Phylogenetics

Course introduction

RL-V3 MPP

Rachel Warnock

14.04.25

About this course

The course is taught in two parts:

- Block course, Mon 14.04.25 - Wed 16.04.25, Henke Str.
- Summer semester, Thursdays 14:00–16:00 CET at Henke Str.

Classes will consist of lectures and exercises + 6 weeks project work

All lecture material available via the course website

Blue underlined text → external links

Course objectives

To learn the application of phylogenetic tools in paleobiology

- Tree building
- Substitution models
- Dating trees
- Clock models
- Tree models
- Diversification rates
- Morphological models
- Continuous trait evolution
- …

Course evaluation

“Phylogenetics” is graded together with “Introduction to Statistical Modelling” (course code: RL-V3 MPP)

Class exercises are mainly in R or the Bayesian phylogenetic software RevBayes

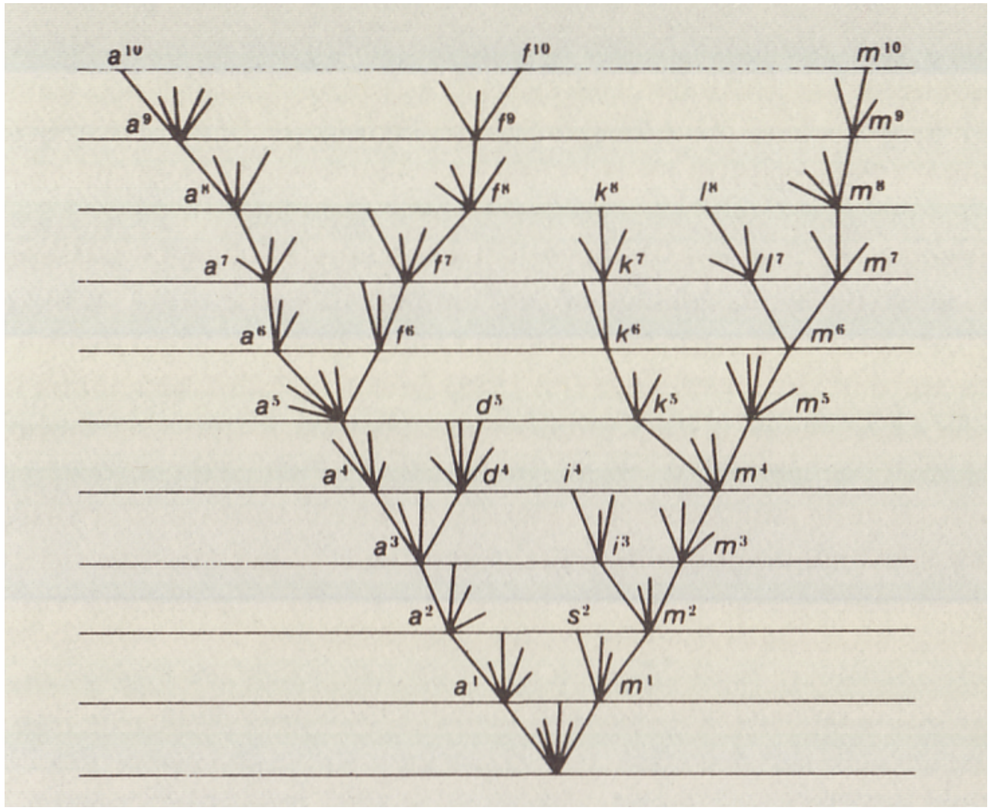
In addition, we have homework exercises that include videos and reading

Evaluation is based on a **written report** (info available on the project page)

Please ask questions!

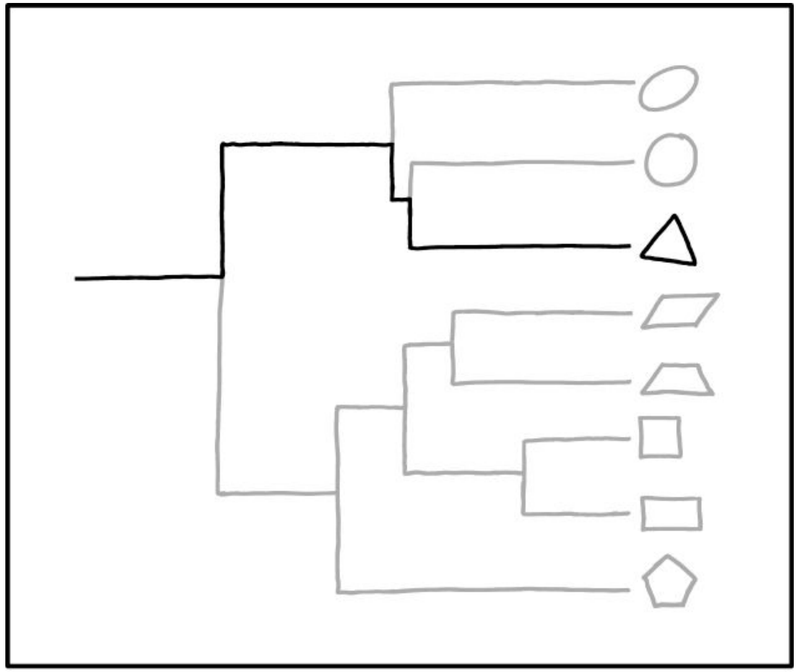
Objectives

- Recap ‘tree-thinking’
- Gain an understanding of the parsimony approach to tree-building and statistical inconsistency



Time tree from Darwin’s *Origin of Species*

What is phylogenetics?



XKDC

THE PHYLOGENETIC REVOLUTION CONTINUES:

TRIANGLES WERE LONG BELIEVED TO BE RELATED TO SQUARES, BUT GENETIC ANALYSIS PROVES THAT THEY ARE ACTUALLY VERY POINTY CIRCLES.

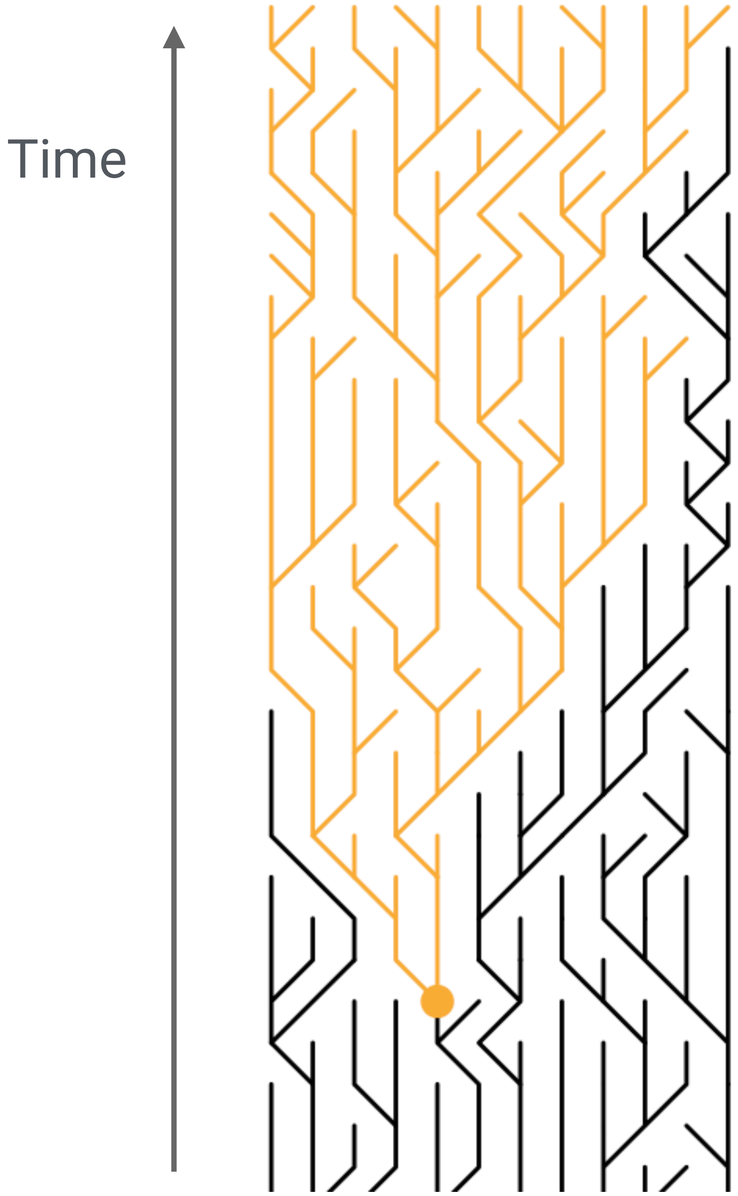
Phylogenetics

Phylogenetics aims to reconstruct the phylogeny of individual samples based on molecular or morphological character data

A phylogeny captures part of evolutionary history that is otherwise not directly observable

Phylodynamics aims to quantify the processes that gave rise to the tree, e.g., speciation, extinction

Explore the tree of life using the Open Tree of Life tool, currently inc. 2,384,572 tips

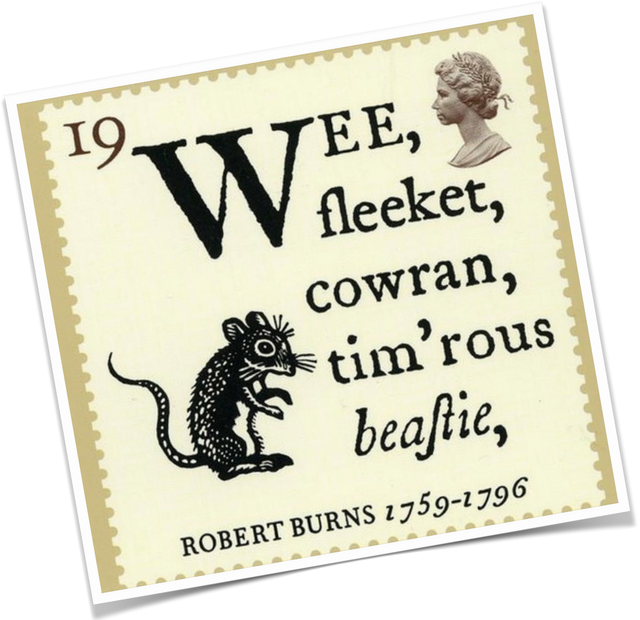


- populations
- species
- viruses
- cells
- languages

Data

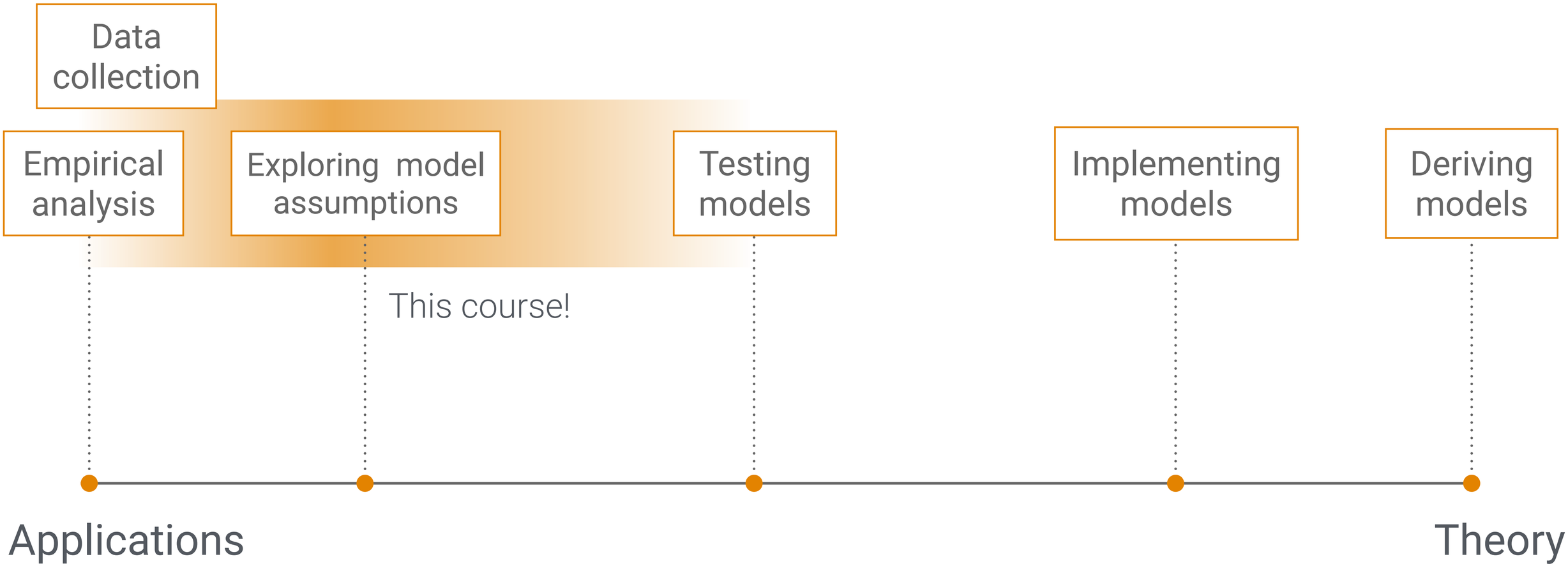
- DNA
- morphology
- words

In this course we mainly focus on trees that include one representative per species



Scots poem - also the BEAST2 logo!

Research topics in phylogenetics

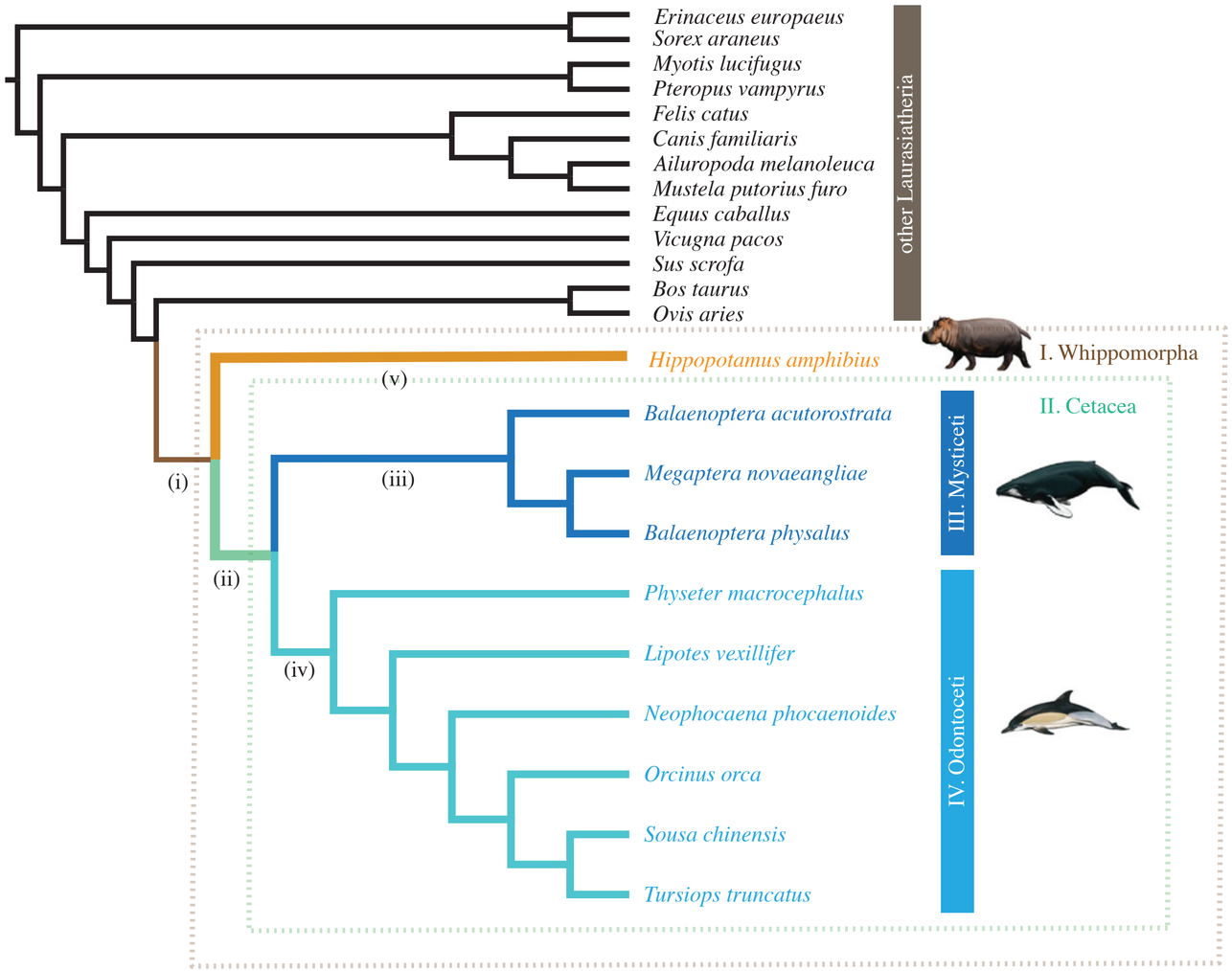


Nothing in biology makes sense except in the light of evolution – *Theodosius Dobzhansky* (1973)

Nothing in evolution makes sense except when seen in the light of phylogeny – *Jay Savage* (1997)

Trees in paleobiology

What can we learn from trees?



