

# Paleobiology of Herbivorous Dinosaurs

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## Keywords

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## Abstract

Herbivorous dinosaurs were abundant, species-rich components of Late Triassic–Cretaceous terrestrial ecosystems. Obligate high-fiber herbivory evolved independently on several occasions within Dinosauria, through the intermediary step of omnivory. Anatomical character complexes associated with this diet exhibit high levels of convergence and morphological disparity, and may have evolved by correlated progression. Dinosaur faunas changed markedly during the Mesozoic, from early faunas dominated by taxa with simple, uniform feeding mechanics to Cretaceous biomes including diverse sophisticated sympatric herbivores; the environmental and biological drivers causing these changes remain unclear. Isotopic, taphonomic, and anatomical evidence implies that niche partitioning reduced competition between sympatric herbivores, via morphological differentiation, dietary preferences, and habitat selection. Large body size in dinosaur herbivores is associated with low plant productivity, and gave these animals prominent roles as ecosystem engineers. Although dinosaur herbivores lived through several major events in floral evolution, there is currently no evidence for plant-dinosaur coevolutionary interactions.

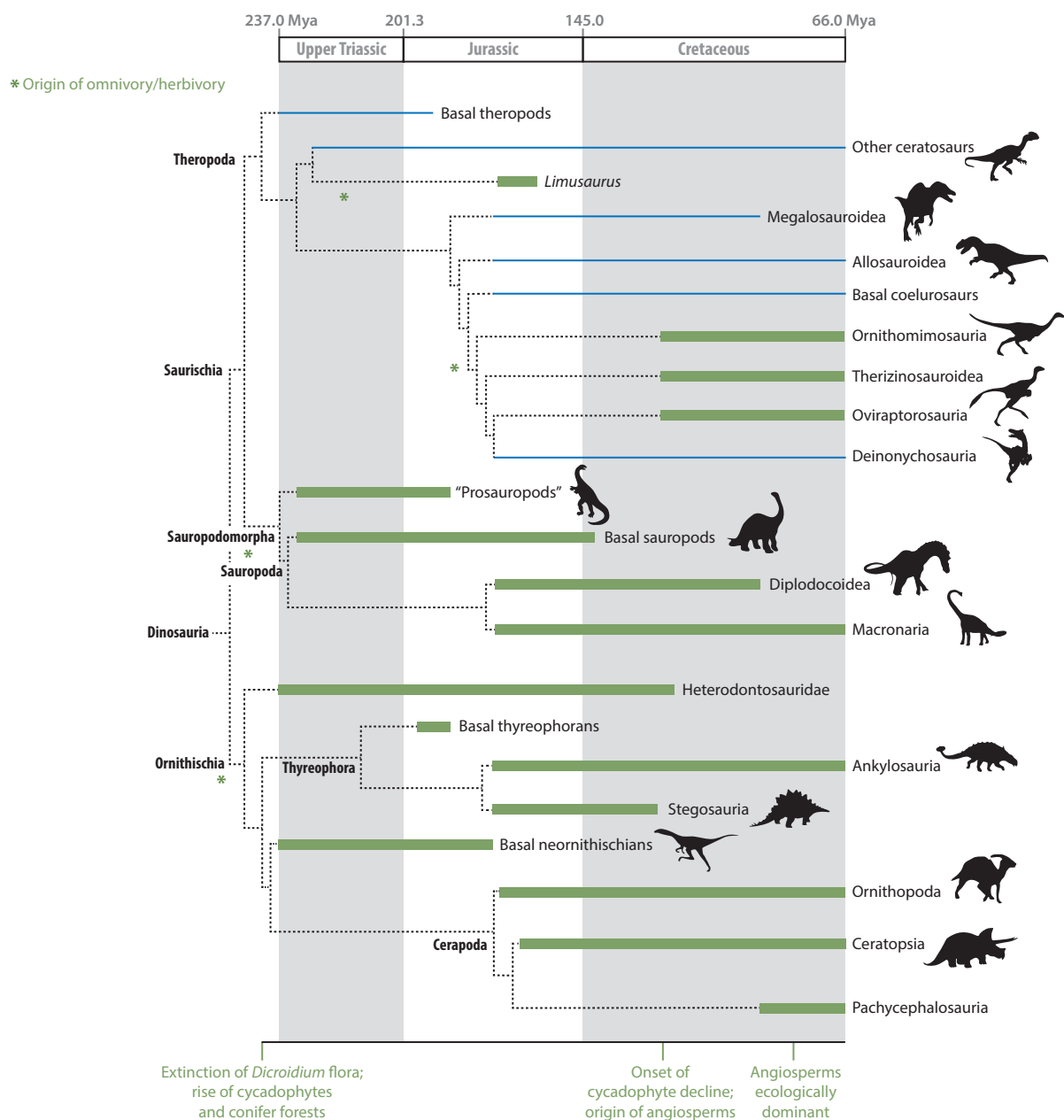
## INTRODUCTION

Herbivore abundance, species richness, food preferences, and feeding mechanisms have profound impacts on the community structure, dynamics, and function of terrestrial ecosystems (e.g., McNaughton et al. 1989, Cyr & Pace 1993, Crawley 1997, Bigger & Marvier 1998, Hawkes & Sullivan 2001). Today, vertebrate herbivores have significant effects on plant communities, due to feeding-related damage, seed dispersal, trampling, and nutrient cycling (e.g., Crawley 1989, 1997; Augustine & McNaughton 1998; Bakker & Olff 2003; Bakker et al. 2006; Danell et al. 2006; Maron & Crone 2006; Doughty et al. 2013). Conversely, plant distribution, life history, and productivity have major repercussions for herbivore population density, survival rates, and distribution (e.g., Owen-Smith 1992).

Herbivory requires numerous physiological, anatomical, and behavioral adaptations to collect, process, and digest vegetation, including modifications to the teeth, jaw musculature, and skull to enable mechanical processing of food; changes in skeletal anatomy to assist food collection; and specialization of the gastrointestinal tract to aid digestion (e.g., Smith 1993; Bels et al. 1994; Stevens & Hume 1995; Fritz et al. 2010, 2011). Conversely, plants have evolved features to deter herbivory, both physical (thorns, tough leaves and bark, hairs, specialist growth forms) and chemical (toxins and other compounds that make plants unpalatable). Plant compensation has also evolved to offset the effects of herbivory by extending growing periods, delaying leaf senescence, and improving nutrient and water availability to surviving leaves (e.g., Weishampel 1984a; Crawley 1989, 1997; Coley & Barone 1996). However, some plants attract herbivores to enable seed dispersal or pollination, usually by producing fleshy fruits or nectar (e.g., Herrera 1985). All of these factors lead to diverse mutualistic interactions between plants and vertebrate herbivores, ranging from herbivore exploitation, with consequent depression of plant selective fitness, to tight and diffuse coevolutionary interactions (e.g., Herrera 1985, Herrera & Pellmyr 2002, Strauss & Irwin 2004, Bascompte & Jordano 2007).

Given the importance of vertebrate herbivory in modern ecosystems, paleontologists have sought to determine how these processes operated in the past. This has involved work on the functional morphology and evolution of feeding in extinct herbivores, characterization of ancient floras, and analyses of regional and global patterns of plant and herbivore distributions. Non-avian dinosaurs (referred to simply as dinosaurs hereafter) have attracted significant attention. Although many dinosaurs were carnivores, the group included the most conspicuous terrestrial vertebrate herbivores of the Mesozoic Era (Sereno 1997, 1999; Weishampel et al. 2004). Approximately 54% of known species were omnivorous or herbivorous, including all sauropodomorphs and ornithischians as well as members of several coelurosaurian theropod clades (Weishampel et al. 2004, Barrett et al. 2011) (**Figure 1**). Herbivory was a major adaptive zone for dinosaurs and contributed greatly to overall dinosaur success.

