The Smallest Diplodocid Skull Reveals Cranial Ontogeny and Growth-Related Dietary Changes in the Largest Dinosaurs

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Sauropod dinosaurs were the largest terrestrial vertebrates; yet despite a robust global fossil record, the paucity of cranial remains complicates attempts to understand their paleobiology. An assemblage of small diplodocid sauropods from the Upper Jurassic Morrison Formation of Montana, USA, has produced the smallest diplodocid skull yet discovered. The ~24 cm long skull is referred to cf. Diplodocus based on the presence of several cranial and vertebral characters. This specimen enhances known features of early diplodocid ontogeny including a short snout with narrow-crowned teeth limited to the anterior portion of the jaws and more spatulate teeth posteriorly. The combination of size plus basal and derived character expression seen here further emphasizes caution when naming new taxa displaying the same, as these may be indicative of immaturity. This young diplodocid reveals that cranial modifications occurred throughout growth, providing evidence for ontogenetic dietary partitioning and recapitulation of ancestral morphologies.

With their titanic bodies and long necks and tails, sauropods are perhaps the most recognizable non-avian dinosaurs. Diplodocus is one of the best-known sauropod taxa, represented by over 100 specimens since its discovery in 18781. Whereas the postcrania of Diplodocus are well represented, cranial remains are exceedingly rare. An adult Diplodocus might attain a body length in excess of 30 m1, but its skull was well under 1 m2. To date only three of these skulls are hypothesized to be from immature animals3–5, thus biasing our understanding of this taxon’s ontogeny, ecology, and evolution towards adult specimens. While few, these immature skulls reveal insights into cranial allometry through ontogeny and suggest that Diplodocus and its Diplodocidae kin underwent radical ontogenetic change. Such changes would have significant effects on the ecology of immature Diplodocidae and the life history of these animals.

The smallest of the three immature skulls (CM 11255) is 29.2 cm in length, slightly over half of the adult cranial length4. Although this specimen reveals critical ontogenetic components, the cranial attributes of much younger diplodocids have remained unknown. Here we describe a new immature cf. Diplodocus skull (CM VP14128), which, with a total cranial length of ~24 cm, represents the smallest known example. This important new specimen reveals hitherto unknown aspects of immature diplodocid anatomy, and shows that juveniles are not merely smaller versions of adults (sensu Whitlock et al.3). Our primary objectives are to test the taxonomic identity of the specimen using phylogenetic analyses, comparative qualitative and quantitative methods, and discuss the ecological implications of cranial ontogeny in diplodocids. We use immature and mature to refer specifically to developmental history, while juvenile, sub-adult, and adult are used as maturational colloquialisms.

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Material and Methods

Specimens. CMC VP14128 was collected in 2010 from the Mother’s Day Quarry (MDQ) of south central Montana (MOR locality no. M-166). The MDQ is a monodominant bone bed containing the remains of at least sixteen small diplodocines (recorded femur lengths between 59.5 cm–120 cm). While five partial braincases have previously been collected from the MDQ, CMC VP14128 is the only complete skull found at the site. The skull of CMC VP14128 is preserved in four major segments (Fig. 1). CMC VP14128 also preserves one half of the proatlas and at least four anterior cervical vertebrae that were clustered with the cranial remains. A second, similarly sized, isolated, and less distorted braincase (CMC VP14129) was also found in the opposite side of the same field jacket.

