

DINOSAUR BIOLOGY

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ABSTRACT

Most aspects of dinosaur biology cannot be observed directly but must be reconstructed by a variety of often speculative approaches. Overall body form can be established if good skeletal material of a dinosaur species is available. From a skeletal reconstruction, interpretations of the animal's soft parts, and inferences about how the creature's skeleton functioned as a living machine, can be made. Inferences about dinosaur habitat preferences and sociality are made from observations of the preservational contexts of skeletons, nesting sites, and trackways. Some aspects of dinosaur biology are interpreted on the basis of relationships between body size and physiological and ecological parameters in living animals, but this involves much uncertainty.

Primary tissues of dinosaur bone suggest that dinosaurs had rapid growth rates, but calibrating dinosaur growth rates in terms of body mass gained per unit time is difficult. It is uncertain whether dinosaurs needed metabolic rates comparable to those of living birds and mammals in order to grow quickly enough to form the primary bone tissues commonly found in dinosaur skeletons.

No evidence convincingly shows that dinosaurs were endotherms, and some evidence suggests that they were not. Dinosaurs routinely achieved considerably larger body sizes than do terrestrial mammals, and they maintained viable

populations in smaller geographic areas than is possible for elephant-sized mammals. This suggests that dinosaurian food requirements were proportionately less than those of birds and mammals, thus permitting large population densities.

INTRODUCTION

Dinosaurs have become such prominent features of popular culture that it is easy to forget that they were once living animals. Countless movies and works of pulp fiction have made them symbols of immense, ravaging destruction, our culture's answer to the dragons of earlier mythology—Rahab, Fafnir, and the Hydra displaced by *Tyrannosaurus*, *Velociraptor*, and Godzilla.

Perhaps contributing to this mythic “monster” image is that so many features that characterize the lives of real animals cannot be observed, but only inferred, for dinosaurs. We do not know exactly what the external appearance of any dinosaur was like. We cannot directly determine how much they weighed, how quickly they grew, how long they lived, or how often they reproduced. It is a real accomplishment when, for any dinosaur species, we can pin down natural history details of the kind that ecologists working on living animals can almost take for granted.

Unfortunately, the popular media often seem unable to distinguish speculation about dinosaur paleobiology from actual observations, and sometimes paleontologists themselves do not make this distinction sufficiently clear. Once published, hypotheses become “evidence” cited to support secondary hypotheses. Hypothetical, artistic restorations of living dinosaurs themselves become rhetorical ammunition in debating interpretations of dinosaur biology.

There is nothing wrong with responsible speculation, though, as long as one remembers that the plausibility of a hypothesis does not guarantee its truth. Informed speculation can focus the attention of paleontologists on questions that might not otherwise be asked, and in the process can suggest new observations, or ways of looking at previous discoveries, that can either disprove or corroborate hypotheses about dinosaur biology.

Here we review the kinds of evidence used to reconstruct dinosaurs as living animals. We then consider selected aspects of dinosaur biology in more detail.

THE “EPISTEMOLOGY” OF DINOSAUR BIOLOGY: WHAT DO WE KNOW, AND WHAT CAN WE KNOW?

The Fossil Record of Dinosaurs

Inferences about dinosaur biology range from the very robust to the highly speculative, depending on the kind of evidence adduced in their support.

Generally, the more directly an interpretation is based on the hard evidence of the fossils themselves, the greater the confidence that can be placed on it. Our primary database for understanding dinosaurs is thus the fossil record itself, with all its biases and imperfections (43). Of 285 genera of dinosaurs recognized in 1988, about 45% were based on only a single articulated specimen, and only about 20% on essentially complete skulls and skeletons. Rough estimates of the total number of dinosaur genera that lived over the course of the Mesozoic Era range from as few as 675 to as many as 3400 (43, 120).

Morphological/Comparative Anatomical Arguments

GROSS BODY FORM The popular stereotype notwithstanding, paleontologists cannot reconstruct an entire skeleton from a single bone unless more complete remains of the same or a closely related taxon have previously been found. Given a reasonable skeletal reconstruction (or better still a complete skeleton), however, paleontologists can make a reasonable conjecture about the soft parts of the living dinosaur. Even without direct fossil evidence, we may confidently assert that dinosaurs had hearts, carotid arteries, lungs, and other organs that all amniotes possess—but we can do much better than that. Comparing the occurrence of soft tissue structures in cladistic crown-groups [the extant phylogenetic bracket (EPB); 15, 138] sharpens our ability to make phylogenetic inferences about their occurrence in extinct forms. Crocodylians and birds form the EPB for dinosaurs. Soft structures that are present (e.g. a four-chambered heart) or absent (e.g. a muscular diaphragm) in both crocodylians and birds probably were correspondingly present or absent in dinosaurs. When a structure occurs in only one of the crown-groups, its presence in dinosaurs is more speculative. A sacral glycogen body occurs in birds, but not in crocodylians. The same body has been thought to have been present in some dinosaurs (58); this is not unlikely but is more speculative on phylogenetic grounds. Even more speculative are structures found neither in crocodylians nor birds, such as the putative “carotid hearts” suggested to have elevated blood up the necks of sauropods (29).

In general, muscles with fleshy attachments leave little osteological evidence of their presence, but muscles with tendinous or aponeurotic attachments are likely to leave skeletal signatures in the form of crests, ridges, or scars. Based on the limited number of species studied so far (15, 88, 94), reptiles and birds seem much less likely to show muscle scars than do mammals—bad news from the standpoint of restoring dinosaur musculatures. More positively, however, body size may correlate positively with the prominence of muscle scars on bones; the large sizes of most dinosaurs may enhance our ability to find and interpret muscle scars on their bones. Use of the EPB (with crocodylians and birds again the crown-groups) extends our interpretation of dinosaurian

musculature beyond the limited evidence from muscle scars, and numerous restorations of muscle arrangements in particular dinosaurs have been published (e.g. 94, 101).

The scant evidence from fossil integument impressions of nonavian dinosaurs shows a skin with a pebbly, reptilian texture (10, 84, 126). Impressions of soft, elevated, rectangular scutes have been reported in the tail of a hadrosaur (64), and conical tail scutes up to 18 cm high from an undescribed sauropod (36). Such finds offer a rare glimpse into species-specific patterns of ornamentation. Dinosaur color patterns and the use of color in behavioral displays are completely conjectural, but the EPB method suggests that it is reasonable to infer that crests, frills, or other features used as display structures were colorful.

FUNCTIONAL MORPHOLOGY Analyses of the shapes of bones and teeth, tooth wear surfaces, skeletal proportions, and joint configurations have been used to reconstruct styles of locomotion, feeding, and even intraspecific courtship and agonistic behavior in dinosaurs (52, 56, 60, 75, 96, 98, 136). Inferences of this kind often rely, at least in part, on comparisons with the functional morphology and natural history of living animals. For example, speculations that the horns of ceratopsids were employed as much or more during intraspecific interactions than as anti-predator devices are based partly on observations of the way horns and hornlike organs are used by living mammals and reptiles (50, 90), and on what is plausibly interpreted as sexual dimorphism in the deployment of ceratopsid horns (81).

Sometimes interpretations based on functional interpretations of skeletal material can be corroborated by other kinds of evidence. The inference that dinosaurs had an erect limb carriage (at least for the hindlimb—75) is amply confirmed by the narrow “gauge” of dinosaur trackways (129). Identification of dinosaur species as carnivores or herbivores on the basis of tooth shapes and wear surfaces can sometimes be corroborated by stable isotope ratios of dinosaur bones (9, 99), the occurrence of bite marks in fossil bone, or the analysis of gut contents or fossilized droppings of dinosaurs (129). Even the occurrence of injuries in fossil bone, or the development of unusual ossifications, may shed light on stresses to which the bones were subjected and thus constrain functional interpretations of osteological structures (115).

BONE HISTOLOGY Although an array of bone tissue types exists in vertebrates, the basic components of bone remain essentially the same (55). Differences in bone tissue types reflect differences in the rate of bone formation (106, 110). Although the organic components of bone decompose after death, the inorganic fraction is remarkably stable, permitting characterization of fossil bone microstructure.

Fibro-lamellar primary bone is formed during very rapid bone deposition;

it is typical of bird and mammal bones but relatively rare in bones of extant reptiles, although it has been reported in turtles and crocodylians (46, 108). More typical of living reptiles is lamellar-zonal bone, indicative of seasonal alternations between fast and slow rates of bone deposition. Zonal bone is uncommon in endotherms but does occur (27).

Because the histology of primary bone provides a record of the processes of growth, it is possible to interpret bone growth patterns in dinosaur species. However, the task is complicated by the fact that, histologically, dinosaur bone is not exactly like that of either modern ectotherms or endotherms (see below).

Taphonomic/Aktuopaleontological Arguments

DINOSAUR HABITATS Dinosaur remains are preserved in environments ranging from shallow marine through arid, eolian deposits, but the most frequently sampled environments are moist lowland settings in the fluvio-deltaic complex (35, 53, 65, 70, 72, 80, 93, 114). Effective use of taphonomic data for interpreting dinosaur paleoecology depends on statistical patterns of occurrence of fossils in different sedimentary situations. It is unwise to draw conclusions from the occurrence of a single skeleton in a single depositional setting. The best bases for making such inferences are situations in which the same taxa are distributed across a suite of environments, or instances in which a transect across contemporaneous, environmentally different rock formations can be made.

In the Late Jurassic Morrison Formation of the western United States, the same dinosaur fauna occurs at sites distributed over a distance of 1000 km. The distribution of sauropod genera across a spectrum of preservational environments demonstrates that these huge herbivores were not confined to single environments, but rather roamed across all habitats, and may even have migrated on an annual basis in the face of periodic drought (44). The Morrison sedimentary record also suggests that stegosaurs may have preferred somewhat drier habitats than did their sauropod neighbors.

Dinosaur diversity of the moist, fluvio-deltaic, coastal lowland environments of the Late Cretaceous Judith River Formation of western North America is high in comparison with that of the drier, more inland Two Medicine Formation of the same age and region; there is little indication of faunal mixing between the two formations (7, 12, 65, 133). The ornithopods *Maiasaura* and *Orodromeus* are absent or uncommon in the lowland faunas, and the common hadrosaurs and ceratopsians from the lowlands do not occur in the upland deposits.

