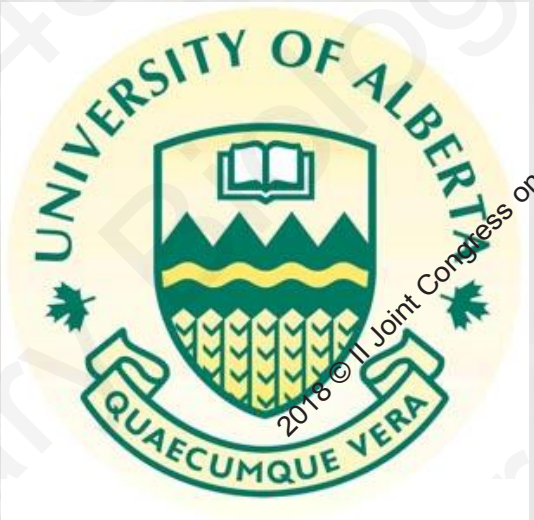
Overhauling the phylogenetic origins and early evolution of lizards and snakes

Tiago R. Simões



Squamata

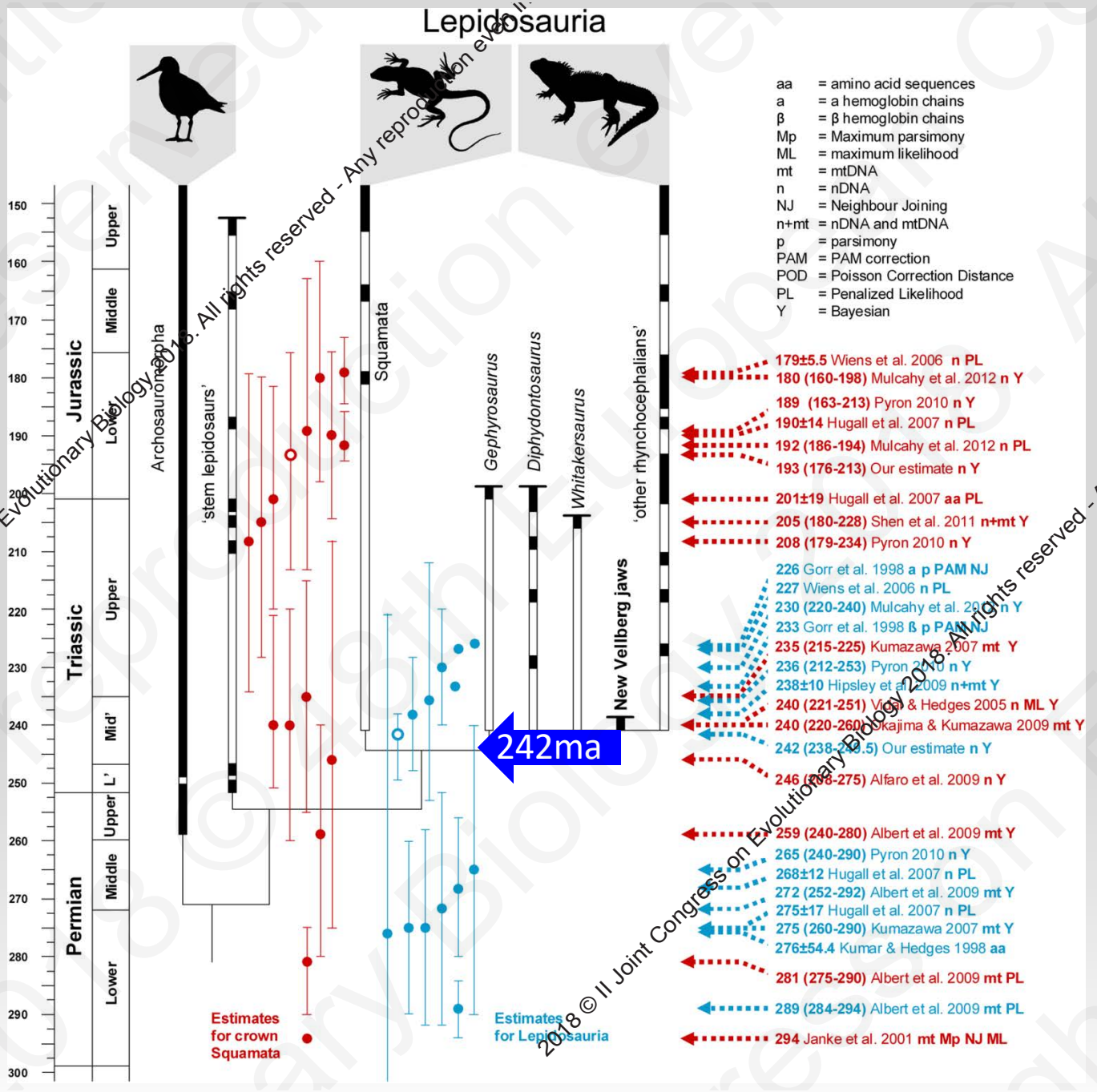
Lizards
Ca. 6.300 spp

Snakes
Ca. 3.500 spp

Amphisbaenians
197 spp

Lepidosauria = Squamata + Rhynchocephalia

Sphenodon punctatus



Jones et al. (2013)

What are the closest relatives to lepidosaurs?

Which were the earliest squamates?

When did the major reptile clades originate?

Early lepidosaur evolution

Current impediments to advance our knowledge

1-

Origin of squamates: ~240 mya (Early-Middle Triassic)

Oldest known fossils: Middle Jurassic (165 MYA) of Britain, Morocco, Central Asia.

2- They look like this:

Balnealacerta silvestris
(NHMUK R12669)

Bellairsia gracilis
(NHMUK R12678)

Oxiella tenuis
(NHMUK R12689)

Early lepidosaur evolution

Current impediments to advance our knowledge

3- Which of these are **lepidosauromorphs?**

Younginiforms: Gauthier 1984; Benton 1985, 1990; Carrol 1988; Evans 1988

Paliguanids: Gauthier 1984; Benton 1985, 1990; Carroll 1975, 1988; Evans 1988

Kuehneosaurids: Gauthier 1984; Evans 1988; Caldwell 1996; Motani et al. 1998; Lee 1997, Lee 2001

Sauropterygians: Rieppel & de Braga 1996; Wilkinson 1997; Motani et al. 1998; Lee 2001; Hill 2005

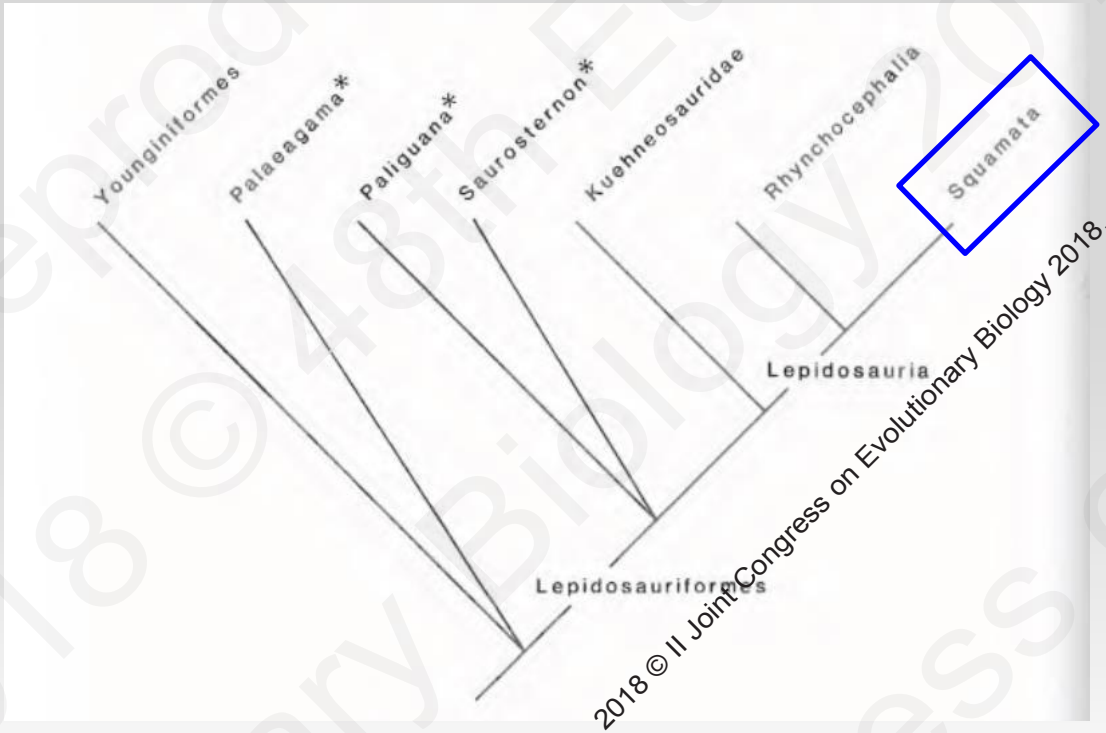
Turtles: Rieppel & de Braga 1996; Caldwell 1996; Motani et al. 1998; Müller 2004; Lyson et al. 2012

Early lepidosaur evolution

Current impediments to advance our knowledge

4- Taxonomic sampling in broad scale reptile relationships:

10,000 species of extant forms (64 families) + hundreds of extinct lineages represented as..

