

FUNCTION AND EVOLUTION OF THE CROCODYLIFORM FEEDING
APPARATUS

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APPARATUS

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Dedication

For Mom. And the rest of my family.

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Abstract

The evolution of crocodylians from their suchian ancestors represents one of the great transformations in vertebrate evolution. Modern crocodylians have flat skulls and generate high forces during feeding, but crocodylian ancestors have tall skulls and lack most of the characters that help crocodylians generate and resist high forces. Thus, the evolution of crocodylians involved a substantial reorganization of the feeding apparatus. Although changes to skull shape in the lineage leading to crocodylians have received a great deal of attention, the functional consequences of shape change on feeding biomechanics are unclear. This dissertation addresses this gap in our knowledge by building high-fidelity biomechanical models to ask questions about the evolution of skull shape and feeding performance in the lineage leading from early suchians to extant crocodylians. I use detailed 3D muscle attachment sites to estimate muscle forces and distribute forces on 3D finite element models using an approach validated against *in vivo* data. These finite element models are used to estimate bite and joint forces. I use traditional linear morphometrics to characterize skull flattening. I also develop novel methods to quantify and visualize joint articular surface shape. These results are analyzed using phylogenetic comparative methods and ancestral character state reconstruction. My results show that skull flatness is linked with inefficient muscle geometries and that these geometries developed stepwise in the lineage leading to crocodylians. I found that joint shape best reflects the highest-magnitude loads that the skull experiences, that the orientation of joint loading tracks with skull flatness, and that peak joint pressure falls within the range predicted by chondral modeling. This study shows

that extant crocodylians rely on extra muscle mass to produce high bite force with inefficient muscle configurations and that the derived, suturally-immobilized cranial joints are key features of the feeding apparatus that mitigate mechanical inefficiencies imposed by a flat skull. Overall, these results depict a coordinated evolution of skull shape, muscle anatomy, joint surface shape, and biomechanical performance in the lineage leading to Crocodylia and have broad implications and applicability to all vertebrate musculoskeletal systems. This dissertation research represents an important step in improving our understanding of the biomechanics of musculoskeletal transitions.

Chapter 1— Introduction

Cranial Function in Vertebrate Feeding

Feeding is one of the most crucial tasks that vertebrates must perform and thus the feeding apparatus is thought to be under immense selective pressure (Dumont et al., 2009; Santana, Dumont and Davis, 2010). In vertebrates, the feeding apparatus is usually centered around the jaws, and the jaw muscles spanning from cranium to mandible are key drivers of the feeding apparatus and provide the input force to be applied to food. The functional and ecological correlates of muscular variation are best known in mammals (Maynard Smith and Savage, 1959; Hylander et al., 2000; Herring, 2007; Ross, Dharia, et al., 2007; Santana, Dumont and Davis, 2010; Santana, Grosse and Dumont, 2012), and investigations of variation in muscular configurations between herbivores and carnivores have revealed key differences between these dietary extremes. Most mammalian herbivores masticate food with a transverse power stroke (Hylander et al., 2005; Ross, Dharia, et al., 2007; Ross, Eckhardt, et al., 2007), and thus the main muscles of mastication are the mediolaterally- pulling masseter and pterygoid. The craniomandibular articulation is elevated above the toothrow by a mandibular condyle (Maynard Smith and Savage, 1959), which affords these muscles with higher mechanical advantage (Maynard Smith and Savage, 1959; Greaves, 1974, 1980). In mammalian carnivores, by contrast, the teeth are designed to shear by sliding past each other dorsoventrally. In such animals, the temporalis muscle is dominant, and it attaches to the mandible above the toothrow via a large coronoid process (Greaves, 1974, 1980; Maynard Smith and Savage, 1959).

Muscles pulling on the jaw often load the jaw joint. During biting, conditions of static equilibrium must be met, and thus all muscle forces acting on the mandible must be resisted by either the food, generating bite force, or by the cranium, generating joint force. In the optimal system, the mandible would channel all of muscle force into food items and act as a link (Hylander, 1975; Gingerich, 1979). However, geometric constraints generally preclude this arrangement, and thus some of muscle force must be resisted by the craniomandibular joint, forcing the mandible to act as a lever. When the mandible acts as a lever, the craniomandibular articulation is loaded compressively because the jaw elevator muscles pull the mandibles against the cranium. Some authors have noted the possibility of unilateral bites in caudal teeth leading to tensile loads at the jaw joint (Bramble, 1978; Greaves, 1978; Crompton and Hylander, 1986; Hylander, 1992; Herring, 2003). In mammals, it is assumed that tensile loading is deleterious to feeding function, as this could result in the mandible being pulled away from the cranium and preventing precise occlusion or permitting a prey item to escape. Thus, some authors have suggested that mammals will differentially recruit jaw muscles to avoid tension (Greaves, 1978, 1995; Hylander, 1975) or use ligaments or the fibrous joint capsule to resist excessive excursion due to tension (Hylander, 1979).

Cranial joint morphology reflects the movement and loading that occur during joint use (Du Brul, 1964; Herring, 2003; Terhune, 2013; Dunn *et al.*, 2014). Compressive joint reaction forces are generated by the traction of one element into another. In joints that allow movement, an oblique joint force could cause

movement. Joints which prevent movement have articular surfaces oriented perpendicular to the restricted direction, whereas an absence of articular surface in an orientation suggests the possibility of joint movement (Herring, 2003). Mammalian herbivores tend to have broad, open craniomandibular articulations. Such joints permit the transverse mandibular movements key to herbivorous oral processing (Maynard Smith and Savage, 1959; Herring, 2003). Similarly, the glenoid fossa of rodents is rostrocaudally- extended, which permits the propalinal mandibular movement characteristic of this group (Herring, 2003). On the other hand, in carnivores, the cranial portion of this joint wraps tightly around the mandibular condyle. This congruent arrangement lets the cranium resist mandibular dislocation caused by the unpredictable forces imposed by struggling prey (Hylander, 2006). Differences in cranial joint morphology provide insights into ecological and functional differences between taxa, and thus changes to joint loading should be reflected in joint morphology.

Major Transitions to the Crocodyliform Skull

Modern crocodylians have extreme feeding performance, subjecting the skulls to tremendous biomechanical loads during feeding (Erickson, Lappin and Vliet, 2003; Fish *et al.*, 2007; Erickson *et al.*, 2012). Correspondingly, many derived features found in crocodylian skulls are associated with generating and resisting large forces (Langston, 1973; Busbey, 1995; Clark *et al.*, 2004; Pol *et al.*, 2013). Cranial strength is afforded by (1) sutural immobilization of the palate and quadrate to the braincase and dermal roof (Langston, 1973; Busbey, 1995; Clark *et al.*, 2004; Metzger, Ross and Spencer, 2004; McHenry *et al.*, 2006; Holliday and Nesbitt, 2013; Pol *et al.*, 2013) and (2) the acquisition of a novel

stabilizing craniomandibular articulation (Iordansky, 1973; Langston, 1973; Busbey, 1995). Bite force is increased by large adductor muscles and novel attachment points including the lateral mandible (Clark *et al.*, 2004). Some studies have suggested that the primary jaw joint may be loaded under tension (Metzger *et al.*, 2004; Sellers *et al.*, 2016), which may be a means of increasing bite force and lowering joint force. This loading pattern may explain the relative increase in the size of the depressor mandibulae muscle and accompanying large retroarticular process.

Crocodylians are often regarded as primitive “living fossils” that are unchanged since the group originated. However, modern crocodylians are the only remaining representatives of a diverse group of suchians called crocodyliforms. The crocodyliform radiation gave included a diverse array of forms with derived skulls and trophic ecologies, often iteratively, including durophagous forms with short rostra and large teeth (Carpenter and Lindsey, 1980), herbivory with oral processing and complex multi-cusped teeth (Clark, Jacobs and Downs, 1989; Ősi, Clark and Weishampel, 2007; Ősi, 2008, 2014; Ősi and Weishampel, 2009; Pol *et al.*, 2014), piscivory found both today and in the past (Young *et al.*, 2010), terrestrial hypercarnivores (Carvalho, Arruda Campos and Henrique Nobre, 2005; Turner and Buckley, 2008), generalist aquatic ambush predators (Ősi, 2014), and forms with no extant analog and unclear trophic strategies (Bona, Degrange and Fernández, 2013). The evolutionary radiation of crocodyliforms has been linked with the taxon’s derived skull (Langston, 1973; Pol *et al.*, 2013). However, the biomechanical

relationships between modifications to the skull, changes in feeding performance, force resistance, and changes to ecology are unclear, which hampers our ability to test hypotheses relating the acquisition of biomechanically- salient innovations and evolution.

Basal suchians possessed skulls like those of stem archosaurs (Figure 1.1). The snout was not flattened and bore the antorbital fenestra typical of archosaurs. Caudally, the skull was dorsoventrally tall (Ewer, 1965). The quadrate proximally articulated with the squamosal and opisthotic in an open otic joint, but the prootic was excluded from this articulation (Mastrantonio et al., 2013). Distally, the quadrate articulated with the articular with two condyles; this articulation was nearly directly ventral to quadrate's articulation with the skull roof, and thus the quadrate was vertically oriented (Figure 1.1). The ventral braincase bore basiptyergoid processes that articulated with the pterygoids in an open palatobasal joint (Figure 1.2; Ewer, 1965). The retroarticular process was relatively small, limiting the maximum size of the depressor mandibulae insertion and constraining its orientation. This process was separated from the articular surface of the articular by a concavity (Ewer, 1965; Nesbitt, 2011). The pterygoid had a vertical quadrate ramus and may have served as the origin for protractor musculature (Ewer, 1965). Although clearly carnivorous, fossils preserve jaw muscle attachments that are broadly typical; neither the temporal muscles nor pterygoid muscles were clearly hypertrophied at the expense of the other (Ewer, 1965). An epiptyergoid united the skull roof and palate (Ewer, 1965).

From this primitive condition, ancestors of crocodylians acquired numerous traits that strengthen the skull and jaw muscles. Until relatively recently, these modifications were thought to have taken place in two steps: once before the origin of Crocodyliformes and once before the origin of Mesoeucrocodylia (Langston, 1973; Clark, 1994). However, recent discoveries of Jurassic “sphenosuchians” such as *Junggarsuchus* and *Almadasuchus* have revealed a mosaic pattern of character acquisition (Clark et al., 2004; Pol et al., 2013; Figure 1.1).

Jaw Muscles— Jaw muscles are a key feature of the vertebrate skull (Holliday, 2009) and are critical for understanding the function of the feeding apparatus. Despite this, a phylogenetically- rigorous reconstruction of suchian jaw muscles has not been attempted. Both geometric and functional concerns altered jaw muscles’ configuration during the transition to crocodyliforms. Cranial widening and flattening at the base of Crocodyliformes led to a reorientation of the jaw muscles. Lateral expansion of the dermal roof and suspensorium shifted jaw muscles into mediolateral orientations (Figure 1.3). Crocodyliforms also have an expanded retroarticular process (Figure 1.4), which expands the size of the depressor mandibulae muscle and gives it a more rostrocaudal orientation.

The pterygoid muscles were also highly modified; the dorsal pterygoid muscle acquired a novel rostral attachment in the caviconchal fossae, interorbital septum, and palatal fenestrae. A specialized ventral belly attaching to the caudolateral surface of the angular bone appeared (Figure 1.4), whose action would tense the quadratoarticular joint, and the expansion of the retroarticular

process suggests an increase in the ability of depressor mandibulae to resist such tension. This resulted in the ventral pterygoid muscle pulling ventrally on the mandible, which likely tenses the jaw joint, possibly accounting for the larger mDM muscle.

Cranial Joints— Along with powerful jaw muscles, crocodyliforms also have strong, rigid skulls afforded by the sutural immobilization of numerous cranial joints. The otic joint was the first to be immobilized. Originally, this was thought to be a crocodyliform synapomorphy (Clark, 1994), but recent discoveries have shown that two derived spheosuchians, *Junggarsuchus* and *Almadasuchus*, sutured the exoccipitals to the distal quadrate (Clark *et al.*, 2004; Pol *et al.*, 2013). The quadrate contacting the basisphenoid was also previously thought to separate crocodyliforms from other crocodylomorphs, but *Almadasuchus* has a pneumatically- inflated basisphenoid that contacts the quadrate (Pol *et al.*, 2013). The otic joint is further reinforced in mesoeucrocodylians, in which the paraoccipital processes of the exoccipitals form a broad sutural contact with the caudal and dorsal surface of the quadrate (Langston, 1973; Figure 1.1).

Changes to the palate followed the immobilization of the quadrate. A suturally- closed palatobasal joint is a crocodyliform synapomorphy (Langston, 1973), but again, recent fossil discoveries have revealed a more complicated pattern. The pterygoids were sutured to the basisphenoid in *Almadasuchus* and in crocodyliforms, and the basiptyergoid processes were lost (Gow, 2000; Pol *et al.*, 2013), precluding movement between the palate and braincase. The pterygoids formed a midline sutural contact with each other, lending further

stability (Sereno and Larsson, 2009). The pterygoids also expanded ventrolaterally to form the pterygoid buttress (Iordansky, 1973; Langston, 1973; Schumacher, 1973). The stability afforded by a closed palatobasal joint and midline pterygoid contact was likely necessary for the evolution of the pterygoid function of stabilizing the mandibles and preventing medial excursion.

The quadrate of crocodyliforms is rotated such that the distal (condylar) portion is caudolaterally tilted with respect to the cranium (Figure 1.5; Busbey, 1989; Langston, 1973; Ortega et al., 2000). Clark et al. (2004) noted that *Junggarsuchus* had sloped quadrates, but in the more primitive crocodylomorph *Sphenosuchus*, Walker (1990) describes the quadrates as “not greatly inclined” (p. 8). Langston (1973) cites a “strongly inclined” (p. 265) quadrate as an apomorphy of what is now termed Crocodyliformes (Figure 1.1). Ortega et al. (2000) cite all studied crocodyliforms as having quadrates sloped “more than 45 degrees”. Some authors have interpreted the rotation of the quadrate in biomechanical terms, noting that the caudal displacement of the quadratoarticular joint increased the moment arm of some of the jaw muscles in producing jaw elevation (Iordansky, 1973; Walker, 1990; Wilberg, 2012); other authors have seen this as an adaptation for aquatic ambush predation (Iordansky, 1973; Grigg and Kirshner, 2015). In mesoeucrocodylians, the caudal rotation of the quadrate results in a dorsoventrally- compressed skull. Intriguingly, some notosuchians have reversed the rotation of the quadrate and placed the quadrate condyle directly ventral to the otic joint (Wilberg, 2012). In early crocodyliforms, changes to the suspensorium flattened the caudal skull but left

the rostrum relatively unmodified. However, in neosuchians, the group of crocodyliforms that includes extant Crocodylia and their closest relatives (Figure 1.1; Figure 1.2), the rostrum was also flattened (Wilberg, 2012). In these forms, the joints within the rostrum were generally broadened (“scarf joints”), the secondary palate was more extensive, and the pterygoid buttresses were greatly expanded. The lateral tilt of the quadrate widened the caudal skull, and the squamosals and parietals expanded mediolaterally to accommodate, which led to a mediolaterally- wide skull (Busbey, 1995).

Outline of Research Objectives

Chapter 2— In Chapter 2, I reconstruct muscle anatomy in select suchians characterizing the transition from early suchians to crown Crocodylians. I develop simple, easily obtained linear measurements to characterize skull size and skull flatness and use these metrics to along with reconstructed muscle anatomy to investigate the relationship between skull flattening and muscle orientation. I also investigate the relationship between the orientation of muscles and the among of muscle mass to test the hypothesis that inefficient muscle configurations in advanced suchians (e.g., crocodylians) are offset by larger overall muscle masses. This work will contribute to our understanding of the coevolution of skull flatness and muscle geometry in suchians. The results also highlight how competing functional demands can sculpt vertebrate cranial morphology and illustrate one way in which evolution can circumvent these limitations.

Chapter 3— In Chapter 3, I create high-fidelity 3D biomechanical models of select suchian skulls and use these models to calculate bite and joint force. I integrate these results with novel methods to quantify the articular surface

morphology of the jaw joint to test the hypothesis that joint shape reflects joint loading. This is, to my knowledge, the first study to quantitatively link joint shape and joint loading. This work will have implications for future investigations into the correspondence of joint articular surfaces and loading environments and will be useful for paleontologists interested in estimating biomechanical parameters from isolated elements.

Chapter 4— In Chapter 4, I integrate the results from previous chapters and use phylogenetic comparative methods to determine how crocodylians can deliver high bite forces with inefficient muscular geometry. I identify key character transitions in the evolution of the lineage leading to extant crocodylians that mitigate inefficient muscle anatomy. This work illustrates the biomechanical evolution of one of the great transformations of vertebrate evolution and opens the door to many promising avenues of future research.

Figure 1.1. Cladogram of Suchia showing specimens used for the present study. A) Suchia, B) Loricata, C) Crocodylomorpha, D) Crocodyliformes, E) Metasuchia, D) Crocodylia, F) Crocodylia, G) Alligatoridae, H) Crocodylidae.

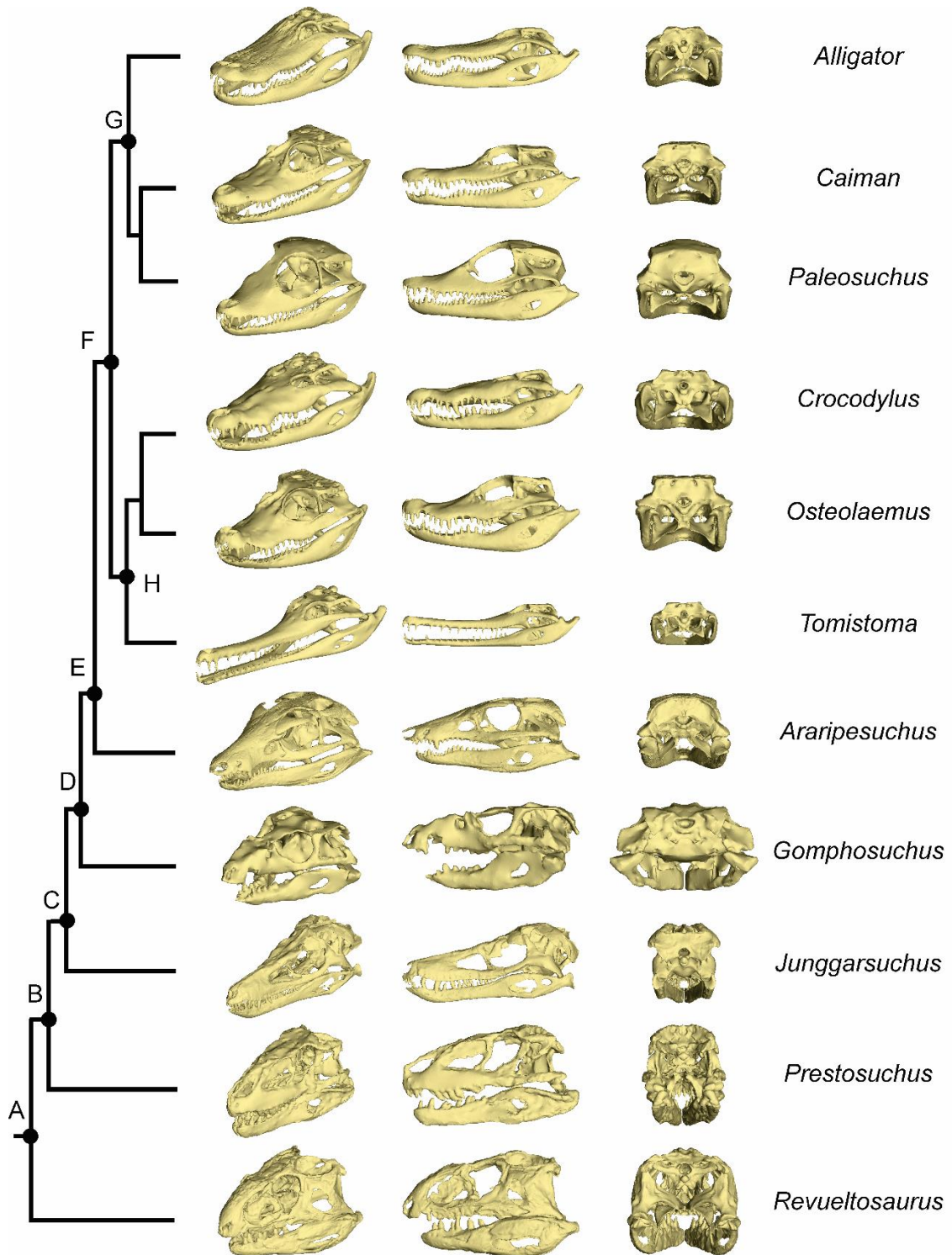


Figure 1.2. Above, Left lateral views of (left) *Prestosuchus* and (right) *Alligator*; vertical line shows slice locations. Below, caudal views of same taxa. The right half of each lower image shows an axial section of the skull through the palatobasal joint. Arrowhead indicates the palatobasal joint. Note the open joint status conferred by a condylar morphology in *Prestosuchus* and the closed sutural morphology of this joint in *Alligator*.

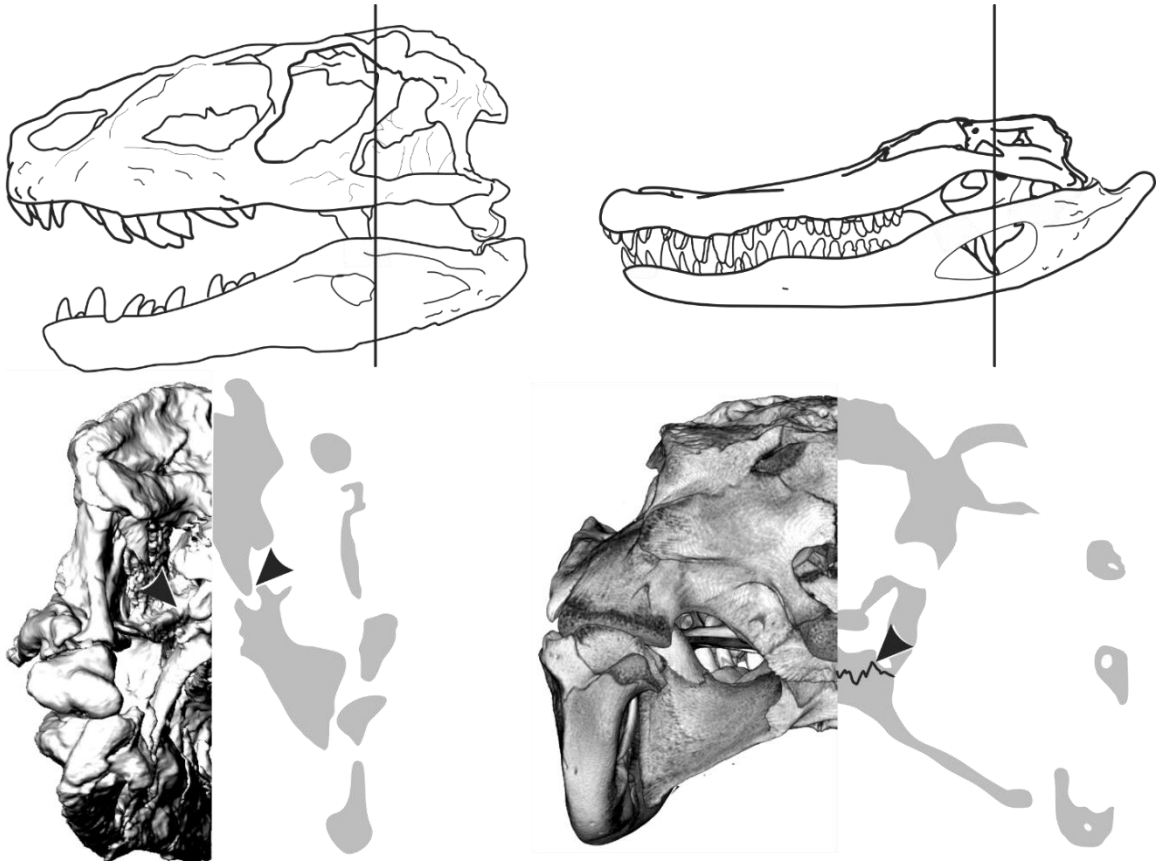


Figure 1.3. Select specimens across the origin of Crocodyliformes in caudal view. Specimens are scaled to the same skull width. A, *Prestosuchus*. B, *Junggarsuchus*. C, “*Gomphosuchus*”. D, *Alligator*. Red arrow shows overall orientation of temporal muscles; note the increasingly- mediolateral components of this group of muscles.

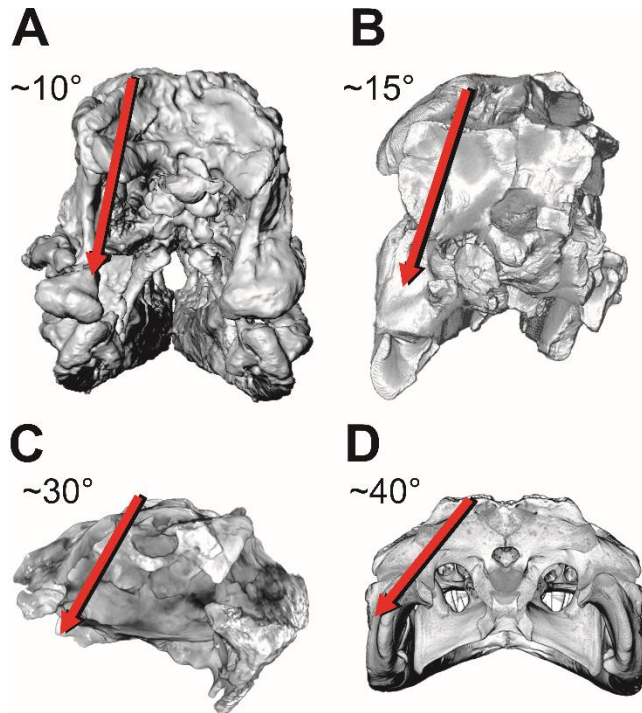


Figure 1.4. Caudal mandibles of (left) *Prestosuchus* and (right) *Alligator*. Note the caudally-expanded retroarticular process and laterally- attaching mPTv in *Alligator*, a crocodyliiform. QAJ, quadratoarticular joint surface. RaP, retroarticular process. Pink, attachment area for mDM. Red, attachment area for mPTv.

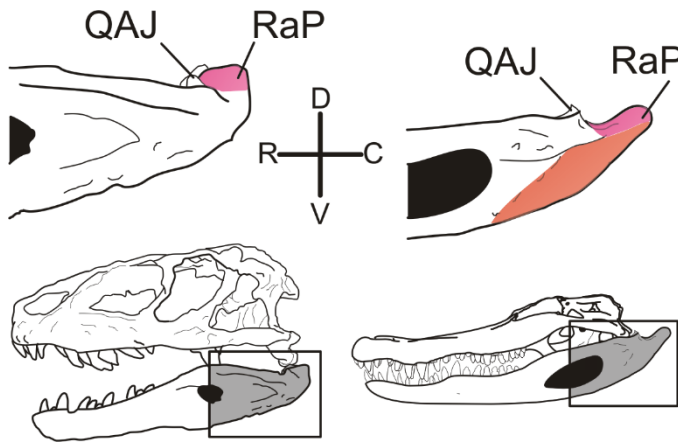
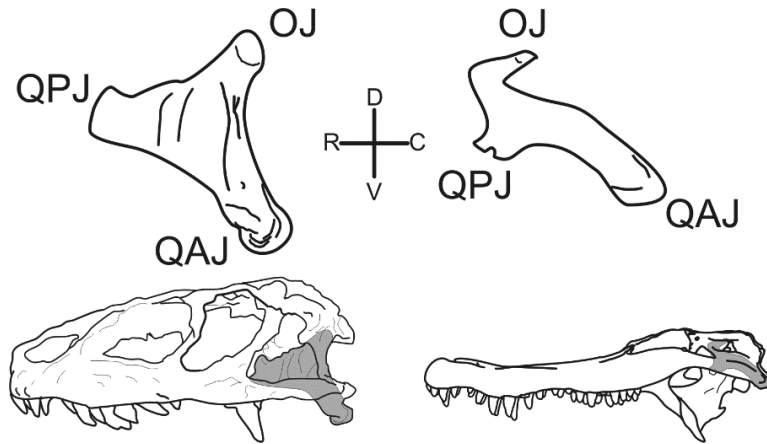


Figure 1.5. Left lateral views of the quadrate of (left) *Prestosuchus* and (right) *Alligator*; location of this bone is highlighted gray in skulls below. Homologous joints are labeled. OJ, otic joint. QPJ, quadratepterygoid joint. QAJ, quadratoarticular joint. D, dorsal. C, caudal. V, ventral. R, rostral. Note the caudal tilt of the quadrate in *Alligator*, a derived crocodyliform.



Chapter 2—The Effects of Skull Flattening on Suchian Jaw Muscle Evolution

INTRODUCTION

Feeding is one of the fundamental tasks faced by organisms, and so the feeding apparatus is thought to be under selective pressure (Lauder, 1995; Dumont *et al.*, 2009; Santana, Dumont and Davis, 2010). The acquisition of jaws and their associated musculature marked the final step in the transition from passive filter feeding to active predation in vertebrates (Gans and Northcutt, 1983; Gans, 1989) and has been linked with the evolutionary success of gnathostomes (Brazeau *et al.*, 2017). Thus, jaw muscles are a key feature of the feeding apparatus (Herrel *et al.*, 2005; Holliday and Witmer, 2007) and essential to understanding the biomechanical consequences of morphological evolution documented by the fossil record.

Jaw muscle anatomy is constrained by the bony anatomy of the adductor chamber (Schumacher, 1973; Holliday and Witmer, 2007) and by diverse functional demands such as generating force for feeding while permitting sufficient gape of the mandibles (Tseng and Wang, 2010; Ósi, 2014). These constraints generally prevent the feeding apparatus from having optimal efficiency in most scenarios (Granatosky and Ross, 2020). The most efficient muscular geometry for producing bite force would direct all of muscle force collinearly through the bite point in a single vector (Greaves, 1978). Additionally, in unilateral bites, contralateral muscle force can only produce bite force by lever action, in which case the optimal muscle orientation would be dorsoventral (Granatosky and Ross, 2020). However, in amniotes (Huber, Dean and

Summers, 2008), these conditions are rarely approached; instead, muscles insert closer to the joint axis than the location where biting occurs, and the mandible acts like a lever even on the working side (Hylander, 1975). When muscle forces are not collinear, the muscle resultant (i.e., the vector sum of each muscle force; F_r) is less than gross muscle force (i.e., the scalar sum of each muscle force; F_g ; Figure 2.1A). Therefore, if the optimal orientation of muscle forces is collinear and dorsoventral, then the medial component of muscle force acting on a hemimandible does not contribute to useful feeding function and is therefore “wasted” muscle force (Figure 2.1B). In taxa with caudally flat skulls like crocodylians, the flattened adductor chamber requires jaw muscles to take on inefficient mediolateral orientations (Figure 2.1B).

The evolution of crocodylians and their fossil relatives (i.e., the crocodyliforms) represents one of the great structural transitions in vertebrate evolution (Figure 2.2; Langston, 1973). Compared to primitive suchian ancestors, modern crocodylians have flat, robust, rigid skulls that are well- suited to resisting the high forces that crocodylians generate during feeding. Crocodylians have relatively massive jaw muscles with novel attachments and deliver the highest- measured feeding forces among vertebrates (Erickson, Lappin and Vliet, 2003), and powerful, whole- body thrashing and rolling augment these forces (Fish *et al.*, 2007). The skull of crocodylians is strengthened by the sutural immobilization of plesiomorphically- mobile joints and the acquisition of new intracranial and craniomandibular linkages (Langston, 1973; Clark *et al.*, 2004; Pol *et al.*, 2013).

Thus, the evolutionary origin of crocodylians and their fossil relatives involved a substantial reorganization of the feeding apparatus.

The paucity of extant crocodylian species and relative ecological homogeneity belies the incredible diversity of feeding ecologies and accompanying craniodental anatomies found in extinct suchians (Brochu, 2001). Rather than unmodified, primitive holdovers, the generalist crocodylians of today are just one tip of a tree full of terrestrial hypercarnivores, herbivores with oral processing, marine piscivore specialists, and taxa with bizarre morphologies adapted to uncertain feeding functions (Langston, 1973; Brochu, 2001; Ősi, 2014; Wilberg, 2017; Cidade, Fortier and Hsiou, 2019). Extant crocodylians and many of their close fossil relatives have flattened skulls relative to basal suchians (Figure 2.2; Iordansky, 1973; Langston, 1973; Busbey, 1989, 1995). Although overall skull size is a primary predictor of muscle mass in various sauropsids (Herrel *et al.*, 2005; Gignac and Erickson, 2016), the relative dimensions of the skull also impact muscle anatomy (Herrel *et al.*, 2005) and bite force (Herrel, De Grauw and Lemos-Espinal, 2001). Thus, the lineage leading to Crocodylia has experienced substantial geometric changes to skull morphology including a flattened adductor chamber with more horizontally oriented muscles (Schumacher, 1973; Busbey, 1989).

Whereas most animals with relatively high bite forces show dorsoventrally tall skulls (Menegaz *et al.*, 2010; Tseng and Stynder, 2011; Cost *et al.*, 2019). A flat skull in a hard-biting animal therefore represents a biomechanical paradox: how to produce high feeding forces with biomechanically disadvantaged muscle

orientations. The evolution of extant crocodylians and their fossil relatives therefore present an ideal opportunity to study the evolution of jaw muscle anatomy, skull shape, and biomechanical performance.

Here, we reconstruct jaw muscle anatomy across a phylogenetic range of crocodylians and fossil suchians to investigate the impact of skull flattening on jaw muscle anatomy. We used osteological correlates, the extant phylogenetic bracket (Witmer, 1995), dissections, and contrast-enhanced imaging (Gignac *et al.*, 2016) to characterize jaw muscle anatomy in a sample of extant crocodylians and fossil suchians, quantify muscle efficiency, and determine geometric correlates of muscle anatomy.

AIMS AND PREDICTIONS

This study aims to characterize jaw muscle anatomy in a diverse sample of extant and extinct crocodylians and determine the effects of skull flattening on muscle performance in a lineage of species that evolved flat skulls yet still bite extremely hard. We use dissection, regular and contrast-enhanced tomography, and biomechanical modeling to reconstruct jaw muscle anatomy in digital models in a comparative sample of crocodylians and fossil relatives (Figure 2.2). Muscle attachment sites were digitally mapped onto skulls and used to estimate each jaw muscle's physiological cross-sectional area (PCSA) and thus its force (Figure 2.3). We use simple linear measurements to characterize skull size and flatness and explore the influence of skull shape and skull flatness on muscle force. These metrics of skull shape and biomechanical performance were mapped onto a phylogeny to reveal patterns of jaw muscle anatomical and functional evolution in crocodylians and their fossil relatives.

We hypothesize that skull flatness will negatively influence jaw muscle resultant force (Hypothesis 1) and that jaw muscles in taxa with flatter skulls will have more inefficient non-collinear orientations (Hypothesis 2). Extant crocodylians may have traits to accommodate inefficient jaw muscle orientation such as larger gross muscle mass than extinct relatives to accommodate inefficient orientations (Hypothesis 3A). Alternatively, the muscle insertions may be placed relatively farther from the jaw joints, reflected in larger sums of moment arms (Hypothesis 3B).

MATERIALS AND METHODS

Study Specimens— The extant sample consisted of one individual from six extant crocodylian species (Table 2.2.1; Figure 2.2): *Alligator mississippiensis* (MUVC 008), *Caiman crocodilus* (FMNH 73711), *Paleosuchus palpebrosus* (FMNH 22817), *Crocodylus moreletii* (TMM M-4980), *Osteolaemus tetraspis* (FMNH 98936), and *Tomistoma schlegelii* (TMM M-6342). Data on extant crocodylian jaw muscles were collected by dissections and regular and contrast-enhanced computed tomography (CT) imaging. Additionally, key fossil suchians that represent important transitional stages were studied (Table 2.1; Figure 2.2): *Araripesuchus gomesii* (AMNH 24450), an undescribed “protosuchian” informally known as “*Gomphosuchus*” sp. (UCMP 97638; Clark, 1986), *Junggarsuchus sloani* (IVPP V14010), *Prestosuchus chiniquensis* (UFRGS PV0629T), and *Revueltosaurus callenderi* (PEFO 34561).

