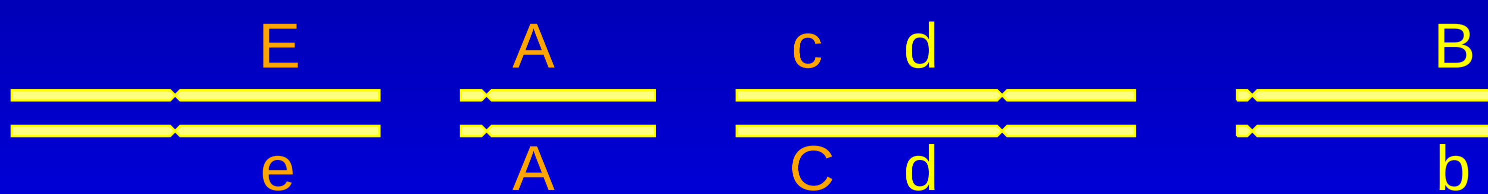

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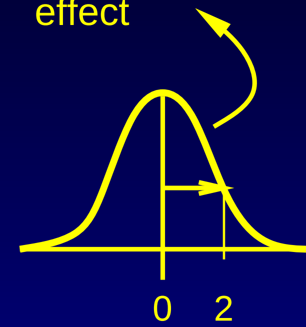

AA	Bb	Cc	dd	Ee
Aa	bb	cc	DD	ee
aa	bb	CC	DD	Ee
aa	bb	Cc	DD	EE
Aa	Bb	Cc	DD	Ee

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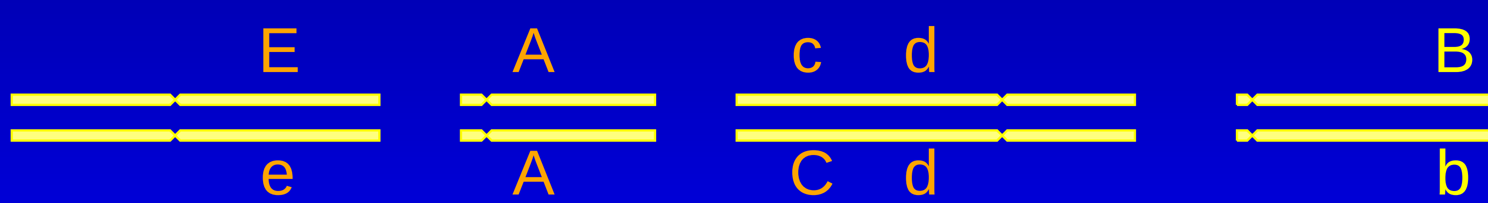

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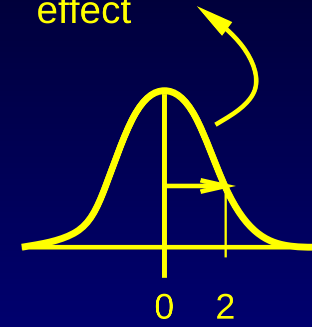

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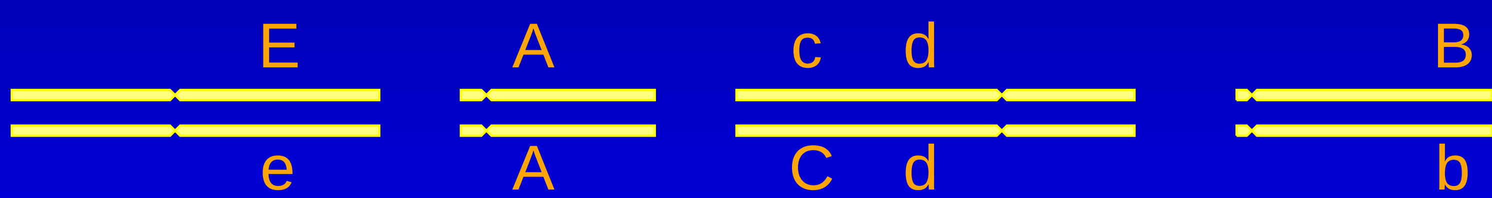

… which leads to various character values

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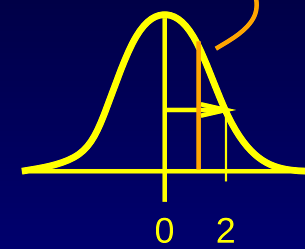

AA	Bb	Cc	dd	Ee	10
Aa	bb	cc	DD	ee	
aa	bb	CC	DD	Ee	
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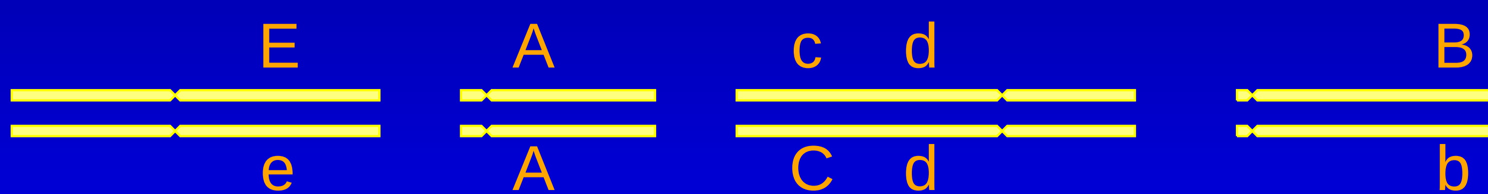

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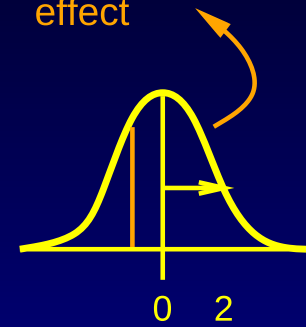
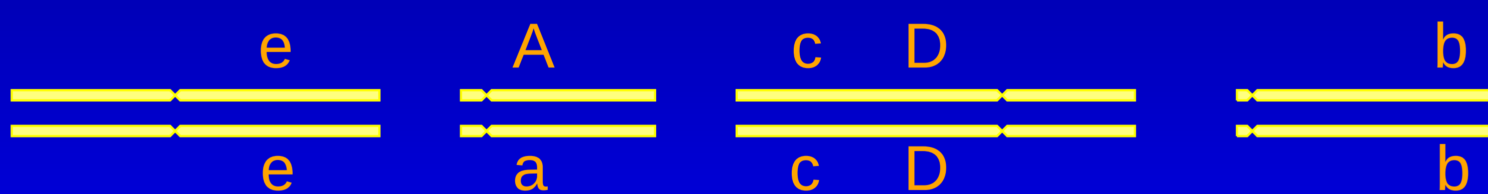


AA	Bb	Cc	dd	Ee	10
Aa	bb	cc	DD	ee	8.8
aa	bb	CC	DD	Ee	
aa	bb	Cc	DD	EE	
Aa	Bb	Cc	DD	Ee	

$$-0.3 + \quad 4 \quad + \quad 6 + 0.3 \qquad -0.2 - 1.0$$



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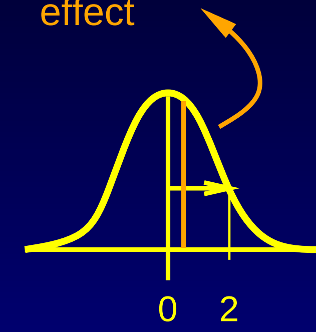
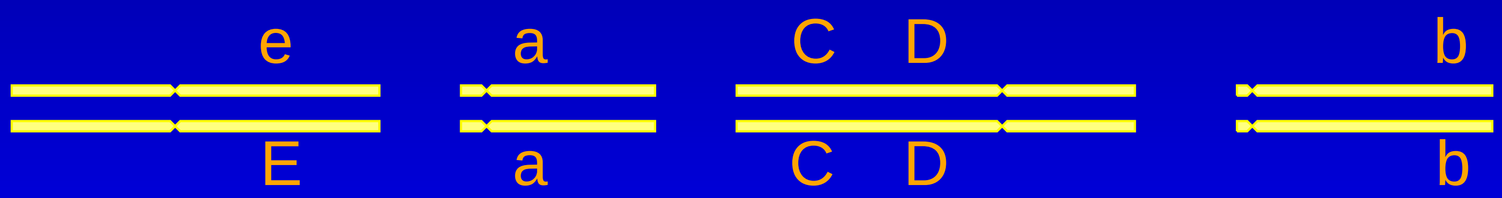


AA	Bb	Cc	dd	Ee	10
Aa	bb	cc	DD	ee	8.8
aa	bb	CC	DD	Ee	6.5
aa	bb	Cc	DD	EE	
Aa	Bb	Cc	DD	Ee	

$$0.3 + 7 + -1 + 0.3 + -0.2 + 0.1$$



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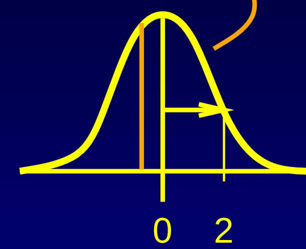
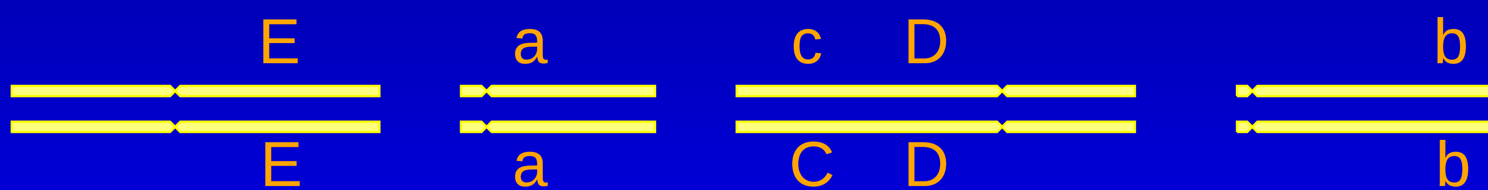


AA	Bb	Cc	dd	Ee	10
Aa	bb	cc	DD	ee	8.8
aa	bb	CC	DD	Ee	6.5
aa	bb	Cc	DD	EE	12.2
Aa	Bb	Cc	DD	Ee	

$$-0.4 + 7 + 6 + 0.3 \qquad -0.2 - 0.5$$



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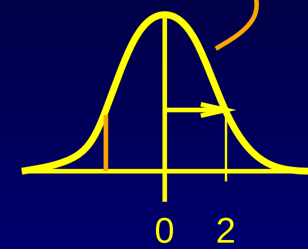
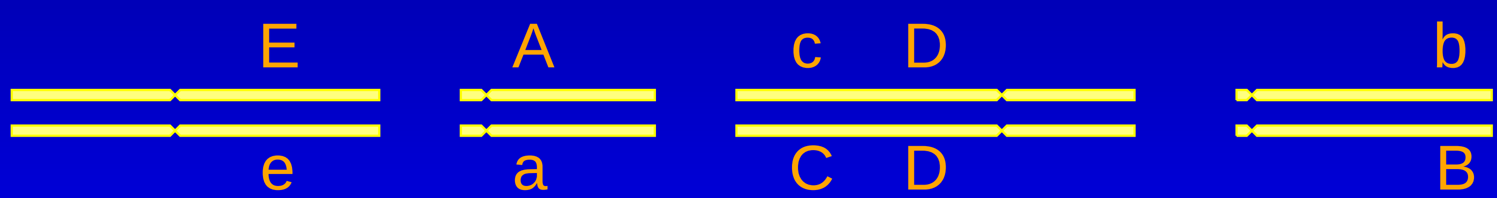


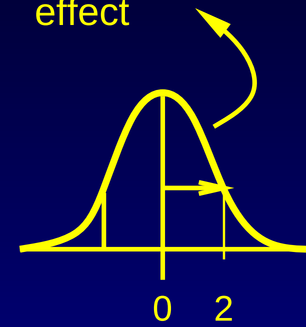
AA	Bb	Cc	dd	Ee	10
Aa	bb	cc	DD	ee	8.8
aa	bb	CC	DD	Ee	6.5
aa	bb	Cc	DD	EE	12.2
Aa	Bb	Cc	DD	Ee	8.9

$$0.3 + 4 + 6 + 0.3 + 0.1 - 1.8$$



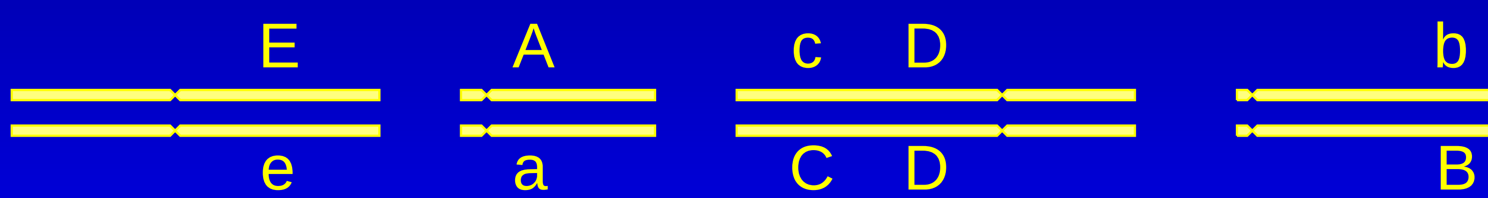
… then we apply a threshold of 9

$$P = \left\{\begin{matrix} AA & 2 \\ Aa & 4 \\ aa & 7 \end{matrix}\right\} + \left\{\begin{matrix} BB & 0.6 \\ Bb & 0.1 \\ bb & -0.2 \end{matrix}\right\} + \left\{\begin{matrix} CC & -1 \\ Cc & 6 \\ cc & 6 \end{matrix}\right\} + \left\{\begin{matrix} DD & 0.3 \\ Dd & 0.3 \\ dd & 0.7 \end{matrix}\right\} + \left\{\begin{matrix} EE & -0.4 \\ Ee & 0.3 \\ ee & -0.3 \end{matrix}\right\} + \text{environmental effect}$$



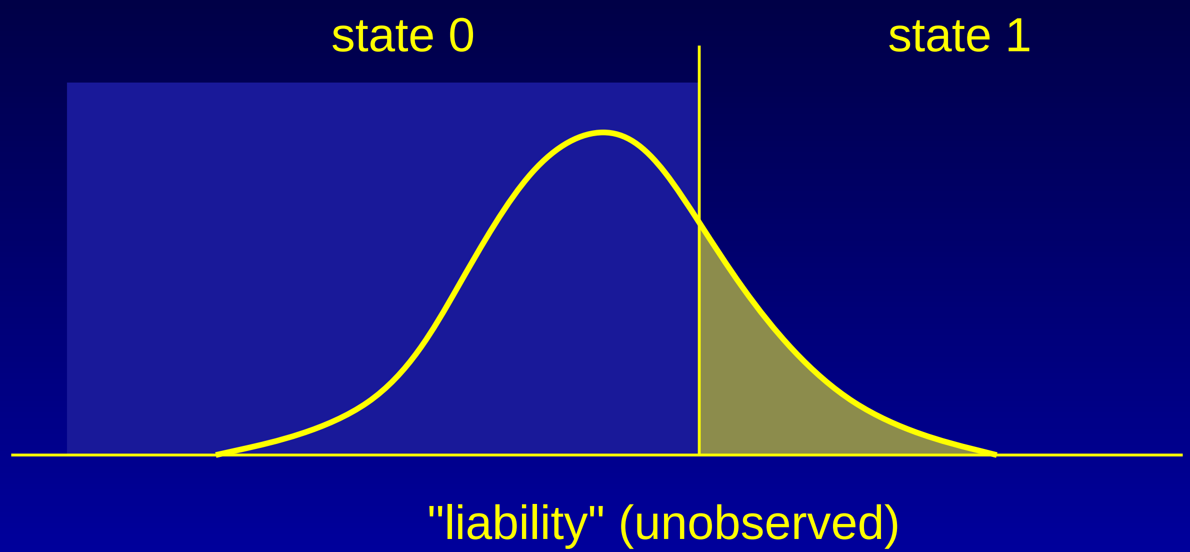
AA	**Bb**	**Cc**	**dd**	**Ee**	**10**	→	**1**
Aa	**bb**	**cc**	**DD**	**ee**	**8.8**	→	**0**
aa	**bb**	**CC**	**DD**	**Ee**	**6.5**	→	**0**
aa	**bb**	**Cc**	**DD**	**EE**	**12.2**	→	**1**
Aa	**Bb**	**Cc**	**DD**	**Ee**	**8.9**	→	**0**

$$0.3 + 4 + 6 + 0.3 + 0.1 - 1.8$$



The threshold model

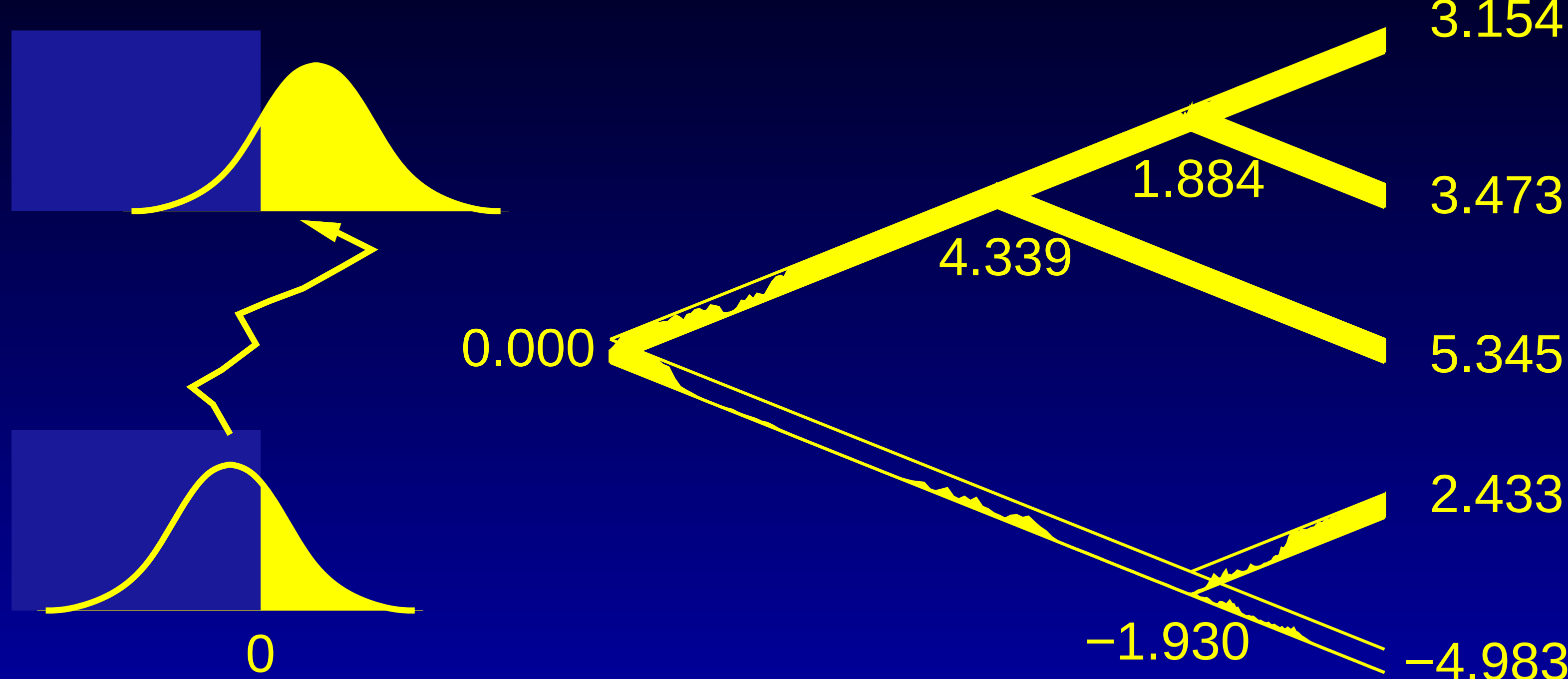
The threshold model (Wright, 1934; Falconer, 1965), plus Brownian motion



Advantages:

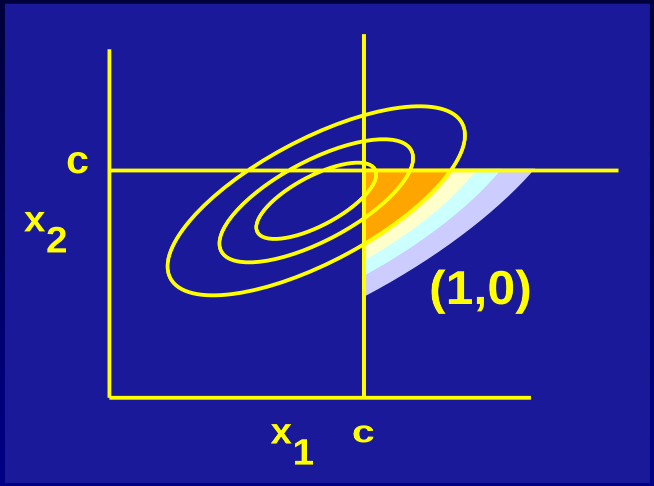
1. Predicts polymorphism as a lineage crosses the threshold
2. Soon after the threshold is crossed, one is more likely to revert. Less later.
3. Can allow covariation of characters

The threshold model on a tree



Computing the likelihood

With two species, one character:



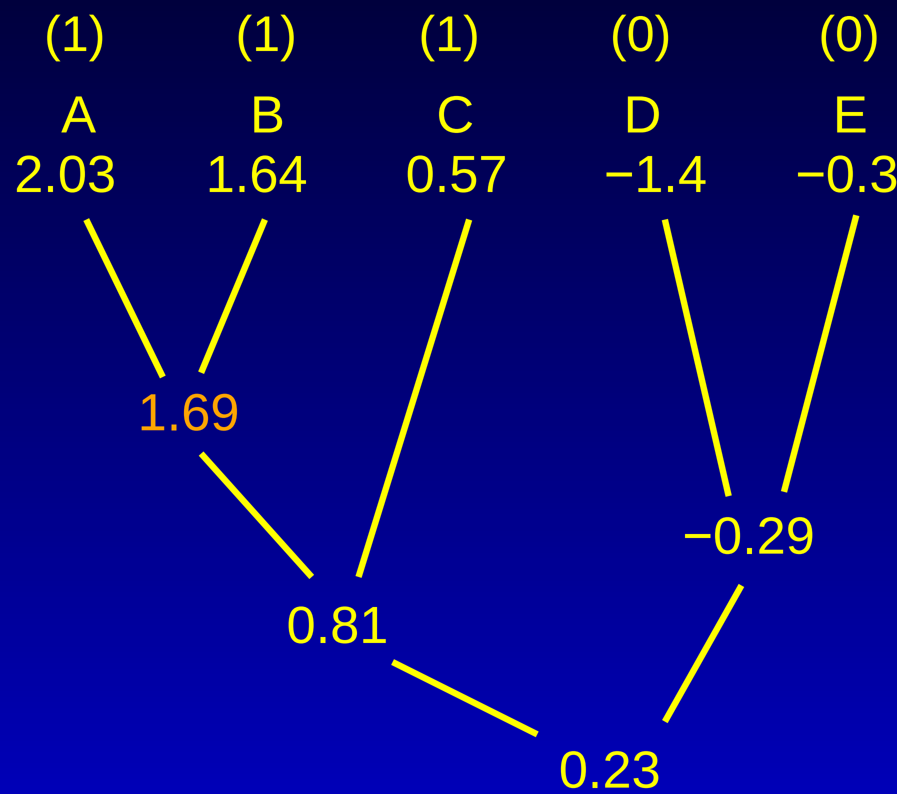
Disadvantages:

Quite hard to compute likelihoods: need to compute area in a corner of a correlated multivariate normal distribution.

