

Paleontology Series

Ecological and evolutionary implications of dinosaur feeding behaviour

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Dinosaurs had a wide variety of feeding mechanisms that strongly impacted on their ecology and evolution. Here, we show how novel application of technologies borrowed from medicine and engineering, such as CT scanning and Finite Element Analysis, have recently been combined with traditional approaches to result in significant advances in our understanding of dinosaur palaeobiology. Taxon-specific studies are providing quantitative data that can be used to generate and test functional hypotheses relating to jaw mechanics and feeding behaviour. In turn, these data form a basis for investigating larger scale patterns of ecological and macroevolutionary change, such as possible coevolutionary interactions and the influence of feeding adaptations on species richness, which are of more general interest to ecologists and evolutionary biologists.

Introduction

Dinosaurs appeared during the Late Triassic period [*ca.* 225 million years ago (Mya)] and diversified rapidly, becoming the dominant terrestrial vertebrates of Jurassic and Cretaceous ecosystems (*ca.* 206–65 Mya) [1–3]. Dinosauria was a successful clade by any standard: it was species rich (with >650 Mesozoic taxa currently considered valid, inclusive of birds), abundant (accounting for >95% of the vertebrate standing biomass in some faunas) and globally distributed. The first dinosaurs were probably small (1–2 m in body length) faunivorous bipeds [4], but, almost immediately after its origin, the group radiated into three distinct monophyletic lineages (Theropoda, Sauropodomorpha and Ornithischia). Each lineage evolved modifications of this *bauplan*, particularly with respect to body size, diet and locomotory adaptations (i.e. bipedality, quadrupedality and flight). This adaptive plasticity enabled Dinosauria to exploit diverse terrestrial niches until the end of the Cretaceous Period (65 Mya), when all non-avian dinosaurs became extinct [1–3]. Dinosaur dietary modes varied from hypercarnivory in predatory theropods to obligate high-fibre herbivory (folivory) in derived sauropodomorphs and ornithischians, as well as piscivory, omnivory, low-fibre herbivory (e.g. frugivory) and possibly other diets such as insectivory and scavenging (Box 1) [1].

One major reason for the ecological and evolutionary success of the dinosaurs during the Mesozoic is likely to have been their diverse feeding mechanisms, which would have promoted niche partitioning and subsequent cladogenesis [5–7]. Feeding behaviour strongly influences most aspects of animal biology, from obvious energetic requirements to reproductive biology, life-history strategies, behavioural ecology, habitat preferences and population ecology [8–10]. Detailed knowledge of dinosaur feeding behaviour not only informs us on the palaeobiology of individual taxa, but also provides a model system for investigating broader ecological and evolutionary questions, such as: how has the occupation of ecological roles and morphospace altered in response to different biotic and abiotic factors through time? How do sophisticated functional complexes evolve? It also enables consideration of the structure and function of ancient ecosystems and the ways in which they compare with those from the Recent. Moreover, feeding mechanisms provide opportunities for assessing large-scale macroevolutionary patterns and processes (e.g. the coevolution of dinosaurian herbivores and plants) [11].

Methods used to infer behaviour and function in extinct animals fall into two broad categories: ahistorical and historical [12]. Ahistorical approaches view organisms as mechanical constructs, whose properties are governed by invariant physicochemical laws: the evolutionary history of the organism(s) is not considered. Methods within this category include the use of form–function correlations based on skeletal architecture (and inferred soft-tissue anatomy) and comparisons with suitable extant analogue taxa, biomechanical modelling and the use of circumstantial palaeoenvironmental evidence (e.g. identification of contemporary food items). Historical methods (such as the ‘Extant Phylogenetic Bracket’ [13]) use information about the phylogenetic position of an organism to infer function by treating it as homology [12,13]. The distribution of the character of interest can be optimised on to a phylogeny and its evolution traced: where the character defines a monophyletic group of organisms, it can be inferred that extinct members of that clade are also likely to have had that feature. Direct evidence of feeding behaviour (e.g. fossilised gut contents) is also informative, but examples are generally rare (Box 2).

