A stable isotopic investigation of resource partitioning among neosauropod dinosaurs of the Upper Jurassic Morrison Formation

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ABSTRACT

For more than a century, morphological studies have been used to attempt to understand the partitioning of resources in the Morrison Fauna, particularly between members of the two major clades of neosauropod (long-necked, megaherbivorous) dinosaurs: Diplodocidae and Macronaria. While it is generally accepted that most macronarians fed 3-5m above the ground, the feeding habits of diplodocids are somewhat more enigmatic; it is not clear whether diplodocids fed higher or lower than macronarians. While many studies exploring sauropod resource portioning have focused on differences in the morphologies of the two groups, few have utilized geochemical evidence. Stable isotope geochemistry has become an increasingly common and reliable means of investigating paleoecological questions, and due to the resistance of tooth enamel to diagenetic alteration, fossil teeth can provide invaluable paleoecological and behavioral data that would be otherwise unobtainable. Studies in the Ituri Rainforest in the Democratic Republic of the Congo, have shown that stable isotope ratios measured in the teeth of herbivores reflect the heights at which these animals fed in the forest due to isotopic variation in plants with height caused by differences in humidity at the forest floor and the top of the forest exposed to the atmosphere. The depositional environment of the Upper Jurassic Morrison Formation has also been highly debated for over a century, but it seems likely that it was a dry environment lacking dense, thick rain forest; however, by measuring carbon stable isotope ratios in leaves from modern plants closely related to those present during the Late Jurassic, it is observed that a significant variation in stable isotope ratios with height is observable not only in trees from a closed canopy forest but also in isolated trees far from a forest environment. With this knowledge, it is now possible to investigate the partitioning of resources via feeding height in herbivorous fossil animals regardless of whether or not they lived in a closed canopy setting as long as it is assumed that they fed largely on the same plants. Applying this to the problem of Morrison neosauropods, it appears that if diplodocids and macronarians likely did not partition resources strictly by height as significant overlap in stable isotope ratio values was observed between the two groups. Instead, it follows that these groups must have partitioned resources by being specialized to feed on different groups of plants, which is consistent with tooth morphology.

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INTRODUCTION

OVERVIEW

The Upper Jurassic Morrison Formation of southern North America preserves a diverse flora and fauna that inhabited a semiarid world. The Morrison Fauna is a characteristic Late Jurassic faunal assemblage (Mateus 2006); it comprises several genera each of large-bodied neosauropod, theropod, and ornithischian dinosaurs that all thrived in the same geographic region at the same time. The number of neosauropod taxa is particularly intriguing. At least nine genera of neosauropods have been described from the Morrison, each estimated to weigh 14,000-35,000 kg. This raises certain questions about how these animals could live in sympatry—that is, how they could live in the same place at the same time. The issue of resource partitioning among neosauropod dinosaurs has been a particularly heavily debated topic. Did neosauropods partition resources via feeding height, eating different types of plants, or both? Since these animals are long since extinct and have no extant ancestors to observe, behavioral reconstructions are particularly difficult and have typically been achieved through morphological studies; however, these morphological analyses are limited. It is generally accepted that macronarian neosauropods fed 3-5 m about the ground given their laterally inflexible necks and proportionately long forelimbs, which built their bodies "uphill" (Foster, 2003). The feeding habits of diplodocid neosauropods are more ambiguous; did these animals feed higher or lower than macronarians? Studies of tooth morphology have also led some to suggest that the robust teeth of macronarians were used to process tougher plant material while the narrow, fragile teeth of diplodocids were used to feed on softer, perhaps aquatic plant material. Stable isotope geochemistry can be used to investigate the partitioning of resources between neosauropod taxa. Animals record the carbon and oxygen characteristics of the food they ingest and the water they drink by incorporating the C and O in their own bodies. Carbon and oxygen isotope ratios of carbonate from bioapatite can be used to make inferences regarding the feeding habits and living environments of fossil animals. Enamel is not easily altered by diagenesis and is thus the best material available to analyze to obtain isotopic information (Kohn & Cerling, 2002).

SAUROPOD BIOLOGY AND EVOLUTION

Sauropoda is a well-supported monophyletic group of saurischian dinosaurs that originated in the Late Triassic Epoch, achieved worldwide distribution and became the predominant terrestrial herbivores of the Mesozoic by the Jurassic Period. These megaherbivores remained an important component of the Mesozoic terrestrial fauna until the clade's extinction at the end of the Cretaceous Period (Barrett and Upchurch 2005, Upchurch *et al.* 2004). Sauropods were the dominant animals in many middle and late Mesozoic ecosystems both in terms of biomass and of numerical abundance. Part of the reason for their success as a group was the evolution of obligate herbivory, as herbivores are generally more speciose than carnivores—the number of species of herbivore in an ecosystem generally tends to be greater than the number of species of carnivore. The group is characterized by large, barrel-shaped bodies with columnar, elephantine limbs; long necks and tails; and relatively small skulls considering their body size.

Sauropoda is defined as a stem-based taxon comprising all sauropodomorphs that are more closely related to *Saltasaurus* than to *Plateosaurus,* and one of the major clades within Sauropoda is Neosauropoda (Upchurch *et al.* 2004, Wilson and Sereno 1998). Neosauropoda is united by a suite of synapomorphic traits (shared, derived traits which set a taxon and its descendants apart from its ancestors), and it is a node-based taxon defined as including the most recent common ancestor of *Diplodocus* and *Saltasaurus* and all of its descendents. Neosauropoda is divided into two major clades, which are the taxa of focus for this study. These two clades are Diplodocidae and Macronaria. Both are stem-based taxa defined as neosauropods more closely related to *Diplodocus* than to *Saltasaurus* or vice versa, respectively (Wilson and Sereno 1998). Neosauropod dinosaurs are the primary focus of this study, particularly the taxa Diplodocidae and *Camarasaurus* (a macronarian). These taxa are the most abundant sauropods in the Morrison Formation (Foster 2005) and are considered in detail in this study. Diplodocidae includes diplodocids and dicraeosaurids, which both appear in the Late Jurassic, and the Early Cretaceous rebbachisaurids. All of the genera of diplodocid relevant to this study are diplodocids, particularly *Diplodocus*, *Apatosaurus*, and *Barosaurus*. *Camarasaurus* is a basal macronarian.

The neosauropods considered in this study are all estimated to have weighed anywhere between 14,000 and 35,000 kg (Sander *et al*. 2010), which has led to much speculation regarding the energy requirements of these megaherbivorous dinosaurs. It has been suggested that sauropods would have had tremendous dietary requirements, but some authors have compared sauropods to mammalian megaherbivores and concluded that large size is actually an advantage for herbivores (Engelmann *et al.* 2004). When plotted on a graph of daily food intake as a % of body mass against body mass in modern mammals, two of the heaviest Late Jurassic sauropods would both require only require <0.5% of the body mass in food per day (Figure 1). This is an extrapolation since the physiologies of mammals and dinosaurs are likely distinct from each other. It is possible that sauropod digestion was extremely efficient; indeed, sauropods do not appear to need to be picky eaters since large herbivores tend to be able to tolerate lower quality forage than small herbivores. This is due to their massive fermentative gut. This may have aided in preventing water loss as well, which would have been a key adaption to survive in dry regions with limited food resources where many individuals of different species of sauropod cohabited. One such region is that preserved in the Morrison Formation, which is the focus of this study. Sauropods exhibit a wide range of morphological characteristics, both cranial and post-cranial, that contribute to feeding diversity. Sauropod taxic diversity estimates reach peak during Kimmeridgian and Tithonian, representing the acme of sauropod diversity with 26 valid genera (Barrett and Upchurch 2005, Upchurch & Barrett 2005, Weishampel *et al* 2004, Upchurch *et al.* 2004), and feeding diversity reached maximum during the Late Jurassic.

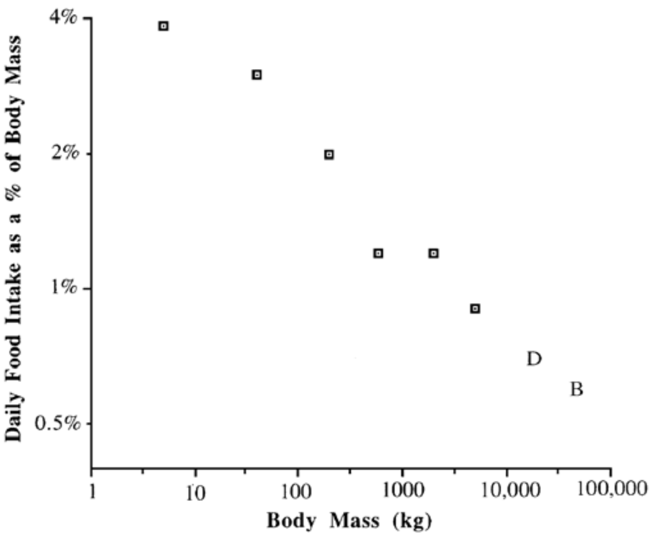


Figure 1. Plot of daily food intake vs. body mass for several mammalian herbivores. The extrapolated positions of *Diplodocus* and *Brachiosaurus* are represented by points D and B, respectively (From Engelmann *et al.*, 2004)

The specialized feeding apparatuses of sauropods have a strong phylogenetic component (Figure 2), and Barrett and Upchurch (2005) identified a suite of "novel feeding mechanisms." Those relevant for this study are reproduced below:

- Novel feeding mechanisms:
    - *Apatosaurus* type: Narrow-crowned teeth; propalinal jaw action; occlusion (apical wear facets); branch-stripping/nipping of vegetation; low forelimb length/hindlimb length ratio (ca. 0.70); elongate (15 cervical vertebrae), laterally and dorsoventrally flexible neck; tripodal ability; low and medium browsing (up to 8m)
    - *Diplodocus* type: Narrow-crowned teeth; lack of occlusion; branch-stripping/nipping of vegetation; low forelimb length/hindlimb length ratio (ca. 0.70); elongate (15 or 16 cervical vertebrae), laterally and dorsoventrally flexible neck; tripodal ability; low, medium, and high browsing (up to 12m)
    - *Camarasaurus* type: Broad-crowned teeth; propalinal jaw action; interdigitating occlusion (mesial and distal wear facets); cropping of vegetation; intermediate forelimb length/hindlimb length ratio (ca. 0.79-0.87); short (12 cervical vertebrae), laterally inflexible and dorsoventrally flexible neck; medium to high browsing (up to 9m)
    - Brachiosaurid type: Broad-crowned teeth (approaching narrow-crowned condition); orthal jaw action; precision-shearing occlusion (apical with occasional mesial and distal wear facets); cropping and nipping of vegetation; high forelimb length/hindlimb length ratio (ca. 1.1); long (12 or 13 extremely elongate cervical vertebrae), laterally inflexible and dorsoventrally flexible neck; high browsing (up to 14m)

