Late Jurassic Climates, Vegetation, and Dinosaur Distributions

P. McAllister Rees, Christopher R. Noto,[1] J. Michael Parrish,[2] and Judith T. Parrish[3]

Department of Geosciences, University of Arizona, Tucson, Arizona 85721, U.S.A.
(e-mail: rees@geo.arizona.edu)

ABSTRACT

The Jurassic and Cretaceous are considered to have been warmer than today on the basis of various climate data and model studies. Here, we use the available global record of climate-sensitive sediments, plants, and dinosaurs to infer broadscale geographic patterns for the Late Jurassic. These provide a context for our more detailed accounts of the Morrison and Tendaguru Formations in North America and East Africa. At the global scale, evaporites predominated in low latitudes and coals in mid- to high latitudes. We ascribe these variations to a transition from drier to wetter conditions between the equator and poles. Plant diversity was lowest in equatorial regions, increasing to a maximum in midlatitudes and then decreasing toward the poles. Most dinosaur remains are known from low-latitude to marginally midlatitude regions where plant fossils are generally sparse and evaporites common. Conversely, few dinosaur remains are known from mid- to high latitudes, which have higher floral diversities and abundant coals. Hence, there is an obvious geographic mismatch between known dinosaur distributions and their primary food source. This may be due to taphonomic bias, indicating that most dinosaur discoveries provide only a small window on the diversity and lifestyles of this group. On the basis of our global- and local-scale studies, we suggest that dinosaur preservation was favored in environments toward the drier end of the climate spectrum, where savannas rather than forests predominated. A holistic approach, incorporating climate and vegetation as well as geography, is required to better understand patterns of dinosaur ecology and evolution.

Introduction

Not surprisingly, dinosaurs arouse intense scientific and public curiosity. Spectacular skeletons, supreme dominance of the terrestrial realm for ~150 m.yr., and scary movies all ensure their role as the subject of serious study as well as popular titillation. However, relatively little is known of dinosaurs in the broader context of climate, geography, and their primary food source, vegetation. Here, we describe distribution patterns of Late Jurassic dinosaurs in that context. Late Jurassic climates have been interpreted from data and model studies (e.g., Vakhrameev 1991; Hallam 1994; Rees et al. 2000; Sellwood et al. 2000) and vegetation patterns outlined (Vakhrameev 1991; Rees et al. 2000). In essence, low-latitude regions were either desert or seasonally summer wet or winter wet, midlatitudes were mostly warm temperate, and high latitudes were cool temperate. Climate was more equable than today, in the sense that there were no polar icecaps and the equator to pole temperature gradient was lower, but vegetation was still far from uniform. There is no evidence of tropical rainforest in the Jurassic; indeed, limited precipitation was the main restriction on plant growth in low latitudes. Although the poles were warmer than today, continuous plant growth there would nevertheless have been constrained by the onset of winter darkness.

The climate data and model results match well in low and midlatitudes although unresolved discrepancies remain in the high latitudes, where the models produce temperatures colder than those estimated by the plant data (e.g., model cold temperate vs. data cool temperate; Rees et al. 2000). This problem has been encountered in all other "hothouse" climate models, which consistently predict cold conditions in high-latitude regions beyond the tolerance limits indicated by the plants

---

Manuscript received February 24, 2004; accepted June 9, 2004.

[1] Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794, U.S.A.

[2] Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois 60115, U.S.A.

[3] College of Science, University of Idaho, Moscow, Idaho 83844, U.S.A.

[The Journal of Geology, 2004, volume 112, p. 643–653] 0022-1376/2004/11206-0003$15.00

(e.g., the Permian; Rees et al. 2002), even for time intervals such as the Late Cretaceous, where quantitative climate estimates have been derived from angiosperm leaf physiognomy (e.g., Spicer et al. 1996; Herman and Spicer 1997).

For the purposes of this article, we focus on the low- and midlatitude regions, simply because it is there that Late Jurassic dinosaur remains are best known. The preceding discussion does, however, raise the question of whether the poleward latitudinal limits of these dinosaur remains is due to climate tolerances of the living animals or taphonomic biases. We address this later, but first we concentrate on the Late Jurassic record of plants, climate-sensitive sediments, and dinosaurs. The global-scale aspects of this study expand on earlier work with A. M. Ziegler on "Correspondence of paleolatitudinal diversity in herbivorous dinosaurs and plants during the Jurassic" (Parrish et al. 1996).

Late Jurassic Global Distribution Patterns

The known paleogeographic distributions of Late Jurassic plants, climate-sensitive sediments, and dinosaurs are described and illustrated here. These are then considered in the context of latitudinal gradients in taxonomic diversity, a well-studied phenomenon in modern biota (Rosenzweig 1992, 1995; Gaston 2000). Present diversity is highest around the equator within tropical regions and decreases toward the poles. There have also been many published accounts of latitudinal gradients in the fossil record (Crane and Lidgard 1989; Kiessling 2002), lending credence to the idea that latitudinal gradients in diversity have been consistent features throughout Earth's history.

Plants and Climate-Sensitive Sediments. The floral and climate-sensitive sediment data used in this study were compiled by A. M. Ziegler and the Paleogeographic Atlas Project. Applying these data, Rees et al. (2000) interpreted Jurassic vegetation patterns. Plant diversity was lowest at the equator and poles but reached a maximum in each hemisphere at the midlatitudes. This is in marked contrast to today, where maximum plant diversity occurs in the equatorial regions. However, measures of diversity provide only a partial insight; it is also important to know the dominant vegetation of each region. For example, boreal conifer forests today have relatively low diversity but high productivity. In the Jurassic, maximum plant diversity (and, apparently, productivity) was concentrated at midlatitudes, where forests were dominated by a mixture of conifers, cycadophytes, pteridosperms, ferns, and sphenophytes. Low-latitude vegetation tended to be xeromorphic (i.e., dry-adapted) and only patchily forested, typified by the presence of small-leafed (microphyllous) forms of conifers and cycadophytes. Polar vegetation was dominated by large-leafed (macrophyllous) conifers and ginkgophytes that were apparently deciduous. Tropical everwet vegetation was, if present at all, highly restricted. Hence, studies of diversity address only part of the question; it is also important to understand the nature of the contributing organisms.

