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Postcranial Morphology and the Locomotor Adaptations of Extant and Extinct Crocodylomorphs  
and Lepidosaur

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A thesis  
presented to  
the faculty of the Department of Geosciences  
East Tennessee State University

In partial fulfillment  
of the requirements for the degree  
Master of Science in Geosciences

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by  
Laura Rooney  
May 2018

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Keywords: Lepidosaur, Crocodylomorph, Morphology, Locomotion, Crocodilian

## ABSTRACT

### Postcranial Morphology and the Locomotor Adaptations of Extant and Extinct Crocodylomorphs and Lepidosauurs

by

Laura Rooney

I have collected a series of linear measurements of the postcranial skeletons of 43 extant crocodylian and lepidosaur taxa to determine if those engaging in similar locomotor behavior display similar morphology despite phylogenetic differences. Stepwise discriminant function analyses reveal reptile locomotor mode can be accurately predicted (over 80% correct) based on morphology. Semi-aquatic taxa are distinguished by a longer ischium relative to pubis length, a longer scapula relative to humerus length, and a broader acetabulum than terrestrial and arboreal taxa. Arboreal taxa display a more elongate, gracile humerus and a smaller acetabulum. This morphometric data can potentially be used to predict the locomotor behavior of a wide range of extinct reptile taxa. Within this study, *Hyposaurus rogersii*, *Necrosuchus ionensis*, *Alligator* sp. of the Gray Fossil Site, *Crocodylus affinis*, and *Allognathosuchus mooki* were examined and all were inferred to be semi-aquatic by the discriminant function analysis.

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## CHAPTER 1

### INTRODUCTION

Studies have shown that the morphology of the postcranial skeleton can be correlated with the known locomotor behavior of extant taxa (e.g. Losos 1990; Wainwright 2007; Samuels and Van Valkenburgh 2008; Samuels et al. 2013; Chen and Wilson 2015). These data can then be used to infer the locomotor modes of extinct taxa based on their morphological similarity to extant groups. Such studies have been conducted on many groups of mammals, however studies on reptiles are less common. Through linear morphometric analysis of extant crocodylian and lepidosaur postcrania, we can determine the presence or absence of convergent morphology in reptile taxa utilizing similar locomotor modes.

## CHAPTER 2

### BACKGROUND

#### Evolution of Crocodylomorph and Lepidosaur Locomotion

##### Locomotor Diversity of Crocodylomorphs and Lepidosaur

Crocodylomorphs are a group of archosaurs that includes extant crocodylians and their extinct relatives. There are 23 known species of extant crocodylians which are placed in three families; Crocodylidae (true crocodiles), Alligatoridae (alligators and caimans), and Gavialidae (gharial and false gharial). All modern crocodylians are semi-aquatic and spend a majority of their life in the water, however they construct terrestrial nests and regularly come ashore to bask. *Gavialis* is considered to be the most aquatic of the extant taxa, while caimans occupy the broadest range of habitats (Vitt and Caldwell 2014). The Order Crocodylia has remained largely unchanged ecomorphologically since its origins approximately 83.5 million years ago with all members engaging in similarly semi-aquatic behavior. Early members of the broader superorder, Crocodylomorpha, originated in the Late Triassic and are considered to have occupied a much wider range of niches, including some fully terrestrial taxa (e.g. *Postosuchus*, *Prestosuchus*, *Poposaurus*) and fully aquatic taxa (e.g. *Metriorhynchus*) (Chatterjee 1985; Grange 1998; Gauthier et al. 2011; Irmis et al. 2013; Liparini and Schultz 2014).

Lepidosauria, is a superorder of reptiles which includes lizards, snakes, amphisbaenians, and tuataras. With over 10,000 extant species, over 6,000 of which are lizards, Lepidosauria is highly diverse and includes many arboreal/scansorial, terrestrial, semi-aquatic, semi-fossorial, fossorial, and saltatorial species. Examples of these taxa include the arboreal chameleon *Bradypodion*, terrestrial agamid *Trapelus*, semi-aquatic varanid *Varanus salvator*, semi-fossorial



skink *Liopholis*, and saltatorial-fossorial lacertid *Acanthodactylus cantoris* (Vitt and Caldwell 2014). Similar to crocodylomorphs, the earliest lizards are thought to have originated during the Late Triassic. Although the diversity of locomotor behavior of crocodylomorphs has greatly decreased since the Mesozoic, lepidosaurs have retained a high distribution of locomotor modes and thus represent potential modern analogs for extinct crocodylomorphs and other amniotes which appear to have engaged in higher degrees of terrestrial behavior.

Several extant families of lepidosaurs display a wide array of locomotor specializations among their taxa. The family Iguanidae, for example, contains arboreal species (e.g. *Iguana iguana*), terrestrial species (e.g. *Cyclura cornuta*), and a semi-aquatic species (*Amblyrhynchus cristatus*) (Vitt and Caldwell 2014). A similar distribution of locomotor behaviors is seen among agamids with arboreal representatives (e.g. *Japalura mitsukurii*), terrestrial species (e.g. *Trapelus sanguinolenta*), and the semi-aquatic *Hydrosaurus pustulatus* and *Physignathus cocincinus* (Vitt and Caldwell 2014). Other lepidosaur families also display species with semi-aquatic adaptations, like the Asian water monitor (*Varanus salvator*) of the family Varanidae, and the northern caiman lizard (*Dracaena guianensis*) of the family Teiidae. Morphometric measurements and comparisons of postcrania for representatives of these locomotor groups within Lepidosauria may reveal that morphology reflects locomotor behavior in reptiles, regardless of evolutionary relationships, and indicate convergence or parallel evolution of locomotor adaptations among clades.

#### Past Studies Inferring Locomotion of Extinct Crocodylomorphs

The locomotor behavior of crocodylomorphs has often been interpreted from crania based on the orientation of the nasals and orbitals, as well as from qualitative analyses of the

postcrania. It is only in recent years that researchers have begun more thorough examinations of crocodylomorph postcrania to interpret their adaptations for aquatic and terrestrial locomotion (Hua and Buffrenil 1996; Hua 2003; Stein et al. 2017). For example, Schachner (2011) reconstructed the muscles of the pelvis and hindlimbs of the extinct crocodylomorph *Poposaurus gracilis* based on the bone and muscle structure found in modern alligators and lepidosaurs. Molnar et al. (2015) examined the lumbar and thoracic vertebrae of modern crocodiles and several extinct crocodylomorphs to determine if variations in the range of motion and joint stiffness of the vertebrae could explain their varying locomotor capabilities. Morphological studies such as these are invaluable to understanding the development of locomotor capabilities through the course of crocodylian evolution. Detailed quantitative studies of extant reptiles can reveal aspects of their morphology that distinguish species with differing locomotor ecology, often based on limited material. The fossil material available for many species of extinct crocodylomorphs is limited, thus it is vital to determine reliable methods of inferring locomotion from whatever skeletal material is present.

#### Skeletal Morphology Reflects Functional Performance

Studies of a wide range of organisms have demonstrated the utility of skeletal morphology in reflecting functional capabilities. Often, patterns have demonstrated that organisms engaging in similar behaviors display similar morphologies (Wainwright 2007; Losos 2011). Cranial, postcranial, and dental morphologies have been used as signals for dietary preferences, locomotor capabilities, and even the evolutionary history of extant taxa (O'Keefe and Carrano 2005; Stayton 2006; Wainwright 2007; Samuels and Van Valkenburgh 2008; Polly et al. 2011; Da Silva et al. 2018). This ability is of great value to paleontologists as, frequently, skeletons are the

only portion of organisms that become fossilized. Extant taxa provide us with the opportunity to examine the morphologies associated with particular ecologies, then quantitatively infer the habits of extinct groups based on their morphology.

### Quantitative Methods of Utilizing Postcrania to Infer Locomotion

#### Past Studies Inferring Locomotion in Mammals

Researchers of mammalian locomotion have repeatedly displayed the utility of using linear morphological measurements of mammal postcrania to create osteological indices that can be used to identify locomotor modes (e.g. Van Valkenburgh 1987; Samuels and Van Valkenburgh 2008; Rose et al. 2014; Chen and Wilson 2015; Tulli et al. 2015). Based on the methodology applied to carnivore locomotion in Van Valkenburgh 1987, Samuels and Van Valkenburgh (2008) took measurements of the limbs of a diverse sample of extant rodent taxa and found their locomotor mode closely reflected their postcranial morphology, despite belonging to evolutionarily distinct groups. Application to extinct rodent species allowed quantitative inference of their locomotor habits. Samuels et al. (2013) utilized the same methodology to interpret locomotor behavior in extant and extinct carnivorans. Both studies measured proportions of the limb bones and calculated a series of osteological indices, which were analyzed using analysis of variance (ANOVA) and stepwise discriminant function analysis (DFA). Chen and Wilson (2015) then displayed that these analyses can be applied on an even broader scale by collecting postcranial data from over 100 small-bodied mammal taxa that spanned 15 orders. With the use of ANOVA and canonical variate analyses (CVA), these researchers once again found that postcranial morphology reflects locomotion and that this

methodology could be applied to infer the locomotor modes of several Mesozoic mammal taxa. Each of these studies indicate that mammal taxa engaging in similar locomotor behavior tend to converge on particular morphologies, regardless of evolutionary relationships.

#### Linking Postcranial Morphology to Locomotor Behavior in Reptiles

Given the diversity of ecology and morphology of extant reptiles, it would be expected that form would reflect function, as similar patterns were observed in studies of mammals. To date, there have been a number of quantitative ecomorphological studies of reptiles that have shown just that (Pianka 1969; Pounds et al. 1983; Garland and Losos 1994). Examinations of postcranial proportions have been applied when interpreting the locomotor systems and ecomorphologies of groups of reptiles such as plesiosaurs (O'Keefe and Carrano 2005) and *Anolis* lizards (Losos 1990); thus, there is potential for applying a similar methodology to other groups of reptiles. In the past, the skull and lower jaw morphology of extant squamates has been used to demonstrate convergence among species with similar diets (Stayton 2006; Klaczko 2016). As crania of reptiles have indicated morphological and functional convergence based on diet, it is possible that reptilian postcrania exhibit similar convergence based on locomotor mode. A wide variety of locomotor specialists are seen in multiple families of extant reptiles, among both crocodylians and lepidosaurs, thus these groups provide the opportunity for examining potential convergent or parallel evolution within reptile clades.

#### Complications When Examining Reptiles vs. Mammals

While several of the simple linear measurements that have been collected from mammals for locomotor studies can easily be applied to reptile taxa, such as lengths of the limb bones and components of the pectoral and pelvic girdles, there are multiple anatomical

distinctions between the two classes that must be noted. For example, mammalian locomotor studies frequently measure the length of the olecranon process of the ulna (ex. Van Valkenburgh 1987; Samuels and Van Valkenburgh 2008; Chen and Wilson 2015), but this feature is not present in reptilian taxa (Romer 1997). In addition, the pectoral girdles of these groups are quite different in that reptiles possess a coracoid which forms the ventral portion of the shoulder girdle (Romer 1997). This feature is absent in all placental mammals, thus new measurements must be determined to accurately represent this feature.

Consideration must also be taken when choosing which postcranial components are to be the primary focus of the study. Mammalian locomotor studies have primarily conducted analyses on the appendicular skeleton as locomotion of most mammals is primarily driven by the limbs, and thus the limbs and girdles display the primary muscle attachment sites for locomotion. However, in reptiles the axial skeleton frequently plays a much larger role in locomotor capabilities, especially for semi-aquatic taxa such as crocodylians. Semi-aquatic crocodylians and lepidosaurs rarely utilize their limbs for aquatic behavior, but rather propel themselves through the water by mediolateral undulation of their paddle-like tails (Hildebrand 1985; Grenard 1991). Therefore, when conducting an ecomorphological analysis of reptilian taxa, the inclusion of measurements of the axial skeleton, particularly the caudal vertebrae, may be key to examining and interpreting locomotor behavior.

## CHAPTER 3

### METHODS

#### Crocodylian and Lepidosaur Taxa

A total of 57 extant crocodylian and lepidosaur specimens from ten families (37 species) are represented within this study (Table 1). Families include Crocodylidae, Alligatoridae, Agamidae, Iguanidae, Varanidae, Teiidae, Dactyloidae, Hoplocercidae, Cordylidae, and Helodermatidae. The majority of species are represented by one specimen, however additional specimens were measured when available to better portray the morphology of the species.

