## Bayesian Inference for Phenotypic and Palaeo Data

- Bayesian phylogenetics (especially BEAST) has a lot to offer for morphologists and palaeontologists
- Peculiarities of morphological / palaeontological data
- Some case studies
  - Cambrian trilobites (evolutionary rates)
  - Crocodile evolution (detecting convergent evolution)
  - Lizard viviparity (ancestral state reconstruction / overparameterisation)

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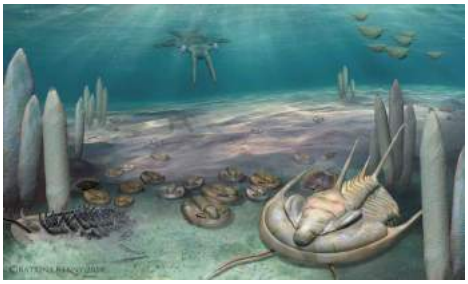
## Trilobites and the Cambrian explosion

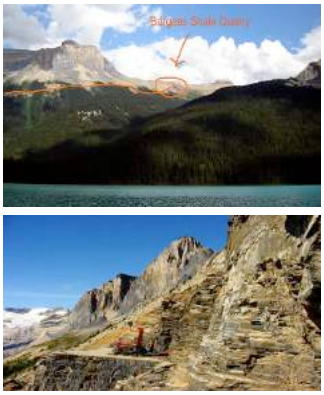
## The Cambrian Explosion



## Cambrian Explosion

| Late Precambrian ~560mya | Cambrian onwards ~540 mya |
|---|---|
| Low diversity | High diversity (nearly all fossilizable phyla) |
| Simple organisms, no complex senses | Complex organisms (eyes, appendages etc) |
| No predation (simple food webs) | Predator-prey interactions (complex food webs) |
| 2d ecosystems: No nekton (active swimmers) | 3D ecosystems: Nekton (active swimmers) |
| No infauna (burrowers) | Infauna (burrowers) |

Burgess shale (Canada)



Burgess shale (Canada)

Emu Bay shale (Australia)

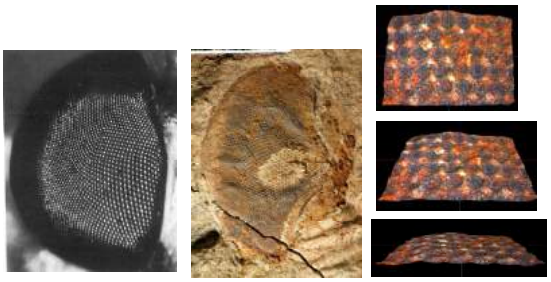
Trilobites and the Cambrian explosion

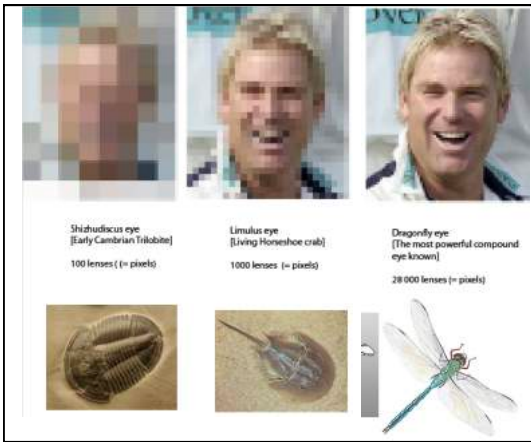
Gould's oddballs are not so odd. EBS includes:

*Hallucigenia* is an onychophoran (velvet worm)

*Anomalocaris* is a stem-arthropod

Fossil eyes of *Anomalocaris* and other taxa






Trilobites and the Cambrian explosion

Causes ?

- Predators
- Vision
- Infauna (burrowing)
- Genetic (hox genes)

← These are potentially interlinked. Explain increase in evolutionary rate (but not the timing)

Trilobites and the Cambrian explosion

Causes ?

- Predators
- Vision
- Infauna (burrowing)
- Genetic (hox genes)

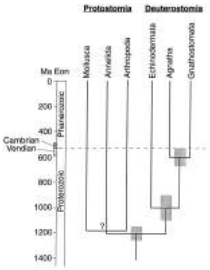
← These are potentially interlinked explain increase in evolutionary rate (but not why timing)

Interesting new idea – which explains Timing:

- Oyxgen levels increased around 540Ma
- Predatory invertebrates have higher metabolisms (and oxygen demands) than herbivores/scavengers
- Hence an increase in global oxygen allowed all the above to occur

## Timing – when did the Cambrian explosion begin ?

Molecular divergences suggests earlier diversification, well within the Precambrian




- (In)Famous 1996 paper dating the radiation of animals
- To twice the age of the Cambrian explosion!
- Used a strict clock and extrapolated slow vertebrate rates across the rest of the invertebrate tree!

