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Physiological constraints on body size distributions in Crocodyliformes

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At least 26 species of crocodylian populate the globe today, but this richness represents a minute fraction of the diversity and disparity of Crocodyliformes. Fossil forms are far more varied, spanning from erect, fully terrestrial species to flippered, fully marine species. To quantify the influence of a marine habitat on the directionality, rate, and variance of evolution of body size in Crocodyliformes and thereby identify underlying selective pressures, we compiled a database of body sizes for 264 fossil and modern species of crocodyliform covering terrestrial, semi-aquatic, and marine habitats. We find increases in body size coupled with increases in strength of selection and decreases in variance following invasions of marine habitats but not of semiaquatic habitats. A model combining constraints from thermoregulation and lung capacity provides a physiological explanation for the larger minimum and average sizes of marine species. It appears that constraints on maximum size are shared across Crocodyliformes, perhaps through factors such as the allometric scaling of feeding rate versus basal metabolism with body size. These findings suggest that broad-scale patterns of body size evolution and the shapes of body size distributions within higher taxa are often determined more by physiological constraints than by ecological interactions or environmental fluctuations.

KEY WORDS: **Crocodile, diving, mass, Ornstein–Uhlenbeck, phylogenetic comparative methods.**

At least 26 species of crocodylian populate the globe today, but this richness represents a minute fraction of the taxonomic and functional diversity and disparity of Crocodyliformes since their origin early in the Triassic. Over their 250 million years of evolution, crocodyliforms have evolved diets ranging from complete herbivory to complete carnivory and adaptations such as heterodonty for insectivory and suction feeding (Gomani 1997; Buckley et al. 2000; O'Connor et al. 2010; Young et al. 2012). Extant crocodylians range between 5 and 1000 kg for adult body mass, whereas extinct crocodyliforms exhibit an even larger range, reaching sizes as small as 0.001 kg and as large as 8000 kg (Steel 1973; Sereno et al. 2001; Pol and Norell 2004; Farlow et al. 2005). Finally, all living crocodiles inhabit semiaquatic environments such as swamps and rivers. Many extinct crocodyliforms also inhabited such environments, but others were fully terrestrial or fully aquatic (Fig. 1; Tennant et al. 2016).

As with other tetrapod groups, crocodyliforms have a long history of living on land. During the Late Triassic, crocodyliforms and their close relatives were important subsidiary and top-tier predators in terrestrial ecosystems (Zanno et al. 2015). The extinction of a number of crocodyliforms and other crurotarsans near the Triassic-Jurassic boundary was followed by the diversification and dominance of dinosaurs in the Early Jurassic (Brusatte et al. 2008). Soon after, the first of three major transitions to a marine lifestyle occurred within Crocodyliformes, this time by members of the clade Thalattosuchia (Fig. 1). Following the extinction of Thalattosuchia in the earliest Cretaceous, another clade, Tethysuchia, invaded the marine realm. These invaders survived the Cretaceous-Paleogene extinction event, only to go completely extinct by the Eocene. The most recent diversification event in the oceans occurred within the crown clade Crocodylia during the latest Cretaceous and Paleogene. In contrast to the previous two invasions, this diversification occurred as several independent evolutionary transitions from semiaquatic to marine forms.

Differences in the physical and chemical boundary conditions in aquatic versus terrestrial habitats have the potential to cause differing morphological responses across evolutionary time.

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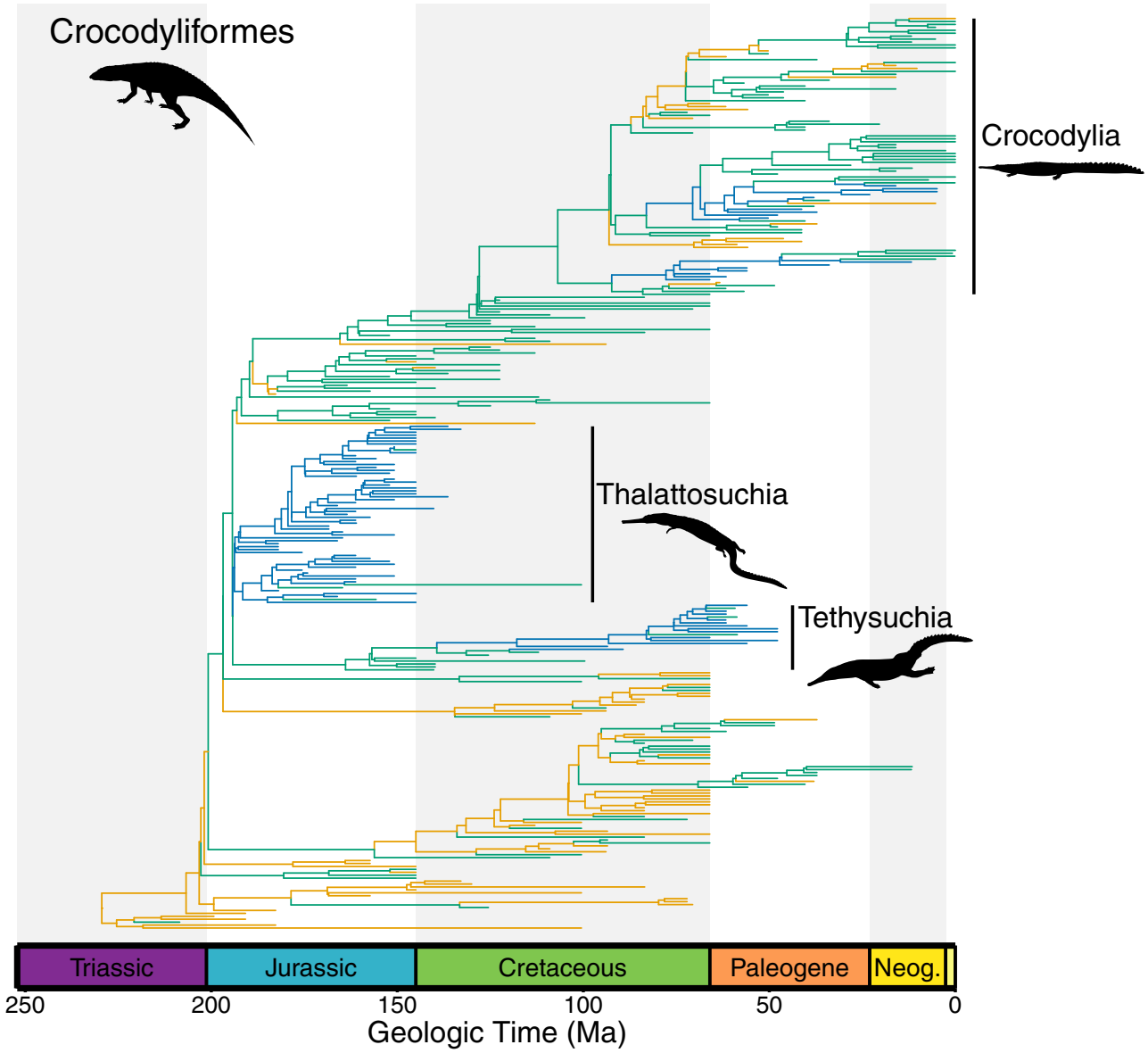

