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PALEONTOLOGY

Theropod dinosaur facial reconstruction and the importance of soft tissues in paleobiology

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Large theropod dinosaurs are often reconstructed with their marginal dentition exposed because of the enormous size of their teeth and their phylogenetic association to crocodylians. We tested this hypothesis using a multiproxy approach. Regressions of skull length and tooth size for a range of theropods and extant varanid lizards confirm that complete coverage of theropod dinosaur teeth with extraoral tissues (gingiva and labial scales) is both plausible and consistent with patterns observed in living ziphodont amniotes. Analyses of dental histology from crocodylians and theropod dinosaurs, including *Tyrannosaurus rex*, further indicate that the most likely condition was complete coverage of the marginal dentition with extraoral tissue when the mouth was closed. This changes our perceptions about the appearance and oral configuration of these iconic predators and has broad implications for our interpretations of other terrestrial animals with large teeth.

The antorbital region of the cranium plays a number of important roles in the biology of terrestrial vertebrates, including respiration, olfaction, and food capture and manipulation. Most known dinosaurs are herbivorous, and some (ornithischians) show evidence for an expanded rictus that formed a superficially cheek-like structure that covered their relatively small dentition externally, with this being particularly relevant for hadrosaurs and ceratopsians (*1*–*3*). By contrast, many non-avian theropod dinosaurs are renowned for possessing very large teeth, which has led to reconstructions in both scientific and popular literature since the 1980s that show maxillary dentition protruding from their closed mouths rather than covered by extraoral tissues, as in most terrestrial vertebrates (Fig. 1 and fig. S2) (*4*, *5*). Among the arguments in favor of this interpretation are the relatively large sizes of some theropod teeth and evidence from the dinosaur phylogenetic bracket, where crocodylians, the closest extant dentigerous relatives of dinosaurs, lack extensive extraoral tissues (*6*–*8*). Some recent research on theropod rostral neurovasculature has argued that direct data and evidence are lacking for extraoral tissue reconstructions (*9*), but rigorous reconstructions of these tissues are important for biological inferences for dinosaurs. Theropod dinosaur teeth have relatively thin enamel, and large theropods retained their dentition for prolonged periods of time (*10*, *11*), potentially exposing them to damaging desiccation and wear (*12*). Here, we use multiple lines of evidence, including dental histology, skull and tooth size regressions, and morphological comparisons, to test alternate hypotheses of theropod facial reconstruction.

In extant reptiles, two major anatomical patterns occur with respect to dentition and extraoral tissues. In crocodylians, about one-quarter of the tooth crown height that extends beyond the labial edge of the maxillary bone is covered by a fleshy gingiva, and the enamel-covered crowns are not covered by labial scales ("lips") (Fig. 2). In extant lepidosaurs, which are more distant reptilian relatives to dinosaurs than crocodiles, the base of the teeth is similarly covered in gingiva; however, the enamel-covered crowns of the teeth are covered externally by labial scales when the mouth