- Great demonstration of the need for relaxed clocks

Molecular Evidence for Deep Precambrian Divergences Among Metazoan Phyla

## Timing – when did the Cambrian explosion begin ?

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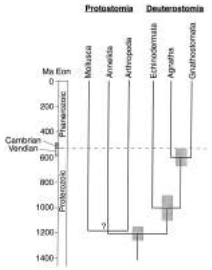
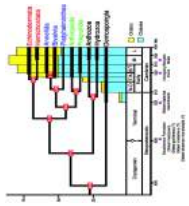


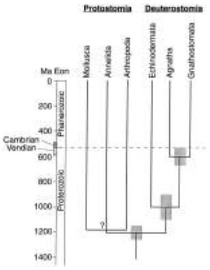
Relaxed clock (r8s) analyses halves the age!

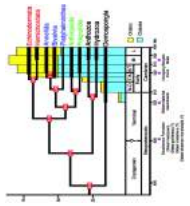
Molecular Evidence for Deep Precambrian Divergences Among Metazoan Phyla

Estimating metazoan divergence times with a molecular clock

## Timing – when did the Cambrian explosion begin ?

Molecular divergences suggests earlier diversification, well within the Precambrian
If rates vary over time, then molecular clock analyses are very challenging



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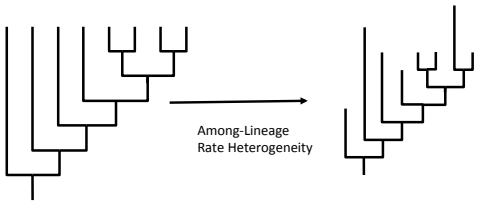
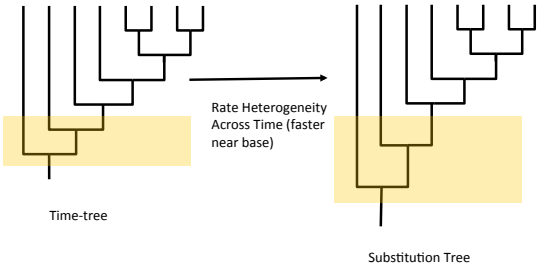



Time-tree

Substitution Tree

## Timing – when did the Cambrian explosion begin ?

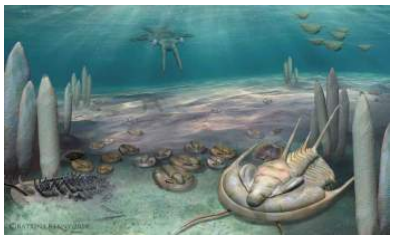



Time-tree

Substitution Tree

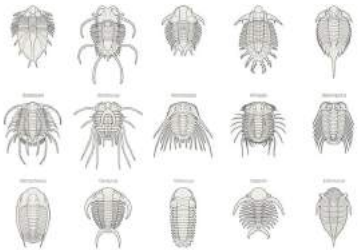
## Timing – when did the Cambrian explosion END?

- When did all the (marine) niches on our planet start to get saturated, with evolution slowing down to Phanerozoic norms ?
- No-one has ever attempted a precise answer to that question



## Trilobites – the best group for Cambrian macrovolutionary analyses

- Extremely abundant & diverse (~12% of species in the EBS); the beetles of the Cambrian
- Lots of hard body parts = lots of characters
- They appear as soon as the Cambrian fossil record starts to get good.



Trilobite evolutionary rates constrain the duration of the Cambrian explosion

## Trilobites – the best group for Cambrian macrovolutionary analyses

- Taxon sampling: >100 species from across most of the Cambrian
- Character sampling:
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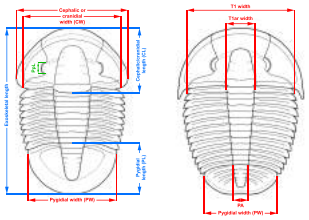
  - continuous traits
  - meristic traits



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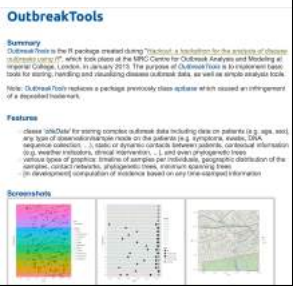

