Elevated evolutionary rates of biting biomechanics reveal patterns of extraordinary craniodental adaptations in some herbivorous dinosaurs

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Abstract: Adaptation to specialist ecological niches is a key innovation that has contributed to the evolutionary success of many vertebrate clades, underpinning the acquisition of diverse skull morphologies. Dinosaurs, which dominated Mesozoic terrestrial faunas, acquired herbivory multiple times, and evolution of these herbivorous adaptations is linked to drastic changes in dental and craniomandibular functional morphology, yet whether changes in functionally relevant phenotypic traits occurred more rapidly in herbivorous lineages compared to in carnivorous lineages remains largely untested in a statistical phylogenetic framework. Here, we infer rates of phenotypic evolution using phylogenetic variable-rate models on relative biting edge (tooth row) lengths of 107 dinosaur taxa to test the hypothesis that the acquisition of herbivory is associated with rapid changes in mandibular biomechanics. We find elevated rates of biomechanical evolution in theropods with foreshortened and beaked skulls (Oviraptorosauria, *Limusaurus*), as well as in ceratopsians and *Diplodocus*. The presence and position of a reduced tooth row and increased jaw efficiency unite these high-rate lineages, indicating selection for greater efficiency in biting biomechanics. Large departures from the isometric scaling of these mandibular characteristics helps explain the differences in evolutionary rates in these clades and those of other herbivorous theropods (Therizinosauria, Ornithomimosauria). Additionally, we hypothesize that extreme ontogenetic changes within species lifetimes may be behind some instances of branch-wise elevated rates. Thus, we show how exceptional rates of biomechanical evolution can reveal signatures of ecological adaptations within dinosaur lineages as well as within-species ontogenetic sequences.

Key words: dinosaur, evolution, specialization, skull, Ceratopsia, Oviraptorosauria.

STUDIES of skull morphology in dinosaurs have revealed a diverse range of dietary modes (Osmólska *et al.* 2004; Barrett & Rayfield 2006), as well as evidence for adaptation to new ecological niches (Benson *et al.* 2014). Many theropod lineages show clear evidence for specialist modes of carnivory, such as bone-crushing in tyrannosaurids (Brusatte *et al.* 2010) and piscivory in spinosaurids (Rayfield 2011; Cruff & Rayfield 2013; Ibrahim *et al.* 2020). Therizinosaurs and ornithomimosaurs show herbivorous adaptations (Currie *et al.* 1993; Barrett 2005; Xu *et al.* 2009; Zanno *et al.* 2009), such as gastric mills and keratinous beaks (Kobayashi *et al.* 1999; Norell *et al.* 2001; Zanno *et al.* 2009; Lee *et al.* 2014). Conversely, the diets of oviraptorosaurs have been the subject of significant debate, including ovivory (Osborn *et al.* 1924; Andrews 1932; Currie *et al.* 1993) molluscivory (Barsbold 1983), and more recently frugivory (Sereno *et al.* 2010; Funston *et al.* 2018) or strict herbivory, (Zanno & Makovicky 2011; Funston *et al.* 2018). The presence of

gastroliths in the basal oviraptorosaur *Caudipteryx*, used to break down plant matter, confirms that at least some members of this clade employed herbivory (Qiang *et al.* 1998).

Herbivorous theropod lineages are known from the Cretaceous (Osmólska *et al.* 2004), and there is evidence for rapid evolution of the skull in oviraptorosaurs compared to other theropods (Diniz-Filho *et al.* 2015), suggesting fast dietary transitions in these clades. Rapid shifts in diet have been hypothesized for other theropod lineages, including alvarezsaurids (Senter 2005; Choiniere *et al.* 2010) and the basal ceratosaur *Limusaurus* (Xu *et al.* 2009; Wang *et al.* 2017a), both of which possess skulls that are poorly adapted to carnivory. *Limusaurus* additionally displays tooth loss with ontogeny, suggesting that an extreme dietary change that may reflect a transition from omnivory to herbivory (Wang *et al.* 2017a). This adaptation is unique within ceratosaurs and is associated with rapid cranial evolution compared to

carnivorous members of the clade, perhaps owing to this dietary adaptation (Diniz-Filho *et al.* 2015). Such shifts in diet within predominantly carnivorous theropod clades suggest that increased rates of evolution in dinosaurs coincide with extreme morphological changes in the skulls.

The specialist skull morphologies found in many herbivorous dinosaurs are often associated with reduced biting edge lengths, allowing for a more consistent mechanical advantage along the tooth row as less force is lost rostrally (Sakamoto 2010; Brusatte *et al.* 2012), thus promoting efficient mastication of plant matter (Longrich *et al.* 2010; Ma *et al.* 2019). This adaptation is exhibited in many clades by foreshortening of the biting edge and development of a beak, such as those of oviraptorosaurs and *Limusaurus* (Barsbold 1983; Xu *et al.* 2009; Longrich *et al.* 2010; Wang *et al.* 2017a; Ma *et al.* 2019). The evolution of a specialist tooth row for herbivory, such as that seen in oviraptorosaurs, is also expressed in the evolution of early ornithiscian clades, such as the emergence of a beak in basal ceratopsians such as *Psittacosaurus* (Button *et al.* 2023), suggesting that a transition to herbivory necessitates the acquisition of specialist skull morphologies, often consisting of a shorter tooth row and reduced biting edge (Button & Zanno 2020).