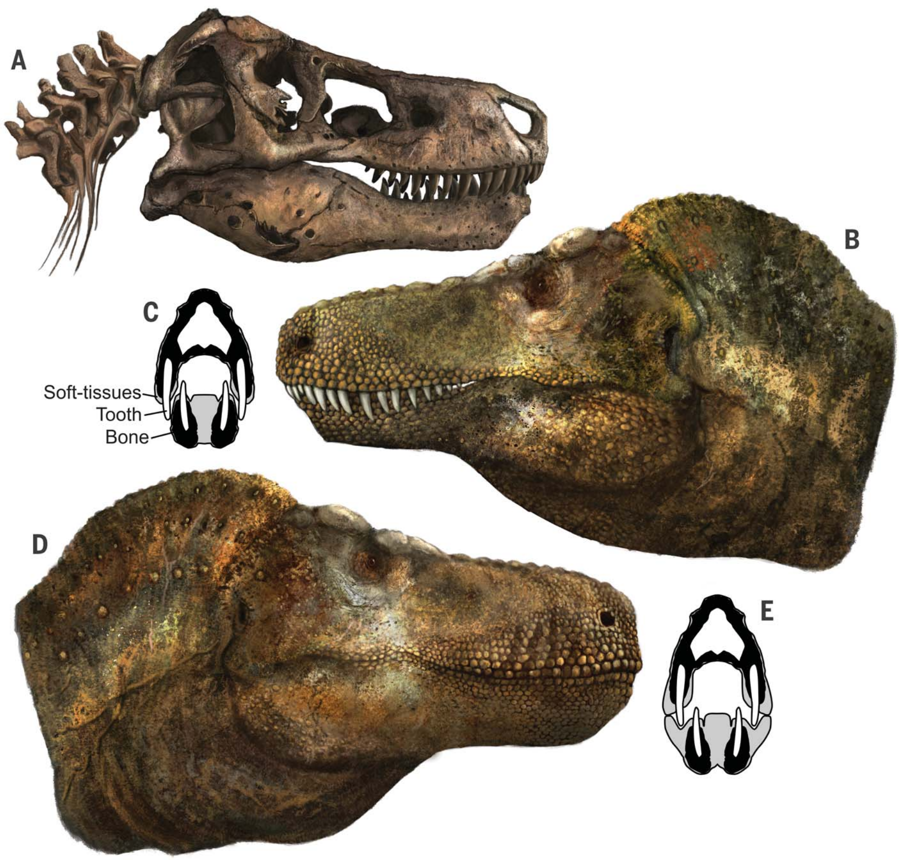

Fig. 1. Comparisons of the reconstructions of *T. rex*. (**A**) Skull, based on Field Museum of Natural History specimen FMNH PR 2081. (**B** to **E**) Two hypothetical flesh reconstructions, one with exposed teeth (B) and an associated cross section of the snout (C) and one with extraoral tissues covering the teeth (D) and an associated cross section of the snout (E).

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is closed (Fig. 2). This applies even in large-toothed taxa such as predatory varanid lizards. Notably, in both these lizards and theropod dinosaurs, the teeth are parasagitally aligned with the vertical plane of the skull and do not lean outward as in extant crocodiles (*13*).

Phylogenetic bracketing, in the absence of evidence from birds and fossils, could support the hypothesis that the large teeth of theropod dinosaurs would show the same pattern as that of extant crocodiles, with the upper marginal dentition being exposed when the mouth is closed (*8*). However, such narrow applications of extant phylogenetic bracketing can be problematic when considering dinosaur facial tissues (*3*, *14*, *15*), especially given recent studies into the derived facial integument of crocodylians and its relation to their aquatic lifestyles and sensory adaptations (*16*–*18*). The foramina that are present along the jaw margins of reptiles facilitate the passage of blood vessels and branches of the trigeminal nerve to the extraoral tissues and, in derived crocodylians, house sensory organs that were more widely distributed across the snout (*9*). Extinct terrestrial crocodylomorphs (e.g., the Late Triassic taxon *Hesperosuchus*; Fig. 2) possess a more theropod-like pattern of linearly arranged jaw foramina, as well as ziphodont dentition (Fig. 2) (*7*). Indeed, a broader extant comparison (Fig. 2) demonstrates that the lower-density, linear pattern of foramina on the face and jaws of theropods, such as tyrannosaurids, is as or more similar in structure to that of many extant squamates, such as *Varanus* or *Amblyrhynchus*, than to the pattern observed in extant crocodylians such as *Alligator*. This is concordant with other work suggesting that similarly low densities of linearly arranged facial foramina are a widespread feature in tetrapods that possess extraoral soft tissues (*1*, *9*).

Dentition in reptiles, including dinosaurs, is characterized by the presence of a relatively thin enamel layer that covers the crown of the tooth. Enamel is formed during tooth development through amelogenesis, is not reparable or replaceable, and is invariably thin in most carnivorous reptiles, both fossil and extant (*19*, *20*). In theropod dinosaurs, the thickness of the enamel is similar on the lingual and labial sides of the tooth crown and is somewhat size dependent, with the largest theropod dinosaurs having the thickest enamel (*20*, *21*). Crocodylians generally have overall thicker enamel than dinosaurs, with thicker regions toward the apex of the crown (*21*). In addition, dentine exposure is common in teeth and tusks that are exposed to the environment (*22*). To investigate the dental histology of large theropods in detail, we removed a functional upper maxillary tooth from a large individual of the tyrannosaurid *Daspletosaurus* and examined it for age and enamel ultrastructure in histological thin section under plane-polarized