Table 1: List of extant species included in analysis

Species #	Family	Species name	N	Locomotor group
1	Agamidae	<i>Hydrosaurus pustulatus</i>	2	Semi-aquatic
2	Agamidae	<i>Trapelus sanguinolentus</i>	1	Terrestrial
3	Agamidae	<i>Japalura mitsukurii</i>	1	Arboreal
4	Agamidae	<i>Stellagama stellio</i>	1	Terrestrial
5	Agamidae	<i>Phrynocephalus przewalski</i>	1	Terrestrial
6	Cordylidae	<i>Cordylus giganteus</i>	1	Terrestrial
7	Agamidae	<i>Bronchocela cristatella</i>	1	Arboreal
8	Agamidae	<i>Physignathus</i> sp.	4	Semi-aquatic
9	Agamidae	<i>Uromastyx</i> sp.	3	Terrestrial
10	Alligatoridae	<i>Paleosuchus trigonatus</i>	2	Semi-aquatic
11	Alligatoridae	<i>Alligator mississippiensis</i>	3	Semi-aquatic
12	Alligatoridae	<i>Alligator sinensis</i> *	1	Semi-aquatic
13	Alligatoridae	<i>Melanosuchus niger</i>	1	Semi-aquatic
14	Alligatoridae	<i>Caiman crocodilus</i>	1	Semi-aquatic
15	Crocodylidae	<i>Crocodylus acutus</i>	1	Semi-aquatic
16	Crocodylidae	<i>Crocodylus moreletti</i>	1	Semi-aquatic
17	Crocodylidae	<i>Crocodylus mindorensis</i>	1	Semi-aquatic
18	Crocodylidae	<i>Gavialis gangeticus</i>	1	Semi-aquatic
19	Crocodylidae	<i>Tomistoma schlegelli</i>	1	Semi-aquatic
20	Dactyloidae	<i>Anolis equestris</i>	1	Arboreal
21	Helodermatidae	<i>Heloderma suspectum</i>	1	Terrestrial
22	Hoplocercidae	<i>Enyalioides oshaughnessyi</i>	3	Arboreal
23	Iguanidae	<i>Amblyrhynchus cristatus</i>	2	Semi-aquatic
24	Iguanidae	<i>Cyclura cornuta</i>	1	Terrestrial
25	Iguanidae	<i>Cyclura cychlura</i>	1	Terrestrial
26	Iguanidae	<i>Iguana iguana</i>	1	Arboreal
27	Iguanidae	<i>Dipsosaurus dorsalis</i>	1	Terrestrial

28	Iguanidae	<i>Callisaurus draconoides</i>	1	Terrestrial
29	Iguanidae	<i>Conolophus subcristatus</i>	1	Terrestrial
30	Iguanidae	<i>Ctenosaura acanthura</i>	1	Arboreal
31	Iguanidae	<i>Ctenosaura similis</i>	2	Terrestrial
32	Iguanidae	<i>Ctenosaura hemilopha</i>	1	Terrestrial
33	Teiidae	<i>Dracaena guianensis</i>	1	Semi-aquatic
34	Teiidae	<i>Tupinambus merianae</i>	1	Terrestrial
35	Teiidae	<i>Ameiva ameiva</i>	1	Terrestrial
36	Iguanidae	<i>Sauromalus ater</i>	1	Terrestrial
37	Varanidae	<i>Varanus bengalensis</i>	1	Terrestrial
38	Varanidae	<i>Varanus griseus</i>	1	Terrestrial
39	Varanidae	<i>Varanus gouldi</i>	1	Terrestrial
40	Varanidae	<i>Varanus salvator</i>	2	Semi-aquatic
41	Varanidae	<i>Varanus komodoensis</i>	1	Terrestrial
42	Varanidae	<i>Varanus exanthematicus</i>	1	Terrestrial
43	Varanidae	<i>Varanus beccarii</i>	1	Arboreal

*Captive specimens are indicated by \*.*

Each species studied was categorized into one of three locomotor modes (Table 2) based on published descriptions of their behavior (Vitt and Caldwell 2014, IUCN). Some taxa are characterized by multiple behaviors and categorizations were made based on the predominance of evidence. Thus, these categories are a simplification of a complex continuum of locomotor behaviors. Lepidosaur families that include members with a variety of locomotor modes were preferentially selected to allow comparisons of closely related taxa with disparate ecology. Specimens were also chosen based on completeness of available postcrania, and the sample includes both male and female individuals. Most of the specimens examined are wild-caught adults; however, occasional juveniles have been used where adult specimens were unavailable. Data for extant specimens were gathered from the reptile collections of the Smithsonian Institution National Museum of Natural History (NMNH), Washington, D.C.; the East Tennessee State University Museum of Natural History (ETMNH), Gray, TN; and the East Tennessee State University modern osteology collections (ETMNH), Johnson City, TN.

Table 2: Locomotor categories used in the analyses and their definitions

Locomotor Mode	Definition
Terrestrial (T)	Primarily displays quadrupedal behavior on land, potentially with slight burrowing behavior. Rarely if ever swims or climbs.
Semi-aquatic (Sa)	Regularly swims for dispersal, escape, or foraging.
Arboreal (A)	Displays frequent climbing behavior for escape, shelter, or foraging. Includes scansorial species.

Table 1 includes a complete list of the included extant species and their designated locomotor modes. Species were assigned to locomotor groups based on descriptions of their behavior found in Vitt and Caldwell, 2014 and IUCN.org.

Nineteen specimens of extinct crocodylomorph taxa (Table 3) spanning ten families were included in the analysis as well to infer their primary locomotor behaviors. Fossil specimens were examined from the vertebrate paleontology collections of the American Museum of Natural History (AMNH), New York, NY and the New Jersey State Museum (NJSM), Trenton, NJ.

Table 3: Extinct crocodylomorph taxa

Family	Species name	N
Alligatoridae	<i>Alligator</i> sp. (Gray Fossil Site)	4
Alligatoridae	<i>Allognathosuchus mooki</i>	1
Alligatoridae	<i>Necrosuchus ionensis</i>	1
Crocodylidae	<i>Bottasaurus harleni</i>	1
Crocodylidae	<i>Crocodylus affinis</i>	1
Crocodylidae	<i>Holops obscurus</i>	1
Dyrosauridae	<i>Hyposaurus rogersii</i>	1
Gavialoidea	<i>Thoracosaurus</i> sp.	3
Goniopholidae	<i>Goniopholis</i> sp.	1
Stem crocodylian	<i>Hesperosuchus agilis</i>	1
Pholidosauridae	<i>Teleorhinus robustus</i>	1
Prestosuchidae	<i>Prestosuchus chiniquensis</i>	1
Pristichampsidae	<i>Pristichampsus vorax</i>	1
Rauisuchidae	<i>Protosuchus</i> sp.	1

### Postcranial Measurements

I used digital calipers to measure a total of 40 linear measurements of the postcranial skeleton (Table 4) using digital calipers to measure to the nearest 0.01 mm. Measurements primarily consisted of total lengths of limb bones as well as proximal, distal, and midshaft



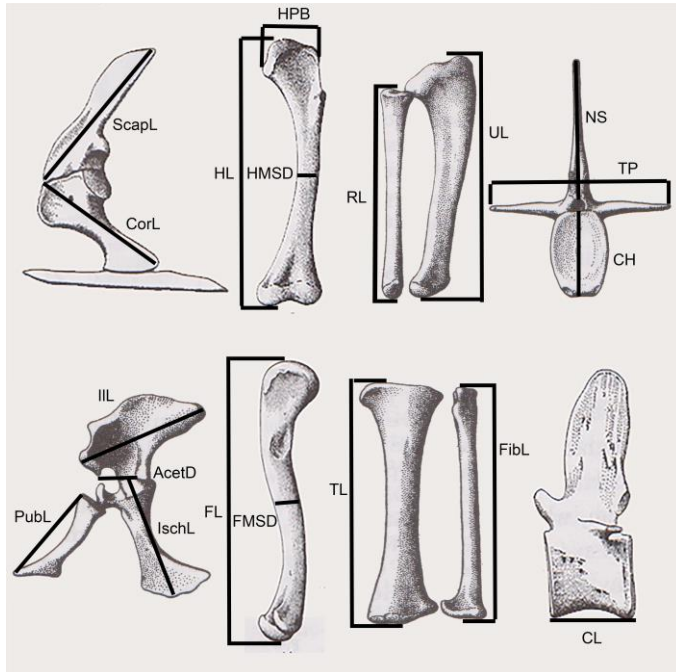
widths of these elements. The bones of the pectoral and pelvic girdles were also measured, along with three caudal vertebrae from each specimen, acting as representatives for three designated segments of the tail (anterior, midway, and posterior). Due to the broad variation in tail lengths and caudal vertebra number across taxa, the caudal vertebrae selected to represent the midway and posterior sections were chosen based on the overall length of the individual's tail.

*Table 4: Postcranial measurements used in the analyses*

<b>Measurement</b>	<b>Abbreviation</b>
Humerus proximal breadth	HPB
Humerus proximal width	HPW
Humerus distal breadth	HDB
Humerus distal width	HDW
Humerus length	HL
Humerus mid-shaft diameter	HMSD
Deltopectoral ridge length	DPRL
Deltopectoral ridge height	DPRH
Radius length	RL
Ulna length	UL
Femur length	FL
Femoral mid-shaft diameter	FMSD
Femur proximal length	FPL
Femur proximal width	FPW
Femur distal length	FDL
Femur distal width	FDW
Linea aspera	LA
Tibia length	TL
Tibia mid-shaft diameter	TMSD
Fibula length	FibL
Fibula mid-shaft diameter	FibMSD
Centrum height of anterior caudal vertebra	CH-ACV
Centrum length of anterior caudal vertebra	CL-ACV
Transverse processes of anterior caudal vertebra	TP-ACV
Neural spine of anterior caudal vertebra	NS-ACV
Centrum height of midway caudal vertebra	CH-MCV
Neural spine of midway caudal vertebra	NS-MCV
Hemal spine height	HSH
Sacrum length	SacL
Acetabulum diameter	AcetD
Ilium length	IIL
Ilium width	IIW

Ischium length	IschL
Ischium width	IschW
Pubis length	PubL
Pubis width	PubW
Scapula length	ScapL
Scapula width	ScapW
Coracoid length	CorL
Coracoid width	CorW

*Measurements are illustrated in Figure 1.*



*Figure 1: Measurements of the axial and appendicular skeleton used in this study*

*Images modified from Romer 1997.*

Since this study covers a wide distribution of taxa across Reptilia, significant size differences between specimens are present. Linear measurements were used to calculate a set of 22 osteological indices (Table 5), which reflect relative proportions and help to account for variations in size between species. These indices allow us to visualize overall limb and tail proportions and interpret variations in velocity ratio and mechanical advantage along these appendages that can reflect particular locomotor adaptations.

Table 5: Osteological indices used in the Indices DFA

Index	Definition
Proximal forelimb index (PFI)	Scapula length divided by humerus length (ScapL/HL). Indicates speed of movement via relative proportions of components of the proximal forelimb.
Humeral robustness index (HRI)	Mid-shaft diameter of humerus divided by humerus length (MSDH/HL). Indicates humeral robustness and resistance to bending and shearing.
Humeral proximal robustness index (HPRI)	Humerus proximal breadth divided by humerus length. Indicates robustness and strength of proximal humerus.
Humeral distal robustness index (HDRI)	Humerus distal breadth divided by humerus length. Indicates robustness and strength of distal humerus.
Shoulder moment index (SMI)	Deltpectoral crest length divided by humerus length (DPCL/HL). Displays mechanical advantage of deltoid and pectoral muscles at the shoulder joint.
Brachial index (BI)	Ulna length divided by humerus length (UL/HL). Indicates relative proportions of proximal and distal elements of the forelimb.
Brachial index 2 (BI2)	Radius length divided by humerus length (RL/HL). Indicates relative proportions of proximal and distal elements of the forelimb.
Middle forelimb index (MFI)	Radius length divided by ulna length (RL/UL). Indicates relative size of musculature controlling extension of distal forelimb.
Crural index (CI)	Tibia length divided by femur length (TL/FL). Indicates relative proportions of proximal and distal elements of the hindlimb.
Femoral robustness index (FRI)	Midshaft diameter of femur divided by femur length (MSDF/FL). Indicates robustness of femur and its resistance to bending and shearing.
Intermembral index (IMI)	Humerus length and radius length divided by femur length and tibia length $[(HL+RL)/(FL+TL)]$ . Indicates relative lengths of forelimb and hindlimb.
Tibial robustness index (TRI)	Midshaft diameter of tibia divided by tibia length (MSDT/TL). Indicates resistance of tibia to bending and shearing.
Body length index (BLI)	Total length of trunk vertebrae (thoracic and lumbar if applicable) divided by total length of caudal vertebrae. Indicates relative proportion of trunk length to tail length.
Neural spine index for anterior caudal vertebra (NSI-ACV)	Height of neural spine divided by centrum height for anterior caudal vertebra. Anterior caudal vertebrae were considered to span first through fourth caudals. First caudal vertebra was measured when available. When unavailable, anterior-most available vertebra was used. Indicates potential dorsal lengthening of anterior portion of tail.

