

A Stable Isotopic Investigation of Resource Partitioning Among Neosauropod Dinosaurs of the Upper Jurassic Morrison Formation

Benjamin T. Breeden, III¹

Advisors: Dr. Thomas R. Holtz¹, Jr., Dr. Alan J. Kaufman², and Dr. Matthew T. Carrano³

¹Department of Geology, The University of Maryland, College Park, MD 20742, USA; ²Department of Geology, Isotope Geochemistry Laboratory, University of Maryland, College Park, Maryland 20742, USA; ³Department of Paleobiology, Smithsonian Institution, Washington, DC 20013, USA



Figure 1. 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.*

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, semiarid 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 occurs not only in trees within 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.

HYPOTHESES

- Morrison neosauropod niche partitioning:
 - H₀. Null hypothesis: There is no isotopic differentiation between Diplodocidae and *Camarasaurus*.
 - H₁. Low-browsing diplodocids: $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for diplodocids will be statistically significantly lower than for *Camarasaurus*.
 - H₂. High-browsing diplodocids: $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for diplodocids will be statistically significantly higher than for *Camarasaurus*.
- Ground-truthing $\delta^{13}\text{C}$ partitioning with height in modern C3 plants:
 - H₀. Null hypothesis: There is no isotopic variation between values of ground cover, low level branches, and high level branches.
 - H₁. Hypothesis 1: Measured $\delta^{13}\text{C}$ values will increase relative to the heights at which samples were collected from the plants.