To date, most work on dinosaur feeding mechanisms and diet [5] has relied upon form–function correlations,

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Box 1. Evolution of dinosaur diets

Outgroup comparisons suggest that dinosaurs were primitively faunivorous [4]. Traditionally, it was thought that herbivory evolved twice in Dinosauria, at the bases of Sauropodomorpha and Ornithischia, respectively [2]. However, more recent work has demonstrated that dietary evolution in the group is likely to have been more complex [59].

Optimization of presumed diets onto a dinosaur phylogeny (Figure 1) indicates that: (i) carnivory was retained in most theropod lineages; (ii) omnivory might have appeared on at least three independent occasions within non-avian dinosaurs; and (iii) that there might have been four or more independent origins of obligate herbivory, often arising via a transitional omnivorous phase [59].

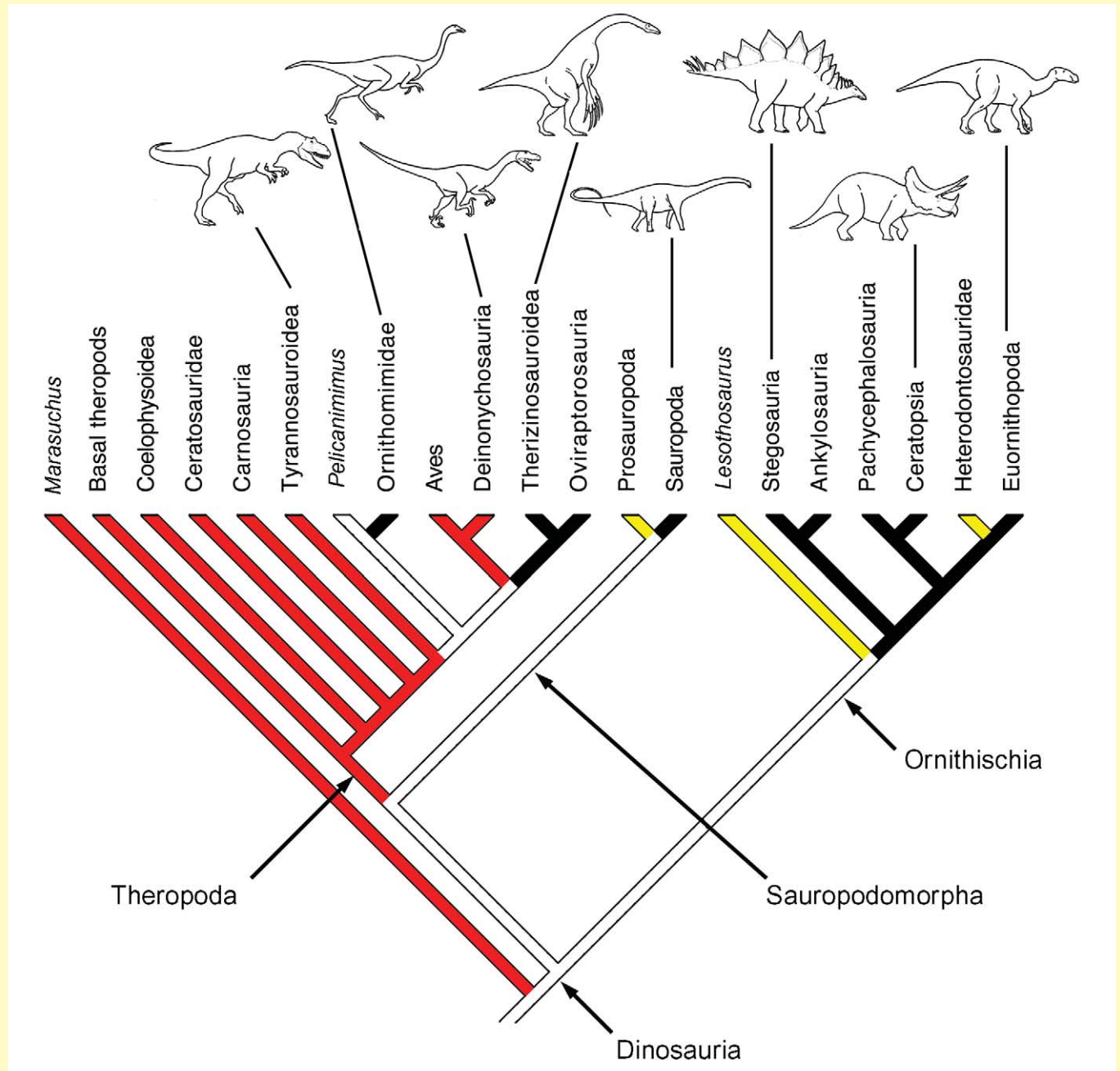


Figure 1. A composite cladogram of Dinosauria, with the non-dinosaurian dinosauromorph *Marasuchus* representing the outgroup. Presumed diets (based on [27,59]) have been optimised (unordered; most parsimonious distribution) onto the tree. Black fill presents obligate herbivory; yellow fill, omnivory; red fill, carnivory; no fill, diet unknown. Dinosaur reconstructions not to scale. Adapted with permission from [2,60].

which enabled qualitative interpretations of feeding behaviour (e.g. the elucidation of jaw mechanisms). However, few of these studies generated robust quantitative data on feeding or attempted to place feeding within

more holistic evolutionary or ecological frameworks (but see [14]).

The past decade has witnessed renewed interest in dinosaur feeding owing to: (i) availability of new

Box 2. Direct evidence of dinosaur diet

Definitive indications of diet and feeding behaviour are rare in the fossil record and rely upon serendipitous discoveries. However, direct evidence of dinosaur diet, including fossilised faeces (coprolites), gut contents (enterolites and cololites) and other feeding traces (e.g. tooth marks on bones [61,62]), is highly informative (although taxon specific) and can be used to test dietary predictions made on the basis of anatomical inferences.