OutbreakTools

Summary

Features

Screenshots

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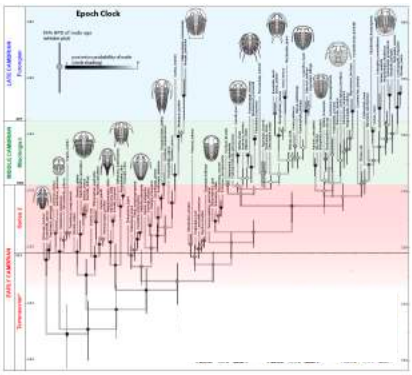
  - Outbreak Tools
- Clock models
  - Strict clock
  - UCLN relaxed clock
  - **Epoch clock**

Inferring Heterogeneous Evolutionary Processes Through Time: from Sequence Substitution to Phylogeography

## Trilobites – the best group for Cambrian macrovolutionary analyses

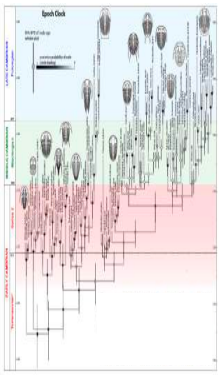



Epoch 3
Late Cambrian)

Epoch 2
(Mid Cambrian)

Epoch 1
(Early Cambrian)

## Trilobites – the best group for Cambrian macrovolutionary analyses



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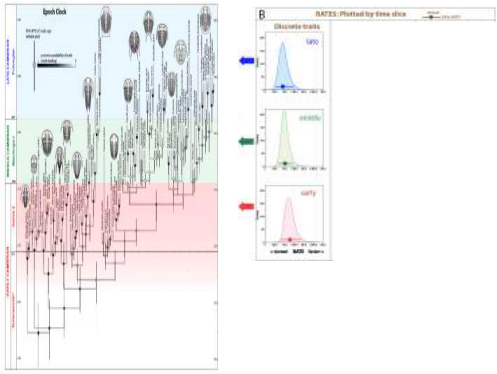

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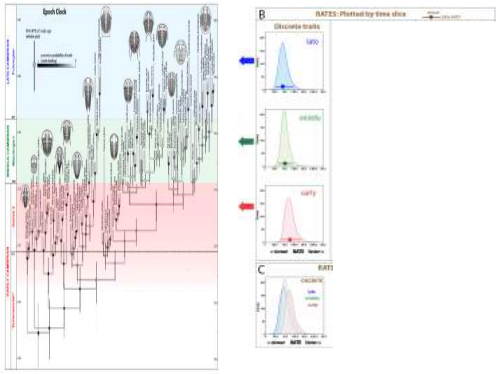

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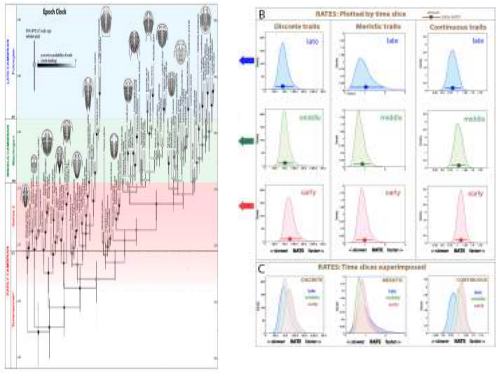

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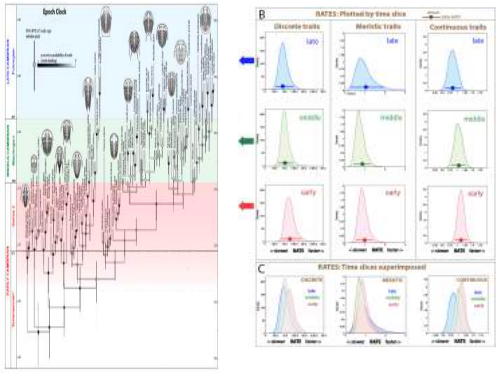

Conclusions

- The Cambrian explosion was already over by the time the first trilobites appear 520 M
- By the time the 'typical' Cambrian fossil record commences, it was evolutionary 'business as usual'
- The Cambrian explosion was briefer, and ended more abruptly, than previously believed
- The Burgess Shale, EBS and other famous Cambrian fossil sites are not windows into the greatest adaptive radiation of all time (*contra* Gould et al).

