SRAS Final Report
Limb morphometry tracks aquatic habits in archosaurs

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Abstract

Crocodilians play a variety of ecologically important roles in modern ecosystems, but are made more vulnerable to anthropogenic stressors by their amphibious habits, which make them reliant on both terrestrial and aquatic environments. Understanding how the functional morphology of crocodilian limbs differs by aquatic affinity can provide insight into how the functional and morphological diversity of modern crocodilians will be affected by future extirpations, which may help by some small measure to inform conservationists concerning the downstream consequences of specific prioritization decisions. Investigating the limb morphometry of aquatic vs. terrestrial crocodilians benefits from sampling the full range of aquatic habits across the crocodilian total-group (Pan-Crocodylia), which includes extinct taxa with exclusively terrestrial and exclusively aquatic lifestyles not represented by modern species. For this report, I scored the aquatic affinities of a large sample of modern and extinct crocodilians and their close relatives (other members of the archosaur total-clade), and I compared their limb morphometries across aquatic affinity bins. I ultimately found that relative hand length and relative foot length are higher in more highly aquatic pan-crocodilians, and that limb proportions may thus serve as a promising metric for future studies to assess ontogenetic and biogeographic changes in their habitat preferences. However, a larger sample size is required to investigate how intraspecific variation affects this perceived signal.

Introduction

Crocodilians play a variety of ecologically important roles in modern ecosystems, serving as possible ecosystem engineers, apex predators that exert top-down control on prey populations, agents of cross-ecosystem (aquatic-to-terrestrial ecosystem) linkage, and ecological indicators of ecosystem health (Somaweera et al. 2020). As of 2025, 42% (11/26) of all crocodilian species were globally threatened (i.e., CR, EN or VU) according to the IUCN Red List (Torres-Romero et al. 2026). Nearly all red-listed crocodilian species face threats from anthropogenic habitat destruction or modification (associated with dam construction and agriculture) or hunting, fishing, and other forms of resource exploitation (Somaweera et al. 2020; Cox et al. 2022). Despite their resilience to past and ongoing conservation threats (Somaweera et al. 2020), crocodilians are made more vulnerable to anthropogenic stressors by their amphibious habits, which make them reliant on both terrestrial and aquatic environments, and thus susceptible to anthropogenic habitat modification and resource exploitation within both media and the liminal coasts or banks between them (Lourenço-de-Moraes et al. 2023). The habitat preferences or aquatic affinities of crocodilians vary widely, both ontogenetically and taxonomically (Ferguson 1985; Vitt & Caldwell. 2014; Gordon et al. 2025, Extended Supplementary Material [ESM]), and these differences in habitat preference have been considered important components of crocodilian functional diversity (Lourenço-de-Moraes et al. 2023).

Understanding how the functional anatomy of crocodilians differs by aquatic affinity can provide insight into how the functional and morphological diversity of modern crocodilians will be affected by future

extirpations, which may help by some small measure to inform conservationists concerning the downstream consequences of specific prioritization decisions. In particular, the functional anatomy and shape (morphometry) of the limbs is a promising system to investigate, as limb morphometry has been shown to vary with aquatic habits in various groups of mammals and reptiles (Joyce & Gauthier 2004; Rothier et al. 2024; Gordon et al. 2025). However, the limb morphometry of these animals is, like all phylogenetically structured traits (Felsenstein 1985), dependent on their phylogenetic relationships as well as their habitats. Thus, any investigation into the limb morphometry of crocodilians should take their phylogeny into account. Moreover, investigating the limb morphometry of aquatic vs. terrestrial crocodilians benefits from sampling the full range of aquatic habits across the crocodilian lineage. Of the 26 species of crocodilians alive today, none are exclusively terrestrial or exclusively aquatic (Gordon et al. 2025). However, the crocodilian total-group (see Gauthier 1984, 2020a, 2020b; Gauthier & Padian 2020), comprising crocodilians and all archosaurs more closely related to them than they are to birds, contains a diverse array of ecologically disparate species that evolved over the past 200+ million years, including various fully terrestrial and fully aquatic taxa (Godoy 2019; Wilberg et al. 2019). For this study, I scored the aquatic affinities of a large sample of modern and extinct crocodilians and other pan-archosaurs, and compared their limb morphometries across these bins. I ultimately found that relative hand and foot length is higher in more highly aquatic crocodilians, and that limb proportions may thus be a promising metric for future studies to assess ontogenetic and biogeographic changes in habitat preference among crocodilians.