Extant vertebrate herbivores occupy a dietary spectrum ranging from obligate, high-fiber herbivory (tough cellulose-rich leaves, stems, bark), through taxa that eat a mixture of low-fiber (new shoots and leaves, fruits) and high-fiber vegetation, to omnivores for which plant material is part of the regular diet or a seasonal resource. Herbivorous dinosaurs likely occupied positions along this continuum (Barrett 2000). Inferences can be made regarding the positions of dinosaurs on this spectrum by documenting the number and complexity of the adaptations to herbivory that they possess. Omnivorous dinosaurs, such as the earliest ornithischians and sauropodomorphs, possessed only a few features indicative of herbivory, including dentitions suitable for shearing plant food (e.g., Norman & Weishampel 1991, Barrett & Upchurch 2007). By contrast, high-fiber herbivores, such as hadrosaurids, had sophisticated cranial and dental adaptations that rivaled those of living mammals. These incorporated the most complex dentitions of any vertebrates, living



**Figure 1**

Simplified time-calibrated dinosaur phylogeny showing the interrelationships of the major clades, with emphasis on those that were omnivorous or herbivorous. A green asterisk denotes the origin of omnivory/herbivory in a clade, and these clades are shown in green, with carnivorous clades represented by blue lines; note, however, that there may have been multiple origins in theropods and that additional acquisitions of herbivory in birds are omitted for clarity. Phylogeny based on Sereno (1999), Butler et al. (2008), Zanno & Makovicky (2011), Carrano et al. (2012), and other sources.

or extinct, with batteries of interlocking teeth, high tooth replacement rates, teeth composed of six different tissue types, and complex jaw mechanisms involving a unique form of intracranial flexibility (pleurokinesis) and both fore-and-aft and vertical movements of the mandible (Norman 1984, Weishampel 1984b, Bell et al. 2009, Williams et al. 2009, Erickson et al. 2012).

Numerous techniques have been used to investigate dinosaur herbivory, including comparative anatomy, functional and ecological modeling, and physiological analogies with extant herbivores. Such studies have provided major insights into the functional morphology of dinosaur herbivores, and many feeding mechanisms of varying complexity have been documented (e.g., Galton 1985, 1986; Crompton & Attridge 1986; Farlow 1987; Weishampel & Norman 1989; Norman & Weishampel 1991; Christiansen 2000; Upchurch & Barrett 2000; Barrett 2001; Rybczynski & Vickaryous 2001; Barrett & Upchurch 2007; Bell et al. 2009; Tanoue et al. 2009; Zanno et al. 2009; Sereno et al. 2010; Hummel & Clauss 2011; Norman et al. 2011; Varriale 2011; Whitlock 2011a; Erickson et al. 2012; Sereno 2012; Young et al. 2012; Zanno & Makovicky 2011). This work has facilitated reconstructions of dinosaur ecology, inferences about dinosaur-plant interactions, and insights into dinosaur evolutionary history (Fastovsky & Smith 2004, Barrett & Rayfield 2006). Herbivorous dinosaurs survived several major floral replacement events (e.g., angiosperm origins), as well as geographic and environmental changes that impacted their evolution. As a result, they are useful models for assessing the long-term influence of herbivory on vertebrate macroecology and macroevolution.

## EVOLUTION OF DINOSAUR HERBIVORY

The ancestral dinosaur is often depicted as a small-bodied, bipedal carnivore, on the basis of the inferred predatory habits of close dinosaur relatives (lagosuchids) and the presence of carnivorous adaptations, including recurved, finely serrated teeth and trenchant claws, in Late Triassic saurischians such as *Herrerasaurus* and *Staurikosaurus* (Sereno 1997). A corollary of this assumption is that omnivory/herbivory appeared on multiple independent occasions within Dinosauria, at the bases of Sauropodomorpha and Ornithischia, respectively, and potentially on several occasions within Theropoda (Barrett 2000, Barrett & Rayfield 2006). However, reappraisal of dinosauromorph phylogeny, and the discovery of new basal dinosaurs and dinosaur outgroups, has undermined this scenario and shown that dietary evolution among Triassic dinosauromorphs was more complex than envisioned previously (Langer et al. 2010, Nesbitt et al. 2010, Barrett et al. 2011, Kubo 2011). Firstly, although lagosuchids have been regarded as carnivores, the evidence for diet in these animals is equivocal, as cranial material is scarce (Langer et al. 2010). Secondly, a recently recognized dinosauromorph group, Silesauridae, has been identified as the immediate sister group to Dinosauria. Most silesaurids were herbivorous, which demonstrates that many close dinosaur relatives were herbivores, rather than carnivores, although the basal-most silesaurid, *Lewisuchus*, is regarded as carnivorous (Nesbitt et al. 2010). Thirdly, early saurischian dinosaur interrelationships are highly unstable; some key taxa, such as *Herrerasaurus* and *Eoraptor*, are recovered in various positions on the dinosaur tree, as either basal saurischians (outside of the clade comprising theropods and sauropodomorphs), early theropods, or basal sauropodomorphs (Sereno et al. 1993, Martínez et al. 2011). Finally, the diet of *Eoraptor* is considered ambiguous; both omnivory and carnivory have been posited for this taxon (Sereno 1999, Langer et al. 2010, Barrett et al. 2011).

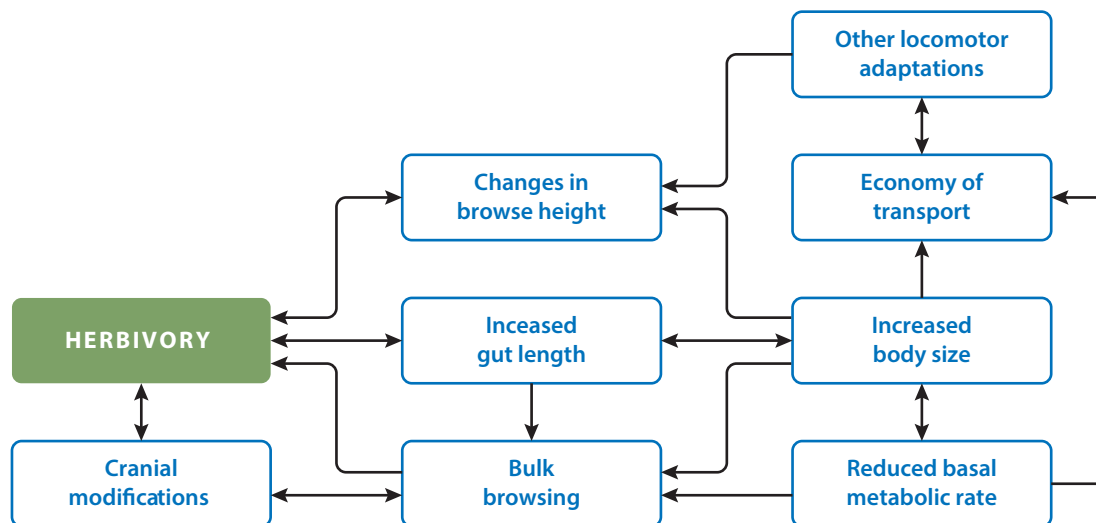
These observations, in combination with the omnivorous/herbivorous diets of all sauropodomorphs and ornithischians, make it difficult to trace dietary evolution in early dinosaurs with confidence. Relatively small changes in the phylogenetic relationships of these taxa, and minor differences in dietary interpretations, have major effects on how different diets are distributed across dinosauromorph phylogeny and on where major dietary shifts occur on the tree. On the