Figure 1. Skeletal reconstruction of CMC VP14128 to scale with a mature *D. carnegii* (dark grey). Grey bones are missing, while those in ivory are those present in CMC VP14128. Skeletal reconstruction based on the *Diplodocus* by S. Hartman. Silhouettes by S. Hartman and PhyloPic (Creative Commons Attribution-ShareAlike 3.0 Unported; http://phylopic.org/image/3cb1d5bf-7db5-4db2-82a6-4c39f6a4411b/; https://creativecommons.org/licenses/by-sa/3.0/), modifications made. Skeletal reconstruction of CMC VP14128 redrawn from *D. carnegii* skeletal by S. Hartman (http://www.skeletaldrawing.com/sauropods-and-kin/diplodocus). Human scale is Andrew Carnegie at his natural height of 1.6 m. Skeletal and silhouettes to scale. (B) CMC VP14128 in right lateral view with accompanying schematic. (C) CMC VP14128 in left lateral view with accompanying schematic. Schematics by DCW. The four portions of the skull numbered on accompanying schematics. Lateral views and schematics to scale. a: angular, al: alisphenoid, ao: antorbital fenestra, d: dentary, f: frontal, h: hyoid, l: lacrimal, m: maxilla, n: nasal, oc: occipital condyle, os: orbitosphenoid, p: parietal, pa: prefrontal, pm: premaxilla, po: postorbital, pro: prootic, q: quadrate, sa: surangular, sq: squamosal. L and r before bone denotes if it is left or right.
Skull length estimates. Anteroposterior skull length was estimated using a linear regression of skull length to lower jaw length in diplodocid genera (Fig. S3). Scaling the anterior and posterior portions of the lower jaw of the immature Diplodocus SMM P84.15.3 results in a total jaw length of 19.9 cm, which indicates approximately 5 cm of missing cranial bone. As the cranial dimensions of smaller (and presumably younger) specimens do not develop isometrically (sensu Whitlock et al.3), from CMC VP14128 it appears that the surangular is proportionally smaller and that most of the lower jaw is represented. This approach produces a conservative estimate of 1 cm of missing bone, which results in a jaw length of 15.6 cm and a skull length of 24.3 cm. This shorter estimate is supported by the preservation of the paired dentaries, posterior portions of the jaw and associated ceratobranchial.

Transformation grid. A transformation grid (Fig. 2E) highlighting shape changes between CMC VP14128 and an adult Diplodocus was produced using the program tpsSplin8. Landmarks were placed on the line drawings of CMC VP14128 and CM 11255 presented in Fig. 2, using the programs tpsUtil9 and tpsDig26410 (see Fig. S4).

Phylogenetic analyses. We tested the taxonomic identity of CM VP14128 by including it in the phylogenetic analyses of Whitlock et al.11 and Tschopp et al.12. As CMC VP14128 is predominantly represented by cranial material, in addition to the full analyses incorporating all skeletal characters, we also phylogenetically analyzed CMC VP14128 using only cranial characters. An approach such as this is certainly not fool-proof, nor should the results be unanimously accepted to represent unequivocal relationships – we simply took this approach to examine what, if any, effects might occur from such extensive missing data. We also combined the matrices (excluding redundant characters) into a single data set – 540 characters for the cranial + postcranial matrix (115 scorable

Figure 2. Cranial ontogeny in Diplodocus sp. (A) CMC VP14128; (B) CM 11255 (redrawn from Whitlock et al.3); (C) CM 11161 (redrawn from Wilson and Sereno69). Skull drawings by K. Scannella. Skulls to scale. (D) Silhouettes of CMC VP14128 and a mature D. carnegii to illustrate body length differences between skulls of A and C size. Diplodocus silhouette by S. Hartman and PhyloPic (Creative Commons Attribution-ShareAlike 3.0 Unported; http://phylopic.org/image/3eb1d5bf-7db5-4dbf-82a6-4c39f6a4411b; https://creativecommons.org/licenses/by-sa/3.0/), modifications made. Skeletal reconstruction of CMC VP14128 redrawn from D. carnegii skeletal by S. Hartman (http://www.skeletaldrawing.com/sauropods-and-kin/diplodocus). (E) Transformation grid highlighting the ontogenetic cranial changes. Adult skull is the same in part C (Wilson and Sereno69).
characters – 21% accounted for, 79% missing), and 153 characters for the cranial only matrix (98 scorable characters – 64% accounted for, 36% missing).

Although cranial and vertebral characters identify CMC VP14128 as a diplodocid, it possesses features seen in more inclusive clades, including an extended tooth row, proportionally small antorbital fenestra, and dorsoventrally tall maxilla and premaxilla, which are seen in derived Eusauropoda and basal Macronaria. Paradoxically, if portions of the skull and vertebrae (such as the spatulate teeth and extended tooth row versus the centroid which lack a strong ventral curvature and possess posteriorly elongate postzygapophyses, see below) of CMC VP14128 had been discovered separately, they could have been misidentified.