Muscle Modeling— To determine muscle force magnitudes and orientations, 3D models of specimens were created following (Sellers *et al.*, 2017). Specimens were scanned with CT or laser scanning. Three-dimensional bony anatomy was

acquired by manually segmenting scan data with Avizo Lite 9.4 (FEI Visualization Science Group; <https://www.thermofisher.com>). Using Geomagic Studio 2013 (Geomagic, Inc.; <https://www.3dsystems.com>), models were cleaned, smoothed, and aligned to global anatomical axes (i.e., x corresponds to mediolateral, y corresponds to dorsoventral, and z corresponds to rostrocaudal), and mandibles were opened to five degrees of gape. Muscular reconstructions in these taxa were informed by first-hand observations, regular and contrast-enhanced computed tomography (CT) imaging, the literature (Busbey, 1989; Holliday and Witmer, 2007, 2009; Ősi, 2014), observations of closely related fossil taxa, and application of the extant phylogenetic bracket (Witmer, 1995). Physiological cross-sectional area (PCSA) is calculated by combining information about attachment site geometry and muscular parameters, described in Equation 1 (Sacks and Roy, 1982):

$$PCSA = \frac{V_M}{l_f} \cdot \cos(\theta) \quad (1)$$

where V_M is volume of the muscle, l_f is the fiber length of the muscle, and θ is the angle of pennation. The ratio between PCSA and force produced is specific tension, defined in Equation 2:

$$F_M = PCSA \cdot T_{\text{specific}} \quad (2)$$

where F_M is muscle force and T_{specific} is specific tension. Muscular parameters that could not be estimated directly from fossil morphology (e.g., relative length of muscle fibers, specific tension, etc.) were given values from *Alligator* (*sensu* Porro et al. 2011). All muscle terminology follows Holliday and Witmer (2007). To compare functional muscle anatomy across this sample, muscle force was

represented as load vectors which were projected into ternary space to facilitate comparisons (Cost *et al.*, 2019).

Skull Shape and Muscle Efficiency— Skull size is known to be a major driver of muscle force. We measured two linear distances in the caudal skull used in recent functional and morphological studies of crocodylians (Iijima, 2017; O’Brien *et al.*, 2019) that capture the size of the adductor chamber: the dorsoventral distance between the ventral margin of the pterygoid flange and the dorsal margin of the skull table (skull height; h_{skull} ; “pterygoid flange depth” of Iijima, 2017; Figure 2.3) and the maximum mediolateral width at the quadrate condyles (skull width; w_{skull} ; Figure 2.3).

For producing useful bite force, non-collinear muscle vectors are less efficient than collinear vectors, as some component of non-collinear vectors is “spent” cancelling out one another. The medial component of muscle force acting on each hemimandible cancels out that from the contralateral hemimandible and cannot contribute to useful feeding function. The mediolateral component of crocodylian jaw muscles is therefore “wasted” force (Figure 2.1). To estimate the degree of wasted muscle force in each taxon, we calculated “muscle efficiency” as the magnitude of the resultant of all muscles acting on the cranium (“resultant muscle force”) divided by the scalar sum of the magnitude of each individual muscle (“gross muscle force”), as defined in Equation 3:

$$E_M = \frac{F_r}{F_g} = \frac{\|\vec{v}_{res}\|}{\sum \|\vec{v}_{muscle_i}\|} = \frac{\|\sum \vec{v}_{muscle_i}\|}{\sum \|\vec{v}_{muscle_i}\|} \quad (3)$$

where E_M is muscle efficiency, F_r is resultant muscle force, F_g is gross muscle force, \vec{v}_{res} is the resultant of all muscle vectors, and \vec{v}_{musci} is the muscle vector of the i th muscle. As muscle geometry become more collinear and thus more efficient, this ratio approaches unity.

Statistical Analyses— Although we hypothesize that the ratio of skull height and skull width is important for muscle force, these measures of size are highly correlated, and thus neither can be used to account for size. Thus, we performed a principal components analysis (PCA) on our linear measurements. Our PCA of skull width and skull height produced a variable linked with overall size (PC1; 97.6% of variance explained; Figure 2.4A) and a variable that is approximately corresponds with aspect ratio, or skull height over skull width (PC2; 2.4% of variance explained; Figure 2.4A). Both skull width and skull height load highly on PC1, suggesting PC1 is broadly equivalent to skull size. PC2 is highly correlated with skull aspect ratio (correlation coefficient = 0.856; Figure 2.4B) and is used to represent skull flatness.

To test our hypothesis that skull flatness influences muscle force (Hypothesis 1), we used phylogenetic generalized least-squares (PGLS) regression of muscle force against PC1 and PC2 using a time-scaled phylogeny modified from Nesbitt (2011) and Wilberg, Turner and Brochu (2019). We modeled the muscle resultant force (F_r) against PC1, (Model 1.1), PC2 (Model 1.2), and PC1 + PC2 (Model 1.3), for a total of three models (Table 2.3). To determine the most appropriate models of muscle force, we calculated the Akaike Information Criterion for each model, corrected for small sample size (AICc). For each hypothesis, the model

with the highest AICc weight was considered the best model. A best-fit model of F_r that includes PC2 would support Hypothesis 1.

To test our hypotheses of relationship between skull shape and muscle force, (Hypothesis 2), we used PGLS regression of muscle efficiency (E_M) against PC1, (Model 2.1), PC2 (Model 2.2), and PC1 + PC2 (Model 2.3), for a total of three models (Table 2.3). A best-fit model of E_M that includes PC2 would support Hypothesis 2, whereas a nonexistent or negative relationship would fail to lend support.

To test our hypothesis that inefficient muscle geometries are “mitigated” by higher muscle mass, (Hypothesis 3A), we used PGLS regression of the gross muscle force (F_g) against PC1, (Model 3.1), PC2 (Model 3.2), and PC1 + PC2 (Model 3.3), for a total of three models (Table 2.3). A best-fit model for gross muscle force including a term for PC2 would support the hypothesis that these skulls rely on extra muscle mass. To test our hypothesis that inefficient muscle geometries are “mitigated” by longer moment arms of muscles (Hypothesis 3B), we used PGLS regression of the sum of muscle moment arms against PC1, (Model 3.4), PC2 (Model 3.5), and PC1 + PC2 (Model 3.6), for a total of three models (Table 2.3). A significant relationship between the moment arms and skull flatness supports the hypothesis that taxa with flat skulls use larger moment arms to mitigate inefficient muscular orientations.

RESULTS

Organization of Results— First, we briefly summarize the primitive condition for suchian jaw muscle anatomy based on comparisons among extant

archosaurs and the literature. Next, we describe major derived features of the extant crocodylian jaw musculature, then evaluate osteological correlates in select fossil suchians to assess the phylogenetic history of these character changes in the context of our 3D muscle-mapped models (Figure 2.5). Finally, we present the results of our quantitative analyses and hypothesis testing.

Primitive Condition for Suchian Jaw Muscles— Early suchians lack many of the osteological correlates of jaw muscles that are found in the skulls of extant crocodylian jaw muscles. In particular, the adductor tubercle of the quadrate for the tendinous attachments of m. adductor mandibulae posterior (mAMP), the cotylar crest of the laterosphenoid for the attachment of m. pseudotemporalis superficialis (mPSTs), and the coronoid eminence of the surangular for the tendinous attachment of the temporal muscles tend to be less well developed in more plesiomorphic crocodylomorphs (Holliday and Witmer, 2009; Ősi, 2014). Thus, our reconstruction of early suchian jaw muscle anatomy is broadly comparable to those of typical sauropsids (Holliday and Witmer, 2007, 2009). The internal mandibular adductor (mAMI) is separated into the pseudotemporalis (mPST) and pterygoid (mPT) bellies. mPSTs originates on the medial border of the dorsotemporal fenestra and the lateral face of the laterosphenoid and inserts on the mandible rostral to the adductor fossa. M. pterigoideus dorsalis (mPTd) retains a primitive morphology in early suchians; its origin is on the lateral surface of the palatine and the lateral surface of the quadrate ramus and caudoventral aspect of the pterygoid flange of the pterygoid bones, and this muscle inserts only onto the medial surface of the articular bone. The external mandibular

adductors (mAME) originates around the edges of the dorsotemporal fenestra and inserts onto the surangular shelf and coronoid bone. The primary jaw opener, depressor mandibulae (mDM), originates on the exoccipital and inserts onto a short retroarticular process. The mAMP originates on the body and pterygoid ramus of the quadrate and inserts onto the adductor fossa.

Extant Crocodylian Jaw Muscles— In extant crocodylians, various muscles have altered bony attachments associated with structural changes in the skull. Numerous works have provided rich and detailed studies of the jaw musculature of extant crocodylian jaw muscles (Iordansky, 1964; Schumacher, 1973; Busbey, 1989; Holliday and Witmer, 2007), and although a thorough summary of their findings is beyond the scope of this paper, we briefly summarize the extant condition below. The rostral portions of the origin of mPTd have expanded to include the maxilla, nasal capsule, prefrontals, jugals, and even the ectopterygoids. This expanded origin is reflected in an enlarged insertion on the expanded articular bone. The insertion of m. pterygoideus ventralis (mPTv) has migrated onto the lateral surface of the mandible, leading this muscle to wrap ventromedially around the mandible. The origin of mPSTs does not lie within the dorsotemporal fenestra in extant crocodylians, as the laterosphenoid no longer participates in the fenestral margin, whereas the insertion of this muscle in extant crocodylians is equivalent to the intramandibularis (mIRA) muscle (Iordansky, 1964; Tsai and Holliday, 2011). The so-called “cartilago transiliens” is a sesamoid within mPSTs. mPSTs/ mIRA travels far rostrally within the primordial canal; in *Alligator*, the rostral extent is the crest that divides the canal for

Meckel's cartilage from the canal for the inferior alveolar nerve (Lessner and Holliday, 2020). The origins of the mAME group are displaced by the diminished size of the dorsotemporal fenestra in crocodylians. Neither m. adductor mandibulae externus superficialis (mAMES) nor m. adductor mandibulae externus medialis (mAMEM) originate on the margin of the dorsotemporal fenestra; rather, both are displaced ventrally onto the quadrate and quadratojugal. The topographic relationships of mAMP are largely unchanged in crocodylians, but the ontogenetic development of a prominent tubercle on the quadrate reflects the presence of a central tendon. The m. depressor mandibulae is large and inserts onto an enlarged retroarticular process.

Muscle Attachments in Fossil Suchians

M. pterygoideus— The antorbital fenestra is closed in extant crocodylians, but soft tissue reconstructions suggest that the extensive pneumatic system of fossil archosaurs excavated the antorbital fossa and perforated the lateral wall of the rostrum, limiting the rostral extent of the origin of mPTd (Witmer, 1997). The shrinkage and closure of the antorbital fenestra has thus been interpreted as an osteological correlate of the expansion of the origin of mPTd onto the nasal capsule, prefrontal, and maxilla in the vicinity of the caviconchal fossa (Witmer, 1997). The antorbital fossa and fenestra are diminished in “protosuchians” and most metasuchians; they are closed in most neosuchians. Thus, we reconstruct the expansion of the rostral origin of mPTd as taking place in two stages—once at the base of Crocodyliformes and once at the base of Neosuchia.

The insertion of mPTv extends onto the lateral surface of the mandible independently in numerous taxa. However, the muscle plesiomorphically attaches to the medial surface of the angular. In our sample, mPTv attaches on the lateral surface of the angular in *Junggarsuchus* (Ruebenstahl *et al.*, in press; Ruebenstahl, 2019), *Araripesuchus* (Nieto *et al.*, 2021), and metasuchians whereas *Prestosuchus* and “*Gomphosuchus*” lack a lateral insertion of mPTv. The distribution of a laterally inserting mPTv is complex within Metasuchia. A laterally inserting mPTv is present throughout basal notosuchians (e.g., *Araripesuchus* and *Mahajangasuchus*; Turner and Buckley, 2008) and basal ziphosuchian notosuchians (e.g., *Simosuchus*; Turner and Sertich, 2010). However, it appears to recede back to the ventromedial surface of the angular and is absent from the lateral surface in most ziphosuchians; e.g., *Malawisuchus*, *Notosuchus*, sphagesaurids, and sebecosuchians (Busbey, 1986; Gomani, 1997; Carvalho, Arruda Campos and Henrique Nobre, 2005; Fiorelli and Calvo, 2008; Campos *et al.*, 2011; Pol *et al.*, 2014). The muscle was also relegated to the medial and ventral mandible in many advanced neosuchians including goniopholids (Martin, Delfino and Smith, 2016; Martin *et al.*, 2020), pholidosaurs (Martin, Raslan-Loubatié and Mazin, 2016), and paralligatorids (Turner, 2015). Basal eusuchians also lack the lateral insertion, including *Bernissartia* (Martin *et al.*, 2020). The ubiquity of a laterally- inserting mPTv in extant crocodylians suggests this trait is a synapomorphy of Crocodylia and that its absence in fossil crocodylians such as *Borealosuchus* (Brochu *et al.*, 2012) resulted from secondary losses.

M. pseudotemporalis— The dorsal skull table is contracted relative to the rest of the skull in metasuchians. In the non-metasuchian *Fruitachampsia* and the non-metasuchian mesoeucrocodylian *Pelagosaurus*, the lateral margin of the laterosphenoid is confluent with the dorsotemporal fenestra and the lateral margins of the skull table are directly dorsal to the jugals (Pierce and Benton, 2006; Clark, 2011). By contrast, in both basal notosuchians and neosuchians, the skull table is narrower than the skull as a whole and the dorsotemporal fenestrae are diminished. We thus reconstruct the exclusion of mPSTs from the dorsotemporal fenestra as originating in metasuchians. This is consistent with previous work on the temporal region of suchians (Holliday and Witmer, 2009).

M. adductor mandibulae externus— In extant Crocodylia, the m. adductor mandibulae externus profundus (mAMEP) is the only muscle that occupies the dorsotemporal fenestra (Holliday and Witmer, 2009; Holliday *et al.*, 2019). The origins of mAMEM and mAMES have been excluded from the fenestra and shifted onto the quadratojugal and quadrate. The shifts in mAME muscles were likely related to the narrow skull table of extant crocodylians. This trait first originated in Metasuchia. The shrinking of the dorsotemporal fenestra also had consequences for mPSTs, as discussed above.

M. adductor mandibulae posterior— In extant Crocodylia, mAMP retains the ancestral attachments and is largely comparable to the ancestral condition, although its orientation is altered by shifts in skull geometry, as discussed below. The adductor tubercle of the attachment of the central tendon of mAMP

(Iordansky, 1964) dates to at least Eusuchia (Holliday and Gardner, 2012; Narváez *et al.*, 2015).

M. depressor mandibulae— Most notosuchians and neosuchians show some form of retroarticular process. The characteristic elongate retroarticular process increases the maximum moment arm available for fibers of mDM. An elongate retroarticular process also provides an enlarged moment arm for portions of mPTd (Gignac and O'Brien, 2016), although the majority of the insertion is not affected by the retroarticular process. Although most “protosuchians” lack this retroarticular process, basal crocodylomorphs close to the ancestry of Crocodyliformes (e.g., *Junggarosuchus* and *Almadasuchus*) constructed a similar process (Ruebenstahl *et al.*, in review; Pol *et al.*, 2013), suggesting an apomorphic loss in “Protosuchia”. All crocodyliforms show a reduced posttemporal fenestra (Iordansky, 1973; Busbey and Gow, 1984), providing a larger surface for the origin of mDM. Thus, we reconstruct an expanded mDM as ancestral for Crocodyliformes. Some “protosuchians” (e.g., *Protosuchus*, “*Gomphosuchus*”) reduced the retroarticular process and evolved an accompanying medial process of the articular (Wu, Brinkman and Lu, 1994), effectively shifting the insertion of mDM medially. Some shartegosuchoids, which are either “protosuchians” or basal mesoeucrocodylians, show a ventrally-angled retroarticular process (Wu, Sues and Dong, 1997; Clark, 2011). This derived mDM morphology may be linked with the active oral processing of plant matter in which “*Gomphosuchus*” probably engaged. Ősi (2014) reported that the worn, bicuspid teeth of “*Gomphosuchus*” are highly indicative of active oral processing

of plant matter. If significant mandibular translational movements were a feature of the power stroke during “*Gomphosuchus*” feeding, an accompanying modification may be expected in the jaw depressors to counter or reverse this translation, but this hypothesis remains to be tested.

Quantitative Reconstructions— Muscle force was dominated by the pterygoideus muscles, with mPTd and mPTv together accounting for ~40-50% of gross muscle force (Figure 2.5; Table 2.2). Adductor mandibulae posterior was the second largest muscle, accounting for ~25-30% (Figure 2.5; Table 2.2). Proportions of muscle force were surprisingly consistent across the sample in light of previous hypothesized relationships between the size of the dorsotemporal fenestra and muscle mass, although recent work has called into question the utility of dorsotemporal fenestra size and muscle anatomy (Holliday *et al.*, 2019). Adductor mandibulae externus muscles accounted for a slightly higher proportion of gross muscle force in early suchians (Figure 2.5; Table 2.2), and within extant crocodylians, the pterygoideus muscles contribute a larger proportion of muscle force in larger individuals, consistent with previously-reported data on muscle scaling in crocodylians (Gignac and Erickson, 2016).

Muscle forces were generally less dorsoventrally- oriented in crocodylians than in extinct suchians (Figure 2.6; Figure 2.7). Temporal muscles in extant taxa are generally ~10% less dorsoventrally oriented than the same muscles in fossil taxa (Figure 2.6; Figure 2.7). Differences in orientations of the pterygoideus muscles are even more dramatic: mPTd is approximately 25% dorsoventrally oriented in fossil taxa, whereas it is nearly in the horizontal plane in extant taxa at

~10% dorsoventrally oriented (Figure 2.6; Table S1). Finally, mDM is nearly 30% less dorsoventrally oriented in extant taxa than in extinct taxa (Figure 2.6; Figure 2.7).

Our analyses show that skull size and skull flatness both jointly influence muscle performance. Gross muscle force was best explained by skull size (i.e., PC1) alone, whereas resultant muscle force was best explained by skull size and skull flatness (i.e., PC1 + PC2). Hypothesis 1 was therefore supported. The relationship between muscle efficiency and skull flatness (i.e., PC2) was significant, supporting Hypothesis 2. There was no relationship between gross muscle force and PC2, failing to support Hypothesis 3A. There was no relationship between the sum of moment arms and PC2, but taxa with flatter skulls had lower sums of moment arms, failing to support Hypothesis 3B (Table 2.3).

DISCUSSION

The Effects of Skull Flattening—Skull flattening is a major feature of crocodylian evolution (Langston, 1973; Busbey, 1995; Cossette, 2018). Numerous derived traits contribute to the complex morphology of skull flattening, including the caudolateral rotation of the quadrate condyles (Langston, 1973; Busbey, 1995), formation of the “skull table” (Langston, 1973; Busbey, 1995; Cossette, 2018), and rostral flattening (Busbey, 1995). Functional explanations of crocodylian skull flattening have focused on presumed adaptations to aquatic ambush predation, such as the dorsal migration of the sensory structures allowing crocodylians to float nearly submerged (Iordansky, 1973; Langston,

1973; Cossette, 2018) or reducing drag during lateral head movements (Busbey, 1995; McHenry *et al.*, 2006). Regardless, this lineage was able to maintain high bite performance despite this arguably suboptimal skull shape.

Although the development of high bite force performance likely played a large role in crocodylian evolution (Langston, 1973), our analyses found that the crocodylian adductor chamber is not optimized for the efficient production of high bite force. Other studies have shown that the geometry of the crocodylian rostrum is not optimized for the resistance of dorsoventral bending or twisting loads (Busbey, 1995; Metzger, Daniel and Ross, 2005; McHenry *et al.*, 2006). This suggests that conflicting functional demands played roles in crocodylian skull shape evolution. Authors have noted that derived traits in the crocodylian rostrum such as a bony secondary palate and broad scarf joints at least partially compensate for the structural inefficiency imposed by a flattened skull (Busbey, 1989, 1995; Metzger, Daniel and Ross, 2005; McHenry *et al.*, 2006; Porro *et al.*, 2011), and derived aspects of the crocodylian jaw adductors may similarly mitigate muscular inefficiencies caused by the flat skull (Salisbury *et al.*, 2006; Gignac and Erickson, 2016; Gignac and O'Brien, 2016; see below).

Some authors have noted ontogenetic and phylogenetic “verticalization” of the braincase of crocodylians and other derived neosuchians (Tarsitano, 1985; Salisbury *et al.*, 2006). Changes to the basisphenoid and basioccipital result in a more dorsoventrally tall braincase. These authors suggested that braincase verticalization may result in *more* dorsoventrally oriented jaw muscles relative to primitive neosuchians, although these studies did not perform quantitative

reconstruction of jaw muscle anatomy. In contrast, this study found the temporal and pterygoideus muscles reoriented to more horizontal orientation despite this pattern of braincase verticalization. This suggests that the braincase, palate, and skull roof elements may have evolved as separate modules, consistent with previous work (Felice *et al.*, 2019).

In addition, this analysis shows signs of ontogenetic recapitulation. Although the focus of this study was a comparison among taxa, smaller extant crocodylians had more dorsoventrally oriented muscles. This matches findings from an ontogenetic sample of *Alligator mississippiensis* (Sellers, Middleton and Holliday, 2018). Heterochronic shifts are a common source of evolutionary shape change, and have been suggested to underlie other aspects of crocodylian skull shape and functional evolution (Gignac and O'Brien, 2016; Morris *et al.*, 2019).

Evolution of Pterygoideus Musculature— The pterygoid muscles have been considered to be key characters in the evolution of the crocodylian feeding apparatus (Iordansky, 1964, 2010; Salisbury *et al.*, 2006; Holliday and Witmer, 2007; Gignac and Erickson, 2016; Gignac and O'Brien, 2016). Previous work has implicated the ventral deflection of the pterygoid flanges in neosuchians in increasing the size of mPTd (Salisbury *et al.*, 2006) and relative size of the jaw adductors (Iijima, 2017). In extant crocodylians, mPTv is especially well-suited to increasing its size, as mPTv is uniquely not bound by the bony adductor chamber (Salisbury *et al.*, 2006; Gignac *et al.*, 2019) and has extensive tendinous origins (Iordansky, 1964, 2010; Schumacher, 1973; Busbey, 1989; Holliday and Witmer, 2007, 2009). This lack of osteological correlates makes predicting the size

(mass, volume) of these muscles challenging. The complex internal anatomy of mPTv and its wrapping geometry also make it difficult to accurately model with traditional approaches (Gignac and Erickson, 2016; Sellers *et al.*, 2017).

Previous studies have reconstructed the pterygoid muscles with widely different proportions relative both to each other and to other jaw muscles (Busbey, 1989: mPTd ~18%, mPTv ~34%; Cleuren, Aerts and De Vree, 1995: mPTd ~18%, mPTv ~34%; Porro *et al.*, 2011: mPTd ~47%, mPTV ~20%; Gignac and Erickson, 2016: mPTd ~17%, mPTv ~62%).

The distribution of a laterally attaching pterygoideus ventralis among crocodylomorphs suggests rampant homoplasy. The distribution of a laterally attaching mPTv suggests this muscle migrated onto the lateral surface of the mandible relatively late in the lineage leading to the crown group and at the base of Notosuchia, followed by a subsequent loss in advanced ziphosuchians (e.g., sebecosuchians). Alternatively, a laterally attaching mPTv may be basal for Metasuchia, although this would require numerous losses within Neosuchia. Taxa just outside of Eusuchia such as *Isisfordia* (Salisbury *et al.*, 2006) were shifting the pterygoid flange ventrally, both widening the space available for mPTd and increasing the attachment area of mPTv. As the flat skull predates the persistent lateral insertion of mPTv in the crown clade, we suggest that the evolutionary hypertrophy of mPTv facilitates high bite force performance despite the geometric inefficiencies imposed by the skull flattening for aquatic ambush predation.

This study highlights the diversity and evolution of jaw muscles in suchians during one of the great transformations in vertebrate evolution. Although many studies have focused on the evolution of shape in the suchian feeding apparatus (Pierce, Angielczyk and Rayfield, 2009; Drumheller and Wilberg, 2020; Stubbs *et al.*, 2021) and the response of the feeding apparatus to forces (McHenry *et al.*, 2006; Walmsley *et al.*, 2013), less attention has been paid to the jaw muscles driving feeding function (but see Schumacher, 1973; Porro *et al.*, 2011, 2013; Ósi, 2014; Gignac and O'Brien, 2016). The reconstruction of jaw muscle evolution presented here clarifies and constrains future functional studies of feeding in Suchia.

CONCLUSIONS

Here, we reconstruct jaw musculature in a sample of suchians leading to the crown group. Muscle proportions show general conservatism across the sample, although the pterygoid muscles did increase their proportion at the expense of temporal muscles in the lineage leading to Crocodylia. Muscles are in less efficient configurations in extant taxa that possess flat skulls, but we found no evidence of taxa with flatter skulls relying on larger gross muscle mass or longer moment arms of muscles to mitigate inefficient muscular geometries. Future studies will analyze the effects of inefficient muscular geometries on feeding performance and evolution.

Table 2.1. Table of taxa included in this study.

Taxon	Specimen Number	Skull Width (cm)	Skull Height (cm)
<i>Alligator mississippiensis</i>	MUVC AL008	24.3	17.3
<i>Caiman crocodilus</i>	FMNH 73711	5.9	4.1
<i>Paleosuchus palpebrosus</i>	FMNH 22817	2.4	1.7
<i>Crocodylus moreletii</i>	TMM M-4980	16.8	8.9
<i>Osteolaemus tetraspis</i>	FMNH 98936	4.9	3.5
<i>Tomistoma schlegelii</i>	TMM M-6342	13.9	7.7
<i>Araripesuchus gomesii</i>	AMNH 24450	4.8	3.4
<i>“Gomphosuchus”</i> sp.	UCMP 97638	4.1	2.3
<i>Junggarsuchus sloani</i>	IVPP V14010	5.5	5.2
<i>Prestosuchus chiniquensis</i>	UFRGS PV0629T	23.5	21.6
<i>Revueltosaurus callenderi</i>	PEFO 34561	9.3	7.1

Table 2.2. Proportion of jaw musculature represented by each muscle belly.

Genus	Jaw Muscle Bellies							
	mAMES	mAMEM	mAMEP	mAMP	mPSTs	mPTd	mPTv	mDM
<i>Alligator</i>	4.5%	1.4%	0.79%	23.9%	7.1%	50.1%	6.2%	6.0%
<i>Caiman</i>	5.0%	1.7%	0.91%	28.5%	7.5%	49.5%	2.7%	4.3%
<i>Paleosuchus</i>	6.0%	2.1%	1.1%	31.0%	9.5%	42.3%	4.1%	4.0%
<i>Crocodylus</i>	5.2%	1.1%	0.6%	26.4%	6.1%	48.6%	5.5%	6.5%
<i>Osteolaemus</i>	4.8%	1.6%	1.00%	29.5%	8.9%	44.2%	4.9%	5.2%
<i>Tomistoma</i>	5.9%	1.6%	0.98%	24.4%	6.8%	47.7%	4.8%	7.9%
<i>Araripesuchus</i>	3.3%	1.8%	0.98%	25.7%	3.7%	53.4%	4.6%	6.5%
<i>“Gomphosuchus”</i>	3.1%	3.2%	2.5%	32.9%	6.4%	39.8%	3.5%	8.7%
<i>Junggarsuchus</i>	4.4%	1.2%	3.3%	34.4%	6.6%	38.2%	6.6%	5.3%
<i>Prestosuchus</i>	6.0%	2.2%	3.6%	25.8%	5.4%	42.6%	8.5%	6.0%
<i>Revueltosaurus</i>	10.3%	1.7%	4.8%	32.8%	6.9%	36.7%	3.1%	3.8%

Table 2.3. Results of statistical analyses. Mod., Model number; Resp. Var., Response variable; Pred. Var(s), Predictor variable(s); β_1 , effect of the first variable; β_2 , effect of the second variable; p_1 , p value of first variable; p_2 , p value of second variable; AICc, Akaike information criterion corrected for small sample size; AICw, AICc weights; $\sum l_m$, sum of moment arms. For hypotheses with multiple significant models, the best-fit model is bolded.

a	Resp. Var.	Pred. Var(s).	β_1	p_1	β_2	p_2	AICc	AICw
1.1	F_r	PC1	-5017 ± 643.3	<0.001	N/A	N/A	207.5	0.04
1.2	F_r	PC2	16283 ± 24773	0.230	N/A	N/A	241.8	0.00
1.3	F_r	PC1 + PC2	-4813 ± 410.9	<0.001	6662 ± 3317	0.004	200.8	0.96
2.1	E_M	PC1	-0.0160 ± 0.034	0.387	N/A	N/A	-8.92	0.00
2.2	E_M	PC2	0.367 ± 0.161	0.0012	N/A	N/A	-20.88	0.92
2.3	E_M	PC1 + PC2	-0.0049 ± 0.0216	0.667	0.360 ± 0.175	0.004	-15.92	0.08
3.1	F_g	PC1	-6217 ± 636.4	<0.001	N/A	N/A	207.2	0.92
3.2	F_g	PC2	13804 ± 31932	0.419	N/A	N/A	247.4	0.00
3.3	F_g	PC1 + PC2	-6171 ± 685.3	<0.001	1466 ± 5531	0.618	212.1	0.08
3.4	$\sum l_m$	PC1	-0.248 ± 0.0099	<0.001	N/A	N/A	-36.38	0.74
3.5	$\sum l_m$	PC2	0.555 ± 1.261	0.187	N/A	N/A	24.35	0.00
3.6	$\sum l_m$	PC1 + PC2	-0.247 ± 0.0094	<0.001	0.063 ± 0.076	0.145	-34.24	0.26

Figure 2.1. Non-orthogonal components of jaw muscles result in lower mechanical efficiency. A, Non-collinear muscles on the left side of the skull result in a lower hemimandibular resultant force (F_r) than gross muscle force (F_g), whereas the right side, these values are identical. B, The skull on the right has a lower total resultant force than the skull on the left.

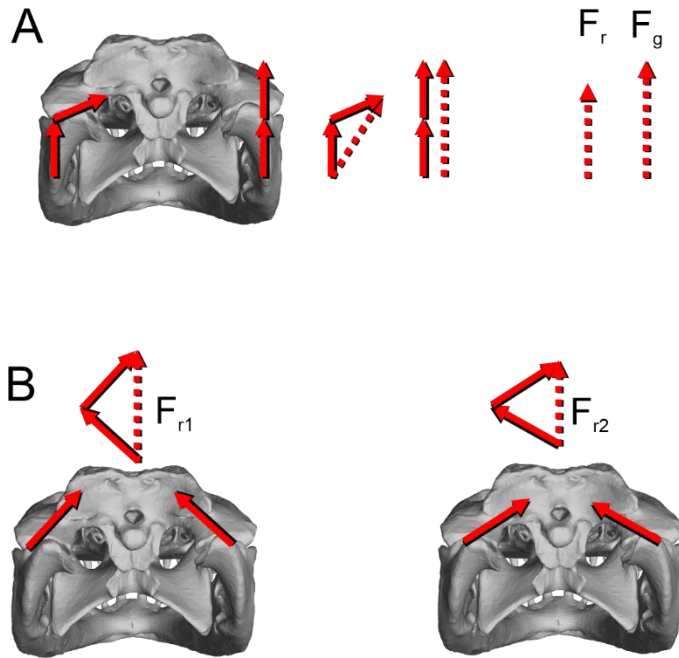


Figure 2.2. Suchian evolution was marked by progressive flattening of the skull. In this cladogram our studied taxa, skulls are scaled to the same skull length. A, Suchia; B, Loricata; C, Crocodylomorpha; D, Crocodyliformes; E, Metasuchia; F, Crocodylia; G, Alligatoroidea; H, Crocodyloidea.

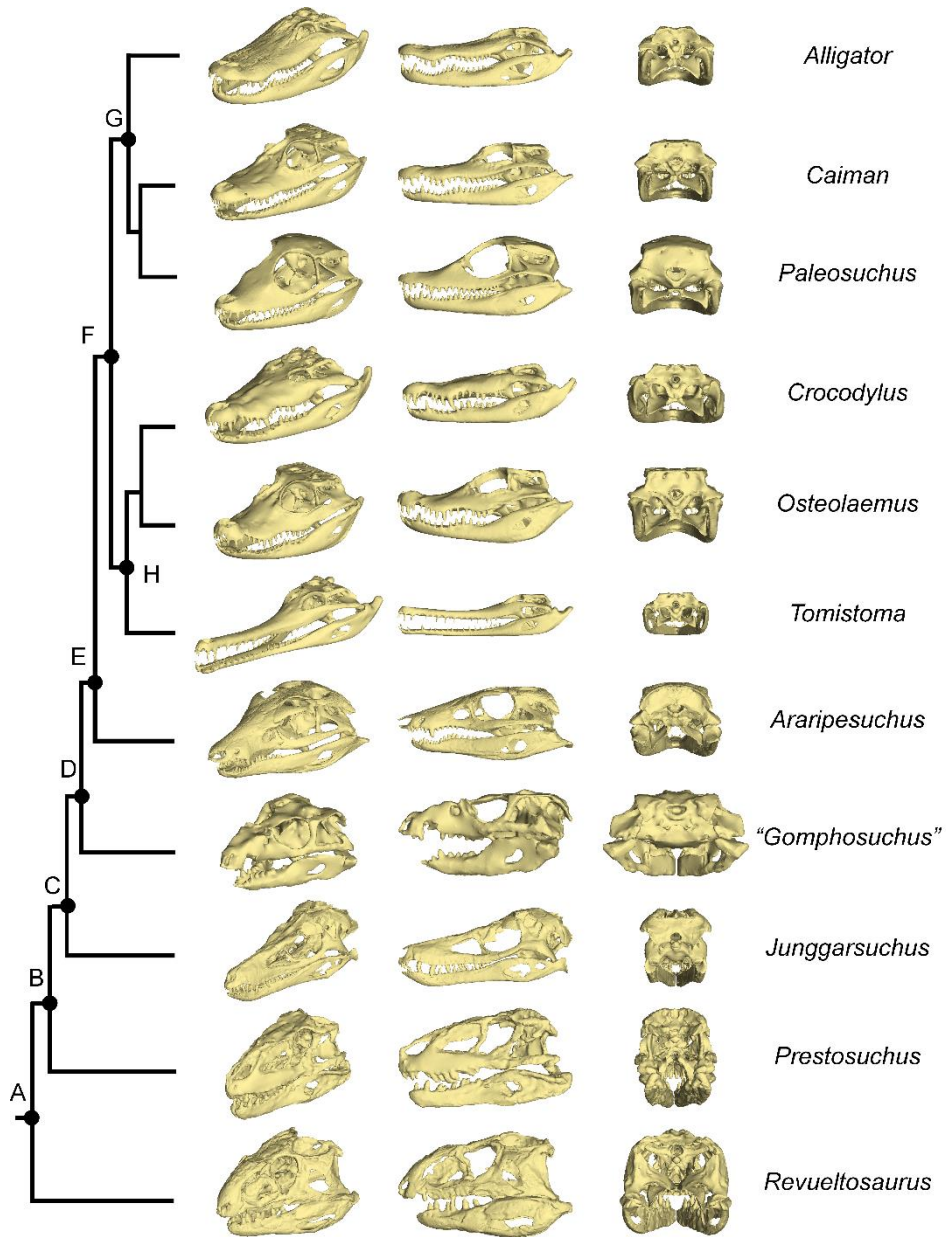


Figure 2.3. Methods used to estimate and quantify muscle force and skull flatness illustrated with *Alligator mississippiensis*. A, CT or laser imaging data were acquired. B, Digital 3D models of cranium and mandible were created. C, Simple linear measures were acquired to characterize skull flatness. D, 3D models were meshed into finite element models. E, Muscle origins and insertions were mapped onto 3D models. F, PCSA was calculated and used to estimate muscle force vectors. G, Muscle force vector orientation was visualized using ternary diagrams.