Although ceratopsids are common members of both lowland and upland faunas of the Late Cretaceous of western North America, protoceratopsids are not found in coastal lowland deposits. Protoceratopsids are rare in North

America, but along with psittacosaur can be abundant in xeric inland deposits of China and Mongolia (40, 74, 80, 97).

In Mongolia, stratigraphically successive Late Cretaceous units demonstrate strong environmental control of faunas (40, 74, 97). In the older Djadochta and Barun Goyot Formations, oxidized red sediments record dry conditions, and the dinosaur fauna is dominated by small and medium-sized species (protoceratopsids, small theropods, a small ankylosaurid), with rare evidence of large hadrosaurs and theropods. The youngest unit, the Nemegt Formation, records the return of moist conditions and fluvial systems. Here large hadrosaurs and tyrannosaurs dominate the fauna, and even rare sauropods are found.

In many Mesozoic sedimentary units, the number of dinosaur skeletons known is greatly exceeded by the number of fossilized dinosaur trackways (82). Jurassic and Cretaceous footprint assemblages in carbonate rocks are often dominated by tracks of large theropods and sauropods, while track assemblages in siliciclastic rocks of comparable age are frequently dominated by ornithopod prints (83). Thus the footprint record, like the skeletal record, allows at least broad inferences about the habitat preferences of particular dinosaur groups.

Paleogeographic reconstructions of continental positions over the course of the Mesozoic Era (123), combined with paleoenvironmental reconstructions for given regions, allow "retrodictions" of ancient climatic regimes (5, 59, 124, 131, 139). The Mesozoic Era seems to have been a time of fairly warm conditions over much of the planet. At least seasonally dry climates were widespread in the Triassic Period, and they remained prevalent at low latitudes through the remainder of the era; moister conditions became established at midlatitudes in the later Mesozoic, however (6). As a group, dinosaurs coped with the entire range of Mesozoic climates; some species occupied high-latitude regions that experienced seasonally dark and cool conditions (30, 91a, 109).

DINOSAUR BEHAVIOR Monotypic bonebeds suggest that certain dinosaurs lived in single-species groups. This interpretation becomes more compelling when multiple bonebeds are known for a particular species of dinosaur, thus demonstrating a repeated tendency rather than a unique event. The Ghost Ranch Quarry, New Mexico, contains remains of 1000 or more juvenile and adult specimens of the small Late Triassic theropod *Coelophysis* that may have perished in a severe drought (122). Because this deposit is unique, it does not form any basis for generalization about sociality in *Coelophysis*. However, the existence of a similar mass kill of a closely related species (105a) supports the idea that these small theropods were gregarious. Monotypic bonebeds are common for the prosauropod *Plateosaurus*, ceratopsids, and hadrosaurids (34,

121, 134), strongly suggesting that these dinosaurs lived (and perished) in herds.

It is common for dinosaur trackway sites to record preferred directions of travel of trackmakers, but in many instances those preferred directions parallel ancient shorelines (82). Although it is possible that such sites record movements of herds along a shore, a bimodal, mirror-image pattern of predominant trackway orientations could merely record movements of solitary animals back and forth along the shoreline. However, if one trackmaker type shows a unimodal pattern of trail orientations, while other kinds of trackmakers left the mirror-image pattern, this suggests that the first set of trails was made by a group of animals. Even more persuasive trackway evidence of dinosaur sociality comes from sites where parallel trails of a particular kind show abrupt, side-by-side changes in direction, suggesting that a group of animals simultaneously adjusted their movements to avoid colliding with one another (33).

Dinosaur nest sites have yielded a wealth of information about dinosaur nest building, egg laying, and clutch sizes (19). The spacing of individual nests, and their occurrence on successive bedding planes, indicate communal nesting behavior and repeated use of particular nest sites by certain ornithopods (63, 69).

However, identification of the egg-layers is only possible when identifiable embryos occur within eggs; the mere discovery of a range of growth stages of a particular dinosaur in the vicinity of a nesting ground is not enough. Mongolian eggs long ascribed to *Protoceratops* turned out, once identifiable embryos were found inside eggs (95), to have been laid by the peculiar theropod *Oviraptor*. This discovery suggests that the parent *Oviraptor* may have guarded its nest in the manner of many birds and crocodylians (32).

Modeling and Scaling Arguments

A fairly speculative approach to dinosaur biology is the use of mathematical or even three-dimensional, experimental models to constrain interpretations of the functions of specialized features of skeletal anatomy. The hollow crests of lambeosaurine hadrosaurs have been viewed as resonating devices, in part on the basis of acoustic modeling of the resonant frequencies of such features (135). The highly vascularized dorsal bony plates of *Stegosaurus* were suggested to have had a thermoregulatory function because wind-tunnel experiments with model stegosaurus indicated that the plates were deployed in an ideal arrangement for dumping excess body heat by forced convection (51).

Among the most interesting ideas about dinosaur biology are those based on scaling arguments, but these are at the same time the interpretations farthest removed from the fossils themselves. A burgeoning literature considers the manifold relationships between animal body size and a variety of physiological

and ecological parameters (16, 37, 100, 104). As the largest land animals in earth history, dinosaurs become highly appropriate fodder for such rumination.

However, there is no way of directly weighing a dinosaur. Given a fairly complete skeleton, a scientific artist can sculpt a life restoration that should come reasonably close to the body proportions of the living animal. From the volume of the model and its scale one can then estimate the volume of the full-sized animal, and given reasonable values of the creature's specific gravity, an estimate of the animal's live mass can be made (1). Alternatively, one can do a regression of body mass on some skeletal measurement of living animals, and use the regression equation to predict dinosaur masses from their bones (2, 17).

Each of these approaches has obvious shortcomings. There is no way to be sure that an artist has correctly restored the musculature and other soft tissues on a dinosaur model. One cannot be certain that regression equations based on living reptiles, birds, or mammals are entirely appropriate for dinosaurs, and there is the additional problem that some dinosaurs were considerably larger than living land animals, such that measurements of their bones may lie well outside the range of data used to create the regression equations. These uncertainties mean that estimates of dinosaur masses are themselves hypotheses and not observations. Arguments that rely on such mass estimates can be considered robust only if they hold true for a range of body mass estimates above and below the estimate actually used.

Scaling arguments and estimates of dinosaur body masses have been used in discussions of dinosaur food consumption rates, predator/prey ratios, reproductive rates, locomotor capabilities, and body sizes (1, 21, 48, 49, 57, 62, 73). Their most sophisticated use has been in models of dinosaur thermoregulation and life history variation, based on data from living reptiles (45, 125).

As useful as such studies have been in focusing attention on plausible scenarios for various aspects of dinosaur biology, they are only as good as the assumptions and data on which they are based. Although their conclusions may be fairly reliable, they probably cannot be considered as well established as interpretations made more directly on fossil material.

ASPECTS OF DINOSAUR BIOLOGY

Reproduction and Growth

SEXUAL DIMORPHISM Recognition of sexual dimorphism in dinosaurs is based on analyses of series of specimens that potentially represent single biological populations (as from a monotypic bonebed) or that putatively represent single species (specimens from a single geologic formation from a particular region).

All or nearly all dinosaurs were oviparous (19). Because dinosaur eggs are

not especially large, compared to the sizes of presumed egg-layers, pelvic architecture is rarely informative as to the sex of individual dinosaurs. However, in male crocodylians the large, first chevron articulates with the second caudal centrum, and it is big in order to serve as an anchor for retractor muscles of an intromittent organ (78). In female crocodylians, in contrast, a relatively smaller first chevron articulates with the third caudal centrum. Consequently the female cloaca is larger than that of males, presumably to allow more room for eggs to pass. The same set of pelvic differences observed in crocodylians is said to occur in *Tyrannosaurus* (78), but unlike crocodylians, and like birds of prey, it is the putative female morph that is larger and more massively built in *Tyrannosaurus*.

Dimorphism of display structures is well known in extant, visually oriented vertebrates. As a working hypothesis, we assume that those individuals of a particular dinosaur species showing the most conspicuously developed potential display structures are males, based on what is commonly seen in living animals. Possible dimorphism of this kind has been inferred for the horns and frills of ceratopsians, the thickened and ornamented skull domes of pachycephalosaurs, the cranial crests of lambeosaurine hadrosaurs, and more subtly in the cranial rugosities of theropods and the body armor of ankylosaurs (18, 41, 42, 81, 91, 128).

Robust and gracile morphs occur in small and large species of theropods (18, 31, 105a). These are usually identified as sexual dimorphs and, as already noted for *Tyrannosaurus*, the female is usually suggested to have been larger and more massively built than the male.

GROWTH RATES Some research has suggested that large ectothermic dinosaurs would have taken several decades to reach maturity (21). Models based on living reptiles, however, indicate that very slow growth rates would require impossibly high juvenile survivorship rates; it is more likely that even the largest dinosaurs reached maturity within 20 years (45).

Dinosaur primary bone commonly shows fibro-lamellar bone deposited in zones separated by lines of arrested growth (LAGs—107, 111). Episodes of fairly rapid growth were punctuated by intervals when growth slowed or even ceased. If growth spurts occurred during a single season of the year, the minimum ages of dinosaurs can be estimated from the number of growth lines preserved in bones. Such LAG counts have been used to suggest that the small theropod *Syntarsus* required 7–8 years to reach full size, another small theropod (*Troodon*) 3–5 years, and the prosauropod *Massospondylus* 15 years (22, 23, 132). However, deposition of azonal fibro-lamellar bone occurs in the small to medium-sized ornithomimid *Dryosaurus*, suggesting continuous rapid growth with no pauses or decelerations (25).

Closely spaced, peripherally positioned lines of arrested growth occur in

compacta formed during late growth in mammals, generated at a time when growth has slowed or ceased upon the attainment of sexual maturity. Similar peripheral LAGs occur in the bones of many dinosaurs (22, 107, 132). However, they are not found in the largest individuals of *Massospondylus* and *Dryosaurus*. Either these individuals do not represent fully grown animals, or these were species with an indeterminate pattern of growth, as opposed to the more determinate growth pattern seen in birds, mammals, and other dinosaurs (23, 25).