basis of current evidence, it is plausible that the ancestral dinosaur was either omnivorous or carnivorous (Barrett et al. 2011, Kubo 2011). Nevertheless, it is clear that obligate, high-fiber herbivory, as evidenced by the appearance of dental occlusion, complex jaw mechanisms, or gastric mills, did appear on multiple occasions within Dinosauria, at least once in Sauropodomorpha, three times in Ornithischia (at the bases of Thyreophora, Ornithopoda, and Ceratopsia), and on several occasions in Theropoda (Barrett & Rayfield 2006, Zanno & Makovicky 2011) (**Figure 1**). In most cases, obligate herbivores are deeply nested within clades that are primitively omnivorous, which implies that obligate herbivory developed via the intermediary condition of omnivory (Barrett 2000), as also occurred in the evolution of mammalian herbivory (Price et al. 2012). Among sauropodomorphs and ornithischians, there are no examples of clades that acquired adaptations associated with obligate herbivory reverting to either omnivory or carnivory. However, reversions to carnivory might have occurred among maniraptoran theropods, especially among paravians and some derived oviraptorosaurians (Zanno et al. 2009, Zanno & Makovicky 2011).

Many functional characters associated with obligate herbivory exhibit high levels of convergence, appearing independently in widely separated parts of the dinosaur tree (Serenó 1997, Barrett 1998). Optimizing herbivorous characters onto dinosaur phylogenies shows, for example, that dental occlusion was derived independently in Eusauropoda and on several occasions in Ornithischia; that complex interlocking dental batteries appeared independently in Ceratopsia and Hadrosauridae; that horny beaks and gastric mills appeared in some ornithischians, several theropod clades, and possibly some sauropodomorphs; that elongate gastrointestinal tracts were present in sauropods, therizinosaurs, and ornithischians (though achieved by different means); and that various complex jaw actions, such as propaliny, had several origins (in ceratopsians, hadrosaurids, and diplodocoids). Repeated evolution of the same characters (and the occurrence of some of these features in other herbivorous archosaurs) might imply that there are underlying developmental or functional constraints that impose a small number of solutions to the problems imposed by herbivory on the archosaur bauplan. If carnivory is the basal dinosaur condition, levels of homoplasy increase further, with the independent evolution of features associated with omnivory/facultative herbivory, such as leaf-like cheek teeth and fleshy cheeks, at the bases of Sauropodomorpha and Ornithischia and in Therizinosauroidea.

Some evidence suggests that the orders in which characters associated with obligate herbivory originate follow common developmental pathways. Analysis of the phylogenetic distributions of characters underpinning theropod herbivory indicates that the key herbivore features of ornithomimosaurs and oviraptorosaurs appeared in the same order within each clade, even though they originated independently in each group (Zanno et al. 2009, Zanno & Makovicky 2011). Similar patterns are also evident in character evolution among ornithischians, in which the evolution of ornithopod and ceratopsian feeding mechanisms shows a number of parallelisms. Each of these clades exhibits (in the same order) phylogenetic trends in the loss of premaxillary and anterior dentary teeth, increases in tooth replacement rates and in the numbers of teeth per tooth position, an increase in prominence of the primary tooth ridges (and the loss of secondary ridges), and the acquisition of complex dental batteries. These changes occurred in concert with trends toward large body size in each clade (Norman 1984, Weishampel 1984b, Sereno 1997, Barrett 1998, Araújo et al. 2011, Varriale 2011).

Following from these character distributions, it is clear that individual herbivorous adaptations contribute to an integrated functional complex of varying sophistication, potentially including modifications to craniodental, postcranial, and gastrointestinal anatomy. In ornithischians, sauropodomorphs, and maniraptoran theropods, the basal members of each of clade were omnivores, with few adaptations for processing or procuring vegetation; in derived members of these clades, incremental modifications to these features produced highly specialized functional



**Figure 2**

Possible reciprocal selective interactions between anatomical and physiological traits in herbivorous dinosaurs. The interplay of these factors, through the process of correlated progression, might have facilitated the evolution of tightly integrated herbivorous character complexes.

complexes. The evolution of such herbivorous character complexes likely impacted the development of other functionally integrated traits: For example, selection for increased gut length might require the evolution of larger body size, which in turn would affect other aspects of biology, such as locomotor mode, browse height, thermal physiology, and life history traits (e.g., reproductive rates). The conserved orders in which herbivorous characters are assembled, and their functional integration, suggest that a macroevolutionary process termed correlated progression (Kemp 2007a,b) was important in the evolution of dinosaur herbivory (Barrett 1998, Barrett & Upchurch 2007). The correlated progression model proposes that the origins of major functional complexes proceed via series of positive feedback loops, in which the appearance of a novel character or function provides a selective advantage that promotes the development of other integrated characters or functions during clade evolution. For example, during sauropodomorph evolution, there are correlations between body size increases, snout width, and other modifications to the teeth and skull (Barrett & Upchurch 2007, Upchurch et al. 2007, Yates et al. 2010, Rauhut et al. 2011, Sander et al. 2011) (**Figure 2**). On the basis of the phylogenetic distribution of these characters, a scenario can be envisioned in which increased body size led to increases in gut length, which in turn allowed longer passage times for digesta, meaning that high-fiber food could form a higher proportion of the diet. This in turn would lead to selection for additional characters related to high-fiber diets, such as increased snout width (enabling higher ingestion rates and bulk browsing) and occlusion (to reduce particle size of the ingested food). Increased body size would also produce changes in maximum browse height, allowing exploitation of new plant resources. Some of these changes are also associated with acquisition of a quadrupedal gait and increases in neck length, which would lead to changes in basal metabolic rate and body temperature and thereby influence the amount and type of food required (Barrett & Upchurch 2007, Yates et al. 2010, Rauhut et al. 2011, Sander et al. 2011). Similar scenarios are also plausible for ornithischians, in which all basal taxa possess beaks, cheeks, simple jaw actions and dentitions, and expanded guts (inferred from their reversed pubic bones), whereas more derived forms show correlated increases in body size

and numerous modifications to the skull and masticatory apparatus. Ornithopods are particularly good candidates for investigation of the potential role of correlated progression in the evolution of herbivory, as incremental increases in tooth replacement rates, reduction in tooth size, changes in tooth shape allowing closer tooth packing, and modified jaw mechanics facilitated the development of dental batteries. These changes occurred in concert with increases in body size, adoption of a quadrupedal stance, and increases in trunk length (and thus additional gut capacity), again allowing bulk feeding on coarse, high-fiber vegetation (Barrett 1998). Maniraptoran theropods possess fewer herbivorous adaptations than do ornithischians or sauropodomorphs, but in their case rigorous analyses of character correlations show that the evolutionary origins of some features, such as the loss of teeth and the downturned tip of the lower jaw, are coupled in a manner compatible with the correlated progression model (Zanno et al. 2009, Zanno & Makovicky 2011). Similar analytical techniques need to be applied to sauropodomorphs and ornithischians to confirm whether the acquisitions of herbivorous features are genuinely correlated.

If herbivorous functional complexes evolved by this mechanism, it provides an explanation for the rarity of reversions to carnivory. The selective advantages for carnivory would have to significantly outweigh the positive selection loops that enabled the evolution of the herbivorous character complexes; moreover, the loss of any one of the characters constituting such a complex would undermine its effectiveness and integration, which would be maladaptive and unlikely to be selected for. Interestingly, the only known reversions to carnivory occur among theropods, which generally possess simpler character complexes than other dinosaur herbivores. Theropod character complexes are thus potentially easier to fragment without compromising function, and the primarily herbivorous features found in this clade, such as toothless beaks, can be more easily retasked for carnivory than could the grinding tooth batteries of ornithischians, for example.

