Crocodile-Like Morphology: Convergence Across Semi-Aquatic Gymnophthalmid Lizards

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Abstract

Examples of convergent morphology abound in lizard taxa, highlighting the role of adaptive processes in generating diverse lizard morphologies and ecologies. Whether such adaptive processes have resulted in convergent morphology across lizards in aquatic habitats remains little explored outside of a few studies on *Anolis* lizards. Previous studies of Gymnophthalmid lizards in the tribe Cercosaurinae have in passing suggested a suite of morphological traits termed "crocodile-like morphology" which is thought to have evolved multiple times in semiaquatic members of the group. Herein, "crocodile-like morphology" is quantified and explored across several taxa of semi-aquatic Cercosaurinae lizards using museum specimens of both semi-aquatic and non-aquatic Gymnophthalmids. PCA is used to explore whether aquatic and non-aquatic Gymnophthalmids group separately based on hypothesized crocodile-like morphology traits. Randomization tests are used to evaluate whether each trait individually differs significantly between aquatic and non-aquatic Gymnophthalmids. Phylogenetic effect is also calculated for each trait, phylogenetic Pearson's correlations are found between traits, and ancestral state reconstructions are performed for some of the analyzed traits. Gymnophthalmid lizards provide novel opportunities to investigate factors which drive convergence, causing convergence to occur in some systems but not others. Additionally, an understanding of ecomorphology in aquatic lizards can help generate hypotheses about the ecology of species which lack ecological data.

Introduction

- Aquatic lizards have evolved in 11 lizard families, with most of aquatic lizard diversity distributed across the families Scincidae, Varanidae and Gymnophthalmidae, and restricted to tropical habitats (Bauer and Jackman 2007). Aquatic lizards are incredibly diverse, with the lack of a suite of characters found across aquatic lizards leading (Bauer and Jackman 2007) to argue that morphology alone does not give insight into the potential aquatic habitats of poorly known species. Most aquatic lizards have laterally compressed tails, however, and many have keeled scales (Bauer and Jackman 2007).
- Within the Cercosaurinae tribe of Gymnophthalmid lizards, aquatic ecologies are thought to have evolved at least four times (Marques-Souza et al. 2018). Aquatic ecologies in this group are accompanied by what Marques-Souza et al. (2018), Rojas-Runjaic et al. (2021), and others referred to as Crocodile-Like Morphology(CLM). CLM consists of traits including heterogeneous dorsal scalation, caudal crests, streamlined bodies, and laterally compressed tails (Marques-Souza et al. 2018).
- While this morphology has been qualitatively described in numerous studies and is likely part of the cause of much taxonomic confusion in this group, little attention has been paid to quantitatively evaluating this hypothesis of convergence and examining variation between taxa in these supposedly convergent traits.
- Reliance on aquatic features of the environment is variable between semi-aquatic lizards, with most of CLM Gymnophthalmids thought to rely on aquatic habitats and supposedly correlated morphology for predator evasion. Other lizard species are often found in close proximity to water, but are less reliant on aquatic habitats (Bauer and Jackman 2007).
- The abundance of both ecological and correlated morphological diversity within Gymnophthalmidae makes it an ideal system for studying adaptive trait evolution and potentially convergent evolution.