Late Jurassic plant localities, scaled according to the number of genera in each, are shown on a paleogeographic map in figure 1*A*. Analysis was restricted to relatively bona fide Late Jurassic floras, so, for example, localities in Argentina, East Antarctica, and eastern Australia were excluded (cf. Rees et al. 2000). There is a paucity of localities between 30°N and 30°S and a high number of genera from localities in present-day India, China, eastern Russia, and Europe. These patterns are instructive in that they show not only the incomplete nature of the geographic record but also some latitudinal control on plant distributions and diversity. However, the plant types preserved in these localities are more significant than the raw numbers of genera in each. Microphyllous forms of conifers and cycadophytes, as well as pteridosperms, tend to be most abundant at low to midlatitudes, along with sphenophytes and ferns. Progressing poleward, ferns, macrophyllous cycadophytes, and sphenophytes become more abundant in mid- to high latitudes, with ginkgophytes and macrophyllous conifers most abundant in the high latitudes. Significantly, low-latitude plant localities have not only relatively low plant diversity but also relatively high proportions of microphyllous taxa. Mid- to high-latitude ones have relatively high diversity as well as more macrophyllous taxa.

Climate-sensitive sediments such as coals and evaporites provide useful indicators of the precipitation/evaporation ratio, indicating relatively wet or dry climate regimes, respectively. Their Late Jurassic distributions are shown in figure 1*B*, from which it is clear that most evaporites occur at low latitudes between ca. 40°N and 40°S of the equator, whereas most coals occur poleward of these limits. This coincides with the floral patterns; low-diversity microphyllous-dominated floras occur in low latitudes, and higher-diversity macrophyllous-dominated ones occur in the mid- to high latitudes. The coal and evaporite patterns shown here are not unique to the Late Jurassic (although, of course, peats occur today in low as well as mid- to high latitudes). Indeed, on the basis of these and other lithologic indicators of climate, Ziegler et al. (2003)

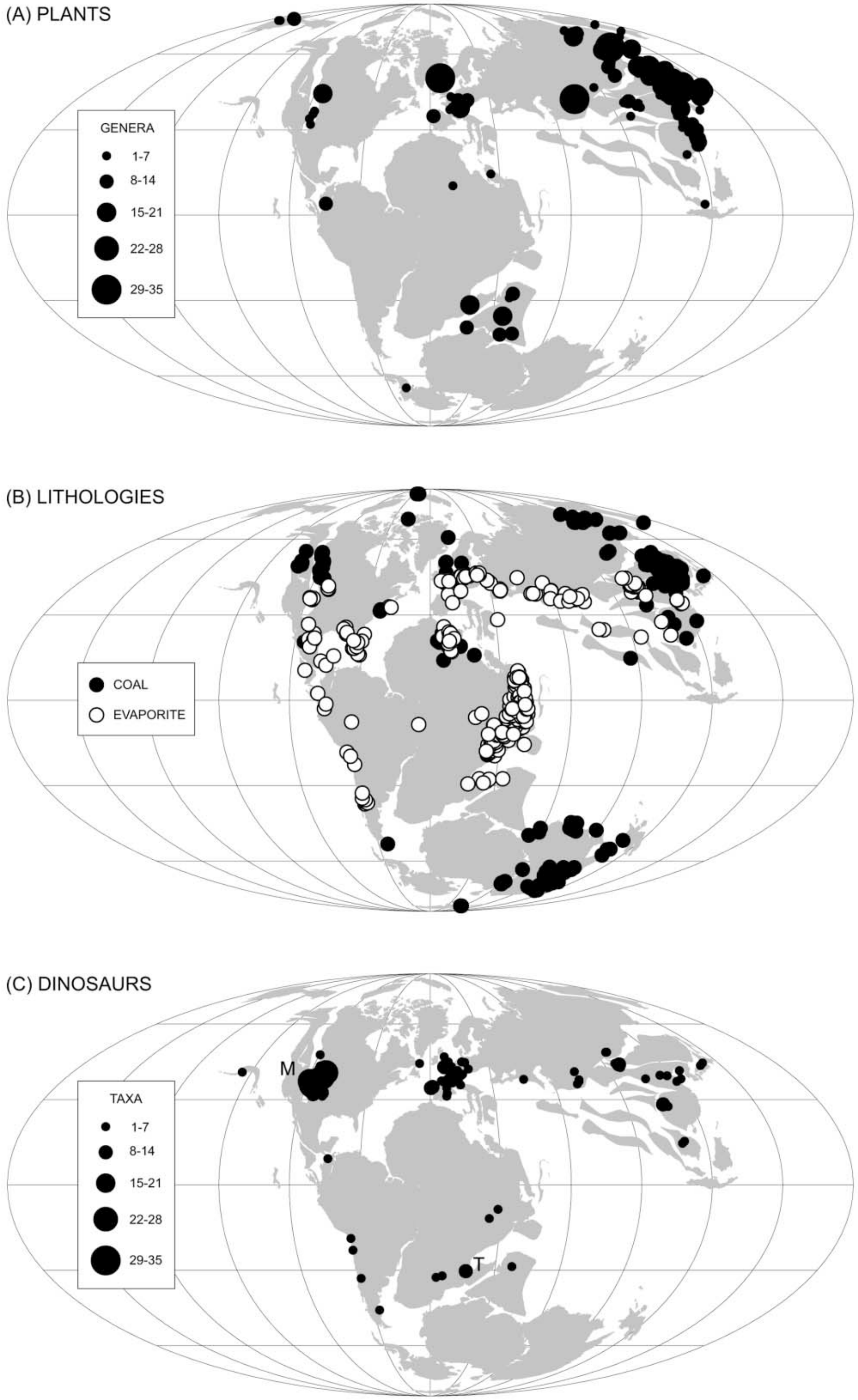

Figure 1. Late Jurassic (150 Ma) paleogeographic maps (Mollweide projection with 30° latitude and longitude lines). *A*, Plant localities, scaled according to the number of constituent genera. *B*, Evaporite and coal deposits. *C*, Dinosaur localities, scaled according to the number of constituent taxa and showing the location of the Morrison (*M*) and Tendaguru (*T*) Formations.