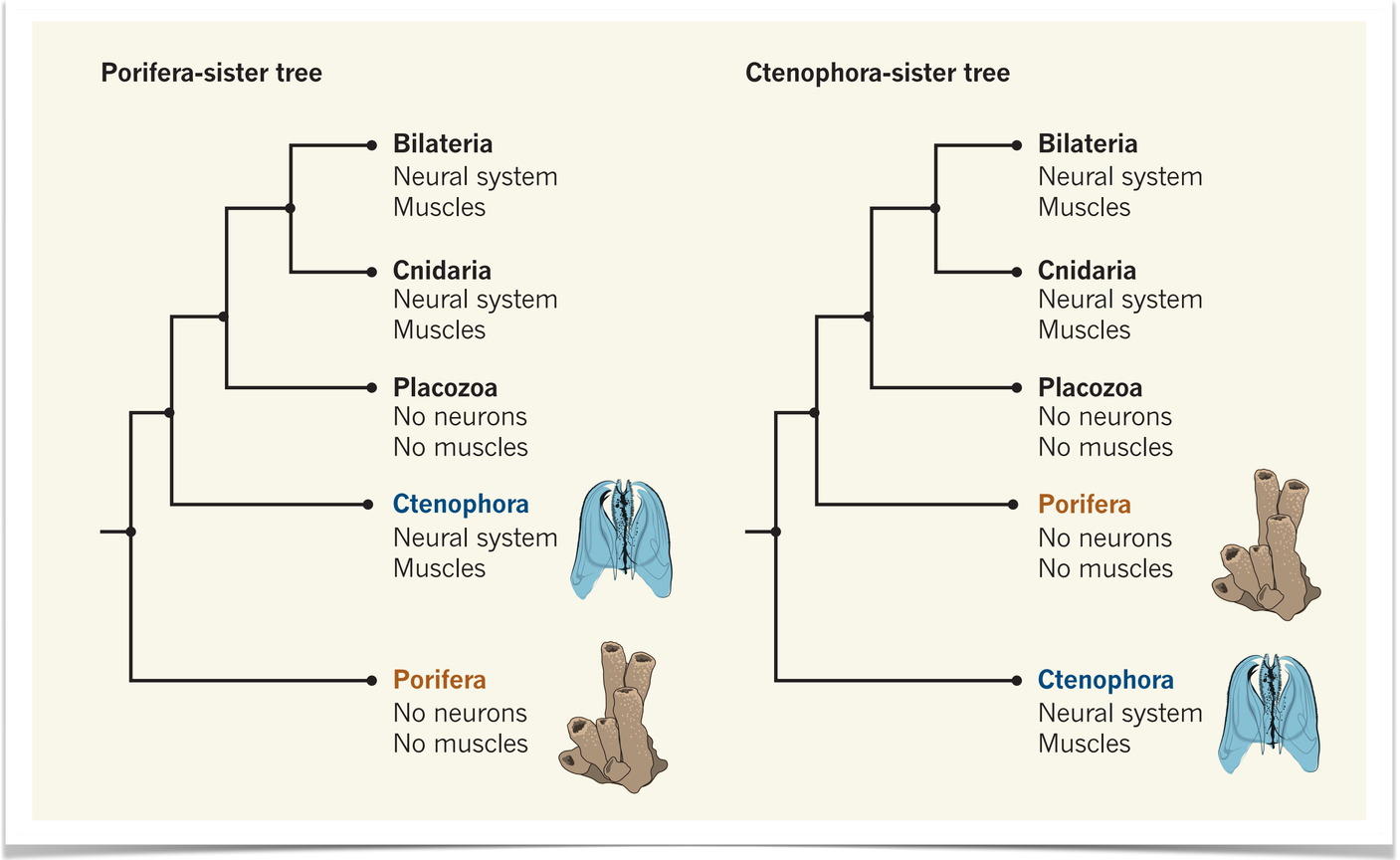
Tsagkogeorga et al. (2015)

How are our favourite species related?

Does the phylogeny support the taxonomy?

What was the sequence of character evolution?

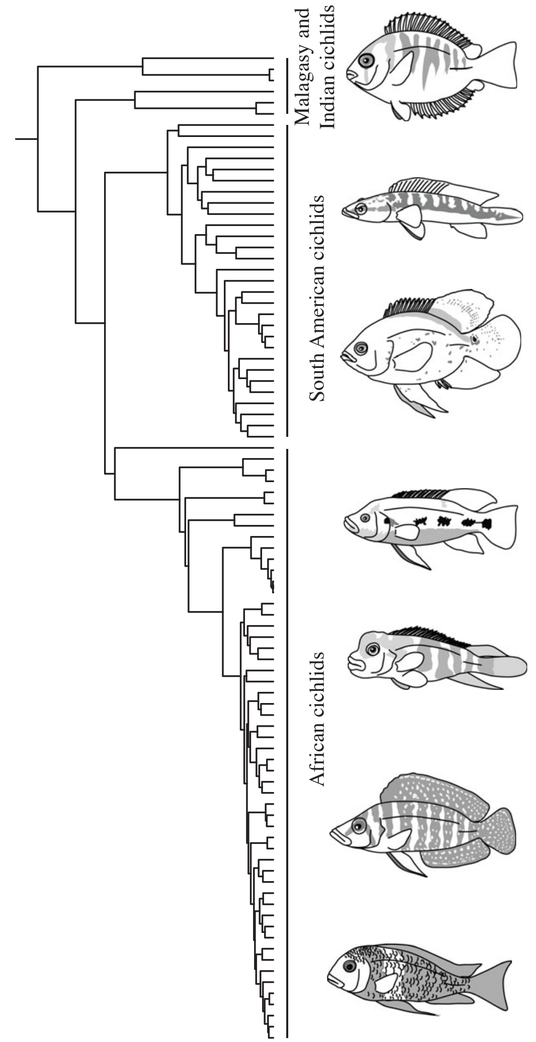
Topology transforms our understanding of character evolution



Telford 2016

What can we learn from trees?

- Evolutionary relationships



What can we learn from trees?

- Evolutionary relationships
- Timing of diversification events
- Geological context
- Rates of phenotypic evolution
- Diversification rates

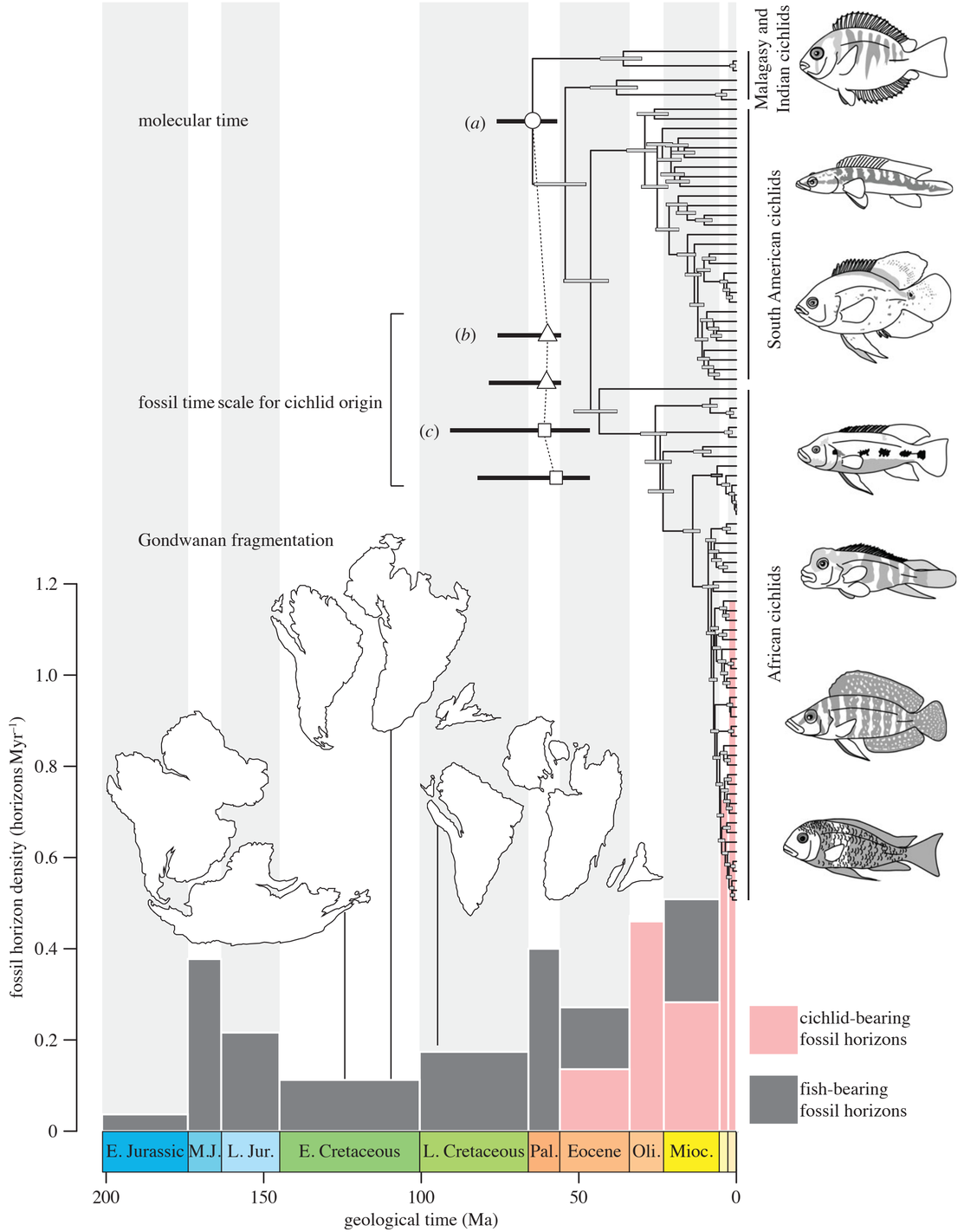
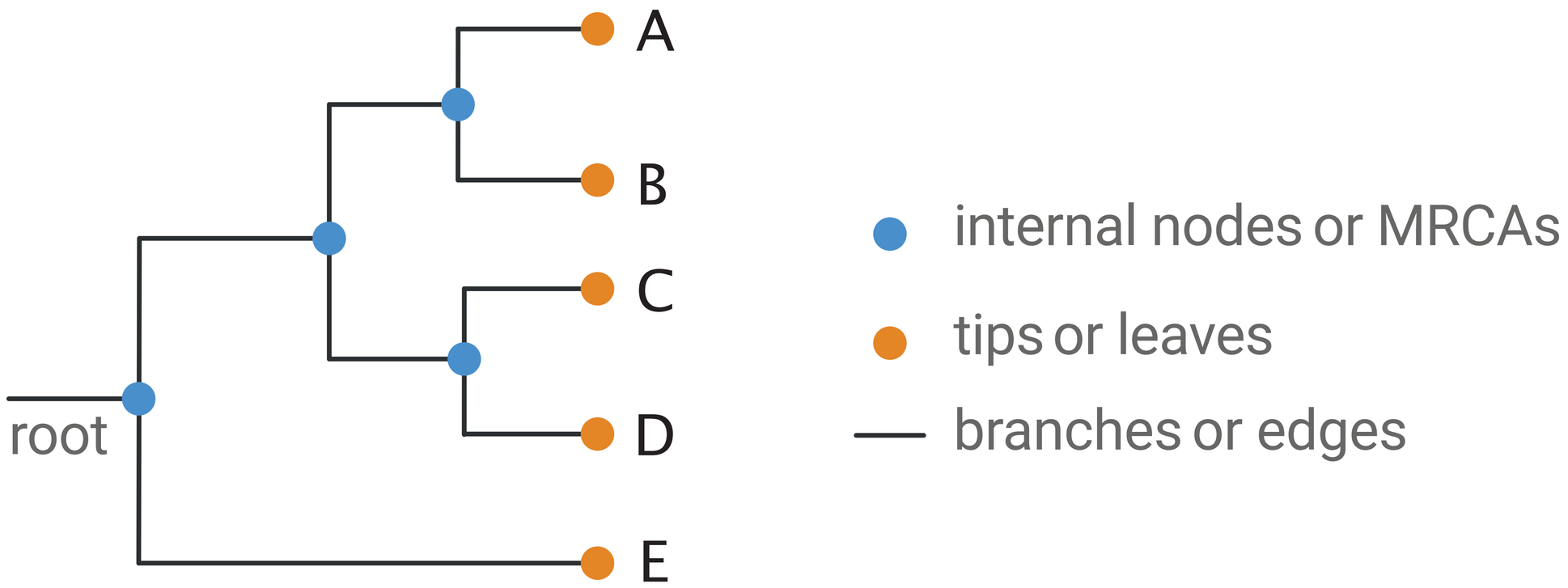


Image adapted from *Friedmann et al.* (2013)

Where do we begin?

Some basic terms

MRCA = most recent common ancestor

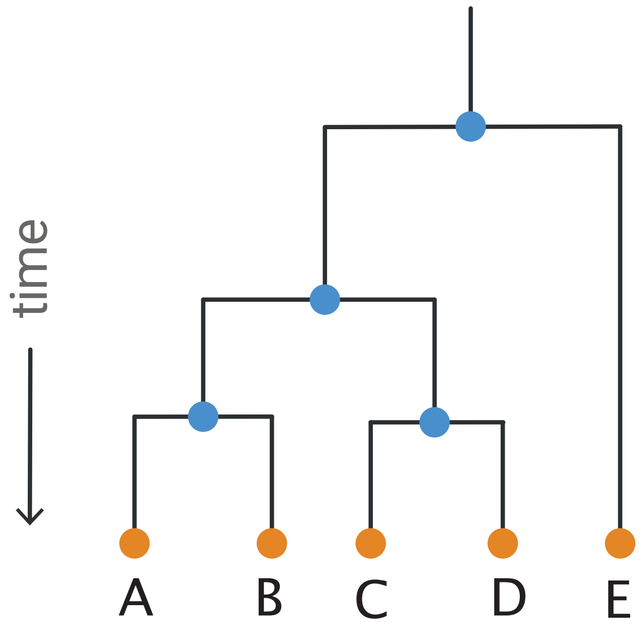


branch lengths = genetic distance *or* time

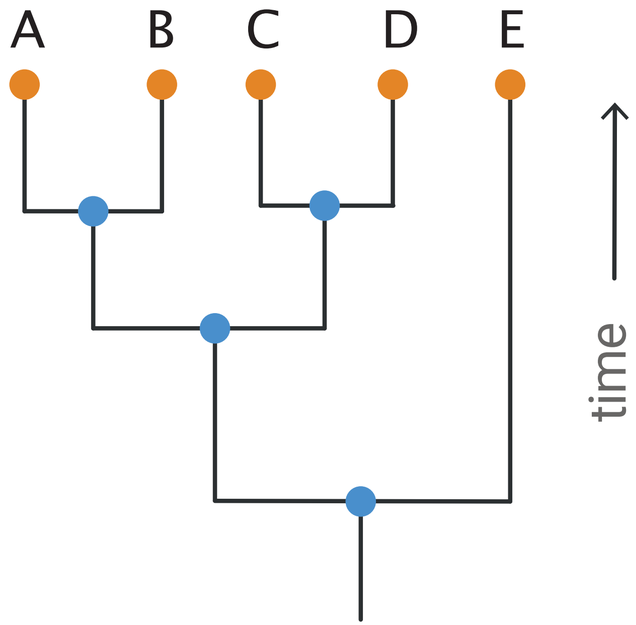
How to read a phylogenetic tree

The direction of time

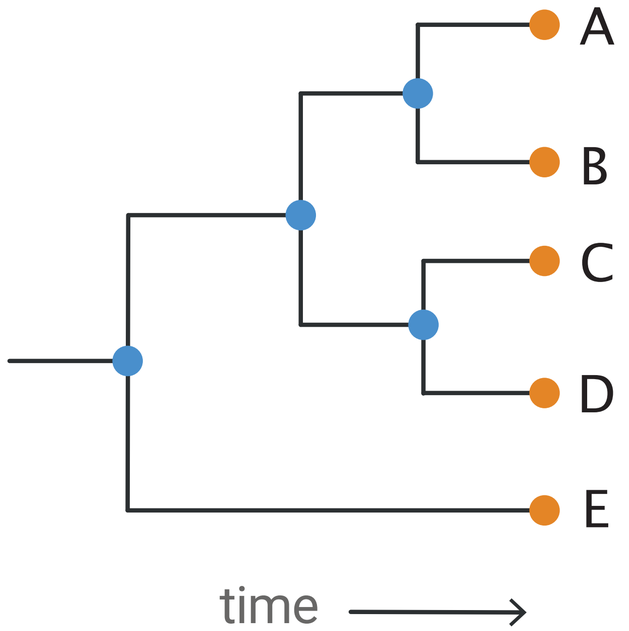
Tip look for the root!