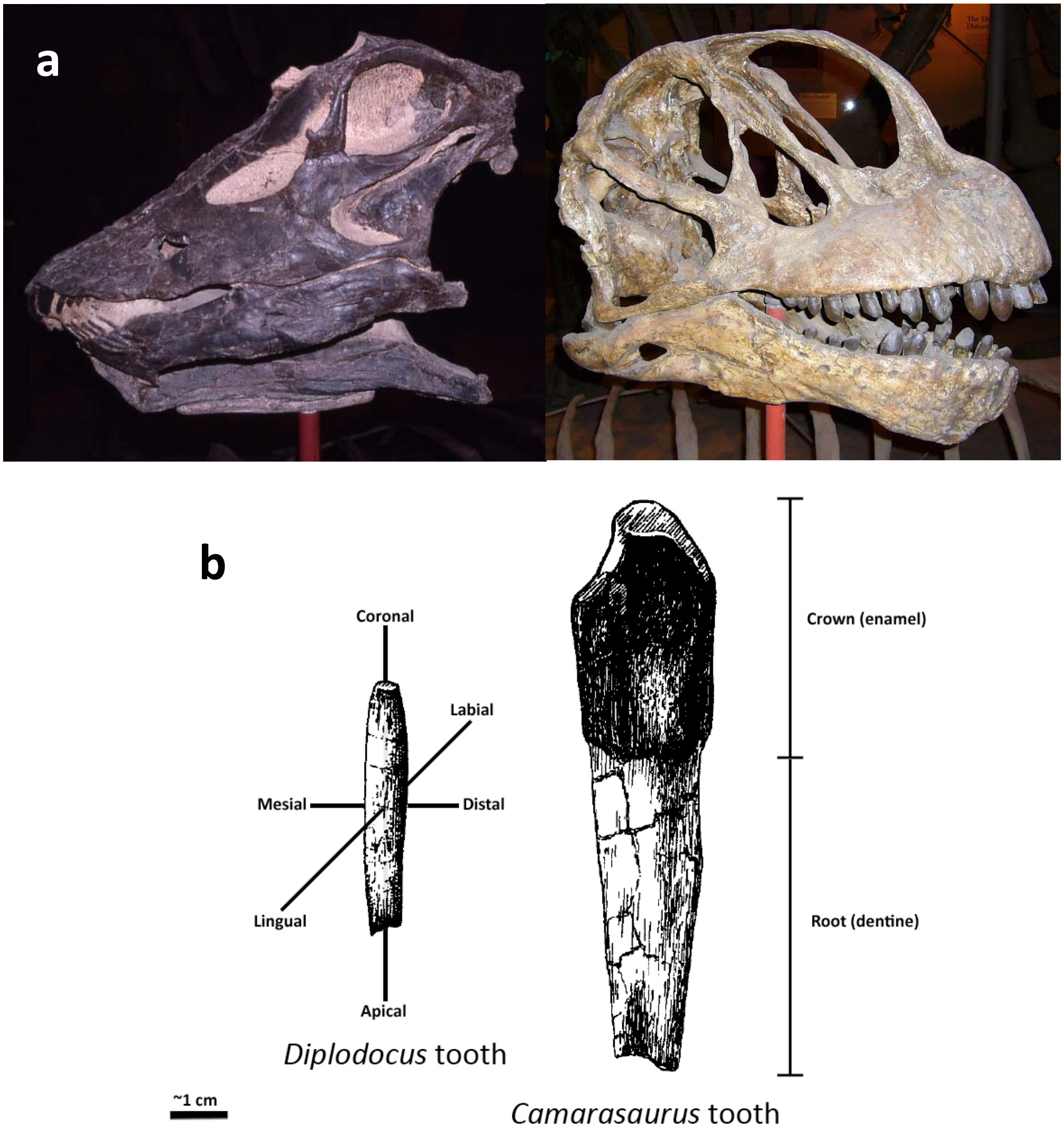


Figure 2. (a) Broad differences in the cranial morphologies of *Diplodocus* (Left, Diplodocidae) and *Camarasaurus* (Right, Macronaria). Diplodocids are characterized by long, squared-off snouts with pencil-shaped teeth that are concentrated at the front of the mouth, and Macronarians are characterized by shorter, box-like skulls with robust teeth extending all the way down the jaw line. Information (images) provided with the permission of the National Museum of Natural History, Smithsonian Institution, 10th and Constitution Ave. N.W., Washington, DC 20560-0193. (http://www.nmnh.si.edu/).
(b) Typical Morrison neosauropod teeth with wear facets visible on the occlusional surfaces. Directional and anatomical terminology indicated on the *Diplodocus* and *Camarasaurus* teeth, respectively. (Modified from Fiorillo 1998).

In these feeding mechanism classifications, broad-crowned teeth are those with slenderness indices (SI) of ≤ 4.0 and a "spatulate" cross-section, and narrow-crowned teeth are those with SI ≥ 4.0 and an approximately cylindrical x-section. SI is calculated by dividing apicobasal length of tooth crown by its mesiodistal width. Broad-crowned genera generally crop vegetation, NC genera generally rake or 'nip' vegetation.

These differences in dentition are highly suggestive of the partitioning of resources among neosauropod groups. Fiorillo (1998) examined the microstructure of wear facets on the teeth of *Diplodocus* and *Camarasaurus.* He noted that differences in the pattern of microwear may be indicative of changes in feeding preferences. He argued that *Camarasaurus* preferentially fed on coarser plants and did some processing in the mouth and that *Diplodocus* fed on much softer material. There is some overlap in wear patterns, particularly between *Diplodocus* and young *Camarasaurus.* It seems that Late Jurassic neosauropods almost certainly partitioned resources. These findings are consistent with other tooth morphological analyses (Chattergee & Zhang 2005).

While sauropods likely partitioned plant resources at least somewhat by utilizing different plants, the vertical partitioning of plant resources has also been proposed. The feeding height of *Camarasaurus* seems to have been relatively fixed at 3-5m above the ground (Foster 2003), but the feeding range of the Diplodocidae has been much more enigmatic. Morphological studies have been used to argue both for and against a high-browsing Diplodocidae. Sauropod head and neck posture has been modeled from comparison to the postures of extant taxa, and many of these analyses are not supportive of a high-browsing Diplodocidae (Stevens & Parrish 2005, Stevens & Parrish 2005, and Rothschild & Molnar 2005); however, other similar analyses have shown that sauropods may be anomalies that cannot be modeled after any living taxa and that diplodocids may possibly have been able to browse high (Taylor *et al.* 2009). Whether or not diplodocids were able to rear into a tripodal position with their forelimbs off the ground remains ambiguous; though, analyses of stress fractures in sauropod limbs are not supportive of this hypothesis (Rothschild & Molnar 2005).

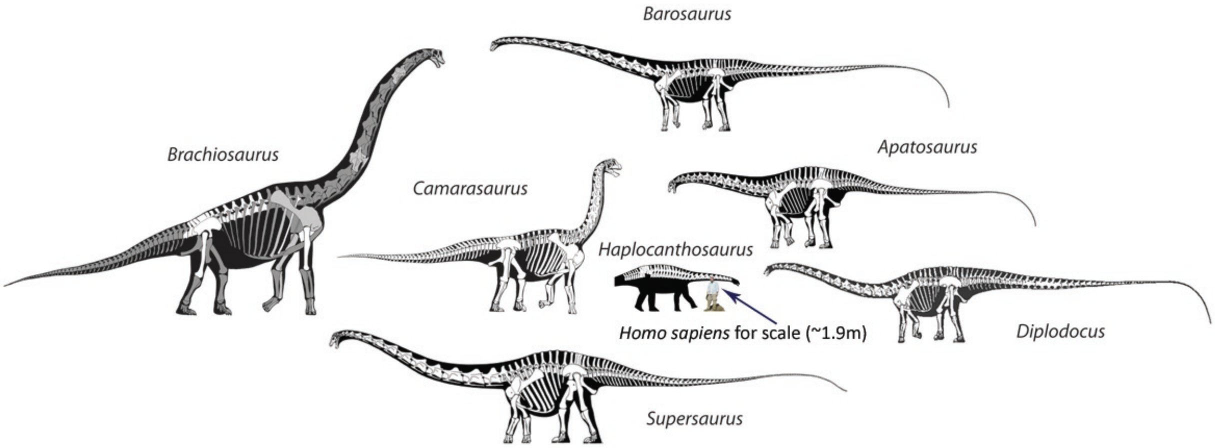


Figure 3. The most common neosauropod taxa of the Morrison Formation. Matt Wedel (~1.9m) for scale.

MORRISON FORMATION

The Morrison Formation is a fossil-rich, Upper Jurassic package of terrestrial sedimentary rocks that crops out in western North America. It preserves an environment with a semiarid climate and wet and dry seasons comprising channel, floodplain, and lacustrine deposits (Foster 2003, Foster 2007, Kirkland and Carpenter 1994, Tütken *et al.* 2004, Turner *et al.* 2004, Engelmann *et al.*2004). Sedimentation in the Morrison is result of the retreat of the Sundance Sea during the early Late Jurassic, and it is characterized by interbedded sandstone, mudstone, and limestone. The Morrison has been dated to 155 to 147 Ma using $^{40}Ar/^{39}Ar$ dating of sanidine in volcanic ash layers that have been mostly altered to bentonite, indicating a mid-Late Jurassic (Kimmeridgian to Tithonian) age (Kowallis *et al.* 1998).

Many lines of evidence support the notion of a semiarid Morrison (Engelmann *et al*. 2004). Evidence from paleosols indicates that the region received annual precipitation of only 600-900mm with a dry season and that the soils likely supported dry, open woodland. Oxygen isotope ratios measured in pedogenic carbonates are characteristic of a rain shadow effect or strong continentality, and high levels of atmospheric CO_2 would have produced warm temperatures. This would have potentially increased plant productivity. Petrological evidence indicates that pedogenic and lacustrine carbonates formed in a region of seasonal drying, with wetter conditions restricted to northernmost and latest locations. Eolian sediments and a preserved large alkaline, saline lake provide strong evidence of episodes of at least semiarid conditions.

The Morrison preserves a diverse flora and fauna, including over 20 genera of dinosaurs. Many species of neosauropod are represented in Morrison deposits, the most well-known from complete samples of which are shown in Figure 3. How so many large-bodied herbivores were able to live in sympatry remains a point of contention. Farlow *et al.* (2010) conducted a paleoecological study of Morrison megaherbivore abundance using carrying capacity, average body mass, and animal energy needs and concluded that there was an upper abundance limit of a few tens of individuals of large subadult and adult animals for every square kilometer of land.

PREVIOUS WORK

Recent studies have used stable isotopic measurements of fossil and recent tooth and bone material to answer questions about paleoecology in a way that strictly morphological studies cannot (Amoit *et al.* 2009, Bryant *et al.* 1996, Cerling *et al.* 2004, Fricke & Pearson 2008, Secord *et al.* 2008, Tütken *et al.* 2004, Zazzo *et al*. 2000). Among these, the research of Cerling *et al.* (2004) and Fricke & Pearson (2008) are the most relevant to this study. Cerling *et al*. (2004) worked in the Ituri Forest, which is a closed canopy forest in Democratic Republic of the Congo. The authors observed that $\delta^{13}C$ values of plants from the canopy top, gaps within the canopy, and the subcanopy average -29.0±1.7‰, -30.4±0.9‰, and -34.0±1.5‰, respectively, and that $\delta^{13}C$ value of tooth enamel forest mammals reflect these differences. ^{13}C-enriched plants are found in water-stressed environments such as the canopy, and ^{13}C-depleted plants are found in low light areas where CO_2 is ^{13}C-depleted such as the understory. Although this study focused on a modern ecosystem, it has tremendous implications for paleoecology. The authors articulate that the stable isotopic composition of animal tissues is an important archive of information about terrestrial ecology. Cerling *et al.* (2004) note that while distinction in diets between C_3 and C_4 biomass in fossil communities is well-studied, there has been little work done to study isotopic variation within the C_3 end member diet. Similar analyses have since followed from other authors (Secord *et al*. 2008).

Fricke & Pearson's 2008 geochemical study of the fauna of the Hell Creek Formation used carbon and oxygen isotope ratios from fossil tooth enamel to make inferences regarding resource partitioning among the major groups of megaherbivorous dinosaurs. The Hell Creek is analogous to the Morrison in that it preserves a dinosaur community living in an environment dominated by C_3 vegetation. The authors found that hadrosaur $\delta^{13}C$ and $\delta^{18}O$ remained relatively consistent over time and with variations in landscape; while $\delta^{13}C$ and $\delta^{18}O$ values in ceratopsians varied with changes in landscape, but remained distinct from those of hadrosaurs within the same sites. Assuming vertical fractionation of isotopes in plants within a closed canopy forest setting, the most parsimonious interpretation of the data is that ceratopsians and hadrosaurs were utilizing different microhabitats of the Hell Creek ecosystem.

Sauropod ecology has been a very prolific research topic recently. Noto and Grossman (2010) investigated the broad-scale paleoecological patterns of Late Jurassic dinosaurs by observing the proportions of high-browsing and low-browsing taxa in dinosaur assemblages that were grouped according to biome. The authors found that high browsing taxa are relatively more abundant in regions categorized as arid, where vegetation is sparser, and low-browsing taxa are more abundant in regions categorized as moist, where vegetation is dense. Semi-arid regions fall in-between with a mix of high- and low-browsing taxa, as is observed in the Morrison. This study suggests that diplodocids are low-browsers as they are more common in moist environments, while macronarians dominate arid environments.

Gee (2011) considered the dietary options for sauropod dinosaurs from a botanical and paleobotanical perspective. In her study, she surveyed the growth habits of close relatives of Jurassic Mesozoic plants, their habitat, the amount of biomass produced by them, and their potential ability to recover from injury through herbivory. She also considered the relative quantities of energy and essential nutrients yielded to herbivores with hindgut fermentation, the consumption of the various plant groups by modern herbivores, and the coeval occurrence of sauropods and the individual plant groups in the fossil record. Considering these factors, it seems likely that *Araucaria, Equisetum*, Cheirolepidiaceae, and *Ginkgo* would have been the most accessible and sustaining sources of food for sauropods and were thus likely preferred. Less so would be the Podocarpaceae, Cupressaceae, and Pinaceae, and even less so would be the forest dwelling ferns. Cycads and bennettitaleans were probably the least frequently eaten plants by sauropods.

Tütken (2011) conducted a study very similar to this thesis. By measuring carbon isotope ratios in plants and sauropod teeth and bones, he investigated the diet of sauropods. His data suggest that sauropods fed primarily on terrestrial C_3 plants and possibly on freshwater aquatic plants. His sample numbers for sauropod teeth were small, but his data provide evidence for sauropod niche partitioning as mean enamel $\delta^{13}C$ values differ by approximately 3‰ in sympatric sauropods. He suggests that low-browsing taxa fed on ferns and horsetails and high-browsing taxa fed on conifers.