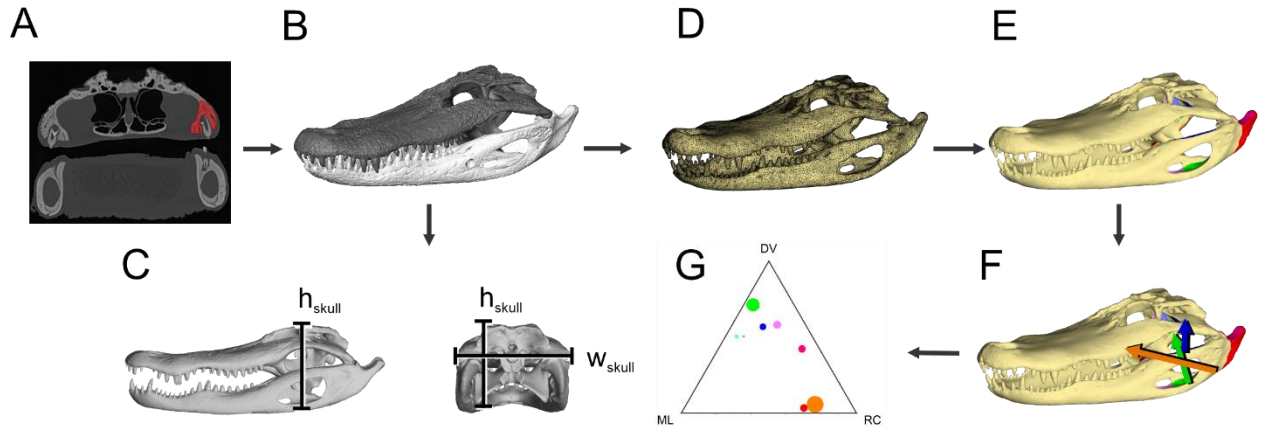


Figure 2.4. Results of principal components analysis of skull measurements. A, PC1 vs PC2. Note that PC1 is related to negative size, so larger skulls are to the left of the plot. B, PC2 vs aspect ratio of skulls in caudal view (i.e., $h_{\text{skull}}/w_{\text{skull}}$). Fossil taxa are represented by crosses whereas extant taxa are circles.

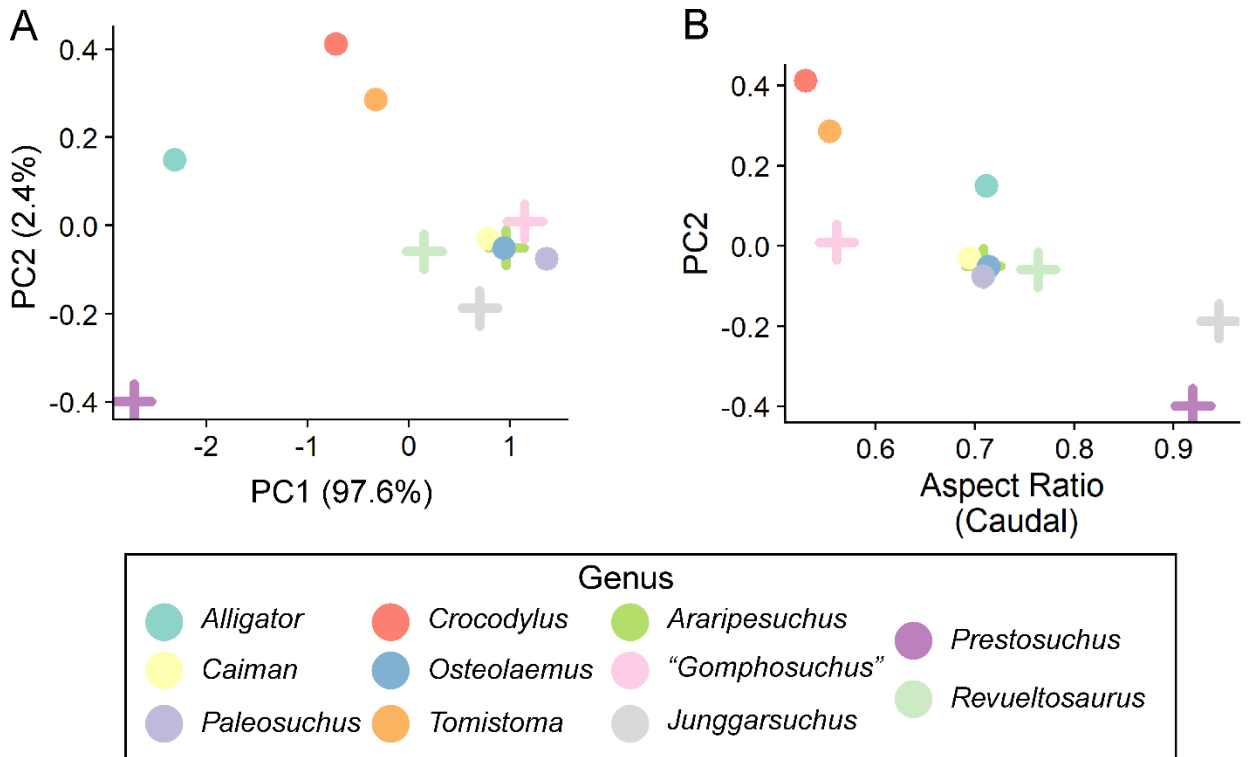


Figure 2.5. Musculus Pterygoideus Dorsalis (mPTd) and Musculus Adductor Mandibulae Posterior (mAMP) were of approximately equal size in early suchians, but in extant crocodylians, mPTd is approximately twice the size of mAMP and accounts for at least ~40% of total muscle force.

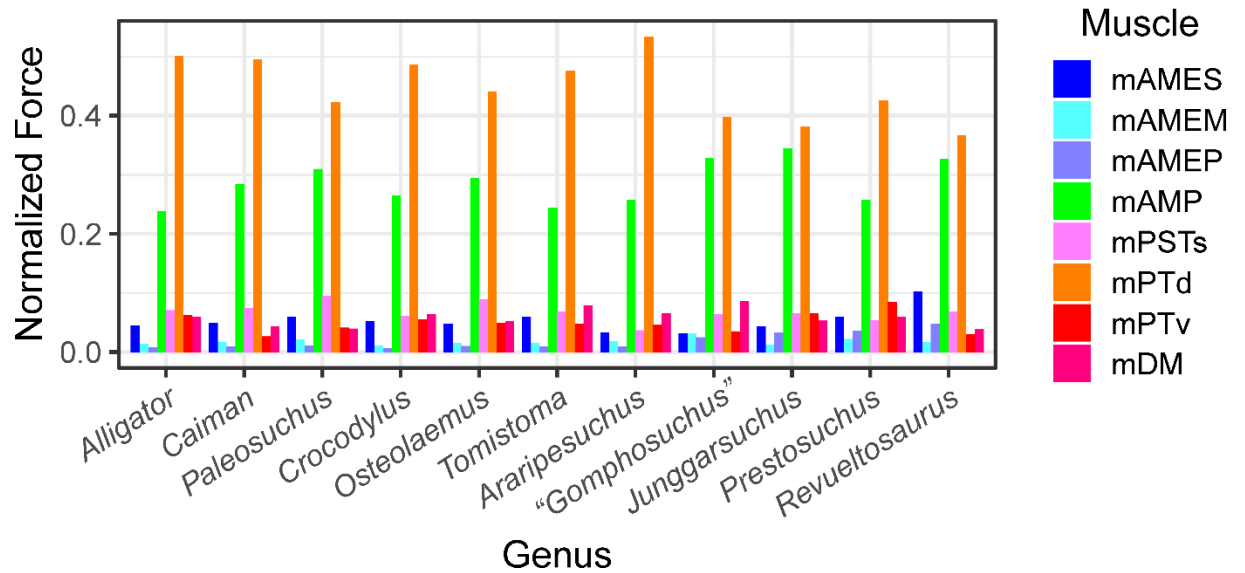


Figure 2.6. Temporal muscles shift from dorsoventrally-oriented to more mediolateral orientations during croc evolution, whereas pterygoideus muscles shifted to more rostrocaudal orientations. Fossil taxa are represented by crosses whereas extant taxa are circles.

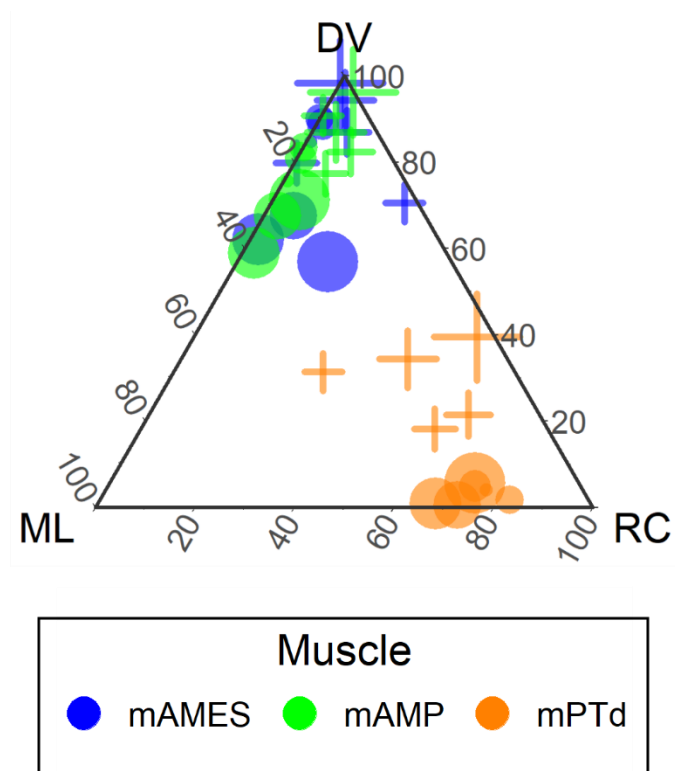
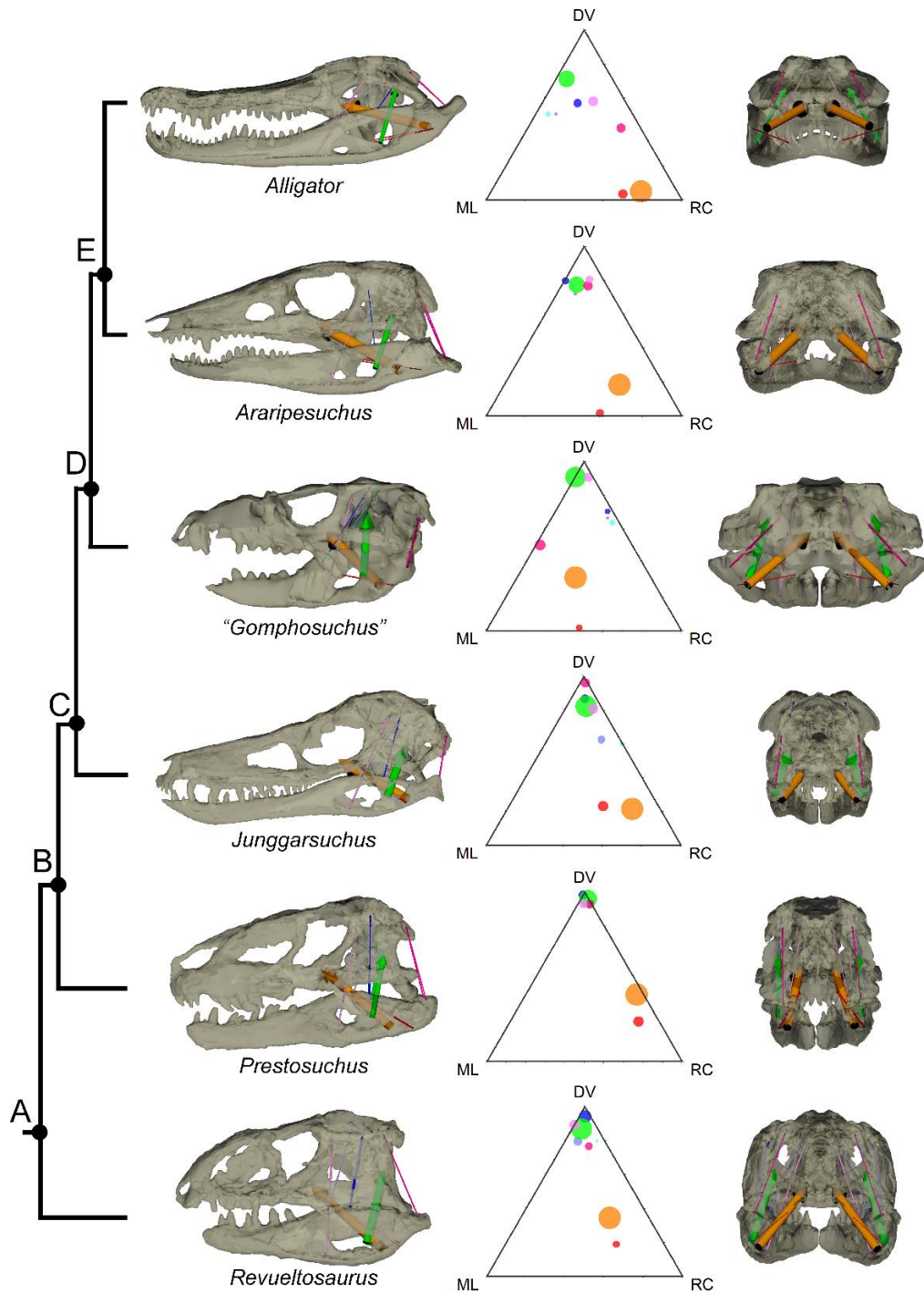


Figure 2.7. Suchian jaw muscle anatomy progressively shifted in the lineage leading to Crocodylia. Reconstructed muscle resultants and accompanying ternary diagrams are displayed for select taxa that characterize changes to muscle anatomy during suchian evolution. Vector thickness corresponds to muscle force. Muscle attachment maps view have been scaled to the same skull height. A, Suchia, B, Loricata, C, Crocodylomorpha, D, Crocodyliformes, E, Metasuchia.



Chapter 3— Cranial Joint Shape and Joint Loading in Suchia

INTRODUCTION

The correspondence between an animal's shape and the forces experienced by that animal is a cornerstone of functional morphology. Animals generate and experience numerous forces during feeding, locomotion, and other behaviors. In vertebrates, the musculoskeletal system ultimately generates and resists most of these forces—muscles generate the input force, and this force is transferred through skeletal elements into the environment as an output force. Skeletal elements and their soft- and hard-tissue linkages must resist the reaction forces that result from interactions with the environment. Because successfully interacting with the environment is crucial to organismal fitness, understanding the link between animal form and biomechanical performance has been a longstanding goal of functional morphologists. The pioneering studies of Maynard Smith and Savage provided early insights into the biomechanical analysis of vertebrate function, showing why cursorial animals lighten distal portions of the limb (Maynard Smith and Savage, 1955) and explained the relative proportions of the temporalis and masseter muscles in mammalian carnivores and herbivores (Maynard Smith and Savage, 1959). In the intervening decades, a great deal of research has investigated the link between an animal's morphology and forces that result from interactions with the environment. For example, Thomason (1985) used biomechanical modeling to show that the transition from subunguligrade to fully unguligrade posture in horses was linked with a decrease in mechanical stress. Herrel *et al.* (2005) found that relative beak width

corresponds with higher bite force in Darwin's finches, which is linked with greater feeding success on hard objects and thus niche differentiation. Kubo and Benton (2007) showed that during archosaur evolution, crocodile-line ancestors adapted an erect posture that was associated with a decrease in limb stress resulting from contact with the ground. By comparison, only a few studies have investigated the correspondence of an animal's form and "intraorganismal" forces such as joint reaction force. However, joints are crucial aspects of musculoskeletal systems, and so understanding the relationship between joint morphology and joint loading is critical.

The craniomandibular articulation (or jaw joint) is a key feature of the gnathostome feeding system. During biting, forces generated by jaw muscles are transferred between cranium and mandible both through the bitten item and through the jaw joint. Indeed, there is mounting evidence that the jaw joint absorbs a greater proportion of adductor muscle force than the bite point in at least some scenarios (Davis, 1955; Cleuren, Aerts and De Vree, 1995; Tseng and Wang, 2010). Thus, the jaw joint plays a primary role in resisting feeding-related forces. However, how cranial joints cope with extreme joint reaction forces, especially such as those in hard-biting species like crocodylians, remains to be understood.

A substantial body of research has focused on loads acting on craniomandibular articulations, although most of these studies focused on the novel mammalian craniomandibular articulation between the dentary and squamosal bones known as the temporomandibular joint (TMJ). Many important

works focused on the mandibular biomechanics of primate feeding and how the primate TMJ is loaded. Hylander conducted early modeling (Hylander, 1975) and experimental (Hylander, 1979) studies in primates and concluded that the joint on the balancing side is loaded more than the biting side during unilateral bites, and that the working side joint is nearly unloaded during unilateral bites at posterior teeth. Other studies in primates disagreed with both the former (Gingerich, 1979) and latter (Smith, 1978; Boyd *et al.*, 1990) points. Some works have focused on the evolutionary origins of the unique mammalian jaw joint. Examinations of transitional fossils suggested a period of reduced joint loading during the origin of the derived mammalian jaw joint. Crompton suggested that the evolutionary reduction in the ancestral quadratoarticular articulation was facilitated by a concomitant reduction in joint loading via reorganization of the adductor musculature (Crompton, 1963) and provided a model describing how these changes have taken place (Crompton and Hylander, 1986). Other works arrived at similar conclusions (Bramble, 1978). The extensive *in vivo* work of Herring and colleagues (Liu and Herring, 2000b, 2000a; Herring *et al.*, 2002; Herring, 2003) has provided support for these hypotheses by showing that joint loading is determined by muscle forces. The quadratoarticular joint (QAJ) typical of most gnathostomes has received less attention. Sinclair and Alexander estimated joint loading in several sauropsid taxa and found that the joint reaction force generally aligns with the structural axis of the quadrate (Sinclair and Alexander, 1987). A similar finding was reported *in vivo* from a caiman (Cleuren, Aerts and De Vree, 1995). Huber *et al.* report that the jaw joint in a durophagous holocephalan is

loaded compressively when biting in anterior loci but is in tension during posterior bites (Huber, Dean and Summers, 2008).

Therefore, we have a reasonable understanding of the loading environment of the mammalian jaw joint and a nascent understanding of the QAJ of other gnathostomes. How these loads are reflected in articular surface morphology, however, is virtually unknown. Hendrickx et al. (2016) performed a geometric morphometric analysis of the quadrate in spinosaurids and other theropods and concluded that the derived shape of the quadrate surface in spinosaurids facilitated a unique type of mandibular movement (Hendrickx, Mateus and Buffetaut, 2016). Bock (1959) investigated the quadrate articular morphology in a variety of birds and reported that some taxa have quadratoarticular joints with morphologies that are incapable of stabilizing the jaw joint. In these taxa, secondary craniomandibular articulations such as a medial process from the articular or derived collateral ligaments are employed to maintain joint stability. Some studies have examined the articular surface of various joints and related its morphology to aspects of animal ecology and behavior. Dunn and colleagues analyzed the relative size of various articular facets on the talus of gorillas to find that gorilla subspecies were able to be distinguished by these metrics and that gorilla populations with different ecologies have different articular morphologies (Dunn *et al.*, 2014; Boyer *et al.*, 2015). Dunn and colleagues also applied similar methods to fossil carnivoran tali, in which different reconstructed locomotor ecologies show different articular morphologies. Terhune (2011) investigated the biomechanical effects of the articular eminence in the primate craniomandibular

articulation to show that more inclined eminences are associated with high bite force. Subsequent work revealed that the morphology of the primate jaw joint is associated with diet (Terhune, 2013). Although these seminal works investigated functional correlates of joint morphological variation, they did not estimate joint loading. Further, mammalian jaw joints utilize secondary cartilage on dermal bones and often possess a fibrocartilaginous disc (Scapino, Obrez and Greising, 2006; Stanković *et al.*, 2013; Robinson *et al.*, 2015). The mammalian craniomandibular articulation is not homologous with the QAJ of other gnathostomes. Thus, our understanding of the patterns of covariation between craniomandibular joint morphology and loading remains limited.

Crocodylians and their fossil relatives are an ideal group in which to explore relationships of cranial joint loading and joint morphology. Extant crocodylians share relatively conserved jaw muscle anatomy (Iordansky, 1964) and simple parasagittal biting kinematics (Busbey, 1989; Cleuren and De Vree, 1992). Crocodylian skulls are akinetic (Iordansky, 1973), and most crocodylians routinely engage in extremely forceful, static crushing bites (Erickson, Lappin and Vliet, 2003). In comparison with fossil relatives, modern crocodylians have dorsoventrally flattened skulls which have reoriented jaw musculature (Figure 3.1; Holliday and Witmer, 2009). Modern forms have a strongly inclined quadrate that places the jaw joint caudal to the occiput (Figure 3.1; Langston, 1973), and so the evolution of crocodylians has been marked by drastic changes to the jaw joint and to the muscles that load it.

Here, we present a description of the jaw joint in a comparative sample of crocodylians and fossil ancestors (Figure 3.2) to investigate the relationship between joint shape and joint loading. We used computational biomechanics and anatomically detailed muscle reconstruction to estimate joint loads on a subset of these samples. We adapted geographic information systems (GIS) techniques and developed novel morphometrics to quantify the shape of articular surfaces. Finally, we compared loading and morphometric data to search for correspondence between joint surface morphology and joint loading.

AIMS AND PREDICTIONS

This study aims to determine the relationship between joint shape and joint loading. Joints are loaded by muscle force that is not resisted by the bite point. In bites at teeth in the caudal dentary, a higher proportion of muscle force is transferred to the bite point. Thus, we hypothesize that working side joint force will be lower when biting occurs at caudal locations and higher when biting at rostral locations (Hypothesis 1A). Because muscle force from the balancing side is only resisted by the jaw joint, we hypothesize that joint force magnitude will be higher on the balancing side than the working side (Hypothesis 1B). Wolff's Law and subsequent developments including the mechanostat hypothesis and chondral modeling predict that skeletal structures maintain roughly stable morphologies so long as they maintain relatively consistent loading regimes (Frost, 1979, 2001; Hamrick, 1999). Thus, we hypothesize that joint surface area will correlate strongly with joint force magnitude (Hypothesis 2). Normal forces most effectively stabilize joints when acting on a surface oriented perpendicularly to the force. Thus, we hypothesize that the amount of force acting in each

direction will correlate with the area of articular surface oriented in that direction (Hypothesis 3).

MATERIALS AND METHODS

Study Specimens— The extant crocodylian sample consisted of one individual from six extant crocodylian species: *Alligator mississippiensis*, *Caiman crocodilus*, *Paleosuchus palpebrosus*, *Crocodylus moreletii*, *Osteolaemus tetraspis*, and *Tomistoma schlegelii* (Table 3.1; Figure 3.2). Data on extant crocodylians were collected by dissections, regular and contrast-enhanced computed tomography (CT) imaging (Gignac *et al.*, 2016), and histological sections. This extant sample was complemented by select fossil suchians that characterize the transitions in QAJ morphology and overall skull shape. Five fossil taxa were studied: *Araripesuchus gomesii* (AMNH 24450), an undescribed “protosuchian” informally known as “*Gomphosuchus*” sp. (UCMP 97638; Clark, 1986), *Junggarsuchus sloani* (IVPP V14010), *Prestosuchus chiniquensis* (UFRGS PV0629T), and *Revueltosaurus callenderi* (PEFO 34561). Data on fossil relatives were collected by first-hand observations, photographs, and/ or CT/ laser imaging.

Joint Force Estimation— To calculate joint forces, we created biomechanical models of our sample of crocodylians and fossil relatives. The biomechanical modeling techniques are described in greater detail elsewhere (Sellers *et al.*, 2017) but will be summarized here (Figure 3.4). Specimens were scanned with regular or micro-computed tomography (CT/ μ CT) imaging or laser scanning (scan details are in Table 3.3.1). Three-dimensional boney anatomy was acquired by manually segmenting scan data with Avizo Lite 9.4 (FEI

Visualization Science Group; <https://www.thermo fisher.com>). Using Geomagic Studio 2013 (Geomagic, Inc.; <https://www.3dsystems.com>), models were cleaned, smoothed, and aligned to global anatomical axes (i.e., x corresponds to mediolateral, y corresponds to dorsoventral, and z corresponds to rostrocaudal), and mandibles were opened to five degrees of gape. Anatomically detailed muscle attachment sites were determined based on osteological correlates, contrast-enhanced CT imaging, dissections, and references to the literature (Iordansky, 1964; Schumacher, 1973; Busbey, 1989; Holliday and Witmer, 2007, 2009; Holliday, 2009). Previously reported muscle architecture (Porro *et al.*, 2011; Sellers *et al.*, 2017), the surface area of muscle attachment size, and its modeled three-dimensional shape were used to estimate physiological cross-sectional area (PCSA) and thus the force each muscle is capable of exerting. The computational package Boneload was used to distribute muscle forces in a realistic fashion (Grosse *et al.*, 2007; Davis *et al.*, 2010). These loads were applied to three-dimensional finite element models in the Strand7 finite element analysis (FEA) software (Strand7 Pty. Ltd.; <http://www.strand7.com>). A single node in the center of the articular surface of both quadrates was constrained in all three translational and all three rotational degrees of freedom. We simulated bites both in rostral and caudal positions unilaterally by constraining a single node at the tip of the biting tooth in all three translational and all three rotational degrees of freedom. All muscles were modeled as contracting maximally, which is consistent with previous EMG data for crushing bites in crocodylians (Busbey, 1989; Cleuren, Aerts and De Vree, 1995).

Joint Articular Surface Morphometrics— We adapted geographic information systems (GIS) approaches akin to methods used by Evans *et al.* (2007) and Melstrom *et al.* (2019) to describe tooth shape complexity, and we developed novel methods to visualize and quantify joint surface topographic morphology. The articular surface of the mandibular condyle of the left quadrate was isolated from the 3D mesh created above. Meshes were smoothed in Avizo using the built-in smoothing algorithm with 20 iterations and scaled to ~1000 triangles. The orientation of a given surface can be described with an orthogonal normal unit vector (Figure 3.5A), and so the 3D model of the articular surface made up of ~1000 surface triangles has a corresponding number of normal vectors (Figure 3.5B). To estimate the correspondence of each patch of surface with the orientation of joint reaction force, we developed a “correspondence index” (CI). For each patch of surface, the load vector calculated from FEA and the local normal vector describe the orientations of joint reaction force and the local surface. When dealing with unit vectors, the cross product of two vectors ranges from zero to one as the angle between the vectors ranges from 0° to 90°. Thus, cross products can serve as a measure of collinearity. In each biting scenario, we calculated the correspondence index for each triangle as the cross product of the normal vector of the triangle with the unit vector of joint reaction force, as shown in Equation 1:

$$CI_{triangle} = \vec{v}_{normal} \times \vec{v}_{JRF} \quad (1)$$

A patch that is perpendicular to the joint load vector would have collinear normal and loading vectors and thus would have a cross product of 0; a patch that is

parallel with the joint reaction force would have with orthogonal orientation and loading vectors would have a cross product of 1. To summarize the correspondence of the total surface, the correspondence index of each patch was normalized by dividing by the relative area of that patch. The overall correspondence index for the joint surface is one minus the sum of these normalized cross products, as shown in Equation 2:

$$CI_{joint} = 1 - \sum I_{triangle} \cdot \left(\frac{A_{triangle}}{A_{joint}} \right)$$

Thus, a joint surface that was entirely orthogonal to the loading vector would have a correspondence index of 1 whereas a joint surface that was entirely parallel with the loading vector would have a correspondence index of 0. To visualize the relationship between the distribution of joint surface orientation and joint loading vectors, we plotted the orientation of each in ternary space.

Statistical Analyses— To test our hypothesis that working side joint force will be lower when biting occurs at caudal locations and higher when biting at rostral locations (Hypothesis 1A), and that joint force magnitude will be higher on the balancing side than the working side (Hypothesis 1B), we used phylogenetic generalized least-squares (PGLS) regression of working and balancing side joint forces for both rostral and caudal bites against skull width using a time-scaled phylogeny modified from Nesbitt (2011) and Wilberg, Turner and Brochu (2019). To test our hypothesis that joint surface area is associated with joint force magnitude (Hypothesis 2), we used PGLS of joint area against each of our calculated joint reaction forces. To test our hypothesis that the amount of force acting in each direction will correlate with the area of articular surface oriented in

that direction (Hypothesis 3), we first had to calculate the amount of surface oriented in each direction. To do this, we multiplied the area of each patch of surface by each component of the proportion vector of that patch. The proportion vector (i.e., the square of the unit vector) is a vector whose components sum to unity. The sum of the products of the area of each patch and each component of the proportion vector represents the amount of joint surface oriented in each direction.

RESULTS

Organization of Results— We first present a description of the caudal quadrate in extant crocodylians to illustrate the anatomy of the region. We subsequently describe the condition of fossil taxa beginning with the most basal and proceeding towards the crown group. Next, we present the results of the joint loading analysis. Finally, results of the quantitative morphometrics and the correspondence of joint surface and joint loading are presented.

Description— In extant crocodylians, the QAJ forms a stable hinge joint. The two hemicondyles are less distinctly separated than in earlier forms, and the articular surface of the quadrate is hourglass to saddle-shaped in ventral view (Figure 3.3). The lateral hemicondyle is larger and more rounded, whereas the medial hemicondyle forms a sharp, laterally oriented lip (Figure 3.3). The extreme reorientation of the distal quadrate caudally causes the articular surface to take on a substantial caudal orientation, especially in larger individuals. The joint capsule and articular cartilage cap together leave a distinct scar delineating the articular portions of the quadrate from other parts of this bone (Figure 3.3). A thickened band of connective tissue forms a lateral collateral ligament which

connects the lateral edge of the quadratojugal to the lateral edge of the surangular (Saber and Hassanin, 2014), leaving a scar on the cranium and mandible in larger individuals. On the mandible, the surangular makes a variable contribution to the glenoid fossa but is never covered in articular cartilage. The quadrate is heavily pneumatized, and in extant forms, the pneumatic cavity invades the articular and forms a soft-tissue tube called the siphonium. The siphonium exits the quadrate caudodorsal to the articular surface and skirts the joint capsule via a membranous tube to enter the articular between the joint capsule and the insertion for m. depressor mandibulae (mDM). The QAJ of the gharial, *Gavialis gangeticus*, deserves special attention. The two hemicondyles are merged in *Gavialis*, presenting as a single convex condyle whose long axis is rostromedial-caudolateral rather than mediolateral as in most extant crocodylians (Langston, 1965; see also Brochu, 2013; Fig 14D). This less restrictive jaw joint morphology in *Gavialis* may be related to the piscivory this species displays, as feeding on compliant items like fish may require less overall feeding forces. Indeed, gharials are the sole outlier of extant crocodylian bite force (Erickson *et al.*, 2012).

In early fossil relatives of crocodylians, the quadrate retained a relatively primitive morphology typical of archosaurs. In basal loricatans (e.g., *Prestosuchus*, *Saurosuchus*), the quadrate is relatively unmodified from the primitive condition. The articular surface bears two distinct hemicondyles separated by a groove that courses rostrally to rostromedially (Figure 3.6A), and the medial hemicondyle is more rostrally placed and rostrally oriented than the

lateral one, as in *Batrachotomus* and *Prestosuchus*. In some specimens, the medial hemicondyle is flexed such that the majority of the medial hemicondyle does not participate in jaw articulation in all poses (Figure 3.6B). A distinct scar for the joint capsule is clearly visible in *Batrachotomus* (Figure 3.6B; see also Gower, 1999) and *Postosuchus* (Weinbaum, 2011). Chatterjee (1985) included a figure that suggests a ligamentous scar on the surangular of *Postosuchus* but did not comment on this feature.

The first steps towards the extant condition are found in Crocodylomorpha. The expansion of the otic notch has already begun to create an angle between the primary head and the body of the quadrate, as in *Macelognathus* (Leardi, Pol and Clark, 2017). Although Walker described the quadrate as “not greatly inclined” in *Sphenosuchus* (Walker, 1990), the articulation with the mandible is caudal to the primary head of the quadrate in *Hesperosuchus* (Clark, Sues and Berman, 2000) and *Dromicosuchus* (Wu and Chatterjee, 1993). In most ‘sphenosuchians’, the dorsal part of the quadrate has elaborated into several distinct processes (Walker, 1990; Wu and Chatterjee, 1993; Leardi, Pol and Clark, 2017). Additionally, basal crocodylomorphs show the first signs of substantial pneumatization of the quadrate (Walker, 1990; Wu and Chatterjee, 1993; Leardi, Pol and Clark, 2017). Walker (1990) reported the presence of a ligament scar between the quadratojugal and surangular in *Sphenosuchus*, suggesting that a lateral collateral ligament goes back to Crocodylomorpha at least. The articulated quadrate of *Hesperosuchus* shows a clear scar for the joint

capsule, but the material is not sufficiently prepared to reveal the majority of the articular surface.

Basal crocodyliforms include the first forms with substantially inclined quadrates, placing the craniomandibular articulation notably caudal to the primary head of the quadrate (Gow, 2000). Some protosuchians seem to have obliterated the bicondylar morphology of the jaw joint in more basal archosaurs (e.g. *Gomphosuchus*; Ősi, 2013). Depending on the polarity of characters, this may be pleisiomorphic for modern crocodylians. If this is the case, the two hemicondyles of modern crocodylians represent a convergence upon or reversion to a bicondylar state. In the slightly more crownward shartegosuchids (e.g., *Fruitachampsia*), the articular surface of the quadrate is described as triangular with the apex pointing dorsally (Clark, 2011). The authors describe a bicondylar morphology, with the smaller medial condyle facing laterally and the larger lateral condyle oriented caudally (Clark, 2011). This suggests that the articular surface morphology present in protosuchians is a derived condition.

By Mesoeucrocodylia, the fundamental modern pattern of a saddle-shaped joint surface with two hemicondyles was established. However, the quadrate is still dorsoventrally tall in many dorsoventrally deep skulled notosuchians (e.g. *Araripesuchus*, present study; *Caipirasuchus*, Pol *et al.*, 2014). In neosuchians such as the goniopholid *Eutretauranosuchus* (Mook, 1967) and basal eusuchians such as *Bernissartia* (Martin *et al.*, 2020), the articular surface is generally comparable to those found in modern forms. In most neosuchians including

extant crocodylians, the entire cranium is dorsoventrally flattened (Iordansky, 1973; Langston, 1973), which displaces the distal quadrate caudally.

Joint Loading— Patterns of joint loading generally conformed to the predicted patterns. The results of the biomechanical analyses are summarized in Tables 2 – 5. In both rostral and caudal bites, both working side and balancing side joint force scale isometrically with skull width (95% CI: 1.76 – 2.29 and 1.82 – 2.32, respectively, for rostral bites; 1.57 – 2.31 and 1.82 – 2.43, respectively, for caudal bites). The expected tradeoff between joint force and bite force along the rostrocaudal axis was observed: bite force was lower in rostral bites and higher in caudal bites whereas the opposite pattern was found in joint force (Tables 2 – 5; Figure 3.7; Figure 3.8), and so Hypothesis 1A was supported. The magnitude of change depended on the length of the rostrum, and so the largest difference was seen in the longirostrine *Tomistoma* where rostral bite force was only ~30% of caudal bite force; among extant taxa, the discrepancy between rostral and caudal bites was lowest in the brevirostrine *Osteolaemus*, in which the rostral bite force was ~45% of caudal bite force. Modeled fossil taxa had no overlap with the proportions found in extant taxa; the *highest* discrepancy was found in *Junggarsuchus* (~46%), and other fossil taxa ranged from ~54% (*Gomphosuchus*) to ~67% (*Prestosuchus*).

