

THE EVOLUTION OF FACIAL KERATIN AND TOOTH DISTRIBUTION:
IMPLICATIONS FOR THE COEVOLUTION OF
TRAITS IN DINOSAURS

by

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GLOSSARY

- **Edentulism:** Toothless condition in the jaws of vertebrates acquired through evolution. This term is sometimes used for specific jawbones. For this study, this term will be used to refer to either the lower jaw or the upper jaw without teeth.
- **Beak:** In archosaurs, it refers to a simple jaw structure consisting of rostral porous jawbones and a horny covering over them. It mainly allows these animals to hold and manipulate objects, like food, from their environment. Identification of this structure in fossils requires finding grooves, and pits of the rostral side [Witton, 2013]. Additionally, the vestigial tooth alveoli of rostral end of jawbones occur in oviraptors and possibly all beaked theropods [Wang et al., 2017c].
- **Diastema:** A space or gap between teeth of the same toothrow.
- **Keratinous cover:** A horny covering in the rostral jawbones of an animal confined to the facial surface, maybe all or just the most rostral portion, or may also include the lingual segment of the jaw. This definition allows for the inclusion of a “true beak”, which is referred to as a “toothless” structure. Identifying this structure in fossils requires finding grooves and patches of foramina on the facial surface of the most jawbones rostral (Fig. 1,2,3,6, 7).

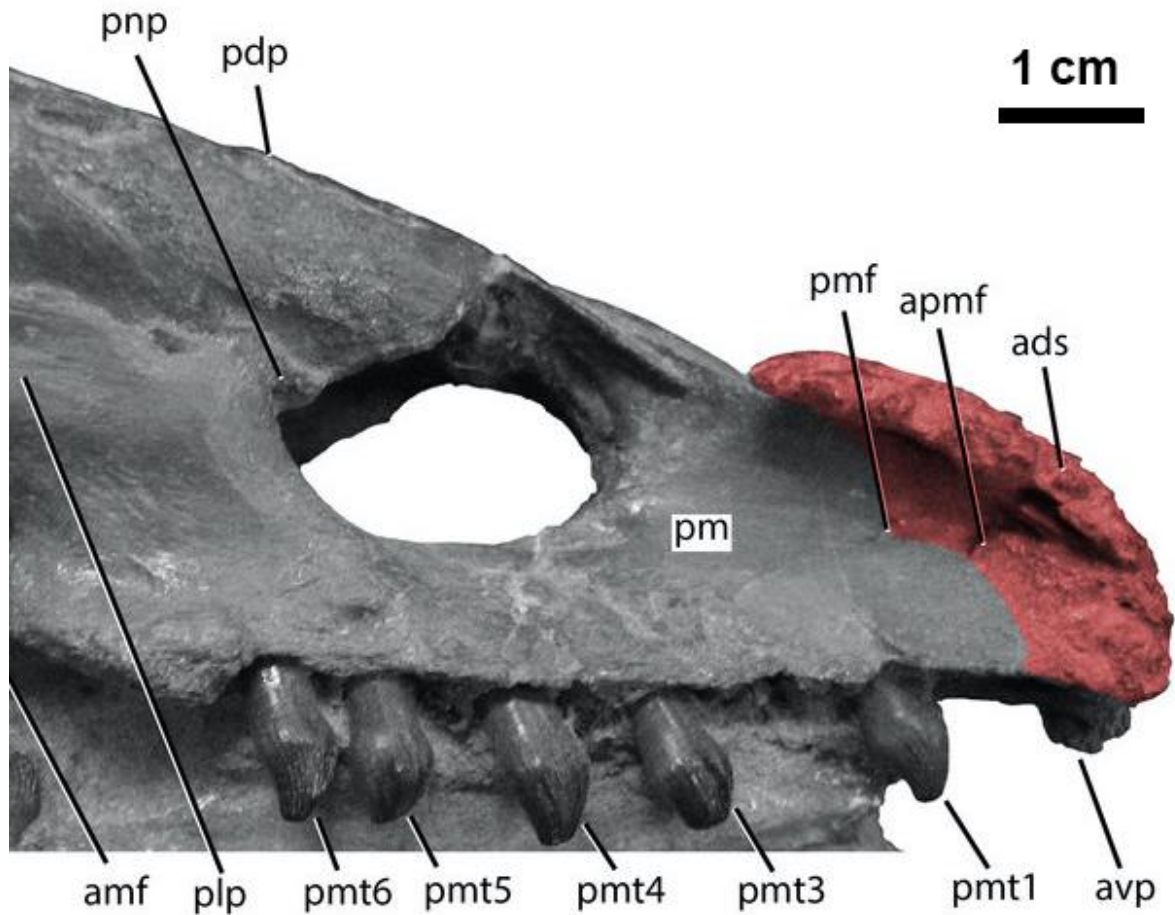


Fig. 1. Facial grooved surfaces with patches of foramina at the tip of the upper jaw (red) identified as proxies for keratinous cover of *Thescelosaurus neglectus* NCSM 15728. Image modified from Boyd [2014]. Abbreviations: ads, anterodorsal shelf of premaxilla; amf, anterior maxillary fossa; apmf, anterior premaxillary foramen; avp, anteroventral tip of premaxilla; pdp, posterodorsal process of the premaxilla; plp, posterolateral process of premaxilla; pm, premaxilla; pmf, premaxillary foramen; pmt, premaxillary tooth/teeth; pnp, premaxillary narial process. Scale bar, 1 cm.



Fig. 2. Facial grooved surfaces with patches of foramina at the tip (red) identified as proxies for keratinous cover of *Camarasaurus* BYU 24688 upper jaw (above) and lower jaw (below). Scale bars, 10 cm.

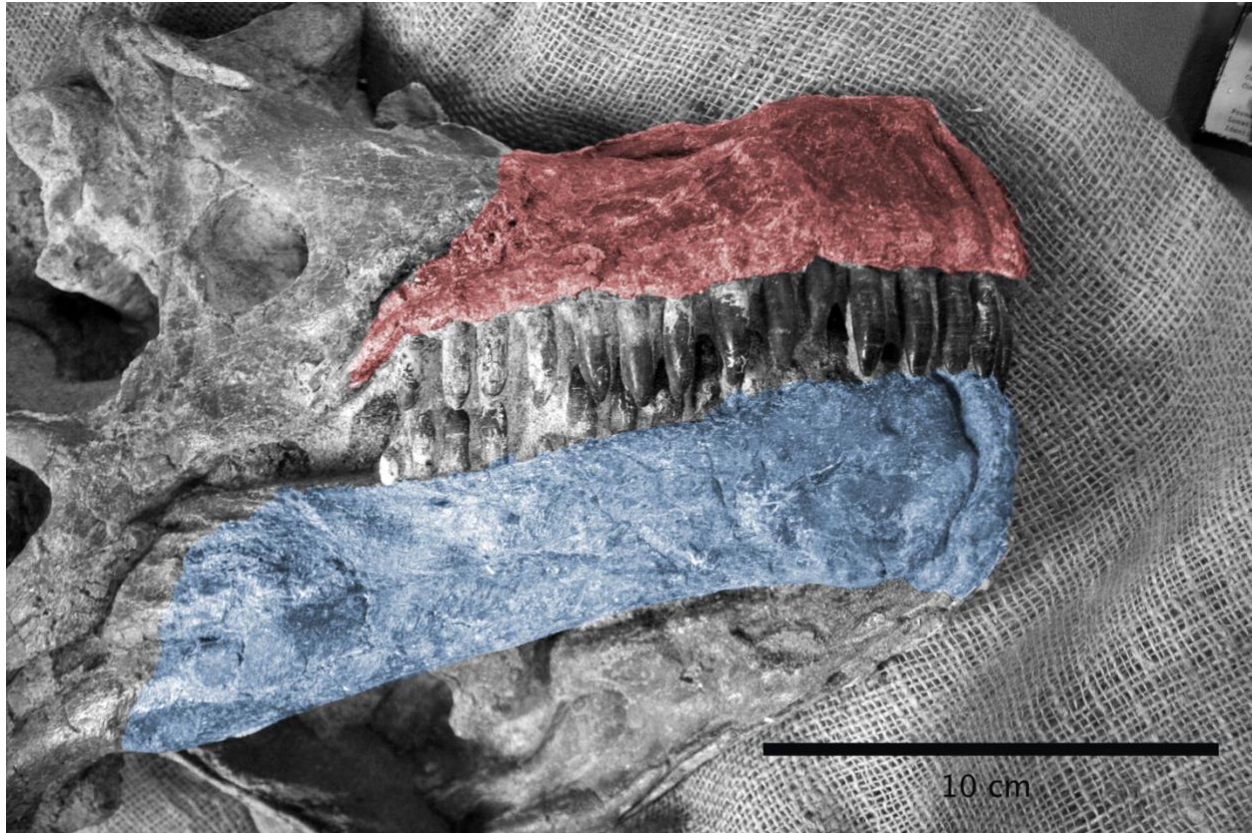


Fig. 3. *Abydosaurus mcintoshi* DINO-16488 skull with grooved surface (red) identified as proxies for keratinous cover in upper jaw and hummocky surface (blue) identified as a proxy for flat facial scales in the lower jaw. Scale bar, 10 cm.

- **Facial:** Refers to the external surface of the face. It includes the labial side of the snout and the area surrounding the ears and eyes (Fig. 4A).
- **Flat facial scales:** Specialize scales on the rostral side of living crocodilians [Hieronymus et al., 2009]. They cover the hummocky jaw surface with rows of foramina (Fig. 5) in crocodiles and are interpreted to have existed in tyrannosaurids [Carr et al. 2017].
- **Labial:** Anatomical term referring to the side of the tooth or mouth that faces the lips or any other facial skin close to the jaws (Fig. 4B) [DeMar, 2013].

- **Lingual:** Anatomical term referring to the side of the tooth or mouth that faces the tongue (Fig. 4B) [DeMar, 2013].

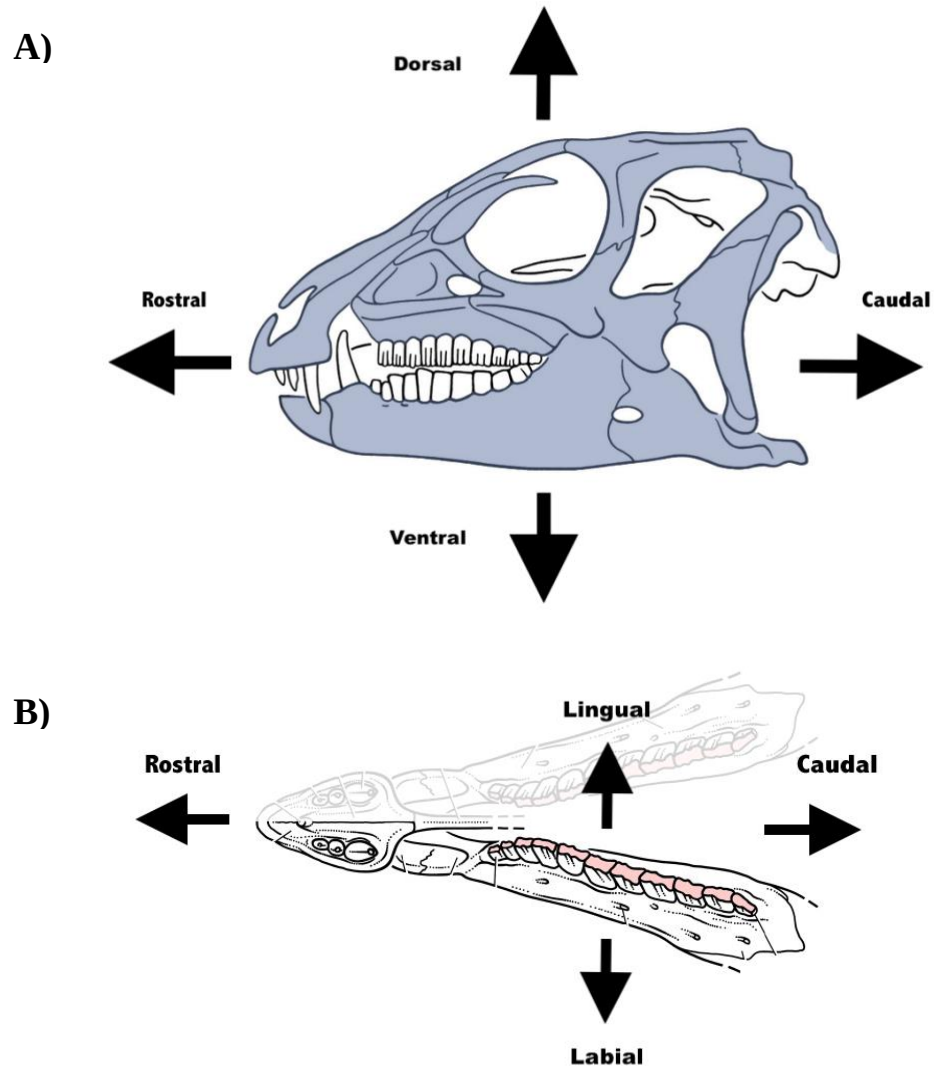


Fig. 4. Modified drawings of *Heterodontosaurus tucki* taken from Sereno [2012]. A) Facial surface of skull highlighted in blue. B) Lower jaw in dorsal view.

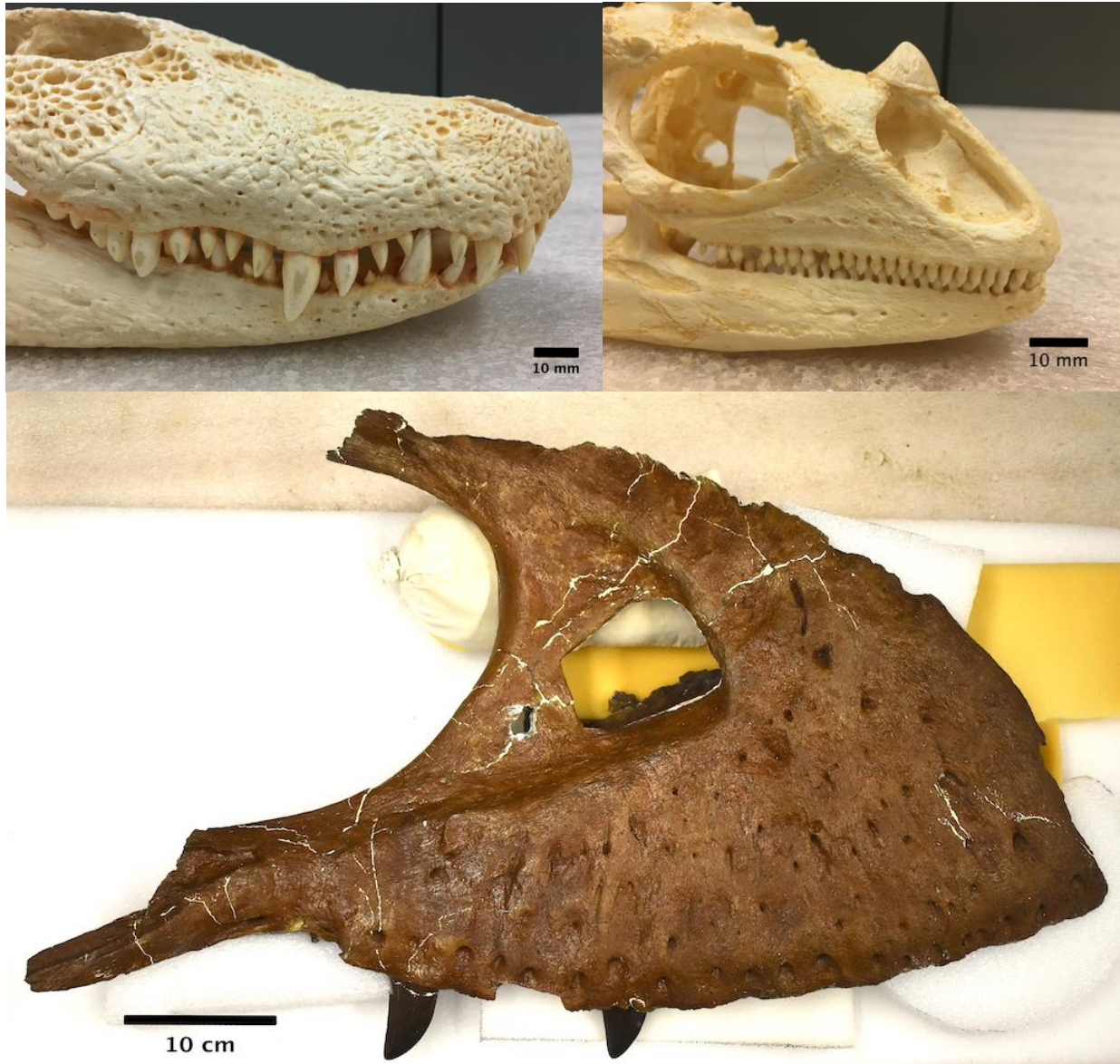


Fig. 5. Examples of facial hummocky jaw surfaces identified as proxies for flat facial scales. From top left to right: *Caiman latirostris* skull replica MOR-OST-872, *Cyclura cornuta* skull replica MOR-OST-257, and *Tyrannosaurus rex* maxilla MOR-1125. Scale bars at 10 mm (upper images) and 10 cm (lower image).

- **Rhamphotheca:** A horny sheath covering [Louchart & Viriot, 2011] or keratinized epidermis [Sturkie, 2012] in the most rostral jawbones of tetrapods. This definition can also be applied when talking exclusively of the upper or lower jaw, but most papers relating to avian and non-avian theropod beak evolution require that it must cover both

the facial and lingual sides, thus disrupting tooth development and forming a “beak”.

This structure has been inferred in fossils from a mosaic of patterns of grooves and pits on the jawbone surface (Fig. 6, 7) [Knusten, 2007; Hieronymus et al., 2009; Witton, 2013] and, in some groups, closure of blood vessel canals, which give nutrients to teeth [Wang *et al.*, 2017c]. However, the grooves tend to have a smoother appearance than the hummocky surface in crocodilian and tyrannosaurids [Carr et al., 2017].



Fig. 6. Example of facial grooved surfaces with foramina identified as proxies for a keratin covers in *Confuciusornis sanctus* skull BMNH-C-98.6 highlighted in yellow. Image modified from Chiappe & Qingjin [2016]. Specimen scale bar data unavailable.

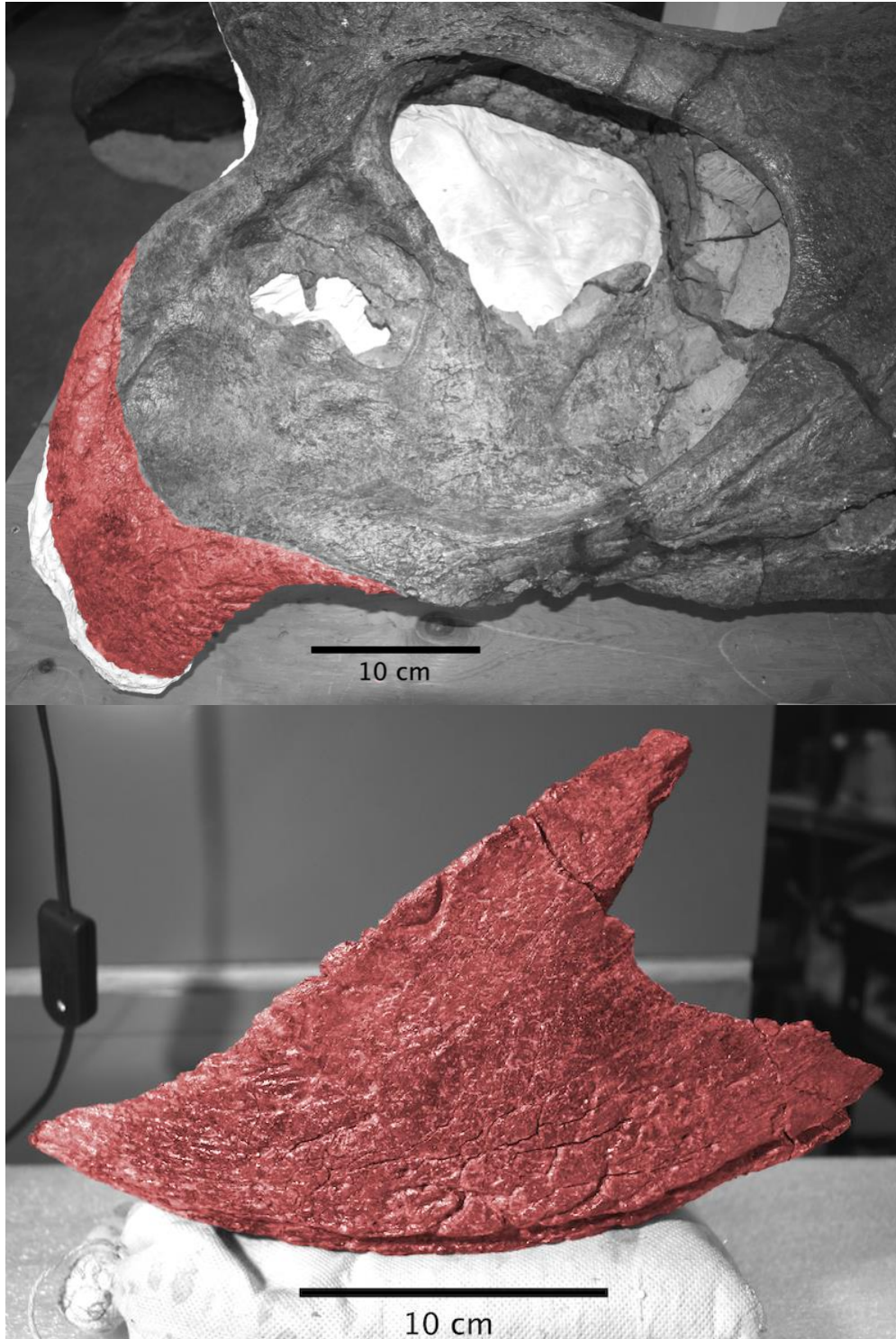


Fig. 7. Example of facial grooved surfaces identified as proxy for keratin covers (red) in *Triceratops prosus* MOR 1604 upper jaw and predentary. Scale bars, 10 cm.