Furthermore, recent analyses indicate that diplodocids, and potentially all sauropods, underwent allometric growth, and consequently radical ontogenetic trajectories. The documentation of specimens that fill voids in our understanding of sauropod ontogeny is critical. As Rozhdestvensky noted, derived immature individuals can appear more morphologically similar to basal adults than to their own adult form; thus, this developmental aphorism reveals the multifaceted importance of such specimens.

Within the Morrison Formation, some relatively small body size diplodocids have been used to establish new genera (including Suuwassea and Kaatedocus), and the taxonomy of some has changed in different analyses. When examined using phylogenetic analyses, while there is more recent taxonomic consensus (again Suuwassea and Galeamopus) some previous analyses placed such taxa in more basal positions. A similar phenomenon has also been seen in other dinosaurian clades. Therefore, CMC VP14128 present the opportunity to assess the phylogenetic position of a demonstrably immature animal in a numerical cladistic analysis. Given the presence of plesiomorphic characters, we predict that it will be recovered in a position basal to Diplodocus. For this purpose, we used recent phylogenetic analyses as a starting point and analyzed the matrices using parsimony and Bayesian algorithms.

Institutional Abbreviations. AMNH, American Museum of Natural History, New York, NY; BYU, Brigham Young University, Provo, UT; CM, Carnegie Museum of Natural History, Pittsburgh, PA; CMC, Cincinnati Museum Center, Cincinnati, OH; HMNS, Houston Museum of Natural Science, Houston, TX; HNM, Humboldt Museum für Naturkunde, Berlin, Germany; MOR, Museum of the Rockies, Bozeman, MT; SMA, Sauriermuseum Aathal, Aathal, Switzerland; SMM, Science Museum of Minnesota, Saint Paul, MN; USNM, United States National Museum, Washington D.C.

Results

Description and comparisons. Skull. Most of the bones are identifiable, but portions of the maxillae, jugals, nasals, and lacrimals are damaged or missing.

The cranium of CMC VP14128 has diagnostic features of Diplodocidae including: a long prefrontal, paroccipital process with a rounded ventrolateral end, external nares that are retracted and dorsally-facing, a tooth row that does not extend the full length of the maxilla and dentary, low coronoid eminence, and absence of a squamosal-quadratojugal contact. Additionally, the morphology of the basal tubera (robust, triangular, and protruding posterovertrally from the basioccipital), the presence of subnarial and maxillary foramina, and the largely peg-like teeth, while not exclusive to Diplodocidae, such morphologies and their combination are commonly observed in diplodocines.

To narrow down the taxonomic identity of CMC VP14128, we compared it with the four Morrison Formation genera of Diplodocinae: Barosaurus, Diplodocus, Galeamopus, and Kaatedocus. Diplodocus is known from eight complete skulls (CM 11255, CM 3452, CM 11161, MOR 7029, SMM P84.15.3, USNM 2672, USNM 2763), Kaatedocus from three skull (AMNH 7530 SMA 0004, SMA D-16/3, USNM 2763), Kaatedocus from three skull (AMNH 7530 SMA 0004, SMA D-16/3, USNM 2763), and Galeamopus is reported from at least three partial skulls (AMNH 969, SMA 0011, and HMNS 175). Fragmentary cranial remains of Barosaurus are reported from the Howe Quarry and recently have been recovered from the Aaron Scott Site in the San Rafael Swell of Utah (CMC VP15544). A tooth row not restricted to the anteriormost portion of the skull is present in CMC VP14128, Kaatedocus (SMA 0004), and Galeamopus (SMA 0011). The premaxillae of the newest and smallest specimen, CMC VP14128, express the Massopoda condition of four teeth - seen in Diplodocus and Kaatedocus. In contrast, the reconstructed skull of the Galeamopus pabsti holotype has five peg-like teeth, while not exclusive to Diplodocidae, such morphologies and their combination are commonly observed in diplodocines.