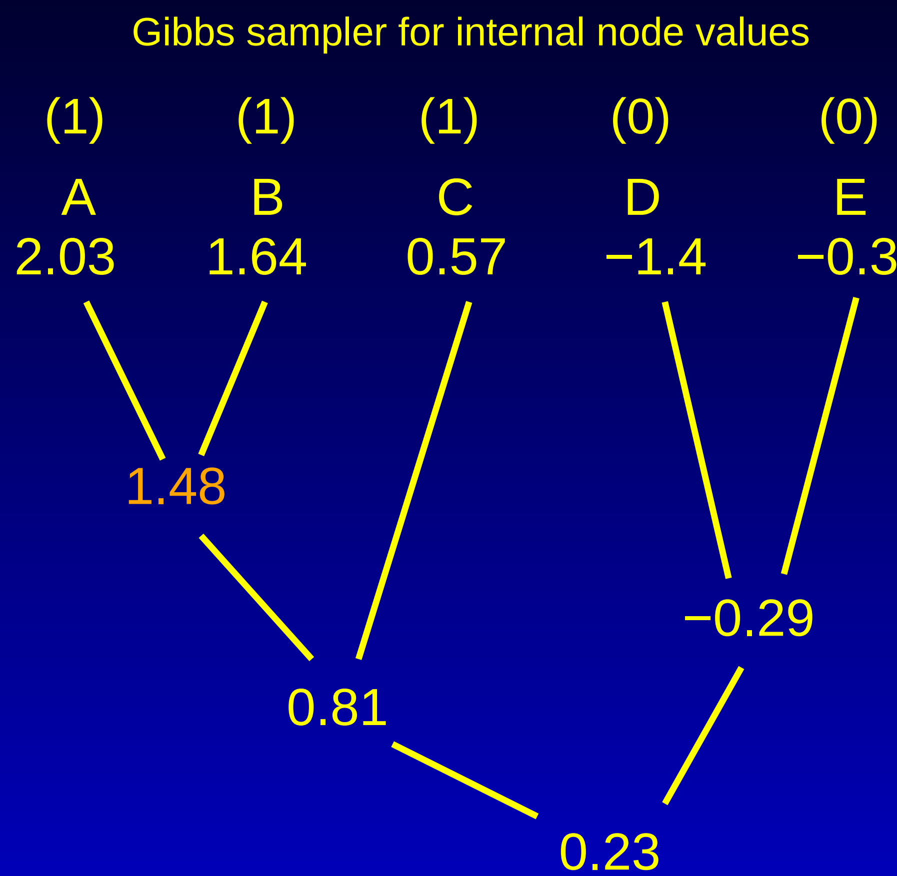
With 5 species, one character:

$$
\begin{aligned}
\mathsf{L} &= \text{Prob}\,(1,1,0,1,1)\\
&= \int_0^\infty \int_0^\infty \int_{-\infty}^0 \int_0^\infty \int_0^\infty \varphi(\mathsf{x}_1,\mathsf{x}_2,\mathsf{x}_3,\mathsf{x}_4,\mathsf{x}_5 \mid \text{Tree})\ \mathsf{dx}_1\ \mathsf{dx}_2\ \mathsf{dx}_3\ \mathsf{dx}_4\ \mathsf{dx}_5
\end{aligned}
$$

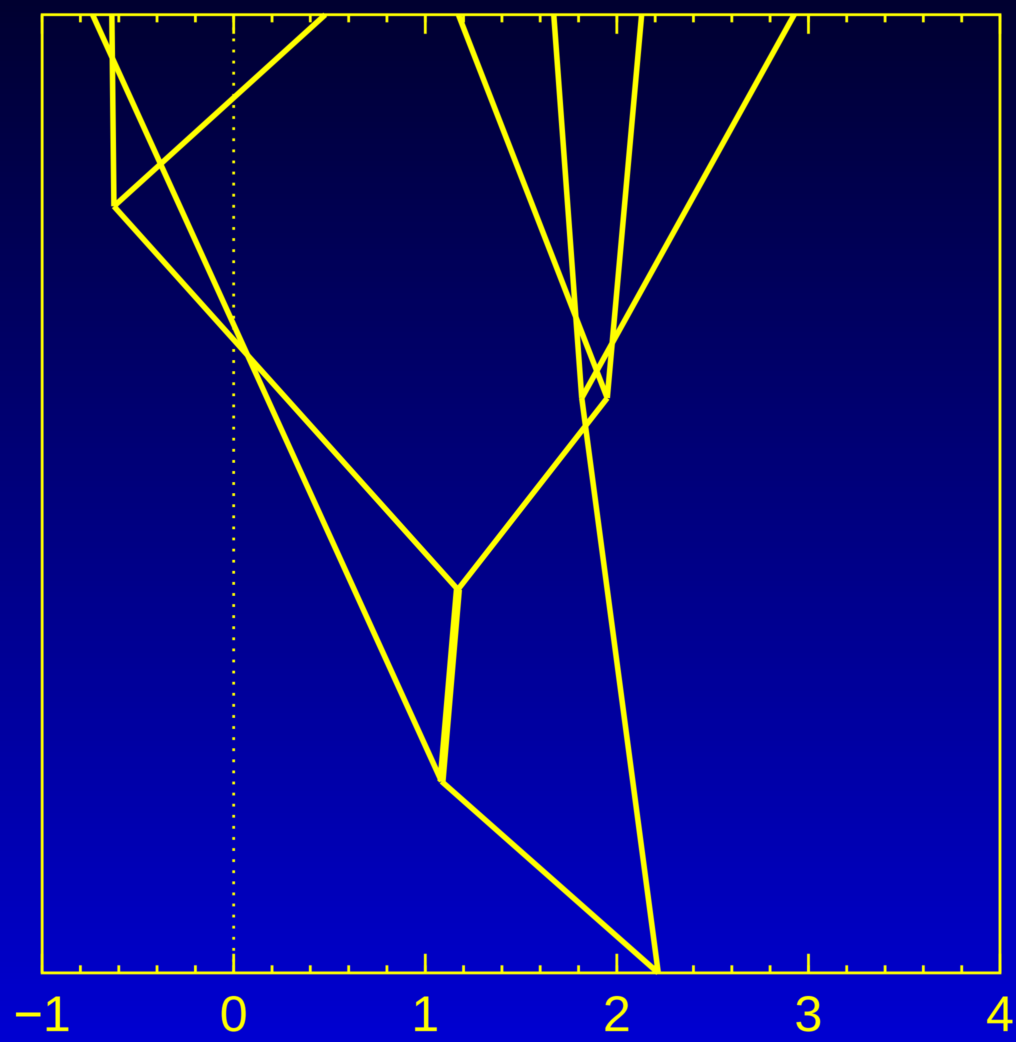
MCMC on liabilities



MCMC on liabilities: result of Gibbs sampling



An example



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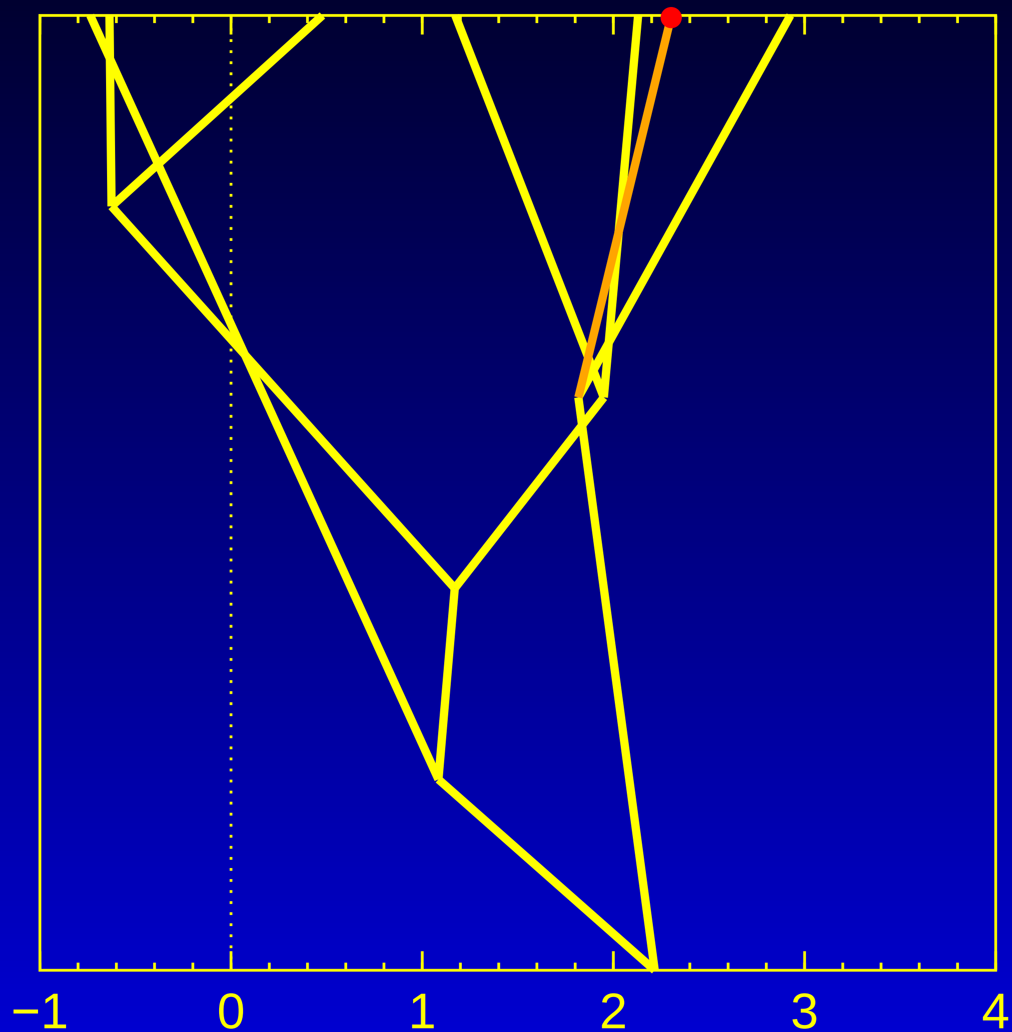

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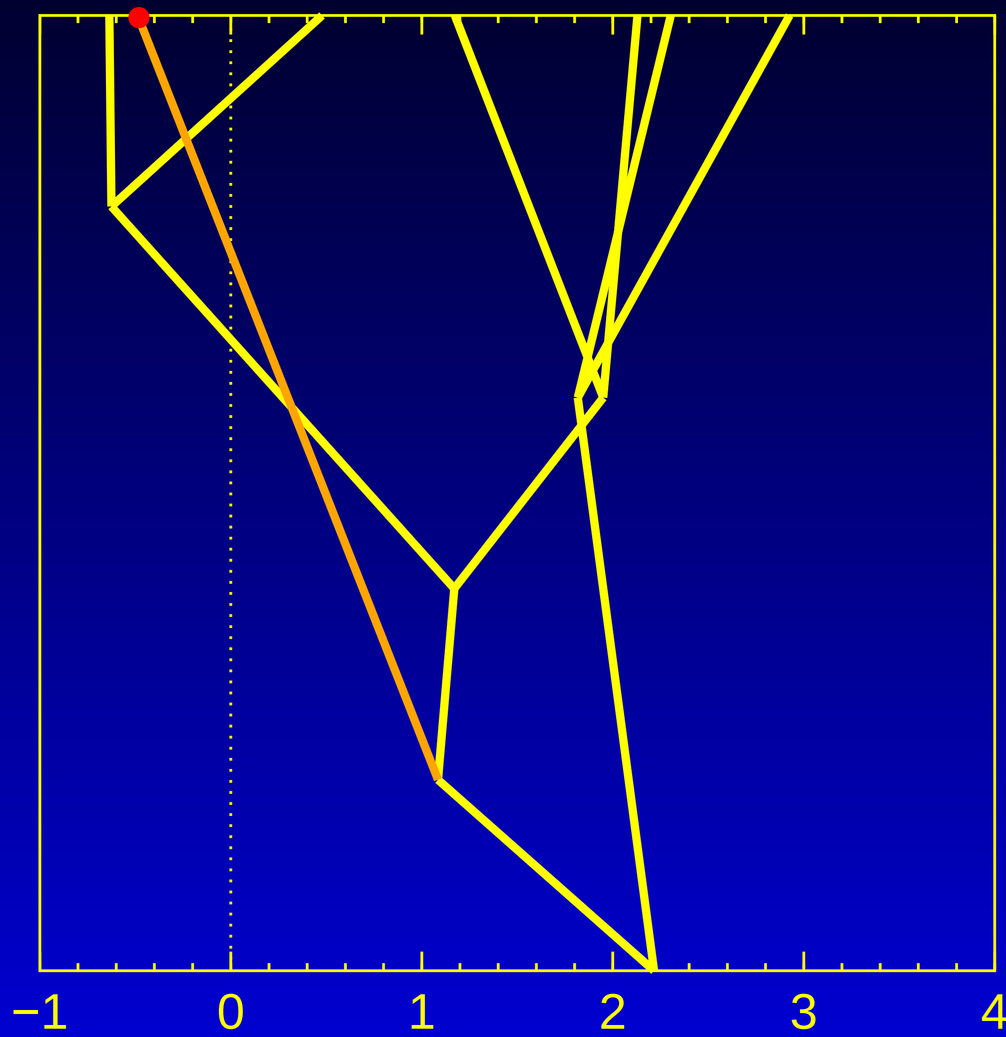
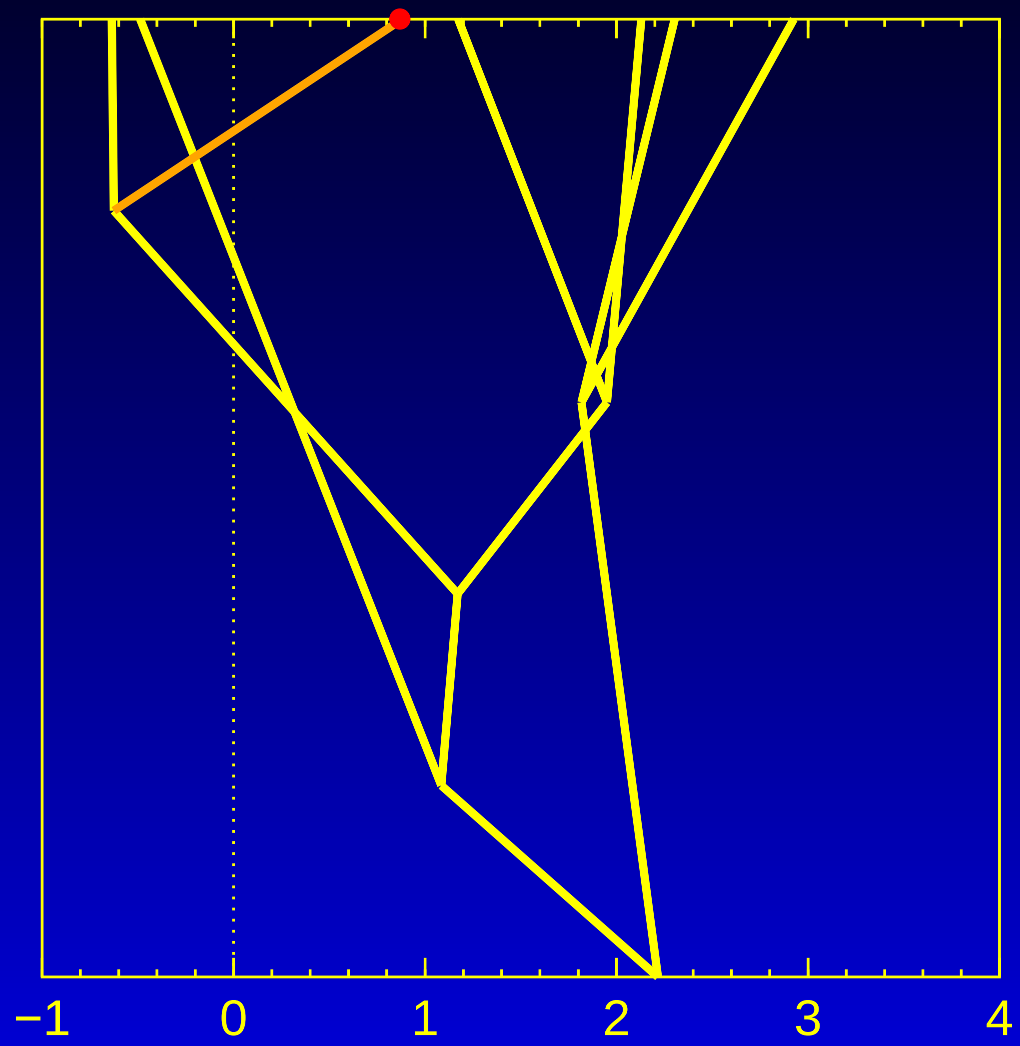
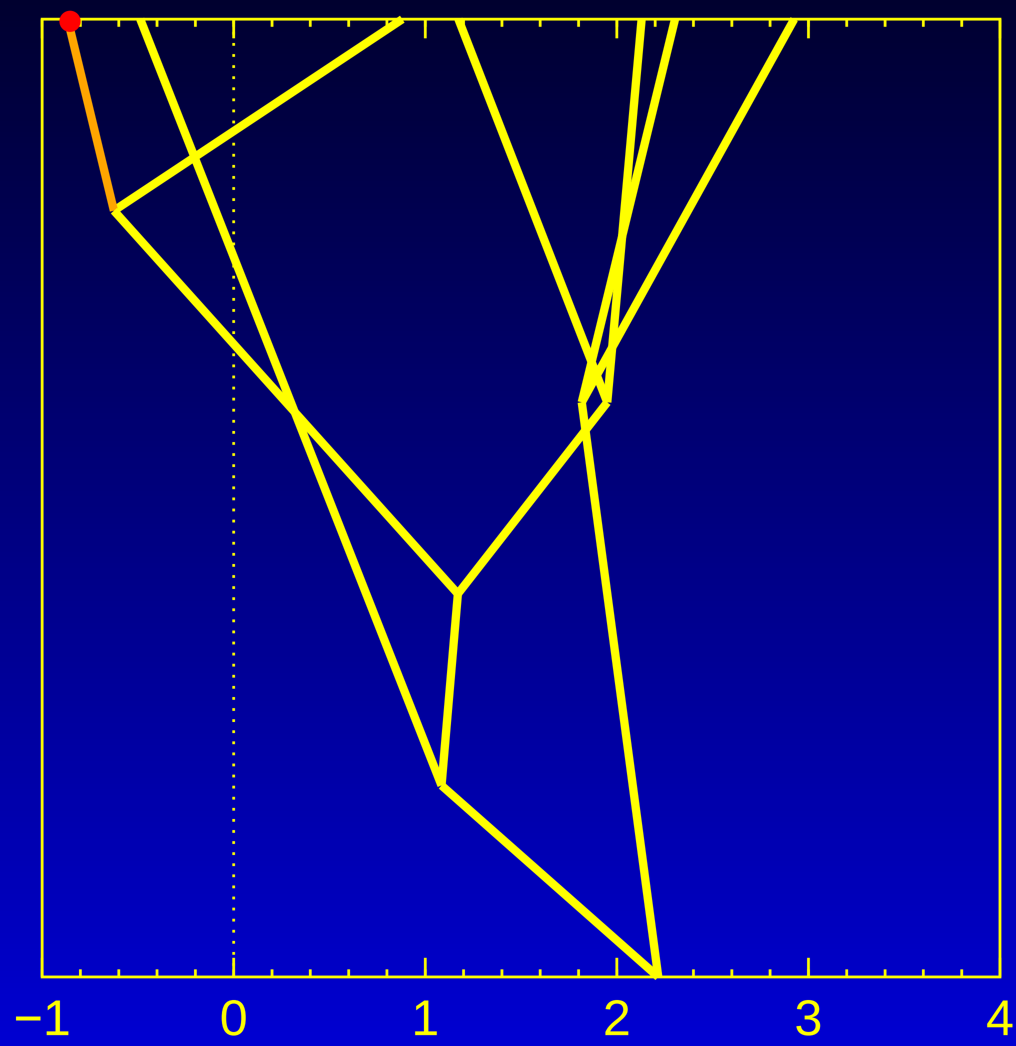


An example



An example



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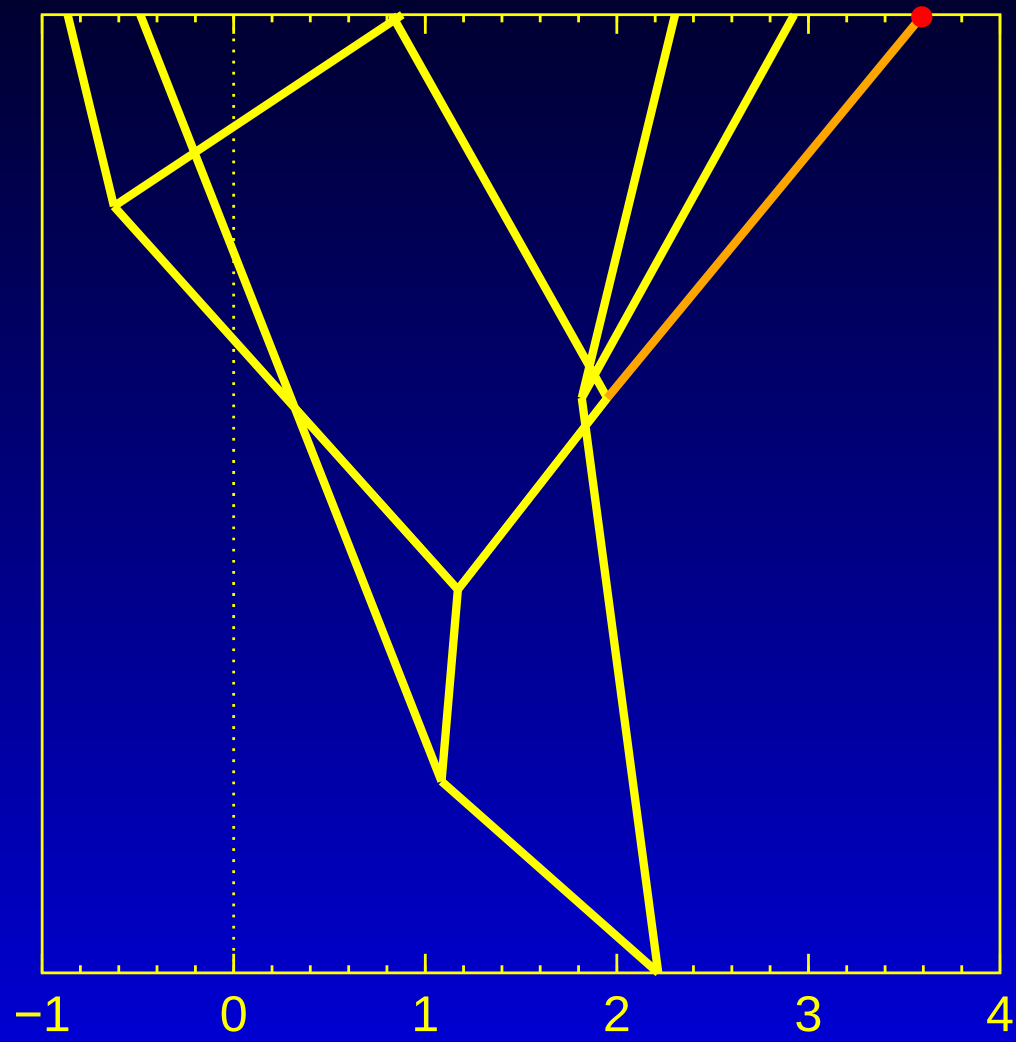