MATERIALS AND METHODS

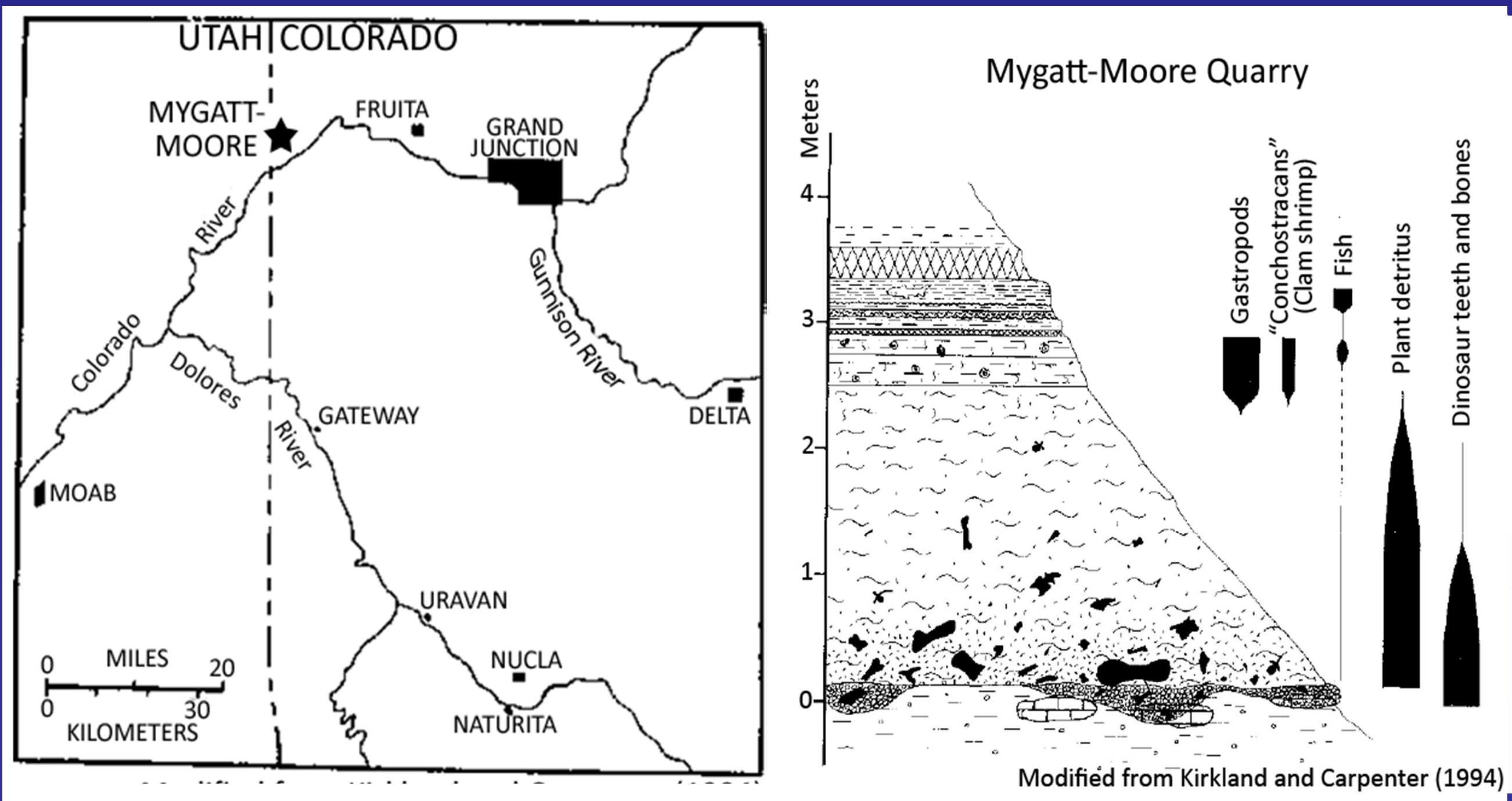


Figure 2. Tooth samples were collected by the Museum of Western Colorado where the Upper Jurassic Morrison Formation crops out at the Mygatt-Moore Quarry (MMQ) site in Western Colorado near the Utah border. Various fossil types are distributed throughout the stratigraphic succession exposed at MMQ, with dinosaur fossils being concentrated at the base of the sectin. Figures modified from Kirkland and Carpenter (1994).



Figure 3. The majority of the plants used in this study were collected at the United States Botanic Gardens (USBG) in Washington, DC. The USBG's Garden Primeval (left) is a reconstructed Mesozoic landscape full of plants closely related to those present in the Jurassic. Some plants were collected on the University of Maryland campus; these similarly selected because of their close relations to Jurassic plants.