The exact morphology of the prefrontal in CMC VP14128 is difficult to determine due to taphonomic distortion, but it appears to exhibit the typical diplodocid posterior hook. The anterior portion of the antorbital fenestra seems to be dorsally situated to the preantorbital fossa as seen in CM 11255, Galeamopus, and possibly in Kaatedocus, although the damaged margin in CMC VP14128 makes this observation tentative. The posterior margin of the postorbital is gracile and more forke – as in Diplodocus and Kaatedocus, in contrast to less forked in Galeamopus, whereas the dorsomedial process is long and tapered as in Diplodocus and Kaatedocus, but not Galeamopus. The squamosal in CMC VP14128 has a tapered and long anterior process approaching the quadrate, as in Diplodocus and Galeamopus, and not Kaatedocus – an autapomorphy of this genus. Due to taphonomic damage and distortion, the morphology of the sagittal nuchal crest cannot be accurately discerned in CMC VP14128 (distinct and narrow vs. wide). In contrast, a distinct crest is found in both Kaatedocus and Galeamopus hayi, and CMC VP14129 does exhibit this feature (see Materials and Methods). Therefore the weight of evidence indicates a referral to Diplodocus over the other taxa.

Mandible. The relative proportions of the dentary and surangular are very similar to the lower jaw of the larger, and slightly more mature Diplodocus (CM 11255). Assuming similar proportions of mandibular bones in a mature Diplodocus to CMC VP14128, the skull would have been disproportionally stretched (see Material & Methods). Instead, CMC VP14128 indicates that in early ontogeny, the bones of the lower jaw were not directly proportionate to those of an adult (e.g. dentary to total jaw length). Regarding the dentary, the dorsoventral thickness post symphysis is more uniform as in Diplodocus and Kaatedocus, opposed to strongly tapered as
in Galeamopus. One of the most interesting features of the lower jaw is the tooth row (Fig. 1B,C). As expressed in the upper jaw, the lower tooth row extends more posteriorly than seen in more mature specimens. In the right dentary of CMC VP14128, the tooth row (which is posteriorly obscured and damaged) is located along the anterior most ~1.5 cm. The left tooth row, however, clearly spans ~6.5 cm of the dentary; approximately 46% the length of the dentary compared to 22% in adults. Comparable to the adult condition, CM 11255 was hypothesized to have had 10–11 dentary teeth, whereas CMC VP14128 possesses 13. This dental variation may represent intraspecific variation, considering that the dentary formula of CMC VP14128 is the same as in immature camarasauromorphs and that ontogenetic dental formula reduction is documented in other dinosaurs.

**Dentition.** The dental formula of CMC VP14128 is 4.8/13; the dental formula of the more mature CM 11255 has a formula of 4.8–9/10–11 dentary teeth, which is comparable to the adult condition of CM 11161 that has a formula of 4.9/11–12.

The premaxillary teeth of CMC VP14128 exhibit the typical diplodocine condition: long, slightly inclined, pointed, and narrow-crowned – the so-called peg-like condition. However, from the second maxillary tooth posteriorly, the teeth are apicobasally short, with mesiodistally wide and more labial convex crowns. Several teeth have a *Camarasaurus*-like distal occlusal wear facet (Fig. 3). This relatively basal tooth morphology is consistent with the overall basal-expression form of the cranium.

**Maturational state of CMC VP 14128.** CMC VP14128 establishes the immature condition for many features of the skull, jaws, dentition, and anterior cervical vertebrae far beyond what has been previously known. We summarize those changes here, and make note of immature features that correspond to the plesiomorphic character states of Diplodocoidea (for a greater discussion on the possibility of ontogenetic recapitulation, please consult the Supplementary Information).
Size. The estimated skull length of CMC VP14128 is 24.29 cm, which is ~40% the length of the largest adult Diplodocus skull (USNM 2673, ~60 cm). Cranial size differences observed between CMC VP14128 and adult skulls attest to changing body size through ontogeny (Fig. 2). The cranial size difference between CMC VP14128 and CM 11255 ~5 cm seems minor, yet the understanding of sauropodomorph paleobiology is dependent on their relative scale. Understanding minor skeletal nuances can have vast ontogenetic repercussions. A mere 25 cm difference in femoral length separates a 6 m 6-year-old from a 27 m 24-year-old Diplodocus (5).