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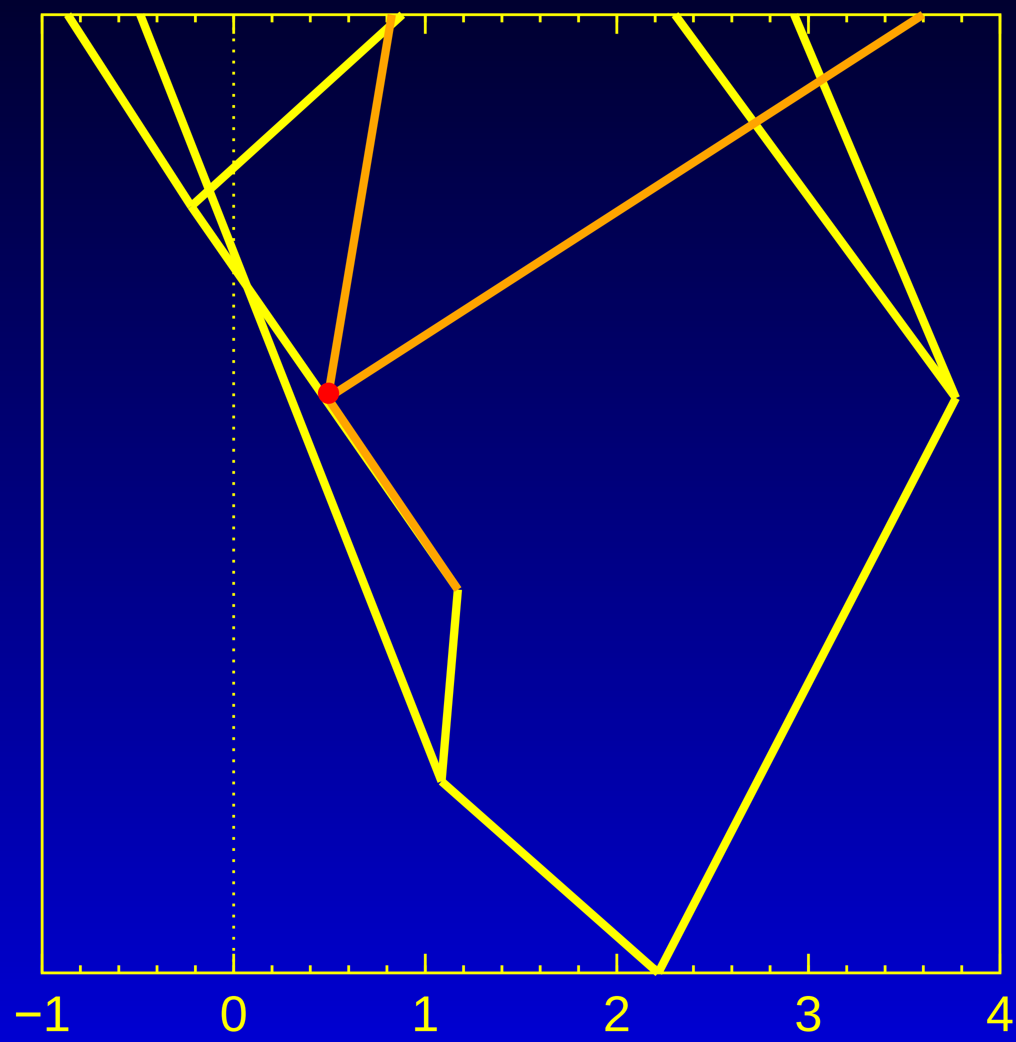

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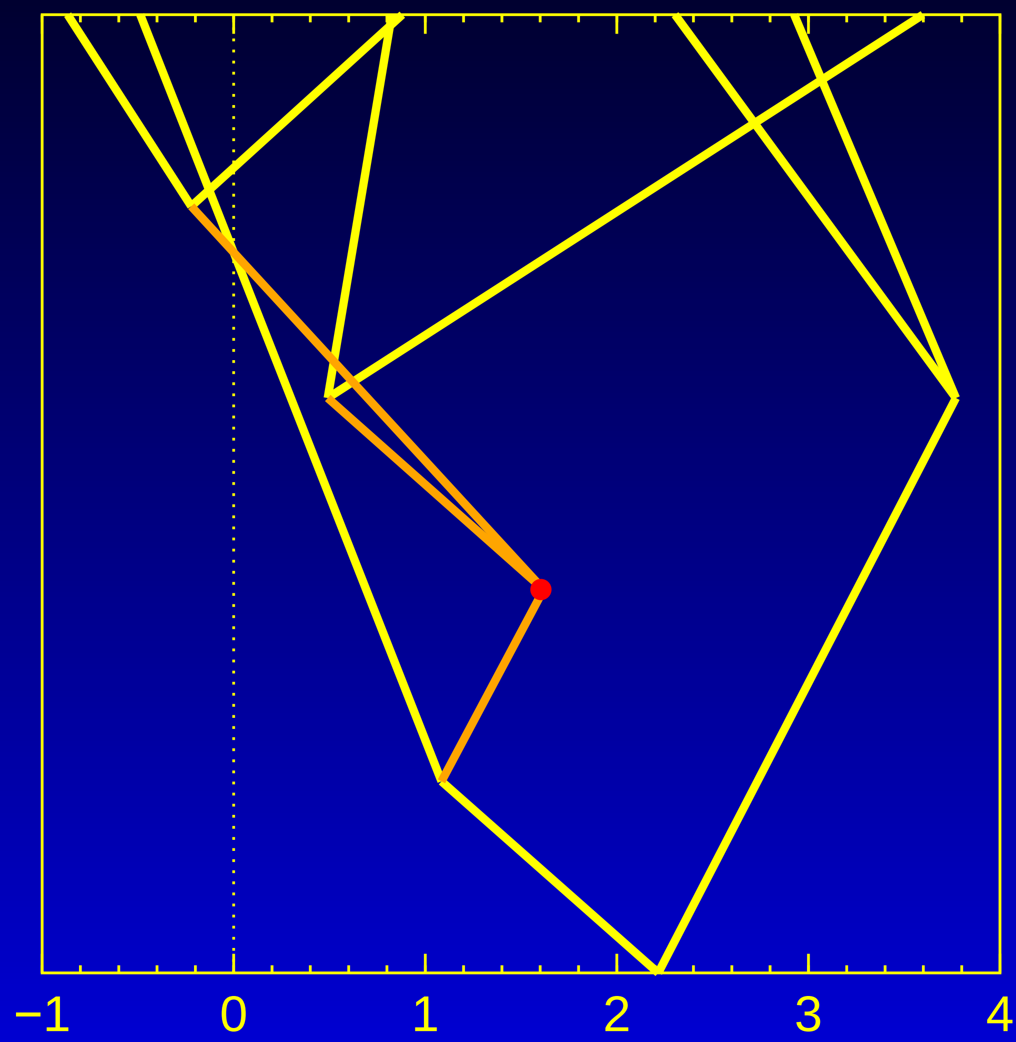

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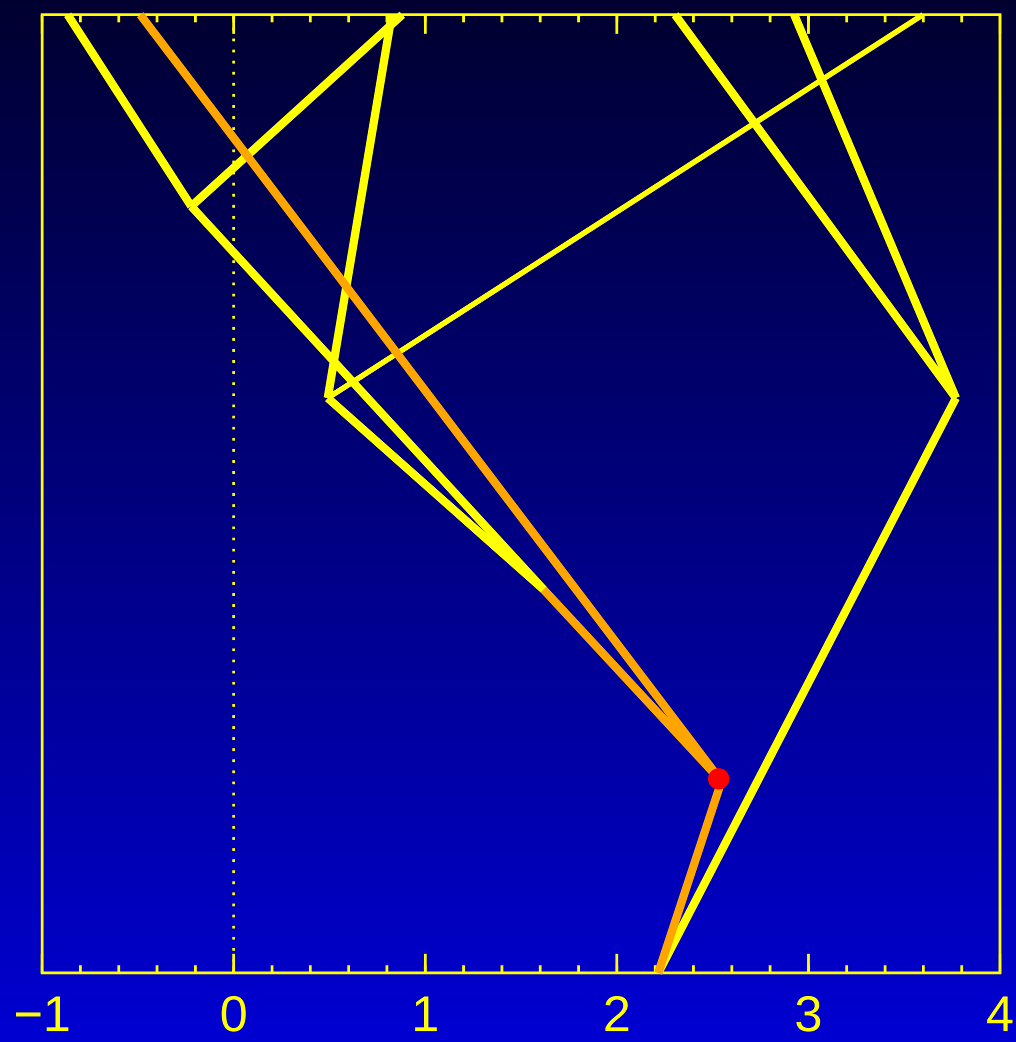

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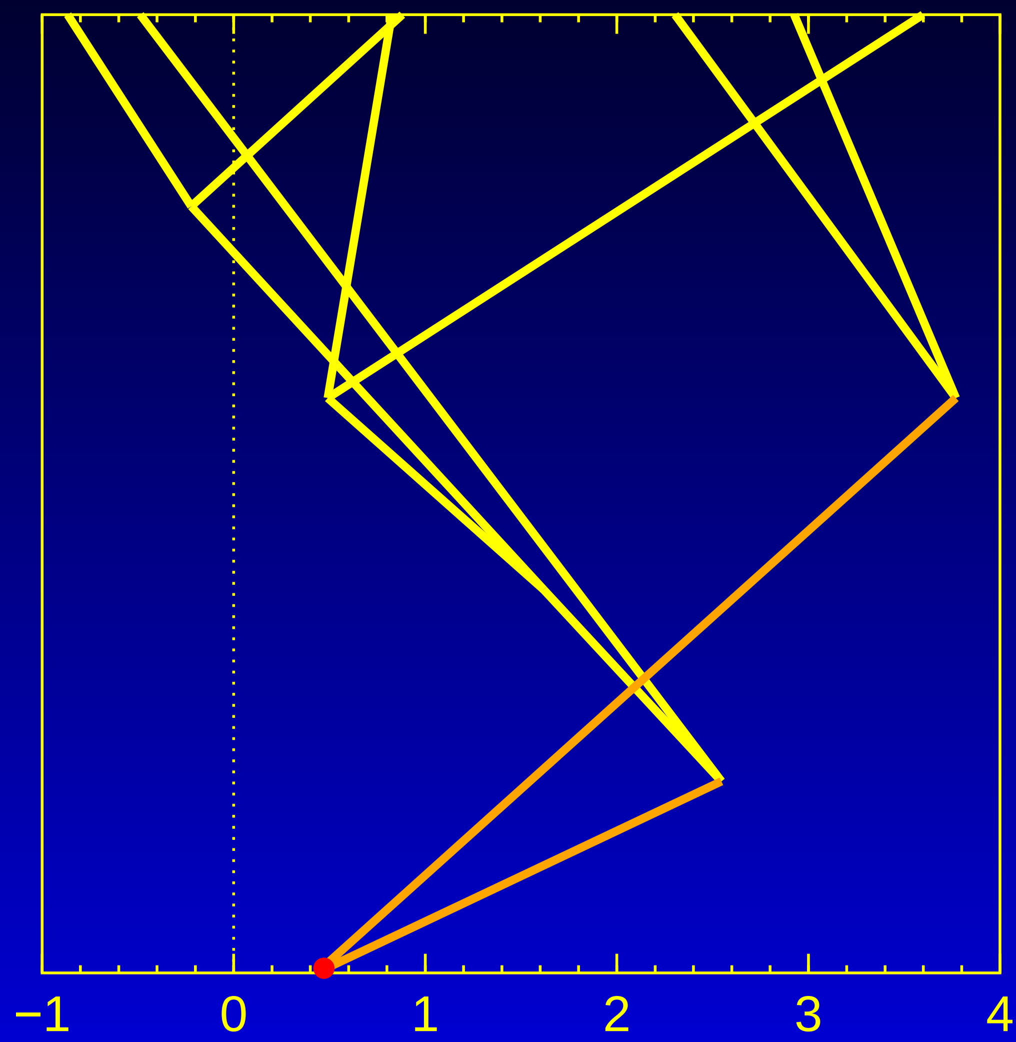
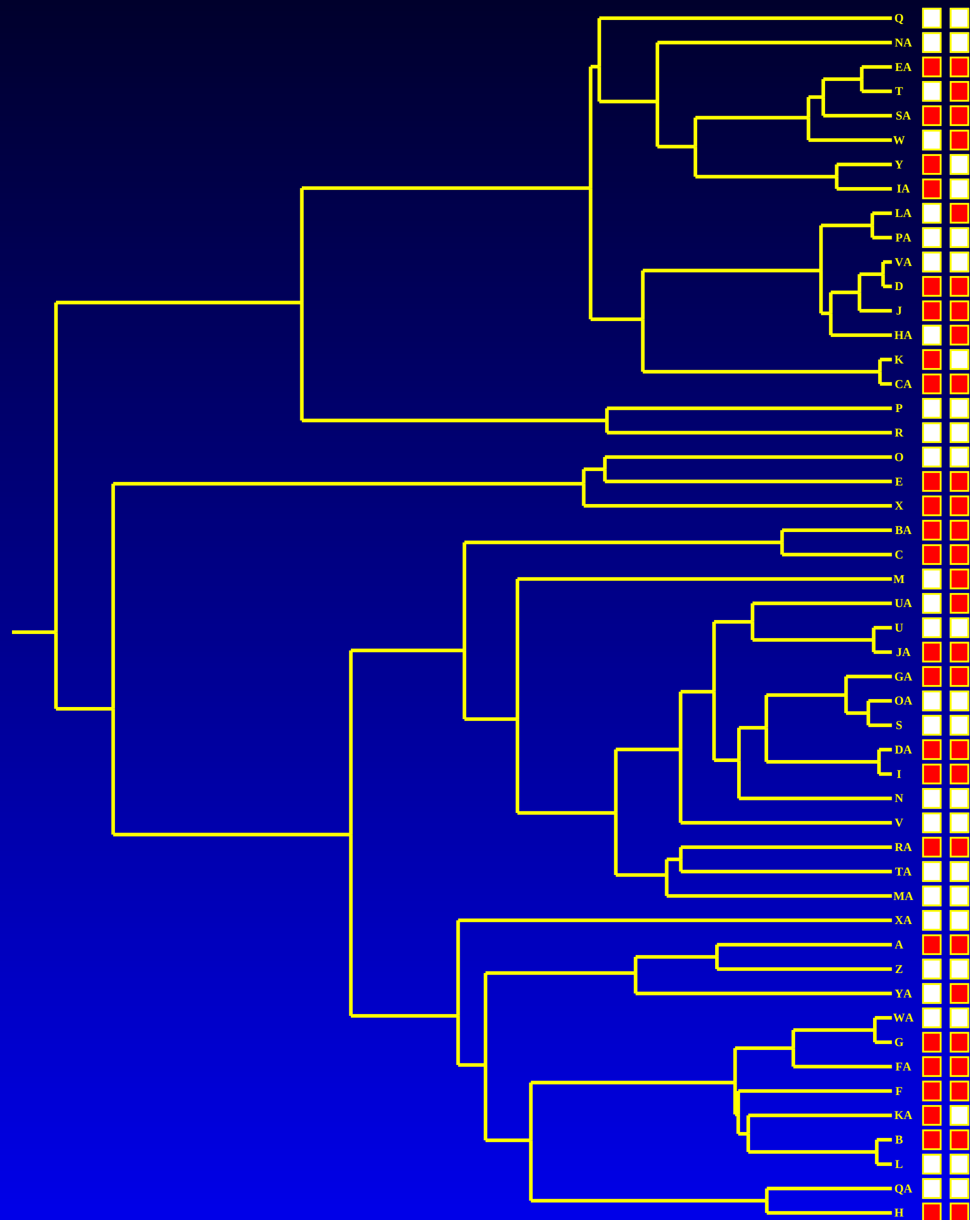


A simulated example, with its true tree



A (very) small-scale simulation

True covariance matrix

1	0.8	0
0.8	1.64	-0.6
0	-0.6	1.36

With 50 species on the given tree:

For the same simulated data set

Run 1			Run 2		
1.70072	1.39356	0.39289	1.68167	1.40056	0.40495
1.39356	1.65104	0.20923	1.40056	1.67836	0.23021
0.39289	0.20923	1.08066	0.40495	0.23021	1.09550

Continuous characters too? Both?

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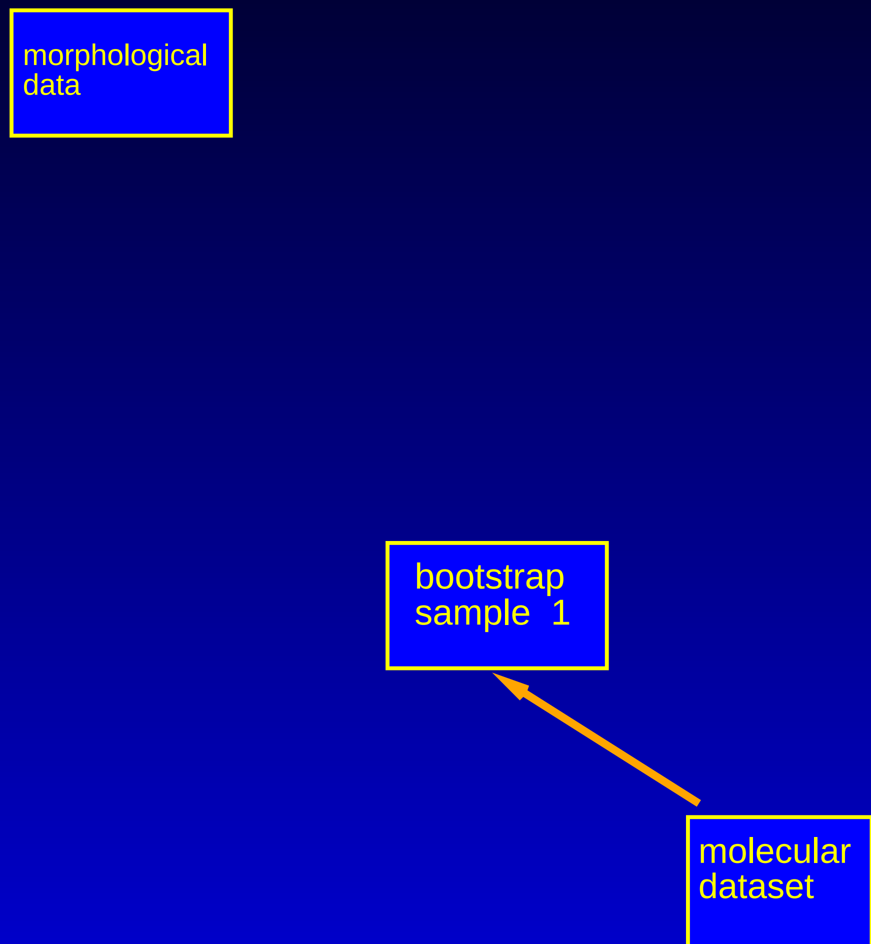
- This would be a noisier version of what we can do exactly already, so there is no point to it, right?
- But ... we could do both discrete and continuous characters together in this way, with almost no extra effort.

When the tree is noisy: Propagating bootstrap sampling

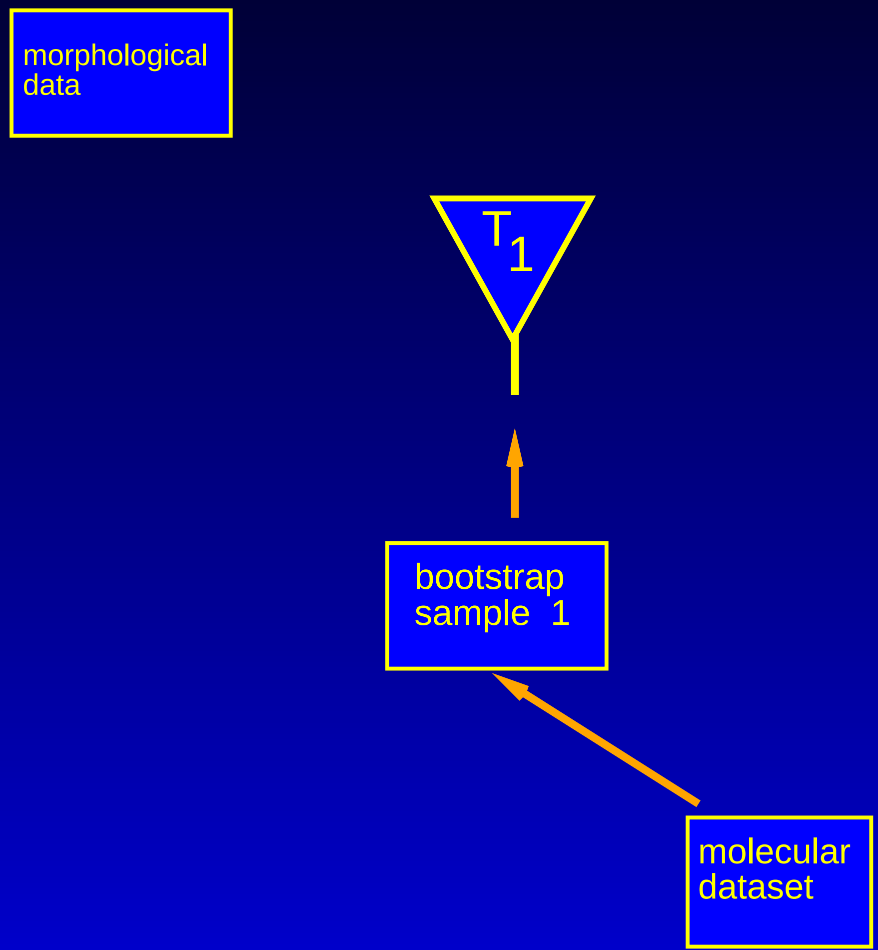
morphological
data

molecular
dataset

Propagating bootstrap sampling



Propagating bootstrap sampling



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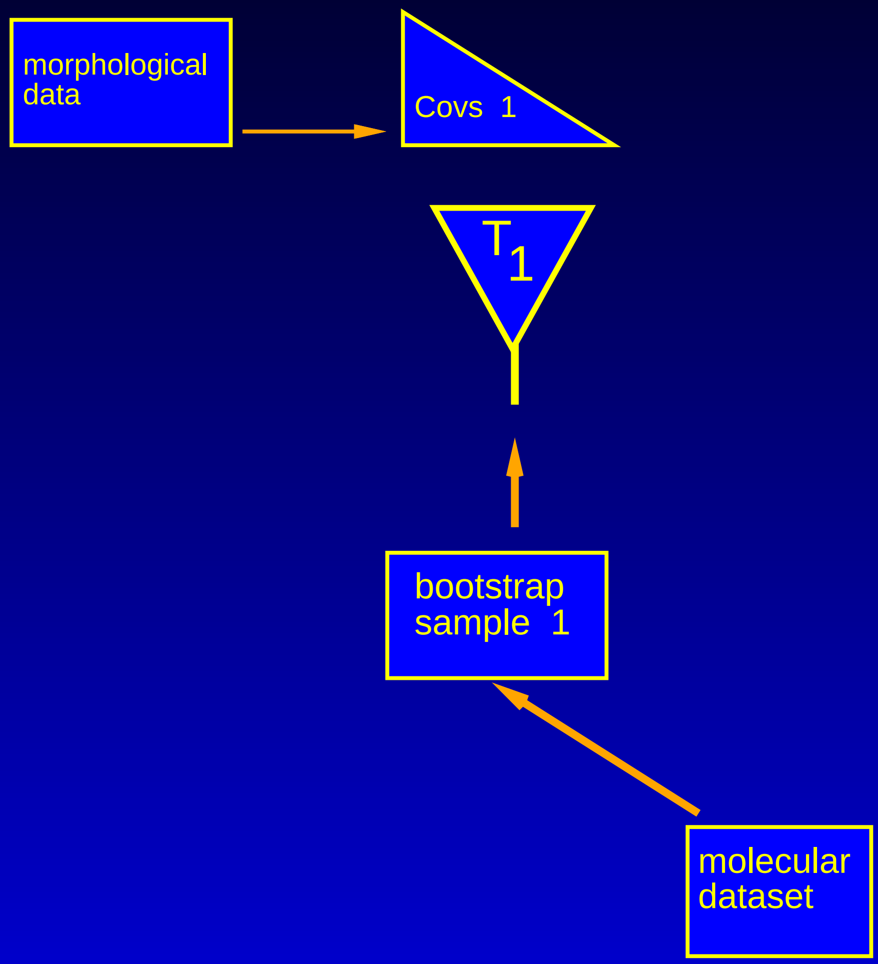

