# **Current Biology**

# **Repeated Evolution of Herbivorous Crocodyliforms during the Age of Dinosaurs**

# **Highlights**

- Some extinct crocodyliforms, relatives of living crocodylians, possess complex teeth
- Quantitative analyses suggest some species with complex teeth were likely herbivores
- Herbivorous crocodyliforms evolved at least three times independently
- Some dentitions rival the complexities of living mammal herbivores

# Authors

Keegan M. Melstrom, Randall B. Irmis

Correspondence keeganmelstrom@gmail.com

# In Brief

Melstrom and Irmis analyze dental complexity of extinct crocodyliforms, relatives of living crocodylians. Many taxa inferred to be herbivorous possess teeth that rival and surpass the complexities of living reptilian herbivores. Herbivorous crocodyliforms lived alongside herbivorous mammals, demonstrating dietary partitioning not observed today.



# Current Biology

# Repeated Evolution of Herbivorous Crocodyliforms during the Age of Dinosaurs

Keegan M. Melstrom<sup>1,2,3,\*</sup> and Randall B. Irmis<sup>1,2</sup>

<sup>1</sup>Department of Geology and Geophysics, University of Utah, 115 S 1460 E, Salt Lake City, UT 84112-0102, USA <sup>2</sup>Natural History Museum of Utah, University of Utah, 301 Wakara Way, Salt Lake City, UT 84108-1214, USA <sup>3</sup>Lead Contact

\*Correspondence: keeganmelstrom@gmail.com https://doi.org/10.1016/j.cub.2019.05.076

#### SUMMARY

Q5 Extinct crocodyliforms from the age of dinosaurs (Mesozoic Era) display an impressive range of skeletal morphologies, suggesting a diversity of ecological roles not found in living representatives [1-6]. In particular, unusual dental morphologies develop repeatedly through the evolutionary history of this group [2, 4-9]. Recent descriptions of fossil crocodyliforms and their unusual teeth provide the inferential basis for a wide range of feeding ecologies. However, tests of these hypotheses are hindered by the lack of directly comparable dental morphologies in living reptiles and mammals, thereby preventing an accurate ecosystem reconstruction. Here, we demonstrate, using a combination of the orientation patch count rotated method and discrete morphological features, that Mesozoic crocodyliforms exploited a much greater range of feeding ecologies than their extant relatives, including likely omnivores and herbivores. These results also indicate that crocodyliforms independently developed high-complexity dentitions a minimum of three times. Some taxa possess teeth that surpass the complexities of living herbivorous lizards and rival those of omnivorous and herbivorous mammals. This study indicates that herbivorous crocodyliforms were more common than previously thought and were present throughout the Mesozoic and on most continents. The occurrence of multiple origins of complex dentitions throughout Crocodyliformes indicates that herbivory was a beneficial dietary strategy and not a unique occurrence. Many of these crocodyliforms lived alongside omnivorous or herbivorous synapsids, illustrating an ecological partition that is not observed today.

#### Q1 Q2 RESULTS

Living crocodylians (alligators, caimans, crocodiles, and gharials) possess a similar general morphology and ecology, being semiaquatic generalist carnivores with relatively simple, conical teeth. This contrasts with the striking morphological disparity seen among their extinct relatives that possess numerous osteological specializations not observed in living taxa [1-6]. One particular specialization, heterodonty-regionalized differences in either the size or shape of dentition-evolved independently multiple times in Crocodyliformes [2, 4-8]. Most crocodyliforms exhibit some form of heterodonty, such as the small premaxillary and large caniniform teeth of living species [10], but taxa with multicusped or ornamented teeth were especially prevalent during the Mesozoic [2]. In some cases, heterodont dentitions even approached a mammal-like condition (i.e., regionalization with a high degree of occlusion in Pakasuchus) [6-8]. These features suggest that extinct crocodyliforms had a much wider dietary breadth than their living relatives [5, 8, 9, 11-13]. Given this heterodont condition, interpretations of extinct crocodyliform feeding ecologies have ranged from carnivores [2] to insectivores [9], omnivores [11, 12], and herbivores [2, 4, 5, 8, 13].

Unfortunately, most extinct heterodont crocodyliforms are outside the living clade (Crocodylia) and frequently express tooth morphologies that have no clear modern analog, making it difficult to reliably assign accurate ecological reconstructions (Figure 1). The diversity of dental morphologies and the taxa that possess them imply that these ecosystems are more complicated than would otherwise be predicted and obfuscate dietary inferences based solely on comparative studies using modern squamates and crocodylians [2].

Quantitative methods offer a solution that allows for the direct comparison of teeth that lack homologous structures. Originally developed for use on living rodents and carnivorans, orientation patch count rotated (OPCR) quantifies complexity of the occlusal dental surface in distantly related animals. This method repeatedly demonstrates a clear relationship between diet and tooth morphology of the upper 4th premolar and all molars [14]. Subsequent studies expanded this method to additional living mammalian groups (e.g., bats, primates, and whales) and extinct clades, such as multituberculates and horses [14-18]. One of use also successfully applied OPCR to living lepidosaurs and crocodylians, although all teeth were evaluated because dentigerous saurians (reptiles herein) lack the clear regionalization that typify mammals (i.e., incisor, canine, premolar, and molar) [17]. Despite this difference, both mammals and reptiles exhibit a similar pattern between diet and tooth complexity; carnivorous animals possess simple teeth, whereas omnivores and herbivores have progressively more complex teeth [17]. Additionally, the most complex tooth in reptile jaws can be used to distinguish taxa with plant-rich diets, even if other teeth are absent [17]. The repeated relationship between diet and dental morphology

### **Cell**Press



Figure 1. Range of Dental Complexity and Morphology among Crocodyliforms

Oblique and occlusal views of false color 3D models of isolated teeth in (A) *Caiman crocodilus*, (B) *Boverisuchus vorax*, (C) *Brachychampsa* sp., (D) *Chimaerasuchus paradoxus*, and (E) UCMP 130082, an undescribed taxon from the Lower Jurassic Kayenta Formation. OPCR maps (right) display tooth complexity; each color represents a different cardinal or ordinal direction. OPCR values are a numerical representation of phenotypic tooth complexity, with lower values belonging to carnivores (red font) and durophages (blue font) and higher values belonging to herbivores (green font). See also Table S1. L, lingual; M, mesial. Scale, 2.5 mm (A); 5 mm (B–E) and Table S2.

suggests that the pattern extends to extinct taxa, and OPCR can be used to reconstruct dietary ecology in animals with unique dental morphologies or without living descendants [16].

