

Complex Molecular Evolutionary Models and Information Theoretic Approaches Provide Genomic Perspectives on Amphibian Evolution



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Blue Waters Symposium

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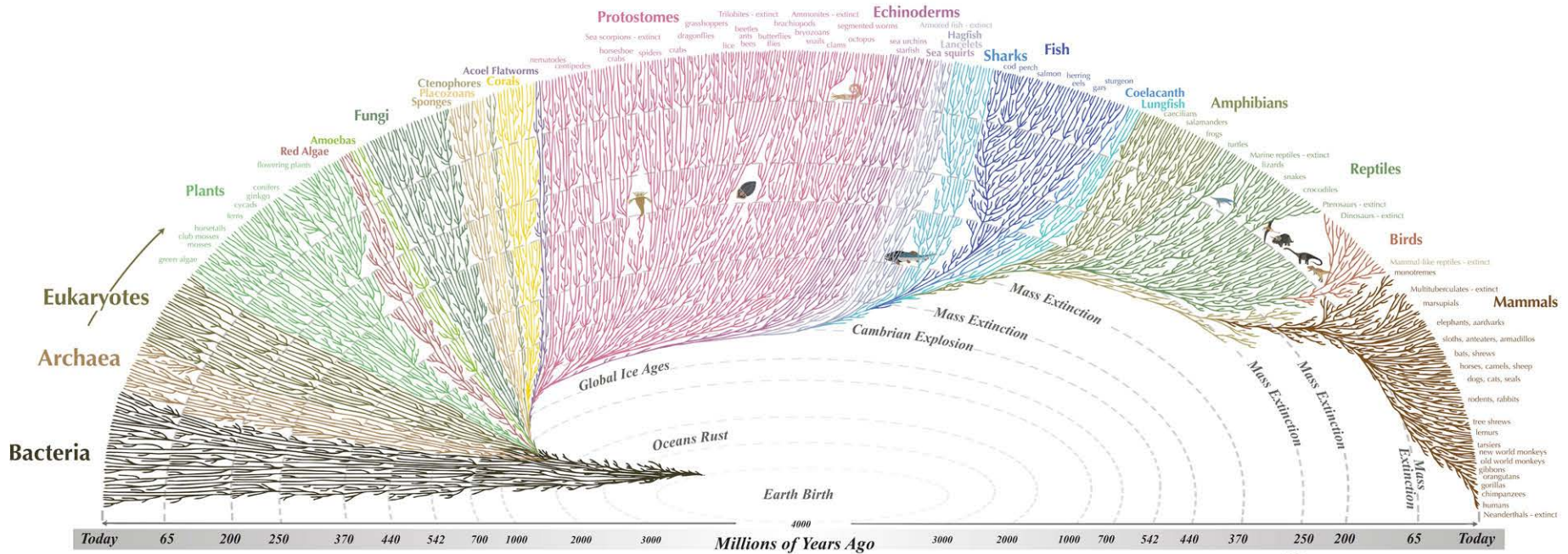



The Evolution of Life on Earth

- All life traces its origins back to a single common ancestor nearly 4 billion years ago
- But today, there are tens of millions of species!
- Reconstructing the genealogy of life is fundamental to nearly all areas of modern biology.



The Evolution of Life on Earth



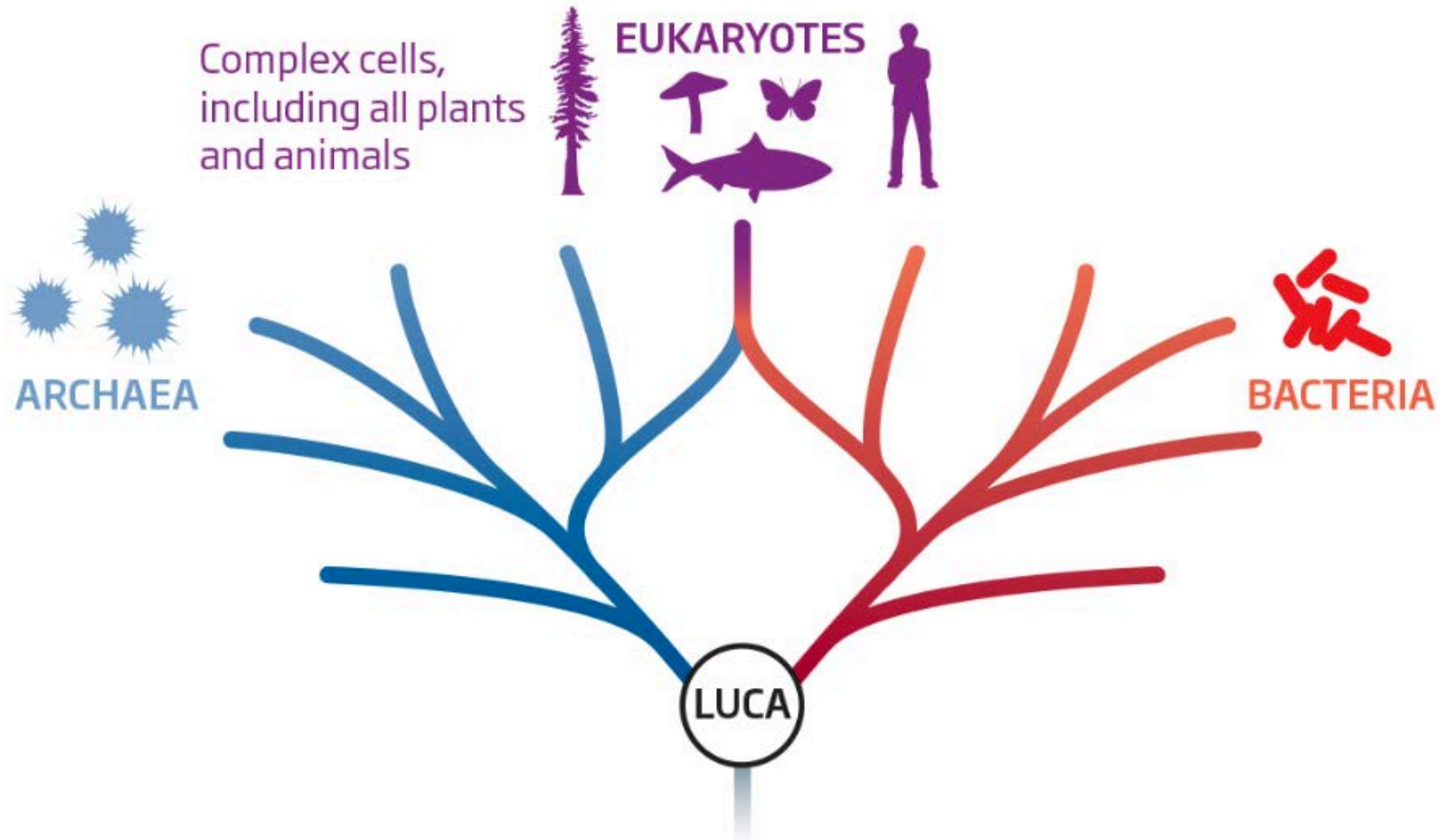
All the major and many of the minor living branches of life are shown on this diagram, but only a few of those that have gone extinct are shown. Example: Dinosaurs - extinct 

“Nothing in biology makes sense, except in light of evolution”

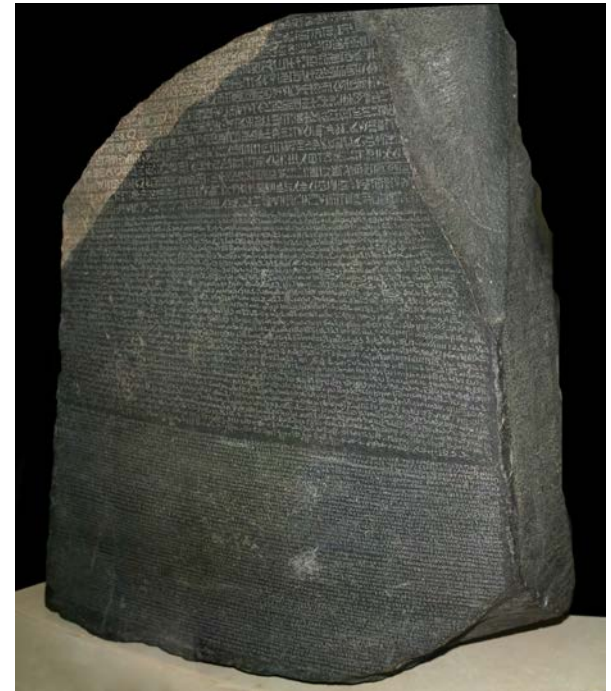
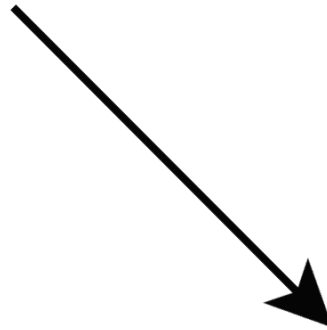
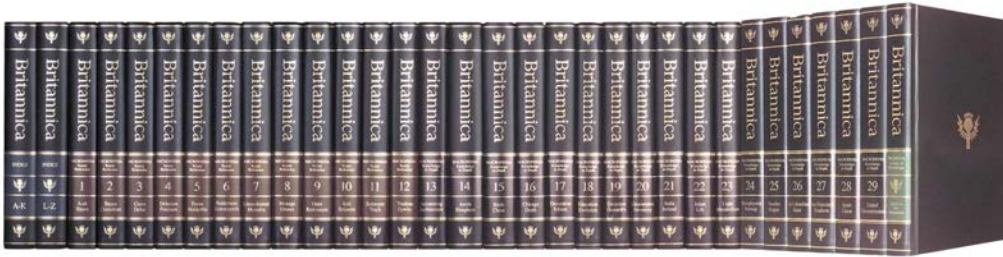
Dobzhansky

“Nothing in evolutionary biology makes sense, except in light of phylogeny”

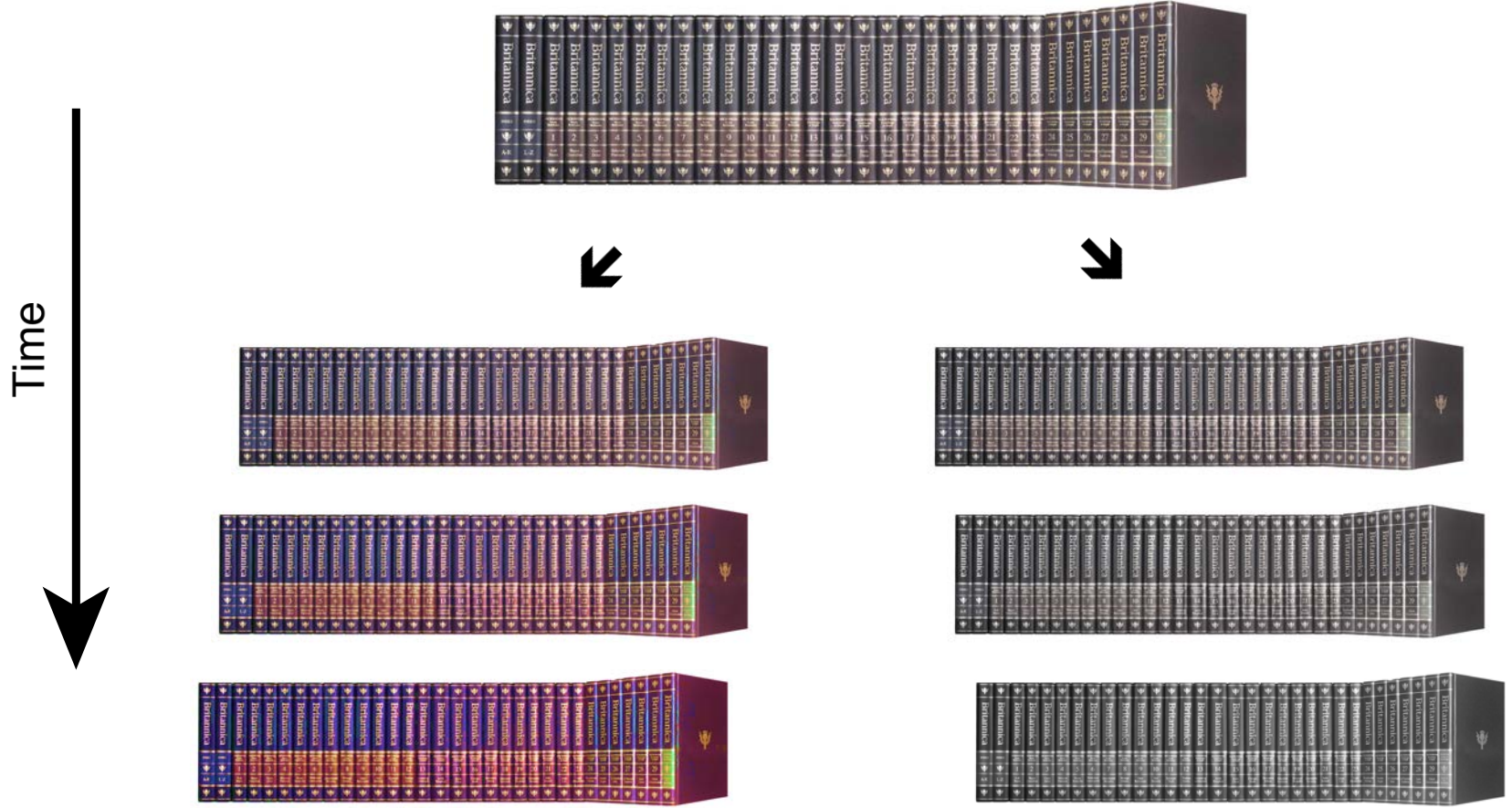
All Organisms on Earth Trace Their Origins Back to a Single Common Ancestor



Genomes Are Documents of Evolutionary History

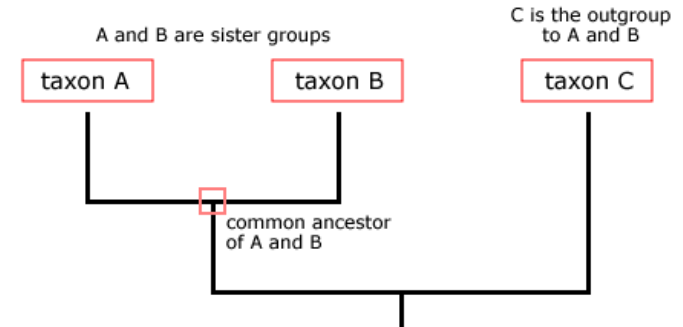


Organisms' Genomes Evolve through Time



Phylogenetic Reconstruction

- Phylogenies are hypotheses about ancestor - descendent relationships.
- These can be estimated from genetic data (in the context of a model).
- Simple case: enumerate all possible trees, pick the “best”.
- Tree space explodes factorially with increasing numbers of taxa.
- Use heuristic search strategies to explore tree- and parameter-space.