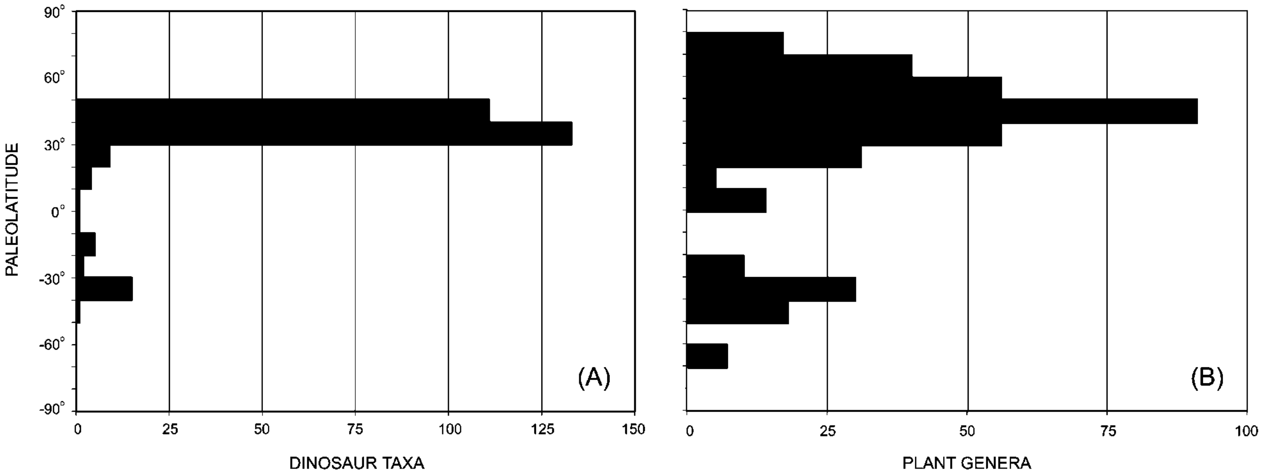

Figure 2. Distributions of dinosaur taxa (*A*) and plant genera (*B*) in 10° paleolatitudinal bins

have documented the latitudinal constancy of climate zones from the Permian to present, relating it to Hadley cell circulation.

Dinosaurs. The topic of dinosaur distribution and diversity has been discussed by paleontologists almost since their initial discovery (see Dodson 1997; Forster 1999 for reviews). Most studies have focused on biogeography, relating continental configurations and tectonic histories to patterns of dinosaur distribution and evolution (e.g., Kalandadze and Rautian 1991; Russell 1993; Dodson 1997; Forster 1999; Sereno 1999*a*, 1999*b*). Attention has also been focused on dinosaurs in the context of ecology as well as biogeography, and the ways in which environmental differences may have determined their distributions (e.g., Lehman 1987, 2000; Parrish et al. 1996; Foster et al. 2001; Noto et al. 2002).

Using the methods for reconstructing paleoclimate and plant distributions mentioned previously, it is now possible to associate dinosaurs with these general climatic regimes, or biomes (see Rees et al. 2000 for details). By assessing dinosaur distributions and diversity in the context of climate and geography, we can gain insights into their paleoecology and the evolutionary pressures exerted by changes in ecological and climatic conditions. Late Jurassic dinosaur data used in this study are from the upcoming second edition of *The Dinosauria* (Weishampel et al. 2004). Remains consist of bones, teeth, tracks, eggs, or coprolites. The last two were excluded from analysis because of the difficulty in assigning these remains to any particular taxon, as well as the possibility that these remains may not belong to dinosaurs at all. Taxonomic diversity was calculated by counting body fossils (bones and teeth) and/or trace fossils (tracks) of taxa within each dinosaur-bearing formation. Fossils unidentifiable to the genus level (e.g., some indeterminate higher taxa or tracks) were counted in a formation only when a representative of that group was not already present. For example, if the genus *Allosaurus* was present, then neither "indeterminate theropod" nor "theropod tracks" was counted for that formation.

Figure 1*C* shows the geographic distribution of Late Jurassic dinosaur remains. From a perusal of figure 1, it is evident that dinosaur fossils are restricted to between ca. 45°N and 45°S of the paleoequator and that this distribution broadly coincides with that of evaporites. High-diversity floral localities do occur at the poleward extremes of dinosaur distributions but, as mentioned earlier, most of the floras where dinosaurs occur have relatively low diversity and comprise higher proportions of microphyllous taxa.

Latitudinal Patterns and Preservational Biases. Floras and dinosaur-bearing formations were assigned to 10° paleolatitudinal bins and the taxa then summed for each bin. An individual taxon was counted only once per bin, regardless of its number of occurrences. Results are shown in figure 2. In the Northern Hemisphere, dinosaur diversity is highest between 30° and 40°N, but plant diversity peaks slightly poleward, between 40° and 50°N. Plant and dinosaur diversity in the Southern Hemisphere peaks at 30°–40°S, although in both cases diversity is lower than in the Northern Hemisphere. This is probably due to factors that include less intensive sampling and smaller land surface area in the Southern Hemisphere (fig. 1). Diversity is otherwise broadly symmetrical about the equator (fig. 2), reaching a maximum in the midlatitudes and a minimum in the low and high latitudes, although the highest levels of dinosaur diversity are restricted latitudinally (30°–50°N), whereas highest plant diversity spans a broader latitudinal range (30°–70°N). The poleward limit of dinosaur fossils is only 40°–50°N and S, whereas plant fossils extend to 70°–80°N and 60°–70°S.

Although figure 2 shows latitudinal distribution patterns, it reveals nothing about longitudinal variations. Dinosaur localities with the highest numbers of taxa are concentrated in Europe and North America (fig. 1*C*). In contrast, genus-rich plant localities are concentrated in China, eastern Russia, India, and Europe, with relatively few in North America (fig. 1*A*). In the case of Europe, dinosaur and plant localities appear to be concentrated together (fig. 1), at least in the southern part. However, compared with more northerly plant localities, the southern European ones have more abundant microphyllous, dry-adapted forms of conifers and cycadophytes.