Here, for the first time, we apply the OPCR method to extinct reptiles, measuring 146 erupted teeth from 16 different taxa of extinct crocodyliforms at a resolution of 25 data rows per tooth ([17]; Supplemental Information). We sample taxa from a broad phylogenetic and temporal range, focusing on fossils that possess heterodont dentitions unobstructed by sediment. Our study chose to concentrate on heterodont species because these specimens frequently possess dental morphologies that have no modern analog, allowing us a novel, independent method of discerning their diet. Using a combination of quantitative dental measurements and discrete morphological features, we reconstruct the extinct crocodyliform diet and demonstrate that these animals occupied a wider range in dental complexities and presumed dietary ecologies than previously appreciated.

Among our sample, Boverisuchus vorax, a crocodylian, and Notosuchus terrestris, a notosuchian, exhibit the simplest sampled dentitions; both the OPCR of the most complex tooth (OPCR<sub>c</sub>) as well as the average OPCR value (OPCR<sub>a</sub>) overlap with the values of living crocodylians (approximately 7 patches per tooth [PPT]). This relatively low dental complexity strongly suggests a carnivorous diet (90% vertebrate material; Figure 2). The reconstruction of carnivory in Notosuchus is surprising, as previous research has hypothesized an herbivorous diet based on a combination of skull and dental morphology [13]. "Allognathosuchus" and Brachychampsa are reconstructed as durophages, given the combination of OPCR values and the presence of specific tooth features shared with extant reptilian durophages, such as wrinkled enamel ([17]; Supplemental Information). The OPCR<sub>c</sub> value of "Allognathosuchus" is likely overestimated because the specimen has a highly worn surface. This is especially apparent when comparing OPCR<sub>a</sub> values, where "Allognathosuchus" has extremely simple teeth, with values even lower than those of the Cretaceous alligatoroid Brachychampsa (Figure 2A).

The notosuchians Araripesuchus gomesii, Mariliasuchus amarali, Armadillosuchus arrudai, and Candidodon itapecuruense have intermediate OPCR<sub>c</sub> (8.25, 8.75, 9.75, and 11.375 PPT, respectively) and OPCR<sub>a</sub> (8.11, 7.77, 9.44, and 7.77 PPT, respectively) values that make dietary reconstructions less certain (Figure 2). These values fall primarily in the range of both insectivorous and omnivorous living reptiles, and three of these taxa do not possess additional discrete dental characters that would allow placement in one of these dietary categories ([17]; Supplemental Information). However, Armadillosuchus has a skull length over 300 mm [2, 11], which places it well outside the body size range ( $\leq$  300 mm) of extant lepidosaur insectivores [17], suggesting an omnivorous diet (Figure 2).

The notosuchian *Simosuchus clarki* possesses a multicusped, heterodont dentition similar to extant herbivorous iguanids (e.g., *Amblyrhynchus cristatus* and *Ctenosaura hemilopha*) [19]. It is not recovered as an unambiguous herbivore based solely on its OPCR<sub>c</sub> value (Figure 2B), but the OPCR<sub>a</sub> clearly recovers *Simosuchus* as an herbivore (Figure 2A), and this is likely an underestimate of dental complexity because the teeth analyzed are the simplest in the dentary [19]. Therefore, even our conservative estimate reconstructs *Simosuchus* with a high dental complexity, supporting the inference that *Simosuchus* was an herbivore [5, 19].

Acynodon iberoccitanus, Chimaerasuchus paradoxus, Edentosuchus tienshanensis, two undescribed Edentosuchus-like taxa from the Kayenta Formation (UCMP 130082 and UCMP 97638), *Iharkutosuchus makadii*, and *Pakasuchus kapilimai* all possess dentitions with complexity values that are equal to or greater than those of living squamate herbivores (OPCR<sub>c</sub> > 14.25 PPT and/or average OPCR<sub>a</sub> > 10 PPT; Figure 2). *Pakasuchus*, a small-bodied notosuchian characterized by extreme variation in dental morphology and mammal-like occlusion [6], and *Acynodon*, a small hylaeochampsid with a wide skull, are reconstructed as probable herbivores based on OPCR<sub>c</sub> values; however, the OPCR<sub>a</sub> values (Figure 2A) of both taxa overlap with those of omnivores. Therefore, other data types (e.g., microwear or stable



#### Figure 2. Comparison of the Dental Complexity of Extinct Crocodyliforms with Extant Reptiles

(A) Diet versus average OPCR value, OPCR<sub>a</sub>, including fossil crocodyliforms with four or more teeth preserved in a single tooth row. One living lizard outlier, *Cyclura cornuta*, is denoted with an asterisk.

(B) OPCR of the most complex tooth, OPCR<sub>c</sub>, values of extinct crocodyliforms compared to those of living saurians. For both plots, the median of each dietary category from living reptiles is indicated by the middle black horizontal line, dark gray boxes are the 25–75% quartiles, and the light gray boxes are the minimum and maximum quartiles. Diet was reconstructed using OPCR data, combined with information on body size (*Armadillosuchus*) and discrete dental features (*"Allognathosuchus"* and *Brachychampsa*). Red symbols indicate a taxon with a carnivorous diet, blue, a durophagous diet, purple, an omnivorous diet, green, an herbivorous diet, and orange are animals whose dental complexities could indicate either an insectivorous or omnivorous diet. *Caiman* included for reference. Extant dataset is from 17. See Figures S1–S3 and Tables S1–S3 for in-depth OPCR results.

isotopes) may be necessary to confirm the herbivorous diet of these taxa.

*Chimaerasuchus*, *Edentosuchus*, UCMP 130082, UCMP 97638, and *Iharkutosuchus* are unambiguous herbivores; among these, UCMP 130082, *Chimaerasuchus*, and *Iharkutosuchus* possess isolated tooth complexity values greater than those of any measured living reptile (Figure 2B). Although *Iharkutosuchus* and *Acynodon* possess labiolingually expanded distal teeth similar to the durophages "*Allognathosuchus*" and *Brachychampsa*, their dentitions are characterized by a combination of prominent cusps, subtle rises, and distinct grooves—features that are not observed in extant durophagous reptiles [2, 17, 19–21].