Neural spine index for midway caudal vertebra (NSI-MCV)	Height of neural spine divided by centrum height for midway caudal vertebra. Midway caudal vertebrae were selected from the halfway point of the total tail length for each specimen. Indicates potential dorsal lengthening of midway portion of tail.
Transverse process index for anterior caudal vertebra (TPI-ACV)	Total length of transverse processes divided by centrum length for anterior caudal vertebra. Anterior caudal vertebrae were considered to span first through fourth caudals. First caudal vertebra was measured when available. When unavailable, anterior-most available vertebra was used. Indicates presence of mediolateral compression.
Ilium index (III)	Ilium length divided by ilium width (ILL/IW). Indicator of relative width of ilium available for muscle attachment.
Pubis index (PubI)	Pubis length divided by pubis width (PubL/PubW). Indicator of relative width of pubis available for muscle attachment.
Ischium index (IschI)	Ischium length divided by ischium width (IschL/IschW). Indicator of relative width of ischium available for muscle attachment.
Ilium-Ischium Index (II-Isch)	Ilium length divided by ischium length (IIL/IschL). Displays relative areas of attachment for various hindlimb, trunk, and tail muscles such as the caudofemoralis, iliocostalis, and ilio-ischio-caudalis.
Ilium-Pubis Index (II-Pub)	Ilium length divided by pubis length (IIL/PubL). Displays relative areas of attachment for various muscles such as the ischiopubis and iliocostalis.
Ischium-Pubis Index (Isch-Pub)	Ischium length divided by pubis length (IschL/PubL). Detects presence of posterior expansion of the pelvis for attachment of tail muscles.

*Measurements indicated above are described in Table 1 and illustrated in Figure 1. Definitions and hypothesized functional meaning of indices are included. Several indices are based on those described in Samuels and Van Valkenburg 2008.*

As an alternative method to correct for body size and account for the influence of allometry, geometric mean (GM), calculated as the  $n^{\text{th}}$  root of the product of  $n$  measurements, was computed for each specimen as a proxy for body size (Mossiman and James 1979). The resulting GM score was then used to calculate a set of GM transformed variables (variable/GM = transformed) from each of the linear measurements, which yield variables corrected for individual body size (Mossiman and James 1979). Additionally, the GM score itself can be used

to study allometry, by regressing other variables (log transformed linear measurements and indices) against log GM score and examining whether slopes are significantly different from isometry (z test).

### Statistical Analyses

Univariate Analysis of Variance (ANOVA) and boxplots were used to assess whether there are significant differences in the osteological indices between locomotor groups and to visualize these differences. I also conducted a stepwise discriminant function analysis (DFA) using the osteological indices to identify which variables can be used to best distinguish between terrestrial, semi-aquatic, and arboreal reptiles. An additional DFA was conducted using GM transformed variables. The DFA based on GM scores is expected to highlight aspects of morphology that best separate groups, while correcting for body size.

The discriminant functions derived from the analysis using osteological indices were then used to infer the locomotor mode of extinct crocodylomorph taxa, which were included as unknowns in the classification phase of the analysis. As osteological indices are easily calculated, even from fragmentary specimens, that analysis has the greatest potential to include and classify the locomotion of extinct species. Ideally, the DFA based on GM scores would also be used to classify the locomotor habits of extinct species, but that would require particularly complete specimens, as all variables are needed to calculate the GM score.

Linear regressions and bivariate plots were also performed on log GM scores versus log transformed linear measurements and osteological indices that displayed significance within the DFAs. Deviations of slopes from expectations (allometry) were tested using a z-test. Z-scores were calculated by subtracting the expected slope from the observed slope produced by

the least squares linear regressions and dividing this by the standard error of the slope. These analyses allowed examination of interspecific allometry and how body size may have an impact on morphological features that distinguish locomotor groups. All statistical analyses were done in IBM SPSS Statistics 24.

## CHAPTER 4

### RESULTS

#### ANOVA Results

The univariate ANOVA (Table 6) aided in identifying several indices that help to distinguish between our locomotor groups. Select indices have been highlighted via the boxplots in Figure 2. The semi-aquatic reptile taxa display a more elongate ischium (high Isch-Pub, low Il-Isch), a short and broad ilium and pubis (Ill and Publ) and a more elongate scapula (high PFI) relative to the other two groups. Arboreal taxa generally showed more slender, gracile limbs (low HPRI, HDRI, FRI, and TRI).

*Table 6: Mean values and standard deviations of indices for each locomotor group*

	<b>Terrestrial</b>	<b>Semi-aquatic</b>	<b>Arboreal</b>
PFI	0.396 (0.057) <sup>Sa</sup>	0.578 (0.175) <sup>T, A</sup>	0.374 (0.091) <sup>Sa</sup>
HRI	0.091 (0.0242)	0.098 (0.020) <sup>A</sup>	0.069 (0.017) <sup>Sa</sup>
HPRI	0.274 (0.046) <sup>A</sup>	0.256 (0.035)	0.213 (0.041) <sup>T</sup>
HDRI	0.305 (0.068) <sup>A</sup>	0.273 (0.052)	0.226 (0.067) <sup>T</sup>
SMI	0.286 (0.059)	0.295 (0.069)	0.239 (0.076)
BI	0.837 (0.078) <sup>Sa</sup>	0.783 (0.070) <sup>T</sup>	0.824 (0.058)
BI2	0.743 (0.067) <sup>Sa</sup>	0.694 (0.069) <sup>T</sup>	0.739 (0.057)
MFI	0.890 (0.053)	0.886 (0.031)	0.897 (0.019)
CI	0.810 (0.096)	0.764 (0.058)	0.797 (0.074)
FRI	0.088 (0.022) <sup>A</sup>	0.090 (0.020) <sup>A</sup>	0.064 (0.021) <sup>T, Sa</sup>
IMI	0.812 (0.082)	0.775 (0.083)	0.795 (0.131)
TRI	0.091 (0.023) <sup>A</sup>	0.095 (0.023) <sup>A</sup>	0.065 (0.026) <sup>T, Sa</sup>
BLI	0.464 (0.212)	0.410 (0.169)	0.283 (0.071)
NSI-ACV	1.937 (0.619)	2.356 (1.074)	2.451 (0.985)
NSI-MCV	2.032 (1.417)	2.878 (1.326)	1.613 (1.041)
TPI-ACV	3.415 (0.623)	3.121 (0.447)	3.028 (0.378)
Ill	2.679 (0.476) <sup>Sa</sup>	2.201 (0.669) <sup>T, A</sup>	2.939 (0.303) <sup>Sa</sup>
Publ	5.539 (2.157) <sup>Sa</sup>	3.383 (2.282) <sup>T, A</sup>	6.131 (1.114) <sup>Sa</sup>
Ischl	1.671 (1.183)	2.034 (1.363)	1.308 (0.168)
Il-Isch	1.516 (0.277) <sup>Sa</sup>	1.260 (0.324) <sup>T, A</sup>	1.687 (0.272) <sup>Sa</sup>
Il-Pub	1.230 (0.212)	1.266 (0.234)	1.199 (0.248)
Isch-Pub	0.822 (0.124) <sup>Sa</sup>	1.036 (0.187) <sup>T, A</sup>	0.712 (0.112) <sup>Sa</sup>

*Indices are defined in Table 4. Significant differences ( $p < 0.05$ ) between groups in univariate ANOVA tests using Scheffe's F post hoc procedure are indicated by superscripts (T = terrestrial, Sa = semi-aquatic, A = arboreal).*

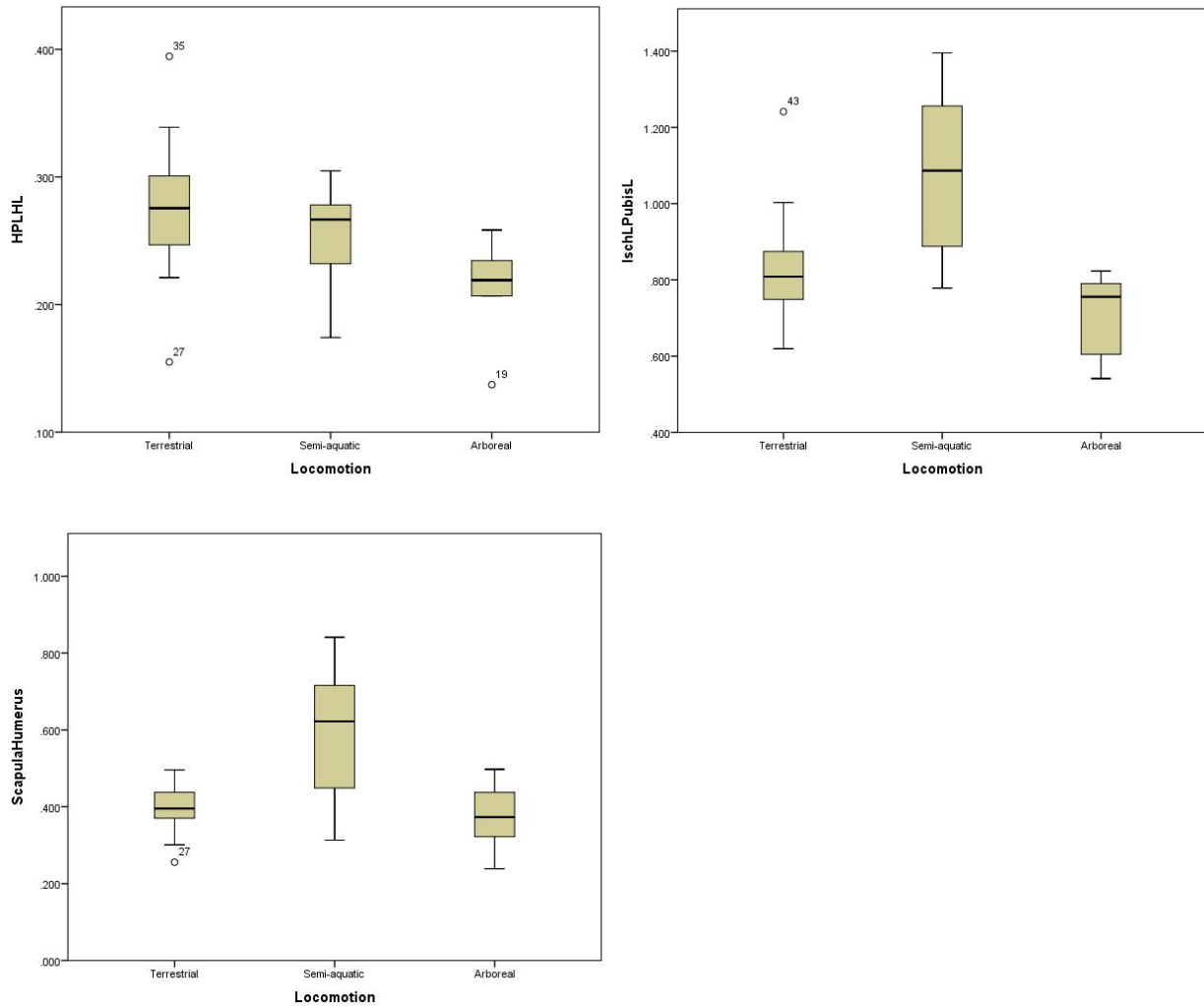


Figure 2: Boxplots of functional indices

The bar displays the median, boxes represent upper and lower quartiles, and whiskers show extreme values for each group. Outliers are represented by individual circles with species numbers (Table 1).

### DFA Using Osteological Indices (Indices DFA)

The stepwise DFA using osteological indices (Indices DFA) included four of the total 22 indices and showed significant separation of locomotor groups based on their morphology (Wilks' lambda = 0.279) (Table 7). The analysis yielded two discriminant functions, the first of which (DF1) accounted for 81.9% of variance and largely separated the terrestrial and semi-aquatic groups. DF1 showed strong negative correlation with PFI (Scapula length to humerus



length) and Isch-Pub (Ischium length to pubis length), but slight positive correlation with Crural Index (Tibia length to femur length) and HPRI (Humerus proximal breadth to humerus length) (Table 7). Terrestrial taxa tended toward more positive scores while semi-aquatic taxa tended toward more negative scores. This indicates the tendency for semi-aquatic reptile species to have a shorter proximal forelimb relative to scapula length, a shorter distal hindlimb, a longer ischium, and a more narrow proximal humerus.

The second discriminant function (DF2) accounted for 18.1% of variance and primarily distinguished arboreal taxa from the terrestrial and semi-aquatic groups. DF2 showed a highly positive correlation with HPRI as well as a somewhat positive correlation with CI and Isch-Pub (Table 7, Figure 3). Arboreal taxa tended toward slightly more negative scores than either terrestrial or semi-aquatic taxa, indicating the tendency for arboreal taxa to have a more narrow proximal humerus relative to a longer overall humerus, a shorter distal hindlimb, and a shorter ischium relative to pubis length.