ABSTRACT

Research on birds indicates that the occurrence of beak keratin and teeth are mutually exclusive, and both traits are widely distributed across Dinosauria. The macroevolution of the antagonistic relationship between keratinous beaks and teeth has only recently been explored, and these studies focus on Aves and non-avian Coelurosauria. Currently, many hypotheses posit an adaptive advantage for the trade-off of these two traits but have not been tested on a macroevolutionary scale. Examples in non-coelurosaurian dinosaurs and non-adaptive alternatives, such as trait evolution correlation and phylogenetic history, have yet to be explored thoroughly.

This study assesses the current evolutionary assumptions of beak-like keratin and tooth distribution across dinosaurs using recently-developed variable rate phylogenetic comparative methods. The diagnostic bone surface used as a proxy for the keratin cover in fossil jaws is smooth grooved textures with foramina at the jaw tips. The effect of a keratin cover on the tooth distribution within individuals is tested with Markov Chain Monte Carlo (MCMC) multinomial regression models. Coevolutionary rates for these structures are evaluated with Bayesian RJ-MCMC algorithms. The best-fit model is determined using Bayes Factors. The taxonomic breadth increased the evolutionary sample size and thus analytical power but forced a simplified coding scheme for beak and tooth traits.

My analysis shows that the presence of a keratin cover influences the evolution of partial tooththrow reduction but not complete tooth loss. Another factor could have driven the evolution of toothless beaks in some dinosaurs. In addition, the evolution of a reduced tooththrow only precedes the presence of a keratin cover in the Theropoda lineage. Furthermore, the evolutionary rate of tooththrow distribution was higher and more diverse when a keratin cover was absent; this suggests that the keratin cover imposes a functional constraint on tooth diversity at macroevolutionary scales.

INTRODUCTION

Across the broad history of animals, diverse jaw structures have evolved for obtaining food. About two-thirds of extant tetrapod species use teeth, and the rest (birds and turtles) have beaks by which they process food. Because mouths function for eating and object manipulation, beaks and teeth may undergo antagonistic coevolution [Louchart & Viriot, 2011]. This hypothesis is supported by avian genetic and developmental biology studies that demonstrate irreversible tooth loss as the beak keratin (the rhamphotheca) expands from a simple egg tooth (caruncle) to a full sheath [Harris et al., 2006; Bhullar, 2016; Wang et al., 2017c].

The rhamphotheca is the keratinized epidermis or sheath covering the upper and lower jaws of extant birds [Sturkie, 2012; Wang et al., 2020] and turtles [Wyneken & Witherington, 2001; Davit-Béal, 2009], both of which lack teeth. Other vertebrates have been classified as “beaked” or “billed”, but these are analogous structures. Tetradontiform fish possess fused teeth that form a “beak-like” structure [Fraser et al., 2012]. Among mammals, the snouts of monotremes are fleshy electrolocation organs resembling the “bills” of birds. In particular, modern platypus “bills” only contain keratin as plates that replace molars in adulthood [Musser & Archer, 1998]. For this study, the presence of a beak or a keratin cover is limited to animals that have direct or indirect evidence of beak-like keratin on the facial side of the jawbones.

The fossil record of primitive bird groups and close relatives exhibit various trends of teeth distribution in the presence of facial keratin at the rostral tips of the jaws [Louchart & Viriot, 2011], with some possible overlap in rare cases [O’Connor, 2020]. Research on birds and non-avian theropods suggest that they independently evolved edentulous beaks [Brocklehurst &

Field, 2021; Elzanowski, 1974; O'Connor, 2020; Wang et al., 2020; Brocklehurst & Field, 2021].

No formal study has explored the macroevolutionary relationship of beak-like keratin and tooth distribution across Dinosauria. However, the fossil record of other non-avian dinosaurs suggests a controversial and complex relationship between these traits: teeth coexist with rhamphotheca-like keratin in the same rostral bones in some primitive sauropodomorphs, sauropods, and ornithischians. The research presented in this thesis aims to explore this taxonomic diversity to test hypotheses about the evolution and coevolution of teeth and beaks.

Teeth Diversity and Biology in Vertebrates: Summary

True teeth are credited to have expanded vertebrate niche exploitation and thus vertebrate diversity [Pough et al., 2009; Bertin et al., 2018] —a tooth consists of a pulp cavity, an inner sheath of dentine and an outer sheath of enamel or enameloid [Davit-Béal, 2009]. Edentulous jaws probably restricted early jawed fishes, primitive gnathostomes, to suction feeding [Reif, 1982; Pough et al., 2009]. The oral processing and handling of food became possible once teeth arose [Reif, 1982; Pough et al., 2009] because teeth are one of the hardest structures in the body [Bertin et al., 2018]. Changes in tooth shape, size and distribution determine an animal's diet [Huysseune & Sire, 1998; Davit-Béal, 2009]. Some tetrapods would later evolve toothless jaws thus handling and food digestion was done by other means, such as having beaks [Louchart & Viriot, 2011], gastric mills [Zanno & Makovicky, 2011; Button & Zanno, 2020], baleen [Davit-Béal, 2009] and stronger chemical digestion [Button & Zanno, 2020].

The evolutionary relationship between dentine, enamel and enameloid is still heavily debated due to doubts regarding homology in the fossil record. Enameloid is not present in

tetrapods [Pough et al., 2009]. Both dentin and enamel might be vertebrate synapomorphies since conodonts, which are stem vertebrates, seem to have them in their dermal bone [Smith, 1995]. However, a recent study revealed that dentine and enamel were absent in basal conodonts thus their “teeth-like” bony elements are analogous to that of other vertebrates [Murdock et al., 2013]. True teeth evolved in vertebrates 450 million years ago in stem gnathostomes [Reif, 1982; Donoghue, 2002; Donoghue & Sansom, 2002; Donoghue et al., 2006; Davit-Béal, 2009].

Tooth attachment tissue types (cementum, periodontal ligament, and alveolar bone) is consistent in amniotes whereas tooth implantation shifts frequently across the clade [Bertin et al., 2018]. Thecodont dentition (teeth in deep sockets) or subthecodont dentition (teeth in shallow sockets with lingual jaw wall lower than labial wall) might have been ancestral to all amniotes [LeBlanc & Reisz, 2013; Bertin et al., 2018]. Along the Eureptilia line some taxa would evolve acrodont dentition (without groove or tooth alveoli attachment) and pleurodont dentition (teeth in sockets with labial wall while lingual wall might be absent) [Edmund et al., 1969; Zaher & Rieppel, 1999; Jenkins et al., 2017; Bertin et al., 2018]. Mammals and archosaurs have thecodont dentition, but independently evolved teeth no longer attached directly to the bone jaw [Bertin et al., 2018]. Tooth-alveoli attachment was thus via the periodontal ligament [Bertin et al., 2018].

Lifetime continuous replacement of teeth (polyphyodonty) is thought to have been ancestral to Amniota [Berkovitz, 2000; Pough et al., 2009; Bertin et al., 2018] but variations of polyphyodonty exist through this clade. Tooth replacement migration could happen either vertically or horizontally, in some non-mammalian synapsids [Crompton, 1972; Sues, 1985; Luo et al., 2004; Bertin et al., 2018], through the jaws. In addition, single replacement of teeth (diphyodonty) evolved in mammaliaforms [Luo et al., 2004; Bertin et al., 2018] while most

acrodont lepidosaurs do not replace teeth at all (monophyodonty) [Cooper et al., 1970; Kieser et al., 2009; Dosedělová et al., 2016; Bertin et al., 2018].

Evolutionary Shift in Theropods and Ontogenetic Shift in Dinosaurs: Summary

A wealth of research on theropod evolution has revealed numerous instances of keratin expansion and tooththrow retraction (Fig. 8, 9). For example, rostral edentulous keratinous tips evolved somewhere within ornithuromorph birds and later expanded caudally while different evolutionary patterns characterize tooth reduction [Bhullar et al., 2016; Field et al., 2018]. A fully edentulous beak evolved three times in this group: *Archaeorhynchus*, *Schizooura*, and crown birds [Brocklehurst & Field, 2021]. In other avialans, beaks evolved once or twice in enantiornithines [Elzanowski, 1974; O'Connor, 2020], and an edentulous beak evolved once in the ancestor of Confuciusornithidae [Wang et al., 2020; Brocklehurst & Field, 2021]. Beaks evolved four times in the non-avian theropods, including the ornithomimosaurs, oviraptors, at least one ceratosaur, and therizinosaurs [Wang et al., 2020].

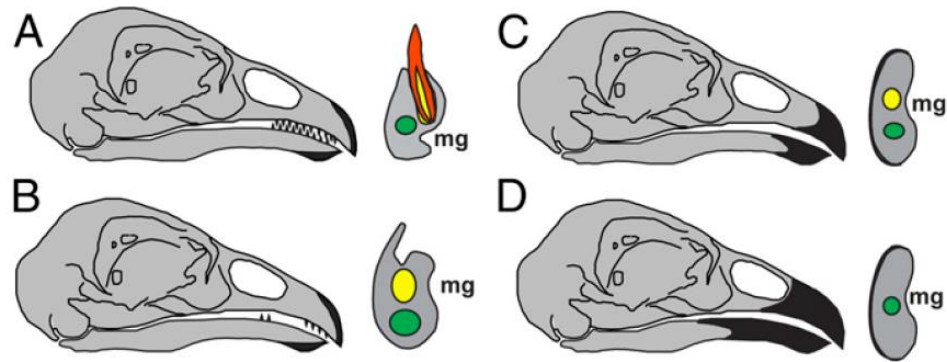


Fig. 8. Evolution of jaw anatomy in theropods. A) Plesiomorphic tooth development with an apomorphic keratinous cover (black) on the labial surface of the rostral portion of the jaws. B) Tooth growth suppressed where vestigial tooth alveoli are located and thus start creating gaps in toothrow. C) Jaws become edentulous and keratin cover becomes a rhamphotheca (black). D) The rhamphotheca expands caudally on both jaws. Orange, tooth; yellow, alveolus; green, mandibular canal; gray, bones; mg, Meckelian groove. Image taken from Wang et al. 2017c.

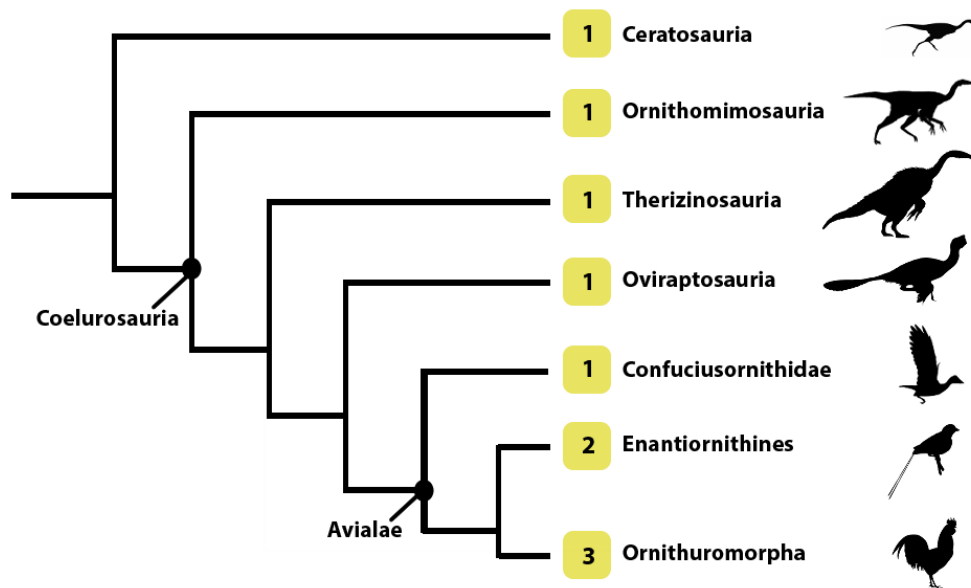


Fig. 9. Simplified phylogeny of theropod dinosaurs taken from Wang et al. 2020. Yellow squares have the number of independent cases of beak evolving in each taxon [Brocklehurst & Field, 2021; Elzanowski, 1974; O'Connor, 2020; Wang et al., 2017b; Wang et al 2017c; Wang et al., 2020; Brocklehurst & Field, 2021]. Silhouettes from *Phylopic.org* [2020-2021]: Ceratosauria (V. V. Sinkkonen); Ornithomimosauria (C. Dylke); Therizinosauria (FunkMonk); Oviraptorosauria (E. Willoughby); Confuciusornis (S. Hartman); Enantiornithines (M. Martyniuk); Ornithuromorpha (S. Traver).

Facial Keratin Reconstructions

Facial tissue reconstruction in extinct dinosaurs has been based on osteological landmarks, bone thickness, and comparison to modern reptiles and birds. The rhamphotheca, in particular, has been inferred from a mosaic of patterns of grooves and pits on the jawbone surface (Fig. 6, 7) [Hieronymus, 2010; Witton, 2013], and closure of blood vessel canals which give nutrients to teeth [Wang et al., 2017c; Wang et al., 2018]. However, the associated grooves tend to have a smoother appearance compared to the hummocky surface in crocodylians and tyrannosaurids (Fig. 5), and foramina are not parallel rows to the teeth [Carr et al. 2017]. In crocodylians, this surface supports flat facial scales [Hieronymus et al., 2009]. Nevertheless, controversy remains when inferring the existence and extent of the rhamphotheca when teeth are present [Sereno, 2007; Falk et al., 2019; O'Connor et al., 2020].

The caudal extension of the rhamphotheca in modern bird skulls does not have an osteological correlate [Zheng et al., 2020]. Jawbone foramina count is unreliable as a rhamphotheca proxy because it varies greatly among extant bird species [Morhardt, 2009]. Reconstruction of rhamphotheca is therefore difficult because jaws with both a rhamphotheca-like keratinous cover and teeth lack consistent proxies. For instance, in avialans and ornithischians, the edentulous jaw tip is the “beak”, whereas the toothed caudal portion is thought to lack a rhamphotheca.

In situ preservation or molds of rhamphotheca are extremely rare. An example of preserved beak keratin is known from a confuciusornithiform fossil [Falk et al., 2019] and a rhamphotheca mold in an *Edmontosaurus* skull [Black, 2012].

Examples where rhamphotheca and teeth might co-occur includes the enantiornithean *Falcatakely forsterae* [O'Connor et al., 2020], several groups within sauropods and basal sauropodomorphs, and some ornithischians. The *Falcatakely* upper jaw resembles the beak of extant toucans (Ramphastidae) with a long and high maxilla and a small premaxilla. This condition is unusual because the maxilla has the osteological proxies for rhamphotheca, but the premaxilla still has a tooth attached to it rostrally.

Probable cases of teeth and beak-like keratin coexistence in ornithischians are rare and are restricted to the upper jaw; specimens with these osteological characteristics lie in different parts of the dinosaur tree. The ornithopodan *Agilisaurus louderbacki* and the ornithischian *Jeholosaurus shangyuanensis* have a complete toothrow with a premaxilla with rhamphotheca bone proxies. The evolutionary implication of both species is hard to establish since there is no general consensus regarding their phylogenetic position [Barret et al., 2005a; Butler et al., 2008]. Another example is *Yinlong downsi*, which is the oldest known ceratopsian. The holotype skull has a small rostral bone and lacks the diastema between the premaxilla and maxilla that is typically found in ceratopodans [Fastovsky & Weishampel, 2016].

The extension of the rhamphotheca in the upper jaw is thought to have covered the premaxilla and rostral bone of *Psittacosaurus* [Serenio et al., 2010] but only the rostral in Ceratopsidae (e.g. *Centrosaurus*, *Triceratops*) [Dodson et al., 2004]. The rostral bone is a ceratopsian autapomorphy that forms the tip of the upper jaw [Hailu & Dodson, 2004]. A toothless prementary is synapomorphic to Ornithischia, which is assumed to have been covered by a rhamphotheca [Galton, 1973; Benton, 2005].

Basal sauropodomorphs and sauropods have a more diverse arrangement of these osteological correlates and teeth. Some titanosaurs, such as *Tapuiasaurus macedoni* and *Nemegtosaurus mongoliensis*, and other sauropods, such as *Camarasaurus* sp. and *Nigersaurus taqueti*, have toothed jaws coexisting with grooves and pits (Fig. 2) [Zaher et al., 2011; Wilson, 2005; Sereno et al., 2007; Wiersma & Sander, 2017; Sereno, 2007]. Floating isolated toothrows (ITRs) that have wrinkled enamel on the labial surface of jawbones in *Camarasaurus* sp. are commonly found, which is interpreted to be covered by “beak keratin” [Wiersma & Sander, 2017]. *Bonitasauria*, which possesses guillotine-like keratin ridges after its frontal teeth, is assumed to have been “beaked” [Apesteguía, 2004].

An alternative hypothesis for the Sauropodomorpha lineage is that the facial grooves with pits are not proxies for beak-like keratin. As explained by Martínez [2009], these osteological features have also been observed in jaws of extant mammals, such as hippopotamuses and manatees, that support highly mobile lips, but dinosaurs lack these facial muscles. Wiersma & Sanders [2017] have proposed that the jaws of sauropods, such as *Camarasaurus* jaws could have been covered by thick gingival connective tissue and scales or beak-like keratin on top.

The Problem with Taxonomic Sampling and Coevolution Inference

Correlation studies are often plagued by easy explanations and *post hoc* hypotheses. Phylogenetic comparative methods can help us assess how much evolution in one trait is associated with the change in another trait. These types of analyses should be applied to *a priori* hypotheses.

Confounding matters, apparent sample sizes can appear inflated in the presence of phylogenetic pseudoreplication [Maddison & FitzJohn, 2015]. That is, data from species tend to

be similar because they are linked in a hierarchically structured phylogeny. Ignoring phylogeny can obscure these associations and lead to incorrect conclusions [Clutton-Brock & Harvey, 1977; Harvey & Mace, 1982; Felsenstein, 1985].

As noted by Maddison & FitzJohn [2015] and Gardner & Organ [2021], it is difficult to ascertain whether correlations are the result of adaptive selection based on statistical models alone. However, statistical correlation can be consistent with *a priori* hypotheses of adaptive correlation given the proper evolutionary sample size or number of independent evolutionary changes of a trait [Gardner & Organ, 2021].

The lack of a general pattern of trait evolution across the clade could indicate that other factors have shaped trait diversity. For example, phenotypic modularity, which consists of the developmental independence of sets of loosely integrated traits may constrain the evolution of trait values [Brocklehurst & Field, 2021; Knapp et al., 2021]. Phylogenetic inertia or stabilizing selection for suites of related features may also constrain trait values. And finally, third variables could always underlie the correlations of variables.

Biases in Adaptive Inferences and the Edentulous Beak Paradigm

Since the publication of *The Origin of Species* [Darwin, 1859], beaks have been extensively studied in birds to understand how and why this quintessential structure evolved [Allen, 1889; Jenkin, 1957; Gill & Wolf, 1978; Boag & Grant, 1981; Abzhanov et al., 2004; Wu et al., 2006; Wu et al., 2006; Bhullar, 2016; Wang et al., 2017b; Wang et al., 2017c; Wang et al., 2020]. However, the ecology and life history of extant birds may not reflect those of other extinct relatives. Many avian traits, such as feathers, genomic contraction, and hollow bones, were thought to be adaptations to flight, but research in the last four decades has revealed otherwise

[Chen et al., 1998; Qiang et al., 1998; Britt, 1994; Xu, 2006; O'Connor & Claessens, 2005; Organ et al., 2007; Organ, 2009a; Benson et al., 2012].