#### DISCUSSION

Our results indicate that heterodont crocodyliforms exhibit a wider range in dietary ecologies than previously hypothesized. Despite having a similar general morphology to Armadillosuchus and possessing dental features previously hypothesized to indicate herbivory (e.g., molariform occlusal surfaces) [13], Notosuchus possesses a surprisingly simple dentition, with an OPCR<sub>c</sub> below that of the extinct Boverisuchus and an extant caiman, taxa whose dietary ecologies are not in question (Figure 2). The absence of major ridges or additional cusps account for this low dental complexity. This is not to say Notosuchus never consumed plant material; many living crocodylians deliberately consume vegetation for a small portion of their diet [22], but it does suggest that animal material likely constituted the majority of its diet. The intermediate complexities of Araripesuchus, Armadillosuchus, Candidodon, and Mariliasuchus make it difficult to confidently reconstruct diet based on dentition alone. It is likely that these genera were dietary generalists, consuming a combination of animal and plant material [2]. In the case of Mariliasuchus, a recent analysis of enamel microstructure and dental microwear support this hypothesis [23]. However, comparisons with extant animals can aid in dietary reconstruction for Armadillosuchus. Both mammals and reptiles who possess a diet comprised primarily of insects are frequently, but not exclusively, associated with a small body size and mass [17, 24-26]. For example, a previous study on reptile dental complexity found that the maximum body size (snout-vent length) of measured insectivores was 300 mm [17]. Similarly, the vast majority of insectivorous mammals fall below a body length of 1 m and under a body mass of 8.5 kg, although the ant-specialist aardvark can be larger (approximately 52 kg) [26]. The skull of Armadillosuchus is approximately 30 cm and has an estimated body length of nearly 2 m, exceeding that of both extant mammalian and squamate insectivores [17, 24-26]. Therefore, Armadillosuchus is reconstructed as an omnivore.

In our dataset, skull length, a general proxy for overall body size, has a weakly negative relationship with dental complexity, with larger taxa having simpler dentitions (Figure S3). Even when phylogenetic history is taken into account, this remains true. It should be noted that this negative relationship is not statistically significant and may change with additional sampling, such as the addition of more protosuchian, goniopholid, and notosuchian taxa. This general trend is expected because most large crocodyliforms appear to be carnivores. It is noteworthy that specimens with high dental complexities, interpreted here as herbivores, are typically smaller bodied (skull length < 20 cm). The smallest taxon included in this analysis, *Edentosuchus*, has a skull approximately 4 cm long and an estimated body size of 40 cm, which falls above that of most



#### Figure 3. Time-Calibrated Phylogeny Displaying Reconstructed Diets of Extinct Crocodyliforms

The geographic location of each taxon is indicated by modern land-mass silhouettes for Africa, Asia, Australia, Europe, Madagascar, North America, and South America. Gold stars represent the inferred evolutionary originations of herbivory, whereas the teal star indicates potential single origin of herbivory in Notosuchia. Inferred carnivores possess teeth that were not sampled for this study but have dentitions that resemble those of measured taxa, primarily conical or labiolingually compressed morphologies. Thalattosuchia is not included because the phylogenetic position of this clade is still disputed [27]. Phylogeny modified from [28]. EJ, Early Jurassic; EK, Early Cretaceous; EO, Eocene; LJ, Late Jurassic; LK, Late Cretaceous; LT, Late Triassic; Mi, Miocene; MJ, Middle Jurassic; OI, Oligocene; Pa, Paleocene; Pe, Pleistocene; PI, Pliocene.

extant insectivores [17, 26], whereas the largest reconstructed herbivore, *Acynodon*, approaches a body length of 1.5 m [2]. Inferred herbivores are found near the middle range of body sizes, unlike extant reptiles and mammals, where many (but not all) herbivores are larger [17, 26]. It remains to be seen if the smaller body size of herbivores is an artifact of the dataset or reflects a broader association of small body sizes and high complexity dentitions. Currently, given the weak relationship between skull length and dental complexity, body size does not appear to explain most variation in dental complexity in this dataset.

Previous workers have suggested that herbivory evolved separately in one or more lineages of Mesozoic crocodyliforms [4, 5, 8, 13], but results presented here demonstrate that the

4 Current Biology 29, 1–7, July 22, 2019

occurrence of herbivory is more common than previously thought. Herbivorous crocodyliforms appeared early in their evolutionary history, shortly after the end-Triassic mass extinction, and persisted until the end-Cretaceous mass extinction. The OPCR results suggest that herbivory independently evolved a minimum of three times, and possibly six times, in Mesozoic crocodyliforms (Figure 3). Among the clade Notosuchia alone, as many as three separate origins of herbivory is not unreasonable, given that many of the intervening unsampled lineages (e.g., uruguaysuchids, peirosaurids, *Caipirasuchus*, and sebecosuchians) have simple dentitions similar to extant carnivorous crocodylians. Other notosuchian taxa with unique dentitions, such as *Malawisuchus*, *Adamantinasuchus*, and *Yacarerani*, have not been tested with our methods [2], and therefore, the

number of inferred origins of herbivory may change as future taxon sampling is increased.

The circumstances leading to the evolution of crocodyliforms with a plant-dominated diet remain unknown. Reconstructing the evolutionary pathways that lead to herbivory in crocodyliforms is beyond the goal of this contribution, but extant organisms offer insight into possible evolutionary transitions. Analyses of living mammals and birds indicate that most dietary transitions occur from other dietary guilds (i.e., carnivory, herbivory) into omnivory, meaning that an animal is more likely to shift from a carnivorous diet to omnivory rather than directly to herbivory [29, 30]. Given that the diet of early crocodylomorphs is inferred to be carnivorous based on their dental morphology (e.g., [31]), it is likely that the closest relatives of herbivorous taxa were omnivores. This transition to omnivory in extinct crocodyliforms is not unreasonable, given that most living crocodylians with wellstudied diets are documented consuming plant material [22, 32, 33]. In the American Alligator, Alligator mississippiensis, individuals who were fed an extruded diet with plant-derived protein for a number of months did not appear to suffer negative side effects [34, 35], suggesting that the ability to efficiently digest plant material is present in living crocodylians without a history of herbivory. This flexibility, if present in extinct representatives, may have contributed to the diversity seen in extinct crocodyliforms. Potential transitions to and from omnivory may be reflected in our results for Notosuchia, where carnivores and herbivores are nested among a variety of omnivores. Nonetheless, reconstructing specific evolutionary transitions requires well-resolved phylogenies and a well-sampled fossil record. Many aspects of crocodyliform phylogeny are still under discussion, and the discovery curve for Mesozoic crocodyliforms (particularly notosuchians) suggests that many taxa remain to be discovered [27, 28, 36].