There is strong anatomical evidence to suggest that rapid transitions to herbivory are associated with rapid shifts in cranial morphology in dinosaurs, including adaptation to increase biting efficiency (Sakamoto 2010; Brusatte *et al.* 2012), but these trends remain largely untested in a statistical phylogenetic framework across Dinosauria (but see Button *et al.* 2017 for a study in Sauropodomorpha). Here, we use phylogenetic variable-rates (VR) regression (Baker *et al.* 2016) to determine which, if any, dinosaurian lineages experience increases in evolutionary rates of biting biomechanics, and if such rate shifts are associated with extraordinary dietary adaptations. We hypothesize that coelurosaurian taxa with adaptations for non-carnivorous diets should experience higher rates of evolution in biting biomechanics. The evolutionary rates for select ornithischian and sauropod taxa will be included for comparison with those of these herbivorous theropods, in addition to determining if any of these herbivorous lineages experienced similar increases in evolutionary rates of biting biomechanics.

Interpreting rates of evolution has been fundamental to the development of evolutionary theories and understanding of the fossil record. Darwin (1859) predicted that evolutionary changes would largely be gradual over macro-evolutionary time but recognized that rates would vary; most notably in slow-evolving lineages. Simpson (1944) proposed mechanisms underlying exceptional rates of evolution, such as quantum evolution in which species drastically shift in phenotype when they transition from one adaptive zone (a set of physical and ecological environments to which species are adapted) to another. Thus, detecting patterns of rates in the evolution of biting biomechanics is key to understanding how morphological features at the interface between the organism (biting edge) and substrate (foods) respond to functional and ecological selection over millions of years.

METHOD

We focus on a biomechanically important feature of dinosaurian skull morphology: the relative lengths of the biting edge. We represented this biomechanical trait as the relationship between the biting edge length (L_{Bite}) and the distance between the posterior-most biting position and the jaw joint (d_{Bite}) in a regression framework ($L_{Bite} \sim d_{Bite}$). This relationship estimates how bite force is lost rostrally along the biting edge, given the position of the biting edge, across a comparative sample of dinosaurs (Sakamoto 2010; Brusatte *et al.* 2012). Given a fixed posterior biting position (d_{Bite}), L_{Bite} then represents the relative lengthening of the biting edge towards the rostrum, meaning that relatively longer L_{Bite} values correspond to relatively longer biting out-lever at the rostral-most biting position. Mechanically, the longer the out-lever, the less force is transferred from the input force, given a fixed in-lever. This means that taxa with relatively longer L_{Bite} will inevitably have relatively weaker bites at the anterior-most biting positions compared to the bite force at their posterior-most biting positions. We also modelled the relationship between d_{Bite} and the length of the skull (L_{Sk}) as an expression of the relative position of the biting edge itself ($d_{Bite} \sim L_{Sk}$). This relationship then represents how the posterior-most biting position (location of maximum bite force along the biting edge) scales with respect to skull length. These measures were taken as Euclidean distances on a two-dimensional projection along the hypothetical midline of the skull, as is the standard approach in approximating a three-dimensional lever in two dimensions (Sinclair 1983; Sinclair & Alexander 1987). This approximation is sufficient for our purposes here as we are interested in the relative differences in out-lever along the biting edge. Similarly, the in-forces (muscle contractile forces) and in-levers (moment arms of the muscle force vectors) are not considered here.

Our taxonomic sample consists of 107 species, chosen to include species from all major dinosaurian lineages (Kunz & Sakamoto 2024). This covers all theropod families, with an emphasis on coelurosaurian clades, as well as representatives from the sauropodomorphs and ornithischians. Our taxonomic sample covers a comprehensive range of skulls and captures the wide diversity in skull morphology and dietary adaptations.

Cranial reconstructions for each species were produced or taken from figures (see Kunz & Sakamoto 2024) in scientific literature and measured using ImageJ v1.51 (Abràmoff *et al.* 2004; Schneider *et al.* 2012). Images were scaled either using a scale bar or the known total length of the skull. The measurements comprise: L_{Sk}, the total length of the skull, from the tip of the premaxilla to the posterior margin of the quadratojugal; L_{Bite}, the total linear length of the biting edge (tooth row or beak) taken as the sum of the lengths along the premaxilla and maxilla respectively; and d_{Bite}, the distance between the posterior point of the biting edge and the jaw joint (Fig. 1). Biting edge length was taken as the linear distance to represent the difference in out-lever between the anterior-most and posterior-most biting positions, but also as it is a good approximation of the arc length of the ventral curvature of the biting edge (the relationship between linear distance and arc length is isometric with the latter on average only being 3% higher than the former; Kunz & Sakamoto 2024). For taxa where multiple images/specimens were available, we selected the largest individual (skull length) as the taxon-representative sample (Kunz & Sakamoto 2024).