A scenario of rapid ontogenetic growth in the hadrosaurid *Maiasaura* has been formulated on studies of nesting sites, young individuals, and monotypic bone beds (63, 66–69, 71, 119, 134). Numerous skeletons of young individuals were found within nests. Wear surfaces on their teeth suggested that they had been feeding prior to death, but the unfinished appearance of bony tissues of femoral epiphyses suggested that the nestlings were altricial (in contrast to another member of the same fauna, the hypsilophodontid *Orodromeus*), and unable to leave the nest. The largest *Maiasaura* found within nests were a little more than a meter long, suggesting that hatchlings were nestbound until they left the nest upon growing to that size. The presence of broken eggshells within *Maiasaura* nests, rather than the more complete half-eggs found in abandoned nests of the precocial *Orodromeus*, was attributed to trampling of hatched eggs by the young hadrosaurs. Adult *Maiasaura* were thought to have fed their young regurgitated plant material during the time they were nestbound.

A catastrophic kill of perhaps thousands of individuals of *Maiasaura* was found in the same formation as the nest sites. There were said to be distinct size classes of individuals, with modes corresponding to body lengths of 3, 4, 5.2, and 7 meters (66, 119, 134). On the assumption that these size classes were year classes, the three-meter-long *Maiasaura* were interpreted as yearlings, and the largest size class as individuals four (or five) years old (and older). Consequently *Maiasaura* was thought to reach full size in roughly 4 or 5 years. If sexual maturity was reached at 67–75% of the final body length (20, 21), this would correspond to the 5.2-m size class, and an age of roughly three years. This is considerably shorter than the 10–12 years to sexual maturity predicted for *Maiasaura* by a model based on the physiological ecology of living reptiles (45).

However, this scenario is obviously based on rather circumstantial evidence. Although it is possible that young *Maiasaura* were nestbound, it would be somewhat surprising for the parents to have left eggshells in the nest where they would be subject to trampling, instead of removing them from the nest (the latter as commonly done by altricial birds—3). The interpretation that the unfinished articular surfaces of young *Maiasaura* indicate altriciality (71) was not documented by a comparison of limb articular surfaces in a variety of altricial as opposed to precocial bird species. In fact, the articular surfaces of

young *Maiasaura* show marked similarities to those of young—and precocial—domestic chickens (4).

The scenario requires the assumption that size classes in *Maiasaura* bonebeds correspond to year classes (not unreasonable), and that the age classes have been correctly identified (less certain). Until independent criteria for assessing ontogenetic ages are established, growth rates interpreted on the basis of the *Maiasaura* scenario should be regarded as hypotheses rather than observations.

Discussions of dinosaur growth rates and primary bone texture figure prominently in interpretations of dinosaur physiology (26, 27, 106–108, 110, 132). The argument usually involves two steps: The presence of fibro-lamellar tissue and a high degree of vascularity are taken as indicative of rapid growth, and rapid growth rates are then presumed to require rapid metabolic rates.

Although a link between fibro-lamellar primary bone and fast growth rates seems likely, calibrating the relationship is difficult. Just how fast bone deposition has to be before an animal shifts from making lamellar-zonal to fibro-lamellar bone, and how this bone deposition rate relates to overall animal growth in units of body mass per time, are uncertain.

The overall vascularity of the femora of juvenile ostriches is greater than for young Nile crocodiles—but not by much—and young crocodiles have more highly vascularized femora than do young secretary birds (24). Although a link between bone vascularity and growth rate is plausible, the correlation does not seem very tight.

The relationship between growth and metabolic rates may be even looser. The absolute mass gain (g/day) during the interval of fastest growth is positively correlated with adult body mass in vertebrates (20), but how the growth rates of reptiles and endotherms of a given mass compare depends on how adult body mass is defined. Birds and mammals first reproduce when they have grown to nearly their final body mass, but reptiles first breed at roughly 30–40% of maximum body mass. If juvenile growth rate is regressed against final adult mass, reptilian growth rates are about an order of magnitude less than those of birds and mammals (20). However, if growth rates are standardized against body mass at sexual maturity, the discrepancy is much less; alligators may equal and even exceed the absolute growth rate observed in some mammals of comparable mass at first reproduction (117).

Were Dinosaurs Endotherms or Ectotherms?

Dinosaur bone histology seems not to provide unambiguous evidence about dinosaur metabolic rates. It therefore joins numerous other lines of evidence that have failed to settle the contentious question of whether dinosaurs were endotherms, ectotherms, or transitional between these two metabolic states (48, 117). Although we wonder if this matter will ever be settled definitively,

some hope is offered by the recent discovery that the presence of respiratory turbinates (which occur in living birds and mammals, but not reptiles) is tightly linked to the rapid rates of pulmonary ventilation associated with endothermy (61). Skeletal attachment sites for respiratory turbinates occur in both birds and mammals, and they are also found in therocephalian and cynodont therapsids (61). So far there is no evidence for such nonsensory, respiratory turbinates in any dinosaurs (J. Ruben, unpublished observations), which suggests that these reptiles were not endotherms.

Body-Size Distributions in Dinosaur Faunas: Ectothermic Giants in a Greenhouse World?

If dinosaurs were metabolically more like living ectothermic reptiles than like endothermic birds and mammals, this may help explain one of the most conspicuous features of these ancient reptiles: the large body sizes of most dinosaur species (103).

Recent studies (14, 87) have described the body-size frequency distributions of Holocene (modern) nonvolant, terrestrial mammalian species and genera on large and small continents. Log body mass distributions are positively skewed for the faunas of large continents, but more nearly normally distributed for the faunas of small continental masses, due to the absence of the right-hand tail of large-bodied species on the smaller continents. Mammalian faunas sampled at a progressively finer scale (continent to biome to "local patches of uniform habitat") show a shift from positively skewed to nearly uniform log body mass distributions.

The present-day North American mammalian fauna is depleted in very large species, reflecting the geologically recent extinction of the megafauna (77). Figure 1 (a—shaded) shows a body-size distribution for the late Pleistocene (25,000–10,000 BP) mammalian fauna of North America (actually the United States), based on species presently known from fossil evidence. Body-size data are also summarized for members of the Order Carnivora and for plant-eating mammals that attain a body size of roughly 1 kg or more (a taxonomically heterogeneous assemblage).

Like that of the modern mammalian fauna, the late Pleistocene body-size distribution is positively skewed. Most species occur in size classes 2 and 3, and the median is size class 3, but the relative importance of these smaller mammals is less marked than in the Holocene body-size distribution. Rather than indicating a real paucity of small mammals in the latest Pleistocene fauna, this probably reflects a taphonomic bias against preservation of the fossils of small-bodied animals. Because all (or nearly all) Holocene mammal species were probably in existence by the latest Pleistocene, a "theoretical" body-size distribution for the latest Pleistocene fauna can be created by adding present-day species not yet found as fossils to those known from fossil deposits (Figure

1 [a—unshaded]). If this is done, the Pleistocene body-size distribution does not look markedly different from that of the Holocene fauna (14).

What is different, of course, is that there are more large-bodied species in the Pleistocene fauna, particularly among the large herbivores. All of the really big (size class 7) latest Pleistocene mammals were plant-eaters, representing a size class not present in the modern fauna.

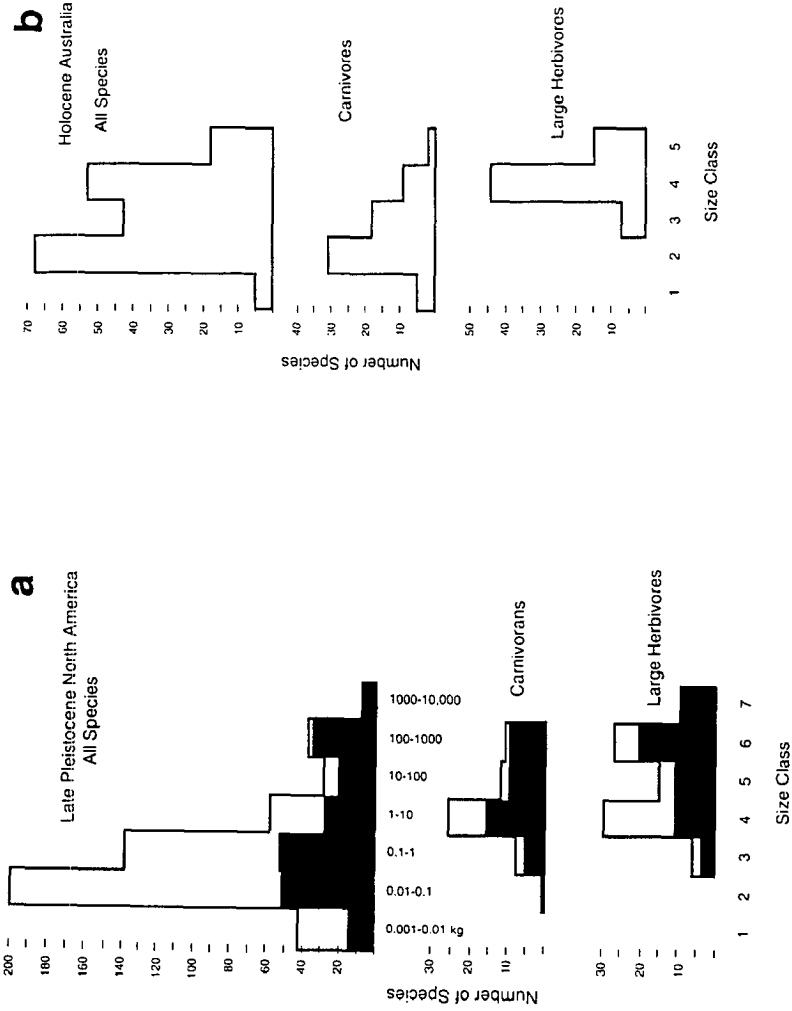
As one of the smaller continents, Holocene Australia has few large-bodied mammalian species (87). The mode for the fauna is size class 2, and the median is size class 3; the largest species occur in size class 5 (Figure 1 [b]). However, like many other parts of the world, Australia has experienced late Quaternary extinctions of megafaunal species (92). The mode and median for Australian Pleistocene megafaunal herbivores are size class 5, and only one species occurs in size class 7 (Figure 1 [c]). The few megafaunal carnivores all occur in size class 5. In fact, the largest Australian megafaunal predator was not even a mammal, but rather a huge varanid lizard (54, 92).