Saurian reptiles, including crocodyliforms, are typically thought of as having simpler dentitions than synapsids, but this work illustrates this is not always the case. When measured at the same resolution as mammals (50 data rows per tooth) [14, 15, 37]. many crocodyliform taxa in this study have comparable dental complexities to those observed in living rodents and carnivorans and extinct primates (compare Table S2 with [14]). The OPCR<sub>c</sub> values of UCMP 130082, Chimaerasuchus, and Iharkutosuchus rival and even surpass the most complex teeth of some extant herbivorous mammals (the rodent Pelomys campanae) [14]. Even then, the dental complexity of Chimaerasuchus is probably an underestimate because some cusps are broken or missing [8] and, therefore, would likely exceed many mammalian herbivores. Unlike living herbivorous reptiles, which frequently converge on a mesiodistally expanded, labiolingually compressed morphology, crocodyliforms independently developed unique dental forms to achieve these extremely high complexities. Increased dental complexity in crocodyliforms, similar to that in multituberculates and extant lizards, is primarily driven by increases in cusp number and relative size of the distal portion of the dentition. However, with the exception of the iguanid-like multicusped, labiolingually compressed tooth morphology of Simosuchus [5, 19], most herbivorous crocodyliforms developed complex, labiolingually expanded molariform teeth superficially resembling various synapsids (e.g., tritylodonts [8, 38]).

Previous studies have suggested that Mesozoic crocodyliform taxa with the highest degree of heterodonty are restricted to

regions with either few or no mammaliamorphs (tritylodontids, mammaliaforms, and relatives) and that the development of mammal-like dental morphologies may be related to this paucity of mammaliamorphs in these ecosystems [2, 6]. Although Iharkutosuchus, Acynodon, Chimaerasuchus, and Edentosuchus were discovered in formations that lack mammaliamorph fossils, mammaliamorphs are known from nearby sites in both the Early to middle Cretaceous of China and latest Cretaceous of Europe (e.g., [39-41]). In contrast, the herbivorous Edentosuchus-like crocodyliforms from the Early Jurassic of western North America are preserved in the same strata as numerous synapsids, including herbivorous tritylodonts and early mammaliaforms [42-44]. The Gondwanan notosuchians Pakasuchus and Simosuchus also are found in assemblages that contain mammaliaforms [45-48], including inferred herbivores and omnivores [46, 47]. This demonstrates that at least some herbivorous Mesozoic crocodyliforms lived in the same regions with synapsids. In cases where they did share the same environments, it remains unknown if these two herbivorous groups directly competed for plant materials or utilized different dietary resources, either partitioning by body size or specializing in different floral groups. In either case, it is clear that during the Mesozoic, crocodyliforms evolved herbivory multiple times alongside mammaliamorphs, suggesting that herbivorous crocodyliforms did not simply occupy a "mammalian" role where mammaliamorphs were absent.

This is the first study to quantitatively reconstruct the diet of extinct crocodyliforms and clearly establishes the applicability of the OPCR method beyond living and extinct mammals, demonstrating a non-destructive avenue for dietary reconstruction in extinct organisms, especially those with no living descendants or unique dental morphologies. Extinct crocodyliforms occupied a much more diverse set of ecological roles, including terrestrial herbivores, than living members of this clade. Our data indicate that herbivorous crocodyliforms were present in both Laurasia and Gondwana during disparate time intervals and independently developed highly complex dentitions, which rival the complexity of living mammalian herbivores. Herbivorous crocodyliforms repeatedly lived in environments with herbivorous synapsids (including mammaliaforms) during the age of dinosaurs, suggesting that these organisms were not simply filling a "mammalian" ecological role (i.e., small-bodied, terrestrial herbivore) or excluding mammals from these ecosystems. Instead, these data suggest an ecological partitioning of plant resources between crocodyliforms and synapsids that does not occur in modern ecosystems. This highlights the uniqueness of these Mesozoic ecosystems, even as many modern components (taxa and interactions) were being assembled.

#### STAR\*METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
  - Specimen Repositories

#### • METHOD DETAILS

- Molding and Casting
- Computed Tomography
- Dietary Categories
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Dental Complexity
  - Data Analyses
- DATA AND SOFTWARE AVAILABILITY

#### SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j. cub.2019.05.076.

#### ACKNOWLEDGMENTS

S. Merchant assisted with the  $\mu$ CT scanning. Thanks to A. Ősi for providing several dental casts; A. Pritchard, N. Kley, A. Turner, P.M. O'Connor, and C. Holliday for providing CT scans; A. Vander Linden, G. Wilson, A. Evans, and D. Boyer for help with the OPCR software; and P. Holroyd, C. Levitt-Bussian, Alejandro Kramarz, and Stella Alvarez for specimen access. This research was supported by a US National Science Foundation Graduate Research Fellow-

Q6 ship (K.M.M.), the Welles Fund from the University of California Museum of Paleontology, and the University of Utah Department of Geology & Geophysics Chapman Fund. We also greatly appreciate the comments provided by the editor and anonymous reviewers that improved the manuscript significantly as well as P.M. O'Connor and M. D'Emic for editing assistance.

#### **AUTHOR CONTRIBUTIONS**

K.M.M. and R.B.I. designed the study. K.M.M. edited CT data. K.M.M. analyzed dental complexity. K.M.M. and R.B.I. wrote the manuscript.

#### **DECLARATION OF INTERESTS**

The authors declare no competing interests.

Received: November 5, 2018 Revised: April 23, 2019 Accepted: May 31, 2019 Published: June 27, 2019

#### REFERENCES

- Young, M.T., Brusatte, S.L., Ruta, M., and De Andrade, M.B. (2010). The evolution of Metriorhynchoidea (mesoeucrocodylia, thalattosuchia): an integrated approach using geometric morphometrics, analysis of disparity, and biomechanics. Zool. J. Linn. Soc. 158, 801–859.
- Ősi, A. (2013). The evolution of jaw mechanism and dental function in heterodont crocodyliforms. Hist. Biol. 26, 279–414.
- Stubbs, T.L., Pierce, S.E., Rayfield, E.J., and Anderson, P.S. (2013). Morphological and biomechanical disparity of crocodile-line archosaurs following the end-Triassic extinction. Proc. Biol. Sci. 280, 20131940.
- Sereno, P., and Larsson, H. (2009). Cretaceous Crocodyliforms from the Sahara. ZooKeys 28, 1–143.
- Buckley, G.A., Brochu, C.A., Krause, D.W., and Pol, D. (2000). A pugnosed crocodyliform from the Late Cretaceous of Madagascar. Nature 405, 941–944.
- O'Connor, P.M., Sertich, J.J., Stevens, N.J., Roberts, E.M., Gottfried, M.D., Hieronymus, T.L., Jinnah, Z.A., Ridgely, R., Ngasala, S.E., and Temba, J. (2010). The evolution of mammal-like crocodyliforms in the Cretaceous Period of Gondwana. Nature 466, 748–751.
- Clark, J.M., Jacobs, L.L., and Downs, W.R. (1989). Mammal-like dentition in a mesozoic crocodylian. Science 244, 1064–1066.