Recent examples include: the presence of a spinosaurid theropod tooth embedded within a pterosaur neck vertebra, which demonstrated a previously undocumented trophic relationship between these taxa [63]; tyrannosaurid enterolites [64] and coprolites [65,66] have provided valuable information on diet and digestive physiology (e.g. passage times through the gut, degree of oral versus gut processing and inferred gut anatomy) in these animals. Furthermore, angiosperm molecular biomarkers detected by geochemical analysis of herbivorous dinosaur coprolites [67], the discovery of a cololite composed exclusively of angiosperm fruits in the ankylosaur *Minmi* [68], and identification of angiosperm-specific parasitic fungi and grass phytoliths in presumed sauropod coprolites [69,70], indicate that flowering plants were a constituent of the diets in at least some Cretaceous dinosaurs.

techniques [e.g. Finite Element Analysis (FEA) and Computer-Assisted Tomography (CT)]; (ii) the discovery of dinosaur taxa with novel anatomical features; and (iii) increased interest in synthesizing palaeobiological data with phylogenetic hypotheses. Here, we review recent work on dinosaur feeding mechanisms, highlighting the contribution made by new technologies. These studies provide the data needed to address broad macroevolutionary questions over a variety of temporal and spatial scales that are relevant to those interested in the function of extinct and extant ecosystems.

Recent advances: novel techniques and new discoveries

Application of methodologies that are novel to palaeobiology is facilitating a greater understanding of dinosaur feeding mechanics (Box 3). The work can be done with analytical rigour and enables hypothesis testing within a quantitative framework. Many of these studies are taxon specific, but the results obtained can inform broader evolutionary questions. An example of this new quantitative approach is the generation of physical models of fossils, which can be subjected to conditions that simulate behavioural hypotheses. By driving replica aluminium-bronze models of *Tyrannosaurus rex* teeth into bovine bone, it has been estimated that 6410 Newtons of bite force were required to penetrate cortical bone of a similar thickness to that seen in a fossilized *Triceratops* pelvis that displays tooth puncture marks characteristic of *T. rex* [15,16]. Further physical modelling has demonstrated how *T. rex* teeth functioned primarily as pegs, gripping food and cutting meat in the manner of a smooth, dull knife blade. Cuboidal serrations along the tooth margins trapped meat fibres and subsequent putrefaction might have enabled *T. rex* to deliver bites loaded with infectious bacteria [17], as in the extant Komodo dragon *Varanus komodoensis*. Small ampullae at the base of each serration prevented the enamel from cracking as the teeth deformed during feeding [18].