The scarcity of large mammalian carnivores in Australia has been attributed to the nutrient-poor nature of Australian soils, and the variability of rainfall patterns due to the El Niño-Southern Oscillation cycle, which are thought to result in low and unpredictable levels of plant productivity (54). This would in turn prevent the establishment of large populations of herbivorous mammals and thus preclude the existence of a sufficiently large resource base to support large carnivorous mammals. However, the small land area of the continent probably is also important in having prevented the evolution of very large Australian mammals (87).

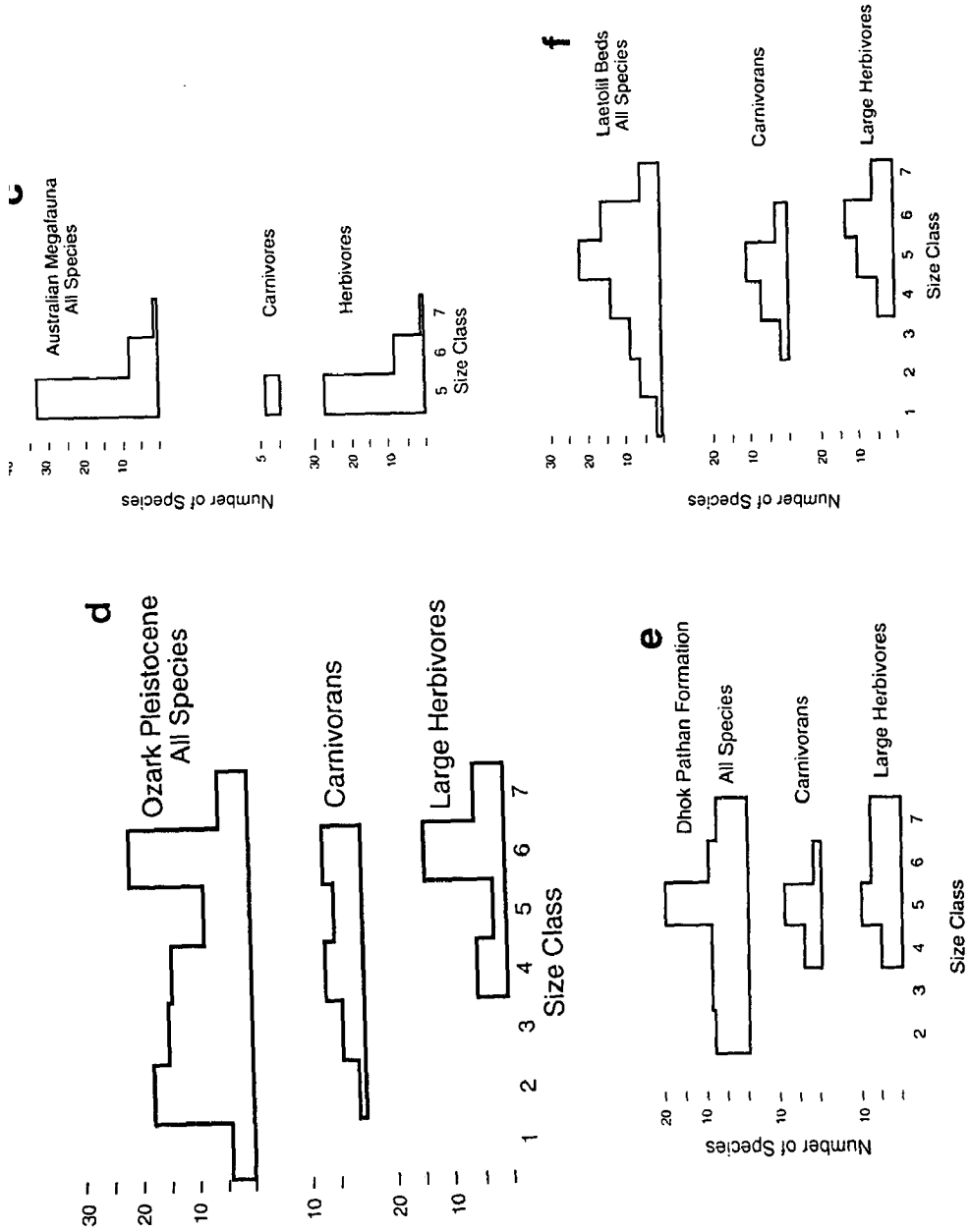
The mammalian faunas of the Pliocene Laetolil Beds of Tanzania, the Miocene Dhok Pathan Formation of Pakistan, and the Pleistocene of the Ozark region of the United States (Figure 1 [d-f]) do not represent the overall mammalian faunas of entire continents, but rather samples of mammals from three geographically circumscribed sets of sites on large continents. The faunas from these three units probably reflect spatial scales intermediate between the biome and the “local patches of uniform habitat” (14) levels. This may partly account for the lesser strength of the smaller size classes in the body-size distributions of these three faunas, with the taphonomic bias against small-bodied animals constituting the rest (perhaps the greater part) of the deficit.

To generalize across the various mammalian faunas, when allowances are made for geographic scale and taphonomic biases, small-bodied species domi-

Figure 1 Body size distributions in mammalian faunas. Body masses are expressed in terms of logarithmic size classes because of the uncertainties in estimating body masses of extinct forms. Size class 1 = mass greater than/equal to (GE) 0.001 kg and less than (LT) 0.01 kg, size class 2 = mass GE 0.01 kg and LT 0.1 kg, and so on. (Data from 14, 39, 77, 79, 85, 92, 127; and C Badgley, J Damuth, R Graham, unpublished observations).



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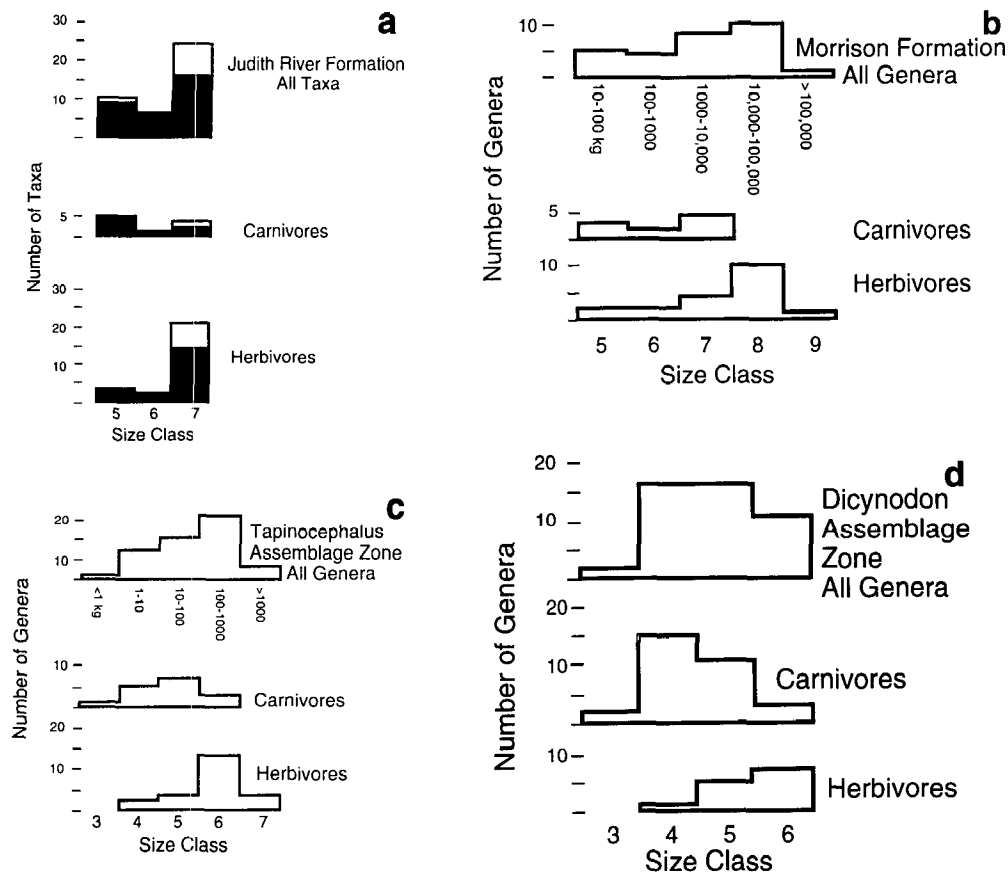


Figure 2 Body-size distributions in dinosaurian (a, b) and therapsid faunas (c, d). Ornithomimosaurs and oviraptorosaurs are included in the distribution for all Judith River dinosaurs, but not in the carnivore or herbivore distributions, due to uncertainty about their diets. Data from 1, 2, 76, 118, 137, and T Holtz, N Hotton, G King, B Rubidge, H-D Sues (unpublished observations).

nate faunas that sample entire continents. The greatest species richness of large carnivores occurs in the 1–10 or 10–100 kg size class. Continent-wide large herbivore faunas show their greatest richness in size class 4 but are also strong in bigger size classes, particularly on large continents. Where really big species occur in a mammalian fauna, these are always plant-eaters.

The situation is very different for dinosaurian faunas. Figure 2 (a—unshaded) shows the body-size distribution of Judith River Formation dinosaurs [based on current species-level classifications (137)]. Figure 2 (a—shaded)

shows the Judith River body-size distribution on the conservative assumption that there is only one valid species per genus.

The present species-level taxonomy of Morrison Formation dinosaurs is almost surely overly split, particularly for sauropods, although there may well be more than one valid species for some Morrison genera (137). We choose not to attempt to decide such systematic questions, and in Figure 2 (b) illustrate only a genus-level body-size distribution.

Like the mammalian faunas of the Laetolil Beds, the Dhok Pathan Formation, and the Ozark Pleistocene, the Judith River dinosaurian fauna probably represents a scale intermediate between the homogeneous local habitat and the biome levels, and so the total taxonomic richness of dinosaurs may reflect a mixture of within-habitat and between-habitat diversity (7, 12). The species-level and genus-level body-size distributions for Judith River dinosaurs show identical patterns. The smallest taxa occur in size class 5—a size class three orders of magnitude larger than the modal size class for North American late Pleistocene mammals (theoretical), and the same as the modal size class for mammals from the Dhok Pathan Formation, the Laetolil Beds (although, as previously noted, these assemblages are likely biased against very small-bodied mammal species), and the Australian Pleistocene megafauna.

