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Unexpected bite-force conservatism as a stable performance foundation across mesoeucrocodylian historical diversity

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Abstract

Effective interpretation of historical selective regimes requires comprehensive *in vivo* performance evaluations and well-constrained ecomorphological proxies. The feeding apparatus is a frequent target of such evolutionary studies due to a direct relationship between feeding and survivorship, and the durability of craniodental elements in the fossil record. Among vertebrates, behaviors such as bite force have been central to evaluation of clade dynamics; yet, in the absence of detailed performance studies, such evaluations can misidentify potential selective factors and their roles. Here, we combine the results of a total-clade performance study with fossil-inclusive, phylogenetically informed methods to assess bite-force proxies throughout mesoeucrocodylian evolution. Although bite-force shifts were previously thought to respond to changing rostridental selective regimes, we find body-size dependent conservation of performance proxies throughout the history of the clade, indicating stabilizing selection for bite-force potential. Such stasis reveals that mesoeucrocodylians with dietary ecologies as disparate as herbivory and hypercarnivory maintain similar bite-force-to-body-size relationships, a pattern which contrasts the precept that vertebrate bite forces should vary most strongly by diet. Furthermore, it may signal that bite-force conservation supported mesoeucrocodylian craniodental disparity by providing a stable performance foundation for the exploration of novel ecomorphospace.

KEYWORDS

Crocodylia, ecomorphology, Notosuchia, performance, stabilizing selection

1 | INTRODUCTION

Throughout the Phanerozoic, organismal design has exhibited regular, historical patterns of form and function. Understanding how these convergent, adaptive patterns have come about requires accurate interpretations of organism–environment interactions across deep time (Larson & Losos, 1996; Lauder, 1996). Such an understanding can be difficult to achieve in vertebrate paleontological systems, however, due to problems inherent in

the fossil record. These may include patchy sampling, small sample sizes, or complex morphologies with many-to-one functional-anatomical mappings—each of which can contribute to misidentification of potential selective factors involved with shaping historical phenotypes (Alfaro, Bolnick, & Wainwright, 2005; Lauder, 1996; Wainwright, 2007; Wainwright, Alfaro, Bolnick, & Hulsey, 2005). Identifying selection on past function is further hindered when imprecise inferences of performance are ascribed to vertebrate fossils. This predicament stems from a relative

paucity of clade-wide, *in vivo* evaluations from modern taxa (Lauder, 1995). To circumvent the need for developing time-intensive empirical assessments of performance, paleontologists have harnessed phylogenetic and comparative analytical methods to test form-function evolutionary hypotheses (see, i.e., Cooke & Terhune, 2015; Emerson, 1988; Irschick, 2002; Lauder, 1995; Schaefer & Lauder, 1996; Westneat, 2001). As a result, inferential methods that draw evolutionary interpretations from single, contemporary time periods are now routinely used to assign functions to fossil forms. Such analytical and temporal disconnects have the potential to result in specious identification of evolutionary signals (Lauder, 1996).

Nonetheless, quantifying deep-time relationships between taxonomic diversity and ecomorphology (e.g., of locomotory or feeding systems; Wainwright & Reilly, 1994) has been a primary focus of studies investigating the phenomena that promote or stabilize clade persistence (Goswami, Binder, Meachen, & O'Keefe, 2015; Higham, Birn-Jeffery, Collins, Hulsey, & Russell, 2015; Hopkins & Lidgard, 2012; Sherratt et al., 2015). For example, crocodile-line archosaurs (Suchia; Figure 1) have survived numerous major extinction events, with crown crocodylians (e.g., alligators, caimans, crocodiles, and gharials) representing the result of more than 240-million years of suchian diversification (Turner & Sertich, 2010). Although adults of all living species are opportunistic feeders (Pooley, 1989; Webb & Manolis, 1989), one reason for crocodylian persistence is that many are successful apex predators within their geographical regions (Grenard, 1991; Grigg & Kirshner, 2015). They demonstrate a wide range of rostridental ecomorphologies that approximate each taxon's specific ecological feeding niche (Figure 1; see Erickson et al., 2012). Crown crocodylian ecomorphologies represent a small historical subset of those known across suchian evolution, and convergence in cranial and dental forms characterize even distantly related clades (Figure 1; Brochu, 2001; Holliday & Nesbitt, 2013; Turner & Buckley, 2008).

In this context, positive correlation of clade persistence and morphological convergence is expected to produce ecomorphological trait variation that should become conserved over time (Hopkins, 2011, 2013). Such stasis should also be accompanied by stable levels of historical taxonomic diversity, which is supported within the more exclusive group, Mesoeucrocodylia (see Figure 1, no. 1), by endeavors that infer logical links between rostridental form and deep-time trends (Godoy, 2020; Morris, Vliet, Abzhanov, & Pierce, 2019; Pierce, Angielczyk, & Rayfield, 2008; Stubbs, Pierce, Rayfield, & Anderson, 2013). Nonetheless, some of these same studies also identify considerable functional and morphological disparity (Godoy, 2020; Pierce et al., 2008; Stubbs et al., 2013). Although convergences are well