OBJECTIVES OF RESEARCH

The primary objective of this study was to contribute geochemical evidence to the ongoing paleontological debate regarding how the megaherbivorous dinosaurs of the Late Jurassic fauna were able to live in sympatry, and how they may have partitioned resources. A secondary objective of this study is to better understand how plants in the late Jurassic Period may have fractionated carbon and oxygen isotopes both intraspecifically and interspecifically. These objectives lead to several alternative hypotheses.

- Neosauropod niche partitioning:
    - H_0. Null hypothesis: There is no isotopic differentiation between Diplodocidae and *Camarasaurus.* Assuming only vertical fractionation of carbon and oxygen isotopes in Late Jurassic plants and not interspecific fractionation, data consistent with this hypothesis would suggest that if plant resources were being partitioned at all, it was likely by plant type rather than height.
    - H_1. Low-browsing diplodocids: $\delta^{13}C$ and $\delta^{18}O$ values for diplodocids will be consistently and statistically significantly lower than for *Camarasaurus.* Assuming only vertical fractionation of carbon and oxygen isotopes in Late Jurassic plants and not interspecific fractionation, data consistent with this hypothesis would suggest that diplodocid dinosaurs were not using their long necks and tripodal ability to reach high into trees. Instead, these data would support the idea that diplodocids remained stationary while feeding and used their long necks to feed from a large area.
    - H_2. High-browsing diplodocids: $\delta^{13}C$ and $\delta^{18}O$ values for diplodocids will be consistently and statistically significantly higher than for *Camarasaurus.* Assuming only vertical fractionation of carbon and oxygen isotopes in Late Jurassic plants and not interspecific fractionation, data consistent with this hypothesis would suggest that diplodocid dinosaurs were utilizing their long necks and tripodal ability to reach high into trees, feeding above the maximum *Camarasaurus* feeding level.
- Ground-truthing $\delta^{13}C$ partitioning with height in modern C3 plants:
    - H_0. Null hypothesis: There is no isotopic variation between values of ground cover, low level branches, and high level branches.
    - H_1. Hypothesis 1: Measured $\delta^{13}C$ values will increase relative to the heights at which samples were collected from the plants.

MATERIALS AND METHODS

COLLECTION, PREPARATION, AND ANALYSIS OF MODERN PLANT MATERIAL

Modern plant material from taxa closely related and morphologically similar to those of the Jurassic flora was collected from sites in College Park, MD and Washington, DC. Carbon isotope ratio measurements will be used in an attempt to ground-truth the vertical fractionation of isotopes in trees and also to observe any variation in isotopic signatures that may be present between plant taxa. This type of analysis is not new, but similar studies (Cerling *et al*., 2004) have tended to focus on modern or recent C_3 plant communities in which the taxa present are quite different from those of the Late Jurassic. For this study, only plants closely related to those known to be closely related to those preserved in the Morrison Formation (Tidwell *et al.*, 1998, Gee 2010, Taylor *et al*. 2009, Chure *et al.* 1998) were considered. There is no easily accessible modern analog to a Morrison floral assemblage, but many appropriate plant taxa are represented as individual isolated trees on campus at University of Maryland, College Park and as a small community called "Garden Primeval" at the United States Botanic Gardens in Washington, D.C., so these were selected these as collection sites for the plant material analyzed here.

The University of Maryland is a recognized arboretum, and many of the plant species present on campus are good modern analogues for Jurassic species. None of these trees are situated such that one would expect to see the vertical isotopic fractionation that has been observed in closed canopy forests, but the material collected on campus can be used to investigate whether there is any general fractionation with height that is independent of varying conditions between the base and the apex of a tree. This is a critical distinction to be made for this study because it is assumed that these neosauropod dinosaurs would have fed in similar regions, and vegetation was sparse in the Morrison, with trees being concentrated only at riparian zones; since the extreme fractionation of carbon and oxygen isotopes observed by Cerling *et al.* (2004) was the result of varying conditions within a dense, closed canopy rainforest, their observations cannot be assumed to be true in the Morrison where dense rainforest did not exist. If isolated trees show isotopic variation with height, all other things being equal, then inferences concerning vertical resource partitioning can be made by observing the isotope ratios of enamel from herbivores feeding in the same region on the same plants. Data collected from the trees on campus can also be used to identify whether any phylogenetic variation in isotopic values exists. Two species of plant on campus were selected for collection: *Taxodium distichum* (baldcypress) and *Ginkgo biloba*. *Taxodium distichum*is a member of the family Cupressaceae, which diversified in the Jurassic Period (Taylor *et al.*, 2009); however, it is important to note that this particular species was not present at the time the Morrison was deposited. Fossils of the genus *Ginkgo* are common in the Morrison (Tidwell *et al.*, 1998), so *Ginkgo biloba* is an excellent modern analog.

Samples were collected from each tree in 2m increments using a bucket truck. The locations of the trees are given on the map in Appendix A. Samples from *T. distichum* were collected on 27 October 2010; however, the sample heights are low precision due to technical issues with the GPS that was intended to be used to determine altitude. The heights were estimated based on the known height of a nearby 25ft light pole.

Figure 4. The “Garden Primeval” at the US Botanic Garden.

The United States Botanic Garden (USBG) provides a much more useful—though by no means a perfect—analog to the representative flora of the Late Jurassic. The USBG’s “Garden Primeval” exhibit (Figure 4) is a reconstructed Jurassic landscape that houses several species of ferns and fern allies, and most are present both along the path through the garden and deep in the shade of other plants. Samples of these ferns and fern allies were collected from both shaded and unshaded settings. Taxa sampled include *Equisetum hyemale* (rough horsetail), *Microlepia speluncae, Microsorum sleerei, Cycas circinalis* (the Queen Sago)*, Araucaria heterophylla* (Norfolk Island pine)*, Araucaria bidwillii* (Bunya pine)*, Zamia pumila* (Coontie)*, Colysis wrightii,* and *Diplazium esculentum*. Most of the samples were collected from ground level, and collection heights of plants taller than 1m were estimated based on the known height of the 10ft specimen of *Araucaria heterophylla.* A complete sample list with taxon names and collection heights is given in Appendix B.

These samples were prepared and analyzed for carbon isotope ratios at the University of Maryland in the Isotope Geochemistry Laboratory. To prepare these materials for analysis, each sample was placed in either a 15mL or 50mL plastic centrifuge tube and dried in a utility oven for 2-3 days. The dried leaves were then crushed into a powder using a ceramic mortar and pestle, and the powder was transferred to smaller plastic sample vials. 60-80μg aliquots of each sample were then weighed into tin cups, which were folded shut and shaped into spheres for combustion.

Carbon isotope ratios were measured using a Eurovector elemental analyzer (EA) coupled to an Isoprime continuous flow (CF) mass spectrometer. Before running any samples for analysis, the CF instrument must be tuned and calibrated. To do this, the voltage must be adjusted for CO_2 so that the ion beams are in optimal position for analysis. The EA must be leak-checked using a pressure test, and then a stability test must be run. In a stability test, the reference gas is checked for consistent peaks. Four to six standards are then run, and the machine is ready for sample measurements.

In a run using the EA and CF machines, the tin sample packets are loaded into a carousel on top of the EA, and the run is started. Each sample is combusted in the combustion column within the EA at 1040°C and reacted in the reduction column at 650°C to form CO_2, which is then passed into the gas chromatograph (GC) column by a continuous flow of pure helium gas at a flow rate of 115mL/min. From here, the gas moves the sample into the mass analyzed of the mass spectrometer where it is bombarded with electrons, making CO_2^+ ions that are separated by mass, resulting in peaks that are measured on the collectors. The batch is started with four to six urea standards, followed by groups of 10 samples + two standards until the end of the run.

Uncertainty for carbon isotope analysis is determined by running the samples along with aliquots of the NIST urea standard, which has a known weight percent value of 20% C and isotopic abundance value ($\delta^{13}C$) of -29.39‰. The average and standard deviation of the weight percent and isotopic abundance values are calculated by using the values of each of the standards analyzed. The calculated average isotopic abundance value is then subtracted from the known value of the standard to determine the offset factor for the isotopic abundance, which is then added to each raw isotopic abundance value to give the corrected value. Corrected weight percent values are determined by dividing the known weight percent value of the standard by the average weight percent value of the measured standards and multiplying the raw weight percent value of each sample by this number. The calculated standard deviation of weight percent and isotopic abundance from the standard values gives the 1σ uncertainty of the respective measurements for each sample. All values are calculated using Microsoft Excel.

Collection, Preparation, and Analysis of Fossil Tooth Material

The fossil teeth analyzed in this study were recovered from Morrison Formation deposits at the Mygatt-Moore Quarry in western Colorado north of the Colorado River near the Utah border (Figure 5). This quarry is notable for yielding the first North American remains of a Jurassic ankylosaur, and it has also produced a number of nearly-complete fish fossils (Foster, 2003). It has also yielded hundreds of isolated dinosaur teeth, mostly pertaining to the genera *Apatosaurus*, *Camarasaurus*, and *Allosaurus.* The Mygatt-Moore Quarry lies in the middle of the Brushy Basin Member of the Morrison Formation, and the majority of the dinosaur fossil material is concentrated at the bottom of the section (Figure 6). The sample set analyzed this this study was provided by the Museum of Western Colorado and comprises 17 neosauropod tooth fragments. Of these fragments, four diplodocid and five macronarian teeth yielded enough enamel to be analyzed. All of the macronarian teeth likely represent the genus *Camarasaurus*; however, it is difficult to identify the diplodocid teeth at the genus level. A complete sample list is included in Appendix B.

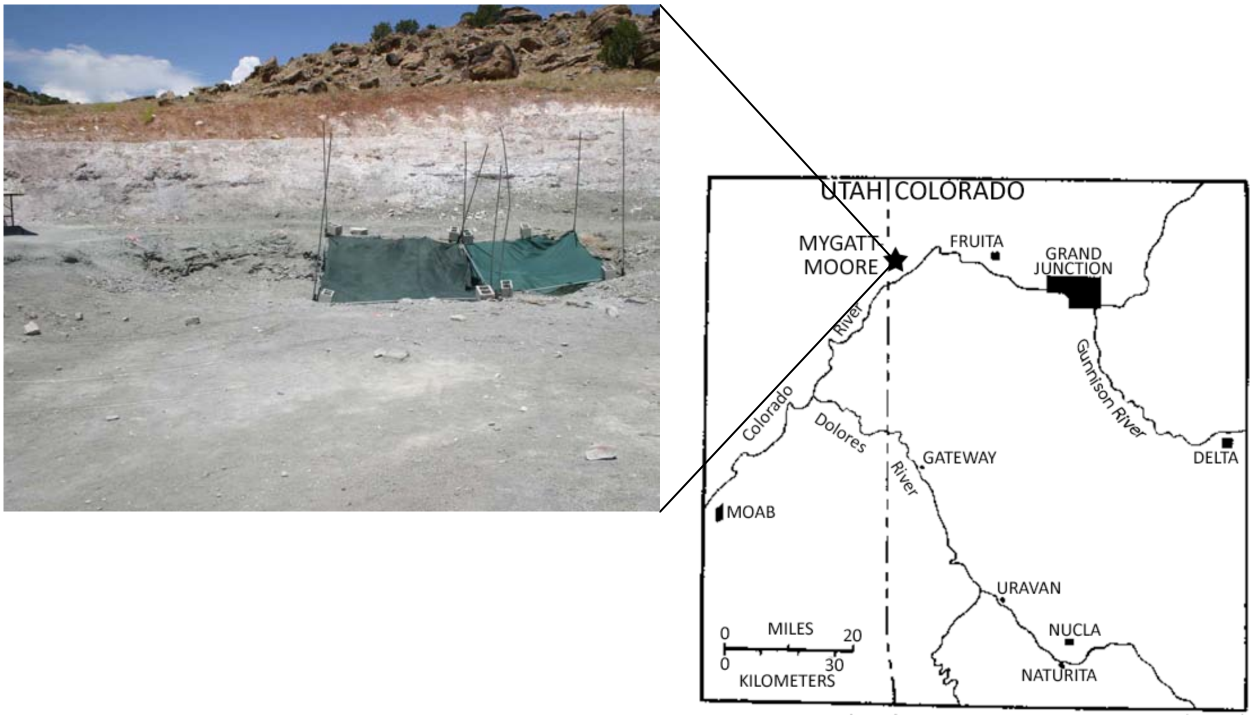
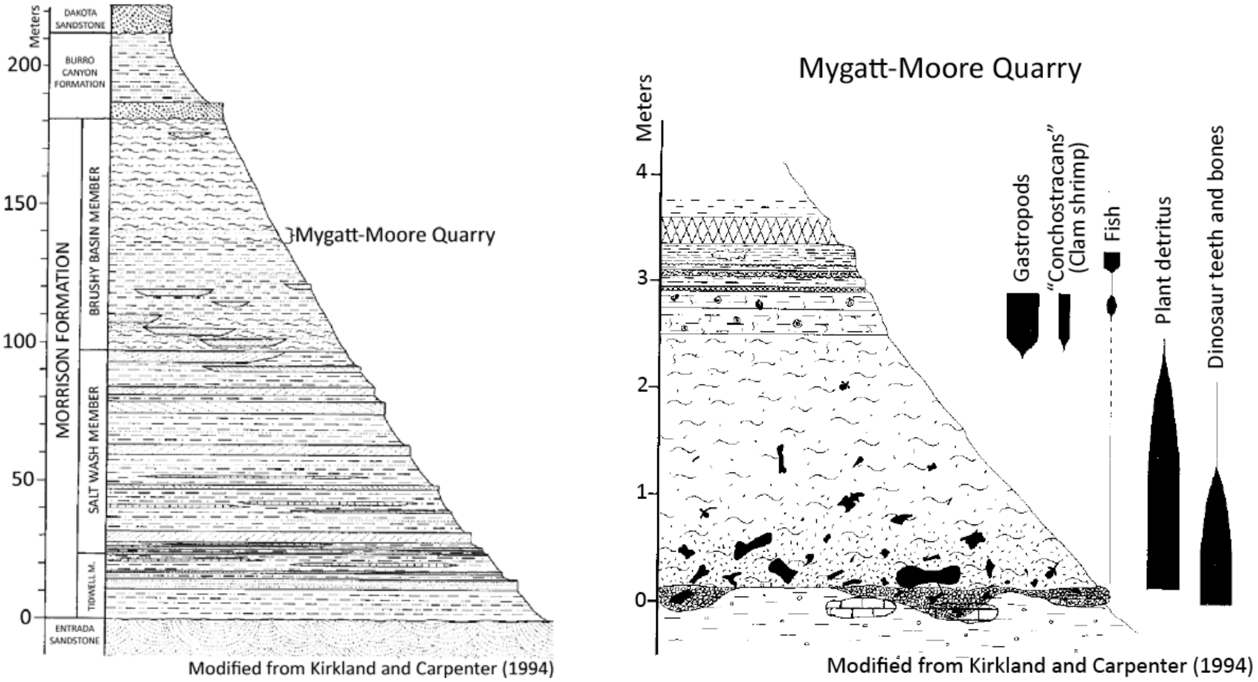