Another measure of the increasing variety of these functional complexes comes from the disparity (total range of variation) of herbivorous dinosaur skull shape. Among sauropodomorphs, omnivorous basal taxa cluster in a small area of skull morphospace, revealing little variation in cranial form, whereas the herbivorous eusauropods occupy a much wider region of morphospace, reflecting substantial experimentation with overall skull shape (Young & Larven 2010). Similarly, the crania of omnivorous and herbivorous theropods occupy substantially larger regions of the total theropod skull morphospace than do those of their carnivorous relatives (Brusatte et al. 2012b, Foth & Rauhut 2013). These studies imply that herbivory is an important factor driving the increases in overall disparity that occur in these clades through time.

Adoption of omnivory/herbivory has been important in shaping the overall trajectory of dinosaur evolutionary history, and these dietary guilds clearly represent major adaptive zones for the clade. The early adoption of herbivory and omnivory in sauropodomorphs may have represented a key innovation that allowed this clade to diversify rapidly in the Late Triassic–Early Jurassic: Sauropodomorpha was considerably more species rich than its carnivorous theropod sister group during the early phases of dinosaur evolution (Barrett et al. 2011). However, herbivorous theropods do not exhibit higher diversity than their carnivorous sister taxa, and ornithischians did not undergo a significant radiation until the Middle–Late Jurassic; it would thus be premature to label herbivory a key innovation in either of these clades (Butler et al. 2007, Barrett et al. 2011). Among ornithischians, reasons for the lag time between the origin of their herbivorous adaptations in the Late Triassic (or earlier) and their mid-Mesozoic diversification are unknown; this situation is paradoxical, as some Late Triassic–Middle Jurassic ornithischians, such as *Heterodontosaurus*, possessed chewing mechanisms better suited to processing tough vegetation than those of contemporary, less specialized, sauropodomorphs (Porro 2009, Norman et al. 2011, Sereno 2012). Potential explanations include physiological differences between these two clades or reliance on different plant resources, but these hypotheses have yet to be tested (Barrett et al. 2011).



## HERBIVOROUS DINOSAUR COMMUNITIES IN TIME AND SPACE

The Mesozoic witnessed the waxing and waning of several distinctive herbivorous dinosaur communities (see Bakker 1978, Weishampel & Norman 1989, Wing et al. 1992, Weishampel & Jianu 2000, Barrett & Willis 2001, Fastovsky & Smith 2004, Upchurch et al. 2011, Benson et al. 2013), and these broad patterns are robust even after geologic and sampling biases are taken into account (Upchurch et al. 2011), although regional variations in community composition occurred (Wing et al. 1992). In the early Late Triassic, dinosaur herbivores were rare (Martínez et al. 2011), but they became established as important components of many ecosystems by the end-Triassic (Galton 1985, 1986; Crompton & Attridge 1986; Barrett et al. 2011). They were the dominant vertebrate herbivores by the early Middle Jurassic, in terms of species richness and biomass (Galton 1985, Barrett et al. 2011), and retained this position until the end of the Cretaceous, surpassing other vertebrate taxa in abundance and diversity (Weishampel & Norman 1989, Wing et al. 1992, Weishampel et al. 2004). Late Triassic–Early Jurassic communities were populated by numerous basal sauropodomorphs (“prosauropods”), with rare ornithischians (heterodontosaurids, basal thyreophorans), and early sauropods. With their elongate necks and large body sizes, basal sauropodomorphs were the first terrestrial vertebrates to exert significant pressure on foliage >1–2 m above ground level and were the earliest high browsers (Bakker 1978). Although early ornithischians and basal sauropodomorphs had many herbivorous adaptations, most of these taxa were probably omnivorous and complex jaw mechanisms were generally absent (except in *Heterodontosaurus*). The extinction of nonsauropod sauropodomorphs at the Early–Middle Jurassic boundary heralded the onset of a major sauropod radiation in the Middle–Late Jurassic; several ornithischian groups also appeared at this time (ornithopods, ankylosaurs, stegosaurs), though they remained subordinate to sauropods in abundance and species richness. During this interval sauropods and ornithischians (particularly ornithopods) developed more sophisticated herbivorous adaptations, including dental occlusion and varied novel jaw mechanisms (e.g., propaliny, pleurokinesis), and increases in sauropod body sizes and neck lengths expanded the vertical reach of the high-browsing guild (Weishampel & Norman 1989, Wing et al. 1992, Fastovsky & Smith 2004). The first known herbivorous theropods occurred in the Late Jurassic (Xu et al. 2009). From the Middle Jurassic onward most dinosaur faunas included dinosaur herbivores from multiple sauropod and ornithischian clades, and the Late Jurassic represents the acme of observed sauropod and stegosaur species richness. However, an extinction at the Jurassic–Cretaceous boundary led to significantly reduced sauropod diversity and the near extinction of stegosaurs (Upchurch & Barrett 2005, Barrett et al. 2009, Mannion et al. 2011, Upchurch et al. 2011). The mechanisms that caused this extinction remain unknown. Following this event, ornithopods, ankylosaurs, and basal ceratopsians became the most conspicuous dinosaur herbivores of the Early Cretaceous, alongside some sauropods, herbivorous theropods (therizinosaurians, oviraptorosaurs, ornithomimosaurs), and rare stegosaurs and heterodontosaurids. Late Cretaceous dinosaur communities in North America were largely populated by ornithischians (ceratopsids, hadrosaurids, ankylosaurs, basal ornithopods, pachycephalosaurs), with herbivorous theropods (ornithomimosaurs, therizinosaurians) and rare titanosaurian sauropods. In Gondwanan faunas (South America, India, Madagascar) titanosaurian sauropods were the principal or only herbivorous dinosaurs, though hadrosaurs and other ornithischians were present in South American faunas. Finally, mixed ornithischian (ankylosaur, ornithopod, ceratopsian), theropod (oviraptorosaur, therizinosaur, ornithomimosaur), and sauropod communities were present in Europe and eastern Asia (Weishampel & Norman 1989, Wing et al. 1992, Barrett & Willis 2001, Fastovsky & Smith 2004, Weishampel et al. 2004, Zanno & Makovicky 2011, Brusatte et al. 2012a, Benson et al. 2013).



The causes of these large-scale replacements are poorly understood; numerous competing hypotheses posit various biotic and abiotic factors (e.g., competition, sea-level fluctuations, climatic changes, extraterrestrial impacts). A subset of these theories is linked to changes in herbivore function, macroecology, and distribution. For example, the rise of diverse Late Triassic (Norian) herbivorous dinosaur communities has been ascribed to major changes in the tetrapod vertebrate guild (Benton 1983; see Irmis 2011 for a review of these and other potential causes). It has been suggested that extinction of an incumbent Middle Triassic–early Late Triassic herbivore fauna dominated by nondinosaurian archosauromorphs (rhynchosaurs, aetosaurs) and basal synapsids (dicynodonts, cynodonts) at the Carnian–Norian boundary might have facilitated the opportunistic radiation of sauropodomorph dinosaurs, by freeing previously occupied ecological space. However, closer scrutiny suggests that the timing of this replacement differs among regions, undermining this hypothesis (Barrett et al. 2011, Irmis 2011). Furthermore, the temporal correlations needed to support this hypothesis are poorly constrained, due to uncertainties in dating key localities and a lack of unbroken Late Triassic depositional sequences that could provide continuous long-term records of faunal change (Irmis 2011). Moreover, Norian sauropodomorphs had substantially different jaw mechanisms and greater body sizes than earlier nondinosaurian herbivores, which suggests that their ecologies were different, so direct ecological replacement (and/or competition for the same resources) seems unlikely (Barrett et al. 2011).