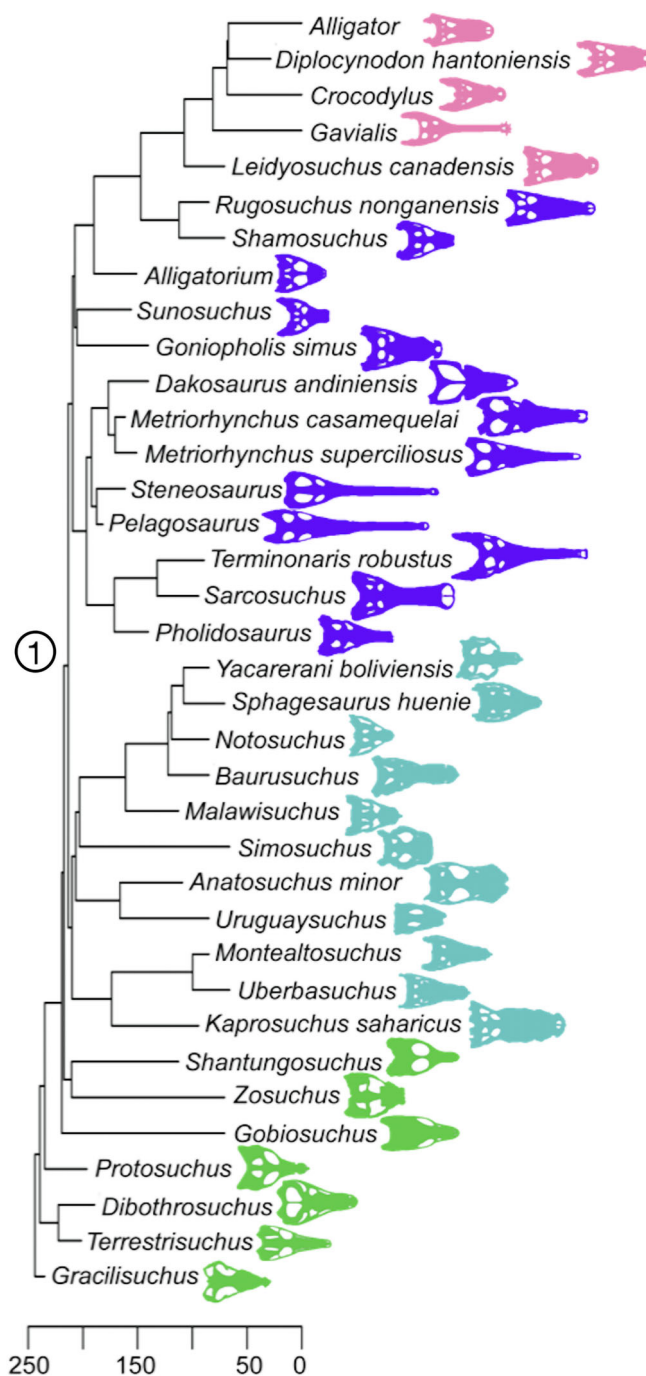


FIGURE 1 Time-scaled suchian phylogeny modified from (Gignac & O'Brien, 2016), reflecting available fossil data. Taxonomic affinities are represented by color, from top to bottom: Crocodylia in pink, remaining Neosuchia in purple, Notosuchia in blue, and early suchians in green. Number 1 indicates the node for Mesoeucrocodylia, the most recent common ancestor of crocodylians and notosuchians. Note convergence in rostral morphotypes, for example, the intermediately broad rostra of *Kaprosuchus* and *Alligator* or the long and slender snouts of *Steneosaurus* and *Gavialis*. Silhouettes by authors

documented, disparity analyses suggest that these convergences are not limited to a single suite of ecomorphological

character traits. Instead, convergent morphologies incorporate a wide array of discrete rostral phenotypes and dental forms (Figure 1; e.g., slender-snouted, intermediate, blunt-snouted, vaulted rostrum, hypercarnivore, “duck faced,” and herbivorous phenotypes; Brochu, 2001; Buckley, Brochu, Krause, & Pol, 2000; Drumheller, Darlington, & Vliet, 2019; Erickson et al., 2012; Ősi, 2013; Sereno & Larsson, 2009; Walmsley et al., 2013). Moreover, disparity patterns are robust across numerous descriptive and functional analyses (McHenry, Clausen, Daniel, Meers, & Pendharkar, 2006; Pierce et al., 2008; Sadlier & Makovicky, 2008; Stubbs et al., 2013; Watanabe & Slice, 2014), suggesting a historical tension between morpho-functional conservation, disparity, and clade persistence.

In this study, we explore the potential for performance stabilization to enable the evolution of morphological disparity and maintenance of clade persistence in extant and extinct mesoeucrocodylians. Living crocodylians are well known for their remarkable bite-force capacities, generating the highest maximum bite forces ever recorded (Erickson et al., 2012). Surprisingly, however, experimentally derived bite-force performance data (Erickson et al., 2012, 2014; Gignac & Erickson, 2016) document no meaningful correlations between jaw or rostrum ecomorphologies with performance in the context of maximum bite-force capacities. Long-standing hypotheses about prey seizure mechanics state that each rostro-dental ecomorphology should result in a unique performance outcome (see McHenry et al., 2006 and references therein). However, *in vivo* studies demonstrate that the maximum bite force—for an individual at any developmental stage in nearly any living taxon—can be explained by body size alone, across 85 million years of diversification (Erickson et al., 2012, 2014). Yet, the fact that crocodylian rostro-dental phenotypes are considerably variable (encompassing gracile, intermediate, and robust forms; Brochu, 2001; Erickson et al., 2012) with no apparent impact on bite-force performance is altogether an enigma. Additionally, the rostro-dental components of the mesoeucrocodylian skull are associated with numerous biological roles such as prey capture, aquatic locomotion, thermoregulation, respiration, and parental care (Busbey, 1995; Grenard, 1991; Grigg & Kirshner, 2015), subjecting them to several potentially conflicting (or conflating) selective regimes. Previous studies examining cranial and dental disparity, therefore, may have identified macroevolutionary patterns that better reflect selection targeting alternative functions of the rostrum, rather than prey-seizure mechanics (see, e.g., Drumheller et al., 2019; Erickson et al., 2012; Gignac & Erickson, 2016; Thorbjarnarson, 1990). These multifunctional demands can render identification of historical selective regimes both difficult and tenuous. Moreover, bite forces are generated by the caudal portion of the cranium via the jaw adductor

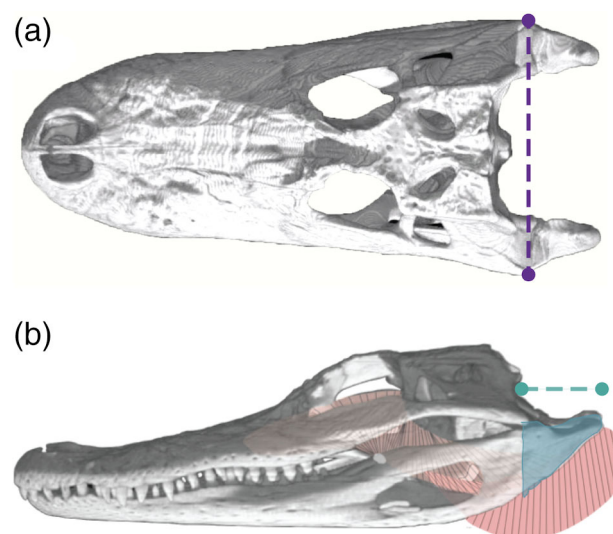


FIGURE 2 Skull of an American alligator, *Alligator mississippiensis*, in (a) dorsal view, demonstrating the linear measurement for head width across the quadrates in purple, and (b) lateral view, with the linear measurement for articular length (i.e., the major anatomical in-lever for jaw adduction; *sensu* Gignac & Erickson, 2016) highlighted in blue and *Musculi pterygoideus dorsalis* and *ventralis* superimposed. Skull accessed from Digimorph.org: Dr. Timothy Rowe, Christopher Brochu, Matthew Colbert, Kyoko Kishi, John Merck, 2003, “*Alligator mississippiensis*” (On-line), Digital Morphology. Accessed July 21, 2016 at http://digimorph.org/specimens/Alligator_mississippiensis/adult/

musculature (Figure 2; see Gignac & Erickson, 2016). If natural selection has acted to promote stable bite-force capacities, then empirically derived data suggest that the adductor region (Gignac & Erickson, 2016; Holliday & Witmer, 2007) may house the most functionally relevant morphological signal.