While we do not have complete Diplodocus specimens, we have composites and referable material enabling us to draw some conclusions about adult proportions. Specifically, here we use D. carnegii CM 84 which is a composite, but represents the informal standard for the genus32. Nevertheless, using a ratio from CM 84 assumes

Comparative description. Comparative description. The Morrison Formation preserves three sauropod clades: Diplodocoidea, Camarasauridae, and Brachiosauridae. The lack of only spatulate teeth, an inclined posterior portion of the pre-maxilla, projecting external naris, cervical ribs shorter than centrum, and rectangular not rhomboidal cervical vertebrae profiles in CMC VP14128 are more diplodocoid than macronarian morphologies. Although many of the diagnostic characters in the sauropod skull are proportionally or ontogenetically variable46 some of the morphologies within CMC VP14128 are different from those expressed in the adult. While a few traits could be outside of the typical adult expressions, we hypothesize that characters/conditions of CMC VP14128 will at least largely associate with a known genus (as previously demonstrated in Europasaurus45).
CMC VP14128 is referable to Diplodocidae based on the presence of: a long posterior process of the prefrontal, teeth that do not span the length of the maxilla and dentary, a low coronoid eminence on the mandible, lack of crown-to-crown occlusion, cervical rib length that is shorter than the corresponding centrum length, and external nares that are retracted and face dorsally. CMC VP14128 is not referable to Apatosaurus given the presence of a basiptyerygoid recess, a basiptyerygoid process that lacks an anteroventral flare, and enlarged cervical ribs that do not project below the centrum. Likewise, CMC VP14128 is not referable to Barosaurus, based on the presence of long postzygapophyses, anteroposteriorly narrow neural spines, and a strongly posteriorly-angled centrum cotyles. CMC VP14128 has its strongest affinities with the slender diplodocines, including Diplodocus, Galeamopus, and Kaatedocus; however, the distribution of shared features is inconsistent, obscuring its lower-level identity. However, based on the number of shared characteristics, CMC VP14128 is most referable to Diplodocus than either Galeamopus or Kaatedocus.

However, it must be stated that specimens previously assigned to Diplodocus, and how we phylogenetically recognize and identify this genus are being reexamined\(^{12,13}\). Some historically recognized Diplodocus specimens are now being referred to other genera – such as USNM 2673 possibly representing Galeamopus\(^{12}\) and even CM 11255 to Barosaurus\(^{48}\). Additionally, some Morrison Formation taxa have little to any known or described cranial material (Barosaurus, Dystrophaeus, Haplocanthosaurus, Supersaurus, Supersaurus, Supersaurus). Therefore, there are several taxa we cannot adequately compare CMC VP14128 to or assess. Additionally, while Whitlock\(^{11}\) identified three cranial autapomorphies for Diplodocus (preantorbital fenestra with well-defined fossa, pterygoid median to ectopterygoid on transverse palatal hook, teeth inclined anteriorly relative to axis of jaw) since no skulls to date are unquestionably associated with post-crania, Tschopp et al.\(^{12}\) questioned these characters. While the latest phylogenetic analysis of Diplodocidae would advocate that no unambiguous diplodocinae cranial synapomorphies are recognized\(^{11,12}\), the exact taxonomic assignment of CMC VP14128 within Diplodocinae remains uncertain. With the current lack of any diplodocinae synapomorphies\(^{12}\), one could taxonomically identify CMC VP14128 simply as diplodocinae indeterminate. However, given the predominance of similar morphologies between CMC VP14128 and Diplodocus sp. in comparison to the other Morrison Formation diplodocids, we tentatively opt to refer CMC VP14128 to cf. Diplodocus. While both identifications (diplo dinosaur indeterminate and cf. Diplodocus) are testable hypotheses, we currently believe that it is more fruitful and more constructive for future works to support/refute our identification of CMC VP14128 as cf. Diplodocus versus reanalyzing starting from a subfamily level identification.

**Phylogenetic analyses.** Separate data sets. The cranial + postcranial parsimony and Bayesian analyses of the Whitlock\(^{11}\) data set recovered CMC VP14128 as the basalmost member of Dicraeosauridae, while the cranial only analysis recovered CMC VP14128 as the sister species of Dicraeosaurus, and Dicraeosaurus + Amargasaurus, respectively. The cranial + postcranial parsimony and Bayesian analyses of the Tschopp et al.\(^{12}\) data set recovered CMC VP14128, as a diplodocine more derived than Diplodocus, while the cranial only analysis recovered CMC VP14128 in a polytomy within Flagellicaudata.