Figure 1. Maximum clade credibility tree of Crocodyliformes showing invasions of the marine realm within three clades. Summary tree of posterior distribution of trees from MrBayes characterless tip-dating analysis of the Crocodyliformes supertree. Tips have been extended to the youngest age estimate of each species' last fossil occurrence for display purposes. Branch colors indicate the most likely habitats of ancestors as estimated across 100 stochastic character maps: terrestrial (orange), semi-aquatic (green), and marine (blue).

Many morphological changes associated with the transition to an aquatic lifestyle have been identified in extinct and extant crocodyliforms, such as osteoderm loss to reduce drag, vertical flattening of the tail for sculling, dorsoventral flattening of the head for capturing prey in water, paddle-like limbs for more efficient swimming, basking for temperature control, and hypometabolism for oxygen conservation (Cott 1961; Smith 1979; Seymour 1982; Seymour et al. 2004; Young et al. 2010). However, one remaining question in the evolution of these invaders is how these differing boundary conditions impacted the evolution of body size within these invading lineages. Similar aquatic invasions in mammals resulted in significant and convergent increases in size (Gearty et al. 2018). Furthermore, the response of body size evolution to these invasions suggest that, contrary to some hypotheses for aquatic gigantism in marine tetrapods, living in water imposes stronger selection on vertebrate body size than does living on land.

The evolution of crocodyliform body size cannot be reconciled with a simple Brownian motion model (Godoy et al. 2019). Rather, the best model of body size evolution is one in which the adaptive landscape contains many unique optimal body sizes. Specifically, shifts to larger sizes are often linked to more aquatic lifestyles (Godoy et al. 2019). However, it has yet to be determined what selective pressure(s) caused these independent size shifts that

are associated with living in water. As in mammals, there are many reasons that one might expect secondarily aquatic crocodyliforms to be larger than their terrestrial counterparts (Gearty et al. 2018). Theories involving neutral buoyancy, increased habitat area, and greater protein availability in the aquatic realm all predict relaxation of selective pressures against increase in the upper end of the body size spectrum (Schmidt-Nielsen 1971, 1984; Reynolds and Karlotski 1977; Anderson et al. 1979; Prange et al. 1979; Williams 1999; Burness et al. 2001; Shurin et al. 2006; Pawar et al. 2012; Tucker and Rogers 2014; Tucker et al. 2014). On the other hand, theories involving increased rates of heat loss in the aquatic realm predict greater selective pressures against small body sizes due to the allometric scaling of surface area to volume (Downhower and Bulmer 1988). For Crocodyliformes, it has also been proposed that the need for increased diving capacity required larger sizes (Seymour et al. 2004). Oxygen stores scale allometrically with body size with an exponent of ~0.9 (Wright and Kirshner 1987), whereas metabolic rate scales allometrically with body size with an exponent of ~0.8 (Seymour et al. 2013). Therefore, the diving capacity of a crocodyliform scales allometrically with body size with an exponent of ~0.1, meaning larger species will have greater capacity to remain under water and dive for prey. Marine mammals spend most of their lives under the surface, foraging, avoiding high drag conditions at the surface to save energy, and to sleep while minimizing the risk of predation (Berta et al. 2006). Marine crocodyliforms must have behaved similarly, and their ability to survive would have been heavily dependent on their ability to dive for extended amounts of time. Shorter dives require more time at the surface to recover, severely limiting the total foraging time. Therefore, there is most likely a minimum diving capacity required to acquire enough food as a fully marine crocodyliform, so it is probable that there would be strong selection against smaller species with shorter diving capacities.