The median and modal size class of Judith River dinosaurs (a size class dominated by herbivorous taxa) is size class 7. This is two orders of magnitude larger than the mode for the Dhok Pathan and Australian megafaunal herbivores, and an order of magnitude larger than the modes for Laetolil and Ozark large herbivores, as well as the second mode (size class 6) seen in the theoretical latest Pleistocene large herbivores of North America. Although there is overlap in body size between herbivorous dinosaurs and large mammalian herbivores, for mammals size class 7 represents a relatively minor category, while for plant-eating Judith River dinosaurs this is the strongest size class.

Judith River carnivorous dinosaurs show a mode in size class 5, as do carnivores from most of the mammalian faunas. In addition, though, the Judith River theropods have representatives in size class 7, a size greater than that reached by any known terrestrial mammalian carnivore, living or extinct (49).

Morrison Formation dinosaurs show much the same pattern as the Judith River dinosaurs (Figure 2 [b]), except that Morrison sauropods attained body masses even greater than those of Judith River herbivores, reaching 10,000–100,000 kg (or more), a size approached by only a few mammalian herbivores.

Although the same taphonomic bias against small-bodied animals undoubtedly occurs in Mesozoic as in Cenozoic terrestrial vertebrate faunas, this is probably not responsible for the scarcity of small-bodied dinosaur species. Dinosaurs with adult masses of a few kilograms are known (137), but the small vertebrates commonly found in well-sampled units like the Judith River and Morrison Formations represent non-dinosaurian groups (6). There is no fossil

evidence that even hints at a diversity of non-avian dinosaurs in size classes 1–4. The shape of the Judith River and Morrison body-size distributions actually suggests that a continent-scale body-size distribution of dinosaur taxa would be negatively skewed (cf. 49, 103, and J Damuth, unpublished observations).

Certain features of the geographic occurrence of dinosaur taxa make the greater body-size of dinosaurs than of terrestrial mammals even more remarkable. During the Campanian Age of the Late Cretaceous (when sediments of the Judith River and Two Medicine Formations were deposited), the western part of North America was separated from the eastern part of the continent by a shallow seaway. Western North America was connected with eastern Asia above the Arctic Circle to form a single landmass, *Asiamerica*, that had a distinctive dinosaurian fauna as compared with the rest of the world.

Although the Asian and American portions of *Asiamerica* have several dinosaurian families and one or more genera in common (74, 137), they seem not to have shared any species, suggesting that the Arctic connection between the two segments of *Asiamerica* acted as an ecological filter preventing free exchange of species. If so, then the Campanian dinosaurs of the Judith River Formation and correlative western North American stratigraphic units were largely restricted to the eastern portion of *Asiamerica*, a landmass with an area approximately the same as that of present-day Australia (49, 120). Judith River dinosaurs not only attained larger sizes than did most terrestrial mammalian species, but also did so on a small landmass—in contrast to what occurs in mammalian faunas.

Among modern mammals, population density decreases with increasing body size, a relationship strongly influenced by diet (37, 38, 112). At any given body mass, carnivores have lower population densities than do herbivores. Population turnover rates likewise decrease with increasing body size (16, 104). Consequently, populations of very large mammals are thinly spread and recover only slowly from environmental perturbations. To maintain viable populations under these conditions, very large mammals should show relatively little habitat specialization or have large geographic ranges, or both (100).

Once again the Campanian dinosaurs of western North America seem at odds with expectations for dinosaur-sized mammals. There is habitat zonation of dinosaur taxa within the Judith River Formation, and between the Judith River and Two Medicine Formations (7, 12, 65, 133). Furthermore, there may be north-south differences in Campanian dinosaur faunas as well (53, 116). It would be surprising to find this much large-vertebrate habitat zonation or biogeographic subdivision in a regional or continental fauna dominated by a diversity of elephant-sized mammals. Not only did dinosaurs routinely reach body sizes much larger than mammals, and on a rather small landmass, but many large-bodied dinosaur species also may not even have occurred in all the available terrestrial habitats on that small landmass.

Dinosaurian oviparity, as opposed to the combination of viviparity and lactation employed by most mammals, has been invoked to explain the ability of dinosaurs to achieve larger body sizes than are typical of mammals (73, 102). As egg-layers, dinosaurs may not have shown the decrease in annual and lifetime reproductive output that in terrestrial mammals accompanies large body size. Dinosaur populations may therefore have been able to recover quickly from environmental catastrophes that would doom elephant-sized mammals.

Although differences in reproductive biology may well have been a contributing factor, we do not think this a sufficient explanation for differences in body-size distributions of dinosaurian as opposed to mammalian faunas. If reproductive differences between dinosaurs and mammals were the single factor that permitted differences in body size in the two groups, we would expect that ground-living, nonpasserine birds, which are thought to be fairly similar to dinosaurs in reproductive biology (73), would have evolved at least some species comparable in mass to large dinosaurs. Although large flightless birds are known from several Cenozoic faunas (17, 86, 92), the largest forms probably weighed only about 500 kg. This is not only much less than the masses routinely achieved by dinosaurs, but it is also smaller than the masses of mammals that were contemporaries of, and in some cases members of the same faunas as, the big ground birds.

Cenozoic birds, like mammals, are endotherms with significantly higher food requirements than ectothermic animals of comparable body mass (16, 104). Elephant-sized birds, like huge mammals, should therefore have very low population densities. To explain how dinosaurian giants maintained viable populations in relatively small areas, it is probably necessary to consider mechanisms that would permit the maintenance of higher dinosaurian population densities than possible for dinosaur-sized birds and mammals.

The Mesozoic Era was a time of warmer climates than at present over much of the earth, possibly due in part to higher concentrations of CO₂ in the atmosphere than in the modern world (5, 8, 131). The combination of warmer temperatures and higher atmospheric CO₂ levels conceivably might have stimulated terrestrial primary productivity, or at least extended growing seasons, and this in turn might have supported larger populations of very large animals than would be possible on the modern earth.

However, although Mesozoic climates were warm, they were also in many places rather dry (6, 133), including (at least at times) much of the area over which Late Jurassic and Late Cretaceous sediments of western North America were deposited. Dry conditions coupled with warm temperatures would probably not have permitted significantly higher levels of primary productivity than seen in the Cenozoic world. Furthermore, many of the plant taxa that dominated Mesozoic vegetations were probably of poor quality as forage (113) and also

slowly growing and/or slow to recover from heavy browsing by herbivores (6, 11, 130).

This leaves us with what seems the most important factor that permitted dinosaurian gigantism: that dinosaurs had lower food consumption rates than expected for equally large birds or mammals. If large dinosaurs had metabolic rates more nearly like those of living reptiles than those of modern endotherms, they might have maintained population densities several times higher than possible for equally large mammals or birds (37, 49, 89). Although most herbivorous dinosaurs were unquestionably megaherbivores (100) in the sense of being large-bodied plant-eaters, the per-animal impact on Mesozoic vegetations may have been less than for elephant-sized mammals. Most ceratopsians and hadrosaurs may have been ecologically more like antelopes than elephants in this regard, and only the biggest herbivorous dinosaurs (particularly sauropods) would have been the energetic equivalents of mammalian megaherbivores. Higher population densities than expected for equally huge mammals may have been even more critical in permitting the evolution of gigantic predatory dinosaurs, given the tighter energetic constraints on large carnivores than on herbivores (49, 54, 112).

Even if low food consumption rates are a precondition for the existence of diverse faunas of very large land animals, this does not mean that tetrapods with low metabolic rates will inevitably evolve such giants. Some of the carnivorous species of Late Permian therapsid faunas may have been endotherms, but herbivorous therapsids probably were not (28, 61, 76). Therapsids were larger on average than terrestrial mammals (Figures 1, 2 [c, d]), but the biggest therapsid size classes are no bigger than those of mammals.

Why Did Plant-Eating Dinosaurs Produce More Very Large Species than Herbivorous Therapsids Did?

Conceivably this relates to changes in vegetation structure between late Paleozoic and early Mesozoic ecosystems, with dinosaurs evolving in association with higher-crowned plants than those typical of the late Permian (6, 130). However, it is intriguing that the first large dinosaurs appeared at a time when atmospheric CO₂ levels are thought to have been well above those of the modern world, and at the high point after recovery from low values of the later Paleozoic Era (8). If greenhouse conditions resulted in longer growing seasons and higher levels of plant productivity than prevailed in the late Paleozoic, this might have permitted larger body sizes in dinosaurs than in late Paleozoic therapsids.

We suggest, then, that dinosaurian gigantism was permitted by a concatenation of factors that made the Mesozoic world and its large-vertebrate inhabitants different from those of the preceding Paleozoic and the following Cenozoic Eras. Although in features of reproductive biology and metabolic rates

dinosaurs were probably similar to herbivorous therapsids, the greenhouse conditions of the Mesozoic world may have been more suitable for the evolution of very large, low-food-requirement herbivores and their predators than were climatic conditions of the late Paleozoic. Even though greenhouse conditions gradually deteriorated as the Cenozoic world lurched toward the modern icehouse configuration (105), levels of plant productivity may have remained comparable to those of the Mesozoic, or even increased, due to the dominance of vegetations by fast-growing angiosperm species that recover quickly from heavy cropping (6, 11, 130). Cenozoic mammals may have been prevented from evolving gigantism to the extent dinosaurs did, not so much because of environmental conditions, but rather because of their higher food requirements and their generally viviparous mode of reproduction.

Even if our speculations about the constraints that prevented gigantism in mammals (and perhaps therapsids), but not dinosaurs, have merit, our hypotheses do not identify the positive selective factors that actually caused dinosaurs to evolve very large body sizes. These might have involved thermoregulation, greater vagility, access to higher plant crowns, digestive physiology, predator-prey interactions, or reproductive dynamics (6, 13, 47, 125, 130; J Damuth, unpublished observations), but evaluating these alternatives would necessitate our being even more speculative than we have already been.

THE VALUE OF DINOSAURS

Because of small sample sizes of specimens of these generally large animals, dinosaurs are not the ideal subjects for studies of evolutionary rates and modes; nor are their remains the most useful fossils for biostratigraphic work. What, then, is the value of dinosaur paleontology?

Dinosaurs push the envelope of what it means to be a large, terrestrial vertebrate. Their very existence poses questions about how body size is related to locomotion, reproduction, growth, metabolism, and trophic ecology that are broader than would be asked if land animals of the modern world were the only terrestrial creatures we knew. Can theories about the factors affecting the structure and function of terrestrial biological communities based on studies of the Holocene biota account for the features of any terrestrial biota, regardless of its taxonomic composition? Or do such theories work only for floras and faunas of the kind we see today? Attempting to understand dinosaur biology confronts us with such questions in an unusually forceful way.