Methods

Specimen dataset

Here I report on patterns in pan-archosaur data collected as part of Gordon et al. (2025). This dataset, of accessioned fossil and zoological specimens within natural history museum collections, included n=123 pan-archosaurs, including n=59 dinosaurs and n=50 pan-crocodilians (n=11 stem crocodilians and n=39 crown-group crocodilians). The crown-group crocodilians sampled included n=20 alligatoroids, n=17 crocodyloids, and n=2 gavialoids. All specimens sampled and their associated taxonomy, as well as definitions for the above taxon names, are provided in Gordon et al. (2025, Table S01 and the ESM).

Linear measurements were taken from either physical skeletons, 3D mesh files, or 2D image files. Mesh files were downloaded from MorphoSource or obtained by original μ-CT scans of Yale Peabody Museum (YPM) Vertebrate Zoology specimens. All scans were constructed using CT Pro 3D software and post-processed, examined, and segmented using VG Studio Max v. 2021–2023. We measured physical specimens with digital calipers, and 3D meshes in 3D Slicer (v. 5.0.3) using the ‘‘line’’ and ‘‘curve’’ tools. Fossil specimens that were splayed within a single 2D plane were measured from scaled high-resolution photographs in planform view, which I either obtained from museum curators or collected ourselves using a DMC-GX8 camera (Panasonic Lumix, 60 mm lens) mounted to a copy stand. Length measurements were then collected from photographs in ImageJ (v. 1.53t) using the straight- and segmented-line tools.

Limb proportions were determined by computing ratios from direct length measurements of the fore- and hindlimb stylopodium, zeugopodium, and acropodium (Figure 2D). Measurements obtained included the lengths of the humerus, femur, radius, ulna, tibia, third manual digit, third pedal digit, and anterior- and posterior-most manual and pedal digits (excluding claw-bearing unguals), as well as third manual and pedal proximal and ungual phalanx lengths and proximal and distal epiphyseal widths. The anatomical points

defining these linear measurements are detailed in Gordon et al. (2025). Stylopodium, zeugopodium, and acropodium length were then combined in various ways to reduce multivariate data on limb proportions into one-dimensional metrics. These included the ratios of acropodium-to-zeugopodium length, acropodium-to-stylopodium length, and stylopodium-to-zeugopodium length, among others. I then compared these ratios among aquatic affinity bins visually with box plots and statistically with phylogenetic comparative tests, as described below.

Classifying aquatic habits

We binned samples by aquatic affinity score using a new scheme that classifies species by the relative frequencies of time they spend on land and in the water on a five point scale from fully terrestrial to fully aquatic (Gordon et al. 2025). In tandem, we also scored aquatic affinity using a previously published scheme that classifies species based on the depth and energy level of the waters they inhabit (Joyce & Gauthier 2004). Our scoring system was designed to be applicable across tetrapods (see Gordon et al. 2025, ESM). Of course, the aquatic habits of tetrapods exist on a continuous and multidimensional spectrum, and any effort to discretize them is inevitably subjective. All we can hope to do is bin species consistently and transparently, in a way that captures broad differences between "more" and "less" aquatic habits, and makes these differences discrete and applicable across amniotes, despite their diverse and nuanced ecologies. To do this, I settled on an original scoring system that separates species into five aquatic affinity "guilds", where a "guild" is defined as a group of species that exploit the same class of environmental resources in the same way, without regard to their phylogenetic positions (Root 1967). Guild groupings are commonly used to classify marine reptiles—most notably into "feeding guilds" based on tooth morphology (Massare 1987; Fischer et al. 2022). For this study, I developed a new guild system under which we classified all sampled specimens into one of five aquatic affinity guilds (fully terrestrial, transiently aquatic, moderately aquatic, highly aquatic, and fully aquatic) based on the relative amount of time they typically spend on (and the relative portion of niche space in which they use) land vs. water: **Fully terrestrial** species spend all of their time on land, seldom intentionally crossing water. **Transiently aquatic** species spend the vast majority of their time on land, but routinely make transient forays into the water. **Moderately aquatic** species are amphibious, spending roughly equal amounts of time on land and in the water—regularly crossing both media. **Highly aquatic** (or transiently terrestrial) species spend the vast majority of their time in the water but routinely bask or nest for short periods on land. **Fully aquatic** species never intentionally leave the water.