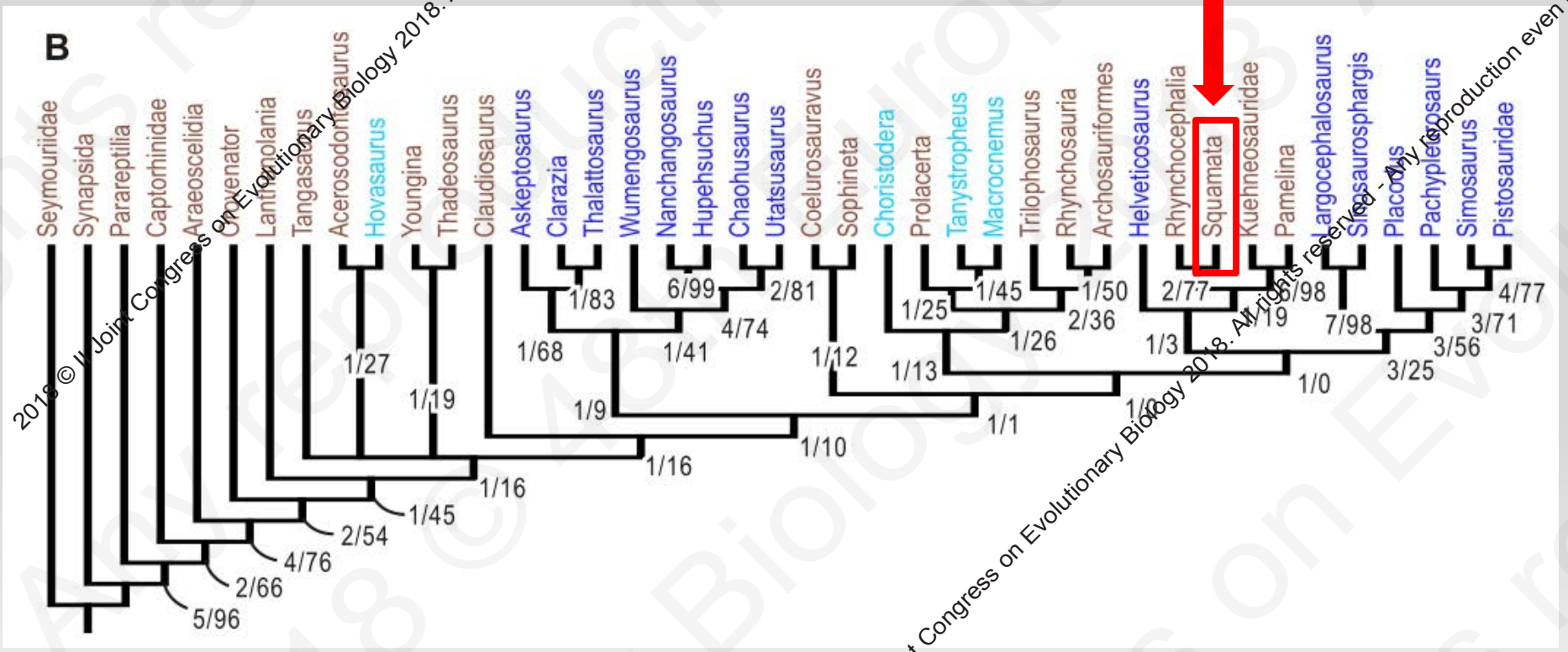


Gauthier et al. (1988)

Early lepidosaur evolution

Current impediments to advance our knowledge

4- Taxonomic sampling in broad scale reptile relationships:



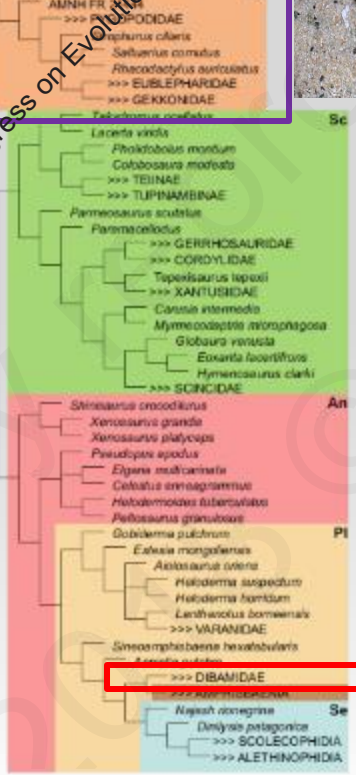
Chen et al. (2014)

Early lepidosaur evolution

Current impediments to advance our knowledge

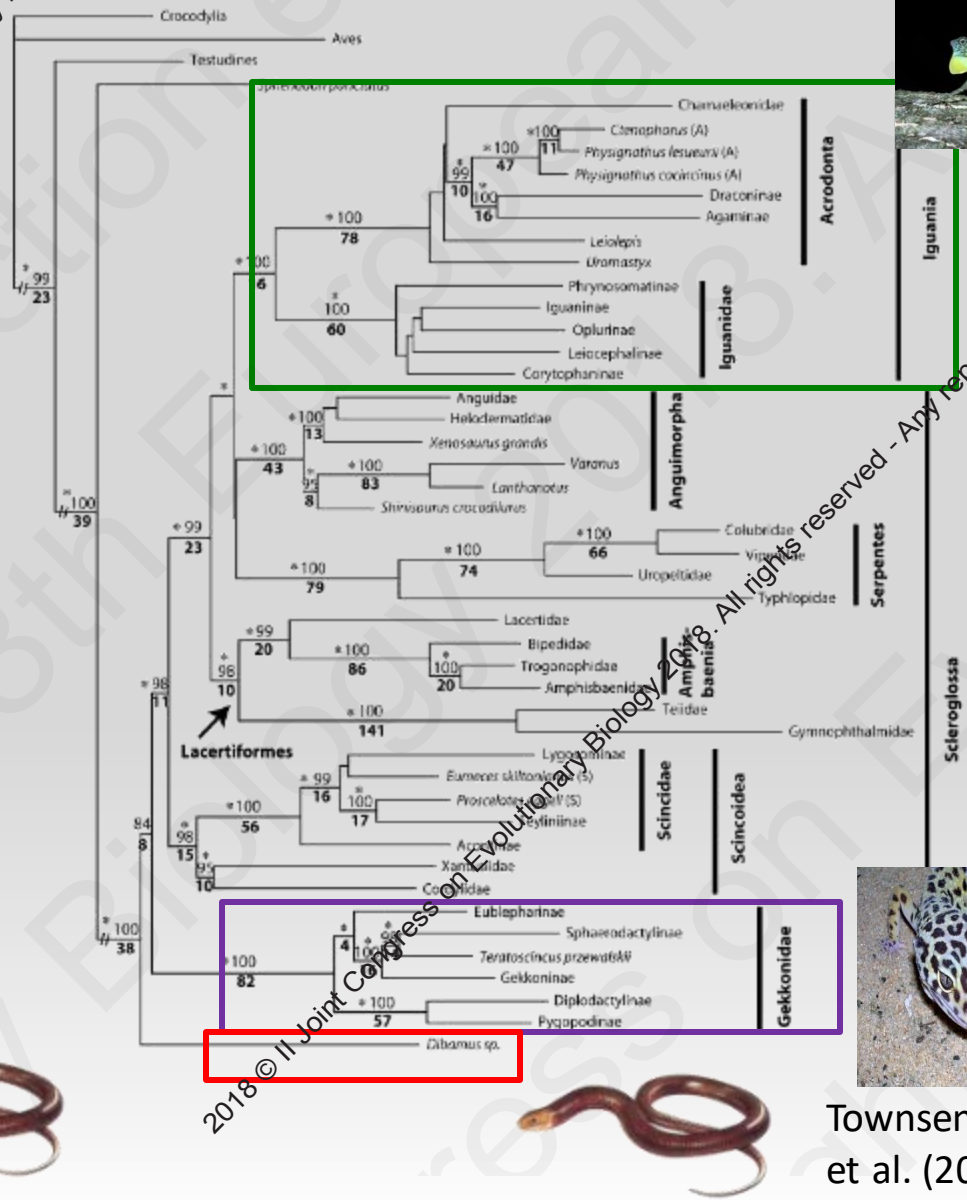
5- How to represent Squamata? What are the earliest squamates?

Morphological signal
(iguanians first)



Gauthier et al. (2012) modified

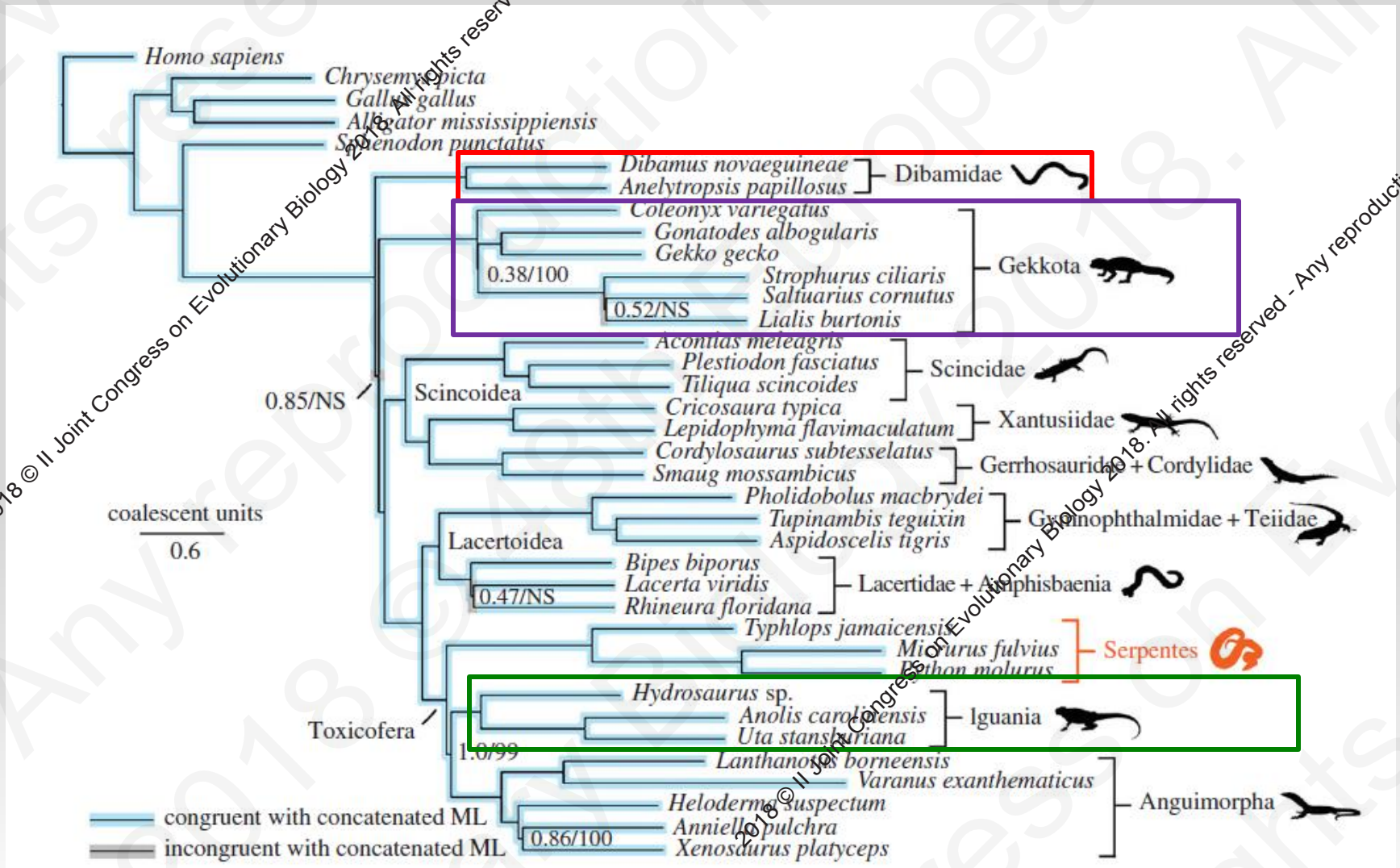
Molecular signal
(geckos + dibamids first)



Townsend et al. (2004)

Phylogenomics

Streicher & Wiens (2017): 4178 nuclear loci (UCEs)



WHAT TO DO, THEN?