Computer science, maths



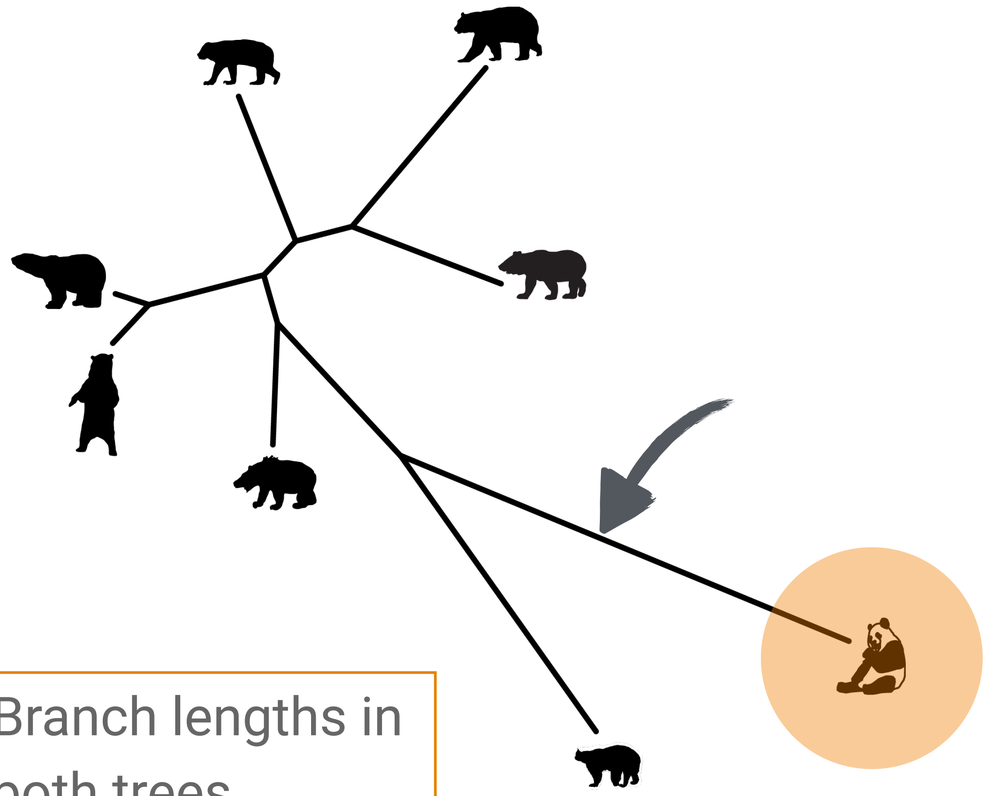
Geology



Evolutionary biology

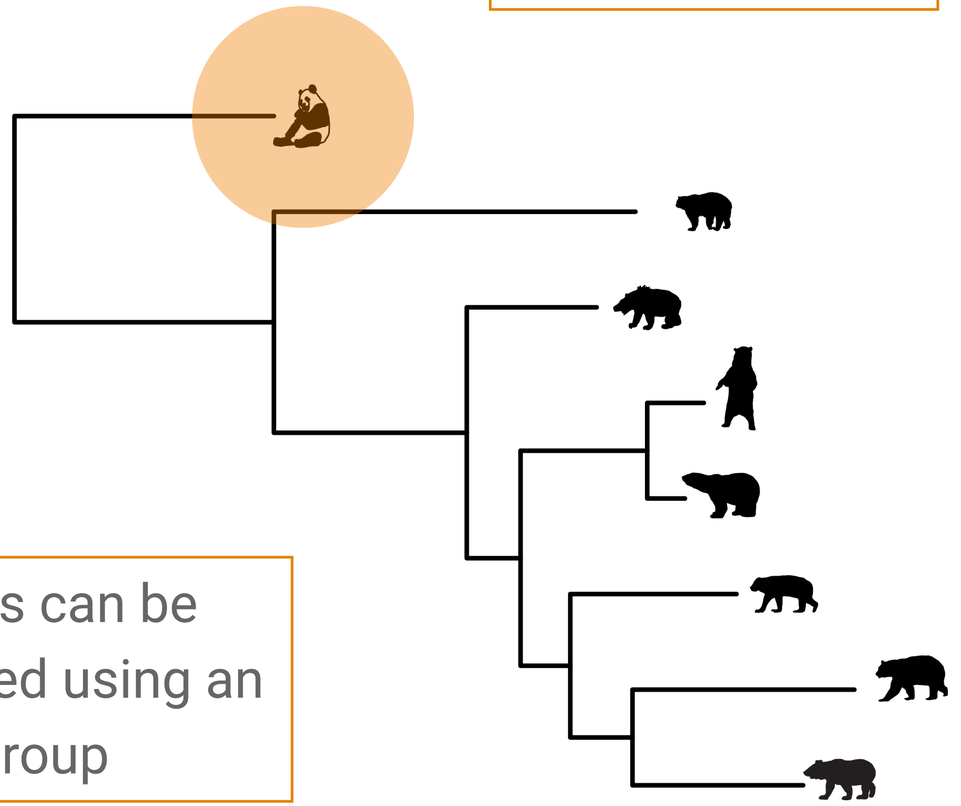
Two types of trees

Unrooted vs. rooted trees



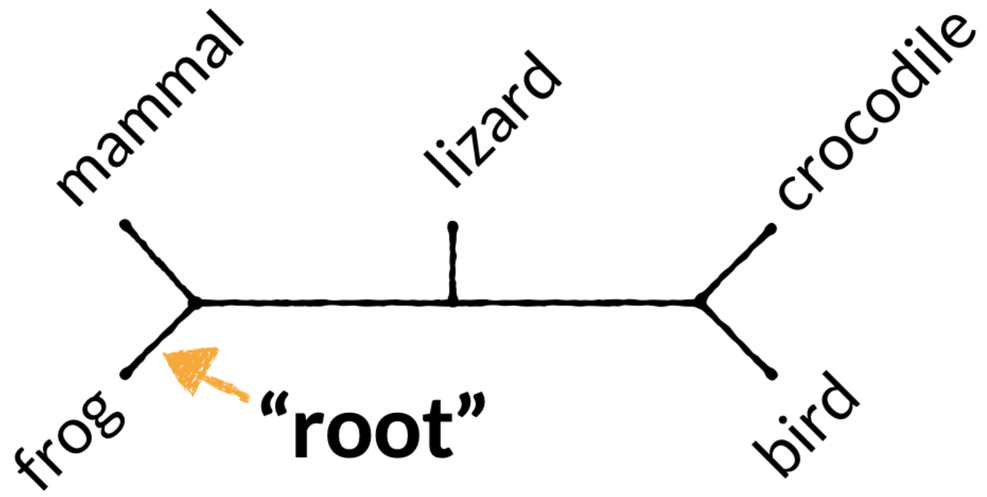
Branch lengths in both trees represents genetic distance

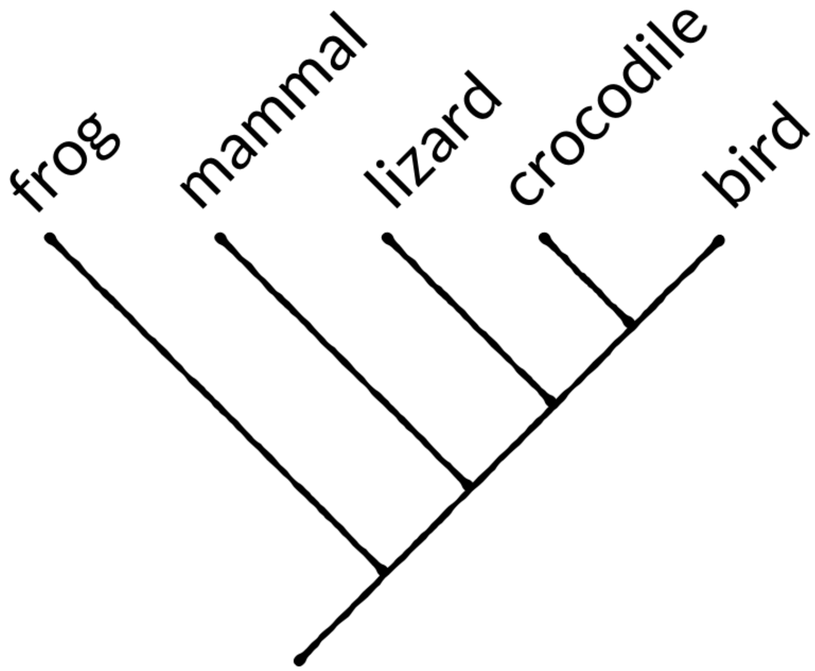
A rooted tree shows the direction of time



Trees can be rooted using an outgroup

Image source Tracy Heath

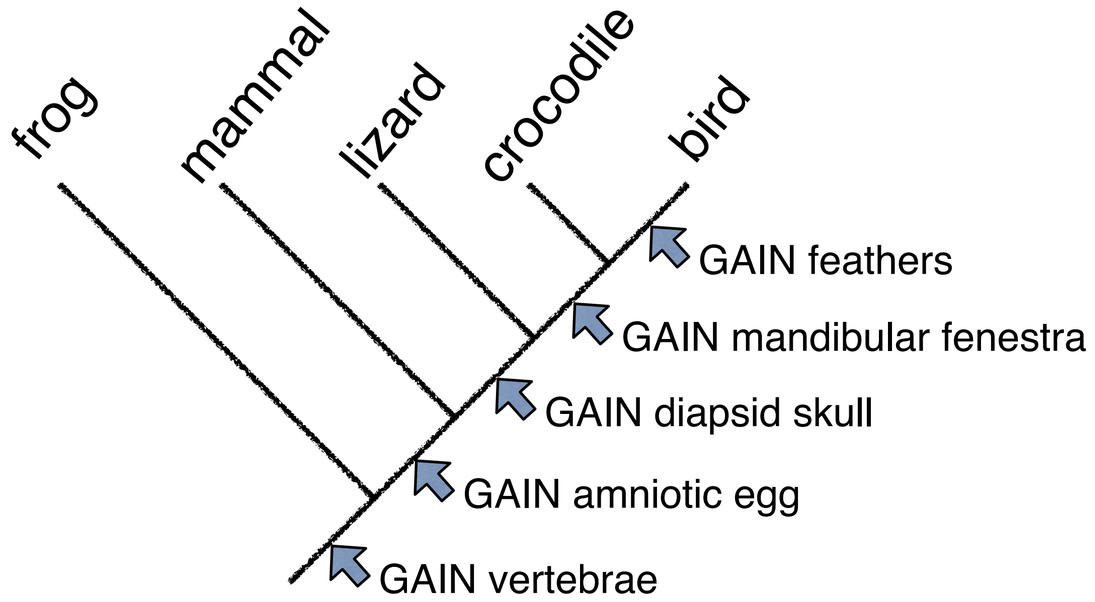




Phylogenies are unrooted by default, because phylogenetic data don't directly contain information about the **direction of time**

data matrix	vertebrae	amniotic egg	diapsid skull	mandibular fenestra	feathers
frog	1	0	0	0	0
mammal	1	1	0	0	0
lizard	1	1	1	0	0
crocodile	1	1	1	1	0
bird	1	1	1	1	1

Tree polarity and rooting



Slides adapted from Philip Donoghue

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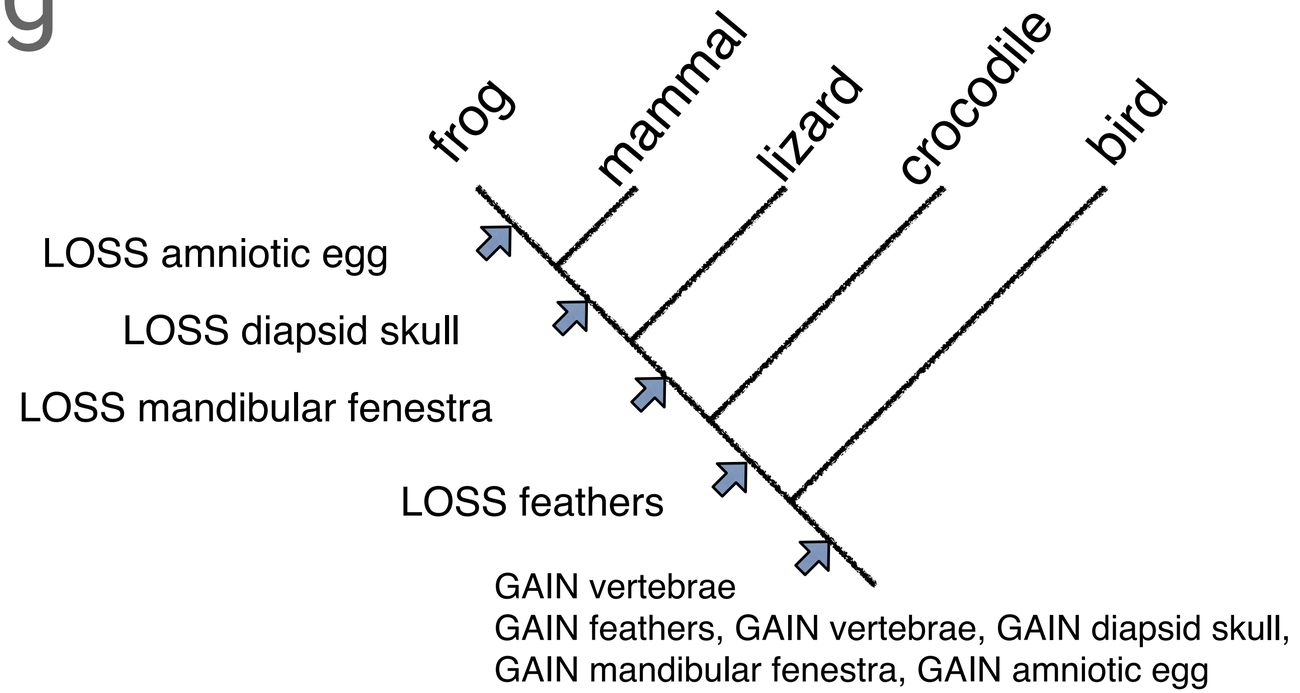
Tree polarity and rooting



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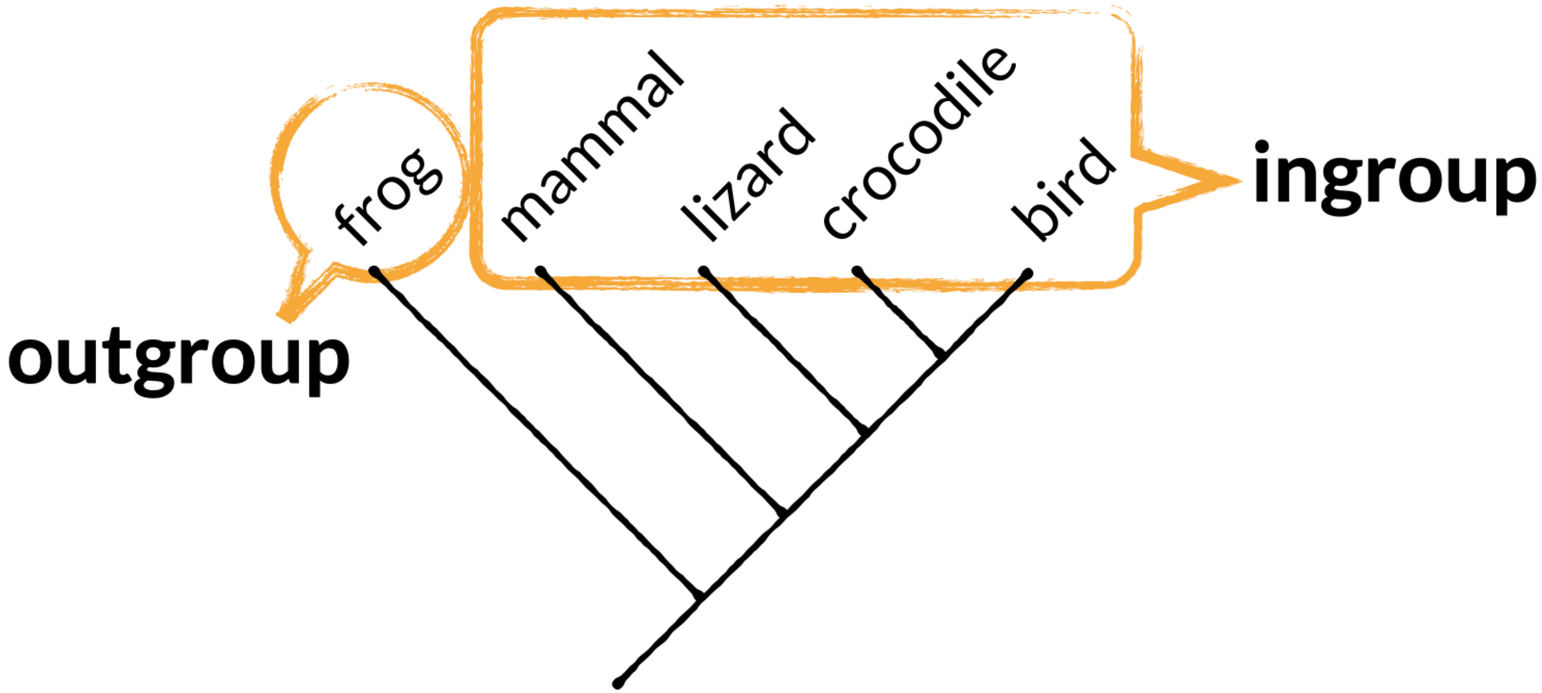