Joint force magnitude was higher in the balancing side joints and lower in working side joints (Tables 2 – 5; Figure 3.7; Figure 3.8); thus, Hypothesis 1B was supported. This effect is more pronounced in caudal bites. In rostral bites, working side joint force was an average of ~85% that of balancing side joint force

(Table 3.4), ranging from 69% in *Paleosuchus* to ~95% in *Caiman*. Bite force is high in caudal bites, causing the working side jaw joint to resist a lower proportion of muscle force. In caudal bites, therefore, working side joint force is on average ~42% that of balancing side joint force (Table 3.5), ranging from ~23% in *Crocodylus* to ~65% in *Tomistoma*. There is little difference in the mean values of this discrepancy between extant crocodylians and fossil taxa in rostral bites; in rostral bites, the mean ratio of working side joint force to balancing side joint force is ~83% in extant crocodylians and ~87% in fossil taxa. By contrast, the discrepancy between working and balancing side joint forces is greater in extant crocodylians than fossil taxa; in caudal bites, the mean ratio of working side joint force to balancing side joint force is ~32% in extant crocodylians and ~53% in fossil taxa.

Because the balancing side of the mandible is not contacting the prey item, all of the muscular force imparted to it is either resisted by the jaw joint or transferred to the balancing side. Accordingly, there is relatively little change in balancing side joint force between rostral and caudal bites; ~12% higher in *Alligator* and ~17% lower in *Gomphosuchus* are the largest changes in balancing side joint force between rostral to caudal bites. Conversely, a substantial proportion of working side muscle force is transferred to the prey item, with the remainder of the force being resisted by the bite point, and so the working side jaw joint experiences substantially lower loading from caudal bites than rostral bites (Tables 2 – 5; Figure 3.7; Figure 3.8), with working side joint force ranging from ~71% lower than balancing side joint force in *Caiman* to ~32% lower in

Tomistoma. Surprisingly, these ratios were more variable among extant crocodylians than extinct taxa, with working side joint force ranging from ~49% lower than balancing side joint force in *Prestosuchus* to ~29% lower in *Araripesuchus*.

Joint Morphometrics and Correspondence with Loading— In general, the joint surfaces reflect loading conditions. Joint articular area (95% CI: 1.83 – 2.38) and both working side and balancing side joint loads (see above) and scale isometrically with skull width, and so joint pressure is relatively consistent across the entire sample (Figure 3.9). Thus, Hypothesis 2 is supported for working and balancing side joints in both rostral and caudal bites (rostral bite working pressure 95% CI: -0.171 – 0.017; rostral bite balancing pressure 95% CI: -0.146 – 0.071; caudal bite working pressure 95% CI: -0.348 – 0.021, caudal bite balancing pressure 95% CI: -0.113 – 0.152).

Across the sample, balancing side correspondence index was more consistent than working side. For rostral bites, balancing side CI ranged from 0.376 in *Araripesuchus* to 0.545 in *Revueltosaurus* with the notable exception of *Gomphosuchus* (0.225). In caudal bites, balancing side CI was very similar to values from rostral bites, ranging from 0.379 in *Araripesuchus* to 0.530 in *Revueltosaurus*, with *Gomphosuchus* again as an outlier (0.226). *Gomphosuchus* had the lowest quality of preservation among the fossil taxa in this study, however, and the *in situ* location of the mandibles required identification of the articular surface on CT data. As such, these anomalous values may represent uncertainty in identifying the articular surface rather than

true anatomy. In rostral bites, working side CI ranged from 0.141 in *Tomistoma* to 0.441 in *Junggarsuchus*. Working side CI in caudal bites was considerably more variable than working side CI in rostral bites or balancing side CI in either biting scenario, ranging from 0.131 in *Tomistoma* to 0.444 in *Junggarsuchus*. *Caiman* and *Paleosuchus* also had CI values below 0.2 for the working side in caudal bites (*Caiman*: 0.162; *Paleosuchus*: 0.192).

Working side and balancing side CIs were more similar in rostral than caudal bites. For the balancing side, the largest change in CI was in *Junggarsuchus*, from 0.489 in rostral bites to 0.530 in caudal bites. For the working side, all large changes in CI between rostral and caudal were in the alligatoroids (*Alligator*: 0.368 in rostral bites to 0.236 in caudal bites; *Caiman*: 0.315 to 0.162; *Paleosuchus*: 0.337 to 0.192). The next-largest change was in *Revueltosaurus* (0.318 to 0.253).

The proportion of force acting in the mediolateral and rostrocaudal directions on a joint showed no correlation with the proportion of surface oriented in a given area in any biting scenarios. However, in every biting scenario, the amount of surface oriented dorsoventrally was predicted by the amount of dorsoventral joint force, and so Hypothesis 3 was partially supported. Further, the amount of surface oriented rostrocaudally modeled by balancing side joint force oriented rostrocaudally was very nearly statistically significant ($p = 0.069$). Joint articular cartilage morphology may account for this mismatch, but articular cartilage is rarely preserved in fossils. Additionally, extant crocodylians employ a pterygomandibular articulation that likely supports (if not supplants) the

quadratoarticular joint's role in resisting mediolateral forces (Iordansky, 1973; Schumacher, 1973; Holliday *et al.*, 2015).

DISCUSSION

Extant crocodylians have flatter jaw joint surfaces than their extinct ancestors. The extant crocodylian articular surface has less pronounced condyles than ancestral suchians, which may reflect less variable loading regimes in crocodylians. Alternatively, the derived joint surface of crocodylians suggests that extant taxa may use additional mechanical means of stabilizing the joint. Extant crocodylians are known to have a second functional articulation between the cranium and mandible; i.e., between the lateral surface of the pterygoid flange and the medial surface of the mandible (Iordansky, 1973; Schumacher, 1973; Holliday *et al.*, 2015). It is possible that the possession of a functional secondary craniomandibular articulation between the pterygoid buttress and caudal mandible in crocodylians freed the quadratoarticular joint to become more specialized to resisting parasagittal forces, as the pterygoid buttress resists medial excursion of the mandibles by bracing them (Langston, 1973). Crocodylians appear to have a distributed joint system in the feeding apparatus.

Quantitative analyses of joint surfaces suggests that crocodylids *sensu* Oaks (2011) possess a derived joint surface compared to alligatorids. The medial hemicondyle of crocodylids is relatively larger and is rostrocaudally expanded relative to those of alligatorids and fossil taxa (Figure 3.10). Further, *Crocodylus*, *Osteolaemus*, and *Tomistoma* all show joint surfaces with a narrower range of orientations than those found in *Alligator*, *Caiman*, and *Paleosuchus* (Figure 3.10).

Joint force magnitude is a measure of the inefficiency of biting (Huber, Dean and Summers, 2008). In a perfectly efficient feeding apparatus, 100% of muscle force is transmitted to the bite point, the mandible acts as a link rather than a lever (Hylander, 1975). Of course, in most real feeding systems, the mandible acts as a lever and a considerable amount of muscle force loads the jaw joints rather than being channeled into bite force. As joint loads are not generally useful in feeding, joint force represents “wasted” muscle force. Thus, joint force is inversely correlated with mechanical efficiency, defined as the ratio of bite force to muscle force (Dumont *et al.*, 2011; Tseng and Flynn, 2018; Ferreira *et al.*, 2020). Results of the present study show that crocodylians have mechanical efficiencies ranging from 0.047 to 0.185 in rostral bites and 0.117 to 0.336 in caudal bites (Table 3.4; Table 3.5). The lowest values are in the longirostrine *Tomistoma* and the highest values are in the protosuchian *Gomphosuchus*. Thus, the most efficient bite in the present study used only ~30% of available muscle force whereas ~70% of muscle force was spent on loading the jaw joints. Recent studies of other amniotes have reported mechanical efficiencies of ~0.1 – 0.3 in rostral bites in turtles (Ferreira *et al.*, 2020), ~0.3 in caudal bites in primates (Dumont *et al.*, 2011), ~0.25 – 0.45 in rostral bites in carnivorans (Tseng and Flynn, 2018), and ~0.15 – 0.3 in rostral bites and ~0.3 – 0.45 in caudal bites in ursids (Pérez-ramos *et al.*, 2020).

Crocodylians have less efficient feeding systems relative to other amniote clades. Although not explicitly reported in these studies, joint force is necessarily relatively lower in taxa with higher mechanical efficiency. If the mechanostat

hypothesis is correct (Frost, 2001), we would expect crocodylians to have relatively larger jaw joints compared to the above taxa with more efficient feeding systems. The finding of low mechanical efficiency suggests that high bite force in crocodylians relative to other clades must have been accomplished via high muscle mass relative to body size, as crocodylians have relatively inefficient bites.

The methods used in the present study can be used to test longstanding hypotheses of biomechanical change, such as the idea that evolutionary acquisition of the mammalian TMJ was associated with a period of proportionally low joint forces (e.g., higher bite force). Various authors have noted both a progressively shrinking QAJ and the evolution of derived jaw musculature. However, there is some disagreement about whether a small or weak jaw joint prompted the evolution of derived jaw musculature (Bramble, 1978) or was allowed by it (Crompton, 1963; Crompton and Parker, 1978). Some studies have provided evidence that mammals have higher mechanical efficiency and thus lower joint force (see above), which is consistent with the hypothesis that mammals have a heritage of lower joint force. Future studies will investigate the relationship between joint area, joint shape, and joint loading in other amniote clades to elucidate evolutionary patterns in the biomechanics of joints.

Despite considerable changes in joint form and joint loading, peak joint pressure was remarkably consistent across the sample. Despite considerable changes in joint form and joint loading, peak joint pressure was remarkably consistent across the sample. The lowest values for peak (i.e., balancing side)

joint pressure was ~6 MPa in a rostral bite in *Alligator*, and the highest values were ~11 MPa in a caudal bite in *Caiman*. Notably, these values are on the same order of magnitude to those reported from *ex vivo* studies in the articular surfaces of other joint systems including the human femoroacetabular joint (~15 MPa; Afoke, Byers and Hutton, 1987), subtalar joint (~5MPa; Wang *et al.*, 1995), and various joints within the wrist (~2 MPa; Hara *et al.*, 1992). These values also fall precisely within the range of joint pressures that articular cartilage is actively maintained (~1-10MPa; Hamrick, 1999). This is consistent with the hypothesis that skeletal structures maintain a constant stress regime (Biewener, 1989), suggesting that crocodylians have maintained biomechanical equilibrium despite profound changes to skull shape.

The protosuchian *Gomphosuchus* has an anomalously convex joint surface without the typical bicondylar morphology found in most suchians, which is reflected in an unusually broad range of orientations on the articular surface. Thus, the quadrate and articular have relatively low congruence. An incongruous joint surface would favor movement over stability, which would facilitate translational movements between the cranium and mandible. This may be indicative of a craniomandibular articulation that orally processed food, which previously has been posited for protosuchians including *Gomphosuchus* (Ősi, 2013). This may also explain why *Gomphosuchus* has a mismatch between its joint surface proportions and the loads acting on the joint (i.e., low correspondence index; Table 3.6; Table 3.7). Future work will investigate the congruence between the quadrate and articular in this sample.

It is possible that relatively high joint forces in crocodylians prompted the evolution of akinesis by suturally immobilizing numerous cranial joints. Previous work (Chapter 2; Sellers et al., in review) has shown that extant crocodylians have inefficient muscle orientations (and thus high joint loads) compared to their fossil relatives, yet this study found that extant crocodylians maintain size-standardized bite force performance values comparable to fossil suchians. If this is the case, akinesis would represent an adaptation to high joint force, and muscular reorganization should evolutionarily precede akinesis. Conversely, akinesis may be a preadaptation to high joint force. In this scenario, akinesis would precede the reorganization of jaw muscles. Protosuchians maintain ancestral jaw adductor anatomy but show the presence of sutured basiptyergoid and otic joint, providing tentative evidence for the latter scenario. Alternatively, the suturing of the quadrate and palate to the braincase may reflect transient tensile loads. Interdigitating sutures are known to be associated with tensile loads (Rafferty and Herring, 1999). Indeed, Bramble (1978) suggested that mammalian akinesis at least in part represents an adaptation to tensile loads acting at the jaw joint.

CONCLUSIONS

The present study illustrates evolutionary patterns of joint loading in one of the great transformations in vertebrate evolution. From the primitive condition, crocodylomorph fossils record the early stepwise acquisition of the extant crocodylian jaw joint, transforming it from a dorsoventrally-oriented bicondylar morphology to a flattened, obliquely oriented hourglass shape. The crocodylian jaw joints resist more force than the bite point during feeding. Mechanical

efficiency in crocodylians is low relative to other clades, which suggests that crocodylians have high joint loads relative to other clades. There is preliminary evidence that early fossil relatives had higher mechanical efficiency and that the joints have become progressively more loaded during crocodylian evolution. Despite these changes in joint shape and joint loading, crocodyliforms maintain a relatively constant joint pressure, suggesting coordinated evolution of these anatomical traits and biomechanical parameters.

Table 3.1. Suchian taxa used in quantitative study.

Taxon	Specimen Number	Skull Width (cm)	Skull Height (cm)
<i>Alligator mississippiensis</i>	MUVC AL008	24.3	17.3
<i>Caiman crocodilus</i>	FMNH 73711	5.9	4.1
<i>Paleosuchus palpebrosus</i>	FMNH 22817	2.4	1.7
<i>Crocodylus moreletii</i>	TMM M-4980	16.8	8.9
<i>Osteolaemus tetraspis</i>	FMNH 98936	4.9	3.5
<i>Tomistoma schlegelii</i>	TMM M-6342	13.9	7.7
<i>Araripesuchus gomesii</i>	AMNH 24450	4.8	3.4
<i>“Gomphosuchus”</i> sp.	UCMP 97638	4.1	2.3
<i>Junggarsuchus sloani</i>	IVPP V14010	5.5	5.2
<i>Prestosuchus chiniquensis</i>	UFRGS PV0629T	23.5	21.6
<i>Revueltosaurus callenderi</i>	PEFO 34561	9.3	7.1

Table 3.2. Components of working (i.e., biting) side and balancing (i.e., non-biting) side joint force and bite force for rostral bites.

Taxon	Working Side Joint Force (N)			Balancing Side Joint Force (N)			Bite Force (N)		
	F _x	F _y	F _z	F _x	F _y	F _z	F _x	F _y	F _z
<i>Alligator</i>	-2310	4490	5530	2960	5510	6120	-3.25	2520	-170
<i>Caiman</i>	-149	258	301	133	302	277	-2.24	142	-30.1
<i>Paleosuchus</i>	-13.6	34.3	28.7	16.4	48.4	44.9	-3.82	24	0.70
<i>Crocodylus</i>	-618	1190	1560	856	1550	2090	-83.7	669	150
<i>Osteolaemus</i>	-66.9	166	168	89.1	207	241	-25.5	111	-6.09
<i>Tomistoma</i>	-945	1290	1470	1020	1310	1560	-15.1	374	-4.86
<i>Araripesuchus</i>	-118	206	147	127	244	170	-7	115	5.58
" <i>Gomphosuchus</i> "	-15.2	100	17.5	19	113	33	-5.97	74.9	-0.48
<i>Junggarsuchus</i>	-144	410	148	124	460	59.4	12.1	106	29.3
<i>Prestosuchus</i>	-1180	6340	2930	1860	7850	3970	-60.9	3170	-300
<i>Revueltosaurus</i>	-334	778	296	326	907	355	-35.8	437	-186

Table 3.3. Components of working (i.e., biting) side and balancing (i.e., non-biting) side joint force and bite force for caudal bites.

Taxon	Working Side Joint Force (N)			Balancing Side Joint Force (N)			Bite Force (N)		
	F _x	F _y	F _z	F _x	F _y	F _z	F _x	F _y	F _z
<i>Alligator</i>	-1370	532	1910	2920	6170	7140	-915	5820	2430
<i>Caiman</i>	-74.8	-15.4	98.3	106	338	298	-49.2	379	152
<i>Paleosuchus</i>	-6.28	-6.84	19	12.1	54.9	43.2	-6.82	58.7	12.2
<i>Crocodylus</i>	-159	97	636	835	1580	2280	-521	1730	883
<i>Osteolaemus</i>	-36.4	33.9	68.9	82.5	226	232	-49.4	224	102
<i>Tomistoma</i>	-657	534	1220	926	1220	1680	-209	1210	129
<i>Araripesuchus</i>	-87.6	137	115	114	241	182	-24.4	188	25.5
" <i>Gomphosuchus</i> "	-9.33	57.9	11.2	14.7	94.5	25.8	-7.52	136	13
<i>Junggarsuchus</i>	-90.7	272	84.6	116	472	157	-33	233	-5.59
<i>Prestosuchus</i>	-756	2980	2000	2190	8700	4830	-813	5680	-217
<i>Revueltosaurus</i>	-277	463	167	375	974	386	-142	686	-88.3

Table 3.4. Comparison of cranial force magnitudes for rostral bites.

Taxon	Sum of Muscle Force (N)	Bite Force (N)	Working Side Joint Force (N)	Balancing Side Joint Force (N)	Mechanical Efficiency	Working Side Joint Pressure (MPa)	Balancing Side Joint Pressure (MPa)
<i>Alligator</i>	29113	2526	7488	8751	0.087	5.40	6.30
<i>Caiman</i>	1415	145.2	423.5	430.8	0.103	10.15	10.32
<i>Paleosuchus</i>	201.8	24.31	46.75	68.03	0.120	6.51	9.47
<i>Crocodylus</i>	10086	690.7	2057	2739	0.068	5.32	7.08
<i>Osteolaemus</i>	1026	114.1	245.5	323.0	0.111	7.55	10.15
<i>Tomistoma</i>	7981	374.3	2172	2278	0.047	6.71	7.04
<i>Araripesuchus</i>	941.5	115.3	279.2	323.4	0.123	6.98	8.09
" <i>Gomphosuchus</i> "	406.9	75.14	102.7	119.2	0.185	7.11	8.26
<i>Junggarsuchus</i>	1573.6	110.6	459.1	480.1	0.070	7.19	7.52
<i>Prestosuchus</i>	23661	3185	7083	8991	0.135	6.72	8.53
<i>Revueltosaurus</i>	2910	476.3	897.0	1027	0.164	8.29	9.49

Table 3.5. Comparison of cranial force magnitudes for caudal bites.

Taxon	Sum of Muscle Force (N)	Bite Force (N)	Working Side Joint Force (N)	Balancing Side Joint Force (N)	Mechanical Efficiency	Working Side Joint Pressure (MPa)	Balancing Side Joint Pressure (MPa)
<i>Alligator</i>	29113	6373	2410	9878	0.219	1.74	7.12
<i>Caiman</i>	1415	411.3	124.5	462.9	0.291	2.98	11.09
<i>Paleosuchus</i>	201.8	60.34	21.15	70.90	0.299	2.94	9.87
<i>Crocodylus</i>	10086	2011	662.7	2897	0.199	1.71	7.49
<i>Osteolaemus</i>	1026	251.0	84.98	334.2	0.245	2.61	10.28
<i>Tomistoma</i>	7981	1235	1485	2273	0.155	4.59	7.03
<i>Araripesuchus</i>	941.5	191.3	199.2	322.8	0.203	4.98	8.07
<i>"Gomphosuchus"</i>	406.9	136.8	59.71	99.06	0.336	4.14	6.86
<i>Junggarsuchus</i>	1574	235.4	298.9	510.8	0.150	4.68	8.00
<i>Prestosuchus</i>	23661	5742	3668	10189	0.243	3.48	9.67
<i>Revueltosaurus</i>	2910	706.1	564.8	1112.8	0.243	5.22	10.28

Table 3.6. Correspondence index for rostral bites shows that the joint surface is more well-suited to dealing with the higher-magnitude balancing side joint forces.

Taxon	Working Side Correspondence Index	Balancing Side Correspondence Index
<i>Alligator</i>	0.368	0.398
<i>Caiman</i>	0.315	0.443
<i>Paleosuchus</i>	0.337	0.462
<i>Crocodylus</i>	0.294	0.434
<i>Osteolaemus</i>	0.354	0.421
<i>Tomistoma</i>	0.137	0.415
<i>Araripesuchus</i>	0.251	0.376
" <i>Gomphosuchus</i> "	0.276	0.225
<i>Junggarsuchus</i>	0.441	0.486
<i>Prestosuchus</i>	0.371	0.403
<i>Revueltosaurus</i>	0.318	0.545

Table 3.7. Correspondence index for caudal bites.

Taxon	Working Side Correspondence Index	Balancing Side Correspondence Index
<i>Alligator</i>	0.236	0.407
<i>Caiman</i>	0.162	0.438
<i>Paleosuchus</i>	0.192	0.464
<i>Crocodylus</i>	0.302	0.435
<i>Osteolaemus</i>	0.312	0.422
<i>Tomistoma</i>	0.131	0.405
<i>Araripesuchus</i>	0.245	0.379
" <i>Gomphosuchus</i> "	0.278	0.226
<i>Junggarsuchus</i>	0.444	0.530
<i>Prestosuchus</i>	0.355	0.400
<i>Revueltosaurus</i>	0.253	0.542

Figure 3.1. Left lateral views of *Prestosuchus* (A) and *Alligator* (B). The quadrate is highlighted in gray. Note the caudal tilt of the quadrate in *Alligator*, a derived extant crocodylian. D, dorsal, C, caudal, V, ventral, R, rostral.

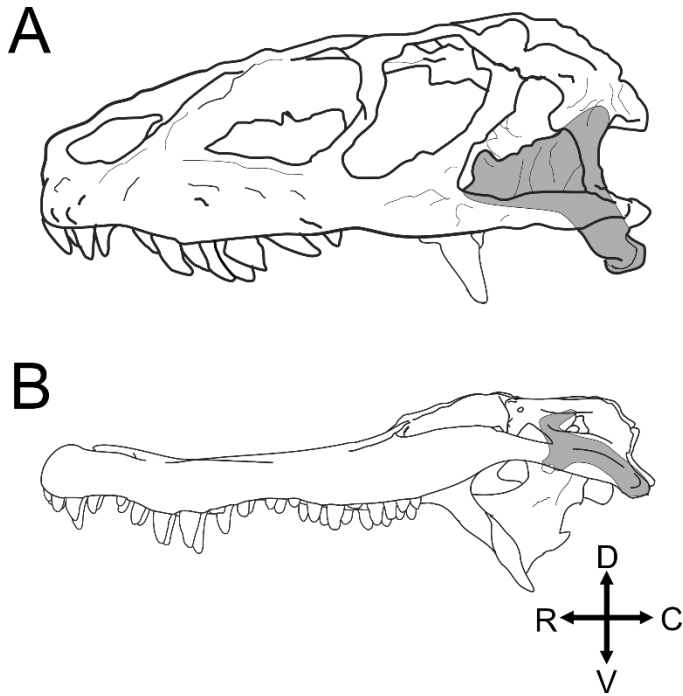


Figure 3.2. Cladogram showing taxa used for quantitative study. A) Suchia, B) Loricata, C) Crocodylomorpha, D) Crocodyliformes, E) Mesoeucrocodylia, D) Crocodylia, F) Crocodylia, G) Alligatoridae, H) Crocodylidae.

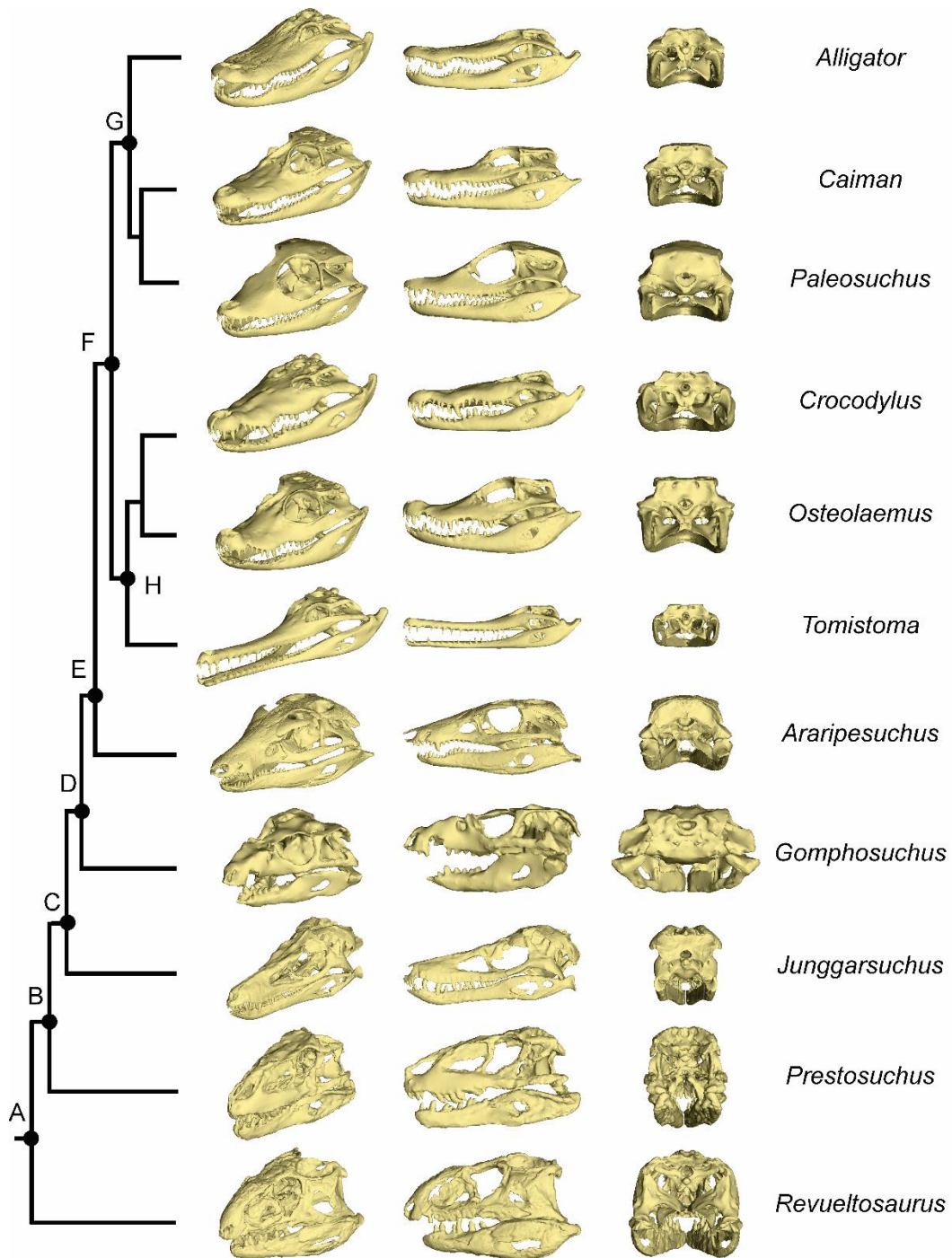


Figure 3.3. Caudal view of the joint surface in an adult individual of *Alligator mississippiensis*. D, dorsal, V, ventral, M, medial, L, lateral.

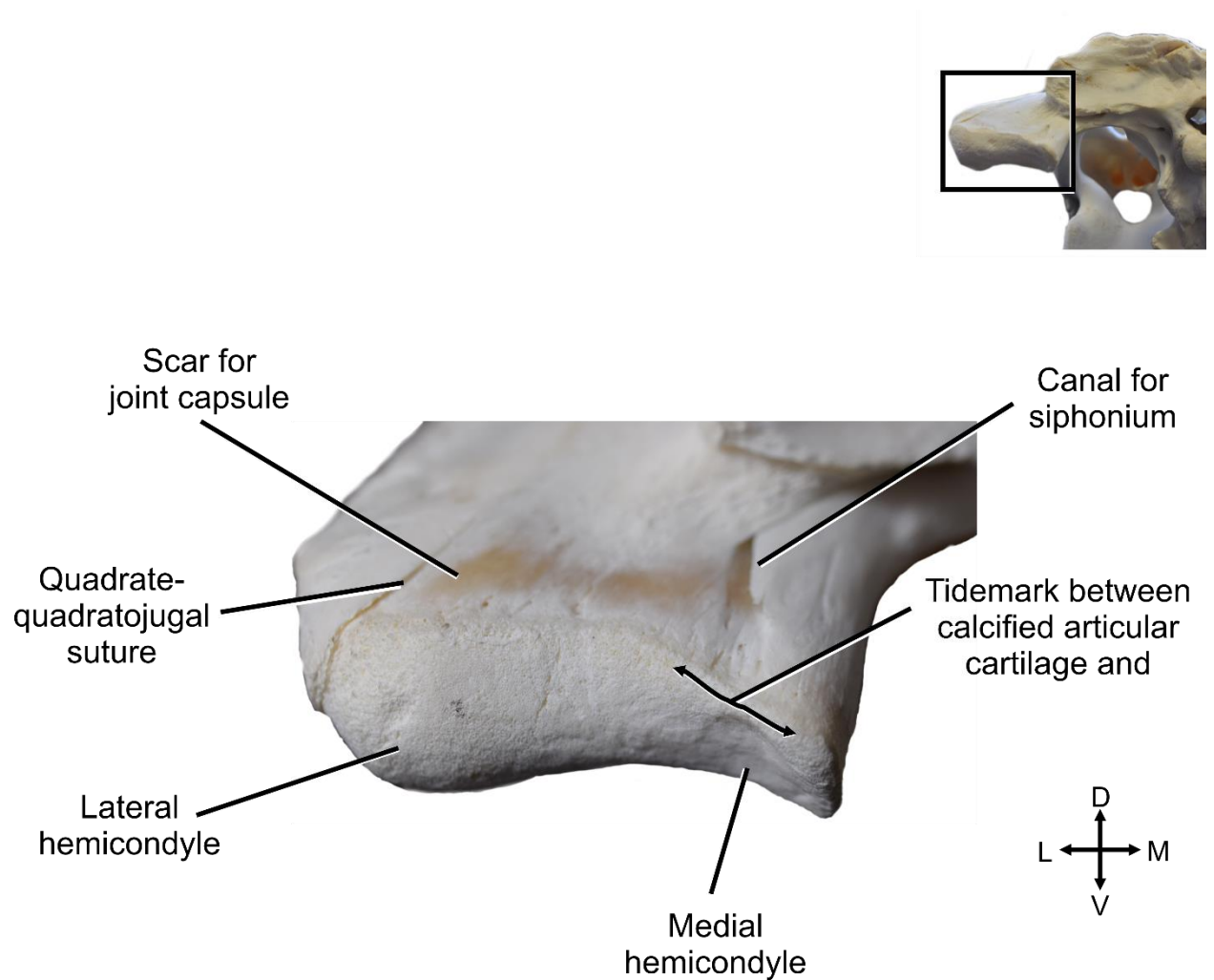


Figure 3.4. Workflow used to estimate joint loading. (A) Computed tomography data were segmented to create three-dimensional meshes of cranial and mandibular morphology (B). These models were cleaned in Geomagic 13 and imported into Strand7 FEA software and meshed (C). Osteological correlates and contrast-enhanced CT imaging were used to digitally “map” muscle attachment sites onto models (D). The computational package Boneload was used to realistically distribute muscle forces (E). These muscle force fields were used to load finite element models and calculate bite and joint reaction forces (F). Joint surfaces were removed in Geomagic 13 (G). Joint surfaces were analyzed using orientation patch counting (H) and by plotting orientation of normal vectors in ternary space (I). Modified from Sellers et al. (2017).

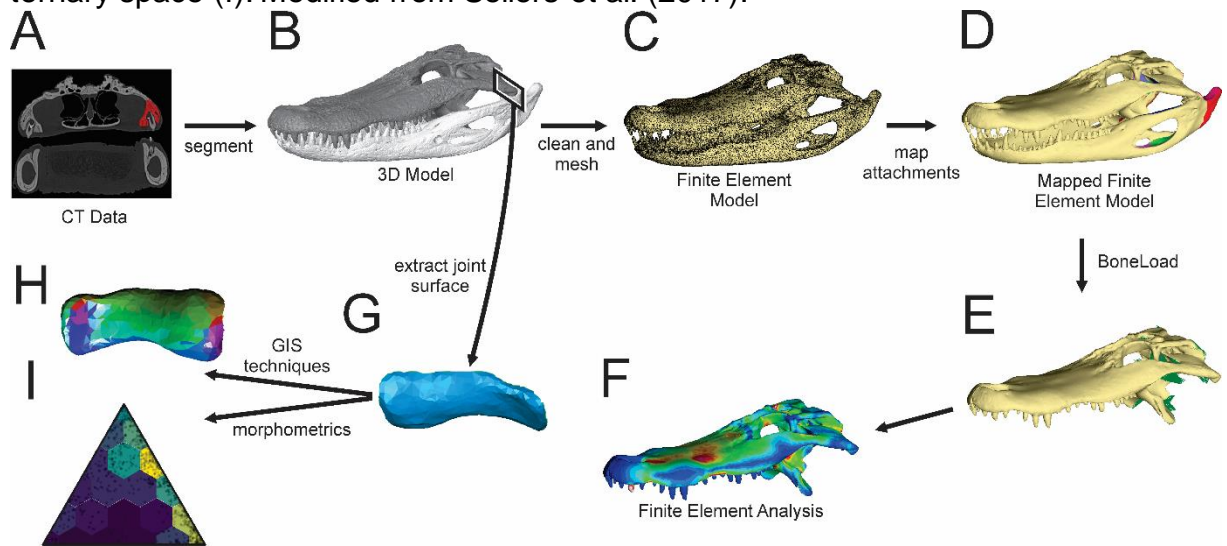


Figure 3.5. A) A given planar surface can be described by a normal vector. B) A smooth surface can be approximated by breaking the surface into triangular patches, each of which can be described by a normal vector.

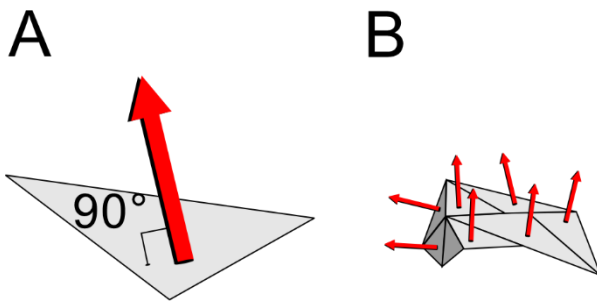


Figure 3.6. (A) Ventral view of left quadrate of *Batrachotomus* (SMNS 52970). Rostral is towards the bottom-right corner of the image. (B) Rostral view of quadrate and mandible of *Batrachotomus* in articulation, highlighting the helical shape of the articular surface. C, caudal, R, rostral, D, dorsal, V, ventral, M, medial, L, lateral.

