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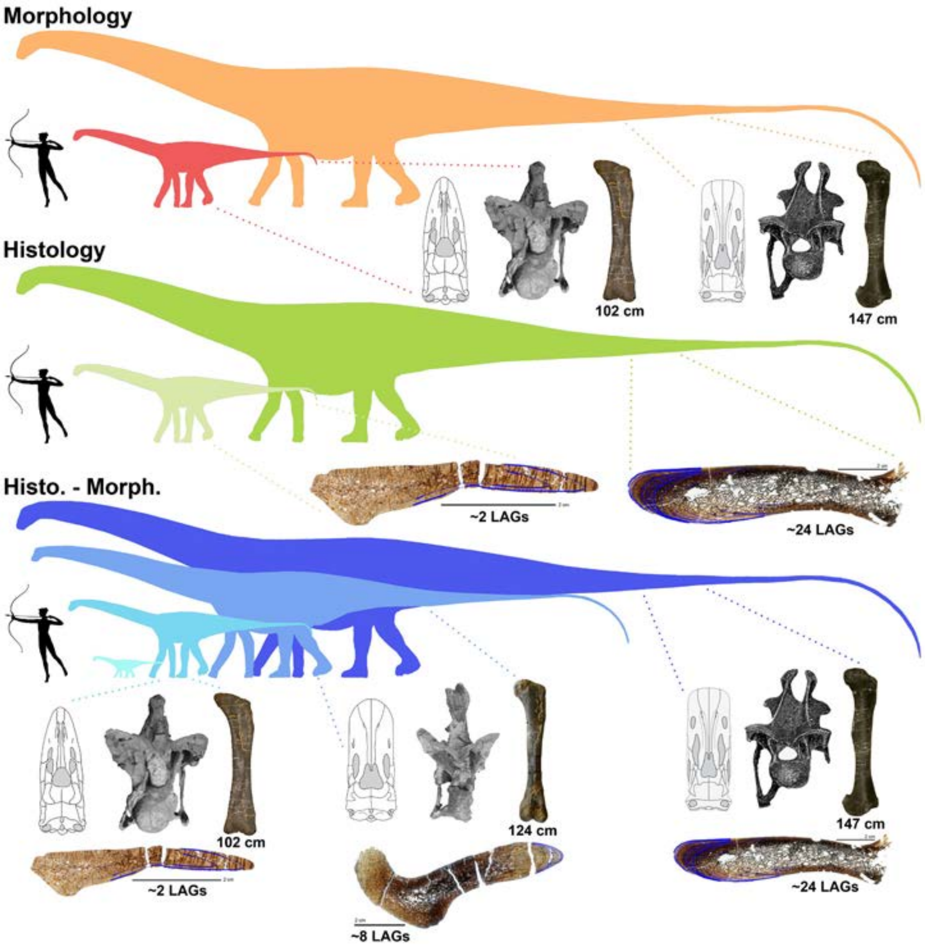
# WHAT FACTORS INFLUENCE OUR RECONSTRUCTIONS OF MORRISON FORMATION SAUROPOD DIVERSITY?

**D. Cary Woodruff**



Theme Issue
An Ecosystem We Thought We Knew—
The Emerging Complexities of the Morrison Formation
SOCIETY OF VERTEBRATE PALEONTOLOGY
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*Based on morphology alone, differing attributes (including body size, cranial, vertebral, and limb morphologies) between two specimens could result in the interpretation that they are distinct. Conversely, from just histology, only age is assessed from a growth perspective. However, by increasing the lines of evidence, by incorporating both morphology and histology, we can more accurately account for a growth series. Growth is gradational, so we should expect to see not just the extremes, but transitional forms as well. Human scale bar is Augustus Saint-Gaudens'* ***Diana of the Tower****, depicting Diana as 1.83 m.* ***Diplodocus*** *sp. silhouettes originally based on art by S. Hartman available via PhyloPic (Creative Commons Attribution-ShareAlike 3.0 Unported).*

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# What Factors Influence our Reconstructions of Morrison Formation Sauropod Diversity?

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## ABSTRACT

The Upper Jurassic Morrison Formation classically represents the "Golden Age" of sauropods, and the Morrison Formation is reported to have yielded 13 genera and 24 species of sauropods. This incredible diversity has produced numerous theories attempting to reconcile the co-occurrence of such large, and similar taxa. Previously, a comparably high diversity has been proposed for the Late Cretaceous Hell Creek Formation of North America – possibly comprising nearly three dozen species from over 20 genera of ankylosaura, caenagnathids, ceratopsians, dromaeosaurids, hadrosaurs, ornithomimids, pachycephalosaurs, thescelosaurs, and tyrannosaurs. However, much of the morphologic variation previously ascribed to taxonomic differences has recently been shown to be a result of stratigraphy and/or ontogeny – resulting in this rich assemblage being downsized to 13 genera and 16 species. Whereas still rich in diversity, such factors have an immediate effect towards our reconstruction of true richness.

Following the example of the Hell Creek Formation, we can investigate the ontogenetic and stratigraphic origin of possible diversity inflation in other formations, and within this study, apply it to the Morrison Formation. New dating techniques are resulting in finer temporal resolution, and are changing the temporal position of well-known quarries. Differences in body size and ontogenetic stages can also affect diversity estimates. Plotting body size stratigraphically, it initially appears that larger specimens (interpreted as different species) occur higher in the section. An increase in average body size may be a legitimate trend, but there are several specimens that counter this "rule" for many genera. Likewise, dramatic allometric ontogenetic trajectories have led to the erection of at least three diplodocid genera – *Amphicoelias*, *Seismosaurus*, and *Suuwassea* – and it is suspected that many more Morrison Formation "species" could alternatively be explained as ontogimorphs. We have a long way to go towards revealing the true nature of Morrison Formation sauropod diversity. Although dietary partitioning undoubtedly occurred at the level of both the species (e.g., *Brachiosaurus* vs. *Diplodocus*) and between ontogenetic stages, a base of 24 levels of co-occurring divisions seems unlikely. The Morrison Formation may have exhibited a sauropod-rich assemblage unlike any other in North America, and the implications of stratigraphy, ontogeny, and variation may be minor, yet these factors alter perceived "diversity." True diversity will not be fully understood unless these factors are considered.

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## INTRODUCTION

The Upper Jurassic Morrison Formation of the western United States of America was home to some of the most classic of dinosaur species. Though the Morrison Formation is well known for theropods (e.g., *Allosaurus*), thyreophorans (e.g., *Stegosaurus*), and ornithopods (e.g., *Camptosaurus*), the sauropods are the quintessential Morrison dinosaurs. Species such as *Apatosaurus*, *Brachiosaurus*, *Camarasaurus*, and *Diplodocus*—discovered well over a century ago—are still famed, highly regarded, and important taxa. It is not just the species of sauropods found in the Morrison Formation that are unique, however, but also their apparent diversity. If interpretations are correct, the Morrison Formation was home to 13 to 14 genera and 24 species of sauropods—*Amphicoelias altus*, *A. fragillimus* (a.k.a., "*Maraapunisaurus*" of Carpenter, 2018), *Apatosaurus ajax*, *A. louisae*, *A. excelsus*, *A. parvus*, *A. yahnahpin* (the last three may alternatively belong to *Brontosaurus* [Tschopp and others, 2015]), *Barosaurus lentus*, *Brachiosaurus altithorax*, *Camarasaurus grandis*, *C. lentus*, *C. lewisi*, *C. supremus*, *Diplodocus carnegii*, *D. hallorum*, *D. longus*, *Dystrophaeus viaemalae*, *Galeamopus hayi*, *G. pabsti*, *Haplocanthosaurus delfsi*, *H. priscus*, *Kaatedocus siberi*, *Supersaurus vivianae*, and *Suuwassea emilieae* (figure 1). Although the Morrison Formation was geographically expansive—representing an area of 1.5 million square km (Dodson and others, 1980; Foster, 2007)—how could 24 of some of the largest terrestrial herbivores ever co-exist? Niche and dietary partitioning could account for some of this species richness, but we can also examine the realities of such seemingly high species co-occurrence.