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Literature Cited

1. Alexander R McN. 1985. Mechanics of posture and gait of some large dinosaurs. *Zool. J. Linn. Soc.* 83:1-25
2. Anderson JF, Hall-Martin A, Russell DA. 1985. Long-bone circumference and weight in mammals, birds and dinosaurs. *J. Zool. Lond. A* 207:53-61
3. Armstrong EA. 1964. Parental care. In *A New Dictionary of Birds*, ed. AL Thomson, pp. 597-600. New York: McGraw-Hill
4. Barreto C, Albrecht RM, Bjorling DE, Horner JR, Wilsman NJ. 1993. Evidence of the growth plate and the growth of long bones in juvenile dinosaurs. *Science* 262:2020-23
5. Barron EJ, Fawcett PJ, Pollard D, Thompson S. 1993. Model simulations of Cretaceous climates: the role of geography and carbon dioxide. *Philos. Trans. R. Soc. Lond. B* 341:307-16
6. Behrensmeyer AK, Damuth JD, Di-Michele WA, Potts R, Sues H-D, Wing SL, eds. 1992. *Terrestrial Ecosystems through Time: Evolutionary Paleocology of Terrestrial Plants and Animals*. Chicago: Univ. Chicago Press. 568 pp.
7. Béland P, Russell DA. 1978. Paleocology of Dinosaur Provincial Park (Cretaceous), Alberta, interpreted from the distribution of articulated dinosaur remains. *Can. J. Earth Sci.* 15:1012-24
8. Berner RA. 1994. Geocarb II: a revised model of atmospheric CO₂ over Phanerozoic time. *Am. J. Sci.* 294:56-91
9. Bocherens H, Brinkman DB, Dauphin Y, Mariotti A. 1994. Microstructural and geochemical investigations on Late Cretaceous archosaur teeth from Alberta, Canada. *Can. J. Earth Sci.* 31: 783-92
10. Bonaparte JF, Novas FE, Coria RA. 1990. *Carnotaurus sastrei*, the horned, lightly built carnivorous from the Middle Cretaceous of Patagonia. *Contrib. Sci. Nat. Hist. Mus. Los Angeles County* 416:1-42
11. Bond WJ. 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biol. J. Linn. Soc.* 36:227-49
12. Brinkman DB. 1990. Paleocology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: evidence from vertebrate microfossil localities. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 78:37-54
13. Brown JH, Marquet PA, Taper ML. 1993. Evolution of body size; consequences of an energetic definition of fitness. *Am. Nat.* 142:573-84
14. Brown JH, Nicoletto PF. 1991. Spatial scaling of species composition: body masses of North American land mammals. *Am. Nat.* 138:1478-512
15. Bryant HN, Seymour KL. 1990. Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. *J. Morphol.* 206:109-17
16. Calder WA. 1984. *Size, Function, and Life History*. Cambridge (MA): Harvard Univ. Press. 431 pp.
17. Campbell KE Jr, Marcus L. 1992. The relationship of hindlimb bone dimensions to body weight in birds. In *Papers in Avian Paleontology*, ed. KE Campbell Jr, pp. 395-412. Los Angeles: Sci. Ser. 36, Nat. Hist. Mus. Los Angeles County
18. Carpenter K, Currie PJ, eds. 1990. *Dinosaur Systematics: Perspectives and Approaches*. Cambridge: Cambridge Univ. Press. 318 pp.
19. Carpenter K, Hirsch KF, Horner JR, eds. 1994. *Dinosaur Eggs and Babies*. Cambridge: Cambridge Univ. Press. 372 pp.
20. Case TJ. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quart. Rev. Biol.* 53:243-82
21. Case TJ. 1978. Speculations on the growth rate and reproduction of some dinosaurs. *Paleobiology* 4:320-28
22. Chinsamy A. 1990. Physiological implications of the bone histology of *Syntarsus rhodensis* (Saurischia: Theropoda). *Palaeont. afr.* 27:77-82
23. Chinsamy A. 1993. Bone histology and growth trajectory of the prosauropod dinosaur *Massospondylus carinatus* (Owen). *Mod. Geol.* 18:319-29
24. Chinsamy A. 1993. Image analysis and the physiological implications of the vascularisation of femora in archosaurs. *Mod. Geol.* 19:101-8
25. Chinsamy A. 1995. Ontogenetic changes in the bone histology of the Late Jurassic ornithomimid *Dryosaurus*

- lettowvorbecki*. *J. Vert. Paleontol.* 15: 96–104
26. Chinsamy A, Chiappe LM, Dodson P. 1994. Growth rings in Mesozoic birds. *Nature* 368:196–97
27. Chinsamy A, Dodson P. 1995. Inside a dinosaur bone. *Am. Sci.* 83:174–80
28. Chinsamy A, Rubidge BS. 1993. Diconodont (Therapsida) bone histology: phylogenetic and physiological implications. *Palaeont. afr.* 30:97–102
29. Choy DSJ, Altman P. 1992. The cardiovascular system of *Barosaurus*: an educated guess. *Lancet* 340:534–36
30. Clemens WA, Nelms LG. 1993. Paleocological implications of Alaskan terrestrial vertebrate fauna in latest Cretaceous time at high paleolatitudes. *Geology* 21:503–6
31. Colbert EH. 1989. The Triassic dinosaur *Coelophysus*. *Bull. Mus. N. Arizona* 57: 1–160
32. Coombs WP Jr. 1989. Modern analogs for dinosaur nesting and parental behavior. In *Paleobiology of the Dinosaurs*, ed. JO Farlow, pp. 21–53. Boulder: Geol. Soc. Am. Spec. Pap. 238
33. Currie PJ. 1983. Hadrosaur trackways from the Lower Cretaceous of Canada. *Acta Palaeontol. Polonica* 28:63–73
34. Currie PJ, Dodson P. 1984. Mass death of a herd of ceratopsian dinosaurs. In *Third Symp. Mesozoic Terrestrial Ecosystems, Short Papers*, ed. W-E Reif, F Westphal, pp. 61–66. Tübingen: Attempto Verlag
35. Currie PJ, Eberth DA. 1993. Palaeontology, sedimentology and palaeoecology of the Iren Dabusu Formation (Upper Cretaceous), Inner Mongolia, People's Republic of China. *Cretac. Res.* 14:127–44
36. Czerkas SA. 1992. Discovery of dermal spines reveals a new look for sauropod dinosaurs. *Geology* 20:1068–70
37. Damuth J. 1987. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biol. J. Linn. Soc.* 31:192–246
38. Damuth J. 1993. Cope's rule, the island rule and the scaling of mammalian population density. *Nature* 365:748–50
39. Damuth J, MacFadden BJ, eds. 1990. *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge: Cambridge Univ. Press. 397 pp.
40. Dashzeveg D, Novacek MJ, Norell MA, Clark JM, Chiappe LM, et al. 1995. Extraordinary preservation in a new vertebrate assemblage from the Late Cretaceous of Mongolia. *Nature* 374:446–49
41. Dodson P. 1975. Taxonomic implications of relative growth in lambeosaurine hadrosaurs. *Syst. Zool.* 24: 37–54
42. Dodson P. 1976. Quantitative aspects of relative growth and sexual dimorphism in *Protoceratops*. *J. Paleontol.* 50:929–40
43. Dodson P. 1990. Counting dinosaurs: How many kinds were there? *Proc. Nat. Acad. Sci. USA* 87:7608–12
44. Dodson P, Behrensmeyer AK, Bakker RT, McIntosh JS. 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. *Paleobiology* 6:208–32
45. Dunham AE, Overall KL, Porter WP, Forster CA. 1989. Implications of ecological energetics and biophysical and developmental constraints for life-history variation in dinosaurs. In *Paleobiology of the Dinosaurs*, ed. JO Farlow, pp. 1–19. Boulder: Geol. Soc. Am. Spec. Pap. 238
46. Enlow DH, Brown SO. 1957. A comparative histological study of fossil and recent bone tissue. Part 2. *Texas J. Sci.* 9:186–214
47. Farlow JO. 1987. Speculations about the diet and digestive physiology of herbivorous dinosaurs. *Paleobiology* 13: 60–72
48. Farlow JO. 1990. Dinosaur energetics and thermal biology. In *The Dinosauria*, ed. D Weishampel, P Dodson, H Osmólska, pp. 43–55. Berkeley: Univ. Calif. Press
49. Farlow JO. 1993. On the rareness of big, fierce animals: speculations about the body sizes, population densities, and geographic ranges of predatory mammals and large carnivorous dinosaurs. *Am. J. Sci.* 293-A:167–199
50. Farlow JO, Dodson P. 1975. The behavioral significance of frill and horn morphology in ceratopsian dinosaurs. *Evolution* 29:353–61
51. Farlow JO, Thompson CV, Rosner DE. 1976. Plates of the dinosaur *Stegosaurus*: forced convection heat loss fins? *Science* 192:1123–25
52. Fiorillo AR. 1991. Dental microwear on the teeth of *Camarasaurus* and *Diplodocus*: implications for sauropod paleoecology. In *Fifth Symp. on Mesozoic Terrestrial Ecosystems and Biota*, ed. S Kielan-Jaworowska, N Heintz, HA Nakrem, pp. 23–24. Contrib. Paleontol. Mus. Univ. Oslo 364
53. Fiorillo AR, Currie PJ. 1994. Theropod teeth from the Judith River Formation