In addition to these empirical approaches, mathematical models have been developed to exploit skeletons and associated soft tissues as structures governed by physical laws: the past five years have witnessed significant advances in the application of these Newtonian principles to feeding behaviour. Measuring cross-sectional surface areas of reconstructed adductor musculature provides estimates of adductor muscle force that, when fed into simple lever arm equations, can be used to estimate dinosaur bite force. In one study [19], this method estimated the maximum mid-tooth row bite force of the theropod *Allosaurus fragilis* to be ~2000 Newtons, similar to that of a leopard. By estimating the mechanical advantage of the jaw-closing musculature and comparing relative mandibular velocities on jaw closure, it was demonstrated that, among theropods, *Carnotaurus sastrei* was optimised for faster jaw closure compared with jaws that were capable of slower, but more forceful, bites in *Ceratopsus nasicornis* and *T. rex* [20]. Beam analysis (a mathematical technique for treating the skull as a 'beam' in engineering terms in order to decipher distributions of stress) has further divided theropods into five feeding categories (including slashing, powerful biting and prey holding) based on the ability of the mandible to resist bending and torsional loads [21]. Furthermore, the principles of beam analysis indicate a relationship between orbit morphology and sagittal bending strength in the skulls of 17 theropod dinosaurs [22]. Stronger skulls generally have narrow orbits that are inclined subparallel to the major inclination of the maxillary teeth and, by inference, could generate a larger bite force [22]. An increase in the surface area of the snout is correlated with an increase in the size and strength of the maxillary teeth in carnivores [23], which has been interpreted as being useful for dispatching prey of equal or greater body size than the predator.

Demonstration of a relationship between bite force and body size in extant taxa led to the prediction that *T. rex* could generate a bite force of between 183000 and 235000 Newtons [24], although this range is substantially higher than empirically derived estimates [16]. Further inferences of skull strength have been provided by space-frame analysis [25], which has suggested that the skull of *T. rex* was constructed primarily to resist strong, vertically directed bite forces during biting: this result has been used to argue for carcass dismemberment through repeated biting rather than extensive lateral shaking of prey, which, by contrast, would have resulted in the application of large, laterally directed loads to the teeth [25].

Inference of feeding behaviour is not restricted to analysis of the cranium. Lever arm mechanics suggest that the diminutive forelimb of *T. rex* had a surprisingly high mechanical advantage. This, coupled with a robust, columnar humerus, shows that the arms were optimised for force generation [26], which could be attributed to prey-handling capabilities.

Another line of mathematical enquiry has been the investigation of dinosaur ecological energetics by the use of calorific data from living organisms and physiological

Box 3. Case study: a holistic approach to feeding in *Tyrannosaurus rex*

By combining evidence from descriptive anatomical work, physical modelling, mathematical approaches and new technologies, palaeontologists are able to gain a more comprehensive knowledge of dinosaur feeding behaviour, which, in turn, improves our understanding of Mesozoic ecology. Here, we demonstrate how this approach can be used to investigate the palaeobiology of *Tyrannosaurus rex*, whose gargantuan size and specialized anatomy have made it a favourite of functional morphologists.