*Table 7: Indices DFA structure matrix and summary statistics*

	Function	
	1	2
PFI	-.643	.375
HPRI	.117	.820
CI	.218	-.051
Isch-Pub	-.631	.626
Eigenvalue	1.636	.361
% Variance	81.9	18.1
Wilks' lambda	.279	.735
p	<0.001	0.002

*All indices are defined in Table 5 (PFI, proximal forelimb index; HPRI, humeral proximal robustness index; CI, crural index; Isch-Pub, ischium-pubis index).*



diameter and a negative correlation with humerus proximal breadth (Table 8). Semi-aquatic taxa tend to have more positive scores than terrestrial and arboreal taxa.

GM DF2 accounts for 9.3% of variance and appears to do play little role in distinguishing between the locomotor groups. GMDF2 is strongly positively correlated with both humerus proximal breadth and acetabulum diameter (Table 8). Semi-aquatic taxa tend to have more negative scores than the other two locomotor groups

*Table 8: GM DFA structure matrix and summary statistics*

	<b>Function</b>	
	1	2
Trans_HP	-.330	.944
Trans_AcetD	.795	.606
Eigenvalue	.723	.074
% Variance	90.7	9.3
Wilks' lambda	.540	.931
p	<0.001	0.068

*Definitions and illustrations of measurements are shown in Table 4 and Figure 1 (HPB, humeral proximal breadth; AcetD, acetabulum diameter).*

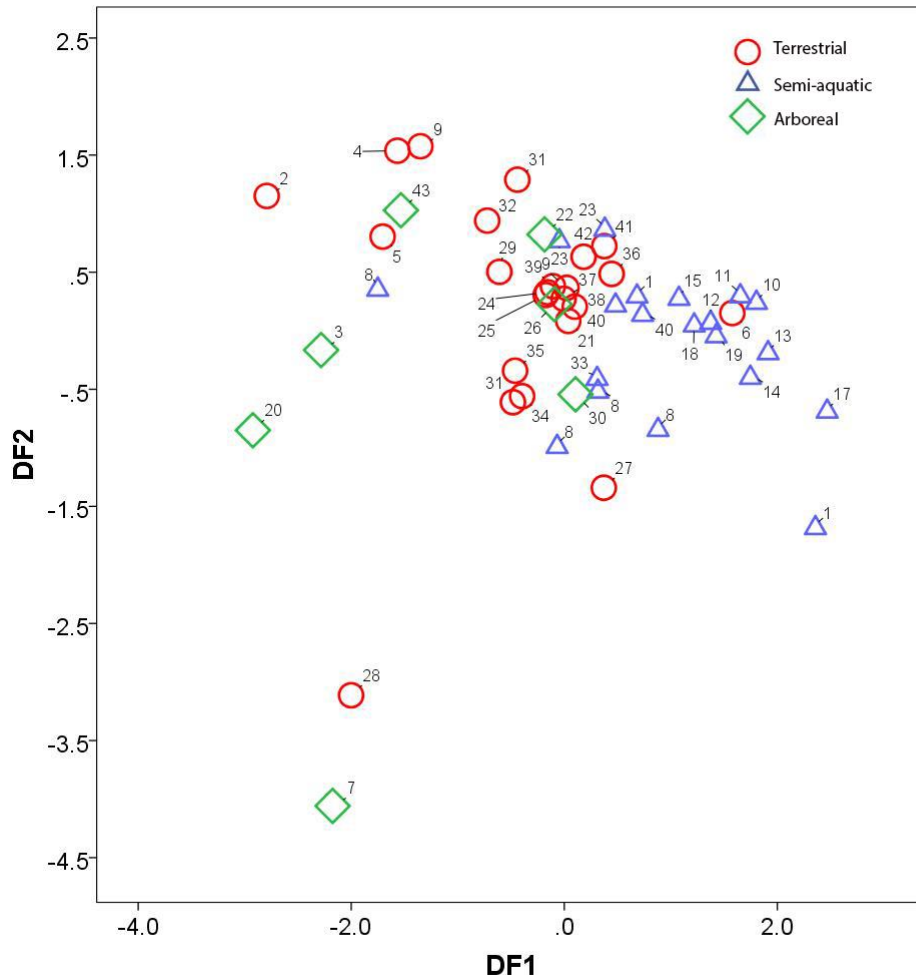


Figure 4: Plot of DF1 and DF2 scores for extant reptile taxa analyzed in the GM DFA

Inferred Locomotor Modes of Extant Lepidosaur and Crocodylian Taxa

The discriminant models' ability to sort the taxa by locomotor group was indicated by the classification matrices in which each specimen was grouped based on the models created using all other specimens.

The classification phase of the Indices DFA correctly classified 81.5% of the extant specimens into their a priori locomotor groups. When cross-validated, 75.9% of the specimens were correctly classified (Table 9). The terrestrial group displayed the highest level of correct

classification at 95%, while the semi-aquatic group was somewhat lower (74% correct), and the arboreal group had much poorer performance (only 57% correct).

A total of 10 out of the 54 specimens were misclassified (Table 10). One taxon, *Physignathus* sp., only partially misclassified with one specimen misclassifying as terrestrial, one misclassifying as arboreal, and the remaining two correctly classifying as semi-aquatic. Both specimens for the semi-aquatic *Amblyrhynchus cristatus* and *Varanus salvator* misclassified as terrestrial. Three arboreal taxa misclassified as terrestrial including *Iguana iguana*, *Enyalioides oshaughnessyi*, and *Ctenosauria acanthura*. One terrestrial taxon, *Uromastix aegypticus*, misclassified as semi-aquatic.

Table 9: Indices DFA classification matrix

	Observed group	% correct	Predicted group membership			Total
			Terrestrial	Semi-aquatic	Arboreal	
Original	Terrestrial	95.8	23	1	0	24
	Semi-aquatic	73.9	5	17	1	23
	Arboreal	57.1	3	0	4	7
Cross-validated	Terrestrial	87.5	21	1	2	24
	Semi-aquatic	69.6	5	16	2	23
	Arboreal	57.1	3	0	4	7

Table 10: Indices DFA misclassified cases

	<b><i>n</i> misclassified</b>	<b>Actual Group</b>	<b>Predicted Group</b>
<i>Amblyrhynchus cristatus</i>	2 of 2	Semi-aquatic	Terrestrial
<i>Iguana iguana</i>	1 of 1	Arboreal	Terrestrial
<i>Enyalioides oshaughnessyi</i>	1 of 1	Arboreal	Terrestrial
<i>Ctenosaura acanthura</i>	1 of 1	Arboreal	Terrestrial
<i>Varanus salvator</i>	2 of 2	Semi-aquatic	Terrestrial
<i>Uromastix aegypticus</i>	1 of 1	Terrestrial	Semi-aquatic
<i>Physignathus</i> sp.	2 of 4	Semi-aquatic	1 Terrestrial, 1 Arboreal

The classification phase of the GM DFA correctly classified 78.0% of the extant specimens into their a priori locomotor groups (Table 11). When cross-validated, 72.0% of the specimens were correctly classified. The terrestrial and semi-aquatic groups showed particularly high rates of correct classification (over 80%), while the arboreal group had much poorer performance (only 57% correct).

Eleven of the 50 total taxa included within the GMDFA were misclassified (Table 12). Once again, both specimens of *Amblyrhynchus cristatus* misclassified as terrestrial and the arboreal taxa *Iguana iguana*, *Enyalioides oshaughnessyi*, and *Ctenosaurua acanthura* misclassified as terrestrial. *Physignathus* sp. again displayed 50% correct classification with two specimens misclassifying as terrestrial, however the specimen that previously misclassified as arboreal within DFA 1 correctly classified as semi-aquatic. Additionally, the terrestrial taxa *Cordylus giganteus* and *Dipsosaurus dorsalis* both misclassified as semi-aquatic while the arboreal *Varanus beccarii* misclassified as terrestrial.

Table 11: GM DFA classification matrix

	Observed group	% correct	Predicted group membership			Total
			Terrestrial	Semi-aquatic	Arboreal	
Original	Terrestrial	87.0	20	2	1	23
	Semi-aquatic	80.0	4	16	0	20
	Arboreal	57.1	4	0	3	7
Cross-validated	Terrestrial	78.3	18	3	2	23
	Semi-aquatic	80.0	4	16	0	20
	Arboreal	28.6	5	0	2	7

Table 12: GM DFA misclassified cases

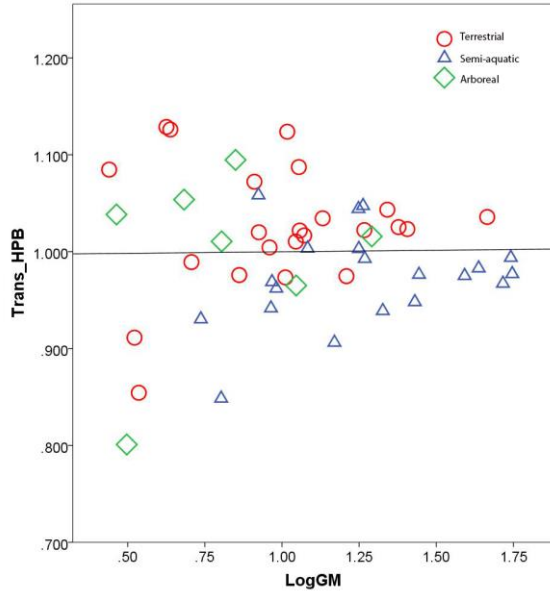
Species	<i>n</i> misclassified	Actual Group	Predicted Group
<i>Cordylus giganteus</i>	1 of 1	Terrestrial	Semi-aquatic
<i>Amblyrhynchus cristatus</i>	2 of 2	Semi-aquatic	Terrestrial
<i>Iguana iguana</i>	1 of 1	Arboreal	Terrestrial
<i>Dipsosaurus dorsalis</i>	1 of 1	Terrestrial	Semi-aquatic
<i>Enyalioides oshaughnessyi</i>	1 of 1	Arboreal	Terrestrial
<i>Callisaurus draconoides</i>	1 of 1	Terrestrial	Arboreal
<i>Ctenosaura acanthura</i>	1 of 1	Arboreal	Terrestrial
<i>Physignathus</i> sp.	2 of 4	Semi-aquatic	Terrestrial
<i>Varanus beccarii</i>	1 of 1	Arboreal	Terrestrial

### Linear Regressions and Interspecific Allometry

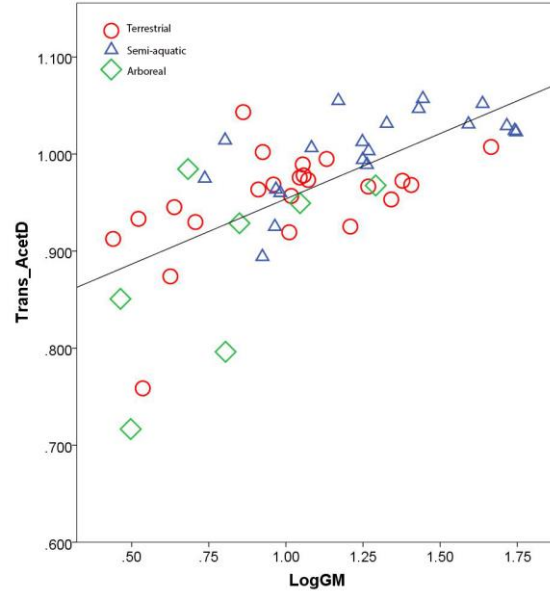
The indices and GM transformed variables that were included in the DFAs have been further analyzed through bivariate plots and linear regressions to better visualize the differences in these variables across the locomotor groups. The linear regressions revealed the presence of positive allometry in acetabulum diameter, proximal forelimb index (PFI), humeral proximal robustness index (HPRI), and ischium-pubis index (Isch-Pub) (Figure 5). The plots

shown in Figure 6 have been used to examine how each variable is contributing to the indices identified within the Indices DFA. These plots revealed that PFI appears to largely be driven by differences in scapula length, with a generally longer scapula present in semi-aquatic taxa relative to the other two groups (Figure 6h) while humerus length relative to body size is fairly uniform across groups (Figure 6g). Similarly, low HPRI values seen in semi-aquatic taxa seem to be the result of more slender proximal humerus compared to other taxa (Figure 6a), whereas the arboreal group's low values for HPRI appear to primarily be the result of a more elongate humerus (Figure 6g). Differences in femur length and tibia length appear to be minimal across the groups, indicating a low level of importance of the crural index in distinguishing locomotor preferences, although semi-aquatic taxa seem to trend toward slightly higher values for both (Figures 6e and 6f). The ischium-pubis index seems to be impacted by both variables with a generally longer ischium and shorter pubis in semi-aquatic taxa and a shorter ischium with a longer pubis in arboreal taxa (Figures 6c and 6d). Figure 7 then displays plots of each individual index, allowing for visual comparisons of additional fossil taxa that could not be incorporated in the original discriminant function analysis due to lack of material.

