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The implications of a dry climate for the paleoecology of the fauna of the Upper Jurassic Morrison Formation

George F. Engelmann^{a,*}, Daniel J. Chure^b, Anthony R. Fiorillo^c

^a*Department of Geography and Geology, University of Nebraska at Omaha, 60th and Dodge Streets, Omaha, NE 68182-0199, USA*

^b*Dinosaur National Monument, P.O. Box 128, Jensen, UT 84035, USA*

^c*Dallas Museum of Natural History, P.O. Box 150349, Dallas, TX 75315, USA*

Abstract

In light of diverse geological evidence that indicates a seasonal, semiarid climate for the time of deposition of the Morrison Formation, one can assume these general environmental conditions for the purpose of reconstructing the ancient ecosystem. Wet environments that preserved plant fossils and some invertebrates and small vertebrates in the Morrison can be interpreted as representing local conditions limited in space and/or time. These elements of the biota and the smaller dinosaurs were probably restricted to such wetland areas at times of environmental stress.

A diverse fauna of large, herbivorous, sauropod dinosaurs ranged throughout the environment. Although this seems to be inconsistent with an environment with sparse resources, large size confers physiologic advantages that are adaptive for just such conditions. The scaling effect of large size makes large herbivores very efficient relative to their size in needing proportionately less food and food of poorer quality than smaller herbivores. They can also survive starvation longer and travel more efficiently to reach widely separated resource patches. Although few in number at any time, the sauropod dinosaurs are locally abundant and seemingly ubiquitous in the fossil record of the Morrison Formation because of overrepresentation of their highly preservable remains in an attritional fossil assemblage.

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1. Introduction

The Morrison Formation has long been known for fossil vertebrates, especially the dinosaur faunas collected by Cope, Marsh, and others over the past 100 years (Ostrom and McIntosh, 1966; Breithaupt, 1998; Monaco, 1998), and, to a lesser extent the fossil

mammals (Engelmann and Callison, 1998). However, additional elements of the flora and fauna represent a diverse biota (Chure et al., 1998). Many depictions of the Morrison ecosystem have been produced over the past century. Such reconstructions followed the broad sedimentologic interpretation of a fluvio-lacustrine environment, but were strongly influenced by assumptions about the needs and characteristics of the dinosaurs, especially the sauropods. The sauropods were once regarded as gigantic lizards that spent much of their time in water, and were pictured in wet, swampy environments with deep bodies of water by Knight, Zallinger, and other artists (Colbert, 1961). Bakker

* Corresponding author. Tel.: +1-402-554-4804; fax: +1-402-554-3518.

E-mail address: george_engelmann@unomail.unomaha.edu, CAS@unomail.unomaha.edu, UNO@unomail.unomaha.edu, UNEHR@unomail.unomaha.edu (G.F. Engelmann).

(1971), Coombs (1975), and others challenged such prevailing interpretations of the sauropods by pointing out that nothing about them was characteristic of aquatic animals. They argued that elephantine reconstructions of sauropods with graviportal limbs implied that they were adapted for dry land rather than marshy conditions.

Dodson et al. (1980) reviewed the evidence of the dinosaur fauna of the Morrison along with that of associated lithologies and saw indications of a relatively dry climate. They proposed a strongly seasonal climate with periods of water scarcity. Discussions of the Morrison paleoenvironment in recent years have tended to follow this interpretation of relatively dry climatic conditions (Farlow et al., 1995).

More recent studies have found further support from diverse sources for interpretation of a semiarid climate with wet and dry seasons as follows.

1.1. *Paleosols*

Retallack (1997) interpreted the Morrison paleosols as indicating annual precipitation of only 600–900 mm with a dry season. He concluded that the soils probably supported dry, open woodland. Demko and Parrish (1998) interpreted the Morrison soils as having formed in a semiarid climate with some seasonal rainfall.

1.2. *Geochemistry*

Isotopic analyses of pedogenic carbonates and other materials by D.D. Ekart (oral communication, 1998) reveal oxygen isotope ratios characteristic of a rain shadow effect or strong continentality in the climate of the Morrison, and high levels of atmospheric CO₂ that would have produced warm temperatures in the Late Jurassic.

1.3. *Petrology*

Pedogenic and lacustrine carbonates of the Morrison were formed in a climate best described as semiarid to transitional (to subhumid), with wetter conditions restricted to the northernmost and latest locations (Dunagan, 2000; Dunagan et al., 1996). Features of these carbonates also support the interpretation of seasonal drying.