When evolutionary hypotheses regarding functional morphology and selection are grounded in extensive performance testing, much can be revealed about the processes influencing macroevolutionary dynamics. Here, we present a case study that capitalizes on experimental performance data to evaluate the hypothesis that bite-force capacity has been a predominant factor in generating mesoeucrocodylian historical diversity. For this function to be linked with clade persistence, the observed morphologies should be relatively unchanged, even across deep time (Hopkins, 2011, 2013). To evaluate these links, we developed bite-force proxies derived from the results of comprehensive, total-clade performance studies with phylogenetically informed, fossil-inclusive evolutionary allometry analyses. Our approach is twofold. First, we focus on the evolution of jaw musculoskeletal features by drawing upon previously established and experimentally

verified bite-force proxies identified from musculoskeletal mathematical models of crown crocodylians (Gignac & Erickson, 2016; Gignac & O'Brien, 2016). These proxies anatomically correlate well with *in vivo* bite-force capacities, which presents a simplified scenario that reduces potential interference from multifunctional systems unrelated to muscle-moment inputs (e.g., snout, jaw out-lever, teeth) in identifying relevant selective regimes (Alfaro et al., 2005; Lauder, 1996; Wainwright, 2007; Wainwright et al., 2005). Additionally, the proxies can be sampled uniformly across evolutionary time because they are preserved in a temporally continuous and evenly distributed phylogenetic series of recent and fossilized specimens (Gignac & O'Brien, 2016). Second, through time-scaled phylogenetically informed analyses, we used these proxies to infer the deep history of bite-force shifts.

Because body size may be particularly important in this system (Erickson et al., 2012, 2014; Erickson, Lappin, & Vliet, 2003), we tested for allometric deviations using phylogenetic analysis of covariance (pANCOVA; Smaers & Rohlf, 2016). Prior research that calculated adductor region evolutionary rates in the context of body-size shifts suggests that two mesoeucrocodylian groups exhibit the most divergent patterns: crocodylians appear to have accelerated bite-force increases, whereas notosuchians (e.g., “mammal-like crocodyliforms”; O'Connor et al., 2010) appear to have accelerated bite-force decreases (Gignac & O'Brien, 2016). This dichotomy provides further opportunity to target our sampling and avoid misidentifying potential selective regimes. Namely, evolutionary rates indicate that if biomechanical performance tradeoffs exist within Mesoeucrocodylia, they should be the most apparent by sampling bite-force proxies within these polarized groups. Under a framework of phylogenetic generalized least-squares (PGLS) regression and pANCOVA, we tested two predictions: (a) crocodylians, known for their extremely robust jaws and high maximum bite forces (Erickson et al., 2012), have greater bite-force potential than the rest of Suchia; and (b) smaller-bodied, occlusally specialized notosuchians had significantly lower bite-force potential as compared to other suchians. If supported, our predictions imply that bite-force proxies have been evolutionarily labile—a characteristic that might be shared with rostrudental phenotypes. If not supported, then conservation of performance proxies may have been essential to enable mesoeucrocodylian feeding diversification through other means, such as rostrudental evolution. We interpret our results in the context of clade persistence, taxonomic diversity, and ecomorphology (Brochu, 2001; Erickson et al., 2012; McHenry et al., 2006; Ősi, 2013; Turner & Buckley, 2008; and references therein) in order to examine patterns of form and function evolution of the mesoeucrocodylian jaw.

2 | MATERIALS AND METHODS

2.1 | Empirically derived performance proxies

Evolutionary stable, functional phenotypes (Wagner & Schwenk, 2000) emerge as a combined result of: (a) their use by organisms for environmental interactions, (b) the principles of physics that govern their functions, and (c) their inheritance from evolutionary precursors (Higham et al., 2021). Accounting for these aspects of potential phenotypic variation provides a framework for evaluation of performance in living and extinct organisms. In the case of bite-force capacity, musculoskeletal performance cannot be measured directly in extinct taxa. Therefore, osteological proxies that represent significant proportions of the performance phenotype present the best opportunity to evaluate differences in functional evolution (Witmer, 1995). Ideally, proxies are identified using empirically demonstrated, form–function relationships that directly link morphology and measured performance (Gignac & Erickson, 2017). What constitutes an appropriate biomechanical proxy for the study of performance variation in the fossil record can be a matter of debate (Lauder, 1995). Here, we propose that such proxies must meet two requirements to provide utility: (a) they must both anatomically correlate with, and (b) mechanistically induce the performance of interest. An ideal means to demonstrate these correlative, mechanistic performance relationships is to evaluate traits within contemporary functional models and quantify the extent to which potential proxies contribute to performance (Higham et al., 2021), prior to application to fossilized forms (Lauder, 1995). The greater a proxy's participation in the generation of performance, the more reliably variation in that proxy correlates to variation in performance. In especially large animals with long periods of growth, a thorough evaluation of how performance is achieved may additionally require examination of proxies within ontogenetic as well as evolutionary time periods (Gignac & Santana, 2016). Indeed, this two-pronged approach can afford opportunities for understanding how developmental variation relates to phylogenetic variation in the both the proxy and its performance output (Gignac & O'Brien, 2016).

In this study, we aim to evaluate bite-force potential as our performance metric of interest. To achieve this, we utilize two linear morphological measurements as proxies: head width (HW, measured across the quadrates) and articular length (AL, measured from the middle of the jaw joint to the caudal end of the articular). To briefly summarize our approach, we examine the evolution of AL relative to HW in a phylogenetic context because AL

× HW approximates relative changes to the area afforded for jaw muscle hyper- or hypotrophy, and both measurements relate directly to the mechanism of bite-force generation. We discuss HW first, followed by AL.