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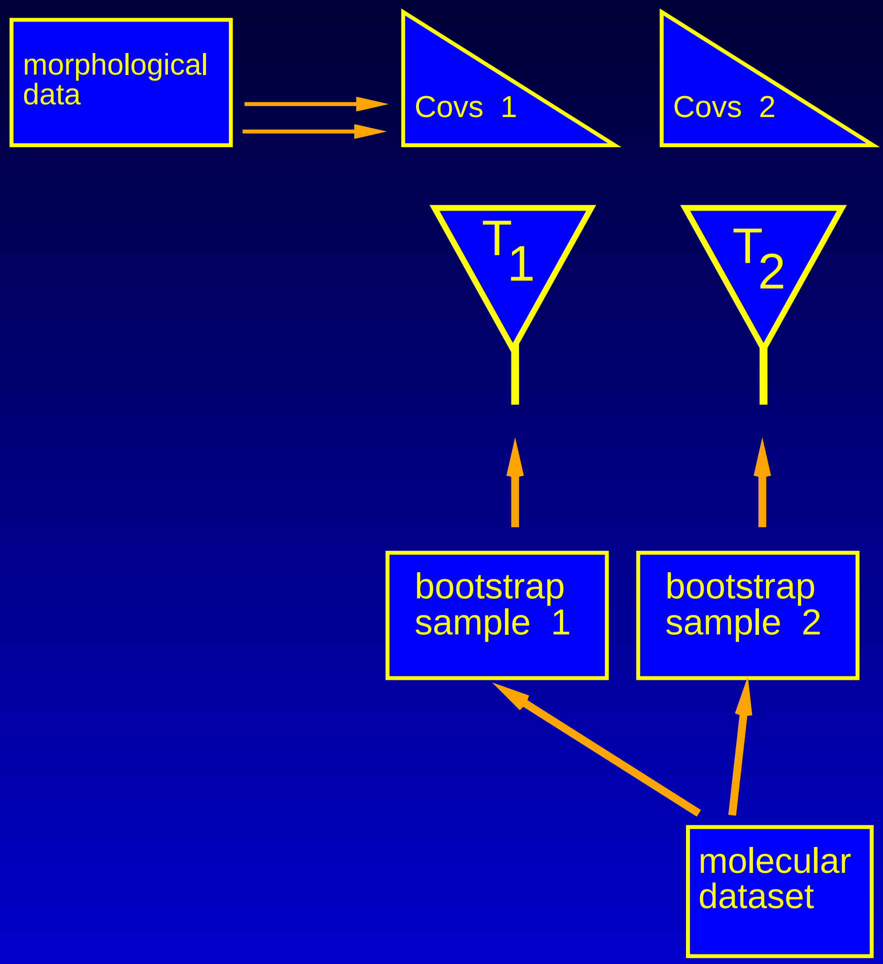

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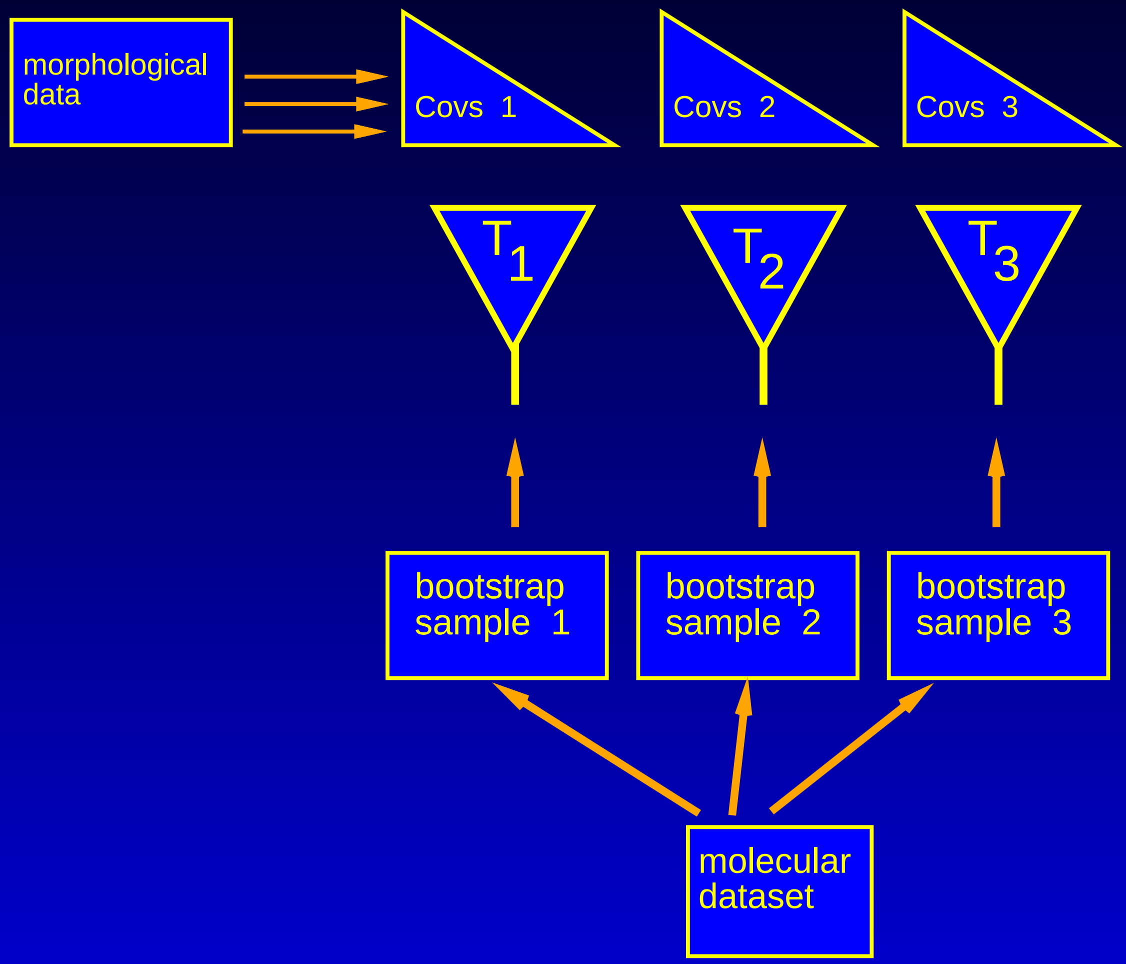

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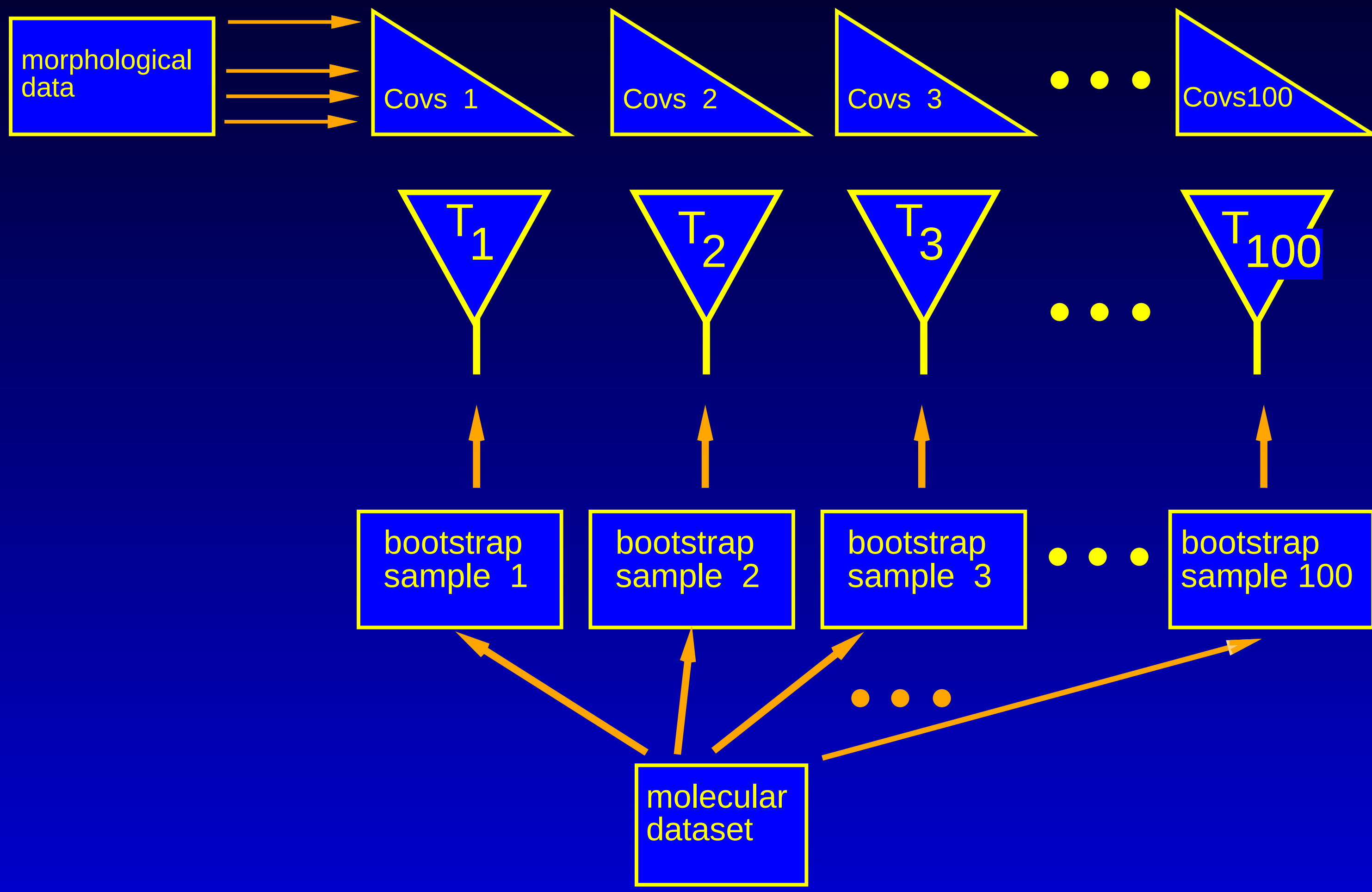
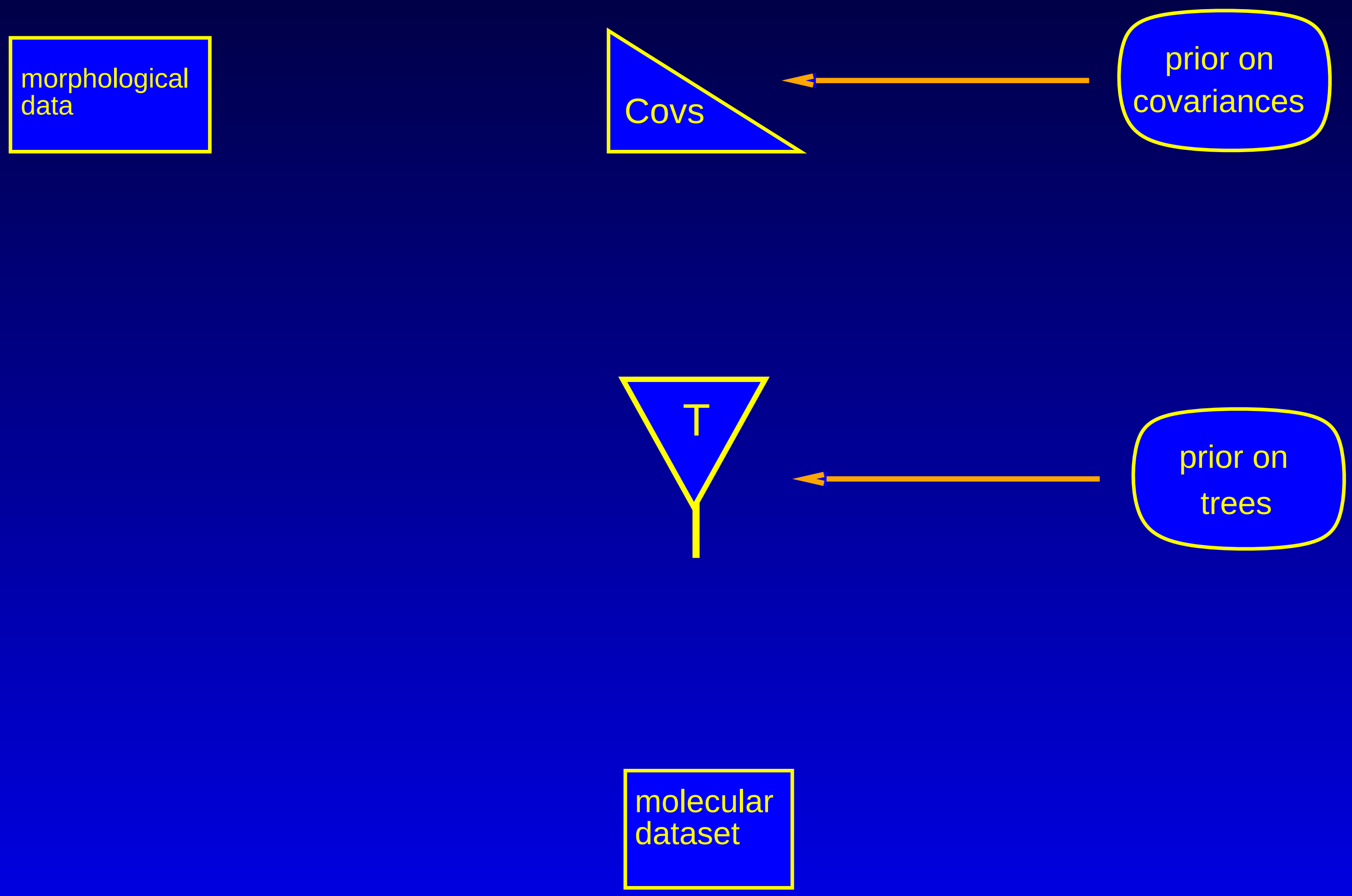


A Bayesian model



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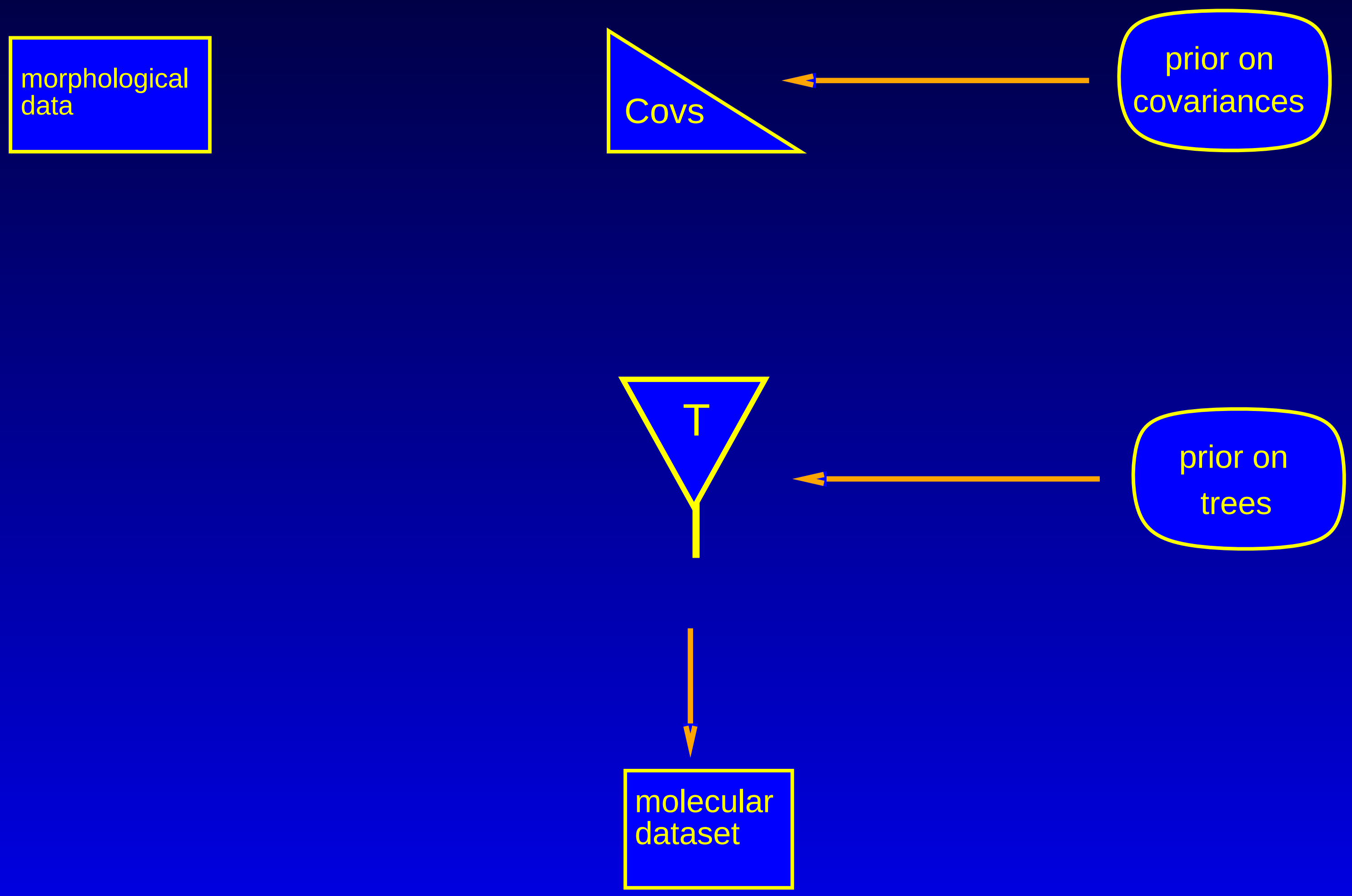

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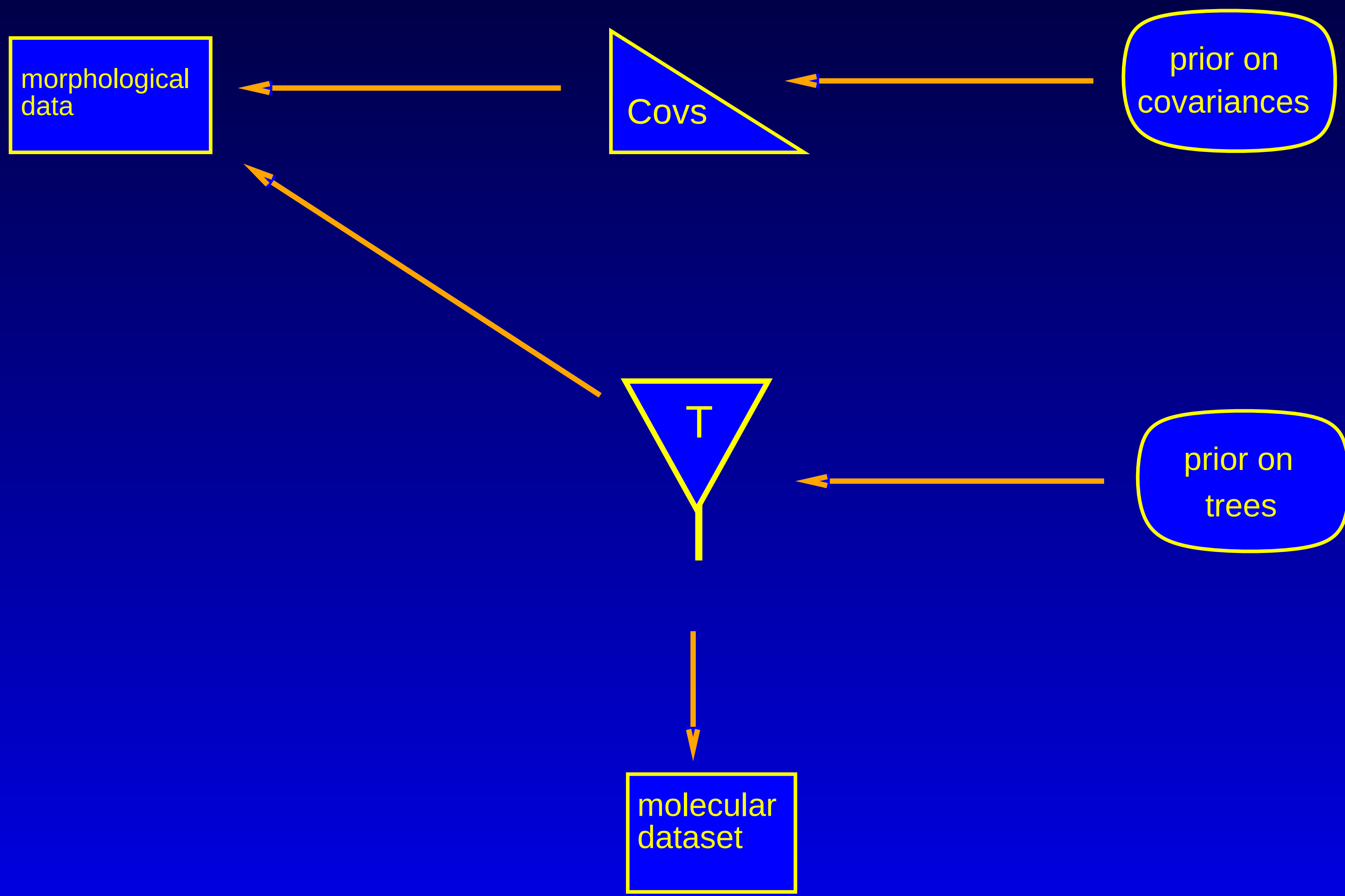
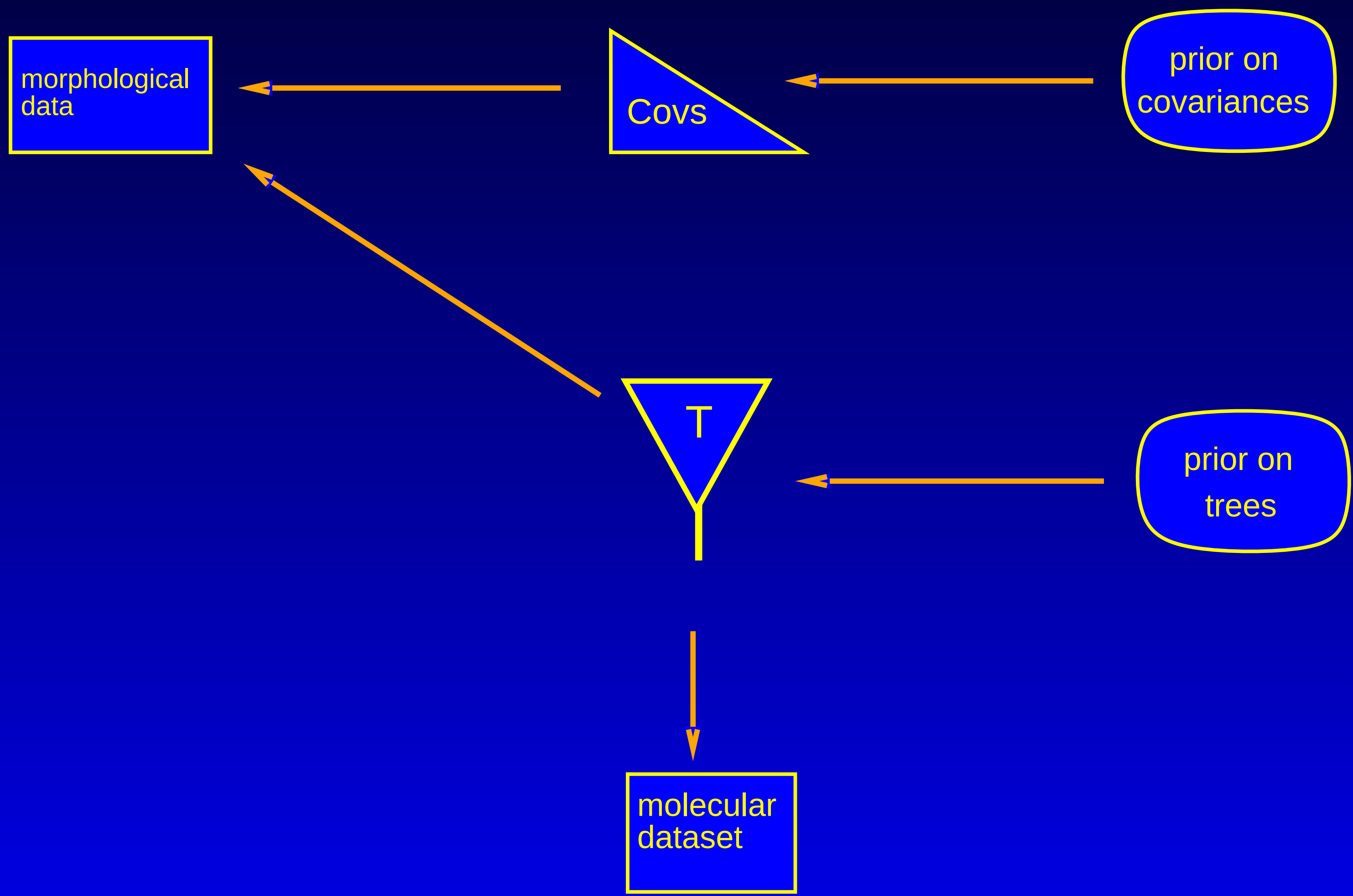