1.4. *Sedimentology*

The presence in the Morrison of eolian sediments and a large alkaline, saline lake provide strong evidence of episodes of at least semiarid conditions (Peterson and Turner-Peterson, 1987; Turner and Fishman, 1991; Peterson, 1994; Dunagan and Turner, this volume).

1.5. *Global climate models*

Demko and Parrish (1998) reviewed the results of qualitative conceptual circulation models and numerical General Circulation Models for the Late Jurassic and found that they predicted a rain shadow effect that would create semiarid to arid conditions over the depositional basin of the Morrison. Computer simulations of Kimmeridgian climate reported on by Valdes (1994) indicate a semiarid climate with estimates of precipitation of 1–2 mm/day in the winter and <1 mm/day in the summer. Sellwood et al. (1998) point out that different climate models for the Late Jurassic all indicate that the climate in which the Morrison was deposited was at least seasonally dry. Moore and Ross (1996) compared the geographic distribution of Late Jurassic dinosaur localities with paleoclimatic models for that time and found that they were concentrated where the model predicted that evaporation exceeded precipitation.

The Morrison biota has provided relatively little help in refining interpretations of climate. This has been especially true for the dominant, large vertebrate fauna, the dinosaurs, because they are so different from their closest living relatives and only distantly related to possible modern ecological analogues. Foster (1998) attempted a comprehensive survey of the Morrison fauna that was corrected for taphonomic bias, and concluded that the Morrison paleocommunity was unlike any modern community or most ancient ones, especially in the abundance and diversity of large herbivores. But, if we cannot rely on the dinosaurs and other elements of the fauna to provide a clear climatic and ecological signal for the Morrison Formation, perhaps it would be informative to accept the constraints on environmental interpretation from the geological evidence and consider how the fauna could have adapted to the conditions indicated. This perspective may help to provide

insights into the paleobiogeography of the Morrison ecosystem.

The evidence cited above seems to most consistently support the interpretation that the overall climate of the Morrison paleoenvironment can best be described as semiarid. There was probably a marked seasonality, with a rainy season of unspecified duration punctuating relatively dry conditions. Semiarid regions can be biologically very productive, with diverse subenvironments, but availability of water is likely to be a limiting factor. Well-adapted communities may not experience severe stress from scarcity of water on an annual basis, but semiarid regions are likely to be vulnerable to severe drought conditions at somewhat longer intervals. It is such physical environmental conditions that we postulate for the Morrison ecosystem.

2. Plants

Plants are represented in the Morrison by plant macrofossils of logs of large trees, leaves, stems and fruiting bodies of conifers, ginkgoes, cycads, ferns, and horsetails (Ash and Tidwell, 1998; Tidwell et al., 1998; Engelmann, 1999; Engelmann and Fiorillo, 2000). There are also charophytes (Schudack et al., 1999), and a diverse palynoflora (Litwin et al., 1998).

Evidence from the plants has been interpreted by some workers as indicating humid or mesic environmental conditions throughout the Morrison depositional basin (Taggart and Cross, 1997; Ash and Tidwell, 1998). Demko and Parrish (1998) and Parrish et al. (this volume) have pointed out that they may only document conditions that are localized in space and time, and are not indicative of climate. Within a semiarid environment, these vegetation samples represent either conditions during the wet season, or those areas that were perennially wet most of the time, such as riparian environments or around ponds and lakes. Such environments were supplied by water from distant sources by through-flowing streams or a shallow water table. In fact, Demko and Parrish (1998) argued that the taphonomy of the plant macrofossils is more consistent with the latter hypothesis. Plant fossils are not widespread in the Morrison but are known from a small number of localities that are not typical of the entire formation. Most of the plant macrofossils on which these interpretations are based

occur in the northernmost and youngest parts of the Morrison.

Parrish et al. (this volume) further develop the idea that details of the taphonomy of plant fossil occurrences indicate a flora in which large woody plants did not thrive in large numbers even when conditions were favorable. They also note that the low diversity of the plant macrofossils compared with the high diversity of the palynoflora is characteristic of a strongly seasonal environment. Much of the floral diversity consists of short-lived, herbaceous plants that could grow rapidly to take advantage of favorable conditions during a wet season, but are seldom preserved. This argument not only supports the climatic interpretations outlined above, but also gives us some idea of the nature of the vegetation in the Morrison.