Trilobite evolutionary rates constrain the duration of the Cambrian explosion

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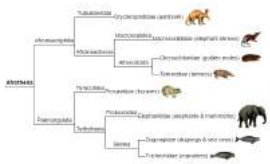


## Crocodile Evolution

## Crocodylians: Diversity and Anatomy

Diversity: ~24 living species

- ~14 species of crocodiles (lower canines exposed)

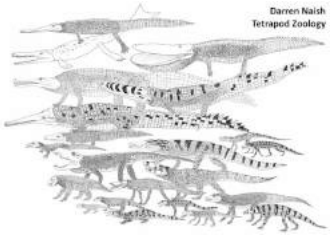
- ~ 8 species of alligators including caimans (lower canines hidden)

- 2 species of gavials/gharials (extremely narrow snouts for fish-eating)

## Crocodylians: Diversity and Anatomy

Diversity:

- All living crocs are sluggish, amphibious predators
- But fossil crocs were much more diverse
  - Active terrestrial forms (cursorial)
  - Small tree-climbing forms (arboreal)
  - Ocean-going forms

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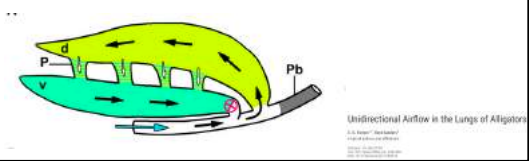
- Living crocs still retain many active, bird-like adaptations (fully-divided hearts and unidirectional lungs).

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- They can also gallop!
- Evidence of agile ancestors?

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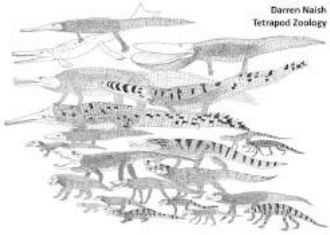


Crocodylians: Long-snouted forms

Indian Gavial (*Gavialis*)

Malayan or "false" Gavial (*Tomistoma*)

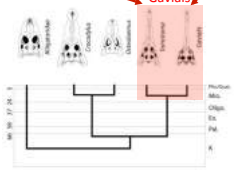
Crocodylians: Long-snouted forms

Malayan or "false" Gavial (*Tomistoma*)

Indian Gavial (*Gavialis*)

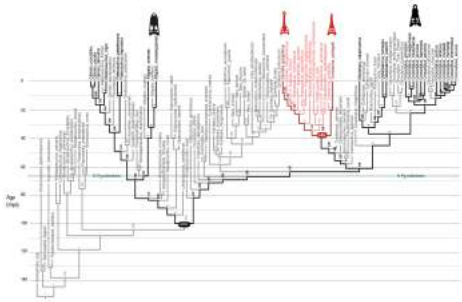
Gavials

Genomic tree:
Long-snouted forms
are a recent clade



Crocodylians: Long-snouted forms

Most fossils fit the genomic scheme.... light = fossils



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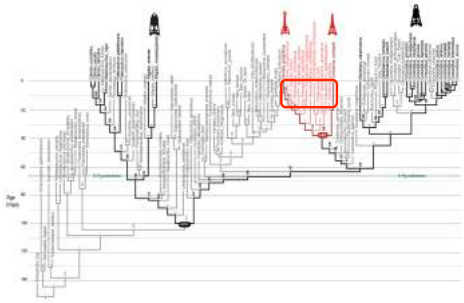


Crocodylians: Long-snouted forms

Most fossils fit the genomic scheme.... Except for thoracosaurs

Malayan or "false" Gavial (Tomistoma)

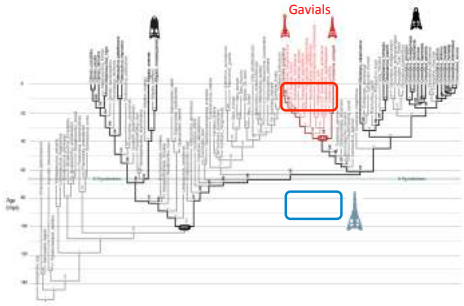
Indian Gavial (Gavialis)

Thoracosaur

Crocodylians: Long-snouted forms

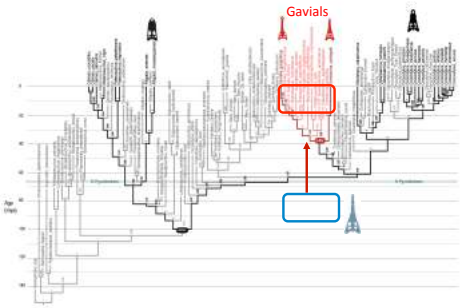
Most fossils fit the genomic scheme.... Except for thoracosaurs
Among the oldest crocs - three times as old as all other gavial fossils!

