

# Evolution: Much on the Menu for Ancient Crocs

Roger B.J. Benson<sup>1,\*</sup> and Pedro L. Godoy<sup>2</sup>

<sup>1</sup>Department of Earth Sciences, University of Oxford, South Parks Road, Oxford OX1 3AN, UK

<sup>2</sup>Department of Anatomical Sciences, Stony Brook University, Stony Brook, NY 11794-8434, USA

\*Correspondence: [roger.benson@earth.ox.ac.uk](mailto:roger.benson@earth.ox.ac.uk)

<https://doi.org/10.1016/j.cub.2019.06.004>

**Crocodylians are carnivores, but their extinct relatives had wider-ranging diets. A new study shows that herbivory evolved often in these animals, and that their teeth rivalled those of mammals in terms of complexity.**

Crocodylians include crocodiles, alligators, caimans and gavials. Today, there are only 27 species, all of which live in warm environments [1,2]. These armoured aquatic reptiles are predominantly predators. Their primeval appearance has caused many to regard them as ‘living fossils’ that have changed little since the time of the dinosaurs (the Mesozoic). However, fossil discoveries, especially of the past few decades, have revealed that the ancient relatives of crocodylians were much more diverse. These animals, known as crocodyliforms, did include very crocodile-like forms, but also lightly-built and probably fast-running terrestrial species, hippo-like herbivores (Figure 1A), short-snouted as well as mega-long snouted forms, and specialised terrestrial predators [3–6]. Some had highly differentiated tooth types, functionally more similar to the teeth of mammals than living reptiles (Figure 1B) [7]. This reveals a hidden history of crocodyliform diversification, one that was unexpected from the study of extant species alone. However, uncertainties about the ecology of extinct species, especially their diets, have limited our understanding of crocodyliform evolution. A new paper in this issue of *Current Biology* by Keegan Melstrom and Randall Irmis [8] provides a path towards resolving these uncertainties, using an index of tooth complexity to infer the diets of extinct crocodyliforms and to characterise their ancient diversification.

Understanding the evolutionary diversification of crocodyliforms requires at least a broad-brush knowledge of their ecology. However, interpreting the ecology of extinct animals known only from fossil skeletons is challenging. This is especially true for diet. Fossil gut contents

can show the last meal consumed by an animal that lived even hundreds of millions of years ago, but such fossils are rare [9]. So, to infer the diet of extinct species, palaeobiologists often rely on the structure of the skeleton (particularly the teeth and jaws) and on patterns of dental microwear — scratches formed by the action of food against the teeth.

Dietary interpretations are difficult for fossils that have no direct living analogues. This is the case with many extinct reptiles, including crocodyliforms. Because of this, widely-varying interpretations have been put forward, based mostly on qualitative appraisal [10] and often without statistical validation from the comparative study of living animals. Only the most obvious and extreme examples of dietary adaptation in extinct crocodyliforms have been identified with confidence. For example, some species closely resembled living crocodylians and were likely aquatic carnivores, while other species share features with large predatory dinosaurs and were likely hypercarnivores [6]. However, the many remaining uncertainties have placed core aspects of crocodyliform evolution on shaky ground.

The new study by Melstrom and Irmis [8] quantifies tooth complexity in extinct crocodyliforms using the orientation-patch-count-rotated method. This method counts the number of individual non-contiguous surfaces with distinct angular orientations as a measure of complexity. It originates from geographic information systems, where it is used for characterising landscapes, and was pioneered for the study of teeth by a previous study [11].

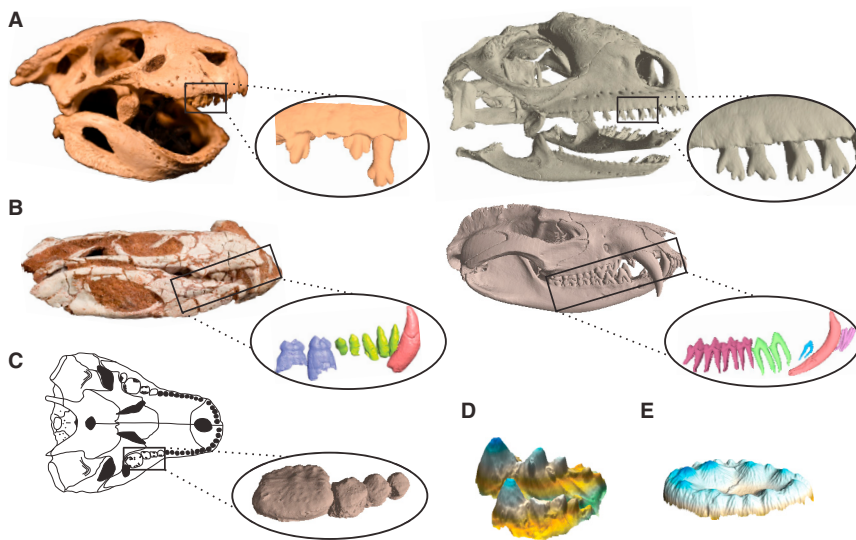
Plant tissues are difficult to digest and can require substantial pre-processing. To do this, herbivores have very complex