3. Invertebrates

Ostracodes (Schudack et al., 1998) and conchostacans (Lucas and Kirkland, 1998) indicate the presence of ephemeral bodies of freshwater, while gastropods (Evanoff et al., 1998) and bivalve mollusks require that some streams had perennial flows for at least periods of several years, but also show evidence of seasonality (Good, this volume). As with the plants, these invertebrates provide evidence of those times and places where water was available.

Trace fossils provide evidence of a diverse arthropod fauna including termites, ants, and other insects, and crayfish (Hasiotis and Demko, 1996, 1998; Hasiotis et al., 1998, 1999; Hasiotis, this volume). Insects as a group inhabit a wide range of climatic conditions, so they cannot be considered diagnostic of any particular climate. Yet, the structure and physiology of insects are well suited to arid climates and they have been one of the more successful animal groups in adapting to such environments. Ants and termites have done very well in semiarid environments. Insects may well represent the principal small herbivores in the Morrison ecosystem. Termites may have been particularly important in recycling the nutrients from buried organic material back to the surface.

Crayfish are an exclusively aquatic group, so it is not surprising that their burrows occur within channel sandstones. However, Hasiotis (this volume) has noted that crayfish burrows in the Morrison occur close

to the channels and do not extend far out into floodplain sediments as they would if there were extensive persistent wetlands beyond the channel.

4. Lower vertebrates

The fish fauna of the Morrison (Kirkland, 1998) includes ray-finned fish that indicate the presence of stable bodies of freshwater. However, lungfish are perhaps the best represented elements of the fish fauna. Lungfish are adapted to stagnant, restricted bodies of water, and some can aestivate in burrows for long periods of time when the water dries up completely.

Frogs and salamanders occur in the wetland deposits of the Morrison (Henrici, 1998), along with turtles and crocodylians that appear to be adapted to the aquatic environment of major river systems and long-lived lakes. However, the example of modern aquatic organisms demonstrates that members of these groups can be adapted to withstand even severe drought. Lizards are present in the same localities with the other small vertebrates (Evans and Chure, 1998, 1999) and presumably shared similar habitat. As in the insects, modern lizards inhabit a wide range of environments and many species are well adapted to semiarid conditions.

5. Dinosaurs

5.1. Sauropods

Sauropod dinosaurs dominated the Morrison ecosystem in many respects. Not only were they the largest animals in the fauna, but at the generic level, sauropods constitute more than half the diversity of herbivorous dinosaurs in the Morrison. Why is there such diversity among the large, sympatric herbivores? Differences in the dentition and body form of the sauropod species suggest the possibility that there may have been some kind of resource partitioning with respect to food and other resources.

Fiorillo (1998) examined the microtexture of the wear facets on the teeth of the sauropods *Camarasaurus* and *Diplodocus*, the commonest sauropod taxa in the Morrison. Each also exemplifies a different one of the two major types of dentition that characterize

the Morrison sauropods. There were consistent differences in the pattern of microwear that indicated that *Camarasaurus* consumed a diet of relatively coarser vegetation than did *Diplodocus*. One notable exception to this distinction between the species was that the microwear observed in a juvenile specimen of *Camarasaurus* was more like that found in *Diplodocus* than that typical of the adult *Camarasaurus*. This study supports the conjecture that there may have been niche partitioning of the food resources (i.e., vegetation) among the adult forms of the sauropods as well as the possibility that there may have been dietary differences between adults and juveniles of the same species.

Because of their long necks, it has been suggested that sauropods were specialized to browse high above the ground (Bakker, 1971), and much discussion has been devoted to how and whether they could accomplish this (Coombs, 1975; Alexander, 1989). But, a recent analysis of the range of movement permitted by the cervical vertebrae of sauropods (Stevens and Parrish, 1999) concluded that, in diplodocids, *Diplodocus* and *Apatosaurus*, the neck could not be lifted high above the horizontal. The diplodocid neck did have considerable flexibility from side to side and even downward in ventriflextion, well below the feet of the dinosaur. Simply because of its tall stature, if the neck were held horizontally, a diplodocid could browse at a moderately high level. However, it seems unlikely that the animal would habitually assume an extreme posture. Rather, they may have utilized the ventral and lateral range of their long necks to feed close to the ground, and to sweep over a large area while standing in one spot, as suggested by Krassilov (1981) and others. Even with limited dorsiflexion of the neck, the long forelimbs of *Brachiosaurus* would place its mouth high above the ground, making it a high browser.