The adaptive advantages of beaks over teeth plausibly include lightening the skeleton for flight [Louchart & Viriot, 2011], the replacement of forelimbs for food probing and manipulation as coincident with the evolution of wings [Davit-Béal et al., 2009], fast embryonic growth and shortening of incubation period [Ericson et al., 2017; Yang & Sanders, 2018], and improve calory extraction from food, such as seeds, by way of the gizzard [Louchart & Viriot, 2011; Larson et al., 2016; Button & Zano, 2020]. These specializations could have given the toothless crown birds a better chance of survival during the K-Pg mass extinction.

Ornithischians, unlike theropods, evolved oral food processing analogous to mammalian chewing [Galton, 1973; Benton, 2005; Button & Zanno, 2020]. The predentary or the maxilla took an active role in cranial kinetics, possibly related to chewing [Norman & Weishampel, 1985; Benton, 2005; Nabavizadeh & Weishampel, 2016].

Most ornithischians were traditionally assumed to be strictly herbivorous. Mallon & Anderson's [2013; 2014] morphometric analyses revealed that different feeding specializations were defined by beak shape, dental batteries and body height, and were unique to other groups of ornithischians. Ankylosaurs most likely fed on fibrous herbage as bulk feeders due to their broad and square beaks and short stature. Ceratopsians could have eaten plant matter that was low in fiber and high in protein due to their narrow triangular beaks, but they most likely fed on fibrous plants due to their body size and shredding dentition. Hadrosaurs could eat both pulpy and fibrous plants because their beak morphology was intermediate between ankylosaur and ceratopsian beaks.

Other studies have hinted at a wider range in diet, such as omnivory in hadrosaurs or ceratopsians, due to preserved and partially digested crustaceans and rotten wood in coprolites [Chin & Tashman, 2017], and insectivory in ankylosaurs due to the inference of a desert paleoenvironment [Nopcsa, 1928; Hill et al., 2015] and robust hyobranchial apparatus [Hill et al., 2015].

Like theropods, different lines of evidence in sauropodomorphs indicate that these animals did little to no chewing [Sander, 2013; Barret, 2014; Button & Zanno, 2020; Singh, 2021], and they might have relied more on extended gut fermentation as their body size increased [Sander, 2013, Barret, 2014; Button & Zanno, 2020]. Sauropodomorph teeth are relatively simple, compared to the complex grinding surface found in many ornithischians, and show little to no variation in tooth size or shape [Galton & Upchurch, 2004; Sereno & Wilson, 2005].

Teeth range from non-sauropod sauropodomorph spatulate shape [Galton & Upchurch, 2004; McPhee et al., 2015] or leaf shape [Brusatte, 2012], to cylindrical (i.e., pencil-shaped) or intermediate shape in sauropods [Upchurch et al., 2004; Canudo et al., 2018]. This morphology, along with a weak bite, suggests that sauropods were specialized for clipping/nipping and procurement of foliage [Button & Zanno, 2020; Singh, 2021]. These lines of evidence also suggest that omnivory may have been prevalent in basal sauropodomorphs since their teeth resemble iguana teeth [Barret, 2000; Brusatte, 2012].

Due to their unique body morphology and large sizes, some authors have proposed that beak-like keratin (“beak”, “bill”, “keratinous sheath”) might have protected jaws from abrasive plant matter while foraging [Wiersma & Sander, 2017; Canudo et al., 2018]. In addition, beak-

like keratin along with gingival connective tissue might have held teeth that have absent or reduced roots, such as in *Camarasaurus*, *Diplodocus*, and *Europasaurus* [Michael et al., 2013; Wiersma & Sander, 2017]. Giraffes, which are analogous models for sauropods [Steven & Parrish, 2005], also deal with abrasive plant matter but use anatomical structures that are uniquely mammalian: they use prehensile lips with long hairs and long dexterous tongues for protection against thorns while they seek out leaves [Dagg, 1971].

Significance, Purpose and Scope of This Study

This study aims to assess the evolutionary relationship between teeth and beak-like keratin using dinosaur diversity. Previous research on the subject focused on theropod fossils closely related to birds. However, tooth and beak coevolution could be biased towards bird physiology, embryology, ecology, and phylogeny.

This research provides a more extensive sampling of the dinosaur clades known to have developed rhamphotheca, increasing the evolutionary sample size of these structures. This increases our analytical power to test for evolutionary patterns and processes.

The long-term goal is to provide insights into the evolution and diversification of dinosaurs and help determine if current hypotheses in the literature apply to all beaked animals or just theropods.

QUESTIONS AND HYPOTHESES

Question: What is the Evolutionary Relationship of the Keratin Cover and Teeth in Dinosaurs?

First Hypothesis

The presence of a beak-like keratin cover influences tooth distribution in dinosaurs.

Rejecting the null hypothesis would imply that part of the variation in tooth distribution can be explained by the presence of beak-like keratin. Failure to reject the null hypothesis suggests that there is no association between the keratin cover and tooth distribution.

Question: Does the Keratin Cover Repeatedly Evolve
Through the Same Sequence of Intermediate Steps?

Second Hypothesis

The keratin cover independently evolved in dinosaurs by a series of intermediate steps.

The intermediate steps in this hypothesis include: 1) Partial tooth loss. 2) Evolution of the keratin cover in a jaw that has toothrow gaps. 3) Finally, evolution of an edentulous jaw with keratin cover. If the null hypothesis is rejected, the evolutionary pattern seen in avialans will have occurred throughout Dinosauria.

Question: How Does the Evolution of the Keratin Cover Influence the Rate of Tooth Evolution?

Third Hypothesis

The appearance of a keratin cover influences the evolutionary rate of tooth loss in dinosaurs. If the evolutionary rate of tooth loss is increased, there may have been an adaptive advantage of a keratin cover over teeth. Conversely, if the evolutionary rate of tooth loss is decreased after the appearance of a keratin cover, the two structures may have functioned

together. If the null hypothesis could not be rejected, the keratin cover had no influence on the rate of tooth loss in dinosaurs.

MATERIALS AND METHODS

The scope of data collection of discrete morphological characters in this study include numerous adult dinosaur specimens. These are divided into three major branches: the Ornithischia lineage, the Sauropodomorpha lineage, and the Theropoda lineage. These groups are further divided into distinct taxa or undetermined classification, as shown in Table 1. Missing data were imputed using phylogenetically-informed methods, as detailed below.

Lineage	Group 1	Group 2	Upper jaw	Lower jaw
Ornithischia	Cerapoda	Ornithopoda	5	4
	Cerapoda	Ceratopsia	7	6
	Cerapoda	Pachycephalosauria	1	1
	Thyreophora	Ankylosauria	4	3
	Thyreophora	Indet. Thyreophora	1	0
	Thyreophora	Stegosauria	2	2
	-	Heterodontosauridae	3	3
	-	Parksosauridae	3	3
	Indet. Ornithischia	-	4	4
Total=			30	26
Sauropodomorpha^I	Prosauropoda ^{II}	Indet. Prosauropoda	6	7
	Prosauropoda	Massospondylidae	5	5
	Prosauropoda	Plateosauridae	1	1
	Sauropoda	Brachiosauridae	1	1
	Sauropoda	Camarasauridae	1	1
	Sauropoda	Diplodocidae	3	3
	Sauropoda	Mamenchisauridae	1	1
	Sauropoda	Rebbachisauridae	1	1
	Sauropoda	Titanosauria	2	3
Total=			21	23
Theropoda	Avetheropoda ^{III}	-	2	3
	Coelurosauria	Aviale	8	8
	Coelurosauria	Paraves ^{IV}	2	2
	Coelurosauria	Oviraptorosauria	5	8
	Coelurosauria	Ornithomimosauria	5	5
	Coelurosauria	Scansoriopterygidae	2	2
	Coelurosauria	Therizinosauria	3	5
	Coelurosauria	Tyrannosauridae	4	4
	Indet. Theropoda	-	2	3
Total=			33	40
Indet. Dinosauria	Herrerasauridae+	-	2	2

Table 1. The number of specimens used in this study for upper jaw data and lower jaw data. They are classified by lineage, taxonomic group (Group 1) and another more inclusive taxonomic group (Group 2). I) Includes both sauropod and prosauropod sauropodomorphs. II) A non-monophyletic group of non-sauropod/archaic sauropodomorphs. III) Refers to non-coelurosaurian avetheropods. IV) Refers to non-avian paravians that exclude Scansoriopterygidae. +) Refers to an indet. dinosaur taxon in addition to Herrerasauridae.

Specimen Selection

Specimens used for phylogenetic analyses [Table A1] have labial and (or) facial surface intact for keratin cover (*KC*) inference. The facial grooves located at the rostral tip of jawbones are used as keratin cover proxies. The term keratin cover is used to refer to jaws with direct or indirect evidence of “facial rhamphotheca”, which avoids the ambiguity with a “rhamphotheca” defined as a “toothless” structure.

Toothrow (*TR*) distribution inference required other anatomical attributes, such as in-place teeth and (or) functional tooth alveoli. The latter refers to tooth alveoli that are not vestigial. Thus, there is evidence that the tooth had access to a blood vessel as a nutrient supply. Any teeth missing due to taphonomic filters or collection errors are therefore accounted for.

Toothrow distribution was coded as a multistate categorical variable, using the following states: (0) edentulous, (1) gaps in *TR*, (2) complete *TR*. This coding accounts for general tooth patterns previously described in the literature. Keratinous cover data was treated as a binary character: (0) without *KC*, (1) with *KC*. Binary coding is less descriptive but offers the advantage of reducing the parameter estimation required by some comparative methods [Hieronymus & Witmer, 2010].

Tooth distribution in both the upper and lower jaw was used over tooth count because there is drastic variability in tooth count, and it is logistically taxing to account for in a large dataset, such as the one used in this research. In addition, accurate data for tooth count is harder to access in literature, limiting data collection. For example, cerapodans, which include ceratopsians and hadrosaurs, possess complex dental batteries. These structures significantly

increase teeth number in the jaws, in the rostral-caudal and labio-lingual sense, and are prone to intraspecific variability.

Species data that lacked cranial material or was inaccessible were omitted unless replaced with another of the same genus. In addition, fragmentary specimens were used in some cases to account for deformation and destruction of traits of interest in otherwise more complete specimens. Only adult or subadult specimens were used to avoid ambiguity of species identity or (and) drastic ontogenic variation of jaw anatomy.

Phylogeny Model

Button & Zanno's [2020] tree was used for the phylogenetic comparative analyses performed in this study. Given the uncertainty of the dinosaurian family tree in recent studies [Baron et al., 2017; Langer et al., 2017; Nesbitt, 2019], a base polytomy that separates the three main dinosaur lineages, Ornithischia, Sauropodomorpha, and Theropoda, at an equal distance was used (Fig. 10). The phylogenetic comparative analyses were run across a posterior sample of 100 time-calibrated trees from Button & Zanno [2020] to assess the accuracy of ancestral reconstruction estimates and evolutionary transitions. The trees incorporate alternative topologies and topological uncertainty.

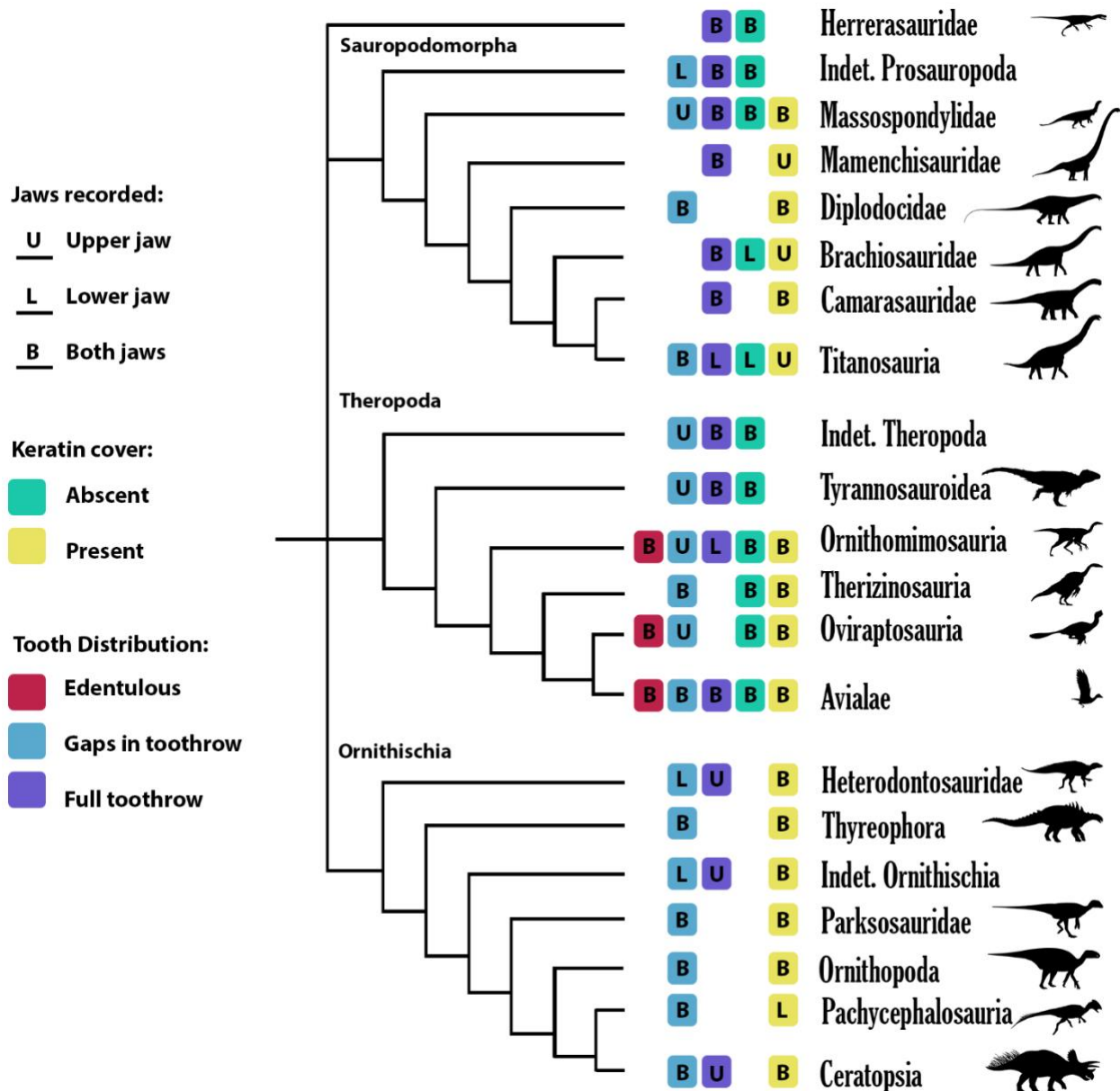


Fig. 10. Simplified Dinosaur phylogeny from Button & Zanno [2020]. Variable states present in different taxa from dataset where added. Silhouettes from *Phylopic.org* [2020-2021]:

Herrerasauridae (O. Alcober & R. Martinez); Massospondylidae and Tyrannosauroidae (T. Dixon); Mamenchisauridae (Fang-Designs); Diplodocidae, Titanosauria and Confuciusornis (S. Hartman); Brachiosauridae, Camarasauridae, Heterodontosauridae and Parksosauridae (M. Wedel); Ornithomimosauria (C. Dylke); Therizinosauria and Ankylosauria (FunkMonk); Oviraptorosauria (E. Willoughby); Ornithopoda (I. Reid); Pachycephalosauria (T. Michael-Keesey); Ceratopsia (D. Tana).

Multiple Imputation Method

The fossil record is inherently incomplete and biased since only a few environments allow for slow body decay and taphonomic preservation needed for forming body fossils. As a result, not all extinct species leave fossils; body fossils tend to be incomplete and thus can present a challenge when trying to infer general properties and parameters of their biology. Therefore, an imputation method was used to overcome this problem and fill in missing data.

The *missForest* R package [Stekhoven & Bühlmann; 2012] uses a multiple imputation method with the same name to fill in these missing values. As with other imputation methods, this increases statistical power and reduces parameter bias. Thus the probability to correctly reject the null hypothesis increases [Nakagawa, 2015].

As mentioned by Stekhoven and Bühlmann [2012], MissForest uses the Random Forest algorithm for each variable to predict missing values; numerical variables with sample means and categorical variables with the sample mode. It then fits a random forest on the observed part of the dataset and “learns” to predict the missing data values. It repeats the process in loops and analyses the imputed datasets. In a final step, the datasets are pooled in one final result when reaching a stopping criterion that gives the uncertainty of estimates. The imputation quality is measured by two types of out-of-bag imputation error estimates: the Normalized Root Mean Square Error (*NRMSE*) for continuous variables and the Proportion of Falsely Classified entries (*PFC*). A zero value means good imputation performance, whereas a value of one implies poor performance.

MissForest can cope with mixed-type variables and nonlinear relationships, and requires little computational time. Imputation accuracy for biological data increases considerably when

including phylogenetic information as originally shown in Garland & Ives [2000] and Organ [2007, 2009a, 2009b], and later tested in MissForest by Penone et al. [2014] and Fournier et al. [2019].

The phylogenetic eigenvectors reflect the differences between the terminal taxa and the nodes at different levels in the tree model. They were extracted from the distance matrix in the phylogenetic tree models using a principal coordinate analysis (*PCoA*) (Fig. 11) [Legendre & Legendre, 1998; Diniz-Filho et al., 2012] using the *ape R* package.

Following Penone's et al. [2014] method (Fig. 11), the eigenvectors' optimal number to do the imputation method was determined with the following steps: 1) Run imputations of missing data with an increasing number of eigenvectors ($k = 1-5, 10, 15, 20, 25, 30, 40, 75, 100, 125$ & 150), starting with the eigenvectors that reflect the longest distances (from the root to of the tree to the terminal taxa). 2) Calculate the imputation error estimates (NRMSE, PFC). 3) Repeat this process nine more times. 4) Do a linear mixed-effects model to test the effects of the number of eigenvectors on the imputation error estimates. 5) Select the lowest number of eigenvectors with the lowest imputation error estimates for creating the final dataset with imputed data.

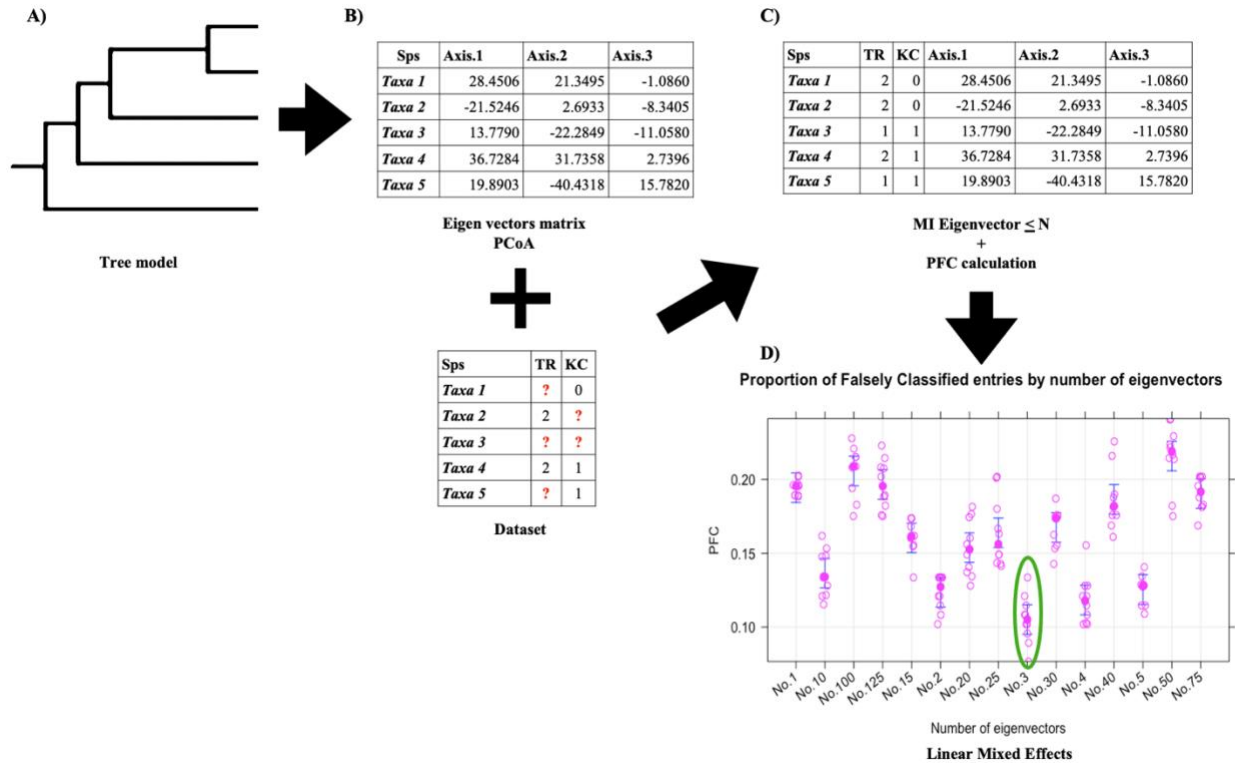


Fig. 11. Multiple imputation method divided into four parts: A) Tree model; B) Extraction of eigenvector from the tree model using PCoA method, and fusion of eigenvector dataset with the dataset of traits of this study; C) Running MissForest with decreasing number of eigenvectors nine times each, and calculate their PFCs; D) Linear mixed-effects model of PFCs by eigenvectors' number.