These bins together form a five-rung scale that stretches the terrestrial-aquatic continuum and allows us to apply the same classification system to all amniotes. Most of these aquatic-affinity bins for extant taxa are intuitive, with short, literature-based justifications provided in Gordon et al. (2025), Table S01. However, scoring the aquatic affinities of extant crocodilians was particularly challenging, and my crocodilian aquatic affinity scores require further clarification. All extant crocodilians are amphibious predators that spend extensive time hunting and wading in the water, but also routinely bask, nest, and travel to some degree on land (Whitaker & Basu 1982; Ferguson 1985; Vitt & Caldwell 2014; Murray et al. 2020). These species nevertheless span a continuum of semi-aquatic lifestyles, which differ intraspecifically, ontogenetically, and depending on weather and other external factors (Vitt & Caldwell 2014; Isberg et al. 2019). Here I assigned scores based primarily on adult habits. Briefly, I called *Gavialis gangeticus* and *Crocodylus acutus* "highly aquatic," and all other crown crocodilian species "moderately aquatic." Perhaps because they descend from marine ancestors (Wilberg et al. 2019), the gavialids *G. gangeticus* and *Tomistoma schlegelli* S. Müller

1838 have longirostrine snouts often treated as specializations for hunting fish, though their diet is actually more varied (Whitaker & Basu 1982). While *T. schlegelli* occupies lentic marsh waters (Staniewicz et al. 2018), *G. gangeticus* often resides in deep, fast-moving rivers, seldom (if ever) moves far from the water's edge, often remains submerged during nest attendance, and has more limited mobility on land than other modern crocodilians (Whitaker & Basu 1982; Vitt & Caldwell 2014; Choudhary et al. 2018; Murray et al. 2020). As a result, *G. gangeticus* is frequently considered the most aquatic crown crocodilian (Vitt & Caldwell 2014). In a similar vein, the saltwater crocodile (*Crocodylus porosus*) may be the most active long-distance swimmer among extant crocodilians, as it regularly makes extended (>1000 km) journeys over open ocean (Fukuda et al. 2019; Spennemann 2020). Because *G. gangeticus* and *C. acutus* spend most of their time in large or fast-moving water bodies, but still occasionally travel over land, we consider these species "highly aquatic." Given that no other extant species of crocodilian typically spends this much time active in large or fast-moving bodies of water, we consider all other crown crocodilians—including alligatorids, other crocodylids, and *Tomistoma schlegelli*—to be "moderately aquatic." This scoring reflects the fact that these species spend extensive time on both land and (typically shallower, more lentic) water. Within this single bin of "moderately aquatic" crocodilians, we stress the existence of a finer continuum, and encourage the reader to review Gordon et al. (2025)'s ESM for additional discussion and qualifications about this scoring system.

Phylogenetic comparative tests

Relationships among all aforementioned length measurements and ratios were compared aquatic affinity bins using statistical tests within a phylogenetic framework and assuming the pan-crocodilian tree topology recovered by Rio and Mannion (2021) (Figure 1). All statistical tests were performed in R (v. 4.2.0-foss-2020b) (R Core Team 2020) on the Grace High-Performance Computing Cluster at Yale University, with varying degrees of parallelization to accelerate computation. To compare variable distributions among all scored limb type and aquatic affinity bins, we performed simulation-based phylogenetic analyses of variance (phylANOVAs) (Garland et al. 1993) and phylogenetic Levene's tests (phyloLevs) with pairwise post-hoc Tukey comparisons for all predictor-response variable pairs in our dataset, using original R functions incorporating the phylANOVA command (nsim=10000, posthoc=T, p.adj="BH") from the R package phytools (v. 1.2-0) (Revell 2012). To assess whether any limb metrics could predict aquatic affinity in pan-archosaurs, I converted the aforementioned five-guild system into a binary scoring system that separated species into "highly or fully aquatic" and "semi-terrestrial" categories, trained and tested a phylogenetic binomial logistic regression model (phybLR) model on the data using a tree subsampling procedure involving 3-fold cross-validation with 100 iterations, and assessed model performance using Receiver-Operating Characteristic (ROC) curve analysis as described in Gordon et al. (2025).

