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Convergent body size evolution of Crocodyliformes upon entering the aquatic realm

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1. Introduction

Twenty-four species of crocodile populate the globe today, but this richness represents a minute fraction of the diversity and disparity of Crocodyliformes since their origin early in the Triassic. Across this clade, three major diversification events into the aquatic realm have occurred. Aquatic and terrestrial habitats impose differing selective pressures on body size. However, previous research on this topic in Crocodyliformes remains qualitative in nature. In this study, our goal was to quantify the influence of habitat (terrestrial versus aquatic) on the evolution of body size in Crocodyliformes. We find a history of repeated body size increase and convergence following shifts to an aquatic lifestyle, suggesting common selective pressures on life in water spanning multiple independent aquatic clades.

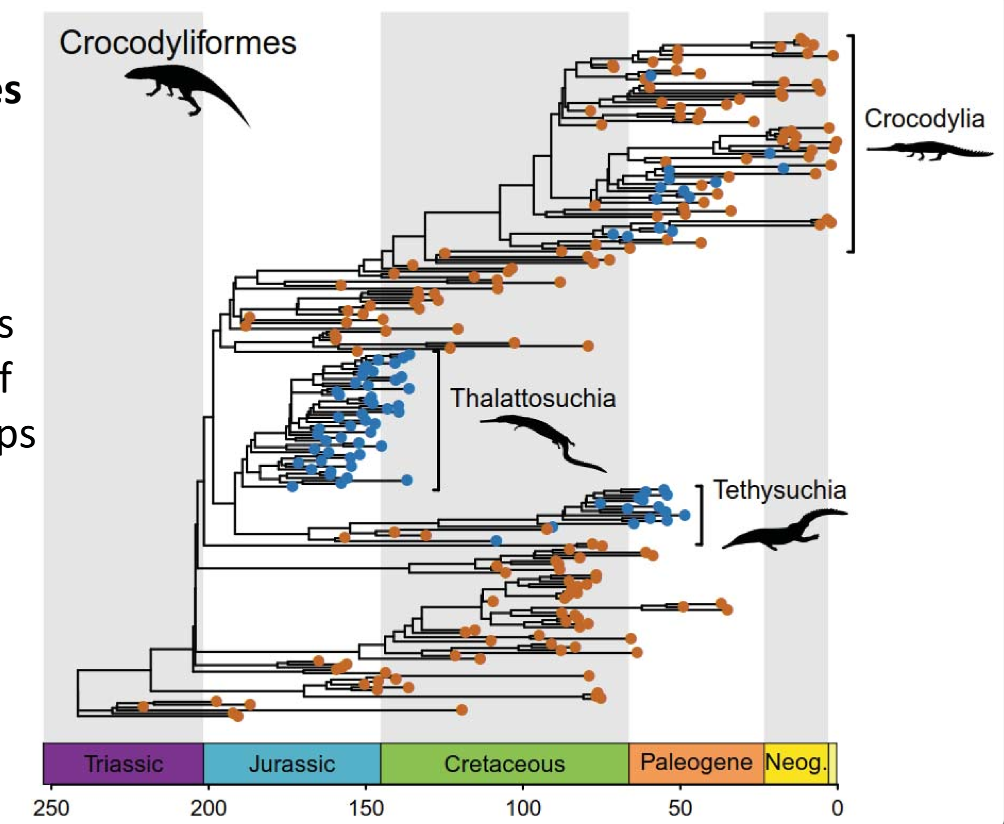
2. Materials and Methods

- Calculated body masses of 249 crocodyliformes (living and extinct) using measurements from primary literature
- Assigned habitats based on compilations and primary literature
- Crocodyliformes supertree (Bronzati et al. 2015)
- Species fossil ranges from compilations and PBDB
- Characterless tip-dating analysis using R and MrBayes
- Macroevolutionary Ornstein-Uhlenbeck (OU) model fitting
  - *OUwie* R package (Beaulieu et al. 2012)
  - Results model-averaged across 17 different models using AIC

General Equation of an OU Model: $dX(t) = \alpha[\theta - X(t)]dt + \sigma dB(t)$	
$X(t)$: initial body size	**α: strength of selection**
$dX(t)$: change in body size	**σ: intensity of random drift**
$dB(t)$: random variation	**θ: body size optimum**

Figure 2.1: **Maximum clade credibility tree of Crocodyliformes showing invasions of the aquatic realm within three clades**

Summary tree of posterior distribution of trees from MrBayes characterless tip-dating analysis of the Crocodyliformes supertree. Tips without habitat and/or size data were dropped. Tip labels indicate terrestrial and aquatic species.