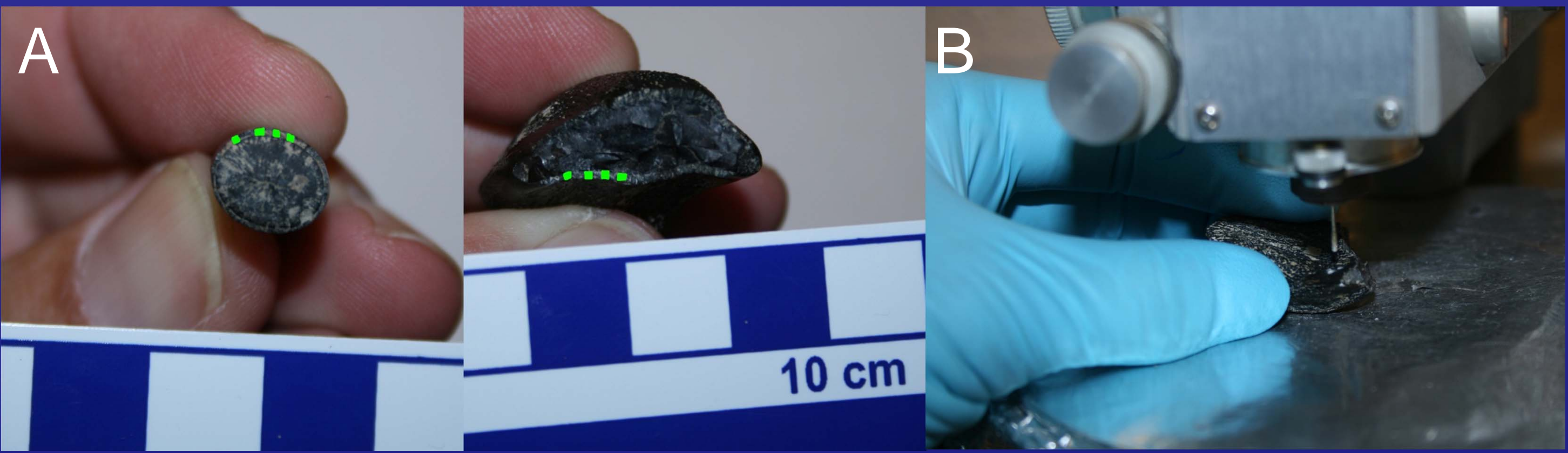


Figure 4. (a) Cross-sectional views of uncataloged NMNH diplodocid (left) and macronarian (right) teeth. A portion of the enamel layer is highlighted in green on each tooth. (b) A Dremel drill with a diamond-tipped bit is used to bore into the thin enamel layer of each tooth. The underlying dentine must be avoided in this process.

Enamel powders were treated with bleach to oxidize and remove lingering organic matter and soluble non-structural minerals and a calcium acetate/acetic acid buffer to remove and non-structurally-bound carbonate. Plant samples were dried in a utility oven and crushed in an aluminum mortar and pestle before being weighed for analysis. Tooth enamel samples were analyzed for carbon and oxygen isotopes using an Elementar Isoprime mass spectrometer coupled to an Elemental Multiflow carbonate autosampler, and the leaf samples were analyzed for carbon isotopes using a Eurovector elemental analyzer (EA) coupled to an Isoprime continuous flow (CF) mass spectrometer at University of Maryland, College Park.

RESULTS AND DISCUSSION

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 Elemental carbonate standards. All ratios of carbon and oxygen isotopes were calculated using standard delta notation where, for example:

$$\delta^{13}\text{C} = \left[\left(\frac{^{13}\text{C}}{^{12}\text{C}} \right)_{\text{sample}} / \left(\frac{^{13}\text{C}}{^{12}\text{C}} \right)_{\text{std}} - 1 \right] \times 1000$$