Gavials



## Crocodylians: Long-snouted forms

Every undated (parsimony, MrBayes) analysis puts thoracosaurs within living gavials

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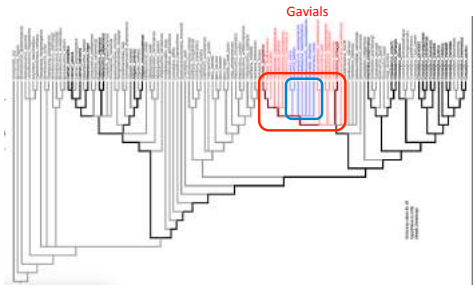
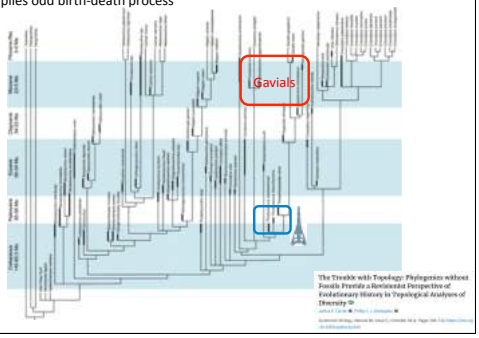



## Crocodylians: Long-snouted forms

Putting thoracosaurs within crown-clade gavials ruins the time-tree...

- 3x more ghost lineage (implying the croc fossil record is terrible)
- Poor stratigraphic concordance (oldest crocs are deeply nested!)
- Implies odd birth-death process

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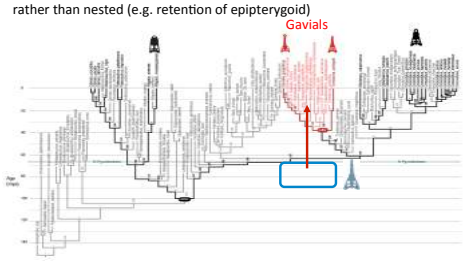
Notably, though, there are a few characters that do suggest thoracosaurs are basal rather than nested (e.g. retention of epipterygoid)



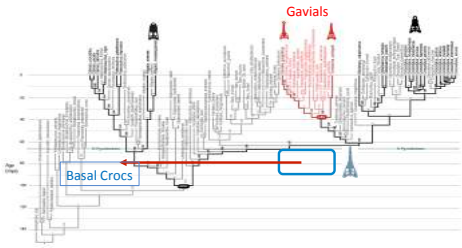

## Crocodylians: Long-snouted forms

Maybe thoracosaurs are basal crocs, which convergently evolved long snouts.

- Slightly less parsimonious (e.g. more convergence in snout characters)

But also

- Much more congruent with DNA
- Much more congruent with rest of stratigraphic record (all gavial fossils young)
- Consistent with some other morphological traits (epipterygoid)

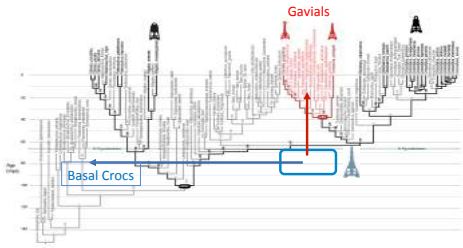



## Crocodylians: Long-snouted forms

2 hypotheses

Within gavials, favoured by parsimony

Basal, Favoured by everything else



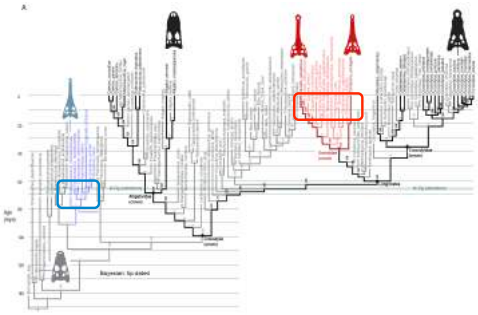
## BEAST to the rescue ?

Data
- 117 taxa including thoracosaurs
- 278 morphological traits
- 9200 bp

Total evidence tip-dating in BEAST / BEASTMC3
- Separate UCLN clocks
- Morph: Lewis, ascertainment, gamma, unpartitioned by state number

## BEAST to the rescue ?

Thoracosaurs are an early, basal lineage of crocs which convergently evolved gavial-like snouts (pp 0.99)



## BEAST to the rescue ?

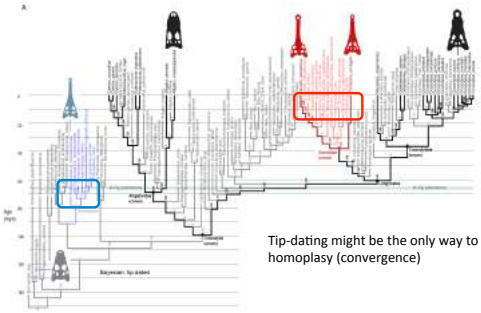
Thoracosaurs are an early, basal lineage of crocs which convergently evolved gavial-like snouts (pp 0.99)

Consistent with old age
Makes tree very congruent with stratigraphy
Reduces inferred ghost lineages
Explains why they retain some primitive bones

**But** slightly more homoplasy (i.e. more convergence)

## BEAST to the rescue ?

When similar organisms evolve multiple times at different ages ...