Models in Evolutionary Biology

- Evolutionary biology is an inherently historical discipline.
- In evolutionary biology, one cannot “replay the tape” of life...
- We use statistical approaches to compare competing sets of models, in the light of data which we collect.

“All models are wrong. Some are useful.”

George Box

Data \approx Information

(Except in the Context of an Appropriate Model)

Species 1 ACCGAGGGC**A**TCGATCGACTACCTTAGGGCTCTAGCCTGTT**T**CGTGCTAGCTGACTGATCGTAGTGTAGCTGACTGTGTG
Species 2 ACCGAGGGC**T**TCGATCGACTACCTTAGGGCTCTAGCCTGTT**A**CGTGCTAGCTGACTGATCGTAGTGTAGCTGACTGTGTG
Species 3 ACCGAGGGC**A**TCGATCGACTACCTTAGGGCTCTAGCCTGTT**A**CGTGCTAGCTGACTGATCGTAGTGTAGCTGACTGTGTG
Species 4 ACCGAGGGC**T**TCGATCGACTACCTTAGGGCTCTAGCCTGTT**A**CGTGCTAGCTGACTGATCGTAGTGTAGCTGACTGTGTG
Species 5 ACCGAGGGC**T**TCGATCGACTACCTTAGGGCTCTAGCCTGTT**A**CGTGCTAGCTGACTGATCGTAGTGTAGCTGACTGTGTG
Species 6 ACCGAGGGC**A**TCGATCGACTACCTTAGGGCTCTAGCCTGTT**T**CGTGCTAGCTGACTGATCGTAGTGTAGCTGACTGTGTG
Species 7 ACCGAGGGC**T**TCGATCGACTACCTTAGGGCTCTAGCCTGTT**C**CGTGCTAGCTGACTGATCGTAGTGTAGCTGACTGTGTG
Species 8 ACCGAGGGC**T**TCGATCGACTACCTTAGGGCTCTAGCCTGTT**T**CGTGCTAGCTGACTGATCGTAGTGTAGCTGACTGTGTG
Species 9 ACCGAGGGC**A**TCGATCGACTACCTTAGGGCTCTAGCCTGTT**T**CGTGCTAGCTGACTGATCGTAGTGTAGCTGACTGTGTG
Species 10 ACCGAGGGC**T**TCGATCGACTACCTTAGGGCTCTAGCCTGTT**T**CGTGCTAGCTGACTGATCGTAGTGTAGCTGACTGTGTG
Species 11 ACCGAGGGC**T**TCGATCGACTACCTTAGGGCTCTAGCCTGTT**T**CGTGCTAGCTGACTGATCGTAGTGTAGCTGACTGTGTG
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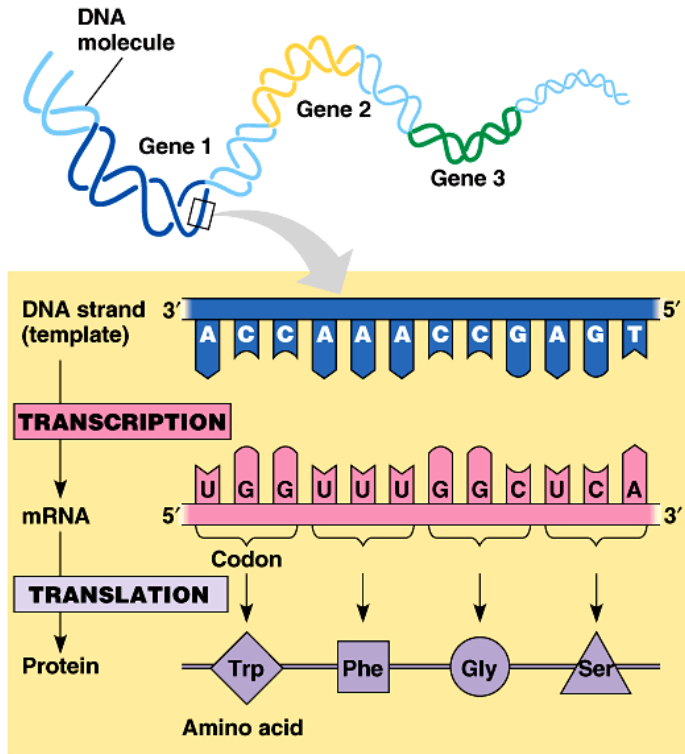
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informative site

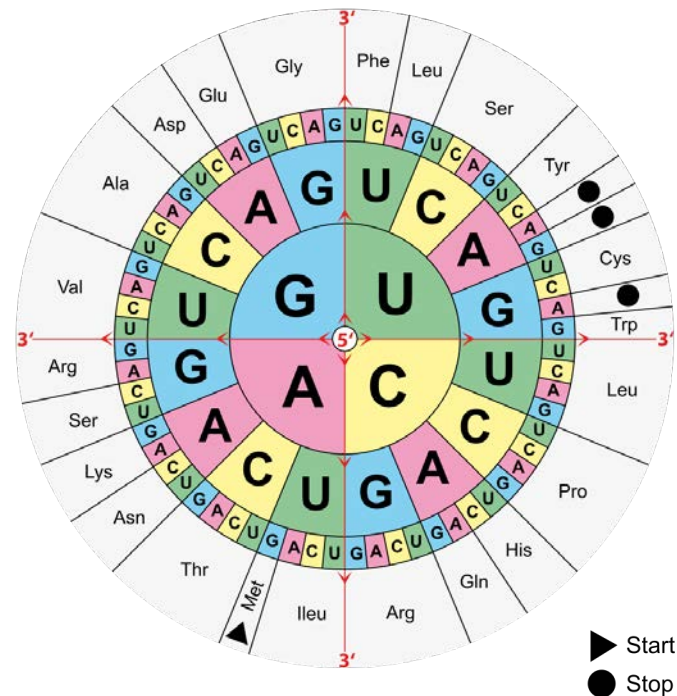
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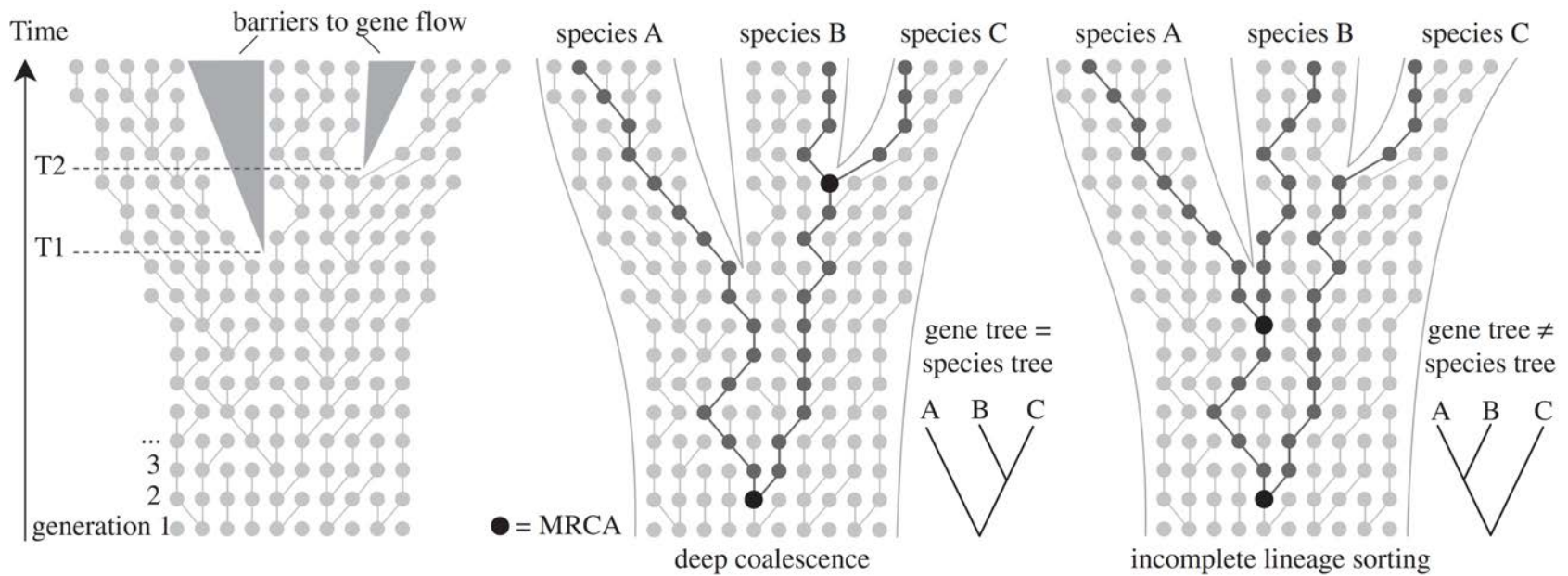
Codon-Based Models of Molecular Evolution



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The Multispecies Coalescent Model

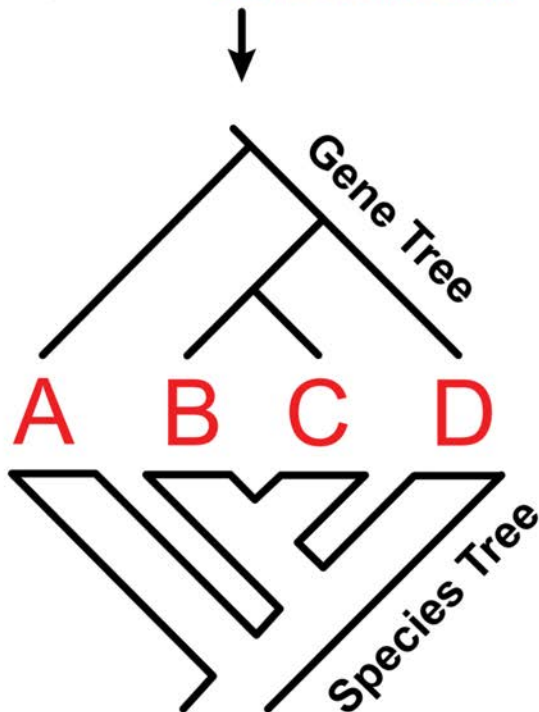


Gene divergences always predate species divergences

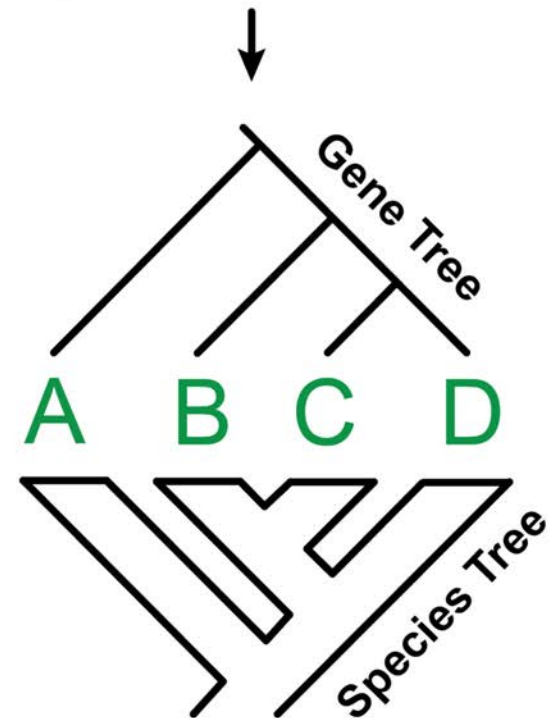
Stochastic coalescent processes can lead to gene tree / species tree discordance

Gene Tree - Species Tree Discordance

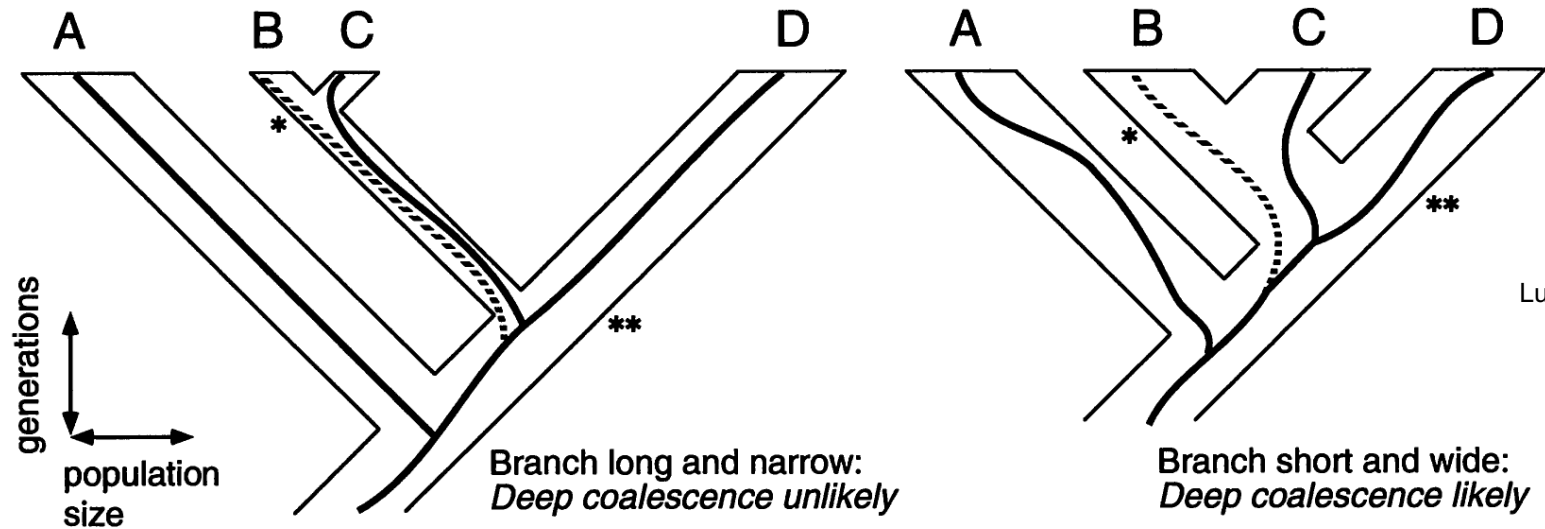
Species A AATCTTCGAATCAG
Species B AGCCTTCTAATCAC
Species C AGCCTTCTAATCAG
Species D AGTCTTTGAATCAG



Species A TTACCTGTTCTCTTT
Species B GTCCCTTTTGTCATT
Species C TTCCCATTTTCTCTAT
Species D GTACCATTTTCTCTAT



Population-Level Processes Affect The Expected Distributions of Gene Coalescence



Conflicting phylogenetic signal from different loci is expected, especially for more recent divergence events and large effective population sizes.