Resource partitioning by vertical stratification and utilization of different plant species helps to explain sauropod diversity, but leaves us with an apparent puzzle. How could populations of such large organisms, the largest known land animals, inhabit a semiarid environment with seasonally scarce resources? One might expect such large creatures to require tremendous plant productivity to support them.

As noted above, modern megaherbivores such as the elephant have been used as functional analogues

in analyzing the skeletal structure of sauropods and recognizing that graviportal limbs could support them on dry land. Although modern megaherbivores are all mammals, and none is as large as the adult sauropod dinosaurs, studies of the physiology and ecology of these modern animals also may be relevant to the interpretation of sauropod adaptation and ecology.

Various authors have discussed the effects of large size on the physiology of sauropod dinosaurs (Alexander, 1989, 1995; McGowan, 1991, 1994; Paul, 1998; Dodson, 1990; Farlow, 1987), usually in grappling with the problem of dinosaur endothermy. Because of the scaling effects of increasing size, the maintenance energy, the energy required by an organism each day to maintain its essential physiological life processes, increases with increasing body mass (M) according to the relationship $M^{0.75}$ (Schmidt-Nielsen, 1984). Another way of expressing this relationship is the prediction that the specific metabolic rate, the metabolic energy requirements per unit body mass, should decrease with increasing size according to $M^{-0.25}$. This relationship has been borne out by field and experimental studies of a number of modern megaherbivores (Owen-Smith, 1988). Because the metabolic energy of an organism is derived from the food it eats, this relationship can be determined empirically by measuring daily food intake for animals of a wide range of sizes. If we assume a similar relationship existed for sauropod dinosaurs, we can use estimates of body mass to arrive at their required daily food intake. Using estimates from Alexander (1989) for *Diplodocus* and *Brachiosaurus*, we indicate where they would fall in Fig. 1. We do not assert, nor intend to argue, that sauropod physiology was similar to that of modern, mammalian megaherbivores, as this extrapolation assumes. It is only intended as an illustration of the effect of this relationship. This effect is a result of the scaling of properties in organisms of varying size, and is independent of the particular physiology of the type of organism considered. Therefore, we would expect food intake for various dinosaurs to plot along a similar line, possibly slightly higher or slightly lower according to differences in physiology. In fact it might be expected that to the extent sauropods differed from mammals in their metabolic level, it would have been lower, as McGowan (1991) has argued. It is also possible that a sauropod's digestion was more efficient than that of

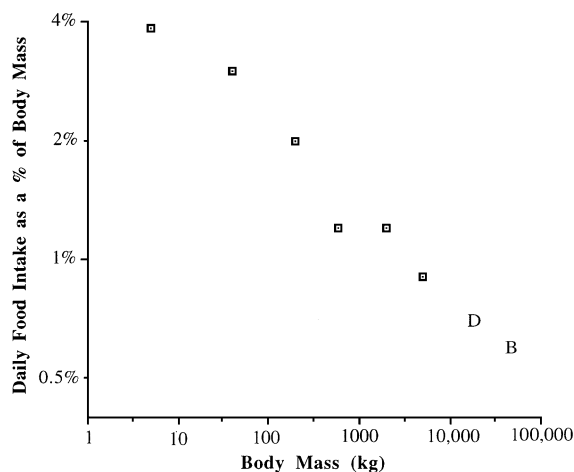


Fig. 1. Plot of daily food intake, represented as a percentage of body mass, against body mass for several mammalian herbivores (after Owen-Smith, 1988). Letters indicate extrapolated position of two sauropods, *Diplodocus* (D) and *Brachiosaurus* (B), based on their body mass as estimated by Alexander (1989).

mammalian megaherbivores in extracting nutrients from its food, reducing food requirements further still. However, even with this uncertainty, whatever the characteristics of the physiology of sauropods they must have a low daily food intake relative to body mass. Thus, the energy demand for maintenance is advantageous for large herbivores.