The Late Cretaceous Hell Creek Formation represents a dinosaur-bearing formation that is historically well known and extensively studied, with similarly high dinosaur diversity to that of the Morrison Formation. However, over the past decade, ontogenetic and stratigraphic assessments (Horner and Goodwin, 2006, 2008, 2009; Scannella and Fowler, 2009; Scannella and Horner, 2010, 2011; Campione and Evans, 2011; Horner and others, 2011; Scannella and Fowler, 2014; Scannella and others, 2014; Goodwin and Evans, 2016; Fowler 2017; Wosik and others, 2017, 2018) have reassessed the diversity, life development, and evolution of the Hell Creek Formation dinosaurs. These analyses alternatively suggest lower species richness. Using the Hell Creek Formation diversity analysis as a guide, we can re-examine the Morrison Formation sauropod diversity, assessing the effect considering ontogeny and stratigraphy.

## INSTITUTIONAL ABBREVIATIONS

ANS: Academy of Natural Sciences, Philadelphia, Pennsylvania; DNM: Dinosaur National Monument, Jensen, Utah; GMNH: Gunma Museum of Natural History, Japan; NMMNH: New Mexico Museum of Natural History, Albuquerque, New Mexico; OMNH: Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma.

## FACTORS INFLUENCING OUR VIEW OF DIVERSITY

### Ontogeny

Compared to many other dinosaur groups, sauropod ontogeny has received relatively less attention, and has been mostly restricted to histologic analysis of relative bone maturity (including Curry, 1999; Sander, 2000; Sander and Tückmantel, 2003; Klein and Sander, 2008; Lehman and Woodward, 2008; Woodward and Lehman, 2009; Sander and others, 2011; Waskow and Sander, 2014; Rogers and others, 2016). Although no sauropod nesting sites are yet known from the Morrison Formation, based on those from South America, such as Auca Mahuevo (Chiappe and others, 1998), the potential difference in body mass between a hatchling and an adult Morrison Formation sauropod is at least four orders of magnitude. Descriptions of immature Morrison Formation sauropods (Gilmore, 1925; Carpenter and McIntosh, 1994; Foster, 1995; Britt and Naylor, 1996; Curtice and Wilhite, 1996; Curry, 1999; Foster, 2005a; Schwarz and others, 2007; Myers and Storrs, 2007; Myers and Fiorillo, 2009; Whitlock and others, 2010; Carballido and others, 2012; Storrs and others, 2012; Tschopp and Mateus, 2013; Hedrick and others, 2014; Tschopp and others, 2015; Woodruff and others, 2015, 2017; Melstrom and others, 2016; Hanik and others, 2017, show that sauropods did not grow iso-

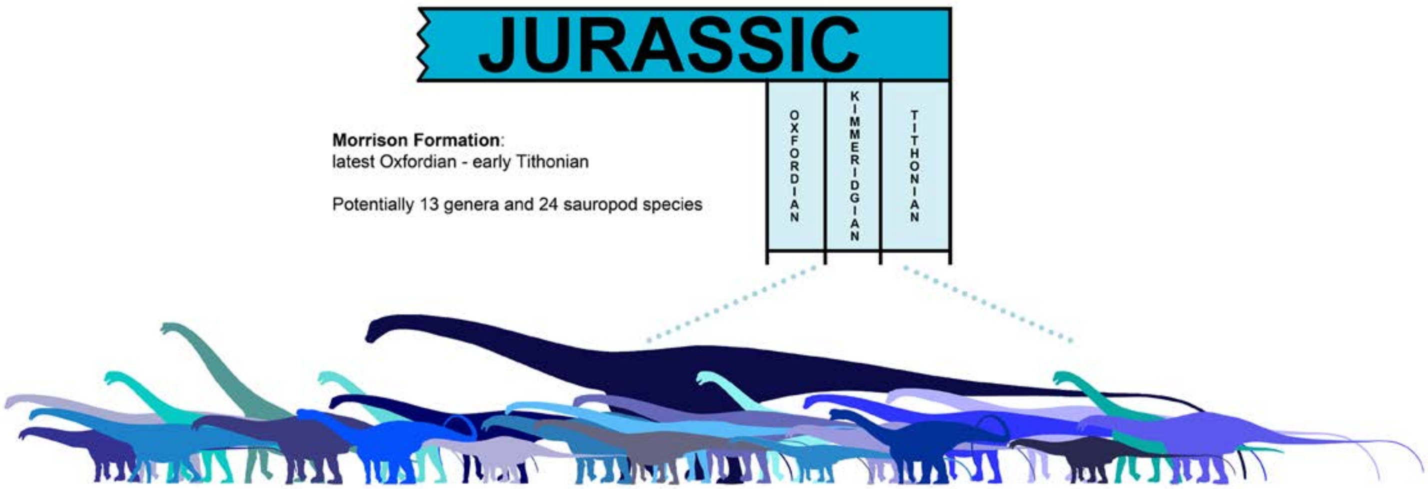

Figure 1. The entirety of possible sauropod species within the Morrison Formation. *Amphicoelias*: *A. altus* (or *Diplodocus altus* [Woodruff and Foster, 2014]), *A. fragillimus* (a.k.a., "*Maraapunisaurus*" of Carpenter, 2018); *Apatosaurus*: *A. ajax*, *A. louisae*, *A. excelsus*, *A. parvus*, *A. yahnahpin* (the last three may alternatively belong to *Brontosaurus* [Tschopp and others, 2015]); *Barosaurus lentus*; *Brachiosaurus altithorax*; *Camarasaurus*: *C. grandis*, *C. lentus*, *C. lewisi*, *C. supremus*; *Diplodocus*: *D. carnegii*, *D. hallorum*, *D. longus*; *Dystrophaeus viaemalae*; *Galeamopus*: *G. hayi*, *G. pabsti*; *Haplocanthosaurus*: *H. delfsi*, *H. priscus*; *Kaatedocus siberi*; *Supersaurus vivianae*; *Suuwassea emilieae*. As historically portrayed in other dinosaur-bearing formations, the sauropods of the Morrison Formation are largely depicted as homogenized – an inaccurate portrayal for numerous reasons outlined in this review. Species to supposed scale. Silhouettes by S. Hartman available via PhyloPic (Creative Commons Attribution-ShareAlike 3.0 Unported).

metrically (though some appendicular elements generally appear more isometric than allometric; Woodruff and others, 2017). Sauropod ontogenetic development is still the subject of much discussion (Whitlock and Harris, 2010; Whitlock and others, 2010; Woodruff and Fowler, 2012; Wedel and Taylor, 2013; Hedrick and others, 2014; Tschopp and others, 2015; Melstrom and others, 2016; Woodruff and others, 2017), and continuing investigations and conversations are invaluable. This review adheres to the hypothesis that sauropods underwent radical ontogenetic development, but I strongly encourage readers to examine all sides of this discussion.

The implications of ontogeny could complicate our understanding of the species richness within Morrison Formation sauropods. If these sauropods did undergo radical size and ontogenetic changes, how do we recognize these growth stages, and how do we assign ontogimorphs to genera?