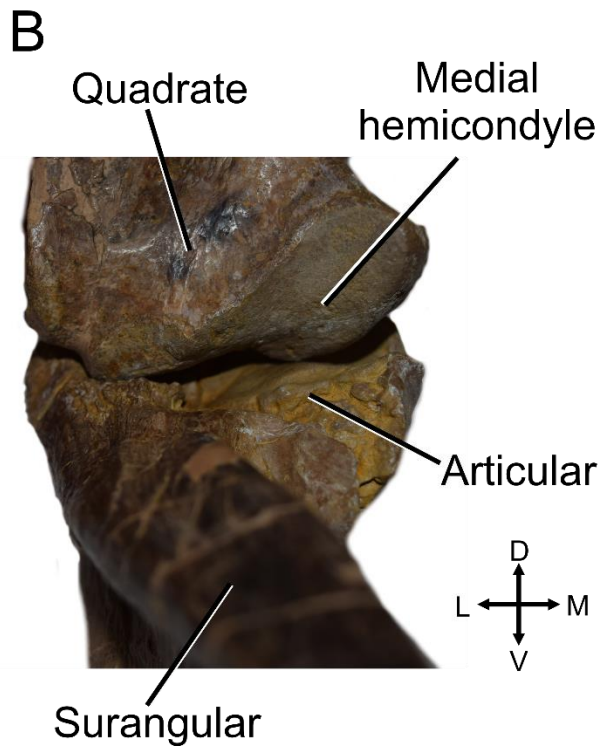
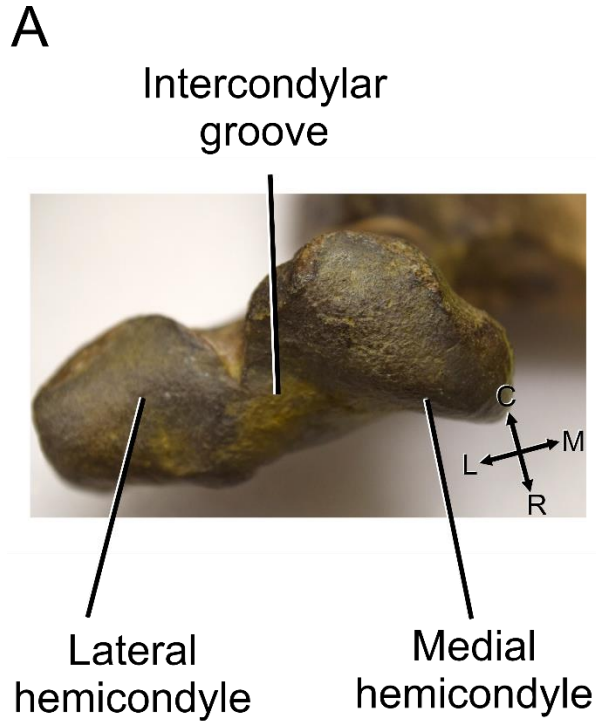


Figure 3.7. Balancing side joint force magnitude remains relatively unchanged from rostral to caudal bites, whereas there is an exchange between working side joint force and bite force. Comparison of cranial force magnitudes in rostral bites (A) and in caudal bites (B).

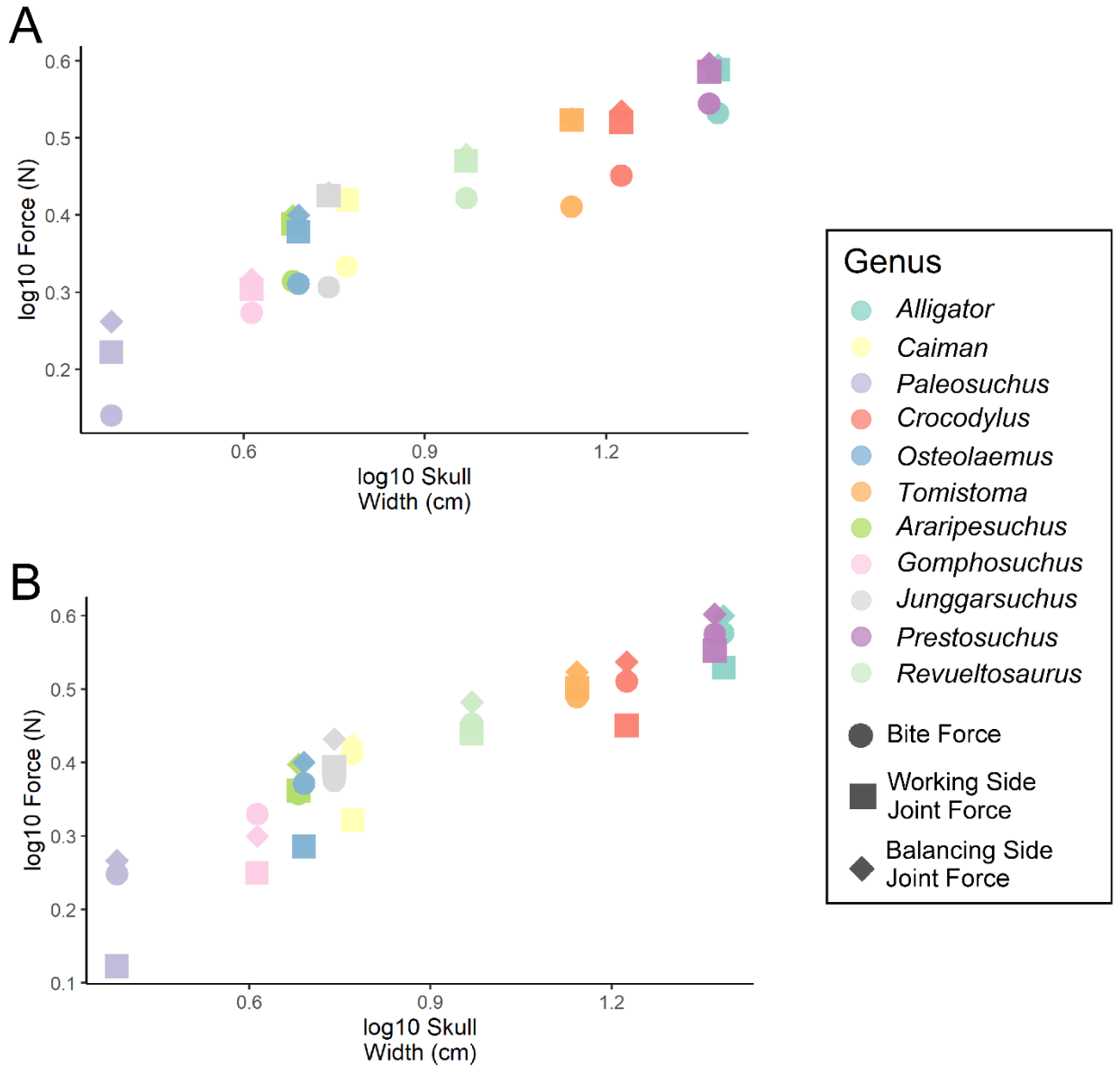


Figure 3.8. Joint reaction forces in extinct suchians are more dorsoventrally oriented compared to reaction forces in extant crocodylians. Comparison of orientations of cranial forces in rostral bites (A) and in caudal bites (B) across the comparative sample. Note that in caudal bites, working side reaction force becomes more variable and loses dorsoventral component, and balancing side joint force remains relatively similar.

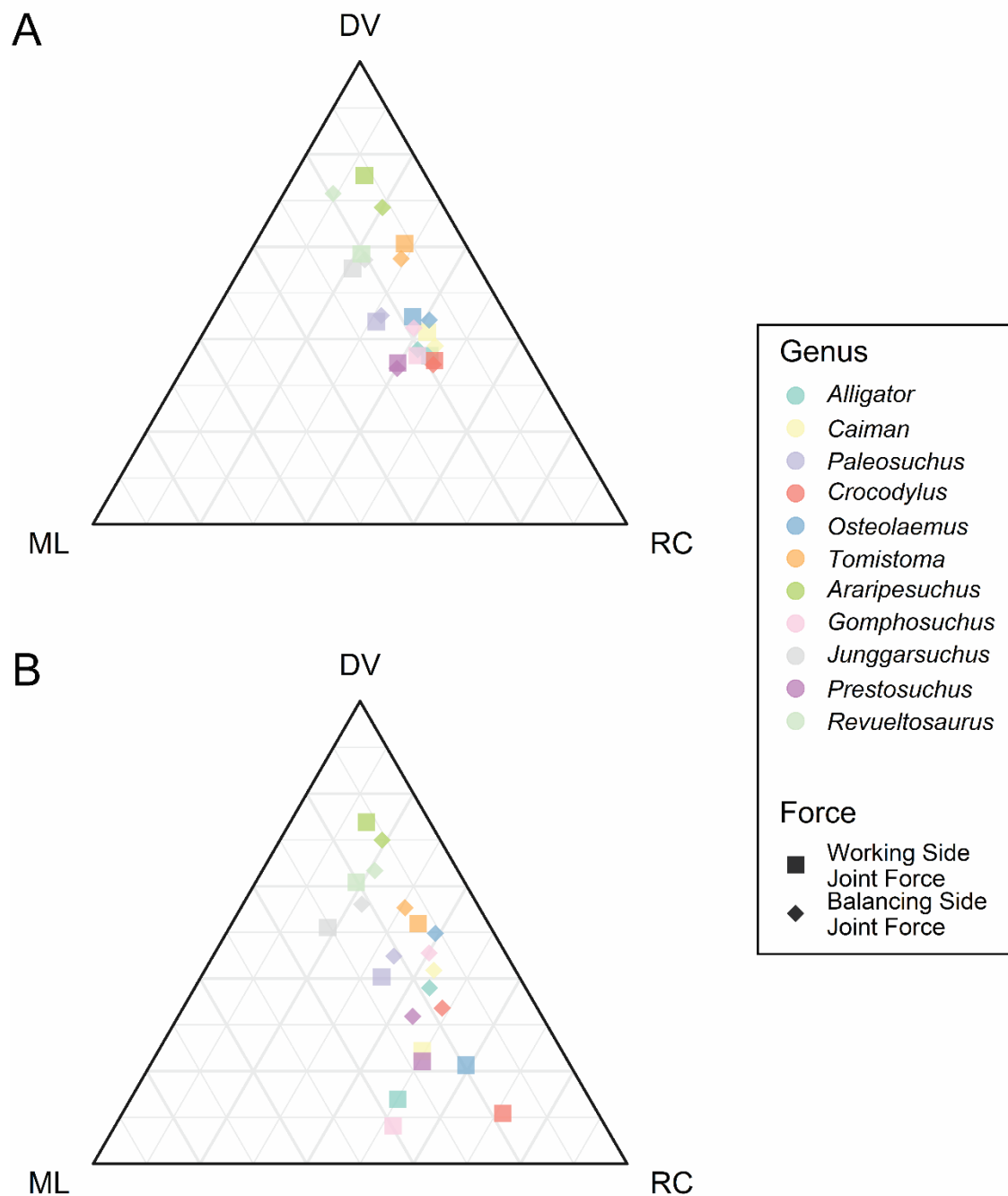


Figure 3.9. Joint pressure is consistent across the entire comparative sample of suchian jaw joints in rostral bites (A) and in caudal bites (B).

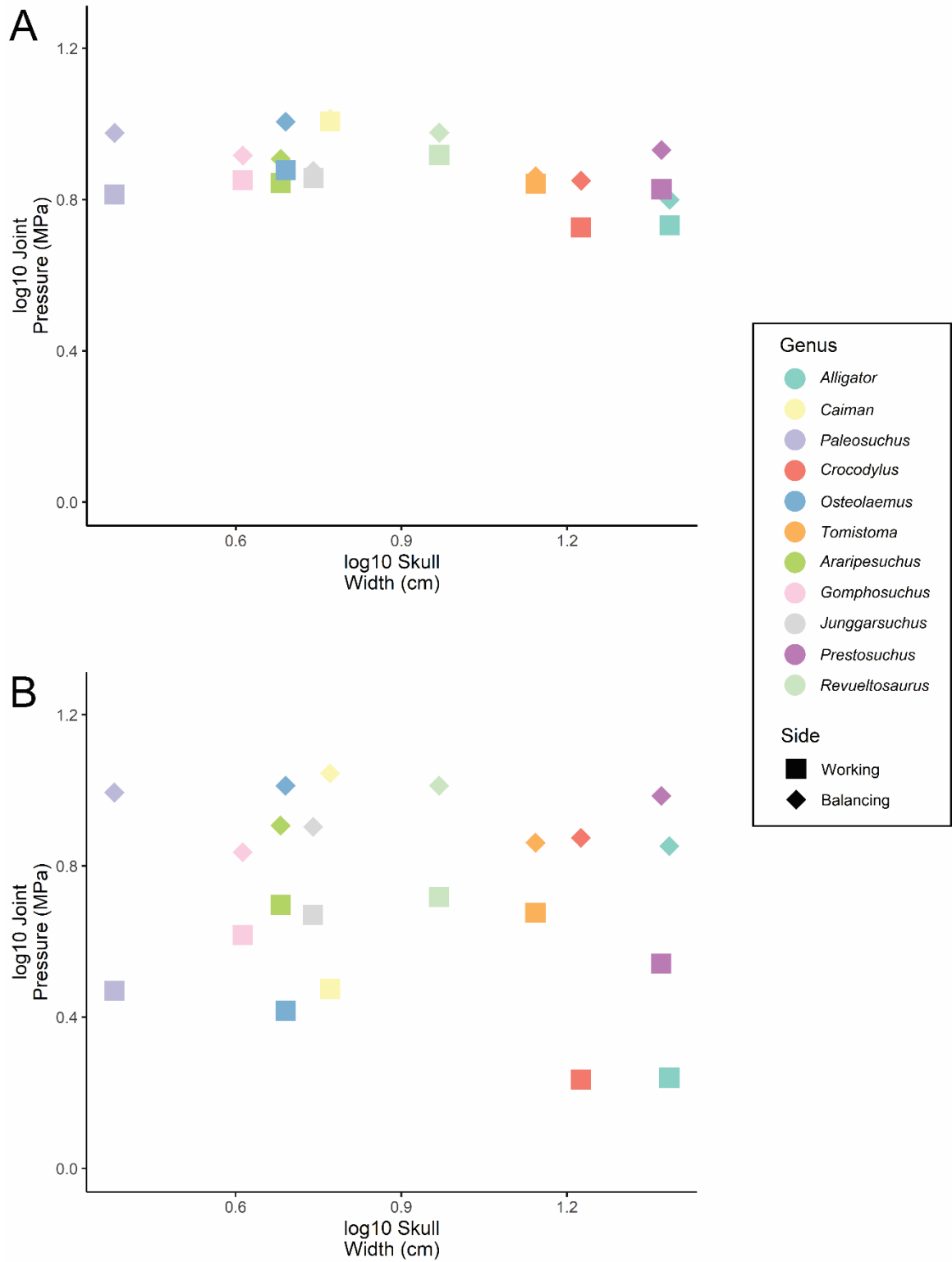
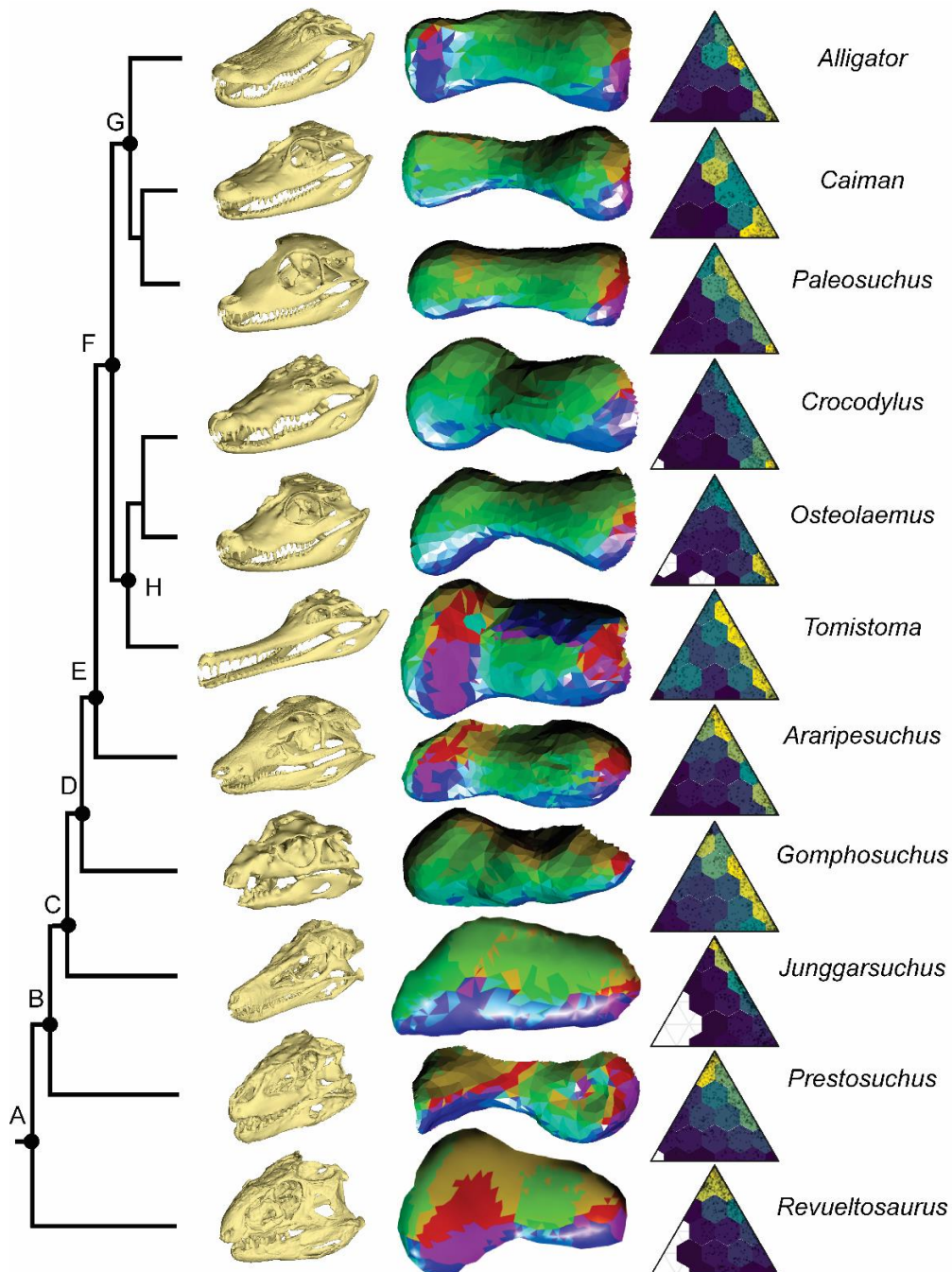


Figure 3.10. The articular surfaces of the quadrate of extant crocodylians have lower range of orientations compared to those from extinct suchians. Left) Skulls used in biomechanical analysis in left oblique view. Middle) Orientation patch counting of articular surfaces of left quadrate in “articular” view in the comparative sample of suchians. The top of each image is the caudodorsal aspect, depending on the degree of rotation of the quadrate. Right) Ternary plot of orientation of normal vectors of joint surface. Yellow: high amount of surface in given orientation. Blue: low amount of surface in given orientation. Node letters are as in Figure 3.2.



Chapter 4— Skull Flattening and Evolution of Feeding Biomechanics in Suchia

INTRODUCTION

Evolutionary transitions have fascinated biologists since Darwin first recognized the common ancestry of life on Earth. Key musculoskeletal innovations such as the origin of jaws or limbs are dramatic examples of phenotypic change associated with increases in performance (Hunter, 1998; Smith, 2003; Dumont *et al.*, 2012). Such innovations are often viewed through the lens of adaptation; novel structures are presumed to confer an adaptive advantage or to permit the exploitation of new niches (Heard and Hauser, 1995). In living organisms, laboratory or field studies can directly correlate an organism's structure with its performance.

The fossil record bears witness to many structural transformations in vertebrate evolution. However, the biomechanical and ecological roles of structures before and during these transitions are often poorly understood, as function cannot be directly assessed in fossil organisms. Thus, even clear instances of evolutionary transformation can involve structures of unknown significance. As feeding is a fundamental task of vertebrates and involves the generation of forces, many of the functionally- and ecologically- salient traits in the skulls of vertebrates are related to the generation or dissipation of forces. If a cranial modification improves an organism's ability to generate or resist higher forces, the change may represent a key innovation linked with an evolutionary transformation.

Crocodylians and their fossil relatives represent one of the great structural transformations in vertebrate evolution (Langston, 1973). Extant crocodylians have robust and akinetic skulls capable of accommodating the high forces that crocodylian skulls experience during feeding. Crocodylians use massive jaw muscles with derived geometry to deliver the highest measured feeding forces among vertebrates (Erickson, Lappin and Vliet, 2003), and powerful, whole-body thrashing and rolling augment these forces (Fish *et al.*, 2007; Drumheller, Darlington and Vliet, 2019). The skulls of crocodylians are strengthened by the sutural immobilization of previously more flexible joints, the elaboration of existing intracranial joints, and the acquisition of new intracranial and craniomandibular linkages. Thus, the evolutionary origin of crocodylians and their fossil relatives involved a substantial reorganization of the feeding apparatus.

The derived feeding apparatus of crocodyliforms has been linked with the evolutionary radiation of the taxon (Langston, 1973; Pol *et al.*, 2013), and Mesozoic fossils document the sequence of character transformations that structurally integrated and strengthened the skull. Crocodyliform lineages equipped with the derived feeding apparatus radiated into many forms with derived craniomandibular morphologies including herbivory, durophagy, and the extreme-performing generalist strategy of modern crocodylians, all of which involve the production of relatively high forces acting on the feeding apparatus. However, the biomechanical effects of many aspects of the derived crocodyliform skull have not been quantitatively evaluated. Thus, the potential adaptive value of this character suite and potential key innovation remains untested.

Here, we integrate three-dimensional reconstructions of jaw muscle anatomy (Sellers *et al.*, 2017; Chapter 2), jaw joint anatomy, skull geometry, and biomechanical performance in a sample of crocodylians and fossil relatives that characterize the transformations to skull shape in this group. We use these data to test the effects of derived character states on the evolution of crocodylian feeding performance and identify which character transitions are most linked with high bite force.

AIMS AND PREDICTIONS

This study aims to elucidate the phylogenetic history of skull shape, muscle geometry, and joint linkages and to determine which are linked with key aspects of feeding biomechanics. As early Crocodyliformes represents a key stage in the evolution of crocodylians (Langston, 1973; Clark, 1986), we hypothesize that most biomechanical evolution will take place by the origin of this group (Hypothesis 1). Dorsoventrally tall muscles and akinetic joint systems should optimize force transfer for biting. Thus, we hypothesize that size-standardized bite force will be associated with dorsoventrally tall skulls and accompanying efficient muscle geometries as well as akinetic joints (Hypothesis 2). We also hypothesize that mechanical efficiency (defined here as the magnitude of bite force divided by the scalar sum of muscle forces) will be associated with dorsoventrally tall skulls and accompanying efficient muscle geometries as well as akinetic joints (Hypothesis 3).

MATERIALS AND METHODS

Studied Specimens— The study sample consists of a single individual from 11 taxa: six extant crocodylians and five suchians that span the transformations

of skull geometry, muscle anatomy, joint linkages, and biomechanical performance (Figure 4.1). The extant crocodylian taxa included three alligatorids: *Alligator mississippiensis* (MUV AL008), *Caiman crocodilus* (FMNH 73711), and *Paleosuchus palpebrosus* (FMNH 22817). The rest of the extant sample consisted of three crocodylids: *Crocodylus moreletii* (TMM M-4980), *Osteolaemus tetraspis* (FMNH 98936), and *Tomistoma schlegelii* (TMM M-6342). Extinct taxa include the basal notosuchians *Araripesuchus gomesii* (AMNH 24450) from the Early Cretaceous of South America, an undescribed protosuchian informally known as “*Gomphosuchus*” (UCMP 97638) from the Early Jurassic of North America, *Junggarsuchus sloani* (IVPP V14010) from the Middle Jurassic of Asia, *Prestosuchus chiniquensis* (UFRGS PV0629T) from the Middle Triassic of South America, and *Revueltosaurus callenderi* (PEFO 34561) from the Late Triassic of North America.

Biomechanical Modeling— The biomechanical modeling techniques are described in greater detail elsewhere (Chapter 2; Sellers *et al.*, 2017) but will be summarized here. Specimens were scanned with regular or micro-computed tomography (CT/ μ CT) imaging or laser scanning. Three-dimensional boney anatomy was acquired by manually segmenting scan data with Avizo Lite 9.4 (FEI Visualization Science Group; <https://www.thermo fisher.com>). Using Geomagic Studio 2013 (Geomagic, Inc.; <https://www.3dsystems.com>), models were cleaned, smoothed, and aligned to global anatomical axes, and mandibles were opened to five degrees of gape. Anatomically detailed muscle attachment sites were determined based on osteological correlates, contrast-enhanced CT

imaging (Gignac *et al.*, 2016), dissections, and references to the literature (Iordansky, 1964; Schumacher, 1973; Busbey, 1989; Holliday and Witmer, 2007, 2009; Holliday, 2009). Previously reported muscle architecture (Sellers *et al.*, 2017), the surface area of muscle attachment size, and its modeled three-dimensional shape were used to estimate physiological cross-sectional area (PCSA) and thus the force each muscle was capable of exerting. The computational package Boneload was used to distribute muscle forces in a realistic fashion (Grosse *et al.*, 2007; Davis *et al.*, 2010). These loads were applied to three-dimensional finite element models in the Strand7 finite element analysis (FEA) software (Strand7 Pty. Ltd.; <http://www.strand7.com>). A single node in the center of the articular surface of both quadrates was constrained in all three translational and all three rotational degrees of freedom. We simulated bites both in rostral and caudal positions unilaterally by constraining a single node at the tip of the biting tooth in all three translational and all three rotational degrees of freedom. All muscles were modeled as contracting maximally, which is consistent with previous EMG data for crushing bites in crocodylians (Busbey, 1989; Cleuren, Aerts and De Vree, 1995).

Geometric and Biomechanical Performance Metrics— We used several metrics to summarize biomechanical performance. In addition to bite force and reaction forces acting on the working (i.e., biting) and balancing (i.e., non-biting) jaw joints, we also calculated mechanical efficiency ($E_{\text{mech.}}$) as the ratio of bite force magnitude over the scalar sum of muscle forces (i.e., bite force over gross muscle force; $E_{\text{musc.}}$). We also used measures of skull size and shape from

Chapter 2. PC1 inversely tracks with skull size (i.e., larger skulls have lower PC1 values), and PC2 is linked with aspect ratio of the skull in caudal view and represents skull flatness (relatively flatter skulls have lower PC2 values). Plotting PC2 values onto cladograms reveal the progressive flattening of the skull in the lineage leading to Crocodylia (Figure 4.2). To determine size-standardized bite force, we used phylogenetic least-squares regression (PGLS) of bite force magnitude against PC1; residuals of this model represent size-standardized bite force and were used in subsequent analyses. All statistical analyses were conducted with R (R Core Team, 2021).

Analyses and Hypothesis Testing— We used ancestral state reconstruction to identify suchian clades with significant shifts in the measured geometric and performance metrics. To test the hypothesis that size-standardized bite force is linked with muscle geometry and joint linkages (Hypothesis 1), we used phylogenetic generalized least-squares (PGLS) regression of size-standardized bite forces against muscle efficiency (defined here as the magnitude of the vector sum of jaw muscle forces divided by the scalar sum of muscle forces; Model 1.1), muscle efficiency and the state of the palatobasal joint (open or closed; after Character 54 of Clark, 1994; Character 99 of Nesbitt, 2011; Model 1.2), muscle efficiency and the state of the paraoccipital process contacting the quadrate (not contacting or contacting, after Character 36 of Clark, 1994; Model 1.3), and muscle efficiency and the state of the mandibular symphysis (Class I, Class II, or Class III; after Holliday and Nesbitt, 2013; Model 1.4), for a total of four models. To test the hypothesis that mechanical efficiency

is associated with muscle geometry and joint linkages (Hypothesis 2), we created linear models of mechanical efficiency against muscle efficiency (Model 2.1), muscle efficiency and the state of the palatobasal joint (Model 2.2), muscle efficiency and the state of the paraoccipital process contacting the quadrate (Model 2.3), and muscle efficiency and the state of the mandibular symphysis (Model 2.4), for a total of four models. For both hypotheses, we used AICc on significant models to determine the best model; the model with the highest AICc weight was considered the best.

RESULTS

Ancestral state reconstruction of muscle efficiency revealed that Crocodylia has significantly less efficient muscular geometry compared to Suchia as a whole (Figure 4.3; Table 4.1; 95% CIs: 0.5524 – 0.7220 vs 0.7835 – 0.8830, respectively). The reconstructed values for Mesoeucrocodylia approached statistical significance, being lower than those in Suchia (95% CIs: 0.6225 – 0.7914 vs 0.7835 – 0.8830, respectively).

Ancestral state reconstruction of size-standardized muscle force revealed several increases in the lineage leading to Crocodyliformes (Figure 4.4, Table 4.2). The clade consisting of *Junggarsuchus* + Crocodyliformes had statistically significantly higher muscle force than Suchia (95% CIs: -2638 – -2328 vs -4475 – -4481, respectively). Crocodyliformes had statistically significantly higher muscle force than the clade consisting of *Junggarsuchus* + Crocodyliformes (95% CIs: -1136 – -871 vs -2638 – -2328, respectively). Ancestral state reconstruction showed that Crocodyliformes had statistically significantly greater size-standardized bite force than Suchia as a whole (Figure 4.5; Table 4.3; 95% CIs: -

382 – 79 vs -934 – -565, respectively). By contrast, no statistically significant shifts in mechanical efficiency were detected (Figure 4.6; Table 4.4). Overall, these results support Hypothesis 1.

The results of statistical analyses are summarized in Table 4.5. Our results show that muscle efficiency alone does not predict size-standardized bite force (muscle efficiency: $p=0.879$). For the model including muscle efficiency and PBJ state, muscle efficiency does not predict size-standardized bite force, but the state of the PBJ does ($p=0.1040$ and $p=0.0462$, respectively). For the model including muscle efficiency and paraoccipital process, neither term was statistically significant ($p=0.272$ and $p=0.211$, respectively). For the model including muscle efficiency and the mandibular symphysis, neither term was statistically significant ($p=0.1456$ and $p=0.151$, respectively). Thus, Hypothesis 2 was not supported.

By contrast, muscle efficiency significantly predicted mechanical efficiency ($p= 0.0106$). For the model including muscle efficiency and palatobasal joint, muscle efficiency was statistically significant and palatobasal joint was nearly statistically significant ($p=0.0023$ and $p=0.0598$, respectively). For the model including muscle efficiency and the paraoccipital process, muscle efficiency was statistically significant but the paraoccipital process was not ($p=0.0500$ and $p=0.3718$, respectively). For the model including muscle efficiency and the mandibular symphysis, muscle efficiency was statistically significant, as was the presence of derived symphyseal morphology ($p=1.1e-6$ and $p=7.7e-5$, respectively). Thus, Hypothesis 3 was supported.

DISCUSSION

Several derived features of the crocodylian skull explain how these animals are able to deliver extreme bite forces despite possessing inefficient muscle orientations (Figure 4.9). The primitive condition of the suchian skull was tall with high muscle efficiency, lower size-standardized muscle mass, and higher mechanical efficiency. The suchian skull primitively had an open palatobasal joint, a simple Class I mandibular symphysis, a paraoccipital process that did not contact the quadrate, and low pneumaticity. In extant crocodylians, larger jaw muscle mass, suturally-immobilized cranial joints, and interdigitated mandibular symphyses are associated with generating high bite force despite inefficient muscular geometry. The progressive skull flattening in the suchian lineage leading to Crocodylia has long been recognized (Figure 4.2; Figure 4.9; Langston, 1973; Busbey, 1989). Results of previous research (Chapter 2) show that the efficiency of muscle geometry decreases concomitantly with skull flatness (i.e., with PC2; Figure 4.3). However, crocodylians are noted for their extreme bite force performance, begging the question of how a lineage with inefficient muscle geometry can bite so hard.

The results of this study show that size-standardized gross muscle force and muscle efficiency underwent coordinated evolution (compare Figure 4.3 with Figure 4.4). In order to generate high bite forces with inefficient muscle orientations, flat-skulled taxa rely on larger jaw musculature. As the efficiency of the muscular system decreased (Figure 4.3), the absolute amount of force generated by the jaw adductors increased (Figure 4.4). Thus, extant crocodylians

rely on greater size-standardized muscle forces to “rescue” the bite performance from the inefficient muscle geometry brought about by skull flattening.

While these changes in muscle proportions and forces evolved, changes in key joints were found. Both a closed palatobasal joint found in crocodyliforms (Figure 4.7A) and the derived, Class III, interdigitated mandibular symphysis of metasuchians (Figure 4.7B) are associated with increased mechanical efficiency for a given muscular arrangement. These changes happened near the base of Crocodyliformes, providing quantitative support for previous research suggesting changes to cranial joints (Langston, 1973; Clark *et al.*, 2004; Pol *et al.*, 2013) and the mandibular symphysis (Holliday and Nesbitt, 2013; Lessner *et al.*, 2019) in Crocodyliformes were key to the success of the group. As the geometry of the skull causes jaw muscles to take on inefficient orientations, these traits enable more effective force transmission in the feeding system.

Taxa near the base of Crocodyliformes passed through an evolutionary bottleneck of a pneumatically inflated basicranium; taxa such as *Dibothrosuchus* (Wu and Chatterjee, 1993; Ruebenstahl, 2019), *Junggarsuchus* (Clark *et al.*, 2004; Ruebenstahl, 2019), *Almdadasuchus* (Leardi, Pol and Clark, 2017), *Macelognathus* (Leardi, Pol and Clark, 2017), *Protosuchus* (Colbert and Mook, 1951; Gow, 2000), and *Gomphosuchus* (Clark, 1986) have dramatically pneumatically-expanded basisphenoids relative to earlier relatives (Character 35 of Pol *et al.*, 2013). The pneumatic expansion of the braincase may have facilitated higher bite forces by providing greater surface area for muscle attachment. Indeed, both the unnamed clade consisting of *Junggarsuchus* +

Crocodyliformes as well as Crocodyliformes show larger size-standardized muscle force than more basal clades (Figure 4.4). Additionally, pneumatic expansion of the basisphenoid may have facilitated the obliteration of the palatobasal joint by opposing large portions of the surface of the basisphenoid to the pterygoids. *Almadasuchus* from the Late Jurassic of South America is more closely related to Crocodyliformes than is *Junggarsuchus*. The pneumatic expansion of the basisphenoid resulted in the basisphenoid contacting the pterygoid, further immobilizing the suspensorium. This key outgroup to Crocodyliformes is the first taxon to eliminate the palatobasal joint (Pol *et al.*, 2013; Leardi, Pol and Clark, 2020). Thus, long after the pneumatically-inflated basisphenoid receded, more crownward taxa still carry the legacy of this pneumatic inflation in the sutural connections between the basicranium and the palate.

High mechanical efficiency in crocodyliforms is linked with herbivory. The herbivorous (Clark, 1986; Ősi, 2014; Melstrom and Irmis, 2019) *Gomphosuchus* had the highest mechanical efficiency among the sample. This is consistent with work in mammalian taxa suggesting higher mechanical efficiency (Maynard Smith and Savage, 1959; Tseng and Flynn, 2018) and size-standardized bite force (Christiansen and Wroe, 2007) are linked with herbivory. In *Gomphosuchus*, the jaw is relatively short and the caudal teeth are relatively caudally shifted, decreasing the length of the out-lever and increasing mechanical advantage. Several crocodyliforms have been reconstructed as omnivorous or herbivorous, usually on the basis of heterodont dentition (Ősi,

2014; Melstrom and Irmis, 2019), and most have relatively tall skulls and relatively efficient jaw muscle orientations. Tall skulls and shortened mandibles that increase mechanical efficiency are reported in *Simosuchus* (Kley *et al.*, 2010). In contrast, the eusuchian *Iharkutosuchus* from the Late Cretaceous of Europe possessed a remarkably flat skull (Ősi, Clark and Weishampel, 2007; Ősi, 2008; Ősi and Weishampel, 2009). Results from the present analysis suggest that the flat skull of this taxon would force jaw muscles to take on inefficient orientations and presumably confer lower mechanical efficiency. Perhaps as a means to overcome this biomechanical disadvantage, *Iharkutosuchus* had an “unusually robust” muscle scar (Iordansky, 1964) for m. adductor mandibulae posterior (Ősi and Weishampel, 2009), and these authors reconstructed a large mAMP in this taxon. The robust osteological correlates for jaw muscle attachments in *Iharkutosuchus* reflect an increase in tendinous and aponeurotic muscle attachments (Iordansky, 1964), which likely evolved as another mechanism to increase surface area available for muscle attachments to offset inefficient orientations caused by the marked cranial flattening in neosuchians.