Owen-Smith (1988) has discussed at some length the consequences of this scaling effect on physiology in modern mammalian megaherbivores. Because gut capacity increases in proportion to body mass while metabolic requirements decrease, large herbivores can tolerate lower dietary quality than can smaller animals. This allows large herbivores to utilize lower quality forage, when higher quality forage is not available. They are therefore able to utilize a broader resource base than smaller herbivores at times of environmental stress such as during drought. Furthermore, because of their lower metabolic requirements, the deterioration of the health of large herbivores that do not eat enough to maintain basic life processes will occur more slowly than for small ones. McGowan (1991, 1994) has pointed out the applicability of this effect to sauropod dinosaurs.

The ability of megaherbivores to exploit a broader resource base including poorer quality forage and the ability to survive longer on a starvation diet can

improve the chances of survival during a time of scarce resources within a given habitat area. As Owen-Smith (1988, p. 86) says, “Hence increased body mass could be an adaptation to compensate for extreme seasonal fluctuations in food availability”. These characteristics can also prove advantageous in an area where food and water resources occur in small, widely separated geographic areas, by allowing the megaherbivores to travel from one resource patch to another across areas that would not provide sufficient resources to maintain them.

Another advantage of large size is the increased energy efficiency of transport. Because the energy cost of transport per unit mass for an animal is the cost of taking a step, as the stride length increases, the cost of travel per distance decreases (Schmidt-Nielsen, 1984). Therefore, large animals can travel with greater energy efficiency than smaller ones (Alexander, 1989, 1995; McGowan, 1991, 1994).

A log–log plot of energy cost of transport, in J per kg m, against mass for a wide variety of animals (Fig. 2) reveals a simple relationship. By using the estimated body masses of *Diplodocus* and *Brachiosaurus*, as before, we can extrapolate the curve to indicate the approximate cost of transport for these sauropod dinosaurs. The low cost of transport beyond the other

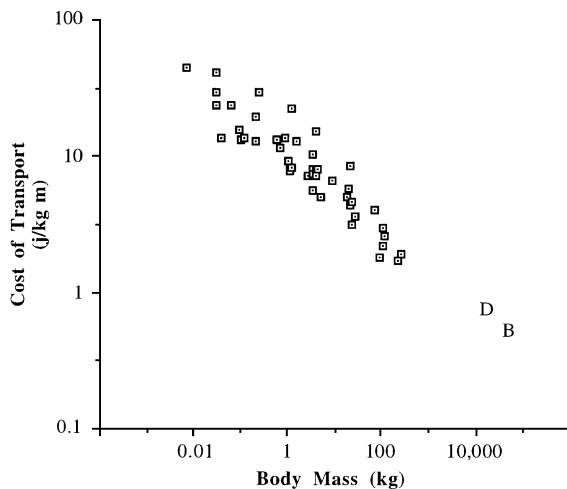


Fig. 2. Cost of transport in J per kg m for vertebrates of varying size, including mammals, birds, and lizards (after Alexander, 1995). Letters indicate extrapolated position of two sauropods, *Diplodocus* (D) and *Brachiosaurus* (B), based on their body mass as estimated by Alexander (1989).

energy needs of the sauropods would make it worthwhile to travel considerable distances in search of resource patches.

The size-related advantages discussed above would only apply to adult or subadult sauropods of a certain size. Until they achieved some critical body size, juvenile sauropods must have faced the same environmental limitations as other small herbivores. As with some modern vertebrate species, the juveniles of a sauropod species may have been ecologically distinct from the adults of that species. The difference between juvenile and adult *Camarasaurus* in micro-wear of the teeth discovered by Fiorillo (1998) lends some support to this idea.

We envision the sauropods as relying on vegetation that may have been seasonally abundant. Based on the analysis of Parrish et al. (this volume) the herbaceous vegetation represented primarily by palynomorphs accounted for much of the floral diversity of the Morrison, and is the most likely resource available to fulfill this need. Krassilov (1981) suggested that the diet of diplodocids consisted of ferns and horsetails while camarasaurids fed on cycads and conifers. Taggart and Cross (1997) seconded this notion, arguing that ferns would have been one of the most abundant plant resources in the Morrison. Although Taggart and Cross (1997) also use the abundance of ferns to argue for a mesic climate, we believe that represents only local and seasonal abundance. Fiorillo (1998) used Weaver’s (1983) estimates of the caloric values of Morrison plants along with the evidence from micro-wear of the teeth to consider possible sauropod diets. Weaver (1983) ranked the caloric content of ferns and horsetails as low, ginkgos intermediate, and cycads highest, with conifers having intermediate to high values. Fiorillo (1998) dismissed the ferns and horsetails from further consideration because of their low caloric value. But the ability of sauropods to utilize poor quality forage by virtue of their large size leads us to reconsider this point and agree that sauropods, especially diplodocids, may have relied heavily on these and possibly other low-growing plants.