Results

Pan-Archosaurian limb morphometries tracked aquatic affinities, with predominantly marine species occupying large or fast-moving water bodies (open oceans, fast rivers) possessing significantly higher or significantly more variant relative acropodium lengths (acropodium-zeugopodium length ratios or AZRs) and markedly but not significantly higher relative stylopodium lengths (stylopodium-zeugopodium length ratios or SZRs) (Figure 2). The highest AZR and SZR values among sampled pan-archosaurs (and pan-crocodilians) were observed in metriorhynchids—a group of highly or fully aquatic pelagic marine crocodylomorphs that lived during the Jurassic Period, whose acropodial and stylopodial regions regularly

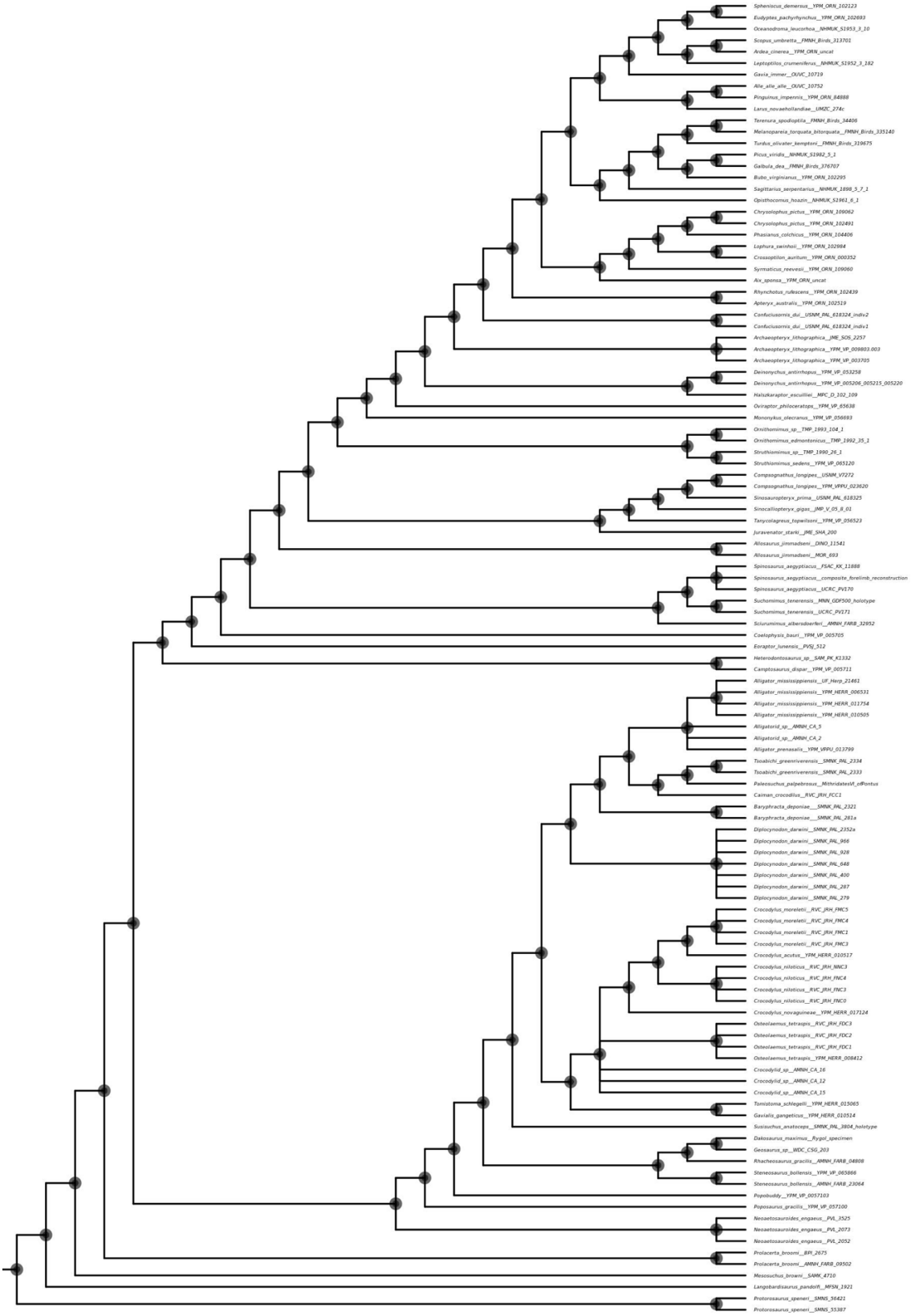


Figure 1. Phylogenetic tree containing all pan-archosaur specimens included in the analysis, in the format *Genus_species__specimenID#*. This tree was used as an input for all phylogenetic comparative tests.