The end-Triassic extinction (ETE) led to the disappearance of some sauropodomorphs, but they remained the dominant herbivores of the Early Jurassic (Barrett & Upchurch 2005, Barrett et al. 2011, Irmis 2011, Mannion et al. 2011, Upchurch et al. 2011). Nevertheless, ornithischians increased in species richness and numbers after the ETE, possibly due to ecological release following the extinction of similarly sized nondinosaurian herbivores (Butler et al. 2007, Barrett et al. 2011, Irmis 2011). Interestingly, the taxonomic and ecological expansion of the Early Jurassic herbivore guild (encompassing a wider range of body sizes, new feeding behaviors, and different community compositions) occurred without significant increases in overall dinosaur morphological disparity (Brusatte et al. 2008). Nonsauropod sauropodomorphs became extinct at the Early–Middle Jurassic boundary, and sauropods replaced them as the dominant herbivores. The causes of this replacement remain unknown. It is possible that basal sauropodomorphs were outcompeted by eusauropods, as the latter possessed dental occlusion, broader muzzles, longer necks, and other adaptations to high-fiber herbivory lacking in basal sauropodomorphs (Barrett & Upchurch 2005). However, this suggestion is tentative, and the possible roles of environmental and geographic changes in this apparent replacement require investigation. Competitive interactions between basal sauropodomorphs and ornithischians probably played no role in basal sauropodomorph extinction, due to major differences in the body sizes, distributions, and feeding mechanics of these groups (Barrett & Upchurch 2005). Many hypotheses proposed to account for Late Jurassic–Cretaceous faunal replacements have linked changes in dinosaur diversity with some of the large-scale floral replacements that occurred during the Mesozoic (see below). Competition has been invoked as a possible mechanism to explain the decline of sauropods and stegosaurs and the rise of ornithomorphs and ceratopsians in the Early Cretaceous (Bakker 1978), but substantial differences in the feeding ecology and morphology of these groups undermine this suggestion (Barrett & Upchurch 2005).

Additional work is needed to disentangle the effects of possible internal and external drivers that might have influenced these large-scale patterns in dinosaur beta diversity and community dynamics. Potential external drivers include geographic changes, caused by variations in sea level and tectonic activity, which influence land area, local environmental conditions, and paleobiogeographic patterns (Vavrek & Larsson 2010, Gates et al. 2012, Mallon et al. 2012, Mannion et al. 2012); climatic and atmospheric changes, which have direct effects on habitability (precipitation,

temperature) and knock-on effects on vegetation type and distribution (Rees et al. 2004, Noto & Grossman 2010); and evolutionary changes in floras, which affect the type of forage available (see below). Internal drivers represent the constraints imposed by dinosaur anatomy and physiology in terms of their feeding adaptations and nutritional requirements, habitat preferences, dispersal ability, independence from environmental conditions (e.g., large body size as a buffer against changing temperatures), and life history. These studies also need to be conducted at global and regional scales to capture a full picture of how such factors might interact; for example, changes in global dinosaur species richness through time do not correlate well with fluctuations in mean global sea level (Butler et al. 2011), but local changes, such as the formation of the Western Interior Seaway in North America (Gates et al. 2012), could have had a profound influence on regional dinosaur habitats and communities. Geologic and sampling biases also have to be accounted for to ensure accurate reconstructions of dinosaur faunal compositions (Mannion et al. 2011, Brown et al. 2013, Evans et al. 2013).

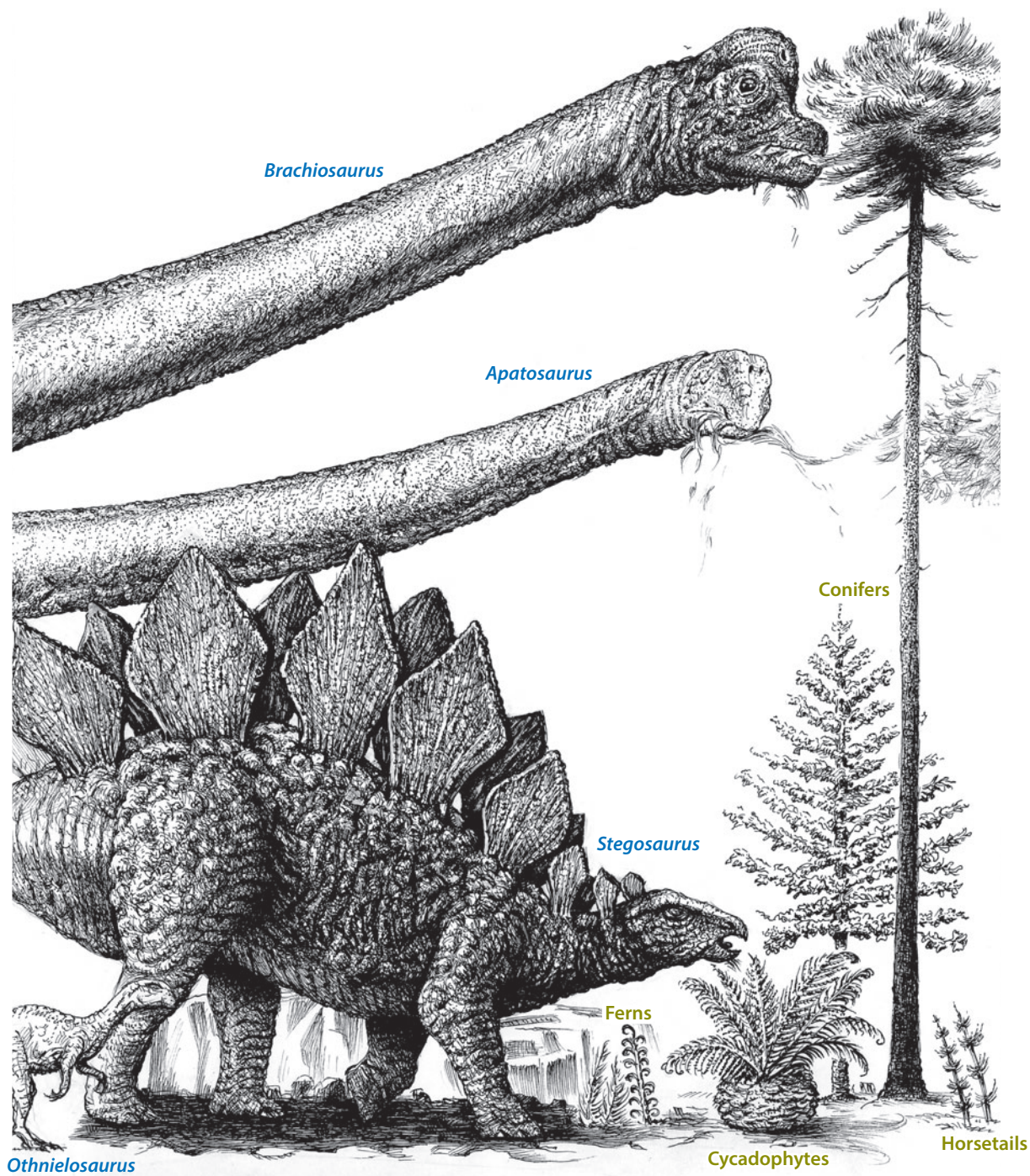
## ECOLOGY OF DINOSAUR HERBIVORY

Paleobiologists have used data on functional morphology, body size, paleoenvironments, and taxon distributions, and a range of modeling approaches, to investigate herbivorous dinosaur paleoecology (e.g., Wing et al. 1992, Fastovsky & Smith 2004). For example, numerous studies have attempted to explain how many Mesozoic ecosystems were capable of supporting a high diversity of sympatric dinosaur herbivores (Weishampel et al. 2004). Perhaps the most extreme example of herbivore sympatry comes from the Late Jurassic Morrison Formation (western United States), which has yielded approximately 20 contemporaneous herbivore genera, ranging from gigantic sauropods to ornithischians with body lengths <1 m (e.g., Foster 2003, 2007; Upchurch et al. 2004; Maidment et al. 2008; Butler et al. 2010b; Carpenter 2010; McDonald 2011; Whitlock 2011a) (**Figure 3**). In this and other speciose dinosaur faunas, the coexistence of so many herbivores would potentially increase competition for available plant resources. This implies either that the productivity of Mesozoic terrestrial ecosystems was unusually high (Burness et al. 2001), that dinosaur nutritional requirements (or population densities) were low (Englemann et al. 2004, Farlow et al. 2010), or that mechanisms existed to enable niche partitioning between sympatric herbivores. These scenarios are not mutually exclusive, and a combination of environmental and biological factors probably shaped dinosaur community composition.