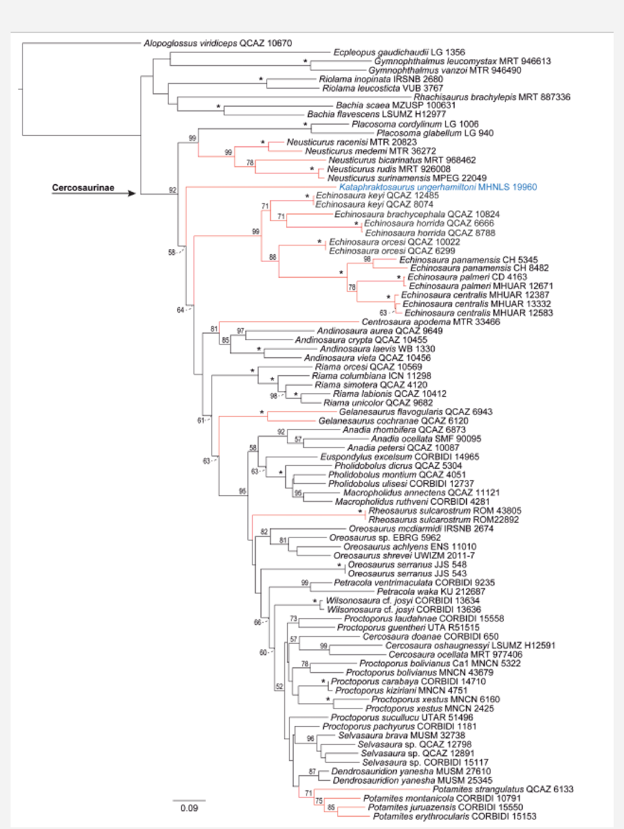


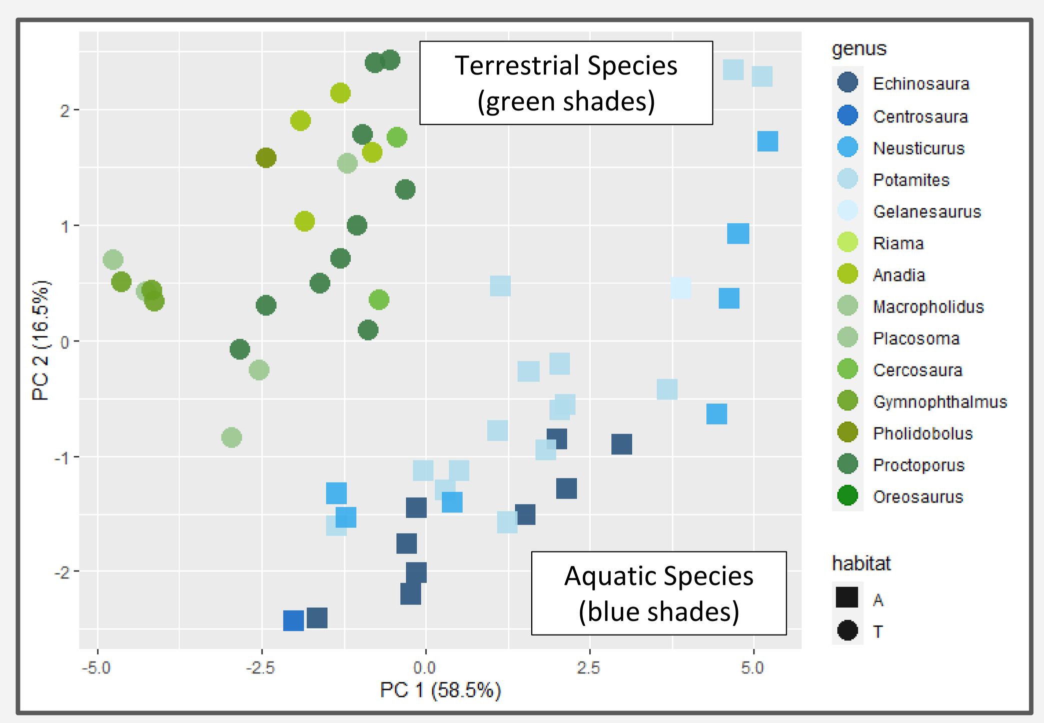
Fig.1: Borrowed from (Rojas-Runjaic et al. 2021) showing Maximum likelihood tree of Cercosaurinae species with species having CLM shown in red.

Methods

- Nine species of aquatic and 11 species of non-aquatic lizard from the Gymnophthalmid tribe Cercosaurinae and one non-aquatic species from outside Cercosaurinae were chosen for which specimens were available in the collections at the American Museum of Natural History in New York.
- Traits which previous literature suggested composed Crocodile-Like Morphology were quantified as described in Table 2. For all characters too small to measure with calipers, photos were taken through a dissecting microscope and measurements were taken using ImageJ (Schneider et al. 2012). Measurements were collected from 58 specimens.
- The package FactoMineR was used to make a PCA plot. PCA and randomization tests were performed on data with no phylogenetic corrections. Randomization tests were performed on residuals of each trait regressed against SVL, except for those traits which were ratios of different measurements. SVL was included as a variable in the PCA plot.
- Geneious was used to align genetic sequences (ND4, 16S, 12S, C-mos) for all species for which genetic data was available on Genbank. 100 bootstrap replicates and a ML analysis were performed in RAxML.
- Phylogenetic effect calculations, phylogenetic Pearson's correlations, and ancestral state reconstructions were performed using the package phytools in R (Revell 2012).