The absence or paucity of dinosaur fossils at higher latitudes is in marked contrast to the abundance of fossil floras and coals. At lower latitudes, the regional co-occurrence of dinosaurs with evaporites and floras containing abundant microphyllous taxa is also noteworthy. These may represent real biological patterns, but first we consider the effects of taphonomic bias. Several traits of the depositional environment will affect its ability to preserve vertebrate material including temperature, precipitation, vegetation, and underlying geology, which determine the chemical and physical properties of a soil.

Arid and semiarid climates result in longer residence times on the surface for vertebrate remains, tending to increase time averaging and concentration of remains, whereas hard parts (e.g., bone) degrade more quickly in humid climates as a result of biotic as well as abiotic processes (Behrensmeyer et al. 2000). Increasing temperature can cause an increase in biotic and chemical activity that may be destructive to the remains (Hare 1980; Yavitt and Fahey 1986). Both pH and Eh (oxidation-reduction) have been shown to be the most important factors determining vertebrate preservation in a variety of depositional environments (Hare 1980; Gordon and Buikstra 1981; Retallack 1998). Precipitation affects bone preservation through its ability to mobilize ions in the soil, leading to the leaching of surface materials, especially organic acids (Yavitt and Fahey 1986). This leaching is what leads to the overall lower pH of forest soils and the eventual dissolution and destruction of bone. Soils in more humid climates also have a greater amount of organic material than in arid and semiarid areas. Floodplain soils are drier, more mineral rich, and have a lower organic content. Consequently, their pH is higher than that of areas with more precipitation (Pritchett 1979). Vegetation plays an important role chemically, through the exchange of materials (water, minerals, and nutrients) that affect soil chemistry, and physically, by the action of roots (Henderson 1987; Berner et al. 2003). Plant roots can adversely affect bone preservation through soil leaching of mineral components as well as physical degradation. Plants also play a role in determining the nature of soils in which an animal is buried, and plants with more complex root systems have been shown to dramatically increase rock weathering rates (Cochran and Berner 1996; Berner et al. 2003).

The interplay between these factors will ultimately be responsible for the destruction or preservation of an animal's remains. This may explain why Late Jurassic dinosaur bones are scarce to nonexistent in higher latitudes, where the prevailing climates were generally warm and wet, albeit seasonal, with broad tracts of gymnosperm forests dominating the landscape.

Case Studies of Late Jurassic Dinosaur-Dominated Ecosystems

A detailed global analysis of the paleoecology of Jurassic dinosaur-bearing deposits is beyond the scope of this study. However, an examination of floral and faunal patterns in two deposits yielding abundant dinosaur remains, the Morrison Formation of North America and the Tendaguru beds of Tanzania (fig. 1*C*), can offer some insights into the kinds of conditions that favored diverse, sauropod-rich faunas in the Late Jurassic. The dinosaurs, plants, and paleoenvironments in both formations have been studied intensively.

Similarities between the faunas of the Morrison Formation and the dinosaur-bearing sediments of the Tendaguru beds of Tanzania have long been noted (Schuchert 1918; Russell et al. 1980; Maier 2003). The deposits both appear to span the Kimmeridgian-Tithonian interval, and their fossil records comprise plants, invertebrates, and a dinosaur-dominated vertebrate assemblage. Some of the greatest similarities are apparent in the dinosaur faunas, each of which is dominated, both in diversity and abundance of individuals, by sauropods and also includes stegosaurs and small ornithopods.

The floras of the Morrison Formation have been studied by numerous workers (see Ash and Tidwell 1998; Litwin et al. 1998; Parrish et al. 2004 for recent reviews). Those of the Tendaguru have been studied by Kahlert et al. (1999), Schrank (1999), and Grube et al. (2001).

Floras. Plant material is particularly sparse in the Kimmeridgian part of the Morrison Formation (Parrish et al. 2004). Microphyllous conifers (e.g., *Brachyphyllum*) are represented by five species, followed by ginkgophytes (e.g., *Czekanowskia*), cycadophytes, and sphenophytes, along with rare ferns and bryophytes.

Parrish et al. (2004) considered the following as possible explanations for the paucity of plant material in most environments: (1) complete mechanical degradation, (2) complete oxidation, and/or (3) a depauperate source. Mechanical degradation by physical and biological processes was clearly important in environments with strong currents or abundant bioturbators, such as channels and lakes, respectively. Oxidation was also likely an important mechanism, given the large volume of fine-grained rocks that have no carbonaceous debris. Most rocks from this interval are light greenish gray, light to medium gray, red, tan, or purple; dark gray rocks are rare. However, even those more reducing lithofacies contain very little plant material, suggesting that, even when conditions were favorable for preservation, few plants were preserved. This indicates that the vegetation was not particularly dense or large-statured in most places. That the plants were mostly small in stature is supported by the fact that evidence for deep rooting or large roots is rare in the Morrison Formation (Hasiotis and Demko 1998). The leaf mats of *Czekanowskia* are the one exception to the general scarcity of plant occurrences in the Kimmeridgian. They are monospecific and limited to narrow intervals, suggesting that the ecology of this plant was different from the others (Parrish et al. 2004).

In contrast to those of the Kimmeridgian, the Tithonian-age rocks tend to be gray and brown, and the red, green, and light brown colors that characterize the Morrison elsewhere are lacking. Plant megafossils are more abundant than in the Kimmeridgian (Parrish et al. 2004) and comprise several species of ferns and cycadophytes, along with macrophyllous conifers, ginkgophytes, sphenophytes, pteridosperms, and bryophytes. This part of the formation also contains thin, high-ash, high-sulfur coal beds (Calvert 1909; Fisher 1909) that were mined mostly between 1885 and 1955 (Silverman and Harris 1967). The sedimentologic evidence indicates that the Morrison in central Montana was deposited in mires and associated rivers, floodplains, and lakes.