Bayesian MCMC

Markov Chain Monte Carlo



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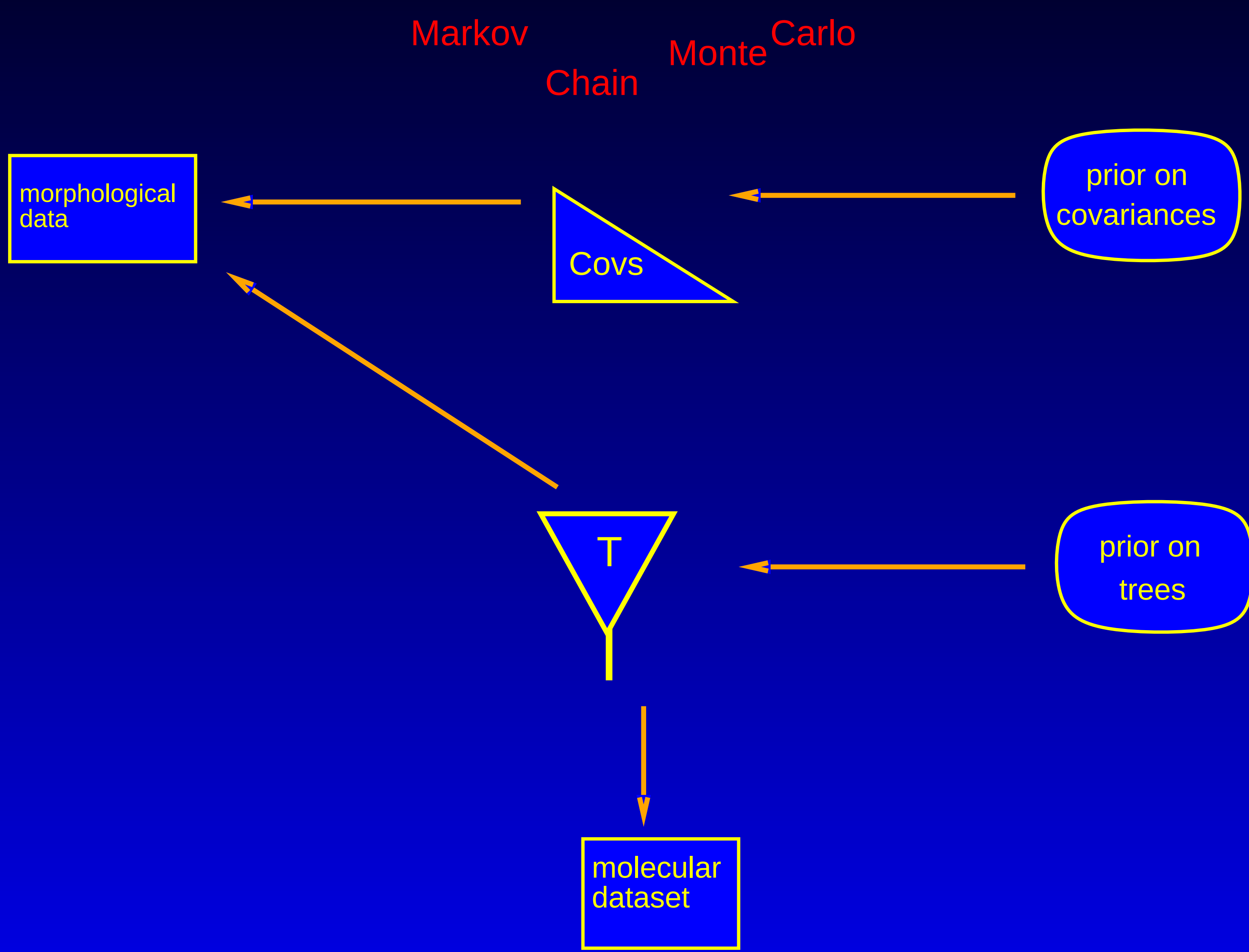

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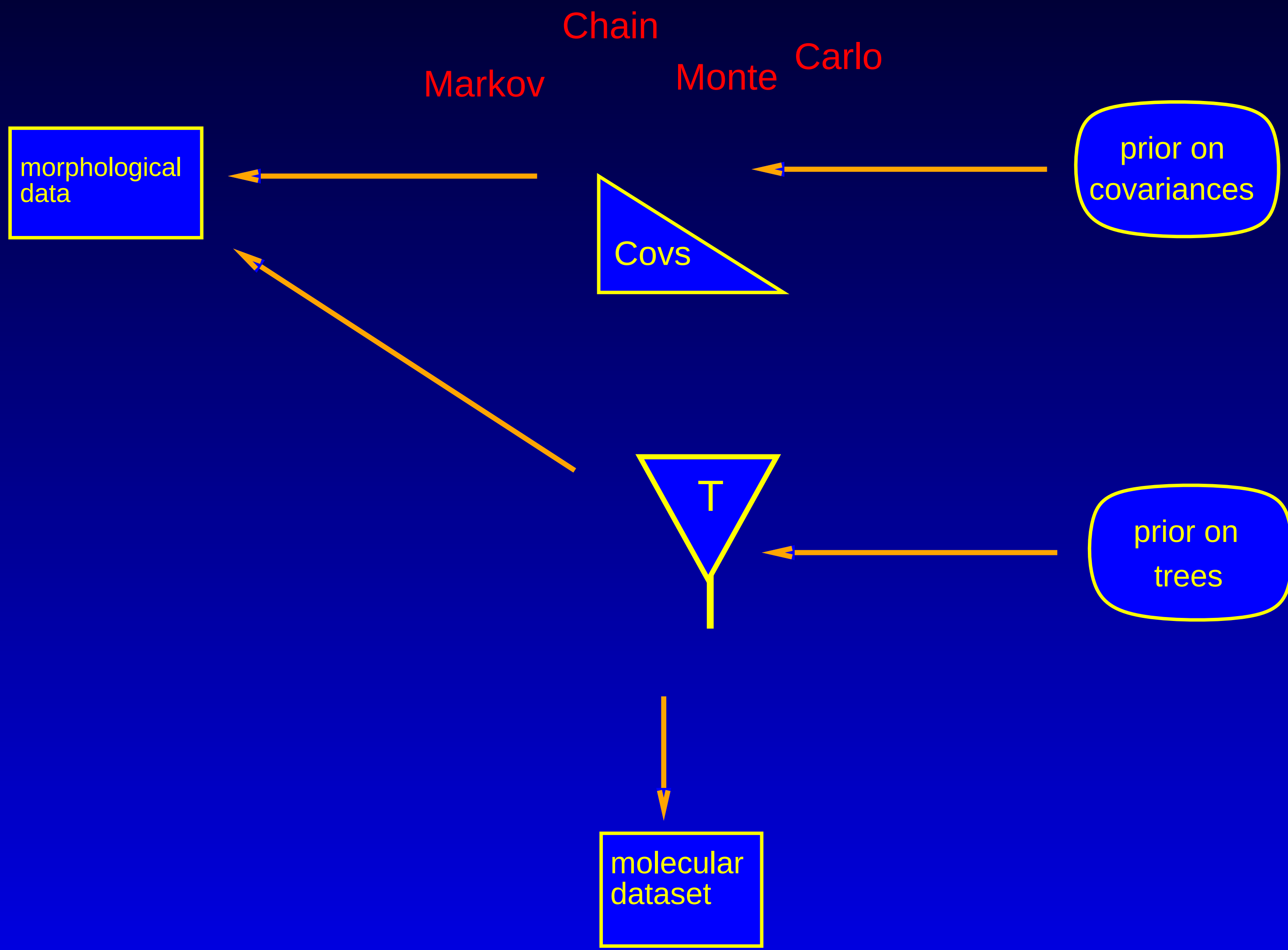

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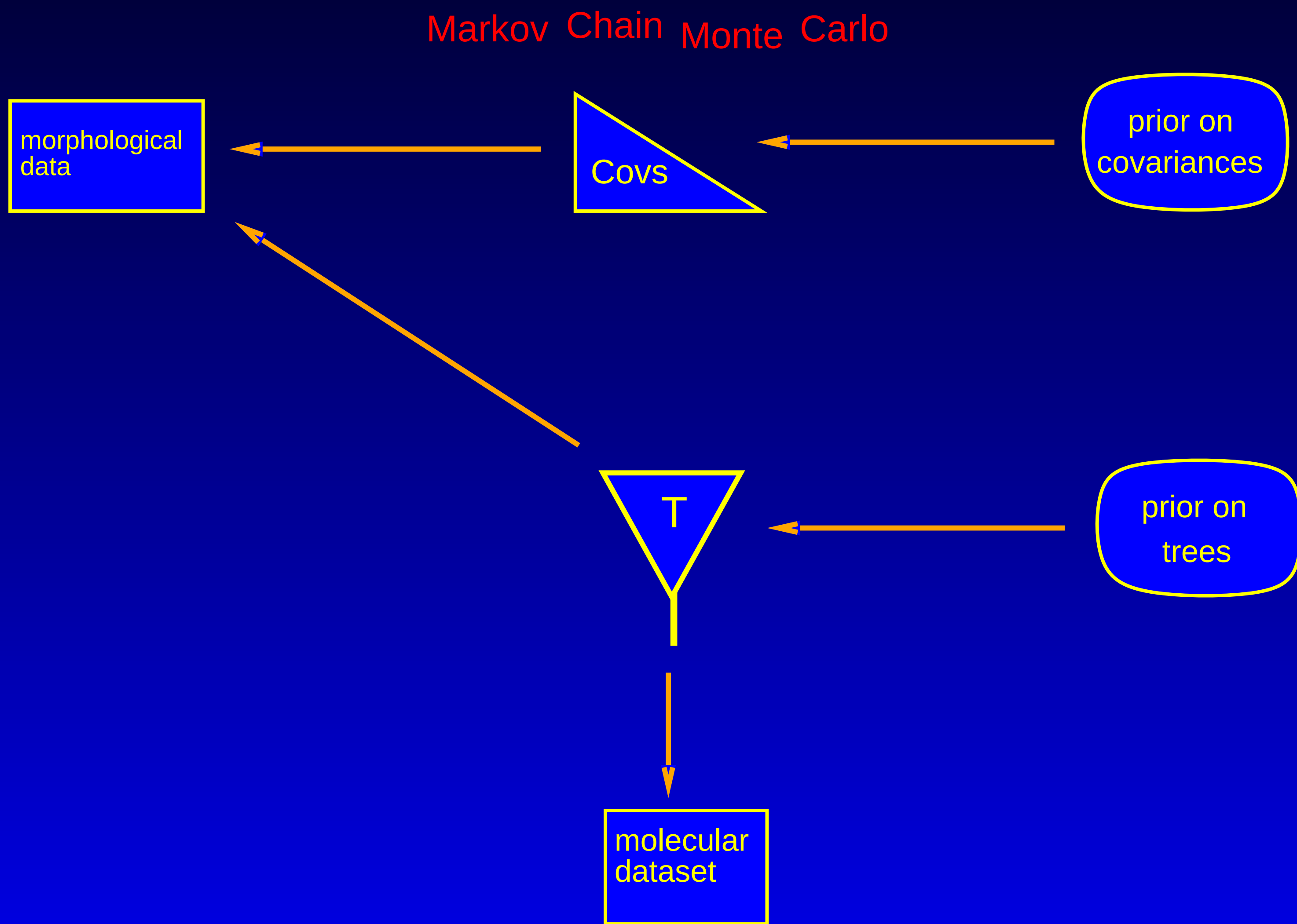
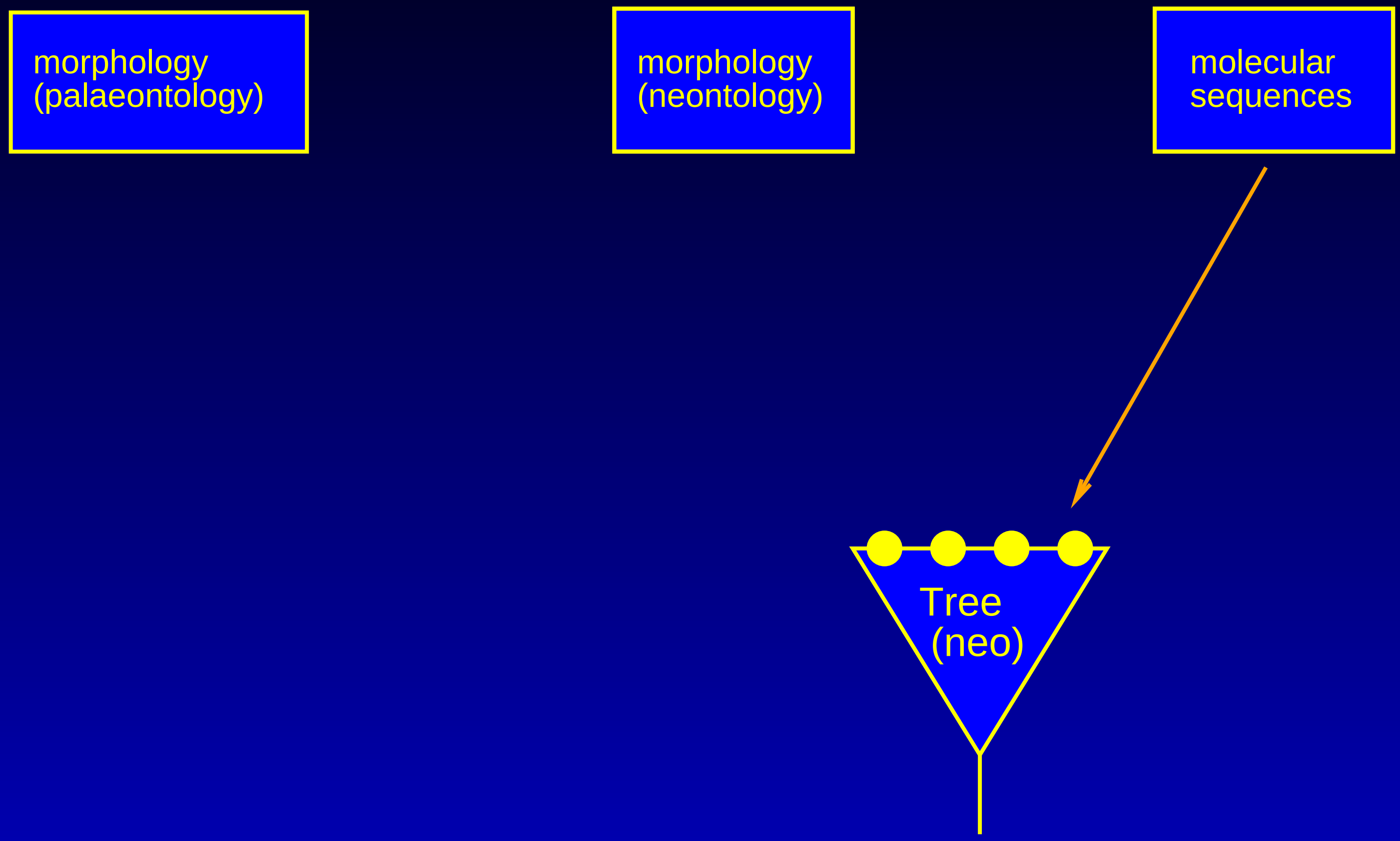
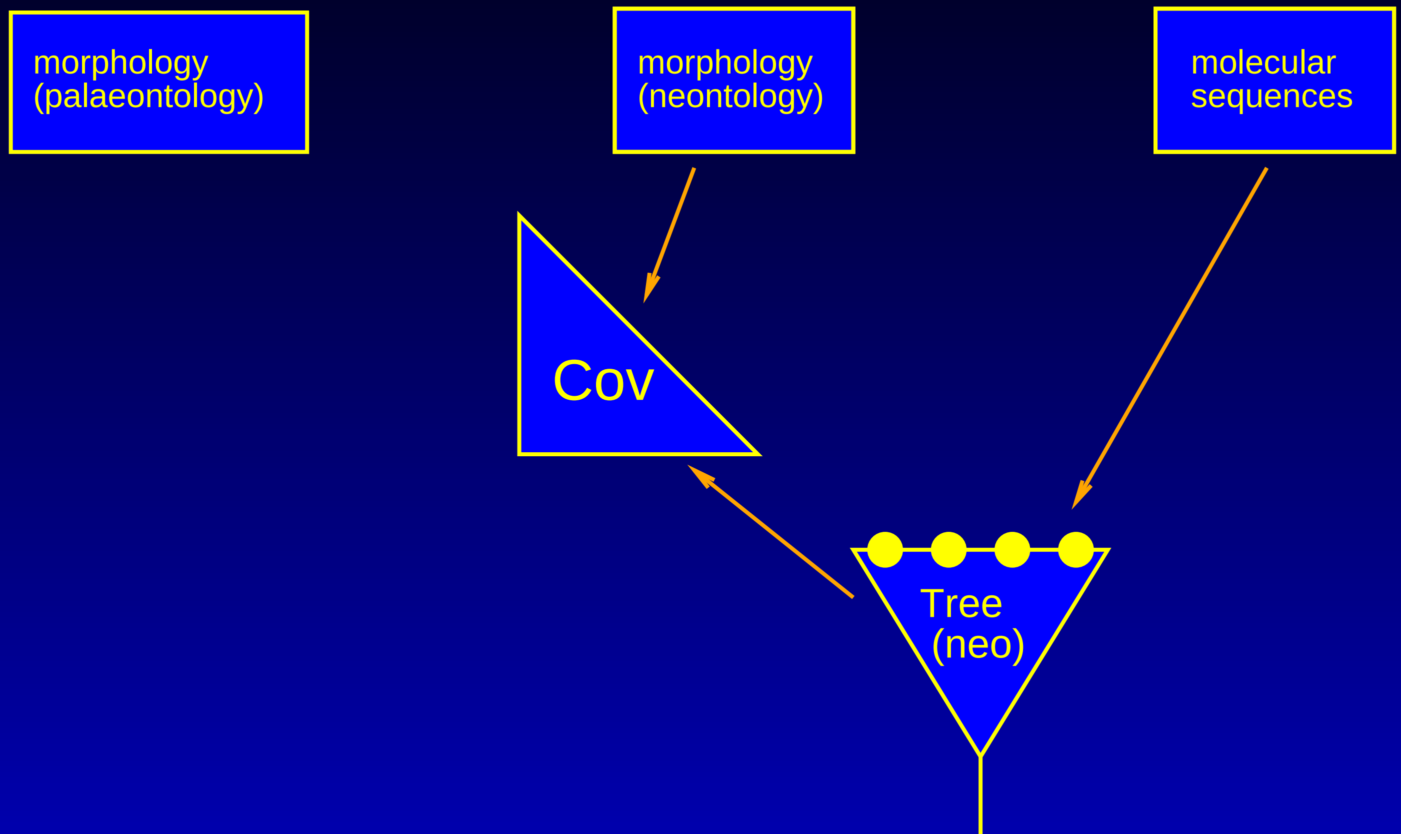


Using fossils sensibly



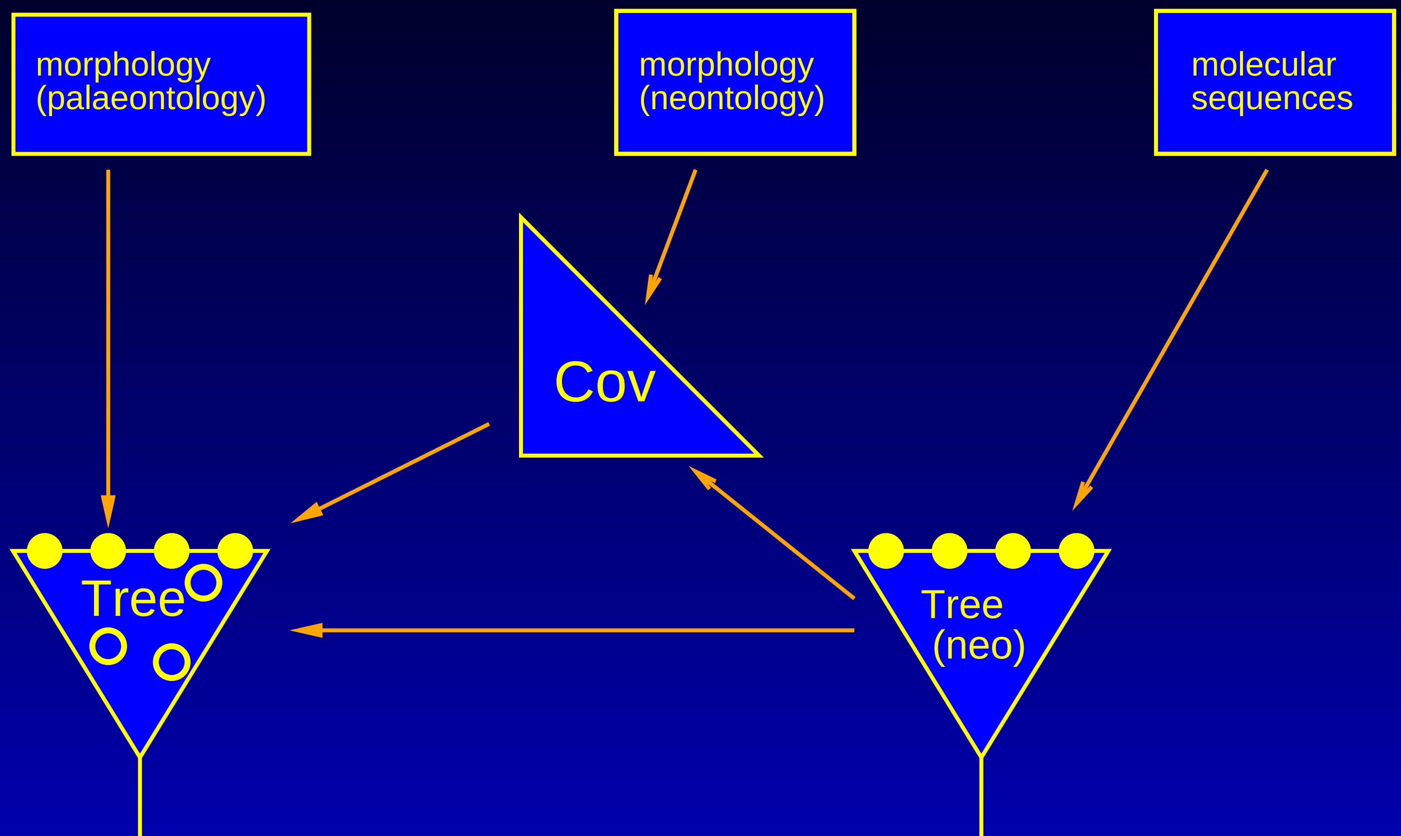
Infer tree of present-day species from molecular sequences