Browse height is a possible niche-partitioning mechanism, allowing vertical separation between herbivores on the basis of body size, stance (quadrupedal versus bipedal or rearing taxa), and additional adaptations such as neck elongation and function (e.g., Bakker 1978, Upchurch & Barrett 2000) (**Figure 3**). Browse height differences might have been especially important in sauropod-rich faunas (Upchurch & Barrett 2000, Sander et al. 2011, Wilkinson & Ruxton 2012) as their long necks varied in absolute and relative length and in range of vertical motion. Some taxa might have fed at heights >9 m, though the degree of dorsal neck flexion is contentious (see Stevens & Parrish 1999, 2005; Upchurch & Barrett 2000; Parrish 2006; Seymour 2009; Taylor et al. 2009; Christian 2010; Ruxton & Wilkinson 2011; Sander et al. 2011). Fiorillo (1998) used variation in sauropod dental microwear patterns to investigate browse heights, using the proportions of

### Figure 3

Representative Morrison Formation herbivores, illustrating the different browse heights of the sympatric taxa *Othnielosaurus*, *Stegosaurus*, *Apatosaurus*, and *Brachiosaurus*, as well as candidate Late Jurassic food plants, including ferns, horsetails, cycadophytes, and conifers. Drawing by Robert Laws.





scratches and pits on the teeth as a proxy for the amount of dietary grit, which varies with canopy height. However, dental microwear reflects the type of browse consumed in addition to cropping height (Whitlock 2011a). Most ornithischians and all herbivorous theropods would have browsed at much lower levels than those habitually exploited by adult sauropods (Bakker 1978, Barrett & Willis 2001, Barrett & Upchurch 2005). However, work on the ceratopsid-, ankylosaur-, and hadrosaurid-dominated communities of Late Cretaceous North America indicates that browse height was not particularly important in niche partitioning among ornithischians: Most of the taxa present had closely overlapping feeding envelopes concentrated within the first 1–2 m above ground level, although larger hadrosaurids might have been able to reach up to 5 m, allowing them to crop vegetation unavailable to ceratopsids and ankylosaurs (Mallon et al. 2013).

Differences in jaw mechanics, dental wear, and skull shape are found among sympatric herbivores and potentially indicate niche partitioning (e.g., Weishampel & Norman 1989, Carrano et al. 1999, Christiansen 2000, Upchurch & Barrett 2000, Barrett & Willis 2001, Barrett & Upchurch 2005, Henderson 2010, Whitlock 2011a, Mallon & Anderson 2013). This assumes that inferred functional differences, such as those between the grinding dentition of a hadrosaur and the slicing dentition of a ceratopsian, imply use of different food plants or plant tissues. Snout shapes are often correlated with dietary preferences in living mammals (e.g., Janis & Ehrhardt 1988); broad-snouted taxa are interpreted as unselective bulk feeders and narrow-snouted taxa as more selective in food choice. Systematic differences in snout width indicative of different browsing modes are found among coexisting sauropods (Whitlock 2011a) and hadrosaurids (Carrano et al. 1999; but see Mallon & Anderson 2013), as well as between coexisting hadrosaurid, ceratopsid, and ankylosaur taxa in the Late Cretaceous Dinosaur Park Formation of Canada (Mallon & Anderson 2013). There is also evidence for different bite strengths in contemporary ceratopsids (Henderson 2010) and jaw actions in hadrosaurids (Erickson et al. 2012), which might indicate divergent dietary preferences. Dietary differences among sauropods have also been identified through dental microwear, though interpretations of this evidence have been contradictory (Fiorillo 1998, Upchurch & Barrett 2000, Whitlock 2011a).

Isotopic evidence supports dietary partitioning and implies distinct habitat preferences for some dinosaur herbivores. Tütken (2011) calculated  $\delta^{13}\text{C}$  values of tooth enamel from the sympatric sauropods of the Tendaguru Beds (Late Jurassic, Tanzania) and found consistent differences between taxa that might reflect preferences for different vegetation types (e.g., conifers versus ferns) and browse heights. In addition, comparisons between the  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  isotopes obtained from ceratopsid and hadrosaurid teeth (Late Cretaceous, Hell Creek Formation, United States) suggest differences in the spatial distributions and possible browse heights of these groups: Ceratopsians were interpreted as preferring open, lowland environments and hadrosaurids as preferring forested areas (Fricke & Pearson 2008). However, taphonomic analyses examining associations between sediment type and dinosaur occurrence data provide contrary evidence on habitat preference: Although they also recover evidence for spatial separation of these groups, they indicate that hadrosaurid remains occur primarily in floodplain or channel environments, whereas ceratopsid specimens are found further inland (Butler & Barrett 2008, Lyson & Longrich 2011). These analyses also suggest that herbivorous theropods, pachycephalosaurs, and ankylosaurids exhibited preferences for inland environments, whereas nodosaurids and other sauropods are preferentially recovered from coastal environments (Butler & Barrett 2008, Mannion & Upchurch 2010). Whitlock (2011b) noted a correlation between the occurrence of high-browsing sauropods and forested environments in the Tendaguru fauna, whereas the less densely wooded and contemporary Morrison Formation had higher abundances of low- to medium-level browsers. These results imply interplay between the spatial distributions of dinosaur herbivores and plant communities, though such patterns require further statistical testing.

Little effort has focused on dinosaur ecological energetics, as this requires numerous assumptions on dinosaur metabolic rate, body mass, and activity levels and on plant productivity and nutritional value (e.g., Farlow 1976; Farlow et al. 1995, 2010; Barrett 2005; Hummel et al. 2008; McNab 2009; Wilkinson & Ruxton 2013). However, these estimates provide a basis for addressing relationships between dinosaur abundance and biomass and plant productivity, as well as potential links with other aspects of dinosaur biology, such as body size evolution. Large size in dinosaurs has been linked to high atmospheric CO<sub>2</sub> during the Mesozoic, which has been suggested to foster higher plant productivity (Farlow et al. 1995, Burness et al. 2001). However, there are no correlations between atmospheric CO<sub>2</sub> changes and events in sauropod body size evolution (Sander et al. 2011), and higher CO<sub>2</sub> levels are unlikely to have increased Jurassic plant productivity (Midgley et al. 2002, Boyce & Zwierniecki 2012). Moreover, many Jurassic ecosystems with diverse large-bodied herbivores are found in the midlatitudes where climates were semiarid with limited primary productivity (Rees et al. 2004, Noto & Grossman 2010, Mannion et al. 2011). An alternative possibility is that large body size evolved in low-productivity scenarios, where available fodder either had low biomass, was sparsely distributed, or was of poor nutritional quality [for example, it has been suggested that Mesozoic fodder, such as conifers and cycads, was a poor source of nitrogen in comparison with modern angiosperms (Midgley et al. 2002, Wilkinson & Ruxton 2013; but see Sander et al. 2011)]. Under any low-productivity scenario, large body size would be advantageous; benefits include lower mass-specific metabolic rates, longer gut passage times (gut length increases in proportion to body mass, whereas metabolic rate decreases with size), and economy of transport, perhaps in combination with low population densities (Midgley et al. 2002, Englemann et al. 2004, Farlow et al. 2010, Sander et al. 2011, Wilkinson & Ruxton 2013). Low population densities would permit vegetation recovery, and there is some isotopic evidence for long-distance sauropod migration (Fricke et al. 2011). It has also been shown that low-productivity environments could support high dinosaur biomass if dinosaurs had field metabolic rates considerably lower than those of mammals (McNab 2009, Farlow et al. 2010, Trammer 2011).