Comparisons of the craniodental morphology of *T. rex* (Figure 1a) to living animals indicate that this animal was a carnivore. Wear facets on the teeth show that tyrannosaurids practiced repeated shearing between upper and lower dentitions [44] (Figure 1b), offering a processing mechanism for flesh and bone. Puncture-like bite marks on a *Triceratops* pelvis [15] (Figure 1c) and extensive damage to the tail of one specimen of the duck-billed dinosaur *Edmontosaurus* [62] demonstrate the ability of *T. rex* to penetrate bone. Two types of repetitive biting behaviour are observed: deep puncture of thinner cortical bone and, in deeper cortical bone, shallow puncture followed by pulling of the teeth across the bone surface [15]. Comparison of the cutting ability of fossilised teeth to that of varied replica blades demonstrated that stout tyrannosaurid teeth (Figure 1d) functioned as pegs with poor cutting ability. Instead, the teeth were used to ‘grip-

and-rip’ prey – the ‘puncture-pull’ feeding hypothesis [17,18]. Space-frame analysis suggests that the *T. rex* skull was constructed to resist strong, vertically directed bite forces [25]. FEA provides information on stress-strain patterns within the skull, and confirms that the *T. rex* cranium could withstand large feeding-induced puncture-pull loads [34] (Figure 1e). Furthermore, FEA studies suggest that tyrannosaurid nasal bones were fused and thickened to withstand large compressive and shear stresses, and that open skull sutures assisted in ‘shock-absorption’ during powerful bites [34].

Replica teeth driven into bovine bone (mimicking the morphology of the bitten *Triceratops* pelvis) indicate that *T. rex* could produce bite forces exceeding 6410 Newtons [16], well in excess of those estimated for modern lions, showing that a *T. rex* bite could shatter bone [16]. This hypothesis is confirmed by the discovery of a *T. rex* coprolite [65] (Figure 1f) that contains large quantities of pulverized bone pertaining to an ornithischian dinosaur. In this instance, the bone of the prey animal was only partially digested, indicating that gut-residence time was short [65]. Finally, although most palaeontologists agree that *T. rex* was an active predator at least some of the time [49,50], recent ecological energetic analysis of the *T. rex*-bearing Hell Creek Formation suggests that, providing competition for carrion was low, it could have survived purely as a scavenger [29].