- Wu, X.-C., Sues, H.-D., and Sun, A. (1995). A plant-eating crocodyliform from the Cretaceous of China. Nature 376, 678–680.
- Gomani, E.M. (1997). A crocodyliform from the Early Cretaceous of Malawi. J. Vertebr. Paleontol. 17, 280–294.
- D'Amore, D.C., Harmon, M., Drumheller, S.K., and Testin, J.J. (2019). Quantitative heterodonty in Crocodylia: assessing size and shape across modern and extinct taxa. PeerJ 7, e6485.
- Marinho, T.S., and Carvalho, I.S. (2009). An armadillo-like sphagesaurid crocodyliform from the Late Cretaceous of Brazil. J. S. Am. Earth Sci. 27, 36–41.
- Soto, M., Pol, D., and Perea, D. (2011). A new specimen of *Uruguaysuchus aznarezi* (Crocodyliformes: Notosuchia) from the middle Cretaceous of Uruguay and its phylogenetic relationships. Zool. J. Linn. Soc. *163*, 173–198.
- Fiorelli, L., and Calvo, J.O. (2008). New remains of *Notosuchus terrestris* Woodward, 1896 (Crocodyliformes: Mesoeucrocodylia) from Late Cretaceous of Neuquen, Patagonia, Argentina. Aq. Mus. Nac., Rio de Jan 66, 83–124.
- Evans, A.R., Wilson, G.P., Fortelius, M., and Jernvall, J. (2007). High-level similarity of dentitions in carnivorans and rodents. Nature 445, 78–81.
- Wilson, G.P., Evans, A.R., Corfe, I.J., Smits, P.D., Fortelius, M., and Jernvall, J. (2012). Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. Nature 483, 457–460.
- Santana, S.E., Strait, S., and Dumont, E.R. (2011). The better to eat you with: functional correlates of tooth structure in bats. Funct. Ecol. 25, 839–847.
- Melstrom, K.M. (2017). The relationship between diet and tooth complexity in living dentigerous saurians. J. Morphol. 278, 500–522.
- Peredo, C.M., Peredo, J.S., and Pyenson, N.D. (2018). Convergence on dental simplification in the evolution of whales. Paleobiology 44, 434–443.
- Kley, N.J., Sertich, J.J.W., Turner, A.H., Krause, D.W., O'Connor, P.M., and Georgi, J.A. (2010). Craniofacial morphology of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. J. Vertebr. Paleontol. 30, 13–98.
- Ősi, A., Clark, J.M., and Weishampel, D.B. (2007). First report on a new basal eusuchian crocodyliform with multi-cusped teeth from the Upper Cretaceous (Santonian) of Hungary. N. Jb. Geol. Paläont. Abh. 243, 169–177.
- Ősi, A., and Weishampel, D.B. (2009). Jaw mechanism and dental function in the late cretaceous basal eusuchian *Iharkutosuchus*. J. Morphol. 270, 903–920.
- Platt, S.G., Elsey, R.M., Liu, H., Rainwater, T.R., Nifong, J.C., Rosenblatt, A.E., Heithaus, M.R., and Mazzotti, F.J. (2013). Frugivory and seed dispersal by crocodilians: an overlooked form of saurochory? J. Zool. (Lond.) 291, 87–99.
- Augusta, B.G., and Zaher, H. (2019). Enamel dentition microstructure of Mariliasuchus amarali (Crocodyliformes, Notosuchia), from the Upper Cretaceous (Turonian–Santonian) of the Bauru Basin, Brazil. Cretac. Res. 99, 255–268.
- 24. Pough, F.H. (1973). Lizard energetics and diet. Ecology 54, 837-844.
- Carbone, C., Mace, G.M., Roberts, S.C., and Macdonald, D.W. (1999). Energetic constraints on the diet of terrestrial carnivores. Nature 402, 286–288.
- Pineda-Munoz, S., Evans, A.R., and Alroy, J. (2016). The relationship between diet and body mass in terrestrial mammals. Paleobiology 42, 659–669.
- Wilberg, E.W. (2015). What's in an outgroup? The impact of outgroup choice on the phylogenetic position of Thalattosuchia (Crocodylomorpha) and the origin of Crocodyliformes. Syst. Biol. 64, 621–637.
- Pol, D., Nascimento, P.M., Carvalho, A.B., Riccomini, C., Pires-Domingues, R.A., and Zaher, H. (2014). A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of advanced notosuchians. PLoS ONE *9*, e93105.