Using fossils sensibly



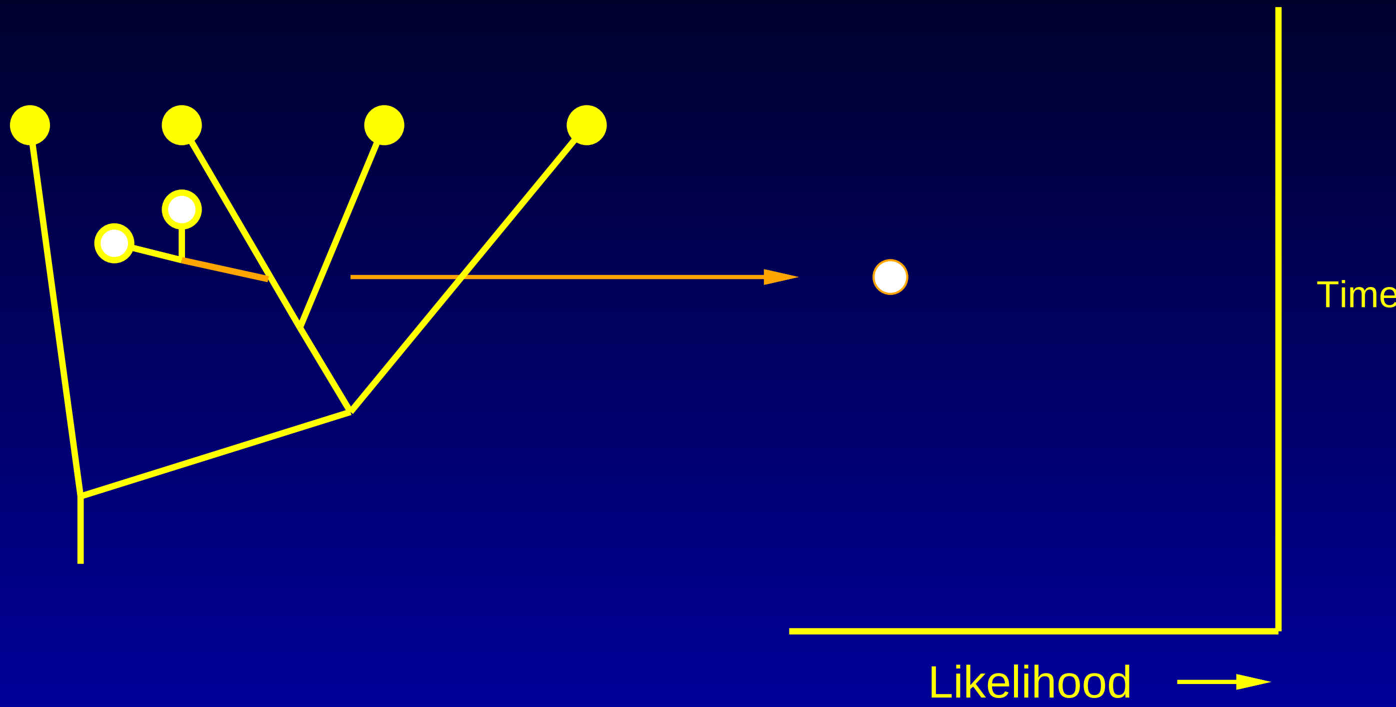
Infer covariances of morphology using it, present-day species

Using fossils sensibly



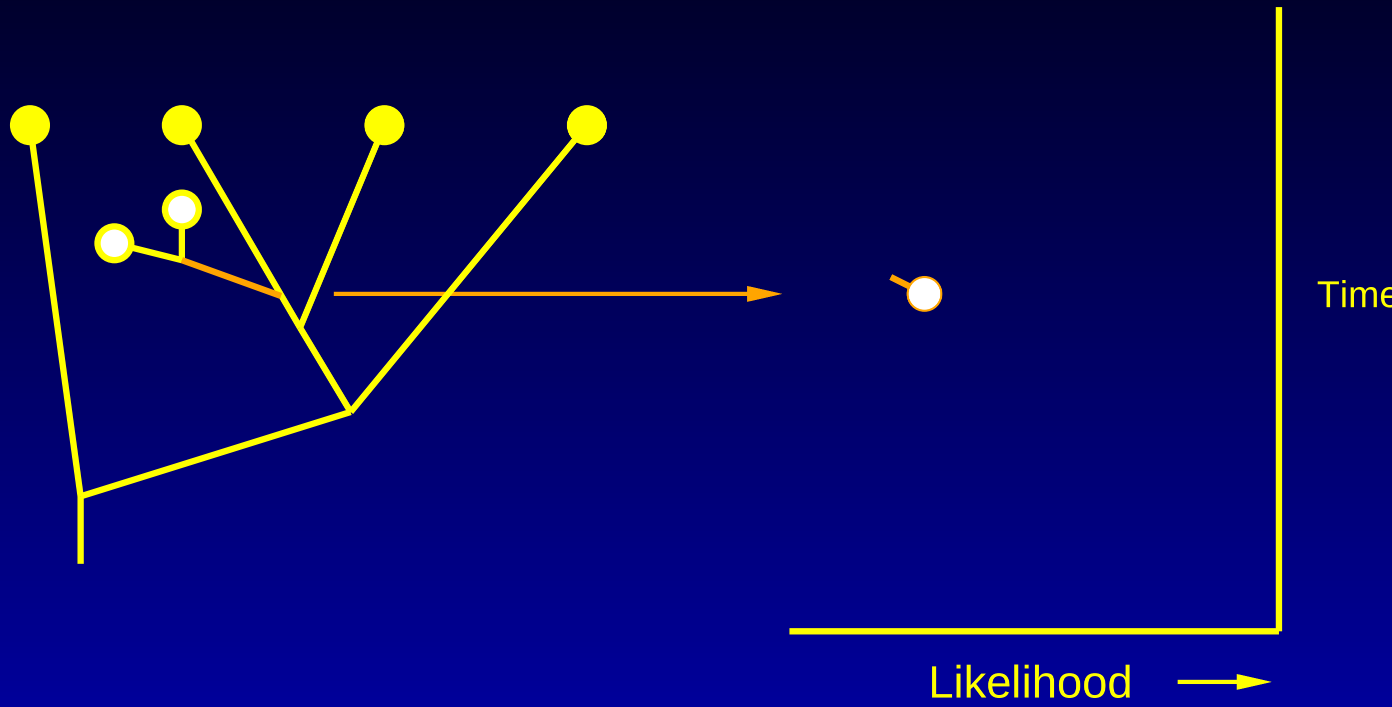
Infer placement of fossil species using their data

Using fossils sensibly



Use fossil and present-day morphology, covariances, tree, also stratigraphic models

Using fossils sensibly



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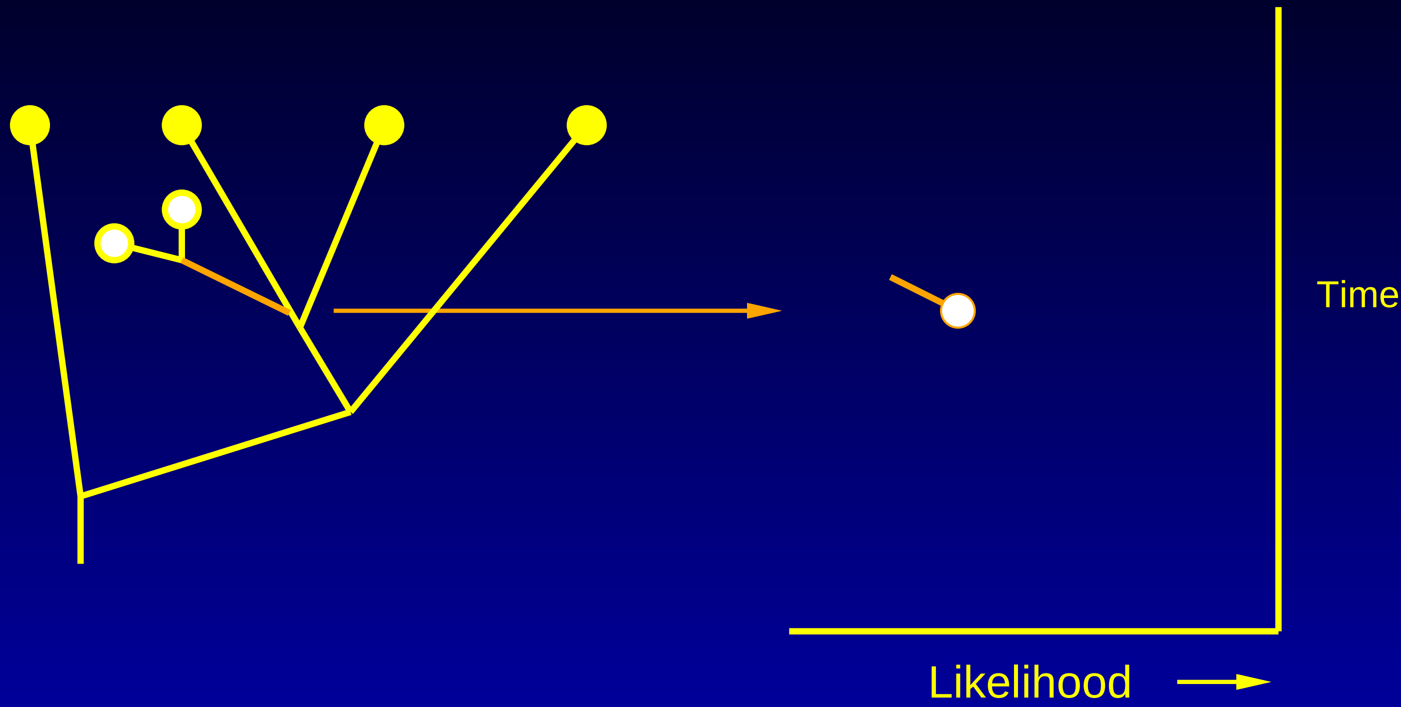

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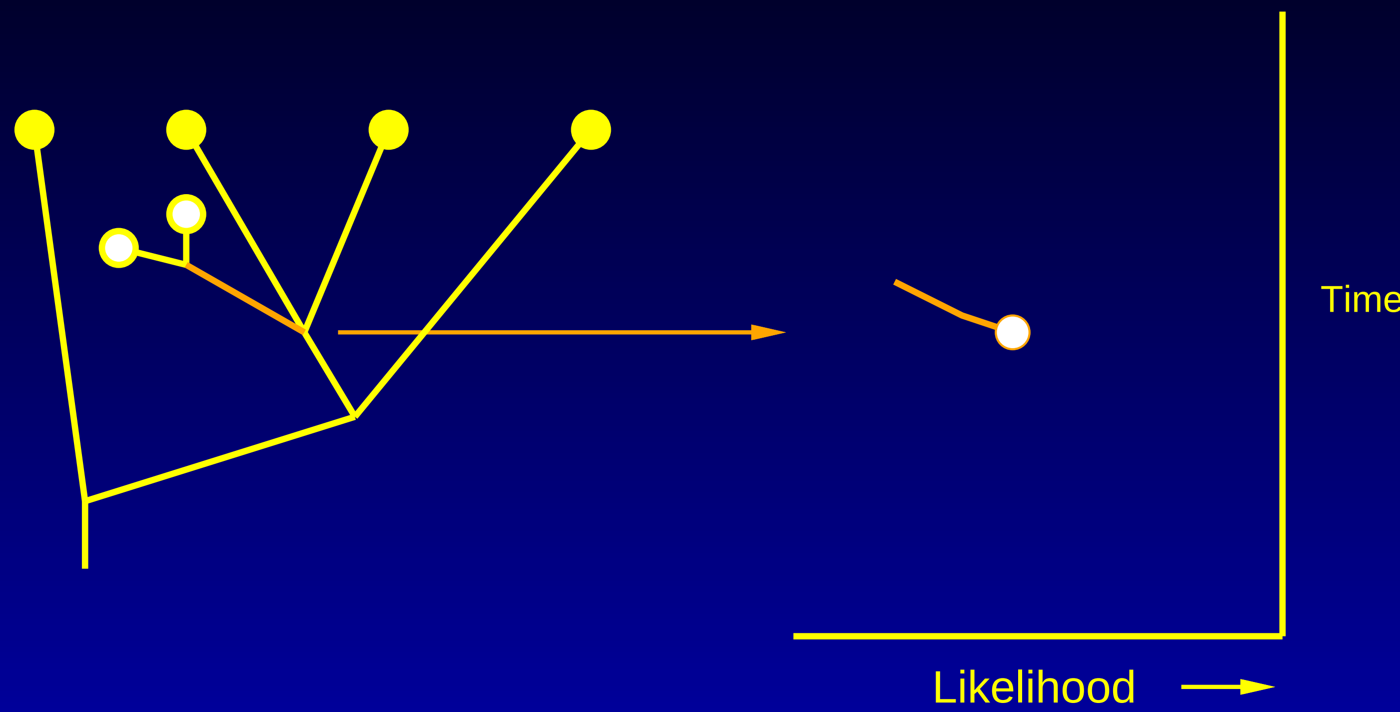

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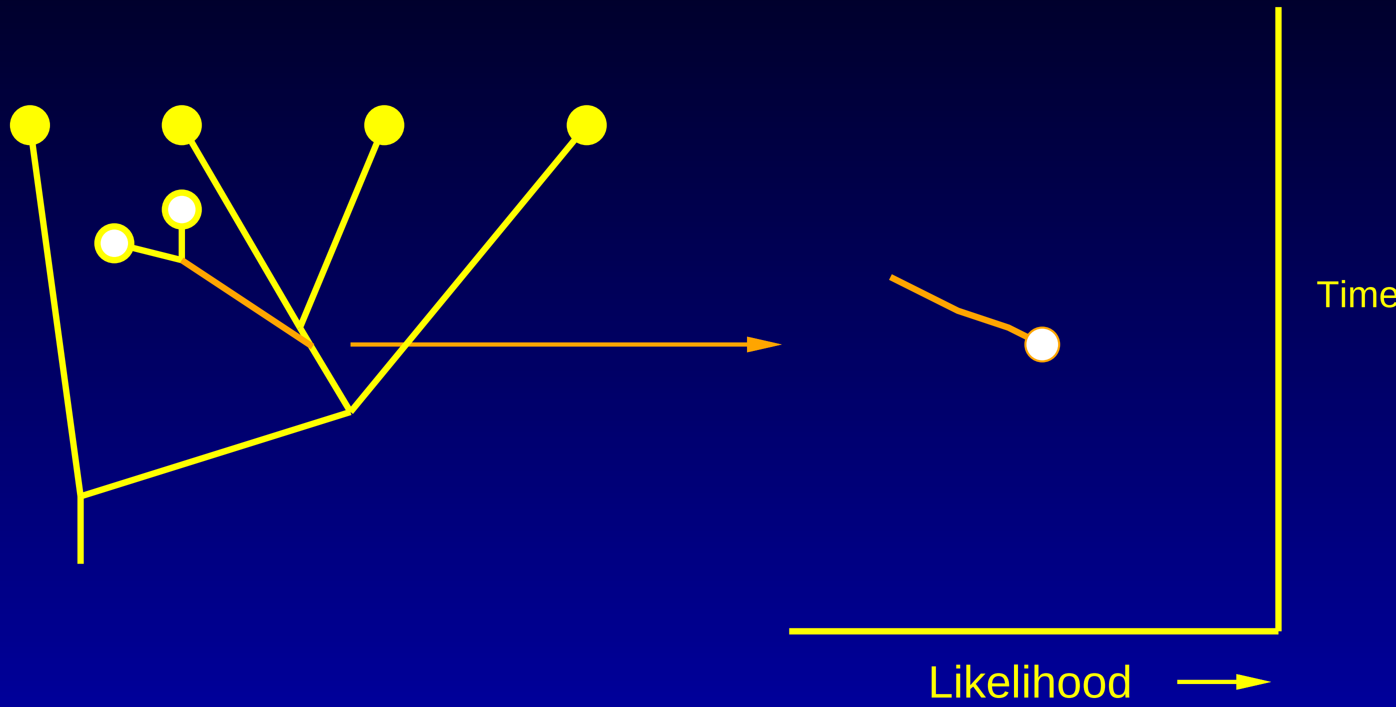

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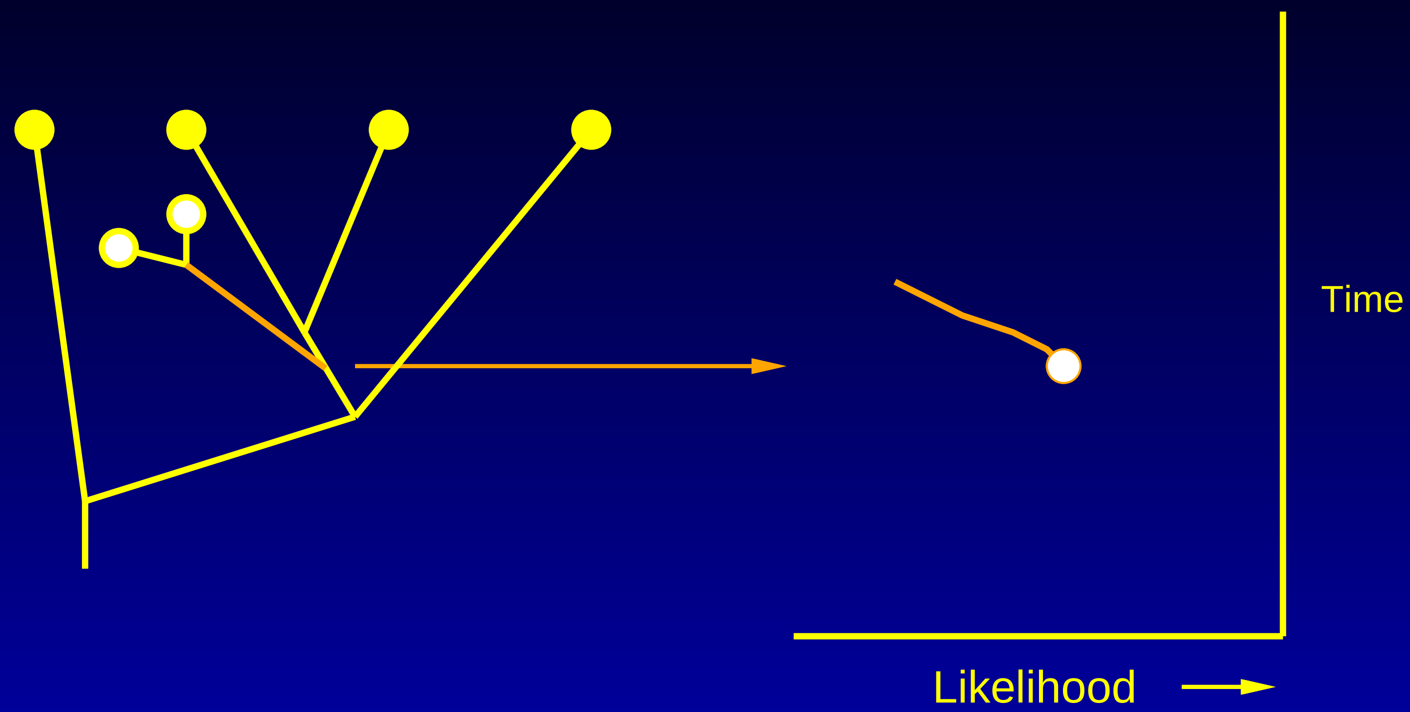

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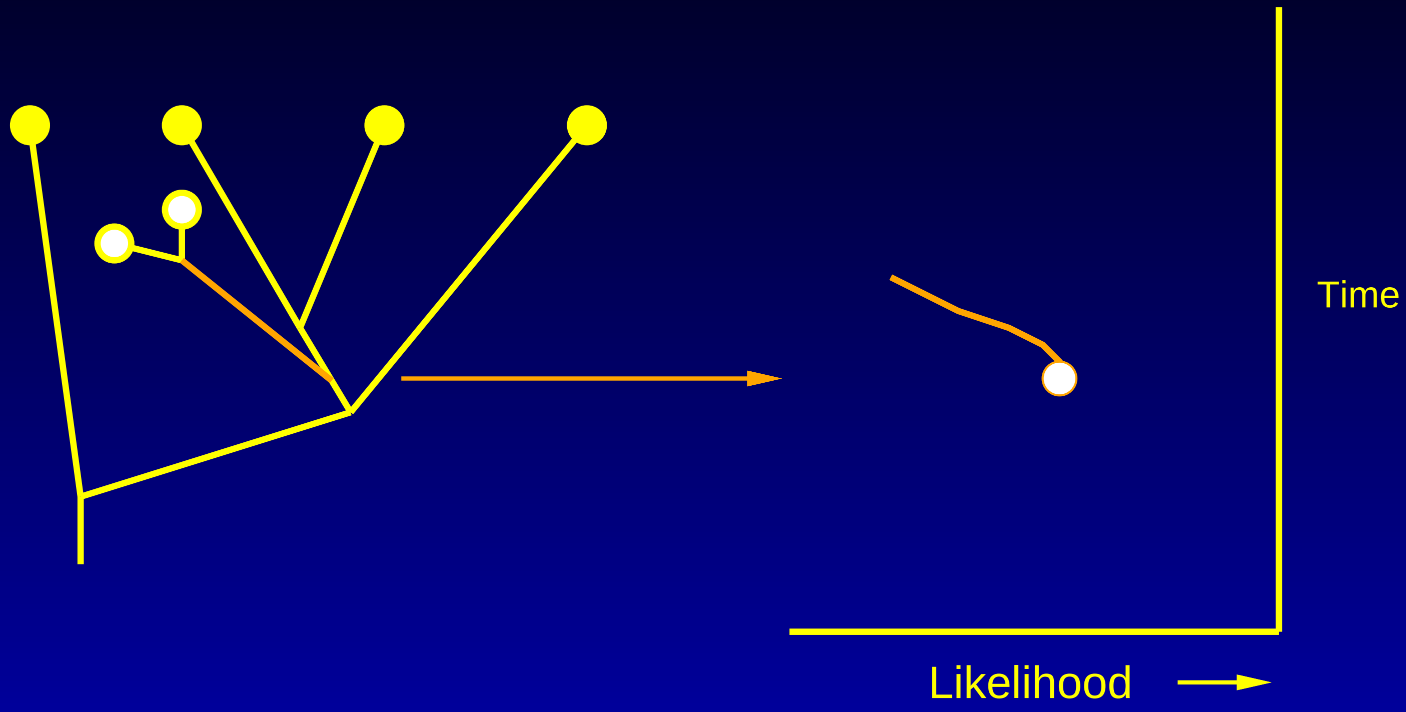