Due to the difficulty of measuring body size in the fossil record, we used an osteological proxy that reliably predicts body size: HW. HW scales isometrically (slope = 2.953 ± 0.193 ; isometry = 3.0) with, and captures 93% of, variation in adult crocodylian body mass (O'Brien et al., 2019). This metric matches or exceeds the precision for the most commonly used linear measure of snout–vent length for assessing size. It is, thus, quantitatively comparable to other approaches for estimating body mass in crocodylians, but it utilizes a linear dimension that is more commonly preserved in fossil specimens (O'Brien et al., 2019; Scheyer et al., 2019; Young & Sachs, 2020).

In addition to representing body mass, HW also benefits the study of bite-force performance evolution in mesoeucrocodylians because it spans the region of the jaw-closing musculature, mediolaterally. Mesoeucrocodylians are unlike mammals and some squamate groups that have jaw adductor musculature exposed laterally. Instead, these muscles are positioned within a bony adductor chamber located between the caudal and lateral skull, braincase, and cranial vault (Holliday & Witmer, 2007). As a result, comparing HW between taxa both standardizes for body size and indicates absolute mediolateral expansions or contractions of the post-orbital cranium surrounding the jaw adductor musculature. Indeed, shape analysis has quantified longstanding stasis in adductor chamber osteology (Piras et al., 2014), indicating the highly conserved nature of the post-orbital cranium in crocodylians (and their mesoeucrocodylian precursors; Felice et al., 2019). It should be little surprise, therefore, that crocodylian bite forces correlate strongly with body-size metrics in ontogenetic and phylogenetic comparisons ($R^2 \geq 0.87$; Erickson et al., 2003, 2012, 2014; Gignac & Erickson, 2016). For example, ontogenetic allometries of bite-force performance do not differ phylogenetically: slopes for measured maximum bite force plotted against body mass differ by only 3% for comparisons between distantly related taxa and between divergent rostrudental ecomorphs (Erickson et al., 2014). This helps to explain why any individual in nearly any extant taxon (excepting *Gavialis gangeticus*; Erickson et al., 2012), is bite-force comparable as a function of just body size.

Even though HW captures signals of adductor chamber width, it alone is insufficient to approximate bite-force potential for taxa outside of the crown clade. This is primarily due to the evolutionary extension of the articular bone caudally, as the retroarticular process, during mesoeucrocodylian evolution. Basal suchians lacked a “pronounced” caudal process of the articular (Wu,

Brinkman, & Lu, 1994) for jaw-closing muscle attachment. Instead, only a single jaw-opening muscle, *Musculus depressor mandibulae*, is interpreted as having attached here. By the origin of Mesoeucrocodylia (Figure 1, no. 1), however, this structure gained attachments for the *Musculi pterygoideus* muscle complex and came to serve as an anatomical in-lever (Gignac & Erickson, 2016) for jaw adduction (Holliday & Witmer, 2007; Turner & Sertich, 2010; Wu et al., 1994).

It should be noted that the retroarticular process serves two functions in mesoeucrocodylians: (a) it is the anatomical in-lever for jaw opening (Sinclair & Alexander, 1987), and (b) it is one of several anatomical in-levers for jaw closure (Gignac & Erickson, 2016). In both cases, muscles pull on the retroarticular process and generate muscle moments. A muscle moment is the product of perpendicular muscle force (i.e., force modeled vertical to the horizontal orientation of the retroarticular process *sensu* Gignac & Erickson, 2016) multiplied by the length of the (horizontal) anatomical in-lever. The anatomical in-lever that is specifically the focus of this study is the length of the (retro)articular process, and it was measured in Gignac and Erickson (2016), Gignac and O'Brien (2016), and in the current study as the linear distance from the mid-point of the quadrate-articular joint to the end of the mandible, caudally (also referred to as “retroarticular process length”, “RAP”, or “in-lever length” for *M. pterygoideus ventralis* in prior studies). We refer to this measurement herein as AL, which is preferred as a more inclusive term for accurately describing historical and contemporary suchian anatomy. As AL increases, it causes a larger muscle moment to be generated about the quadrate-articular joint during jaw adduction, which induces a higher value of bite-force performance at any bite point (i.e., as a necessary result of lever mechanics; Cochran, 1982; Gignac & Erickson, 2015, 2016). Although AL might seem to represent many-to-one functional mapping (Alfaro et al., 2005; Lauder, 1996; Wainwright, 2007; Wainwright et al., 2005) because it instigates both jaw depression and elevation, these actions are diametrically opposed. As a result, contraction of the *M. pterygoid* muscle complex produces a muscle moment along AL, about the jaw joint, regardless of *M. depressor mandibulae* function (i.e., even when *M. depressor mandibulae* contracts during jaw closure; Cleuren, Aerts, & de Vree, 1995).

Refocusing the general features of functional phenotypes, outlined above by Higham et al. (2021), onto our particular study system, when a mesoeucrocodylian interacts with its environment by generating a bite force upon a food resource, physics—in the form of lever mechanics—dictates that contractile muscle forces applied to the retroarticular process must generate a

moment that contributes to the sum (along with all other relevant jaw muscle moments) of bite-force performance. (To review mathematical, bite-force model methodologies in crocodylians, see Busbey, 1989, Cleuren et al., 1995, van Drongelen and Dullemeijer (1982), Gignac & Erickson, 2016, Porro et al., 2011; Sellers, Middleton, Davis, & Holliday, 2017, and Sinclair & Alexander, 1987.) To compare bite-force potential, we sampled AL because it is a critical component of the force-generating system. It correlates strongly with measured maximum bite forces over ontogeny ($R^2 = 0.95$; supplemental table 5 of Gignac & O'Brien, 2016), and the (retro)articular process mechanically contributes to bite-force generation in all mathematical models of neonate, juvenile, and adult crocodylians to date (Busbey, 1989; Cleuren et al., 1995; van Drongelen and Dullemeijer, 1982; Gignac & Erickson, 2016; Porro et al., 2011; Sellers et al., 2017; Sinclair & Alexander, 1987) as well as those developed for other archosaurs (Bates & Falkingham, 2012; Gignac & Erickson, 2017; Lautenschlager, 2015; Nieto, Degrange, Sellers, Pol, & Holliday, 2021; Sustaita, 2008). The broad use of the (retro)articular in archosaur bite-force models is, perhaps, unsurprising when considering prior assertions of extreme evolutionary-developmental conservation of the jaw adductor morphology among extant crocodylians (Bona & Desojo, 2011; Busbey, 1989; Cleuren et al., 1995; Endo et al., 2002; Iordansky, 1964; Schumacher, 1973; Sinclair & Alexander, 1987) and between crocodylians, nonavian dinosaurs, and neornithine birds (Holliday, 2009). Among archosaur clades, however, mesoeucrocodylians uniquely expand the adductor musculature caudally through extreme articular elongation. This occurs to such an extent that musculoskeletal bite-force models developed from lever mechanics for the exemplar taxon *Alligator mississippiensis*, estimate that AL transmits 60 to 70% of maximum bite-force capacity in adults (see table 6 of Gignac & Erickson, 2016). This value derives from the combined muscle moments for the two adductor muscles that insert onto the retroarticular process: *M. pterygoideus ventralis*, which contributes 61.63% of maximum bite force, and the caudal half of *M. pterygoideus dorsalis*, which contributes ~8.65% of maximum bite force (for explanation about how these values were calculated, see supplemental Materials and Methods of Gignac & Erickson, 2016). Two reasons account for such a high combined percentage: (a) the *M. pterygoideus ventralis* and (caudal portion of) *dorsalis* muscles that attach to the retroarticular process are large jaw adductors, and (b) the extended length of the retroarticular process mechanically induces relatively high-valued muscle moments, and thus disproportionately contributes to bite-force generation (Gignac & Erickson, 2016). Even neonate *A. mississippiensis*, which have