We used a VR regression (Baker *et al.* 2016) performed in a Bayesian framework in BayesTraits (Meade & Pagel 2019) to model the relationships between L_{Bite} and d_{Bite} and between d_{Bite} and L_{Sk} while accounting for statistical non-independence owing to shared ancestry, uncertainties in phylogenetic relationships, and heterogeneous processes of phenotypic evolution. The VR regression works in much the same way as normal phylogenetic regression to minimize the residuals on a best-fit regression model, but accounts for extremely large/small residuals by treating them as increases/decreases in the rates of phenotypic evolution (Baker *et al.* 2016; Sakamoto *et al.* 2019). Rates are inferred for individual branches of the phylogenetic tree by stretching or compressing the branches so that their modified lengths are proportional to the amount of trait change under Brownian motion (constant rate of evolution) (Venditti *et al.* 2011). Thus, large deviations away from the modelled general relationships ($L_{Bite} \sim L_{Skull}$; $d_{Bite} \sim L_{Skull}$), or large residuals, are detected as shifts in the rate of phenotypic evolution, which can be interpreted as instances of exceptional adaptive changes (Baker *et al.* 2016; Sakamoto *et al.* 2019).

To take phylogenetic uncertainties into account, we used a sample of trees for our input tree in the VR regression model (implemented in BayesTraits v4.0.0; unpub. data, MS, J. Baker, M.J. Benton, A. Meade, C. Organ, M. Pagel, C. Venditti). We sampled 100 most-parsimonious trees from Lloyd *et al.* (2016) and scaled the branches using the first and last appearance dates (FAD and LAD respectively) in R v3.4.2 (R Core Team 2013). We took FADs as the minimum node ages, sharing branch lengths equally with adjoining branches to adjust internal branches with lengths of zero using the paleotree R library (v3.4.5; Bapst 2012). We then extended the terminal branches to their LADs. We repeated this process for all trees in the sample. The sample of trees from Lloyd *et al.* (2016) is from a meta-tree analysis (a variation of the matrix-represented supertree approach) and is thus a quantitatively derived comprehensive summary of dinosaur phylogenetic topologies across the literature (as of 2016).

At each iteration along the Markov Chain Monte Carlo (MCMC) run, a tree is taken from the sample of trees, and rate scalars are applied to the branches. The rate scalars and tree are accepted and retained in the posterior sample in proportion to the likelihood. We ran the chain for 10^7 iterations (discarded as burn-in) before sampling every 10^6 iterations over a period of 10^9 iterations, resulting in a posterior sample of 1000 rate-scaled trees and model parameters. Branches are determined to have undergone exceptional rate shifts if they are scaled in the majority (over 50%) of the posterior sample of rate-scaled trees (Sakamoto *et al.* 2019). Regression model parameters

FIG. 1. Example of a typical skull image included in data-set, and measurements of skull length and biting edge length used in analysis. Measurements: A, length of premaxilla; B, length of maxilla; C, total length of skull; D, length of biting edge position. Skull of *Deinonychus antirrhopus*, AMNH.5232 (American Museum of Natural History, New York). Scale bar represents 50 mm.
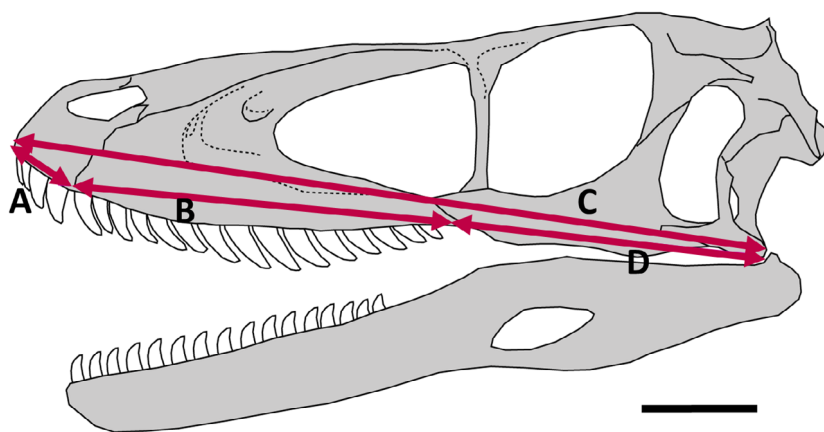
are taken as statistically significant if less than 95% of the posterior sample of coefficients lie beyond zero ($p_{MCMC} < 0.05$), in other words, the posterior distribution of regression coefficients is different from zero. We coloured the branches of the maximum clade credibility tree of the sample of time-scaled trees (Lloyd *et al.* 2016) according to a colour gradient based on the rate scalars.

RESULTS

There is an isometric scaling relationship between L_{Bite} and d_{Bite} (median slope = 0.922, $p_{MCMC(slope = 1)} = 0.073$); changes in rostral force loss along the biting edge are proportional to changes in relative biting edge positions. By contrast, d_{Bite} scales with a weak negative allometry to L_{Sk} (median slope = 0.941, $p_{MCMC(slope = 1)} = 0.025$); bite force diminishes rostrally along the biting edge as the lever length increases.