Several studies have examined sauropod maturational states. Some of these studies rely on morphology (Whitlock and others, 2010; Woodruff and Fowler, 2012; Wedel and Taylor, 2013; Carballido and Sander, 2014), whereas others rely on histology (Curry, 1999; Sander, 1999, 2000; Klein and Sander, 2008; Lehman and Woodward, 2008; Griebeler and others, 2013; Mitchell and others, 2017). Whereas histology is the demonstrably proven way to assess and verify maturity in dinosaurs (see Padian and Lamm [2013] and the sources therein), given the extreme changes throughout growth, understanding the development and life history of a sauropod represents a complex association with both morphology and histology.

Contrary to previous speculation, sauropods did not take centuries to mature (sensu Curry, 1999; Sander, 1999, 2000; Erickson and others, 2001; Sander and Tückmantel, 2003; Sander and others, 2004; Rogers and Erickson, 2005; Lehman and Woodward, 2008; Woodward and Lehman, 2009; Griebeler and others, 2013; Waskow and Sander, 2014; Woodruff and others, 2017).

Recent histologic analyses have recorded an estimated maximum age-of-death in the thirties to forties in specimens of *Camarasaurus* and *Diplodocus* (Waskow and Sander, 2014; Woodruff and Foster, 2017; Woodruff and others, 2017). Although maximum longevity is unattainable, the majority of sauropods likely fell within the half century interval, although some exceedingly rare specimens may have extended this envelope (Wings and others, 2007; D.C. Woodruff, personal observations). Thanks to the pioneering work of Waskow and Sander (2014), sauropod dorsal rib histology allows for numerical age estimates as opposed to maturational rankings (Histological Ontogenetic Stage; Klein and Sander, 2008).

As paleontology relies on morphology in part to distinguish different species, these growth differences/changes are quantifiable with radical ontogenetic trajectories. If we had several specimens that unbeknownst to us represented a growth series, given their "unique" and "defining" characters/combinations, one could identify each specimen as a separate taxon. How then are we to separate taxa from ontogimorphs?

The case for *Triceratops* ontogeny and synonymy, although still debated, (Scannella and Horner, 2010, 2011; Longrich and Field, 2012; Mairoino and others, 2013) represents a good case study. This species-rich genus was previously thought to consist of over a dozen species, all co-existing. However, analyses by Horner and Goodwin (2006, 2008) demonstrated that this high degree of morphologic variability was largely caused by ontogenetic development within two species. Thus, the Hell Creek Formation chasmosaurines were reduced to *T. horridus*, *T. prorsus*, and *Torosaurus latus*. Scannella and Horner (2010) later "reduced" this diversity even more by identifying that *Torosaurus* was an extremely mature individual of *Triceratops*. From the studies of Horner and Goodwin (2006, 2008) and Scannella and Horner (2010), the Hell Creek Formation "lost" over 90% of its chasmosaurine diversity.

The conclusions of Horner and Goodwin (2006; 2008) were reached based on morphology that was ultimately corroborated via histology (Scannella and Horner, 2010; Horner and Lamm, 2011); thus, histology proved to be the test. Combining morphology and histology allowed for the recognition of ontogenetic change, and how these changes occurred (echoed by Hone and others, 2016). As done for *Triceratops*, we should be taking a similar approach towards the Morrison Formation sauropods. Once several specimens have been morphologically and histologically studied, then comparisons can be made regarding (1) changes through ontogeny and (2) differences among taxa. In doing so, groupings or patterns may start to occur, such as different growth stages grouping together ("juveniles" will group separately from "adults"), and similarities and/or differences among taxa will become more evident (i.e., immature *Diplodocus* and *Apatosaurus* are more alike, but both are more distinct from immature *Camarasaurus*; Woodruff and others, 2017; figure 2).

Given the incompleteness of the fossil record, many purportedly new genera may represent immature specimens of known taxa. The Morrison Formation sauropod *Suuwassea emilieae* may be one such example. Recognized from a single individual (specimen ANS 21122), the taxonomy of *Suuwassea* has been debated (Harris and Dodson, 2004; Lovelace and others, 2008; Whitlock and Harris, 2010; Whitlock, 2011a; Woodruff and Fowler, 2012; Wedel and Taylor, 2013; Hedrick and others, 2014; Tschopp and others, 2015; Woodruff and others, 2017). Histology shows that specimen ANS 21122 lacks an External Fundamental System (EFS) (Hedrick and others, 2014; Woodruff and others, 2017; EFS, the skeletal indicator of osteogenesis—Padian and Lamm, 2013). Yet the morphologies have been interpreted to be valid, distinguishable characters (Harris and Dodson, 2004; Wedel and Taylor, 2013; Hedrick and others, 2014), or alternatively ontogenetic (Woodruff and Fowler, 2012; Woodruff and others, 2017). Aside from the differing taxonomic interpretations, the holotype of *Suuwassea* represents a relatively small-statured immature animal with intriguing morphologies (see a list of these features in Woodruff and Fowler, 2012). Currently the holotypic material of *Suuwassea* could equally represent an immature individual from a known taxon, a distinct taxon, a maturationally varied individual or taxon with pedomorphic attributes, and possibly a combination of these conditions. At this time the holotype does not unanimously support one distinct interpretation.

Another example from the Morrison Formation is the sauropod *Diplodocus hallorum*. Originally known