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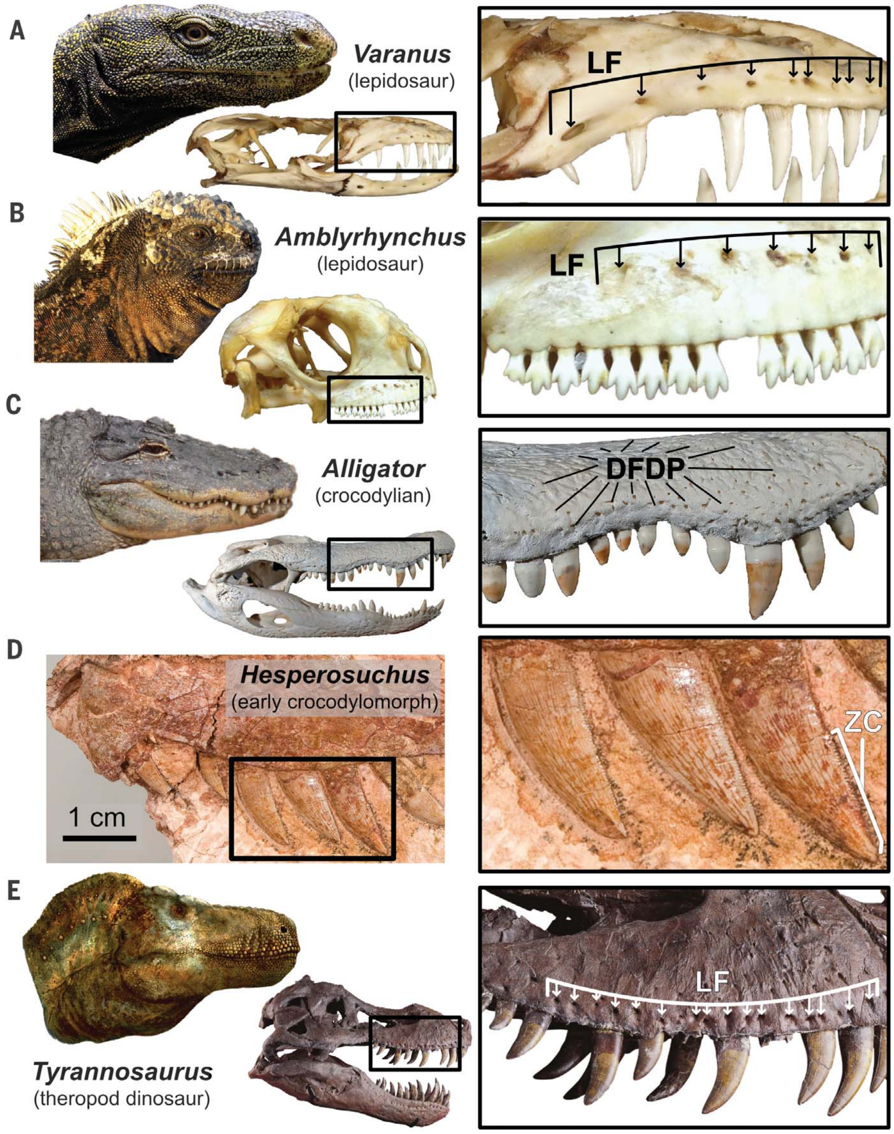

Fig. 2. Comparisons of life appearance and reconstructions, skull shape, and maxillary morphology in lepidosaurs and archosaurs. (**A**) *V. salvadorii*. (**B**) *Amblyrhynchus cristatus*. (**C**) Extant crocodylian *A. mississippiensis*. (**D**) Extinct crocodylomorph *Hesperosuchus agilis*. (**E**) Extinct theropod *T. rex*. Note the linear pattern of foramina (LF) along the extraoral margin in sampled lepidosaurs and theropods in contrast to the broadly distributed pattern of foramina and dome pressure sensor pores (DFDP) in *Alligator*. Also note the ziphodont tooth condition (zc) in the inset image of *Hesperosuchus* (D) compared with the condition present in extant crocodylians. [Image credits: *V. salvadorii*, *A. cristatus*, and *A. mississippiensis* in-life photographs from Wikimedia Commons (public domain); *A. cristatus* skull photograph from E. Graslie (used with permission); *A. mississippiensis* skull photograph from D. Descouens (CC-ASA-4.0); *T. rex* skull photograph from J. Weinstein at FMNH (used with permission); remaining images are from the authors]