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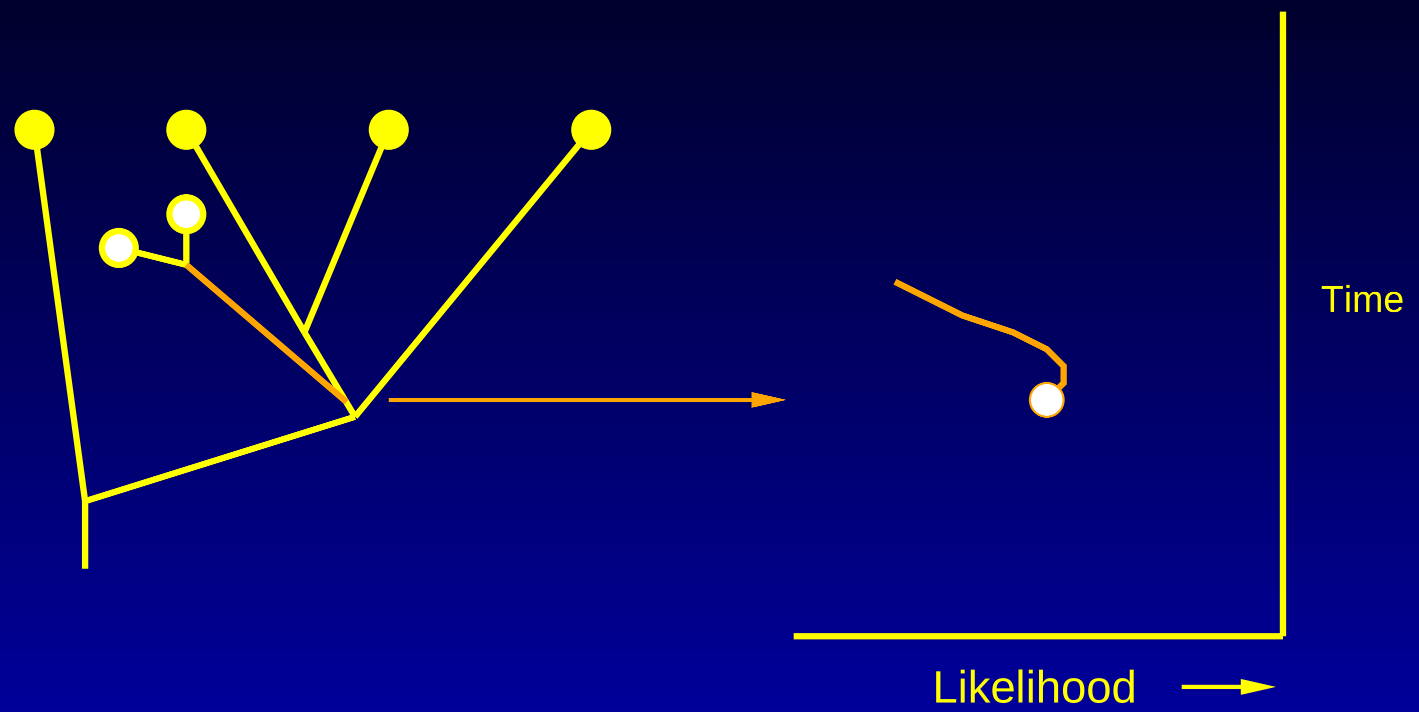

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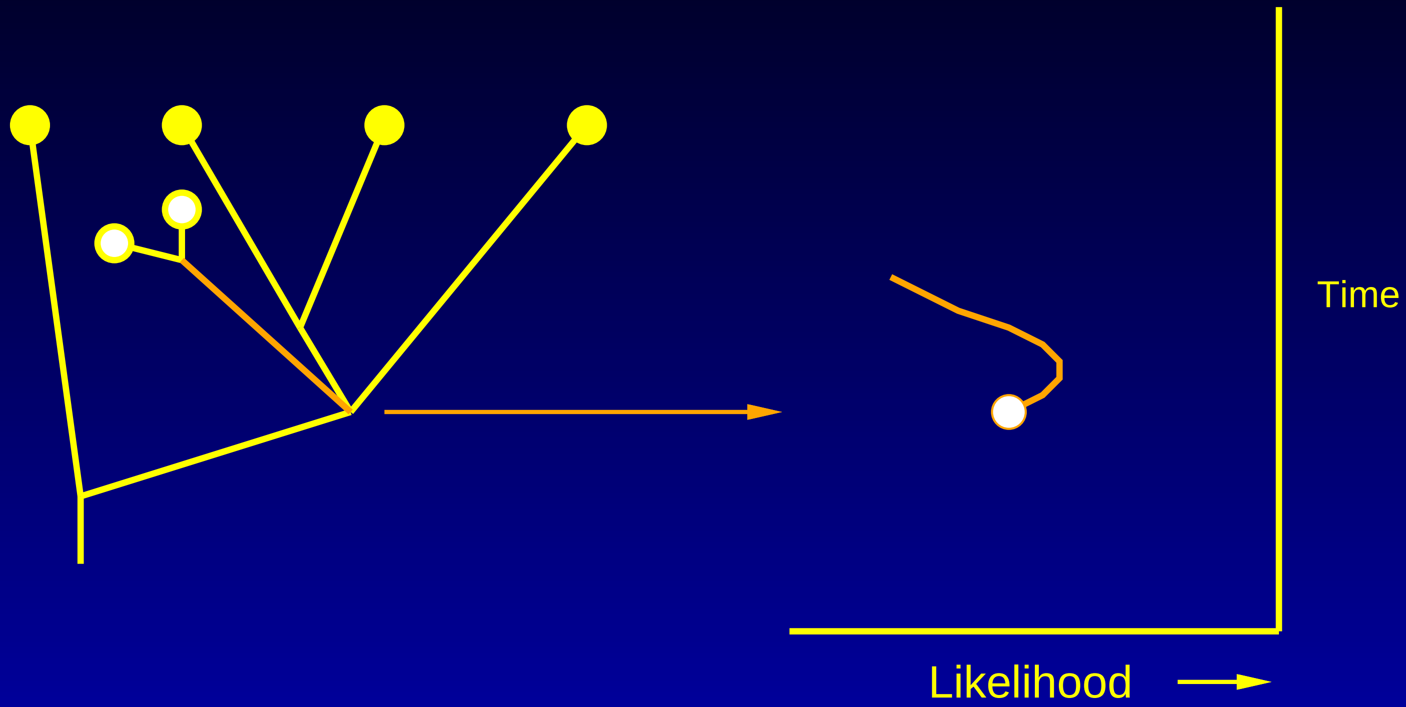

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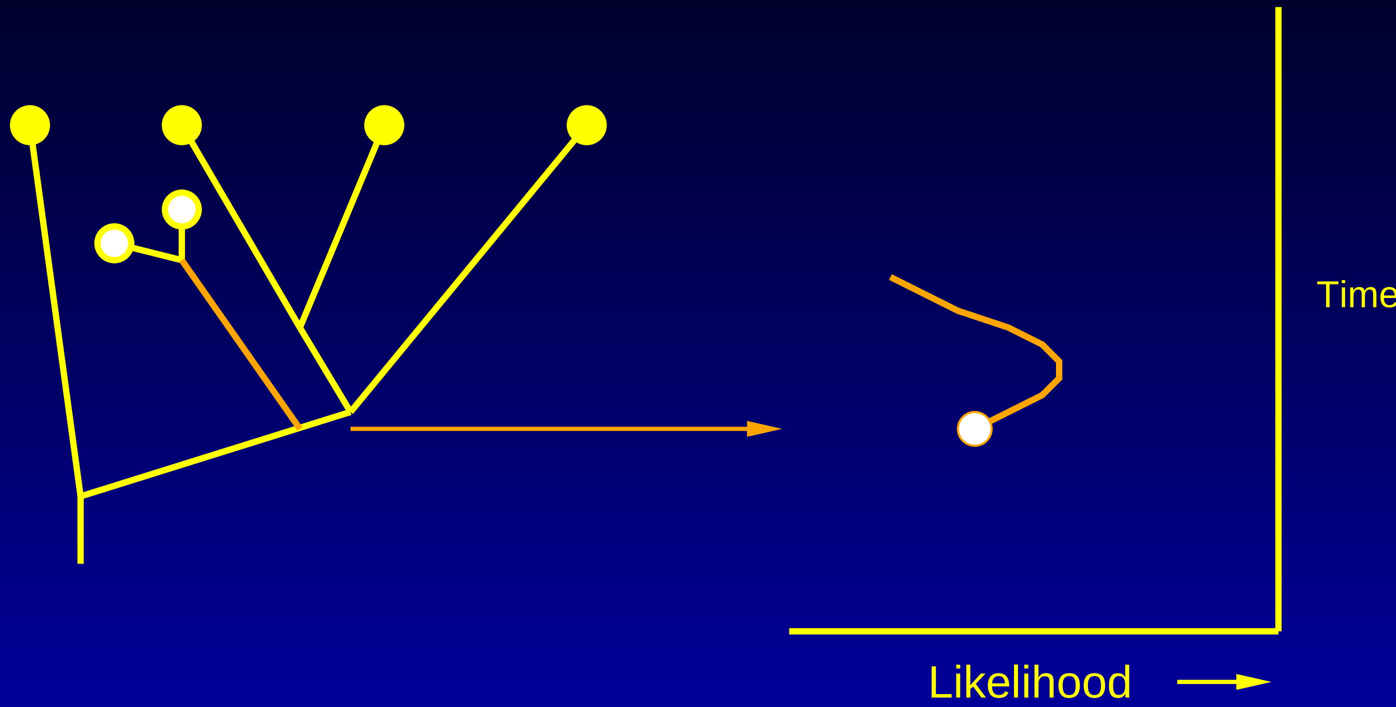

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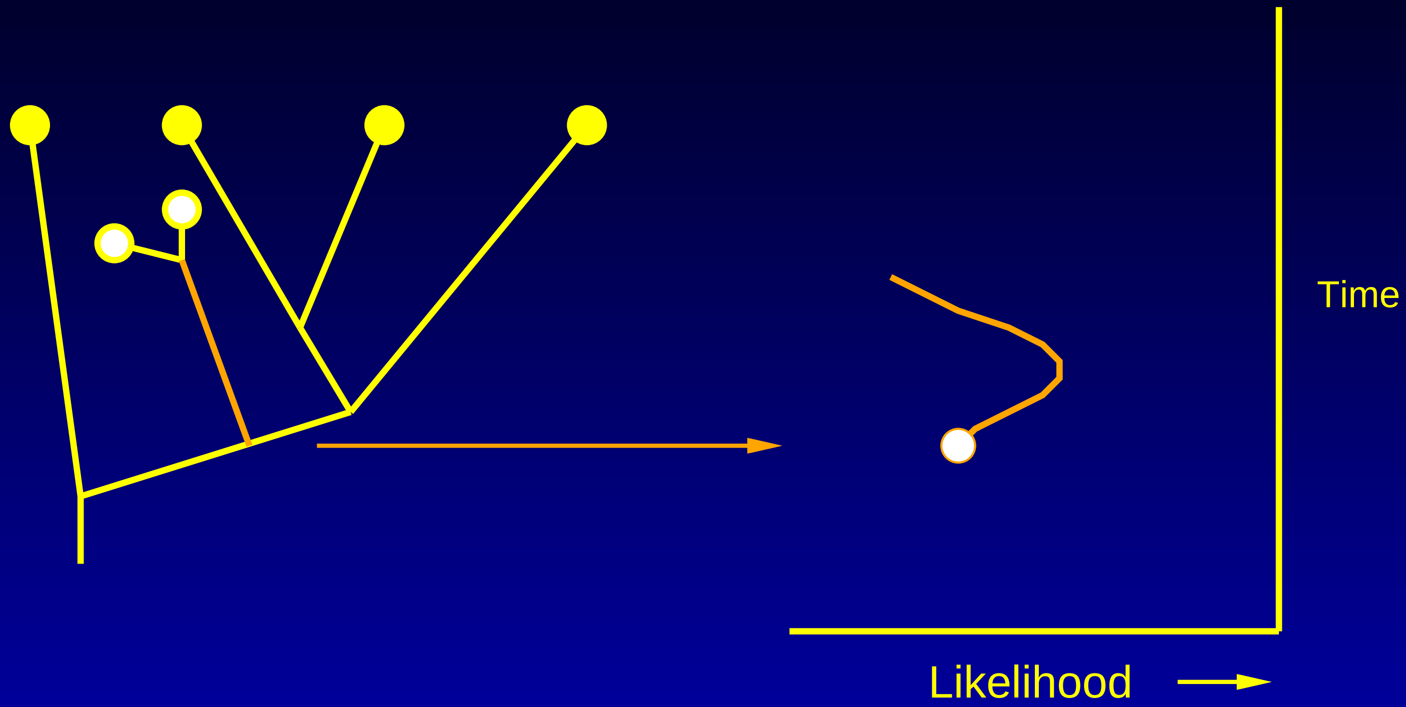

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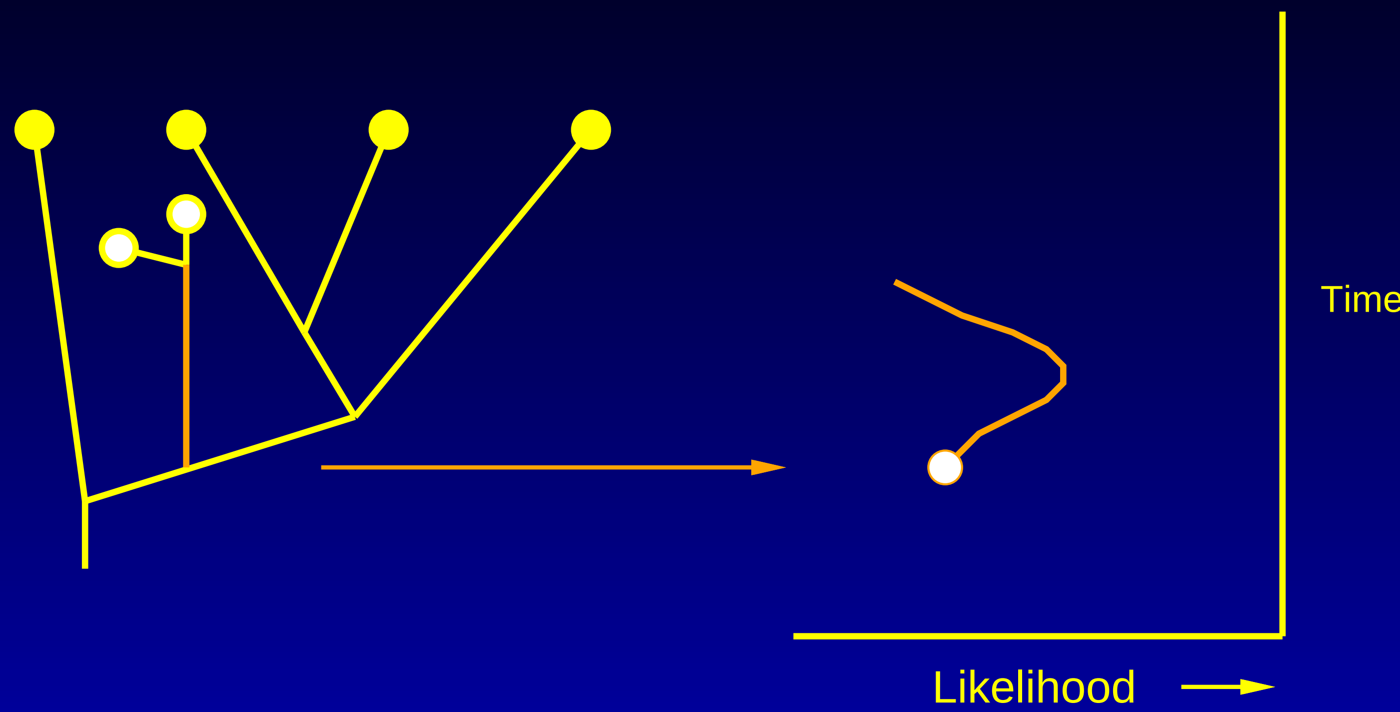

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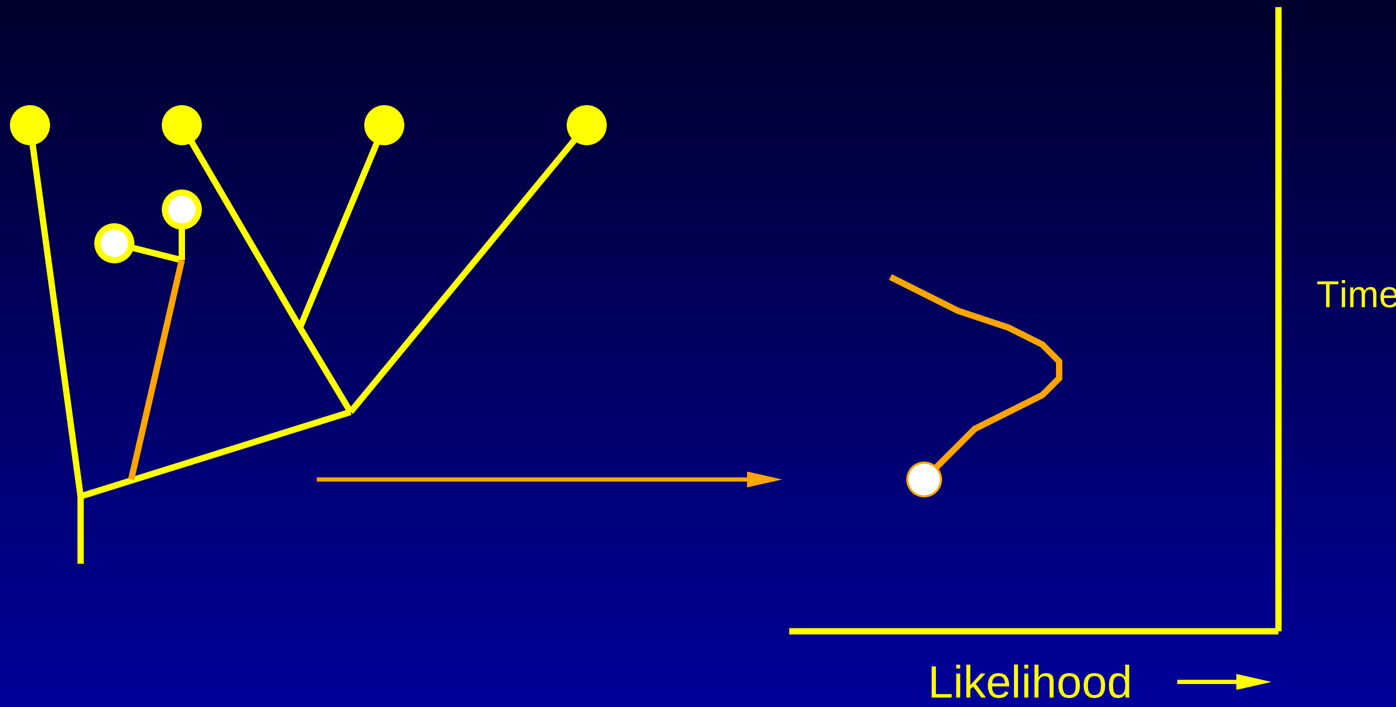

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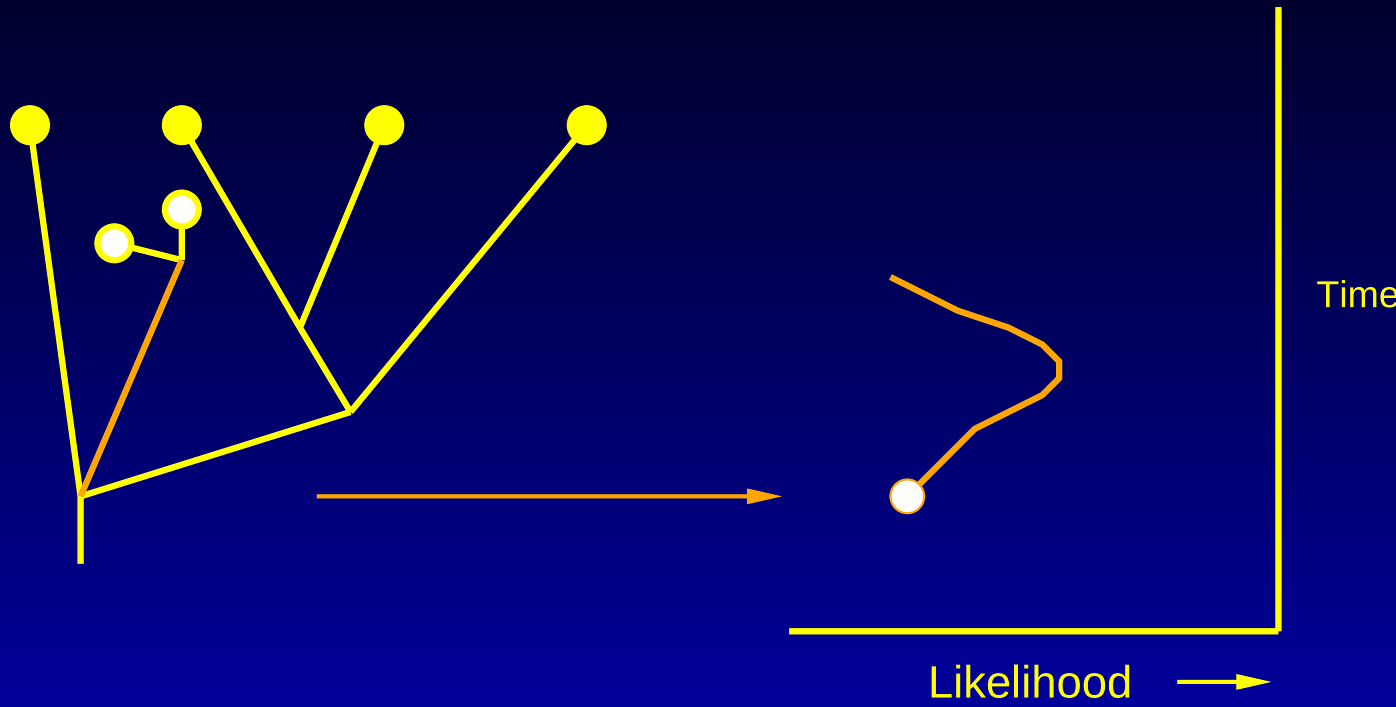

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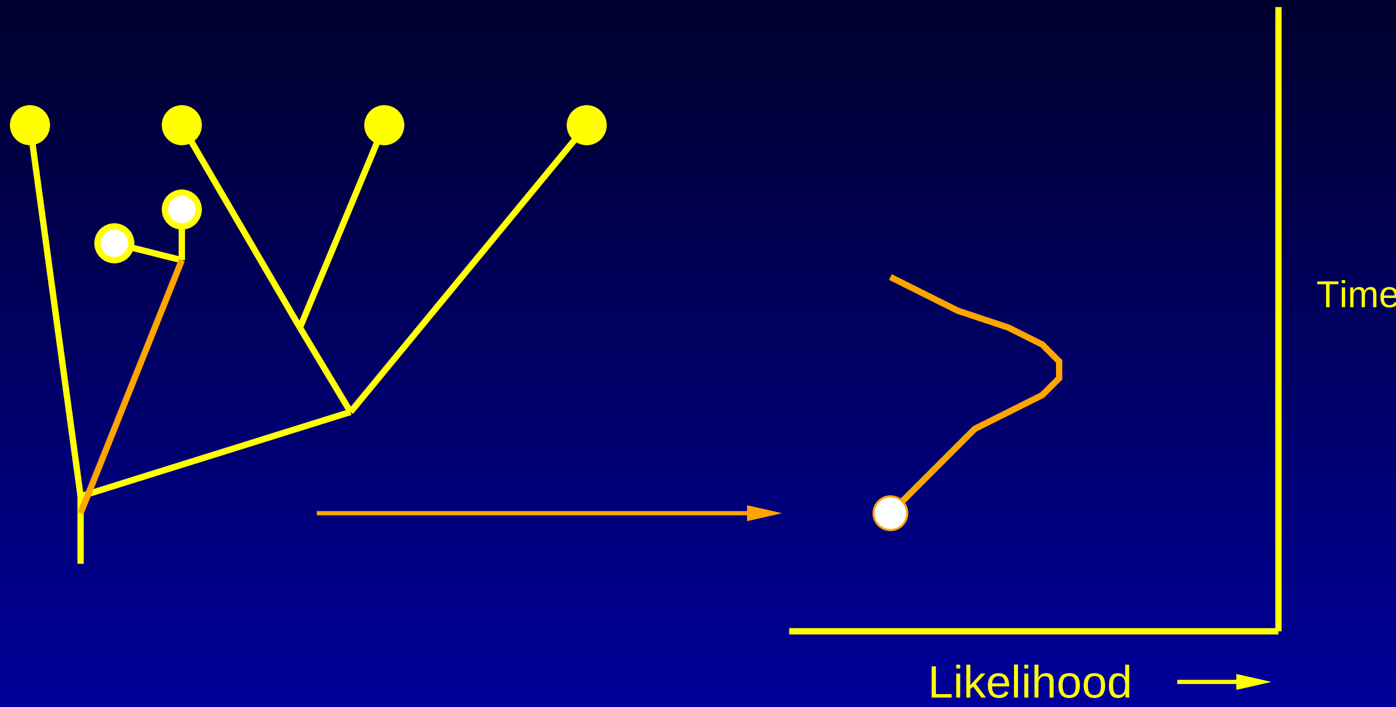

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Physical Anthropology – current methodology?