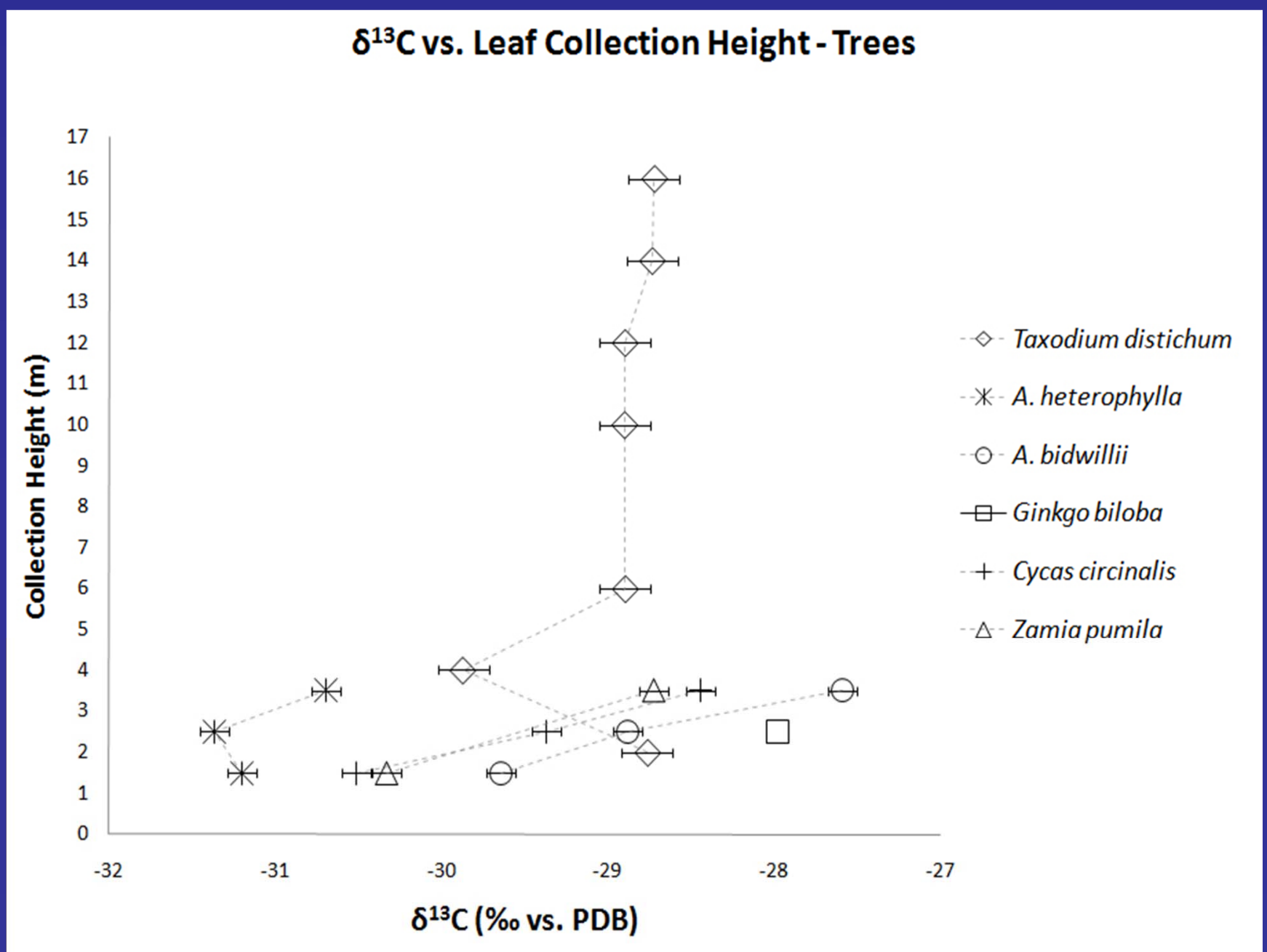


Figure 5. Carbon isotope ratio measurements for trees; each tree has higher $\delta^{13}\text{C}$ at the top of the tree than at the bottom.