- (Upper Cretaceous) of South-Central Montana. *J. Vert. Paleontol.* 14:74–80
54. Flannery T. 1991. The mystery of the Meganesian meat-eaters. *Australian Natural History* 23:722–29
55. Francillon-Vieillot H, de Buffrénil V, Castanet J, Géraudie J, Meunier FJ, et al. 1990. Microstructure and mineralization of vertebrate skeletal tissues. In *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends*, ed. JG Carter, 1:471–529. New York: Van Nostrand Reinhold
56. Gatesy SM. 1990. Caudofemoral enlargements and the evolution of theropod locomotion. *Paleobiology* 16:170–86
57. Gatesy SM. 1991. Hind limb scaling in birds and other theropods: implications for terrestrial locomotion. *J. Morphol.* 209:83–96
58. Giffin EB. 1991. Endosacral enlargements in dinosaurs. *Mod. Geol.* 16:101–12
59. Hallam A. 1993. Jurassic climates as inferred from the sedimentary and fossil record. *Philos. Trans. R. Soc. Lond. B* 341:287–96
60. Heinrich RE, Ruff, CB, Weishampel DB. 1993. Femoral ontogeny and locomotor biomechanics of *Dryosaurus lettowvorbecki* (Dinosauria, Iguanodontia). *Zool. J. Linn. Soc.* 108:179–96
61. Hillenius WJ. 1994. Turbinates in therapsids: evidence for Late Permian origins of mammalian endothermy. *Evolution* 48:207–29
62. Holtz TR Jr. 1994. The arctometatarsalian pes, an unusual structure of the metatarsus of Cretaceous Theropoda (Dinosauria: Saurischia). *J. Vert. Paleontol.* 14:480–519
63. Horner JR. 1982. Evidence of colonial nesting and 'site fidelity' among ornithischian dinosaurs. *Nature* 297:675–76
64. Horner JR. 1984. A "segmented" epidermal tail frill in a species of hadrosaurian dinosaur. *J. Paleontol.* 58:270–71
65. Horner JR. 1984. Three ecologically distinct vertebrate faunal communities from the Late Cretaceous Two Medicine Formation of Montana, with discussion of evolutionary pressures induced by interior seaway fluctuations. *Montana Geol. Soc. 1984 Field Conf.*, pp. 299–303
66. Horner JR. 1992. Dinosaur behavior and growth. In *Fifth North American Paleontological Convention, Abstracts and Program*, ed. RS Spencer. *Paleontol. Soc. Special Publ.* 6:135 (Abstr.)
67. Horner JR. 1994. Comparative taphonomy of some dinosaur and extant bird colonial nesting grounds. In *Dinosaur Eggs and Babies*, ed. K Carpenter, KF Hirsch, Horner JR, pp. 116–123. Cambridge: Cambridge Univ. Press
68. Horner JR, Gorman J. 1988. *Digging Dinosaurs*. New York: Workman. 210 pp.
69. Horner JR, Makela R. 1979. Nest of juveniles provides evidence of family structure among dinosaurs. *Nature* 282:296–98
70. Horner JR, Varricchio DJ, Goodwin MB. 1992. Marine transgression and the evolution of Cretaceous dinosaurs. *Nature* 358:59–61
71. Horner JR, Weishampel DB. 1988. A comparative embryological study of two ornithischian dinosaurs. *Nature* 332:256–57
72. Insole AN, Hutt S. 1994. The palaeoecology of the dinosaurs of the Wessex Formation (Wealden Group, Early Cretaceous), Isle of Wight, Southern England. *Zool. J. Linn. Soc.* 112:197–215
73. Janis CM, Carrano M. 1992. Scaling of reproductive turnover in archosaurs and mammals: why are large terrestrial mammals so rare? *Ann. Zool. Fennici* 28:201–16
74. Jerzykiewicz T, Russell DA. 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretac. Res.* 12:345–77
75. Johnson R, Ostrom JH. The forelimb of *Torosaurus*, and an analysis of the posture and gait of ceratopsian dinosaurs. In *Functional Morphology in Vertebrate Paleontology*, ed. J Thomason. Cambridge: Cambridge Univ. Press. In press
76. King G. 1990. *The Dicotylodons: a Study in Palaeobiology*. London: Chapman and Hall. 233 pp.
77. Kurtén B, Anderson E. 1980. *Pleistocene Mammals of North America*. New York: Columbia Univ. Press. 442 pp.
78. Larson PL. 1994. *Tyrannosaurus* sex. In *Dino Fest*, ed. GD Rosenberg, DL Wolberg, pp. 139–155. *Paleontol. Soc. Spec. Pub.* 7
79. Leakey MD, Harris JM, eds. 1987. *Laeloli: a Pliocene Site in Northern Tanzania*. Oxford: Clarendon Press. 561 pp.
80. Lehman TM. 1987. Late Maastrichtian paleoenvironments and dinosaur biogeography in the western interior of North America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 60:189–217
81. Lehman TM. 1990. The ceratopsian family Chasmosaurinae: sexual dimorphism and systematics. In *Dinosaur Systematics: Approaches and Perspectives*,

- ed. K Carpenter, PJ Currie, pp. 211–29. Cambridge: Cambridge Univ. Press
82. Lockley MG. 1991. *Tracking Dinosaurs: A New Look at an Ancient World*. Cambridge: Cambridge Univ. Press. 238 pp.
83. Lockley MG, Hunt AP, Meyer CA. 1994. Vertebrate tracks and the ichnofacies concept: implications for palaeoecology and palichnostratigraphy. In *Paleobiology of Trace Fossils*, ed. S Donovan. New York: Belhaven
84. Lull RS, Wright NE. 1942. Hadrosaurian dinosaurs of North America. *Geol. Soc. Am. Spec. Pap.* 40:1–242
85. Lundelius EL Jr, Graham RW, Anderson E, Guilday J, Holman JA, et al. 1983. Terrestrial vertebrate faunas. In *Late-Quaternary Environments of the United States: The Late Pleistocene*, ed. SC Porter, 1:311–53. Minneapolis: Univ. Minn. Press
86. Marshall LG. 1994. The terror birds of South America. *Sci. Am.* 270(2):90–95
87. Maurer BA, Brown JH, Rusler RD. 1992. The micro and macro in body size evolution. *Evolution* 46:939–53
88. McGowan C. 1979. The hind limb musculature of the brown kiwi, *Apteryx australis mantelli*. *J. Morphol.* 160:33–74
89. McNab BK. 1994. Resource use and the survival of land and freshwater vertebrates on oceanic islands. *Am. Nat.* 144: 643–60
90. Molnar RE. 1977. Analogies in the evolution of combat and display structures in ornithopods and ungulates. *Evol. Theor.* 3:165–90
91. Molnar RE. 1991. The cranial morphology of *Tyrannosaurus rex*. *Palaeontographica A* 217:137–76
- 91a. Molnar RE, Wiffen J. 1994. A Late Cretaceous polar dinosaur fauna from New Zealand. *Cretac. Res.* 15:689–706
92. Murray P. 1991. The Pleistocene megafauna of Australia. In *Vertebrate Paleontology of Australasia*, ed. P Vickers-Rich, JM Monaghan, RF Baird, TH Rich, EM Thompson, C Williams, pp. 1071–1164. Melbourne: Pioneer Design Studio/Monash Univ.
93. Nadon GC. 1993. The association of anastomosed fluvial deposits and dinosaur tracks, eggs, and nests: implications for the interpretation of floodplain environments and a possible survival strategy for ornithopods. *Palaios* 8:31–45
94. Nicholls EL, Russell DA. 1985. Structure and function of the pectoral girdle and forelimb of *Struthiomimus altus* (Theropoda: Ornithomimidae). *Palaeontology* 28:643–77
95. Norell MA, Clark JM, Dashzeveg D, Barsbold R, Chiappe L, et al. 1994. A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. *Science* 266:779–82
96. Norman DB. 1980. On the ornithischian dinosaur *Iguanodon bernissartensis* of Bernissart (Belgium). *Mem. de l'Inst. Roy. Sci. Nat. Belg.* 178:1–103
97. Osmólska H. 1980. The Late Cretaceous vertebrate assemblages of the Gobi Desert, Mongolia. *Mem. Soc. Geol. France* 139:145–50
98. Ostrom JH. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bull. Peabody Mus. Nat. Hist.* 30: 1–165
99. Ostrom P, Macko SA, Engel MH, Russell DA. 1993. Assessment of trophic structure of Cretaceous communities based on stable nitrogen isotope analyses. *Geology* 21:491–94
100. Owen-Smith RN. 1988. *Megaherbivores: The Influence of Very Large Body Size on Ecology*. Cambridge: Cambridge Univ. Press. 369 pp.
101. Paul GS. 1987. The science and art of restoring the life appearance of dinosaurs and their relatives: a rigorous how-to guide. In *Dinosaurs Past and Present* Vol. II, ed. SJ Czerkas, Olson EC, pp. 4–49. Seattle: Univ. Wash. Press
102. Paul GS. 1994. Dinosaur reproduction in the fast lane: implications for size, success, and extinction. In *Dinosaur Eggs and Babies*, ed. K Carpenter, KF Hirsch, JR Horner, pp. 244–255. Cambridge: Cambridge Univ. Press
103. Peckzis J. 1994. Implications of body-mass estimates for dinosaurs. *J. Vert. Paleontol.* 14:520–33.
104. Peters RH. 1983. *The Ecological Implications of Body Size*. Cambridge: Cambridge Univ. Press. 329 pp.
105. Prothero DR. 1994. *The Eocene-Oligocene Transition: Paradise Lost*. New York: Columbia Univ. Press. 291 pp.
- 105a. Raath MA. 1990. Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodensis*. In *Dinosaur Systematics: Approaches and Perspectives*, ed. K Carpenter, PJ Currie, pp. 91–105. Cambridge: Cambridge Univ. Press
106. Reid REH. 1987. Bone and dinosaurian “endothemy.” *Mod. Geol.* 11:133–54
107. Reid REH. 1990. Zonal “growth rings” in dinosaurs. *Mod. Geol.* 15:19–48
108. Reid REH. 1993. Apparent zonation and slowed growth in a small Cretaceous theropod. *Mod. Geol.* 18:391–406
109. Rich THV, Rich, PV. 1989. Polar di-