Objectives

New reptile phylogeny:

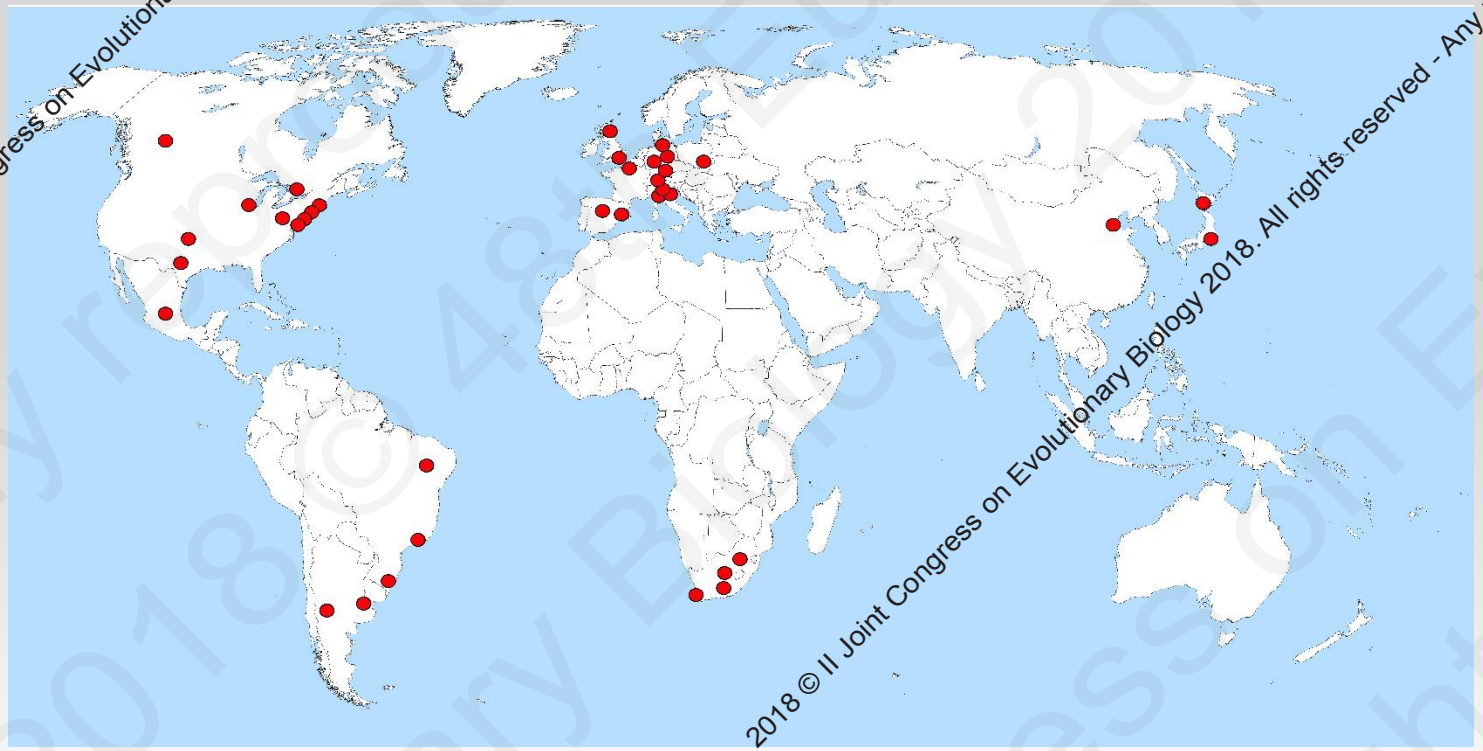
- Rich sampling of **taxa within and outside the Squamata**
- **Morphological and Molecular** data
- Rigorous criteria for **morphological character constructions**
- **Primary data collection** of morphological data

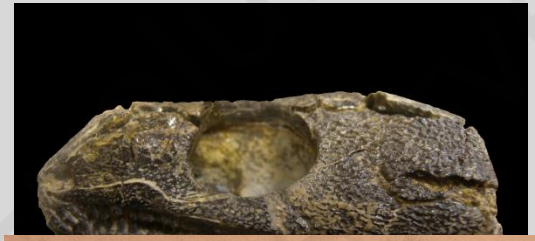
Macroevolutionary inferences:

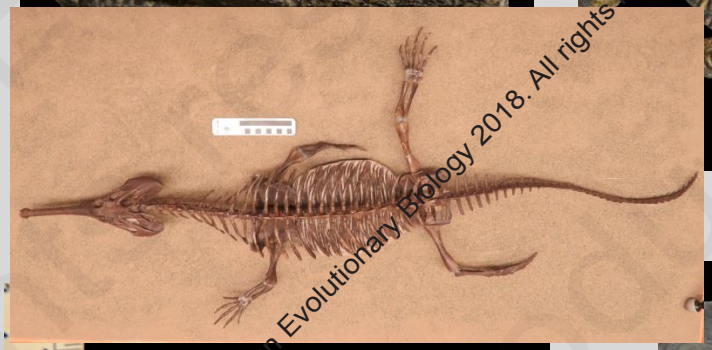
- **Divergence time estimates**
- **Evolutionary rates**

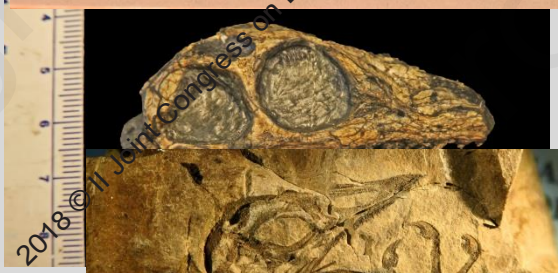
After nearly **400 days of trips to collections** in museums and universities:

- **51 collections** visited in university and museums in **17 countries**
- **Personally observed specimens from 129 species** of fossil and extant reptiles

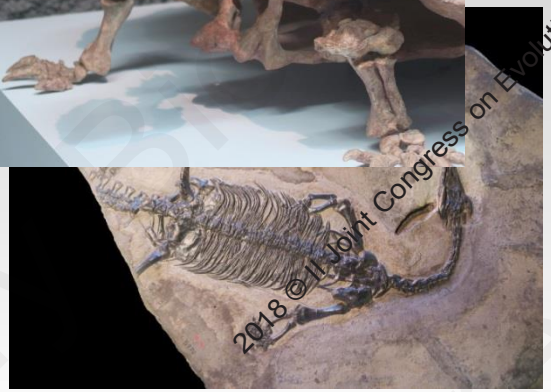
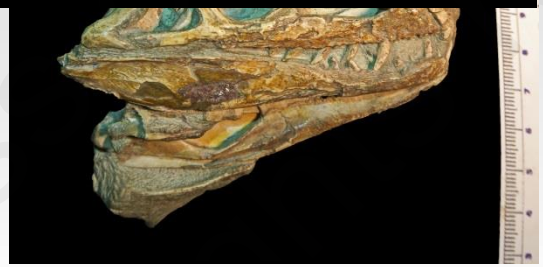