Tip-dating might be the only way to detect this homoplasy (convergence)

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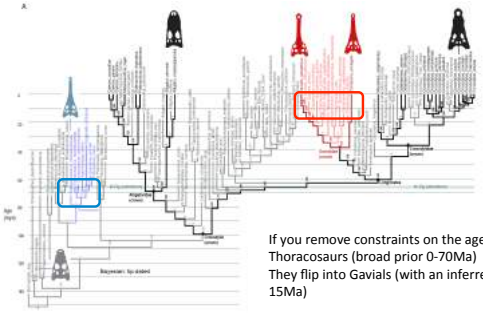
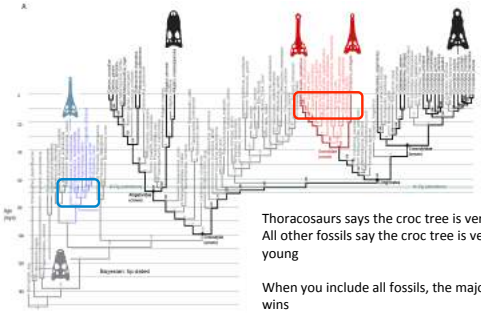


If you remove constraints on the age of Thoracosaurs (broad prior 0-70Ma)
They flip into Gavials (with an inferred age of 15Ma)

## BEAST to the rescue ?

Calibrations 'sort it out' among themselves in tip-dating ....



Thoracosaurs says the croc tree is very old
All other fossils say the croc tree is very young

When you include all fossils, the majority wins

## Bayesian Inference and Phenotypic Data

- Bayesian phylogenetics (especially BEAST) has a lot to offer for morphologists and palaeontologists
- Peculiarities of morphological / palaeontological data
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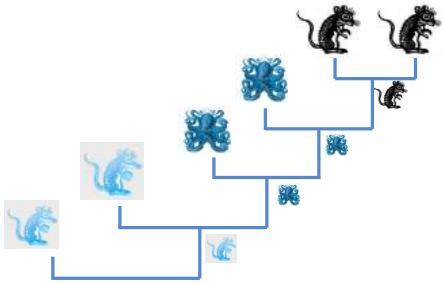
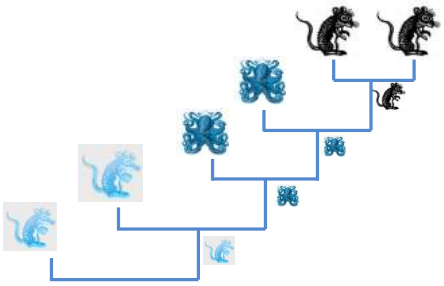
  - Lizard viviparity (ancestral state reconstruction)

## Ancestral State Reconstruction

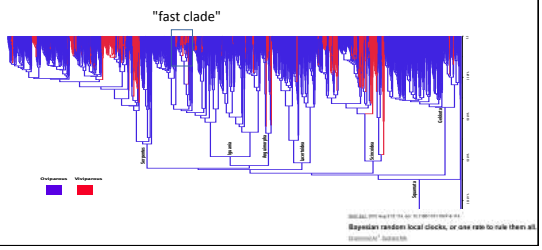


## Ancestral State Reconstruction



## Ancestral States: Why relaxed clocks matter!

- Biologists are tracing the evolution of traits on increasingly large trees (e.g. 10 000 birds, 6000 mammals, 4000 lizards and snakes).

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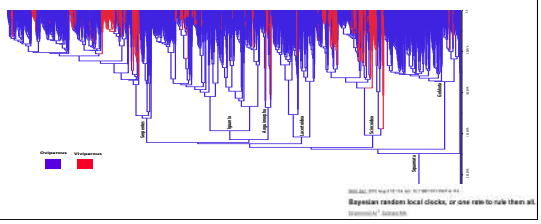
- Traits are never going to evolve at the same rate across such large swathes of the tree of life …