- nosauurs and biotas of the Early Cretaceous of southeastern Australia. *Nat. Geogr. Res.* 5:15-53
110. Ricqlès A de. 1980. Tissue structure of dinosaur bone: functional significance and possible relation to dinosaur physiology. In *A Cold Look at the Warm Blooded Dinosaurs*, ed. RDK Thomas, EC Olson, pp. 103-139. Boulder: Westview
 111. Ricqlès A de. 1983. Cyclical growth in the long limb bones of a sauropod dinosaur. *Acta Palaeontol. Polonica* 28: 225-32
 112. Robinson JG, Redford KH. 1986. Body size, diet, and population density of Neotropical forest mammals. *Am. Nat.* 128: 665-680
 113. Robinson JM. 1990. Lignin, land plants, and fungi: biological evolution affecting Phanerozoic oxygen balance. *Geology* 18:607-10
 114. Rogers RR. 1990. Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of northwestern Montana: evidence for drought-related mortality. *Palaios* 5: 394-413
 115. Rothschild BM, Martin LD. 1993. *Palaeopathology: Disease in the Fossil Record*. Boca Raton: CRC. 386 pp.
 116. Rowe T, Cifelli RL, Lehman TM, Weil A. 1992. The Campanian Terlingua local fauna, with a summary of other vertebrates from the Aguja Formation, Trans-Pecos, Texas. *J. Vert. Paleontol.* 12:472-93
 117. Ruben J. 1995. The evolution of endothermy in mammals and birds: from physiology to fossils. *Annu. Rev. Physiol.* 57:69-95
 118. Rubidge B, ed. *Biostratigraphy of the Beaufort Group (Karoo Supergroup), South Africa*. South African Committee for Stratigraphy. In press
 119. Russell DA. 1989. *An Odyssey in Time: The Dinosaurs of North America*. Toronto: Univ. Toronto Press. 240 pp.
 120. Russell DA. China and the lost worlds of the dinosaurian era. *Hist. Biol.*. In press
 121. Sander PM. The Norian *Plateosaurus* bonebeds of central Europe and their taphonomy. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 93:255-99
 122. Schwartz HL, Gillette DD. 1994. Geology and taphonomy of the *Coelophysis* quarry, Upper Triassic Chinle Formation, Ghost Ranch, New Mexico. *J. Paleontol.* 68:1118-30
 123. Scotese CR, Golonka J. 1992. *Paleogeographic Atlas*, PALEOMAP Project, Univ. Texas, Arlington. 38 pp.
 124. Sellwood BW, Price GD, Valdes PJ. 1994. Cooler estimates of Cretaceous temperatures. *Nature* 370:453-55
 125. Spotila JR, O'Connor MP, Dodson P, Paladino FV. 1991. Hot and cold running dinosaurs: body size, metabolism and migration. *Modern Geol.* 16:203-27
 126. Sternberg CM. 1925. Integument of *Chasmosaurus belli*. *Can. Field-Nat.* 39: 108-10
 127. Strahan R, ed. 1983. *The Australian Museum Complete Book of Australian Mammals: the National Photographic Index of Australian Wildlife*. London: Angus and Robertson. 530 pp.
 128. Sues H-D, Galton PM. 1987. Anatomy and classification of the North American Pachycephalosauria (Dinosauria: Ornithischia). *Palaeontographica A* 198:1-40
 129. Thulborn T. 1990. *Dinosaur Tracks*. London: Chapman and Hall. 410 pp.
 130. Tiffney BH. 1992. The role of vertebrate herbivory in the evolution of land plants. In *Essays in Evolutionary Plant Biology*, ed. BS Venkatachala, DL Dilcher, HK Maheshwari, pp. 87-97. Lucknow: Birbal Sahni Inst. Palaeobotany
 131. Valdes P. 1993. Atmospheric general circulation models of the Jurassic. *Philos. Trans. R. Soc. Lond. B* 341:317-26
 132. Varricchio DJ. 1993. Bone microstructure of the Upper Cretaceous dinosaur *Troodon formosus*. *J. Vert. Paleontol.* 13:99-104
 133. Varricchio D. 1993. Montana climatic changes associated with the Cretaceous Claggett and Bearpaw transgressions. In *Energy and Mineral Resources of Central Montana: 1993 Field Conference Guidebook*, ed. LDV Hunter, pp. 97-102. Billings: Montana Geol. Soc.
 134. Varricchio DJ, Horner JR. 1993. Hadrosaurid and lambeosaurid bone beds from the Upper Cretaceous Two Medicine Formation of Montana: taphonomic and biologic implications. *Can. J. Earth Sci.* 30:997-1006
 135. Weishampel DB. 1981. Acoustic analyses of potential vocalization in lambeosaurine dinosaurs (Reptilia: Ornithischia). *Paleobiology* 7:252-61
 136. Weishampel DB. 1984. Evolution of jaw mechanisms in ornithomimid dinosaurs. *Adv. Anat. Embry. Cell Biol.* 87:1-110
 137. Weishampel DB, Dodson P, Osmólska H, eds. 1990. *The Dinosauria*. Berkeley: Univ. CA Press. 733 pp.
 138. Witmer LM. 1994. The extant phylogenetic bracket and the importance of

reconstructing the soft parts of fossils. In *Functional Morphology in Vertebrate Paleontology*, ed. J Thomason, pp. 19–33. Cambridge: Cambridge Univ. Press

139. Ziegler AM, Parrish JM, Jiping Y, Gyllenhaal ED, Rowley DB, et al. 1993. Early Mesozoic phytogeography and climate. *Philos. Trans. R. Soc. Lond. B* 341:297–305



CONTENTS

Special Section on Sustainability Issues

THE CONCEPT OF ENVIRONMENTAL SUSTAINABILITY, <i>Robert Goodland</i>	1
SUSTAINABILITY OF SOIL USE, <i>S. W. Buol</i>	25
SUSTAINABLE EXPLOITATION OF RENEWABLE RESOURCES, <i>R. Hilborn, C. J. Walters, D. Ludwig</i>	45
CAN WE SUSTAIN THE BIOLOGICAL BASIS OF AGRICULTURE, <i>Carol A. Hoffman, C. Ronald Carroll</i>	69
MEASURING BIODIVERSITY VALUE FOR CONSERVATION, <i>Christopher J. Humphries, Paul H. Williams, Richard I. Vane-Wright</i>	93
HUMAN ECOLOGY AND RESOURCE SUSTAINABILITY: THE IMPORTANCE OF INSTITUTIONAL DIVERSITY, <i>C. Dustin Becker, Elinor Ostrom</i>	113
SUSTAINABILITY, EFFICIENCY, AND GOD: ECONOMIC VALUES AND THE SUSTAINABILITY DEBATE, <i>Robert H. Nelson</i>	135
ECOLOGICAL BASIS FOR SUSTAINABLE DEVELOPMENT IN TROPICAL FORESTS, <i>Gary S. Hartshorn</i>	155
MANAGING NORTH AMERICAN WATERFOWL IN THE FACE OF UNCERTAINTY, <i>James D. Nichols, Fred A. Johnson, Byron K. Williams</i>	177
THE ECOLOGICAL BASIS OF ALTERNATIVE AGRICULTURE, <i>John Vandermeer</i>	201
ECONOMIC DEVELOPMENT VS SUSTAINABLE SOCIETIES: REFLECTIONS ON THE PLAYERS IN A CRUCIAL CONTEST, <i>John G. Clark</i>	225
* * * * *	
VESTIGIALIZATION AND LOSS OF NONFUNCTIONAL CHARACTERS, <i>Daniel W. Fong, Thomas C. Kane, David C. Culver</i>	249
THE QUALITY OF THE FOSSIL RECORD: POPULATIONS, SPECIES, AND COMMUNITIES, <i>Susan M. Kidwell, Karl W. Flessa</i>	269
HIERARCHICAL APPROACHES TO MACROEVOLUTION: RECENT WORK ON SPECIES SELECTION AND THE "EFFECT HYPOTHESIS," <i>Todd A. Grantham</i>	301

WOMEN IN SYSTEMATICS, <i>Diana Lipscomb</i>	323
A GENETIC PERSPECTIVE ON THE ORIGIN AND HISTORY OF HUMANS, <i>N. Takahata</i>	343
HISTORICAL BIOGEOGRAPHY: INTRODUCTION TO METHODS, <i>Juan J. Morrone, Jorge V. Crisci</i>	373
MOLECULAR EVIDENCE FOR NATURAL SELECTION, <i>Martin Kreitman, Hiroshi Akashi</i>	403
GENETIC MOSAICISM IN PLANTS AND CLONAL ANIMALS, <i>Douglas E. Gill, Lin Chao, Susan L. Perkins, Jason B. Wolf</i>	423
DINOSAUR BIOLOGY, <i>James O. Farlow, Peter Dodson, Anusuya Chinsamy</i>	445
THE ROLE OF NITROGEN IN THE RESPONSE OF FOREST NET PRIMARY PRODUCTION TO ELEVATED ATMOSPHERIC CARBON DIOXIDE, <i>A. David McGuire, Jerry M. Melilo, Linda A. Joyce</i>	473
FOOD WEB ARCHITECTURE AND POPULATION DYNAMICS: THEORY AND EMPIRICAL EVIDENCE, <i>Peter J. Morin, Sharon P. Lawler</i>	505
ARCHITECTURAL EFFECTS AND THE INTERPRETATION OF PATTERNS OF FRUIT AND SEED DEVELOPMENT, <i>Pamela K. Diggle</i>	531
MUTATION AND ADAPTATION: THE DIRECTED MUTATION CONTROVERSY IN EVOLUTIONARY PERSPECTIVE, <i>P. D. Sniegowski, R. E. Lenski</i>	553
SPECIATION IN EASTERN NORTH AMERICAN SALAMANDERS OF THE GENUS <i>PLETHODON</i> , <i>Richard Highton</i>	579
MULTIPLE FITNESS PEAKS AND EPISTASIS, <i>Michael C. Whitlock, Patrick C. Phillips, Francis B-G. Moore, Stephen Tonsor</i>	601
ECOLOGY AND EVOLUTION OF SOCIAL ORGANIZATION: INSIGHTS FROM FIRE ANTS AND OTHER HIGHLY EUSOCIAL INSECTS, <i>Kenneth G. Ross, Laurent Keller</i>	631
SEPARATE VERSUS COMBINED ANALYSIS OF PHYLOGENETIC EVIDENCE, <i>Alan de Queiroz, Michael J. Donoghue, Junhyong Kim</i>	657
ANTARCTIC TERRESTRIAL ECOSYSTEM RESPONSE TO GLOBAL ENVIRONMENTAL CHANGE, <i>Andrew D. Kennedy</i>	683
PLANT-VERTEBRATE SEED DISPERSAL SYSTEMS IN THE MEDITERRANEAN: ECOLOGICAL, EVOLUTIONARY, AND HISTORICAL DETERMINANTS, <i>Carlos M. Herrera</i>	705
INDEXES	
SUBJECT INDEX	729
CUMULATIVE INDEX OF CONTRIBUTING AUTHORS, VOLUMES 22–26	751
CUMULATIVE INDEX OF CHAPTER TITLES, VOLUMES 22–26	753