Iharkutosuchus and other eusuchians including Crocodylia inherited flat skulls from a bottleneck of skull flatness around the base of Neosuchia. The most basal neosuchians such as *Goniopholis* (de Andrade *et al.*, 2011), *Bernissartia* (Norell and Clark, 1990; Martin *et al.*, 2020), and stomatosuchids including *Stomatosuchus* and *Laganosuchus* (Serenó and Larsson, 2009) showed some of the flattest skulls from the suchian record. This trend continued into Eusuchia as

documented by *Isisfordia* (Salisbury *et al.*, 2006), *Iharkutosuchus* (Ősi, Clark and Weishampel, 2007; Ősi, 2008) and aegyptosuchids (Holliday and Gardner, 2012). Some eusuchians including *Isisfordia* and Crocodylia extended the pterygoid flange ventrally (Salisbury *et al.*, 2006), which increases the available attachment area for m. pterygoideus ventralis and permits a larger m. pterygoideus dorsalis to course dorsal to this element. Thus, the appearance of elaborate crests and tubercles on the quadrate of neosuchians helps to offset the inefficient muscle orientations inherited from neosuchians and serves as further evidence that derived suchians rely on increasing muscle mass to facilitate the generation of bite force.

Extant crocodylians show a marked asymmetry in joint loading in caudal bite locations (Figure 4.8). In most of the extant sample, the working-side jaw joint experienced $\leq 30\%$ of the force acting on the balancing side. The exception was the longirostrine *Tomistoma*, in which the working side jaw joint experienced $\sim 65\%$ of the force acting on the balancing side jaw joint. This pattern may be contrasted with the fossil taxa, in which the working side jaw joint of most of the sample experienced $\geq 50\%$ the force acting on the balancing side. The exception was *Prestosuchus*, in which the working side jaw joint experienced $\sim 35\%$ the force acting on the balancing side. The reduction of the magnitude of working side jaw joint force was driven by a drop in the dorsoventral component of joint reaction force; that is, the mandible is pulled dorsally against the quadrate less in Crocodylia relative to earlier taxa. In some feeding behaviors (e.g., the death roll), the working side jaw joint may be loaded in net tension. This may explain

the large medial and lateral collateral ligaments of the jaw joints in extant crocodylians (Saber and Hassanin, 2014).

CONCLUSIONS

Here, we found evidence for the phylogenetically significant geometric and functional traits responsible for the high bite performance and evolutionary success of Crocodylians. Muscle efficiency decreased concomitantly with skull flatness in the lineage leading to Crocodylia, whereas size-standardized muscle force increased, perhaps ameliorating inefficient muscle geometries found in more crownward groups. Derived features of crownward taxa such as a closed palatobasal joint and an interdigitated Class III symphysis also mitigate inefficient muscle geometries by permitting more efficient force transfer to and through the feeding apparatus. The evolutionary bottleneck of a pneumatically-inflated basicranium near the base of Crocodyliformes may have facilitated both an increase in muscle mass and the sutural immobilization of cranial joints. Later, the lineage leading to Crocodylia passed through a bottleneck of particularly flat skulls, which likely prompted an increase in soft-tissue muscle attachments to further ramp up muscle mass. Together, these results represent a step forward in resolving the paradox of high bite force in a flat-skulled vertebrate and help elucidate the biomechanical transitions underlying one of the great transformations in vertebrate evolution.

Table 4.1. Ancestral state reconstruction shows that muscle efficiency in the pan-suchian and pan-loricatan nodes are significantly higher than that of Crocodylia. Muscle efficiency in the pan-loricatan node is significantly higher than that of Metasuchia.

Clade	2.5% Confidence Interval	97.5% Confidence Interval
Suchia	0.784	0.883
Loricata	0.801	0.876
Crocodyliformes + <i>Junggarsuchus</i>	0.718	0.850
Crocodyliformes	0.696	0.821
Metasuchia	0.623	0.791
Crocodylia	0.552	0.722
Crocodylidae	0.526	0.682
<i>Crocodylus</i> + <i>Osteolaemus</i>	0.531	0.657
Alligatoridae	0.564	0.720
Caimaninae	0.600	0.726

Table 4.2. Ancestral state reconstruction shows that size-standardized muscle force is significantly lower in the pan-loricatan node than in the Crocodyliformes + *Junggarsuchus*. Size-standardized muscle force is significantly lower in the the Crocodyliformes + *Junggarsuchus* node than in Crocodyliformes. Thus, size-standardized muscle force experienced two increases in the lineage leading to crown Crocodylia.

Clade	2.5% Confidence Interval	97.5% Confidence Interval
Suchia	-4775	-4881
Loricata	-4740	-4555
Crocodyliformes + <i>Junggarsuchus</i>	-2638	-2328
Crocodyliformes	-1136	-871
Metasuchia	-742	-551
Crocodylia	-723	-332
Crocodylidae	-1865	-1348
<i>Crocodylus</i> + <i>Osteolaemus</i>	-2193	-1775
Alligatoridae	334	865
Caimaninae	127	587

Table 4.3. Ancestral state reconstruction shows that size-standardized bite force is significantly higher in Crocodyliformes than in the pan-suchian and pan-loricatan nodes.

Clade	2.5% Confidence Interval	97.5% Confidence Interval
Suchia	-934	-565
Loricata	-843	-564
Crocodyliformes + <i>Junggarsuchus</i>	-658	-172
Crocodyliformes	-382	79
Metasuchia	-479	138
Crocodylia	-553	46
Crocodylidae	-870	-311
<i>Crocodylus</i> + <i>Osteolaemus</i>	-833	-374
Alligatoridae	-236	334
Caimaninae	-151	315

Table 4.4. Ancestral state reconstruction of mechanical efficiency shows no significant changes along the lineage leading to Crocodylia.

Clade	2.5% Confidence Interval	97.5% Confidence Interval
Suchia	0.199	0.288
Loricata	0.210	0.277
Crocodyliformes + <i>Junggarsuchus</i>	0.189	0.308
Crocodyliformes	0.228	0.341
Metasuchia	0.159	0.310
Crocodylia	0.154	0.306
Crocodylidae	0.140	0.280
<i>Crocodylus</i> + <i>Osteolaemus</i>	0.161	0.275
Alligatoridae	0.177	0.317
Caimaninae	0.222	0.335

Table 4.5. Results of statistical analyses. H., Hypothesis; Mod., Model number; Resp. Var., Response variable; Pred. Var(s), Predictor variable(s); $\beta_{cont.}$, parameter estimate of continuous variable; $\beta_{cat.,1}$, parameter estimate of first category of discrete covariate second variable; $\beta_{cat.,2}$, effect of second category of discrete covariate; $p_{cont.}$, p value of continuous variable; $p_{cat.}$, p value of categorical variable; AICc, Akaike information criterion corrected for small sample size; AICw, AICc weights; Stand. F_{bite} , size-standardized bite force; $E_{mech.}$, mechanical efficiency; $E_{musc.}$, muscular efficiency; PBJ, state of palatobasal joint; paraocc., state of paraoccipital process; chin, state of mandibular symphysis.

Mod.	Resp. Var.	Pred. Var(s).	$\beta_{cont.}$	$p_{cont.}$	$\beta_{cat.,1}$	$\beta_{cat.,2}$	$p_{cat.}$	AICc	AICw
1.1	Stand. F_{bite}	$E_{musc.}$	318.5	0.879	N/A	N/A	N/A	180.6	0.39
1.2	Stand. F_{bite}	$E_{musc.} + \text{PBJ}$	4408 ± 5542	0.104	1205 ± 1179	N/A	0.046	180.1	0.51
1.3	Stand. F_{bite}	$E_{musc.} + \text{paraocc.}$	3802 ± 7424	0.272	862.2 ± 1462	N/A	0.211	183.6	0.09
1.4	Stand. F_{bite}	$E_{musc.} + \text{chin}$	4886 ± 7062	0.146	1091 ± 1552	1305 ± 1496	0.151	187.3	0.01
2.1	$E_{mech.}$	$E_{musc.}$	0.601 ± 0.367	0.011	N/A	N/A	N/A	-25.69	0.22
2.2	$E_{mech.}$	$E_{musc.} + \text{PBJ}$	0.778 ± 0.346	0.002	0.131 ± 0.118	N/A	0.060	-25.62	0.21
2.3	$E_{mech.}$	$E_{musc.} + \text{paraocc.}$	0.500 ± 0.425	0.050	-0.0445 ± 0.092	N/A	0.372	-21.62	0.03
2.4	$E_{mech.}$	$E_{musc.} + \text{chin}$	0.642 ± 0.258	$1.1e-6$	0.184 ± 0.089	0.094 ± 0.086	$7.7e-5$	-27.53	0.55

Figure 4.1. Cladogram of Suchia showing specimens used for the present study. A) Suchia, B) Loricata, C) Crocodylomorpha, D) Crocodyliformes, E) Metasuchia, D) Crocodylia, F) Crocodylia, G) Alligatoridae, H) Crocodylidae.

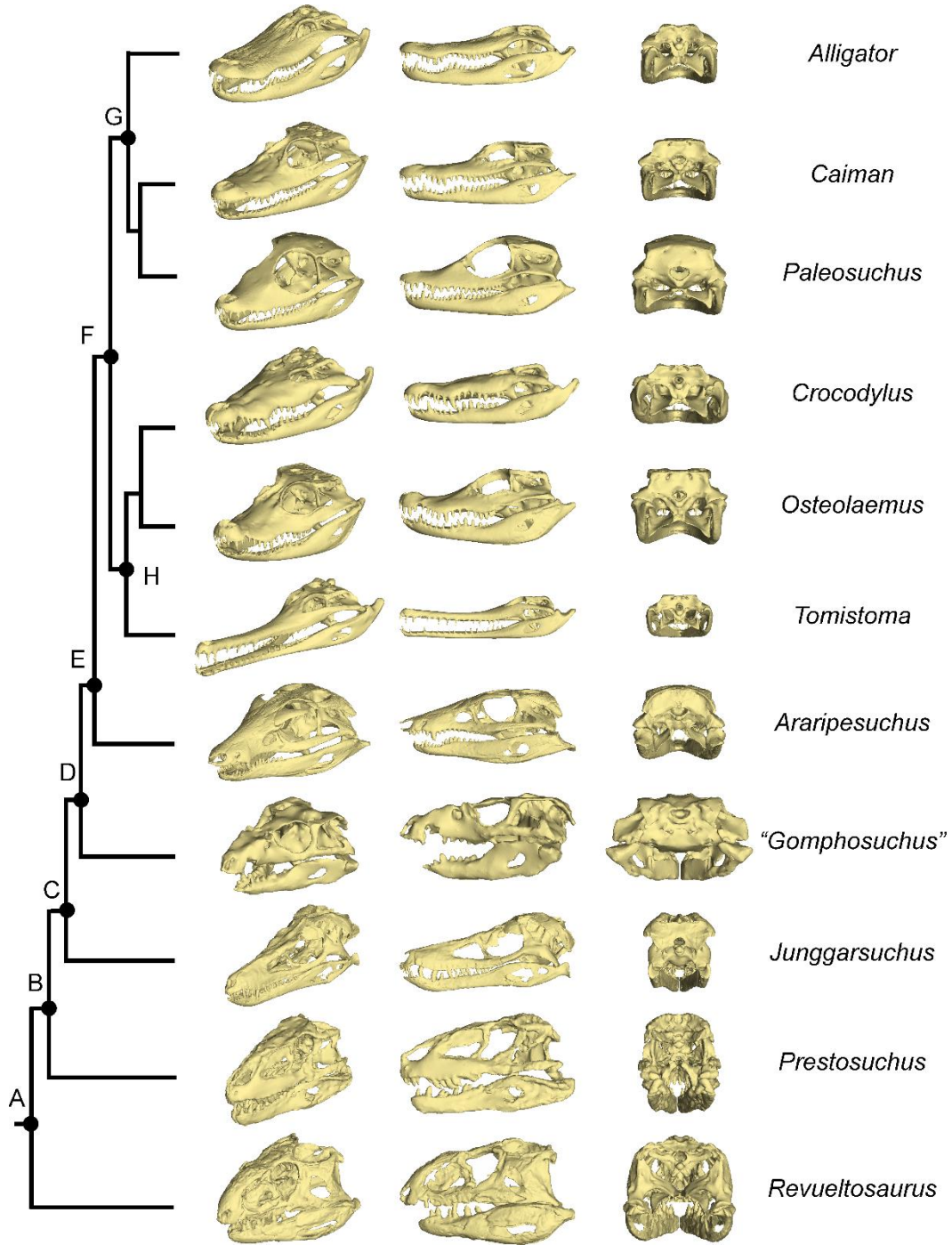


Figure 4.2. Heat-mapped cladogram (top) and phenogram (bottom) showing progressive skull flattening (corresponding to low PC2 values) in Suchia.

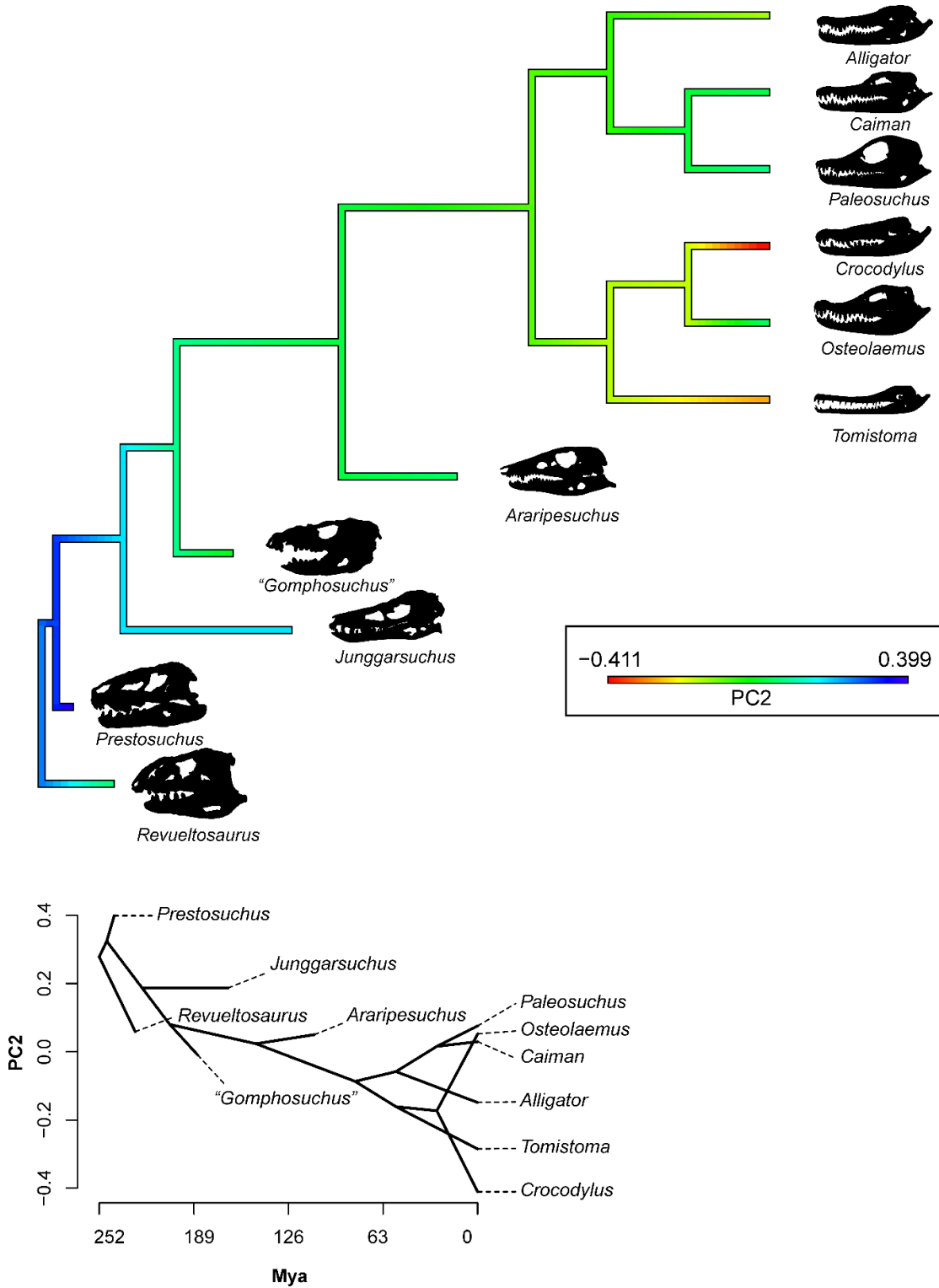


Figure 4.3. Heat mapped cladogram (top) and phenogram (bottom) showing the progressive decrease in muscle efficiency in the lineage leading to Crocodylia.

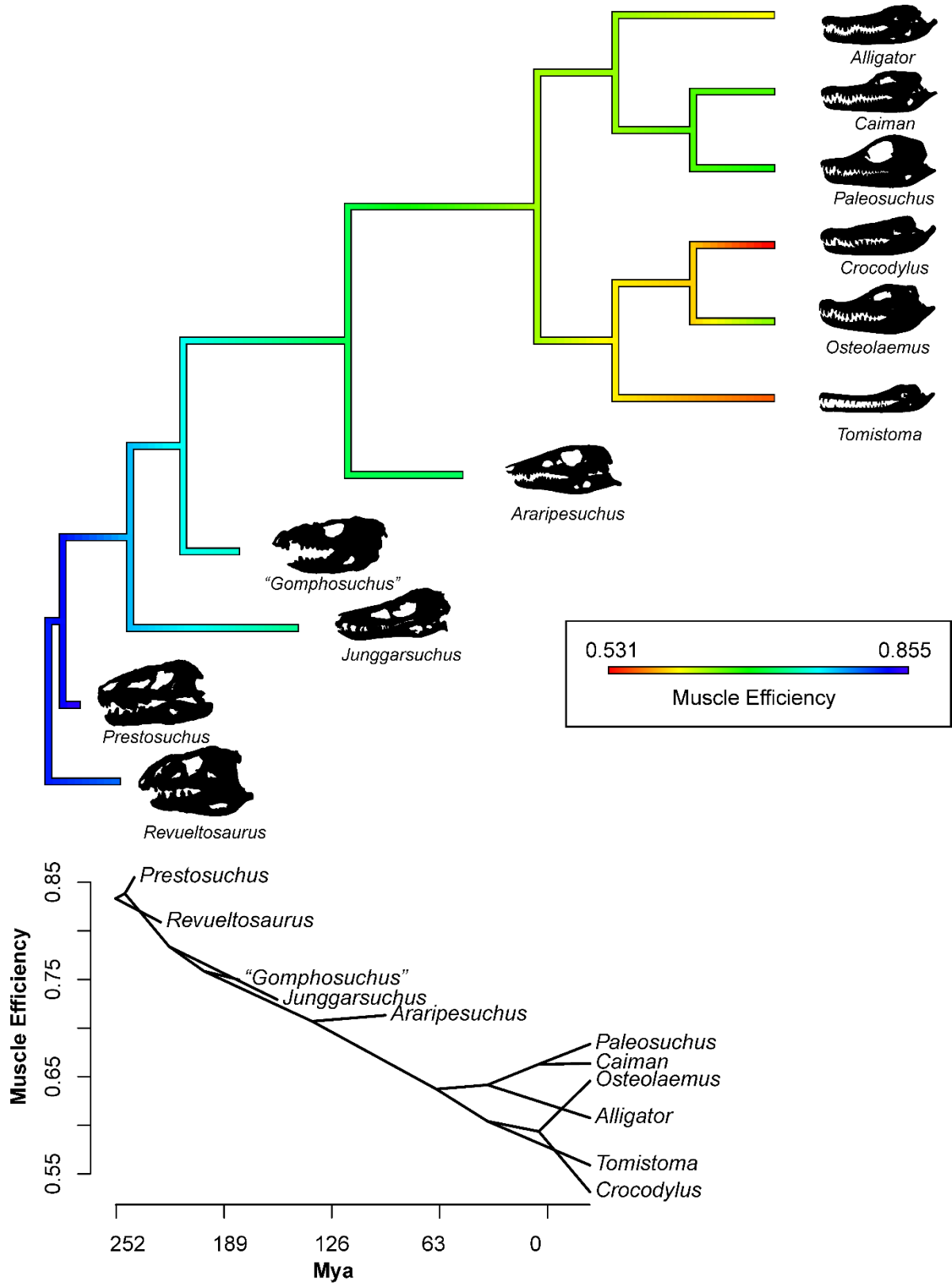


Figure 4.4. Heat-mapped cladogram (top) and phenogram (bottom) showing an increase in size- standardized muscle force near the base of Crocodyliformes.

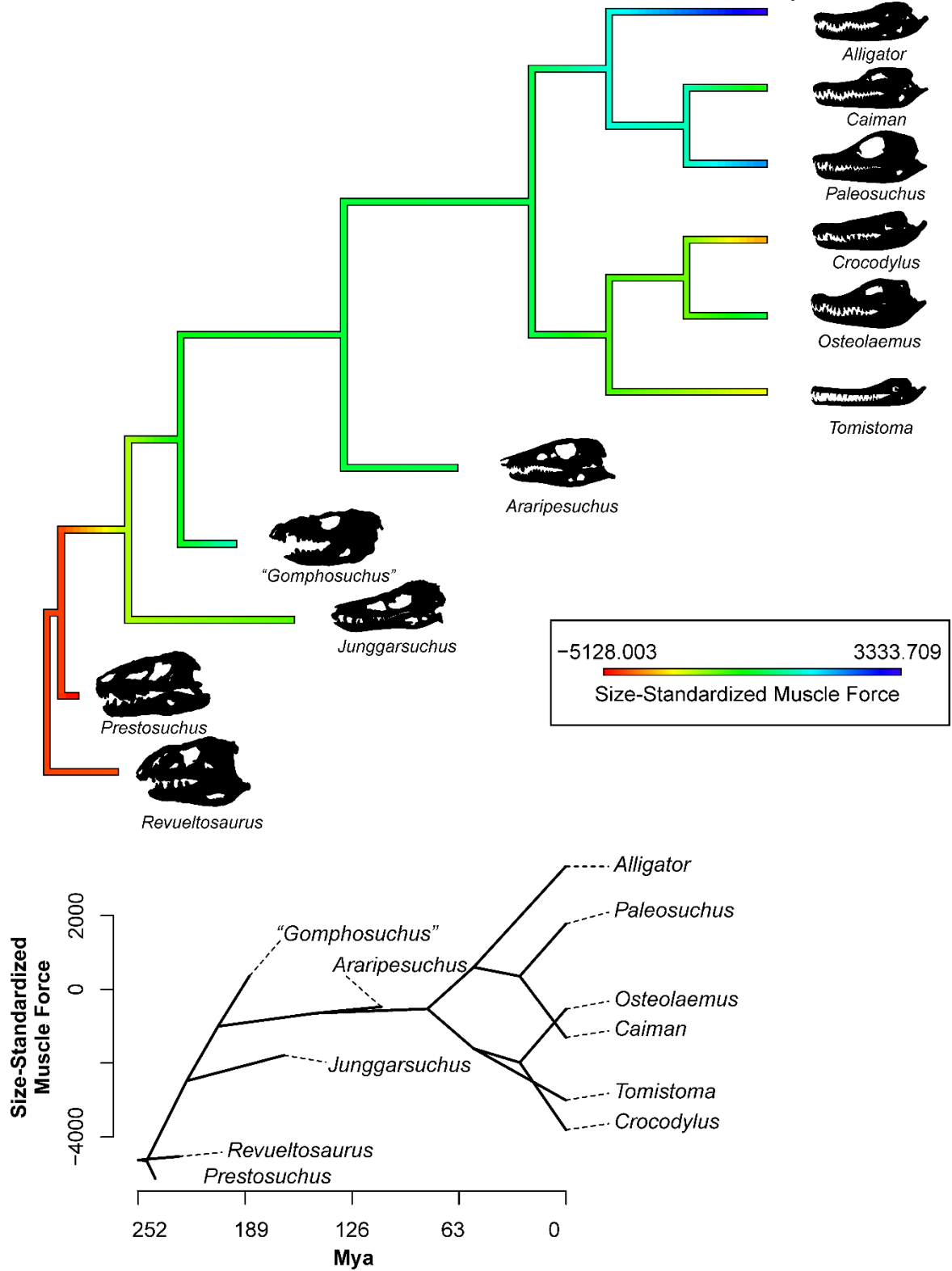


Figure 4.5. Heat-mapped cladogram (top) and phenogram (bottom) showing relative stasis in size-standardized bite force performance in Suchia.

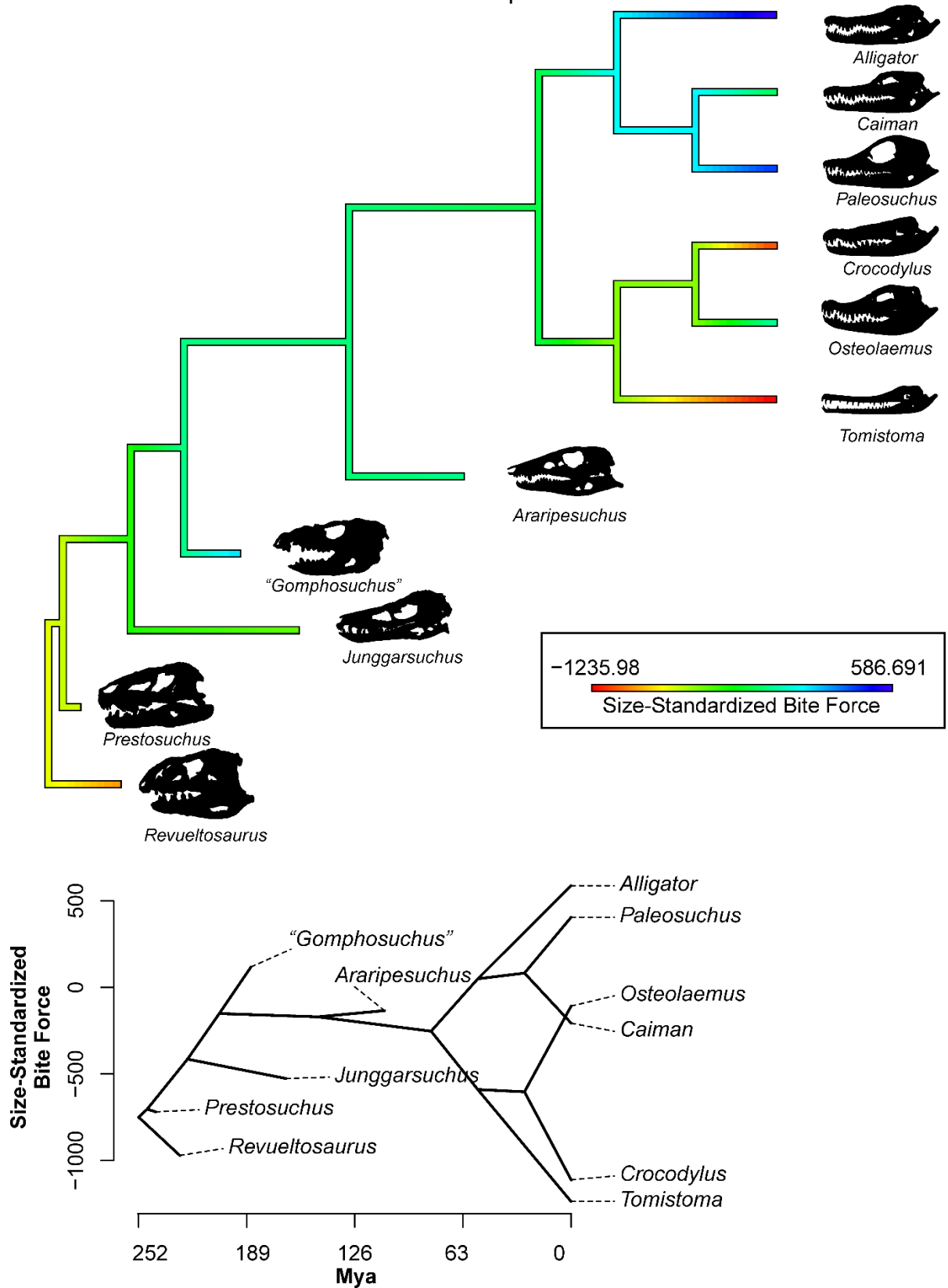


Figure 4.6. Heat mapped cladogram (top) and phenogram (bottom) showing relative stasis in mechanical efficiency in Suchia.

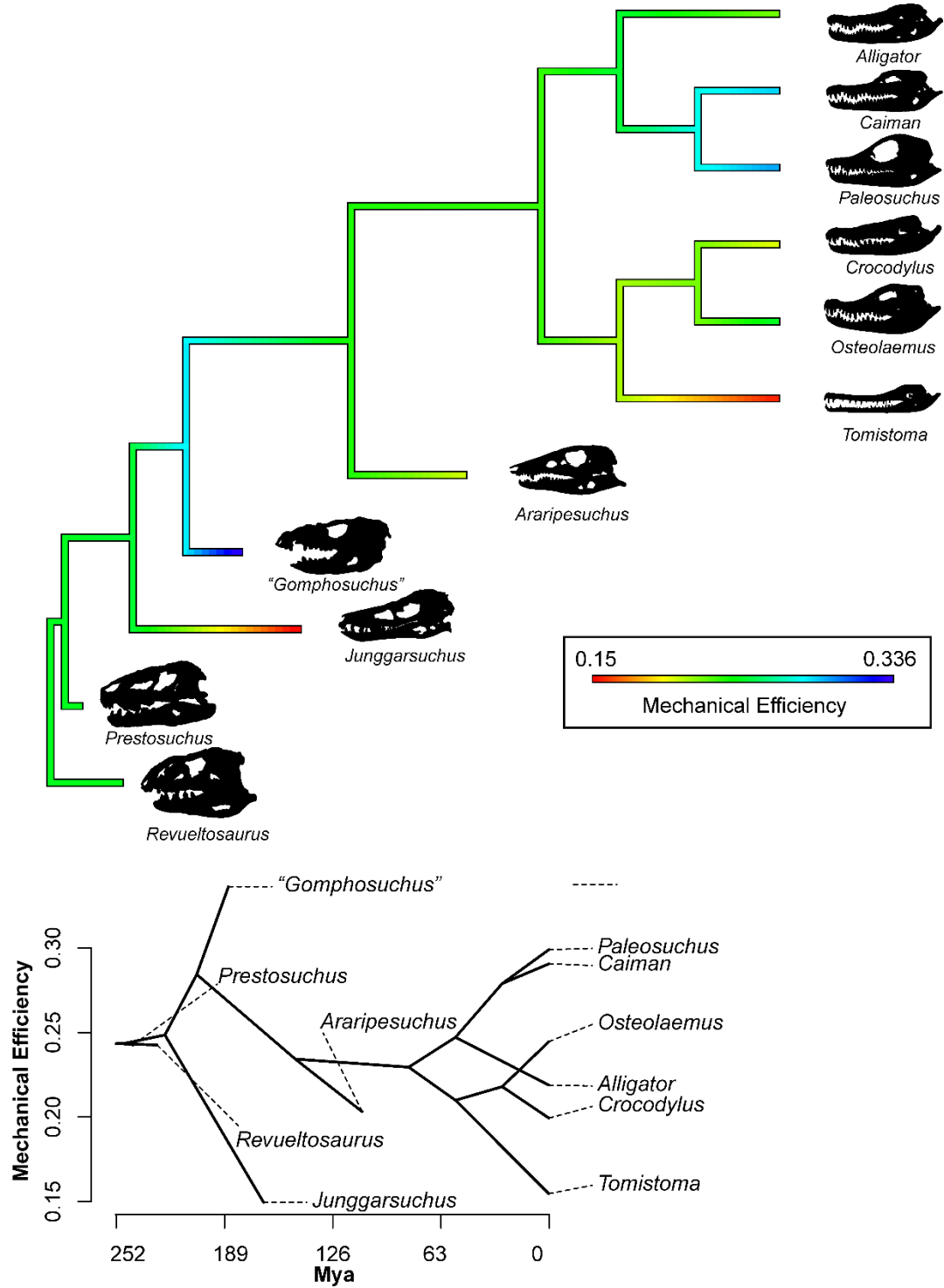


Figure 4.7. Mechanical efficiency (i.e., the proportion of muscle force transmitted as bite force) for a given muscle geometry is higher in taxa with a closed palatobasal joint (top) and in taxa with derived symphyseal morphologies (bottom).

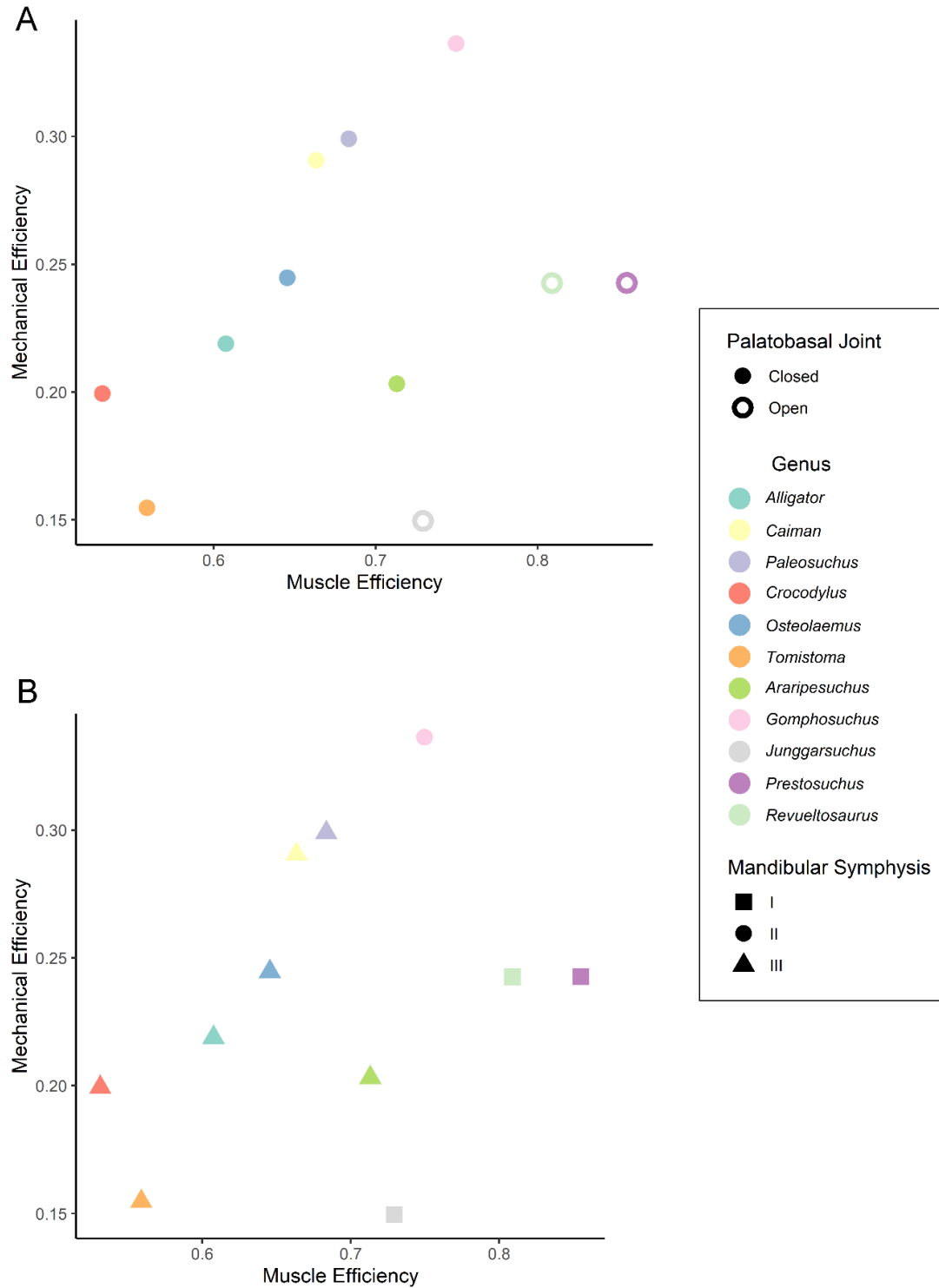


Figure 4.8. Working side jaw joint force is higher in fossil taxa relative to extant Crocodylians.