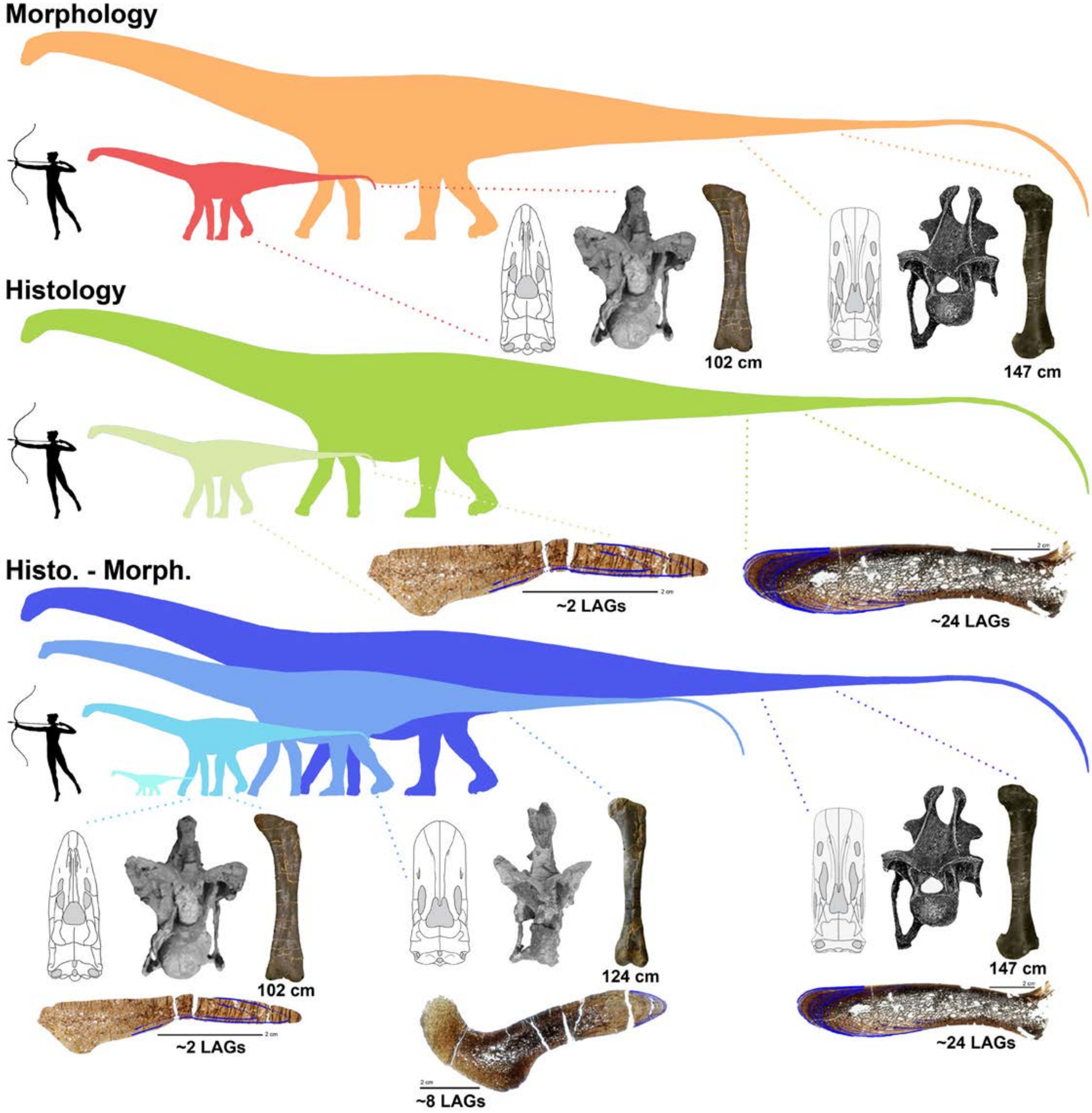

Figure 2. Caption is on the following page.

Figure 2 is on the previous page. The interpretations that could result from single lines of evidence. Morphology: not only differing body sizes, but the differing cranial, vertebral, and limb morphologies between two specimens could result in the two being interpreted as separate taxa. Histology: from just the histology, only the individual ages of these specimens could be assessed from a growth perspective. However, by increasing the lines of evidence (here with histology and morphology), and additionally by incorporating more specimens, we see a growth series. Growth is gradational, so we should expect to see not just the extremes, but transitional forms (so "unique" character combinations may instead represent hallmarks of ontogeny). Human scale bar is Augustus Saint-Gaudens' *Diana of the Tower*, depicting Diana as 1.83 m. Femora and histologic images modified from Woodruff and others (2017). *Diplodocus* sp. silhouettes modified from Woodruff and others (2017) and originally based on art by S. Hartman available via PhyloPic (Creative Commons Attribution-ShareAlike 3.0 Unported). Immature *Diplodocus* sp. skull drawing in Histology and Histo. - Morph. by K. Scannella, adult *Diplodocus* sp. and *Suuwassea emilieae* skulls in Histology and Histo. - Morph. from Whitlock (2011b).

as "*Seismosaurus*" (specimen NMMNH P-3690; Gillette, 1991), this specimen likely represents one of the largest Morrison Formation sauropods (Woodruff and Foster, 2014). Whereas this taxon was originally diagnosed mainly on postcranial proportional differences, in a reassessment of the genus, Lucas and others (2006) proposed that these differences were simply due to its extreme body size (and the "hook-like" ischium was found to be inaccurate; Lucas and others, 2006). Now indistinguishable from *Diplodocus*, Lucas and others (2006) synonymized "*Seismosaurus*" into a species of *Diplodocus*. In their taxonomic revision of Diplodocidea, Tschopp and others (2015) phylogenetically recognized several specimens now referable to *D. hallorum*; however, the question remains whether the holotype of *D. hallorum* represents a distinct species, or an incredibly elderly *Diplodocus*. (Histologic analysis of specimen NMMNH P-3690 is currently underway by DCW and K. Waskow). Similar to the case of *D. hallorum* is that of *Amphicoelias*. The holotype material of *A. fragillimus* hints at a posterior dorsal vertebra in excess of 2.8 m – making it unquestionably the largest vertebrate ever (Carpenter, 2006; Woodruff and Foster, 2014; see also Carpenter, 2018). Serious doubt should be raised to the validity of this taxon (as all of the holotype material vanished; Woodruff and Foster, 2014), whereas we now have revised autamorphies for this species (Tschopp and others, 2015), as some of the first autamorphies for *D. hallorum* were size related (such as a more robust pubis; Lucas and others, 2006), does "big" necessarily equal distinct?

Ontogeny should not just be considered when examining small-bodied individuals; large-bodied specimens can be just as guilty (Trujillo and others, 2011). The rarity of *Torosaurus* compared to the prolific *Triceratops* was proposed by Scannella and Horner (2010) to be the result of "*Torosaurus*" being a senescent *Triceratops*. Nature is unkind to the young and old, and attritional mortality shows that samples of specimens in these age ranges should be underrepresented (Lyman, 1994). Whereas immature sauropods are known from the Morrison Formation (Gilmore, 1925; Carpenter and McIntosh, 1994; Foster, 1995; Britt and Naylor, 1996; Curtice and Wilhite, 1996; Curry, 1999; Foster, 2005a; Myers and Storrs, 2007; Schwarz and others, 2007; Myers and Fiorillo, 2009; Whitlock and others, 2010; Carballido and others, 2012; Storrs and others, 2012; Tschopp and Mateus, 2013; Hedrick and others, 2014; Tschopp and others, 2015; Woodruff and others, 2015, 2017; Melstrom and others, 2016; Hanik and others, 2017), it might be possible that a few of these specimens, though identified as different species, may alternatively represent differing ontogenetic stages of known taxa. And while not yet histologically demonstrated, the case of "*Elosaurus*" *parvus* (Peterson and Gilmore, 1902) representing an immature *Apatosaurus* (McIntosh, 1995; or *Brontosaurus* by Tschopp and others, 2015), or *Diplodocus* "*lacustris*" (Marsh, 1884) being an immature *Diplodocus* (Upchurch and others, 2004; although see Tschopp and others, 2015), demonstrate that even previously, Morrison Formation sauropod diversity reconstructions have been altered by ontogeny.

## Biostratigraphy

The Morrison Formation represents a time interval of approximately 7 million years and spanning a geographical range of about 14° latitude and to 12° longitude (Kowallis and others, 1998; Turner and Peterson, 1999; Foster, 2007; Trujillo and Kowallis, 2015). Thus, the Morrison Formation represents a significant geographic region and temporal interval. Historically, the biota appeared to be homogeneously distributed within the formation with little if any recording of stratigraphic occurrence (especially during the "Bone Wars" of O.C. Marsh and E.D. Cope; Foster, 2007). In a pioneering attempt to correlate localities and compile the stratigraphic distribution of dinosaurs, Turner and Peterson (1999) correlated 230 Morrison Formation localities to the DNM section. From such correlations, Turner and Peterson (1999) claimed the formation could be better understood as a single functional unit. Not only did Turner and Peterson (1999) claim to correlate sections over vast areas with the aid of the so-called "clay change" (the sudden shift between the lower and upper Brushy Basin Member from non-smectitic to smectitic clays, which denotes increased volcanism), but they also claimed to see diversity and species patterns change. *Camarasaurus* lasted longer than *Apatosaurus*, *Diplodocus* survived longer than its sister taxon *Barosaurus*, and the perhaps distinct *Amphicoelias* appeared to be the last surviving sauropod within the formation (Turner and Peterson, 1999). The incredibly detailed and thorough work of Turner and Peterson (1999) has served as a platform for subsequent Morrison Formation studies.