reached 2–5x the length of their zeugopodials (Gordon et al. 2025, Table S01). There were also some notable but non-significant differences in acropodial planform dimensions among pan-archosaurs occupying larger or faster-moving water bodies (Figure 2). Phalanx dimensions were not associated with aquatic habits in sampled pan-archosaurs (Gordon et al. 2025, Data S2).

Phylogenetic binomial logistic regression models using limb region proportions (AZRs and SZRs) varied widely in accuracy, with individual Receiver-Operating Characteristic (ROC) curves varying greatly in Area Under the Curve (AUC) values, and the resulting consensus ROC (cROC) curves achieving low to moderate AUCs. Taken together, these results indicate a predictive landscape that is highly sensitive to input parameter values, casting doubt on the robustness of limb morphometry for predicting aquatic affinity in pan-archosaurs. However, the best-performing models selected via cROC curve analysis achieved high accuracies (each shown best-model accuracy >90%, Figure 3), correctly classifying specimens in the training data set in significantly more than 75% of cases (one-sample binomial tests, each $p < 0.05$). Despite their apparent high accuracies, these "best models" were highly conservative, with low false positive rates but similarly low true positive rates, indicating that they will seldom misclassify terrestrial species as aquatic (generate false positives), but will often misclassify aquatic species with moderate AZR and SZR values as terrestrial (generate false negatives).

Discussion

This study builds upon findings reported in Gordon et al. (2025), which demonstrated that acropodial-to-zeugopodial ratios (AZRs) tend to be significantly higher and more variable in highly aquatic amniotes across multiple major tetrapod clades, including pan-archosaurs, turtles, lizards, and mammals. The present analysis expands specifically upon the pan-archosaur component of that work and confirms that AZRs remain informative predictors of aquatic affinity within Archosauria, although the relationship appears weaker than that observed in turtles and lizards (Gordon et al. 2025). Nevertheless, these results suggest that AZRs may provide a useful framework for reconstructing finer-scale shifts in habitat preference among extinct crown-group crocodilians. Such reconstructions could complement broader paleoecological studies of crocodilian habitat evolution (e.g., Wilberg et al. 2019) by enabling higher temporal and ecological resolution inferences regarding transitions between more terrestrial and more aquatic lifestyles. More refined reconstructions of crocodilian aquatic affinity could also have conservation relevance. If robustly reliable morphometric proxies for habitat preference can be identified, local extirpation or range contraction events in extinct crocodilian lineages could potentially be compared directly with paleoclimatic and paleoenvironmental data. This may help identify which environmental conditions have historically posed the greatest risks to crocodilian populations and could improve our understanding of how future climatic shifts may affect extant species and isolated populations.

However, several important limitations in this study are worth noting. First, the aquatic-affinity scoring system employed here was intentionally coarse-grained because it was designed for broad applicability across Tetrapoda. Consequently, it does not fully capture the subtler ecological differences among extant crocodilian species. For example, *Osteolaemus tetraspis* and *Paleosuchus trigonatus* are generally less aquatic than many other crocodilians classified here as "moderately aquatic," yet both species regularly utilize both terrestrial and aquatic habitats and were therefore assigned the same categorical score. A more continuous ecological scoring framework tailored more specifically to crocodilians may improve future analyses.