Phylogenetic Analysis

The *R* package *MCMCglmm* [Hadfield, 2010] was used to test for correlation between the variables of interest after being normalized for common descent. It is a phylogenetic regression program that implements a generalized linear mixed model (glmm) with the Bayesian framework. This approach permits the analysis of binary dependent variables against independent variables after accounting for residual variation (uncertainty: u) and phylogeny as the random effect (s) [Ives & Garland, 2014]. The model is:

$$\begin{aligned}
\Pr(Y = 1) &= p \\
\text{probit}(p) &= b_o + b_1x + s + u \\
s &\sim N(0, \sigma_s^2 C) \\
u &\sim N(0, \sigma_u^2 I)
\end{aligned}$$

Equation 1.

The glmm can be used for other types of dependable variables (such as count or discrete nominal data). In addition, this method is suitable for data with non-normal distributions.

Bayesian inference is premised on the likelihood (conditional probability) of a parameter value (hypothesis) given the known data (evidence). This is calculated by multiplying the probability of the evidence given the hypothesis by the prior probability, and divided by the probability of the evidence; this is summarized in the following formula:

$$P(H|E) = \frac{P(E|H) * P(H)}{P(E)}$$

Equation 2.

The Markov Chain Monte Carlo (MCMC) algorithm searches through parameter space and samples values in proportion to their posterior probability to estimate the posterior distributions of a model and its parameter values [Ives & Garland, 2014]. The search has two phases: the burn-in, where it searches randomly through parameter space, and the stationary phase, where the search explores parameter values of high likelihood.

The Bayesian inference using MCMCglmm can also be divided into three main parts: the unknown parameter value, the generative model and the known variable values (Fig. 12).

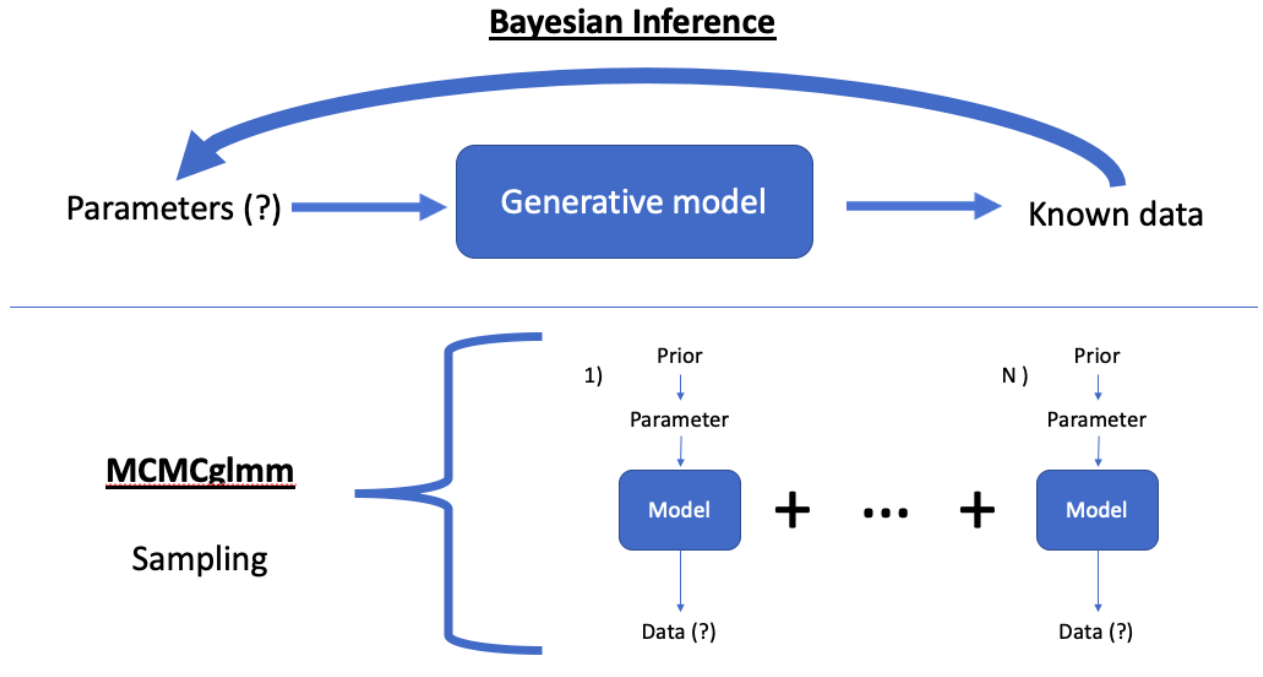


Fig. 12. Bayesian inference is divided into three parts and MCMCglmm sampling of parameter values. N represents the specified maximum number of iterations that the MCMC algorithm would run when searching parameter space.

Generative Model

Multinomial regression models were fitted to test coevolution of the traits of interest for this project because the response variable, tooththrow distribution, is a categorical variable with three different responses: (0) edentulous, (1) gaps in *TR*, (2) complete *TR*. This model determines whether the logged probability of Y , as a categorical response variable, is determined by X , the independent variable. In this case, X is a binomial variable describing the absence (0) or the presence of *KC* (1).

This model uses maximum likelihood to determine if the probabilities of the categories of the response variable depend on an explanatory variable. It is a multi-response model that is good for dealing with missing data. The different tooth distribution conditions are set as mutually

exclusive. A dimension reduction was used to constrain the probability of expressing either tooth distribution category:

$$\Pr(TR[i] = \textit{Edentulous}) + \Pr(TR[i] = \textit{Partial dentition}) + \Pr(TR[i] = \textit{Full dentition}) = 1$$

Equation 3.

Since there are more than two categories (J) of the dependent variable, the model needed $J-1$ latent variables. This is the log-odds ratio of “succeeding” over “failing” in one category. Both latent variables used the “edentulous” category as the baseline, as shown in the following formulas:

$$l_i \textit{ partial dentition} = \log \left(\frac{\Pr(TR) = \textit{Partial dentition}}{\Pr(TR) = \textit{Edentulous}} \right) = b_{1,0} + b_{1,1}(KC = \textit{abscent}) + b_{1,2}(KC = \textit{present})$$

Equation 4.

$$l_i \textit{ full dentition} = \log \left(\frac{\Pr(TR) = \textit{Full dentition}}{\Pr(TR) = \textit{Edentulous}} \right) = b_{2,0} + b_{2,1}(KC = \textit{abscent}) + b_{2,2}(KC = \textit{present})$$

Equation 5.

Log odds ratio, also known as the logit function, is a symmetrical distribution that looks like a normal distribution. This is useful for determining the probabilities of an event occurring. Odds is a ratio of one state of tooththrow condition expressing against the “base” state—it is a true/false situation. One can infer with logit standard distributions and thus p-values. Coefficients for the intercept and slope are inferred through a t-test. The Y-axis must be continuous to calculate the mean Y for each category X and the mean Y difference between the two X categories. Logit transforms the Y categorical variable values into a continuous variable.

Two versions of this model were tested for each jaw (upper and lower) to see which fitted the data better: one with phylogeny as the random effect and a simpler model without phylogeny. This was repeated again using the imputed dataset for each jaw. Both the deviance information criterion (DIC) and the Bayesian information criterion (BIC) were used to determine the best model – both are optimal for a Bayesian framework and they penalize a model for including too many terms that are not useful [Wasserman, 2000; Spiegelhalter et al., 2002; Felsenstein, 2004].

The DIC is used in Bayesian model selection without making assumptions of a “true model”, it estimates the adequate number of parameters, and the posterior distribution is searched with an MCMC, such as in MCMCglmm [Spiegelhalter et al., 2002; Alastair, 2004; Hadfield, 2010]. The BIC, in contrast, attempts to identify the “true model” given the data, requires prior specification of the number of parameters, and is an approximation to a model’s log marginal likelihood [Kass & Raftery, 1995; Wasserman, 2000; Alastair, 2004]. The smallest value of DIC or BIC means that the model is the best fit for the data.

Ancestral Reconstruction & Evolutionary Rates

A reversible-jump Markov Chain Monte Carlo (RJ-MCMC) algorithm was employed using *BayesTraits V3* [Pagel, 1999; Meade & Pagel, 2016] to look into the evolutionary changes of the two traits of interest that took place along the dinosaur clade (Table 2). The RJ-MCMC algorithm randomly sets parameters equal to one another and to zero, thereby automatically finding the fewest number of parameters supported by the data.

Transition probabilities	0	1	2	3	4	5
0	-	q01	q02	q03	q04	q05
1	q10	-	q12	q13	q14	q15
2	q20	q21	-	q23	q24	q25
3	q30	q31	q32	-	q34	q35
4	q40	q41	q42	q43	-	q45
5	q50	q51	q52	q53	q54	-

Table 2. Median transition probabilities ($q_{\#,\#}$) of changing from one state to another for trait U (upper jaw) or L (lower jaw). Rows represent states in an ancestor, and columns represent states in the descendants. Red: impossible transition probabilities due to the absence of state 0 in the dataset. The value of each valid square would be 0.05 if all valid transitional probabilities were equal.

First, KC and TR states were recorded as a single multistate trait for the upper jaw (U), and another equivalent trait for the lower jaw (L), as seen in Table 3 and Figure 13. Then, the algorithm was run for 500,000 iterations with a 10,000 burn-in, 100 stepping-stone sampling (SS) for every 10,000 iterations, the reversible jump (RJ) exponential hyperprior 0 10, and an empirical base frequency. The stepping-stone sampling (SS) method uses a posterior and prior distribution for estimating the marginal likelihood, and it is much more accurate than the harmonic mean (HM) method [Xie et al., 2011, Meade & Pagel, 2016]. Empirical base frequencies are drawn directly from the frequencies of state values and are ideal for working with an imbalanced dataset of large sample size [Jiang & Zhang, 2010].

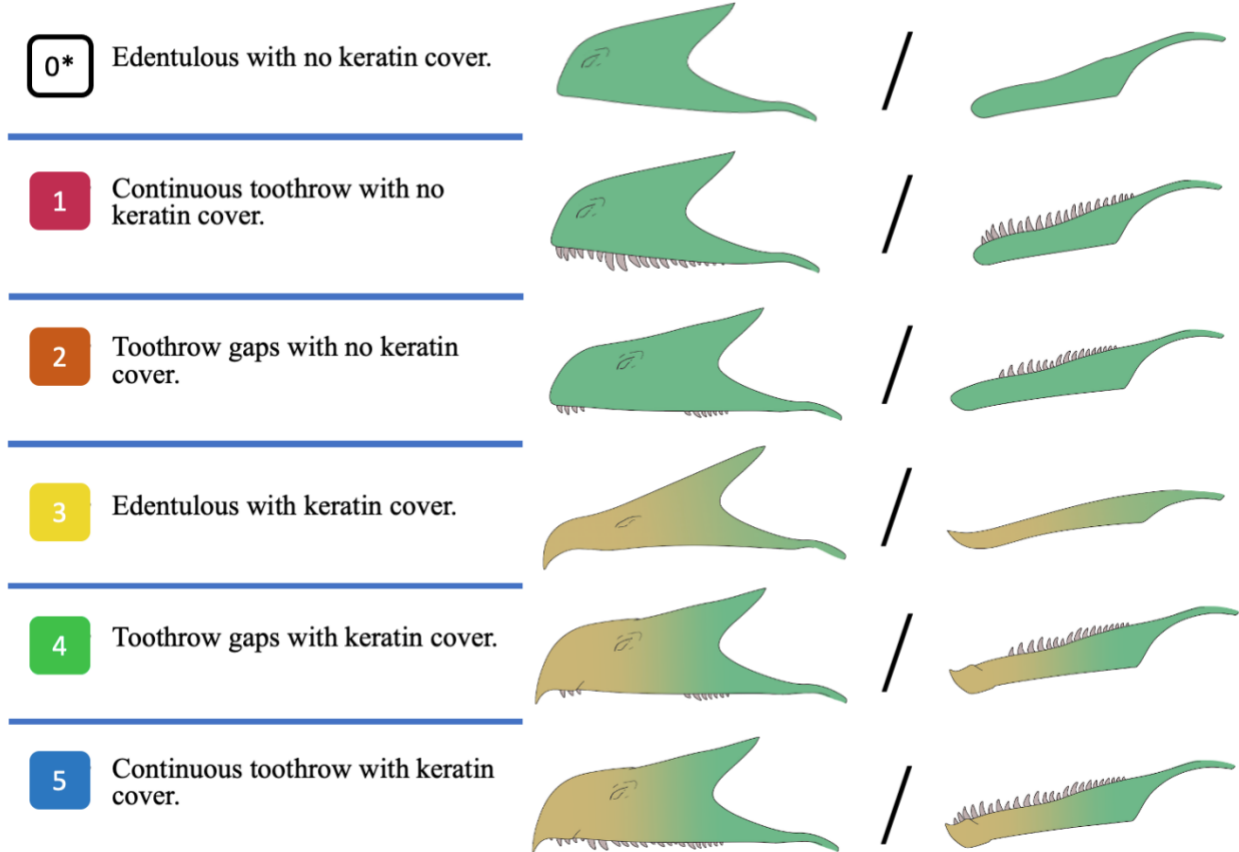
Trait state

Fig. 13. The five states of the upper jaw trait (*U*) and the equivalent states in the lower jaw trait (*L*). From left to right: the coded number and coded color of trait states, the trait state description, the upper jaw representation of the trait, and the lower jaw representation of the trait. Colors in jaw figures: green for absence of keratin cover, and yellow with green to represent the presence of keratin cover without assuming the exact caudal extension of the keratin cover. Location of gaps in tooththrow differ between species of dinosaurs. * There were no specimens in the original dataset that had this combination of traits.

U/L	Color code	TR	KC
0*		0	0
1		1	0
2		2	0
3		0	1
4		1	1
5		2	1

Table 3. Table showing the trait *U* and its states that represent the different combinations of possible tooththrow states (*TR*) with keratin cover (*KC*) in the upper jaw. *TR* states: edentulous (0), tooththrow with gaps (1), and complete tooththrow (2). *KC* states: absent (0), and present (1). Trait *L* is equivalent to trait *U*, but it uses data from the lower jaw of the specimens sampled for this study. * There were no specimens in the original dataset that had this combination of traits.

The RJ-MCMC algorithm was used to avoid over-parameterization, which are problematic in complex models [Pagel & Meade, 2006; Pagel & Meade, 2007]. This Bayesian methodology explores different models, visiting them directly proportional to their posterior probabilities [Pagel & Meade, 2006]. This avoids manually testing many distinct models of correlated evolution between the discrete traits of interest.

To evaluate the effect of using empirical base frequencies, an RJ-MCMC unrestricted model was compared to a model equal ($q_{21} = q_{54} = q_{53}$) frequencies. A log Bayes Factor test (*BF*) was performed for model selection based on the Raftery et al. [1996] (Table 4). This last step compares the average stepping-stone logged marginal likelihoods (*SS LMh*) of two models (*i*: no restriction, *j*: model with restriction). If the *BF* favors the unrestricted model, a difference between the tooth loss rate between lineages with keratin cover and those without is supported.

$$BF = 2(SMh_i - SMh_j)$$

Equation 6.

Log Bayes Factors	Interpretation
<0	Evidence for model <i>j</i>
0-2	Weak evidence for model <i>i</i> *
>2	Positive evidence model <i>i</i>
5-10	Strong evidence model <i>i</i>
>10	Very strong evidence model <i>i</i>

Table 4. Interpretation of Log Bayes Factors [Raftery et al, 1996]. * Not included as evidence for model *i* since it is not statistically significant.

Dollo's Law was assessed by fixing the transitional probabilities that increased tooth gain from ancestors with gaps in toothrow (q12, q15, q42 & q45) to 0. A model with restrictions for evolving teeth from edentulous ancestors (q31, q32, q34, q35) was not performed because the model without restrictions already favored this scenario, and the BayesTraits program would not allow all transitional probabilities to be manually fixed. A similar approach was used for cases where ancestral node reconstruction was edentulous but had toothed descendants: the unrestricted RJ-MCMC model was compared against models with internal nodes fixed to states of U/L that had teeth. These fixed models were created using the *Fossil* command.

RESULTS

Assessing CoevolutionModel Selection

There is strong evidence against the multinomial regression model that does not include phylogeny as a random effect (simple model) when compared against the model with phylogeny as a random effect (complex model) when using the original and the imputed datasets for the upper jaw (Table 5); this was supported by low DIC and BIC values for the model with phylogeny, and their respective weights close to 1. There is also strong evidence against the simple model when using the original and the imputed datasets for the lower jaw.

Dataset	Models	DIC	DIC w	BIC	BIC w
Original	<i>U.Cm</i>	98.4	1 ~	1 ~	112.2
	<i>U.Sm</i>	110.5	0 ~	0 ~	124.2
	<i>L.Cm</i>	80.2	1	1	93.9
	<i>L.Sm</i>	102.8	0	0	117.3
—	—	—	—	—	—
Imputed	<i>U.Cm</i>	441.8	1 ~	1 ~	422.4
	<i>U.Sm</i>	626.3	0 ~	0 ~	608
	<i>L.Cm</i>	164.6	~1	~1	171
	<i>L.Sm</i>	353.3	~0	~0	356.8

Table 5. Model selection of multinomial regression models for upper jaw data (*U*) and lower jaw data (*L*) from the original dataset and the imputed dataset. This classification is furtherer divided as the complex model (*Cm*) and the simple model (*Sm*).

Assessing the Effect of KC

Imputation Data. The results of the model for the upper jaw (Table 6) show strong evidence ($pMCMC < 0.01$) that when keratin cover is present, the mean odds of having toothrow gaps is 11.91 times more likely than having no teeth (95% profile likelihood of CI: 2.38-82.80).

In the lower jaw, there is stronger evidence (pMCMC<0.001) that when keratin cover is present, the mean odds of having tooth row gaps is 21.48 more times than having no teeth (95% C.I. profile likelihood: 3.97-143.36).

Data and model	Latent variables	β	e^β	95% C.I.	$e^{95\% \text{ C.I.}}$	E.S.S.	pMCMC
<i>U.Cm</i>	a)	3.1586	23.5376	1.4375 - 4.9233	4.21-137.45	316.4	<0.001 ***
	b)	5.5385	254.2963	3.7142 - 7.3385	41.02-1538.40	426.3	<0.001 ***
	c)	2.4775	11.9114	0.8692 - 4.4165	2.38-82.80	689.8	0.00667 **
	d)	0.9359	2.5495	(-) 0.7965 - 2.733	0.45-15.37	703.4	0.31111
—	—	—	—	—	—	—	—
<i>L.Cm</i>	a)	2.1677	8.7381	0.3729 - 4.1673	1.45-64.54	195.1	0.020 *
	b)	6.2285	506.9944	4.309 - 7.7941	74.36-2426.24	290.7	<0.001 ***
	c)	3.0675	21.4881	1.3802 - 4.9654	3.97-143.36	311.8	<0.001 ***
	d)	-1.3444	0.2606	(-) 3.6043 - 0.499	0.02-1.64	184.4	0.173

Table 6. Fixed effects of *U.Cm* and *L.Cm* using the imputed dataset. It includes the log-odd posterior probability mean (β), of one tooththrow state succeeding against the edentulous condition, the mean odds (e^β), the 95 % confidence interval (C.I.), the mean odds 95 % confidence interval ($e^{95\% \text{ C.I.}}$), the effective sample size (E.S.S.), and the pMCMC statistic. Green highlights the latent variables (log-odds tooththrow states) that are associated with a jaw without keratin cover, yellow highlights the latent variables that are associated with a jaw with keratin cover. Row classification represent latent variables: a & c) P(Gap / Edentulous); b & d) P(Full / Edentulous). * Indicates statistical significance (pMCMC<0.05), ** indicates a stronger significance than * (pMCMC<0.01), and *** indicates the strongest significance (pMCMC<0.001).

When there is keratin cover in the upper jaw, the mean odds of having a complete tooththrow is 2.54 times more than having no teeth (95% profile likelihood CI: 0.45-15.37). When there is keratin cover in the lower jaw, the mean odds of having a complete tooth row is 0.26 higher than having no teeth (95% profile likelihood CI: 0.02-1.64). Both probabilities are not statistically significant (pMCMC> 0.05).

When there is no keratin cover in the upper jaw, there is strong evidence (pMCMC < 0.001) that the mean odds of having gaps in tooththrow in the upper jaw is 3.15 times more likely

than having no teeth (95% profile likelihood of CI: 4.21-137.45). In the lower jaw, there is evidence ($pMCMC < 0.05$) that the mean odds of having a complete tooth row in the lower jaw is 6.22 times more likely than having no teeth (95% profile likelihood of CI: 1.45-64.54).