Figure 5. Field photo and location of the Mygatt-Moore Quarry site in Western Colorado. Map modified from Kirkland and Carpenter (1994). Photo courtesy of Dr. Thomas Holtz.

To prepare the fossil teeth for analysis, a method discussed with Dr. Christine France of the Smithsonian Museum Conservation Institute was used. Variations of the method are common in the literature (Koch *et al* 1997, Secord *et al.* 2008, Zazzo *et al.* 2000). Following this method, a Dremel drill with a diamond-tipped bit was used to bore into the enamel of each tooth create at least 10-15mg of powder (Figure 7), taking care to avoid dentine contamination by drilling too deep. This powder was weighed into a 15mL plastic centrifuge tube, and the weight of both the powder and the empty tube are recorded. 10mL of 2-3% sodium hypochlorite was added to the tube in order to oxidize and remove any lingering organic matter that could interfere with carbon and oxygen isotopic analyses. The power samples sat in the sodium chlorite at room temperature overnight and were then rinsed five times with ultra-pure Milli-Q water to ensure that the samples reached neutrality. The remaining solid was then dried in a utility oven at approximately 60°C, and the dried sample was weighed to determine percent loss. This weight is subtracted from the initial weight of the powder sample to establish the mass of organic matter and soluble minerals in each sample. A 1M acetic acid/calcium acetate buffer solution was prepared by mixing equal parts of a 2M acetic acid solution and a 2M calcium acetate solution. In order to dissolve all of the calcium acetate powder into solution, the solution was left on a stirring plate for several hours. The pH of the resulting buffer solution must be near 4.5 and was be measured before proceeding since structural carbonate from the enamel may be dissolved if the pH is too low. 10mL of the 1M acetic acid/calcium acetate buffer solution was then added to the dried sample to remove non-structurally-bound carbonate, and the sample was left to soak for four hours at room temperature. Allowing the sample to soak for any longer than four hours can compromise the



Modified from Kirkland and Carpenter (1994)

Modified from Kirkland and Carpenter (1994)

Figure 6. (*a*) General stratigraphy of the Morrison formation in the region surrounding the Mygatt-Moore Quarry indicating the location of the quarry in the stratigraphic section. The rocks exposed at the quarry represent middle portion of the Brushy Basin Member. (*b*) Higher resolution stratigraphy of the Mygatt-Moore quarry showing fossil distribution; dinosaur fossil material is concentrated toward the bottom of the exposure.

integrity of the structural carbonate of the enamel. After soaking in the buffer solution, the sample was rinsed five times with ultra-pure Milli-Q water. The remaining solid was then dried and weighed again to determine the amount of sedimentary carbonate present in each sample. The samples were then ready for analysis, and 1-2mg aliquots were weighed using a Sartorious Microbalance and loaded into Labco Exetainers®.

Enamel samples were analyzed for carbon and oxygen isotopes using an Elementar Isoprime mass spectrometer coupled to an Elemental Multiflow carbonate autosampler at University of Maryland, College Park. The sample vials were loaded into a 180-sample tray kept at 65°C and were individually flushed with a stream of UHP He carrier gas for 300 seconds, and then acidified using 0.1 ml of 100% phosphoric acid. Reactions were allowed to proceed for one hour before extraction of the evolved gas. Samples were run under continuous flow conditions with a trap current of 175μA, producing peak heights of 6 to 9 nA. Measurements are expressed in the standard delta notation as per mille values relative to Vienna PeeDee Belemnite (V-PDB), and uncertainties are determined by comparing sample measurements against those of the NBS-19 and Elementar carbonate standards. All ratios of carbon and oxygen isotopes were calculated using standard delta notation where, for example:

$$\delta^{13}C = [(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard} - 1]\times 1000$$

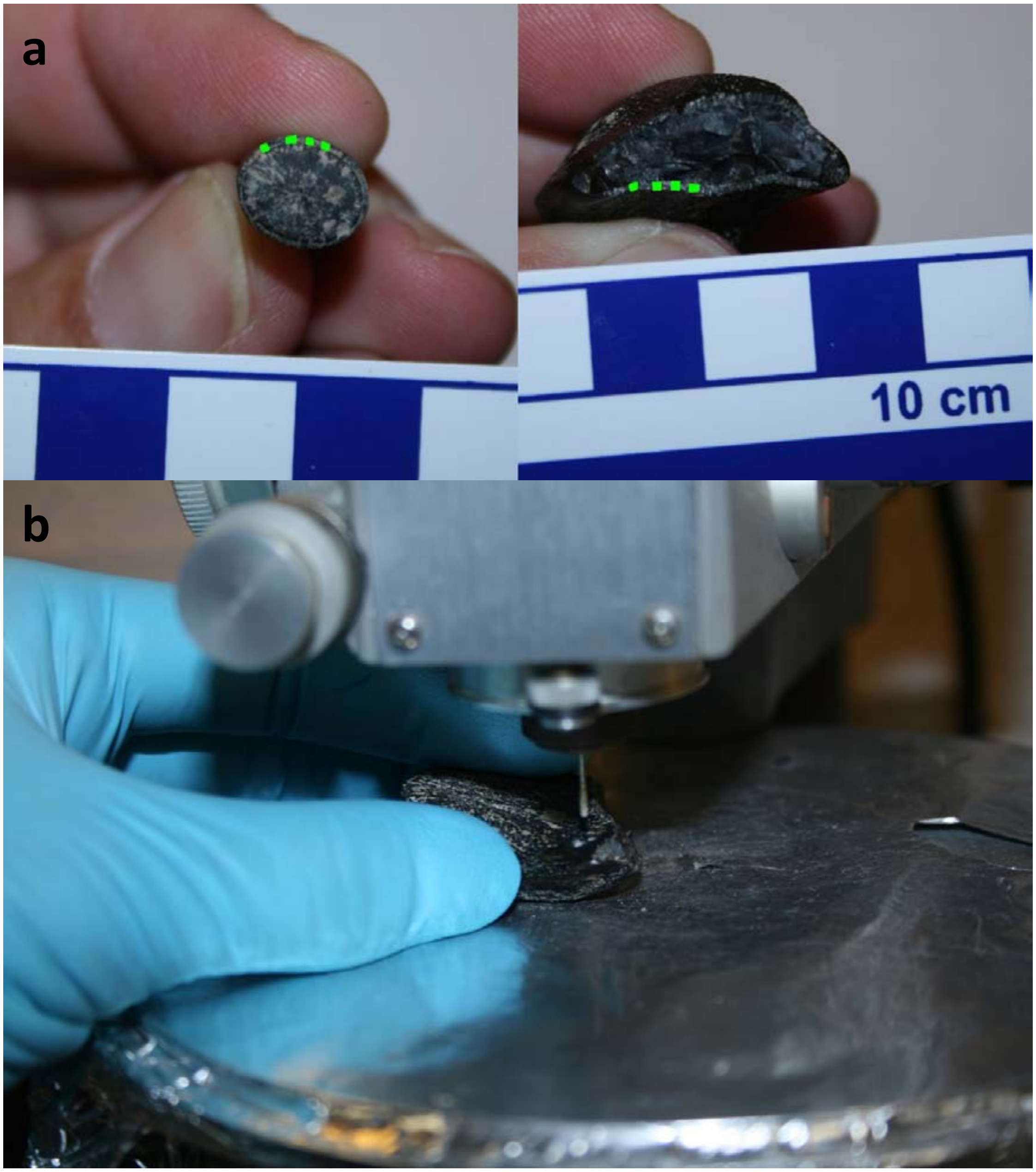


Figure 7. *(a)* Cross-sectional views of uncataloged NMNH diplodocid (left) and macronarian (right) teeth. A portion of the enamel layer is highlighted in green on each tooth.
(b) A Dremel drill with a diamond-tipped bit is used to bore into the thin enamel layer of each tooth. The underlying dentine must be avoided in this process.

RESULTS

All stable isotope data for sauropod tooth enamel and modern plant leaves are given in Appendix B. The analytical precision is ±0.087‰ for $\delta^{13}C$ (1σ) in the plant study; it is ±0.13‰ for $\delta^{13}C$ (1σ) and ±0.1‰ for $\delta^{18}O$ (1σ) in the enamel study (an example of how uncertainty was calculated is included in Appendix C). Modern plant samples yielded $\delta^{13}C$ values between -33.39‰ and -26.08‰ (Figure 8, Appendix B). Sauropod tooth enamel samples yielded $\delta^{18}O$ values between -9.89‰ and -6.12‰ and $\delta^{13}C$ values between -9.02‰ and -7.58‰ (Figure 9).

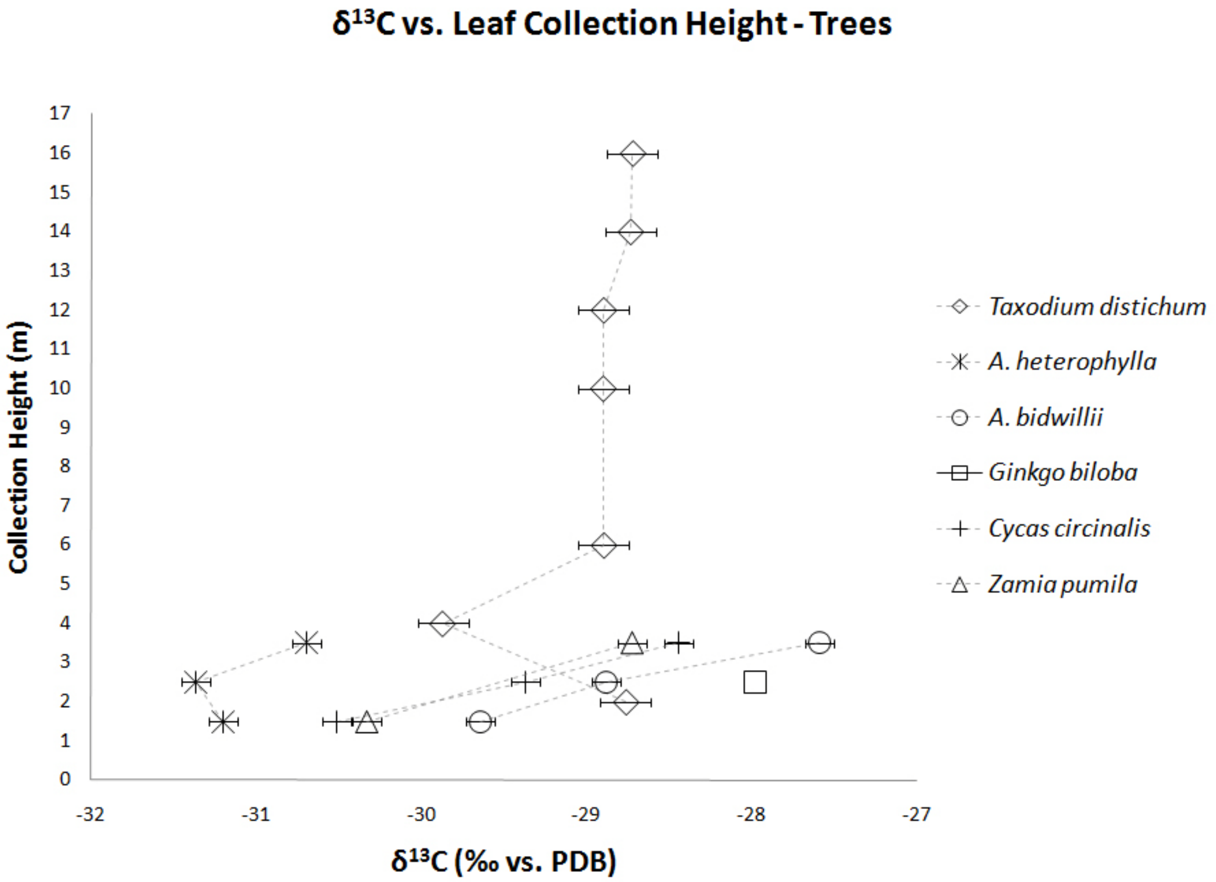


Figure 8. Carbon isotope ratio measurements for trees; each tree has higher $\delta^{13}C$ at the top of the tree than at the bottom.