As demonstrated within the Hell Creek Formation, stratigraphy is an important consideration for diversity estimates (Horner and others, 2011; Scannella and others, 2014; Fowler, 2017). While Horner and Goodwin (2006) were able to show that *Triceratops* species diversity was a false artifact from ontogimorphs of two species, Scannella and others (2014) was able to refine this image by incorporating stratigraphic information. By plotting the stratigraphic position of over 50 specimens of *Triceratops* and noting their ontogenetic states, Scannella and others (2014) were able to plot evolutionary patterns. Not only did they document morphological details (such as the nasal horn increasing in size through time), but more importantly, they were able to plot the evolution of *T. horridus* to *T. prorsus* through anagenesis (Scannella and others, 2014).

From the change in *Triceratops* within only ~1 million years (Scannella and others, 2014), one might expect to see evolutionary changes in sauropods over the course of ~7 million years (Kowallis and others, 1998; Turner and Peterson, 1999; Trujillo and Kowallis, 2015) in the Morrison Formation. By correlating species occurrence within the formation, a body size trend may exist: *Apatosaurus yahnahpin* (or *Brontosaurus yahnahpin*; Tschopp and others, 2015) occurs prior to *A. louisae*, *Camarasaurus lentus* occurs before *C. supremus*, and *Diplodocus carnegii* occurs prior to *D. hallorum* (Turner and Peterson, 1999; figure 3). It would seem that all of the smaller species occur before the larger; therefore, one could say that Morrison Formation sauropods increased in size through time. However, when plotting additional species and specimens, it becomes apparent that this is not a strict rule. An *Apatosaurus* sp. (Museum of the Rockies [MOR] 857) from the stratigraphically lower Salt Wash Member of the Morrison Formation equivalent may be comparable in size to the largest specimen ever collected (specimen OMNH 1670) from the higher Brushy Basin Member equivalent levels of the Morrison Formation in western Oklahoma. The smallest species of *Camarasaurus*, *C. lewisi*, occurs stratigraphically between the larger *C. lentus* and *C. supremus*, and *Diplodocus carnegii* occurs before the larger *D. hallorum*. However, we should not think of this as a strict trend, as the stratigraphically highest occurrence of *Apatosaurus* (within the upper meters of the Brushy Basin Member in Arches National Park, Utah), is of a size typical for the average adult lower in the formation (Foster, 2005b). Tentatively, whereas body size increase is *not* a strict rule throughout the formation, *average* body size increases may be a legitimate trend (sensu Foster, 2007).

Plotting sauropod genera stratigraphically may even have the potential to highlight major evolutionary processes. In 2013, the diplodocid *Kaatedocus siberi* (Tschopp and Mateus, 2013) was named from the Howe-Stevens Quarry in north-central Wyoming. Whereas there has been some informal discussion as to whether this taxon is distinct or not,

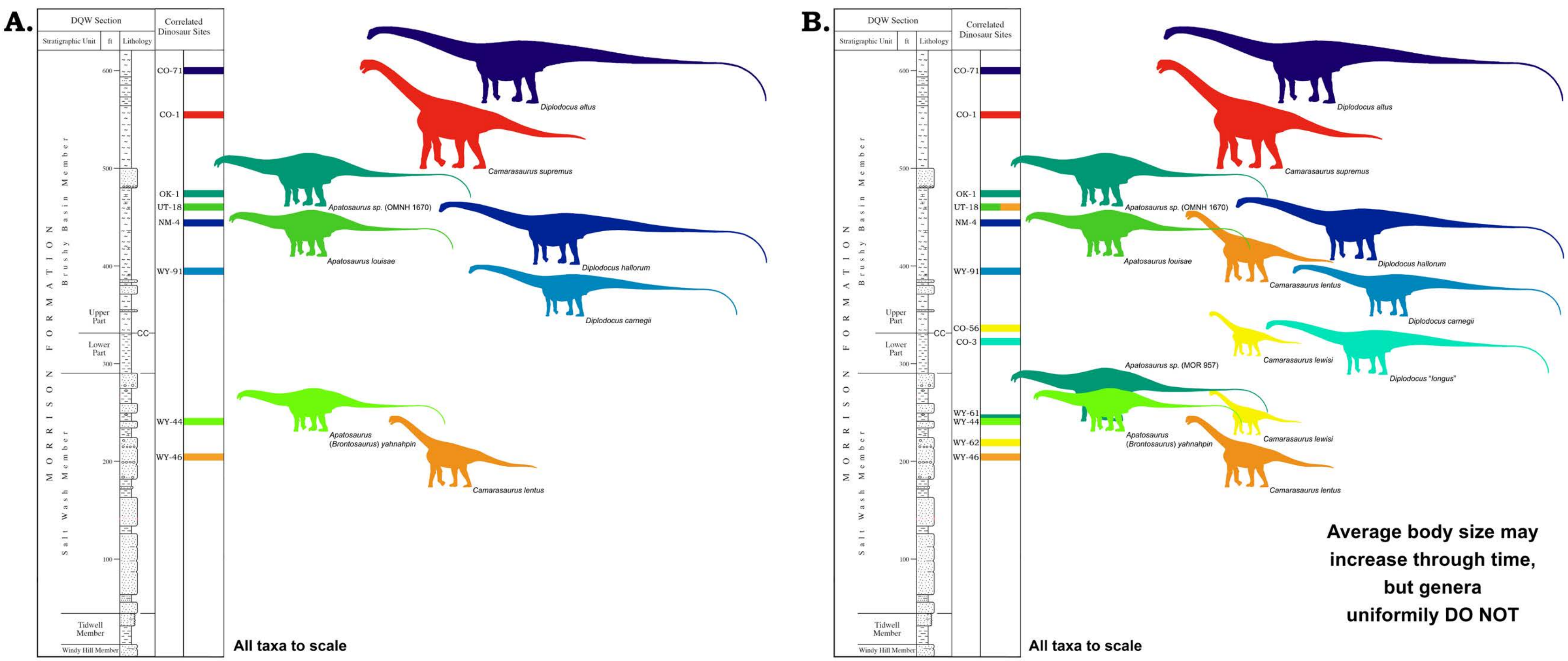

Figure 3. The largest species of *Apatosaurus*, *Camarasaurus*, and *Diplodocus* appear stratigraphically higher compared to their smaller counterparts. Thus, one might infer that Morrison Formation sauropod genera increase in body size through time (A). However, by plotting more specimens/species (B), we see that the previous assumption is not a rule nor a strict pattern. Whereas an increase in average body size amongst sauropod taxa may be a legitimate trend observed within the Morrison Formation, we are not advocating or suggesting Cope's Law (that lineages must increase in size through time). Silhouettes by S. Hartman available via PhyloPic (Creative Commons Attribution-ShareAlike 3.0 Unported). A full-size version of figure 3 is in the Attachements pane.

based on cranial and vertebral morphologies the holotype of *Kaatedocus* may represent an immature individual (D.C. Woodruff, personal observations; and note not a synonymous ontogimorph). What has not been discussed in-depth is the stratigraphic occurrence. Correlated to the DNM stratigraphic section (Turner and Peterson, 1999), *Kaatedocus* appears to be stratigraphically lower than any reported *Diplodocus*. According to Turner and Peterson (1999), all *Diplodocus* and *Barosaurus* specimens occur within the upper part of the Salt Wash or Brushy Basin Members or their equivalents, whereas *Kaatedocus* may occur equivalently in the lower regions of the Salt Wash Member. More work and better resolution is needed—both ontogenetic and stratigraphic—but the apparent stratigraphic distinctness could be used as evidence in favor for the validity of *Kaatedocus*. Furthermore, given that *Kaatedocus* is geologically one of oldest Morrison Formation diplodocids known, it could represent part of a diplodocine cladogenic or anagenetic lineage (figure 4). As the Morrison Formation temporally represents an increasing terrestrial space (Foster, 2007), and as fauna migrate into this newly acquired space through time, could we expect to document evolutionary changes? Anagenesis (potentially with *Kaatedocus* and the co-occurring diplodocid *Galeamopus*) and cladogenesis (*Apatosaurus* vs. *Brontosaurus*?) are evolutionary processes that should be considered. Fortunately, due to the wealth of time spent exploring the Morrison Formation and the vast number of specimens collected (Foster, 2007; Brinkman, 2010), these kinds of questions have the potential to be examined.