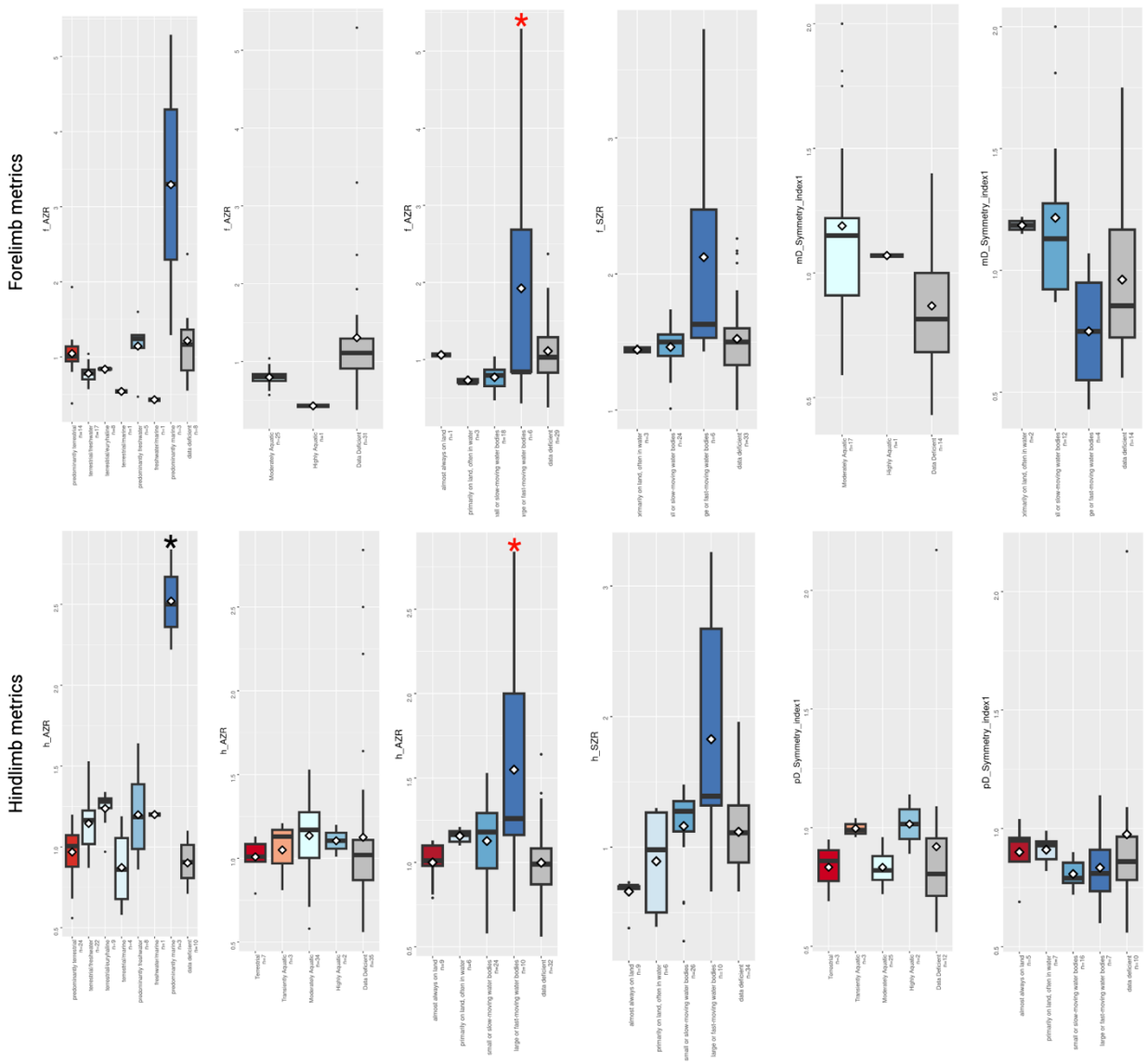


Figure 2. Key differences in pan-archosaur (including crocodilian) forelimb (top row) and hindlimb (bottom row) morphometry across aquatic affinity bins. Asterisks indicate that the highlighted aquatic affinity bin had a significantly different limb morphometry from the other bins sampled. Black asterisks indicate significantly higher means (phylogenetic ANOVA with pairwise post-hoc tests, each $p < 0.05$); red asterisks indicate significantly higher variances (phylogenetic Levene's test with pairwise post-hoc tests, each $p < 0.05$). Abbreviations: f_AZR, forelimb acropodium-to-zeugopodium length ratio; f_SZR, forelimb stylopodium-to-zeugopodium length ratio; h_AZR, hindlimb acropodium-to-zeugopodium length ratio; h_SZR, hindlimb stylopodium-to-zeugopodium length ratio; mD_Symmetry_Index1 and pD-Symmetry_index1: scalar metrics devised to summarize acropodial dimensions in planform view of the manus (mD) or pes (pD), defined in Gordon et al. (2025).