teeth with many and multifunctional surfaces. In contrast, carnivores have simpler teeth [11,12]. Melstrom and Irmis [8] use this relationship to test hypothesised diets of some of the most enigmatic extinct crocodyliforms. Surprisingly, they find that the teeth of extinct crocodyliforms show a diverse range of tooth complexity that is similar to that of today’s mammals: the most complex crocodyliform teeth, for example those of *Iharkutosuchus* and *Chimaerasuchus* (Figure 1C,D), are similar to those of some herbivorous mammals. Mammals are the champions of tooth complexity among vertebrates. So, this finding is particularly surprising for reptiles, and especially given the simplicity of the teeth of extant crocodylians, which mostly are simple cones for snagging prey.

The study by Melstrom and Irmis [8] firmly refutes some older hypotheses. For example, the Late Cretaceous small-bodied *Notosuchus* was previously conjectured as a possible herbivore [13] but is now found to be almost certainly carnivorous, with simple teeth. The study also confirms some previous hypotheses, such as herbivory in the Malagasy *Simosuchus*, whose dentition is very similar to that of herbivorous lizards (Figure 1A) [5,10]. It also proposes some surprising but well-supported interpretations for species that were not much discussed before. For example, strong support for herbivory was found for the protosuchid *Edentosuchus* and some of its close relatives (Figure 1E).

By taking an explicitly quantitative approach, Melstrom and Irmis [8] recognise the limits of current interpretations. Durophages (which crush hard prey) aren’t readily distinguished from omnivores or insectivores based on





**Figure 1. Mesozoic herbivorous crocodyliforms, their teeth and some modern analogues.** (A) *Simosuchus clarki* and herbivorous marine iguana (*Amblyrhynchus cristatus*). (B) *Pakasuchus kapilimai*, showing mammal-like heterodonty (tooth differentiation indicated by colours), and the Virginia opossum (*Didelphis virginiana*). (C) *Iharkutosuchus makadlii*. (D) *Chimaerasuchus paradoxus*. (E) An undescribed protosuchid (UCMP 130082). Skulls and teeth not to scale. Photos of fossils by Pedro Godoy and Patrick O'Connor (Ohio University); CT scan data made available by Roger Benson and Keegan Melstrom; *Iharkutosuchus* outline modified from [19] [www.schweizerbart.de/journals/njgpa](http://www.schweizerbart.de/journals/njgpa); teeth in (b) reprinted by permission from Springer Nature: Nature [7] © 2010; teeth in D and E from [8].

tooth complexity alone, indicating that other forms of evidence must be leveraged. This shows where other types of investigation might bear the most fruit. For example, biomechanical modelling or study of dental microwear could distinguish among food types.

By mapping their dietary inferences onto an evolutionary tree, the authors propose that herbivory evolved multiple times independently among distantly-related groups of crocodyliforms. The first occurred almost 200 million years ago, in protosuchids, a group of long-limbed small-bodied terrestrial species. Another group of crocodyliforms, the Cretaceous notosuchians, included several herbivores. Although they might represent just a single evolutionary origin of herbivory, the herbivorous notosuchians nevertheless show striking variation in the details of their tooth morphology (Figure 1A,B,D). Notosuchians as a whole also included carnivores, omnivores and insectivores, suggesting a high degree of versatility in the evolution of their diets.

Overall, a striking pattern emerges: many Mesozoic groups of crocodyliforms show far greater evolutionary variation in diet than seen in crocodylians, the group that includes all living crocodyliforms.