These proposed mechanisms all predict increases in average size upon invading the marine realm. Theories related to neutral buoyancy, increased habitat area, and greater protein availability predict this increase in size is due to a relaxation of selection against larger sizes, which would be characterized by decreased rates of evolution and increased variation. On the other hand, theories related to heat loss and diving capacity predict that this increase in size is due to an increase in selection for larger sizes, which would be characterized by increased rates of evolution and decreased variation. Therefore, one can begin to distinguish among these theories by modeling and estimating body size variation and rates of body size evolution across these invasions.

Here, we compile an extensive body size and habitat database of 264 fossil and modern crocodyliforms and time-scale a preexisting supertree. We then estimate these body size dynamics across three marine invasions within the clade using a phylogenetic model fitting approach. Finally, we use these estimates to test among the various potential selective pressures that may result in increased sizes in secondarily aquatic vertebrates.

Materials and Methods

We collected 36 femur, 269 skull, and 31 total length measurements from the primary literature spanning 264 extant and extinct crocodyliform species, covering approximately 46% of the 580 currently accepted species (according to data downloaded from the Paleobiology Database on January 11, 2019). We checked an additional 50 species that have figured specimens, but they lacked complete femora or skulls for proper measurements. We estimated body masses, along with the standard error of these estimates, using scaling relationships specific to each of the osteological measurements that have been derived from living alligators (Table S1, Farlow et al. 2005). When multiple body mass estimates (and associated standard errors) existed for a single species, we calculated the weighted mean of these estimates and the standard error of the weighted mean to characterize the species. Interspecific body size variation is much higher than intraspecific variation across extinct and extant crocodyliforms (Farlow et al. 2005), so these estimates should capture the evolutionarily significant differences across many species, despite potential differences in body proportions in some extinct taxa (Young et al. 2011, Young et al. 2016).

We assigned each species to one of three habitats: terrestrial, semi-aquatic, or marine. We used previous habitat compilations as a starting point for this assignment process, including the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), the Paleobiology Database, and primary literature (Mannion et al. 2015; Tennant et al. 2016; Wilberg et al. 2019). When different resources had conflicting information for a single species, we used the most recent publication to assign a habitat to that species. We then assigned the remaining species to habitats based on specimen presence in terrestrial, semiaquatic/freshwater, or marine sediments (specimen information was downloaded from the Paleobiology Database on January 24, 2019).

We used a previously constructed supertree for Crocodyliformes combined with a large tree for Crocodylia to build a combined supertree of 311 tips (Bronzati et al. 2012, 2015; Brochu 2013). The Paleobiology Database (PBDB) has been shown to have taxonomic errors that may impact biodiversity studies, particularly within Crocodyliformes (Jouve et al. 2017). The misassignment of taxa to species within the PBDB may result in biased FAD and LAD estimates. Therefore, we built a new database of tip ages using data on the age uncertainty associated with the measured specimens. When multiple specimens were measured for a species, the oldest maximum age for any specimen was used as the oldest age for the tip, whereas the oldest minimum

age for any specimen was used as the youngest age for the tip. When specimens were not measured for a species, the age uncertainty for the type specimen was used. We used the Paleobiology Database to get the most recently updated ages for the localities associated with the specimens (these ages are not necessarily the most recent opinions in the primary literature, but the most recently documented opinions in the PBDB). We created a MrBayes nexus file using the "createMrBayesTipDatingNexus" function in the *paleotree* R package (Bapst 2012). Uniform age constraints were assigned to tips using the tip age database, and the tree age prior was set as an offset exponential distribution with a minimum of 228 million years (the oldest fossil in our dataset) and a mean of 238 million years. Other priors and constraints were guided by the best practices of Matzke and Wright (Ronquist et al. 2012; Matzke and Wright 2016). Specifically, we used the fossilized birth death model, with a uniform speciation prior between 0 and 10, a flat extinction prior with extinction relative to speciation between zero and one, a random stratigraphic sampling prior, and a modern sampling probability of one. We ran two Metropolis-coupled Markov chain Monte Carlo runs, with four chains each, of a Bayesian tip dating analysis using MrBayes version 3.2.7a for 150,000,000 generations. We removed the first half of the generations to account for burn-in, then used Tracer version 1.7.1 (Rambaut et al. 2018) to visually confirm that the runs had reached stationarity and converged and that the combined effective sample sizes of all parameters were greater than 200.

To account for variation in the dating of the phylogeny and resolution of its 39 polytomies, we sampled 100 trees from the post-burn-in posterior. We then used the *phytools* R package (Revell 2012) to create 50 stochastic character maps of the ancestral habitats for each posterior tree using an all-rates-different ordered character model (Huelsenbeck et al. 2003). We then dropped any tips for which we lacked body mass data, resulting in trees with 263 species. Finally, we randomly sampled 500 trees from the 5000 total trees for subsequent analyses.

To study the overall trends of body mass through time across Crocodyliformes, we constructed a phenogram combining the information available from the fossil record and from the supertree. During the extent of a species' fossil range, we assumed the species' body size remained constant. We used the tip age from the maximum clade credibility tree of the tip-dating results as the maximum extent of the fossil range and used the youngest possible age for the most recent fossil as the minimum extent of the fossil range. We then used the "fastAnc" function from the *phytools* R package (Revell 2012) to estimate the ancestral body sizes at the divergence points between these fossil ranges within the tree. We then used this phenogram to estimate the mean, variance, and 5th and 95th percentiles of body mass through time. We also used the phenogram to estimate skewness and the standard error of skewness through time (Cramer 1998). We calculated these statistics through time both across all species and separated by habitat.