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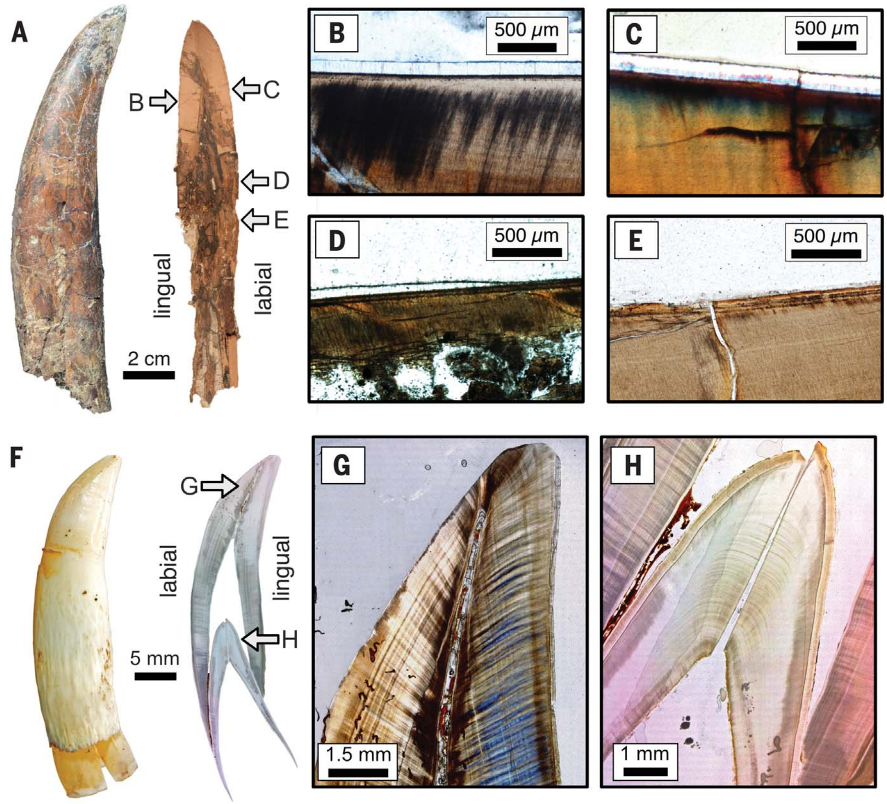

Fig. 3. Histological thin sections of teeth from the large theropod *Daspletosaurus* and *Alligator*. (**A** to **E**) *Daspletosaurus* tooth (Royal Tyrrell Museum of Palaeontology specimen TMP 2003.010.0003) (A) showing relatively unworn enamel of equal thickness on the lingual (B) and labial (C) surfaces of this functional tooth, as well as a reduction of enamel at the base of the crown (D) and cementum present along the root (E). (**F** and **G**) *Alligator* tooth (Royal Ontario Museum specimen ROM R600) (F) showing highly uneven wear patterns between the labial and lingual surfaces (G), with all enamel and some dentine worn away along the labial surface and thick enamel still present on the lingual surface. (**H**) Unerupted *Alligator* tooth without any wear and with the presence of even enamel thickness. See fig. S1 for images of the maxilla of TMP 2003.010.0003 and additional information on the sampled tooth. Images in (B) to (E) and (G) and (H) are thin sections photographed using a petrographic microscope, under plane-polarized [(E) and (H)] and cross-polarized [(B), (D), and (G)] light.