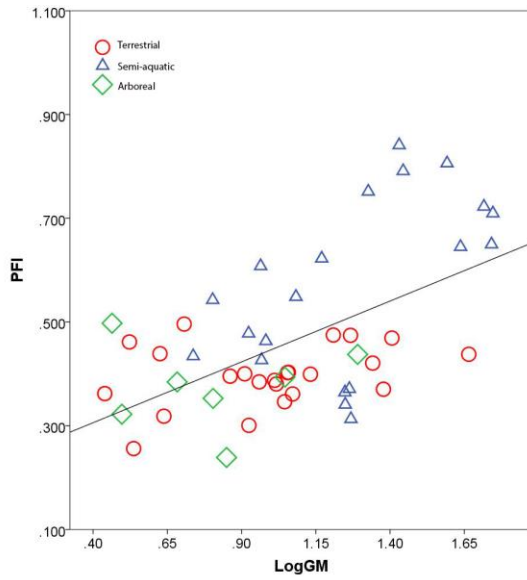




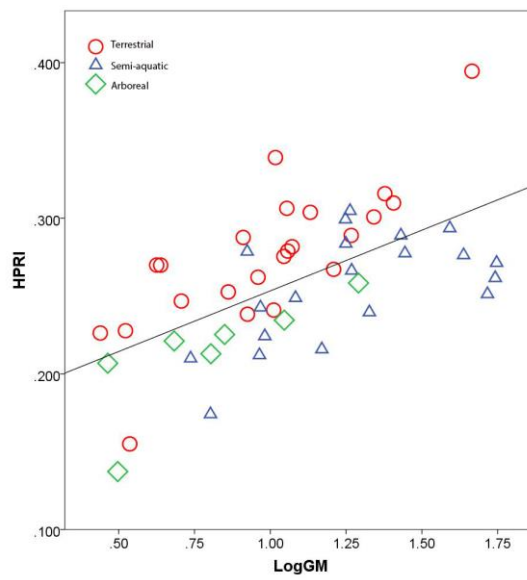
**a**



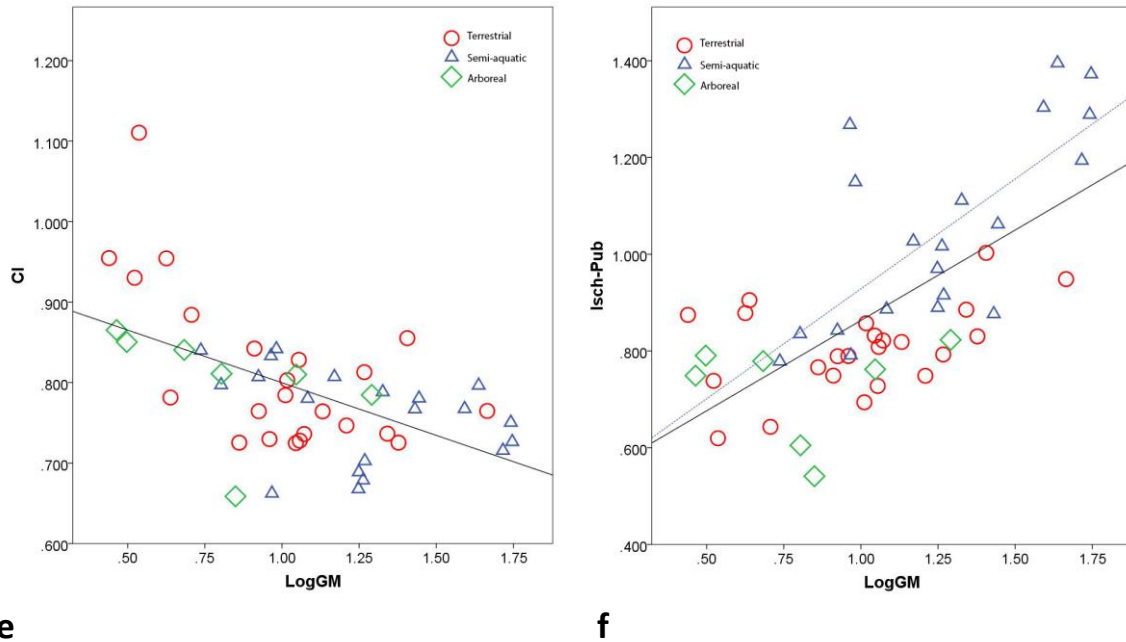
**b**



**c**



**d**



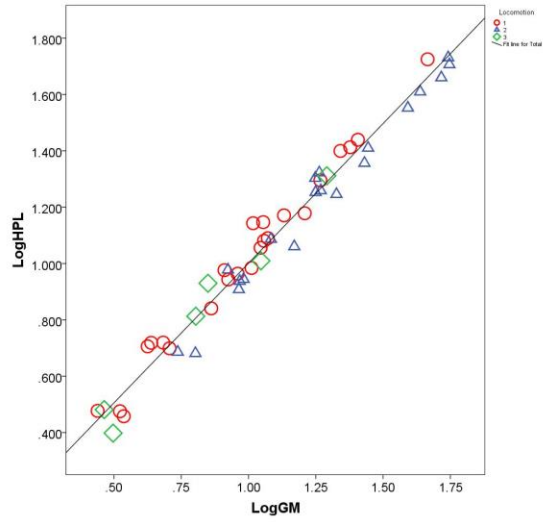
**e** **f**  
 Figure 5: Plots of selected functional indices and GM transformed variables versus the log geometric mean (a proxy for body size).

**a:** Humerus proximal breadth. Total fit line:  $y=1+3.17E-3*x$ . **b:** Acetabulum diameter. Total fit line:  $y=0.82+0.13*x$ . **c:** Proximal forelimb index. Total fit line:  $y=0.21+0.23*x$ . **d:** Humeral proximal robustness index. Total fit line:  $y=0.18+0.08*x$ . **e:** Crural index. Total fit line:  $y=0.93-0.13*x$ . **f:** Ischium pubis index. Total fit line (solid):  $y=0.49+0.37*x$ . Semi-aquatic fit line (dashed):  $y=0.47+0.45*x$ .

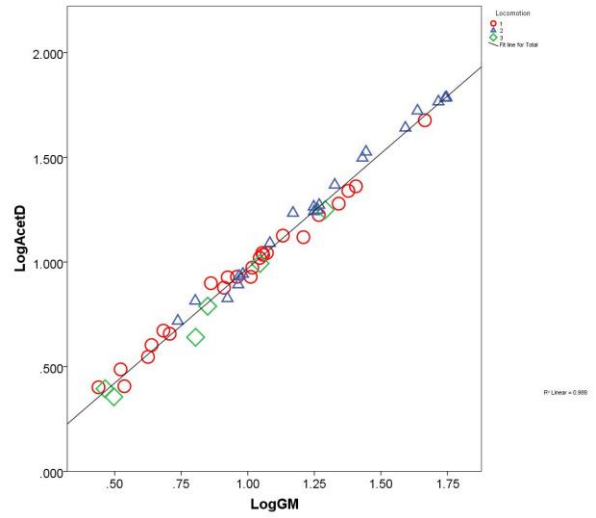
Table 13: Z-scores displaying the influence of allometry on variables identified by the DFAs

Variable	Observed Slope	Std. Error of Slope	Z-Score
PFI	0.006416	0.001203	5.33
HPRI	0.001542	0.000400	3.86
CI	-0.002167	0.000810	-2.68
Isch-Pub	0.010159	0.001513	6.71
Trans_HP	-0.000205	0.000695	-0.29
Trans_AcetD	0.002703	0.000618	4.37

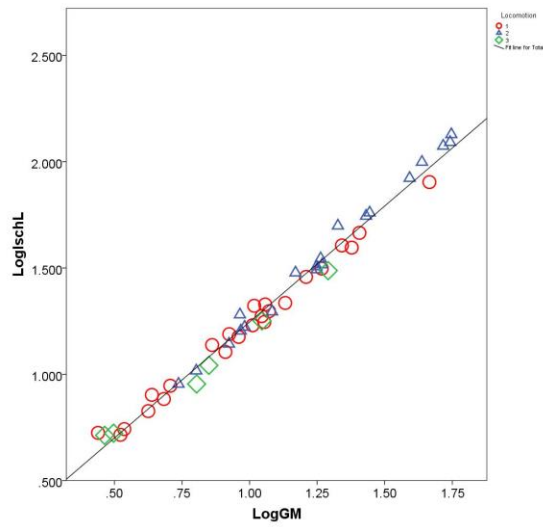
Z-scores were calculated by subtracting the expected slope (0) from the observed slope produced by the least squares linear regressions and dividing this by the standard error of the slope. Z-scores greater than 2 indicate positive allometry, while scores less than -2 indicate negative allometry.



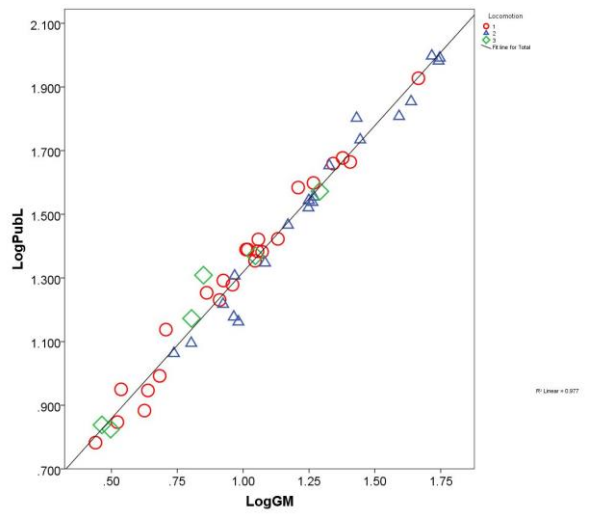
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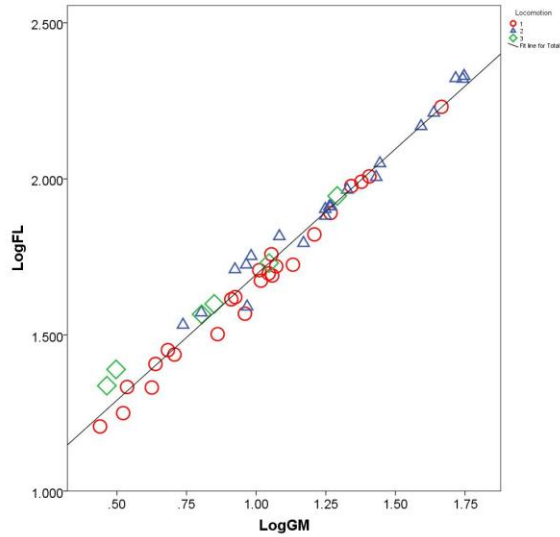
**b**



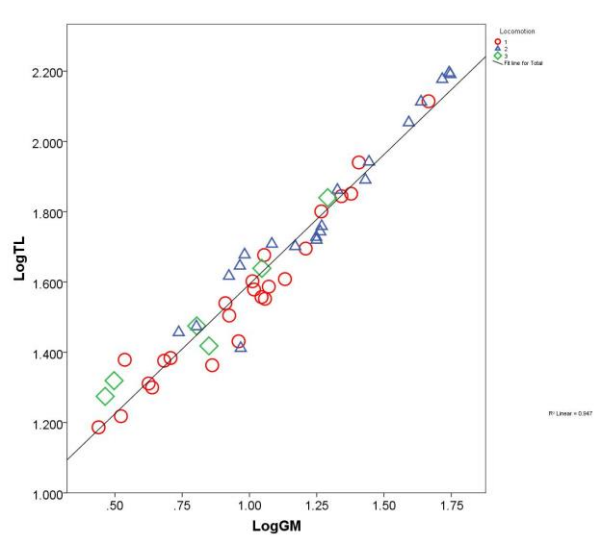
**c**



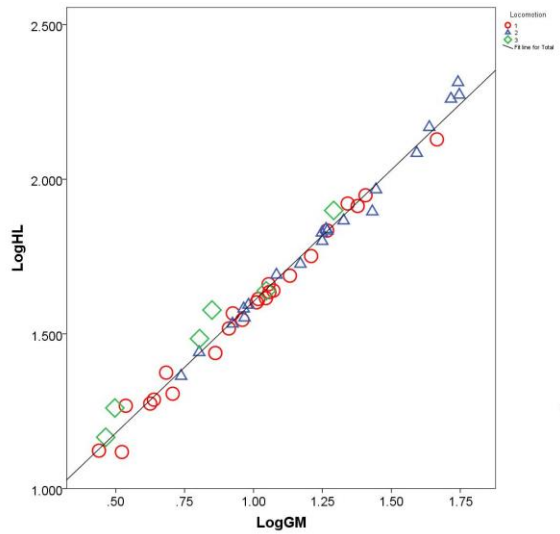
**d**



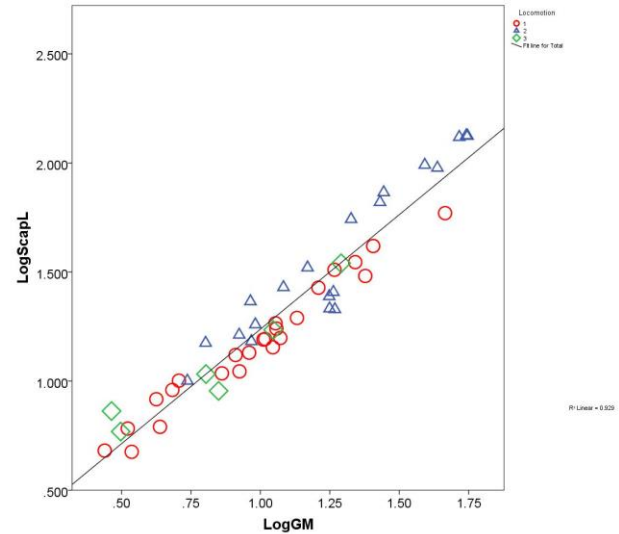
**e**



**f**



**g**



**h**

Figure 6: Log/log plots of variable components that displayed significance within the Indices DFA and the GM DFA