We further tested the influence of habitat on body size evolution using generalized Ornstein–Uhlenbeck (OU) process modeling using the *OUwie* R package (Hansen 1997; Butler and King 2004; Beaulieu et al. 2012), as has been used in previous studies (Jaffe et al. 2011; Benson et al. 2014; Price and Hopkins 2015; Gearty et al. 2018). The OU process (Hansen 1997) represents a model of adaptive evolution appropriate to the question of size evolution across a transition in habitat, where the change of body mass, X, over time, t, is the result of the interactions between the body mass optimum, θ, the strength of selection toward the optimum, α, the intensity of random drift away from the optimum, σ, and white noise, B:

$$dX(t) = \alpha\,[\theta - X(t)]\,dt + \sigma dB(t) \tag{1}$$

Model-fitting can be used to compare the likelihoods of Brownian motion models (in which $\alpha = 0$) to those of any number of different OU processes. We tested two different types of Brownian motion models: one in which all taxa evolved according to the same σ^2 (BM), and one in which each habitat had a separate σ^2 (BMS) (in this case, we used the noncensored BMS model by O'Meara et al. (2006) as suggested in the OUwie documentation). We also tested five different OU models: one in which all taxa evolved according to the same σ^2, α, and optimum (θ) (OU), one in which each habitat had its own optimum, but all taxa shared the same σ^2 and α (OUM), one in which each habitat had its own optimum and α, but all taxa shared the same single σ^2 (OUMA), one in which each habitat had its own optimum and σ^2, but all taxa shared the same α (OUMV), and one in which each habitat had its own optimum, σ^2, and α (OUMVA). We also tested this same set of models for cases where the terrestrial and semiaquatic habitats were combined (to test for a marine vs. non-marine signal) and where the semiaquatic and marine habitats were combined (to test for an aquatic vs. nonaquatic signal). Finally, we tested the same set of models for a case that included a clade effect. We divided the terrestrial habitat into two regimes: terrestrial species within Neosuchia and those outside of Neosuchia ("Basal"); the semi-aquatic habitat into three regimes: semiaquatic species within Thethysuchia or Thalattosuchia, those otherwise within Neosuchia, and those outside of Neosuchia; and the marine habitat also into three regimes: marine species within Tethysuchia, those in Thalattosuchia, and those otherwise within Neosuchia. In total, we assessed support across 22 potential models for size evolution for each of the 500 sampled trees.

We determined the proportional support for each model relative to each tree using weighted Akaike information criterion values, corrected for sample sizes, hereafter referred to as AIC_c *weights* (Sugiura 1978; Burnham and Anderson 2002). When

individual analyses did not converge, we excluded their likelihood results from the calculation of AIC_c weights. This was infrequent for most models (<11% of trees) but occurred frequently for the more complex models that incorporated a clade effect (OUM: 27%, OUMV: 29%, OUMA: 60%, and OUMVA: 65%). The most complex models (OUMA and OUMVA) are hard to fit with many regimes and small sample sizes within those regimes (Beaulieu et al. 2012). However, even in the worst case of the OUMVA model, our analyses still converged on results for more than 170 of the trees, suggesting that it can still provide useful information. In all AIC_c weight calculations, the sample size is taken to be the total number of tips within the clade of interest (Butler and King 2004). To account for the various degrees of support for the different models and for the inclusion of different parameters in each of the models, we calculated model-averaged parameter estimates using the formulae of Burnham and Anderson (2002). In the case of the BM and BMS models, we treated alpha as zero.

Differences among OU models are typically described in terms of the phylogenetic half-life ($\ln(2)/\alpha$), which represents the time it takes to evolve halfway toward the optimum, as well as the stationary variance ($\sigma^2/2\alpha$), which represents the expected variance when the process is at equilibrium (Hansen et al. 2008; Gearty et al. 2018). We calculated these transformations using the raw parameter estimates and model-averaged these values as above to provide metrics for describing the rate of evolution relative to units of time and the variance relative to units of mass.

Results

BODY SIZE TRENDS THROUGH TIME

Terrestrial and semiaquatic crocodyliforms have evolved nearly in tandem throughout the history of the clade (Fig. 2B). They maintained an average body mass of about 10 kg for their first 100–150 million years, followed by a steep increase of more than an order of magnitude through the Cenozoic to the modern mean of about 150 kg. In contrast, marine crocodyliforms originated at sizes much larger than their nonmarine counterparts, near 500–1000 kg, and maintained these larger sizes for their duration, with limited variation (Fig. 2).

In aggregate, the body size distribution of Crocodyliformes is negatively skewed, even when the habitats are treated separately (Fig. 3). The amount and direction of skewness has varied substantially across time and is associated with large uncertainty, suggesting that the overall negative skewness cannot be interpreted as a strong and consistent property of the body size distribution in Crocodyliformes as a whole.

MODEL SUPPORT

Of the 22 evolutionary models that were tested, there is overwhelming support for adaptive OU models over Brownian motion models (Fig. 4). The model with the strongest support was the OUMVA model with all three habitats treated separately and with a clade effect, the second most supported model was the OUMVA model with all three habitats treated separately, and the third most supported model was the OUMVA model with terrestrial and semi-aquatic habitats combined. Across these three models, they share a treatment of the marine habitat separately from other habitats, with a different optimum, strength of selection, and amount of variation.