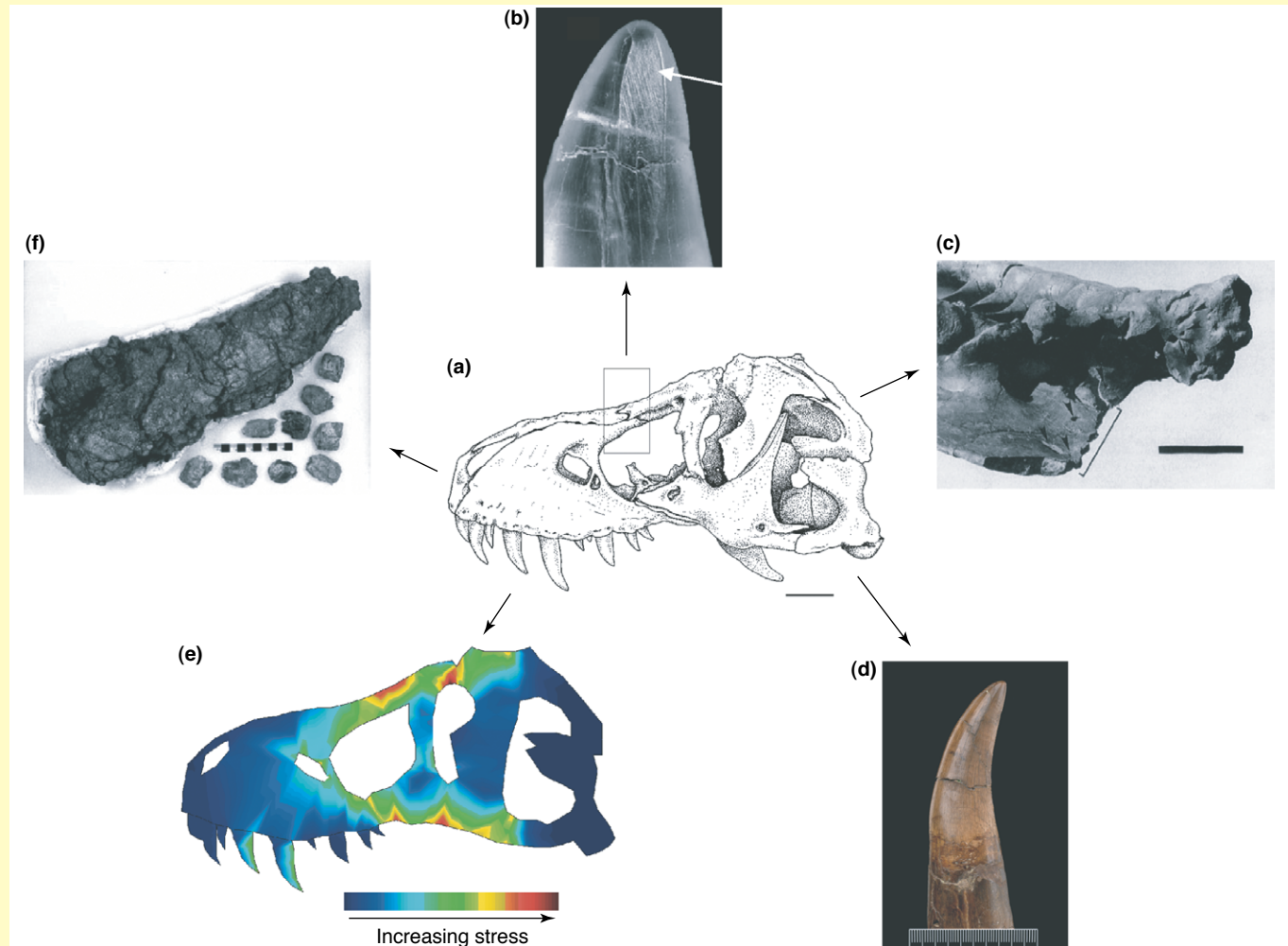


Figure 1. A holistic approach to *Tyrannosaurus rex* feeding behaviour. (a) The skull of *T. rex*, left lateral view; (b) Wear facets on tyrannosaurid teeth as indicated by the white arrow; (c) *Triceratops* pelvis, bitten repeatedly by *T. rex* (arrow indicates a ‘pull’ scrape); (d) tyrannosaurid tooth [Natural History Museum (BMNH) specimen R4863]; (e) Finite element model demonstrating stress distributions in the *T. rex* skull during a bite; (f) Probable *T. rex* coprolite. Scale bars = 100 mm (a,f), 10 mm (b and d) and 250 mm (c). Reproduced with permission from [34] (a), [44] (b), [16] (c), E.J. Rayfield (e), [65] (f).

models to estimate daily food requirements and to test hypotheses relating to diet and foraging strategies [27–29]. Calculation of daily energy budgets for ornithomimosaurian theropods demonstrated that, contrary to a recent suggestion [30], filter feeding was not a tenable lifestyle for these animals [27]. Similar approaches have also suggested that sauropod dinosaurs needed to consume $> 170 \text{ kg fodder d}^{-1}$ to meet their prodigious energy requirements [28].

CT scans have become an important tool in palaeontological research, owing largely to advances in scan resolution, imaging software and the increased availability of machines in industrial and academic environments. Previously unseen internal geometry of bones can be captured and reconstructed in 2D and 3D. CT data can inform studies of dinosaur feeding in tangential ways: for example, by elucidating the morphology of the brain and sense organs [31]. Moreover, CT can generate data sets that can then be utilized for beam analysis or computer modelling, although these avenues have been little explored with the exception of FEA. Laser surface scanning of bones also yields digital 3D morphological data; however, this process captures only the external geometry of the specimen and neglects important internal structural information (e.g. cortical thickness and internal buttressing). Yet, this approach is important because it enables ‘virtual’ manipulation of skeletal elements that are often large, unwieldy and/or fragile, enabling functional experimentation. For example, computer modelling of sauropod necks has provided estimates of the range of vertical and horizontal movement, which would have influenced browsing heights and foraging strategies in these animals [32].