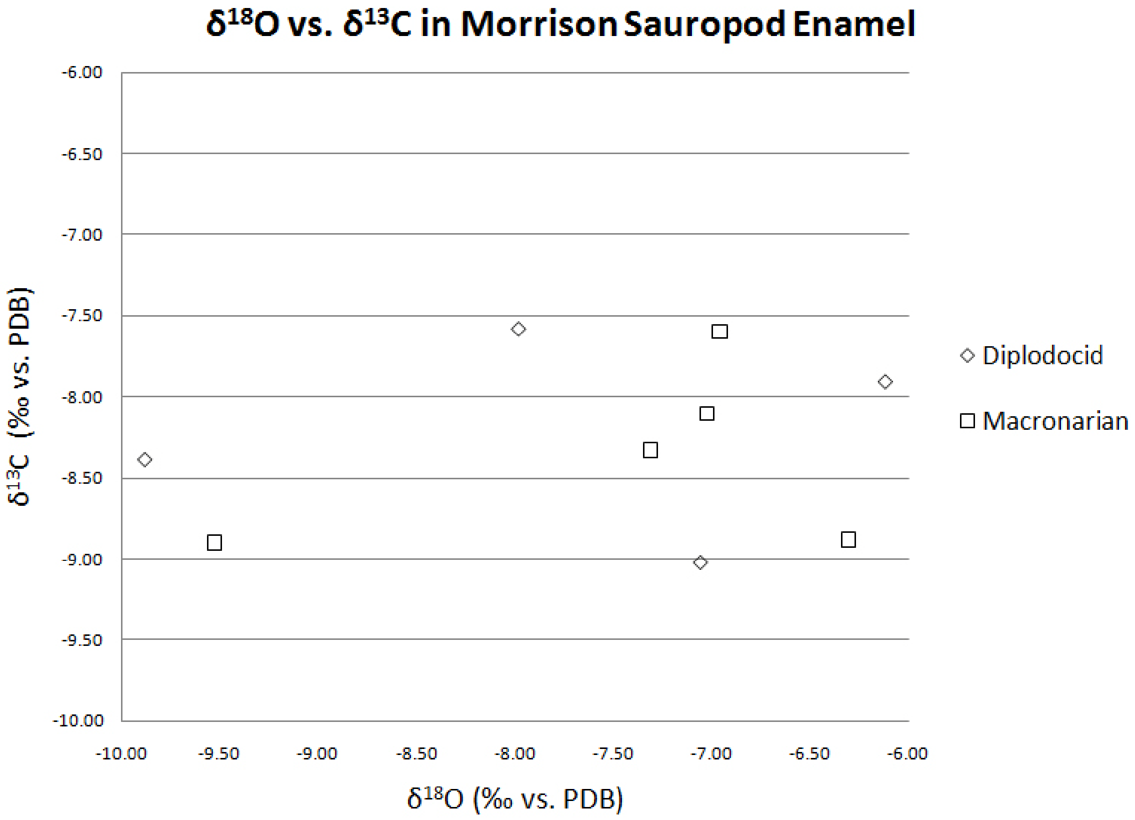


Figure 9. δ^{13}C and δ^{18}O values show no significant difference between diplodocids and macronarians. This is consistent with the null hypothesis that dipolodocid and macronarian sauropods were not partitioning resources exclusively by plant height. Note that sample numbers are small for each taxon, so these results should be treated as preliminary.

DISCUSSION

From the results of the plant analysis, some interesting and surprising trends emerge. Of the ground-level plants, those samples collected from shaded environments were not always depleted in ^{13}C relative to those collected from unshaded environments as was expected from the Cerling *et al.* (2004) study, in which ^{13}C is depleted in the shaded understory due to recycling of CO_2. This could be because many of the “shaded” samples were not collected from as deep in the underbrush as others simply because they weren’t present there; however, there is up to a 4‰ variation in δ^{13}C between several of the shaded and unshaded samples of single taxa. These variations were unexpected, but it seems likely that the collection site at the US Botanic Gardens is not a useful analog for a natural closed canopy forest system.

In the samples collected from trees, a statistically significant isotope effect is consistently observed, with δ^{13}C values being lower in samples collected toward the base of the tree than those collected toward the top in any given tree. This phenomenon—here proposed to be named *dendrostratigraphy*—is consistent with my running hypothesis that measured δ^{13}C values will increase relative to the heights at which samples were collected from the plants.

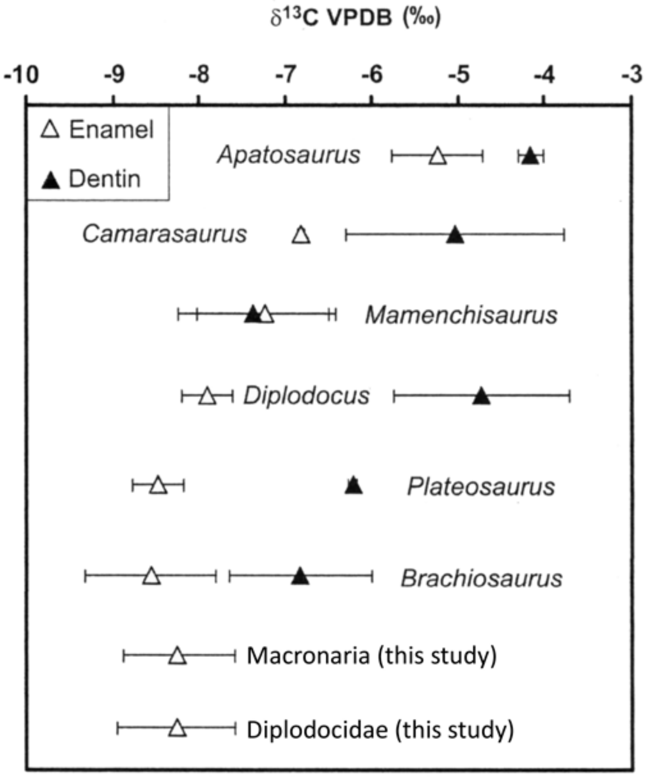


Figure 10. Tütken's $\delta^{13}C$ measurements for the enamel and dentine of various sauropod groups with the values from this study included. The diplodocid measurements from this study are consistent with the measurements for the genus *Diplodocus* from Tütken's study. The macronarian measurements from this study are most consistent with Tütken's *Brachiosaurus* measurements; however, the morphology the teeth in this study suggests that they are almost certainly the teeth of *Camarasaurus*. It should be noted that Tütken only has a single measurement for *Camarasaurus*. Modified from Tütken (2011).

This phenomenon was unexpected considering that the trees were not truly part of a closed canopy forest system as was the case in the Cerling *et al.* (2004) Ituri Forest study, but it does appear to be valid—repeated measurements consistently yielded a statistically significant increase in $\delta^{13}C$ values with height for every tree. Why dendrostratigraphy occurs is not well-understood; perhaps it has to do with the vertical fractionation of CO_2 as it diffuses upwards from the surface of the Earth. That is, perhaps as CO_2 is formed at the surface via the combustion of fuel and it diffuses vertically, the lighter $^{12}CO_2$ is preferentially used by plants for photosynthesis such that the lowest leaves on a tree get "first dibs", so to speak, and the CO_2 molecules comprising the light isotope get more and more depleted as the gas diffuses upward. This is speculative, and a more thorough systematic study on the matter would be useful in understanding this phenomenon.

Even without understanding why dendrostratigraphy occurs, it still has tremendously important implications for this study since dense rainforest was likely not present in the region of Morrison deposition during the Late Jurassic. The observation of dendrostratigraphy in isolated trees suggests that it doesn't matter that there may not have been dense, closed-canopy forest in the Morrison. This means that paleoecological inferences can be made of two or more different taxa potentially utilizing the same resources in the same region and partitioning plant resources by height alone. This is an important assumption for the hypotheses this study seeks to test—that sauropods were feeding on the same plant resources. These hypotheses only consider the vertical partitioning of plant resources.

No isotopic offset is observable between diplodocid and macronarian enamel in the tooth samples from the Mygatt-Moore Quarry (Figure 9). Both groups have $\delta^{18}O$ values ranging from ~-10.00‰ to ~-6.00‰ and $\delta^{13}C$ values ranging from ~-9.00‰ to ~-7.50‰. This overlap is not the result of diagenesis; enamel was selected as the material to analyze because of its high density and resistance to diagenetic alteration (Kohn & Cerling, 2002). These values are also consistent with the $\delta^{13}C$ values obtained by Tütken (2011) (Figure 10). Although the dendrostratigraphy of carbon in isolated trees has been demonstrated in this study, the same is not true of oxygen, so little can be inferred from the oxygen isotopic measurements. Even so, this overlap is consistent with the null hypothesis that the two groups were not feeding on the same plants and partitioning resources exclusively by height. This conclusion is not altogether surprising—it would be remarkable for the paleoecology of the two groups to be so simple, but this study provides quantitative evidence that Morrison sauropods likely partitioned resources by feeding on different plant groups or possibly by feeding in different regions.

CONCLUSIONS AND FURTHER WORK

Exactly how megaherbivorous neosauropod dinosaurs of the Late Jurassic were able to coexist without competing for resources has been a point of contention for well over a century. Most of the arguments put forth to date have been concerned with wear facets on the teeth of neosauropods or with postcranial morphological traits that can potentially by used to identify biomechanical constraints on the behaviors of the dinosaurs, but very few studies have considered geochemical evidence. In this study, geochemical analyses have been used to suggest that trees exhibit an increase in $\delta^{13}C$ values with tree height regardless of environment (dendrostratigraphy), which can be used to infer the relative feeding heights of two or more taxa feeding in the same region. A more thorough systematic investigation of the nature of dendrostratigraphy would be useful, measuring not only carbon isotopes but also oxygen isotopes in a much larger sample set than that considered in this study.

Isotope ratio measurements of diplodocid and macronarian sauropod enamel are consistent with the null hypothesis that the two groups did not partition resources exclusively by height, though a more thorough study utilizing a larger sample set would be useful. This should not be altogether surprising given the differences in both overall morphology, but these data provide quantitative evidence that vertical fractionation alone did not occur. This implies that the two groups likely partitioned resources by feeding on different types of plants. This issue is further investigated in Appendix D using taxic abundance data from the Paleobiology Database to look for correlations in the relative abundances of major plant and sauropod groups from the Late Jurassic worldwide and ultimately to make inferences regarding sauropod paleoecology in the Morrison.