What about at deep scales?

Many loci (regions of the genome) may be needed for difficult questions.

The Genomics Revolution in Evolutionary Biology

It has never been easier to collect genomic data in non-model organisms.



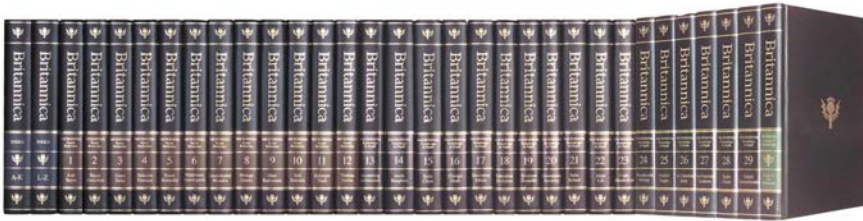
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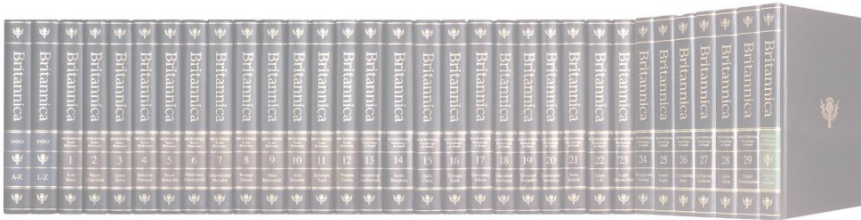
Data ≠ Information

(Except in the Context of an Appropriate Model)



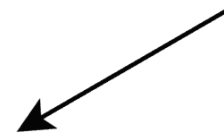
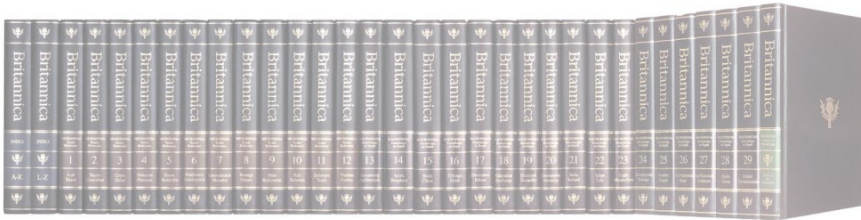
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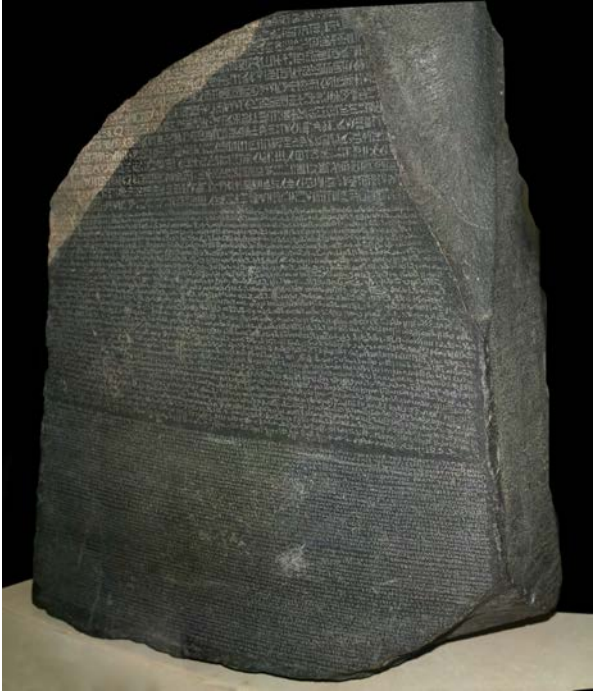
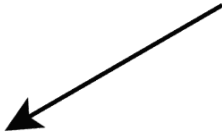
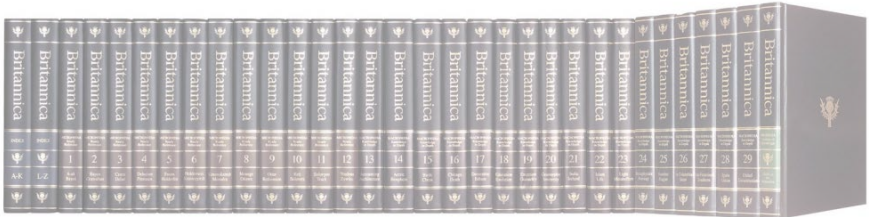
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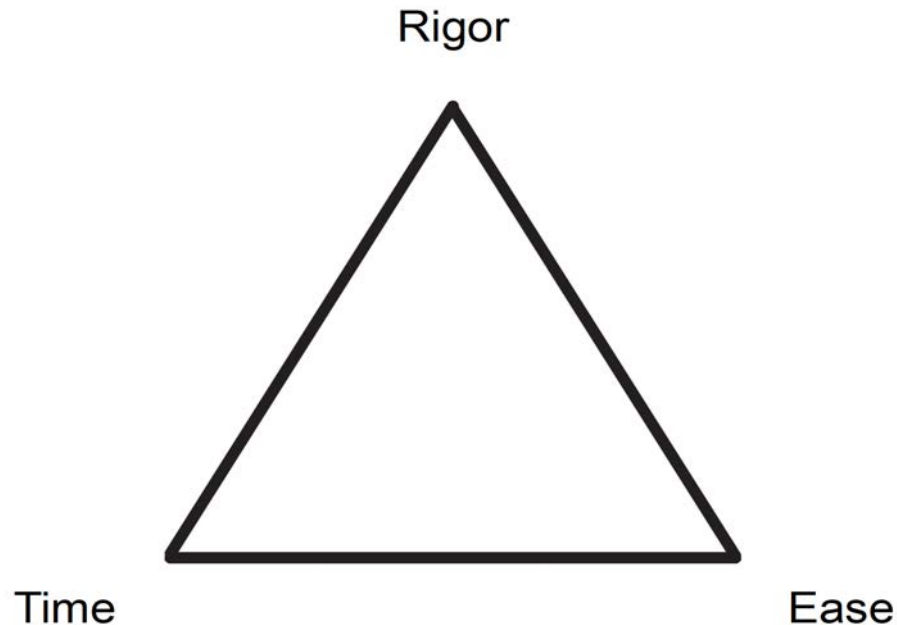
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Some of the Many Tradeoffs in Phylogenomics

The genomic revolution is now offering unprecedented opportunities to tackle thorny questions in evolutionary biology.

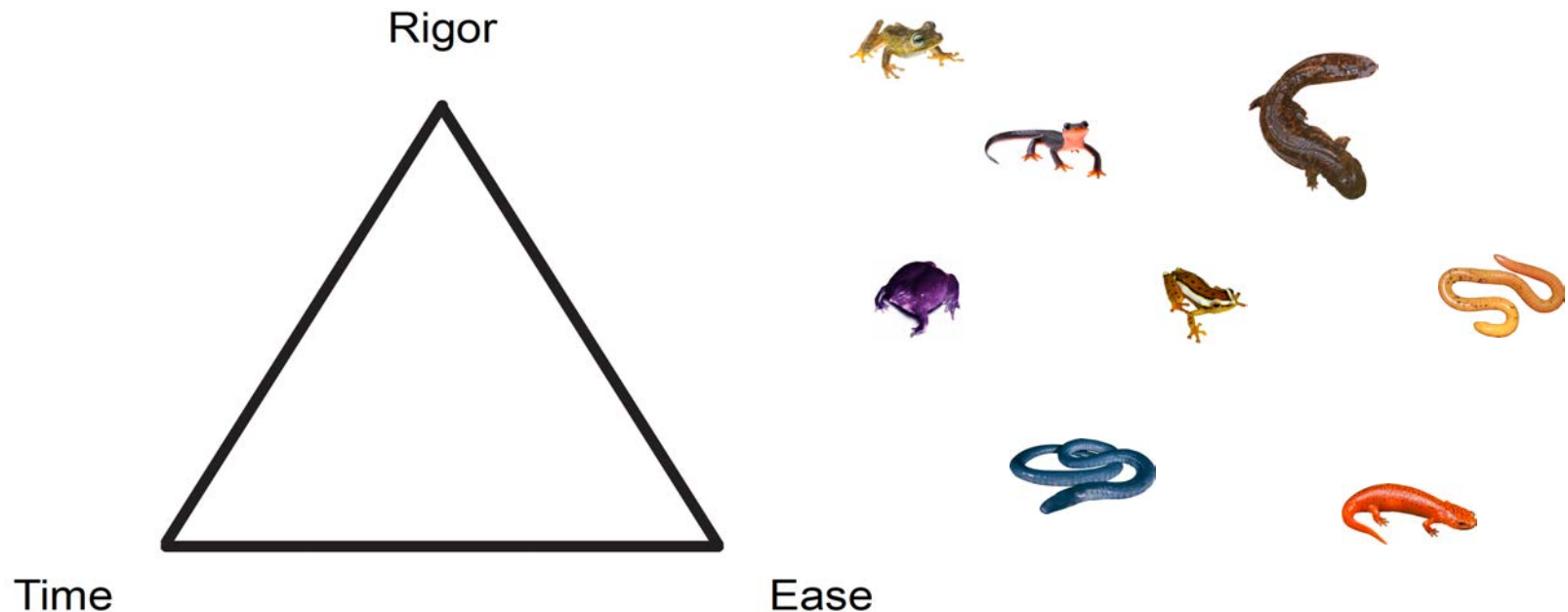
But these opportunities bring analytical and computational costs.



Some of the Many Tradeoffs in Phylogenomics

The genomic revolution is now offering unprecedented opportunities to tackle thorny questions in evolutionary biology.

But these opportunities bring analytical and computational costs.



Genomic perspectives on the amphibian tree of life

- Amphibians provide a rich system for testing phylogenetic hypotheses at both deep and shallow scales of divergence.

- What is the topology of the amphibian Tree of Life???

- How confident are we in that topology?

- What are the inter-ordinal relationships?

- What is the nature of support across the genome?

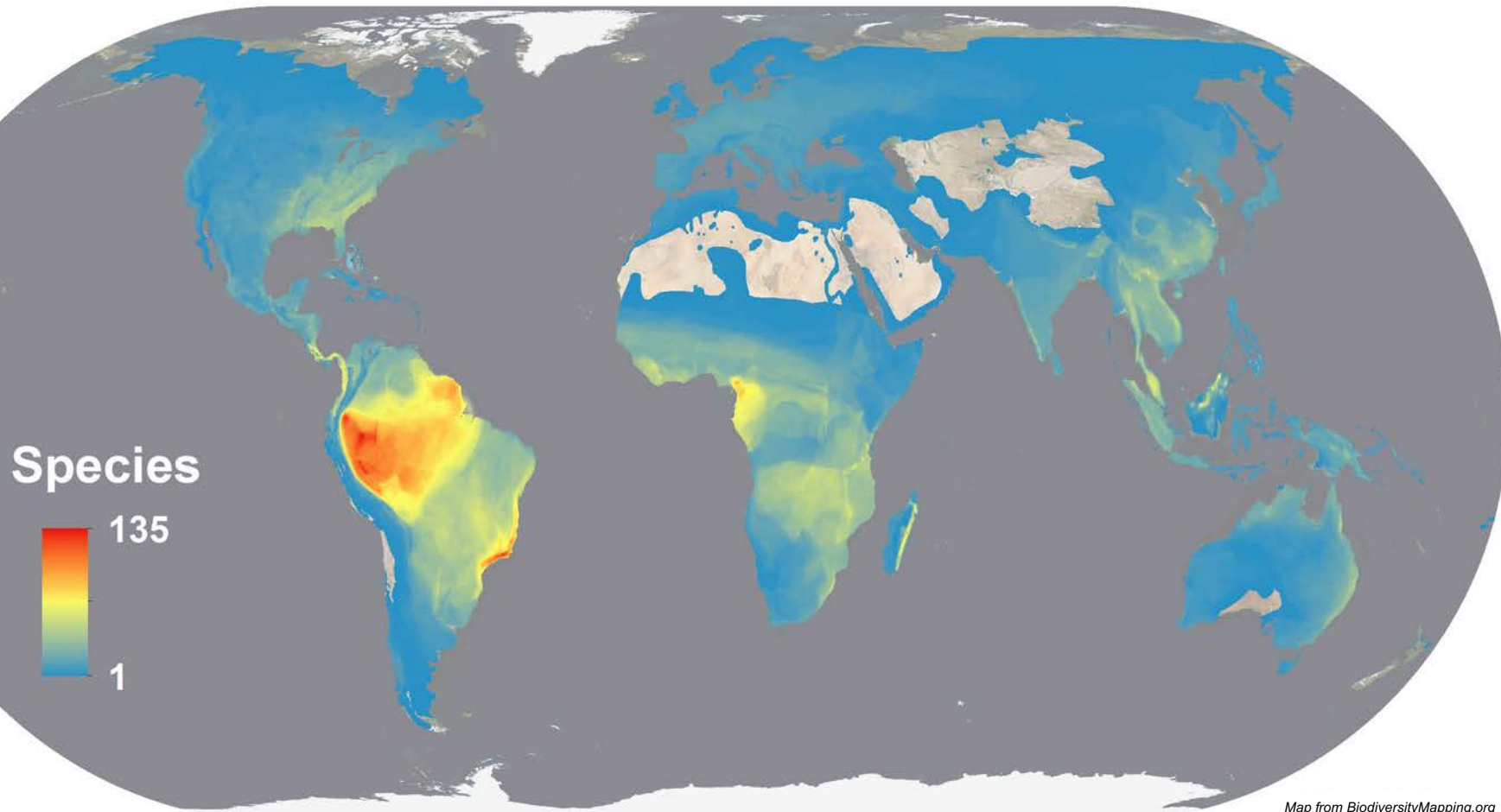
- What are “best” practices with large phylogenomic data sets???