In the VR regression model, $L_{Bite} \sim d_{Bite}$ (Fig. 2), we detected clade-wide rate shifts in three clades, Chasmo-saurinae, Oviraptorosauria and the basal tetanuran clade,

Carnosauria (Allosauroidea + Megalosauroidea). Rate increases were detected in branches within Chasmosauri-nae and Oviraptorosauria while rate decreases were detected in carnosaurian branches. Additionally, we detected branch-wise rate increases in the basal cerato-saurid *Limusaurus*, the sauropod *Diplodocus* and the coe-lurosaur *Ornitholestes*.

Similarly, in the VR regression model $d_{Bite} \sim L_{Sk}$ (Fig. 3), we detected a clade-wide rate increase in Cera-topsidae, and branch-wise rate increases in *Diplodocus*, *Limusaurus*, *Ornitholestes*, and the branch subtending the *Coelophysis* + *Megapnosaurus* clade (*C. bauri* and *M. rhodesiensis*).
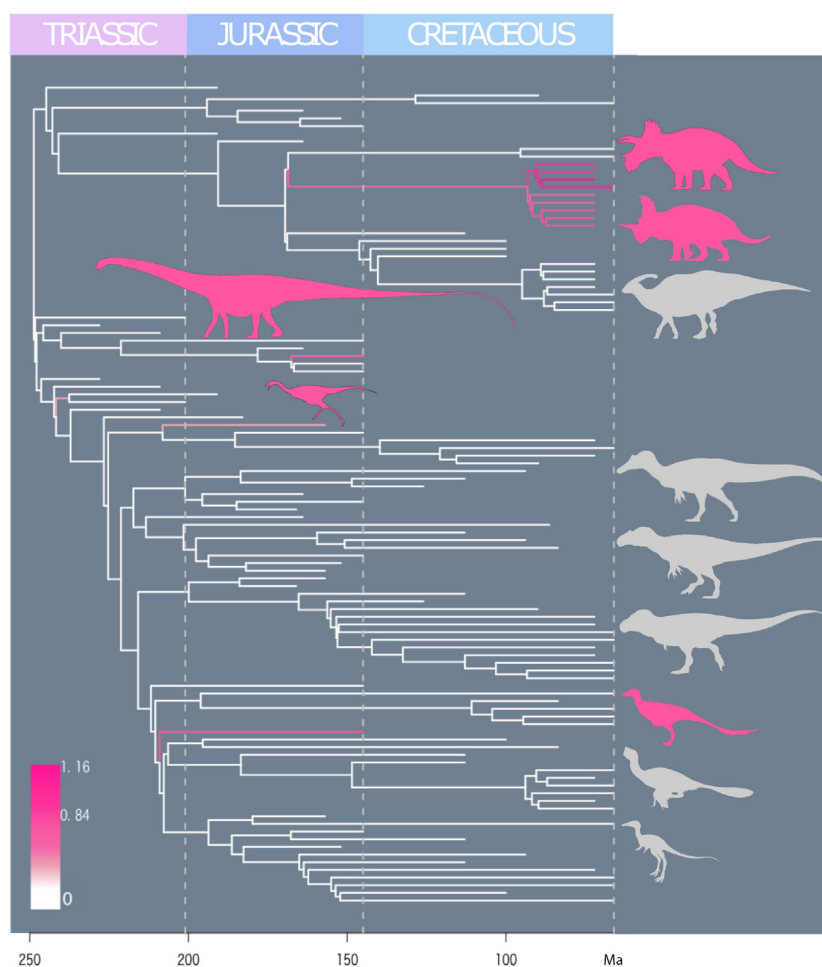
DISCUSSION