relatively short ALs (i.e., comparable to, or shorter than, the estimated ancestral AL reconstructed at the node for Mesoeucrocodylia; see fig. 3 and supplemental tables S9 and S10 of Gignac & O'Brien, 2016), transmit more than half of maximum bite-force capacity through this structure (table 6 of Gignac & Erickson, 2016).

Our proxies, taken together, standardize for body size as well as capture evolutionary variation in the area of the adductor chambers (e.g., regardless of lineage-specific changes to the relative size of each muscle within the chamber). Both HW and AL anatomically correlate with bite-force potential and biomechanically contribute to bite-force capacity in crocodylians. In addition, HW spans the adductor chamber approximately orthogonal to the orientation of AL (see Figure 2), meaning that the two variables can change independently without an increase or decrease in one trait necessarily requiring an increase or decrease in the other. The conservation of post-orbital cranial morphology and bite-force performance in crown crocodylian evolution since the Late Cretaceous are a testament to the utility these metrics hold for studying bite-force potential in deep time. If conserved in even older clades as well, then they stand to inform us about bite-force evolution from as far back as the Early Jurassic. Within Mesoeucrocodylia (which includes Crocodylia and Notosuchia but excludes basal suchians), HW and AL are readily measurable, and we compare these values as a minimum representative unit for bite-force capacity in order to provide a conservative examination of relative performance evolution. For example, in taxa with relatively short ALs, we interpret the minimum representative unit of bite-force capacity to be lower as compared to those with long ALs. This is because short ALs are indicative of smaller *M. pterygoideus* muscle complexes (due to less space available in the adductor region for jaw musculature) and are lower-valued in-levers, which are smaller mathematical multipliers and induce proportionally lower-valued muscle moments (Cochran, 1982). By contrast, caudal length shifts in the articular bone provide the opportunity for hypertrophy of the jaw adductor musculature by enlarging the (especially pennate) muscles caudal and ventral to the adductor chamber (Gignac & O'Brien, 2016). In these cases, we interpret the minimum representative unit of bite-force capacity to be relatively higher.

Notably, Mesoeucrocodylia includes several bizarre taxa or those with extreme phenotypes (e.g., *Kaprosuchus*, *Simosuchos*). However, conservation of jaw adductor chamber osteology (Felice et al., 2019; Holliday, 2009; Holliday & Witmer, 2007; Piras et al., 2014) and our mechanical understanding of the role that AL plays in bite-force generation indicate that the potential for unforeseen form-functional

relationships in taxa with otherwise unusual cranial phenotypes is unlikely. The exception to this generalization may lie within piscivorous thalattosuchians (e.g., *Pelagosaurus*, *Metriorhynchus*) with their rostrally elongate adductor chambers that greatly increase all adductor in-lever lengths and, thus, muscle moments and bite forces. However, data on the most ecomorphologically analogous extant crocodylian (*G. gangeticus*) suggests that these changes would have been (at least somewhat) counteracted by fusiform *M. pterygoideus ventralis* muscle-fiber arrangements (Endo et al., 2002) that enable faster jaw closure by reducing maximum bite-force capacity in this, and presumably other, exceptionally piscivorous species (Erickson et al., 2012; Ballell, Moon, Porro, Benton, & Rayfield, 2019; also see Piras et al., 2014 for discussion of postorbital skull shape convergences among long-snouted forms). We also note that HW and AL can be measured reliably for basal suchians such as *Dibothrosuchus*, *Gracilisuchus*, *Protosuchus* (even though jaw adductor muscles are not thought to attach to the articular bone), and we do so—but only to provide additional historical context. See below for our treatment of AL data in these taxa.

Finally, it is also important to recognize that our proxies are unable to register traits that do not fossilize, such as behavioral differences in neuromuscular activation (Cleuren et al., 1995), myosin subtype (Hoh, 2002), muscle fiber shortening parameters (Porro et al., 2011), fiber pennation angles (Scott and Winter, 1991), and specific bite point along the jaw (Gignac & Erickson, 2016)—all of which are important factors for accurate bite-force modeling in living vertebrates. Nonetheless, the anatomically correlative and directly causal relationships that HW and AL have with bite-force performance in extant mesoeucrocodylians demonstrate their unambiguous functions for extinct forms. To summarize, the foundation set by prior biomechanical modeling efforts meaningfully implicates the utility of these simple linear measurements for identifying functional patterns in adductor chamber variation. Thus, we interpret relative AL changes to indicate shifts in a minimum representative unit for bite-force capacity, not as indicative of specimen-specific bite-force values. By tracking and comparing AL alongside body size in a phylogenetic context, we exemplify how well-informed singular traits can be used to identify macroevolutionary patterns in functional morphologies.

2.2 | Data

We measured rostral-caudal AL and HW in mm for 36 suchian taxa (extant, $n = 3$; extinct, $n = 33$; Figure 2; Table S1; for full details of measurement protocols, see

Gignac & O'Brien, 2016). All species are represented by mature individuals as indicated by known ages (when available), and/or alveolar and sutural completeness (Brochu, 1996; LeBlanc, Brink, Cullen, & Reisz, 2017). As described in the previous section, AL was used to indicate caudal expansion of the adductor system (Figure 2b), and HW (Figure 2a) was used as a proxy for body size (O'Brien et al., 2019). Prior to analyses, all measurements were natural-log-transformed, and regression diagnostics found each variable to be normally distributed and homoscedastic with no outliers. For phylogenetic context, we utilized the Bayesian, morphologically based, time-calibrated phylogeny of Gignac and O'Brien (2016). This phylogeny was generated using modifications of the character matrix of Turner and Sertich (2010). The original phylogeny includes 81 taxa of both extant and extinct suchians. It was pruned to those taxa with available AL and HW data using the R-package APE (Paradis, Claude, & Strimmer, 2004; R Core Team, 2016). The pruned tree contains no polytomies (Figure 1).