Extant Amphibian Diversity

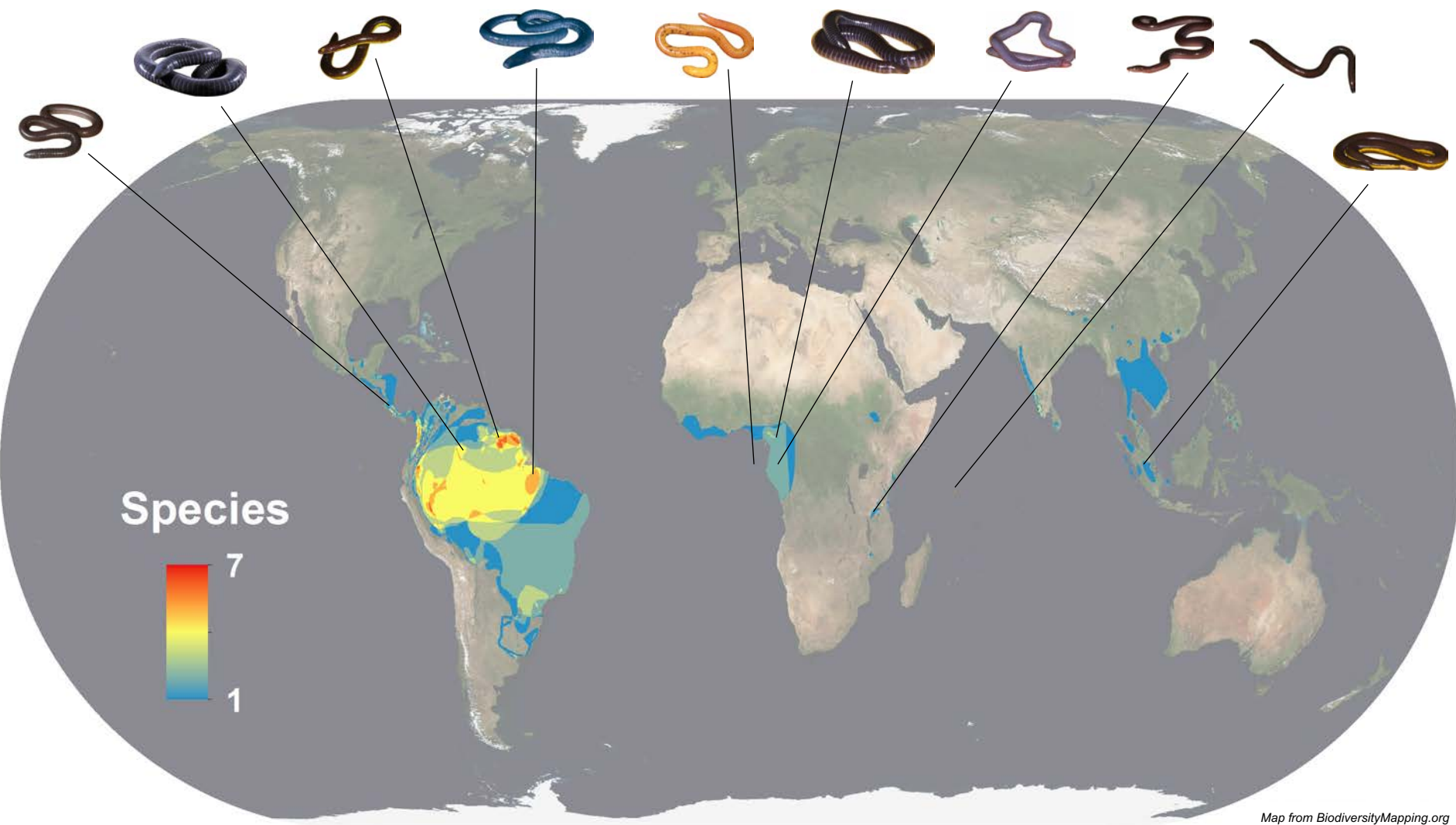
Amphibians - 7,660 species as of 28 April, 2017 (<http://AmphibiaWeb.org>)

The three amphibian orders likely diverged 300+ MYA.



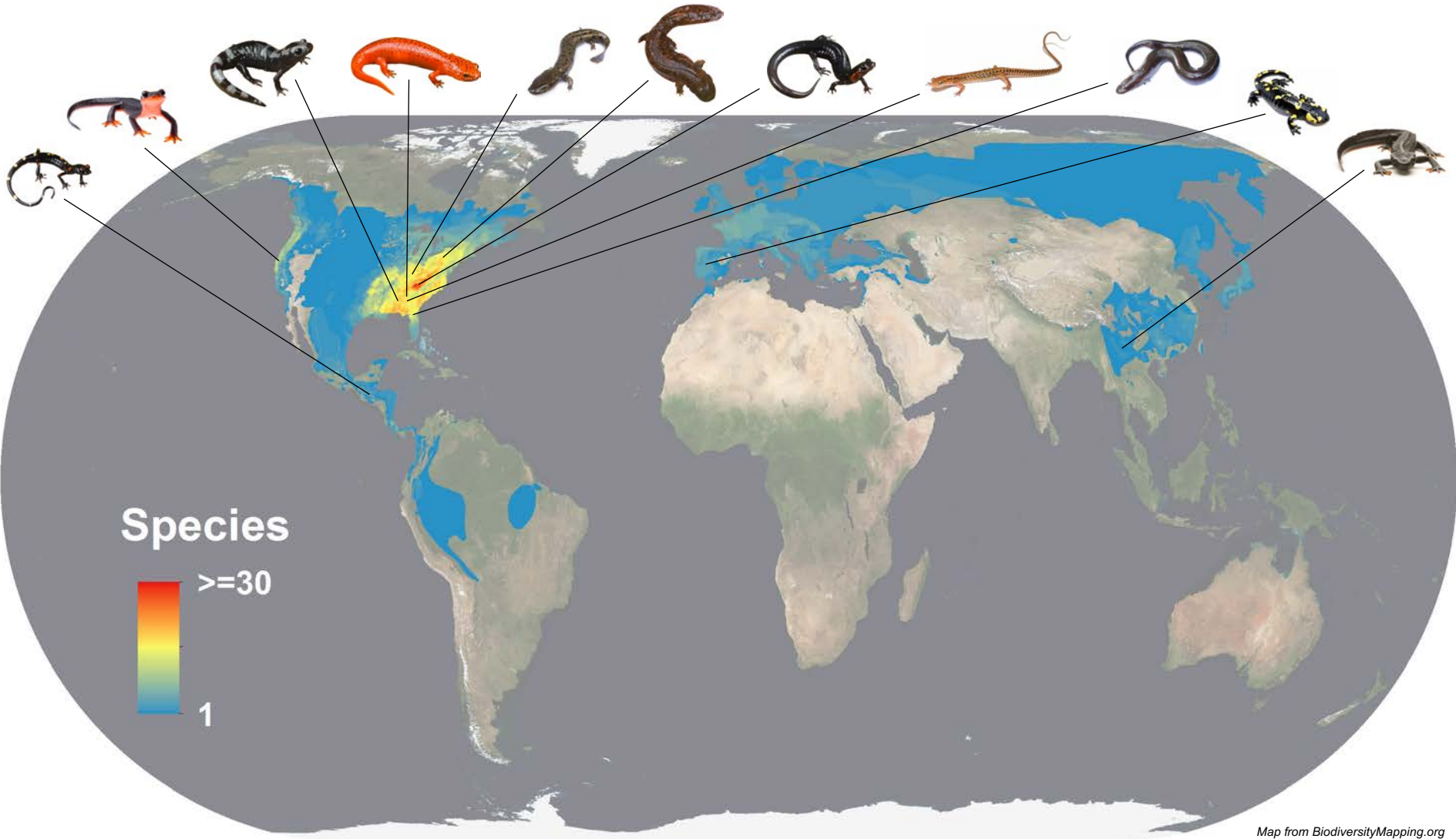
Extant Amphibian Diversity

Caecilians (Gymnophiona) - 205 species, 33 genera, 10 families



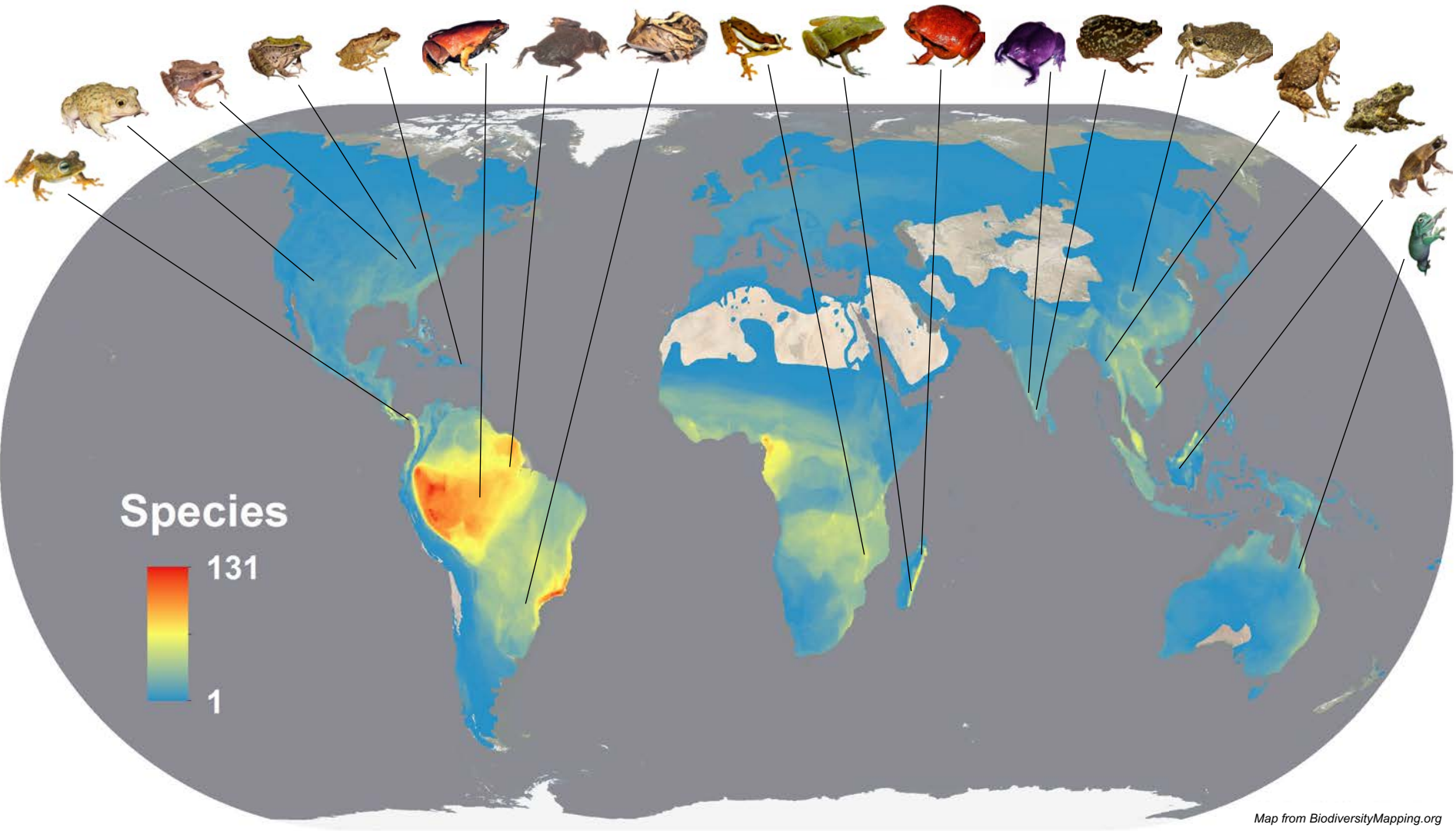
Extant Amphibian Diversity

Salamanders (Caudata) - 695 species, 68 genera, 10 families



Extant Amphibian Diversity

Frogs and Toads (Anura) - 6,760 species, 448 genera, 55-65 families



Amphibian Relationships

Hundreds of studies have addressed phylogenetic affinities of amphibians...