Scaling biting edge in Dinosauria

Amongst all dinosaurs, the vast majority of lineages main-tain a constant proportion between L_{Bite} and d_{Bite} (iso-metric scaling) under Brownian motion, meaning that
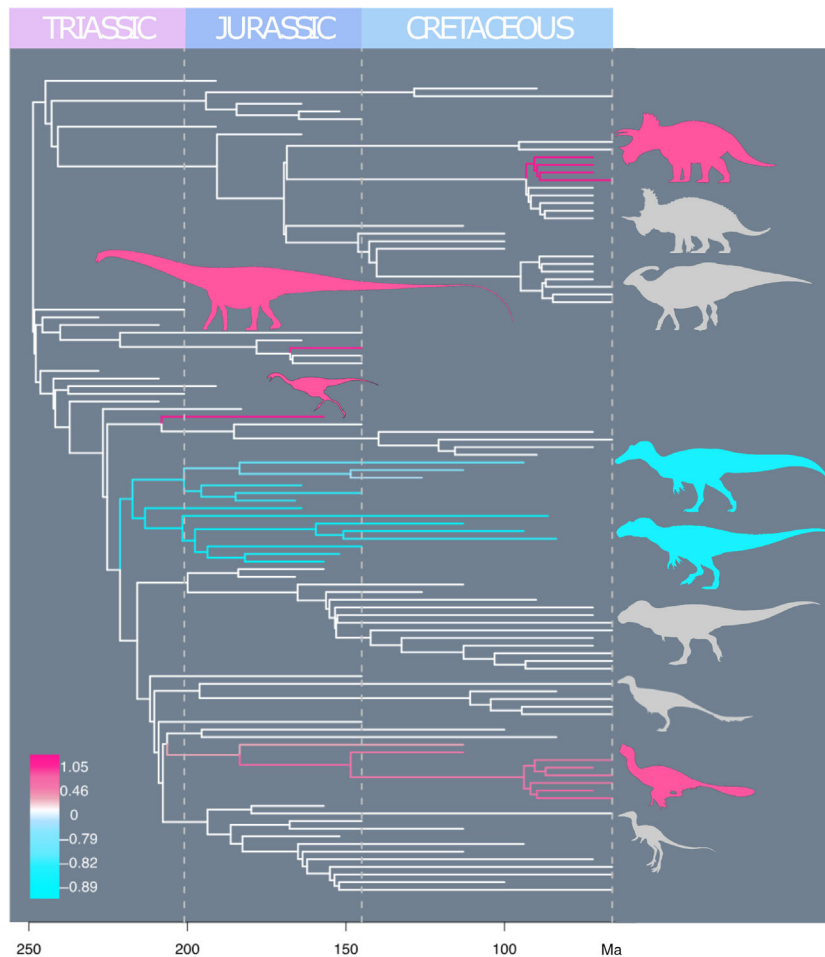
FIG. 2. Relative length of the bit-ing edge with respect to the distance between the posteriormost biting position and the jaw joint, plotted on a time-scaled tree of dinosaurs with branches coloured according to rates of evolution. Background rate is in white with increasing and decreasing rates represented by the intensity of the colour gradient towards pink and blue respectively. Rates are mapped onto a maximum clade credibility tree of the sample of trees from Lloyd *et al.* 2016. Sil-houettes from PhyloPic (http://phylopic.org): *Tyrannosaurus rex* by Jack Mayer Wood, *Triceratops poro-sus* by Raven Amos, *Diplodocus car-negii* by Scott Hartman (all CC BY 3.0); *Limusaurus inextric-abilis* by Ville-Veikko Sinkkonen, *Ornitholestes hermanni* by Matt Martynuik (both CC BY-NC-SA 3.0; reproduced with permis-sion); *Citipati osmolskae* by Emily Willoughby (CC BY-SA 3.0); *Baryo-nyx walkeri* by Ivan Iofrida (CC BY 4.0); *Allosaurus jimmadseni* and *Centrosaurus apertus* by Tasman Dixon, *Shuvuuia deserti* by thefunk-monk, *Parasaurolophus walkeri* by Jack Mayer Wood (all CC0 1.0).

FIG. 3. Relative position of the biting edge with respect to skull length plotted on a time-scaled tree of dinosaurs with branches coloured according to rates of evolution. Background rate is in white with increasing rates represented by the intensity of the colour gradient towards deep pink. Rates are mapped onto a maximum clade credibility tree of the sample of trees from Lloyd *et al.* 2016. Silhouettes from PhyloPic (http://phylopic.org): *Tyrannosaurus rex* by Jack Mayer Wood, *Triceratops porosus* by Raven Amos, *Diplodocus carnegii* by Scott Hartman (all CC BY 3.0); *Limusaurus inextricabilis* by Ville-Veikko Sinkkonen, *Ornitholestes hermanni* by Matt Martynuik (both CC BY-NC-SA 3.0; reproduced with permission); *Citipati osmolskae* by Emily Willoughby (CC BY-SA 3.0); *Baryonyx walkeri* by Ivan Iofrida (CC BY 4.0); *Allosaurus jimmadseni* and *Centrosaurus apertus* by Tasman Dixon, *Shuvuuia deserti* by thefunkmonk, *Parasaurolophus walkeri* by Jack Mayer Wood (all CC0 1.0).

evolutionary changes in both variables occurred at the same pace and in proportion to each other. A similar pattern can be observed for d_{Bite} with L_{Sk} albeit with a slight but significant negative allometry. Biomechanically, bite force diminishes rostrally along the biting edge as the lever length increases (Gröning *et al.* 2013). The degree to which this rostral reduction occurs in a given taxon depends on its L_{Bite}; the longer the L_{Bite} the greater the bite force reduction at rostral biting positions relative to the posterior-most biting position, or the maximum bite force. A constant L_{Bite} relative to d_{Bite}, is therefore associated with a constant degree of force reduction along the biting edge across size classes and phylogeny.

While the retention of constant proportions between two morpho-functional variables can be considered to have evolved under stabilizing selection (Martins & Hansen 1997; Butler & King 2004), the residual variance in phylogenetic regression is modelled under Brownian motion. As such, deviations around the regression line (the isometric or nearly isometric relationship) may still occur steadily through time as the result of adaptive changes in response to natural selection, rather than

displaying strict adherence to the optimum. We also find multiple instances of true departures from Brownian motion, however, in the form of increases and decreases in evolutionary rates (see below).

Rates of biomechanical evolution

Phenotypic changes on macro-evolutionary time scales (over millions of years) have been widely accepted as indicative of adaptive responses to natural selection (Darwin 1859; Simpson 1944; Venditti *et al.* 2011; Baker *et al.* 2016). Variation in rates of phenotypic evolution is therefore expected to reflect the relative strengths of natural selection acting on the phenotype of interest (Baker *et al.* 2016), with patterns in the rate of phenotypic change being a potential proxy for responses to intensifying or relaxing selection pressures across phylogeny and through time.