In this scenario, at some time of the year, or at longer intervals, the vegetation became progressively more restricted to riparian zones along major through-flowing watercourses. Although these wetland areas may have remained reliable resources throughout the dry season, at least in most years, they may not have

been sufficient to sustain the demands of even a small resident population of adult sauropods. But the ability of the adult sauropods to efficiently travel long distances would have allowed them to follow these linear food resource belts, or even travel from one belt to another across terrain that could not sustain the sauropods. Dodson (1990) suggests a similar model of migratory, wide-ranging sauropods. Rather than being a liability, the large size of sauropods was an adaptive asset in a seasonally dry, semiarid climate.

Modern elephants again provide a useful analogue. African elephants include distinct subspecies that inhabit very different environments. The bush elephant inhabits the savannas, and ranges widely throughout an environment characterized by a pronounced dry season and occasional drought. The forest elephant inhabits the rain forest. Adult forest elephants are distinctly smaller than adult bush elephants, and exhibit a smaller home range. A small population of bush elephants inhabit the Namib Desert of Namibia (Viljoen, 1992). These elephants survive in the harsh, arid environment by having a very large home range (on the order of 2000 km²) in comparison with other elephants. Within this vast range, they travel from one source of food and/or water to another, typically 25 km per day, but at times much greater distances. It is particularly interesting to note that individual elephants from this population are among the largest of African elephants. Even within the species, large size seems to be an asset in a dry climate.

The strategy described above would distribute the resource demands of the sauropods over a large area, enabling them to survive in a relatively unproductive environment, but it would mean that the number of sauropods living within the Morrison ecosystem at one time was not very great. The relative abundance of sauropod fossils in the Morrison Formation seems to belie this conclusion. However, as we have suggested elsewhere (Engelmann and Fiorillo, 2000), the dinosaur fauna of the Morrison is an attritional accumulation, and the high preservability of sauropod skeletons may cause them to be overrepresented in the fauna.

The previous discussion has been concerned with the ability of sauropods to meet food requirements in an environment with limited water availability. It has not considered more direct water requirements. Modern megaherbivores have substantial water needs and must have water to drink. How did sauropods obtain

sufficient water during times of scarcity? Unfortunately, there are too many unknowns concerning the physiology of sauropods to constrain possible answers to this question. For one thing, modern megaherbivores are mammals. Mammalian physiology may be more profligate in its use of water for cooling and waste processing than were the life processes of sauropods. It may be that water content of the vegetation consumed by sauropods was sufficient to meet all or most of their water requirements. This would give them access to a ground water resource that would otherwise be difficult to exploit. Carbon isotope ratios in dinosaur teeth and eggshells from the Morrison (Ekart and Cerling, *this volume*) seem to support this suggestion. Finally, as noted above, the population of elephants that inhabit the Namib Desert, by utilizing a strategy of resource exploitation similar to that suggested here for sauropods, must be able to find water even in an environment that is probably more severe than that experienced in the Morrison ecosystem most of the time.

Another important concern is with one of the chief disadvantages of large size. Modern mammalian megaherbivores have difficulty dissipating excess metabolically generated heat. If the physiology of sauropods were similar to that of elephants, this problem would be magnified many times. This problem would only be aggravated by solar heating in a semiarid climate where there was little shelter from the sun. McGowan (1991, 1994) argues that this effect of very large size makes it very unlikely that sauropods could have been endotherms with mammalian or avian metabolic levels. Having a relatively low metabolic level, whether retained from its primitive archosaurian ancestry or developed as an adaptation within the Sauropoda, could provide a solution to this problem and would also reduce the dietary requirements for sauropods. McGowan (1991, 1994) also mentions the possibility that the long neck and tail of a sauropod may have served as heat dissipation structures. The long cylindrical structure of the legs would also increase the surface area for heat loss (McIntosh et al., 1997).