Contents lists available at ScienceDirect
Molecular Phylogenetics and Evolution
journal homepage: www.elsevier.com/locate/ympev

A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians

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Biogeographic Analysis Reveals Ancient Continental Vicariance and Recent Oceanic Dispersal in Amphibians

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THE AMPHIBIAN TREE OF LIFE

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Number 297, 370 pp., 71 figures, 5 tables, 7 appendices
Issued March 15, 2006

RESEARCH ARTICLE Open Access

Molecular phylogeny of microhylid frogs (Anura: Microhylidae) with emphasis on relationships among New World genera

Rafael O de Sá¹, Jeffrey W Stoecher², Rebeקה Selkova³, Mauricio C Forlani⁴, Simon P Loader⁵, El Greenbaum⁶, Stephen Richards⁶, and Célio F B Haddad⁷

Global patterns of diversification in the history of modern amphibians

Kim Roolants¹, David J Gower¹, Mark Wilkinson², Simon P Loader³, S. D. Biju⁴, Karen Guillemae⁵, Linde Molisau⁶, and Franky Bossuyt^{1*}

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A Phylogenomic Approach to Vertebrate Phylogeny Supports a Turtle-Archosaur Affinity and a Possible Paraphyletic Lissamphibia

Jonathan J. Feng^{1,2,3}, Jeremy M. Brown¹, Matthew K. Fujita^{1,2,4,5}, Bastien Boussau^{6,7}

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66 THE QUARTERLY REVIEW OF BIOLOGY VOLUME 82

ever. Unfortunately, despite much data and many pages, it is a disaster. The data must be reanalyzed, and the phylogeny and taxonomy should not be used unless the specific results are confirmed by other analyses. So what went wrong?

Frost et al. present a new taxonomy for all amphibians based (more or less) on a phylogenetic analysis of 522 species of amphibians from combined parsimony analysis of two mitochondrial taxonomic changes will almost certainly prove to be correct. But at this point, how does one know which are right and which are not? Given all of these problems, it seems that the safest bet is to simply ignore this study until someone takes the time to do it right. What a waste.

JOHN J. WIENS, Editor The Quarterly Review of Biology

WILEY-BLACKWELL Cladistics

Is The Amphibian Tree of Life really fatally flawed?

Darrel R. Frost^{1*}, Taran Grant², Julian Faivovich³, Raouï H. Bain⁴, Alexander Haas⁵, Célio F. B. Haddad⁶, Rafael O. de Sá⁷, Alan Channing⁸, Mark Wilkinson⁹, Stephen C. Donnellan¹⁰, Christopher J. Raxworthy¹, Jonathan A. Campbell¹¹, Boris L. Blotto¹², Paul Molér¹³, Robert C. Drewes¹⁴, Ronald A. Nussbaum¹⁵, John D. Lynch¹⁶, David M. Green¹⁷ and Ward C. Wheeler¹⁸

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Efficient Sequencing of Anuran mtDNAs and a Mitogenomic Exploration of the Phylogeny and Evolution of Frogs

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Molecular Evidence for the Early History of Living Amphibians

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A multilocus timescale for the origin of extant amphibians

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Phylogeny, evolution, and biogeography of Asiatic Salamanders (Hynobiidae)

Peng Zhang¹, Yue-Qin Chen¹, Hui Zhou¹, Yi-Fei Liu¹, Xiu-Ling Wang¹, Theodore J. Papenfuss², David B. Wake³, and Liang-Hu Qu⁴

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Contributed by David B. Wake, March 22, 2006

The Palaeozoic Ancestry of Salamanders, Frogs and Caecilians

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A Versatile and Highly Efficient Toolkit Including 102 Nuclear Markers for Vertebrate Phylogenomics, Tested by Resolving the Higher Level Relationships of the Caudata

Xing Xing Shen¹, Dan Liang¹, Yan Jie Feng¹, Meng Yun Chen¹, and Peng Zhang^{1*}

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Associate editor: Xun Gu

Amphibian Relationships

Hundreds of studies have addressed phylogenetic affinities of amphibians...

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Molecular Phylogenetics and Evolution

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BMC Evolutionary Biology

Efficient Sequencing of Anuran mtDNAs and a Mitogenomic Exploration of the Phylogeny and Evolution of Frogs

This project aims to sample hundreds of nuclear genes for hundreds of amphibian species

DARREL R. FROST,^{1,2} TARAN GRANT,^{1,*} JULIAN FAIVOVICH,^{1,3} RAOUL H. BAIN,^{1,2} ALEXANDER HAAS,² CÉLIO F.B. HADDAD,⁴ RAFAEL O. DE SA,⁵ ALAN CHANNING,⁶ MARK WILKINSON,⁷ STEPHEN C. DONNELLAN,¹⁰ CHRISTOPHER J. RAXWORTHY,¹ JONATHAN A. CAMPBELL,¹¹ BORIS L. BLOTTO,¹² PAUL MOLER,¹³ ROBERT C. DREWES,¹⁴ RONALD A. NUSSBAUM,¹⁵ JOHN D. LYNCH,¹⁶ DAVID M. GREEN,¹⁷ AND WARD C. WHEELER³

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Paraphyletic Lissamphibia

Jonathan J. Feng,^{1,2,3} Jeremy M. Brown,^{4,5} Matthew K. Fujita,^{1,2,3,4,6} Bastien Boussau^{1,7}

¹Museum of Vertebrate Zoology, University of California, Berkeley, California, United States of America; ²Department of Integrative Biology, University of California, Berkeley, California, United States of America; ³College of Natural Sciences, San Jose State University, San Jose, California, United States of America; ⁴Department of Biological Sciences, Indiana State University, Bates Stage, Terre Haute, United States of America; ⁵Museum of Comparative Zoology & Department of Organismal and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, United States of America; ⁶Department of Biology, University of Texas at Austin, Austin, Texas, United States of America; ⁷Department of Statistics, University of California, Berkeley, California, United States of America

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VOLUME 82

ever. Unfortunately, despite much data and many pages, it is a disaster. The data must be reanalyzed, and the phylogeny and taxonomy should not be used unless the specific results are confirmed by other analyses. So what went wrong?

Frost et al. present a new taxonomy for all amphibians based (more or less) on a phylogenetic analysis of 522 species of amphibians from combined parsimony analysis of two mitochondrial

taxonomic changes will almost certainly prove to be correct. But at this point, how does one know which are right and which are not? Given all of these problems, it seems that the safest bet is to simply ignore this study until someone takes the time to do it right. What a waste.

JOHN J. WENNS, *Editor, The Quarterly Review of Biology*



Cladistics 24 (2008) 385–395

Cladistics

10.1111/j.1365-3113.2007.00314.x

Is *The Amphibian Tree of Life* really fatally flawed?

Darrel R. Frost^{1*}, Taran Grant², Julian Faivovich³, Raoul H. Bain⁴, Alexander Haas⁵, Célio F. B. Haddad⁶, Rafael O. de Sa⁷, Alan Channing⁸, Mark Wilkinson⁹, Stephen C. Donnellan¹⁰, Christopher J. Raxworthy¹, Jonathan A. Campbell¹¹, Boris L. Blotto¹², Paul Moler¹³, Robert C. Drewes¹⁴, Ronald A. Nussbaum¹⁵, John D. Lynch¹⁶, David M. Green¹⁷ and Ward C. Wheeler¹⁸

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A multilocus timescale for the origin of extant amphibians

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Phylogeny, evolution, and biogeography of Asiatic Salamanders (Hynobiidae)

Peng Zhang¹, Yue-Qin Chen¹, Hui Zhou¹, Yi-Fei Liu¹, Xiu-Ling Wang¹, Theodore J. Papenfuss¹, David B. Wake^{1,2}, and Liang-Hu Qu^{1,3}

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Contributed by David B. Wake, March 22, 2006

Evolutionary Journal of the Linnean Society, 2007, 130 (Suppl. 1), 1–180. With 75 figures

The Palaeozoic Ancestry of Salamanders, Frogs and Caecilians

ROBERT L. CARROLL FLS¹

¹Redpath Museum, McGill University, 859 Sherbrooke St W, Montreal, P.Q. Canada, H3A 2K6

A Versatile and Highly Efficient Toolkit Including 102 Nuclear Markers for Vertebrate Phylogenomics, Tested by Resolving the Higher Level Relationships of the Caudata

Xing Xing Shen¹, Dan Liang¹, Yan Jie Feng¹, Meng Yun Chen¹, and Peng Zhang^{1*}

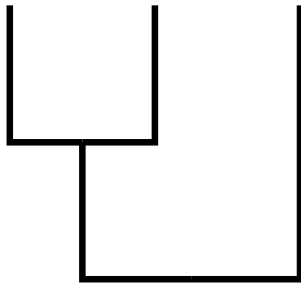
¹Key Laboratory of Gene Engineering of the Ministry of Education, State Key Laboratory of Biocatalysis, School of Life Sciences, Sun Yat-Sen University, Guangzhou, China

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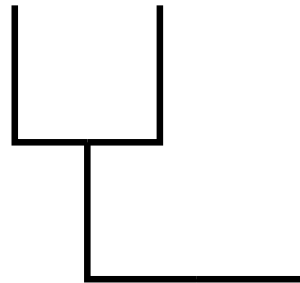
Associate editor: Scott Stepien

Inter-Ordinal Amphibian Relationships

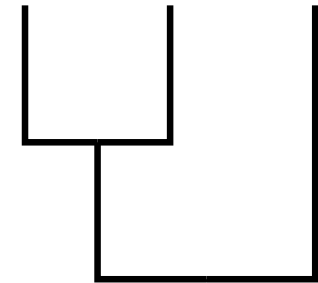
Three main hypotheses for phylogenetic relationships among the three amphibian orders (assuming that Amphibia is monophyletic...)



Batrachia



Acauda

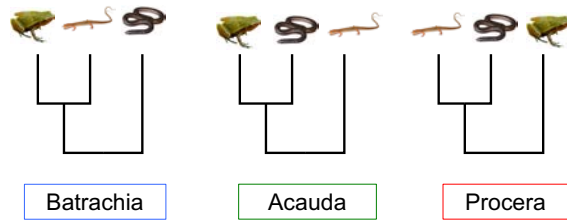


Procera

The potential resolutions of these deep branches each have very different implications for our understanding of amphibian evolution.

Inter-Ordinal Amphibian Relationships

- There are **15** possible topologies for the three amphibian orders and amniotes, assuming that Amphibia may or may NOT be monophyletic..



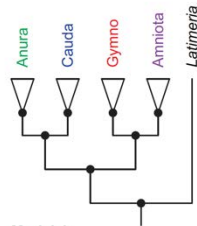
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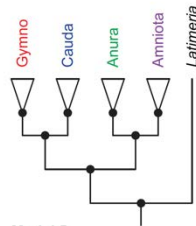
A Phylogenomic Approach to Vertebrate Phylogeny Supports a Turtle-Archosaur Affinity and a Possible Paraphyletic Lissamphibia

Jonathan J. Fong^{1,2,3}, Jeremy M. Brown^{2,4}, Matthew K. Fujita^{1,2,5,6}, Bastien Boussau^{2,7}

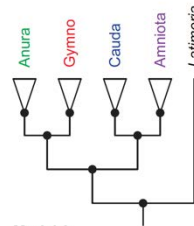
1 Museum of Vertebrate Zoology, University of California, Berkeley, California, United States of America, 2 Department of Integrative Biology, University of California, Berkeley, California, United States of America, 3 College of Natural Sciences, Seoul National University, Seoul, Republic of Korea, 4 Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana, United States of America, 5 Museum of Comparative Zoology & Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, United States of America, 6 Department of Biology, University of Texas-Arlington, Arlington, Texas, United States of America, 7 Laboratoire de Biométrie et Biologie Evolutive, Université de Lyon, Villeurbanne, France



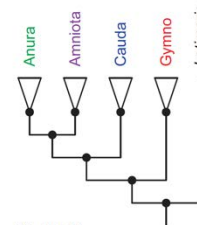
Model 4:
Paraphyletic Lissamphibia
Batrachia Hypothesis



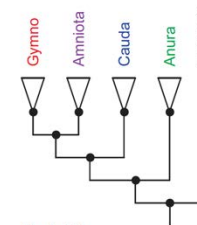
Model 5:
Paraphyletic Lissamphibia
Procera Hypothesis



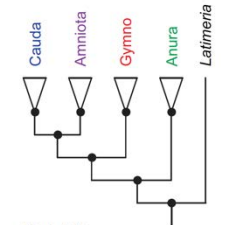
Model 6:
Paraphyletic Lissamphibia
Acauda Hypothesis



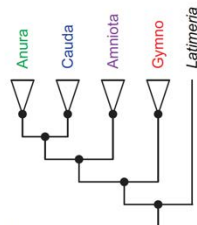
Model 10:
Paraphyletic Lissamphibia
Anura+Amniota, Gymno Basal



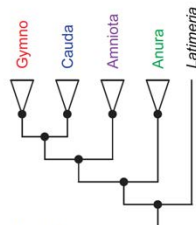
Model 11:
Paraphyletic Lissamphibia
Gymno+Amniota, Anura Basal



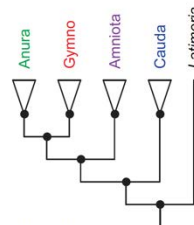
Model 12:
Paraphyletic Lissamphibia
Cauda+Amniota, Anura Basal



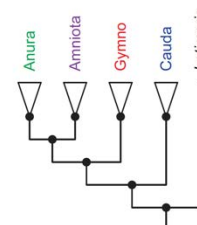
Model 7:
Paraphyletic Lissamphibia
Batrachia Hypothesis



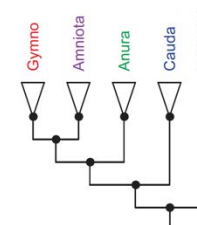
Model 8:
Paraphyletic Lissamphibia
Procera Hypothesis



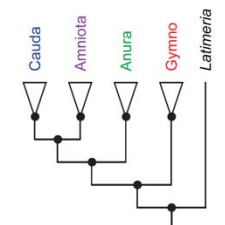
Model 9:
Paraphyletic Lissamphibia
Acauda Hypothesis



Model 13:
Paraphyletic Lissamphibia
Anura+Amniota, Cauda Basal



Model 14:
Paraphyletic Lissamphibia
Gymno+Amniota, Cauda Basal



Model 15:
Paraphyletic Lissamphibia
Cauda+Amniota, Gymno Basal

Taxonomic Sampling across Amphibia

- We targeted 325 amphibian taxa (296 “worked”).
- 276 genera (> 50% of recognized genera)...
- 96% of recognized families (and most subfamilies)...
- Taxa were sampled roughly in proportion to species richness.