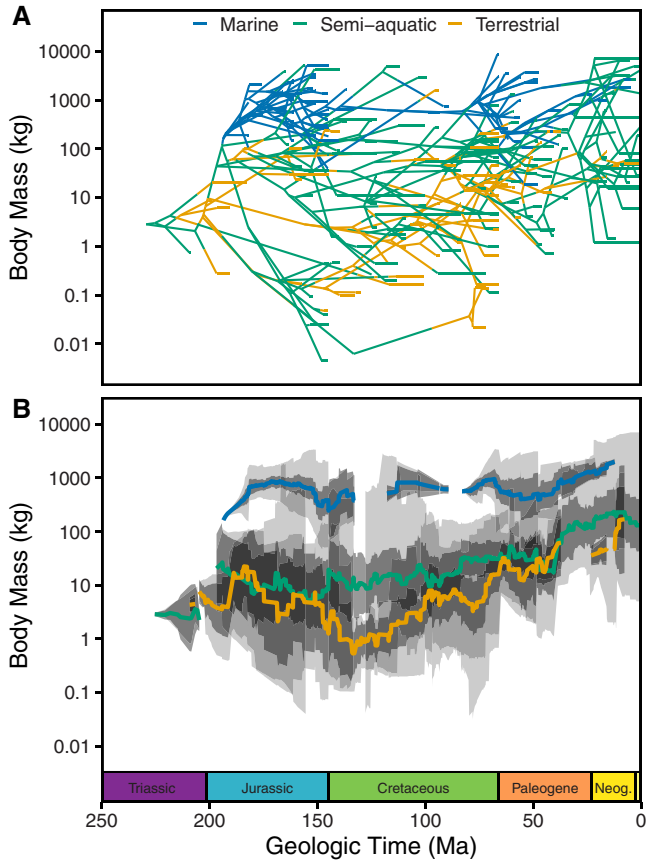

Figure 2. Crocodyliformes body mass trends through time show marine lineages originate at larger sizes. (A) A phenogram of Crocodyliformes showing the evolution of body mass along the maximum clade-credibility tree, with tips extended based on the fossil record. (B) Calculated means and associated error of Crocodyliformes body mass split by habitat through time. Colored lines represent mean body mass. Dark shaded zones represent the 95% confidence intervals of the means (calculated as the mean plus/minus 1.96 standard errors). Light shaded zones represent the intervals between the 5th and 95th quantiles. Colors as in Fig. 1.

MODEL PARAMETERS

The estimated body mass optima of all three independent marine lineages are much closer to each other (~500–700 kg) than they are to that of the nonmarine groups (~5–15 kg) (Fig. 5A),

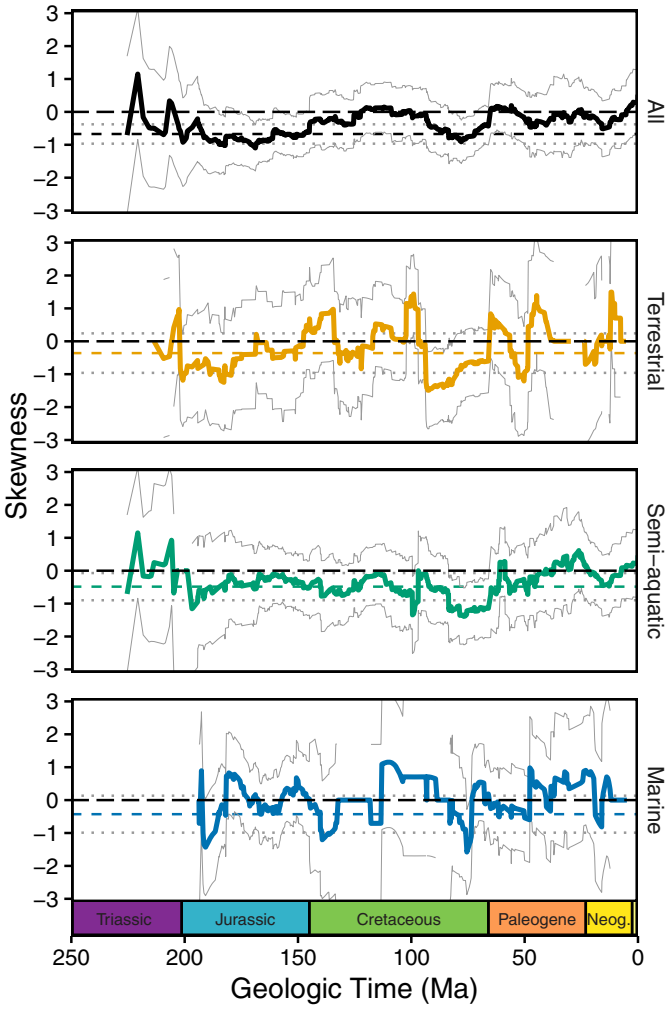

Figure 3. Body mass skewness fluctuates through time, but estimates have large error. Solid lines represent body mass skewness through time. Solid gray lines represent the 95% confidence interval of the skewness (calculated as the mean plus/minus 1.96 standard errors). Dashed lines represent the aggregate body mass skewness estimates. Dotted lines represent the 95% confidence intervals of these estimates (calculated as the mean plus/minus 1.96 standard errors).