Unlike other thin coal-bearing units (e.g., the Cretaceous Kogosukruk tongue of the Prince Creek Formation, Alaska; Spicer and Parrish 1987; Parrish and Spicer 1988), the Tithonian part of the Morrison Formation is depauperate of fossil wood. The coal beds themselves contain little vitrinite, indicating that the mire community was also depauperate in woody plants (Parrish et al. 2004). However, the density of identifiable leaf remains on bedding planes is higher in the Tithonian than in the Kimmeridgian of the Morrison, although the rootlets and rhizomes in these younger floras are the same small size as in the rocks elsewhere in the Morrison. This is consistent with the paucity of wood and the low vitrinite content of the coals.

Whereas the Morrison Formation has been variously described as humid or arid, recent work suggests that the climate was predominantly semiarid, with slight variations in moisture availability owing to climate and/or higher water tables (Demko 1998; Parrish et al. 2004). For example, Demko (1998) described fluvial and floodplain deposits that contain calcareous, vertic paleosols, as well as eolian sandstone, bedded gypsum, and lacustrine deposits that formed in a large saline-alkaline lake (Turner and Fishman 1991).

The Tendaguru macroflora is best represented in the Middle Saurian bed, which also includes the most abundant dinosaur fossils. Cuticle analysis indicates four families of gymnosperms: Taxaceae, Cupressaceae, Cycadaceae, and Ginkgoaceae (Grube et al. 2001). The upper Saurian beds also preserve a diverse cuticle flora, including Podocarpaceae and Cheirolepidiaceae. Palynological analysis of the entire section at Tendaguru indicates a dominance of the Cheirolepidiaceae taxon *Classopollis*, with the Araucariaceae taxon *Araucariacites* also common. These are conifer pollen, and it is noteworthy that the corresponding leaf fossils (e.g., *Frenelopsis*, *Brachyphyllum*; Vakhrameev 1991) are typically microphyllous. The Middle Saurian beds also yield spores of ferns and bryophytes.

Sedimentology and Paleoenvironments. Parrish et al. (2004) documented sedimentological characteristics of the Morrison Formation that are relevant to a climate interpretation. These include: (1) eolian sandstone of the Bluff Sandstone and Recapture Members in the southern part of the Morrison Formation and equivalent beds as far north as north-central Wyoming and western South Dakota (Peterson 1988); (2) thick beds of gypsum of the terrestrial and marginal-marine Tidwell Member; (3) aridisols and gypsic entisols of the Tidwell and

Salt Wash Members, calcisols and argillic calcisols of the Salt Wash Member, vertic and argillic calcisols of the Brushy Basin Member, weakly developed entisols and calcisols in the upper Brushy Basin Member and equivalent rocks to the north, all of which were in the Kimmeridgian part of the Morrison, and gleysols and histosols in the Tithonian parts of the Morrison (Demko 1998); and (4) saline-alkaline lake deposits, with characteristic zonation of authigenic minerals, including zeolites of the Brushy Basin Member (Lake Too'dich'i'; Turner and Fishman 1991). As with the plants, the differences between the Kimmeridgian and Tithonian characteristics of the Morrison are noticeable but not large, and the differences are consistent with a slightly greater supply of moisture, through higher groundwater levels, lower evaporation rates, and/or higher precipitation rates during deposition of the upper part of the Brushy Basin Member and correlative rocks elsewhere.

The succession of dinosaur-bearing beds in Tendaguru is similarly dominated by calcareous sandstones and siltstones, but their estuarine, coastal, and shallow marine origin is demonstrated by the abundance of marine invertebrate taxa including dinoflagellates, corals, ammonites, and gastropods (Aberhan et al. 2002). The vertical succession at the dinosaur-bearing site captures a succession of transgressions dominated by marine taxa and regressions that mix articulated and disarticulated dinosaurs with the marine fauna. Calcrete horizons in the dinosaur-bearing intervals indicate alternating wet-dry conditions similar to those observed for the Morrison.

Dinosaur Distributions and Feeding. A quantitative comparison of the abundance of various taxa in the two deposits is instructive. In the Tendaguru, the most abundant sauropod taxon is *Brachiosaurus* (Russell et al. 1980; minimum number of individuals [MNI] = 26), compared with an MNI of 11 observed for the second-most abundant taxon, the smaller, low-browsing diplodocid *Dicraeosaurus*. In contrast, the Morrison fauna is dominated by diplodocids (principally *Diplodocus* and *Apatosaurus*) and the sauropod *Camarasaurus*, with *Brachiosaurus* a consistently rare element of the fauna (Foster 2003).

The Morrison dinosaur fauna is dominated by taxa that appear to be low to medium browsers, based on computer modeling of feeding heights (e.g., Stevens and Parrish 1999 and in press). The presence of a marked ventral inclination of the skull relative to the vertebral column in diplodocids is consistent with their occupation of a low browsing guild (Parrish 2003). This interpretation of sauropod feeding correlates with the abundance of aquatic, herbaceous, and ground-covering plants in the Morrison.

By contrast, the Tendaguru sequence, particularly the best-represented fauna of the Middle Saurian beds, is dominated quantitatively by the giant sauropod *Brachiosaurus* (Russell et al. 1980). Although the morphology of the neck of *Brachiosaurus* is not completely known, and differences exist in interpretation of the neck inclination of this animal (e.g., Paul 1988; Christian and Heinrich 1999; Stevens and Parrish, in press), different researchers agree that this animal was probably the highest-browsing member of the Late Jurassic sauropod faunas. This is consistent with the abundance in the Tendaguru of Cheirolepidiaceae and Araucariaceae as both pollen and cuticle. The presence of low-browsing taxa such as the diplodocid sauropod *Dicraeosaurus* and the stegosaur *Kentrosaurus* in the Tendaguru beds suggests that, as in the Morrison, these animals may have been feeding on low- to medium-height plants such as bryophytes, ferns, and sphenophytes (e.g., *Equisetum*).

In summary, the Morrison and the Tendaguru dinosaur-rich deposits occur at similar paleolatitudes but in different hemispheres. They appear to represent semiarid paleoenvironments with the greatest abundance and diversity of herbaceous and arborescent plants concentrated near bodies of water. Significant family and genus-level differences in the dinosaurs present in the two deposits may relate to differences in the structure of their plant communities.