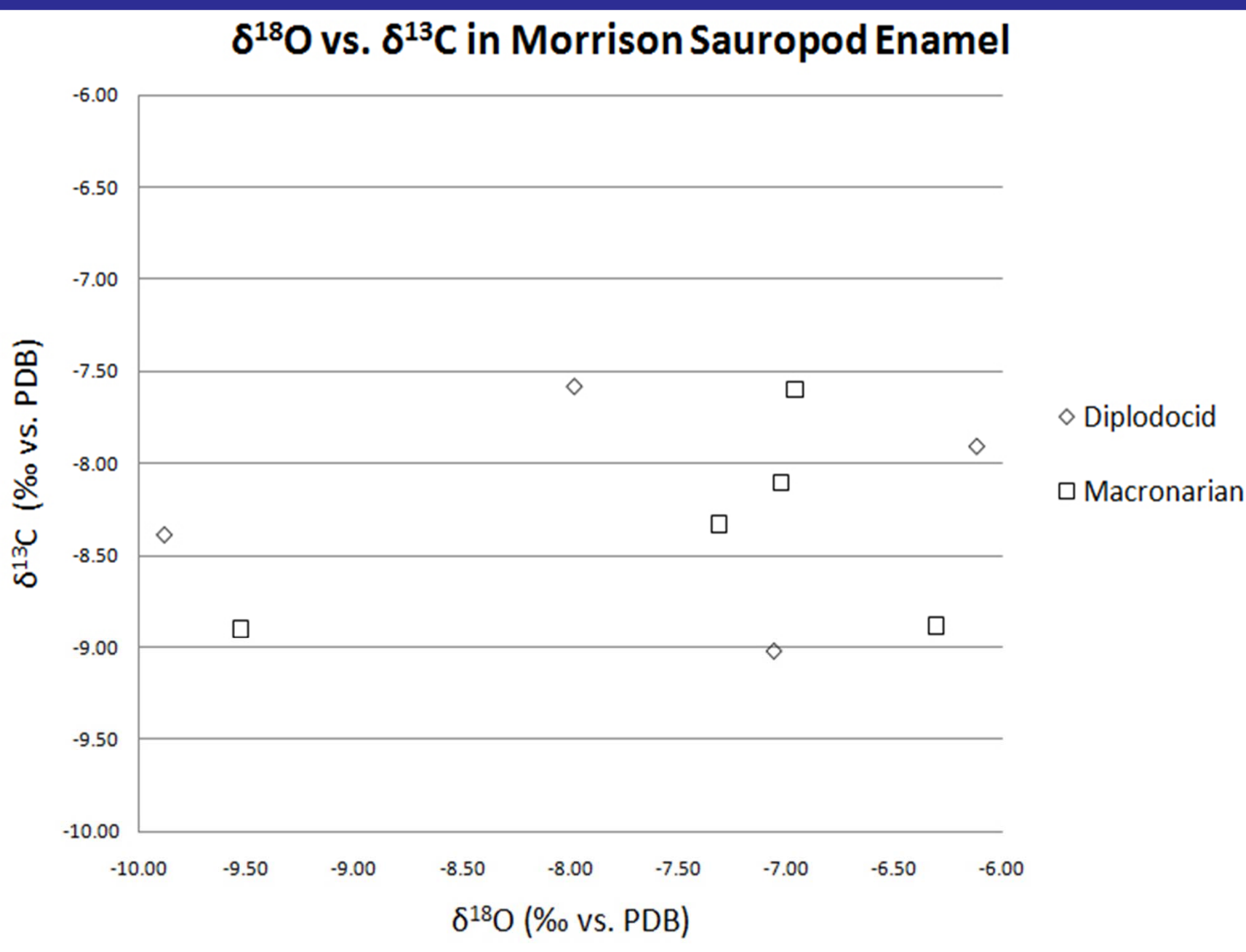


Figure 6. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values show no significant difference between diplodocids and macronarians. This is consistent with the null hypothesis that diplodocid and macronarian sauropods were not partitioning resources exclusively by plant height. Note that sample numbers are small for each taxon, so these results should be treated as preliminary.