Individual points represent individual specimens included in the analysis. **a**: Humerus proximal breadth. Regression line:  $y = 9.54E-3+0.88*x$ . Standard error of the estimate = 0.056. Correlation coefficient  $r = 0.987$ . **b**: Acetabulum diameter. Regression line:  $y = -0.13+1.1*x$ . Standard error of the estimate = 0.043. Correlation coefficient  $r = 0.994$ . **c**: Ischium length. Regression line:  $y = 0.15+1.09*x$ . Standard error of the estimate = 0.044. Correlation coefficient  $r = 0.993$ . **d**: Pubis length. Regression line:  $y = 0.4+0.92*x$ . Standard error of the estimate = 0.050. Correlation coefficient  $r = 0.988$ . **e**: Femur length. Regression line:  $y = 0.89+0.81*x$ . Standard error of the estimate = 0.044. Correlation coefficient  $r = 0.988$ . **f**: Tibia length. Regression line:  $y = 0.86+0.74*x$ . Standard error of the estimate = 0.061. Correlation coefficient  $r = 0.973$ . **g**:

Humerus length. Regression line:  $y = 0.75 + 0.85 * x$ . Standard error of the estimate = 0.037. Correlation coefficient  $r = 0.993$ . **h**: Scapula length. Regression line:  $y = 0.19 + 1.05 * x$ . Standard error of the estimate = 0.103. Correlation coefficient  $r = 0.964$ .

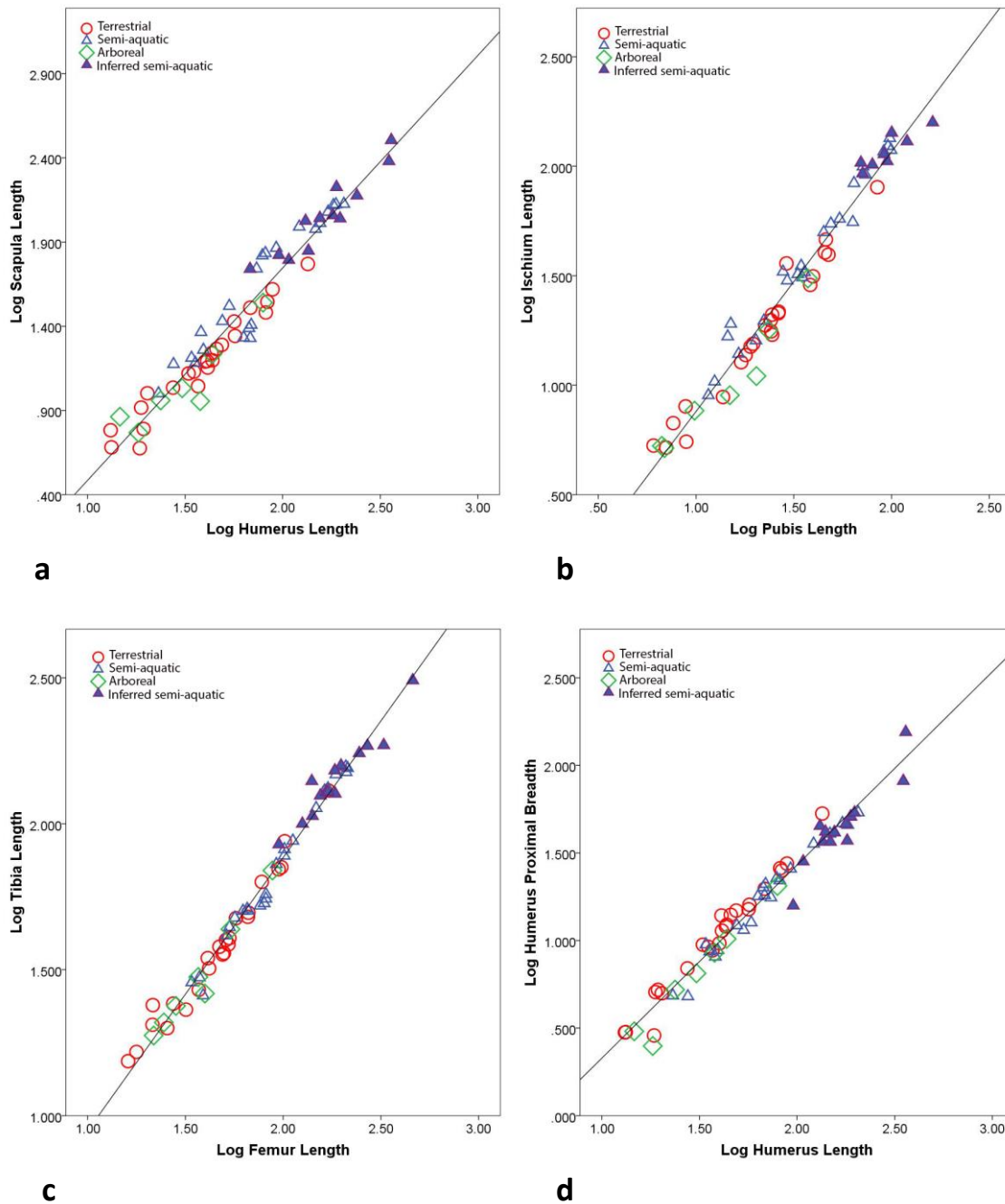


Figure 7: Log/log plots of indices components

The y-axis represents the numerator and the x-axis represents the denominator. Units are in log (mm). **a**: Proximal forelimb index (PFI). Regression line:  $y = -0.78 + 1.26 * x$ . Standard error of the estimate = 0.038. Correlation coefficient  $r = 0.983$ . **b**: Ischium Pubis Index (Isch-Pub). Regression line:  $y = 0.31 + 1.19 * x$ . Standard error of the estimate = 0.027. Correlation coefficient  $r = 0.984$ . **c**:

Crural index (CI). Regression line:  $y = 0.01 + 0.94 * x$ . Standard error of the estimate = 0.015. Correlation coefficient  $r = 0.992$ . **d**: Humeral proximal robustness index (HPRI). Regression line:  $y = 0.77 + 1.1 * x$ . Standard error of the estimate = 0.026. Correlation coefficient  $r = 0.983$ .

### Inferred Locomotor Modes of Extinct Crocodylians

Five of the 18 examined fossil crocodylomorph taxa were classified into a locomotor group by the Indices DFA. All other fossil specimens lacked sufficient fossil material to be grouped. The five taxa presented include *Hyposaurus rogersii*, *Necrosuchus ionensis*, *Alligator* sp. of the Gray Fossil Site, *Crocodylus affinis*, and *Allognathosuchus mooki*. All five were inferred to be semi-aquatic based on their negative values for DF1 within the Indices DFA (Figure 8). These taxa also displayed high probabilities ( $\geq 0.9$ ) of belonging to the semi-aquatic group (Table 14).

Table 14: Indices DFA classification of extinct species

Taxa	Predicted Group	P (D G)	P (G D)
<i>Hyposaurus rogersii</i>	Semi-aquatic	0.717	0.99294
<i>Crocodylus affinis</i>	Semi-aquatic	0.343	0.99736
<i>Allognathosuchus mooki</i>	Semi-aquatic	0.225	0.98436
<i>Necrosuchus ionensis</i>	Semi-aquatic	0.490	0.91964
<i>Alligator</i> sp.	Semi-aquatic	0.390	0.99769

$P(D|G)$  represents the conditional probability of the observed canonical score, given membership in the most likely group.  $P(G|D)$  represents the posterior probability that a case belongs in the predicted group, given the sample used to create the discriminant model (Samuels et al., 2013).

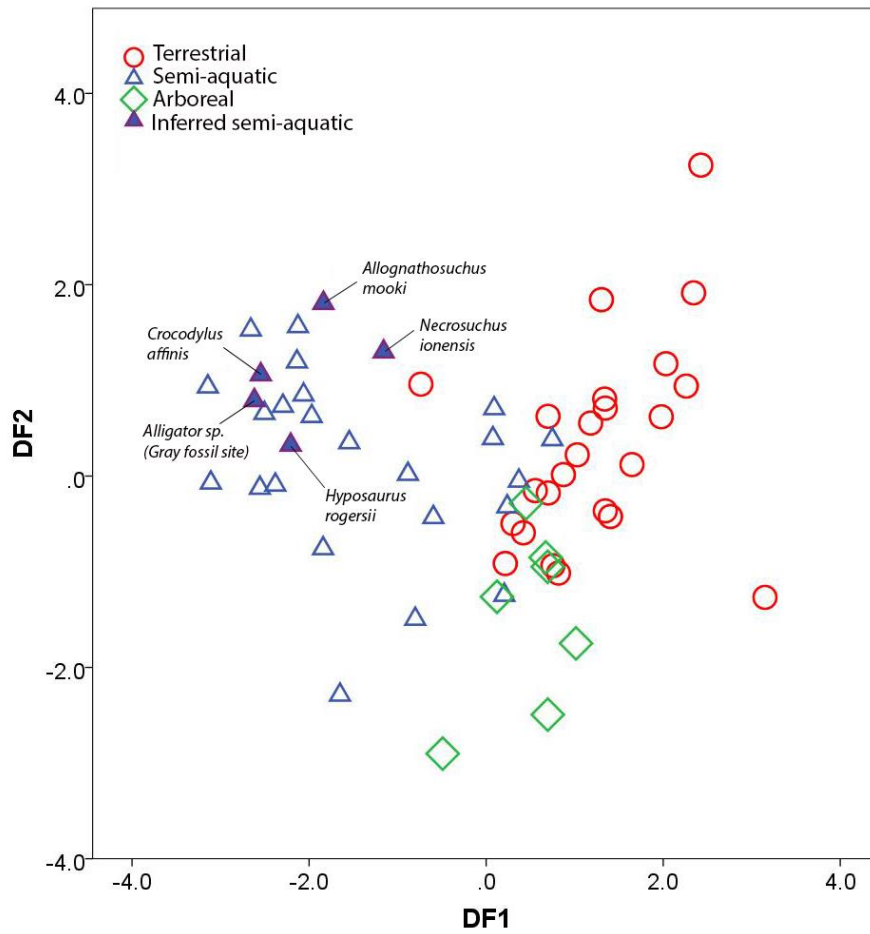


Figure 8: Plot of DF1 and DF2 discriminant scores for the Indices DFA including extinct taxa

## CHAPTER 5

### DISCUSSION

While many modern reptiles are locomotor generalists and display a combination of climbing, swimming, and terrestrial capabilities, there are several examples of species that have developed locomotor specializations. These specializations have evolved independently several times across multiple reptile lineages. Within this study, I found that convergent morphologies are present across reptile taxa utilizing similar locomotor modes, regardless of the distance in their evolutionary relationships. The locomotor groups each display significant morphological differences that allow these groups to be distinguished from one another. These distinctions also allowed for a high rate of success in correctly classifying members belonging to each of these groups.

#### Correlation of Postcranial Morphology with Locomotor Mode in Extant Crocodylians and Lepidosaurus

The statistical analyses conducted within this study revealed multiple features of the postcrania that enable us to differentiate between reptiles engaging in different locomotor behavior. The ANOVA and boxplots (Table 6, Figure 2) emphasize the utility of several of the indices in distinguishing between locomotor groups. The semi-aquatic group appeared to display the most deviations from both of the other two groups, potentially suggesting that semi-aquatic behavior requires more significant morphological adaptations.