FEA is a computerized technique that calculates stress and strain within a virtual structure under an applied load. FEA offers a quantitative framework in which to construct hypotheses of skeletal evolution and function that can then be tested by the manipulation of model parameters and comparison with extant animal models [33]. Although routinely applied in engineering and orthopaedics, its use in zoology and palaeontology has been limited thus far. FEA has demonstrated that the cranium of *Allosaurus fragilis* was extremely strong, but a relatively weak bite force resulted in high safety factors (the ratio of the highest habitual stress experienced *in vivo* to the ultimate failure stress of the structure concerned), a result of either evolutionary constraint and poor optimisation of the cranium for feeding or the adoption of a feeding strategy that applied large, dynamic loads to the skull [19]. FEA has informed broad functional questions such as the behaviour of sutures during feeding: for example, in *T. rex*, that fused nasal bones correspond to regions of high compressive and shear stress, and cranial sutures might act as ‘shock-absorbers’ to contain large, powerful bites [34]. Further work on *Allosaurus* showed that cranial suture morphology is adapted to the stress experienced across the sutures [35]. An FEA study on the mandible of *Carnotaurus sastrei* suggests that the intramandibular joint common to theropod mandibles functions in a similar shock-absorbing manner [36]. Most FEA studies so far are taxon or even element specific [37],

but recently an attempt was made to place FEA results within a phylogenetic framework (see below) [38].

Information about the relative motion of the jaws can also be obtained from analysis of dental microwear, the microscopic scratches and pits left on the teeth by the action of food–tooth and tooth–tooth wear during feeding. Few studies have been carried out on dinosaurs to date [39–45], but these have revealed hitherto unsuspected diversity and complexity in the jaw mechanics of ankylosaurs [41,42] and ceratopsians [43]. Furthermore, differences in dental microwear patterns between sympatric sauropod taxa can be used to support hypotheses of niche partitioning [39,40].

Finally, discovery of new material and/or taxa can also lead to the generation of novel functional observations and hypotheses. For example, two new theropod taxa, *Incisivosaurus* [46] and *Masiakasaurus* [47], have bizarre and previously undocumented combinations of cranial and dental features, which presumably reflect highly specialized diets.

Palaeoecological and evolutionary implications

Knowledge of feeding mechanics and behaviour provides the raw information that is needed to study niche construction and community structure within Mesozoic ecosystems. Until recently, niche partitioning among dinosaur taxa was poorly understood, particularly as many sympatric taxa (among both the herbivore and carnivore guilds) showed considerable overlap in habitat preference and body size [48,49]. Nevertheless, better functional characterization of theropod dinosaur feeding systems has revealed that these animals radiated into several distinct ecomorphotypes, distinguished by differences in the form or function of the skull, teeth and postcranial skeleton [6,50]. These ecomorphotypes form a basis for dietary differentiation and the establishment of distinct predatory guilds within faunas [6,50]. Similarly, differences in maximum vertical and horizontal browsing ranges and jaw mechanics are likely to have formed the basis for niche separation in herbivorous dinosaur communities [14,40,51]. New information about dietary composition can also enable more confident reconstructions of fine-scaled trophic relationships, such as the identification of specific predator–prey interactions [52,53].

Combinations of functional and phylogenetic data are useful for investigating the evolution of the various functional complexes associated with particular feeding modes (e.g. specific jaw mechanisms, combinations of postcranial features affecting browsing ability, etc.). First, the optimisation of characters onto phylogenetic trees enables us to trace the sequence of character acquisition within functional complexes, offering insights into how they were assembled [40,54,55]. Feeding complexes in herbivorous dinosaurs usually evolved in an incremental manner, beginning with relatively simple, generalised systems that become progressively more sophisticated in derived members of the group [54,55]. For example, the evolution of the elaborate pleurokinetic jaw mechanisms and dental batteries of hadrosaurs occurred in a step-wise manner, shown by the sequential modification and/or

addition of characters present in more primitive ornithomorphs [54,55]. Second, phylogenetic hypotheses provide a comparative context for the interpretation of results obtained from taxon-specific biomechanical modelling. A preliminary attempt to analyse the evolution of theropod feeding on the basis of FEA showed that all of the taxa included shared several cranial stress distributions in common, suggesting that these conditions should be regarded as symplesiomorphic for Theropoda, whereas other mechanical features of the skull were limited to individual taxa and could be regarded as derived [38].