Taxonomic Sampling across Amphibia

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- 276 genera (> 50% of recognized genera)...
- 96% of recognized families (and most subfamilies)...
- Taxa were sampled roughly in proportion to species richness.
- Multiple outgroups were included to root the phylogeny.



Anolis



Chrysemys



Gallus



Homo



Latimeria

Generating Genomic Data in Amphibians

- We developed an amphibian-specific gene capture system which targets 366 semi-conserved nuclear exons.
- Probes were designed from genomic/transcriptomic* resources for:

1 Caecilian:



Ichthyophis

4 Salamanders:



*Ambystoma**



*Cryptobranchus**



Desmognathus



*Notophthalmus**

6 Frogs:



Ascaphus



Gastrophyne



Mixophyes



Pseudacris



Rana
(*Lithobates*)



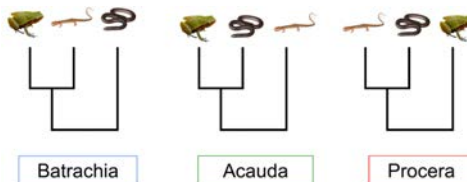
Xenopus
(*Silurana*)

Nuclear Gene Tree Estimation

- Independently estimated ML gene trees for all genes in RAxML.



- Used separate (best-fit) partitioning schemes and nucleotide substitution models for each gene (GTR+ Γ).
- Conducted 500 non-parametric bootstrap replicates (across sites) to assess “support” for branches in these gene trees.
- Identified outlier taxa for each gene (and removed those taxa).
- Conducted analyses with unconstrained and constrained topological backbones.



Species Tree Estimation

- Use multiple algorithms to estimate the topology of the species tree.
- “Shortcut” methods attempt to reconcile collections of gene trees into an estimate of the species tree (`Astral` and `MulRF`).



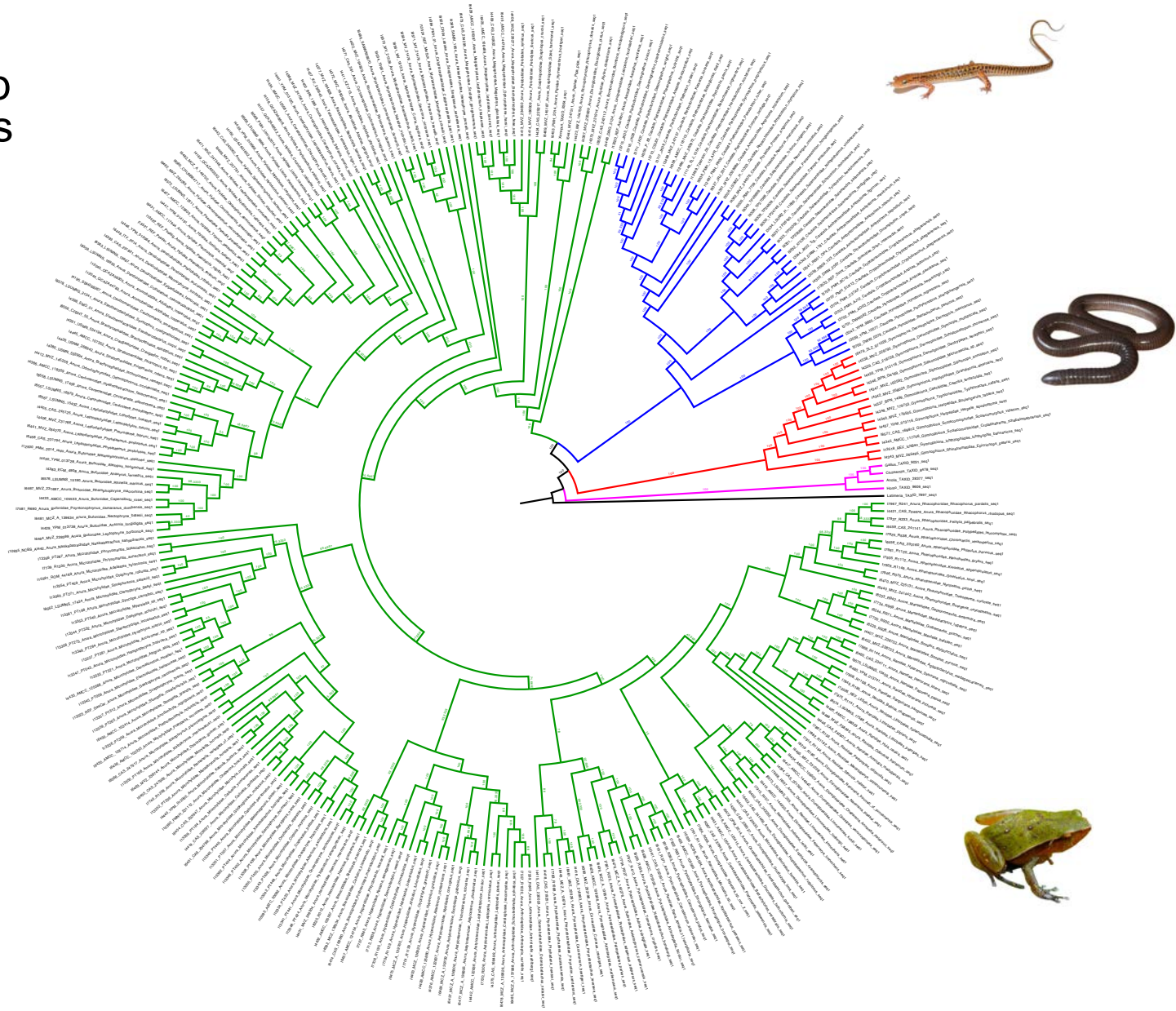
- Also implemented a gene-tree-free approach (`SVDQuartets`).
- Lastly, estimated a concatenated ML tree in `RAxML`, using a best-fit partitioning scheme of 76 distinct partitions (separate `GTR+ Γ` models).
- Used the non-parametric bootstrap across sites to assess “support” (sites and genes for `Astral`).

Brief Overview of Results

- Nearly all families are recovered as monophyletic.
- Shallow-scale relationships are largely in line with previous studies.
- Most higher-order clades are recovered.
- Deep branches receive strong bootstrap support in species tree analyses...

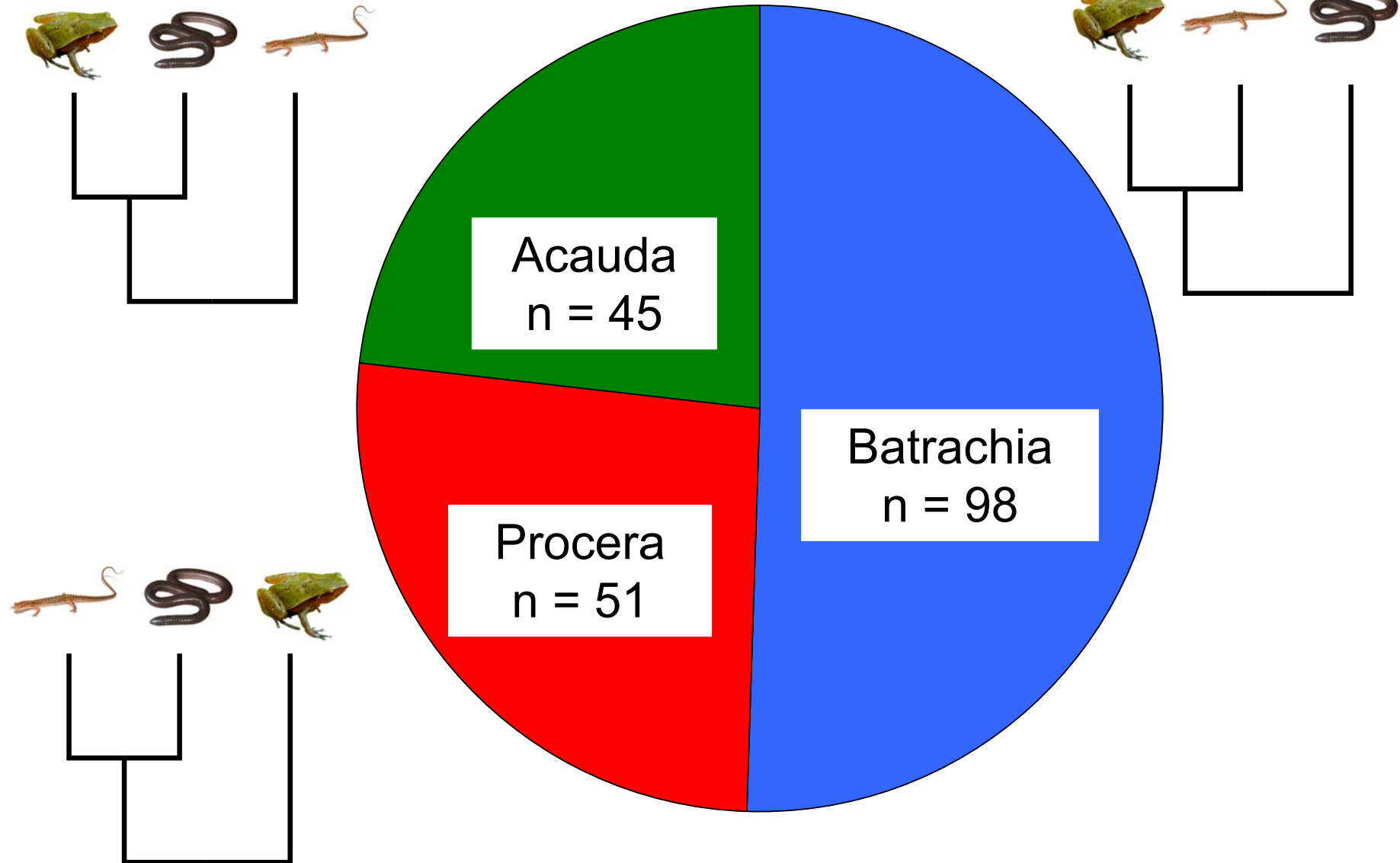
Astral12 Species Tree

- High bootstrap support across the tree
- Inter-ordinal support is for Batrachia (BS = 100)
- We're done, right??!
- Scrutinize phylogenetic signal across the genome...