Finally, the assumptions and inferences regarding Morrison Formation stratigraphy could be derived from a false signal. As presented herein, stratigraphic distribution of sauropods within the Morrison has been based around the framework created by Turner and Peterson (1999). Within the past decade, the reliability of Turner and Peterson (1999) has been questioned. Starting with Trujillo (2006), it was demonstrated that the "clay change" was not supported by clay mineralogy nor X-ray diffraction (XRD) data. According to Trujillo (2006), this marker unit was not a consistently developed horizon, and within a given section numerous clay-type alterations could occur. These findings meant that correlating sections in this manner, particularly over such long distances, was not reliable (Trujillo, 2006).

After the Trujillo (2006) "clay change" study, there were a series of seminal papers reporting on U-Pb dates and recalibrated $^{40}$Ar/$^{39}$Ar dates for several Morrison Formation localities (Trujillo and Chamberlain, 2013; Trujillo and others, 2014; Trujillo and Kowallis, 2015). Radiometric dating (such as K/Ar or $^{40}$Ar/$^{39}$Ar) can rely on silicate (or potassium feldspar) minerals from overlying or underlying volcaniclastic deposits to determine a relative temporal interval (Olsson, 1986). However, by using non-detrital zircon crystals from smectitic mudstones, some of these newer studies were able to determine dates for localities previously dated with detrital material, in addition to new, and geographically distant localities (Trujillo and Chamberlain, 2013; Trujillo and others, 2014; Trujillo and Kowallis, 2015). As the standard used for $^{40}$Ar/$^{39}$Ar dating and decay constants became over time more refined, these necessitated recalibration; and these recalibrated dates now correspond more favorably to the same derived from U-Pb (Trujillo and Kowallis, 2015). With these refined dates, while relative stratigraphic position of many localities remains the same, their position within a chronostratigraphic context has changed. From $^{40}$Ar/$^{39}$Ar dating, Turner and Peterson (1999) had the Mygatt-Moore Quarry in western Colorado correlated within the upper portion of the upper Brushy Basin Member between 147.8 ± 0.6 and 150.3 ± 0.3 Ma. However, new studies conducted using zircon U-Pb chemical abrasion (CA-TIMS), still place this locality within the lower portion of the upper Brushy Basin Member, but with a date of 152.18 ± 0.29 Ma (Trujillo and others, 2014; figure 4). In fact, based on recalibrated $^{40}$Ar/$^{39}$Ar dates, the entire temporal positioning has likewise changed. From $^{40}$Ar/$^{39}$Ar dating, Turner and Peterson (1999) chronostratigraphically placed the correlated dinosaur quarries between 148.1 ± 0.5 and 154.8 ± 0.6 Ma, yet $^{40}$Ar/$^{39}$Ar recalibration by Trujillo and Kowallis (2015) refined this range to 150.00 ± 1.03 and 156.84 ± 1.18 Ma, respectively.

Newer magnetostratigraphic and sequence stratigraphic studies are also changing the interpretation of the northern extent of the formation. Following the correlated section of Turner and Peterson (1999), lo-