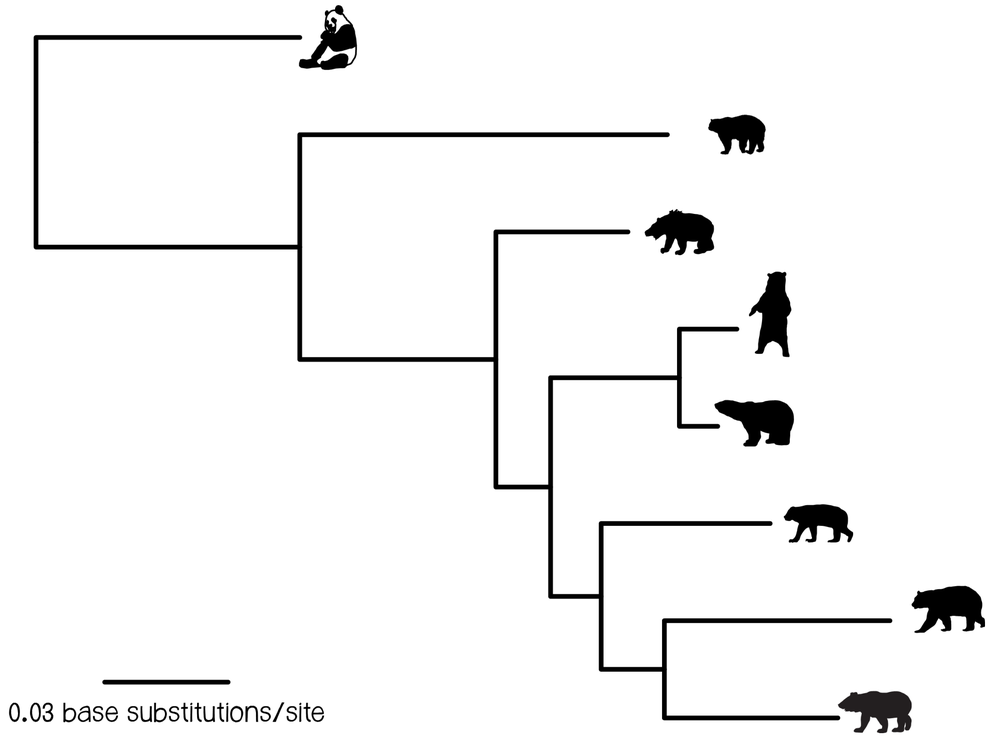
We have to find a way of breaking one of the branches in two, where the break represents the oldest point in our tree

The most common approach is to use an outgroup — a taxon that we know is more distantly related to everything else

Branch lengths = genetic *or* time

Tip look at the axis

Trees show the relationships among **extant** (living) bear species



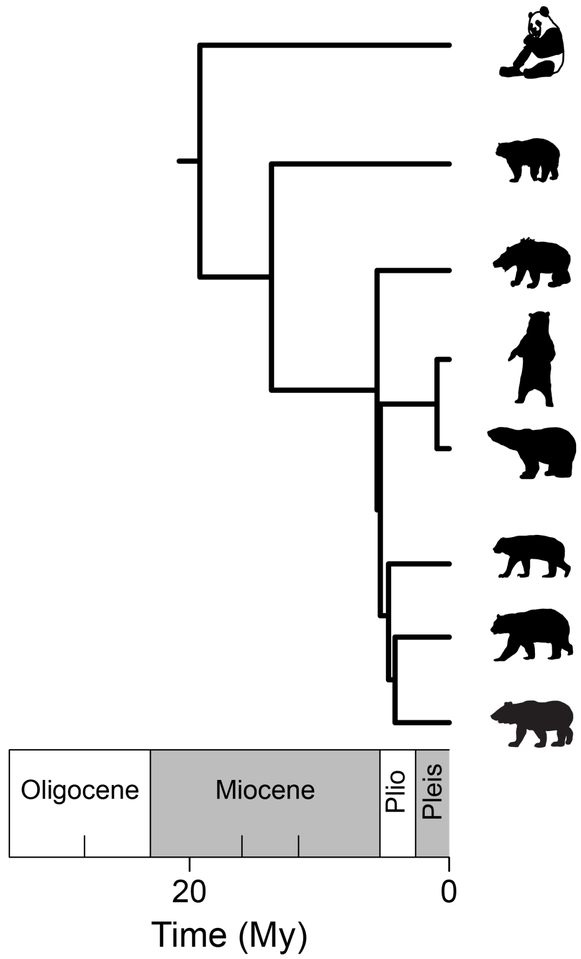


Image source Tracy Heath

Dated tree showing the relationship of extant *and* fossil bear species

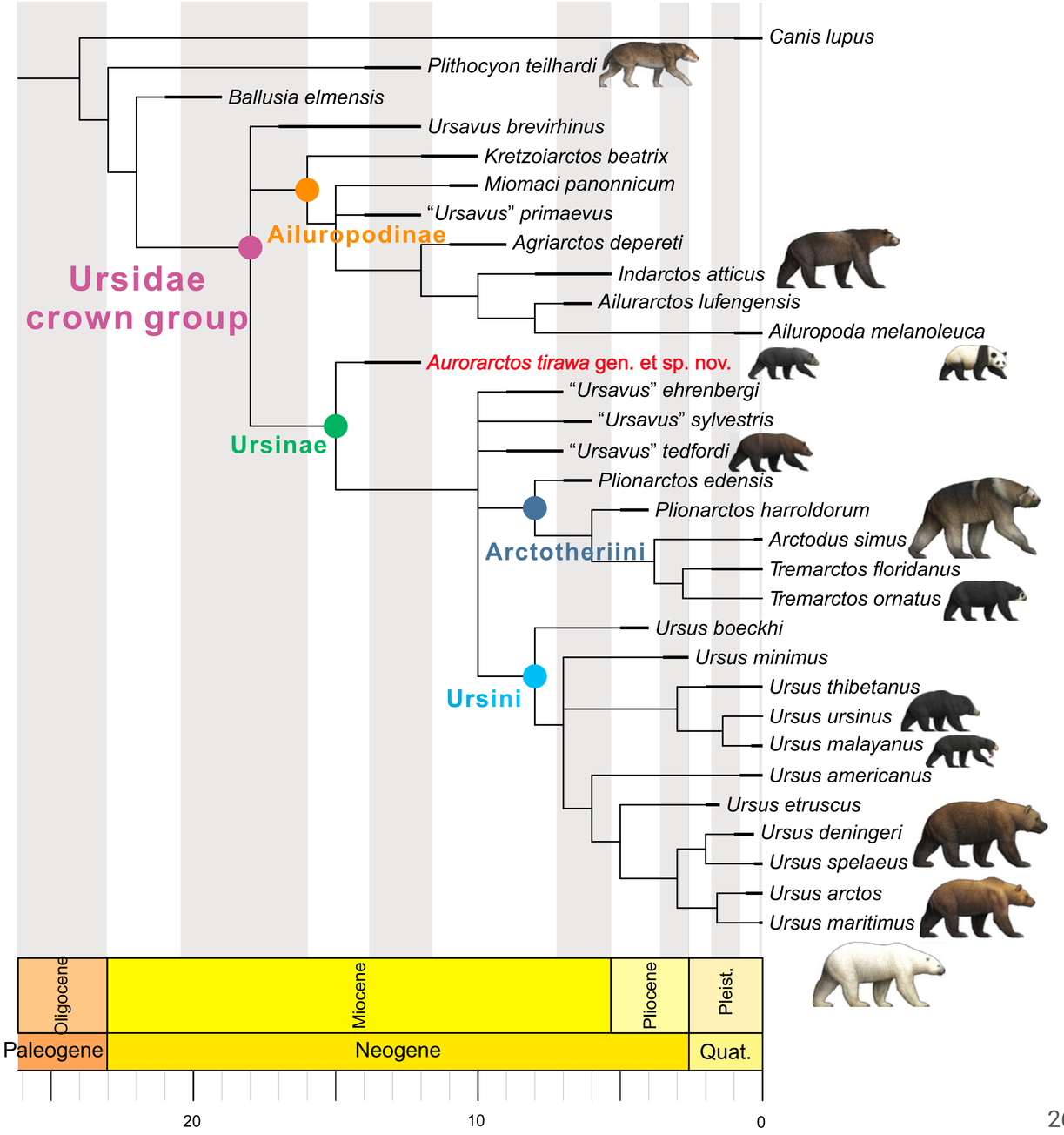


Image adapted from *Jiangzuo and Flynn.* (2020)

Character	Lamprey	Antelope	Bald eagle	Alligator	Sea bass
Lungs	0	1	1	1	0
Jaws	0	1	1	1	1
Feathers	0	0	1	0	0
Gizzard	0	0	1	1	0
Fur	0	1	0	0	0

- What do you think the correct rooted tree should be?
  Write down your logic
- How many possible unrooted or rooted trees are there?

‘0’ and ‘1’ represent **absence** or **presence**

Source *Khan Academy*

There are a huge number of possible trees!

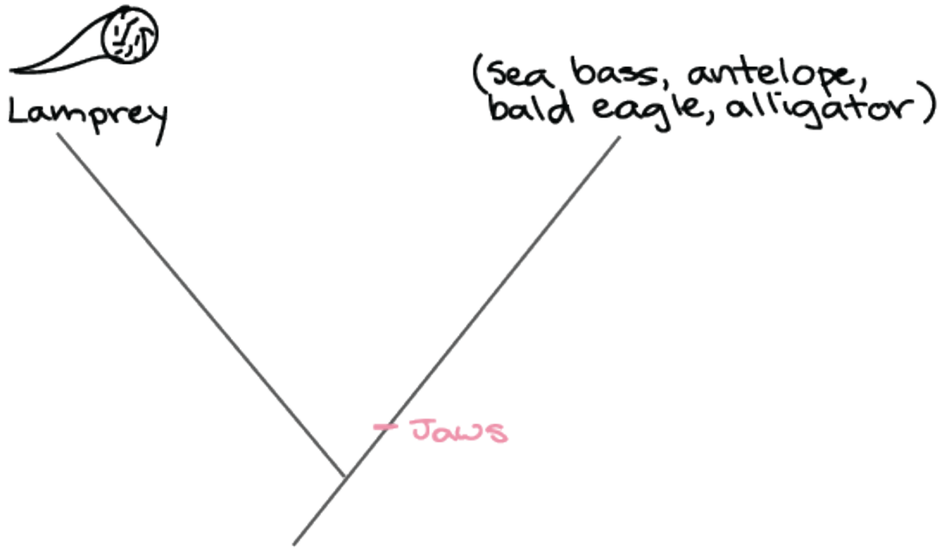
n tips	unrooted trees	rooted trees
3	1	3
4	3	15
5	15	105
6	105	945
7	945	10395
8	10395	135135
9	135135	2027025
10	2027025	34459425

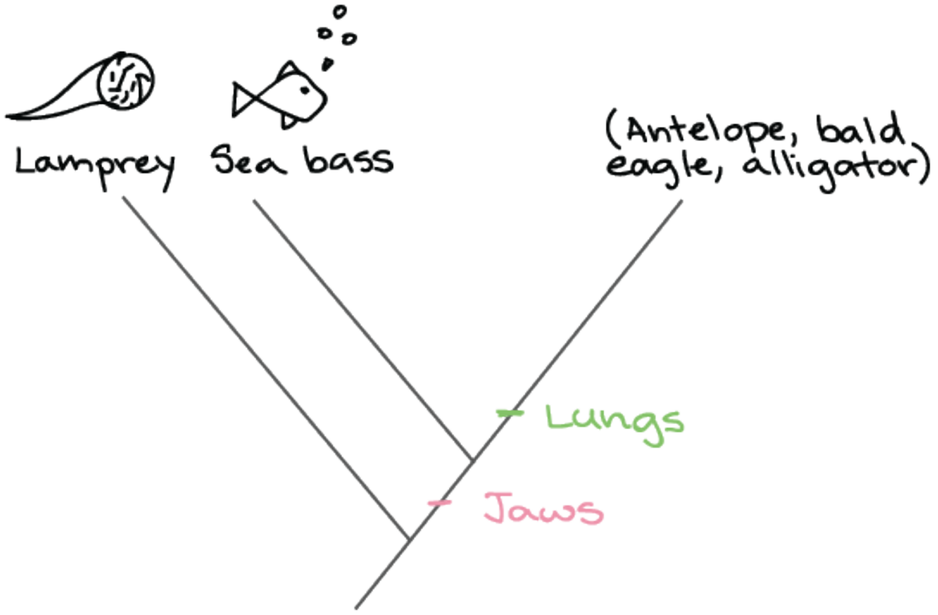
See wiki for more on where these numbers come from

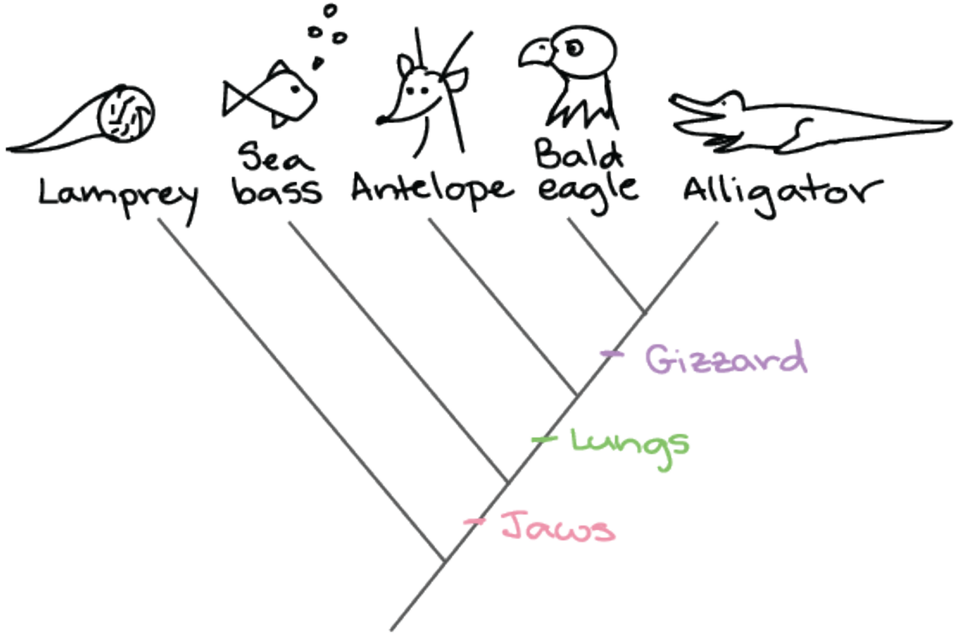
Number of **branches**, *n*

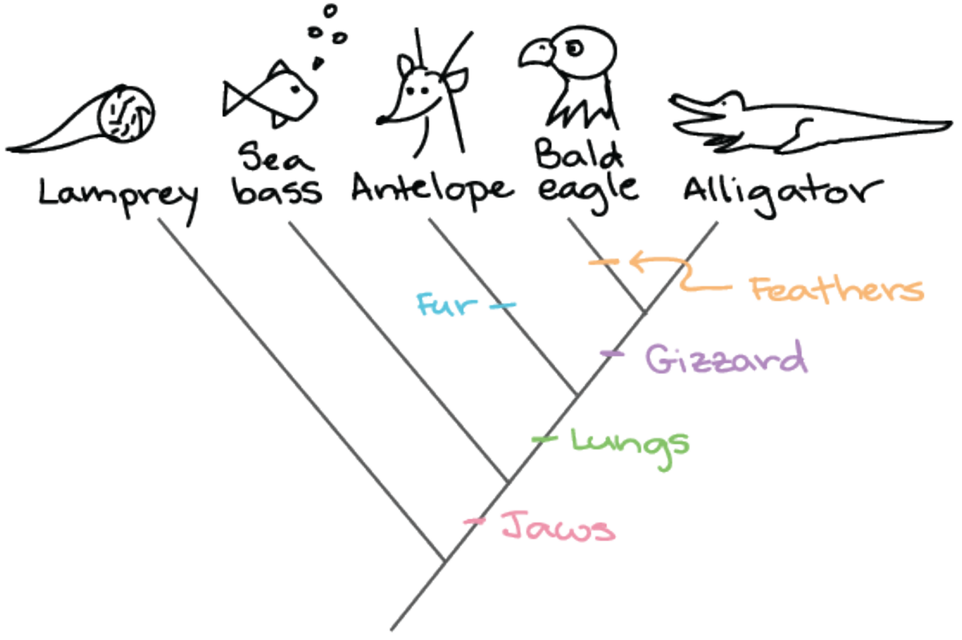
unrooted tree
$2n-3$

rooted tree
$2n-2$









Source *Khan Academy*

- *Write down your logic*

→ Most people intuitively assume the tree with the fewest changes is correct

→ This approach to tree building is called maximum parsimony

How do we find the ‘best’ tree?