Crocodylian diets span narrow range, and have done so since the Mesozoic, including just durophages and carnivores [8]. They could, therefore, be regarded as evolutionarily constrained dietary specialists. Although not completely understood yet, the reduction of ecological diversity among crocodyliforms through time could involve selective extinction of the groups that once flourished during the Mesozoic during climate change and mass extinctions.

The study adds to our understanding of the general roles of crocodyliforms in Mesozoic ecosystems. Ranging from ocean-going to fully terrestrial species, from diminutive animals weighing perhaps 5 kilograms [14] to giants of 8 tonnes [15] and exhibiting varied diets [8], these crocodyliforms were interacting with other tetrapods including dinosaurs and the largest Mesozoic mammals. Nevertheless, as with their extant members, Mesozoic crocodyliforms achieved their highest diversities in warm environments at low latitudes, and were absent from high latitudes [2,16]. Furthermore, studies of bone microstructure [17] indicate slow, reptile-like growth rates. Most likely the

metabolisms of these species were more similar to those of living crocodylians than to warm-bodied mammals, birds and other dinosaurs [18]. It is therefore striking that Mesozoic crocodyliforms achieved wide-ranging ecological diversity, analogous to that of mammals or dinosaurs, whilst having an essentially reptilian physiology. This may only have been possible in the ancient greenhouse Earth, which was substantively warmer than today. Or perhaps crocodyliforms became excluded from these ecologies by the Cenozoic radiation of placental mammals. It may be some time before we know the answers.

Melstrom and Irmis [8] draw a line in the sand for crocodyliform palaeobiology, providing a firm platform from which to move forward in future studies, and will certainly stimulate further research into the crocodyliform diversification. Ultimately, this work deepens our appreciation of the spectacular evolutionary history of crocodylians and their fascinating but long-extinct relatives.

## REFERENCES

1. Grigg, G., and Kirshner, D. (2015). *Biology and Evolution of Crocodylians* (New York: Cornell University Press).
2. Markwick, P.J. (1998). Crocodylian diversity in space and time: the role of climate in paleoecology and its implication for understanding K/T extinctions. *Paleobiology* 24, 470–497.
3. Turner, A.H., and Pritchard, A.C. (2015). The monophyly of Suisuchidae (Crocodyliformes) and its phylogenetic placement in Neosuchia. *PeerJ* 3, e759.
4. Sereno, P.C., and Larsson, H.C. (2009). Cretaceous crocodyliforms from the Sahara. *ZooKeys* 28, 1–143.
5. Buckley, G.A., Brochu, C.A., Krause, D.W., and Pol, D. (2000). A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. *Nature* 405, 941.
6. Godoy, P.L., Ferreira, G.S., Montefeltro, F.C., Vila Nova, B.C., Butler, R.J., and Langer, M.C. (2018). Evidence for heterochrony in the cranial evolution of fossil crocodyliforms. *Palaeontology* 61, 543–558.
7. 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.
8. Melstrom, K.M., and Irmis, R.B. (2019). Repeated evolution of herbivorous crocodyliforms during the age of dinosaurs. *Curr. Biol.* 29, 2389–2395.