2.3 | Analysis

We used PGLS regression and pANCOVA to test for significant deviations from allometric predictions of a minimum representative unit of bite-force capacity for Crocodylia and Notosuchia. This least-squares pANCOVA procedure calculates the change associated with the groups of interest in the residual variance simultaneously with the phylogenetic regression parameters (Smaers & Rohlf, 2016). This approach allows for a direct least-squares test of whether a model with multiple grades (assuming multiple groups with different mean trait values) indicates a significantly better statistical fit to the data than a model with only a single grade (assuming that no particular group indicates a significantly different mean trait value). In doing so, the pANCOVA procedure effectively tests for differences in mean value (after controlling for the covariate) among groups. Technical details and examples of implementation of this procedure are available in Smaers and Rohlf (2016).

In order to test species' deviations from allometric predictions using the phylogenetic regression, least-squares pANCOVA (as implemented here) is preferred over methods that detect "evolutionary singularities" (Nunn & Zhu, 2014) because such methods do not provide a direct test for differences in intercepts and slopes in a regression, nor do they provide a direct test comparing the fit of multiple grades relative to a single grade. Least-squares pANCOVA is also preferred over the procedure to remove the datum of interest, fitting a regression line to the remaining data points, and calculating

intervals for a new observation (Garland & Adolph, 1994; Garland, Dickerman, Janis, & Jones, 1993), because such a procedure is not a correct statistical test as it does not account for the variance of the predicted means (Smaers & Rohlf, 2016). In terms of minimal reliable sample size, conventional wisdom is that at least 10 data points are needed per parameter to be estimated (Freckleton & Watkinson, 2001). However, this cutoff is trivial and is suggested to apply to multidimensional data. Considering that our data are bivariate only, and that calculations are done using standard least-squares procedures only (which provide correct calculations of regression parameters irrespective of sample size and automatically penalize for parameterization and low sample size in the estimation of the probabilities through the use of degrees of freedom), parameterization based on as few as five data points (i.e., Crocodylia, the smallest subsample size in our group membership indicator variables) poses no statistical issue.

Using the least-squares pANCOVA procedure described above, we compared different models each representing a particular hypothesis about clade differences. In pANCOVA, the indicator variables are conceptually and quantitatively the same as an interaction term, and hypotheses are implemented by comparing different multiple treatment groups to a control group. The first model compared differences among Crocodylia, Notosuchia, and other suchians (the “among” group model in Table 1). The second model compares Crocodylia to other suchians while holding constant any differences with Notosuchia. The third model compares Notosuchia to other suchians while holding constant any differences with Crocodylia. Basal suchians (Figure 1) were retained in these analyses in order to represent trait values near the base of Suchia, prior to caudal jaw adductor expansion. However, we do not interpret these data points to be indicative of minimum representative units of bite-force capacity. Instead, they illustrate the ancestral morphospace from which mesoeucrocodylian ALs evolved. These analyses were carried out using the R packages “APE,” “geiger,” “caper,” “rms,” and “evomap” (Paradis et al., 2004; Smaers & Rohlf, 2016; Harmon, Weir, Brock, Glor, & Challenger, 2008; Harrell Jr, 2016; Orme et al., 2013, respectively). For further details of our analysis, see the R code provided (SI Text).

3 | RESULTS

PGLS regression of AL allometry indicates a consistent relationship between AL and HW across all suchian taxa for the past 240-million years (Figure 3; Figure S1).

TABLE 1 Results of phylogenetic analysis of covariance. These results indicate that there are no significant differences in relative articular length (a proxy for bite-force potential) among suchian groups

	<i>df</i>	<i>F</i>	<i>p</i>
Among groups	2.32	1.087	0.349
Crocodylia versus other Suchia	1.32	1.764	0.194
Notosuchia versus other Suchia	1.32	0.565	0.458

Abbreviations: *df*, degrees of freedom, *F*, *F*-statistic; *p*, level of significance.

The PGLS regression yielded a lower slope (scaling coefficient = 1.363, adjusted $R^2 = 0.823$, $\lambda = 0.369$) relative to the ordinary least squares (OLS) regression (scaling coefficient = 1.450, $R^2 = 0.887$), suggesting that AL would be overestimated without phylogenetic correction (Figure S1). Both regression models indicate a significant relationship between AL and HW ($p_{\text{PGLS}} < .0001$; $p_{\text{OLS}} < .0001$). pANCOVA was used to test for significance in slope and y-intercept differences between (a) Crocodylia and the rest of Suchia—with the former presumed to be evolutionarily optimized for high bite forces (fig. 3; Gignac & O'Brien, 2016); and (b) Notosuchia and the rest of Suchia—with the former presumed to have lower on-average bite forces concomitant with specialized, heterodont dentitions (fig. 3; Gignac & O'Brien, 2016). Neither crocodylian nor notosuchian subsamples indicate a slope that is significantly different from the slope of the rest of the sample ($F = 0.583$, $p = 0.451$ and $F = 0.159$, $p = 0.693$, respectively). Therefore, pANCOVA can be used to test for differences in intercepts among these subsamples while holding the slope constant (equality of slopes is an assumption of pANCOVA). Table 1 reports results for the pANCOVA when testing for differences in the intercept among subsamples. No significant differences were found among groups ($F = 1.087$, $p = 0.349$; Table 1) or for either pairwise comparison: Crocodylia versus other suchians ($F = 1.764$, $p = 0.194$), or Notosuchia versus other suchians ($F = 0.565$, $p = 0.458$). (A more conservative test including the comparison of multiple treatment groups to a control group also reveals no significant differences: Crocodylia versus other suchians while controlling for differences with Notosuchians [$F = 1.527$, $p = 0.226$] and Notosuchians versus other suchians while controlling for differences with Crocodylia [$F = 0.053$, $p = 0.819$].)