When there is no keratin cover in the upper jaw, there is strong evidence ($pMCMC < 0.001$) that the mean odds of having a complete toothrow in the upper jaw is 254.29 times more likely than having no teeth (95% profile likelihood of CI: 41.02-1538.403). In the lower jaw, there is strong evidence ($pMCMC < 0.001$) that the mean odds of having a complete tooth row in the lower jaw is 6.22 times more likely than having no teeth (95% profile likelihood of CI: 74.36-2426.24).

Original Data. The models for the upper jaw and lower jaw original data (Table 7) are similar to the models for the imputed data. Yet, the models for the original data do not detect a significant ($pMCMC > 0.05$) higher mean odds of toothrow gaps against the edentulous condition in the upper jaw (e^{β} : 6.11; 95% profile likelihood of CI: 1.16-51.93) or the lower jaw (e^{β} : 5.87; 95% profile likelihood of CI: 1.09-34.81) when there is no KC.

In summary, the multinomial regression analysis results show strong support for the hypothesis of toothrow reduction when keratin cover is present. Keratin cover is more likely to be associated with partial tooth loss than losing the whole toothrow.

Data and model	Latent variables	β	e^β	95% C.I.	$e^{95\% \text{ C.I.}}$	E.S.S.	pMCMC
<i>U.Cm</i>	a)	1.81	6.1104	0.15-3.95	1.16-51.93	536.8	0.5
	b)	3.55	34.8133	1.96-5.33	7.09-206.43	561.2	<0.05*
	c)	2.01	7.4633	0.73-3.43	2.07-30.87	729.6	<0.05*
	d)	0.32	1.3771	(-) 1.2-1.73	0.30-5.64	551.8	>0.05
—	—	—	—	—	—	—	—
<i>L.Cm</i>	a)	1.77	5.8708	0.09-3.55	1.09-34.81	541.8	0.5
	b)	3.38	29.3707	1.69-4.94	5.41-139.77	449.3	<0.05*
	c)	2.42	11.2458	0.95-3.97	2.58-52.98	406.0	<0.05*
	d)	-0.93	0.3945	(-) 2.7-1.24	0.06-3.45	284.0	>0.05

Table 7. Fixed effects of *U.Cm* and *L.Cm* using the original dataset. It includes the log-odd posterior probability mean (β), of one toothrow state succeeding against the edentulous condition, the mean odds (e^β), the 95 % confidence interval (C.I.), the mean odds 95 % confidence interval ($e^{95\% \text{ C.I.}}$), the effective sample size (E.S.S.), and the pMCMC statistic. Green highlights the latent variables (log-odds toothrow states) that are associated with a jaw without keratin cover, yellow highlights the latent variables that are associated with a jaw with keratin cover. Row classification represent latent variables: a & c) P(Gap / Edentulous); b & d) P(Full / Edentulous). * Indicates statistical significance (pMCMC<0.05), ** indicates a stronger significance than * (pMCMC<0.01), and *** indicates the strongest significance (pMCMC<0.001).

Ancestral Reconstruction

Theropods

RJ-MCMC ancestral reconstruction for the Theropoda lineage (Fig. 14; Table 8, 9) suggests that toothrow reduced in size in coelurosaurian ancestors before or when keratin cover evolved. Toothrow reduction differs between the upper jaw and the lower jaw in Ornithomimosauria, Oviraptorosauria, and Ornithomura. The results also are inconsistent with the hypothesis of intermediate states of toothrow reduction. The steps of this hypothesis are: 1) Partial tooth loss. 2) Evolution of the keratin cover in a jaw that has toothrow gaps. 3) Finally, evolution of an edentulous jaw with keratin cover.

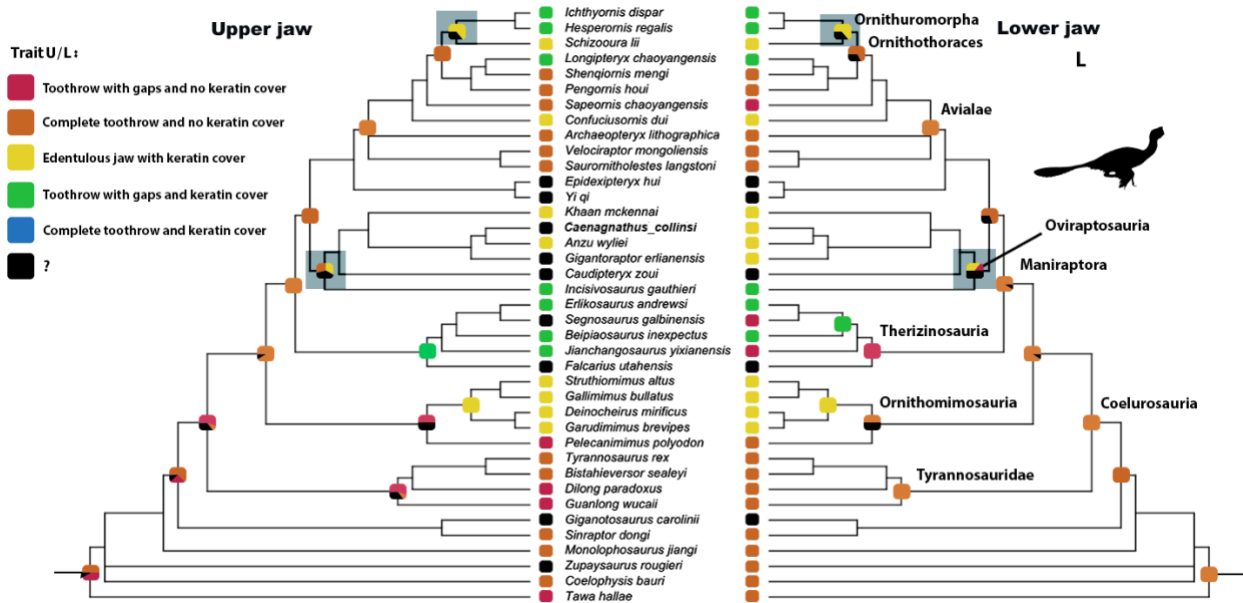


Fig. 14. Ancestral reconstruction of the upper jaw trait (U) and the lower jaw trait (L) in theropods. Missing data or uncertain ancestral reconstruction highlighted in black, states of traits highlighted in five different colors (red, orange, yellow, green, blue) following Table 3, and grey squares indicate where the BF test was performed. Phylogeny follows the tree of Button & Zanno [2020] using *ape* and *phytools* R packages. The tree excludes most species that were not included in the project. Dinosaur silhouette from *Phylopic.org* [2020]: E. Willoughby.

Groups	Toothrow with gaps and no keratin cover (1)	Complete toothrow and no keratin cover (2)	Edentulous jaw with keratin cover (3)	Toothrow with gaps and keratin cover (4)	Complete toothrow and keratin cover (5)
Theropoda	0.470	0.507	0.001	0	0~
<i>Sinraptor</i> +	0.315	0.670	0~	0	0~
Coelurosauria	0.681	0.270	0.004	0	0
Tyrannosauridae	0.658	0.304	0.003	0~	0~
Ornithomimosauria +	0.094	0.853	0.003	0~	0~
Ornithomimosauria	0.569	0.151	0.057	0~	0.009
Ornithomimosauria -	0.005	0.005	0.982	0	0~
Maniraptora	0.009	0.953	0~	0~	0.001
Therizinosauria	0.009	0.022	0~	0.928	0.024
Oviraptosauria +	0.020	0.928	0.004	0~	0~
Oviraptosauria	0.0836	0.264	0.299	0.045	0.083
Aviale	0.041	0.910	0.002	0	0
Ornithothoraces	0.006	0.963	0~	0	0~
Ornithuromorpha	0.052	0.135	0.653	0~	0~

Table 8. Summary of median posterior predictive results for ancestral reconstruction for states of the upper jaw of Theropoda. All measurements truncated to the third decimal. Rows ordered from inclusive to least inclusive taxonomic groups. The highest posterior probability for each taxonomic group is highlighted in green. “+” refers to the ancestor that includes the taxon name that is written before it and the taxa that is written in the rows below, and “-” refers to an inclusive group within the taxon named before this symbol.

Groups	Toothrow with gaps and no keratin cover (1)	Complete toothrow and no keratin cover (2)	Edentulous jaw with keratin cover (3)	Toothrow with gaps and keratin cover (4)	Complete toothrow and keratin cover (5)
Theropoda	0.007	0.980	0~	0	0.004
<i>Sinraptor</i> +	0.008	0.984	0~	0	0.002
Coelurosauria	0.046	0.915	0.002	0	0.017
Tyrannosauridae	0.030	0.942	0.002	0	0.012
Ornithomimosauria +	0.099	0.805	0.007	0	0.011
Ornithomimosauria	0.104	0.575	0.140	0	0.084
Ornithomimosauria -	0.003	0.003	0.985	0	0.001
Maniraptora	0.095	0.840	0.002	0	0.005
Therizinosauria	0.863	0.067	0.006	0	0.022
Therizinosauria -	0.033	0.007	0.002	0.922	0.013
Oviraptosauria +	0.051	0.717	0.028	0	0.024
Oviraptosauria	0.288	0.091	0.318	0	0.097
Aviale	0.062	0.808	0.014	0	0.030
Ornithothoraces	0.053	0.667	0.019	0	0.009
Ornithuromorpha	0.041	0.057	0.651	0	0.036

Table 9. Summary of median posterior predictive results for ancestral reconstruction for states of the lower jaw of Theropoda. All measurements truncated to the third decimal. Rows ordered from inclusive to least inclusive taxonomic groups. The highest posterior probability for each taxonomic group is highlighted in green. “+” refers to the ancestor that includes the taxon name that is written before it and the taxa that is written in the rows below, and “-” refers to an inclusive group within the taxon named before this symbol.

The RJ-MCMC model estimated Ornithuromorpha and Oviraptosauria as two independent cases where the ancestral node has a high posterior probability of having an edentulous upper jaw or lower jaw with keratin cover despite having at least one toothed descendant. The BF tests for Oviraptosauria (Table 10) do not show support for these reconstructions ($BF < 2$) when compared to models where the ancestral node is fixed to toothrow with gaps and no keratin cover (Fossil 1) or complete toothrow with no keratin cover (Fossil 2). In contrast, the BF test for Ornithuromorpha do show support for the RJ-MCMC model ($BF > 2$) when compared to any model where the ancestor is fixed at any state other than an edentulous jaw with keratin cover.

Groups	Trait	Models	SS LMh	BF
Ornithuromorpha	<i>Upper jaw (U)</i>	<i>RJ-MCMC</i>	-80.269027	-
		<i>Fossil 1</i>	-83.975334	7.412614**
		<i>Fossil 2</i>	-81.624435	2.710816*
		<i>Fossil 4</i>	-86.407661	12.277268***
		<i>Fossil 5</i>	-86.244806	9.169456**
	<i>Lower jaw (L)</i>	<i>RJ-MCMC</i>	-72.627537	-
		<i>Fossil 1</i>	-74.023941	2.792808*
		<i>Fossil 2</i>	-72.336148	-0.582778
		<i>Fossil 4</i>	-79.823207	14.39134***
		<i>Fossil 5</i>	-74.229226	2.646614*
	—	—	—	—
Oviraptosauria	<i>Upper jaw (U)</i>	<i>RJ-MCMC</i>	-81.660078	-
		<i>Fossil 1</i>	-82.603939	1.887722
		<i>Fossil 2</i>	-81.683858	0.04756
		<i>Fossil 4</i>	-83.961612	4.603068*
		<i>Fossil 5</i>	-86.330854	12.123654***
	<i>Lower jaw (L)</i>	<i>RJ-MCMC</i>	-72.905919	-
		<i>Fossil 1</i>	-72.555705	-0.700428
		<i>Fossil 2</i>	-73.790157	1.768476
		<i>Fossil 4</i>	-78.516764	11.22169***
		<i>Fossil 5</i>	-75.647971	6.040868**

Table 10. Stepping Stone Sampler Log Marginal likelihoods (SS LMh) of the ancestral node reconstruction models in Ornithuromorpha and Oviraptosauria for the upper jaw trait and the lower jaw trait, and the Bayes Factor (BF). RJ-MCMC model without restrictions (*RJ-MCMC*), model with node fixed at state 1 (*Fossil 1*), model with node fixed at state 2 (*Fossil 2*), model with node fixed at state 4 (*Fossil 4*) and model with node fixed at state 5 (*Fossil 5*). Trait *U* (upper jaw) and trait *L* (lower jaw) and their respective states are defined in Table 3. Degree of evidence for model RJ-MCMC based on Table 4: *, positive evidence; **, strong evidence; ***, very strong evidence.

Sauropodomorphs

The RJ-MCMC ancestral reconstruction for the Sauropodomorpha lineage (Fig. 15, Table 11, 12) have a high posterior probability for keratin covers evolving at least two times independently: in a single event for both jaws in prosauropods within Massospondylae, whereas sauropods could have evolved keratin covers in each jaw at different points within their evolutionary history.

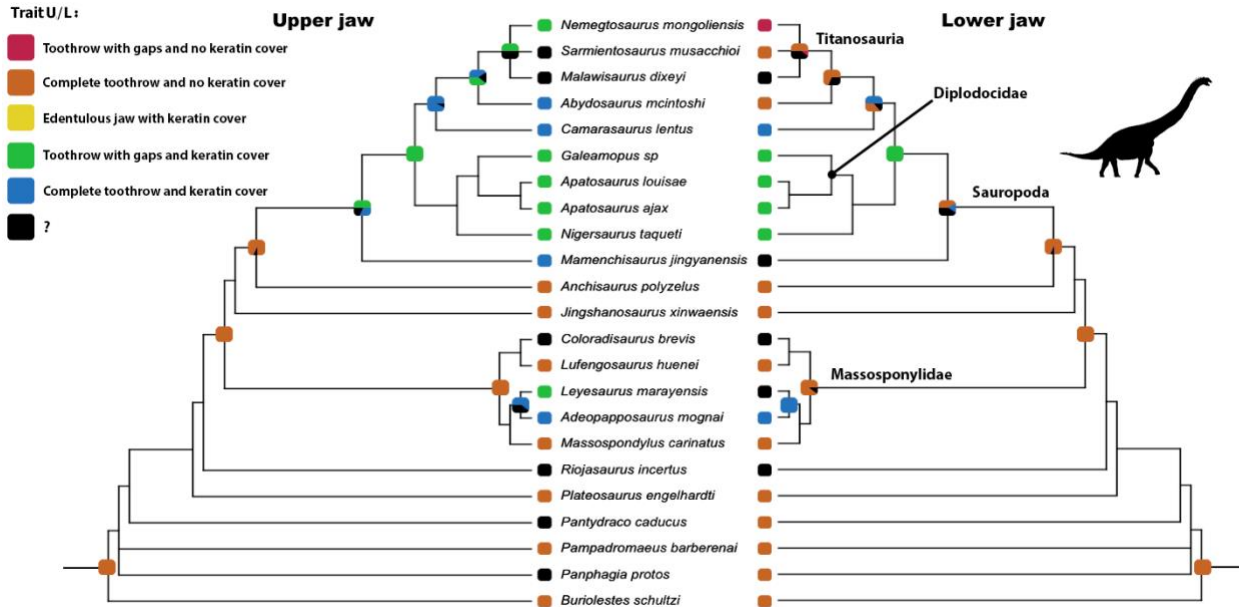


Fig. 15. Ancestral reconstruction of the upper jaw trait (U) and the lower jaw trait (L) in the Sauropodomorpha lineage. Missing data or uncertain ancestral reconstruction highlighted in black, states of traits highlighted in five different colors (red, orange, yellow, green, blue) following Table 3, and grey squares indicate where the BF test was performed. Phylogeny follows the tree of Button & Zanno [2020] using *ape* and *phytools* R packages. The tree excludes most species that were not included in the project. Dinosaur silhouette from *Phylopic.org* [2020]: S. Hartman.

The common ancestor of Massospondylae likely had no keratin covers and had a complete tooththrow. The common ancestor of *Leyesaurus* and *Adeopaposaur* is reconstructed to have had both jaws with keratin cover and a complete tooththrow.

Adeopaposaur mognai is odd among prosauropods since it has the osteological correlates for keratin cover associated with a complete tooththrow, which has been interpreted as a horny beak in both jaws [Martínez, 2009]. Some authors have proposed some prosauropods had horny beaks [Attridge et al. 1985; Crompton and Attridge, 1986; Sereno, 1997, 2007], but this view is controversial due to incomplete fossil remains [Barrett and Upchurch, 2007].

Leyesaurus marayensis is another prosauropod that is classified as a sister taxon to *Adeopaposaur* [Apaldetti et al., 2011] and has a similar facial texture in both jaws. However,

teeth in the lower jaw are partially hidden. Determining toothrow state with confidence is thus impossible.

Results of this analysis indicate, a keratin cover with gaps in the toothrow in the upper jaw evolved in the sauropod common ancestor. In contrast, a lower jaw with a keratin cover has a lower posterior probability than one having no keratin cover. *Mamenchisaurus jingyanensis* lacks a lower jaw, making this inference ambiguous with current data. Unlike theropods and ornithischians, most sauropods species share the same evolutionary pattern: rostral teeth coexist with bone proxies for keratin while caudal segment of the jaws do not acquire keratin cover proxies and lose teeth. Within the Sauropodomorpha lineage, tooth reduction does not occur before the appearance a keratin cover.

Groups	Toothrow with gaps and no keratin cover (1)	Complete toothrow and no keratin cover (2)	Edentulous jaw with keratin cover (3)	Toothrow with gaps and keratin cover (4)	Complete toothrow and keratin cover (5)
Sauropodomorpha	0.022	0.953	0~	0~	0.002
Massospondylidae +	0.001	0.992	0	0	0
Massospondylidae	0.034	0.907	0~	0	0
Massospondylidae -	0.002	0.004	0~	0.284	0.697
<i>Anchisaurus</i> +	0.053	0.820	0.001	0~	0.013
Sauropoda	0.072	0.114	0.040	0.373	0.416
Diplodocidae +	0.011	0.006	0~	0.921	0.032
Camarasauridae +	0.010	0.014	0.001	0.076	0.851
Brachiosauridae +	0.053	0.086	0.017	0.410	0.416
Titanosauria	0.130	0.169	0.062	0.490	0.166

Table 11. Summary of median posterior predictive results for ancestral reconstruction for states of the upper jaw of Sauropodomorpha. All measurements truncated to the third decimal. Rows ordered from inclusive to least inclusive taxonomic groups. The highest posterior probability for each taxonomic group is highlighted in green. “+” refers to the ancestor that includes the taxon name that is written before it and the taxa that is written in the rows bellow, and “-” refers to an inclusive group within the taxon named before this symbol.

Groups	Toothrow with gaps and no keratin cover (1)	Complete tooththrow and no keratin cover (2)	Edentulous jaw with keratin cover (3)	Toothrow with gaps and keratin cover (4)	Complete tooththrow and keratin cover (5)
Sauropodomorpha	0.011	0.977	0~	0	0.002
Massospondylidae +	0.006	0.970	0~	0	0.015
Massospondylidae	0.019	0.819	0.003	0	0.141
Massospondylidae -	0.042	0.024	0.003	0	0.900
Anchisaurus +	0.055	0.794	0.017	0	0.103
Sauropoda	0.197	0.355	0.109	0	0.257
Diplodocidae +	0.018	0.004	0.001	0.948	0.008
Camarasauridae +	0.050	0.378	0.002	0	0.511
Brachiosauridae +	0.121	0.738	0.021	0	0.077
Titanosauria	0.198	0.536	0.059	0	0.128

Table 12. Summary of median posterior predictive results for ancestral reconstruction for states of the lower jaw of Sauropodomorpha. All measurements truncated to the third decimal. Rows ordered from inclusive to least inclusive taxonomic groups. The highest posterior probability for each taxonomic group is highlighted in green. “+” refers to the ancestor that includes the taxon name that is written before it and the taxa that is written in the rows bellow, and “-” refers to an inclusive group within the taxon named before this symbol.

Ornithischians

Both the upper and the lower jaw RJ-MCMC reconstruction suggest that jaws with keratin cover and gaps in tooththrow were ancestral for Ornithischia (Fig. 16; Table 13, 14) and is consistent with the Ornithischian synapomorphy of having an edentulous beak confined to the prementary [Galton, 1973; Benton, 2005]. In the upper jaw, the character coding used here conceals a diversity of tooththrow gap locations regarding evolutionary rates and ancestral conditions.

Heterodontosaurs, and basal species of Thyreophora, Cerapoda, and other ornithischians have a tooththrow gap between the premaxilla and maxilla [Fastovsky & Weishampel, 2016]. Later forms evolve an edentulous premaxilla.

The facial texture and a toothless area at the tip of jaws, before the first premaxilla tooth in the upper jaw and the edentulous prementary in the lower jaw, in *Heterodontosaurus tuckii* and

Lesothosaurus diagnosticus, suggest these taxa likely possessed a small keratin cover on the premaxilla [Serenó, 2012; Porro et al., 2015]. This structure later expanded to form the rhamphotheca in some descendants. Edentulous beaks confined to the premaxilla evolved independently in thyreophorans, ornithomimids, neoceratopsians and pachycephalosaurs.