3. Results

Figure 3.1: **Aquatic clades converge on larger body size optima**

Weighted means and 2σ confidence intervals of model-averaged body mass optima (θ) as estimated by OUwie analyses for terrestrial and aquatic regimes. Aquatic clades have statistically greater body mass optima than the terrestrial regime ($p < .001$, Mann-Whitney test).

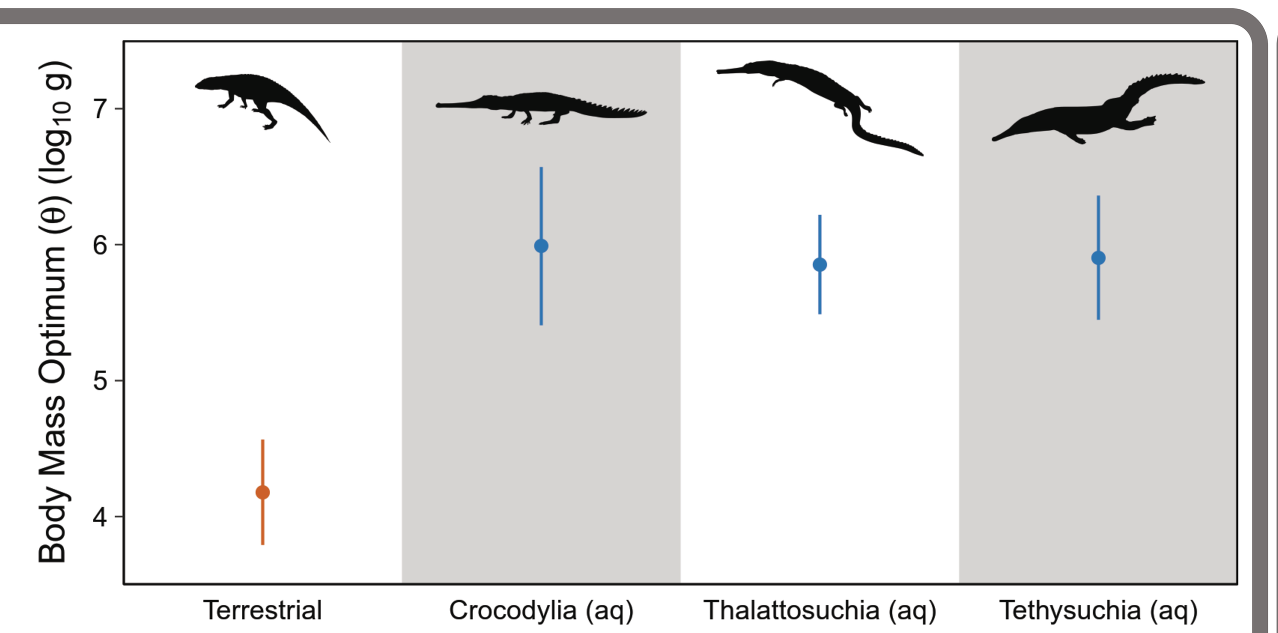


Figure 3.2: **Aquatic clades converge on shorter phylogenetic half-lives**

Boxplots of model-averaged phylogenetic half-lives (ln(2)/α) as estimated by OUwie analyses for terrestrial and aquatic regimes. Outliers have been removed. Aquatic clades have statistically shorter phylogenetic half-lives compared to the terrestrial regime ($p < .001$, Mann-Whitney test).