Dinosaur herbivores were ecosystem engineers that influenced the ecology of other organisms (Farlow et al. 2010). They trampled and denuded vegetation, disturbed soil, and produced feces, and their carcasses provided sustenance for scavengers and decomposers (e.g., Chin & Gill 1996, Farlow et al. 2010). Their high reproductive rates (in comparison with large-bodied herbivorous mammals), enabled by oviparity, large clutch sizes, and brief posthatching parental care, may have had a role in fostering the high diversity of large-bodied carnivorous dinosaurs by providing a constantly high level of standing herbivore biomass (Hummel & Clauss 2008). It has also been suggested that sauropod methane emissions, a by-product of digestion, contributed to high Mesozoic temperatures (Wilkinson et al. 2012), although there is currently no geochemical evidence to support this. Finally, it has been suggested that Pleistocene megafaunal herbivores had a significant effect on nutrient availability, due to their extensive home ranges (Doughty et al. 2013); it is tempting to speculate that large dinosaurs had similar effects on their environments.

## PLANT-DINOSAUR INTERACTIONS: COEVOLUTION OR COINCIDENCE?

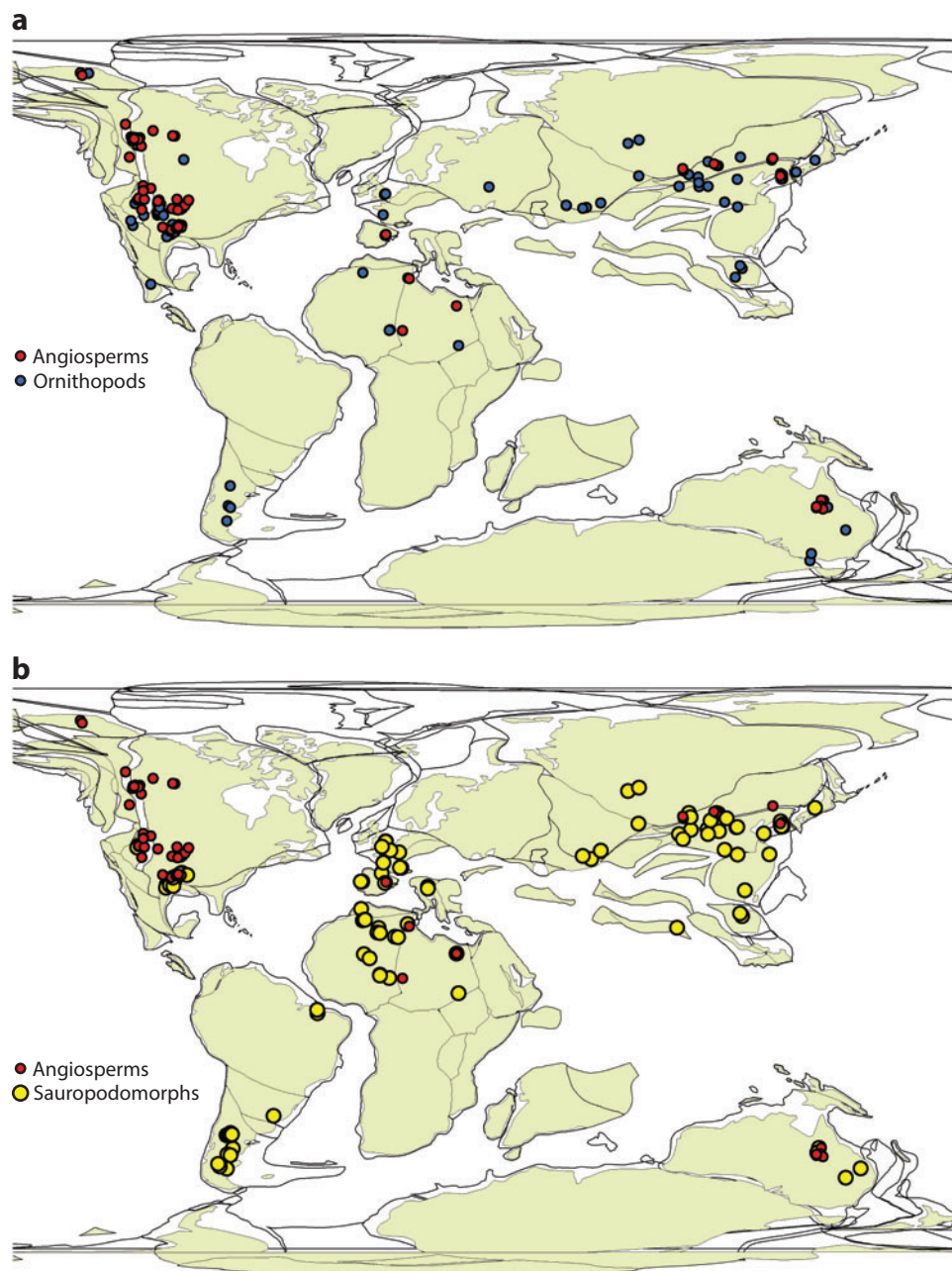
The Mesozoic witnessed profound changes in floral composition and structure, including the extinction of the Middle Triassic *Dicroidium* seed-fern flora in Gondwana; the rise of fern-, cycadophyte-, and conifer-dominated biomes during the Triassic and Jurassic; the sharp decline of cycadophyte abundance and richness in the Early Cretaceous; and the origin and subsequent diversification of angiosperms from the Early Cretaceous onward, with angiosperms achieving floral dominance by the Late Cretaceous (e.g., Niklas et al. 1985, Wing et al. 1992). Each of

these floral events has been linked to changes in dinosaur ecology (e.g., faunal composition, clade species richness, biomass) or functional morphology/physiology (e.g., food preferences, novel feeding mechanisms), thereby implying a variety of coevolutionary interactions (e.g., Bakker 1978; Benton 1983; Coe et al. 1987; Wing & Tiffney 1987; Weishampel & Norman 1989; Tiffney 1992, 2004; Taggart & Cross 1997; Coria & Salgado 2005; Mustoe 2007). Most of these hypotheses are based on potential temporal coincidences between floral and faunal events, but for a candidate interaction to qualify as coevolutionary, other factors—such as spatial distribution, long-term species richness and evenness data, and functional morphological evidence (from both the plants and animals)—are required (e.g., Thompson 1994, Butler et al. 2010a).