The ancestor of ceratopsians is reconstructed as having a complete toothrow with a keratin cover, an inference influenced by *Yinlong downsi*, which has a complete toothrow and is the most basal ceratopsian. The ancestral node that includes *Agilisaurus louderbacki*, *Jeholosaurus shangyuanensis*, and Cerapoda is also reconstructed as having a complete toothrow, again influenced by the two most basal species which have this condition.

Yinlong downsi is the only ceratopsian in the dataset that has a complete toothrow. The holotype skull has three teeth of different sizes that occupy the total length of the premaxilla [Han et al., 2016]. The first maxillary tooth begins immediately behind the premaxillary suture, eliminating any diastema [Han et al., 2016]. *Y. downsi* is thus unusual because the diastema between the premaxilla and the maxilla is present in other basal ceratopsians and in cerapodans generally [Fastovsky & Weishampel, 2016]. It has a small toothless rostral bone, which is unique to ceratopsians. This bone has been interpreted to form a beak. In more advanced ceratopsians, such as *Triceratops horridus*, this bone becomes enlarged.

Agilisaurus louderbacki (Jurassic) and *Jeholosaurus shangyuanensis* (Cretaceous) are two basal ornithischians of unknown taxonomic affinity. Both possess a complete toothrow in the upper jaw that coexists with a shallow grooved premaxilla surface [Guanzhao, 1997; Barret et. al., 2005a].

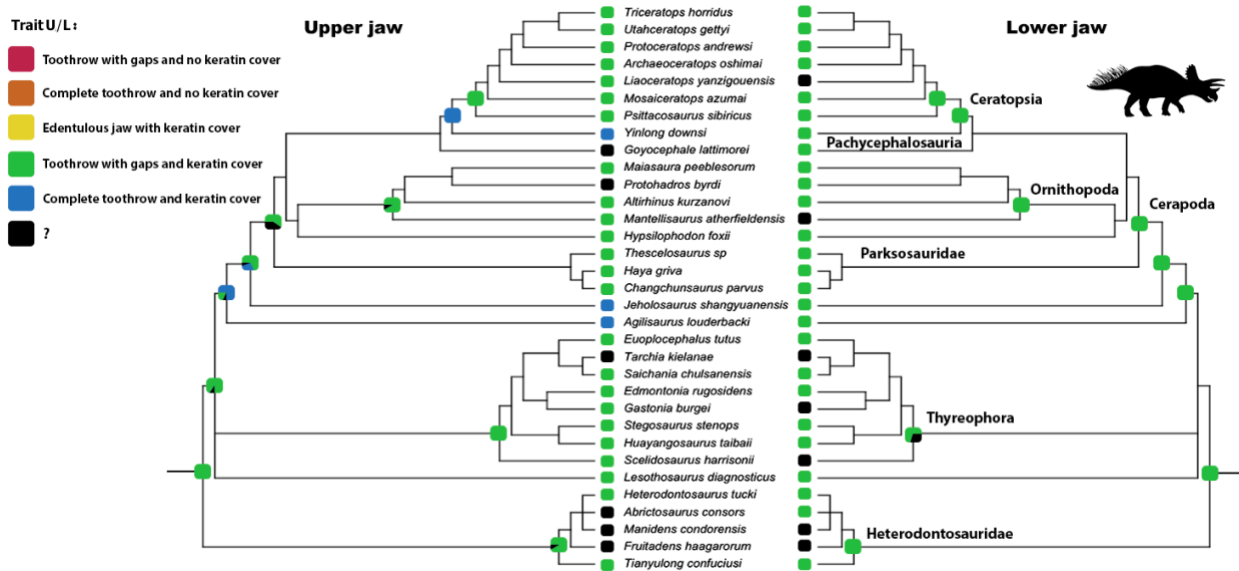


Fig. 16. Ancestral reconstruction of the upper jaw trait (U) and the lower jaw trait (L) in ornithischians. Missing data or uncertain ancestral reconstruction highlighted in black, states of traits highlighted in five different colors (red, orange, yellow, green, blue) following Table 3, and grey squares indicate where the BF test was performed. Phylogeny follows the tree of Button & Zanno [2020] using *ape* and *phytools* R packages. The tree excludes most species that were not included in the project. Dinosaur silhouette from *Phylopic.org* [2020]: D. Tana.

Groups	Tooththrow with gaps and no keratin cover	Complete tooththrow and no keratin cover	Edentulous jaw with keratin cover	Tooththrow with gaps and keratin cover	Complete tooththrow and keratin cover
	(1)	(2)	(3)	(4)	(5)
Dinosauria	0~	0.998	0	0	0
Ornithischia	0.007	0.014	0~	0.957	0.015
Heterodontosauridae	0.024	0.023	0.001	0.871	0.052
Thyreophora	0.002	0.010	0~	0.971	0.009
Agilisaurus +	0.010	0.006	0~	0.230	0.740
Jeholosaurus +	0.007	0.018	0~	0.688	0.265
Cerapoda	0.009	0.011	0~	0.595	0.356
Ornithomimidae	0.039	0.044	0.003	0.810	0.062
Ceratopsia	0~	0.001	0~	0.015	0.917
Ceratopsia -	0.005	0.007	0~	0.963	0.012

Table 13. Summary of median posterior predictive results for ancestral reconstruction for states of the upper jaw of Dinosauria and Ornithischia. All measurements are truncated to the third decimal. Rows ordered from inclusive to least inclusive taxonomic groups. The highest posterior probability for each taxonomic group is highlighted in green. “+” refers to the ancestor that includes the taxon name that is written before it and the taxa that is written in the rows below, and “-” refers to an inclusive group within the taxon named before this symbol.

Groups	Toothrow with gaps and no keratin cover (1)	Complete toothrow and no keratin cover (2)	Edentulous jaw with keratin cover (3)	Toothrow with gaps and keratin cover (4)	Complete toothrow and keratin cover (5)
Dinosauria	0.001	0.998	0~	0	0~
Ornithischia	0.006	0.002	0~	0.979	0.002
Heterodontosauridae	0.018	0.007	0.001	0.946	0.011
Thyreophora	0.103	0.051	0.028	0.739	0.066
Agilisaurus +	0.014	0.001	0~	0.966	0.004
Jeholosaurus +	0.026	0.004	0.002	0.943	0.009
Cerapoda	0.005	0.003	0~	0.982	0~
Ornithopoda	0.046	0.029	0.011	0.860	0.031
Ceratopsia	0.002	0~	0~	0.991	0.001
Ceratopsia -	0.012	0.004	0~	0.965	0.006

Table 14. Summary of median posterior predictive results for ancestral reconstruction for states of the lower jaw of Dinosauria and Ornithischia. All measurements are truncated to the third decimal. Rows ordered from inclusive to least inclusive taxonomic groups. The highest posterior probability for each taxonomic group is highlighted in green. “+” refers to the ancestor that includes the taxon name that is written before it and the taxa that is written in the rows bellow, and “-” refers to an inclusive group within the taxon named before this symbol.

Evolutionary Rates

The evolutionary rates analysis (Table 15) for both jaws does not reject the null hypothesis ($BF < 2$) that the presence or absence of a keratin cover does not affect the tooth loss rate in both jaws for dinosaurs (ET 1). There is support against Dollo’s Law ($BF > 2$) in the upper jaw when evolving a complete toothrow from ancestors with gaps (ET 2).

Trait	Models	SS LMh	BF
<i>Upper jaw (U)</i>	<i>RJ-MCMC</i>	-81.053556	-
	<i>ET 1</i>	-80.332429	-1.442254
	<i>ET 2</i>	-83.499709	4.892306*
<i>Lower jaw (L)</i>	<i>RJ-MCMC</i>	-72.665854	-
	<i>ET 1</i>	-72.301957	-0.727794
	<i>ET 2</i>	-72.005348	-1.321012

Table 15. Evolutionary transition models in Dinosauria for the upper jaw trait and the lower jaw trait, and their respective Stepping-Stone Sampler Log Marginal likelihoods (SS LMh) and Bayes Factor (BF). Traits defined in Table 3. RJ-MCMC model without restrictions (RJ-MCMC), evolutionary transitions for tooth loss fixed to be equal (ET1), tooth increase evolutionary transitions fixed to 0 (ET2) to test whether KC affects tooth loss rate. * RJ-MCMC model without restrictions is supported (BF>2).

The RJ-MCMC model without restrictions for both the upper jaw trait (*U*) and lower jaw trait (*L*) showed different probabilities for evolutionary transitions (Table. 16, 17; Fig. 17, 18).

Both *U* and *L* show transition probabilities of 0 to evolve teeth from an edentulous ancestor.

Another common pattern is a higher variation in rates of tooththrow evolution condition when ancestors do not have a keratin cover, whereas ancestors with keratin cover have a lower variation in rates of tooththrow evolution. In addition, both allow for tooth gain and tooth loss.

Unlike the model for trait *U*, the model for trait *L* does allow evolutionary transitions where there is keratin cover gain or loss while the tooththrow condition does not change.

Transition probabilities	0	1	2	3	4	5
0	-	0	0	0	0	0
1	0	-	0.029531	0.0259925	0	0
2	0	0.0313265	-	0.030812	0.031113	0
3	0	0	0	-	0	0
4	0	0	0	0	-	0.031218
5	0	0.0073685	0	0.0004995	0.0307125	-

Table 16. RJ-MCMC model without restrictions of trait *U* in Dinosauria. Trait *U* is defined in Table 3. Trait states: Toothrow with gaps and no keratin cover (1), complete toothrow and no keratin cover (2), edentulous jaw with keratin cover (3), toothrow with gaps and keratin cover (4), complete toothrow and keratin cover (5). Light orange highlights the probability of evolving teeth from and edentulous ancestor. Blue highlights the probabilities of evolving a complete toothrow from and ancestor with gaps in the toothrow. Yellow highlights the probabilities of losing teeth.

Transition probabilities	0	1	2	3	4	5
0	-	0	0	0	0	0
1	0	-	0.027363	0.020725	0.02544	0.0212695
2	0	0.0296285	-	0.0200985	0.018565	0.0197515
3	0	0	0	-	0	0
4	0	0	0	0	-	0
5	0	0.0198755	0.0222905	0.0196025	0.0212235	-

Table 17. Rates of reversible jump model of trait *L* in Dinosauria. Trait *L* is defined in Table 3. Trait states: Toothrow with gaps and no keratin cover (1), complete toothrow and no keratin cover (2), edentulous jaw with keratin cover (3), toothrow with gaps and keratin cover (4), complete toothrow and keratin cover (5). Light orange highlights the probability of evolving teeth from and edentulous ancestor. Blue highlights the probabilities of evolving a complete toothrow from and ancestor with gaps in the toothrow. Yellow highlights the probabilities of losing teeth.

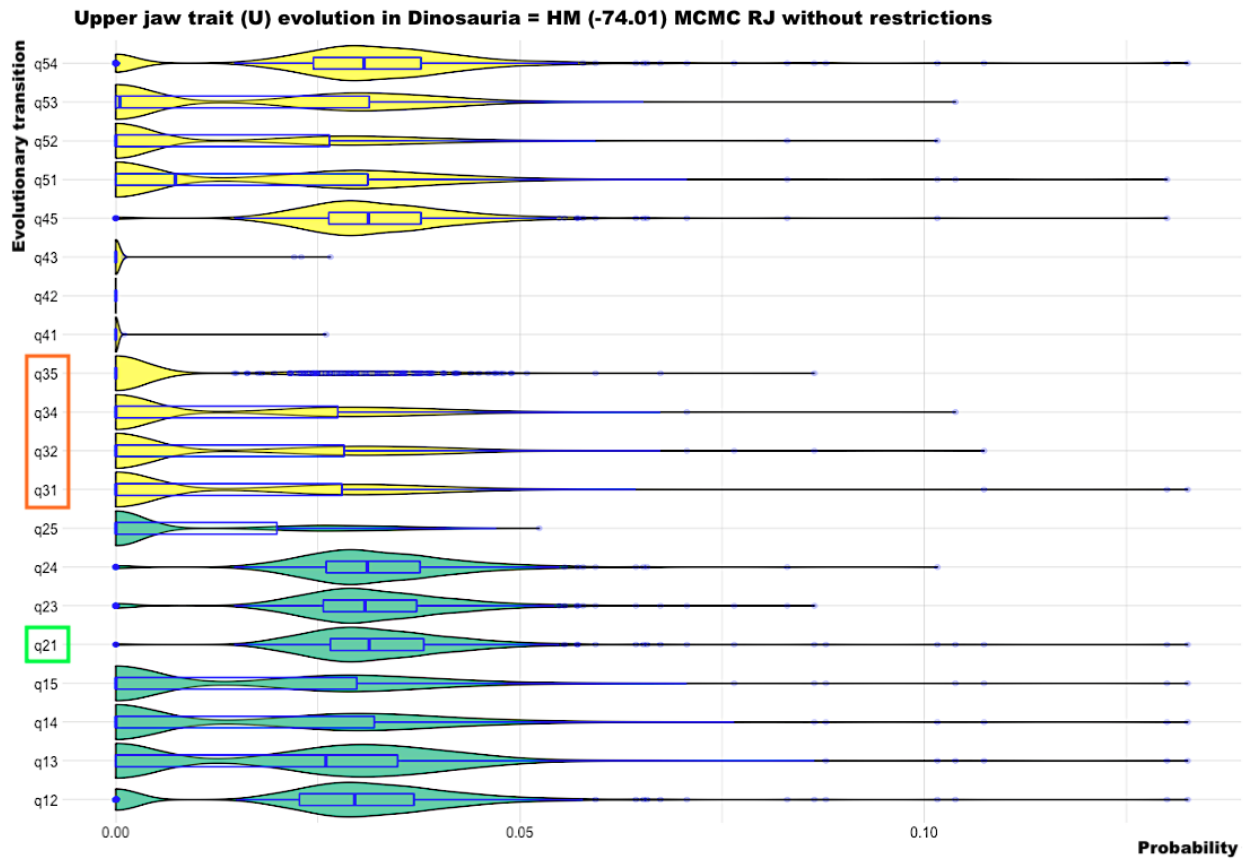


Fig. 17. Violin plots with whisker plots showing probabilities of evolutionary transitions of trait *U* in Dinosauria. Trait *U* is defined in Table 3. Evolutionary transitions with keratin cover in yellow and without keratin cover in aquamarine. The orange box highlights transitions from edentulous to toothed and the green box highlights the highest evolutionary transition probability. HM: Harmonic mean.

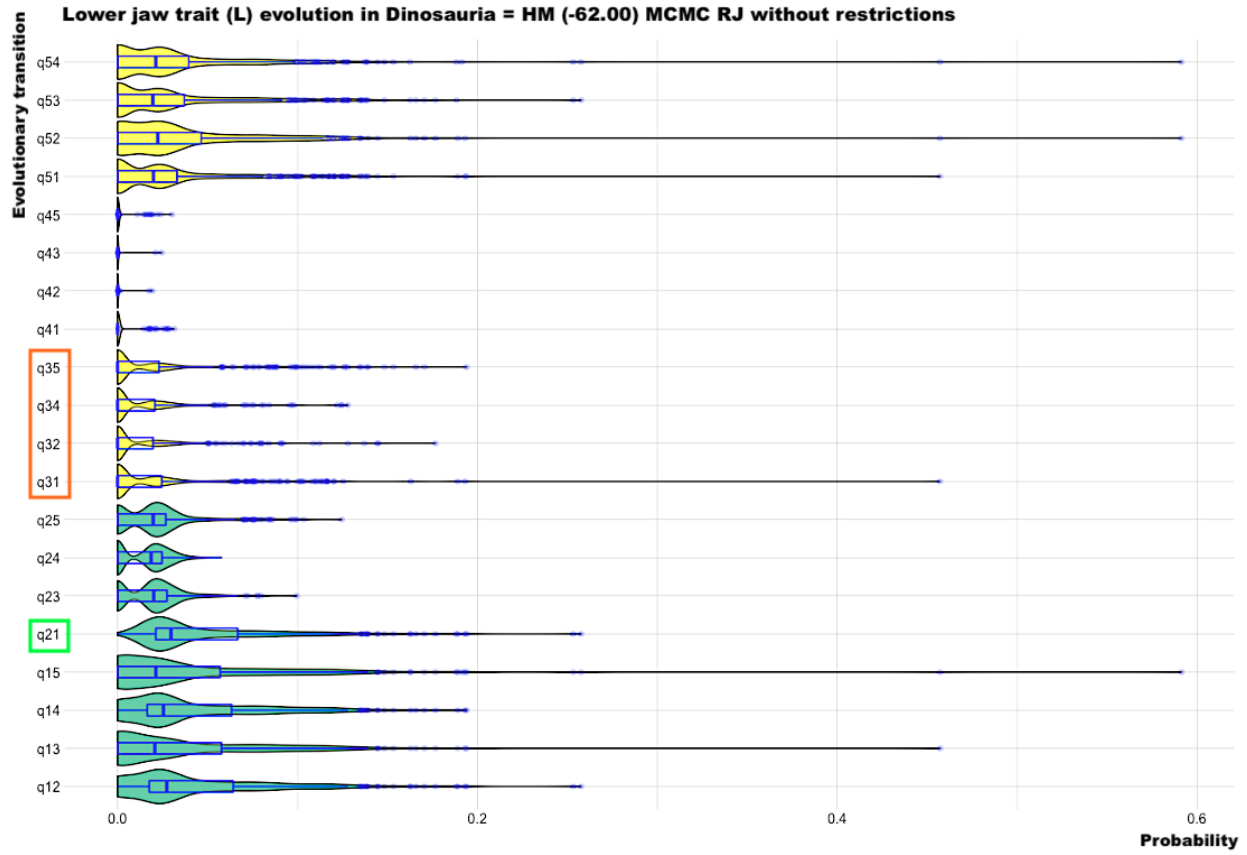


Fig. 18. Violin plots with whisker plots showing probabilities of evolutionary transitions of trait *L* in Dinosauria. Trait *L* is defined in Table 3. Evolutionary transitions with keratin cover in yellow and without keratin cover in aquamarine. The orange box highlights transitions from edentulous to toothed and the green box highlights the highest evolutionary transition probability. HM: Harmonic mean.

DISCUSSION

Coevolution Assessment

In extant birds and turtles, there is a negative relationship between teeth and rhamphotheca development. However, the fossil record shows that forms unseen in extant taxa can exist and some non-avian dinosaur fossils suggest that these structures may have co-occurred in the past. This study finds support for the hypothesis that toothrow reduction in dinosaurs, including Mesozoic birds, was driven by the evolution of beak-like keratin on the margin of the jaws. That said, the analyses conducted here do not explain complete tooth loss.

Ancestral Reconstruction

According to Brocklehurst & Field, 2021, there is no overarching trend towards edentulism in avialans. Nevertheless, there is partial tooth reduction before the evolution of the rhamphotheca. In our study, analyses suggest that most theropod groups underwent an independent reduction in the toothrow before evolving beaks. The evolutionary reduction of teeth occurs in Ornithischia and Sauropodomorpha but not before the appearance of keratin covers, suggesting a much wider state space is possible for tooth and beak morphology in vertebrates than would be suggested by extant taxa. An edentulous beak confined to the predentary is a synapomorphy for Ornithischia. The transition from partial dentition to a complete toothrow may have occurred in isolated ornithischian and sauropodomorph groups with keratin covers.

There are two caveats with the ancestral reconstruction analyses: tooth location in relation to the keratin cover and sample size. Ornithischian toothrow distribution in the upper

jaw is more diverse than the lower jaw, but this difference is not included in the character coding. Sauropods are the only group of dinosaurs where tooth-bearing jawbones have a large area for keratin cover proxies, whereas the portion of the jaws that lose teeth do not have the keratin cover proxies. This is also hidden by the character coding.

Parameter estimation, such as ancestral state reconstruction and evolutionary rate, is also difficult to estimate with small sample sizes (of character state changes) in RJ-MCMC models. Statistical power is low in small sample sizes and thus parameter estimations are prone to bias [Ackerly, 2000; Heath et al., 2008]. For example, in this study the ancestor of oviraptor and the ancestor of ornithuromorph birds are reconstructed to have edentulous jaws with keratin cover despite having a toothed descendant. Oviraptor ancestral reconstruction is not supported by the BF tests when compared to models where the ancestors are toothed instead. The absence of basal taxa could also explain the lack of intermediate steps of tooth reduction before keratin cover evolution in ornithischians and most sauropodomorphs.

An alternative hypothesis to explain “beak” and teeth evolution in sauropodomorphs is that the facial grooves with pits are not proxies for beak-like keratin. As explained by Martínez [2009], these osteological features have also been observed in jaws of extant mammals, such as hippopotamuses and manatees, that have highly mobile lips. Non-avian dinosaurs are thought to have lacked facial muscles associated with mobile or prehensile lips. Wiersma & Sanders [2017] have proposed that the jaws of sauropods, such as *Camarasaurus*, could have been covered by thick gingival connective tissue and scales or beak-like keratin on top. The jaws were thus protected from abrasive plant matter and had biomechanical support for teeth with reduced roots.