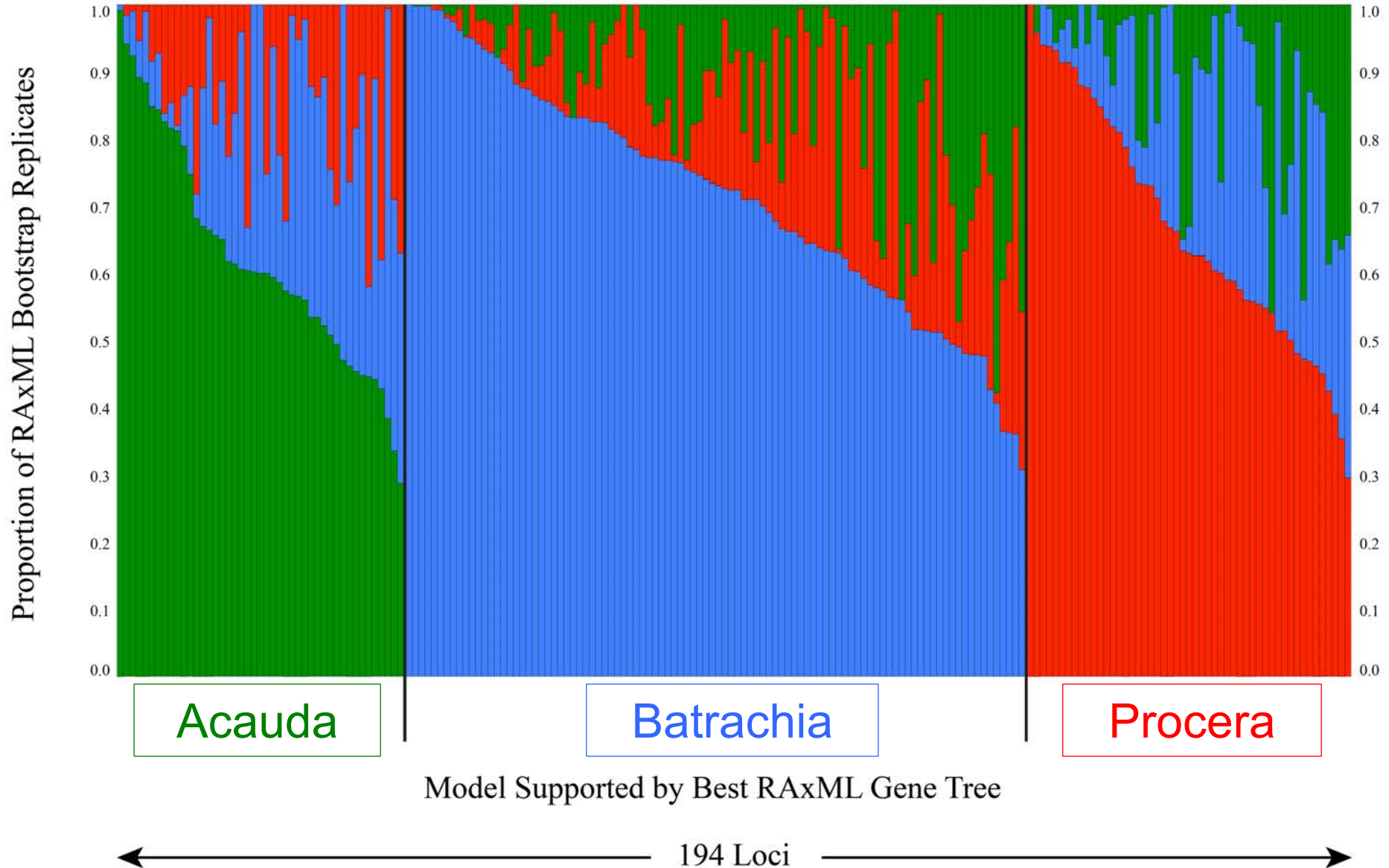


Inter-Ordinal Support Varies across Loci

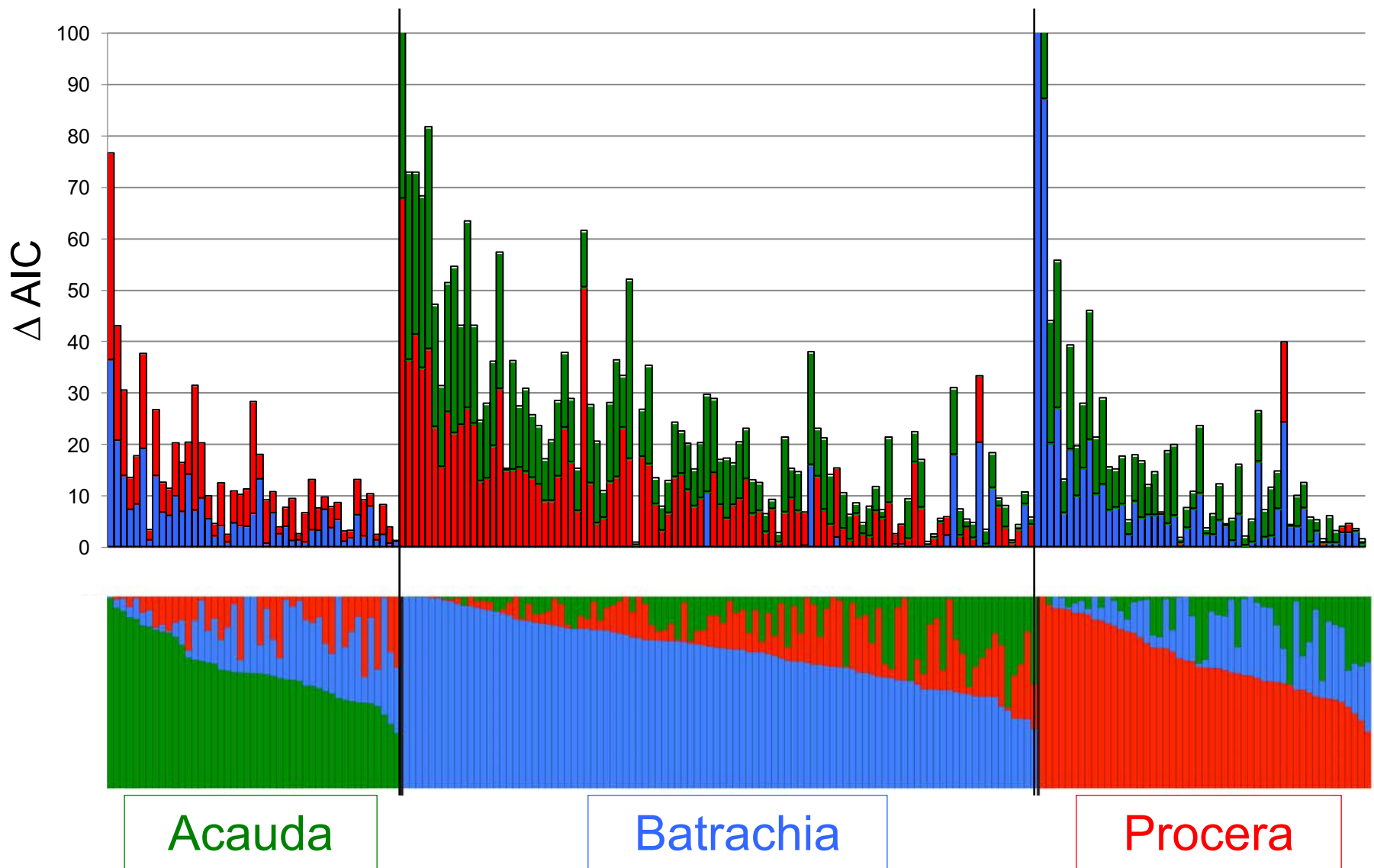
(RAxML "Best" Gene Trees)



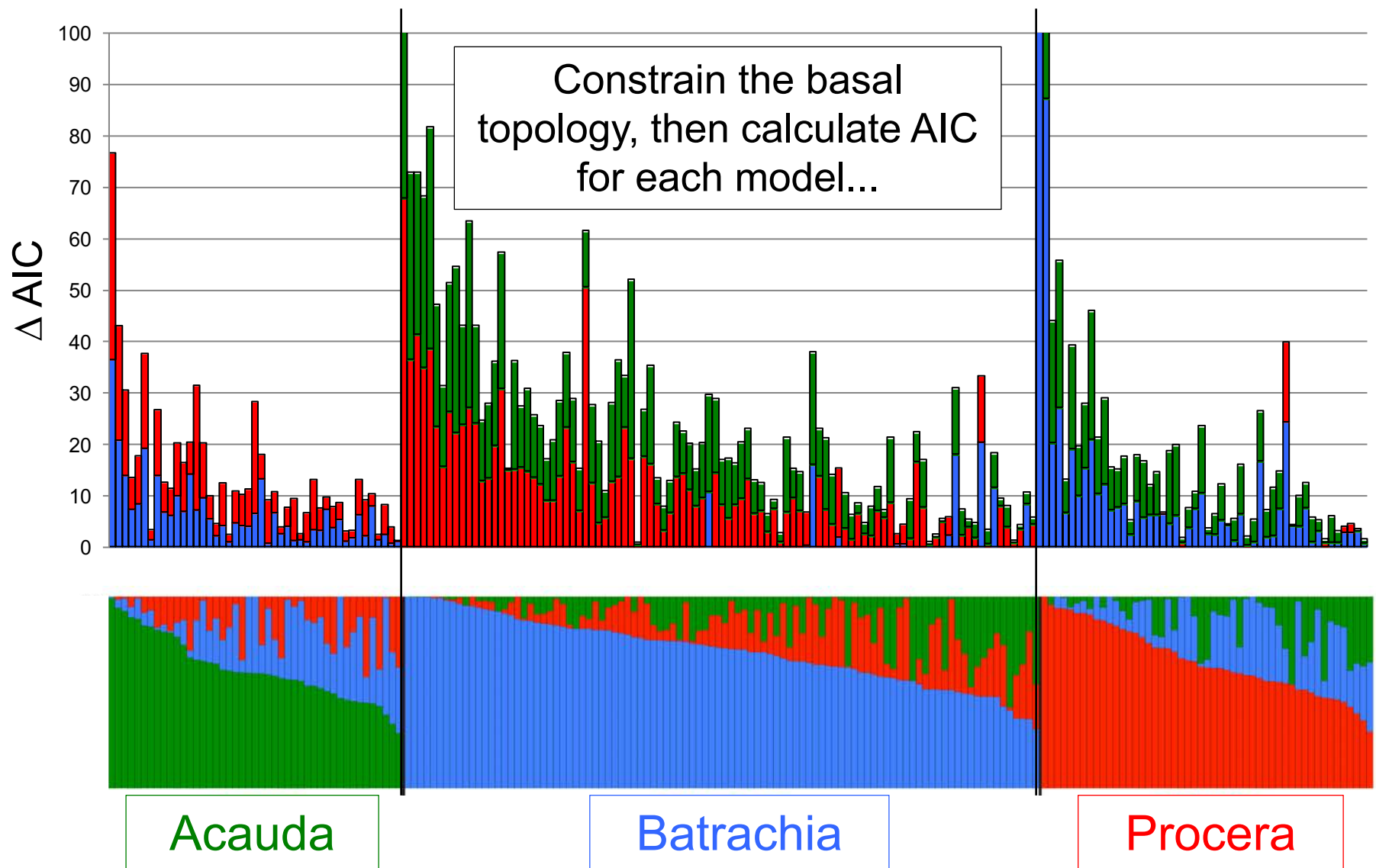
Support across 500 Bootstrap Replicates



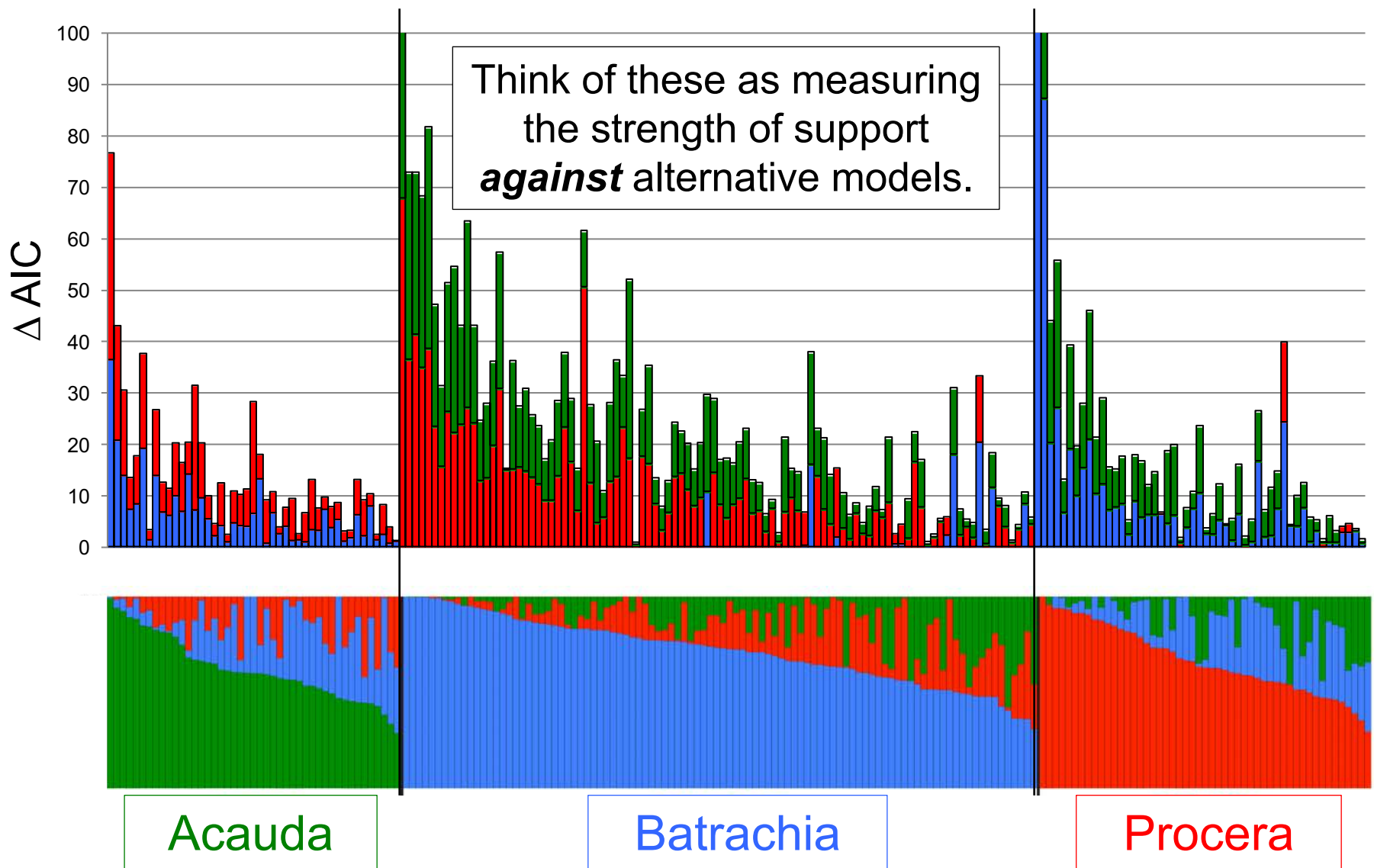
Unbounded Support Using the AIC



Unbounded Support Using the AIC



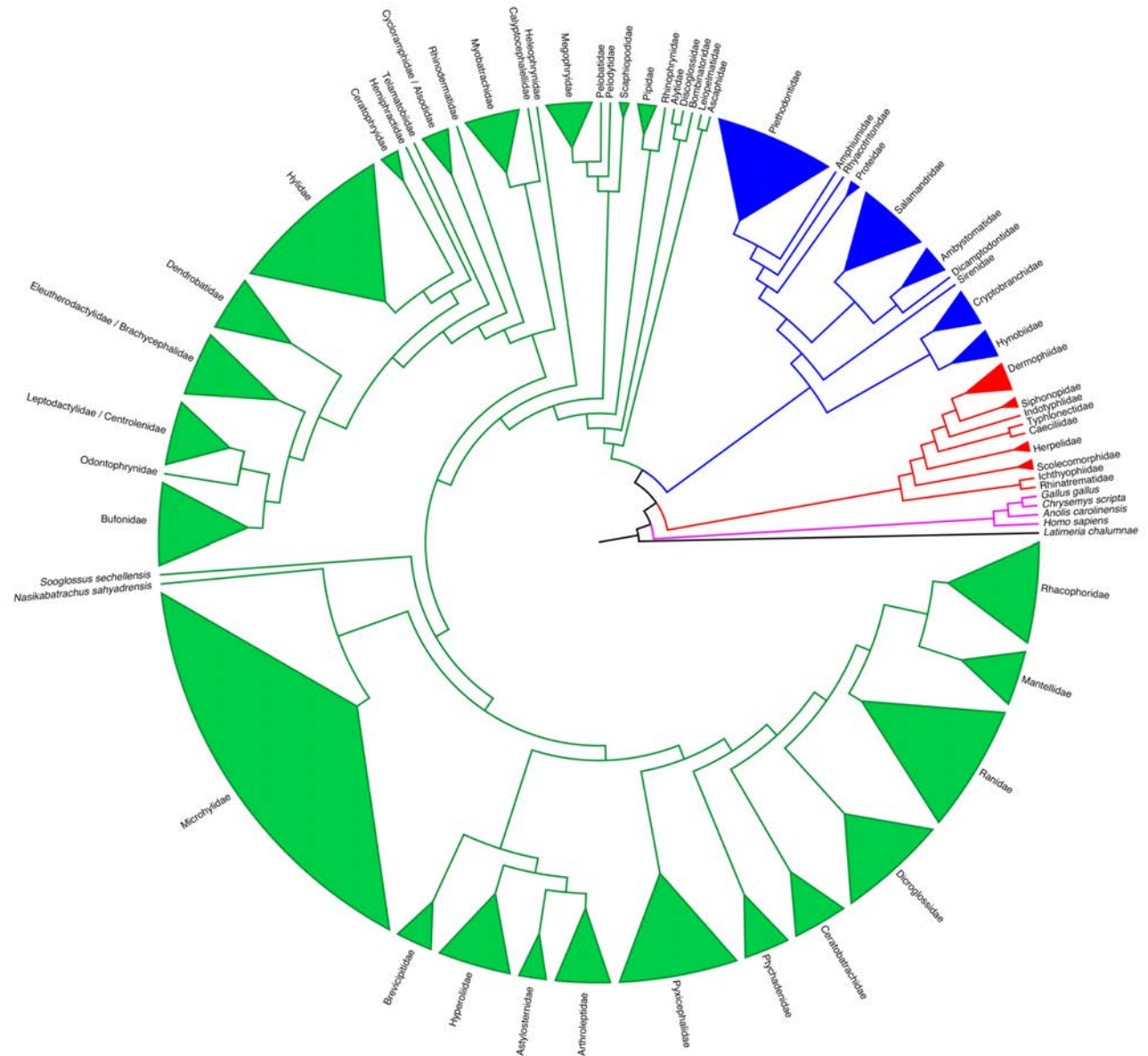
Unbounded Support Using the AIC



Backbone of the Amphibian Tree of Life

These topologies are largely concordant with previous studies..