ACKNOWLEDGEMENTS

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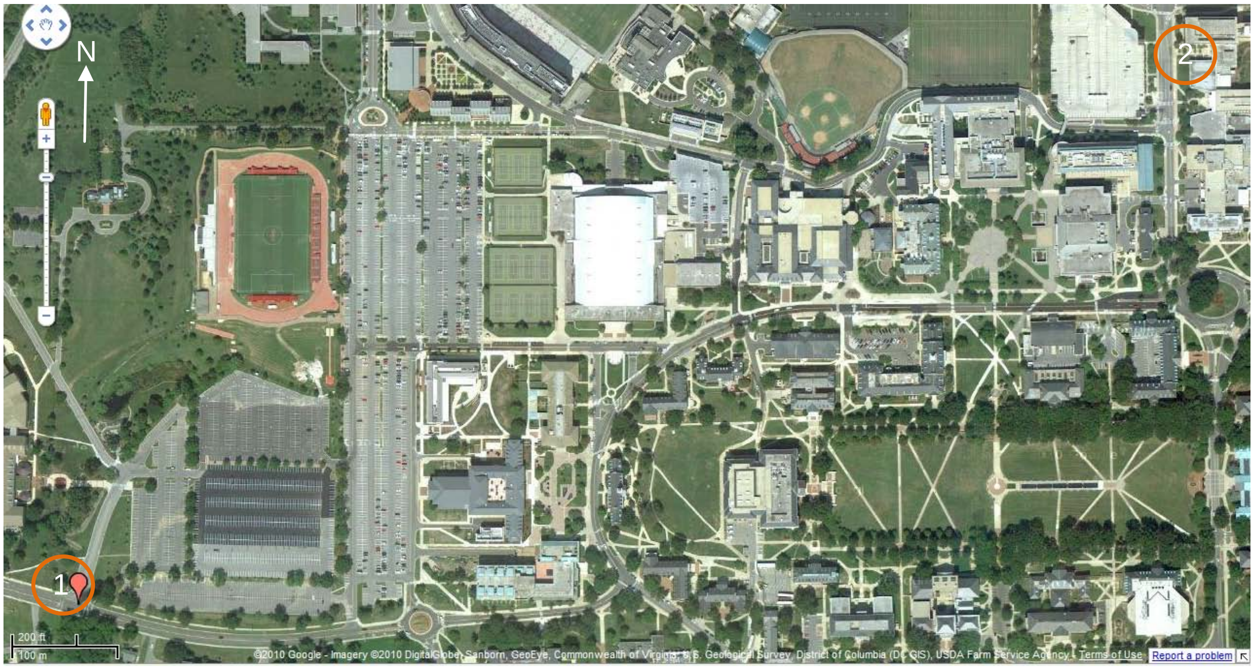
APPENDIX A



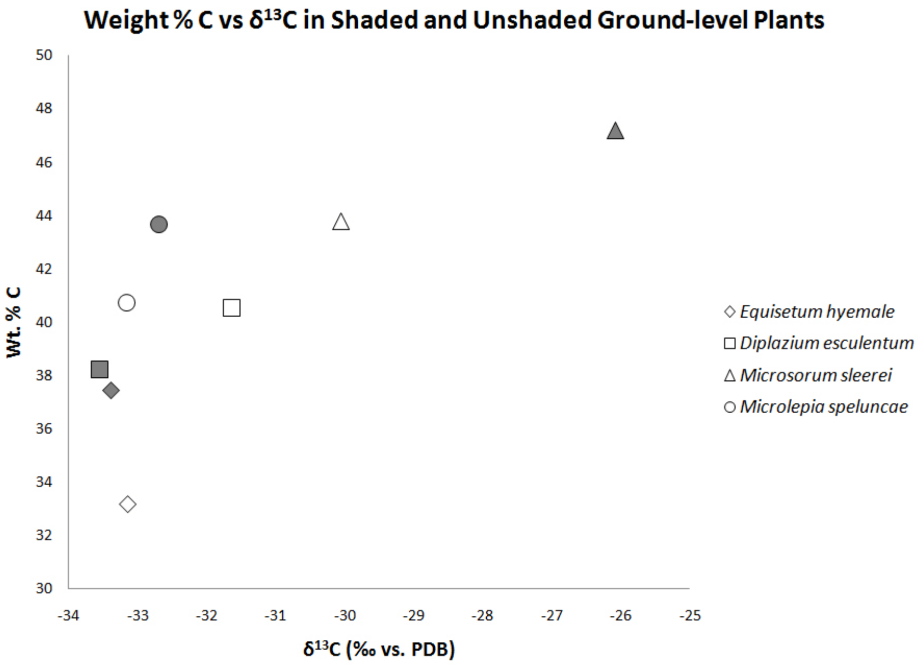
Taxon locations on University of Maryland, College Park campus. Map from google.com.

1. *Taxodium distichum*
2. *Ginkgo biloba*

APPENDIX B – EXPERIMENTAL RESULTS

Tooth Enamel Isotope Ratio Values

Name	Sample Description	$\delta^{13}C$ (‰ vs. PDB)	$\delta^{18}O$ (‰ vs. PDB)
MWC6985	Diplodocid	-9.02	-7.06
MWC6818	Diplodocid	-7.58	-7.99
MWC6814	Diplodocid	-7.905	-6.12
MWC5716	Diplodocid	-8.385	-9.885
MWC4316	Macronarian	-8.90	-9.53
MWC5719	Macronarian	-8.88	-6.31
MWC4258	Macronarian	-8.11	-7.03
MWC6996	Macronarian	-7.60	-6.96
MWC4303	Macronarian	-8.33	-7.31

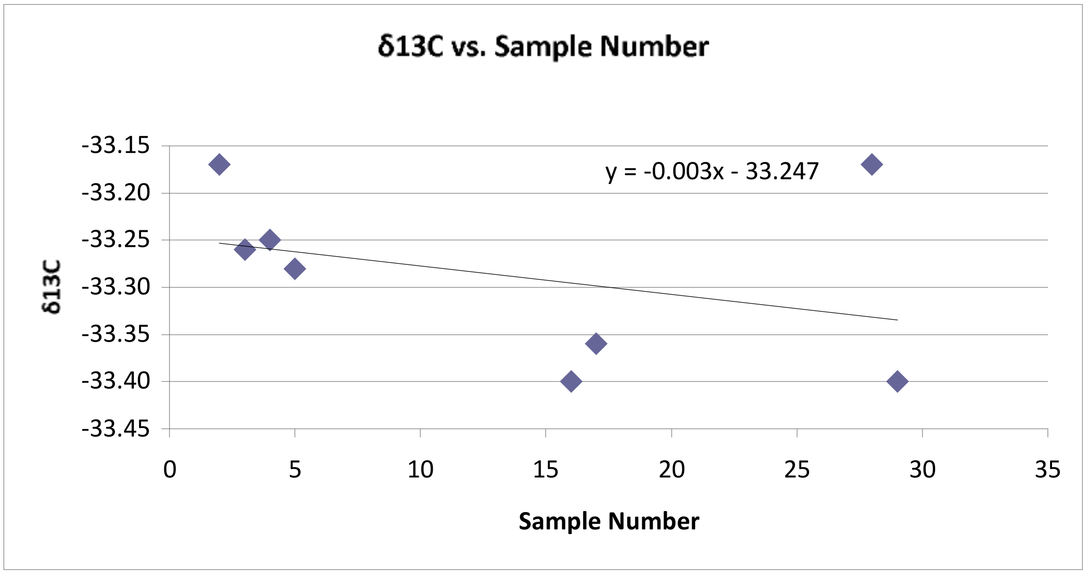


Plant Isotope Ratio Values

Taxon	Condition	$\delta^{13}C$ (‰ vs. PDB)	Sample Height (m)	Wt. %
Taxodium distichum		-28.76	2	
Taxodium distichum		-29.87	4	
Taxodium dstichum		-2890	6	
Taxodium distichum		-28.90	10	
Taxodium distichum		-28.90	12	
Taxodium distichum		-28.74	14	
Taxodium distichm		-28.72	16	
Equisetum hyemale	Unshaded	-33.39	0	37.4692
Equisetum hyemale	Shaded	-33.15	0	33.1828
Diplazium esculentum	Unshaded	-31.64	0	40.5564
Diplazium esculentum	Shaded	-33.55	0	38.25
Microlepia speluncae	Unshaded	-33.16	0	40.7436
Microlepia speluncae	Shaded	-32.69	0	43.6772
Microsorum sleerei	Unshaded	-30.06	0	43.778
Microsorum sleerei	Shaded	-26.08	0	47.2016
Araucaria heterophylla		-30.39	1.5	
Araucaria heterophylla		-31.29	1.5	
Araucaria heterophylla		-31.40	2.5	
Araucaria heterophylla		-30.76	3.5	
Araucaria heterophylla		-30.69	1.5	
Araucaria heterophylla		-31.12	1.5	
Araucaria heterophylla		-31.34	2.5	
Araucaria heterophylla		-30.62	3.5	
Colysis wrightii		-30.71	0	
Zamia pumila		-30.33	1.5	
Zamia pumila		-28.73	3.5	
Cycas circinalis		-30.52	1.5	
Cycas circinalis		-29.38	2.5	
Cycas circinalis		-28.44	3.5	
Araucaria bidwillii		-29.65	1.5	
Araucaria bidwillii		-28.89	2.5	
Araucaria bidwillii		-27.59	3.5	
Ginkgo biloba		-27.98	2.5	

APPENDIX C – UNCERTAINTY ANALYSIS

Sample #	Name	$\delta^{13}C$ Raw (‰)	$\delta^{13}C$ CORR (‰)	
2	BB 11-22-10 urea R1	-33.17	-33.16	
3	BB 11-22-10 urea R2	-33.26	-33.25	
4	BB 11-22-10 urea R3	-33.25	-33.24	
5	BB 11-22-10 urea R4	-33.28	-33.27	
16	BB 11-22-10 urea R5	-33.40	-33.35	
17	BB 11-22-10 urea R6	-33.36	-33.31	
28	BB 11-22-10 urea R7	-33.17	-33.09	
29	BB 11-22-10 urea R8	-33.40	-33.31	
		-33.29	-33.25	AVERAGE
		0.093	0.087	STDEV
		3.90	3.86	OFFSET



Uncertainty for $\delta^{13}C$ and $\delta^{18}O$ measurements is determined using repeated measurements of the the appropriate standards. In the example above, raw $\delta^{13}C$ measurements are plotted against sample numbers, and the slope of the resulting trendline is subtracted from each of the raw measurements and multiplied by its sample number for corrected $\delta^{13}C$ values. The standard deviation of these corrected values is calculated to give the uncertainty of the measurements. For this example, $\sigma = \pm 0.087$‰.

APPENDIX D – COMPARISON OF THE RELATIVE ABUNDANCES OF THE FLORA AND SAUROPODOMOPRH FAUNA OF THE MORRISON TO THOSE OF OTHER UPPER JURASSIC FORMATIONS

Here, the relative abundances of sauropod and plant taxa from the Morrison are compared to those of other similar synchronous terrestrial deposits in order to investigate the way Morrison sauropods partitioned resources by plant type or height or otherwise.

OTHER UPPER JURASSIC FORMATIONS

The Morrison Formation has many faunal, floral, sedimentological, and age similarities to Upper Jurassic deposits from other parts of the world (Mateus 2006). The Lourinhã and Alcobaça formations of Portugal are Kimmeridian and Tithonian continental and shallow marine sand and mud deposits. These deposits preserve alluvial fan and fluvio-deltaic depositional environments punctuated by periodic marine transgressions. The Tendaguru Beds are also Kimmeridgian and Tithonian in age and comprise calcareous sandstone and siltstone deposits. The Morrison is the largest of these formations, with outcrops occupying 2000 times the area of Lourinhã outcrops. These paleoregions also share some dinosaurian fauna between them: *Ceratosaurus, Torvosaurus,* and *Apatosaurus* are all present in the Late Jurassic of both North America and Portugal, and *Allosaurus* may be present in all three regions. All of the families of dinosaur present in Late Jurassic deposits in Portugal are also present in the Morrison, with distinct but closely-related generic pairs present between the two regions such as *Lusotitan* and *Brachiosaurus*, *Lourinhasaurus* and *Camarasaurus*, and *Dinheirosaurus* and *Diplodocus*. A major difference in the the dinosaurian faunas of these regions is that ornithischians are more generically abundant than sauropods in Portuguese deposits, while the opposite is true of the Morrison and Tendaguru. While these three regions have much in common, Asia developed a dinosaurian fauna distinct from the rest of the world, with Chinese deposits from the Shaximiao, Suining, and Shishugou formations providing the unique mamenchisaurid sauropods.