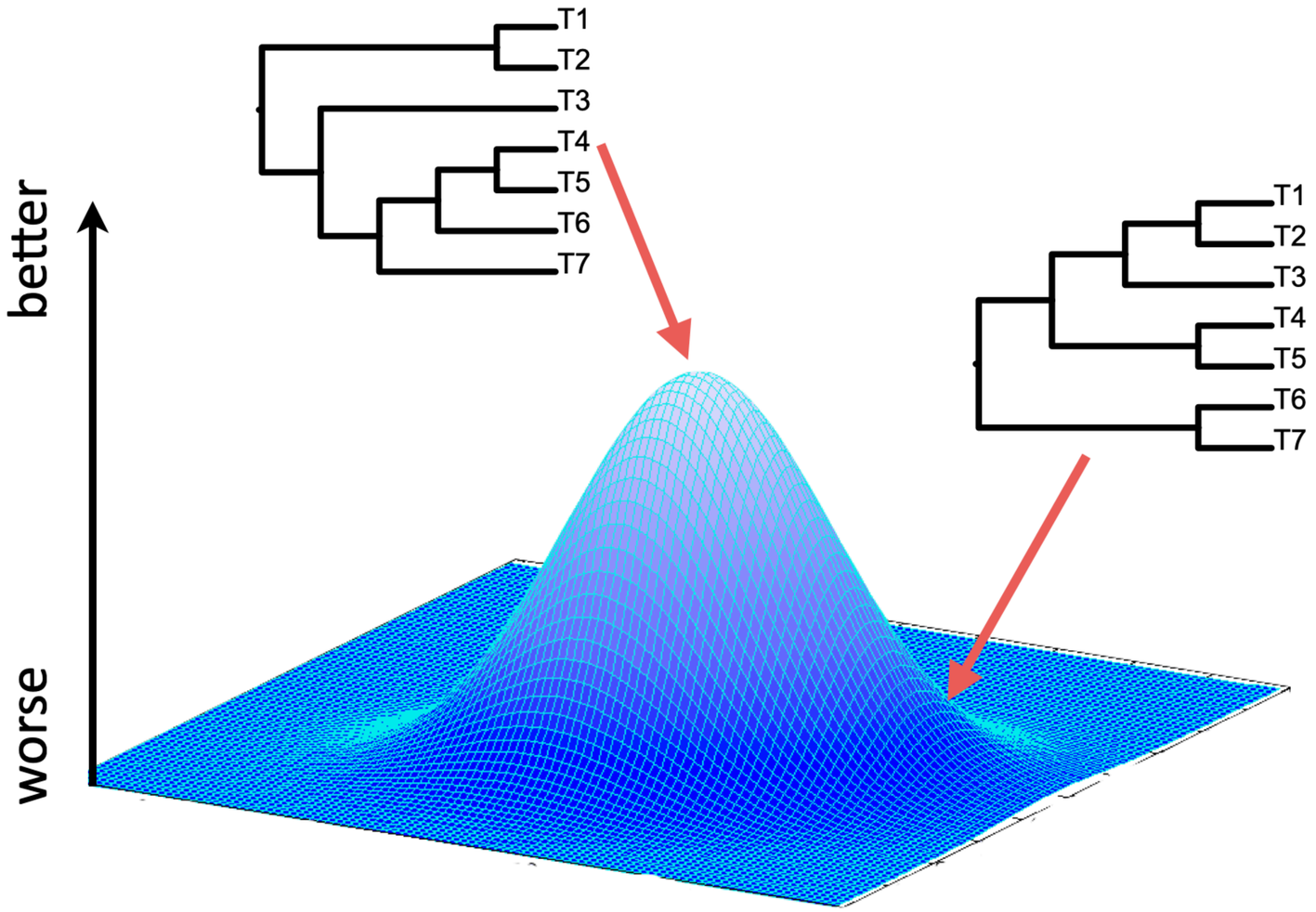


Image source Tracy Heath

It depends how you measure ‘best’

Method	Criterion (tree score)
Maximum parsimony	Minimum number of changes
Maximum likelihood	Likelihood score (probability), optimised over branch lengths and model parameters
Bayesian inference	Posterior probability, integrating over branch lengths and model parameters

Both maximum likelihood and Bayesian inference are model-based approaches

Note these are not the only approaches to tree-building but they are the most widely used

Maximum parsimony

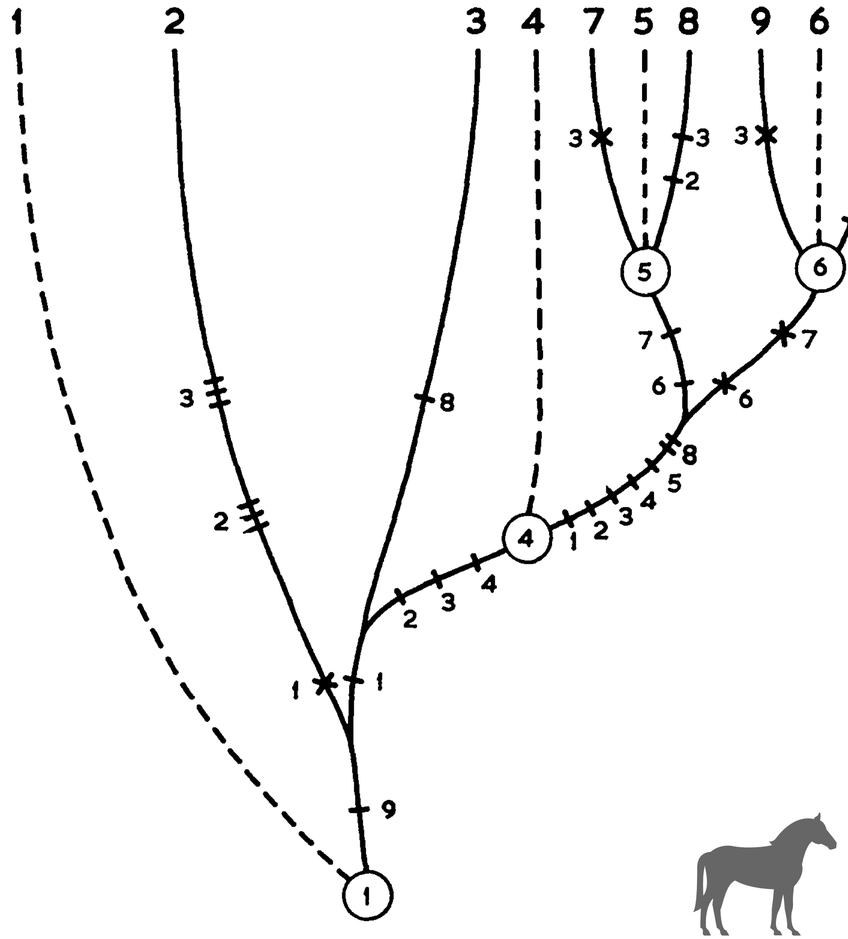
(also sometimes known as the minimum evolution method)

Maximum parsimony

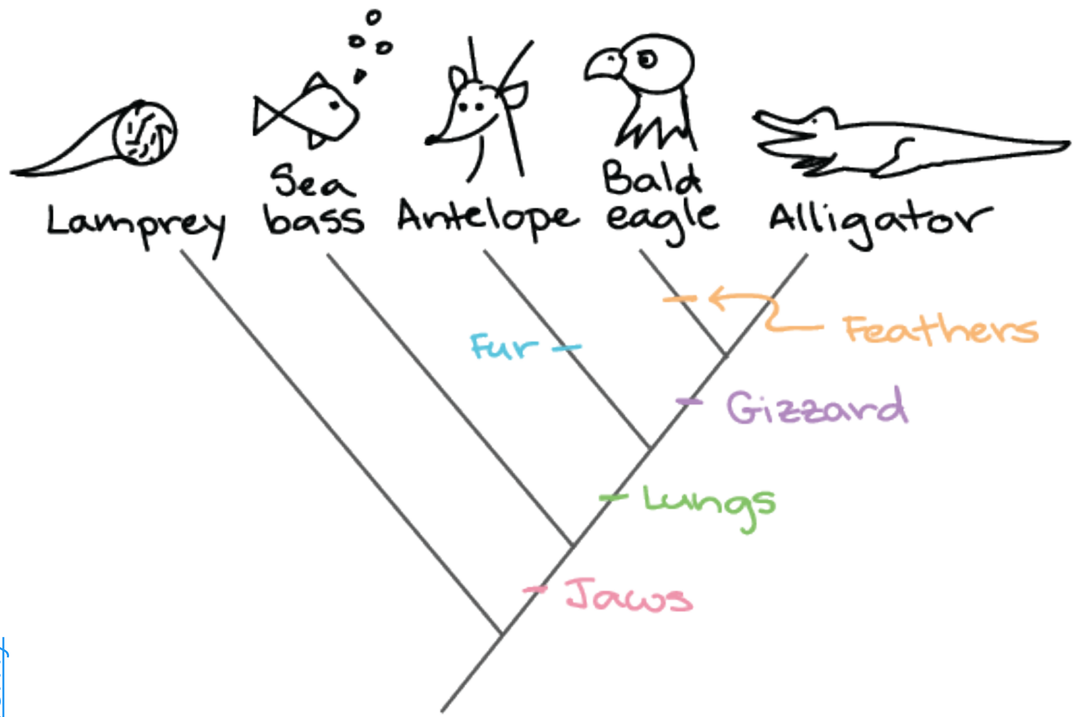
The maximum parsimony tree is the unrooted tree with the *lowest parsimony score*

The parsimony score of a tree is defined as the *minimum number of changes* required to explain the data summed across characters

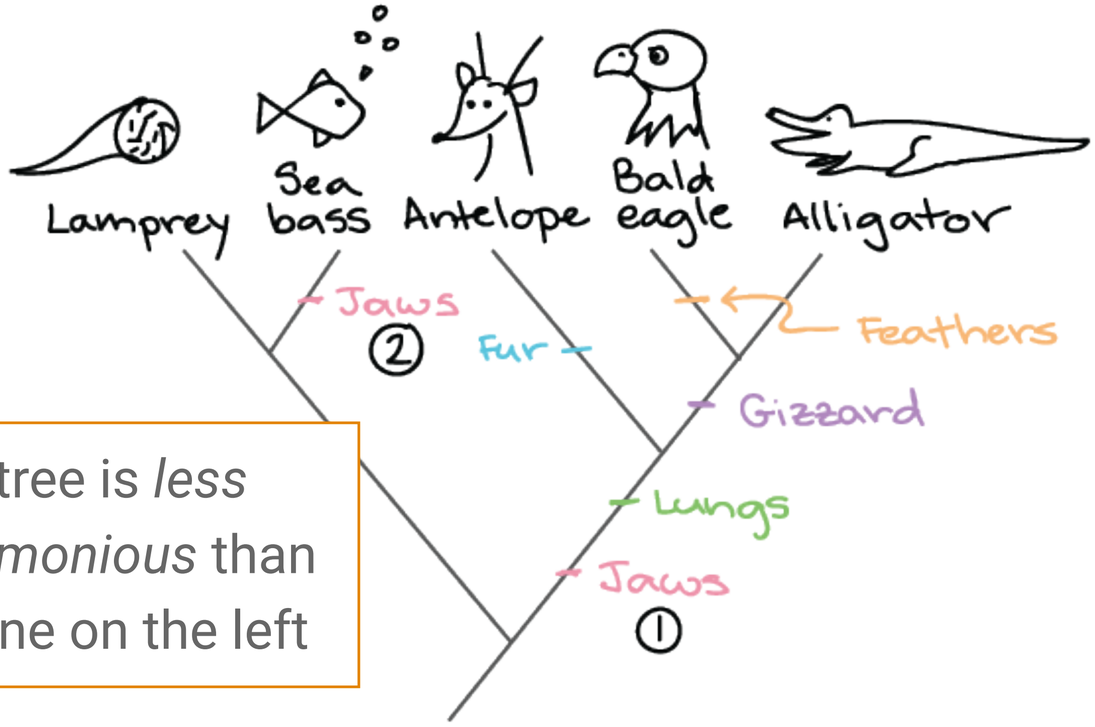
Maximum parsimony first described in *Edwards and Cavalli-Sforza* (1964)



Phylogeny of fossil horses. It was (I think) the first tree constructed using parsimony and discrete morphological characters by *Camin and Sokal* (1965) — this study popularised the use of parsimony among systematists



This tree is *less parsimonious* than the one on the left



Source *Khan Academy*

Maximum parsimony

Parsimony can not identify the location of the root, so we can use an outgroup to root the tree

There can be more than one tree with the same parsimony score

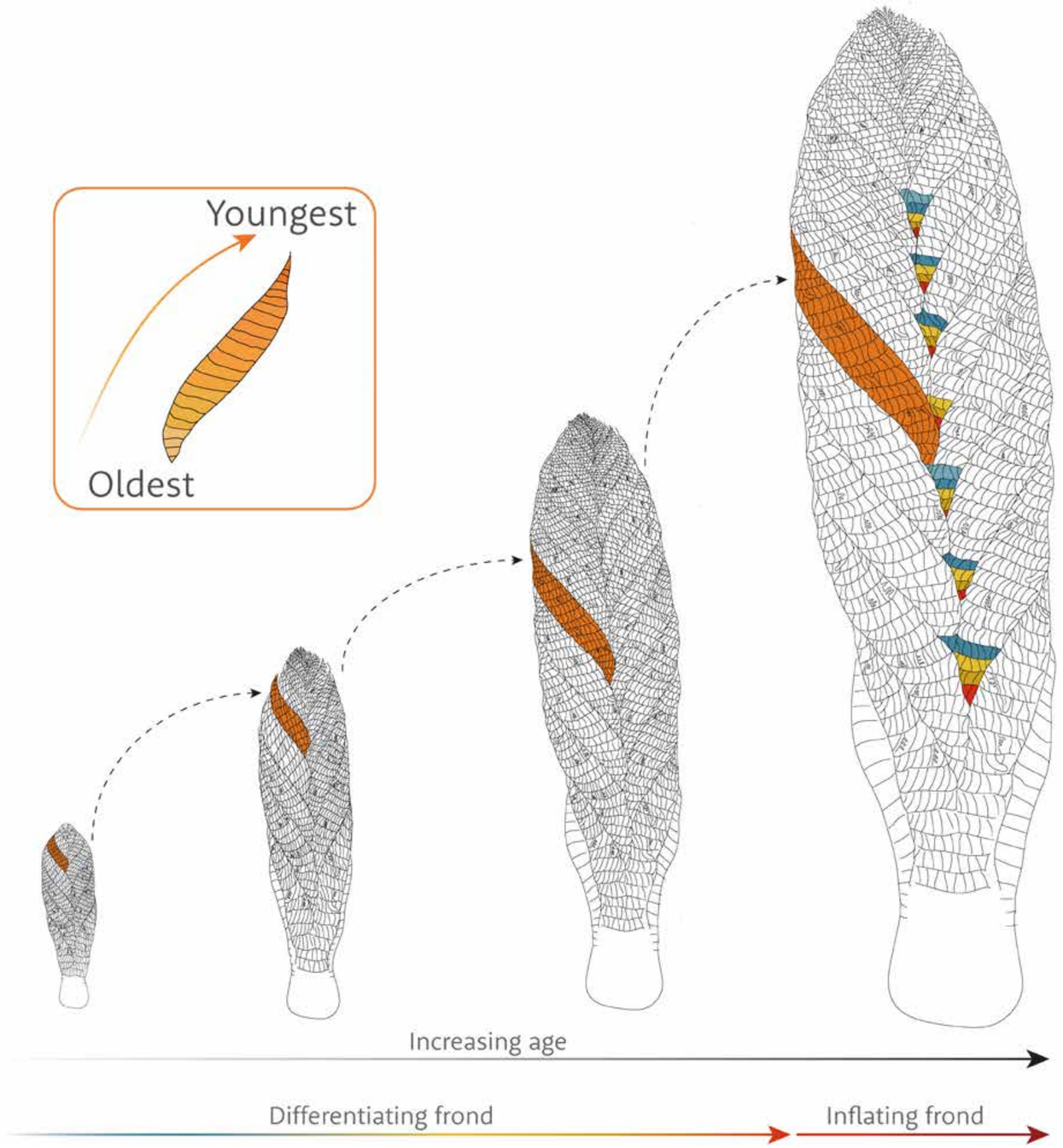
Parsimony does not make explicit assumptions about the evolutionary process

Maximum parsimony can only be used to estimate tree topology

Exercise

Tree building using parsimony

Data from *Dunn* (2016). See also *Dunn et al.* (2021) Phylogenetic affinity of the enigmatic *Charnia*