9. Godoy, P.L., Montefeltro, F.C., Norell, M.A., and Langer, M.C. (2014). An additional baurusuchid from the Cretaceous of Brazil with evidence of interspecific predation among Crocodyliformes. *PLoS One* 9, e97138.
10. Ősi, A. (2014). The evolution of jaw mechanism and dental function in heterodont crocodyliforms. *Hist. Biol.* 26, 279–414.
11. Evans, A.R., Wilson, G.P., Fortelius, M., and Jernvall, J. (2007). High-level similarity of dentitions in carnivorans and rodents. *Nature* 445, 78.
12. Melstrom, K.M. (2017). The relationship between diet and tooth complexity in living detritivorous saurians. *J. Morphol.* 278, 500–522.
13. Fiorelli, L.E., and Calvo, J.O. (2008). New remains of *Notosuchus terrestris* Woodward, 1896 (Crocodyliformes: Mesoeucrocodylia) from Late Cretaceous of Neuquén, Patagonia, Argentina. *Arq. Mus. Nac.* 66, 83–124.
14. Clark, J.M., Xu, X., Forster, C.A., and Wang, Y. (2004). A Middle Jurassic “sphenosuchian” from China and the origin of the crocodylian skull. *Nature* 430, 1021–1024.
15. Aureliano, T., Ghilardi, A.M., Guilherme, E., Souza-Filho, J.P., Cavalcanti, M., and Riff, D. (2015). Morphometry, bite-force, and paleobiology of the Late Miocene Caiman *Purussaurus brasiliensis*. *PLoS One* 10, e0117944.
16. Mannion, P.D., Benson, R.B., Carrano, M.T., Tennant, J.P., Judd, J., and Butler, R.J. (2015). Climate constrains the evolutionary history and biodiversity of crocodylians. *Nat. Commun.* 6, 8438.
17. Cubo, J., Köhler, M., and de Buffrénil, V. (2017). Bone histology of *Iberosuchus macrodon* (Sebecosuchia, Crocodylomorpha). *Lethaia* 50, 495–503.
18. Erickson, G.M. (2014). On dinosaur growth. *Annu. Rev. Earth Planet. Sci.* 42, 675–697.
19. Osi, A., Clark, J.M., and Weishampel, D.B. (2007). First report on a new basal eusuchian crocodyliform with multicusped teeth from the Upper Cretaceous (Santonian) of Hungary. *N. Jb. Geol. Paläont. Abh.* 243, 169–177.

## Transcription Regulation: Tales of a Divergent Mediator

Xiaolu Zhao and Yifan Liu\*

Department of Pathology, University of Michigan, Ann Arbor, MI 48109, USA

\*Correspondence: [yifan@med.umich.edu](mailto:yifan@med.umich.edu)

<https://doi.org/10.1016/j.cub.2019.06.033>

**Mediator is a large, multi-module complex that plays a key role in transcription regulation in eukaryotes. A divergent Mediator from a unicellular eukaryote has been identified and characterized, revealing novel adaptations to mRNA and ncRNA transcription.**

The Mediator complex is a key regulator in eukaryotes for RNA polymerase II (Pol II) transcription [1]. In addition to its classic function as a bridge between DNA-binding transcription factors and the pre-initiation complex (comprising Pol II and general transcription factors), Mediator is also involved in many other aspects of transcription, including elongation, termination, RNA processing, as well as its epigenetic regulation [2]. Mediator is most likely universally present in eukaryotes as a transcription coactivator: it is well characterized in yeasts (*Saccharomyces cerevisiae* and *Schizosaccharomyces pombe*) and mammalian cells, and also studied in *Caenorhabditis elegans*, *Drosophila melanogaster* and *Arabidopsis thaliana*, even though many of its subunits (over 20 in these species) have diverged over the course of evolution, accompanied by the emergence of species-specific subunits [3–5]. However, the eukaryotic tree of life is far from thoroughly sampled; the

divergence of Mediator and the diversity of its functions remain to be fully explored. In independent studies reported in this issue of *Current Biology* [6,7], two teams led by Jeff Fillingham and Miao Tian identified the Mediator complex in *Tetrahymena thermophila*, a ciliated protist, and characterized its roles in transcription regulation, revealing a recurrent theme with novel compositions.

Fillingham and colleagues purified proteins associated with the conserved Med31 subunit in *Tetrahymena*. They identified 10 subunits sharing sequence homology with established Mediator components in other species (named conventionally), and 13 novel subunits (named as Med31-interacting *Tetrahymena*-specific (MITS) 1–13) (Figure 1A) [6]. This composition is very similar to that described in Tian’s work, which is identified by an orthogonal approach [7]. The case for a functional *Tetrahymena* Mediator complex is further boosted by the fact that these subunits

share similar expression profiles under different physiological conditions [6] as well as their association with Pol II subunits [7] and general transcription factors like TFIIS [6]. The 10 conserved subunits are distributed in the head, middle, and tail modules, supporting a deep evolutionary origin for the large, multi-module complex (Figure 1A) [3]. However, no apparent homologues were found for the kinase module components, or the structurally and functionally important Med14 subunit (Figure 1A). Association with the kinase module, generally implicated in transcription repression, may be more dynamic or contingent on certain stimuli and/or physiological conditions, as is well-documented in yeasts and mammalian cells [1,2]; in *A. thaliana*, the Mediator core complex is also not co-purified with the kinase module subunits [8]. The apparent lack of Med14 may be due to difficulties in identifying highly divergent Mediator homologues by primary sequences alone.

