

A Review on the Evolutionary Perspective of Snout Elongation in Extant Crocodilians

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Abstract: *The evolutionary morphology of snout elongation in extant crocodilians reflects a complex interplay of ecological adaptation, biomechanical constraints, and phylogenetic history. This review explores how craniofacial variations categorized into semi-altirostral, longirostral, platyrostral, and brevirostral morphotypes correlates with foraging strategies, hydrodynamic requirements, and habitat specialization. Emphasis on convergent and parallel evolution of longirostry and brevirostry across monophyletic and non-monophyletic lineages is also provided. Comparative biomechanical stresses and von Mises factors also highlighted for differences in bite force distribution between snout morphologies. Longirostrals show adaptations for ichthyophagy, while brevirostrals demonstrate secondarily derived traits largely suitable for terrestrial crushing of prey. We hypothesize that post-Cretaceous ecological filtering and spatio-trophic competition with dominant reptilian clades including Theropods shaped the morphological stasis and niche conservatism observed in extant Esuchians. Moreover, paleoenvironmental shifts during the Cenozoic further constrained the range and diversity of crocodilians. Despite their retention of plesiomorphic body plans, crocodilians demonstrate key evolutionary innovations in jaw shapes enabling resource partitioning and survival through mass extinctions. This review also synthesizes evolutionary ecology and biomechanical informations to propose a power cascade jaw width expansion in clade Crocodylia.*

Keywords: craniofacial morphology, longirostry, brevirostry, convergent evolution, power cascade model

1. Introduction

The clade Archosauria (the ruling reptiles) includes the Crurotarsal lineages, largely defined by a distinct ankle morphology in which a hemicylindrical condyle on the calcaneum bone articulates with a concave astragalus. This configuration, where the calcaneum forms a stout lever to ventroflex the pes, is characteristic of the extant Eusuchians, the only surviving lineage within the Order Crocodylia [11]. These reptiles are recognized by their secondary palate an apomorphic trait, thecodont dentitions, heavily covered body armours (osteoderms) and are currently represented by 27 valid taxa, inhabiting swamps, marshes, rivers, lagoons and even marine habitats. Largely distributed across central and south America, Africa, India, parts of Asia, the Malay Archipelago and Australia. The Family Gavialidae includes monotypic genera such as *Gavialis* sp. and *Tomistoma* sp. the Family Crocodylidae encompasses genera like *Crocodylus* spp., *Osteolaemus* spp., and *Mecistops* spp. while *Alligator* spp., *Caiman* spp., monotypic genus *Melanosuchus* sp. and *Palaeosuchus* spp. belongs to the family Alligatoridae.

Evolutionary Perspective

One of the most intriguing aspects of archosaurian evolution is associated with variation in locomotive postures depending on different osteological tarsal joint types and craniofacial morphology, both these traits are closely tied to ecological adaptation. The transformation of locomotive postures and skull shape particularly elongation of rostrum are traits that evolved independently in multiple archosaurian lineages,

likely in response to acquisition of vacant eco-spaces for the utilization of resources, niche partitioning and ecological competition over the past 230 million years of their evolutionary history. The early archosauria including Triassic Pseudosuchians exhibited oreinirostral cranium where the length is lesser than its width, perhaps more advantageous for facultative bipedal or quadrupedal semi erect gaits and terrestrial foraging. In contrast, later Eusuchians displayed an accelerated rate in craniofacial disparity, indicating an evolutionary radiation linked to aquatic specialization along with dietary shifts [1,2,5,11].

In evolution the spatio-trophic acquisition of vacant eco-spaces often drives specialization among species over time intra or interspecific competition for resources may ultimately lead to trait divergence, adaptive convergent evolution and character displacements. Thus, it is hypothesised that early Eusuchians in their evolutionary origin and diversification in the Cretaceous (125-100 million years ago) encountered intense resource competition in volcanogenic terrestrial landscapes from the already established much older clade the non-avian Dinosauria which were largely terrestrial and evolving from mid Triassic some 240 million years ago. The dominance, minor extinctions and diversification of dinosaurs throughout the Cretaceous (145-66 million years ago) largely shaped by geographic isolation (allopatric speciation), vicariant events (plate tectonics) and dispersals likely influenced the evolutionary trajectory of Eusuchians. The terrestrial competition and the extinction of various

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Neosuchian lineages might have forced Eusuchians into semi-aquatic or amphibious niches [4, 8,9,10,11].