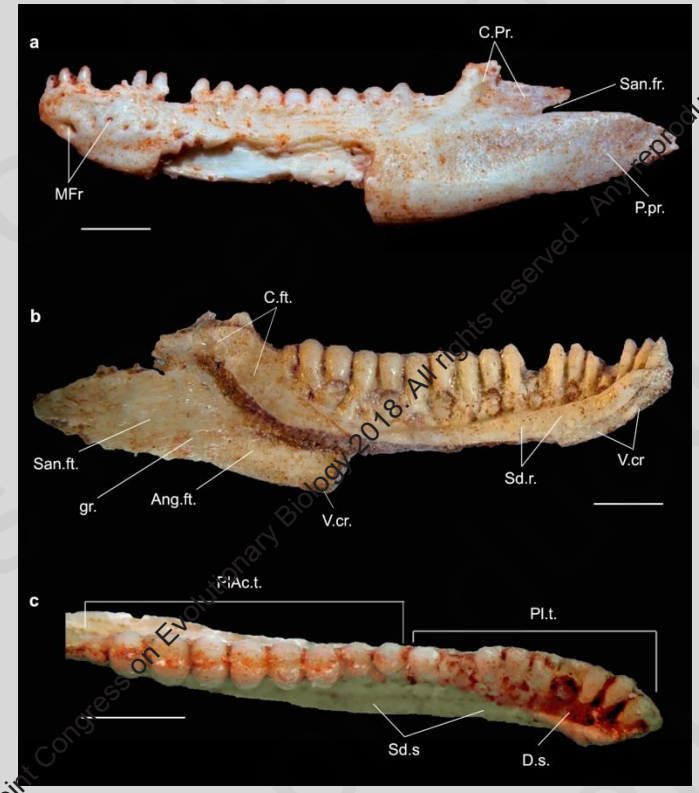


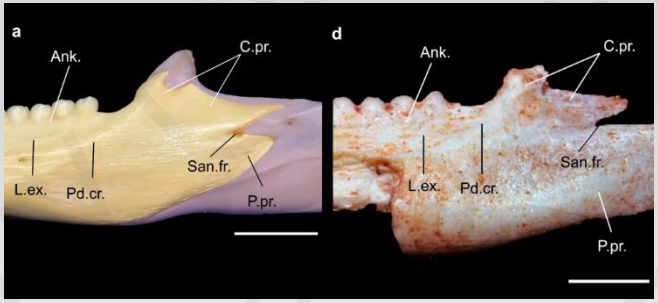



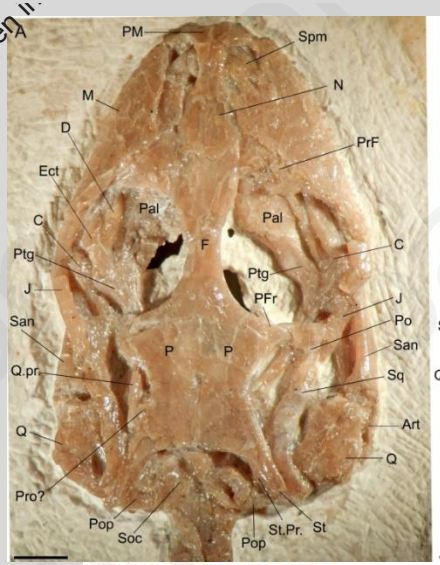



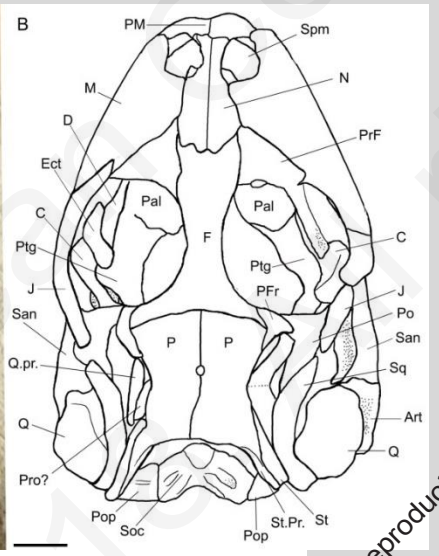


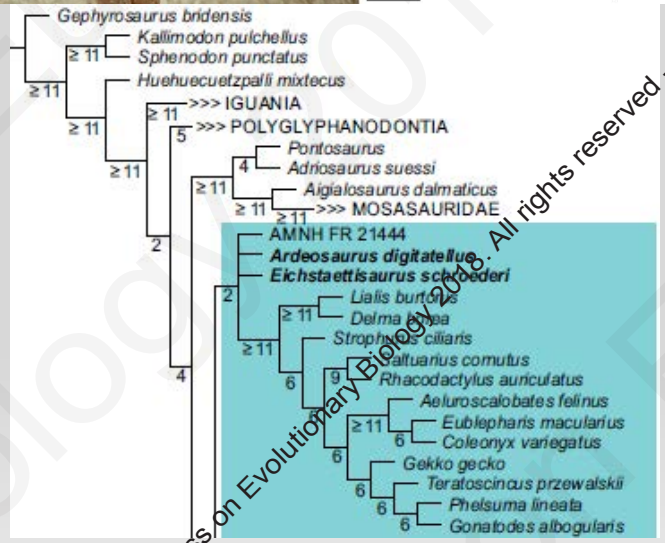














Gueragama sulamericana (90-75 MYA)

Eichstaettisaurus schroederi (155 MYA)

Simões et al. (2015), *Nature Comm.*, 6(8149)

Simões et al. (2017a), *Zool. J. Linn. Soc.* 180, 216-241

Morphological characters

Examples of common practices in character construction that should be avoided:

- **One transformation series split into other ones**

e.g. Ch.1: Supratemporal shortens…: absent (0)/ present (1)"
Ch.2: Supratemporal lengthens…: absent (0)/ present (1)"

Redundant

- **Characters dependent on other characters**

e.g.: nasal longer than frontal - But which one is actually changing in size?

-
-

And more!

30% - 45% of characters in squamate Datasets

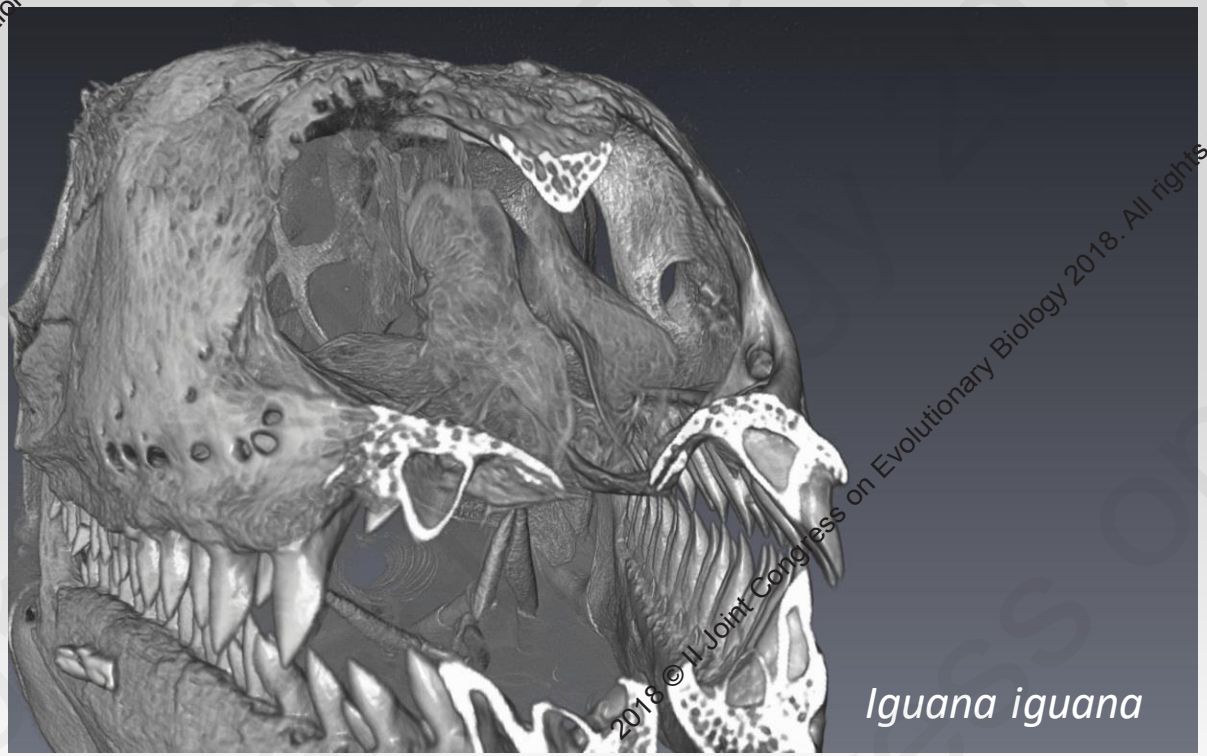
Among 1,000 characters

Simões et al. (2017b), *Cladistics* 33, 198-219

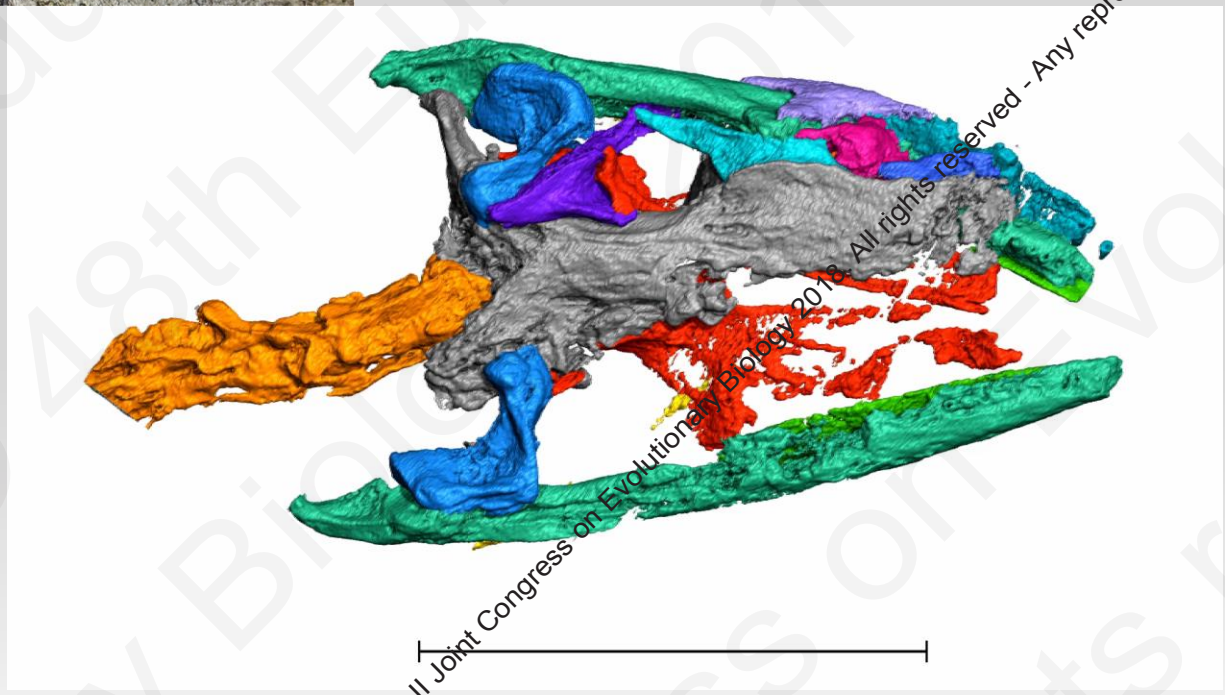
Morphological data:

347 morphological characters
129 terminal taxa (91 extinct and 38 extant)

- **Largest taxon sampling** ever collected for **diapsids**
- **First** with **deep sampling** of **squamates**