Images Charnwood Forest Geopark

Reconstructed Ediacaran fauna, 560 Ma

Charnia specimen

#NEXUS

Initiates the nexus block

```
[Matrix modified from Dunn (2016)]

BEGIN DATA;

DIMENSIONS  NTAX=10 NCHAR=117;
    FORMAT DATATYPE = STANDARD SYMBOLS= " 0 1 2 3" MISSING=? GAP=- ;

MATRIX

Charnia         00?1??1??????????0???1?211201??????????0-?-????????
Laccaria        110?001000000000-000--00--00---00--0--------000-
Capsaspora      001011-00------000-00---00--------0----------0-0-
Monosiga        001000-11------000-00---00--------0----------0-0-
Sycon           00110011111111111110100110--0000000000----0---000-
Amphimedon      00110011111111111121100110--00000000000---0---000-
Trichoplax      0011001111111100000-0000210--01111110000--00---000-
Mnemiopsis      0011001111111100000-00112112001100101111121110011110
Nematostella    00110011111110000000112111001100101111111101111111
Hydra           0011001111111100000-00112111001100101111111110111111

;

END;
```

```
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[Matrix modified from Dunn (2016)]

BEGIN DATA;

DIMENSIONS  NTAX=10 NCHAR=117;
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MATRIX

Charnia         00?1??1???????????0???1?211201??????????0-?-????????
Laccaria        110?001000000000000-000--00--00---00--0--------000-
Capsaspora      001011-00------000-00---00--------0----------0-0-
Monosiga        001000-11------000-00---00--------0----------0-0-
Sycon           00110011111111111110100110--0000000000----0---000-
Amphimedon      00110011111111111121100110--00000000000---0---000-
Trichoplax      0011001111111100000-0000210--01111110000--00---000-
Mnemiopsis      0011001111111100000-00112112001100101111121110011110
Nematostella    00110011111110000000112111001100101111111101111111
Hydra           0011001111111100000-00112111001100101111111110111111

;

END;
```

Comments go in square brackets

Great for keeping track of data sources

```
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[Matrix modified from Dunn (2016)]

BEGIN DATA;

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MATRIX

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Laccaria        110?001000000000000-000--00--00---00--0--------000-
Capsaspora      001011-00------000-00---00--------0----------0-0-
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Trichoplax      0011001111111100000-0000210--01111110000--00---000-
Mnemiopsis      0011001111111100000-00112112001100101111211100111110
Nematostella    00110011111110000000112111001100101111111101111111
Hydra           0011001111111100000-00112111001100101111111110111111

;

END;
```

Initiates the data block

```
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[Matrix modified from Dunn (2016)]

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MATRIX

Charnia         00?1??1???????????0???1?211201??????????0-?-????????
Laccaria        110?001000000000000-000--00--00---00--0--------000-
Capsaspora      001011-00------000-00---00--------0----------0-0-
Monosiga        001000-11------000-00---00--------0----------0-0-
Sycon           00110011111111111110100110--0000000000----0---000-
Amphimedon      00110011111111111121100110--00000000000---0---000-
Trichoplax      00110011111100000-0000210--01111110000--00---000-
Mnemiopsis      00110011111100000-00112112001100101111211100111110
Nematostella    00110011111110000000112111001100101111111101111111
Hydra           00110011111100000-00112111001100101111111110111111

;

END;
```

Number of taxa and characters in the matrix

```
#NEXUS

[Matrix modified from Dunn (2016)]

BEGIN DATA;

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    FORMAT DATATYPE = STANDARD SYMBOLS= " 0 1 2 3" MISSING=? GAP=- ;

MATRIX

Charnia         00?1??1???????????0???1?211201??????????0-?-????????
Laccaria        110?001000000000000-000--00--00---00--0--------000-
Capsaspora      001011-00------000-00---00--------0----------0-0-
Monosiga        001000-11------000-00---00--------0----------0-0-
Sycon           00110011111111111110100110--0000000000----0---000-
Amphimedon      00110011111111111121100110--00000000000---0---000-
Trichoplax      0011001111111100000-0000210--01111110000--00---000-
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Nematostella    00110011111110000000112111001100101111111101111111
Hydra           0011001111111100000-00112111001100101111111110111111

;

END;
```

Details about the data

```
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Monosiga        001000-11------000-00---00--------0----------0-0-
Sycon           00110011111111111110100110--0000000000----0---000-
Amphimedon      00110011111111111121100110--00000000000---0---000-
Trichoplax      0011001111111100000-0000210--01111110000--00---000-
Mnemiopsis      0011001111111100000-00112112001100101111211100111110
Nematostella    00110011111110000000112111001100101111111101111111
Hydra           0011001111111100000-00112111001100101111111110111111

;

END;
```

Initiates the data matrix

```
#NEXUS

[Matrix modified from Dunn (2016)]

BEGIN DATA;

DIMENSIONS  NTAX=10 NCHAR=117;
    FORMAT DATATYPE = STANDARD SYMBOLS= " 0 1 2 3" MISSING=? GAP=- ;

MATRIX

Charnia         00?1??1??????????0???1?211201??????????0-?-????????
Laccaria        110?00100000000000-000--00--00---00--0--------000-
Capsaspora      001011-00------000-00---00--------0----------0-0-
Monosiga        001000-11------000-00---00--------0----------0-0-
Sycon           00110011111111111110100110--0000000000----0---000-
Amphimedon      00110011111111111121100110--00000000000---0---000-
Trichoplax      00110011111100000-0000210--01111110000--00---000-
Mnemiopsis      00110011111100000-00112112001100101111211100111 10
Nematostella    00110011111110000000112111001100101111111101111111
Hydra           00110011111100000-00112111001100101111111110111111

;

END;
```

Phylogenetic data matrix

Taxon names left, characters right after tabs or spaces

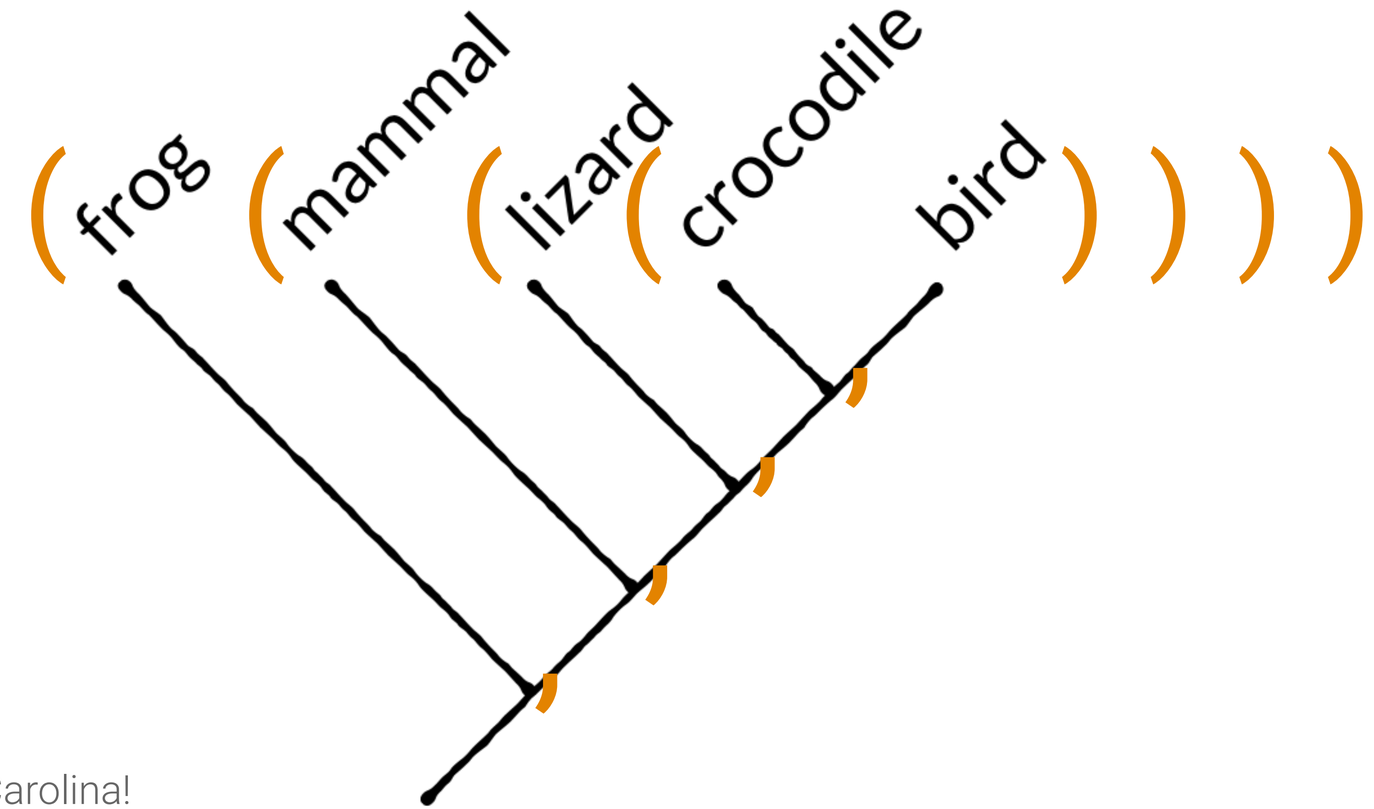
```
#NEXUS

[Matrix modified from Dunn (2016)]

BEGIN DATA;

DIMENSIONS  NTAX=10 NCHAR=117;
    FORMAT DATATYPE = STANDARD SYMBOLS= " 0 1 2 3" MISSING=? GAP=- ;

MATRIX

Charnia        00?1??1???????????0???1?211201??????????0-?-????????
Laccaria       110?001000000000-000--00--00---00--0--------000-
Capsaspora     001011-00------000-00---00--------0----------0-0-
Monosiga       001000-11------000-00---00--------0----------0-0-
Sycon          00110011111111111110100110--0000000000----0---000-
Amphimedon     00110011111111111121100110--00000000000---0---000-
Trichoplax     0011001111111100000-0000210--01111110000--00---000-
Mnemiopsis     0011001111111100000-00112112001100101111211100111110
Nematostella   00110011111110000000112111001100101111111101111111
Hydra          0011001111111100000-00112111001100101111111110111111

;

END;
```

Initiates the end of the data matrix

```
#NEXUS

[Matrix modified from Dunn (2016)]

BEGIN DATA;

DIMENSIONS  NTAX=10 NCHAR=117;
    FORMAT DATATYPE = STANDARD SYMBOLS= " 0 1 2 3" MISSING=? GAP=- ;

MATRIX

Charnia         00?1??1???????????0???1?211201??????????0-?-????????
Laccaria        110?001000000000-000--00--00---00--0--------000-
Capsaspora      001011-00------000-00---00--------0----------0-0-
Monosiga        001000-11------000-00---00--------0----------0-0-
Sycon           00110011111111111110100110--0000000000----0---000-
Amphimedon      00110011111111111121100110--00000000000---0---000-
Trichoplax      0011001111111100000-0000210--01111110000--00---000-
Mnemiopsis      0011001111111100000-00112112001100101111211100111110
Nematostella    00110011111110000000112111001100101111111101111111
Hydra           0011001111111100000-00112111001100101111111110111111

;

END;
```

Initiates the end of the nexus block

Newick format



Named after Newick's Lobster House, North Carolina!

```
(frog, (mammal, (lizard, (crocodile, bird))));
```

Statistical inconsistency

The following slides are adapted from Tracy Heath (in turn adapted from Mark Holder)

Statistical consistency

Ideally, we want an inference method to return the correct answer if we provide enough data

An estimator is statistically consistent if it is guaranteed to get the correct answer with an infinite amount of data

It has been demonstrated that in some scenarios, parsimony is statistically inconsistent. The issue is known as long branch attraction

Convergent evolution

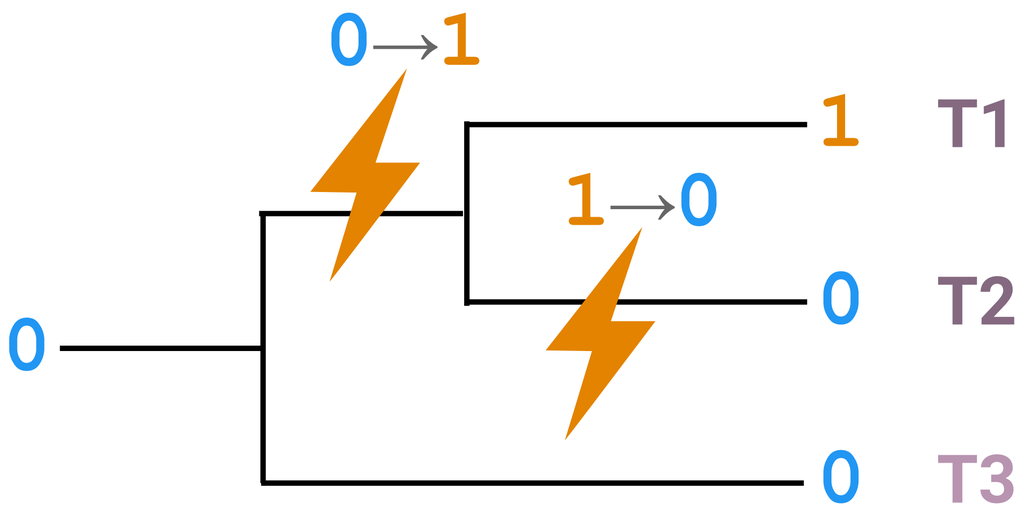
A trait that is found in two species, but not in their common ancestor is an example of homoplasy

We find widespread homoplasy in both morphological and molecular datasets

Bird, Pterosaur (extinct), fruit bat: 3 different vertebrates independently lightened bones and transformed hands into wings

Image source *Convergent Evolution: an introduction*

Convergence and parsimony



Hypothetical tree showing multiple transitions at the same character

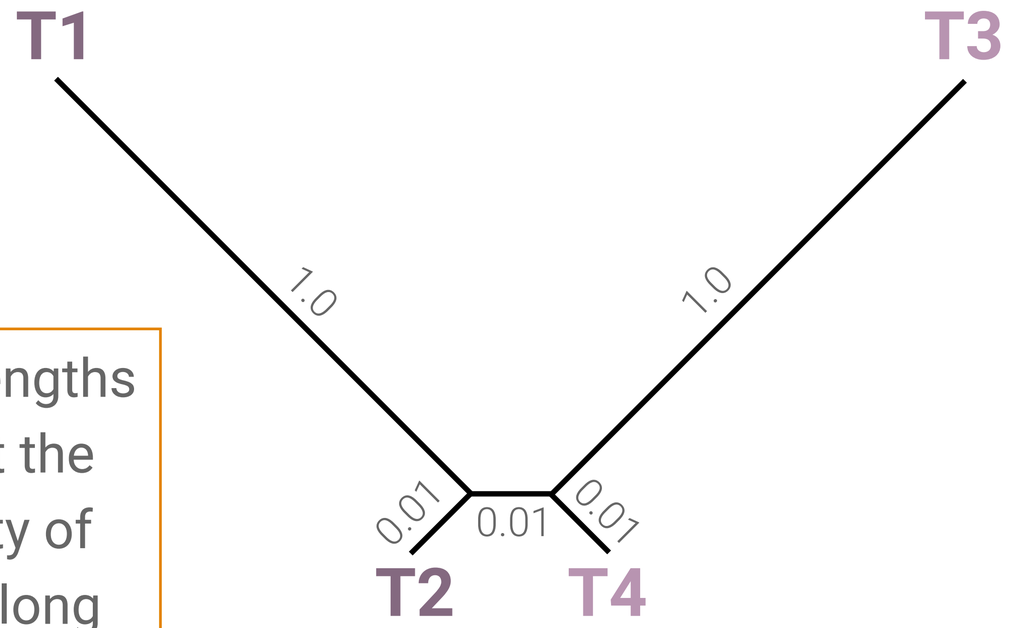
Parsimony will always favour the tree with the smallest number of changes

The method does not account for multiple transitions (or “hits”), e.g., 0 → 1 → 0

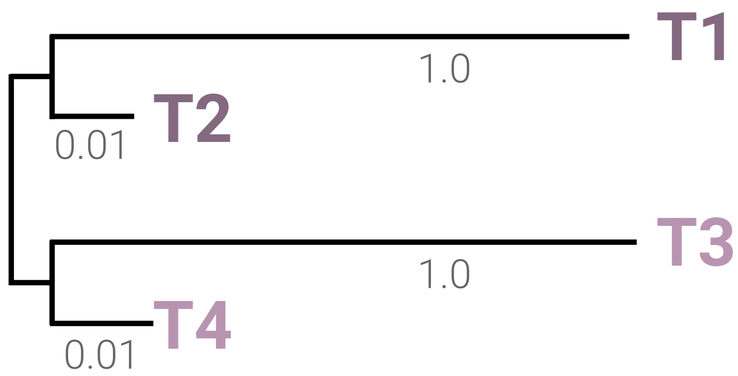
We can only invoke convergent evolution *ad hoc* after inference