After the extraterrestrial catastrophic event which eliminated the dominant terrestrial, volant and marine reptiles (non-avian Dinosaurs, Pterosaurs, Plesiosaurs and Mosasaurs) in the end Cretaceous, 66 million years ago (K-Pg mass extinction), the much smaller creatures those are ecologically more adaptive to sustain mass extinction such as Squamata reptiles, mammals and birds rapidly evolved and diversified to fill the newly vacant niches. While Eusuchians faced selective ecological pressures on terrestrial ecosystems with limited phenotypic plasticity, likely retained plesiomorphic traits optimized for semi-aquatic life [4, 8, 9, 10, 11].

Despite retaining ancestral body plans, extant Eusuchians exhibit notable craniofacial disparity which is more hydrodynamic and also reflects adaptations for specific foraging strategies. The cranio-kinesis (craniostylic jaw suspension) in modern Crocodylians where bite forces are transferred from the snout tip inward while catching and engulfing prey the von Mises stress occurs at the middle of maxilla and mandible. In longirostral forms bite force at the tip of snout is reduced due to mechanical disadvantages. In Crocodylids median von Mises stress is highest in the lower jaw than the upper jaw which dissipates posteriorly. Thus, reduction of skull depth from oreinirostral to longirostral craniofacial morphology is a key innovative adaptive trait not only restricted to Eusuchians but also independently evolved as character convergence among several Spinosauroid lineages of Theropod dinosaurs for specialized dietary preference such as Ichthyophagy which further allowed them to reduce intense spatio-trophic resource competition with other Theropods [2,4,5,6,7,8,10,11].

Extant Crocodylians

The modern Crocodylians displayed further modifications in skull morphology largely associated with their foraging ecology and hydrodynamic structures helps them to move efficiently in water. Here we categorise them into semi altirostral (e.g. *Crocodylus* spp.), longirostral (*Gavialis* sp. *Tomistoma* sp. and *Mecistops* spp.) platyrostral (*Alligator mississippiensis*) and brevirostral (*Osteolaemus* spp., *Caiman*

spp., *Melanosuchus* sp., *Palaeosuchus* spp. and *Alligator sinensis*).

We hypothesize that longirostry in *Gavialis* sp. and *Tomistoma* sp. is an example of parallel trait evolution, driven by similar environmental pressures and ichthyophagus diets in similar ecological niches but in different geographical areas; *Crocodylus* spp. display broader ecological plasticity while *Mecistops* spp. remained niche conservative being ichthyophagous. Whereas several Caimaninae genera have independently evolved brevirostry as their dietary preference varies from large to medium size fishes in south American river system, while *Osteolaemus* spp though also brevirostral have secondarily adapted to a terrestrial cave dwelling life as their short snouts are much more efficient to catch much agile bats (chiropterophagy) a notable case of convergent trait evolution. Although congeneric *Alligator mississippiensis* is platyrostral while *Alligator sinensis* is brevirostral. Among many taxa species retained more ancestral plesiomorphic traits through phylogenetic conservatism and these traits sustained through long evolutionary time as long as its beneficial for survival as platyrostry in *Alligator mississippiensis* an evolutionary advantage to reduce resource competition with more generalist American Crocodile *Crocodylus acutus*. The geographic isolation through allopatric speciation lead *Alligator sinensis* to be much more specialist in Chinese swamps to feed on hard shelled Crabs, Molluscs and Crustaceans. It is also noted that in the closely related sympatric taxa specialization in resource use may have led to character convergence enabling niche partitioning and species coexistence [1,2,5,6,7].