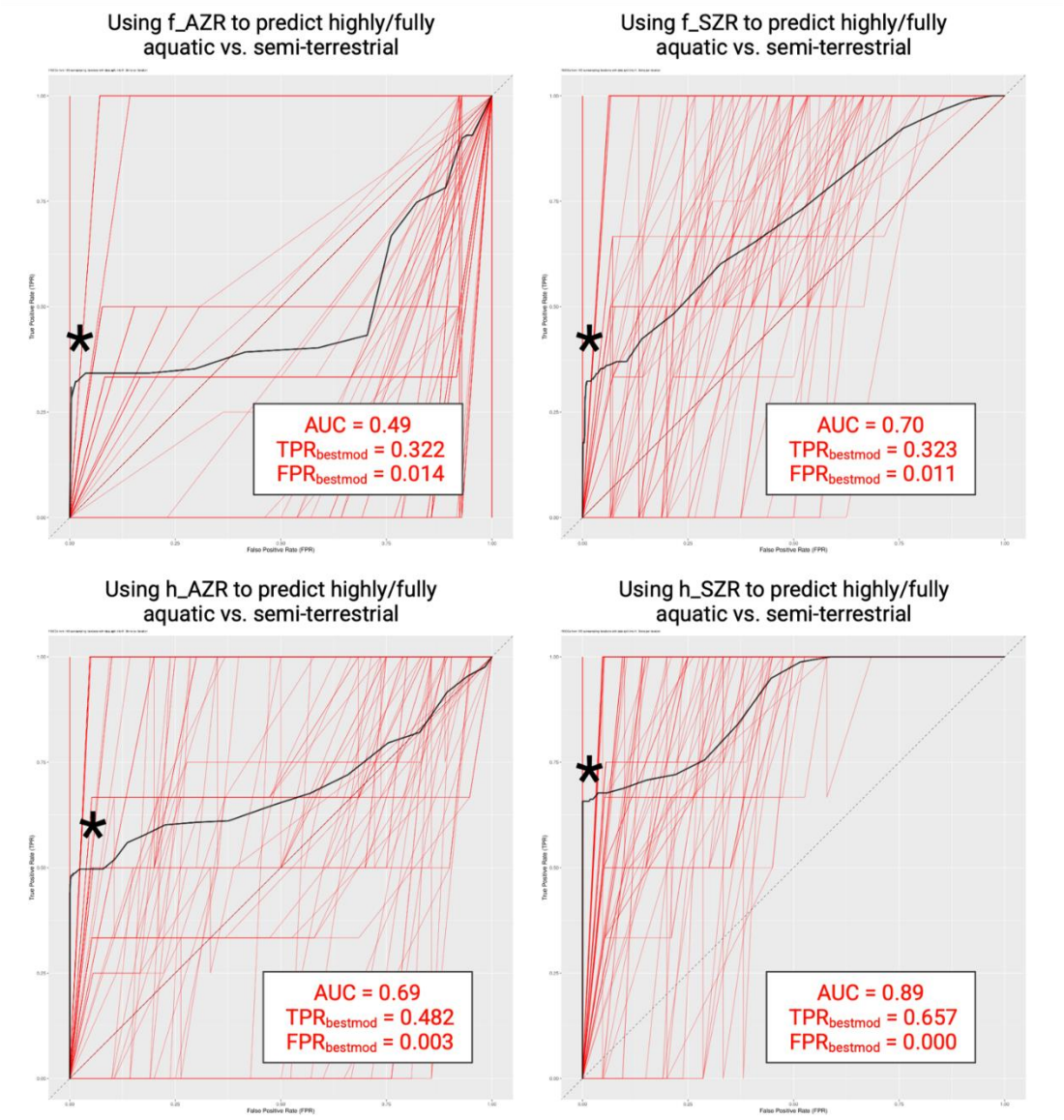


Figure 3. Consensus Receiver-Operating Characteristic (cROC) curves (black lines) averaged from 100 replicate ROC curves (red lines) fit for phylogenetic binomial logistic regression models. Asterisks indicate that the best-performing logistic regression model, selected using cROC curve analysis as the model whose parameters predictive maximize accuracy, correctly classifies species by their binary aquatic affinity in >75% of cases (one-sample binomial test for best model, $p < 0.05$).