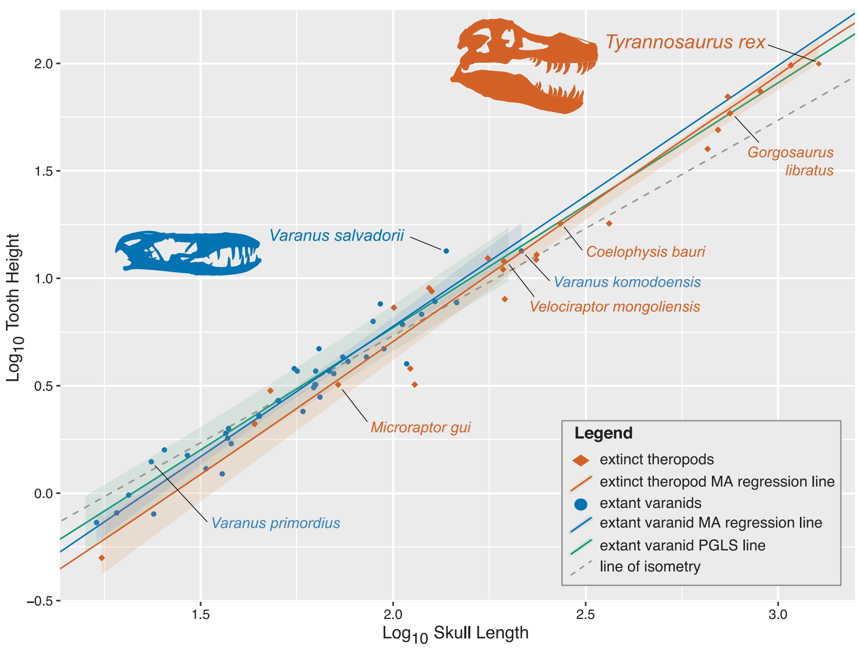

Fig. 4. Plot of $\log_{10}$ skull length to $\log_{10}$ tooth height for a range of extant varanids and extinct theropods. Model II major axis (MA) regressions run on extant varanids (all of which have extraoral tissues covering teeth) (blue points, line, and shaded confidence intervals) and extinct theropods (orange points, line, and shaded confidence intervals). Also plotted are a phylogenetic generalized least squares (PGLS) line for the same extant varanids (green) and the line of isometry (dashed gray). Goodness-of-fit for *Varanus* data is as follows: coefficient of determination (r^2) = 0.9285, and $p < 0.001$. The slope of the *Varanus* MA regression line is 1.215, the slope of the PGLS line is 1.140, and the slope of the theropod MA regression line is 1.218. The *Varanus* and theropod lines are not significantly different ($p = 0.97$).

and cross-polarized light using a petrographic microscope (Fig. 3 and fig. S1; see supplementary text). The thin section confirmed that this tooth was fully developed, with an estimated 512 von Ebner lines being present, consistent with tooth development and replacement rates of well over 1 year that have been estimated in other large tyrannosaurids, including *Tyrannosaurus rex* (*11*). The enamel was found to be of similar thickness on both the lingual and labial sides, with no evidence of any substantial wear (Fig. 3, A to E). Despite its advanced age, the tooth still carried well-formed mesial and distal cutting edges (carinae) with delicate serrations [ziphodont (*23*) or incrassate (*24*)]. Wear on tyrannosaurid teeth occurs rarely and primarily on the medial surface of the maxillary dentition because of tooth-on-tooth contact with the opposing dentary teeth (*25*). By contrast, the enamel of the largest teeth of *Alligator mississippiensis*, like the one in tooth position 4 (Fig. 3, F to H), frequently becomes eroded on the exposed labial side, with even a substantial portion of the dentine occasionally worn away.

Enamel has a relatively low water content but is still hydrated and maintained in extant terrestrial vertebrates by glandular secretions in the mouth (*12*, *26*), which arrest detrimental changes in enamel hardness and elasticity (*12*, *27*). Dry enamel has a higher nanohardness and elastic modulus, resulting in stiffer tissue (*12*, *27*), whereas wet enamel is better

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at resisting wear and abrasion (*12*). Given the relationship between hydration and wear resistance, and the difficulty of maintaining hydration if a tooth is exposed to air for long periods of time, it is unlikely for functional teeth to remain relatively unworn if exposed, unless the enamel structure and thickness are considerably modified. The comparative lack of wear and abrasion in theropod teeth (Fig. 3, A to E) (*23*), in contrast to the extensive and asymmetric wear [Fig. 3, F to H; see also (*28*–*30*)] and breakage (*31*) observed through ontogeny in crocodylians, suggests that theropod teeth existed under hydrated conditions consistent with the possession of extraoral tissues.