Tooth Rate Evolution and Dollo's Law

We would expect a statistically significant higher evolutionary rate of tooththrow reduction in dinosaurs with keratin cover if beak-like keratin provided an adaptive advantage over teeth. This does not seem to be the case: our analysis does not detect an effect of the keratin cover on the rate of tooththrow evolution. The evolutionary rate of tooth loss is higher in species without a keratin cover. This finding obscures the developmental and function antagonistic relationship between teeth and beaks.

According to Gould [1970], Dollo's law states that complex morphological features that are lost through evolution can never be acquired back. Jaw edentulism is thought to be permanent for tetrapods [Louchart & Virrot, 2011; Collin & Miglietta, 2008; Brocklehurst & Field, 2021]. The sole exception would be the frog species *Gastrotheca guentheri*, which evolved back a complete lower jaw tooththrow despite its absence since 225-330 million years in the common ancestor of frogs [Wiens, 2011]. Possible explanations include duplication and migration of existing functional tooth genes nearby [Collin & Miglietta, 2008; Yedid et al., 2008; Wiens, 2011], such as the upper jaw.

This study's tooth rate analysis support Dollo's law in lineages that have lost the entire tooththrow in either jaw. However, there is evidence for evolving a continuous tooththrow from an ancestor with gaps, but this is not evidence against Dollo's Law. The evolution of a complete tooththrow can occur due to subnarinal gap reduction, rostral-caudal enlargement of teeth, and (or) an increase in the number of teeth. Coding used in this analysis does not allow for distinguishing between these situations and thus cannot be used to test Dollo's Law. Ornithuromorpha is the

only group where teeth evolve again from an edentulous ancestor, but this ancestral reconstruction might be due to small sample size of the taxon.

CONCLUSIONS

According to my results, the three dinosaur lineages had distinct patterns of “evolutionary steps” of tooththrow variation in relation to keratin cover absence/ presence. Tooththrow reduction occurs in all three, but tooththrow reduction happens before keratin only along the theropod line. Ornithischian and Sauropod lineages could have larger gaps in the fossil record, where the missing diversity might confound (or explain) the patterns uncovered in this work.

Future research with more complete sampling of basal sauropodomorphs and ornithischians might shed light on the differences detected among the three main dinosaur lineages. Furthermore, additional morphological studies on extant/extinct animals are needed to determine what other bone landmarks (superficial and internal) help differentiate beak-like keratin and other facial structures in fossils.

The findings of this study suggest that a partial tooththrow reduction occurs when beak-like keratin proxies are present. The results do not support complete tooth loss associated with “beaks”. My results are ambiguous as to whether tooth reduction is dependent on keratin cover location. The first two statements align with current macroevolution research in avialans, whereas the latter is not.

This research only accounted for facial keratin and thus might not apply for “true” rhamphotheca, which covers both the facial and oral sides of the jaw. However, facial beak-like keratin was widespread through Mesozoic dinosaurs, and toothless beaks seen in extant birds are just one variation on this theme. Oral expansion of facial keratin evolved later in some groups of dinosaurs independently.

APPENDICES

APPENDIX A

SPECIMEN LIST WITH CODED TRAITS, TAXONOMIC CLASSIFICATION AND CITED
REFERENCE

Species	Other	Identification	Source	Upper jaw			Lower jaw			Group 1	Group 2	Lineage
				T R	K C	U	T R	K C	L			
<i>Anzu_wyliei</i>		CM 78000	Lamanna et al., 2014	0	1	3	0	1	3	Oviraptorosauria	Coelurosauria	Theropoda
<i>Apatoraptor_pennatus</i>		TMP 1993.051.0001	Funston & Currie, 2016	-	-	-	0	1	3	Oviraptorosauria	Coelurosauria	Theropoda
<i>Archaeopteryx_lithographica</i>		"Eichstätt specimen", WDC-CSG-100	Wellnhofer, 1990; Rahut, 2014	2	0	2	2	0	2	Archaeopteryx	Aviale	Theropoda
<i>Beipiaosaurus_inexpectus</i>		IVPP V 11559	Liao & Xu, 2018	1	1	4	1	1	4	Therizinosauria	Coelurosauria	Theropoda
<i>Bistahieversor_sealeyi</i>		NMMNH P-27469	Carr & Williamson, 2010	2	0	2	2	0	2	Tyrannosauridae	Coelurosauria	Theropoda
<i>Caenagnathus_collinsi</i>		CMN 8776	Currie et al., 1993	-	-	-	0	1	3	Oviraptorosauria	Coelurosauria	Theropoda
<i>Caudipteryx_zoui</i>		NGMC 97-4-A	Qiang et al., 1998	1	-	-	0	-	-	Oviraptorosauria	Coelurosauria	Theropoda
<i>Coelophysis_bauri</i>		MCZ 4327; AMNH 7224	Colbert, 1989	2	0	2	2	0	2	-	Indet. Theropoda	Theropoda
<i>Confuciusornis_dui</i> *	<i>Confuciusornis_sanctus</i>	BMNHC-PH986	Martin et al., 1998; Chiappe & Qingjin, 2016	0	1	3	0	1	3	Confuciusornithidae	Avialae	Theropoda
<i>Deinocheirus_mirificus</i>		MPC-D 100/127	Lee et al., 2014	0	1	3	0	1	3	Ornithomimosauria	Coelurosauria	Theropoda
<i>Dilong_paradoxus</i>		IVPP V14243	Xu et al., 2004	1	0	1	2	0	1	Tyrannosauridae	Coelurosauria	Theropoda
<i>Epidexipteryx_hui</i>		IVPP V15471	Zhang et al., 2008	1	-	-	1	-	-	Scansoriopterygidae	Coelurosauria	Theropoda
<i>Erlikosaurus_andrewsi</i>		PST 100/110	Clark et al., 1994	1	1	4	1	1	4	Therizinosauria	Coelurosauria	Theropoda
<i>Falcarius_utahensis</i>		UMNH VP 14526	Kirkland et al., 2005	-	-	-	2	-	-	Therizinosauria	Coelurosauria	Theropoda
<i>Gallimimus_bullatus</i>		G.I.No.DPS 100/11	Osmolska et al., 1972	0	1	3	0	1	3	Ornithomimosauria	Coelurosauria	Theropoda
<i>Garudimimus_brevipes</i>		GIN 100/13	Kobayashi & Barsbold, 2005	0	1	3	0	1	3	Ornithomimosauria	Coelurosauria	Theropoda

Table A1. Specimen list with coded traits used in this study. * Replaced with species of the same genus. + Included specimens from a different species of the same genus. Specimens observed at museums in blue.

<i>Giganotosaurus_ carolinii</i>		MUCPv-95	Calvo & Coria, 1998	-	-	-	-	0	-	Carnosauria	Avetheropoda	Theropoda
<i>Gigantoraptor_ erlianensis</i>		LH V0011	Xu et al, 2007	-	-	-	0	1	3	Oviraptosauria	Coelurosauria	Theropoda
<i>Guanlong_wucaii</i>		IVPP V14531	Xu et al, 2006	1	0	1	2	0	2	Tyrannosauridae	Coelurosauria	Theropoda
<i>Hesperornis_ regalis</i>		YPM 1206	Olso, 1976	1	1	4	1	1	4	Ornithothoraces	Aviale	Theropoda
<i>Ichthyornis_ dispar</i>		YPM 1450; FHSM VP- 18702	Oslo, 1976; Field et al., 2018	1	1	4	1	1	4	Oviraptosauria	Coelurosauria	Theropoda
<i>Incisivosaurus_ gauthieri</i>		IVPP V13326	Xu et al., 2002a	1	1	4	1	1	4	Oviraptosauria	Coelurosauria	Theropoda
<i>Jianchangosaurus_yi xianensis</i>		41HIII-0308A	Pu et al., 2013	1	1	4	1	0	1	Therizinosauria	Coelurosauria	Theropoda
<i>Khaan_mckennai</i>		IGM 100/973	Balanoff & Norell, 2012	0	1	3	0	1	3	Oviraptosauria	Coelurosauria	Theropoda
<i>Longipteryx_ chaoyangensis</i>		BMNHC- PH826; DNHM- D2889; V 12325	Zhang et al, 2001; Wang et al, 2015; Chiappe & Qingjin, 2016	1	1	4	1	1	4	Enantiornithes	Aviale	Theropoda
<i>Monolophosaurus_ jiangi</i>		IVPP 84019	Brusatte et al., 2010	2	0	2	2	0	2	-	Non-Avetheropoda Tetanura	Theropoda
<i>Pelecanimimus_ polyodon</i>		LH 7777	Pérez-Moreno et al., 1994	1	0	1	2	0	2	Ornithomimosauria	Coelurosauria	Theropoda
<i>Pengornis_ houi</i>		IVPP V15336	Zhou et al., 2008	2	0	2	2	0	2	Enantiornithes	Aviale	Theropoda
<i>Sapeornis_ chaoyangensis</i>		STM 16-18; HGM- 41HIII0405; BMNHC- PH1067	Zhou & Zhang, 2003; Chiappe & Qingjin, 2016; Wang et al, 2017a	2	0	2	1	0	1	Sapeornis	Aviale	Theropoda
<i>Saurornitholestes_ langstoni</i>		UALVP 55700	Currie & Evans, 2019	2	0	2	2	0	2	Paraves	Coelurosauria	Theropoda
<i>Schizoura_lii</i>		IVPP V 16861	Shuang et al., 2012	0	1	3	0	1	3	Ornithothoraces	Aviale	Theropoda

Table A1. Continued.

<i>Segnosaurus_galbinensis</i>		MPC-D 100/80; GIN 100/111	Barsbold & Perle, 1980; Zanno et al., 2016	-	-	-	1	1	4	Therizinosauria	Coelurosauria	Theropoda
<i>Shenqiornis_mengi</i>		DNHM D2950/1	Wang et al., 2010	2	0	2	2	0	2	Enantiornithes	Aviale	Theropoda
<i>Sinraptor_dongi</i>		IVPP 10600	Currie & 1993; Brusatte et al., 2010	2	0	2	2	0	2	Carnosaurs	Avetheropoda	Theropoda
<i>Struthiomimus_altus</i>		RTMP 1990.026.0001; AMNH 5339	Osborn, 1917; Cuff & Rayfield, 2015	0	1	3	0	1	3	Ornithomimosauria	Coelurosauria	Theropoda
<i>Tawa_hallae</i>		GR 241	Nebitt et al., 2009	1	0	1	2	0	2	-	Indet. Theropoda	Theropoda
<i>Tyrannosaurus_rex</i>		MOR-1125	MOR visit	2	0	2	2	0	2	Tyrannosauridae	Coelurosauria	Theropoda
<i>Velociraptor_mongoliensis</i>		GIN 100/25	Barsbold & Osmolska, 1999	2	0	2	2	0	2	Paraves	Coelurosauria	Theropoda
<i>Yi_qi</i>		STM 31-2	Xu et al., 2015	1	-	-	1	-	-	Scansoriopterygidae	Coelurosauria	Theropoda
<i>Zupaysaurus_rougieri</i>		PULR-076	Arcucci & Rodolfo, 2003; Ezcurra & Novas, 2007	-	-	-	2	0	2	-	Indet. Theropoda	Theropoda
<i>Abydosaurus_mcintoshi</i>		DINO-16488	BYU visit	2	1	5	2	0	2	Brachiosauridae	Sauropoda	Sauropodomorpha
<i>Adeopapposaurus_mognai</i>		PVSJ610	Martínez, 2009	2	1	5	2	1	5	Massospondylidae	Prosauropoda	Sauropodomorpha
<i>Anchisaurus_polyzelus</i>		YPM 1883	Yates, 2010	2	0	2	2	0	2	Indet. Sauropodomorpha	Prosauropoda	Sauropodomorpha
<i>Apatosaurus_ajax</i> *	<i>Apatosaurus</i>	BYU 16874; BYU 16825	BYU visit	1	1	4	1	1	4	Diplodocidae	Sauropoda	Sauropodomorpha
<i>Apatosaurus_louisae</i> *	<i>Apatosaurus</i>	BYU 16874; BYU 16825	BYU visit	1	1	4	1	1	4	Diplodocidae	Sauropoda	Sauropodomorpha
<i>Buriolestes_Schultzi</i>		ULBRA-PVT280; CAPP/UFESM 0035	Cabreira et al., 2016; Müller et al., 2018	2	0	2	2	0	2	Indet. Sauropodomorpha	Prosauropoda	Sauropodomorpha
<i>Camarasaurus_lentus</i> *	<i>Camarasaurus</i> _sp.	BYU 24688; BYU 24688	BYU visit	2	1	5	2	1	5	Camarasauridae	Sauropoda	Sauropodomorpha
<i>Coloradisaurus_Brevis</i>		PVL 3967	Apaldetti, 2014	2	-	-	2	-	-	Massospondylidae	Prosauropoda	Sauropodomorpha
<i>Galeamopus_sp</i>		SMA 0011	Tschopp & Mateus, 2017	1	1	4	1	1	4	Diplodocidae	Sauropoda	Sauropodomorpha

Table A1. Continued.

<i>Jingshanosaurus_xinwaensis</i>		LFGT-ZLJ0113	Zhang et al., 2019	2	0	2	2	0	2	Indet. Sauropodomorpha	Prosauropoda	Sauropodomorpha
<i>Leyesaurus_marayensis</i>		PVSJ 706	Apaldetti et al., 2011	1	1	4	-	1	-	Massospondylidae	Prosauropoda	Sauropodomorpha
<i>Lufengosaurus_huenei</i>		IVPP V15	Barret et al., 2005b	2	0	2	2	0	2	Massospondylidae	Prosauropoda	Sauropodomorpha
<i>Malawisaurus_dixeyi</i>		MAL-174	Jacobs et al., 1993	-	-	-	2	-	-	Titanosauria	Sauropoda	Sauropodomorpha
<i>Mamenchisaurus_jingyanensis</i>		CV00734	Zhang et al., 1998	2	1	5	2	-	-	Mamenchisauridae	Sauropoda	Sauropodomorpha
<i>Massospondylus_carinatus</i>		BP/1/4934; BP/1/5241; BP/1/4376	Gow, et al., 1990; Chapelle, 2018	2	0	2	2	0	2	Massospondylidae	Prosauropoda	Sauropodomorpha
<i>Nemegtosaurus_mongoliensis</i>		Z.PAL.MgD-I/9	Wilson, 2005	1	1	4	1	0	1	Titanosauria	Sauropoda	Sauropodomorpha
<i>Nigersaurus_taqueti</i>		MNN GAD 512	Sereno et al., 2007	1	1	4	1	1	4	Rebbachisauridae	Sauropoda	Sauropodomorpha
<i>Pampadromaeus_barberenai</i>		ULBRA-PVT016	Cabreira et al., 2011	2	0	2	1	0	1	Indet. Sauropodomorpha	Prosauropoda	Sauropodomorpha
<i>Panphagia_protos</i>		PVSJ 874	Martinez & Alcober, 2009	-	-	-	2	0	2	Indet. Sauropodomorpha	Prosauropoda	Sauropodomorpha
<i>Pantydraco_caducus</i>		A-M: P24	Galton & KerMack, 2010	2	-	-	2	-	-	Indet. Sauropodomorpha	Prosauropoda	Sauropodomorpha
<i>Plateosaurus_engelhardti</i>		SMNS 13200	Galton, 2012	2	0	2	2	0	2	Plateosauridae	Prosauropoda	Sauropodomorpha
<i>Riojasaurus_incertus</i>		ULR 56	Bonaparte & Pumares, 1995	2	-	-	2	-	-	Indet. Sauropodomorpha	Prosauropoda	Sauropodomorpha
<i>Sarmientosaurus_musacchioi</i>		MDT-PV 2	Martinez et al., 2016	2	-	-	2	0	2	Titanosauria	Sauropoda	Sauropodomorpha
<i>Eoraptor_lunensis</i>		PVSJ 512	Sereno et al., 2012	2	0	2	2	0	2	-	-	Indet. Dinosauria
<i>Herrerasaurus_ischigualastensis</i>		PVSJ 407	Sereno et al., 1994	2	0	2	2	0	2	-	Herrerasauridae	Indet. Dinosauria
<i>Abrictosaurus_consors</i>		NHMK RU	Sereno, 2012	-	-	-	1	1	4	-	Heterodontosauridae	Ornithischia
<i>Agilisaurus_louderbacki</i>		ZDM T6011	Guangzhao, 1997	2	1	5	1	1	4	-	Indet. Ornithischia	Ornithischia
<i>Altirhinus_kurzanovi</i>		PIN 3386/8	Norman, 1998	1	1	4	1	1	4	Ornithopoda	Cerapoda	Ornithischia

Table A1. Continued.

<i>Archaeoceratops_oshimai</i>		IVPP V 11114	You & Dodson, 2003	1	1	4	1	1	4	Ceratopsia	Cerapoda	Ornithischia
<i>Changchunsaurus_parvus</i>		JLUM L0403-j-Zn2	Liyong et al., 2010	1	1	4	1	1	4	Parksosauridae	Indet. Ornithischia	Ornithischia
<i>Edmontonia_rugosidens</i>		TMP 98.98.01	Vickaryous, 2006	1	1	4	1	1	4	Ankylosauria	Thyreophora	Ornithischia
<i>Euoplocephalus_tutus</i>		AMNH 5405	Vickaryous & Russell, 2002	1	1	4	1	1	4	Ankylosauria	Thyreophora	Ornithischia
<i>Fruitadens_haagarorum</i>		LACM 115747; LACM 128258	Butler et al., 2012	1	-	-	-	-	-	-	Heterodontosauridae	Ornithischia
<i>Gastonia_burgei</i>		CEUM 1307	Kirkland, 1998	1	1	4	-	-	-	Ankylosauria	Thyreophora	Ornithischia
<i>Goyocephale_lattimorei</i>		GI SPS 100/1501	Perle et al., 1982	1	-	-	1	1	4	Pachycephalosauria	Cerapoda	Ornithischia
<i>Haya_griva</i>		IGM 100/2016	Makovicky et al., 2011	1	1	4	1	1	4	Parksosauridae	Cerapoda	Ornithischia
<i>Heterodontosaurus_tucki</i>		SAM-PK-K337	Norman et al., 2010	1	1	4	1	1	4	-	Heterodontosauridae	Ornithischia
<i>Huayangosaurus_taibaii</i>		IVPP V6728	Sereno & Zhimin, 1992	1	1	4	1	1	4	Stegosauria	Thyreophora	Ornithischia
<i>Hypsilophodon_foxii</i>		R 197; BMNH R2477	Huxley, 1870; Galton, 2001	1	1	4	1	1	4	Ornithopoda	Cerapoda	Ornithischia
<i>Jeholosaurus_shangyuanensis</i>		IVPP V12530 ;IVPP V15716	Barret et al., 2005a; Barret & Han, 2009	2	1	5	1	1	4	-	Indet. Ornithischia	Ornithischia
<i>Lesothosaurus_diagnosticus</i>		NHMUK PV RU B23; NHMUK PV RU B17	Porro et al., 2015	1	1	4	1	1	4	-	Indet. Ornithischia	Ornithischia
<i>Liaoceratops_yanzigouensis</i>		IVPP V12738	Xu et al., 2002b	2	1	5	-	-	-	Ceratopsia	Cerapoda	Ornithischia
<i>Maiasaura_peeklesorum</i>		PU 22405	Horner, 1983	1	1	4	1	1	4	Ornithopoda	Cerapoda	Ornithischia
<i>Mantellisaurus_atherfieldensis</i>		BMNH R5764; BMNH 3741	Hooley, 1925; Paul, 2008	1	1	4	-	-	-	Ornithopoda	Cerapoda	Ornithischia
<i>Mosaiceratops_azumai</i>		ZMNH M8856	Zheng et al, 2015	1	1	4	1	1	4	Ceratopsia	Cerapoda	Ornithischia
<i>Protoceratops_andrewsi</i>		AMNH 6251	Granger, 1923	1	1	4	1	1	4	Ceratopsia	Cerapoda	Ornithischia
<i>Protihadros_byrdi</i>		SMU 74582	Head, 2010	1	-	-	1	1	4	Ornithopoda	Cerapoda	Ornithischia

Table A1. Continued.