A second limitation is sample size. The present study included a relatively small number of crocodilian species and insufficient specimen-level sampling to robustly assess intraspecific variation. In addition, many of the observed morphometric trends are currently driven primarily by metriorhynchids, which are a highly specialized and long-extinct Jurassic group of near-fully aquatic crocodylomorphs that do not resemble any modern species. Although these taxa provide an important signal regarding extreme aquatic adaptation, broader sampling of crown-group crocodilians is necessary to determine whether the trends

identified here persist among extant taxa alone. Expanding the dataset to include a much larger sample of extant crocodilian specimens would help determine whether the observed relationships are robust ecological signals or artifacts of limited sampling.

Increased sampling would also permit investigation of how AZRs and stylopodial-to-zeugopodial ratios (SZRs) vary intraspecifically across ontogenetic stages, habitats, and geographically isolated populations. Such analyses may be particularly informative in species exhibiting broad ecological variability. For example, some *Osteolaemus tetraspis* populations inhabit inland cave systems (Crocodile Specialist Group 1996; Vitt & Caldwell 2014; Shirley et al. 2017), and frequently consume terrestrial prey (Pauwels et al. 2007). Similarly, *Paleosuchus trigonatus* is often associated with small inland streams in heavily forested environments (Medem 1958; Magnusson et al. 1987; Brochu 2001), and adults of both consume substantial quantities of terrestrial prey (Jackson et al. 1974; Magnusson et al. 1987; Shirley et al. 2017). In contrast, the closely related *Paleosuchus palpebrosus* more frequently inhabits larger aquatic systems and consumes proportionally less terrestrial prey (Magnusson et al. 1987). These ecological differences, and the morphometric patterns described above, raise the possibility that limb-region proportions may vary predictably with habitat use, ontogeny, or local environmental conditions. For example, it would be informative to test whether AZRs decrease as *P. trigonatus* individuals mature into more terrestrially inclined adults that consume more terrestrial prey, or whether isolated inland populations differ morphometrically from populations inhabiting larger aquatic systems. Similarly, future studies could investigate whether limb proportions correlate with environmental variables such as water depth or current velocity. If such relationships are confirmed, AZRs may prove useful as indicators of local adaptation in isolated crocodilian populations occupying distinct ecological niches.

From a conservation perspective, these morphometric indicators could potentially help identify populations that are poorly matched to rapidly changing environments. For instance, if AZRs reliably track aquatic specialization, unusually high AZRs in an inland P. trigonatus population might indicate relatively recent inland colonization by a population still adapted to more aquatic conditions. Such populations could conceivably occupy positions farther from local adaptive optima and therefore exhibit heightened vulnerability to anthropogenic stressors or environmental change. Although speculative at present, these hypotheses illustrate the potential for integrating functional morphology, paleoecology, and conservation biology to better understand both the evolutionary history and future resilience of crocodilian populations.

Acknowledgments

I would particularly like to thank Ruth Elsey, Pablo Siroski, Sally Isberg, and the whole IUCN SSC Crocodile Specialist Group for considering my application and granting me the Fritz-Huchzermeyer Student Research Assistance Scheme to help support my PhD research. I would also like to thank Thomas Langford, Aya Nawano, and the Yale Center for Research Computing (YCRC) for assistance with Yale's Grace High-Performance Computing Cluster; Brandon Mercado and Yale's Chemical and Biophysical Instrumentation Center for access to and training on the micro-computed tomography (μCT) scanner; and Zachary S. Morris for feedback on crocodilian aquatic affinity scorings. This research was conducted as part of a PhD in Bhart-Anjan S. Bhullar's lab in the Department of Earth and Planetary Sciences at Yale University, and was also supported by the Yale Institute of Biospheric Studies (Doctoral Pilot Grant, Doctoral Dissertation Improvement Grant) and a National Science Foundation Graduate Research Fellowship under grant no. DGE1752134. The results reported herein were collected as part of a previous

paper (Gordon et al. 2025), published with co-authors Lisa S. Freisem, Christopher T. Griffin, Jacques A. Gauthier, and Bhart-Anjan S. Bhullar.

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