It may be that, as a group, sauropod dinosaurs were adapted to relatively dry environments. Dodson's (1990) review of sauropod occurrences led him to conclude that they were most successful in humid regions. Yet, a review of Jurassic and Cretaceous

formations that have produced sauropods (Weishampel, 1990) shows that many were deposited in relatively dry environments. For example, Lucas (1981) interpreted the Late Cretaceous dinosaur fauna of the San Juan Basin, which includes *Alamosaurus*, as an upland community in a region with a seasonally dry climate, and sauropods are unknown from contemporaneous, wet, coal-forming environments elsewhere in North America. It is also interesting to note that the presumed sister group to the sauropods, the prosauropods, occur primarily within sediments indicative of arid conditions (Weishampel, 1990; Russell, 1989; Galton, 1990).

5.2. Other dinosaurs

No other Morrison dinosaurs approach the size of the sauropods, although some are moderately large in comparison with modern terrestrial vertebrates. The other herbivorous dinosaurs of the Morrison are not abundant in the fossil record and, as noted above, are only as diverse at the generic level, as the sauropods alone. These smaller, herbivorous species may have been resident populations in those areas where there was a reliable supply of food and water, and the diversity of such populations was limited by the small areal extent of consistent plant productivity.

The carnivorous theropod dinosaurs, however, feeding at a higher trophic level, were less directly constrained by the vegetation. The theropods are relatively diverse and display a wide and continuous range of body sizes. They could have preyed on or scavenged the remains of all of the dinosaurian and nondinosaurian herbivores down to the size of large insects, and may have preyed on smaller theropods as well.

6. Mammals

The mammals of the Morrison Formation (Engelmann and Callison, 1998) are far removed from any living mammals in their history of adaptive modification. They are therefore of little value as environmental indicators. The specific adaptations of the Morrison mammals are not apparent from what is known of their anatomy. It seems likely that at least some, such as the triconodonts and dryolestoids, depended on a diet of small invertebrates and possibly small vertebrates.

Whether some of the Morrison mammals, such as the multituberculates, may have been partly or completely herbivorous, cannot be determined with confidence. Thus, some, and possibly all of the Morrison mammals, as secondary consumers, were not immediately dependent on the vegetation for food.

One characteristic common to the Morrison mammals is their small size. The largest were only the size of a modern ground squirrel, and many were much smaller. Because of their small size, the mammals probably would have been restricted to areas where water was continuously available. However, resource requirements for very small individual organisms are small, and a population of mammals could survive on very limited resources. Small animals also may be able to take advantage of microhabitats that offer more favorable conditions. For example, they may have been primarily nocturnal, sheltering in burrows to avoid the heat of the day. On the other hand, small size also implies short generation times, allowing surviving populations to expand rapidly when resources are relatively abundant.

We would expect the mammals of the Morrison to have been part of a riparian or lake-margin community that flourished during wet seasons when resources were readily available, and expanded to cover a greater geographic area. But this community would have diminished during dry intervals, surviving only as small populations in those areas where water and vegetation persisted.

7. Taphonomic considerations

Apparent contradictions in climatic indicators between the physical features of the stratigraphic record and the characteristics of the fossil record, particularly the plants, have led us to follow Demko and Parrish (1998) and Retallack (1997) in postulating an environment in a semiarid climate with a diverse habitat structure. Within that environment, elements characteristic of wetter conditions are considered spatially and temporally local. We have given a brief overview of the entire ecosystem in terms of this model, and find that the sauropod dinosaurs in particular require special consideration. But is it really necessary to explain the sauropod dinosaurs' adaptation to dry conditions? Might they not be just another element

of an ecosystem that required mesic conditions and was displaced by episodes of aridity through time?

Evidence from the lithofacies in which the fossils of the flora and fauna are preserved argues against this. The plant fossils occur virtually exclusively within gray mudstones that accumulated in wetland environments, but this lithofacies is uncommon in the Morrison (Parrish et al., this volume). Similarly, aquatic invertebrates occur in the gray mudstones and the sandstones of fluvial channels (Engelmann and Fiorillo, 2000). The microvertebrates, including frogs, salamanders, lizards and mammals, occur in mudstones that appear to represent ponds and other environments within fluvial complexes (Engelmann and Callison, 1998; Engelmann and Fiorillo, 2000). The dinosaurs, on the other hand, occur in all lithofacies of the Morrison (Dodson et al., 1980; Engelmann and Fiorillo, 2000). They appear to have ranged throughout the environment. Dinosaurs are also found throughout the stratigraphic range of the Morrison and over most of its geographical extent (Turner and Peterson, 1999; Engelmann, 1999).