Megachirella wachtleri



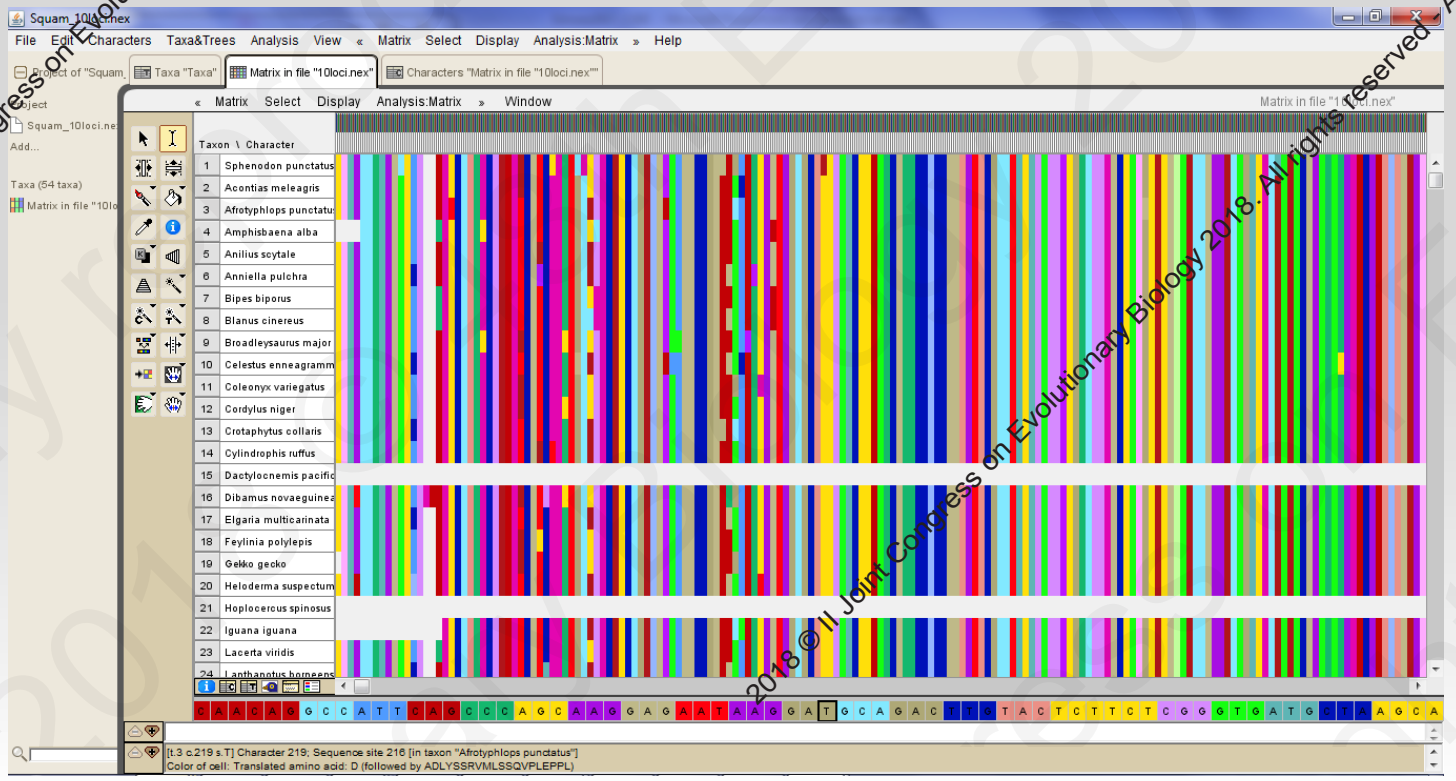
Simões et al. (2018), *Nature* 557:706-709.

Molecular data:

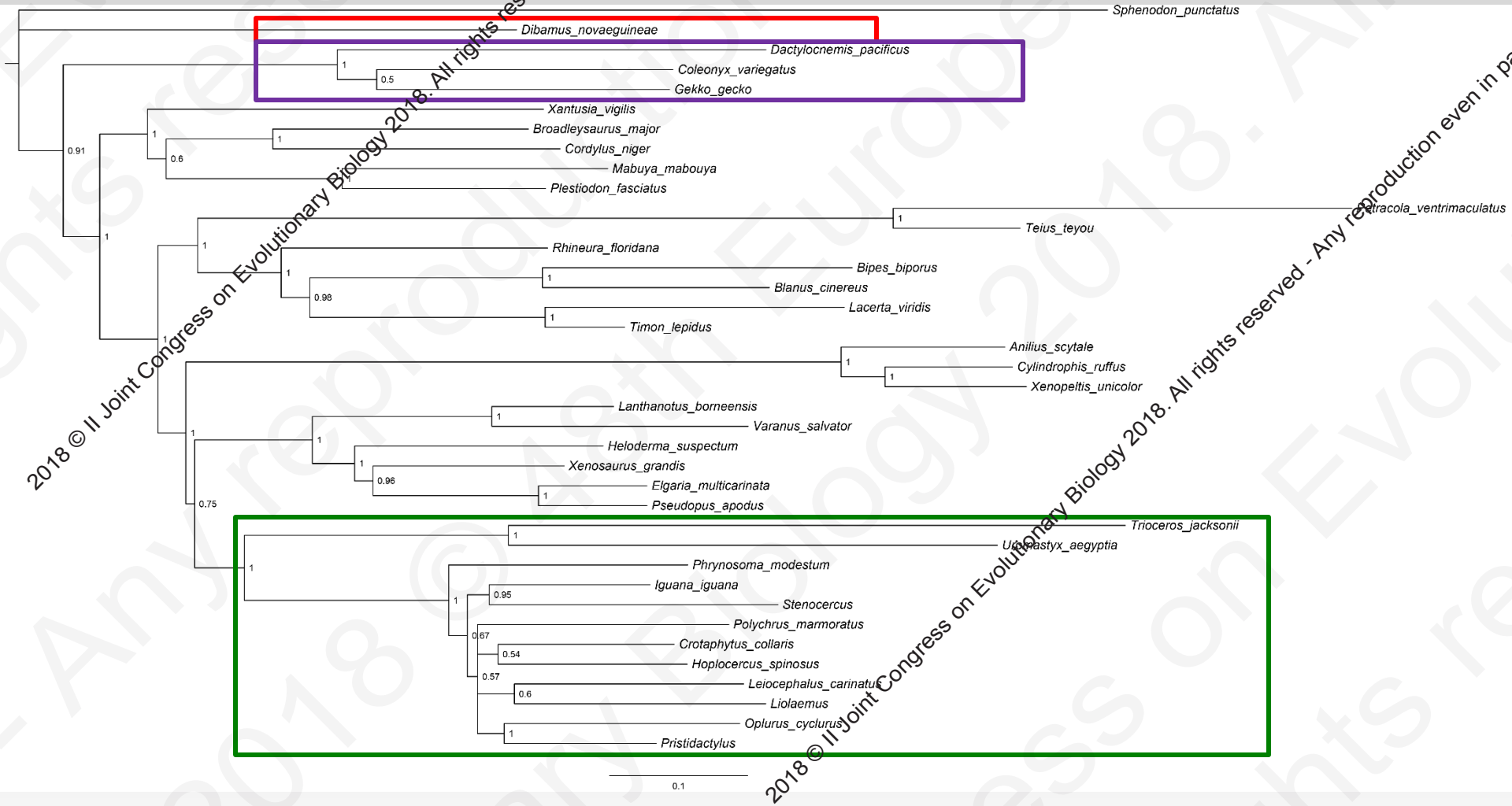
11532 bp from **16 loci (13 nuclear + 3 mitochondrial)** from 38 extant taxa (GenBank)

Alignments : MAFFT v. 7 → global alignment strategy + iterative refinement with consistency scores (G-INS-i).

Partitions and **substitution models** assessed with PartitionFinder v.1.1:



Bayesian inference
Molecular
(Majority rule consensus)



Tree inference procedures

Maximum parsimony (Equal weights): TNT v.1.1 (New Technology Search algorithms)→ protocol of Simões et al. (2015a)

Bayesian Inference (non-clock): Mr. Bayes v. 3.2
Morphology:
-MkV
-GA vs LN rate variation across characters (Bayes Factor non-significant)

Time calibrated Bayesian Inference
Relaxed morpho-molecular clock analysis (FBD model + Diversity sampling):
Mr. Bayes v. 3.2
- MkV (Morphology)
- IGR clock vs TK02 clock (Bayes Factor = 230.36 → favors IGR)
- Tip-dating/ tip+node dating

Maximum parsimony
Morphology
(Strict consensus
621 most parsimonious trees)

Captorhinidae
Araeoscelidia
"Younginiformes"
Ichthyopterygia
Thalattosauria
Sauropterygia
Protorosauria
Kuehneosaurids
Choristodera
Testudinata
Rhynchosauria
Archosauriformes
Rhynchocephalia
Gekkota
Megachirella
Lacertoidea
Squamata
Iguania
Anguimorpha
Mosasauria
Amphisbaenia
Serpentes

Maximum parsimony
(Equal Weights)
Morphology
(Strict consensus
621 most parsimonious trees)

Captorhinidae
Araeoscelidia

"Younginiformes"

Ichthyopterygia

Thalattosauria

Sauropterygia

Protorosauria

Kuehneosaurids

Choristodera

Testudinata

Rhynchosauria

Archosauriformes

Rhynchocephalia

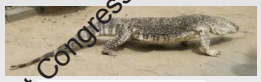
Gekkota

Teiioidea

~TOXICOFERA
(but with dibamids +
amphisbaenians)