Long branch attraction

Say we have the following tree, with 2 long and 2 short branches

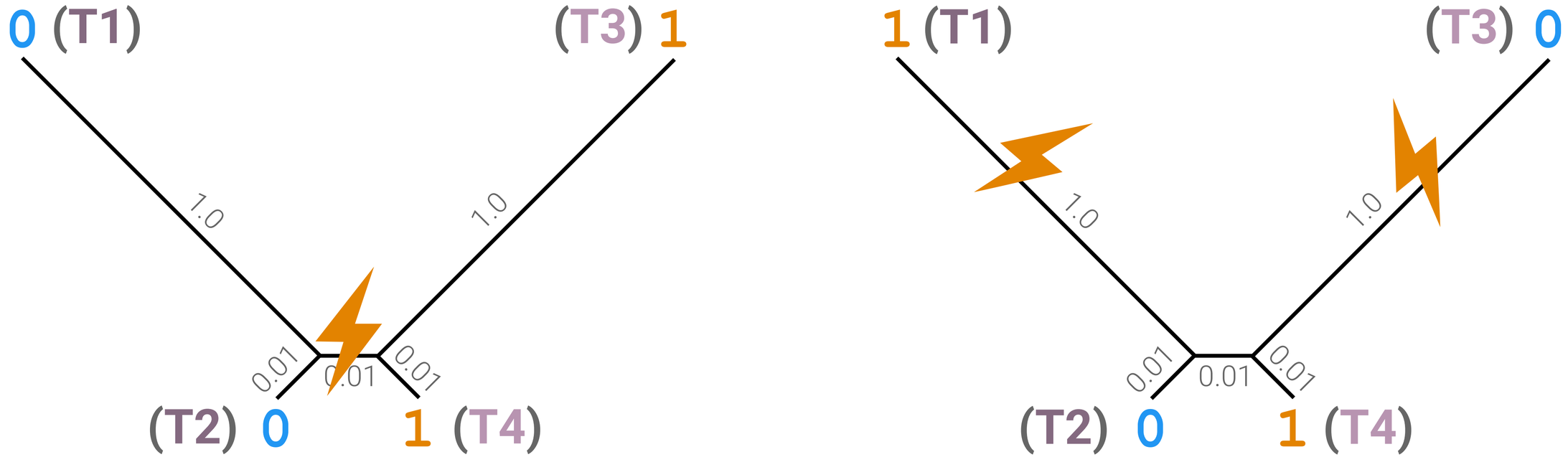


Branch lengths represent the probability of change along that branch



The rooted version of the same tree

Long branch attraction



Some time in the past

A transition somewhere along the branch that separates (T1, T2) and (T3, T4)

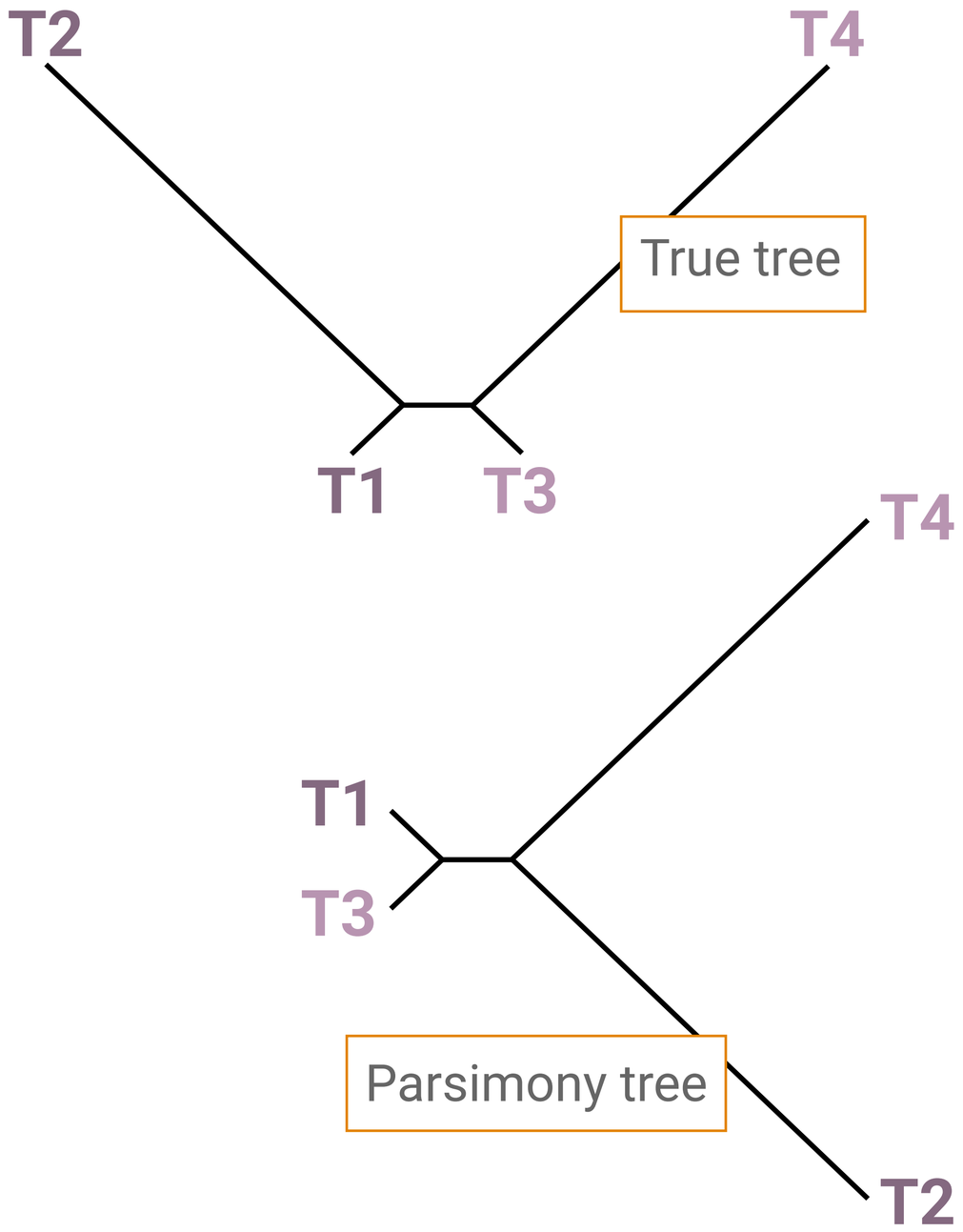
Subsequent transitions along the branches leading to T1 and T3

Long branch attraction

Parsimony is almost guaranteed to get this tree wrong

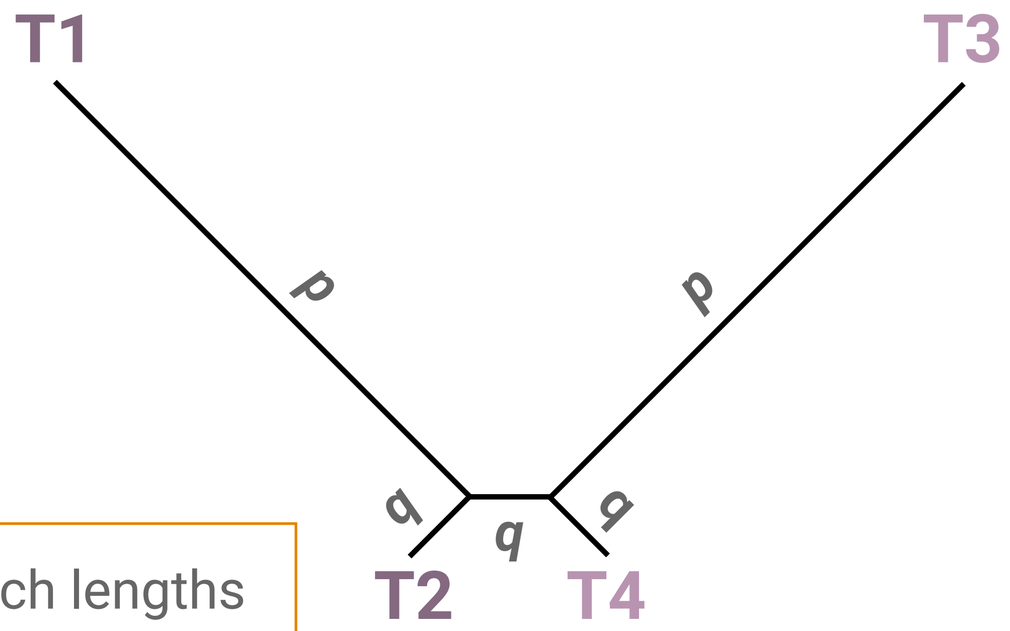
And more data makes this problem worse, meaning this approach is statistically inconsistent

This issue has been thoroughly characterised for molecular data



Felsenstein (1978)
Felsenstein (2004), *Inferring Phylogenies*

Long branch attraction



Branch lengths represent the probability (***p***, ***q***) of change along that branch

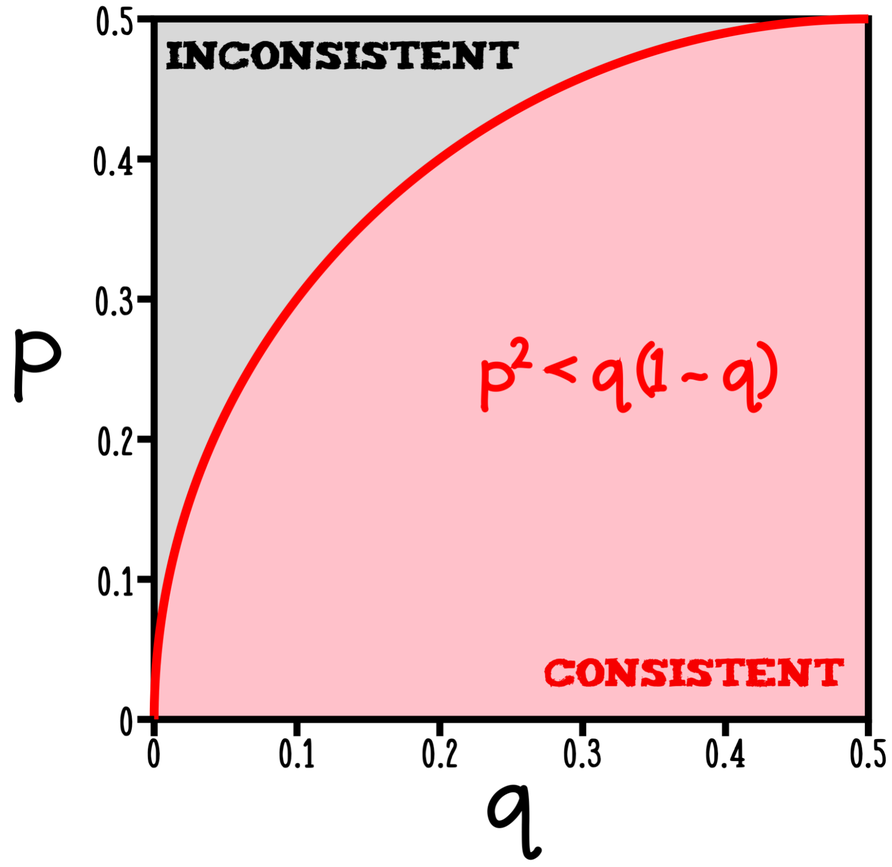
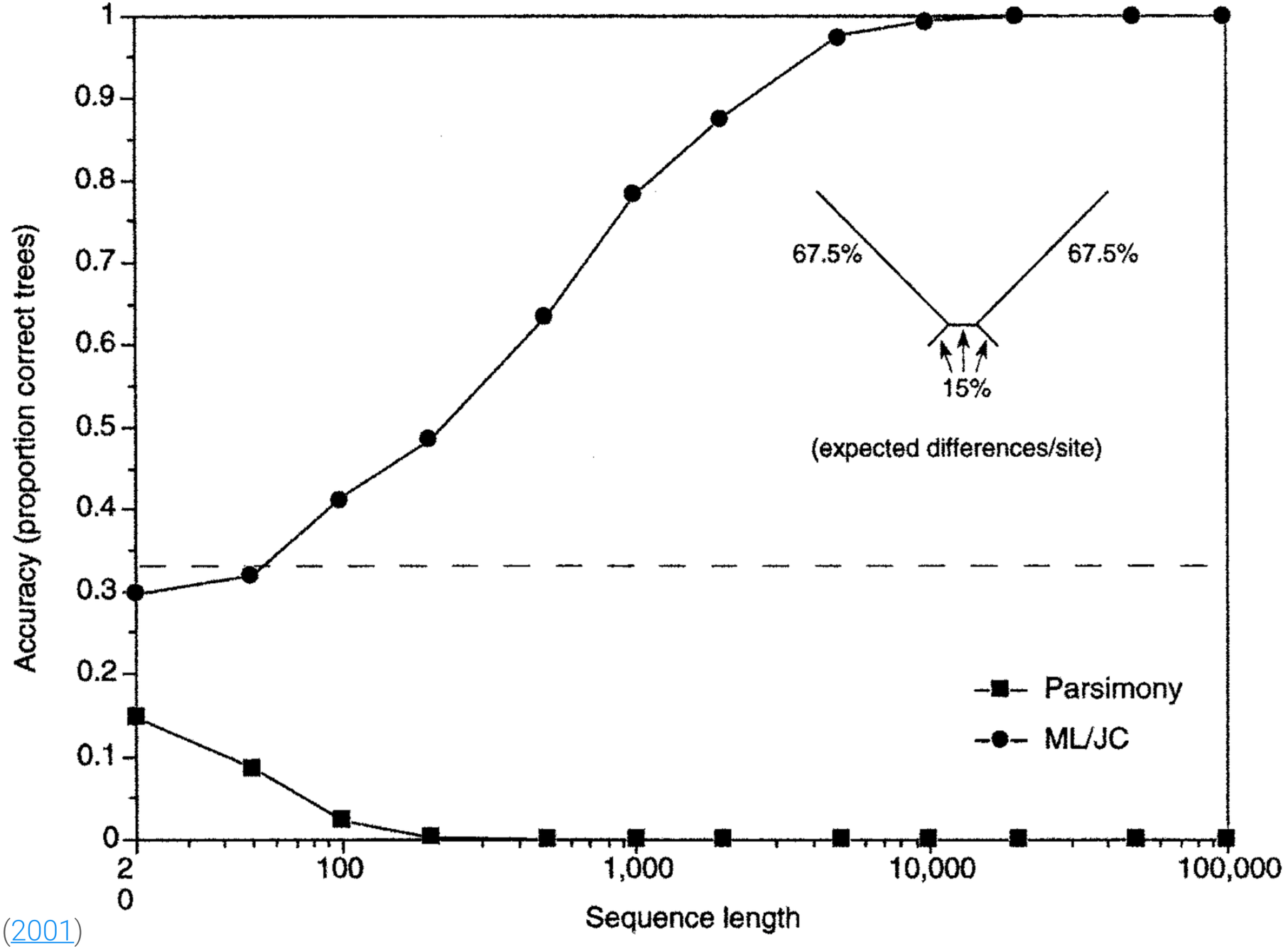


Image source Tracy Heath

The area in grey, is the area of parameter space where you are almost guaranteed to recover the wrong tree, with increasing certainty the more data you have

Felsenstein (2004), *Inferring Phylogenies*

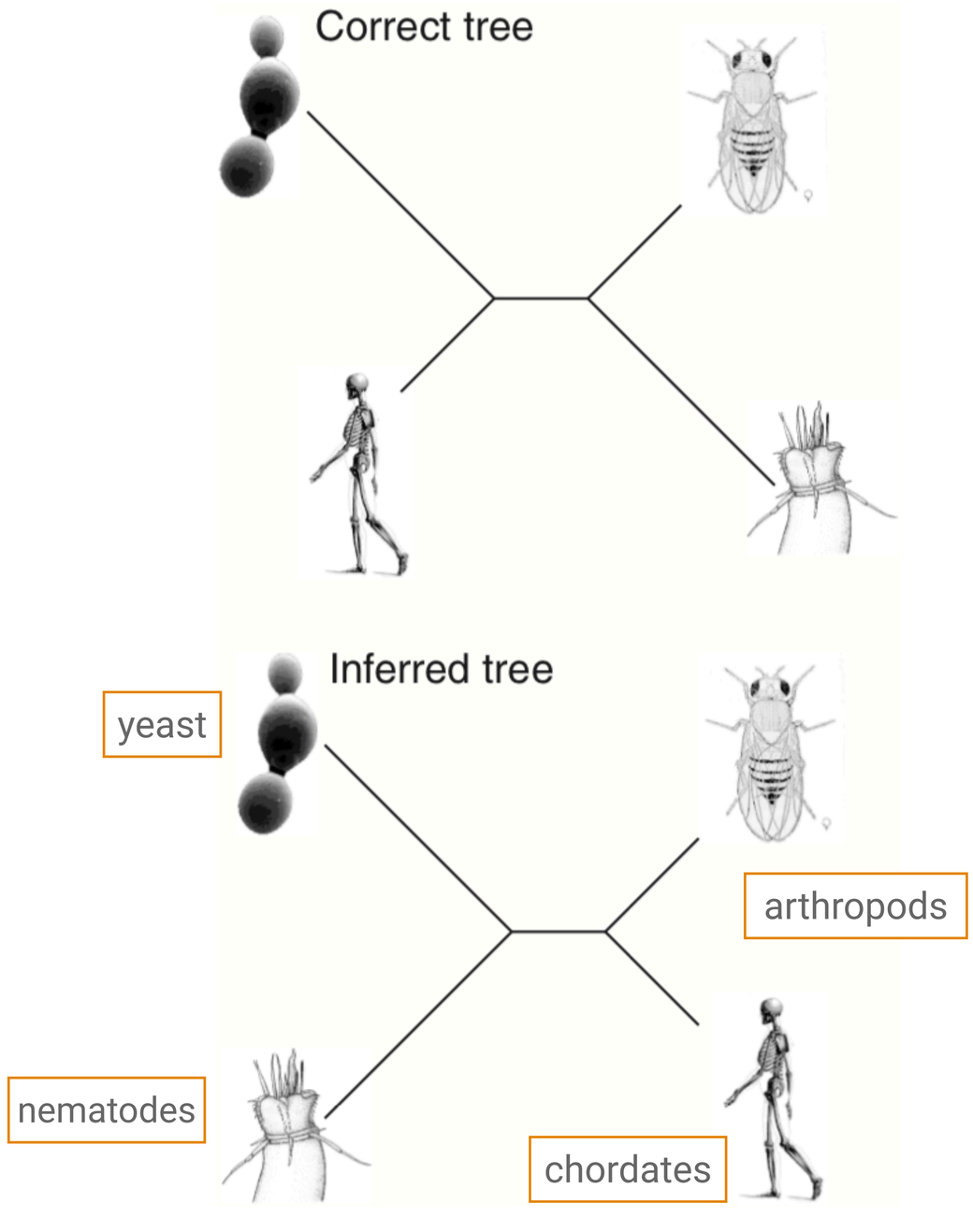


Swafford et al. (2001)