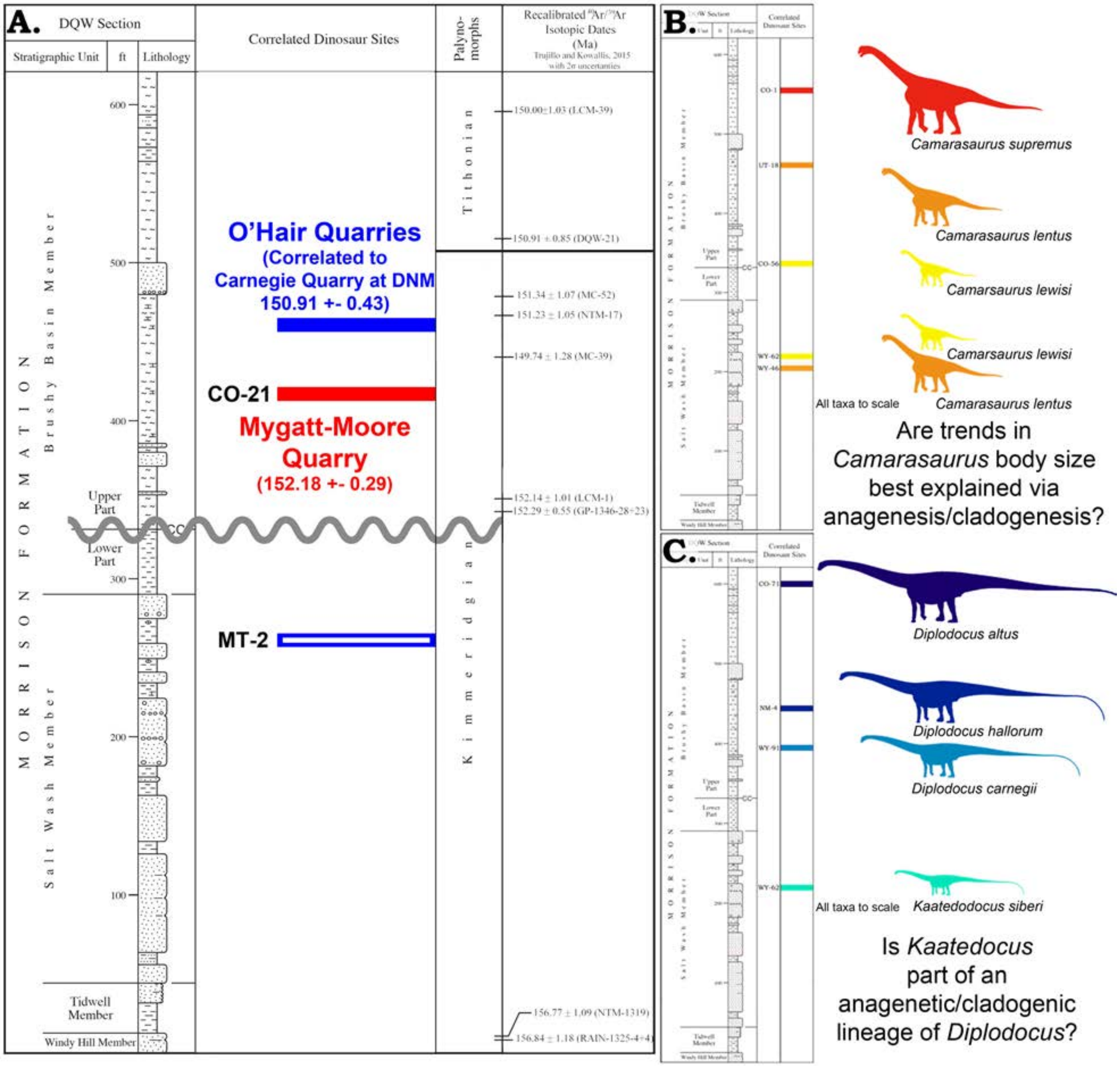

Figure 4. (A) The stratigraphic section of the Morrison Formation (from Turner and Peterson, 1999) with the recalibrated dates of Trujillo and Kowallis (2015). Note the locations of the Mygatt-Moore Quarry (CO-21; red) and the O'Hair Quarries (MT-2; blue). In Turner and Peterson (1999) the Mygatt-Moore Quarry was correlated within the upper portion of the upper Brushy Basin Member between 147.8 ± 0.6 and 150.3 ± 0.3 Ma. With the recalibrated $^{40}$Ar/$^{39}$Ar dates of Trujillo and others (2014), this locality still remains within the upper portion of the upper Brushy Basin Member, but now at 152.18 ± 0.29 Ma. The outlined blue box represents the correlated position of O'Hair Quarries (MT-2) from Turner and Peterson (1999). The solid blue box represents this locality's new correlated position based on new magnetostratigraphic (Maidment and Muxworthy, 2016) and sequence stratigraphic studies (McMullen and others, 2014; McMullen, 2016). The undulating gray line is to cross out the "clay change" of Turner and Peterson (1999). Portions of this image – particularly those pertaining to the palynomorph zones and the recalibrated $^{40}$Ar/$^{39}$Ar dates – are modified from Trujillo (2016). (B) Possible trends in *Camarasaurus* body size throughout the formation. (C) Possible explanation of *Kaatedocus* within the evolutionary trajectory of *Diplodocus*. Silhouettes by S. Hartman available via PhyloPic (Creative Commons Attribution-ShareAlike 3.0 Unported).

calities from Montana were placed equivalently within the upper portion of the Salt Wash Member (specifically the O'Hair Quarries; Cooley and Schmitt, 1998; Schimelfening and others, 2014). In addition to correlation with the DNM section, association with the underlying marine Swift Formation and the predominance of sandstone to mudstone beds, all supported a Salt Wash Member-equivalent position (Cooley and Schmitt, 1998; Turner and Peterson, 1999; Schimelfening and others, 2014). However, new magnetostratigraphic (Maidment and Muxworthy, 2016) and sequence stratigraphic analyses (McMullen and others, 2014; McMullen, 2016) are changing the position of these localities. The magnetostratigraphic analyses of Maidment and Muxworthy (2016) proposes that the O'Hair Quarries are temporally equivalent to the upper Brushy Basin Member in Dinosaur National Monument (figure 4).

How then can stratigraphic correlation and magnetostratigraphy produce such different results? In the beginning of the deposition of the Morrison Formation, the terrestrial area in the southwest was adjacent to the Sundance Sea. Later this same region was seasonally arid, or savanna-like (Foster, 2007). But as the Sundance Sea kept retreating northwards, the contiguous terrestrial deposits would continue to have a coastal composition. Systems and environments do vary latitudinally, but the lower stratigraphic placement of the Montana localities could be due to an inaccurate stratigraphic signal. A time-transgressive Morrison Formation has been previously proposed by Harris and Dodson (2004) and Harris (2005), and perhaps the geographical extremes of the formation are the better locations to study this phenomenon. If this is correct, then due to the regression of the Sundance Sea, by the time Montana had become terrestrial, it would have been temporally equivalent to Dinosaur National Monument. But the coastal environment in Montana would result in depositional systems similar to those recognized in the lower and earlier portions of the formation.

In light of these newer and ongoing studies, the work of Turner and Peterson (1999) should still be commended. Prior to Turner and Peterson (1999), Morrison Formation stratigraphic research had little, if any, cohesion or unity. Workers outside of the Colorado Plateau region were unable to place and understand their localities within the context of the entire formation. The correlatable "clay change" of Turner and Peterson (1999) at the time seemed to change that. Even in consideration of these studies incorporating new techniques/recalibration (Trujillo and Chamberlain, 2013; Trujillo and others, 2014; Trujillo and Kowallis, 2015), the Morrison Formation may be too large to correlate, and perhaps geographical regions are not a part of the same depositional system (S. McMullen, Hess Corporation, written communication, 2018). Certainly, regional correlation may still possible, but the aforementioned radiometric, magnetostratigraphic, and sequence stratigraphic studies collectively suggest that incorporating all of this new information should result in a better and more accurate reconstruction of these localities. An initial blend of this new information is already being performed by Tschopp and others (2016). By taking Morrison Formation diplodocid occurrences and incorporating them into the magnetostratigraphy of Maidment and Muxworthy (2016), Tschopp and others (2016) may be able to reanalyze these basic Morrison Formation sauropod questions, and I greatly await these results and future works.

Furthermore, while we continue to relocate, recalibrate, and reanalyze specimens within a stratigraphic context, we can thus far identify—even at coarse resolution—some levels of biozones (sensu Foster, 2003, 2007; figure 5). Due to the inherent inaccuracies in assuming formational homogeneity, Foster (2003, 2007) suggested that differing paleoenvironments throughout the formation would consist of differing groups of dinosaurs. The benefits of biozone demarcations are that they reflect environmental groupings throughout the course of the formation (i.e., environments + time versus strictly time). Until we have a better understanding of the time component, which admittedly could significantly alter the biozone signals, grouping via biozones may be a more neutral way to group or demarcate Morrison Formation sauropod taxa. There are four tentative biozone signals that we may see within the Morrison Formation. (1) The lowermost occurrence of *Barosaurus*, *Dystrophaeus*, and *Haplocanthosaurus* in Zone 1 may indicate that these forms could represent or be relics of pre-Morrison Formation sauropod genera. (2) The low sauropod diversity of Zones 1, 3, and 6 could indicate

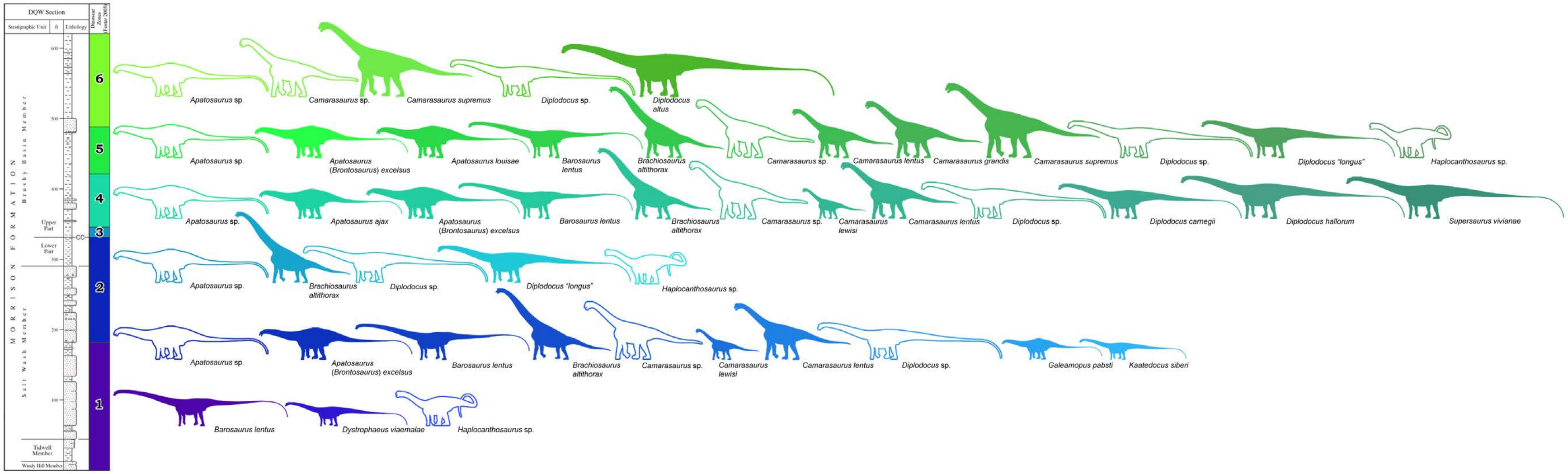

Figure 5. Biozone demarcations of sauropods within the Morrison Formation. Biozones are from Foster (2003) with additional specimens plotted according to stratigraphic placement via Turner and Peterson (1999). Stratigraphic section is from Foster (2003). Closed silhouettes represent genera with identified species, open silhouettes represent only generic level referral. Silhouettes by S. Hartman available via PhyloPic (Creative Commons Attribution-ShareAlike 3.0 Unported). Silhouettes to relative scale. A full-size version of figure 5 is in the Attachements pane.