- Price, S.A., Hopkins, S.S.B., Smith, K.K., and Roth, V.L. (2012). Tempo of trophic evolution and its impact on mammalian diversification. Proc. Natl. Acad. Sci. USA 109, 7008–7012.
- Burin, G., Kissling, W.D., Guimarães, P.R., Jr., Şekercioğlu, Ç.H., and Quental, T.B. (2016). Omnivory in birds is a macroevolutionary sink. Nat. Commun. 7, 11250.
- Irmis, R.B., Nesbitt, S.J., and Sues, H.-D. (2013). Early crocodylomorpha. In Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and Their Kin, S.J. Nesbitt, J.B. Desojo, and R.B. Irmis, eds. (Geological Society, London), pp. 275–302.
- Rosenblatt, A.E., Zona, S., Heithaus, M.R., and Mazzotti, F.J. (2014). Are seeds consumed by crocodilians viable? A test of the crocodilian saurochory hypothesis. Southeast. Nat. 13, 29.
- Somaweera, R., Brien, M.L., Platt, S.G., Manolis, C., and Webber, B.L. (2019). Direct and indirect interactions with vegetation shape crocodylian ecology at multiple scales. Freshw. Biol. 64, 257–268.
- Reigh, R.C., and Williams, M.B. (2018). Plant products in compounded diets are effectively utilized by American Alligator, *Alligator mississippiensis*. J. World Aquacult. Soc. 49, 1014–1018.
- DiGeronimo, P.M., Di Girolamo, N., Crossland, N.A., Del Piero, F., Reigh, R.C., and Nevarez, J.G. (2017). Effects of plant protein diets on the health of farmed American alligators (*Alligator mississippiensis*). J. Zoo Wildl. Med. 48, 131–135.
- Pol, D., and Leardi, J.M. (2015). Diversity patterns of Notosuchia (Crocodyliformes, Mesoeucrocodylia) during the Cretaceous of Gondwana. Publ Electrón Asoc Paleontol Argent 15, 172–186.
- Boyer, D.M., Evans, A.R., and Jernvall, J. (2010). Evidence of dietary differentiation among late Paleocene-early Eocene plesiadapids (Mammalia, primates). Am. J. Phys. Anthropol. *142*, 194–210.
- Wu, X.-C., and Sues, H.-D. (1996). Anatomy and phylogenetic relationships of *Chimaerasuchus paradoxus*, an unusual crocodyliform reptile from the Lower Cretaceous of Hubei, China. J. Vertebr. Paleontol. *16*, 688–702.
- Csiki-Sava, Z., Buffetaut, E., Ősi, A., Pereda-Suberbiola, X., and Brusatte, S.L. (2015). Island life in the Cretaceous - faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. ZooKeys 469, 1–161.
- 40. Zhou, Z., Barrett, P.M., and Hilton, J. (2003). An exceptionally preserved Lower Cretaceous ecosystem. Nature *421*, 807–814.
- Smith, T., and Codrea, V. (2015). Red iron-pigmented tooth enamel in a multituberculate mammal from the Late Cretaceous Transylvanian "Hateg Island". PLoS ONE 10, e0132550.
- 42. Sues, H.D., Clark, J.M., and Jenkins, F.A. (1994). A review of the Early Jurassic tetrapods from the Glen Canyon Group of the American Southwest. In In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods, N. Fraser, and H.D. Sues, eds. (Cambridge University Press), pp. 284–294.
- 43. Kühne, W.G. (1956). The Liassic Therapsid *Oligokyphus*, (British Museum [Natural History]).
- Jenkins, F.A., Crompton, A.W., and Downs, W.R. (1983). Mesozoic mammals from Arizona: new evidence on mammalian evolution. Science 222, 1233–1235. 24.

- Rogers, R.R., Krause, D.W., Kast, S.C., Marshall, M.S., Rahantarisoa, L., Robins, C.R., and Sertich, J.J.W. (2013). A new, richly fossiliferous member comprised of tidal deposits in the Upper Cretaceous Maevarano Formation, northwestern Madagascar. Cretac. Res. 44, 12–29.
- Krause, D.W., Gottfried, M.D., O'Connor, P.M., and Roberts, E.M. (2003). A Cretaceous mammal from Tanzania. Acta Palaeontol. Pol. 48, 321–330.
- Schultz, J.A., Krause, D.W., von Koenigswald, W., and Dumont, E.R. (2014). Dental function and diet of *Vintana sertichi* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. J. Vertebr. Paleontol. 34, 182–202.
- O'Connor, P.M., Krause, D.W., Stevens, N.J., Groenke, J.R., MacPhee, R.D.E., Kalthoff, D.C., and Roberts, E.M. (2019). A new mammal from the Turonian–Campanian (Upper Cretaceous) Galula Formation, southwestern Tanzania. Acta Palaeontol. Pol. 64, 65–84.
- Turner, A.H. (2006). Osteology and phylogeny of a new species of Araripesuchus (Crocodyliformes: Mesoeucrocodylia) from the Late Cretaceous of Madagascar. Hist. Biol. 18, 255–369.
- Lecuona, A., and Pol, D. (2008). Tooth morphology of *Notosuchus terrest*ris (Notosuchia: Mesoeucrocodylia): New evidence and implications. C. R. Palevol 7, 407–417.
- Clark, J.M., and Fastovsky, D.E. (1986). Vertebrate biostratigraphy of the Glen Canyon Group in northern Arizona. In The Beginning of the Age of Dinosaurs: Faunal Change across the Triassic-Jurassic Boundary, K. Padian, ed. (Cambridge University Press), pp. 285–301.
- Teaford, M.F., and Oyen, O.J. (1989). Live primates and dental replication: new problems and new techniques. Am. J. Phys. Anthropol. 80, 73–81.
- Cooper, W.E., and Vitt, L.J. (2002). Distribution, extent, and evolution of plant consumption by lizards. J. Zool. (Lond.) 257, 487–517.
- Rieppel, O., and Labhardt, L. (1979). Mandibular mechanics in *Varanus niloticus* (Reptilia: Lacertilia). Herpetologica 35, 158–163.
- 55. Furness, R.W. (1988). The predation of Tern chicks by sheep. Bird Study 35, 199–202.
- Furness, R.W. (1988). Predation on ground-nesting seabirds by island populations of red deer *Cervus elaphus* and sheep *Orvis*. J. Zool. (Lond.) 216, 565–573.
- Greene, H.W. (1982). Dietary and phenotypic diversity in lizards why are some organisms specialized? In Environmental Adaptation and Evolution, D. Mossakowski, and G. Roth, eds. (Gustav Fischer), pp. 107–128.
- Iverson, J.B. (1979). Behavior and ecology of the rock iguana Cyclura carinata. Bull. Fla. State Mus. Biol. Sci. 24, 175–358.
- 59. Loftin, H., and Tyson, E.L. (1965). Iguanas as carrion eaters. Copeia 1965, 515.
- Martin, J.E. (2007). New material of the Late Cretaceous globidontan Acynodon iberoccitanus (Crocodylia) from southern France. J. Vertebr. Paleontol. 27, 362–372.
- Hammer, O., Harper, D.A.T., and Ryan, P.D. (2001). PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electronica 4, 1–9.
- Midford, P.E., Garland, T., Jr., and Maddison, W.P. 2005. PDAP Package of Mesquite. Version 1.16.
- 63. Maddison, W.P., and Maddison, D.R. 2006. Mesquite: a modular system for evolutionary analysis. Version 3.03. (Mesquite Project).