With a few distinct exceptions...



Conflict in the Frog Tree: *Nasikabatrachus*

New frog family from India reveals an ancient biogeographical link with the Seychelles

S. D. Biju^{1,2*} & Franky Bossuyt^{2*}

¹Tropical Botanic Garden and Research Institute, Palode, Thiruvananthapuram, 695562 Kerala, India

²Biology Department, Unit of Ecology & Systematics, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium

*The authors contributed equally to this work

About 96% of the more than 4,800 living anuran species¹ belong to the Neobatrachia or advanced frogs²⁻⁴. Because of the extremely poor representation of these animals in the Mesozoic



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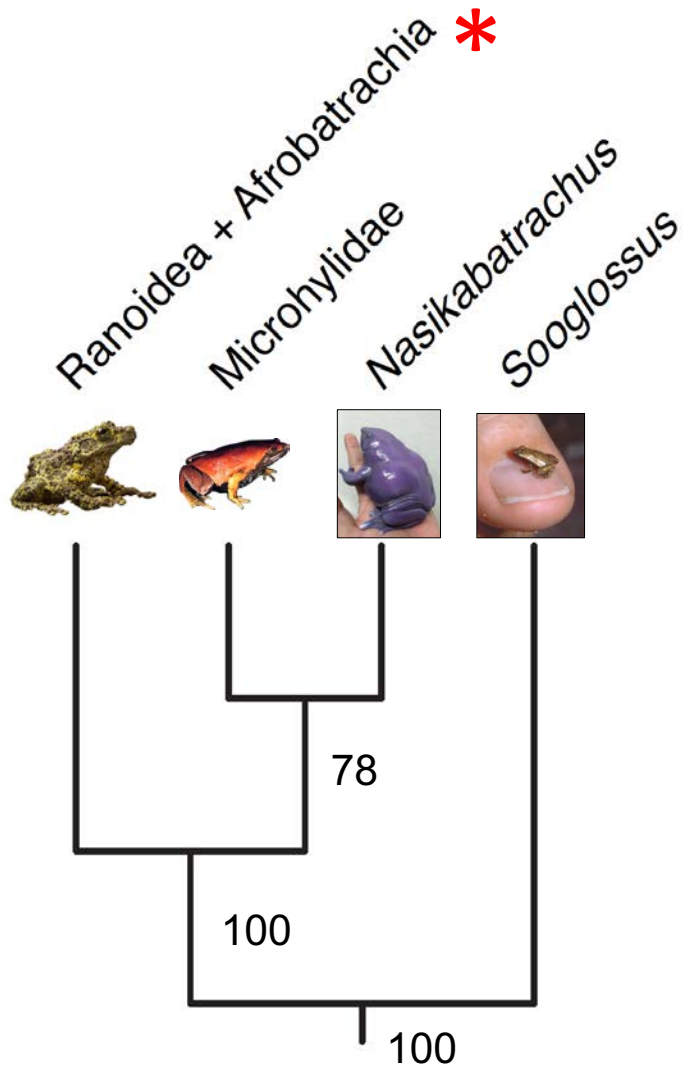
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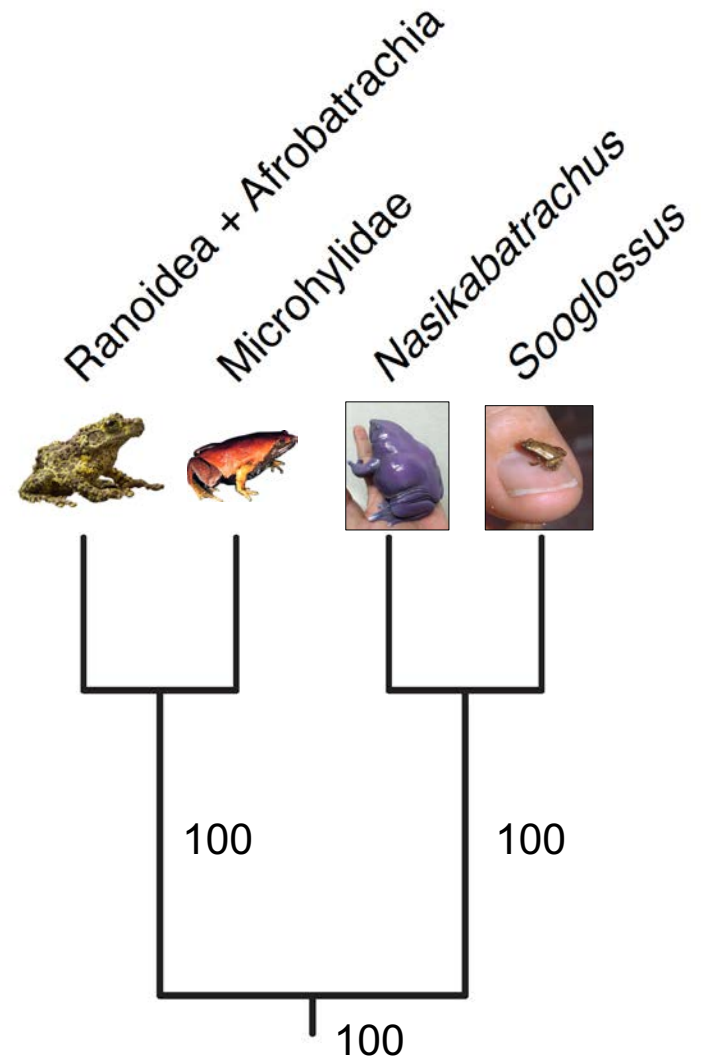


Different Methods Yield Different Topologies

ASTRAL Tree

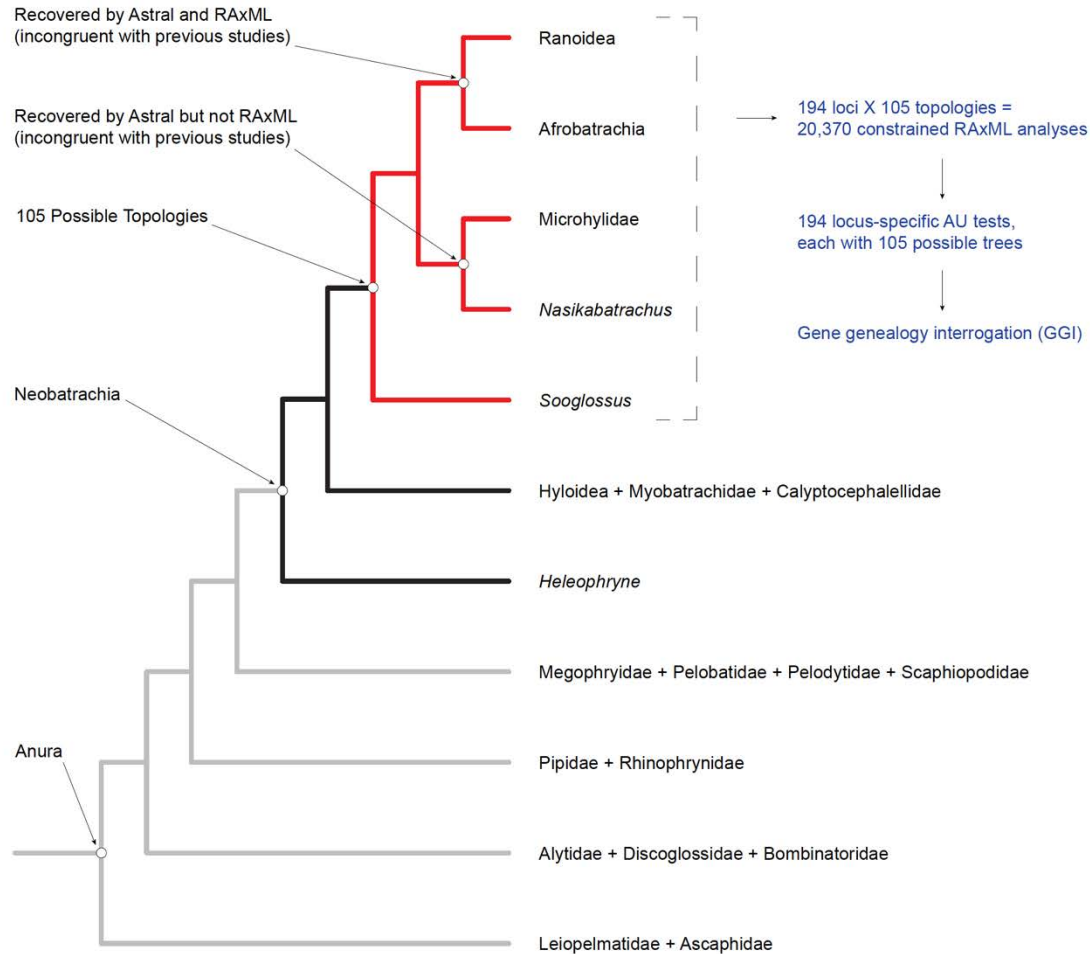


RAXML Tree



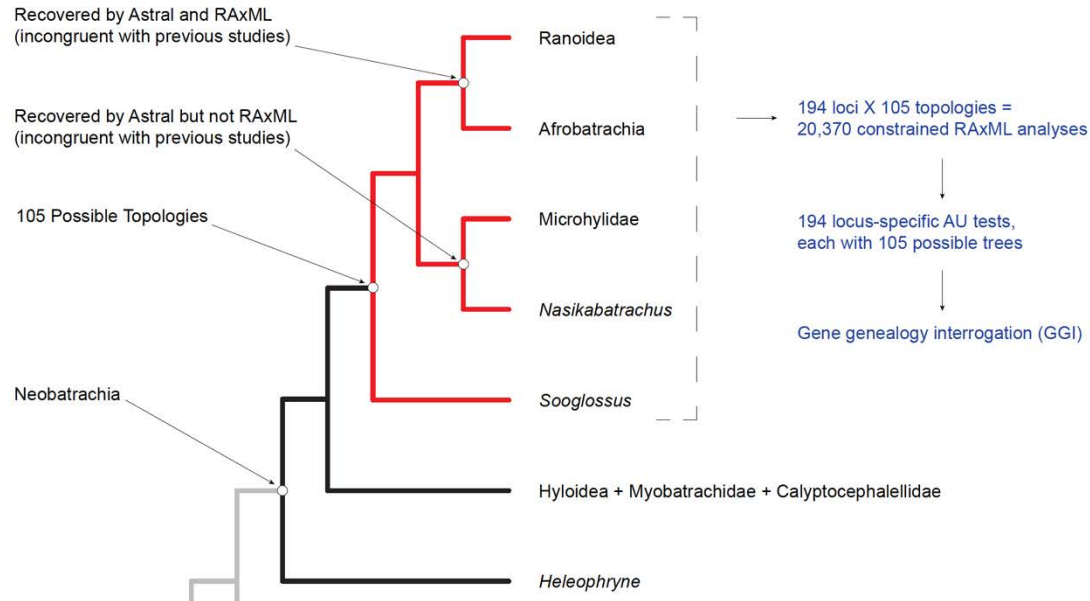
A Framework for Testing Neobatrachian Relationships

■ Topology congruent with previous studies ■ Topology incongruent with previous studies ■ Non-Neobatrachians excluded for GGI



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Conclusions

- The illusion of “support” for topological hypotheses depends on how hard one looks.
- The bootstrap can help determine the direction of support, but may not be informative about its magnitude.
- Substantial discordance across loci exists at the base of the amphibian tree (and may not all be noise!).
- Genomic data and new statistical models are providing novel insights into evolutionary relationships of amphibians.
- More data \neq easy answers (that are credible...).

Why Blue Waters?

- Rigorously testing competing topological models across large numbers of genes is computationally demanding.
- Even embarrassingly parallel approaches (gene-by-gene AIC) overwhelm typical HPC clusters' resources.
- MCMC sampling for rugged likelihood surfaces can be improved with large numbers of Metropolis coupled chains.
- For Bayes factor tests (with N taxa):

Markov chain Monte Carlo scales as N^2

Hamiltonian Monte Carlo scales as $N^{1.2}$



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