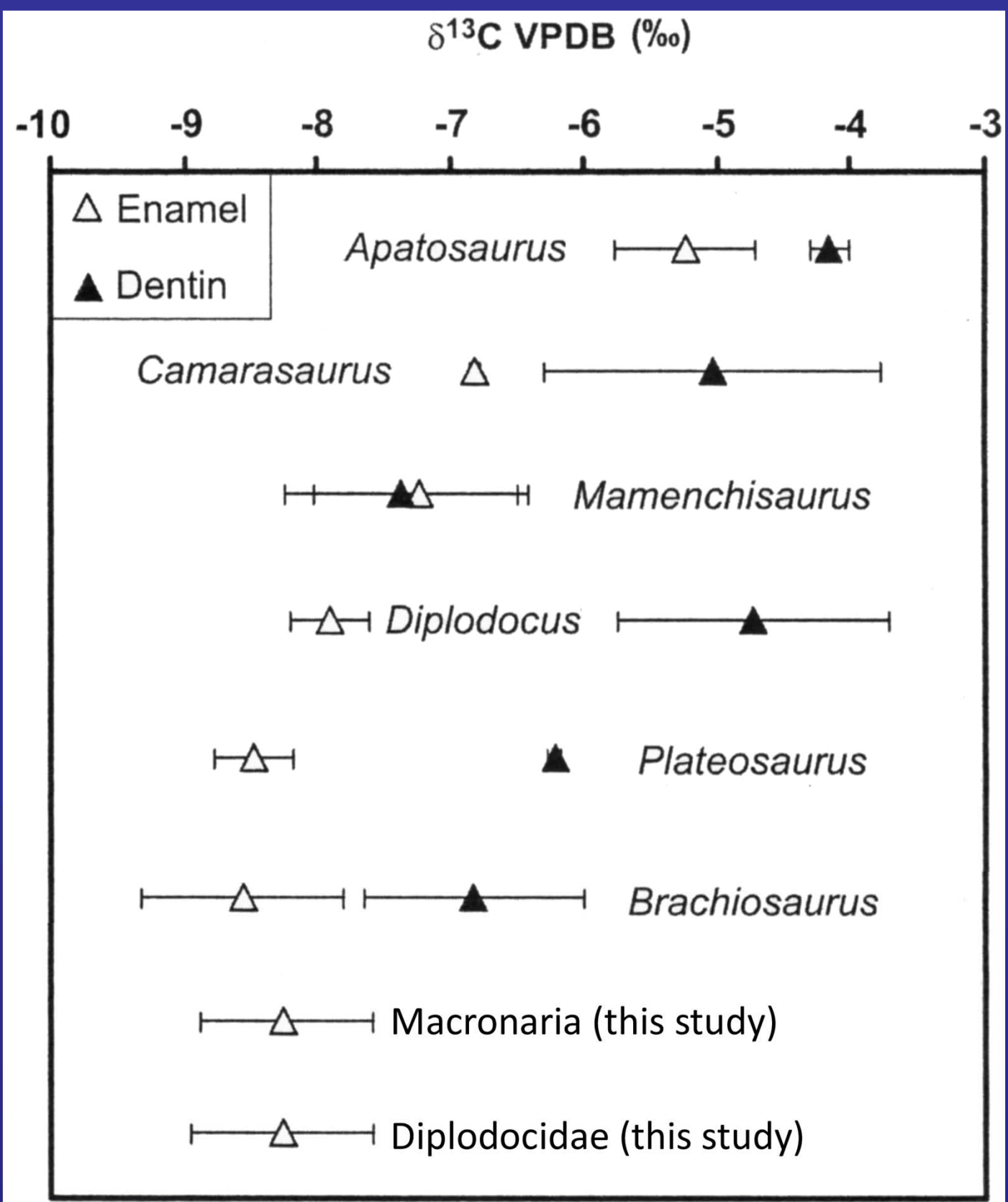


Figure 7. Tütken's $\delta^{13}\text{C}$ measurements for the enamel and dentine of various sauropod groups with the values from this study included. The diplodocid measurements from this study are consistent with the measurements for the genus *Diplodocus* from Tütken's study. The macronarian measurements 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).

CONCLUSIONS

- Morrison neosauropod niche partitioning:
 - The null hypothesis is supported by the isotopic data collected from the sauropod enamel powder, so it is unlikely that sauropods partitioned food resources by vertical partitioning alone.
- Ground-truthing $\delta^{13}\text{C}$ partitioning with height in modern C3 plants:
 - The data collected from plants is consistent with H₁; $\delta^{13}\text{C}$ increases with height in trees not only in a closed canopy forest setting as previously thought but also in isolated trees in open environments. This observation can be used to investigate vertical resource partitioning not only in dense rainforests but also in arid environments like the Morrison paleoenvironment where vegetation is less dense.

REFERENCES

- Cerling, T.E., J.A. Hart, & T.B. Hart. 2004. Stable isotope ecology in the Ituri Forest. *Oecologia* **138**:5-12.
- Kirkland, J.I. & K. Carpenter. 1994. North America's first pre-Cretaceous ankylosaur (Dinosauria) from the Upper Jurassic Morrison Formation of western Colorado. *Brigham Young University Geology Studies* **40**:25-42.
- Tütken, T. 2011. The diet of sauropod dinosaur: implications of carbon isotope analysis on teeth, bones, and plants. Pp. 57- 79 in Klein, N., K. Remes, C.T. Gee, and P.M. Sander (eds.), *Biology of the sauropod dinosaur: understanding the life of giants*. Indiana University Press.

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