4 | DISCUSSION

In our examination of the evolutionary dynamics of mesoeucrocodylian performance proxies, we sampled the

PGLS of bite-force allometry

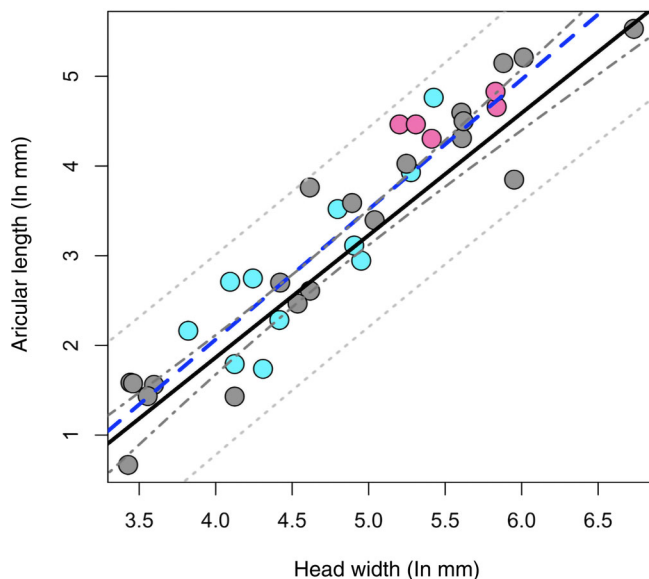


FIGURE 3 Phylogenetic generalized least-squares regression (black solid line) of articular length allometry plotted against head width. Phylogenetic analyses of covariance found neither Crocodylia (pink) nor Notosuchia (turquoise) to be significantly different from other suchians (gray) as a whole (see Table 1). Dark gray dashed lines indicate 95% confidence intervals; light gray dashed lines indicate 95% prediction intervals; blue dashed line shows an overlay of the ordinary least squares regression for visual comparison. (Grayscale-formatted figure available with taxon names listed as Figure S1)

relative length of the (retro)articular process as a minimum representative unit for bite-force capacity (as opposed to an indicator of specimen-specific bite-force values). Our findings document longstanding conservation in the relationship between AL and HW. When framed through the lens of two highly divergent clades, Crocodylia and Notosuchia, an unexpectedly common trend appears: a key osteological feature of bite-force generation is not significantly different between groups relative to body size, regardless of within-clade morphological disparity, longevity, inferred niche breadth, or taxonomic diversity. Instead of co-varying with these or other factors, AL exhibits positive evolutionary allometry (isometry = 1; PGLS scaling coefficient = 1.363) and is dominated primarily by changes in body size ($R^2 = 0.825$). There are no significant deviations from this allometry (Figure 3). Thus, it can be determined that the lack of musculoskeletal plasticity in AL is ancestral for Mesoeucrocodylia (Felice et al., 2019), supporting prior assertions of extreme developmental conservation in the jaw adductor morphology of extant crocodylians (Bona & Desojo, 2011; Busbey, 1989; Cleuren et al., 1995; Endo et al., 2002; Holliday & Witmer, 2007;

Iordansky, 1964; Schumacher, 1973; Sinclair & Alexander, 1987).

Although not significantly different from other suchians as a group (Figure 3; Table 1), crocodylians are characterized by net positive allometry and higher-than-expected bite forces for adult body sizes. Indeed, crocodylian positive AL allometry is consistent with positive evolutionary allometry among crown taxa for *in vivo* measured maximum bite forces reported previously. For example, smaller-sized adult specimens such as *Osteolaemus tetraspis* and *Paleosuchus palpebrosus* generate pound-for-pound comparable bite forces as large-bodied taxa, like *A. mississippiensis* and *Crocodylus porosus* (Erickson et al., 2012, 2014). Furthermore, these findings are robust to ontogenetic stage and phylogenetic relationships, which explain their ubiquity among the crown (Piras et al., 2014). Such conservation suggests that our findings for Crocodylia would persist even if we had selected a different sample of extant species. Still, mesoeucrocodylians with large HWs (including crocodylians) tend to have disproportionately high AL values (Figure 3), which is consistent with a deep history of positive evolutionary allometry (Piras et al., 2014). This pattern may be the result of a greater influence of ontogenetic inertia with increasing body-size evolution that was more common than previously considered (Gignac & O'Brien, 2016; Gignac & Santana, 2016; O'Brien et al., 2019). Under this paradigm, first identified within Neosuchia, stronger performance selection during early life-history stages of crocodylians would have led to disproportionate gains in AL during early ontogeny (Gignac & O'Brien, 2016). These developmental gains (see Gignac & Erickson, 2016 for a detailed analysis) would have been further amplified by long periods of adult growth (Erickson & Brochu, 1999; Grenard, 1991), manifesting as convergences in absolutely high performance potential such as those implied here for other large, predatory mesoeucrocodylians (e.g., *Kaprosuchus*; Figure S1).

Conversely, notosuchian taxa trending toward either smaller adult body sizes or heterodonty were expected to have relatively shorter AL values collectively (although see Melstrom & Irmis, 2019) (Figure 3). Previous work considering evolutionary rates illustrated that many notosuchians are characterized by an accelerated decrease in AL relative to HW (Gignac & O'Brien, 2016), suggesting evolutionary trade-offs for reduced bite-force potential. However, as demonstrated by the current analysis, relative AL in notosuchians, as a group, were not significantly different than those of other suchians. Within Notosuchia, however, a significant difference is observed between *Uberabasuchus*, *Notosuchus*, *Simosuchus*, *Uruguaysuchus*, and *Yacarereni* versus other notosuchians

after controlling for any differences with other suchians ($F = 7.7219$, $p = 0.009$). This indicates the potential for performance grades within Notosuchia, even though each subgroup on its own is not significantly different from the whole ($F = 3.279$, $p = 0.080$; $F = 2.951$, $p = 0.096$). In contrast to *Uberabasuchus*, which was likely a terrestrial carnivore (Carvalho, Ribeiro, & dos Santos, 2004), the remaining short-AL notosuchians (i.e., those below the 95% CI in Figure 3; Figure S1) are interpreted to be primarily or fully herbivorous forms. These three taxa (*Simosuchus*, *Uruguaysuchus*, *Yacarereni*) have complex, heterodont cusp morphologies and inferred wider-ranges of jaw mobility in addition to orthal movements (Carvalho et al., 2004; Kley et al., 2010; Ősi, 2013)—hallmarks of herbivory. Indeed, these forms would be excellent targets for more intensive jaw adductor muscle reconstructions to address potential within-clade, ecomorphological gradations in more detail. The results of such approaches may point to convergent phenotypes, wherein herbivorous-grade notosuchians trended toward the jaw-adductor muscle features of their herbivorous relatives (e.g., *Edentosuchus*; Melstrom & Irmis, 2019). Such forms with multicusped teeth presumably also lacked elongate ALs. However, cranial material is too incomplete to clarify these phenotypes (Ősi & Weishampel, 2009; Pol, Ji, Clark, & Chiappe, 2004), and the signal of decreasing AL that we identified here is weak.