Combined data set. In the combined cranial + postcranial parsimony and Bayesian topology, there is a degree of basal uncertainty (no united Macronaria), yet there is a structured and organized Diplodocoidea (Fig. 4). In the parsimony topology, CMC VP14128 is recovered as the sister species to Diplodocus, while in the Bayesian analysis, it is recovered as a derived member of Flagellicaudata and basal to Diplodocidae. For the combined cranial only analyses, the topologies are similar to that of the cranial + postcranial analyses. There are distinct Rebbachisauridae, Dicraeosauridae, and Diplodocidae branches, and CMC VP14128 is recovered as the sister taxon to Diplodocus. Apart from minor changes in posterior probability, the Bayesian topology is very similar to the earlier analysis\(^{12}\). It likewise recovers CMC VP14128 in a flagellicaudatan polytomy in which Dicraeosauridae forms one branch. Yet we would caution that while these two analyses superficially produce similar results, the low support for groupings indicates that these relations are not definitive.

The minutia between the parsimony and Bayesian analyses do vary, but in general the encompassing skeletal analyses do little to elucidate the taxonomic identity of CMC VP14128. In the analysis of Whitlock\(^{11}\), CMC VP14128 is recovered in the same dicraeosaurid position, while in the analysis of Tschopp et al.\(^{12}\) taxonomy is slightly more refined as CMC VP14128 is recovered as a derived diplodocine versus a flagellicaudatan polytomy, and finally in the combined analysis, CMC VP14128 is still recovered as a diplodocoid. Certainly the encompassing analyses do reveal much more overall taxonomic resolution, but said resolution is largely irrespective to CMC VP14128. A cranial only approach could appear redundant or unnecessary, yet given the vastly differing phylogenetic placements between the matrices used herein, we would suggest that an elemental or regional styled analyses can be used to further check or verify specimens that are recovered in seemingly unusual or suspect positions.

**Discussion**

**Phylogeny.** Parsimony analyses of CMC VP14128 produced a conflict. One resulted in only a generic level association with Diplodocus, while the other advocated a unique basal position. If our cranial-only analyses represent true phylogenetic patterns, then relatively small morphological matrices (in terms of number of characters, percentage of each character region, and/or taxa) can be sensitive to inclusion of juvenile specimens\(^{4}\), as demonstrated by the more basal positioning of CMC VP14128. This is expected as even a few characters that change with ontogeny will have a large effect on the outcome of the analysis. In the larger\(^{12}\) and combined analyses, CMC VP14128 is recovered amongst other flagellicaudatans (including diplodocids), albeit in large polytomes, agreeing with our previous diagnosis. This suggests including additional characters can override the effect of a few characters that are ontogenetically biased, but as paleontological phylogenetic analyses are often based on small datasets, this bias can be significant.
In regard to the plesiomorphic characters in CMC VP14128, we theorize these might be evidence of recapitulation; i.e., the ephemeral presence of plesiomorphic characters that transition into their derived states by adulthood. Recapitulation has been documented in other basal and derived immature sauropods. Morphologies in CMC VP14128 – such as the posterior tooth row, lower jaw proportions, and rounded snout – could be recapitulatory in origin (see Supplementary Material); yet given the relationship between cranial attributes and feeding strategy, these morphologies could also derive from ontogenetic ecomorphological relationships (see below). More specimens and analyses are need to substantiate either possibility, and we note that these hypotheses are not mutually exclusive.

Despite the presence in CMC VP14128 of phylogenetically plesiomorphic features that are not seen in adult Diplodocus, this does not mean that the entire skeleton of CMC VP14128 is plesiomorphic, (or that it is a misidentified basal taxon), since the specimen does have characters of Diplodocus. Instead, this combination of characters is evidence that 1: not all parts of the skeleton develop at the same rate, and 2: regardless of rate, ontogenetic skeletal changes followed the phylogenetic progression from plesiomorphic to derived states. Recognition of this phenomenon strongly cautions against diagnosing new taxa based on small statured specimens displaying a combination of basal and derived characters, which might instead be evidence of immaturity. Interestingly, similar findings were reported by Tschopp et al. regarding "Elosaurus" parvus (CM 566). While originally thought to be a valid taxon, "Elosaurus" is now regarded as an immature Brontosaurus parvus (however, while this analysis believes this maturational inference is highly likely, we cautiously note that this hypothesis has not been histologically tested). Including CM 566 into a specimen-level analysis, Tschopp et al. recovered the specimen not only within the species B. parvus, but also as the basalmost specimen. We would agree with Tschopp et al. that more studies are needed to address this issue, and this further highlights the multifaceted relationship between ontogenetically variable characters and taxonomic recovery.