implying convergence on a shared marine optimum of about 600 kg. Although the model-averaged values obtained across the 500 analyzed trees do differ significantly between most pairs of groups, any pairwise differences among the marine groups are within an order of magnitude (Mann–Whitney test, $P > 0.01$) compared to the two orders of magnitude pairwise differences between marine and nonmarine groups (Mann–Whitney test, $P < 0.001$). The average estimates of phylogenetic half-life for the three marine groups are statistically indistinguishable (Mann–Whitney test, $P > 0.05$), and all three groups have significantly shorter phylogenetic half-lives (~100 Ma) than the nonmarine groups (~200–300 Ma) (Mann–Whitney test, $P < 0.001$) (Fig. 5B). Finally, the three marine groups also show convergence in their stationary variances with statistically indistinguishable averages (Mann–Whitney test, $P > 0.05$), and all three groups have significantly smaller stationary variances (~1–2 $\log_{10}g^2$) than the nonmarine groups (~5–12 $\log_{10}g^2$) (Mann–Whitney test, $P < 0.001$) (Fig. 5C).

Discussion

In concert, the model selection results indicate that a marine lifestyle imposes selective pressures that favor larger body sizes than those selected for on land or in semi–aquatic habitats. Furthermore, these pressures are stronger than those imposed by living on land and constrain the size range of crocodyliforms living in the ocean more than those living on land. There is ubiquitous support for these selective pressures across three independent marine groups despite their different taxonomic affinities and ages of origin and evolution.

Several factors have been put forward previously in studies of body size evolution in vertebrates as potential influences on size evolution that differ between aquatic and terrestrial species. Hypotheses for the observed large sizes of aquatic mammals include neutral buoyancy, greater habitat area, greater protein availability, and greater rates of heat loss (Schmidt-Nielsen 1971, 1984; Reynolds and Karlotski 1977; Anderson et al. 1979; Prange et al.

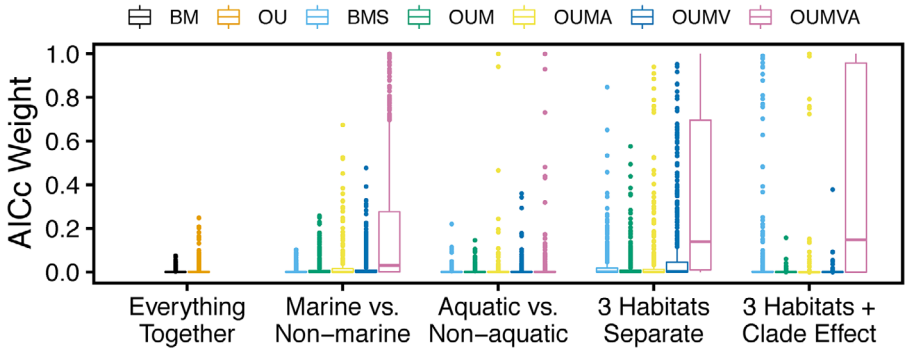

Figure 4. Model support from OUwie analyses. Higher AICc weights indicate stronger relative support.

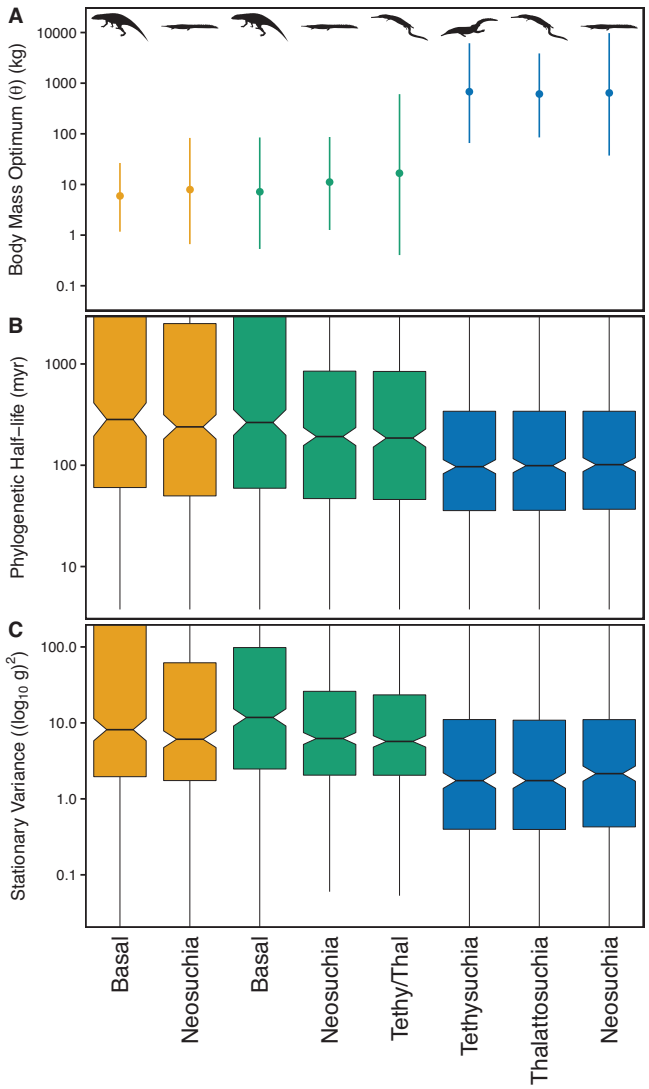

Figure 5. Marine invasions converge on larger body size optima, shorter half-lives, and smaller variance. Plots of estimated body mass optima (A), phylogenetic half-lives (B), and stationary variances (C) by clade and habitat (colors as in Fig. 1). Optima (θ) are reported as weighted means with 2σ confidence intervals of model-averaged values. Phylogenetic half-lives [ln(2)/α] and stationary variances ($\sigma^2/2\alpha$) are reported as box plots of model-averaged values.