Instances of elevated rates indicate episodes of exceptional adaptive changes, or intensification of selection pressures (Baker *et al.* 2016). Two clades in which we

observed elevated rates are the oviraptorosaurs (but in only the regression $L_{Bite} \sim d_{Bite}$) and ceratopsians. Both clades exhibit specialized skull morphologies (Longrich *et al.* 2010; Mallon & Anderson 2015; Maiorino *et al.* 2015; Meade & Ma 2022), with adaptations for efficient biting. Oviraptorosaurs attained efficient biting through foreshortening of the skull (Osborn *et al.* 1924; Currie *et al.* 1993; Sereno 1997, 1999; Osmólska *et al.* 2004; Barrett 2014; Meade & Ma 2022) thereby achieving a large mechanical advantage along their biting edges (Sakamoto 2010). Additionally, the beaks of oviraptors are significantly different from those of other beaked theropods (such as ornithomimosaurs), and more closely resemble those of ornithischian taxa (Osborn *et al.* 1924; Currie *et al.* 1993). Interestingly, oviraptorosaurs do not exhibit rate increases in the evolution of biting edge positions ($d_{Bite} \sim L_{Sk}$). Their biting edges are positioned as expected given background evolution even compared to other theropod lineages, demonstrating that their unique morphology for biting biomechanics lies in the relatively short biting edge lengths.

Conversely, decreases in rates suggest that adaptive changes along the corresponding branches occur at rates lower than expected given background rate, implying weaker selection pressures. We observe such decreased rates of evolution of biting edge lengths in carnosaurs (basal tetanurans including megalosauroids and allosauroids), indicating that relative biting edge lengths did not undergo substantial evolutionary changes through time and across phylogeny in this clade. This decrease in evolutionary rates within carnosaurs is consistent with evolutionary patterns observed in function-space occupation of biting performance within basal tetanuran clades (Sakamoto 2010), in which tetanuran taxa formed a continuous distribution within function space, indicating an overall similarity in the biomechanical profile of biting in this clade. Carnosaurs generally maintained consistent biting efficiencies throughout their evolutionary history. Specialized feeding adaptations observed within this group (i.e. spinosaurs) are likely to be the result of selection on other features associated with feeding (e.g. overall skull and snout morphology/geometry or tooth shape) not biting efficiency as measured as relative changes in mechanical advantage along the biting edge.

Possible influence of feeding ecology on evolutionary rates in theropods

Oviraptorosaur diet has been the subject of much debate for decades, with studies proposing a variety of ecological niches for this clade (Osborn *et al.* 1924; Barsbold 1983; Currie *et al.* 1993; Sereno *et al.* 2010; Zanno & Makovicky 2011; Funston *et al.* 2018). Oviraptorosaur beaks feature a sharp shearing edge, suited for cutting through tough food, rather than a flat surface like durophagous mammals (Longrich *et al.* 2010). This skull morphology would have been effective at slicing up vegetation but may not have been best suited for crushing tough material (Longrich *et al.* 2010). Previous studies (Tsuihiji *et al.* 2016; Funston *et al.* 2018), have suggested that oviraptorosaurs mainly occupied arid environments, and therefore the diet of these taxa could incorporate both herbivory and frugivory in a facultatively opportunistic manner underpinned by food availability within this ecosystem. It is possible that this resulted in niche partitioning within this clade, as suggested by the presence of many similar species in some locations (Tsuihiji *et al.* 2016; Funston *et al.* 2018; Ma *et al.* 2019). In particular, oviraptorids demonstrate a higher diversity in craniomandibular morphology and function (Ma *et al.* 2019), consistent with our findings of higher variation in L_{Bite} with respect to d_{Bite}. It is possible that oviraptorosaurs experienced a transition from one form of vegetation to another as a response to environmental changes or food availability (Tsuihiji *et al.* 2016; Funston *et al.* 2018; Ma *et al.* 2019).

There is evidence for the presence of gastroliths in basal oviraptorosaurs (Qiang *et al.* 1998; Wang *et al.* 2017b) as well as in *Limusaurus*, another lineage for which we observe elevated rates, suggesting a possible convergent evolution of dietary adaptations in these two lineages. *Limusaurus*, a basal ceratosaur, has a skull anatomy which is much more similar to the oviraptorosaurs than to other ceratosaurs (Carrano & Sampson 2008; Wang *et al.* 2017b). Adaptive processes underlying the foreshortening of the skull and acquisition of a beak in both lineages, such as a possible adaptation towards specific niches of herbivory (Longrich *et al.* 2010) or in response to competition between clades (Fricke & Pearson 2008), may be responsible for their respective increases in rates of biomechanical evolution.