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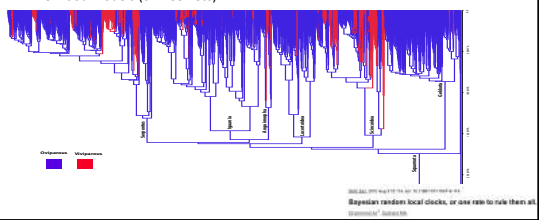
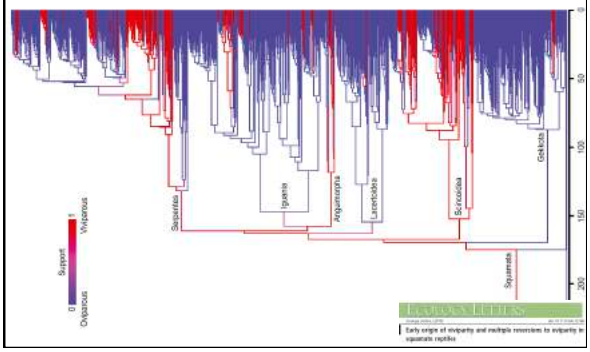
- Traits are never going to evolve at the same rate across such large swathes of the tree of life …
- If you don't account for this (e.g. random local clocks) , you can get ***totally erroneous*** ancestral state reconstructions under Bayesian or Likelihood models (or BiSSE etc).



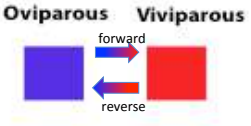
Ancestral state reconstruction (using strict clock) gave ludicrous results

- Ancestral lizard was live bearing (but all basal lineages are egg laying)
- Live-bearers reverted back to egg-laying over 100 times




The likelihood model used by most people..

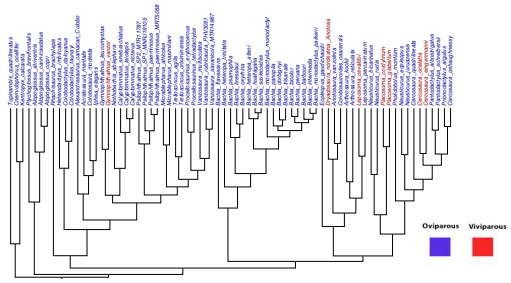
- Rate of evolution is homogenous throughout the tree (strict clock)
- But the asymmetry (forward-reverse bias) is estimated, ie a parameter that can be optimised and used to explain the observed data




- Likelihood's goofy solution to explain "fast evolving" clades:
  - Give one particular transition (e.g. reversals) a very high rate, so it should occur often
  - contrive a reconstruction that has lots of these transitions in fast clades

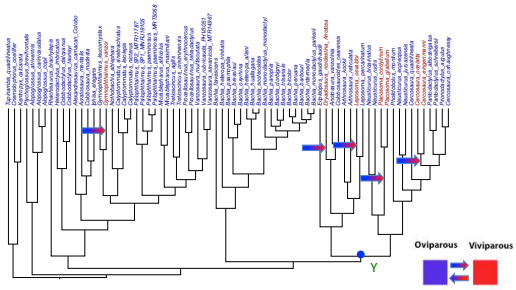
The Epic Fail explained …

- How would you map reproductive mode on this (hypothetical) tree?



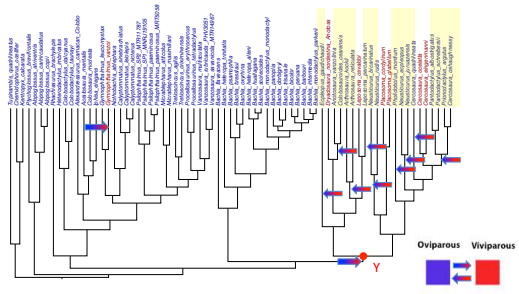

The Epic Fail explained …

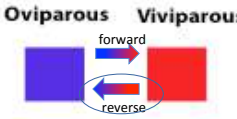
- Common-sense and parsimony says
  - lots of forward transformations (O-V)
  - Clade Y has a faster rate of change, ie 4 forward changes