1979; Downhower and Bulmer 1988; Williams 1999; Burness et al. 2001; Shurin et al. 2006; Pawar et al. 2012; Tucker et al. 2014; Tucker and Rogers 2014), all of which could also be applied to crocodyliforms. The neutral buoyancy, habitat area, and protein availability hypotheses predict relaxation of constraints on maximum body size associated with transitions from terrestrial to aquatic habitats, and therefore increases in variance that would also be associated with increases in average body size (Gearty et al. 2018). Contrary to the expectations associated with these hypotheses, the increase in mean and optimum size in marine crocodyliforms is associated with an increase in the minimum body size but little or no change in the maximum body size, leading to a decrease in variance. They are also associated with a decrease in the phylogenetic half-life. The reduced phylogenetic half-life of body size evolution in the marine realm suggests that, if anything, selective pressures on body size are greater in the ocean than on land for crocodyliforms, contrary to hypotheses involving the relaxation of selective pressures resulting in extreme sizes.

Two hypotheses are consistent with the findings from the model fitting exercise. First, the allometric scaling of oxygen stores to body size causes the relative volume of oxygen to be much smaller at smaller body sizes (Seymour et al. 2004). This constraint does not apply to terrestrial crocodyliforms because they can breathe at will nor does it apply to semiaquatic crocodyliforms because they spend much of their time living and hunting on land. By contrast, marine crocodyliforms rely solely on diving to acquire food and are therefore highly dependent on the ability to function without breathing for extended periods of time. Second, the allometric scaling of surface area to volume causes the relative rate of heat loss to be much greater at smaller sizes (Downhower and Bulmer 1988). This constraint from heat loss is minimal in air, where the rate of heat loss is slow due to low thermal conductivity and specific heat capacity. However, it is a constraint on marine crocodyliforms due to a greater rate of heat loss to water that is cooler than body temperature due to high thermal conductivity. Because diving requires submergence in water that is typically cooler than body temperature, constraints from heat loss should be most severe for marine species, and because crocodyliforms are ectothermic, the only way for them to reacquire heat is to return to the surface for basking. This rapid loss of body heat in water constrains diving capacity. Both hypotheses predict greater selective pressures against small body sizes, resulting in an increase in optimum size and decreases in phylogenetic half-life and variance in association with the transition to the marine realm. Because both factors limit diving time, one can investigate the relative impact of both factors at different sizes of crocodyliforms to determine if either or both can explain the body size changes we have observed.

The maximum diving time given the volume of oxygen available for aerobic activity, here estimated using the lung volume, V_L, and the rate at which that oxygen is consumed, or the standard metabolic rate, SMR, can be given by:

$$T_{\text{diving}} = V_L/\text{SMR} \tag{2}$$

Using an allometric equation for lung volume, in milliliter, based on voluntary submergence of *Crocodylus porosus*, where mass, m, is measured in gram (Wright and Kirshner 1987):

$$V_L = 0.09 \times m^{0.90} \tag{3}$$

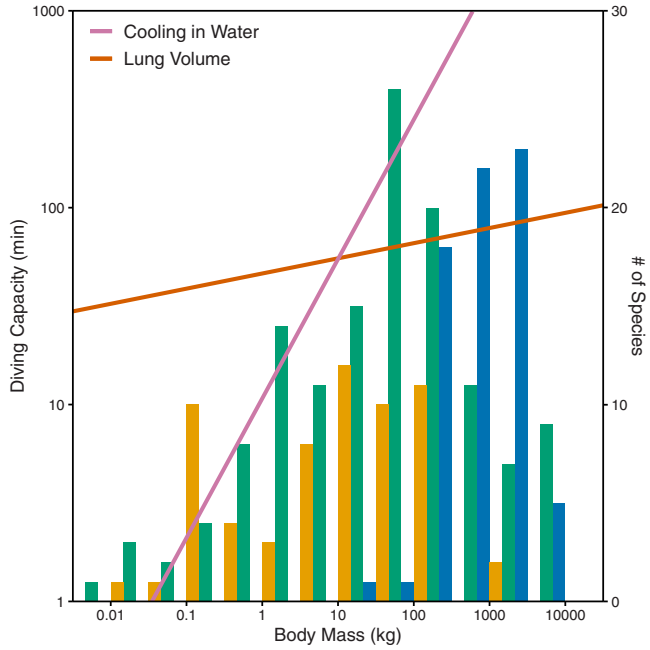

Figure 6. Lung volume and cooling enforce diving capacity constraints at different sizes. Lung volume and cooling limits on the diving capacity of crocodyliforms compared to histograms of crocodyliform body mass split by habitat (colors as in Fig. 1). Cooling rapidly restricts diving capacity at smaller sizes. The smallest marine crocodyliforms are at the smallest size where lung volume is more limiting than heat loss.