Results

Do aquatic and terrestrial species have different morphologies? YES.



← Fig.2: Principal component analysis of measured morphological traits. Traits were not size corrected, and SVL is included as a trait. Each point is a specimen. PC 1 accounts for 57.63% of the variance and PC2 17.16% in the data.

Aquatic and non-aquatic Gymnophthalmids formed two non-overlapping clusters based on morphometric data, indicating the presence of distinct ecomorphs. Within aquatic and non-aquatic species, there was overlap between genera. Members of *Echinosaura* overlap with other aquatic species, but nonetheless have an aquatic morphology unique from other aquatic genera.

Do crocodile-like traits co-evolve across the phylogeny? YES.

Table 1: A table showing Pearson correlation coefficients and P values for several pairs of traits. →

Pearson Correlation with Phylogenetic Data			
Trait 1	Trait 2	r	p
Keel height	Scale surface Area	-0.4577499	0.04240874
Keel height	Tail width/height at .2 SVL	-0.4790781	0.03258282
Keel height	Eye to snout length	0.4187447	0.06612059
Keel height	Limb length proximal	0.5387852	0.01730383
Limb length proximal	Tail width/height at .2 SVL	-0.6736113	0.001567983
Tail width/height at .2 SVL	Scale surface Area	0.5357152	0.0149129

Pearson correlations with phylogenetic data were significant for all pairs of traits tested excluding the test of correlation between keel height and eye to snout length, which had a P value above .05.

Are crocodile-like traits influenced by evolutionary history? YES.

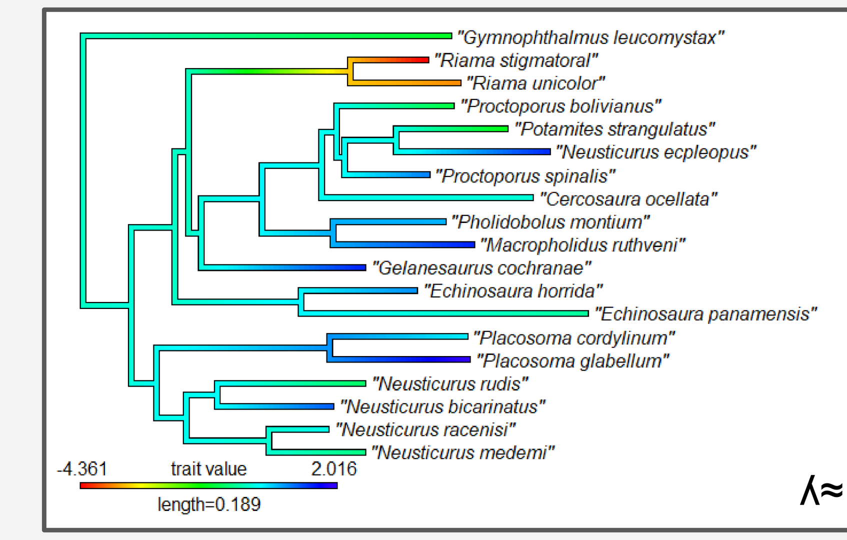
Trait	Description	Size Corrected?	Phylogenetic Effect (λ)	Randomization Test P Value
Head width	Distance between front of eyes with callipers	Y	0.240629	0.2194
Width/SVL	Width of body measured at widest point dived by the snout to vent length	N	0.844198	0.295995
Tail width/height at .2 SVL	The tail's width divided by the height measured .2 of the SVL down from the posterior margin of the cloaca	N	6.61E-05	0
Tail width/height at .4 SVL	The tail's width divided by the height measured .4 of the SVL down from the posterior margin of the cloaca	N	0.999934	0
Keel height	The avergae height of five largest keels sampled at a random location on the dorsum	Y	6.61E-05	0
Keel length	The avergae length of five largest keels sampled at a random location on the dorsum	Y	6.61E-05	0.172
Scale surface area	The 2D surface area of scale was measured from photos using ImageJ. Values were averaged across five scales for each specimen. For species with heterogeneous dorsal scalation, smaller scales were preferentially selected.	Y	6.61E-05	0
Limb length proximal	The length of the proximal portion of the right hindlimb measured with callipers	Y	0.948544	0
Limb length distal	The length of the distal portion of the right hindlimb measured with callipers	Y	0.746111	0
Eye to snout length	Distance from the front of the eye to the tip of the snout measured along the right side of the head	Y	0.34021	0.0005

← Table 2: A table describing the morphological traits used to quantify "Crocodile-like morphology", whether they were size corrected for analyses, Pagel's λ, and P values from randomization tests of each trait between aquatic and non-aquatic species.