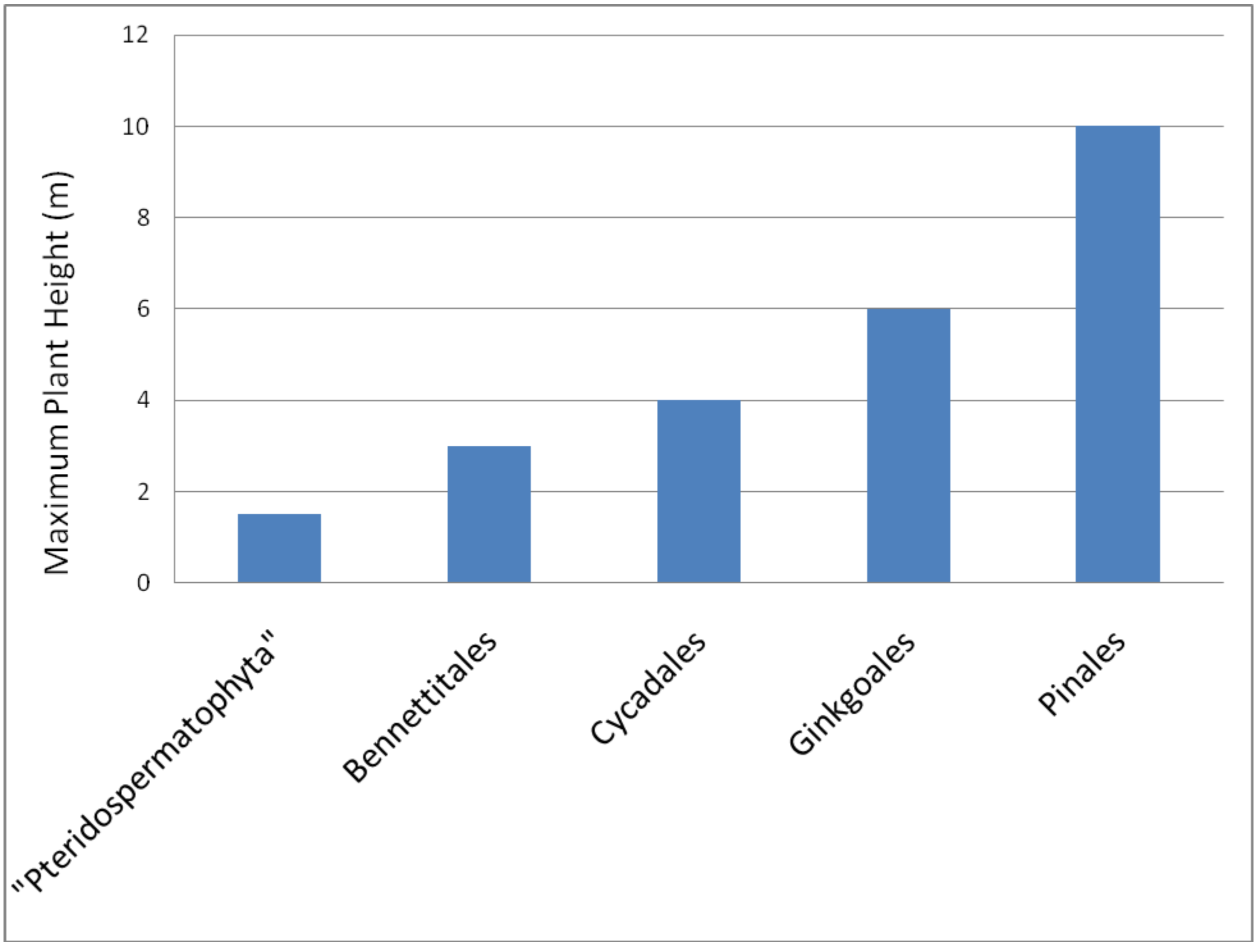


Figure 11. Average maximum potential plant heights of common Late Jurassic plant taxa. (Modified from Stevens & Parrish (2005)).

OBJECTIVES AND METHODS

While the floras and faunas of Late Jurassic deposits in Portugal, western North America, and Africa are all similar to each other, there are distinct differences in the relative abundances of major plant and sauropodomorph dinosaur taxa. Identifying correlations between abundances of plant and sauropod taxa may be useful in identifying broad paleoecological patterns that can be used to infer feeding habits in Morrison sauropods. Since the feeding heights of macronarians and the maximum heights of plants are relatively fixed and well-understood, these can be used as standards in understanding how diplodocids may have fed. The feeding heights of camarasaurids and diplodocids have potential overlap when assuming that all four legs remain on the ground and that the head is being held as high as possible, so evidence for the presence or absence of feeding overlap in brachiosaurids and diplodocids is like the most useful relationship in determining whether or not diplodocids habitually fed in a tripod stance. Assuming that brachiosaurids fed at the height of the full extent of their necks, they likely fed exclusively on pinale plants, which were the only plants during the Late Jurassic to exceed heights of approximately six meters (Figure 11). If adult diplodocids fed reared on their hindlimbs, they would also have been limited to eating pinale plants, so the relative abundances of pinale groups will be of particular significance to this study.

The hypotheses for this analysis are as follows:

> $H_{0:}$ Low-browsing diplodocids: Diplodocids do not demonstrate the same response to changes in relative abundances of the major Late Jurassic plant taxa that brachiosaurids do in deposits from the Western Laurasian, Eastern Gondwanan, and Eastern Paleotethyian regions and are thus not competing for the same plant resources as brachiosaurids.
>
> $H_{1:}$ High-browsing diplodocids: Diplodocids demonstrate the same response to changes in relative abundances of the major Late Jurassic plant taxa that brachiosaurids do in deposits from the Western Laurasian, Eastern Gondwanan, and Eastern Paleotethyian regions and are thus likely competing for the same plant resources as brachiosaurids.

In order to test these hypotheses, data obtained from The Paleobiological Database were utilized. Three broad paleoregions were analyzed for relative sauropod and plant abundances: Western Laurasia, Eastern Gondwana, and Eastern Paleotethys (Figure 12). These abundances were calculated by dividing the number of collections of each taxa by the total number of collections of taxa in each respective region. Each taxon was assigned to a larger family- or order-level group to the best of the author's ability, and these groups were lumped together for each region. The resulting abundances were then plotted on a stacked area graph (Figure 13).

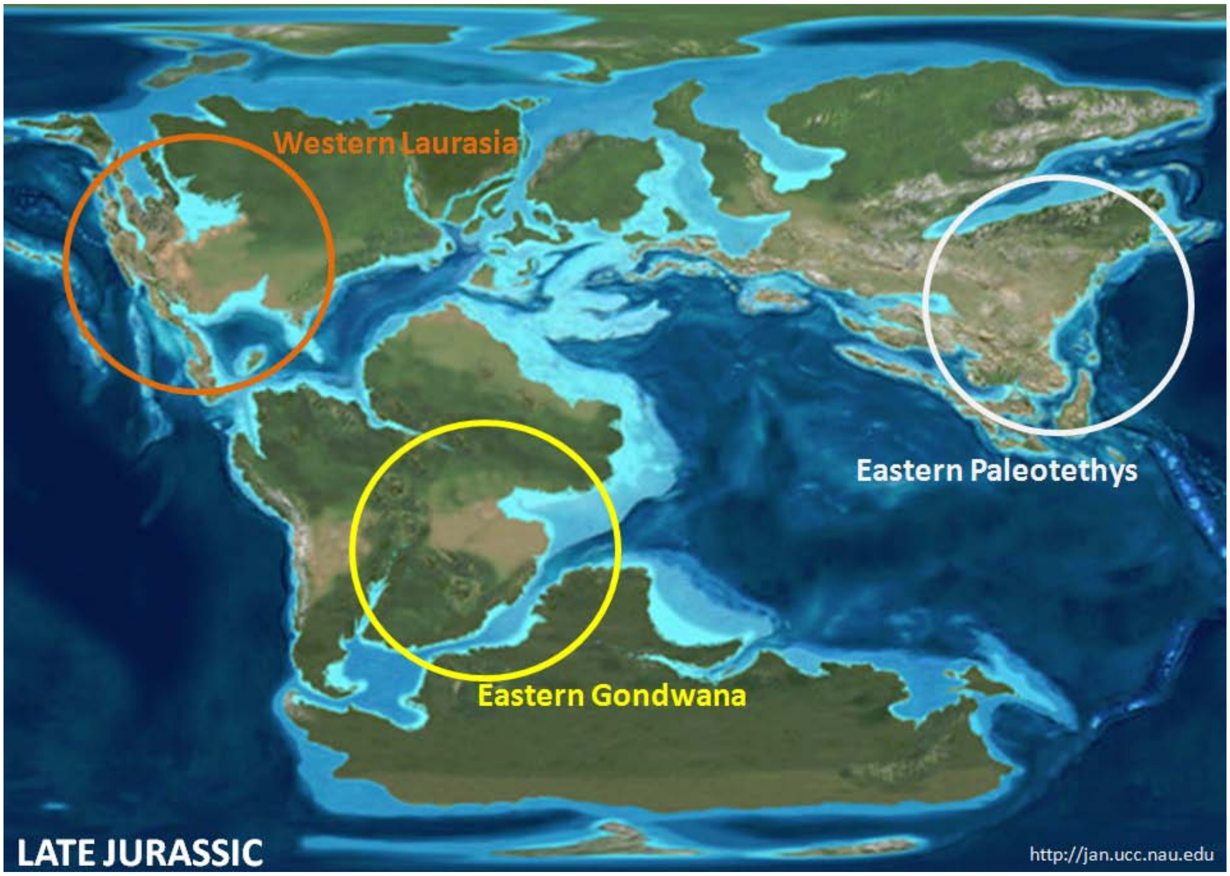


Figure 12. Paleogeographic map of the Late Jurassic with regions considered in this study highlighted. (http://jan.ucc/nau/edu)

RESULTS AND DISCUSSION

Each of the three paleoregions included in this study is dominated by a different group of sauropod dinosaur: Western Laurasia is diplodocoid-dominated, Eastern Gondwana is macronarian-dominated, and Easern Paleotethys is “basal eusauropod”-dominated. The sauropod faunas of Western Laurasia and Eastern Gondwana are more similar to each other than either is to Eastern Paleotethys. The floras of these regions are largely similar and in the groups present, with some notable and significant differences in relative abundances. Since very little faunal overlap is observed between Paleotethys and Laurasia/Gondwana, it does not provide much insight for the inference of diplodocoid feeding height. An interesting difference between the Laurasian and Gondwanan taxa is that the relative abundances of both brachiosaurids and araucareaceans are much higher in the Gondwanan deposits.

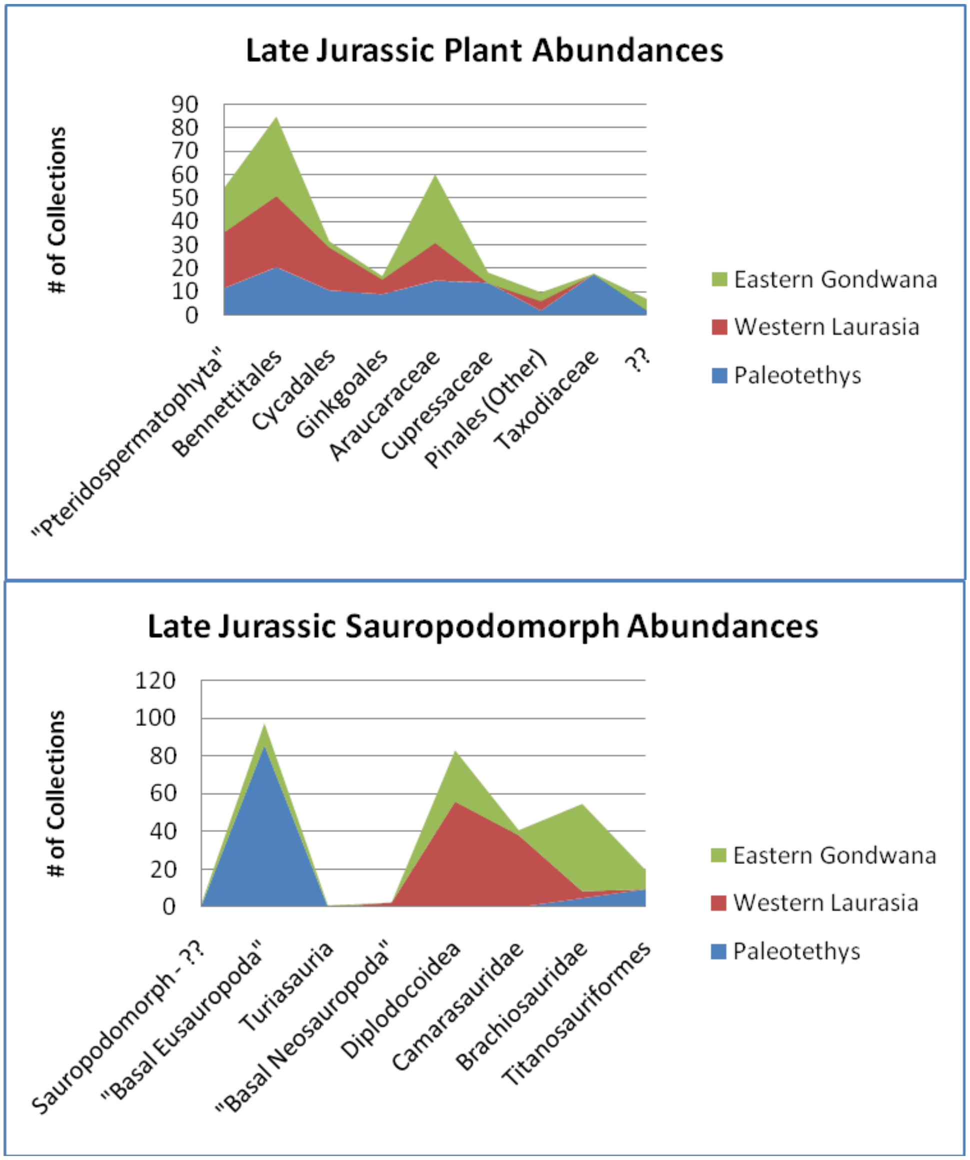


Figure 13. Stacked area plots of the relative abundances of Late Jurassic plant and sauropodomorph taxa.