Conclusions

The exact nature and spatial distribution of vegetation and environments present in the Morrison and Tendaguru ecosystems is difficult to interpret conclusively; however, it can be seen that an immense biomass and diversity of dinosaurs was apparently supported by sparse vegetation. Modern tropical savannas, which are composed of grasses and scattered shrubs and trees, with a higher density of shrubs and trees along the water courses, are the obvious choice for comparison with these extinct ecosystems. Although the plant groups in these ecosystems are different (e.g., Jurassic sphenophytes and ferns vs. modern grasses), they share many characteristics, such as broad, open areas of low-standing vegetation surrounding concentrations of arborescent plants near bodies of water. This spatial arrangement may determine the diversity and biomass of herbivores in an ecosystem more than the potential productivity of the vegetation (Taggart and Cross 1997).

Modern tropical savannas are broad summer wet zones transitional between deserts and humid forests, where the growing season is controlled by alternating wet and dry periods (Bourlière and Hadley 1983). The Late Jurassic Morrison and Tendaguru formations occupied a winter wet biome, between desert and warm temperate biomes (see Rees et al. 2000 for maps and biome descriptions). We emphasize that these Late Jurassic "savannas" occurred in midlatitudes and were bounded equatorward by desert belts; they do not, therefore, indicate poleward expansion of the tropical savanna biome. However, conditions were seasonally wet and temperatures relatively high, so a comparison with modern summer wet savannas is valid. Compared with forested ecosystems, tropical savannas can have a higher net productivity during the wet season if soil fertility is not limiting. Much of this biomass is readily available because it is more palatable and easily acquired as leaves or seasonally regenerating shoots, in contrast to the large amounts of relatively unattainable wood that makes up the majority of biomass in forests (Bourlière and Hadley 1983). Seasonal productivity leads to herbivores (e.g., African elephants) that are nomadic or long-range migrants.

The tropical savanna model fits well with reconstructions of the Morrison environments (Dodson et al. 1980; Engelmann and Fiorillo 2000). Some of the confusion surrounding descriptions of the Morrison climate may be due to the time-averaging and/or differential preservation of sediments from wet and dry seasons. Recent work by Dunagan (2000) shows that Morrison paleoclimate was at least semiarid and perhaps at times even intermediate between semiarid and subhumid. Late Jurassic savannas may have covered a considerable area, allowing herds of sauropods and other large dinosaur herbivores to roam vast distances in search of food, through drier areas to more riparian settings. Aggregation of various species around water sources is not uncommon today and may partially explain the abundance of fossils in the Morrison that have been recovered from lacustrine, fluvial, and adjacent floodplain deposits (Engelmann and Fiorillo 2000).

Modern tropical savannas are important centers of ecological diversity. A relatively simple trophic structure allows small perturbations to lead to changes in the dominant species. Species turnover due to difficult conditions favors rapid evolution, possibly acting as a "species pump," distributing new species to surrounding habitats. Over geologic time, xeric habitats such as savannas may have supported more species than mesic ones (Bourlière and Hadley 1983). In this regard, pregrassland savannas may have been a significant vegetation type during the Mesozoic.

Vegetation and climate reconstructions indicate that the Late Jurassic lacked a tropical everwet biome, which is associated in today's world with high biodiversity. Instead, Late Jurassic midlatitude and high-latitude regions supported high-diversity forest communities growing in temperate climates. However, the dinosaur remains are known mostly from areas that occupied only seasonally wet biomes at lower latitudes, where vegetation was relatively sparse and of lower diversity. Dinosaurs did exist at higher latitudes at other times during the Mesozoic. They were most likely smaller than those of the "savannas" because of size restrictions placed on forest-dwelling animals and may have had lower taxonomic diversity due to the relative inaccessibility of a large portion of the forest biomass. In contrast, relatively dry environments as in savannas tend to favor large herbivores (Engelmann et al. 2004). Coupled with taphonomic conditions that would have inhibited vertebrate preservation, the high-latitude record of Late Jurassic dinosaurs remains sparse.

ACKNOWLEDGMENTS

We are indebted to F. Ziegler for his advice, encouragement, and friendship over the years and for his ideas during the early stages of this work. We thank C. Scotese for the use of his plate reconstruction software and D. Rowley for discussions and help with other global-scale aspects of this study. We also thank two anonymous reviewers for their insightful comments.

REFERENCES CITED

Aberhan, M.; Bussert, R; Heinrich, W.-D.; Schrank, E.; Schultka, S.; Sames, B.; Kriwet, J.; and Kapilima, S. 2002. Paleoecology and depositional environments of the Tendaguru beds (Late Jurassic to Early Cretaceous, Tanzania). Mitt. Mus. Natkd. Berl. Reihe 5:19–44.

Ash, S. R., and Tidwell, W. D. 1998. Plant megafossils from the Brushy Basin Member of the Morrison Formation near Montezuma Creek Trading Post, southeastern Utah. Mod. Geol. 22:321–339.

Behrensmeyer, A. K.; Kidwell, S. M.; and Gastaldo, R. A.

2000. Taphonomy and paleobiology. *In* Erwin, D. H., and Wing, S. L., eds. Deep time: paleobiology's perspective. Paleobiology 26(suppl.):103–147.

Berner, E. K.; Berner, R. A.; and Moulton, K. L. 2003. Plants and mineral weathering: present and past. *In* Drever, J. I., ed. Treatise on geochemistry. Vol. 5. New York, Elsevier, p. 169–188.

Bourlière, F., and Hadley, M. 1983. Present-day savannas: an overview. *In* Bourlière, F., ed. Ecosystems of the world. Vol. 13. Tropical savannas. New York, Elsevier, p. 1–18.

Calvert, W. R. 1909. Geology of the Lewistown Coal Field, Montana. U.S. Geol. Surv. Bull. 39.

Christian, A., and Heinrich, W.-D. 1999. The neck posture of *Brachiosaurus brancai*. Mitt. Mus. Natkd. Berl. Reihe 1:73–80.