Next, using the standard metabolic rate, of *C. porosus*, in mL/min, again with mass, m, in gram (Seymour et al. 2013):

$$\mathrm{SMR} = 1.01 \times \left(\frac{m}{1000}\right)^{0.83} \tag{4}$$

Combined, these equations provide an estimate of the length of time, in minutes, for which a crocodyliform can dive on a single breath, with mass, m, in gram, confirming that diving time does indeed gradually increase with body mass when constrained by oxygen stores (Fig. 6, dark orange line):

$$T_{\mathrm{diving}} = 27.20 \times m^{0.08} \tag{5}$$

Heat loss to the aquatic medium should also scale allometrically due to changes in the ratio of surface area to volume with body mass. Under the assumption that marine crocodyliforms were ectothermic (Hua and De Buffrenil 1996), they would have lost heat to the water around them until they had reached equilibrium with the temperature of the liquid. Because these marine crocodyliforms could not leave the water to gape and bask in the sun like extant crocodylians, the only way to warm their bodies would be to return to the surface, where the water was warmest and there was direct sunlight. Smith (1976) determined heat loss rates for *Alligator mississippiensis* on land and in water experimentally and computed the amount of time, in minutes, that it would take for the temperature of the alligator to travel 63% of the way to equilibrium, here taken to be the temporal limit on diving due to heat loss, with mass, m, in gram:

$$T_{\mathrm{diving}} = 0.08 \times m^{0.71} \tag{6}$$

This relationship also extends the potential diving time for crocodyliforms as they increase in size; however, the relationship of heat loss with body mass is steeper than that of diving time with body mass (Fig. 6, purple line). Although lung volume and oxygen storage capacity place a stronger constraint on diving capacity at sizes larger than 10 kg, heat loss should be the more important constraint below this size. Lung volume constraints alone would permit dive times greater than 40 minutes for sizes smaller than 10 kg, but the rate of heat loss constrains diving times to less than 1 minute for the smallest crocodyliforms. Not a single recorded marine crocodyliform was smaller than this cross-over point between physiological constraints on diving time at 10 kg. Therefore, a model that combines these two constraints provides a more complete model for the potential diving time, in minutes, of a crocodyliform as a function of body mass, m, in gram:

$$T_{\mathrm{diving}} = \min\left(27.20 \times m^{0.08} | 0.08 \times m^{0.71}\right) \tag{7}$$

Within this model, heat loss enforces a hard constraint on the minimum size of marine crocodyliforms. Invasions of the marine realm would be difficult below this threshold, as divers would be limited to less than 1 minute under water before they would have to resurface. Therefore, this strong constraint also explains why marine crocodyliforms have only evolved from significantly larger than average ancestors (Fig. 2). The positive allometric relationship between oxygen stores and body mass favors even larger sizes beyond this minimum, resulting in a larger average size than that of nondiving crocodyliforms. This model explains the larger lower size limit and increased optimal body size of marine crocodyliforms.

Marine and nonmarine crocodyliforms have nearly identical maximum body sizes. The allometric scaling of heat loss and lung capacity (eq. 7) only constrains minimum size. Allometric scaling of feeding and basal metabolic rate may together limit the overall maximum sizes in groups where basal metabolic rate increases more steeply than feeding rate with body mass (Gearty et al. 2018). Feeding data for modern crocodylians record behavior over short intervals and so are difficult to extrapolate to long-term average rates relevant for this calculation. However, given the similar maximum sizes across habitats and the shared feeding modes of carnivory in these largest crocodyliforms, we hypothesize that allometric scaling of feeding rate versus basal metabolic rate may ultimately explain the upper limit on size in Crocodyliformes.

Conclusion

Phylogenetic comparative methods reveal consistent increases in minimum and average body size across all three groups of marine crocodyliforms, accompanied by significant decreases in phylogenetic half-life and variance. We interpret this convergence as strong selective pressures that have imposed physiological constraints on marine crocodyliforms, regardless of ancestry. At sizes smaller than 10 kg, the rate at which crocodyliforms lose stored heat to the water greatly limits the capacity to dive for long periods of time. At sizes larger than 10 kg, lung volume and metabolic rate play the major role in limiting diving capacity. The former constraint imposes such a strong selective pressure against small size that marine crocodyliforms do not cross the 10 kg threshold, no matter their taxonomic affinities or marine adaptations. We hypothesize that marine crocodyliforms have not evolved to sizes larger than their largest nonmarine counterparts due to shared limits in the rates of food acquisition and consumption.

Many drivers have been proposed to explain variation in body size across the tree of life. Interactions between predators and prey can cause selection and coevolution (Vermeij 1994). Fluctuations in the abiotic environment can have short- or long-term impacts on the evolutionary capacities of species (Holland 2006). Finally, intrinsic factors such as physiology can impose constraints, which select for or against particular sizes (Vermeij 1994; Ernest et al. 2004; Heim et al. 2017). Furthermore, previous studies have demonstrated that body size distributions at higher taxonomic levels can be driven by size-biased extinction and origination rates (Maurer et al. 1992; Clauset and Erwin 2008). The findings herein, coupled with related findings for marine mammals (Gearty et al. 2018), suggest that broad-scale patterns of body size evolution and the shapes of body size distributions within higher taxa are often determined by physiological constraints more than by ecological interactions or environmental fluctuations. The model that we have developed provides a physiological basis for the factors that may drive differential extinction and origination dynamics as a function of body size. Further studies testing for the drivers of selection across the tree of life are needed to better understand how the interplay between the biological and physical realms drives the evolution of life at various taxonomic levels.

AUTHOR CONTRIBUTIONS

WG conceived of the study, carried out the data collection and statistical analyses, and drafted the manuscript. JLP participated in the design of the study and helped draft the manuscript. Both authors gave final approval for publication.

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DATA ARCHIVING

The code and data for all analyses are archived in the Stanford Digital Repository (https://purl.stanford.edu/fd595ms6824).

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