Possible influence of feeding ecology on evolutionary rates in non-theropods

Within the Ornithischia, ceratopsids also show clade-wide increases in evolutionary rates. However, the underlying selection pressures may differ from those of *Limusaurus* or oviraptorosaurs; ceratopsids retain a relatively long L_{Bite} but have substantial variation in d_{Bite} with many species showing exceptionally short d_{Bite} for their L_{Sk}. That is, ceratopsids exhibit adaptions associated with biting efficiency via modifications to the lever arm of the biting moment for the maximum bite force (d_{Bite}) (Nabavizadeh 2018, 2019, 2023). Ceratopsids show additional adaptations for varying mechanical advantages, most notably in the size and position of the coronoid process. The coronoid process is enlarged and lies labially to the biting

edge, resulting in a long lever arm of the temporal-group muscle forces. This implies that ceratopsids were under selection associated with the overall increase in mechanical advantage of the biting lever. Then, given d_{Bite}, only the subfamily Chasmosaurinae show further variation, and thus exceptional adaptive changes, in L_{Bite}. This may indicate that selection acting on d_{Bite}, and therefore its functional significance, is stronger than on that on L_{Bite} in ceratopsids as a whole.

Within Ceratopsidae, there is evidence for a possible dietary shift in chasmosaurines, which possessed different biomechanical adaptations in the lower jaw than centrosaurines (Maiorino *et al.* 2015; Mallon & Anderson 2015). Differences in the patterns of evolutionary rates in L_{Bite} with respect to d_{Bite} between chasmosaurines and centrosaurines suggest that chasmosaurines may have been adapted for a diet of less abrasive vegetation than centrosaurines. This difference is likely to be due to the transition from tougher gymnosperms to softer angiosperms that occurred during the Late Cretaceous (Lupia *et al.* 2000; Arens & Allen 2014). In the Hell Creek Formation (Maastrichtian) of North America, where the chasmosaurine *Triceratops* is one of the most common dinosaurs (Scanella *et al.* 2014), angiosperms are the most abundant and widespread plants (Arens & Allen 2014). As both clades coexisted during the Late Cretaceous (Mallon & Anderson 2013), this diversity in diet could also suggest evidence of further niche partitioning within ceratopsians, with centrosaurines feeding on tougher vegetation than chasmosaurines (Maiorino *et al.* 2015).

Despite having similar skull adaptations (e.g. dental battery) to ceratopsids (Norman & Weishampel 1985; Weishampel 2012), we found no rate shifts in ornithopods. These two clades were both widespread in Asia and North America throughout the Cretaceous (Osmólska *et al.* 2004) and, unlike many other dinosaur clades, were experiencing increases in speciation during this time (Sakamoto *et al.* 2016). Both ceratopsids and hadrosaurs are believed to have coexisted during the Late Cretaceous (Fricke & Pearson 2008), and fossils of both have been found in the same locations, such as the Dinosaur Park Formation (Upper Campanian) of Alberta, Canada (Gates *et al.* 2012; Mallon & Anderson 2013). It has therefore been suggested that these two dinosaur clades experienced niche partitioning, similar to different herbivore species in modern ecosystems (Fricke & Pearson 2008; Mandlate *et al.* 2019). However, unlike in ceratopsids, the evolutionary rate of the biting edge in ornithopods is not significantly different from background rate, indicating that the amount of evolutionary change accrued along the relevant branches is proportional to the passage of time. This also means that ornithopods exhibit less variation in L_{Bite} compared to ceratopsids, supporting the notion that these two clades were under different ecological selection despite convergent

acquisition of the dental battery (Fricke & Pearson 2008). Compared to hadrosaurids, which appeared to feed mainly on the forest canopy (Fricke & Pearson 2008), ceratopsids are likely to have preferred floodplain or forest understory environments (Fricke & Pearson 2008), and it has previously been suggested that they primarily consumed highly-fibrous plants (Ostrom 1966; Dodson 1993; Maiorino *et al.* 2017). This diet of tougher, more abrasive vegetation might have necessitated in more efficient feeding adaptations, such as the shorter beak and longer tooth row (with shorter d_{Bite}) than hadrosaurids.

The skull of *Diplodocus*, a species that also experienced an exceptional rate increase, possesses a reduced tooth row, along with specialist teeth for an herbivorous diet (Calvo 1994; Woodruff *et al.* 2018). The characteristic peg-like teeth of diplodocids, located at the anterior tip of the jaws, are thought to indicate a diet consisting of soft foliage (Calvo 1994; Fiorillo 1998), facilitating possible adaptations to specialist feeding methods such as branch stripping (Barrett & Upchurch 1994; Young *et al.* 2012). This differs from the skulls of macronarian sauropods such as *Camarasaurus*, which have longer tooth rows consisting of spatulate teeth that suggest a diet of coarser vegetation (Fiorillo 1998; Button *et al.* 2014). Similar to the oviraptorosaurs and ceratopsians, these morphological differences and elevated rates of evolution of the biting edge in *Diplodocus* suggest that niche partitioning occurred within the Jurassic sauropods (Fiorillo 1998; Button *et al.* 2014).