It is somewhat surprising that relative bite-force potential should be comparable across mesoeucrocodylian clades, even for non-predatory taxa. Other vertebrates with highly specialized dentitions, such as mammals that have a single set of permanent adult teeth, broadly exhibit inverse relationships between occlusal complexity and maximum-force biting (Binder & Van Valkenburgh, 2000; Evans, Wilson, Fortelius, & Jernvall, 2007; Kiltie, 1982; Wroe, McHenry, & Thomason, 2005). Mesoeucrocodylians, however, are polyphyodont (O'Connor et al., 2010; Wu et al., 2013), and modern taxa with either delicate or stout dentitions commonly shed or break teeth during biting (Erickson, 1996a, 1996b; Poole, 1961; Singh & Bustard, 1982) but with negligible long-term impact on feeding success (Erickson, 1996b). Although not used for prey capture in herbivorous notosuchians, polyphyodonty may have insulated these animals from functional limitations on maximum bite force related to masticatory reflex arcs (Yamada & Harguchi, 1995) and issues of tooth strength and dental safety factor that are thought to place an upper limit on maximum-force biting in many adult mammals (Dan, Azuma, Hayakawa, & Kohyama, 2005; Kohyama et al., 2004; Paphangkorakit & Osborn, 1998). Our findings signal that herbivorous notosuchian jaw mechanics, while broadly conserved, may have responded in a limited way to selective regimes that uniquely shaped each taxon's life history

(e.g., divergent habitats, diets, ecologies). For example, recent analyses of dental evolution in notosuchians by Melstrom and Irmis (2019) indicate that herbivory evolved independently at least three times in the clade (perhaps as many as six). This presents the opportunity for the lineage-specific, residual decreases in AL identified here to also represent modest convergent ecomorphological performance shifts. Whatever the mechanism, evolutionary trends and tradeoffs between dental complexity and mechanical performance of the unique notosuchian feeding complex are in need of significant further study.

Low levels of interspecific morphological disparity are typically indicative of generalist life histories that presumably served as morphological refugia from which more specialized forms evolved in response to novel paleoenvironments (Futuyma, 2001; Futuyma & Moreno, 1988; Hopkins, 2011, 2013). In our mesoeucrocodylian model, scaling-mediated differentiation of bite-force performance implied by relative AL shifts might have promoted clade longevity by facilitating expansions into divergent feeding niches, such as those occupied by many small-bodied omnivorous and herbivorous notosuchians (Ősi, 2013). This is supported by evidence of longstanding constraints in relative AL as illustrated by the basal suchians we sampled, which—although lacking the jaw-adductor muscle attachments of their descendants—fail to deviate from the scaling relationship that also describes mesoeucrocodylians (Figure 3; Figure S1). This consistency is further reflected in the early development of the crocodylomorph cranial bauplan reported by Araújo and colleagues from Portugal (Araújo et al., 2015). Remarkably, the ossification sequence and bone morphologies from a 13-egg clutch of 150-million-year-old crocodylomorph embryos are strikingly similar to those of extant crocodylians. This points to extreme conservation during the *in ovo* unfolding of development, which may have limited potential pathways for performance evolution since at least the Late Jurassic. Namely, if the adductor anatomy typically develops as an integrated unit and has a function critical for hatchling survival (e.g., for prey capture), the potential for post-hatchling excursions into unique regions of morphospace may be limited (see Goswami et al., 2016). In such a case, scaling-mediated shifts in performance and overall body-size changes—like those suggested here—would be the remaining primary means by which mesoeucrocodylians were capable of changing absolute bite-force capacities (Felice et al., 2019; Piras et al., 2014). Presumably, residual shifts would then be due to unique selective optima, such as for enhanced herbivory via the reduction and loss of selection on hatchling prey capture or other clade-specific selective regimes.

5 | CONCLUSIONS

By integrating performance evolution, ecology, clade dynamics, and deep historical diversity, our study suggests that the force-generating apparatus of the mesoeucrocodylian jaw is an evolutionarily stable configuration (Wagner & Schwenk, 2000), and one that is not coupled to variation in rostrudental anatomy (Figure 1; Felice et al., 2019). We, therefore, hypothesize that stable bite-force potential may have facilitated repeat rostrudental and cranial evolution that promoted convergent incursions into a wide array of niches in response to a suite of selective pressures acting on the mesoeucrocodylian head (e.g., prey capture and manipulation, thermoregulation, hydrodynamics, respiration, etc.). This non-integration of rostral and caudal cranial functional morphology may be a hallmark of how mesoeucrocodylians have invaded new ecological niches: a foundation of neutral variation in the function of force generation directly facilitated reliable exploration of novel snout shapes and dental morphologies at cladogenic events. Our results suggest that this combination has driven clade longevity by providing opportunities for extreme convergence onto a limited range of ecomorphs (e.g., Crocodylia) as well as by enabling rapid expansion into novel and specialized feeding niches (e.g., Notosuchia). In addition, our findings align with Erickson et al. (2012) and underscore that the organization of the tetrapod head may not require a *de facto* coordination between maximum-force biting and rostral morphology (e.g., as it relates to bending, torsional, or shear strength). We agree with numerous prior interpretations that have pointed toward rostrudental variations in living and fossils mesoeucrocodylians as honest indicators of ecomorphology, specifically because such phenotypes appear to vary freely of relative bite-force capacity and its proxies (i.e., measured *in vivo* or inferred) but in coordination with ecological factors. This is supported by studies of cranial integration, which indicate that rostral and caudal components of the skull are weakly covarying modules (Araújo et al., 2015; Felice et al., 2019; Iijima, 2017; Piras et al., 2014; Morris et al., 2019). Finally, our study reiterates the importance of comprehensive, *in vivo* performance evaluations and sampling of fossil groups for aiding in the interpretation of deep-time responses to selective regime shifts, without which this unexpected and plesiomorphic performance regime, apparently maintained across the entirety of mesoeucrocodylian evolutionary history, could not have been recognized.

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CONFLICT OF INTEREST

The authors report no conflicts of interest.

DATA AVAILABILITY STATEMENT

R code provided as SI text, which is available on FigShare (<https://figshare.com/s/64576ea2ce3582da5aac>).

AUTHOR CONTRIBUTIONS

Paul Gignac: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); writing – original draft (equal); writing – review and editing (equal). **Jeroen Smaers:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); software (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Haley O'Brien:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); software (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal).

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