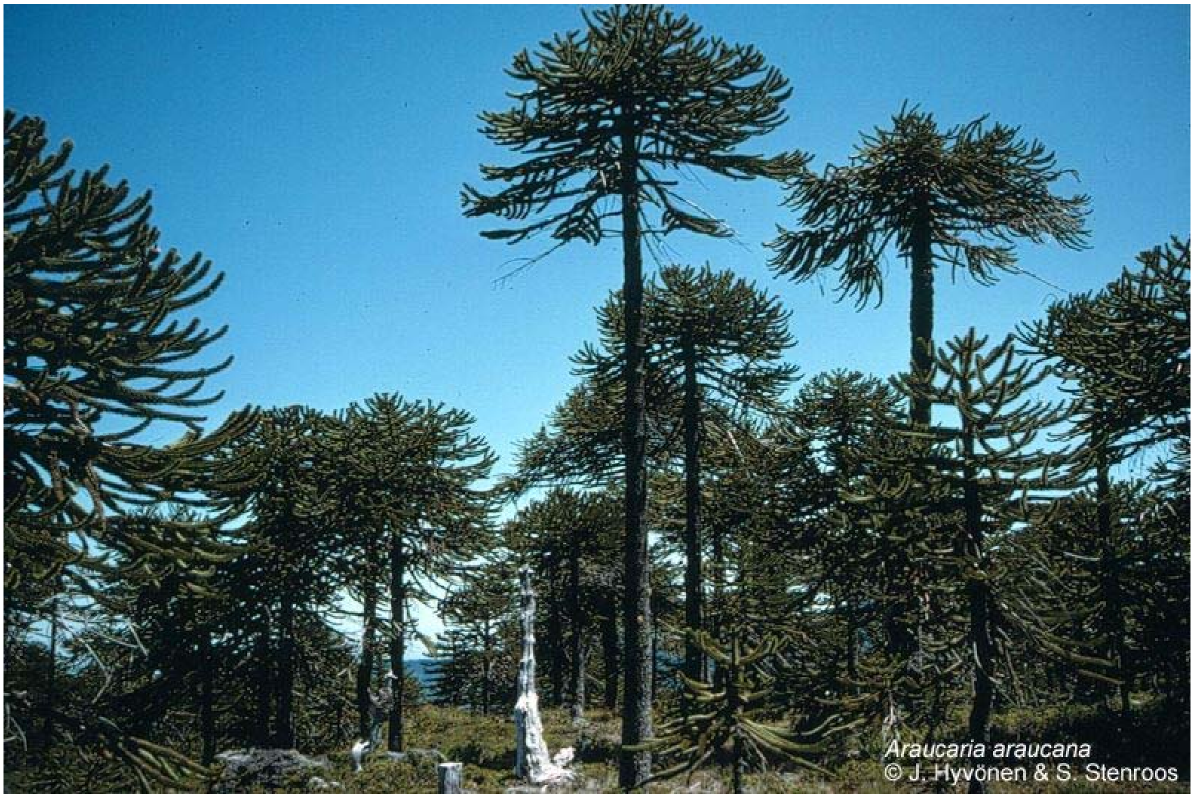


Figure 14. Modern Araucariaceae taxon *Araucaria araucana*.

Araucariacea is a family of the order Pinales, and trees of modern araucariacean taxa can grow to astounding heights far exceeding 30 meters. None of the sauropods discussed would have been able to feed at such heights, but there is another interesting aspect of Araucariaceae. Some species of the genus *Araucaria* concentrate the majority of their leaves at the top of the tree (Figure 14). If this was a common morphology of Late Jurassic members of Araucariaceae, it could have serious implications for sauropod niche partitioning. With relatively abundant Araucariaceae, they would be a vast untapped source of food just out of reach for herbivores, and it might be expected that not only brachiosaurids would flourish with increased abundance of Araucariaceae but also diplodocids if they were feeding as tripodal high browsers. In fact, the opposite is observed. In Gondwana, where Araucariacea is at its most abundant, diplodocoids are relatively less abundant than they are in Laurasia. Instead, diplodocid abundance seems to correlate with Cycadales and Ginkgoales, all of which are relatively abundant in Laurasia but are not so in Gondwana. Interestingly, *Araucaria* also offers more energy than other plant groups, and would likely have grown in vast monospecific stands (Sander *et al.*2010).

CONCLUSIONS

While the sample set utilized for this study was rather small and there was significant lumping of taxa, some interesting trends do emerge in Late Jurassic plant and sauropod taxa. Given the correlative abundances of brachiosaurids with Araucariaceae and diplodocids with Cycadales and Ginkgoales, I very tentatively conclude that my first hypothesis H_1 is refuted in light of the given data, and that the null hypothesis H_0 for a low-browsing Diplodocidae is better supported by these data. A more thorough, systematic analysis of sauropod and plant abundances at the Formation level could prove fruitful for providing more confident interpretations of diplodocid feeding.

Paleotethys			
Genus	**Collections**	**Taxonomic Notes**	**Relative Abundance (%)**
Araucarites	1	Pinales (Araucariaceae)	0.41
Brachyphyllum	34	Araucariaceae leaves	14.11
Cupressinocladus	33	Pinales (Cupressaceae)	13.69
Desmiophyllum	4	Pinales	1.66
Elatocladus	37	Taxodiaceae	15.35
Ginkgo	13	Ginkgoales (Ginkgoaceae)	5.39
Nilsonia	25	Cycadales	10.37
Otozamites	20	Cycadopsida - Bennettitales	8.30
Pterophyllum	9	Cycadopsida - Bennettitales	3.73
Ptilophyllum	14	Cycadopsida - Bennettitales	5.81
Sagenopteris	14	Pteridospermatophyta	5.81
Sphenobaiera	8	Ginkgoales (Ginkgoaceae)	3.32
Sphenolepis	5	Pinales (Taxodiaceae)	2.07
Sphenopteris	13	Pteridospermatophyta	5.39
Taeniopteris	5	??	2.07
Zamites	6	Cycadopsida - Bennettitales	2.49
TOTAL	241		
Western Laurasia			
Genus	**Collections**	**Taxonomic Notes**	**Relative Abundance (%)**
Araucaria	3	Pinales (Araucariaceae)	3.26
Araucarites	3	Pinales (Araucariaceae)	3.26
Brachyphyllum	9	Araucariaceae leaves	9.78
Cycadolepis	1	Cycadopsida - Bennettitales	1.09
Desmiophyllum	2	Pinales	2.17
Elatocladus	2	Pinales (Podocarpaceae)	2.17
Ginkgo	3	Ginkgoales (Ginkgoaceae)	3.26
Nilsonia	17	Cycadales	18.48
Otozamites	1	Cycadopsida - Bennettitales	1.09
Pachypteris	8	Pteridospermatophyta	8.70
Pterophyllum	16	Cycadopsida - Bennettitales	17.39
Ptilophyllum	1	Cycadopsida - Bennettitales	1.09
Sagenopteris	5	Pteridospermatophyta	5.43
Sphenobaiera	3	Ginkgoales (Ginkgoaceae)	3.26
Sphenopteris	9	Pteridospermatophyta	9.78
Weltrichia	1	Cycadopsida - Bennettitales	1.09
Williamsonia	3	Cycadopsida - Bennettitales	3.26
Zamites	5	Cycadopsida - Bennettitales	5.43
TOTAL	92		

Eastern Gondwana

Genus	**Collections**	**Taxonomic Notes**	**Relative Abundance (%)**
Alethopteris	1	Pteridospermatophyta	0.38
Araucaria	4	Pinales (Araucariaceae)	1.54
Araucarites	22	Pinales (Araucariaceae)	8.46
Brachyphyllum	50	Araucariaceae leaves	19.23
Bucklandia	2	Cycadales	0.77
Carpolithes	2	??	0.77
Cupressinocladus	12	Pinales (Cupressaceae)	4.62
Cycadolepis	19	Cycadopsida - Bennettitales	7.31
Desmiophyllum	2	Pinales	0.77
Elatocladus	8	Pinales (Podocarpaceae)	3.08
Ginkgo	4	Ginkgoales (Ginkgoaceae)	1.54
Nilsonia	5	Cycadales	1.92
Otozamites	7	Cycadopsida - Bennettitales	2.69
Pachypteris	7	Pteridospermatophyta	2.69
Pecopteris	2	??	0.77
Pterophyllum	2	Cycadopsida - Bennettitales	0.77
Ptilophyllum	9	Cycadopsida - Bennettitales	3.46
Rhaphidopteris	6	Pteridospermatophyta	2.31
Sphenolepis	1	Pinales (Taxodiaceae)	0.38
Sphenopteris	35	Pteridospermatophyta	13.46
Taeniopteris	9	??	3.46
Williamsonia	7	Cycadopsida - Bennettitales	2.69
Zamites	44	Cycadopsida - Bennettitales	16.92
TOTAL	260		

Regional Taxon Abundances

Taxon	**Paleotethys**	**Western Laurasia**	**Eastern Gondwana**
"Pteridospermatophyta"	11.2	23.91	18.85
Bennettitales	20.33	30.43	33.85
Cycadales	10.37	18.48	2.69
Ginkgoales	8.71	6.52	1.54
Araucaraceae	14.52	16.3	29.23
Cupressaceae	13.69	0	4.62
Pinales (Other)	1.66	4.35	3.85
Taxodiaceae	17.43	0	0.38
??	2.07	0	5

Appendex B: Sauropodomorph Data

Western Laurasia			
Genus	**Collections**	**Taxonomic Notes**	**Relative Abundance (%)**
Amphicoelias	4	Diplodocoidea	1.62
Apatosaurus	61	Diplodocoidea	24.70
Barosaurus	14	Diplodocoidea	5.67
Brachiosaurus	9	Macronaria - Brachiosauridae	3.64
Camarasaurus	94	Macronaria - Camarasauridae	38.06
Diplodocus	53	Diplodocoidea	21.46
Dystrophaeus	1	Diplodocoidea	0.40
Dystylosaurus	1	Diplodocoidea	0.40
Haplocanthosaurus	6	Basal Neosauropod	2.43
Supersaurus	3	Diplodocoidea	1.21
Suuwassea	1	Diplodocoidea	0.40
TOTAL	247		
Eastern Gondwana			
Genus	**Collections**	**Taxonomic Notes**	**Relative Abundance (%)**
Amphicoelias	1	Diplodocoidea	0.91
Australodocus	1	Diplodocoidea	0.91
Barosaurus	1	Diplodocoidea	0.91
Brachiosaurus	3	Macronaria - Brachiosauridae	2.73
Brohisaurus	2	Macronaria - Titanosauria	1.82
Camarasaurus	3	Macronaria - Camarasauridae	2.73
Dicraeosaurus	19	Diplodocoidea	17.27
Dinheirosaurus	1	Diplodocoidea	0.91
Galvesaurus	1	Eusauropoda - Turiasauria	0.91
Giraffatitan	42	Macronaria - Brachiosauridae	38.18
Janenschia	7	Macronaria - Titanosauria	6.36
Lourinhasaurus	13	Basal Eusauropoda	11.82
Lusotitan	6	Macronaria - Brachiosauridae	5.45
Ornithopsis	1	Macronaria - Titanosauria	0.91
Pleurocoelus	1	Macronaria - Basal Titanosauriform	0.91
Tendaguria	1	Sauropodomorph - ??	0.91
Tornieria	7	Diplodocoidea	6.36
TOTAL	110		

Paleotethys			
Genus	**Collections**	**Taxonomic Notes**	**Relative Abundance (%)**
Daanosaurus	1	Macronarian - Brachiosauridae	4.76
Euhelopus	2	Basal Titanosauriform	9.52
Mamenchisaurus	13	Basal Eusauropoda	61.90
Omeisaurus	4	Basal Eusauropoda	19.05
Shunosaurus	1	Basal Eusauropoda	4.76
TOTAL	21		

Regional Taxon Abundances

Taxon	Paleotethys	Western Laurasia	Eastern Gondwana
Sauropodomorph - ??	0	0	0.91
"Basal Eusauropoda"	85.71	0	11.82
Turiasauria	0	0	0.91
"Basal Neosauropoda"	0	2.43	0
Diplodocoidea	0	55.87	27.27
Camarasauridae	0	38.06	2.73
Brachiosauridae	4.76	3.64	46.36
Titanosauriformes	9.52	0	10

These data were downloaded from the Paleobiology Database (http://www.paleodb.org) on 07 December, 2010, using the group name 'marine' and the following parameters: time intervals = Late Jurassic, region = Paleotethys and Eastern Gondwana and Western Laurentia, paleoenvironment = terrestrial, class = Sauropoda and Plantae.

THE UNIVERSITY OF MARYLAND HONOR PLEDGE

I pledge on my honor that I have not given or received any unauthorized assistance or plagiarized on this assignment.

Benjamin T. [illegible], III

29 April 2011