Cochran, M. F., and Berner, R. A. 1996. Promotion of chemical weathering by higher plants: field observations on Hawaiian basalts. Chem. Geol. 132:71–77.

Crane, P. R., and Lidgard, S. 1989. Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. Science 246:675–678.

Demko, T. M. 1998. Paleosols in the upper Jurassic Morrison Formation: implications for paleoclimate, paleohydrology, and sequence stratigraphy. *In* Turner, C. E., and Peterson, F., eds. The Morrison Formation extinct ecosystems project, final report. Report to the National Park Service, interagency agreement 1443-IA-1200-94-003, p. 33–54.

Dodson, P. 1997. Distribution and diversity. *In* Currie P. J., and Padian, K., eds. Encyclopedia of dinosaurs. San Diego, Calif., Academic Press, p. 186–188.

Dodson, P.; Behrensmeyer, A. K.; Bakker, R. T.; and McIntosh, J. S. 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. Paleobiology 6:208–232.

Dunagan, S. P. 2000. Constraining Late Jurassic paleoclimate within the Morrison paleoecosystem: insights from the continental carbonate record of the Morrison Formation (Colorado, USA). *In* Hall, R. L., and Smith, P. L., eds. GeoResearch Forum. Vol. 6. Proceedings of the 5th Jurassic Symposium, Vancouver. Switzerland, Trans Tech, p. 523–532.

Engelmann, G. F.; Chure, D. J.; and Fiorillo, A. R. 2004. The implications of a dry climate for the paleoecology of the fauna of the upper Jurassic Morrison Formation. Sediment. Geol. 167:297–308.

Engelmann, G. F., and Fiorillo, A. R. 2000. The taphonomy and paleoecology of the Upper Jurassic Morrison Formation determined from a field study of fossil localities. *In* GeoResearch Forum. Vol. 6. Proceedings of the 5th Jurassic Symposium, Vancouver. Switzerland, Trans Tech, p. 533–540.

Fisher, C. A. 1909. Geology of the Great Falls Coal Field, Montana. U.S. Geol. Surv. Bull. 356, 85 p.

Forster, C. A. 1999. Gondwanan dinosaur evolution and biogeographic analysis. J. Afr. Earth Sci. 28: 169–185.

Foster, J. R. 2003. Paleoecological analysis of the vertebrate fauna of the Morrison Formation (upper Jurassic), Rocky Mountain Region, USA. Bull. N. M. Mus. Nat. Hist. Sci. 23, 95 p.

Foster, J. R.; Holtz, T. R.; and Chure, D. J. 2001. Contrasting patterns of diversity and community structure in the theropod faunas of the Late Jurassic and Late Cretaceous of western North America. J. Vertebr. Paleontol. 21(suppl.):51A.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405:220–227.

Gordon, C. G., and Buikstra, J. E. 1981. Soil pH, bone preservation, and sampling bias at mortuary sites. Am. Antiq. 46:566–571.

Grube, R.; Schultka, S.; and Süß, H. 2001. Kutikulen und Fusite: Hinweise auf eine oberjurassi-sche Flora vom Tendaguru (Tansania). Laboratorium für Paläobotanik und Palynologie, Utrecht: 19. Jahrestagung des Arbeitskreises für Paläobotanik und Palynologie, Programm und Beitrags-kurzfassungen, p. 8.

Hallam, A. 1994. Jurassic climates as inferred from the sedimentary and fossil record. *In* Allen, J. R. L.; Hoskins, B. J.; Sellwood, B. W.; Spicer, R. A.; and Valdes, P. J., eds. Palaeoclimates and their modelling: with special reference to the Mesozoic Era. London, Chapman & Hall, p. 79–88.

Hare, P. E. 1980. Organic geochemistry of bone and its relation to the survival of bone in the natural environment. *In* Behrensmeyer, A. K., and Hill, A. P., eds. Fossils in the making: vertebrate taphonomy and paleoecology. Chicago, University of Chicago Press, p. 208–219.

Hasiotis, S. T., and Demko, T. M. 1998. Ichnofossils from Garden Park Paleontological Area, Colorado: implications for paleoecologic and paleoclimatic reconstructions of the upper Jurassic. Mod. Geol. 22:461–479.

Henderson, J. 1987. Factors determining the state of preservation of human remains. *In* Boddington, A.; Garland, A. N.; and Janaway, R. C., eds. Death, decay, and reconstruction: approaches to archaeology and forensic science. Manchester, Manchester University Press, p. 43–54.

Herman, A. B., and Spicer, R. A. 1997. New quantitative palaeoclimate data for the Late Cretaceous Arctic: evidence for a warm polar ocean. Palaeogeogr. Palaeoclimatol. Palaeoecol. 128:227–251.

Kahlert, E.; Schultka, S.; and Süß, H. 1999. Die mesophytische Flora der Saurierlagerstätte am Tendaguru (Tansania). Mitt. Mus. Natkd. Berl. Geowiss. Reihe 2: 185–199.

Kalandadze, N. N., and Rautian, A. S. 1991. Late Triassic zoogeography and a reconstruction of the terrestrial tetrapod fauna of North Africa. Paleontol. Zh. 1:3–14.

Kiessling, W. 2002. Radiolarian diversity patterns in the latest Jurassic-earliest Cretaceous. Palaeogeogr. Palaeoclimatol. Palaeoecol. 187:179–206.

Lehman, T. M. 1987. Late Maastrichtian paleoenvironments and dinosaur biogeography in the western interior of North America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 60:189–217.

———. 2000. Late Cretaceous dinosaur provinciality. *In* Tanke, D. H., and Carpenter, K., eds. Mesozoic vertebrate life. Bloomington, Indiana University Press, p. 310–328.

Litwin, R. J.; Turner, C. E.; and Peterson, F. 1998. Palynological evidence on the age of the Morrison Formation, Western Interior U.S. Mod. Geol. 22:297–319.

Maier, G. 2003. African dinosaurs unearthed. The Tendaguru expeditions. Bloomington, Indiana University Press, 380 p.