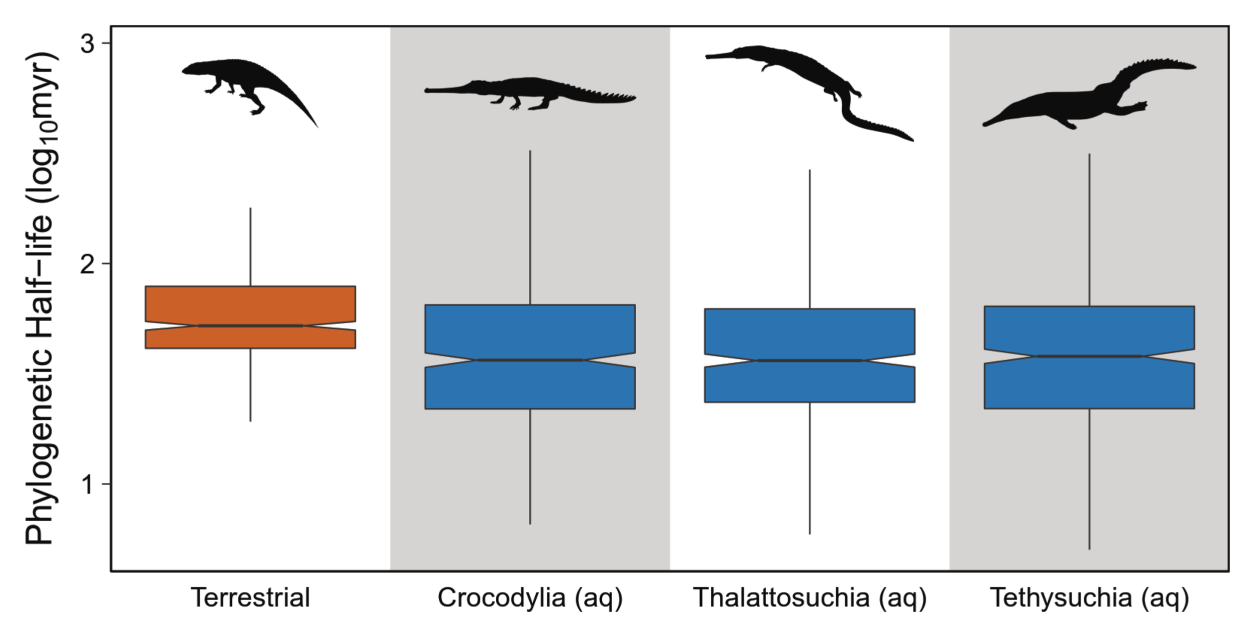


Figure 3.3: **Aquatic clades converge on smaller stationary variances**

Boxplots of model-averaged stationary variances ($\sigma^2/(2*\alpha)$) as estimated by OUwie analyses for terrestrial and aquatic regimes. Outliers have been removed. Aquatic clades have statistically smaller stationary variances compared to the terrestrial regime ($p < .001$, Mann-Whitney test).