### Q3 Q4 STAR ★ METHODS

#### **KEY RESOURCES TABLE**

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological Samples		
Acynodon iberoccitanus	[2]	ACAP-FX2 (for institutional abbreviations, see Table S1)
"Allognathosuchus"	This paper	UCMP 150180
Armadillosuchus arrudai	[2]	MPMA-64-0001-04
Araripesuchus gomesii	[49]	AMNH 24450
Boverisuchus vorax	This paper	UCMP 170767
Brachychampsa sp.	This paper	UCMP 159000
Candidodon itapecuruense	[2]	UFRJ DG 114-R
Chimaerasuchus paradoxus	[2]	IVPP V8274
Edentosuchus tienshanensis	[2]	IVPP V3236
Iharkutosuchus makadii	[2]	MTM 2006.52.1
Mariliasuchus amarali	[2]	MN 6756-V
Notosuchus terrestris	[50]	MACN-RN 1127
Pakasuchus kapilimai	[6]	RRBP 08631
Simosuchus clarki	[19]	UA 8679
UCMP 97638	[51]	UCMP 97638
UCMP 130082	[51]	UCMP 130082
Deposited Data		
MorphoSource, STL files of teeth	This paper	https://www.morphosource.org/
Software and Algorithms		
Surfer Manipulator	[14, 15]	http://evomorph.org/surfermanipulator
MeshLab	N/A	http://www.meshlab.net/

#### **CONTACT FOR REAGENT AND RESOURCE SHARING**

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Keegan Melstrom (keeganmelstrom@gmail.com).

#### **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

#### **Specimen Repositories**

The experimental subjects are fossilized crocodyliform dentitions from a wide temporal and geographic range. The dentitions of *Brachychampsa, Araripesuchus, Pakasuchus, Simosuchus*, UCMP 97638, and UCMP 130082 were scanned directly and are currently found at their original repositories. The remaining taxa were molded and cast by either K.M.M or A. Ősi [2]. All cast teeth are reposited at the Natural History Museum of Utah (NHMU; see Table S1 for specimen numbers and locations).

#### **METHOD DETAILS**

#### **Molding and Casting**

We molded and cast "*Allognathosuchus*" and *Boverisuchus* specimens from the University of California Museum of Paleontology (UCMP) and *Notosuchus* from the Museo Argentino de Ciencias Naturales, Buenos Aires (MACN). We applied Reprosil light body catalyst and base molding material directly to the specimens to generate molds. Casts were produced at the NHMU by pouring EPOTEK 301 epoxy resin into each mold and placing in a vacuum chamber for 5–10 min to remove air bubbles. Additional casts were provided by A. Ősi. Each cast has submicron resolution [52], capturing minor dental features (e.g., serrations), which are subsequently detected by the  $\mu$ CT scanner.

#### **Computed Tomography**

Dental casts of *Acynodon, "Allognathosuchus", Armadillosuchus, Boverisuchus, Candidodon, Chimaerasuchus, Edentosuchus, Iharkutosuchus, Mariliasuchus, and Notosuchus* were  $\mu$ CT scanned at the University of Utah Small Animal Imaging Core Facility using a Siemens INVEON  $\mu$ CT scanner. Dentitions were digitized at a voxel resolution of 35 microns, a voltage of 80 kVp, and a current of 150  $\mu$ A. Multiple specimens were often scanned together, due to their small size, at a pixel resolution of 1152. Taxa scanned in previous studies were  $\mu$ CT scanned in different locations. *Simosuchus* was  $\mu$ CT scanned at the University of Texas at Austin High Resolution X-ray Computed Tomography Facility (HRXCT), whereas *Araripesuchus* was scanned using a GE v|tome|x  $\mu$ CT scanner at the American Museum of Natural History Microscopy and Imaging Facility and had a voxel resolution of 62  $\mu$ . *Pakasuchus* was  $\mu$ CT scanned at Ohio University  $\mu$ CT Facility using the protocol: 85 kVp, 400 mA and a slice thickness of 0.045 mm with detailed report of the scanning protocol available in its description [6]. UCMP 97638 and UCMP 130082 were scanned at the HRXCT facility by C.M. Holliday (University of Missouri) using the following protocol: 80 kVp, 10W, total slices of 864 and 806, respectively, and a voxel resolution of 12.11 and 14.75 microns, respectively. 3D models of teeth were exported both as STL (binary) files (made available on MorphoSource) and STL (ASCII) files (for analysis in Surfer Manipulator) using the freeware program MeshLab (http://www.meshlab.net/).

#### **Dietary Categories**

Definitions for dietary categories follow Cooper and Vitt [53] and Melstrom [17], both of which investigated diet in living saurians. Carnivores are defined as animals that primarily consume vertebrate material for greater than 90% of their diet. The teeth of most extant carnivorous saurians are relatively simple, though morphologies can vary, between labiolingually compressed, knife-like teeth to conical teeth with blunted apices [17]. Durophages are a special category of carnivores that preferentially consume shelled organisms, such as snails or mollusks, for a large portion of their diet. Extant durophages, such as *Dracaena guianensis* and *Varanus niloticus*, are often characterized by large, labiolingually and mesiodistally expanded teeth in the posterior portion of the jaw [17, 54]. These bulbous teeth are frequently distinguished by small enamel wrinkles or crenulations, which are only detected by OPCR analyses at high resolutions (50 data rows per tooth). Previous studies hypothesize that these minor ridges help increase friction and distribute pressure over the tooth during the consumption of hard-shelled organisms [54]. Insectivores, similar to carnivores, are defined as organisms whose diet is over 90% animal material, but has a reliance on terrestrial arthropod prey (e.g., insects), as opposed to vertebrates. Living insectivorous saurians exhibit a wide range of dental complexities and morphologies, which often overlap with those of omnivores.

The diet of omnivores varies between 10% and 90% vegetation. Coupled with this diversity in diet is a wide range in dental complexities and morphologies. Although dental complexities frequently overlap with insectivores, some discrete features can be used to distinguish diets. In particular, the omnivore tooth cusps are frequently duller than those of insectivores, which may reflect differences in breaking down insect versus plant material [17]. Additionally, in a previous study on saurian dental complexity, measured insectivores did not exceed a snout-vent length 300 mm, whereas omnivores frequently possessed much larger body sizes, suggesting taxa that a large body size may help discriminate between insectivores and omnivores [17]. Herbivores are defined as animals where plants make up over 90% of the diet [53]. The selection of 10% animal material in a diet is arbitrary, but it allows for taxa that rarely or accidentally consume animal matter to still be considered herbivores, as both mammalian and reptilian herbivores are also known to occasionally, but purposely, consume animal material [55–59]. Therefore, an herbivore may have a diet that is occasionally supplemented with vertebrate and/or invertebrate material. Herbivorous saurians possess a wide range in dental morphologies, but are most often characterized by relatively high complexities, despite differences in morphology [17].