Noto, C. R.; Rees, P. M.; Ziegler, A. M.; and Weishampel, D. B. 2002. Rocks, bones, and plants: a pattern of latitudinal dependence demonstrated by the distribution of Jurassic dinosaurs. J. Vertebr. Paleontol. 22:92A–93A.

Parrish, J. M. 2003. Mapping ecomorphs onto sauropod phylogeny. J. Vertebr. Paleontol. 20:85A–86A.

Parrish, J. M; Rees, P. M.; and Ziegler, A. M. 1996. Correspondence of paleolatitudinal diversity in herbivorous dinosaurs and plants during the Jurassic. *In* Repetski, J. E., ed. 6th North American paleontological convention: abstracts of papers. Paleontol. Soc. Spec. Publ. 8:301.

Parrish, J. T.; Peterson, F.; and Turner, C. E. 2004. Jurassic "savannah": plant taphonomy and climate of the Morrison Formation (Upper Jurassic, Western USA). Sediment. Geol. 167:137–162.

Parrish, J. T., and Spicer, R. A. 1988. Late Cretaceous terrestrial vegetation: a near-polar temperature curve. Geology 16:22–25.

Paul, G. S. 1988. The brachiosaur giants of the Morrison and Tendaguru with a description of a new genus and a comparison of the world's largest dinosaurs, *Giraffotitan*. Hunteria 2:1–14.

Peterson, F. 1988. Pennsylvanian to Jurassic eolian transportation systems in the western United States. Sediment. Geol. 56:207–260.

Pritchett, W. L. 1979. Properties and management of forest soils. New York, Wiley, 500 p.

Rees, P. M.; Ziegler, A. M.; Gibbs, M. T.; Kutzbach, J. E.; Behling, P.; and Rowley, D. B. 2002. Permian phytogeographic patterns and climate data/model comparisons. J. Geol. 110:1–31.

Rees, P. M.; Ziegler, A. M.; and Valdes, P. J. 2000. Jurassic phytogeography and climates: new data and model comparisons. *In* Huber, B. T.; Macleod, K. G.; and Wing, S. L., eds. Warm climates in earth history. Cambridge, Cambridge University Press, p. 297–318.

Retallack, G. J. 1998. Fossil soils and completeness of the rock and fossil records. *In* Donovan, S. K., and Paul, C. R. C., eds. The adequacy of the fossil record. New York, Wiley, p. 133–163.

Rosenzweig, M. L. 1992. Species-diversity gradients: we know more and less than we thought. J. Mammal. 73: 715–730.

———. 1995. Species diversity in space and time. Cambridge, Cambridge University Press, 436 p.

Russell, D.; Beland, P.; and McIntosh, J. S. 1980. Paleoecology of the dinosaurs of Tendaguru (Tanzania). Mem. Soc. Geol. Fr. 139:169–175.

Russell, D. A. 1993. The role of central Asia in dinosaurian biogeography. Can. J. Earth Sci. 30:2002–2012.

Schrank, E. 1999. Palynology of the dinosaur beds of Tendaguru (Tanzania): preliminary results. Mitt. Mus. Natkd. Berl. Geowiss. Reihe 2:171–183.

Schuchert, C. 1918. Age of the American Morrison and east African Tendaguru formations. Bull. Geol. Soc. Am. 29:245–280.

Sellwood, B. W.; Valdes, P. J.; and Price, G. D. 2000. Geological evaluation of multiple GCM simulations of Late Jurassic palaeoclimate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 156:147–160.

Sereno, P. C. 1999*a*. Dinosaurian biogeography: vicariance, dispersal and regional extinction. *In* Tomida, Y.; Rich, T. H.; and Vickers-Rich, P., eds. Proceedings of the second Gondwanan dinosaur symposium. Tokyo, National Science Museum Monographs, p. 249–257.

———. 1999*b*. The evolution of dinosaurs. Science 284: 2137–2147.

Silverman, A. J., and Harris, W. L. 1967. Stratigraphy and economic geology of the Great Falls-Lewistown Coal Field, central Montana. Mont. Bur. Mines Geol. Bull. 56, 20 p.

Spicer, R. A., and Parrish, J. T. 1987. Plant megafossils, vertebrate remains, and paleoclimate of the Kogosukruk tongue (Late Cretaceous), North Slope, Alaska. U.S. Geol. Surv. Circ. 998:47–48.

Spicer, R. A.; Rees, P. M.; and Herman, A. B. 1996. The Cretaceous vegetation and climate of Asia: some insights. Mem. Geol. Soc. India 37:405–433.

Stevens, K. A., and Parrish, J. M. 1999. Neck posture and feeding habits of two Jurassic sauropod dinosaurs. Science 284:798–800.

———. In press. Biological implications of reconstructions of the whole body of sauropod dinosaurs. *In* Chure, D.; Curry Rogers, K.; and Wilson, J., eds. Sauropod evolution and paleobiology. Cambridge, Cambridge University Press.

Taggart, R. E., and Cross, A. T. 1997. The relationship between land plant diversity and productivity and patterns of dinosaur herbivory. *In* Wolberg, D. L.; Stump, E.; and Rosenberg, G., eds. Dinofest International: proceedings of a symposium held at Arizona State University. Philadelphia, Academy of Natural Sciences, p. 403–416.

Turner, C. E., and Fishman, N. S. 1991. Jurassic Lake T'oo'dichi': a large alkaline, saline lake, Morrison Formation, eastern Colorado Plateau. Geol. Soc. Am. Bull. 103:538–558.

Vakhrameev, V. A. 1991. Jurassic and Cretaceous floras and climates of the earth. Cambridge, Cambridge University Press, 318 p.

Weishampel, D. B.; Dodson, P.; and Osmolska, H. 2004. The dinosauria (2d ed). Berkeley, University of California Press, 880 p.

Yavitt, J. B., and Fahey, T. J. 1986. Litter decay and leaching from the forest floor in *Pinus contorta* (lodgepole pine) ecosystems. Ecology 74:525–545.

Ziegler, A. M.; Eshel, G.; Rees, P. M.; Rothfus, T. A.; Rowley, D. B.; and Sunderlin, D. 2003. Tracing the tropics across land and sea: Permian to present. Lethaia 36:227–254.