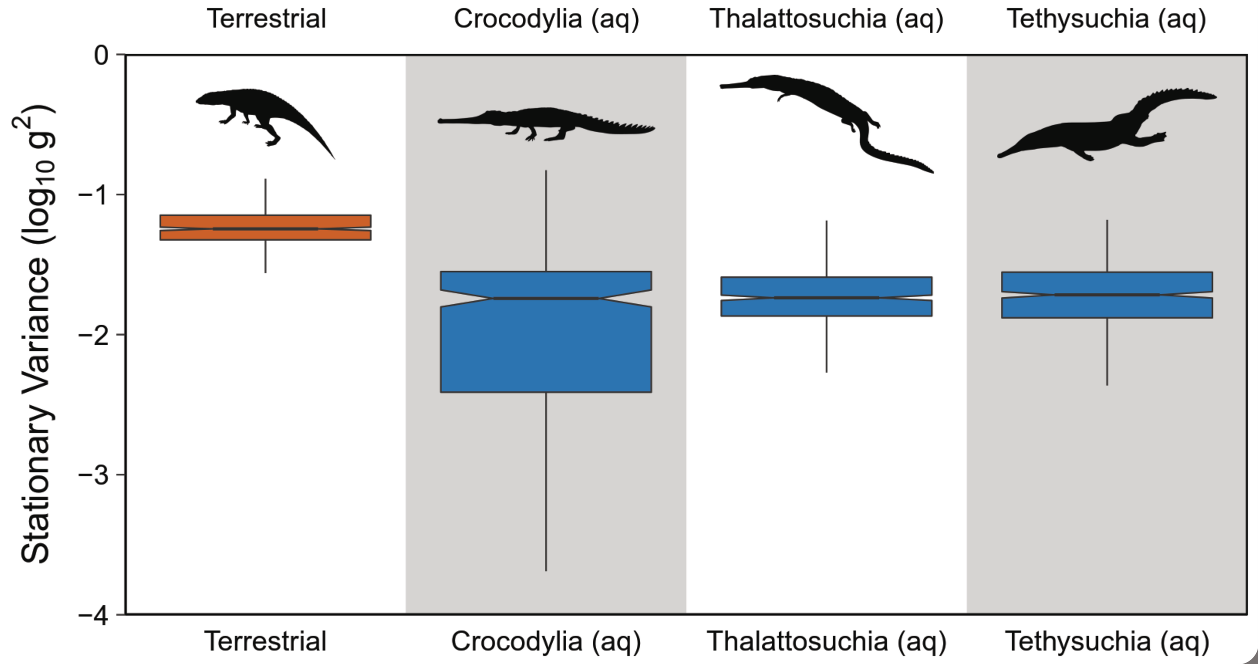


Figure 3.4: **Body size governs relative time invested in temperature regulation**

Ratios of the time it takes to cool down versus the time it takes to warm up in crocodiles in air and in water (Smith 1976) compared to a stacked histogram of terrestrial and aquatic body masses. Larger sizes require less warming time with respect to cooling time. Living in air is thermally advantageous at smaller size whereas living in water is preferable at larger size.