We propose that semi-altirostral and platyrostral forms are hydrodynamically favourable for prey capture in water as well as to drag larger prey from lands. longirostral jaws are optimized for fish capture, while brevirostry enhances bite forces at the mid-point of upper and lower jaw (maxilla and mandible) ideal for seizing agile or hard-shelled prey, especially on land. A log exponential power cascade model for expanding jaw width from the tip to the base may further clarify the current review (Fig. 1, 2, 3) [3].

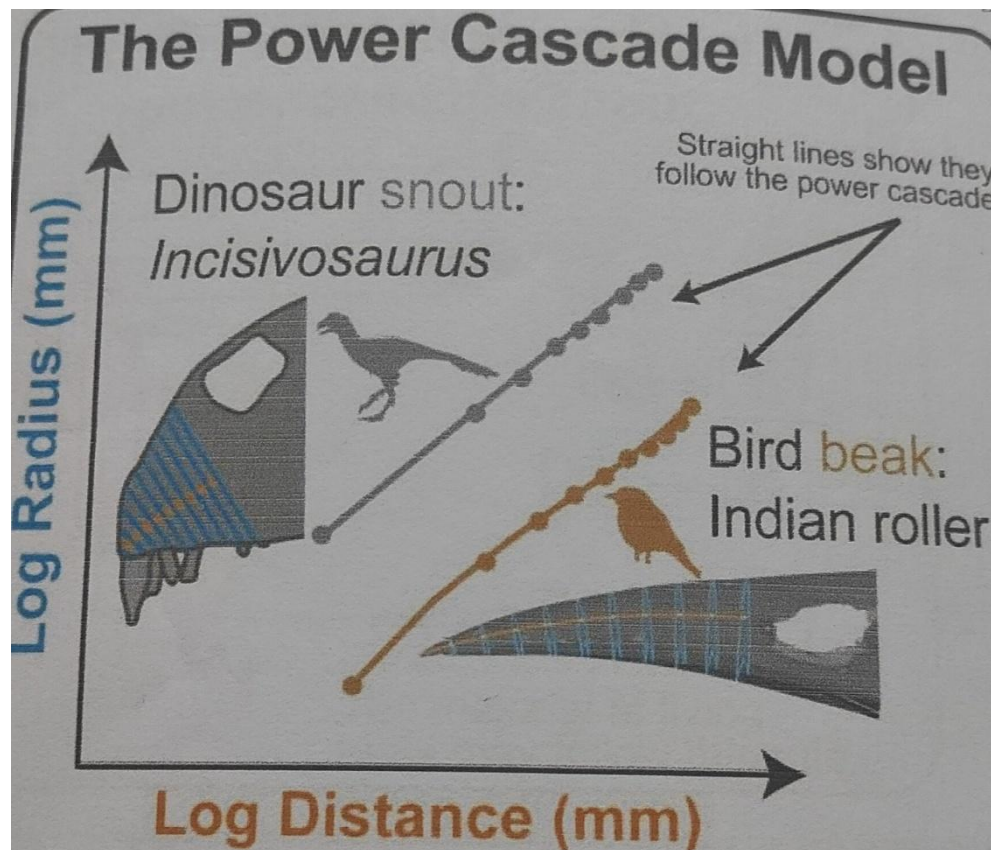


Figure 1: Rostrum of Maniraptoran Oviraptorosaurid Dinosaur *Incisivosaurus gautheieri* from China and beak of modern birds follow the hypothetical log exponential power cascade model where the width of jaw increases from tip to the base after Garland et.al. 2025 [3].



Figure 2: The semi-altirostral skull of salt water crocodile *Crocodylus porosus* supports log exponential model of jaw widening from the tip of snout to the base (Courtesy of Indian Museum, Calcutta, West Bengal, India).



Figure 3: The longirostral skull of freshwater Indian Gharial *Gavialis gangeticus* an exception of power cascade model and its dietary specialization supports this species to coexist in sympatry with generalist *Crocodylus palustris*. (Courtesy of Indian Museum, Calcutta, West Bengal, India).