Both discriminant function analyses had high degrees of success in distinguishing semi-aquatic taxa from terrestrial and arboreal taxa, however grouping arboreal individuals proved to be more challenging. This may be the result of a limited sample size of arboreal lepidosaurs. In addition, many lepidosaurs are small-bodied generalists and thus are capable of a



combination of scansorial and terrestrial locomotor behaviors without the need for extensive morphological adaptations, which may help to explain the overlap between these groups in morphospace. A more extensive examination of lepidosaur taxa that engage in higher degrees of arboreal behavior, such as chameleons and geckos, may aid in identifying morphological features indicative of this type of locomotion. Future analyses may also incorporate fossorial, saltatorial, and cursorial lepidosaurs to encompass an even broader range of morphological specializations (Vanhooydonck and van Damme 1999; Toro et al. 2004; Verwaijen and van Damme 2007).

The Indices DFA identified a variety of features as potential indicators of semi-aquatic behavior including longer scapulae (indicated by low values for PFI), a more slender proximal humerus (indicated by high values for HPRI) a slightly low crural index, and an elongated ischium (high values for ischium length to pubis length index).

The reduction of the proximal end of the humerus as well as the shortening of the distal hindlimb can aid these animals in holding their limbs close to the body to maintain a more streamlined body shape and thus reduce drag during aquatic locomotion (Stein 1988; Fish 1996; Gingerich 2003; O'Keefe and Carrano 2005). Unlike many aquatic mammals that utilize their limbs as the primary propulsive forces during swimming, reptiles instead tend to use their tails to generate thrust (Webb and Blake 1985). As a result, while several aspects of the limbs of semi-aquatic reptiles tend to be reduced as they do not require a high mechanical advantage, the tails require substantial muscle to drive their locomotion.

One of the muscles that forms the ventral wall of the tails in reptiles is the ilio-ischio-caudalis muscle (Mallison et al. 2015). A large portion of this muscle originates from the distal-

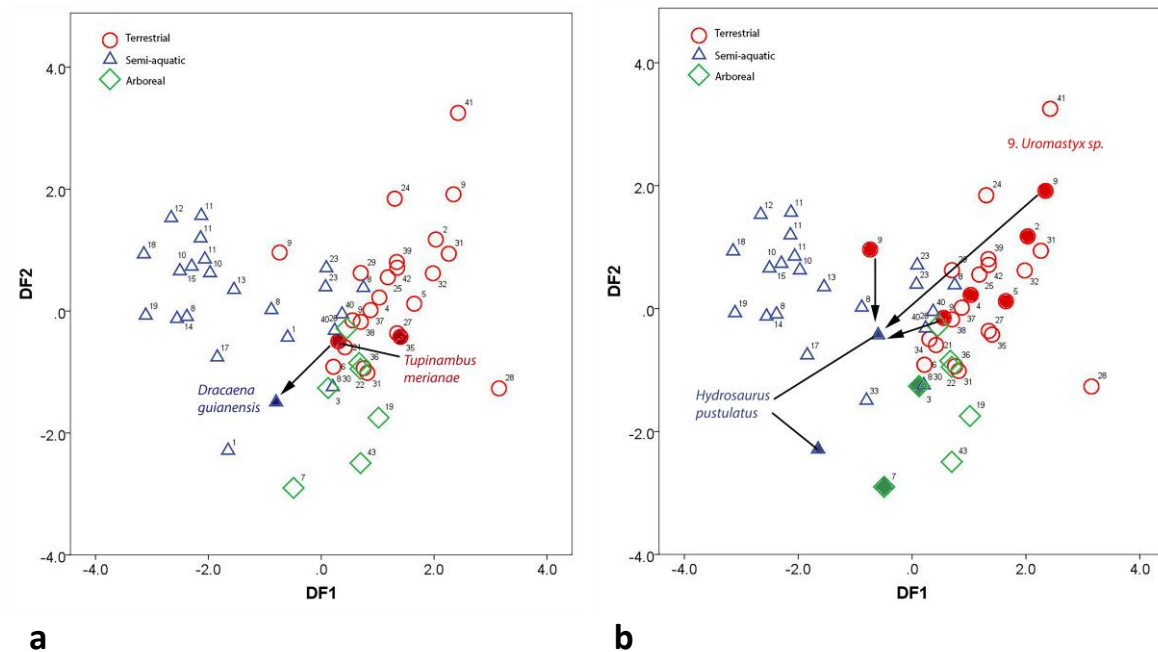
most extent of the ischium and has been found to insert at the transverse processes and hemal spines of the caudal vertebra in several crocodylians (Persons and Currie 2013; Mallison et al. 2015). The larger length of the ischium encountered in semi-aquatic reptiles may be the result of increasing surface area for the attachment of this muscle to produce more powerful mediolateral undulations of the tail while in the water.

While the number of arboreal taxa included within the analysis was limited, certain morphological trends did appear to aid in characterizing the group. Arboreal specimens trended toward a longer, more slender humerus (low value for HPRI), a longer proximal hindlimb (low crural index), and a longer pubis (low value for Isch-Pub). The extended length of the proximal forelimb and hindlimb in arboreal taxa can allow for a longer reach while moving through branches of trees, while the more narrow proximal end of the humerus may indicate an overall thinner bone to promote speed and flexibility rather than supporting heavy muscle mass. A longer pubis relative to ischium length may be a manner of repositioning the center of gravity toward the center of the body to maintain better stability while climbing. It is important to note that while both semi-aquatic and arboreal taxa exhibit proximal reduction of the humerus, this adaptation is serving very different purposes in their locomotor behavior and thus should be examined with caution when inferring locomotor behaviors.

The GM DFA also identified semi-aquatic taxa as having a more gracile proximal humerus as well as a larger acetabulum diameter in comparison to terrestrial and arboreal reptiles. The broad acetabulum diameter encountered in semi-aquatic taxa may serve as an adaptation to improve terrestrial locomotion despite the group's many adaptations to movement in the water. This larger acetabulum may accommodate a larger femoral head that

provides semi-aquatic taxa with more structural stability when carrying the weight of their heavily muscled tails during movement on land. Willey et al. (2003) found that the center of gravity of an alligator is focused closer to the hip than the shoulder joint. This may explain why we encounter proximal shortening in the forelimbs of semi-aquatic taxa, but relative distal shortening in the hindlimbs. The femur likely needs to remain a relatively significant size to be able to support the weight of a heavy, muscularized tail when on land compared to terrestrial taxa that have less musculature in that area.

Assessment of Convergence in Lepidosaurs and Crocodylians



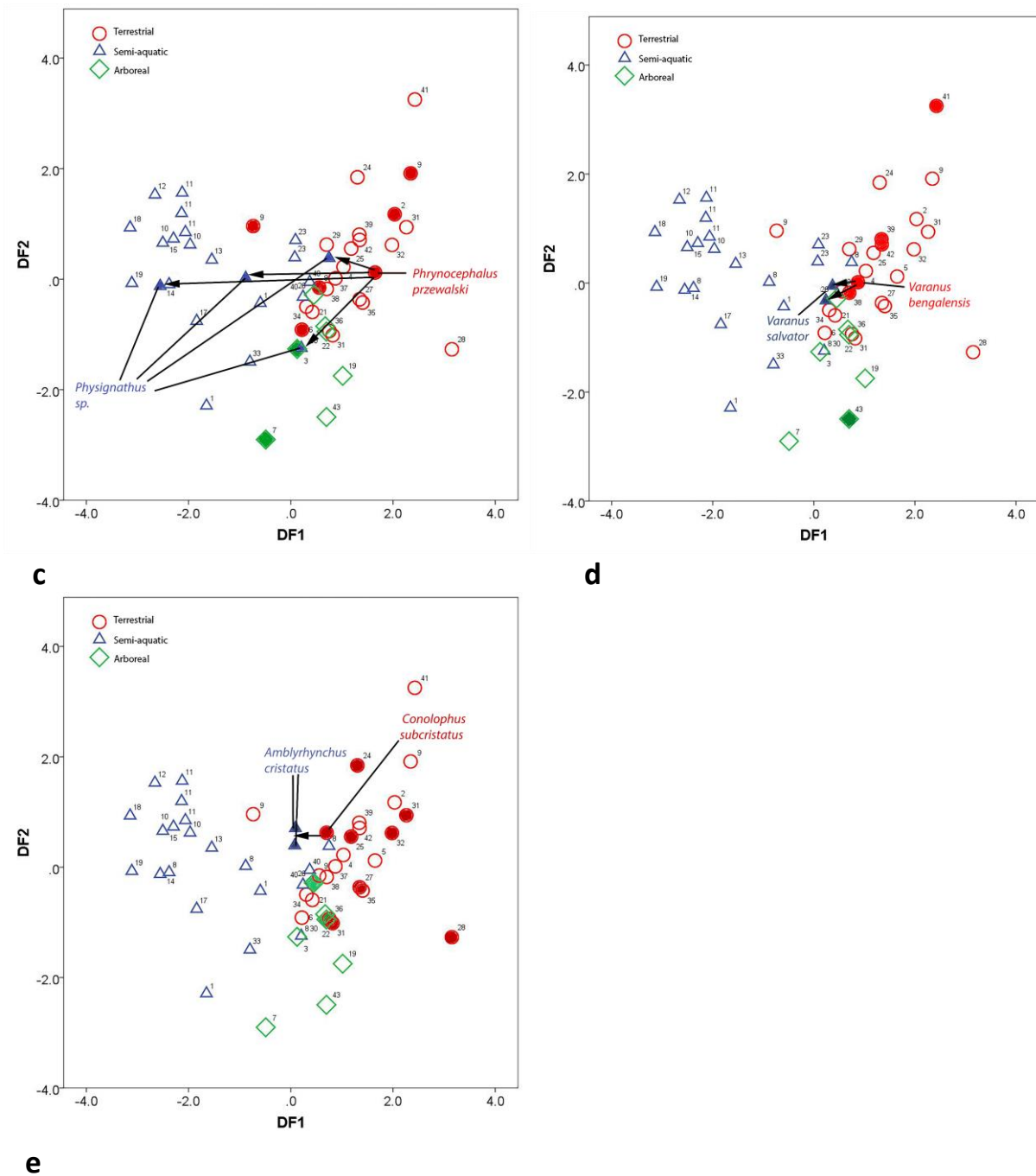


Figure 9: Plots of DF1 and DF2 scores for extant reptile taxa analyzed in the Indices DFA

Plots used to highlight divergence of semi-aquatic lepidosaur taxa from their terrestrial relatives. Within each plot, members belonging to the same family are represented by filled-in symbols. Arrows display the general direction of divergence in morphospace of semi-aquatic taxa from their closest terrestrial relative examined within the analysis. Relationships between taxa can be viewed in the phylogenies displayed in Figure 10. **a:** Teiidae; **b:** Agamidae,

*Hydrosaurus pustulatus*; **c.** *Agamidae*, *Physignathus* sp.; **d.** *Varanidae*; **e.** *Iguanidae*

Several semi-aquatic lepidosaur taxa examined within this analysis appear to display convergence of morphological features with similarly semi-aquatic crocodylians. Members of *Agamidae*, *Iguanidae*, *Teiidae*, and *Varanidae* diverge in a similar direction from their terrestrial relatives.

*Dracaena guianensis*, the northern caiman lizard (*Teiidae*), was correctly classified as semi-aquatic, displaying a clear divergence in morphology from its terrestrial relatives (Figure 9a). Two specimens of *Hydrosaurus pustulatus*, the Phillipine sailfin lizard (*Agamidae*), were also correctly classified as semi-aquatic (Figure 9b). Out of four total *Physignathus* specimens, two properly classified as semi-aquatic while one misclassified as terrestrial and the other as arboreal. Specimens that were incorrectly classified, such as these two *Physignathus*, still displayed a divergence from the centroid in the same direction as other semi-aquatic taxa (Figure 9c). Both specimens of *Amblyrhynchus cristatus* and *Varanus salvator* were also misclassified as terrestrial; however, these specimens had relatively low discriminant scores for function one, trending closer toward the more negative scores characteristic of other semi-aquatic taxa (Figures 9d and 9e). Within the Indices DFA, one example of *Uromastyx* sp. is the only specimen to have misclassified as semi-aquatic. This taxon displays burrowing behavior (Nemtzov 2005) and suggests the future incorporation of a separate locomotor group for fossorial taxa could aid in discrimination of similar taxa.