negative events/environments, or this signal could indicate poor sampling. (3) The ecology of Zones 5 and 6 may have been more conducive to speciation—these zones exhibit the most genera and the greatest number of species. (4) Out of all of the sauropod genera that appear in at least two zones, only *Barosaurus* and *Brachiosaurus* have a single species—such could indicate something special about their biology (being longer occurring species), or their diversity (number of species) may be incorrect (note that Woodruff and others, 2017 suggest that based on possible morphologic differences seen stratigraphically, *Barosaurus* may represent more than a single species).

## Ecological Capacity

In addition to ontogeny and stratigraphy, there are several other factors at play that could equally be interfering with our signal of Morrison Formation sauropod diversity. As previously mentioned, 24 different kinds of multi-ton herbivores across a single landscape would theoretically be ecologically taxing. Many studies have proposed ecological segregation among the Morrison Formation sauropods including feeding height (Bakker, 1971; Dodson and others, 1980; Bakker, 1986; Martin, 1987; Stevens and Parrish, 1999, 2005; Upchurch and Barrett, 2000; Christian, 2002; Foster, 2003, 2007; Dzemski and Christian, 2007; Christian, 2010; Hummel and Clauss, 2011), dietary niche partitioning (Galton, 1986; Fiorillo, 1998; Upchurch and Barrett, 2000; Christian, 2002; Foster, 2003, 2007; Engelmann and others, 2004; Stevens and Parrish, 2005; Carpenter, 2006; Whitlock and others, 2010; Hummel and Clauss, 2011; Young and others, 2012; D'Emic and others, 2013; Button and others, 2014; Woodruff and others, 2015), or ontogenetic segregation (Dodson and others, 1980; Foster, 2003; Myers and Storrs, 2007; Myers and Fiorillo, 2009; Woodruff and others, 2015). Such ecological segregation undoubtedly had to occur, and likely several of these forms co-occurred—such as young sauropods feeding on different plant material than their adult forms (sensu Whitlock and others, 2010 and Woodruff and others, 2015). Not only are feeding-related factors important, but so too is their respect to body size. The African savanna today is made up a multitude of co-occurring herbivores ranging from the dik-dik (up to 6 kg; Grubb, 2005) to the African elephant (up to 10,400 kg; Larramendi, 2016). Several exemplary studies have examined the relationship between body size and foraging height to explain the extreme prevalence of herbivores in this ecosystem (Du Toit, 1990, 2003; Woolnough and Du Toit, 2001; Fritz and others, 2003; Cameron and Du Toit, 2006; Anderson and others, 2016), and possibly a similar body size to feeding height/vegetation type stratification occurred within the sauropods of the Morrison Formation. Perhaps the predominance of smaller body sized Morrison Formation sauropods, such as *Camarasaurus* (approximately 12,530 kg for *C. grandis*; specimen GMNH 101 – *this analysis*) versus the rarity of larger body sized taxa, such as *Supersaurus* (36,287 kg; Lovelace and others, 2008) may be analogous to the pattern seen in the African savanna.

## Individual Morphological Variation within Species

Another possible confounding factor is individual variation. Unlike the degree of variation observed within hadrosaurs (Campione and Evans, 2011; Fowler and Horner, 2015; Woodward and others, 2015; McFeeters and others, 2018; Takasaki and others, 2018) and ceratopsians (Scannella and Horner, 2010; Frederickson and Tumarkin-Deratzian, 2014; Scannella and others, 2014; Campbell and others, 2016, 2018), the exacting degrees of morphologic variation in Morrison Formation sauropods have not been precisely quantified. Morrison sauropod workers have colloquially referred to observed variation, but as morphologic variation in sauropods can derive from taxonomy or body size (among others), denoting whether a character is taxonomically distinct or within the range of variation can become more nebulous (Foster, 2015). Also, treating what may be continuous variation as discrete characters from low sample sizes is likely to be problematic (J. Foster, Utah Field House of Natural History State Park Museum, written communication, 2018). As an example, let us examine cranial openings. One could presume that the number of cranial openings would be a significant taxonomic signal. Therefore, said number or presence/absence of specific openings would seemingly be a strong phylogenetic indicator. And yet, this is absolutely not the case in *Camarasaurus*. The frontal aperture (Woodruff and Foster, 2017) is variably present among *Camarasaurus* specimens of various species and body sizes (echoed in Madsen and others, 1995). If the presence of an extra cranial opening is demonstrably not a taxonomically viable character in a Morrison Formation sauropod, then what characters are significant, and how do we begin to measure and quantify such variability?

## CONCLUSIONS

The information presented herein and throughout this themed set of Morrison Formation papers, beginning in 2016 in the *Geology of the Intermountain West*, will hopefully contribute to a shift in our understanding of the true nature and complexities within the Morrison. In regard to the sauropod diversity, the Morrison Formation may have legitimately exhibited unparalleled sauropod diversity. However, stratigraphy and ontogeny, among others, have been demonstrated to have repercussions on diversity estimates.

Previously, the Hell Creek Formation was thought to harbor nearly three dozen dinosaurian species. However, subsequent analyses examining the critical variables of ontogeny, stratigraphy, and variation have shown that while still highly diverse, this diversity is in actuality constructed by less than half of the perceived species (Carr and Williamson, 2004; Horner and Goodwin, 2009; Scannella and Horner, 2010; Campione and Evans, 2011). Certainly, there are unique attributes of the Morrison Formation, one such is clade representation. Within the Hell Creek Formation, species richness seems fairly evenly distributed across the different clades. Yet, in the Morrison Formation, the dominating clade constitutes almost an equal number of species to all the other clades combined (26 versus 24, respectively). As in the Hell Creek Formation, the Morrison Formation was likely very species rich. This review is not meant to admonish against richness, merely to contemplate the multifaceted factors that could affect said richness.

In consideration of the expanse that is the Morrison Formation, approximately 7 million years, and a geographical range of 14 degrees of latitude and 12 degrees of longitude (Kowallis and others, 1998; Turner and Peterson, 1999; Foster, 2007; Trujillo and Kowallis, 2015), stratigraphy, ontogeny, variation, evolutionary patterns, and environments should have some effect on sauropod diversity. Currently the degree or significance of these factors towards Morrison Formation sauropod diversity is unresolved; yet in another formation it has been demonstrated that these factors do alter diversity reconstructions. Therefore, until these factors are accounted for, we may not be accurately reconstructing the true diversity of sauropods within the Morrison Formation.

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