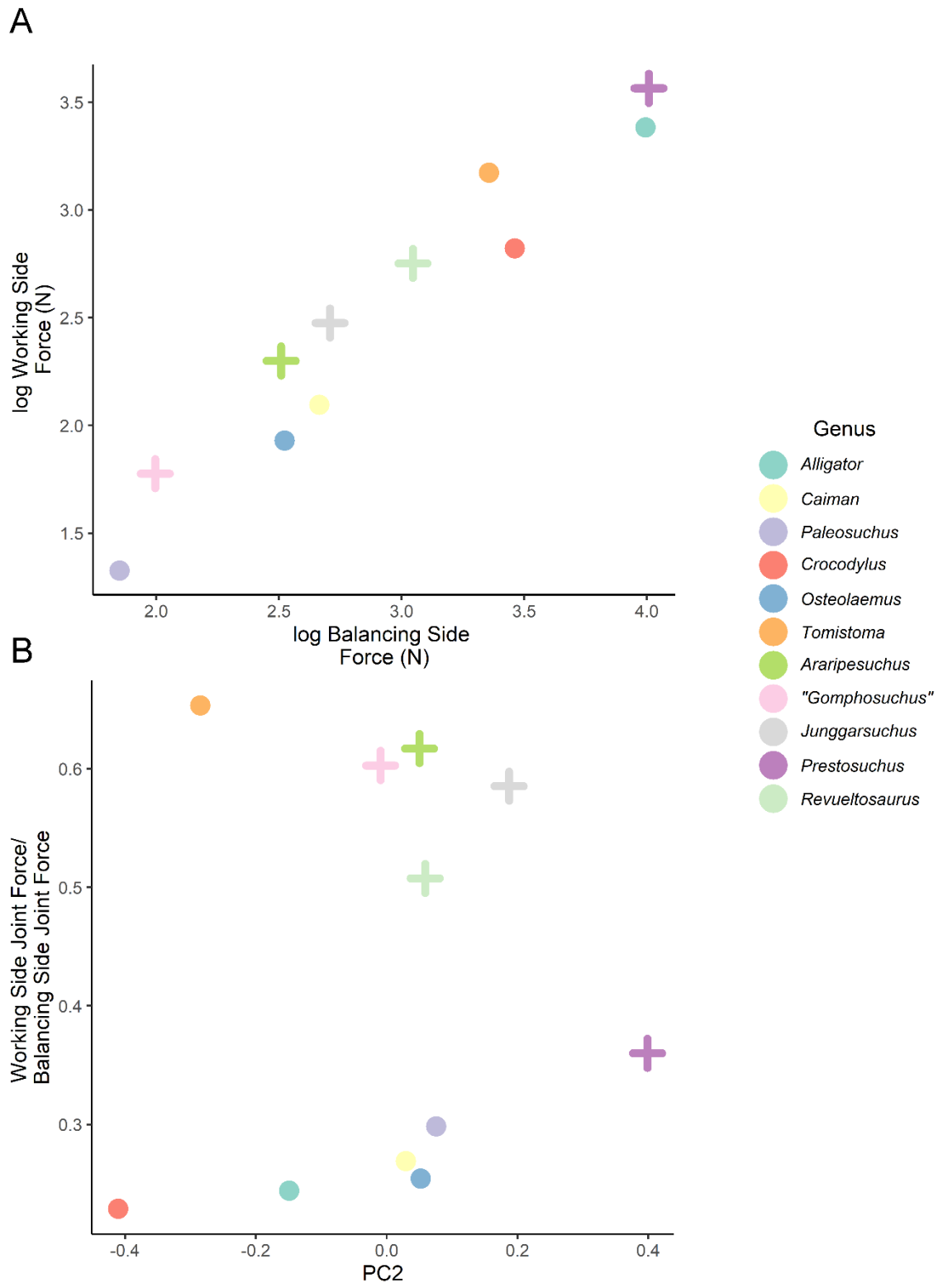
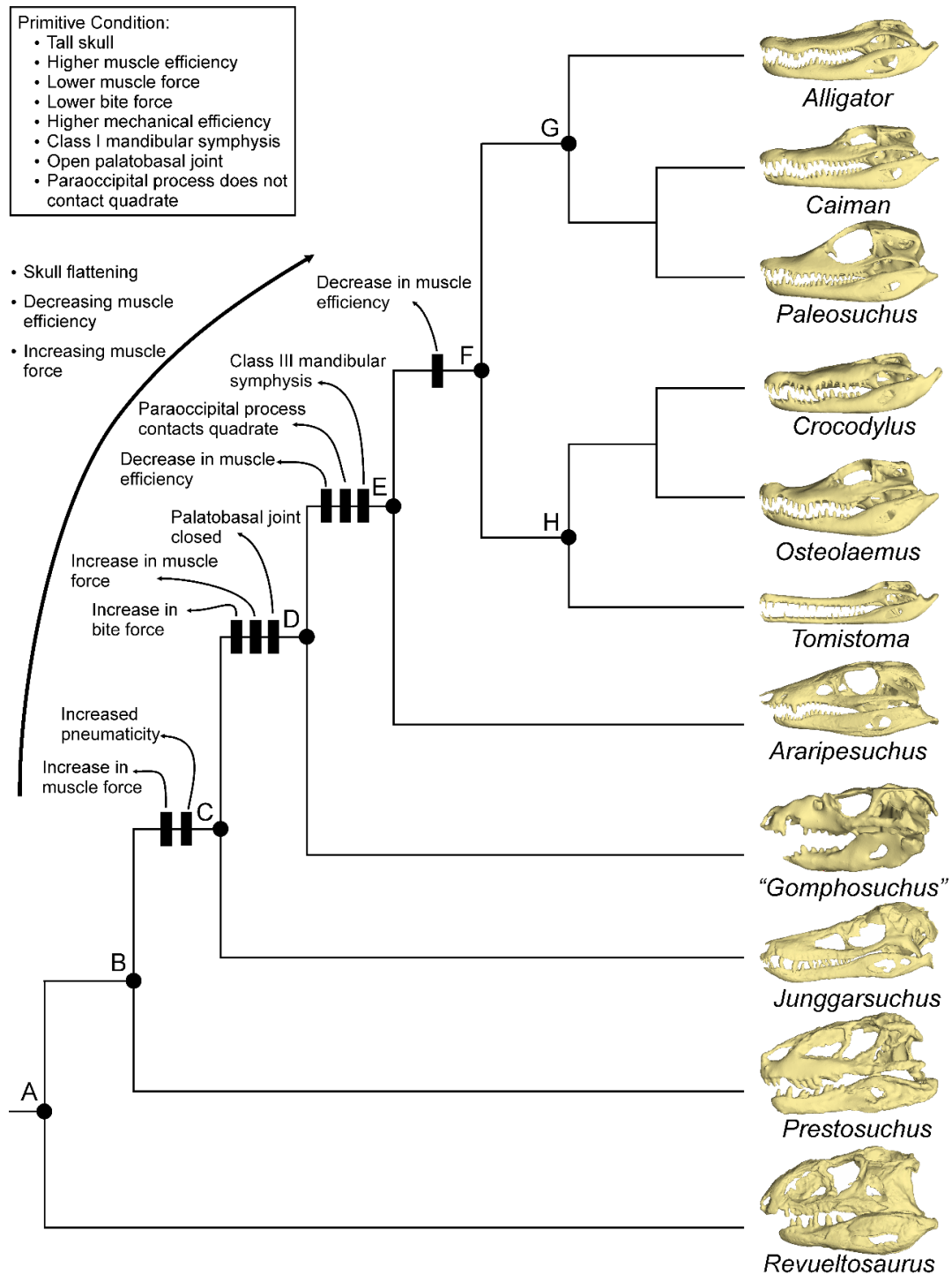


Figure 4.9. Skull flattening and the accompanying inefficient jaw muscle orientations in Suchia were offset by increasing muscle mass, locking up of cranial joints, and interdigitation of the mandibular symphysis. A) Suchia, B) Loricata, C) Crocodylomorpha, D) Crocodyliformes, E) Metasuchia, D) Crocodylia, F) Crocodylia, G) Alligatoridae, H) Crocodylidae.



Chapter 5— Conclusion

Introduction

This dissertation investigated the evolution of high feeding performance in crocodylians and their fossil relatives. Feeding is one of the most important tasks animals must accomplish (Dumont *et al.*, 2009; Santana, Dumont and Davis, 2010), yet the vertebrate skull houses numerous structures involved in a variety of roles, including feeding but also protecting the brain and sensory structures, ventilation, communication, and defense. Further, even a single function such as feeding can be subject to multiple selective pressures that are at odds with one another. Skulls therefore feature tradeoffs between conflicting functional demands and often represent a “compromise” that satisfies these disparate functions.

The evolution of the crocodylian skull represents one of the great transformations in vertebrate evolution. Early fossil pseudosuchians, the clade of archosaurs more closely related to crocodylians than birds, had tall skulls with flexible cranial joints and jaw muscle anatomy typical of early archosaurs. From this configuration, the lineage leading to extant crocodylians evolved robust but flat skulls that deliver the highest bite forces ever measured. The cooccurrence of a flat skull with high bite performance represents a paradox: how does an animal with a flat skull bite so hard? This dissertation research aims to characterize the effects of skull flattening on muscle and joint anatomy and to elucidate the means by which crocodylians are able to deliver powerful bites with seemingly inefficient muscular anatomy.

Below, I briefly summarize the methods and major findings of the three research chapters of this dissertation research. I then consider the results together to describe the biomechanical evolution of the lineage leading to crocodylians. Finally, I illustrate how the results of the present study might be applied to address outstanding questions in vertebrate evolution.

The Effects of Skull Flattening on Suchian Jaw Muscle Evolution

This study aimed to characterize jaw muscle anatomy in a diverse sample of extant and extinct suchians and determine the effects of skull flattening on muscle performance. In an ideal biomechanical system, jaw muscles would pull completely dorsally and all of the force would pull the mandible dorsally, producing maximal bite force. In most animals with high bite forces, including hyenas (Tanner *et al.*, 2008, 2010), sharks (Huber *et al.*, 2005; Ferrara *et al.*, 2011), and *Tyrannosaurus* (Cost *et al.*, 2019), the jaw muscles are relatively upright. Thus, oblique muscle orientations in a hard-biting group like crocodylians is surprising (Iordansky, 1964).

I used dissections, contrast-enhanced imaging (Gignac *et al.*, 2016), and the extant phylogenetic bracket (Witmer, 1995) to reconstruct jaw muscle anatomy in a sample of extant crocodylians and fossils that characterize the transition from early suchians to extant crocodylians. I used simple linear measurements to characterize skull flatness and skull size, and phylogenetic generalized least-squares (PGLS) regression to test hypotheses relating muscle anatomy to skull flatness.

Results of this study showed that the *m. pterygoideus dorsalis* gradually increased its relative size throughout suchian evolution until it was the dominant jaw adductor, accounting for ~50% of total jaw muscle force, largely at the expense of the temporal muscles. As the skull flattened, the jaw muscles also took on increasingly mediolateral orientations. This was reflected by a negative relationship between skull flatness and muscle efficiency, here calculated as the sum of muscle force magnitudes divided by the magnitude of the vector sum of muscle forces. This study did not find evidence that taxa with flat skulls relied on larger muscle masses to mitigate the biomechanical consequences of inefficient muscle orientations, although a later chapter with more sophisticated statistical analyses (Chapter 4) found support for this hypothesis. Overall, this study confirmed the hypothesis that muscles are forced into inefficient orientations in taxa with flat skulls, which has dramatic consequences for feeding biomechanics.

Cranial joint shape and joint loading in Suchia

This study aimed to quantify the anatomy of the articular surface of the jaw joint and test the hypothesis that joint articular surface morphology reflects joint loading. One of the hallmarks of the crocodylian skull is a rotation of the quadrates that places the jaw articulation caudal to the occiput (Walker, 1990). In such taxa, the structural axis of the quadrate is greatly inclined (Langston, 1973; Walker, 1990; Wilberg, 2012). It has been hypothesized that reaction forces acting on the jaw joint should align with this axis to prevent excessive bending moments (Sinclair and Alexander, 1987). If this is true, then the articular surface of the quadrate in flat-skulled taxa with inclined quadrates should be oriented more caudally rather than ventrally.

I used the muscle reconstructions performed in Chapter 2 as input for high-fidelity biomechanical models (Sellers *et al.*, 2017) to estimate bite and joint force in a sample of suchians with a range of quadrate morphologies. I developed novel methods of quantifying and visualizing joint articular surface morphology and developed a “correspondence index” that summarizes the concordance between the vector of joint force and the distribution of surface orientations on the articular surface.

Results of this study showed that the balancing-side jaw joint experiences higher load magnitudes than the working-side jaw joint, and that joint load generally decreases as the bite location moves caudally. I found that articular surface is oriented to resist the highest magnitude forces that it encounters (i.e., balancing-side joint force). In general, taxa with flatter skulls and tilted quadrates had more oblique orientations of joint force, suggesting that joint surface morphology tracks both with the orientation of the structural axis of the quadrate and the orientation of the forces acting on the quadrate during feeding. I also show that peak joint pressure is remarkably consistent across the sample, falls in line with most previously reported joint pressures, and falls within the range predicted by chondral modelling (Frost, 1979; Hamrick, 1999) for the maintenance of joint articular cartilage. Overall, this study suggests that joint articular surface morphology, jaw muscles, and skeletal elements experience coordinated evolution that maintain biomechanical equilibrium. These results illustrate how data from skeletal tissue biology and biomechanics can be integrated to test evolutionary hypotheses.

Skull Flattening and the Evolution of Feeding Biomechanics in Suchia

This study aimed to integrate muscle anatomy, joint loading, skull geometry, and biomechanical performance to test the hypothesis that derived key features of the crocodylian skull linked with high bite force performance act to counter the deleterious biomechanical effects of skull flattening. Researchers have long noted that the crocodylian skull has many derived characters that distinguish crocodylians from both other sauropsid taxa and fossil suchians (Iordansky, 1973; Langston, 1973). Although these characters are often linked with feeding performance (Iordansky, 1973), a holistic analysis of quantitative feeding forces and cranial modifications has not been attempted.

I integrated the feeding forces calculated in Chapter 3 with skull flatness and discrete character shifts to elucidate patterns of transformation in biomechanical performance. I used phylogenetic generalized least squares regression of various biomechanical parameters against skull flatness to reveal which character states increase feeding performance for a given muscular configuration.

I found that as the skull flattened in the lineage leading to modern crocodylians, muscle geometry was forced into inefficient orientations. To mitigate inefficient jaw muscle anatomy, jaw muscle mass and thus force was increased near the base of Crocodyliformes. The fossil record shows an increase in crests and tuberosities indicating increased aponeurotic and tendinous muscle attachments in taxa with the flattest skulls near the origin of Crocodylia. Thus, modern crocodylians likely inherited large muscle masses to overcome the geometric inefficiencies imposed by their flat skulls. Derived characters such as a

suturally immobilized palatobasal joint, an interdigitated mandibular symphysis, and a paraoccipital process contacting the quadrate were also linked with more effective production of bite force for a given muscle geometry. Overall, these results highlight the utility of studies combining traditional character analysis with high-fidelity biomechanical modeling.

Synthesis

The overall goal of this dissertation research was to characterize the evolution of feeding biomechanics in one of the great transformations in vertebrate evolution. A great deal of work has investigated evolution of skull shape in suchians (Piras *et al.*, 2014; Godoy, 2019; Stubbs *et al.*, 2021) and feeding biomechanics (McHenry *et al.*, 2006; Pierce, Angielczyk and Rayfield, 2008; Walmsley *et al.*, 2013; Gignac and O'Brien, 2016; McCurry *et al.*, 2017). Most of these studies have focused on the rostrum and have used two-dimensional representations of morphology. Most biomechanical studies in a sample of suchians have used proxies, artificially applied a bite force, and ignored the effects of muscle and joint forces. However, to my knowledge, this is the first study that uses high-fidelity biomechanical models with biologically-realistic loads estimated from detailed muscle anatomy in a sample of crocodylians and fossil suchians based on methods verified against *in vivo* data (Sellers *et al.*, 2017). Thus, the biomechanical findings of this study likely represent reliable estimates of feeding performance in suchians.

The flat skulls of extant crocodylians are thought to represent an adaptation to their aquatic ambush predatory lifestyle. A dorsoventrally flat skull allows crocodylians to float nearly submerged (Iordansky, 1973; Langston, 1973;

Cossette, 2018) and reduces drag during lateral head movements for prey capture (Busbey, 1995; McHenry *et al.*, 2006). However, as the results of the present study have shown, a flat skull also leads to inefficient muscle orientations. Thus, the flat skull of crocodylians represents conflicting functional demands on the feeding system. Although many studies have identified scenarios in which the skull is faced with conflicting functional demands (Van der Leeuw *et al.*, 2003; Albertson *et al.*, 2005), these usually pertain to the skull being involved in multiple biological roles (e.g., feeding, drinking, housing the brain and sensory structures). An exception is Rayfield (2019), who identified the flat skull of crocodylians as an instance of competing functional demands, although in this case rostral flatness was identified as less effective at resisting dorsoventral bending forces.

The results of this study depict coordinated evolution between jaw muscles, jaw joints, skeletal elements, and overall skull shape in the evolution of the lineage leading to crocodylians. Coordinated evolution is a common pattern found in skeletal elements that serve similar functions (Monteiro and Nogueira, 2010; Kelley and Motani, 2015). Although often viewed through the lens of morphological integration (Monteiro and Nogueira, 2010; Rossoni *et al.*, 2019; Michaud, Veron and Fabre, 2020), the results presented in this dissertation show that coordinated evolution can also be analyzed by detailed reconstructions of biomechanical performance in deep time. Overall, these results contribute to our understanding of one of the great transformations in vertebrate evolution.

Future Directions

The findings of this study set the stage for numerous avenues of future work. All the chapters in this dissertation investigated soft-tissue or skeletal aspects of skull morphology that underlie biomechanical performance of the feeding system. Although this study used a sample of suchians that characterized the evolution of the lineage leading to crown Crocodylia, various other lineages explored other derived morphologies, especially among the diverse notosuchians, sister group to Neosuchia. The findings presented here could be applied to assess putatively-herbivorous taxa for salient biomechanical features. Finally, with a denser sampling of fossil taxa, the methods presented here will enable us to investigate rates of biomechanical evolutionary change.

The present study identified a significant decrease in muscle efficiency at the base of Mesoeucrocodylia. Thus, basal notosuchians such as *Araripesuchus* inherited lower muscle efficiency and associated mitigated factors such as the closed palatobasal joint, an interdigitated Class III mandibular symphysis, and paraoccipital processes sutured to the quadrate. However, some derived members of Notosuchia evolved dorsoventrally-tall skulls and deep mandibles associated with herbivory (e.g., *Simosuchus*; Krause *et al.*, 2010; Ősi, 2014) or terrestrial hypercarnivory (e.g., baurusuchids; Pol and Leardi, 2015). In these clades, we may expect to find evidence of evolutionary “reversals” in some of the performance metrics reported in the present study. Using the methods described in Chapters 2 and 4, we can reconstruct biomechanical function in the lineages leading to these derived taxa. We can hypothesize that due to the more efficient muscular geometry made possible by a tall skull, derived taxa such as these may

decrease the amount of muscle mass, as efficient geometries will transfer more of input muscle force into useful bite force. These methods could be used to identify notosuchians clades in which there are significant changes in biomechanical performance. This line of inquiry also highlights the notion that very different biological roles (i.e., herbivory and hypercarnivory) can lead to similar forms and functions (*sensu* Bock and von Wahlert, 1965).

In addition to lineage-specific questions, these studies can be used to explicitly evaluate the biomechanics of herbivory in suchians. Some herbivorous suchians are noted for dorsoventrally-tall skulls and deep mandibles, presumably to increase muscle and mechanical efficiency (Ősi, 2014). However, some herbivorous suchians, particularly eusuchians (e.g., *Iharkutosuchus*), have incredibly flat skulls. Although the findings of Chapter 2 suggest this would imply very oblique muscle orientations, many such eusuchians have a medially-shifted pterygoid flange (Buscalioni *et al.*, 2011), suggesting a lack of medially-oriented muscle force for these structures to resist (Iordansky, 1964, 1973). The quadrate of these taxa have elaborated crests and tuberosities, suggesting they may instead rely on increasing the mass of the relatively-upright m. adductor mandibulae posterior. This inquiry highlights the “many-to-one” mapping of form to function (Wainwright, 2007; Collar *et al.*, 2014) involved in adaptations to a new diet. In addition to derived muscular features, many putatively-herbivorous suchians show derived jaw joint morphologies (Ősi, 2014). In many (e.g., “*Gomphosuchus*”), the articular surface of the quadrate is rostrocaudally shorter than that of the articular, suggesting the potential for proal or palinal translational

movements of the mandible. In a taxon with jaw movement, the jaw joint likely experiences a wide range of joint reaction force orientations. The methods of analyzing joint shape and joint force developed in Chapter 3 could be used to investigate the jaw joints of putatively-herbivorous and identify the full range of joint force orientations throughout the chewing cycle. “*Gomphosuchus*” also had the highest mechanical efficiency among our sample, which necessarily means it had the lowest joint force relative to size. It is possible that lower joint force is a requirement for translational jaw movement.

Finally, future research could identify evolutionary rates. Using the modest sample, this study was able to identify nodes at which biomechanical performance experienced significant shifts. By expanding the sample and filling key gaps in the tree (particularly between Crocodyliformes and Metasuchia and between Metasuchia and Crocodylia), the methods presented in this study could be expanded to identify nodes at which evolutionary rates of biomechanical change shifted. Previous studies have identified rate shifts in shape evolution in suchians (Stubbs *et al.*, 2021). However, to my knowledge, no study has attempted to identify rate shifts in biomechanical performance in Suchia before.

References

- Afoke, N. Y. P., Byers, P. D. and Hutton, W. C. (1987) 'Contact pressures in the human hip joint', *Journal of Bone and Joint Surgery - Series B*, 69(4), pp. 536–541. doi: 10.1302/0301-620x.69b4.3611154.
- Albertson, R. C. *et al.* (2005) 'Integration and evolution of the cichlid mandible: the molecular basis of alternate feeding strategies.', *Proceedings of the National Academy of Sciences of the United States of America*, 102(45), pp. 16287–16292.
- de Andrade, M. B. *et al.* (2011) *A new Berriasian species of Goniopholis (Mesoeucrocodylia, Neosuchia) from England, and a review of the genus, Zoological Journal of the Linnean Society*. doi: 10.1111/j.1096-3642.2011.00709.x.
- Biewener, A. A. (1989) 'Mammalian terrestrial locomotion and size Mechanical design principles define limits', *BioScience*, 39(11), pp. 776–783.
- Bock, W. J. (1959) 'Preadaptation and Multiple Evolutionary Pathways', *Evolution*, 13(2), pp. 194–211.
- Bock, W. J. and von Wahlert, G. (1965) 'Adaptation and the Form-Function Complex', 19(3), pp. 269–299.
- Bona, P., Degrange, F. J. and Fernández, M. S. (2013) 'Skull Anatomy of the Bizarre Crocodylian *Mourasuchus nativus* (Alligatoridae, Caimaninae)', *Anatomical Record*, 296(2), pp. 227–239. doi: 10.1002/ar.22625.
- Boyd, R. L. *et al.* (1990) 'Temporomandibular joint forces measured at the

condyle of *Macaca arctoides*', *American Journal of Orthodontics and Dentofacial Orthopedics*, 97(6), pp. 472–479.

Boyer, D. M. *et al.* (2015) 'Evolution of postural diversity in primates as reflected by the size and shape of the medial tibial facet of the talus', *American Journal of Physical Anthropology*, 157(1), pp. 134–177. doi: 10.1002/ajpa.22702.

Bramble, D. M. (1978) 'Origin of the Mammalian Feeding Complex: Models and Mechanisms', *Paleobiology*, 4(3), pp. 271–301.

Brazeau, M. D. *et al.* (2017) 'A three-dimensional placoderm (stem-group gnathostome) pharyngeal skeleton and its implications for primitive gnathostome pharyngeal architecture', *Journal of Morphology*, 278(9), pp. 1220–1228. doi: 10.1002/jmor.20706.

Brochu, C. A. (2001) 'Crocodylian Snouts in Space and Time: Phylogenetic Approaches Toward Adaptive Radiation', *American Zoologist*, 41(3), pp. 564–585. doi: 10.1668/0003-1569(2001)041[0564:CSISAT]2.0.CO;2.

Brochu, C. A. *et al.* (2012) 'A NEW SPECIES OF BOREALOSUCHUS (CROCODYLIFORMES, EUSUCHIA) FROM THE LATE CRETACEOUS – EARLY PALEOGENE OF NEW JERSEY', *Journal of Vertebrate Paleontology*, 32(1), pp. 105–116.

Brochu, C. A. (2013) 'Phylogenetic relationships of Palaeogene ziphodont eusuchians and the status of *Pristichampsus* Gervais, 1853', *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 103(3–4), pp. 521–550. doi: 10.1017/S1755691013000200.

Du Brul, E. L. (1964) 'Evolution of the Temporomandibular Joint', in *The Temporomandibular Joint*, pp. 1–27.

Busbey, A. B. (1986) 'New Material of *Sebecus* cf. *huilensis* (Crocodilia: Sebecosuchidae) from the Miocene La Venta Formation of Colombia', *Journal of Vertebrate Paleontology*, 6(1), pp. 20–27. doi: 10.1080/02724634.1986.10011595.

Busbey, A. B. (1989) 'Form and Function of the Feeding Apparatus of *Alligator mississippiensis*', *Journal of Morphology*, 202, pp. 99–127.

Busbey, A. B. (1995) 'The Structural Consequences of Skull Flattening in Crocodilians', in *Functional Morphology in Vertebrate Paleontology*, pp. 173–192.

Busbey, A. B. and Gow, C. (1984) 'A new protosuchian crocodile from the upper Triassic Elliot Formation of South Africa', *Palaeotologia Africana*, 25, pp. 127–149.

Buscalioni, A. D. *et al.* (2011) 'Early eusuchia crocodylomorpha from the vertebrate-rich Plattenkalk of Pietraroia (Lower Albian, southern Apennines, Italy)', *Zoological Journal of the Linnean Society*, 163(SUPPL. 1). doi: 10.1111/j.1096-3642.2011.00718.x.

Campos, D. A. *et al.* (2011) 'On a new peirosaurid crocodyliform from the Upper Cretaceous, Bauru group, southeastern Brazil', *Anais da Academia Brasileira de Ciencias*, 83(1), pp. 317–327. doi: 10.1590/S0001-37652011000100020.

Carpenter, K. and Lindsey, D. (1980) 'The Dentary of *Brachychampsia montana* Gilmore (Alligatorinae; Crocodylidae), A Late Cretaceous Turtle-Eating Alligator', *Journal of Paleontology*, 54(6), pp. 1213–1217.

Carvalho, I. D. S., Arruda Campos, A. D. C. and Henrique Nobre, P. (2005) 'Baurusuchus salgadoensis, a New Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil', *Gondwana Research*, 8(1), pp. 11–30. doi: 10.1016/S1342-937X(05)70259-8.

Chatterjee, S. (1985) 'Postosuchus, a New Thecodontian Reptile from the Triassic of Texas and the Origin of Tyrannosaurs', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 309(1139), pp. 395–460. doi: 10.1098/rstb.1985.0092.

Christiansen, P. and Wroe, S. (2007) 'Bite forces and evolutionary adaptations to feeding ecology in carnivores', *Ecology*, 88(2), pp. 347–358. doi: 10.1890/0012-9658(2007)88[347:BFAEAT]2.0.CO;2.

Cidade, G. M., Fortier, D. and Hsiou, A. S. (2019) 'The crocodylomorph fauna of the Cenozoic of South America and its evolutionary history: a review', *Journal of South American Earth Sciences*. Elsevier, 90(December 2018), pp. 392–411. doi: 10.1016/j.jsames.2018.12.026.

Clark, J. M. (1986) *Phylogenetic Relationships of the Crocodylomorph Archosaurs*.

Clark, J. M. (1994) 'Patterns of evolution in Mesozoic crocodyliforms', in *In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods*, pp. 84–97.

Clark, J. M. *et al.* (2004) 'A Middle Jurassic "sphenosuchian" from China and the origin of the crocodylian skull.', *Nature*, 430(7003), pp. 1021–4. doi: 10.1038/nature02802.

Clark, J. M. (2011) 'A new shartegosuchid crocodyliform from the Upper Jurassic Morrison Formation of western Colorado', *Zoological Journal of the Linnean Society*, 163(SUPPL. 1), pp. 152–172. doi: 10.1111/j.1096-3642.2011.00719.x.

Clark, J. M., Jacobs, L. L. and Downs, W. R. (1989) 'Mammal-like dentition in a mesozoic crocodylian.', *Science (New York, N. Y.)*, 244(4908), pp. 1064–1066. doi: 10.1126/science.244.4908.1064.

Clark, J. M., Sues, H.-D. and Berman, D. S. (2000) 'A New Specimen of *Hesperosuchus agilis* From the Upper Triassic of New Mexico and the Interrelationships of Basal Crocodylomorph Archosaurs', *Journal of Vertebrate Paleontology*, 20(4), pp. 683–704. doi: 10.1671/0272-4634(2000)020[0683:ANSOHA]2.0.CO;2.

Cleuren, J., Aerts, P. and De Vree, F. L. (1995) 'Bite and Joint Force Analysis in *Caiman crocodilus*', *Belgian Journal of Zoology*, pp. 79–94.

Cleuren, J. and De Vree, F. L. (1992) 'Kinematics of the Jaw and Hyolingual Apparatus During Feeding in *Caiman crocodilus*', *Journal of Morphology*.

Colbert, E. H. and Mook, C. C. (1951) 'The Ancestral Crocodilian *Protosuchus*', *American Museum of Natural History*, 97(3), pp. 143–182.

Collar, D. C. *et al.* (2014) 'Imperfect morphological convergence: variable changes in cranial structures underlie transitions to durophagy in moray eels.', *The American Naturalist*, 183(6), pp. E168-84. doi: 10.1086/675810.

Cossette, A. P. (2018) 'The early history of character evolution in alligatoroids. Ph.D. dissertation, University of Iowa, Iowa', p. 271 pp.

Cost, I. N. *et al.* (2019) 'Palatal Biomechanics and Its Significance for Cranial Kinesis in *Tyrannosaurus rex*', *The Anatomical Record*, (June 2018), pp. 1–19. doi: 10.1002/ar.24219.

Crompton, A. W. (1963) 'On the lower jaw of *Diarthognathus* and the origin of the mammalian lower jaw', *Journal of Zoology*, 140, pp. 697–749.

Crompton, A. W. and Hylander, W. L. (1986) 'Changes in Mandibular Function Following the Acquisition of a Dentary-squamosal Jaw Articulation', in *Ecology and Biology of Mammal-Like Reptiles*, pp. 263–282.

Crompton, A. W. and Parker, P. (1978) 'Evolution of the Mammalian Masticatory Apparatus: The fossil record shows how mammals evolved both complex chewing mechanisms and an effective middle ear, two structures that distinguish them from reptiles', *American scientist*, 66(2), pp. 192–201.

Davis, D. D. (1955) 'Masticatory apparatus in the spectacled bear, *Tremarctos ornatus*', *Fieldiana*, 37(2), pp. 25–46. doi: 10.5962/bhl.title.2809.

Davis, J. L. *et al.* (2010) 'Predicting bite force in mammals: two-dimensional versus three-dimensional lever models.', *The Journal of experimental biology*,

213(11), pp. 1844–1851. doi: 10.1242/jeb.041129.

Drumheller, S. K., Darlington, J. and Vliet, K. A. (2019) 'Surveying death roll behavior across Crocodylia', *Ethology Ecology and Evolution*. Taylor & Francis, 0(00), pp. 1–19. doi: 10.1080/03949370.2019.1592231.

Drumheller, S. K. and Wilberg, E. W. (2020) 'A synthetic approach for assessing the interplay of form and function in the crocodyliform snout', *Zoological Journal of the Linnean Society*, 188(2), pp. 507–521. doi: 10.1093/zoolinnean/zlz081.

Dumont, E. R. *et al.* (2009) 'Built to bite: cranial design and function in the wrinkle-faced bat', *Journal of Zoology*, 279(4), pp. 329–337. doi: 10.1111/j.1469-7998.2009.00618.x.

Dumont, E. R. *et al.* (2011) 'Finite element analysis of performance in the skulls of marmosets and tamarins', *Journal of Anatomy*, 218(1), pp. 151–162. doi: 10.1111/j.1469-7580.2010.01247.x.

Dumont, E. R. *et al.* (2012) 'Morphological innovation, diversification and invasion of a new adaptive zone', *Proceedings of the Royal Society B: Biological Sciences*, 279(1734), pp. 1797–1805. doi: 10.1098/rspb.2011.2005.

Dunn, R. H. *et al.* (2014) 'Ecological divergence and talar morphology in gorillas', *American Journal of Physical Anthropology*, 153(4), pp. 526–541. doi: 10.1002/ajpa.22451.

Erickson, G. M. *et al.* (2012) 'Insights into the ecology and evolutionary

success of crocodilians revealed through bite-force and tooth-pressure experimentation.', *PloS one*, 7(3), p. e31781. doi: 10.1371/journal.pone.0031781.

Erickson, G. M., Lappin, A. K. and Vliet, K. A. (2003) 'The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*)', *Journal of Zoology*, 260(July), pp. 317–327. doi: 10.1017/s0952836903003819.

Evans, A. R. *et al.* (2007) 'High-level similarity of dentitions in carnivorans and rodents.', *Nature*, 445(7123), pp. 78–81. doi: 10.1038/nature05433.

Ewer, R. F. (1965) 'The Anatomy of the Thecodont Reptile *Euparkeria capensis* Broom', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 237(641), pp. 37–72.

Felice, R. N. *et al.* (2019) 'Evolutionary Integration and Modularity in the Archosaur Cranium', *Integrative and Comparative Biology*, 59(2), pp. 371–382. doi: 10.1093/icb/icz052.

Ferrara, T. L. *et al.* (2011) 'Mechanics of biting in great white and sandtiger sharks', *Journal of Biomechanics*. Elsevier, 44(3), pp. 430–435. doi: 10.1016/j.jbiomech.2010.09.028.

Ferreira, G. S. *et al.* (2020) 'Feeding biomechanics suggests progressive correlation of skull architecture and neck evolution in turtles', pp. 1–11. doi: 10.1038/s41598-020-62179-5.

Fiorelli, L. E. and Calvo, J. (2008) 'New remains of *Notosuchus terrestris* Woodward, 1896 (Crocodyliformes: Mesoeucrocodylia) from Late Cretaceous of

Neuquén, Patagonia, Argentina', *Arquivos do Museu Nacional*, 66(1), pp. 83–124.

Fish, F. E. *et al.* (2007) 'Death roll of the alligator: mechanics of twist feeding in water.', *The Journal of experimental biology*, 210(Pt 16), pp. 2811–8. doi: 10.1242/jeb.004267.

Frost, H. M. (1979) 'A Chondral Modeling Theory', *Calcified Tissue International*, 28, pp. 181–200.

Frost, H. M. (2001) 'From Wolff's Law to the Utah Paradigm: Insights About Bone Physiology and Its Clinical Applications', 419(February), pp. 398–419.

Gans, C. (1989) 'Stages in the origin of vertebrates: analysis by means of scenarios.', *Biological reviews of the Cambridge Philosophical Society*, 64(3), pp. 221–68. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/2675997>.

Gans, C. and Northcutt, R. G. (1983) 'Neural crest and the origin of vertebrates: a new head.', *Science (New York, N.Y.)*, 220(4594), pp. 268–73. doi: 10.1126/science.220.4594.268.