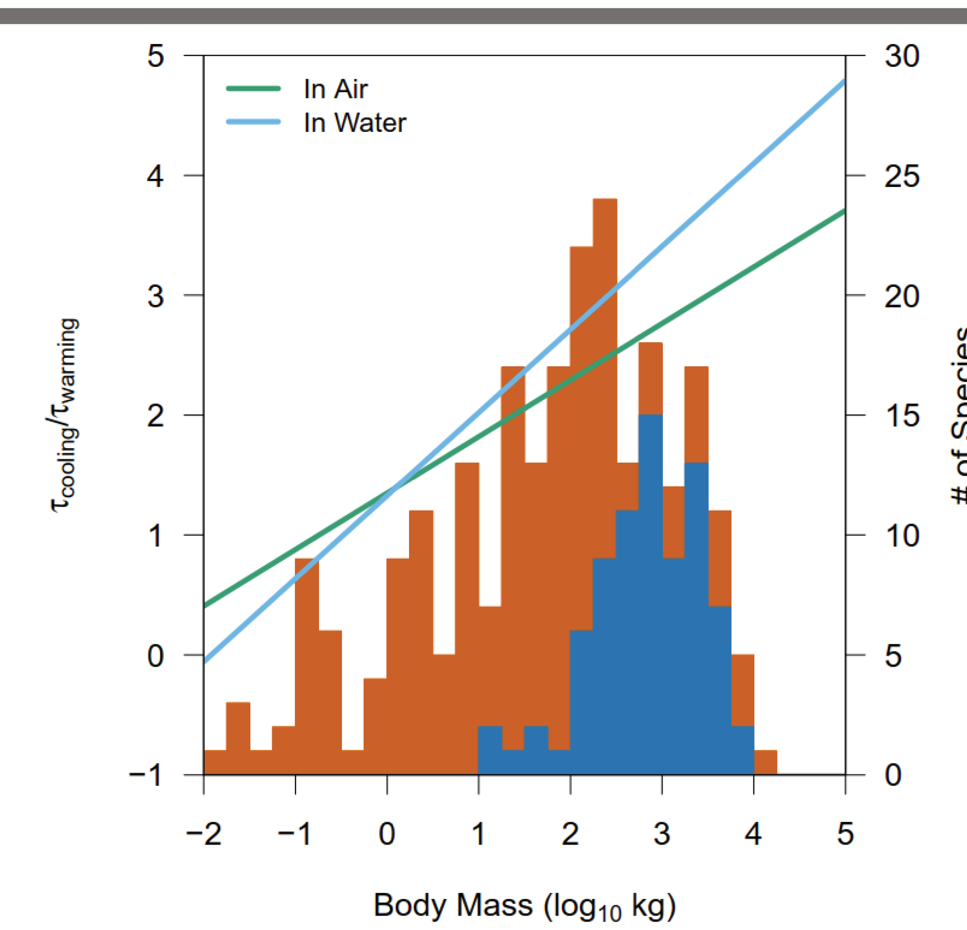
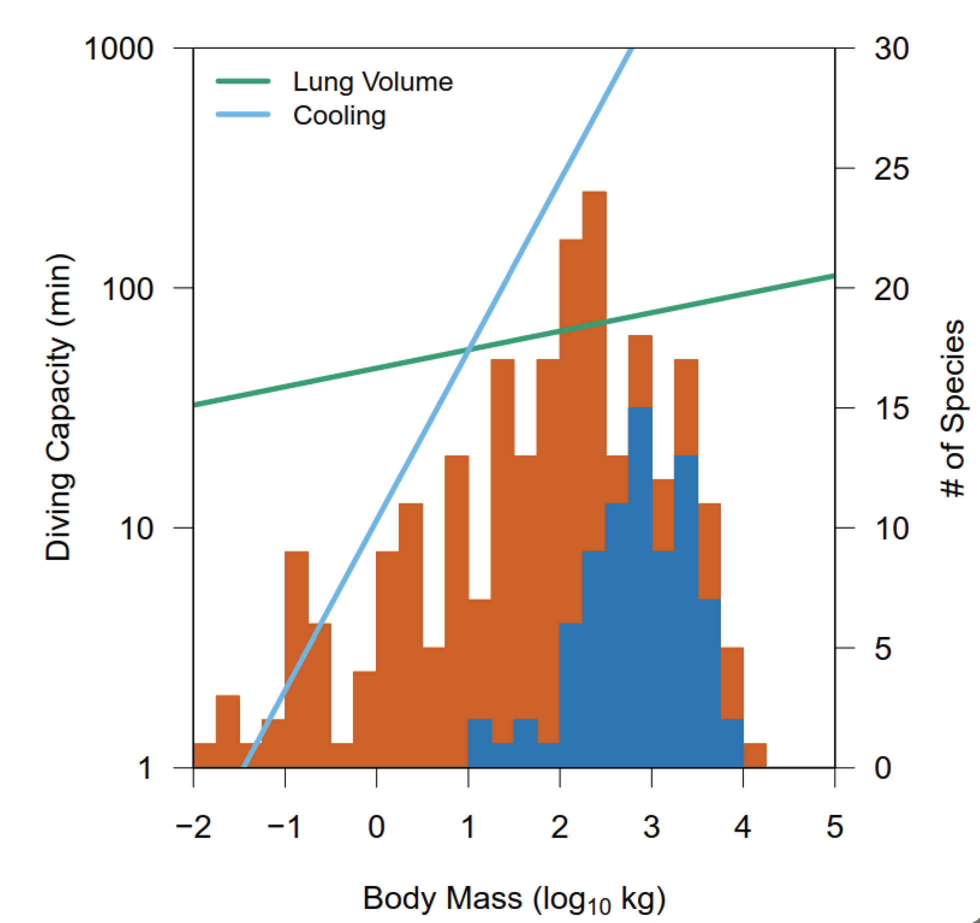


Figure 3.5: **Lung volume and cooling enforce diving capacity constraints at different sizes**

Lung volume (Wright and Kirshner, 1987; Seymour et al. 2013) and cooling (Smith 1976) limits on the diving capacity of crocodiles compared to a stacked histogram of terrestrial and aquatic body masses. Cooling rapidly restricts diving capacity at smaller sizes. The smallest aquatic crocodiles are at the smallest size where lung volume is more limiting than heat loss.



4. Conclusions

- All three aquatic clades converge on *greater optima*, with *shorter phylogenetic half-lives* and *smaller stationary variances*
- *Lung volume*, which has long been proposed as the main constraint on diving capacity, is only a constraint at sizes greater than 10 kg
- The *rate of cooling* strongly constrains diving capacity at sizes smaller than 10 kg and may be the primary driver of larger body sizes in diving crocodyliformes

References and Acknowledgements

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