Iguania

Anguimorpha



Mosasauria

Amphisbaenia

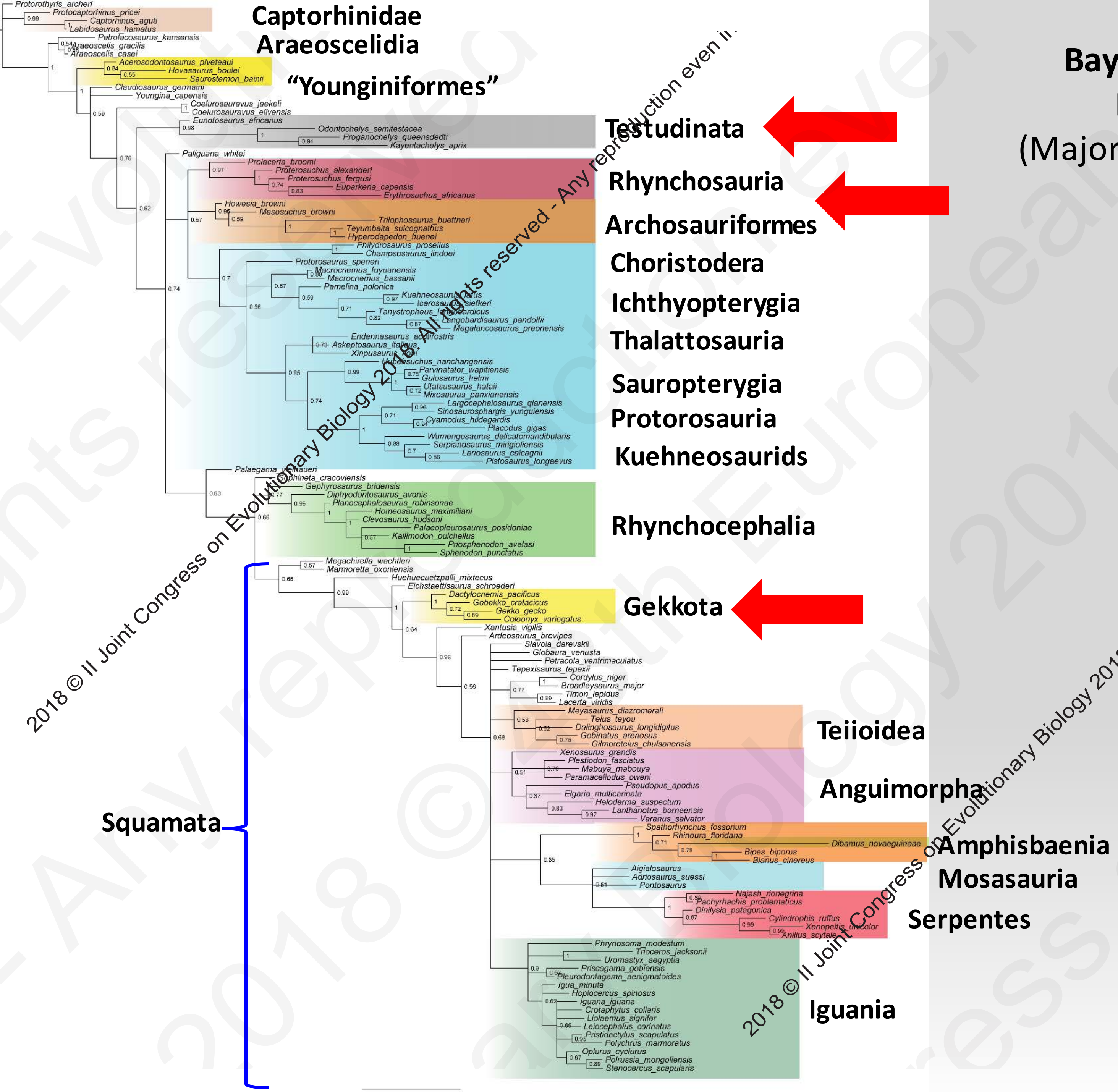
Serpentes

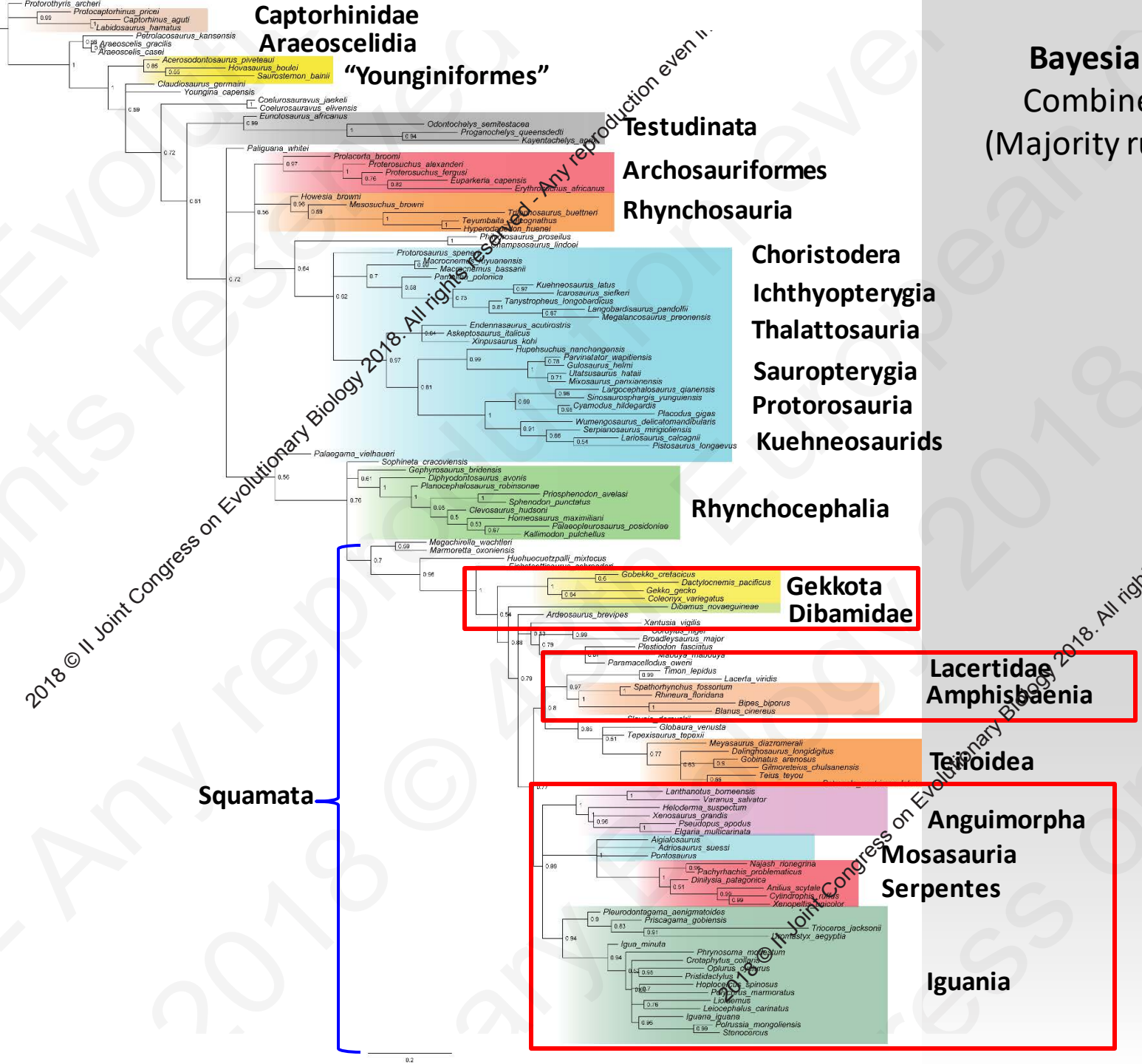
Squamata

Bayesian inference

Morphology

(Majority rule consensus)




Captorhinidae
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Kuehneosaurids
Rhynchocephalia
Gekkota
Dibamidae
Lacertidae
Amphisbaenia
Teioidea
Squamata
Anguimorpha
Mosasauria
Serpentes
Iguania
Bayesian inference
Combined evidence
(Majority rule consensus)
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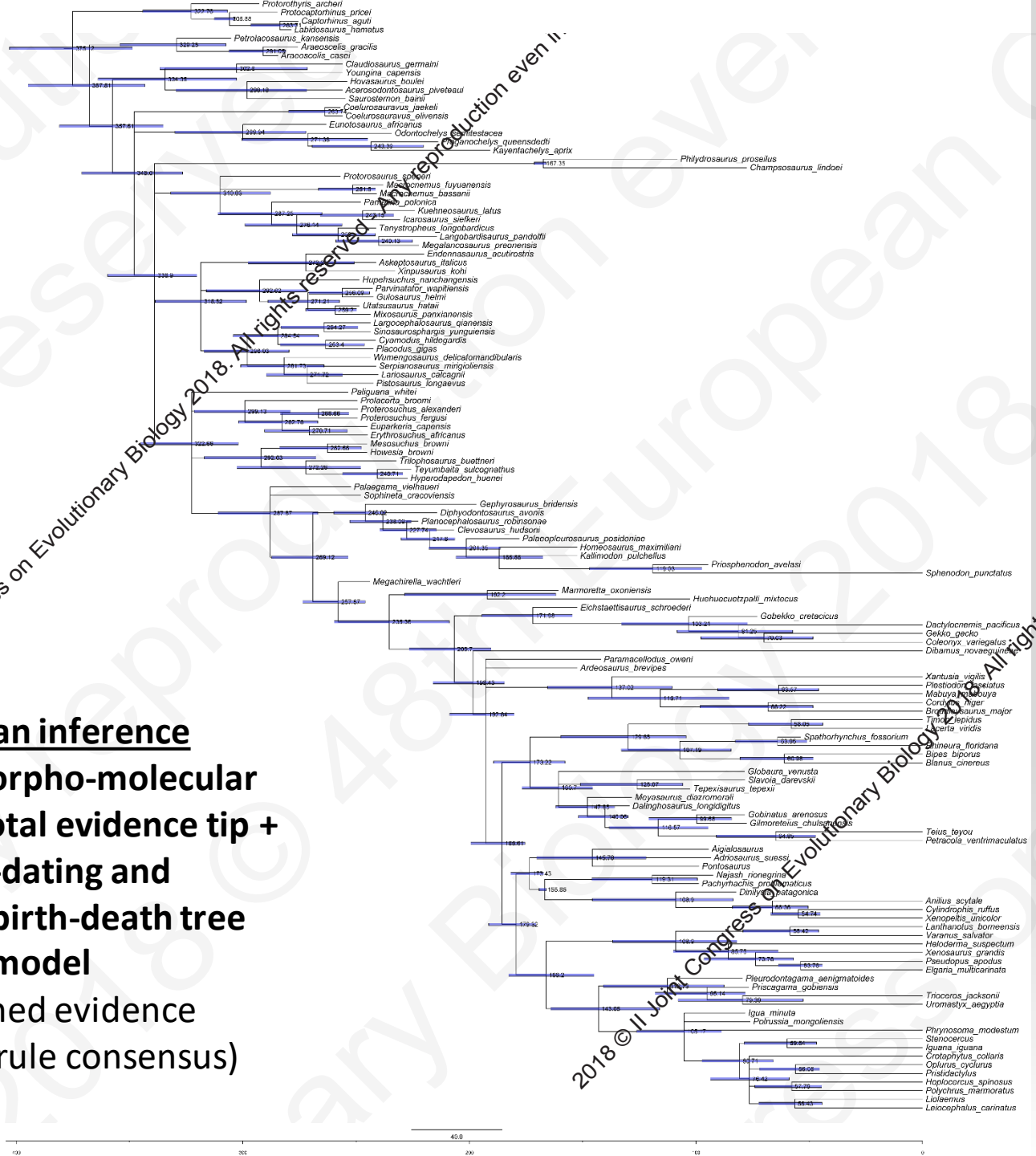
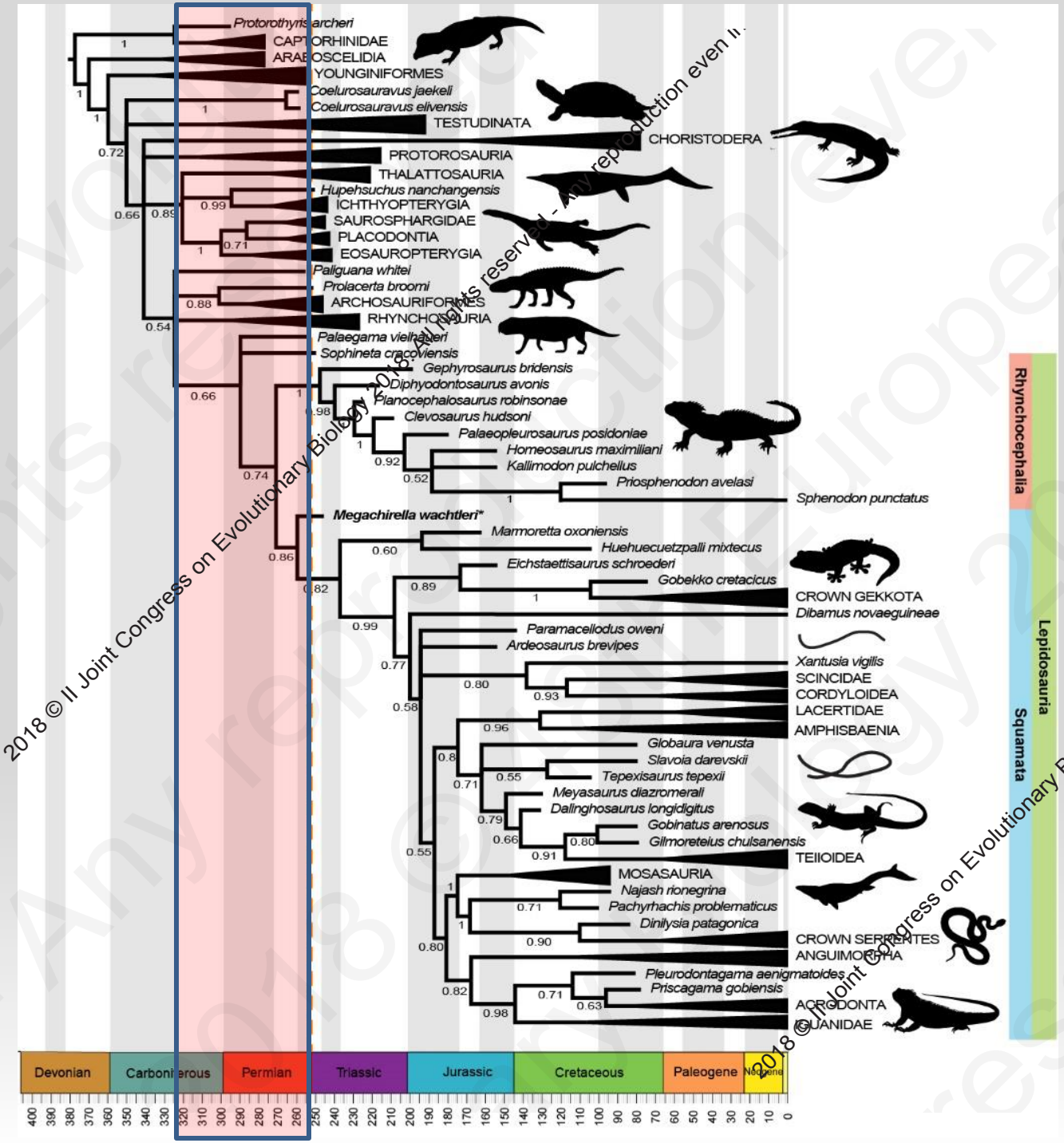