Gignac, P. M. *et al.* (2016) 'Diffusible iodine-based contrast-enhanced computed tomography (diceCT): An emerging tool for rapid, high-resolution, 3-D imaging of metazoan soft tissues', *Journal of Anatomy*, 228(6), pp. 889–909. doi: 10.1111/joa.12449.

Gignac, P. M. *et al.* (2019) *Feeding in Crocodylians and Their Relatives: Functional Insights from Ontogeny and Evolution*. Springer International

Publishing. doi: 10.1007/978-3-030-13739-7.

Gignac, P. M. and Erickson, G. M. (2016) 'Ontogenetic bite-force modeling of Alligator mississippiensis: implications for dietary transitions in a large-bodied vertebrate and the evolution of crocodylian feeding', *Journal of Zoology*, 299(4), pp. 229–238. doi: 10.1111/jzo.12349.

Gignac, P. M. and O'Brien, H. (2016) 'Suchian Feeding Success at the Interface of Ontogeny and Macroevolution', *Integrative and Comparative Biology*, p. icw041. doi: 10.1093/icb/icw041.

Gingerich, P. D. (1979) 'The human mandible: lever, link, or both?', *American journal of physical anthropology*, 51(1), pp. 135–7. doi: 10.1002/ajpa.1330510116.

Godoy, P. L. (2019) 'Crocodylomorph cranial shape evolution and its relationship with body size and ecology', *Journal of Evolutionary Biology*, (August), p. 724609. doi: 10.1101/724609.

Gomani, E. M. (1997) 'A Crocodyliform from the Early Cretaceous Dinosaur Beds, Northern malawi', *Journal of Vertebrate Paleontology*, 17(2), pp. 280–294. doi: 10.1080/02724634.1997.10010975.

Gow, C. E. (2000) 'The Skull of Protosuchus Haughtoni, an Early Jurassic Crocodyliform From Southern Africa', 20(March), pp. 49–56.

Gower, D. J. (1999) 'The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany', *Stuttgarter*

Beiträge zur Naturkunde Serie B (Geologie und Paläontologie) , 280, pp. 1–49.

Available at: <http://www.naturkundemuseum->

[bw.de/sites/default/files/publikationen/serie-b/B280.pdf](http://www.naturkundemuseum-bw.de/sites/default/files/publikationen/serie-b/B280.pdf).

Granatosky, M. C. and Ross, C. F. (2020) 'Differences in muscle mechanics underlie divergent optimality criteria between feeding and locomotor systems', *Journal of Anatomy*, (May), pp. 1–15. doi: 10.1111/joa.13279.

Greaves, W. S. (1974) 'Functional Implications of Mammalian Jaw Joint Position', *Forma et Functio*, 7, pp. 363–376.

Greaves, W. S. (1978) 'The jaw lever system in ungulates: a new model', *Journal of Zoology*, 184(2), pp. 271–285. doi: 10.1111/j.1469-7998.1978.tb03282.x.

Greaves, W. S. (1980) 'The Mammalian Jaw Mechanism-- The High Glenoid Cavity', *The American Naturalist*, 130(4), pp. 526–543. doi: 10.2307/2678832.

Greaves, W. S. (1995) 'Functional predictions from theoretical models of the skull and jaws in reptiles and mammals', in *Functional Morphology in Vertebrate Paleontology*, pp. 99–115.

Grigg, G. C. and Kirshner, D. (2015) *Biology and Evolution of Crocodylians*. Ithaca, New York: Cornell University Press. doi: 10.1146/annurev.ento.52.110405.091303.

Grosse, I. R. *et al.* (2007) 'Techniques for modeling muscle-induced forces in finite element models of skeletal structures.', *Anatomical Record*, 290(9), pp.

1069–1088. doi: 10.1002/ar.20568.

Hamrick, M. W. (1999) 'A Chondral Modeling Theory Revisited', *Journal of Theoretical Biology*, pp. 201–208.

Hara, T. *et al.* (1992) 'Force distribution across wrist joint: Application of pressure-sensitive conductive rubber', *Journal of Hand Surgery*, 17(2), pp. 339–347. doi: 10.1016/0363-5023(92)90417-N.

Heard, S. B. and Hauser, D. L. (1995) 'Key Evolutionary Innovations and Their Ecological Mechanisms', *Historical Biology*, 10, pp. 151–173.

Hendrickx, C., Mateus, O. and Buffetaut, E. (2016) 'Morphofunctional analysis of the quadrate of Spinosauridae (Dinosauria: Theropoda) and the presence of Spinosaurus and a second spinosaurine taxon in the Cenomanian of North Africa', *PLoS ONE*, 11(1), pp. 1–49. doi: 10.1371/journal.pone.0144695.

Herrel, A. *et al.* (2005) 'Evolution of bite force in Darwin's finches: A key role for head width', *Journal of Evolutionary Biology*, 18(3), pp. 669–675. doi: 10.1111/j.1420-9101.2004.00857.x.

Herrel, A., De Grauw, E. and Lemos-Espinal, J. a. (2001) 'Head shape and bite performance in xenosaurid lizards', *Journal of Experimental Zoology*, 290(2), pp. 101–107. doi: 10.1002/jez.1039.

Herring, S. W. *et al.* (2002) 'Temporomandibular joint in miniature pigs: Anatomy, cell replication, and relation to loading', *Anatomical Record*, 266(3), pp. 152–166. doi: 10.1002/ar.10049.

- Herring, S. W. (2003) 'TMJ anatomy and animals models', *Journal Musculoskelet Neuronal Interact.*, 3(4), pp. 997–1003. doi: 10.1016/j.biotechadv.2011.08.021.Secreted.
- Herring, S. W. (2007) 'Masticatory Muscles and the Skull: A Comparative Perspective', 52(4), pp. 296–299.
- Holliday, C. M. (2009) 'New Insights Into Dinosaur Jaw Muscle Anatomy', *Anatomical Record*, 292(9), pp. 1246–1265. doi: 10.1002/ar.20982.
- Holliday, C. M. *et al.* (2015) 'The functional and evolutionary significance of the crocodyliform pterygomandibular joint', *Integrative and Comparative Biology*, 55, p. E81.
- Holliday, C. M. *et al.* (2019) 'The Frontoparietal Fossa and Dorsotemporal Fenestra of Archosaurs and Their Significance for Interpretations of Vascular and Muscular Anatomy in Dinosaurs', *The Anatomical Record*, p. ar.24218. doi: 10.1002/ar.24218.
- Holliday, C. M. and Gardner, N. M. (2012) 'A new eusuchian crocodyliform with novel cranial integument and its significance for the origin and evolution of crocodylia', *PLoS ONE*, 7(1). doi: 10.1371/journal.pone.0030471.
- Holliday, C. M. and Nesbitt, S. J. (2013) 'Morphology and diversity of the mandibular symphysis of archosauriforms', *Geological Society, London, Special Publications*, 379(1), pp. 555–571. doi: 10.1144/SP379.2.
- Holliday, C. M. and Witmer, L. M. (2007) 'Archosaur Adductor Chamber

Evolution: Integration of Musculoskeletal and Topological Criteria in Jaw Muscle Homology', *Journal of Morphology*, 268, pp. 457–484. doi: 10.1002/jmor.

Holliday, C. M. and Witmer, L. M. (2009) 'THE EPIPTERYGOID OF CROCODYLIFORMS AND ITS SIGNIFICANCE FOR THE EVOLUTION OF THE ORBITOTEMPORAL REGION OF EUSUCHIANS', *Journal of Vertebrate Paleontology*, 29(September), pp. 715–733.

Huber, D. R. *et al.* (2005) 'Analysis of the bite force and mechanical design of the feeding mechanism of the durophagous horn shark *Heterodontus francisci*', *The Journal of Experimental Biology*, 208(Pt 18), pp. 3553–3571. doi: 10.1242/jeb.01816.

Huber, D. R., Dean, M. N. and Summers, A. P. (2008) 'Hard prey, soft jaws and the ontogeny of feeding mechanics in the spotted ratfish *Hydrolagus coliei*.', *Journal of the Royal Society, Interface / the Royal Society*, 5(25), pp. 941–952. doi: 10.1098/rsif.2007.1325.

Hunter, J. P. (1998) 'Key innovation and ecology of macroevolution', *Trends in Ecology and Evolution*, 13(1995), pp. 31–36.

Hylander, W. L. (1975) 'The Human Mandible: Lever or Link?', *American Journal of Physical Anthropology*, 43(2), pp. 227–242.

Hylander, W. L. (1979) 'An Experimental Analysis of Temporomandibular Joint Reaction Force in Macaques', *American Journal of Physical Anthropology*, 51, pp. 433–456.

Hylander, W. L. (1992) 'Functional Anatomy', in Sarnat, B. G. and Laskin, D. M. (eds) *The Temporomandibular Joint: a Biological Basis for Clinical Practice. Fourth Edition.*, pp. 60–92.

Hylander, W. L. *et al.* (2000) 'Symphyseal fusion and jaw-adductor muscle force: an EMG study.', *American journal of physical anthropology*, 112(4), pp. 469–92. doi: 10.1002/1096-8644(200008)112:4<469::AID-AJPA5>3.0.CO;2-V.

Hylander, W. L. *et al.* (2005) 'Temporalis function in anthropoids and strepsirrhines: An EMG study', *American Journal of Physical Anthropology*, 128(1), pp. 35–56. doi: 10.1002/ajpa.20058.

Hylander, W. L. (2006) 'Functional Anatomy and Biomechanics of the Masticatory Apparatus', *Temporomandibular disorders: an evidence approach to diagnosis and treatment*, (January 2006), pp. 3–34. Available at: <http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Functional+Anatomy+and+Biomechanics+of+the+Masticatory+Apparatus#0>.

Iijima, M. (2017) 'Assessment of trophic ecomorphology in non-alligatoroid crocodylians and its adaptive and taxonomic implications', *Journal of Anatomy*, 231(2), pp. 192–211. doi: 10.1111/joa.12626.

Iordansky, N. N. (1964) 'The jaw muscles of the crocodiles and some relating structures of the crocodilian skull', *Anat. Anz.*, 115, pp. 256–280.

Iordansky, N. N. (1973) 'The Skull of the Crocodilia', in Gans, C. (ed.) *Biology of the Reptilia*, Vol. 4, pp. 201–261.

Iordansky, N. N. (2010) 'Pterygoideus muscles and other jaw adductors in amphibians and reptiles', *Biology Bulletin*, 37(9), pp. 905–914. doi: 10.1134/S1062359010090050.

Kelley, N. P. and Motani, R. (2015) 'Trophic convergence drives morphological convergence in marine tetrapods', *Biology Letters*, 11(1), pp. 20140709–20140709. doi: 10.1098/rsbl.2014.0709.

Kley, N. J. *et al.* (2010) 'Craniofacial Morphology of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar', *Memoirs of the Society of Vertebrate Paleontology*, 10(6), pp. 122–153. doi: 10.1080/02724634.2010.532674.

Krause, D. W. *et al.* (2010) 'OVERVIEW OF THE DISCOVERY, DISTRIBUTION, AND GEOLOGICAL CONTEXT OF SIMOSUCHUS CLARKI (CROCODYLIFORMES: NOTOSUCHI) FROM THE LATE CRETACEOUS OF MADAGASCAR', *Journal of Vertebrate Paleontology Memoir*, 30, pp. 4–12.

Kubo, T. and Benton, M. J. (2007) 'Evolution of hindlimb posture in archosaurs: Limb stresses in extinct vertebrates', *Palaeontology*, 50(6), pp. 1519–1529. doi: 10.1111/j.1475-4983.2007.00723.x.

Langston, W. (1965) 'Fossil Crocodilians from Colombia and the Cenozoic History of the Crocodilia in South America', *Copeia*, 1965(3), p. 392. doi: 10.2307/1440820.

Langston, W. J. (1973) 'The Crocodilian Skull in Historical Perspective', in *Biology of the Reptilia*, Vol. 4, pp. 263–284.

Lauder, G. V. (1995) 'On the Inference of Function from Structure', in Thomason, J. J. (ed.) *Functional Morphology in Vertebrate Paleontology*, pp. 1–18.

Leardi, J. M., Pol, D. and Clark, J. M. (2017) 'Detailed anatomy of the braincase of *Macelognathus vagans* Marsh, 1884 (Archosauria, Crocodylomorpha) using high resolution tomography and new insights on basal crocodylomorph phylogeny', *PeerJ*, 5, p. e2801. doi: 10.7717/peerj.2801.

Leardi, J. M., Pol, D. and Clark, J. M. (2020) 'Braincase anatomy of *Almadasuchus figarii* (Archosauria, Crocodylomorpha) and a review of the cranial pneumaticity in the origins of Crocodylomorpha', (September 2019), pp. 1–26. doi: 10.1111/joa.13171.

Van der Leeuw, A. H. J. *et al.* (2003) 'Conflicting demands on the trophic system of Anseriformes and their evolutionary implications', *Animal Biology*, 53(3), pp. 259–301. doi: 10.1163/157075603322539453.

Lessner, E. J. *et al.* (2019) 'Anatomy and Ontogeny of the Mandibular Symphysis in *Alligator mississippiensis*', *Anatomical Record*, 302(10), pp. 1696–1708. doi: 10.1002/ar.24116.

Lessner, E. J. and Holliday, C. M. (2020) 'A 3D ontogenetic atlas of *Alligator mississippiensis* cranial nerves and their significance for comparative neurology of reptiles', *Anatomical Record*, (September), pp. 1–29. doi: 10.1002/ar.24550.

Liu, Z.-J. and Herring, S. W. (2000a) 'Bone surface strains and internal bony pressures at the jaw joint of the miniature pig during masticatory muscle

contraction', *Archives of Oral Biology*, 45(2), pp. 95–112. doi: 10.1016/S0003-9969(99)00127-2.

Liu, Z.-J. and Herring, S. W. (2000b) 'Masticatory Strains on Osseous and Ligamentous Components of the Temporomandibular Joint in Miniature Pigs', *Journal of Orofacial Pain*, 14(4), pp. 265–278.

Martin, J. E. *et al.* (2020) 'Virtual reconstruction of the skull of *Bernissartia fagesii* and current understanding of the neosuchian–eusuchian transition', *Journal of Systematic Palaeontology*. Taylor & Francis, 0(0), pp. 1–23. doi: 10.1080/14772019.2020.1731722.

Martin, J. E., Delfino, M. and Smith, T. (2016) 'Osteology and affinities of Dollo's goniopholidid (*Mesoeucrocodylia*) from the Early Cretaceous of Bernissart, Belgium', *Journal of Vertebrate Paleontology*, 36(6). doi: 10.1080/02724634.2016.1222534.

Martin, J. E., Raslan-Loubatié, J. and Mazin, J. M. (2016) 'Cranial anatomy of *Pholidosaurus purbeckensis* from the Lower Cretaceous of France and its bearing on pholidosaurid affinities', *Cretaceous Research*, 66, pp. 43–59. doi: 10.1016/j.cretres.2016.05.008.

Mastrantonio, B. M. *et al.* (2013) 'The braincase of *Prestosuchus chiniquensis* (Archosauria: Suchia)', *Geological Society, London, Special Publications*, 379, pp. 425–440. doi: 10.1144/SP379.10.

Maynard Smith, J. and Savage, R. J. G. (1955) 'SOME LOCOMOTORY ADAPTATIONS IN MAMMALS', (September).

Maynard Smith, J. and Savage, R. J. G. (1959) 'The Mechanics of Mammalian Jaws', *The School Science Review*.

McCurry, M. R. *et al.* (2017) 'The biomechanical consequences of longirostry in crocodilians and odontocetes', *Journal of Biomechanics*. Elsevier Ltd, 56, pp. 61–70. doi: 10.1016/j.jbiomech.2017.03.003.

McHenry, C. R. *et al.* (2006) 'Biomechanics of the Rostrum in Crocodilians: A Comparative Analysis Using Finite-Element Modeling', *The anatomical record. Part A, Discoveries in molecular, cellular, and evolutionary biology*, 288(8), pp. 827–849. doi: 10.1002/ar.a.20360.

Melstrom, K. M. and Irmis, R. B. (2019) 'Repeated Evolution of Herbivorous Crocodyliforms during the Age of Dinosaurs', *Current Biology*. Elsevier Ltd., 29(14), pp. 2389-2395.e3. doi: 10.1016/j.cub.2019.05.076.

Menegaz, R. A. *et al.* (2010) 'Evidence for the influence of diet on cranial form and robusticity', *Anatomical Record*. doi: 10.1002/ar.21134.

Metzger, K. A., Daniel, W. J. T. and Ross, C. F. (2005) 'Comparison of Beam Theory and Finite-Element Analysis With In Vivo Bone Strain Data From the Alligator Cranium', *Anatomical Record - Part A Discoveries in Molecular, Cellular, and Evolutionary Biology*, 283(2), pp. 331–348. doi: 10.1002/ar.a.20167.

Metzger, K. A., Ross, C. F. and Spencer, M. A. (2004) 'Does the constrained lever model describe an optimality criterion in crocodilian jaw mechanics?', pp. 6–8.

Michaud, M., Veron, G. and Fabre, A. -C. (2020) 'Phenotypic integration in feliform carnivores: covariation patterns and disparity in hypercarnivores versus generalists', *Evolution*, p. evo.14112. doi: 10.1111/evo.14112.

Monteiro, L. R. and Nogueira, M. R. (2010) 'Adaptive radiations, ecological specialization, and the evolutionary integration of complex morphological structures', *Evolution*, 64(3), pp. 724–744. doi: 10.1111/j.1558-5646.2009.00857.x.

Mook, C. C. (1967) 'Preliminary Description of a New Goniopholid Crocodilian', *Kirtlandia*, 2, pp. 1–10.

Morris, Z. S. *et al.* (2019) 'Heterochronic shifts and conserved embryonic shape underlie crocodylian craniofacial disparity and convergence', *Proceedings of the Royal Society B: Biological Sciences*, 286(1897), p. 20182389. doi: 10.1098/rspb.2018.2389.

Narváez, I. *et al.* (2015) 'New crocodyliforms from southwestern Europe and definition of a diverse clade of European late cretaceous basal eusuchians', *PLoS ONE*, 10(11), pp. 1–34. doi: 10.1371/journal.pone.0140679.

Nesbitt, S. J. (2011) 'THE EARLY EVOLUTION OF ARCHOSAURS: RELATIONSHIPS AND THE ORIGIN OF MAJOR CLADES', *Bulletin of the American Museum of Natural History*, 352, pp. 1–292.

Nieto, M. N. *et al.* (2021) 'Biomechanical performance of the cranio-mandibular complex of the small notosuchian *Araripesuchus gomesii* (Notosuchia, Uruguaysuchidae)', *Anatomical Record*.

Norell, M. A. and Clark, J. M. (1990) 'A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia', *Bulletin - Institut royal des sciences naturelles de Belgique. Sciences de la terre*, 60, pp. 115–128. Available at: <http://cat.inist.fr/?aModele=afficheN&cpsidt=19656862>.

O'Brien, H. D. *et al.* (2019) 'Crocodylan Head Width Allometry and Phylogenetic Prediction of Body Size in Extinct Suchians', *Integrative Organismal Biology*, 7063. doi: 10.1093/iob/obz006.

Oaks, J. R. (2011) 'A time-calibrated species tree of crocodylia reveals a recent radiation of the true crocodiles', *Evolution*, 65(11), pp. 3285–3297. doi: 10.1111/j.1558-5646.2011.01373.x.

Ortega, F. *et al.* (2000) 'A new species of Araripesuchus (Crocodylomorpha, Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina)', *Journal of Vertebrate Paleontology*, 20(1), pp. 57–76. doi: 10.1671/0272-4634(2000)020[0057:ANSOAC]2.0.CO;2.

Ősi, A. (2008) 'Cranial osteology of *Iharkutosuchus makadii*, a Late Cretaceous basal eusuchian crocodyliform from Hungary', *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 248(3), pp. 279–299.

Ősi, A. (2014) 'The evolution of jaw mechanism and dental function in heterodont crocodyliforms', *Historical Biology*, 26(3), pp. 279–414. doi: 10.1080/08912963.2013.777533.

Ősi, A., Clark, J. M. and Weishampel, D. B. (2007) 'First report on a new

basal eusuchian crocodyliform with multicusped teeth from the Upper Cretaceous (Santonian) of Hungary', *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 243(2), pp. 169–177. doi: 10.1127/0077-7749/2007/0243-0169.

Ósi, A. and Weishampel, D. B. (2009) 'Jaw mechanism and dental function in the late cretaceous basal eusuchian *Iharkutosuchus*', *Journal of Morphology*, 270(8), pp. 903–920. doi: 10.1002/jmor.10726.

Pérez-ramos, A. *et al.* (2020) 'Biomechanical simulations reveal a trade-off between adaptation to glacial climate and dietary niche versatility in European cave bears', pp. 1–11.

Pierce, S. E., Angielczyk, K. D. and Rayfield, E. J. (2008) 'Patterns of morphospace occupation and mechanical performance in extant crocodilian skulls: a combined geometric morphometric and finite element modeling approach.', *Journal of Morphology*, 269(7), pp. 840–864. doi: 10.1002/jmor.10627.

Pierce, S. E., Angielczyk, K. D. and Rayfield, E. J. (2009) 'Shape and mechanics in thalattosuchian (Crocodylomorpha) skulls: implications for feeding behaviour and niche partitioning.', *Journal of anatomy*, 215(5), pp. 555–576. doi: 10.1111/j.1469-7580.2009.01137.x.

Pierce, S. E. and Benton, M. J. (2006) 'Pelagosaurus typus Bronn, 1841 (Mesoeucrocodylia: Thalattosuchia) from the Upper Lias (Toarcian, Lower Jurassic) of Somerset, England', *Journal of Vertebrate Paleontology*, 26(3), pp. 621–635. doi: 10.1671/0272-4634(2006)26[621:PTBMTF]2.0.CO;2.

Piras, P. *et al.* (2014) 'Morphological integration and functional modularity in the crocodilian skull', *Integrative Zoology*, 9(4), pp. 498–516. doi: 10.1111/1749-4877.12062.

Pol, D. *et al.* (2013) 'A new fossil from the Jurassic of Patagonia reveals the early basicranial evolution and the origins of Crocodyliformes.', *Biological reviews of the Cambridge Philosophical Society*, 88(4), pp. 862–72. doi: 10.1111/brv.12030.

Pol, D. *et al.* (2014) 'A new notosuchian from the late cretaceous of Brazil and the phylogeny of advanced notosuchians', *PLoS ONE*, 9(4). doi: 10.1371/journal.pone.0093105.

Pol, D. and Leardi, J. M. (2015) 'Diversity Patterns of Notosuchia (Crocodyliformes, Mesoeucrocodylia) During the Cretaceous of Gondwana', *Publicación Electrónica de la Asociación Paleontológica Argentina*, (October 2016). doi: 10.5710/PEAPA.10.06.2015.108.

Porro, L. B. *et al.* (2011) 'Free body analysis, beam mechanics, and finite element modeling of the mandible of Alligator mississippiensis.', *Journal of Morphology*, 272(8), pp. 910–37. doi: 10.1002/jmor.10957.

Porro, L. B. *et al.* (2013) 'In vivo bone strain and finite element modeling of the mandible of Alligator mississippiensis.', *Journal of anatomy*, 223(3), pp. 195–227. doi: 10.1111/joa.12080.

Rafferty, K. L. and Herring, S. W. (1999) 'Craniofacial sutures: Morphology, growth, and in vivo masticatory strains', *Journal of Morphology*, 242(2), pp. 167–

179. doi: 10.1002/(SICI)1097-4687(199911)242:2<167::AID-JMOR8>3.0.CO;2-1.

Rayfield, E. J. (2019) 'What Does Musculoskeletal Mechanics Tell Us About Evolution of Form and Function in Vertebrates?', in *Feeding in Vertebrates*, pp. 45–70. doi: 10.1007/978-3-030-13739-7_3.

Robinson, J. *et al.* (2015) 'Progenitor Cells of the Mandibular Condylar Cartilage', pp. 110–114. doi: 10.1007/s40610-015-0019-x.

Ross, C. F., Eckhardt, A., *et al.* (2007) 'Modulation of intra-oral processing in mammals and lepidosaurs', *Integrative and Comparative Biology*, 47(1), pp. 118–136. doi: 10.1093/icb/icm044.

Ross, C. F., Dharia, R., *et al.* (2007) 'Modulation of mandibular loading and bite force in mammals during mastication.', *The Journal of Experimental Biology*, 210(Pt 6), pp. 1046–63. doi: 10.1242/jeb.02733.

Rossoni, D. M. *et al.* (2019) 'A multiple peak adaptive landscape based on feeding strategies and roosting ecology shaped the evolution of cranial covariance structure and morphological differentiation in phyllostomid bats', *Evolution*, 73(5), pp. 961–981. doi: 10.1111/evo.13715.

Ruebenstahl, A. *et al.* (no date) 'Anatomy and Relationships of the Basal Crocodylomorphs *Junggarsuchus sloani* and *Dibothrosuchus elaphros*', *Anatomical Record*. doi: 10.4103/JCD.JCD_353_16.

Ruebenstahl, A. A. (2019) 'Junggarsuchus sloani, an Early Late Jurassic Crocodylomorph with Crocodyliform Affinities'.

Saber, A. S. and Hassanin, A. (2014) 'Some Morphological Studies on the Jaw Joint of the Australian Saltwater Crocodile (*Crocodylus porosus*)', *Journal of Veterinary Anatomy*, 7(2), pp. 55–74.

Sacks, R. D. and Roy, R. R. (1982) 'Architecture of the Hind Limb Muscles of Cats: Functional Significance', *Journal of Morphology*, 173, pp. 185–195.

Salisbury, S. W. *et al.* (2006) 'The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia.', *Proceedings. Biological sciences / The Royal Society*, 273(1600), pp. 2439–48. doi: 10.1098/rspb.2006.3613.

Santana, S. E., Dumont, E. R. and Davis, J. L. (2010) 'Mechanics of bite force production and its relationship to diet in bats', *Functional Ecology*, 24(4), pp. 776–784. doi: 10.1111/j.1365-2435.2010.01703.x.

Santana, S. E., Grosse, I. R. and Dumont, E. R. (2012) 'Dietary Hardness, Loading Behavior, and the Evolution of Skull Form in Bats', pp. 2587–2598. doi: 10.5061/dryad.d548646j.

Scapino, R. P., Obrez, A. and Greising, D. (2006) 'Organization and function of the collagen fiber system in the human temporomandibular joint disk and its attachments', *Cells Tissues Organs*, 182(3–4), pp. 201–225. doi: 10.1159/000093969.

Schumacher, G.-H. (1973) 'The head muscles and hyolaryngeal skeleton of turtles and crocodilians', *Biology of the Reptilia Volume 4*, (2), pp. 101–199. Available at: papers2://publication/uuid/86DB0F05-E994-46A0-BA97-E9FB604F7759.

Sellers, K. C. *et al.* (2017) 'Ontogeny of bite force in a validated biomechanical model of the American alligator', *The Journal of Experimental Biology*, 220(11), pp. 2036–2046. doi: 10.1242/jeb.156281.

Sellers, K. C., Middleton, K. M. and Holliday, C. M. (2018) 'Biomechanics and Evolution of the Crocodyliform Skull', in *Society for Integrative and Comparative Biology*, pp. 117–6.

Sereno, P. C. and Larsson, H. C. E. (2009) 'Cretaceous crocodyliforms from the Sahara', *ZooKeys*, 28(SPEC. ISSUE 4), pp. 1–143. doi: 10.3897/zookeys.28.325.

Sinclair, A. G. and Alexander, R. M. (1987) 'Estimates of forces exerted by the jaw muscles of some reptiles', *Journal of Zoology, London*, pp. 107–115.

Smith, M. M. (2003) 'Vertebrate dentitions at the origin of jaws: When and how pattern evolved', *Evolution and Development*, 5(4), pp. 394–413.

Smith, R. J. (1978) 'Mechanical Biomechanics and Temporomandibular Joint Function in Primates', *American Journal of Physical Anthropology*, 49, pp. 341–350.

Stanković, S. *et al.* (2013) 'Morphological and biomechanical features of the temporomandibular joint disc: An overview of recent findings', *Archives of Oral Biology*, 58(10), pp. 1475–1482. doi: 10.1016/j.archoralbio.2013.06.014.

Stubbs, T. L. *et al.* (2021) 'Ecological opportunity and the rise and fall of crocodylomorph evolutionary innovation'.

Tanner, J. B. *et al.* (2008) 'Of arcs and vaults: The biomechanics of bone-cracking in spotted hyenas (*Crocuta crocuta*)', *Biological Journal of the Linnean Society*, 95(2), pp. 246–255. doi: 10.1111/j.1095-8312.2008.01052.x.

Tanner, J. B. *et al.* (2010) 'Ontogenetic change in skull morphology and mechanical advantage in the spotted hyena (*Crocuta crocuta*)', *Journal of Morphology*, 271(3), pp. 353–365. doi: 10.1002/jmor.10802.

Tarsitano, S. F. (1985) 'Cranial Metamorphosis and the Origin of the Eusuchia', *Neues Jahrbuch fur Geologie und Palantologie*, 170(1), pp. 27–44.

Team, R. C. (2021) 'R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>'.

Terhune, C. E. (2011) 'Modeling the biomechanics of articular eminence function in anthropoid primates', *Journal of Anatomy*, 219(5), pp. 551–564. doi: 10.1111/j.1469-7580.2011.01424.x.

Terhune, C. E. (2013) 'Dietary correlates of temporomandibular joint morphology in the great apes', *American Journal of Physical Anthropology*. Elsevier Ltd, 150(2), pp. 260–272. doi: 10.1002/ajpa.22204.

Thomason, J. J. (1985) 'Estimation of locomotory forces and stresses in the limb bones of Recent and extinct equids', *Paleobiology*, 2(2), pp. 209–220. doi: 10.1017/S0094837300011519.

Tsai, H. P. and Holliday, C. M. (2011) 'Ontogeny of the Alligator cartilago

transiliens and its significance for sauropsid jaw muscle evolution', *PLoS ONE*, 6(9). doi: 10.1371/journal.pone.0024935.

Tseng, Z. J. and Flynn, J. J. (2018) 'Structure-function covariation with nonfeeding ecological variables influences evolution of feeding specialization in Carnivora', *Science Advances*, 4(2). doi: 10.1126/sciadv.aao5441.

Tseng, Z. J. and Stynder, D. (2011) 'Mosaic functionality in a transitional ecomorphology: skull biomechanics in stem Hyaeninae compared to modern South African carnivorans', *Biological Journal of the Linnean Society*, 102(3), pp. 540–559. doi: 10.1111/j.1095-8312.2010.01602.x.

Tseng, Z. J. and Wang, X. (2010) 'Cranial functional morphology of fossil dogs and adaptation for durophagy in Borophagus and Epicyon (Carnivora, Mammalia)', *Journal of Morphology*, 271(11), pp. 1386–1398. doi: 10.1002/jmor.10881.

Turner, A. H. (2015) 'A Review of Shamosuchus and Paralligator (Crocodyliformes, Neosuchia) from the Cretaceous of Asia', *PLoS ONE*, 10(2), pp. 1–39. doi: 10.1371/journal.pone.0118116.

Turner, A. H. and Buckley, G. A. (2008) 'Mahajangasuchus insignis (Crocodyliformes: Mesoeucrocodylia) cranial anatomy and new data on the origin of the eusuchian-style palate', *Journal of Vertebrate Paleontology*, 28(2), pp. 382–408. doi: 10.1671/0272-4634(2008)28[382:MICMCA]2.0.CO;2.

Turner, A. H. and Sertich, J. W. (2010) 'PHYLOGENETIC HISTORY OF SIMOSUCHUS CLARKI (CROCODYLIFORMES: NOTOSUCHIA) FROM THE

LATE CRETACEOUS OF MADAGASCAR', *Journal of Vertebrate Paleontology*, 30(Supplement 6), pp. 177–236.

Wainwright, P. C. (2007) 'Functional Versus Morphological Diversity in Macroevolution', *Annual Review of Ecology, Evolution, and Systematics*, 38(1), pp. 381–401. doi: 10.1146/annurev.ecolsys.38.091206.095706.

Walker, A. D. (1990) 'A revision of *Sphenosuchus acutus* Haughton, a crocodylomorph reptile from the Elliot Formation (late Triassic or early Jurassic) of South Africa', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 330(1256), pp. 1–120. doi: 10.1098/rstb.1990.0185.

Walmsley, C. W. *et al.* (2013) 'Why the long face? The mechanics of mandibular symphysis proportions in crocodiles.', *PloS one*, 8(1), p. e53873. doi: 10.1371/journal.pone.0053873.

Wang, C. L. *et al.* (1995) 'Contact areas and pressure distributions in the subtalar joint', *Journal of Biomechanics*, 28(3). doi: 10.1016/0021-9290(94)00076-G.

Weinbaum, J. C. (2011) 'The skull of *Postosuchus kirkpatricki* (Archosauria: Paracrocodyliformes) from the Upper Triassic of the United States', *PaleoBios*, 30(1), pp. 18–44.

Wilberg, E. W. (2012) 'Phylogenetic and morphometric assessment of the evolution of the longirostrine crocodylomorphs', *University of Iowa*, p. 250.

Wilberg, E. W. (2017) 'Investigating patterns of crocodyliform cranial disparity

through the mesozoic and cenozoic', *Zoological Journal of the Linnean Society*, 181(1), pp. 189–208. doi: 10.1093/zoolinnea/zlw027.

Wilberg, E. W., Turner, A. H. and Brochu, C. A. (2019) 'Evolutionary structure and timing of major habitat shifts in Crocodylomorpha', *Scientific Reports*, 9(1), p. 514. doi: 10.1038/s41598-018-36795-1.

Witmer, L. M. (1995) 'The Extant Phylogenetic Bracket and the Importance of Reconstructing Soft Tissue in Fossils', in *Functional Morphology in Vertebrate Paleontology*, pp. 19–33.

Witmer, L. M. (1997) 'The Evolution of the Antorbital Cavity of Archosaurs: A Study in Soft-Tissue Reconstruction in the Fossil Record with an Analysis of the Function of Pneumaticity', *Journal of Vertebrate Paleontology*, 17(sup001), pp. 1–76. doi: 10.1080/02724634.1997.10011027.

Wu, X.-C. and Chatterjee, S. (1993) 'Dibothrosuchus elaphros, a crocodylomorph from the Lower Jurassic of China and the phylogeny of the Sphenosuchia', *Journal of Vertebrate Paleontology*, 13(1), pp. 58–89. doi: 10.1080/02724634.1993.10011488.

Wu, X.-C., Sues, H.-D. and Dong, Z.-M. (1997) 'Sichuanosuchus shuhanensis, a new ?Early Cretaceous Protosuchian (Archosauria: Crocodyliforms) from Sichuan (China), and the monophyly of Protosuchia', *Journal of Vertebrate Paleontology*, 17(1), pp. 89–103. doi: 10.1080/02724634.2014.956877.

Wu, X. C., Brinkman, D. B. and Lu, J. C. (1994) 'A new species of

Shantungosuchus from the lower cretaceous of Inner Mongolia (China), with comments on S. Chuhsienensis Young, 1961 and the phylogenetic position of the genus', *Journal of Vertebrate Paleontology*, 14(2), pp. 210–229. doi: 10.1080/02724634.1994.10011553.

Young, M. T. *et al.* (2010) 'The evolution of Metriorhynchoidea (mesoeucrocodylia, thalattosuchia): An integrated approach using geometric morphometrics, analysis of disparity, and biomechanics', *Zoological Journal of the Linnean Society*, 158(4), pp. 801–859. doi: 10.1111/j.1096-3642.2009.00571.x.

Vita

Kaleb Sellers was born in the Ozarks and grew up among the hills and trees and rivers near Dixon, Missouri. His favorite question was always “Why?” He attended undergraduate at the University of Missouri and was part of the Conley Scholars Program. In his last semester of college, he realized that his passions and interests were broader than those of medicine and decided not to join the medical school. He read and rediscovered his love of evolution and deep time. Fortuitous circumstances led him to find the lab of Dr. Casey Holliday, where he found a welcoming group of colleagues who became friends.