The misclassification of several semi-aquatic lepidosaurs may be explained by an influence of allometry on semi-aquatic taxa. Figure 10 displays a plot of the specimens' discriminant function scores relative to their body size measured by the geometric mean. Both

the terrestrial and arboreal groups have only slightly sloping lines and their z-scores are not significant (Table 15), indicating overall isometric growth. The semi-aquatic group, however, displays a clear negative slope and a z-score lower than -2 (Table 15) which indicates a significant deviation from isometry. With increases in body size come lower discriminant function scores as semi-aquatic adaptations appear to become more pronounced. Within the group of sampled *Physignathus* specimens, the two smaller individuals are those that misclassified while the larger specimens correctly classified as semi-aquatic. This may be related to larger individuals requiring more well-developed semi-aquatic adaptations.

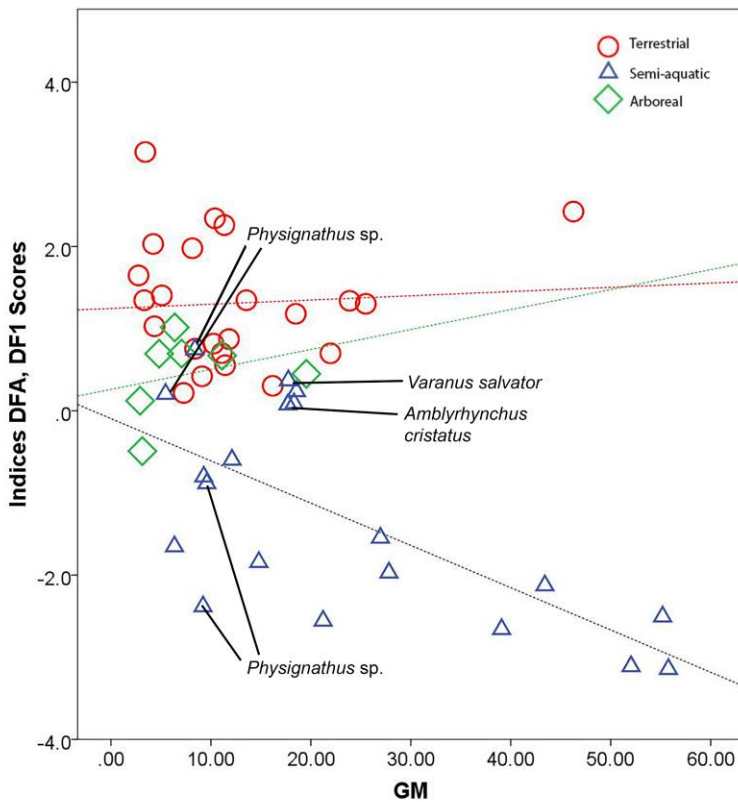


Figure 10: Plot of geometric mean versus DF1 scores of the Indices DFA

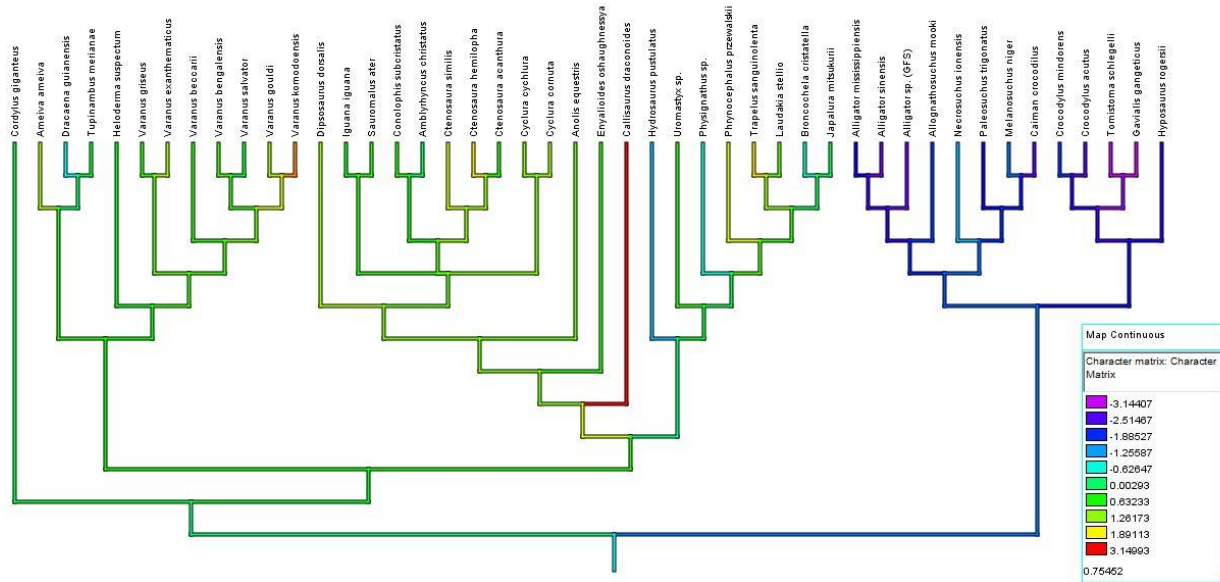
Terrestrial fit line (red dashed):  $y=1.25+5.14E-3*x$ . Semi-aquatic fit line (blue dashed):  $y=-0.1-0.05*x$ . Arboreal fit line (green dashed):  $y=0.26+0.02*x$ .

Table 15: Z-scores displaying the influence of allometry on different locomotor groups

<b>Locomotor Group</b>	<b>Observed Slope</b>	<b>Std. Error of Slope</b>	<b>Z-Score</b>
Terrestrial	0.005144	0.016955	0.303
Semi-aquatic	-0.051461	0.013197	-3.899
Arboreal	0.024289	0.036333	0.669

*Z-scores were calculated by subtracting the expected slope (0) from the observed slope produced by the least squares linear regressions and dividing this by the standard error of the slope. Z-scores greater than 2 indicate positive allometry, while scores less than -2 indicate negative allometry.*

A)



B)

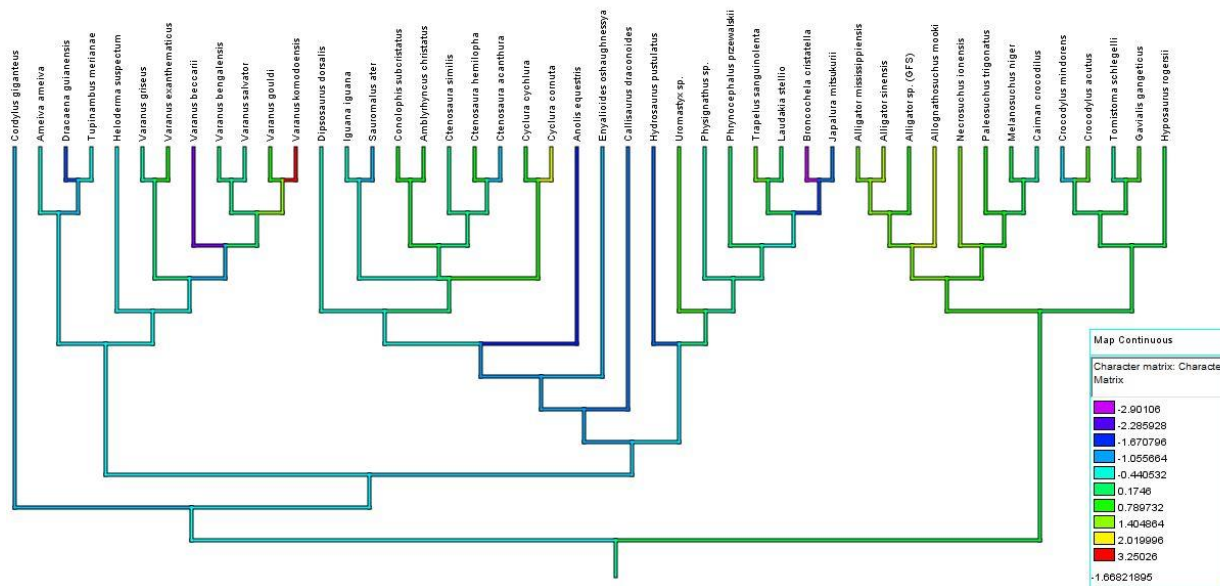


Figure 11: Composite phylogenetic tree of reptile species included within the study

Based on molecular and morphological analyses (Nesbitt, 2011; Bronzati et al., 2012; Pyron et al, 2013; Tucker et al., 2017). Branch colors represent discriminant function scores. **a**: Indices DF1 scores; **b**: Indices DF2 scores



## Applications for Analyzing Locomotor Diversity of Extinct Reptiles

Although several past studies have qualitatively examined the morphologies of extinct crocodylomorphs in order to determine their primary locomotor capabilities (Clark et al. 2004; Kellner et al. 2014; Blanco et al. 2015), this study has provided a unique quantitative assessment of morphological variation in extant reptile groups that can aid in more accurately interpreting the behavior and ecologies of fossil taxa. Fossil crocodylomorphs with morphologies that fall within the range of modern semi-aquatic taxa determined by these analyses were likely engaging in a very similar form of semi-aquatic behavior. There is no ideal modern analog for extinct crocodylomorph taxa, which are interpreted as engaging in higher degrees of terrestrial behavior as indicated by the presence of a more upright posture with legs oriented underneath the body versus the sprawled posture of extant terrestrial lepidosaurs. Despite this, the current ecomorphological framework would enable me to more easily determine if particular extinct species were utilizing a different form of locomotion, based on how similar they are to the morphospace ranges of modern groups.

The primary limitations of this study lie in a frequent lack of postcranial material for extinct specimens. Access to more complete specimens of extinct species and expansion into other groups of pseudosuchians, such as aetosaurs, would aid in inferring their locomotor modes and developing a more complete understanding of locomotor transitions in archosaurs through time.

All of the fossil crocodylomorphs included within this analysis classified as semi-aquatic and fall relatively closely within the range of modern semi-aquatic reptiles (Figure 8). *Alligator* sp. of the Gray Fossil Site, *Allognathosuchus mooki*, and *Necrosuchus ionensis* all group within

Alligatoridae and *Crocodylus affinis* belongs to Crocodylidae (Simpson 1930; Brochu 2011; Puértolas et al. 2011). These two families both span over 50 million years and still have living members today. My results indicate that even early members of these families, such as *Allognathosuchus mooki* and *Necrosuchus ionensis* from the Paleocene and *Crocodylus affinis* of the Eocene, were doing similar semi-aquatic behavior to more recent extinct taxa such as the Mio-Pliocene *Alligator* from the Gray Fossil Site and even modern crocodylian species.

Of the five fossil taxa that were classified, *Hyposaurus rogersii* (Family Dyrosauridae) displayed the highest value for P (D|G) (Table 14), indicating it falls close to the centroid of the modern semi-aquatic group. Initial studies of *Hyposaurus rogersii* suggested that the species was largely marine, likely coming on land only to reproduce (Troxell 1925). More recent studies, however, have drawn attention to the well-developed limb morphology present in this species which potentially indicates terrestrial ancestry or a higher degree of terrestrial behavior than previously hypothesized (Denton Jr. et al., 1997). Specimens of this species have also been found in both marine and shallow subtidal environments. My results indicate that *Hyposaurus rogersii* displays distinct morphological similarities to extant semi-aquatic taxa, thus supporting more recent analyses that this species was engaging in a combination of both aquatic and terrestrial behavior similar to modern semi-aquatic reptiles.

While this study focused on examining extinct crocodylomorph taxa, these results have much broader potential applications. Phytosaurs, for example, display highly convergent morphologies with crocodylians and thus may have similarly identifiable aquatic or terrestrial adaptations. Examination of early archosaurs like *Euparkeria* could also help reveal the ancestral condition for that clade. Fossils of lepidosaurs may be examined as well to interpret

their primary locomotor modes and gain a better understanding of the evolution of the wide diversity of locomotor behavior that we see within the clade today. Today's reptiles also bear distinct similarities to early amniotes; therefore, they may be able to act as a modern analog for early amniotes and reptiles, including well-known species like *Seymouria*, *Hylonomus*, and *Petrolacosaurus*, and also the early synapsids like pelycosaurs. Through the use of broader taxonomic sampling across groups such as chameleons, geckos, and phrynostomatids, we can span an even wider range of locomotor modes (fossorial, saltatorial, cursorial) and potentially identify shifts in predominant locomotor adaptations in these groups through time that could be the result of ecological shifts connected to the first transitions from life in water to life on land.

## CHAPTER 6

### CONCLUSIONS

Through the use of simple linear morphometric analysis, I have determined that several features of the axial and appendicular skeleton reflect the locomotor modes of extant reptiles. Semi-aquatic species across both Crocodylia and Lepidosauria display convergent morphologies that reflect their similar locomotor adaptations despite significant phylogenetic separation between the groups. These methods may then be applied to extinct reptile groups to make more objective inferences of their past locomotor behavior based on quantitative analyses. Future expansion of this study into additional locomotor groups and reptile taxa may reveal other postcranial adaptations to these behaviors that will allow us to better understand the evolution of locomotion in this clade and examine the shifts in ecosystems through time that likely drove these changes.

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