The wetland lithofacies are of limited lateral and vertical extent and are embedded within the lithofacies that provide the evidence for a semiarid climate (Demko and Parrish, 1998; Peterson and Turner-Peterson, 1987). The various lithofacies are so thoroughly enmeshed over most of the geographic and stratigraphic range of the Morrison, that it would be difficult to explain the distributions of fossils and sedimentologic features as a large-scale alternation in time between semiarid and mesic conditions.

8. Conclusions

The fossil flora and fauna of the Morrison Formation offer little help in constraining the general climatic conditions of the paleoenvironment. Although sedimentologic evidence of diverse types seems to consistently indicate strongly seasonal, semiarid conditions during the time of deposition of the Morrison, the plants and some invertebrates and small vertebrates seem to indicate wet conditions. These conflicting interpretations can be resolved if one assumes an overall semiarid environment throughout the extent of the Morrison, with geographically limited areas, such as riparian zones along major through-

flowing streams or shallow lakes or wetlands supplied by ground water, where water was consistently available. In this context, the plants, aquatic invertebrates, and small vertebrates can be useful indicators of the time and place of such locally wet conditions. Given these assumptions we provide the following scenario to summarize our interpretations of the possible characteristics of the Morrison ecosystem.

Consistent plant productivity along through-flowing rivers and around lakes and wetlands fed by these and by groundwater supported a riparian fauna. The vegetation consisted of an open gallery forest of coniferous trees along the larger, more persistent rivers and few long-lived lakes. An understory of smaller conifers, ginkgos and cycads may have extended beyond the larger trees varying distances depending on how consistent rainfall was over any given period of years. A carpet of ferns and other herbaceous vegetation may have extended further still depending on the current and recent history of rainfall. Aquatic forms, including mollusks, crayfish, ray-finned fish, lungfish, frogs, salamanders, turtles, and crocodylians inhabited the rivers, streams and adjacent bodies of water. Small terrestrial vertebrates such as lizards, terrestrially adapted crocodylians, small dinosaurs (including the juveniles of larger species) and mammals ranged throughout this well-vegetated habitat, the extent of their range varying with size and water requirements. Diverse insect life may have constituted the principal small herbivores in the environment and probably the primary food resource for the small vertebrates.

Sauropod dinosaur species partitioned the food resources by varied feeding strategies, possibly including vertical stratification of browsing levels. High-browsing brachiosaurs were probably relatively rare, while camarasaur browsing on coarse vegetation at intermediate height were more common. Diplodocids browsed on the low-growing herbaceous plants. Predatory dinosaurs of varying size occupied the same range as their prey species. The very large predatory dinosaurs may have specialized as scavengers on the large carcasses of sauropods.

This habitat might expand during a wet season or be reduced to small, widely separated refugia during periods of severe drought. Relatively small populations of adult sauropods utilized very large geographic ranges, traveling long distances between resource areas, especially during times of drought. Other,

smaller, herbivorous dinosaurs, including juvenile sauropods, may have been more specialized feeders and ranged less widely than the adult sauropods.

In his study of the paleoecology of the Morrison, Foster (1998) analyzed the various ecological guilds represented in the Morrison with respect to taxonomic diversity and adult body mass. He found that for herbivores, the greatest diversity occurs at very large and very small body size, with much lower diversity in intermediate sizes. He offered two possible explanations for this pattern: that the intermediate body size classes may have been filled by the juveniles of the very large species (sauropods), or that the intermediate size herbivores may have been more vulnerable to predation by moderate to large predators.

This size distribution of species might also be explained as a result of two successful strategies for survival in an environment such as that postulated for the Morrison. At times of limited availability of water, the large sauropods could survive by traveling from one resource patch to another. Smaller species were confined to those small areas with persistent water resources, but smaller body size enabled them to maintain larger populations and greater diversity, and rapidly expand their populations when resources were more abundant. Times of severe drought would be especially harsh on herbivores of intermediate body size. Sauropods would have to grow through such an intermediate size, and would be especially vulnerable to severe drought at that point in their development.

The extinct ecosystem of the Morrison does appear to be unique, with no completely satisfactory modern analogue. One of its most peculiar features is the diverse fauna of sauropod dinosaurs. They undoubtedly had a central role in the ecosystem, and their presence and activities probably affected it in ways we have not considered or even imagined. However, we believe the scenario we have suggested resolves the information we have about the Morrison from diverse sources.

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