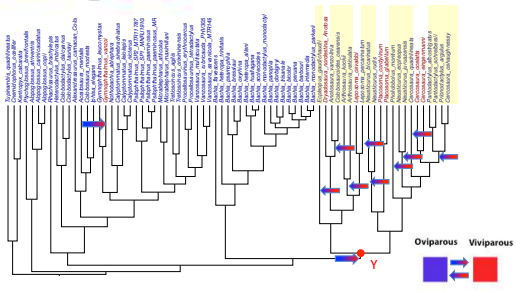

The Epic Fail explained …

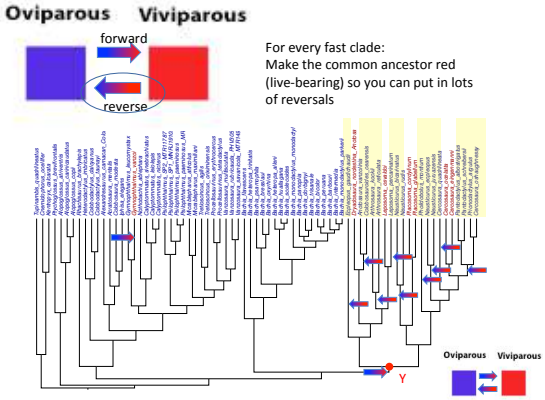
- Likelihood (rate-constant) reconstructs live-bearing at node Y on this tree, and then ~9 reversals back to egg-laying in lots of taxa (shaded)
- How does it converge on this ludicrous optimisation?




Make one transition
(e.g. reversals away from live bearing)
occur at a very fast rate

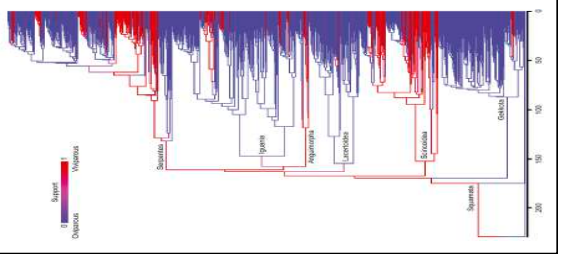





## Mis-paramaterised model

- The tree has lots of rate variability
- But model has no relaxed clock to account for it
- But model has asymmetric evolution – so that is hijacked to account for it

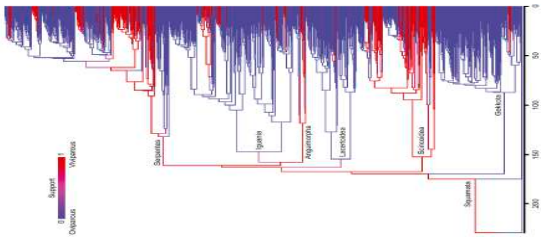
- It uses the substitution model to account for among-lineage rate heterogeneity.



## Mis-paramaterised model

Hijacking the substitution model to account for among-lineage rate heterogeneity, results:

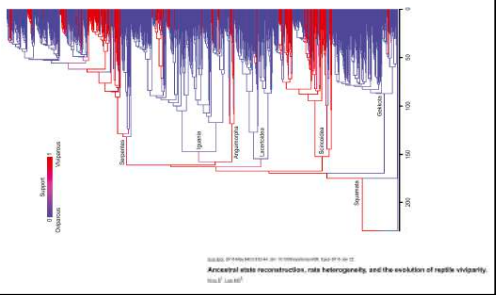
- Weird ancestral state reconstructions
- Weird substitution model
- Paper in high-impact journal



## BEAST to the rescue (again)

Reanalysed the data with BEAST using

- Random local clock
- Asymmetric (time-irreversible) matrix
- Traced character over a fixed tree (starting tree, turned off all branch swapping)



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Results – normality restored

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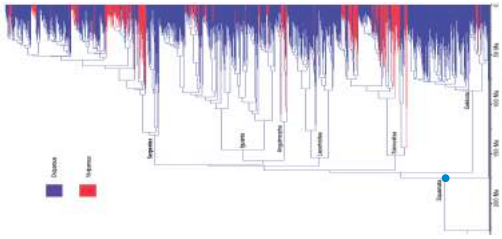
- Egg-laying is ancestral for lizards and snakes
- About 100 convergent evolutions of live-bearing
- Only 3-4 reversals back to egg laying (all biologically sensible)
- Rate shifts all very sensible



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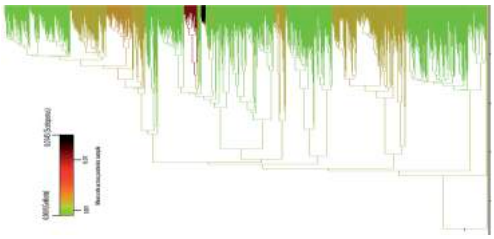

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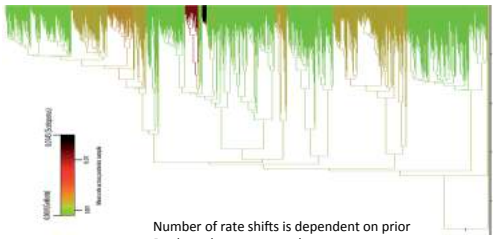

Number of rate shifts is dependent on prior
But branch rates are not!

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- You don't need to be a programming whiz to good stuff in BEAST(2)