A classic case of LBA

The relationship between nematodes, arthropods, and chordates was misunderstood for a long time

- **Ecdysozoa***
  (arthropods, nematodes), vertebrates
- **Coelomata**
  (arthropods, vertebrates), nematodes



*widely accepted today, Image: *Telford et al.* (2005)

Parsimony in paleobiology

PLOS ONE

OPEN ACCESS Freely available online

Bayesian Analysis Using a Simple Likelihood Model Outperforms Parsimony for Estimation of Phylogeny from Discrete Morphological Data

April M. Wright*, David M. Hillis

Department of Integrative Biology, University of Texas at Austin, Austin, Texas, United States of America

Abstract

Despite the introduction of likelihood-based methods for estimating phylogenetic trees from phenotypic data, parsimony remains the most widely-used optimality criterion for building trees from discrete morphological data. However, it has been known for decades that there are regions of solution space in which parsimony is a poor estimator of tree topology. Numerous software implementations of likelihood-based models for the estimation of phylogeny from discrete morphological data exist, especially for the Mk model of discrete character evolution. Here we explore the efficacy of Bayesian estimation of phylogeny, using the Mk model, under conditions that are commonly encountered in paleontological studies. Using simulated data, we describe the relative performances of parsimony and the Mk model under a range of realistic conditions that include common scenarios of missing data and rate heterogeneity.

Citation: Wright AM, Hillis DM (2014) Bayesian Analysis Using a Simple Likelihood Model Outperforms Parsimony for Estimation of Phylogeny from Discrete Morphological Data. PLoS ONE 9(10): e109210. doi:10.1371/journal.pone.0109210

Editor: Art F. Y. Poon, British Columbia Centre for Excellence in HIV/AIDS, Canada

Received July 23, 2014; **Accepted** September 3, 2014; **Published** October 3, 2014

Data Availability: The authors confirm that all data underlying the findings are fully available without restriction. Data are available from Figshare using the DOI http://dx.doi.org/10.6084/m9.figshare.1160541.

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Competing Interests: The authors have declared that no competing interests exist.

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Introduction

For many decades, parsimony methods have been the most widely used approaches for estimation of phylogeny from discrete phenotypic data, despite the availability of likelihood-based methods for phylogenetic analysis. Maximum likelihood and Bayesian methods are commonly used in data sets combining molecules and morphology [1–5], but are used less frequently in morphology-only data sets [6]. As such, the efficacy of these methods under a range of conditions is not well-explored. In particular, the conditions that are investigated in most paleontological studies (many characters missing across sampled taxa, and rate heterogeneity among different sampled characters) lead some investigators to raise questions about the applicability of model-based approaches under these conditions [6–9].

At the present, the most widely implemented (in both pure likelihood and Bayesian contexts) model for estimating phylogenetic trees from discrete phenotypic data is the Mk model proposed by Lewis [10]. This model is a generalization of the 1969 Jukes-Cantor model of nucleotide sequence evolution [11]. The Mk model assumes a Markov process for character change, allowing for multiple character-state changes along a single branch. The probability of change in this model is symmetrical; in other words, the probability of changing from one state to another is the same as change in the reverse direction. This assumption can be relaxed in Bayesian implementations through the use of a hyperprior allowing variable change probabilities among states [12–14]. As many morphologists collect only variable or parsimony-informative characters (i.e., characters that can be used to discriminate among different tree topologies under the parsimony criterion), the distribution of characters collected does not reflect the distribution of all observable characters. This sampling bias can lead to poor estimation of the rate of character evolution within a data set, as well as inflated estimates of character change along branches of the estimated tree. To counteract this bias, Lewis [10] introduced versions of the Mk model that correct for biases in character collection. These versions were subsequently shown to have the desirable quality of statistical consistency [15].

Sampled characters within data sets typically evolve under different rates, developmental processes, and modes of evolution [7,16,17]. Although heterogeneity in the underlying evolutionary processes can present challenges to the application of evolutionary models [18], a distribution of different evolutionary rates of characters can be helpful for resolving branches at different levels in the tree. Extremely labile characters, for example, are useful for resolving recently diverged lineages, whereas slowly evolving characters may be more useful for resolving deep divergences in the tree. Likelihood-based methods can benefit from this heterogeneity by accounting for different rates of character evolution and the amount of time available for change (based on the estimated branch lengths in the tree; [19]). In contrast, high levels of rate heterogeneity among characters can be more problematic for parsimony methods, especially if all character changes are weighted equally [20].

This was the first paper to show that the same LBA issues that affect molecular data probably also affect morphology

Wright and Hillis (2014)

A slue of papers followed…

OPEN ACCESS Freely available online

PLOS ONE

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Advance Access publication February 19, 2020

Morphological Phylogenetics Evaluated Using Novel Evolutionary Simulations

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Associate Editor: Jeanne Serb

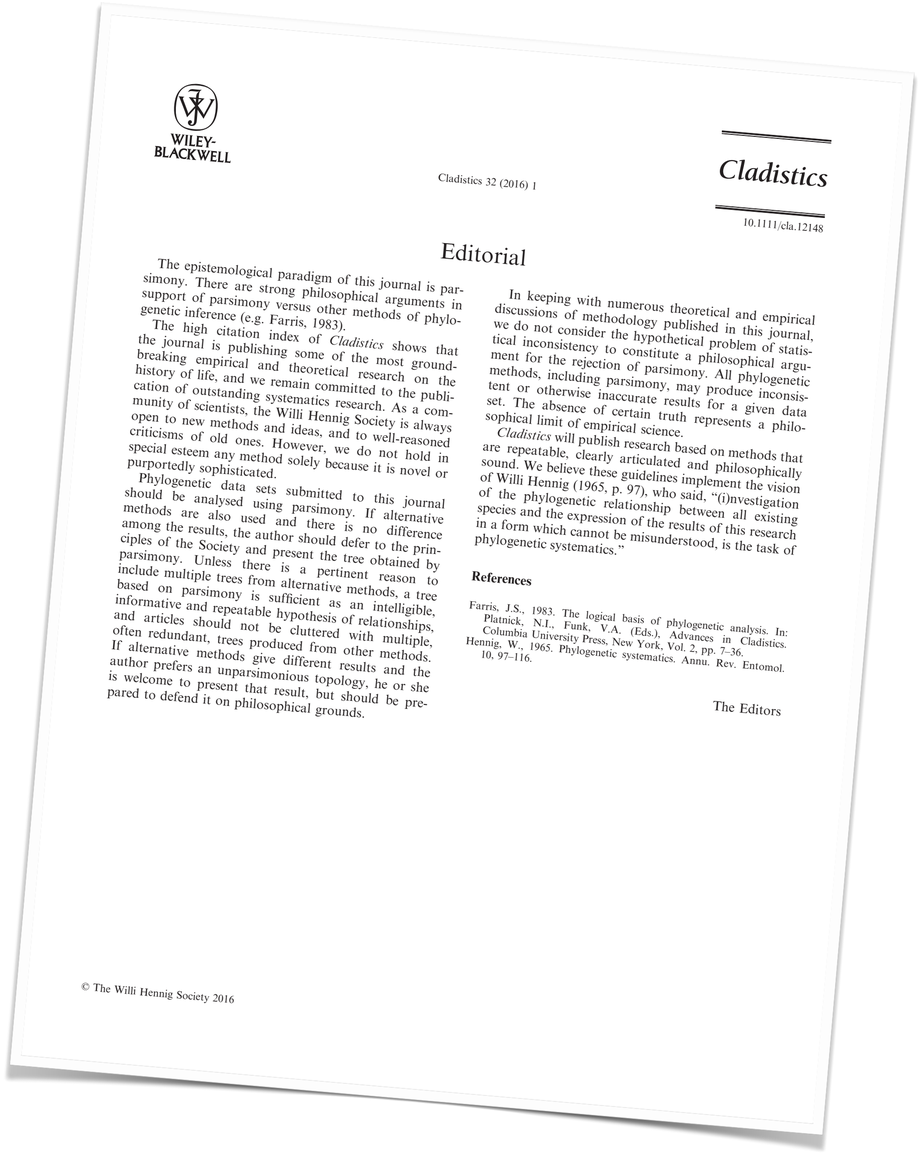
Abstract.—Evolutionary inferences require reliable phylogenies. Morphological data have traditionally been analyzed using maximum parsimony, but recent simulation studies have suggested that Bayesian analyses yield more accurate trees. This debate is ongoing, in part, because of ambiguity over modes of morphological evolution and a lack of appropriate models. Here, we investigate phylogenetic methods using two novel simulation models—one in which morphological characters evolve stochastically along lineages and another in which individuals undergo selection. Both models generate character data and lineage splitting simultaneously: the resulting trees are an emergent property, rather than a fixed parameter. Standard consensus methods for Bayesian searches (Mk) yield fewer incorrect nodes and quartets than the standard consensus trees recovered using equal weighting and implied weighting parsimony searches. Distances between the pool of derived trees (most parsimonious or posterior distribution) and the true trees—measured using Robinson-Foulds (RF), subtree prune and regraft (SPR), and tree bisection reconnection (TBR) metrics—demonstrate that this is related to the search strategy and consensus method of each technique. The amount and structure of homoplasy in character data differ between models. Morphological coherence, which has previously not been considered in this context, proves to be a more important factor for phylogenetic accuracy than homoplasy. Selection-based models exhibit relatively lower homoplasy, lower morphological coherence, and higher inaccuracy in inferred trees. Selection is a dominant driver of morphological evolution, but we demonstrate that it has a confounding effect on numerous character properties which are fundamental to phylogenetic inference. We suggest that the current debate should move beyond considerations of parsimony versus Bayesian, toward identifying modes of morphological evolution and using these to build models for probabilistic search methods. [Bayesian; evolution; morphology; parsimony; phylogenetics; selection; simulation.]

Phylogenetic trees provide a vital framework for evolutionary inferences. Consequently, the accuracy of phylogenetic estimates built using empirical characters underpins our understanding of evolutionary history. Morphology was fundamental to the conception and development of phylogenetic methods (Hennig 1950, 1965). However, in the genomic age, sequence data have replaced morphology as both the dominant source of phylogenetic information for estimating tree topology and the basis of numerical phylogenetic method development (Lee and Palci 2015; Lartillot et al. 2016). Molecular characters are more numerous than morphological ones and their evolution can be modeled based on empirical observations (Kimura 1980; Felsenstein 1981; Hasegawa et al. 1985). Nevertheless, morphology still plays a fundamental role. It is the only form of data by which we can incorporate fossils, and thus a deep-time perspective, in phylogenies. Fossil taxa allow the calibration of molecular clocks (Donoghue and Yang 2016); offer an independent test of evolutionary developmental hypotheses (Raff 2007); break long branches, and thus clarify otherwise intractable relationships (Donoghue et al. 1989; Wiens and Soltis 2005; Legg et al. 2013); and provide the only means of understanding diversity and evolution in deep time (Raup and Sepkoski 1982). For these reasons, integrating fossils in phylogenies is necessary in order to derive accurate phylogenies and reconstructions of character and clade evolution.

Morphological data have conventionally been analyzed using maximum parsimony (Kitching et al. 1998) in which trees that necessitate the fewest character changes are considered optimal. Characters are either treated as weighted equally or rescaled in relation to their homoplasy, for example, using implied weighting (IW; Goloboff 2013). Likelihood-based models have also been used to analyze morphological data, primarily through Bayesian analysis using the Mk model of character evolution (Lewis 2001). The Mk model is a k-parameter model, where k is the number of possible unordered states for a discrete morphological character (e.g., in an M2 model, characters could have $k = 2$ states). The model assumes that character state changes follow a Markov process, and thus the likelihood of changing from one state to another is determined only by the current state. The basic Mk model assumes that all state changes are equally likely and occur at the same rate, although these assumptions are not always true (Lewis 2001). Some characters might be gained or lost much faster or slower than others; as such numerous refinements have been proposed to account for asymmetrical evolutionary rates. For instance, the symmetrical (SYM) and all-rates-different (ARD) models (Paradis et al. 2004) are two extensions of the Mk model that can relax this assumption.

In 2016 the journal *Cladistics* published an editorial stating

“If alternative methods give different results and the author prefers an unparsimonious topology, he or she is welcome to present that result, but should be prepared to defend it on philosophical grounds”



WILEY-BLACKWELL

Cladistics 32 (2016) 1

Cladistics

10.1111/cla.12148

Editorial

The epistemological paradigm of this journal is parsimony. There are strong philosophical arguments in support of parsimony versus other methods of phylogenetic inference (e.g. Farris, 1983).

The high citation index of *Cladistics* shows that the journal is publishing some of the most groundbreaking empirical and theoretical research on the history of life, and we remain committed to the publication of outstanding systematics research. As a community of scientists, the Willi Hennig Society is always open to new methods and ideas, and to well-reasoned criticisms of old ones. However, we do not hold in special esteem any method solely because it is novel or purportedly sophisticated.

Phylogenetic data sets submitted to this journal should be analysed using parsimony. If alternative methods are also used and there is no difference among the results, the author should defer to the principles of the Society and present the tree obtained by parsimony. Unless there is a pertinent reason to include multiple trees from alternative methods, a tree based on parsimony is sufficient as an intelligible, informative and repeatable hypothesis of relationships, and articles should not be cluttered with multiple, often redundant, trees produced from other methods. If alternative methods give different results and the author prefers an unparsimonious topology, he or she is welcome to present that result, but should be prepared to defend it on philosophical grounds.

In keeping with numerous theoretical and empirical discussions of methodology published in this journal, we do not consider the hypothetical problem of statistical inconsistency to constitute a philosophical argument for the rejection of parsimony. All phylogenetic methods, including parsimony, may produce inconsistent or otherwise inaccurate results for a given data set. The absence of certain truth represents a philosophical limit of empirical science.

Cladistics will publish research based on methods that are repeatable, clearly articulated and philosophically sound. We believe these guidelines implement the vision of Willi Hennig (1965, p. 97), who said, “(i)nvestigation of the phylogenetic relationship between all existing species and the expression of the results of this research in a form which cannot be misunderstood, is the task of phylogenetic systematics.”

References

Farris, J.S., 1983. The logical basis of phylogenetic analysis. In: Platnick, N.I., Funk, V.A. (Eds.), Advances in Cladistics. Columbia University Press, New York, Vol. 2, pp. 7–36.
Hennig, W., 1965. Phylogenetic systematics. Annu. Rev. Entomol. 10, 97–116.

The Editors

The debacle was written up in Wired Magazine
See also #ParsimonyGate: The Perspective of a Reformed ‘Hardcore’ Cladist by Prosanta Chakrabarty

Final notes on parsimony

The greatest advantage of parsimony is its beautiful simplicity (Yang, 2014)

Computationally fast, often produces sensible results and still serves practical purposes

Some argue that parsimony is assumption free. Others argue parsimony does make assumptions, even if we don't know what they are, referred to as implicit assumptions

We are often interested in more than just the topology

Model-based approaches on the other hand make explicit assumptions about evolutionary processes

They are also flexible and have many more applications, e.g., rate estimation, phylogenetic dating

We will therefore turn our focus to model-based inference

Reading

Re-familiarise yourself with how to read a phylogenetic tree and rooting

A Brief History of Computational Phylogenetics *Joe Felsenstein*