#### **QUANTIFICATION AND STATISTICAL ANALYSIS**

#### **Dental Complexity**

To infer robust ecological reconstructions of extinct crocodyliforms, we calculated dental complexity using a geographic information systems (GIS) analysis called orientation patch count rotated (OPCR) [14, 15]. This method employs the GIS software Surfer (Golden Software) and SurferManipulator, the latter of which digitizes dental complexity and is freely available (http://evomorph.org/surfermanipulator). OPCR is a quantitative method that measures dental complexity by converting dentitions into digital elevation models and grouping together contiguous pixels with a similar orientation (based on their cardinal and ordinal directions) into patches (Figures 1 and S1–S3). This analysis does not require morphological homologies to be established, which allow the dental complexity of distantly related taxa to be directly compared [14]. OPC quantifies dental complexity by determining the surface orientation of each pixel in the digital elevation model and grouping contiguous pixels facing the same cardinal and ordinal directions (e.g., north, south, south, we southwest) into 'patches'. The number of patches in the tooth row is the numerical representation of dental complexity. Slight variations in tooth orientation are mitigated by repeating the OPC calculation eight times at rotations of multiples of 5.625°. The mean of these separate tests is called Orientation Patch Count Rotated (OPCR), which is reported here.

Previous studies have demonstrated phenotypic tooth complexity is related to diet in extant and extinct mammals [14–16] and extant saurians [17]; thus, this method is broadly applicable for amniote dentitions and is appropriate to use with crocodyliforms. In living reptiles and mammals, OPCR values increase in relation to the relative proportion of consumed plant matter, with herbivores (diet composed of  $\geq$  90% plant material) typically possessing more complex dentitions than carnivores (Figure 2) [14, 16, 17].

To infer dietary categories for the extinct crocodyliforms sampled, we calculated OPCR values for tooth rows and individual teeth from high-resolution CT scans of 16 taxa; these results were then compared with the range of values across dietary categories (carnivore, durophage, insectivore, omnivore, and herbivore) observed for the same measurements in extant saurian reptiles (Figure 2) [17]. In living lizards and crocodylians, both the OPCR of the most complex tooth (OPCR<sub>c</sub>) as well as the average OPCR value (i.e., total OPCR for the tooth row divided by number of teeth; OPCR<sub>a</sub>) are related to diet [17]. Sampled extinct crocodyliform taxa included three crocodylians (*Boverisuchus, Brachychampsa, and "Allognathosuchus*"; Figure S3, two early eusuchians (*Acynodon* and *Iharkutosuchus*; Figure S3), eight notosuchians (*Candidodon, Simosuchus, Chimaerasuchus, Pakasuchus, Mariliasuchus, Armadillosuchus, Notosuchus, and Araripesuchus gomesii*; Figures S1 and S2), and three early branching crocodyliforms (*Edentosuchus* and two unnamed taxa from the Lower Jurassic Kayenta Formation; Figure S1).

Complete dentitions are rare in fossil crocodylomorphs and this is reflected in our dataset, with completeness differing between sampled taxa. *Chimaerasuchus* and the two unnamed early crocodyliforms from the Kayenta Formation (UCMP 97638, UCMP 130082) are known from poorly preserved dentitions (1–3 teeth). These three taxa were included in the OPCR<sub>c</sub> analysis under the assumption that they are the most complex teeth in their dental elements. This is a conservative assumption, because if they are not the most complex tooth, then these values are an underestimate relative to other sampled specimens. *Chimaerasuchus,* UCMP 97638, and UCMP 130082 were not included in OPCR<sub>a</sub> analyses because they did not reach the threshold of a relatively complete dental row (~1/3 of teeth preserved in a given jaw element). Anterior teeth are frequently simple, which reduce OPCR<sub>a</sub> relative to OPCR<sub>c</sub>, thereby making these isolated teeth appear complex compared to taxa with more complete jaws. *Acynodon, "Allognathosuchus," Boverisuchus, Iharkutosuchus, and Simosuchus preserved incomplete, but critical, portions of the dentition,* most importantly the distal teeth (i.e., molariform). *Armadillosuchus, Araripesuchus gomesii, Brachychampsa, Candidodon, Edentosuchus, Mariliasuchus, Notosuchus,* and *Pakasuchus* preserve complete or nearly complete dentitions of either the maxilla or dentary.

#### **Data Analyses**

To reduce the impact of size on shape, all teeth were scaled to the same sizes, 25, 40, and 50 pixel rows ([17]; Table S2). Pixel row count is also related to analysis resolution, with higher number of rows representing higher resolutions. Previous work on mammals has scaled mammal cheek teeth to 150 data rows [14]. In this work, many mammals studied had only three teeth, which comes out to an analysis of 50 data rows per tooth (RPT). In extant squamates, 50 RPT OPCR analyses detect fine-scale structures, such as the small cusps on *Iguana* teeth (but not carnivore serrations), frequently resulting in herbivores having even higher complexities [17]. In fact, 50 RPT analyses better demonstrate the relationship between diet and dental complexity in living saurians (although omnivores and insectivores still overlap).

Unfortunately, higher resolution OPCR analyses are more sensitive to variations in scan resolution, cast quality, and, more importantly for fossils, preservation issues. Many fossil crocodyliform teeth are often damaged, partially worn, or are somewhat covered in matrix. We avoided most dentitions with these issues, but in some cases they were critical to test (e.g., avoiding missing cusps in *Chimaerasuchus*). Cracks, pits, or broken surfaces can be seen when viewing higher resolution OPCR maps, allowing for these data to be discarded. The data presented in the main contribution are the results of 25 RPT analyses. Although they represent the lowest resolution tests, the effect of large cracks, tooth wear, and other damage are removed, which is not the case in higher resolution OPCR analyses. Herbivores frequently possess minor dental features which result in higher complexities, so lower resolutions analyses are a conservative estimation of diet.

To test the relationship between dental complexity and skull size, we measured skulls either in person or used published data [2, 6, 11, 19, 60]. In cases where linear measurements were not available, we used ImageJ (NIH) to calculate skull length. Ordinary least-squares regression on skull length and dental complexity were performed in the PAST3 software package [61]. To account for the effect of phylogeny on this potential relationship, phylogenetically independent contrasts tests were conducted in the PDAP-module (version 1.16) for the Mesquite software package (version 3.03) [62, 63].

#### DATA AND SOFTWARE AVAILABILITY

3D reconstructions (STLs) generated from high-resolution µCT scan of dental casts are available on MorphoSource (https://www. morphosource.org/) project P731.