2. Conclusions

While the crocodilians closest phylogenetic relatives the birds diversified through key innovative evolutionary traits such as gradually attaining body insulation as well as endothermy, modifications of forelimbs into wings for powered flights and different beak structures for foraging in diverse ecosystems, crocodilians retained a more ancestral morphology, during the Eocene-Oligocene and Miocene (55-24 million years ago) the climatic shifts towards global cooling resulted in spatio-temporal changes in habitats as well as habitat shrinking impacted on many of the crocodilian species to decline. The Pleistocene Interglacial period (1.8 million years ago) during the last ice age crocodilians suffered intense trophic resource crunches along with competition, which perhaps compelled many species to decline particularly in northern hemisphere.

However, their ectothermic metabolic rate as well as heliothermic body physiology allowed them to thrive in much

warmer parts of the globe and gradual ontogenetic craniofacial disparity enabled them to utilize a wide range of trophic resources these are the key survival strategies to outcompete dinosaurs and still surviving today, where crocodilians are still dominant predators such as in Central America, Africa and Australia may even offer powerful competition to mammals and birds. The iconic examples include the solitary *Alligator mississippiensis*, the gregarious massive African *Crocodylus niloticus* while the undisputed largest living reptiles the Australian salt water crocodile *Crocodylus porosus* which may grow over 7 meters in length, inhabit in brackish water lagoons have already invaded into oceans. With lifespans exceeding 100 years for many species, crocodilians have endured through massive ecological upheavals and mass extinctions. However, ongoing threats from habitat destruction, poaching for skin and anthropogenic climate change and global warming largely affecting on their breeding biology as the sex determinations of the hatchlings is largely dependent on atmospheric temperature (TSD)

which is intensely challenging their survival in the face of what may be the Earth's Seventh Mass Extinctions.

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References

- [1] Walter JD, Massonne T, Paiva ALS, Martin JE, Delfino M, Rabi M. Expanded Phylogeny elucidates *Deinosuchus* relationships, crocodylian osmoregulation and body-size evolution. *Comm Bio*. 2025; 8:611:1-12.
- [2] Ballell A, Moon BC, Porro LB, Benton MJ, Rayfield EJ. Convergence and functional evolution of Longirostry in Crocodylomorphs. *Paleontology*. 2019:1-21.
- [3] Garland KLS, Hay EM, Field DJ, Evans AR. Common developmental origins of beak shapes and evolution in theropods. *iScience* 2025; 28:1-10.
- [4] Brusatte SL, Benton MJ, Ruta M, Lloyd GT. The first 50Myr of dinosaur evolution: Macroevolutionary pattern and morphological disparity. *Biology Letters* 2008; 4:733-6.
- [5] Ballell A, Moon BC, Porro LB, Benton MJ, Rayfield EJ. Data from: Convergence and functional evolution of longirostry in crocodylomorphs. *Dryad Digital Repository*.
- [6] Erickson GM, Gignac PM, Stepan SJ, Lappin AK, Vliet KA, Brueggen JD, Inouye BD, Kledzik D, Webb GJW. Insights into the ecology and evolutionary success of crocodilians revealed through bite-force and tooth-pressure experimentation. *PloS One* 2012;7: e3178.
- [7] McHenry CR, Clausen, PD, Daniel WJT, Meers MB, Pendharkar A. Biomechanics of the rostrum in crocodilians: a comparative analysis using finite element modelling. *Anatomical Record Part A* 2006; 288A:827-849.
- [8] Bernardi M, Gianolla P, Petti FM, Mietto P, Benton MJ. Dinosaur diversification linked with the Carnian Pluvial Episode. *Nature Communications* 2018; 9:1499:1-10
- [9] Mukherjee D. A brief introduction: origin and evolution of Squamate Reptiles. *International Journal of life Sciences Research* 2014; 2:8-10
- [10] Benton MJ, Forth J, Langer MC. Models for the rise of the Dinosaurs. 2014; 24:87-95
- [11] Benton MJ. *Vertebrate Palaeontology*. Blackwell Publishing Ltd. UK; 2005