Ontogenetic change in *Diplodocus* and *Limusaurus*

There is evidence for extreme ontogenetic changes in the skulls of some taxa with elevated rates. Skulls of an immature *Diplodocus* reveal greater similarities in tooth shape and tooth row length to macronarian sauropods than to adult diplodocids (Woodruff *et al.* 2018). This suggests a change in diet and ecology for these sauropods during their lifespan, accompanied by a reduction in the L_{Bite}. It is possible that the ontogenetic change experienced by *Diplodocus* was accompanied by an ecological transition from a dense forest environment to a more open environment (Woodruff *et al.* 2018). This implies niche partitioning between adult and juvenile *Diplodocus*, along with extreme change in L_{Bite} with respect to d_{Bite} throughout the lifespan of the animal. Such drastic ontogenetic change may in part explain the observed rate increase along this branch. L_{Bite} development in *Diplodocus* is substantially greater during the lifetime of an individual than might be expected given the background rate of evolution.

Limusaurus is an outlier within the basal Ceratosauria (Guinard 2016) and represents the only non-coelurosaurian theropod to show an increase in evolutionary rate. *Limusaurus* is also characterized by extreme

morphological changes in the skull over its lifespan, which are likely to have coincided with dietary shifts. Teeth are present in the juvenile skull of *Limusaurus*, but are lost on reaching adulthood, and replaced with a beak (Wang *et al.* 2017a). As we used the adult skull in our study, it is likely that the elevated rate we observed for this taxon represents extreme ontogenetic changes in the biting edge similar to that in *Diplodocus*. The morphology of the adult skull, along with the presence of gastroliths, indicate adaptations for herbivory (Xu *et al.* 2009; Wang *et al.* 2017a). It is probable that adult and juvenile *Limusaurus* occupied different ecological niches in order to avoid intraspecific competition (Wang *et al.* 2017a), representing yet another example of niche partitioning in species with elevated evolutionary rates.

LIMITATIONS

As with most analyses in cross-species comparative palaeontology (but also zoology in general), our results will undoubtedly be affected by incomplete sampling, whether this is due to gaps in the fossil record or simply unsampled taxa. How incomplete sampling affects detection of rates along the branches of the phylogenetic trees is still largely unknown but we can make some predictions. With respect to observed rate shifts along terminal branches (e.g. *Diplodocus* or *Limusaurus*) additional taxonomic sampling along these branches will break up the number of changes inferred to have occurred, thereby potentially distributing rate scalars across multiple branches instead of one. If these additional samples shared similar biomechanical adaptations to the taxa included, then the drastic changes would be predicted to have occurred along the stem subtending the clade. However, if these additional taxa were more conservative in biomechanical adaptations then this may exemplify the uniqueness of the evolutionary changes occurring along the relevant terminal branches. The exact nature of how these additions may alter patterns of rate scalars is unfortunately unpredictable without more data. On the other hand, the clade shifts that we observe, such as those in ceratopsians and oviraptorosaurs, are likely to remain with increased taxonomic sampling.

One issue that is difficult to resolve is the effect of uncertainty about the lengths of the internal branches, which are largely determined by divergence dates of nodes. Rate shifts observed along basal branches (e.g. that observed at the base of the *Coelophysis* + *Megapnosaurus* clade) could potentially be an artefact of artificially short branch lengths induced by the tree dating approach taken here, in which zero-length branches are scaled in proportion to the branch lengths of ancestral and descendant branches (Brusatte *et al.* 2008). The pros and cons of different divergence dating methods are a topic of its own (e.g. Bapst & Hopkins 2017) and is beyond the scope of this study, but they all introduce artefacts in various ways. The approach we took in this study is to integrate uncertainty into the analysis, by using a sample of trees during the MCMC procedure to estimate a posterior sample of rate-scaled trees, instead of using a single tree.

CONCLUSION

Our results indicate a link between the scaling relationship of biting edges and the presence of elevated evolutionary rates. It is very likely that these increased rates occurred due to ecological changes, facilitating the adaptation of more efficient biting biomechanics for specialist diets. The similarities in ceratopsian and oviraptorosaurian skulls could suggest that the evolution of efficient biting biomechanics relates to the diets of these taxa. Taxa such as *Diplodocus* and *Limusaurus* show evidence for the ontogenetic change of the skull (Wang *et al.* 2017a; Woodruff *et al.* 2018), accompanied by a reduction of the tooth row, suggesting a change in the scaling relationships of the biting edge throughout the lifespan of the animal.

Other taxa with specialized adaptations in the tooth row, such as alvarezsaurs, lack evidence of evolutionary rate increases. This may be due to these groups lacking extreme deviations in biting edge lengths from the isometric scaling relationship. This suggests that, despite the clear link between increased rate-shifts in the evolution of relative biting edge lengths and the acquisition of specialist herbivorous adaptations, this is not the case across all dinosaur clades. In other words, acquisitions of herbivorous adaptations do not always alter biting efficiencies along the biting edge lengths. However, that we can still detect signatures of selection associated with the acquisition of herbivory in the evolution of relative biting edge lengths, demonstrates the utility of simple measures of biomechanical performance in illuminating the evolution of functional morphology through time and across phylogeny.

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DATA ARCHIVING STATEMENT

Raw and processed data collected for and analysed in this work are available in the Dryad digital repository: https://doi.org/10.5061/dryad.h70rxwdqk.

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