Bayesian inference

Relaxed morpho-molecular clock with total evidence tip + node-dating and fossilized birth-death tree model

Combined evidence

(Majority rule consensus)



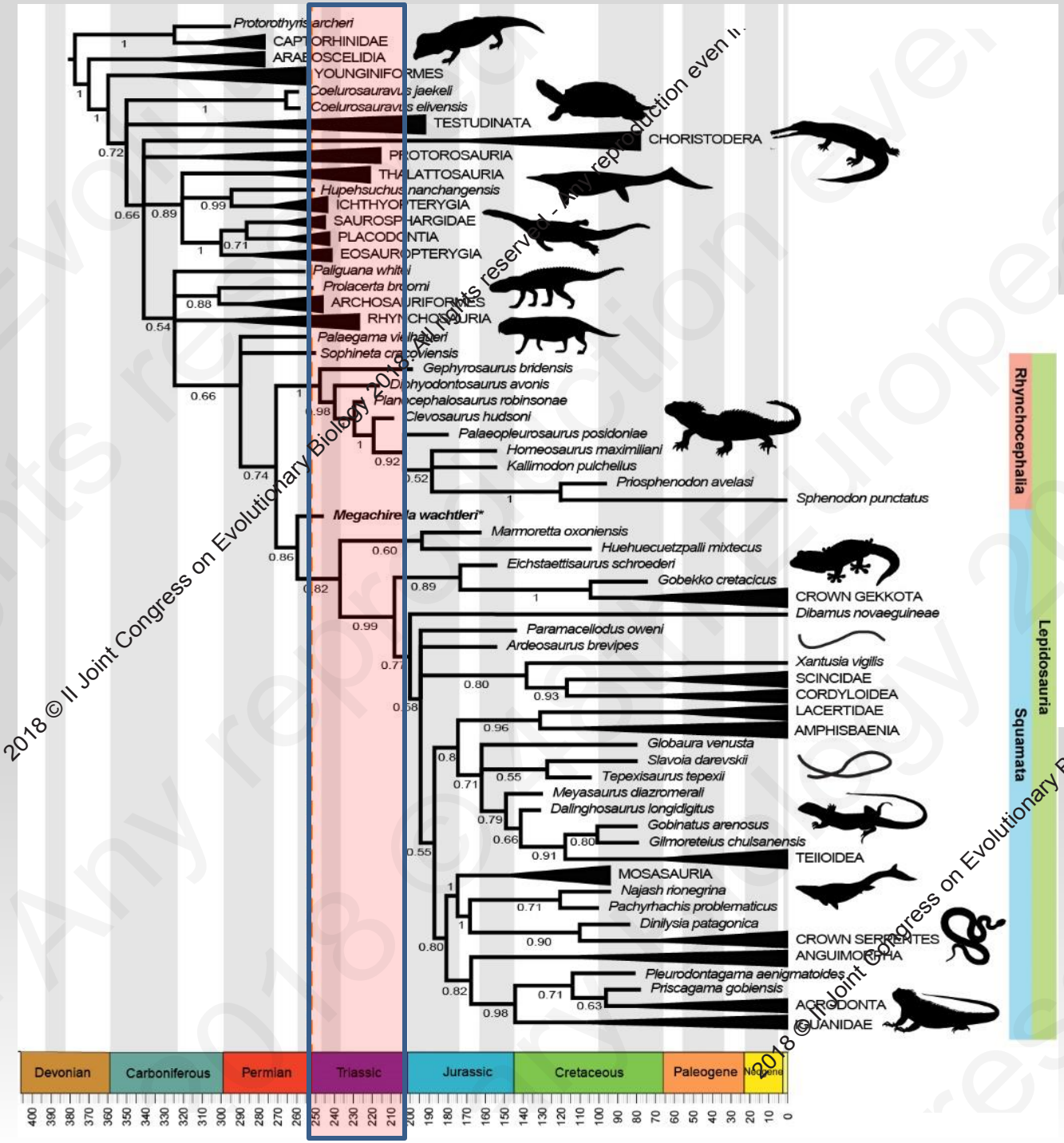
Bayesian inference

Relaxed morpho-molecular clock with total evidence node+tip dating

Combined evidence

Permian:

Origin of most diapsid lineages



Bayesian inference

Relaxed morpho-molecular clock with total evidence node+tip dating

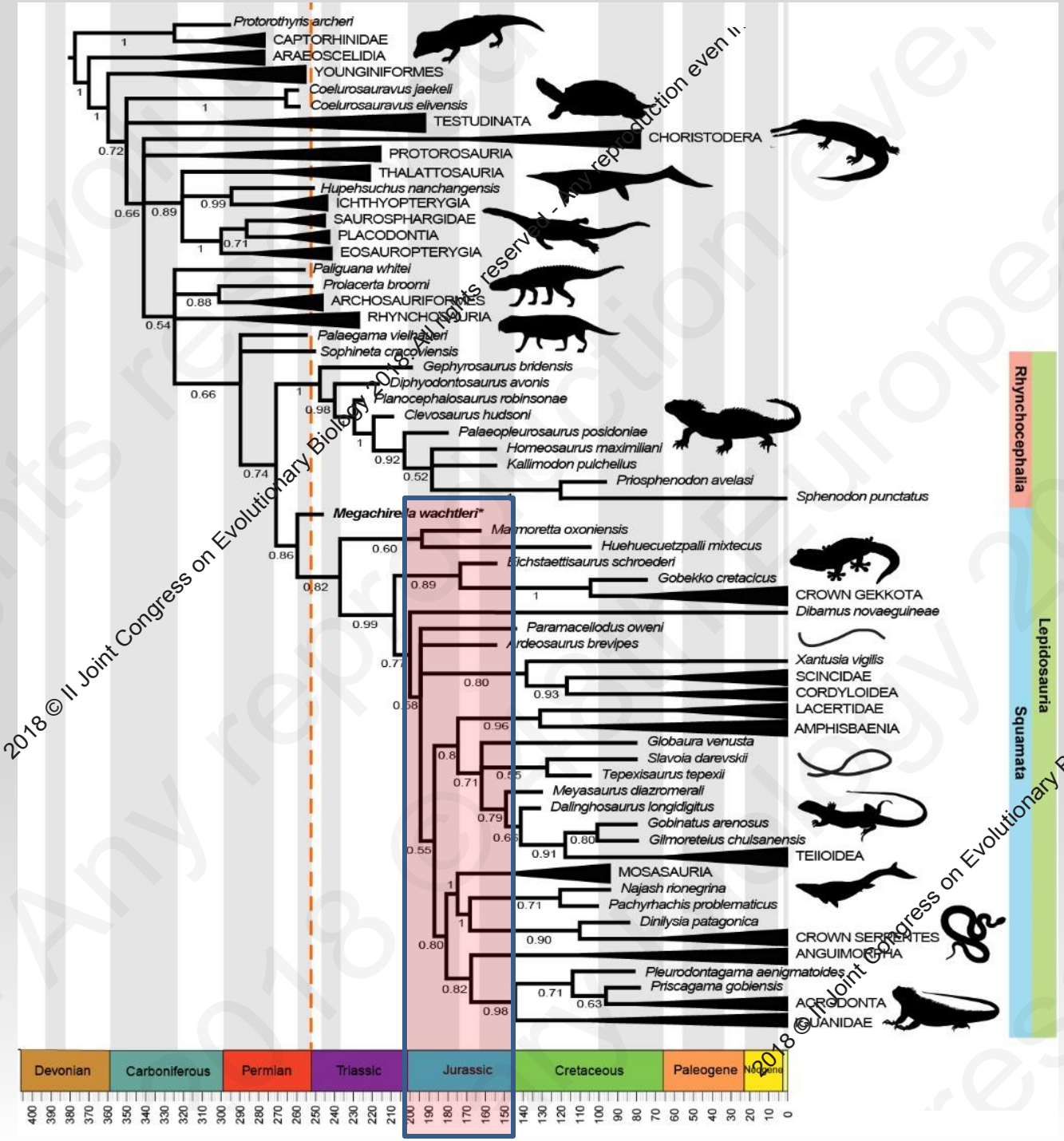
Combined evidence

Triassic:

An era of diversification:

Radiation of most other lineages

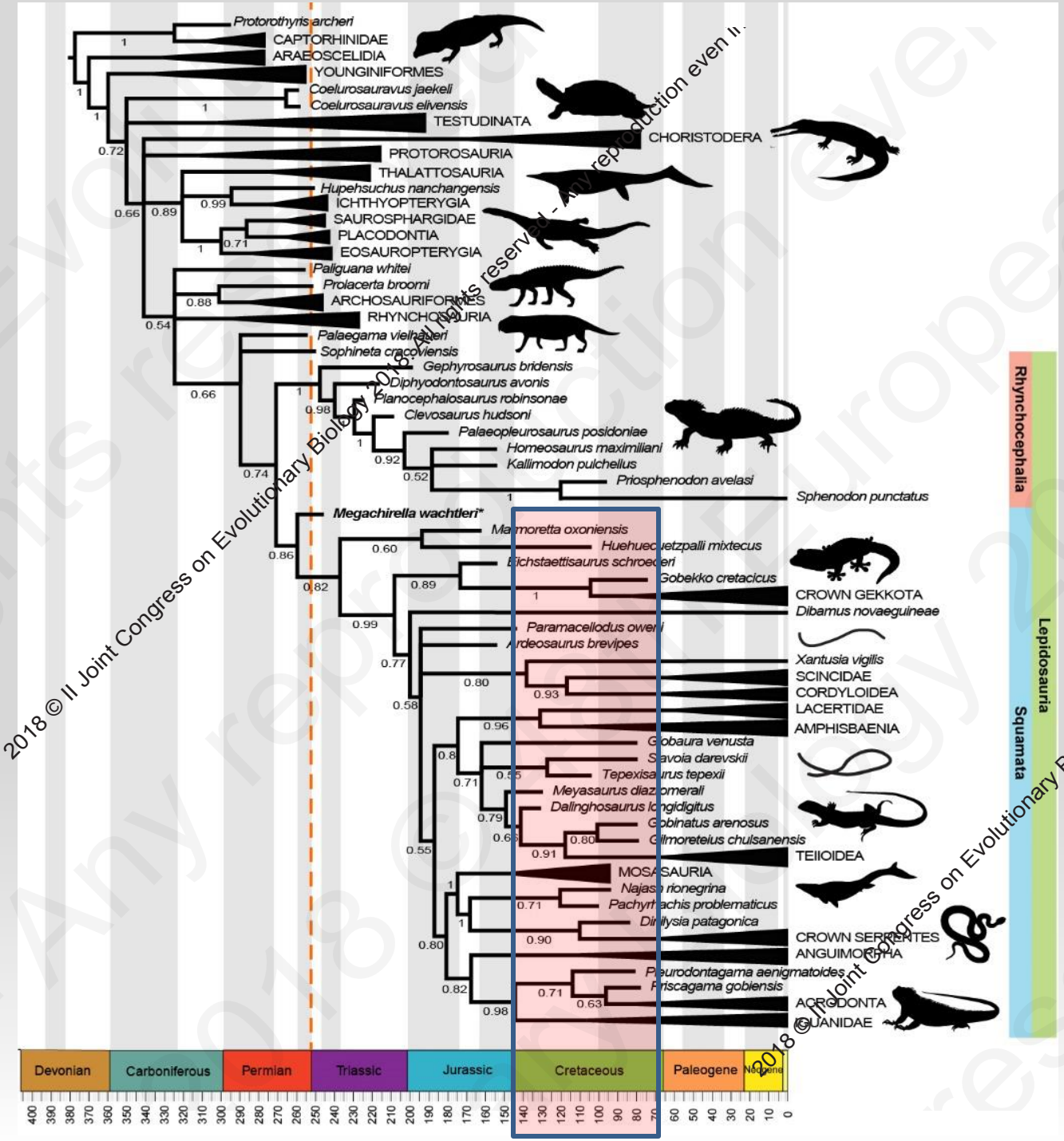
- Explains why most fossils are from this age, although lineages are much older



Bayesian inference

Relaxed morpho-molecular clock with total evidence node+tip dating

Combined evidence

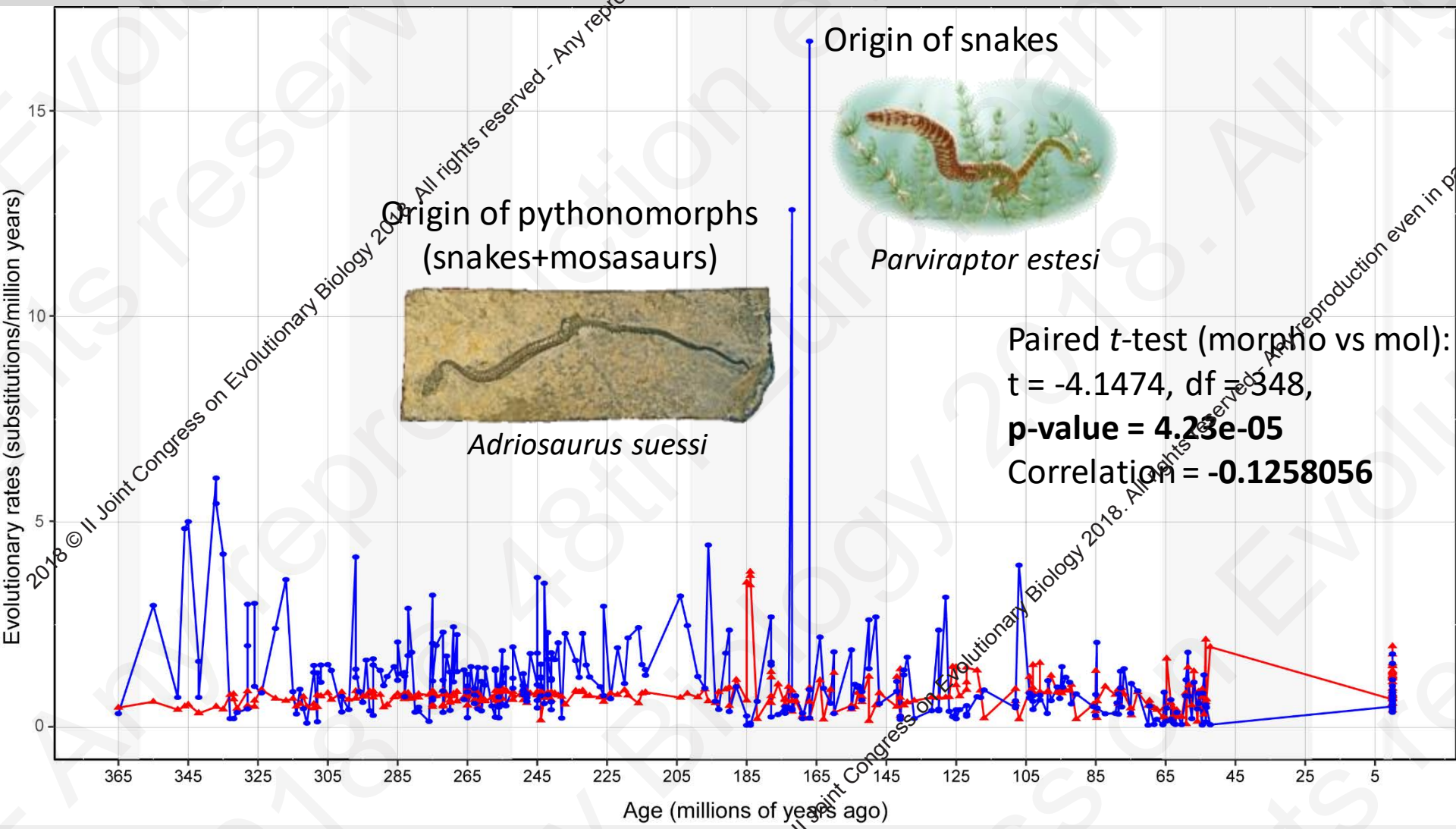


Bayesian inference

Relaxed morpho-molecular clock with total evidence node+tip dating

Combined evidence

Evolutionary rates



*Red = molecular rate of evolution

*Blue = morphological rate of evolution

Conclusions

- Some "**early lepidosauromorphs**" actually fall among **other reptilian clades**
- Other "**early lepidosauromorphs**" are the **earliest known squamates (filling squamate "fossil gap")**
- **First agreement** between **morphological and molecular data** on the **origin of squamates**
- Major reptilian clades ***originated*** **before the P-T extinction**, but ***diversified*** **in the Triassic**
- Sustained **high rates of morphological evolution in reptiles** during the past 350 million years when compared to molecular rates of evolution.
- **High evolutionary rates** associated with the **origin of pythonomorphs and snakes.**

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