Although the skulls and teeth of theropod dinosaurs, such as *Daspletosaurus* and *Tyrannosaurus*, are indeed very large compared to those of extant reptiles, major-axis regression analyses demonstrate that the slope of the tooth-skull size relationship in theropods closely matches that observed for extant varanids (Fig. 4), thus refuting interpretations that their teeth were unusually large to the extent that tooth size could preclude extraoral tissue coverage. Even the varanid with the largest relative tooth size (*Varanus salvadorii*) does not have exposed dentition (Figs. 2A and 4), and it possesses greater tooth height–to–skull length ratios (0.096) than the largest sampled theropod, *T. rex* (0.074). These data indicate that theropod teeth were not too large to be covered with extraoral tissues when the mouth was closed and that such a condition would be consistent with what is observed in living amniotes.

The scaling relationships of tooth to skull size between varanids and theropods (Fig. 4) provide further support for the potential inference of soft tissue coverings of the marginal dentition in theropods. Although the relationship between tooth and skull size is weakly positively allometric, the relationship does not greatly affect expected tooth size over the scales represented (dashed versus solid lines in Fig. 4), and data comparing tooth crown height to extraoral tissue height, where available, suggest that a weakly negative allometric-to-isometric relationship exists between these measures (i.e., crown height increases at a slower rate than extraoral tissue height with increasing body size; fig. S4). No change in the presence of complete coverage of teeth with extraoral tissues is noted over a 12-fold increase in size between the smallest and largest *Varanus* skulls in the dataset, despite the inclusion of *Varanus* species with teeth that are proportionally larger (relative to skull size) than those observed in most theropods (e.g., *V. salvadorii*). It would therefore be inconsistent with the data to expect the extraoral tissues to deviate from this pattern over the sixfold size increase between *Varanus komodoensis* and *T. rex*. Given the close fit of multiple lineages of small theropods to the tooth-to-skull size relationship documented in varanids, well-developed extraoral tissues appear likely in smaller members of all major theropod groups, and it is unlikely for tooth height to have exceeded facial soft tissue growth, even in larger theropods.

These comparisons show that extraoral tissues of nonavian theropods (Fig. 1 and fig. S2; see supplementary text) were more like those of extant lepidosaurs and other tetrapods than those of birds or crocodylians and that the faces of extant archosaurs do not accurately reflect the ancestral condition of the archosaurian clade. The results of this study strongly support "lipped" facial reconstructions in theropods with wide-reaching implications for their portrayal in science and popular culture. More importantly, the presence of extensive extraoral tissues has implications for tooth strength, feeding ecology, and biomechanics and therefore may have played an important role in how carnivorous theropod dinosaur teeth resisted forces associated with feeding close to the bone and even may have permitted carcass dismemberment while reducing spalling in large tyrannosaurids. Finally, we posit a lepidosaur-like plesiomorphic condition for extraoral tissues in Dinosauria and expect that our results not only will provide a deeper understanding of the evolution of buccal soft tissues generally and advanced oral processing in ornithischians in particular but also, more broadly, will open new directions of research into the relationships between oral soft tissues and feeding behavior in terrestrial vertebrates with large teeth.

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SUPPLEMENTARY MATERIALS

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Supplementary Text
Materials and Methods
Figs. S1 to S4
Tables S1 to S3
References (*32*–*68*)
MDAR Reproducibility Checklist
Data S1 and S2

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Not a toothy grin

Theropod dinosaurs such as the iconic *Tyrannosaurus rex* have long been portrayed with their teeth fully visible, similar to extant crocodilians. This pattern of portrayal largely had to do with relatedness between dinosaurs and crocodilians and the relationship between tooth and jaw size. Cullen *et al*. tested hypothesized facial reconstruction in this group using histological analysis of tooth wear patterns and quantitative relationships between skull length and tooth size in both extinct and extant reptiles. Contrary to depictions that have dominated for more than a century, they found that theropods, including *T. rex*, had lips that covered their teeth, leaving them looking more like modern Komodo dragons than crocodiles. —SNV

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