The most prevalent coevolutionary hypothesis proposed that changes in dinosaur browsing behavior fostered the origin and radiation of angiosperms (Bakker 1978). Bakker noted that Late Jurassic dinosaur communities were dominated by high-browsing sauropods, which were assumed to feed primarily on fully grown conifers; by contrast, Early Cretaceous faunas consisted largely of low-browsing ornithischians (sauropods having endured a major crash in species richness at the Jurassic–Cretaceous boundary), and the floras included the first angiosperms. This faunal turnover was posited to change overall herbivore browse pressure, switching from Late Jurassic canopy browsing to Early Cretaceous ground-level feeding. The new regime was suggested to select against slow-growing conifers, whose saplings are vulnerable to herbivore damage, and to favor the newly appearing angiosperms, whose life cycles allow them to thrive in highly disturbed conditions. This elegant thought experiment was extended to account for the evolution of novel jaw mechanisms and seed dispersal syndromes (e.g., Wing & Tiffney 1987, Weishampel & Norman 1989, Tiffney 1992). However, detailed evaluations of the dinosaur and plant records do not support these hypotheses; the faunal and floral summaries forming the basis for these scenarios are now known to be oversimplified, and in some cases erroneous, depictions of Jurassic and Cretaceous paleoecology. For example, Bakker (1978) characterized Jurassic sauropods as high browsers, whereas there is a growing consensus that many were low browsers and that the low-browsing community (including sauropods and ornithischians) was already well established in the Late Jurassic (e.g., Barrett & Willis 2001; Whitlock 2011a,b). Moreover, although angiosperms originated in the Early Cretaceous, they did not become ecologically abundant, and were probably not major components of dinosaur diet, until the early Late Cretaceous, which invokes significant time lags (>10 million years) between the radiation of low-browsing ornithischian groups, such as ornithomimids and ceratopsians, and increases in angiosperm abundance (Weishampel & Jianu 2000, Barrett & Willis 2001, Lloyd et al. 2008, Butler et al. 2009a). Qualitative and statistical comparisons demonstrate that other events in dinosaur evolution, such as major changes in clade species richness patterns/abundance and inferred origination times for novel feeding adaptations, also lack strong temporal linkage to episodes in angiosperm evolution (Weishampel & Jianu 2000, Barrett & Willis 2001, Butler et al. 2009a). Spatial coincidence is also a prerequisite for coevolution but was overlooked in previous work on dinosaur–plant interactions that relied solely on temporal congruency between the dinosaur and plant records. Statistical comparisons between the spatiotemporal distributions of Cretaceous angiosperms and herbivorous dinosaurs, using geographic information systems to visualize this distributional data, indicate no significant associations between the occurrences of these groups, further undermining coevolutionary scenarios (Butler et al. 2010a) (**Figure 4**).

Similar scenarios have linked cycadophyte diversification and decline to sauropod and stegosaur diversity (summarized in Mustoe 2007). These dinosaurs lacked sophisticated chewing mechanisms, and it has been proposed that they would have swallowed cycad seeds whole and transported them in their guts, acting as their major dispersal agents. This hypothesis was supported by the observation that all three groups simultaneously increased in diversity during the Jurassic and





**Figure 4**

Distributions of Cretaceous angiosperm and herbivorous dinosaur localities, plotted on a paleogeographic reconstruction for 100 Mya (modified with permission from Butler et al. 2010a). Statistical comparisons between these distributions within and between time intervals enable testing of long-term patterns of spatial association that might be indicative of coevolutionary interactions. (a) Distributions of ornithopods and angiosperms. (b) Distributions of sauropods and angiosperms. Statistically significant associations between these groups were not recovered in either case, which undermines coevolutionary hypotheses.

declined in concert during the Cretaceous. However, phylogenetic evidence indicates that most of the features present in cycads that have been attributed to coevolution with dinosaur herbivores (e.g., brightly colored seeds, toxins) appeared in the Permian, prior to dinosaur origins (Butler et al. 2010b). Moreover, few statistically significant correlations exist between changes in dinosaur abundance/diversity and cycad decline, and there are no consistent spatial correlations between cycadophyte distributions and those of their proposed dispersers during the Cretaceous (Butler et al. 2009b, 2010a).

Current evidence for diffuse coevolutionary interactions between dinosaurs and plants is weak; other factors, such as the evolution of insect predators/pollinators, changes in fire regimes, and variations in atmospheric gas concentrations, should be explored as potential drivers of Mesozoic floral evolution (e.g., Labandeira et al. 1994, McElwain et al. 2005, Bond & Scott 2010). However, other coevolutionary hypotheses have been proposed. For example, potential correlations have been noted between the distributions and diversity of sauropods and several conifer families during the Jurassic and Cretaceous (Taggart & Cross 1997, Coria & Salgado 2005, Hummel et al. 2008); in addition, the major radiations of ceratopsids and hadrosaurids occurred in angiosperm-dominated environments. Moreover, most analyses have focused on clade-level comparisons between dinosaurs and plants, but might have missed potential region-specific or taxon-specific patterns. Finally, although hypotheses relating to Triassic floral change, such as the extinction of the *Dicrodium* flora and its effect on early dinosaur evolution (Benton 1983) and the rise of cycadophytes (Mustoe 2007), have been tested qualitatively (Barrett & Upchurch 2005, Butler et al. 2010a), they have yet to be subjected to rigorous statistical analysis. Ongoing evaluation of these hypotheses is required as additional ecological data are incorporated and spatiotemporal sampling of dinosaur and plant localities improves.

## SUMMARY POINTS

1. Herbivores accounted for >50% of dinosaur species richness; obligate herbivory appeared on at least three occasions in Ornithischia, once in Sauropodomorpha, and on several occasions in Theropoda.
2. Basal members of most herbivorous clades were likely omnivorous, with sophisticated adaptations to herbivory appearing in derived taxa; many adaptations to herbivory exhibit high levels of homoplasy.
3. The character complexes associated with herbivory evolved in an incremental fashion that might have been driven by reciprocal interactions between improvements in functional traits, consistent with the correlated progression model.
4. Herbivorous dinosaur faunas changed markedly throughout the Mesozoic, though the intrinsic and extrinsic drivers of these changes remain poorly understood.
5. Sympatric dinosaur herbivores employed niche partitioning to reduce competition, as reflected by ecologically significant morphological, sedimentological, and isotopic differences between co-occurring taxa.
6. Herbivorous dinosaurs had significant effects on other organisms, through physical disturbance and provision of dung and standing biomass.
7. Low productivity levels in the Mesozoic might have fostered gigantism, enabling high standing biomass at low population densities.

8. Although several large-scale episodes of faunal and floral change are suggestive of coevolutionary interactions, the evidence in favor of these hypotheses is weak; other biological and environmental factors need to be investigated in connection with these events.

## FUTURE DIRECTIONS

1. Most existing work on herbivorous dinosaurs is qualitative; additional rigor can be introduced by applying statistical and modeling techniques, especially in the areas of paleoecology and macroevolution.
2. Herbivorous theropods have yet to be incorporated into paleoecological scenarios or considerations of large-scale macroevolutionary patterns.
3. Isotopic analyses, dental microwear, disparity analyses, and detailed taphonomic/sedimentological work all have significant potential to add valuable data for assessing niche partitioning among sympatric herbivore taxa.
4. Additional qualitative and quantitative work is required on the functional morphology of herbivorous dinosaurs, and rigorous documentation of character evolution is needed for many major herbivorous clades.
5. Rigorous analyses of hypotheses relating to broad scale Triassic–Jurassic dinosaur–plant interactions have yet to be attempted; similarly, there is scope for exploring examples of coevolutionary interactions at higher taxonomic levels than attempted previously.
6. The effects of dinosaurs as ecological engineers could be explored in more depth by attempting to integrate biological data from modern herbivores and dinosaurs with paleontological proxy data on environmental variables including lithology, climate, nutrient cycling, and productivity.

## DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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## Errata

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