<i>Psittacosaurus_sibiricus</i>		PM TGU 16/4-20	Haily & Dodson, 2004; Averianov et al., 2006	1	1	4	1	1	4	Ceratopsia	Cerapoda	Ornithischia
<i>Saichania_chulsanensis</i>		GI SPS 100/151; IGM 100/1305	Maryanska et al., 1977; Carpenter et al., 2011	1	1	4	1	1	4	Ankylosauria	Thyreophora	Ornithischia
<i>Scelidosaurus_harrisonii</i>		NHMUK R1111; BRSMG Ce12785; BRSMG LEGL 0004	Norman, 2020	1	1	4	-	-	-	-	Thyreophora	Ornithischia
<i>Stegosaurus_stenops</i>		USNM-4934	Czerkas & Gillette, 1999	1	1	4	1	1	4	Stegosauria	Thyreophora	Ornithischia
<i>Thescelosaurus_sp*</i>	<i>Thescelosaurus_neglectus</i>	NCSM 15728	Boyd, 2014	1	1	4	1	1	4	Parksosauridae	Cerapoda	Ornithischia
<i>Tianyulong_confuciusi</i>		STMN 26-3	Zheng et al., 2009	1	1	4	1	1	4	-	Heterodontosauridae	Ornithischia
<i>Triceratops_horridus</i> +	<i>Triceratops_prosus</i>	AMNH 5116; MOR 1604	Scannella & Horner, 2009; MOR visit.	1	1	4	1	1	4	Ceratopsia	Cerapoda	Ornithischia
<i>Utahceratops_gett yi</i>		UMNH VP 12198; UMNH VP 16675; UMNH VP 16672; UMNH VP 12198	Sampson et al., 2010	1	1	4	1	1	4	Ceratopsia	Cerapoda	Ornithischia
<i>Yinlong_downsi</i>		IVPP V14530	Han et al., 2016	2	1	5	1	1	4	Ceratopsia	Cerapoda	Ornithischia

Table A1. Continued.

APPENDIX B

INSTITUTION ABBREVIATIONS

Abbreviation	Name	State/Province	Country
AMNH	American Museum of Natural History	New York	U.S.A.
BMNH [BM]	Natural History Museum [formerly British Museum " "]	England	U.K.
BP	Bernard Price Institute for Paleontological Research	Johannesburg	R.S.A.
BYU	Brigham Young University Earth Science Museum	Utah	U.S.A.
CAPPA/UFSM	Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia da Universidade Federal de Santa Maria	São Paulo	Brazil
CEUM	College of Eastern Utah Prehistoric Museum	Utah	U.S.A.
CMN [CM]	Canadian Museum of Nature	Ontario	Canada
DNHM	Dalian Natural History Museum	Liaoning	China
GIN	Mongolia Academy of Sciences	Ulan Baatar	Mongolia
GI SPS	Geological Institute, Academy of Sciences of the Mongolian People's Republic	Ulan Baatar	Mongolia
GR	Ghost Ranch Ruth Hall Museum	New Mexico	U.S.A.
IGM	Institute of Geology, Mongolia	Ulan Baatar	Mongolia
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology	Beijing	China
JLUM	Jilin University Museum	Changchun	China
LACM	Natural History Museum of Los Angeles County	California	U.S.A.
LFGT-ZLJ	Bureau of Land and Resources of Lufeng County	Guangdong	China
MAL	Malawi Department of Antiquities	-	Malawi
MCZ	Museum of Comparative Zoology	England	U.K.
MDT-PV	Museo Desiderio Torres, Paleovertebrados	Sarmiento	Argentina
MNN	Musée National du Niger	Miamey	Nigeria
MPC-D	Mongolian Paleontological Center, Mongolian Academy of Sciences	Ulan Baatar	Mongolia
MOR	Museum of the Rockies	Montana	U.S.A.
NCSM	North Carolina Museum of Natural Sciences	North Carolina	U.S.A.
NGMC	National Geological Museum of China	Beijing	China
NHUK	The Natural History Museum	England	U.K.
NMMNH	New Mexico Museum of Natural History and Science	New Mexico	U.S.A.
NMW	Naturhistorisches Museum	Vienna	Austria
PIN	Palaeontological Institute of Nauk	Moscow	Russia
PM TGU	Paleontological Museum, Tomsk State University	Tomsk Oblast	Russia
PU	Museum of Natural History, Princeton University	New Jersey	U.S.A.
PULR	Paleontología de Vertebrados, Fundación "Miguel Lillo"	Tucumán	Argentina
PVL	Instituto Miguel Lillo, Universidad de Tucumán	Tucumán	Argentina
PVSJ	Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan	San Juan	Argentina
SAM-PK	Iziko South Africa Museum	Western Cape	R.S.A.

Table B1. Institution abbreviation.

SMA	Sauriermuseum Aathal	Seegräben	Switzerland
SMNS	Staatliches Museum für Naturkunde, Stuttgart	Baden-Württemberg	Germany
SMU	South Methodist University	Texas	U.S.A.
STMN [STM]	Shandong Tianyu Museum of Nature	Shandong Province	China
RTPM [TMP]	Royal Tyrrell Museum of Palaeontology	Alberta	Canada
UALVP	University of Alberta Laboratory for Vertebrate Palaeontology	Alberta	Canada
ULBRA-PVT	Universidade Luterana do Brasil	Rio Grande do Sul	Brazil
ULR	University of La Rioja	La Rioja	Argentina
UMNH	Utah Natural History	Utah	U.S.A.
USNM	National Museum of Natural History, Smithsonian Institution	Washington, D.C.	U.S.A.
WDC	Wyoming Dinosaur Center	Wyoming	U.S.A.
YPM	Yale University, Peabody Museum of Natural History	Connecticut	U.S.A.
ZDM	Zigong Dinosaur Museum	Sichuan	China
ZMNH	Zhejiang Museum of Natural History	Zhejiang	China

Table B1. Continued.

APPENDIX C

COMPUTER PROGRAMS AND CITED REFERENCE TABLE

Name	Function	Source
<i>ape</i>	R package for phylogenetic analyses.	Paradis et al., 2004.
<i>BayesTraits V3</i>	Program for running phylogenetic comparative analysis among group species from a phylogeny or sample of phylogenies. It is used to test evolutionary hypothesis: coevolution of traits, evolutionary rates, ancestral reconstructions, etc.	Pagel & Meade, 2007.
<i>dplyr</i>	R package for data manipulation.	Wickham et al., 2015
<i>geiger</i>	R package for fitting macroevolutionary models to phylogenetic trees.	Harmon et al., 2009
<i>readxl</i>	R package for importing Excel datasets in R.	Wickham et al., 2019.
<i>MCMCglmm</i>	R package for running MCMCglmm.	Hadfield, 2010
<i>missForest</i>	R package for running MissForest MI.	Stekhoven & Bühlmann, 2012
<i>MuMIn</i>	R package for Comparing best model with information criterions.	Barton, 2009.
<i>phytools</i>	R package for plotting and manipulation of phylogenetic trees.	Revell, 2012.
<i>phangorn</i>	R package for computing the non-negative least-squares edge lengths with the condition that the tree is ultrametric.	Schliep, 2018

Table C1. Computer programs and cited references.

APPENDIX D

PFC VALUES TABLES AND PLOTS

Upper jaw			Lower jaw		
Vec_No	PFC	IdMiDat	Vec_No	PFC	IdMiDat
No.1	0.1871175	1	No.1	0.1381885	1
No.2	0.123623	1	No.2	0.1100987	1
No.3	0.1185741	1	No.3	0.1157166	1
No.4	0.119339	1	No.4	0.09838312	1
No.5	0.1127601	1	No.5	0.1157166	1
No.10	0.124388	1	No.10	0.1386681	1
No.15	0.1623317	1	No.15	0.1625788	1
No.20	0.1739596	1	No.20	0.1391477	1
No.25	0.1805386	1	No.25	0.1462044	1
No.30	0.1623317	1	No.30	0.1747739	1
No.40	0.1813035	1	No.40	0.1344889	1
No.75	0.1959914	1	No.75	0.15792	1
No.100	0.1871175	1	No.100	0.15792	1
No.125	0.1863525	1	No.125	0.1518224	1
No.150	0.2235312	1	No.150	0.1681968	1
No.1	0.1805386	2	No.1	0.1381885	2
No.2	0.1003672	2	No.2	0.1100987	2
No.3	0.1178091	2	No.3	0.1157166	2
No.4	0.1185741	2	No.4	0.09838312	2
No.5	0.130967	2	No.5	0.1157166	2
No.10	0.1425949	2	No.10	0.1386681	2
No.15	0.1491738	2	No.15	0.1625788	2
No.20	0.1681457	2	No.20	0.1391477	2
No.25	0.1987454	2	No.25	0.1462044	2
No.30	0.1646267	2	No.30	0.1747739	2
No.40	0.1987454	2	No.40	0.1344889	2
No.75	0.2045594	2	No.75	0.15792	2
No.100	0.2045594	2	No.100	0.15792	2
No.125	0.1820685	2	No.125	0.1518224	2
No.150	0.2111383	2	No.150	0.1681968	2
No.1	0.1871175	2	No.1	0.1381885	2
No.2	0.1178091	2	No.2	0.1100987	2
No.3	0.1003672	2	No.3	0.1157166	2
No.4	0.1135251	2	No.4	0.09838312	2

Table D1. PFC values by entry (IdMiDat), number of eigenvectors (Vec_No) and jaw.

No.5	0.1127601	2	No.5	0.1157166	2
No.10	0.1425949	2	No.10	0.1386681	2
No.15	0.1433599	2	No.15	0.1625788	2
No.20	0.1739596	2	No.20	0.1391477	2
No.25	0.1565177	2	No.25	0.1462044	2
No.30	0.1840575	2	No.30	0.1747739	2
No.40	0.1762546	2	No.40	0.1344889	2
No.75	0.1878825	2	No.75	0.15792	2
No.100	0.2060894	2	No.100	0.15792	2
No.125	0.1987454	2	No.125	0.1518224	2
No.150	0.2053244	2	No.150	0.1681968	2
No.1	0.1673807	3	No.1	0.1381885	3
No.2	0.1352509	3	No.2	0.1100987	3
No.3	0.1127601	3	No.3	0.1157166	3
No.4	0.1069461	3	No.4	0.09838312	3
No.5	0.1069461	3	No.5	0.1157166	3
No.10	0.1433599	3	No.10	0.1386681	3
No.15	0.1441248	3	No.15	0.1625788	3
No.20	0.1623317	3	No.20	0.1391477	3
No.25	0.1572827	3	No.25	0.1462044	3
No.30	0.1565177	3	No.30	0.1747739	3
No.40	0.1855875	3	No.40	0.1344889	3
No.75	0.1747246	3	No.75	0.15792	3
No.100	0.2068543	3	No.100	0.15792	3
No.125	0.1871175	3	No.125	0.1518224	3
No.150	0.2242962	3	No.150	0.1681968	3
No.1	0.1797736	4	No.1	0.1381885	4
No.2	0.1352509	4	No.2	0.1100987	4
No.3	0.1061812	4	No.3	0.1157166	4
No.4	0.1077111	4	No.4	0.09838312	4
No.5	0.1484088	4	No.5	0.1157166	4
No.10	0.1317319	4	No.10	0.1386681	4
No.15	0.1813035	4	No.15	0.1625788	4
No.20	0.1696756	4	No.20	0.1391477	4
No.25	0.1855875	4	No.25	0.1462044	4
No.30	0.1863525	4	No.30	0.1747739	4

Table D1. Continued.

No.40	0.1731946	4	No.40	0.1344889	4
No.75	0.1820685	4	No.75	0.15792	4
No.100	0.2134333	4	No.100	0.15792	4
No.125	0.1747246	4	No.125	0.1518224	4
No.150	0.2250612	4	No.150	0.1681968	4
No.1	0.1979804	5	No.1	0.1381885	5
No.2	0.129437	5	No.2	0.1100987	5
No.3	0.1185741	5	No.3	0.1157166	5
No.4	0.130202	5	No.4	0.09838312	5
No.5	0.1127601	5	No.5	0.1157166	5
No.10	0.124388	5	No.10	0.1386681	5
No.15	0.1790086	5	No.15	0.1625788	5
No.20	0.1681457	5	No.20	0.1391477	5
No.25	0.1739596	5	No.25	0.1462044	5
No.30	0.1565177	5	No.30	0.1747739	5
No.40	0.1608017	5	No.40	0.1344889	5
No.75	0.2045594	5	No.75	0.15792	5
No.100	0.1871175	5	No.100	0.15792	5
No.125	0.2293452	5	No.125	0.1518224	5
No.150	0.2126683	5	No.150	0.1681968	5
No.1	0.1995104	6	No.1	0.1381885	6
No.2	0.129437	6	No.2	0.1100987	6
No.3	0.1069461	6	No.3	0.1157166	6
No.4	0.1367809	6	No.4	0.09838312	6
No.5	0.124388	6	No.5	0.1157166	6
No.10	0.1600367	6	No.10	0.1386681	6
No.15	0.1681457	6	No.15	0.1625788	6
No.20	0.1797736	6	No.20	0.1391477	6
No.25	0.1754896	6	No.25	0.1462044	6
No.30	0.1696756	6	No.30	0.1747739	6
No.40	0.1615667	6	No.40	0.1344889	6
No.75	0.1813035	6	No.75	0.15792	6
No.100	0.2119033	6	No.100	0.15792	6
No.125	0.1813035	6	No.125	0.1518224	6
No.150	0.2192472	6	No.150	0.1681968	6
No.1	0.1936965	7	No.1	0.1381885	7

Table D1. Continued.

No.2	0.1119951	7	No.2	0.1100987	7
No.3	0.1127601	7	No.3	0.1157166	7
No.4	0.124388	7	No.4	0.09838312	7
No.5	0.130967	7	No.5	0.1157166	7
No.10	0.1185741	7	No.10	0.1386681	7
No.15	0.1507038	7	No.15	0.1625788	7
No.20	0.1615667	7	No.20	0.1391477	7
No.25	0.1921665	7	No.25	0.1462044	7
No.30	0.1630967	7	No.30	0.1747739	7
No.40	0.1944614	7	No.40	0.1344889	7
No.75	0.1914015	7	No.75	0.15792	7
No.100	0.1894125	7	No.100	0.15792	7
No.125	0.1929315	7	No.125	0.1518224	7
No.150	0.1936965	7	No.150	0.1681968	7
No.1	0.1871175	8	No.1	0.1381885	8
No.2	0.123623	8	No.2	0.1100987	8
No.3	0.1185741	8	No.3	0.1157166	8
No.4	0.124388	8	No.4	0.09838312	8
No.5	0.1650857	8	No.5	0.1157166	8
No.10	0.1367809	8	No.10	0.1386681	8
No.15	0.1324969	8	No.15	0.1625788	8
No.20	0.1572827	8	No.20	0.1391477	8
No.25	0.1936965	8	No.25	0.1462044	8
No.30	0.1871175	8	No.30	0.1747739	8
No.40	0.1921665	8	No.40	0.1344889	8
No.75	0.1747246	8	No.75	0.15792	8
No.100	0.2045594	8	No.100	0.15792	8
No.125	0.1929315	8	No.125	0.1518224	8
No.150	0.2119033	8	No.150	0.1681968	8
No.1	0.1381885	9	No.1	0.1381885	9
No.2	0.1100987	9	No.2	0.1100987	9
No.3	0.1157166	9	No.3	0.1157166	9
No.4	0.09838312	9	No.4	0.09838312	9
No.5	0.1157166	9	No.5	0.1157166	9
No.10	0.1386681	9	No.10	0.1386681	9
No.15	0.1625788	9	No.15	0.1625788	9

Table D1. Continued.

No.20	0.1391477	9	No.20	0.1391477	9
No.25	0.1462044	9	No.25	0.1462044	9
No.30	0.1747739	9	No.30	0.1747739	9
No.40	0.1344889	9	No.40	0.1344889	9
No.75	0.15792	9	No.75	0.15792	9
No.100	0.15792	9	No.100	0.15792	9
No.125	0.1518224	9	No.125	0.1518224	9
No.150	0.1681968	9	No.150	0.1681968	9

Table D1. Continued.

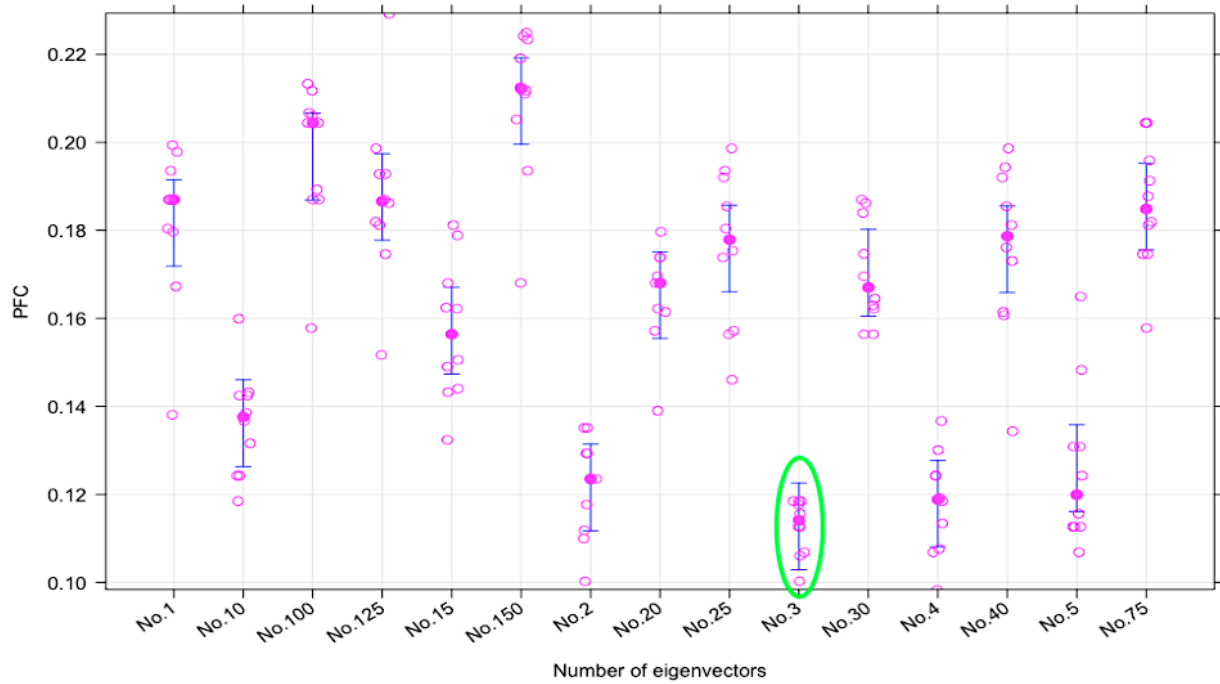


Fig. D1. PFC values by number of eigenvectors residual plot of imputed upper jaw datasets.

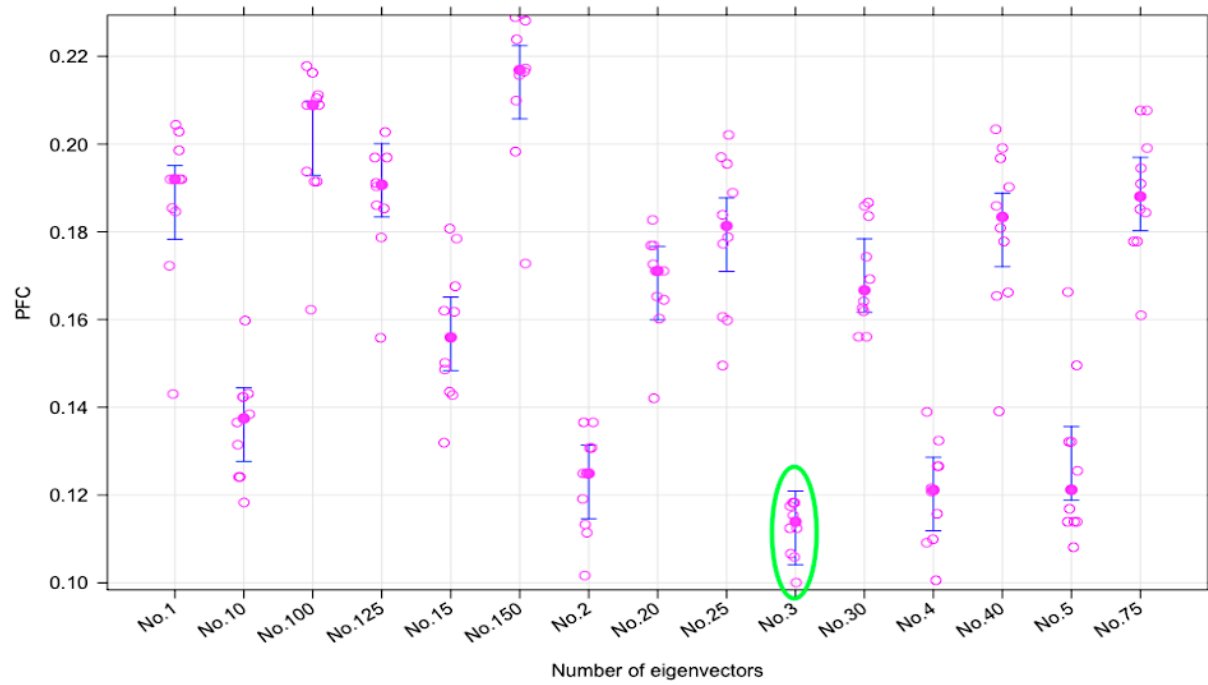


Fig. D2. PFC values by number of eigenvectors residual plot of imputed lower jaw datasets.

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