(An outsider's caricature)

- Find one bone

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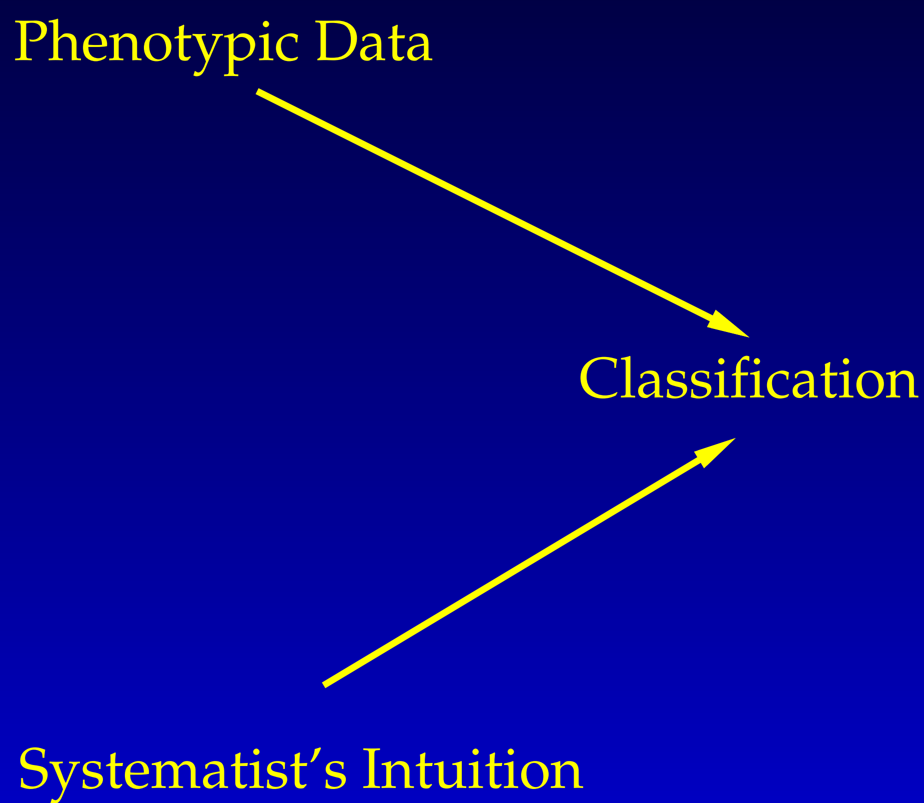
This creates pressure for splitting species, ignoring within-species variation, and overinterpreting data.

Then: the importance of (beta) classification!



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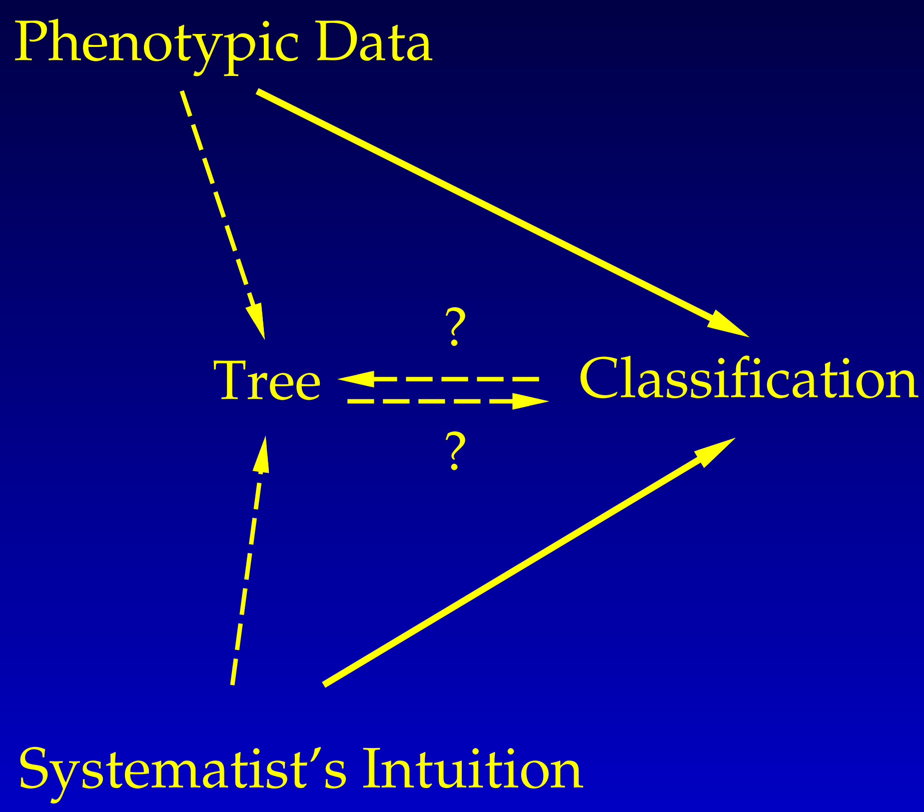

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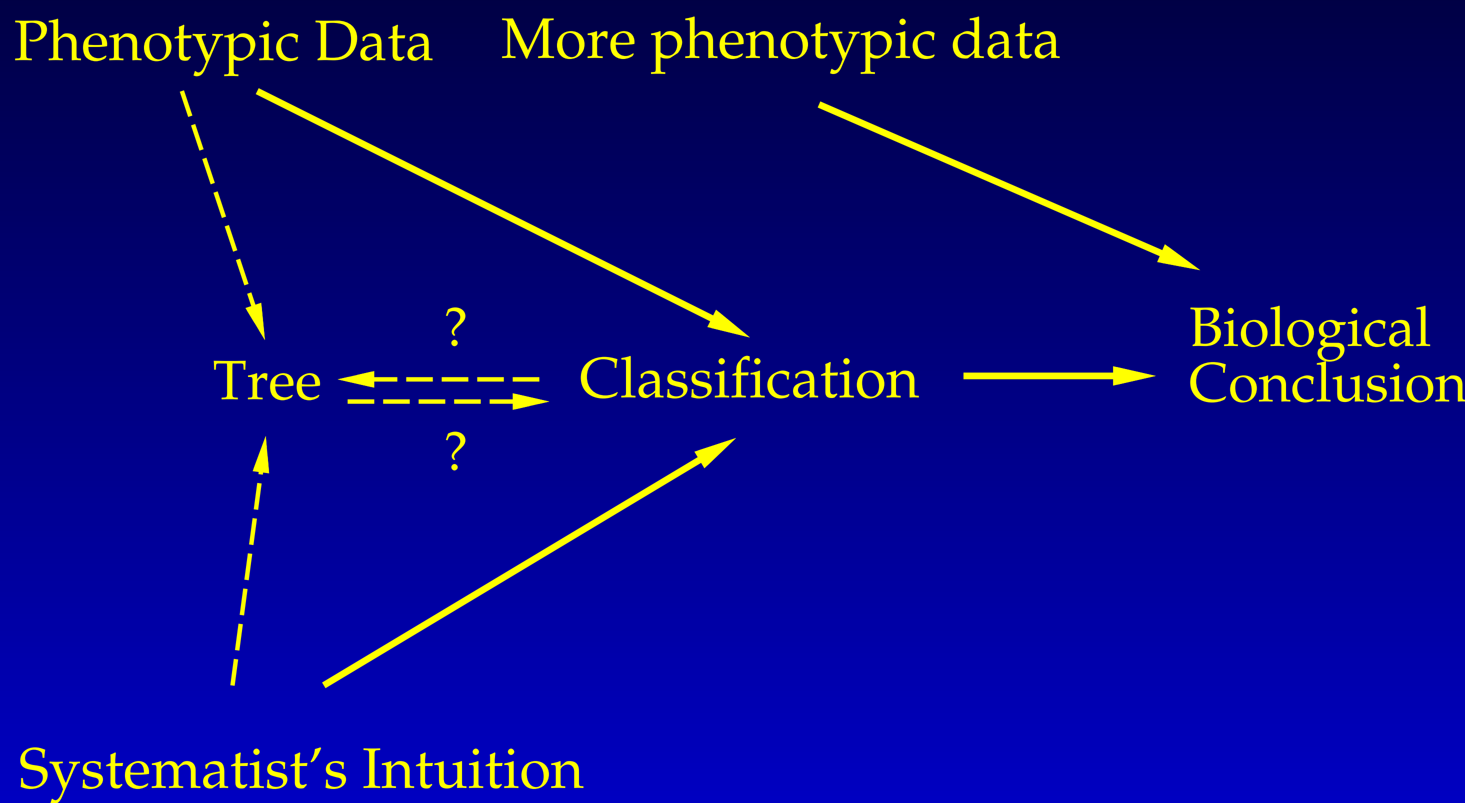

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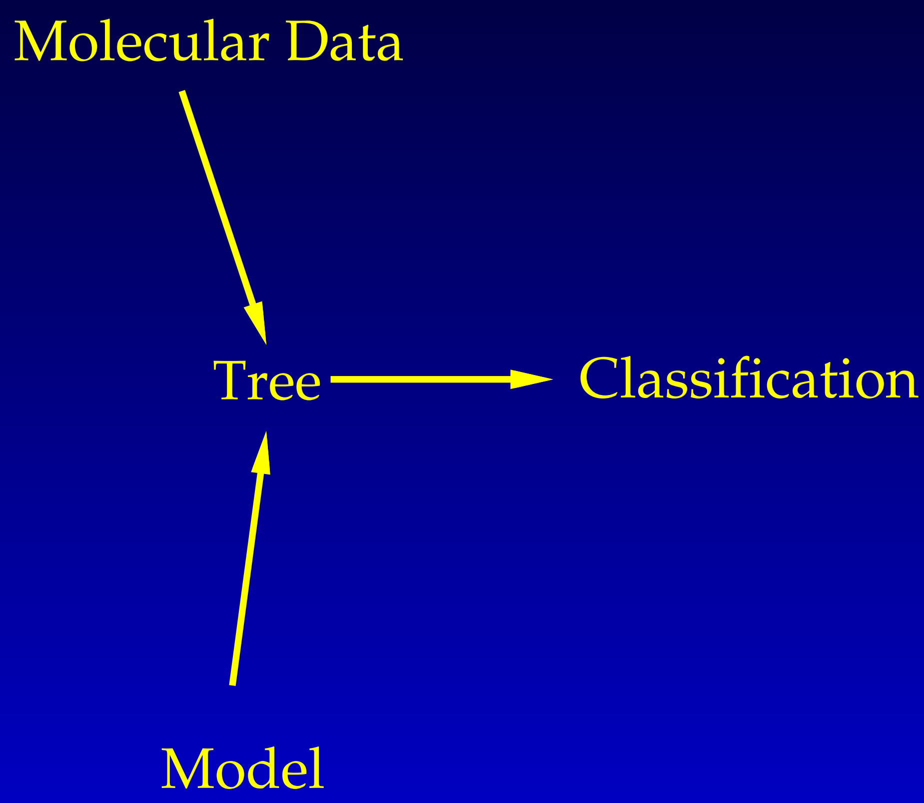

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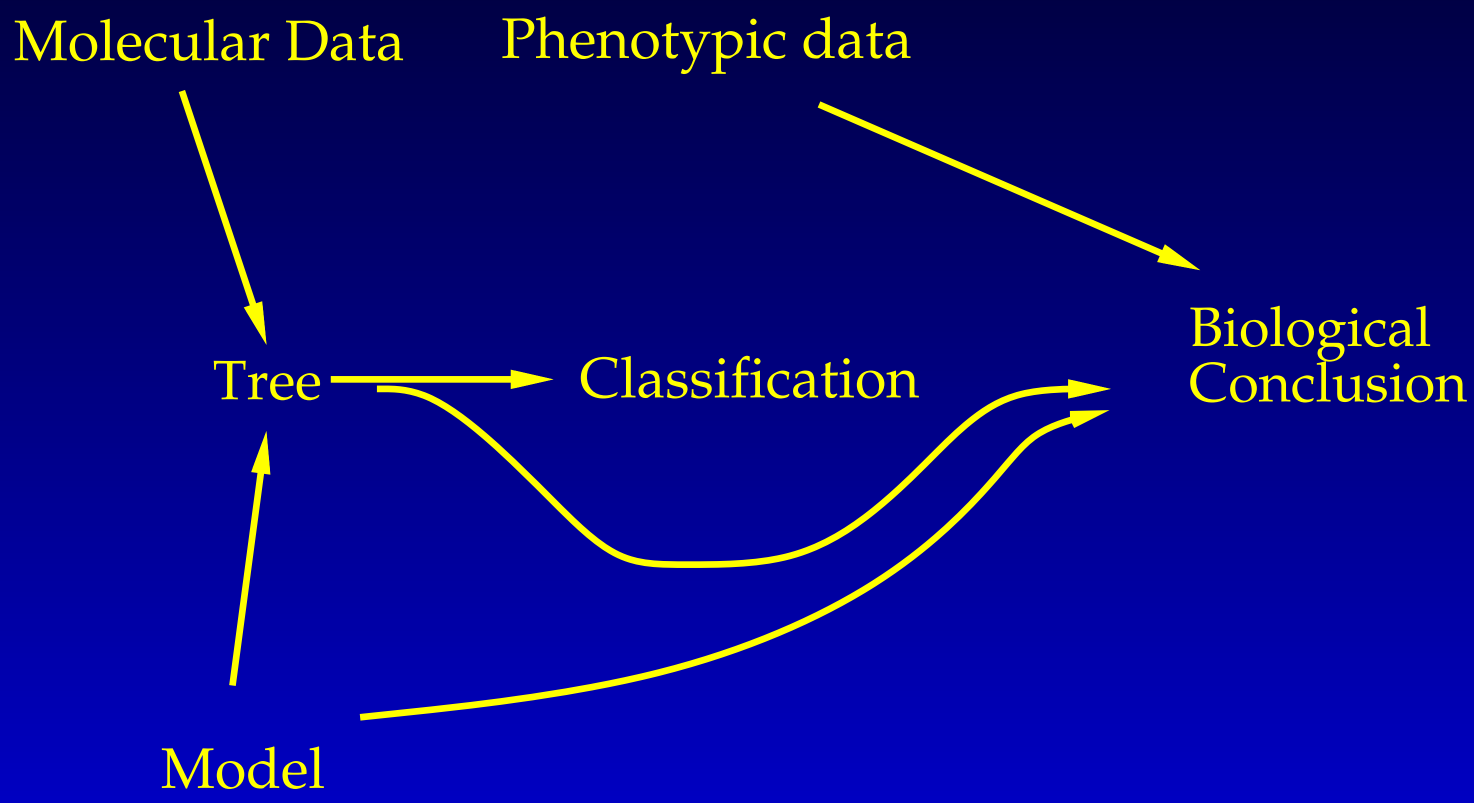

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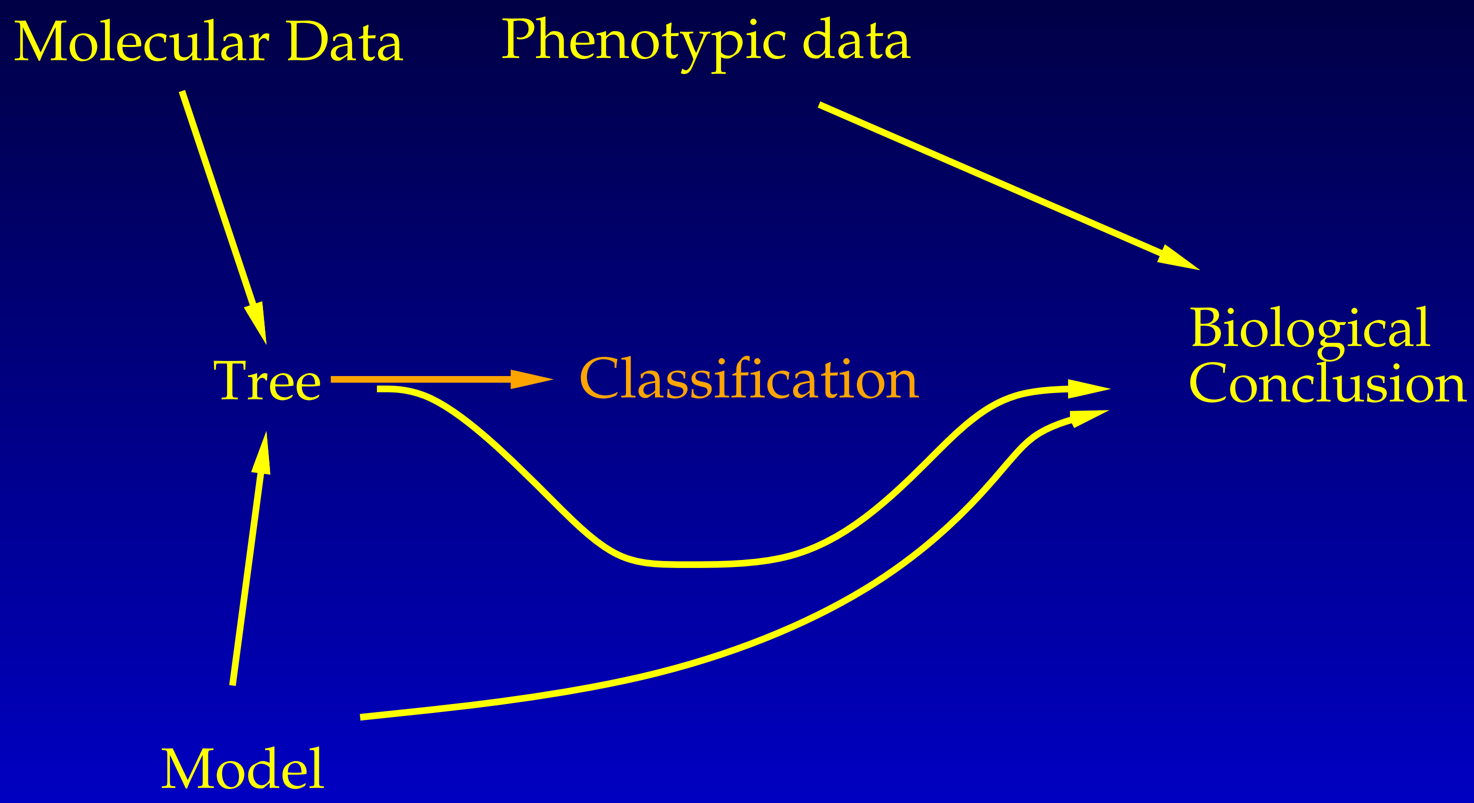
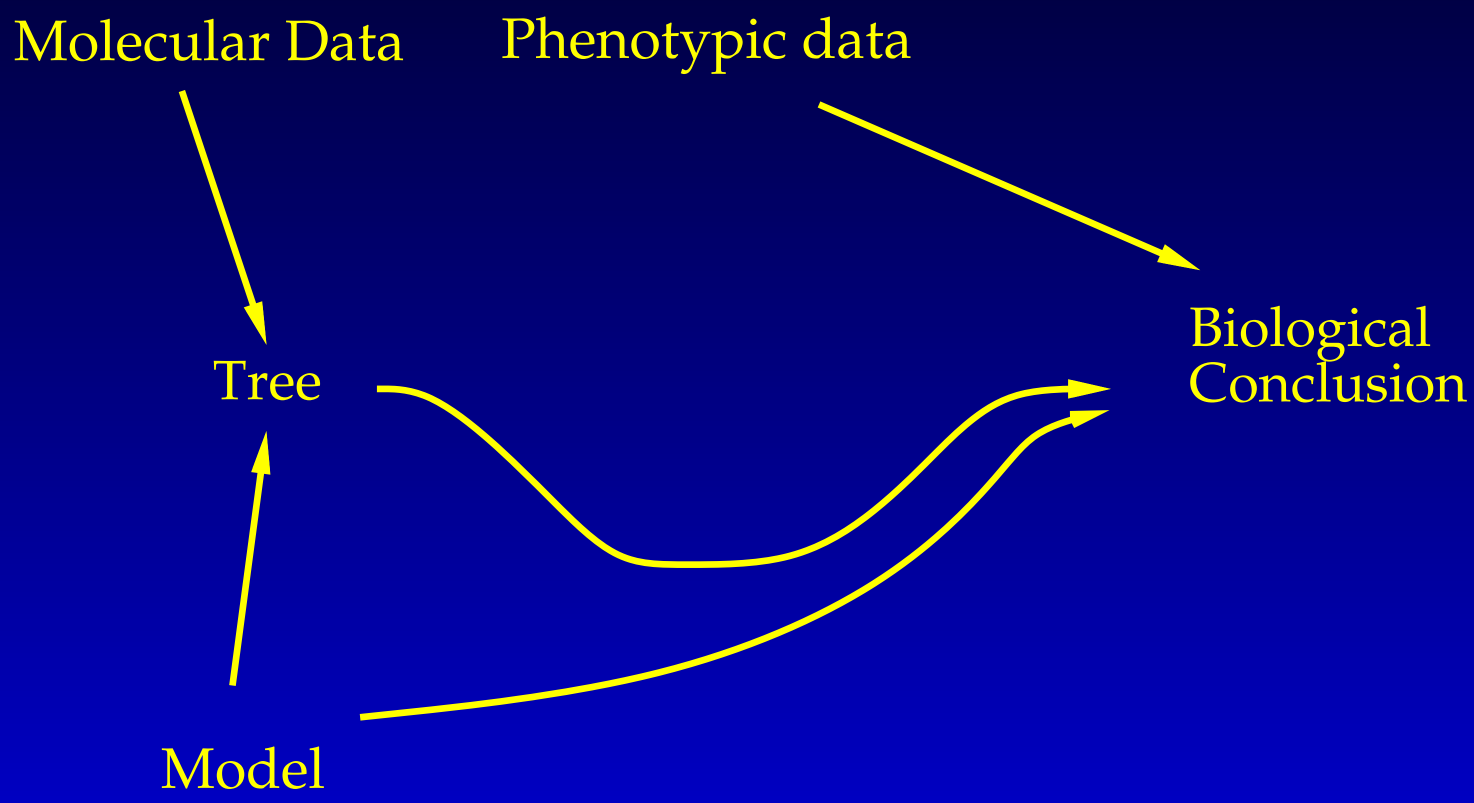


Future? the unimportance of (beta) classification



“But you need names to be able to talk about organisms!”

Yes, but …

- Why then do we need names that describe nonoverlapping sets?
- Why require monophyly?
- In short, does the need for names specify that we must have a hierarchical classification?

What would Julian Huxley have thought?

Julian Huxley as Fellow of New College, Oxford, 1922

What would Julian Huxley have ordered?

The Sir Julian Huxley, 152-154 Addington Road, Selsdon, Surrey

References for the threshold method

Wright, S. 1934. An analysis of variability in number of digits in an inbred strain of guinea pigs. *Genetics* **19:** 506-536. **[The threshold model for discrete traits]**

Falconer, D. S. 1965. The inheritance of liability to certain diseases, estimated from the incidence among relatives. *Annals of Human Genetics* **29:** 51-76. **[Threshold model applied to human diseases]**

Lewis, P. O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology* 50: 913-925. **[Uses 0/1 stochastic process to infer morphological phylogenies]**

Pagel, M. 1994. Detecting correlated evolution on phylogenies: A general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London Series B Biological Sciences.* **255:** 37-45. **[0/1 stochastic model for discrete characters]**

Felsenstein, J. 2005. Using the quantitative genetic threshold model for inferences between and within species. *Philosophical Transactions of the Royal Society of London, series B* **360:** 1427-1434. **[This project in a slightly earlier version]**

How it was done

This presentation was prepared using freeware:

- LaTeX (mathematical typesetting and PDF preparation)
- `prosper` class for projection slides
- Idraw (drawing program to modify plots and draw figures)
- `dvips` to prepare Postscript file
- `ps2pdf` to turn this into a PDF
- Adobe Acrobat Reader (to display the PDF in full-screen mode)
- Linux (operating system)