Dinosaurs can be used as model organisms for investigating questions of macroevolutionary pattern and process: they have an extensive fossil record; are diverse and have a wide variety of morphological adaptations; and they fit into a relatively stable phylogenetic framework [1]. Feeding mechanisms of herbivorous dinosaurs have been used to address the prevalence of competitive replacement events in the fossil record [7]; the influence of coevolutionary interactions on clade diversification over extended geological timescales [11,56]; and the effects of key innovations on diversification patterns [7]. The integration of information on sauropodomorph feeding mechanisms with dinosaur diversity curves and distribution data has indicated that improvements in the feeding mechanisms of sauropods (such as the development of dental occlusion and greater browsing ranges) might have enabled these animals to replace prosauropods (which had relatively simple feeding adaptations) as the dominant herbivores of Lower–Middle Jurassic ecosystems (*ca.* 206–159 Mya) [7], a rare example of a possible ‘candidate competitive replacement event’ [57]. Moreover, a statistical correlation can be demonstrated between sauropod diversity through time and the number of different feeding mechanisms present within the group, suggesting that acquisitions of new feeding adaptations can be regarded as key innovations that promoted the radiation of the clade [7]. Diffuse coevolution with plants has also been proposed as a mechanism for driving dinosaur diversification [14,58]: it was suggested that the initial radiation of angiosperms was fostered by changes in dinosaur browsing behaviour and, conversely, that the evolution of new feeding mechanisms among ornithischian dinosaurs was promoted by the availability of this new food source. However, detailed comparisons between the dinosaur and angiosperm fossil records no longer support these hypotheses: the first appearance of angiosperms in the Early Cretaceous (at ~125 Mya) does not coincide with any major events in dinosaur evolution, such as peaks in speciation rates or the appearance of new jaw mechanisms [11,56]. Nevertheless, some circumstantial evidence does suggest that dinosaur–plant coevolution was possible in the last few million years of the Cretaceous (99–65 Mya) [11], although this suggestion remains to be tested.

Summary and prospects

Recent work is providing insights into aspects of dinosaur feeding that have hitherto eluded quantitative analysis, enabling palaeobiological reconstructions at a high level of detail. Some preliminary attempts to integrate feeding data with phylogenetic and palaeoecological information

have demonstrated that dinosaur feeding has the potential to inform broader conceptual issues that are pertinent to evolutionary studies in general.

Nevertheless, many aspects of dinosaur feeding require further investigation. Relatively few taxa have been studied in detail and more information is needed to provide a comprehensive overview of feeding in this important clade. For example, although quantitative analyses of theropod feeding (e.g. FEA modelling) have revealed aspects of their behaviour unidentified by earlier qualitative studies, similar analyses have not yet been applied to herbivores. In the first instance, we advocate further taxon-specific studies to provide much needed qualitative and quantitative baseline data.

Knowledge of specific dinosaur feeding mechanisms informs macroevolutionary and palaeoecological studies involving processes that are thought to occur over wide spatial and temporal scales. To date, most of the palaeoecological studies have focused on herbivorous dinosaurs (e.g. interactions with plants and the evolution of jaw mechanisms) and the evolutionary context of theropod feeding has been neglected. Important questions that remain include: what is the relationship between species richness and the evolution of specific feeding adaptations? (are certain features ‘key innovations’?) Is it possible to erect testable hypotheses of tight or diffuse coevolutionary interactions between dinosaurs and contemporary floras? Is the species richness of carnivores tied to diversity and community structure of herbivores? Finally, the evolution of avian feeding mechanisms has yet to be addressed from a dinosaurian perspective. A marriage of classic palaeontological analysis and new technologies will further our understanding of these problems and provide fertile avenues for future research.

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