The strength of phylogenetic effect was highly varied between different traits, with only width/SVL, tail width/height at .4*SVL, and both measures of limb length showing high values of lambda indicative of phylogenetic effect. Randomization tests found that all traits examined were significantly different between aquatic and non-aquatic Gymnophthalmids except for head width, width/SVL, and keel length.

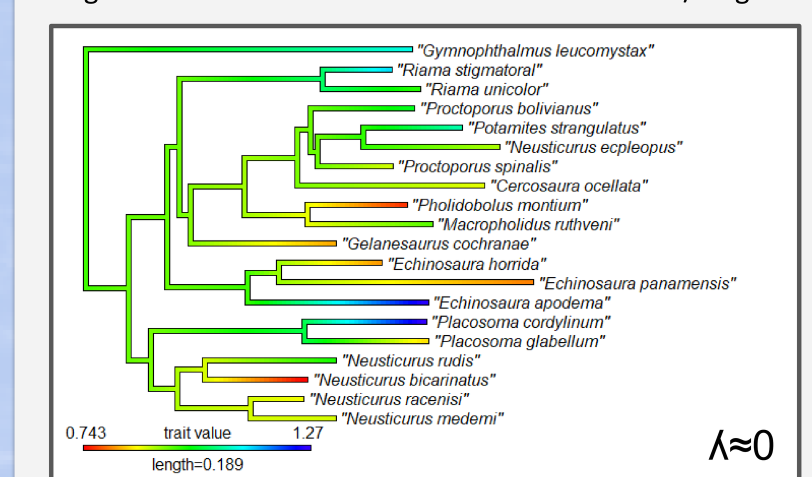
Results continued

Trait values can be explained by tree data. Similar colors at tree tips indicate species with similar morphologies. Limb length shows strong phylogenetic signal.



^Fig.3: Ancestral state reconstruction of limb length (proximal).

˅Fig.4: Ancestral state reconstruction of tail width/height at .2*svl.



The high color variation across the tips of this tree indicates that these species have diverse morphologies for degree of tail compression. Tail compression does not show strong phylogenetic signal, indicating that the trait is evolutionarily labile and not evolutionarily constrained.

Discussion

- Past research has found that CLM evolved at least four times convergently, and likely arose during the Miocene when Pebas Lake was forming (Marques-Souza et al. 2018). Convergence in Gymnophthalmids provides another system in which to study convergent evolutionary processes and adaptive traits, though caution must be taken in interpreting this convergence as the quantitative analyses explored herein reveal that treating CLM as a single discrete trait ignores significant variation between the evolutionary histories of the traits thought to comprise this convergent morphology; CLM traits vary in phylogenetic effect and correlation coefficients. Non-phylogenetic multi and univariate analyses did confirm significant differences in morphology between aquatic and non-aquatic Gymnophthalmids, however, indicating that there is a quantitative basis to the previously qualitatively described convergence.
- Analyses herein were limited by the small sample size, and by the lack of genetic and ecological data. Additionally, the randomization tests and the multivariate trait analysis which here was performed using PCA would be more informative if they took phylogenetic relationships between species into account.
- Crocodile-Like Morphological traits were highly varied between different species of Gymnophthalmids, with many aquatic species lacking the supposed aquatic adaptations and many non-aquatic species appearing to have aquatic adaptations. This is possibly due to selection unrelated to aquatic locomotion; the Gymnophthalmids described as semi-aquatic might more accurately be described as leaf-litter dwellers or semi-arboreal lizards which enter water only occasionally. Additionally, due to the lack of ecological knowledge for lizards in this group, it is possible that some non-aquatic species are actually semi-aquatic; *Placosoma glabellum* has been classified as non-aquatic following other studies mentioning CLM but Pontes et al. (2018) reported collecting an individual on a rock in a stream. Furthermore, traits which are thought to be adaptations for aquatic locomotion in Gymnophthalmids and other taxa (e.g., lateral tail compression) are associated with other ecological purposes in other taxa (e.g., arboreal Pythonids and Boids have laterally compressed bodies (Pizzatto et al. 2007)).

Acknowledgements & Works Cited

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