**Ecomorphology and behavior implications.** The unique cranial and dental characters seen in the immature CMC VP14128 suggest resource partitioning between juvenile and adult Diplodocus. Like the immature Diplodocus CM 11255, CMC VP14128 has a mediolaterally narrow snout, in stark contrast to more mature individuals that express a wide and squared snout. These differences have been hypothesized to indicate dietary niche-partitioning through ontogeny, and the narrow snout of CMC VP14128 is consistent with the hypothesis that immature diplodocids had a selective feeding strategy, while fully mature animals were ground-level browsers. CMCVP14128 also has spatulate teeth and an extended tooth row. Spatulate teeth are more efficient for coarse vegetation and bulk feeding, and non-spatulate teeth are beneficial for softer foliage and browsing. This combination of dental morphologies in CMC VP14128 may indicate that very immature diplodocids were feeding on a greater variety of plant materials, and orally processed them differently than their more mature counterparts.

Figure 4. Dendrograms of parsimony (left column) and Bayesian (right column) phylogenetic analyses. (A–C) Consist of cranial and postcranial characters, while (D,E) consist of only cranial characters. (A and D) CMC VP14128 coded into the matrix of Whitlock. (B and E) CMC VP14128 coded into the matrix of Tschopp et al. (C and F) CMC VP14128 coded into a combined matrix.

While each of these differing matrices (cranial + postcranial vs. cranial) generally recover CMC VP14128 in the same or similar position, no identical typology or placement is recovered amongst these different analyses (Whitlock, Tschopp et al., and Combined).
However, previous studies show that nutrition selectivity is problematic in animals exceeding a certain size and that there is a selection pressure towards browsing for large herbivores. Another recent analysis showed that narrow, short, and rounded macronarian snouts were more efficient for forested environments while broader and longer diplodocoid snouts suggest open, ground-level browsing. This could also be interpreted as indicators of different ecological environments, implying macronarians would have been adapted for more forested environments while diplodocids were more specialized for open environments. Therefore, the plesiomorphic macronarian-like characters seen in CMC VP14128 could also indicate that juvenile diplodocids lived in more forested environments than the adults that (restricted and protected by their size) were most likely browsing in more open habitats. Foraging in forests would have provided the juveniles with protective cover from predators, a danger that colossal adults would not share.

The skull and tooth morphology of *Diplodocus* suggests that these animals transitioned through distinct feeding roles over their lifespan. This inference is supported by a study of *Alligator mississippiensis* tooth change through ontogeny. Dental changes coincided with changes in diet, thus dental allometry could be attributed to dietary partitioning.

Though it is currently unknown which specific plant species Morrison Formation sauropods ate, based on δ13C relationships between modern plant equivalents and tooth enamel implies that *Diplodocus* may have fed on ferns and horsetail, while *Camarasaurus* was generalized, feeding on a wide range of foliage, including ferns, horsetails, conifers, and cycads. An immature *Diplodocus* may have foraged for itself (or possibly as part of an age-segregated herd) and fed on differing foliage to gain more nutrients during critical development.

The ontogenetic change in dental morphologies observed within *Diplodocus* also gives evidence for the lack of parental care in sauropods (along with nest structures and histology). If adults fed hatchlings - potentially the foliage they ate - then there would be no reason for the changes in tooth morphology. Evidence of precocial juvenile sauropods was also found in a recent histologic assessments of a very immature titanosaur. Furthermore, the extreme size differences between parent and hatchlings could have resulted in high infant mortalities due to trampling.

The differences in cranial morphology between CMC VP14128 and more mature *Diplodocus* specimens (such as CM 11255; Whitlock et al.) highlights extreme cranial changes that occurred rapidly over a short increase in size. In addition to the narrow snout, the proportionally enlarged braincase and extremely large orbits are both infantile attributes observed in many other immature vertebrates. The more box-like cranial condition and the extended tooth row in CMC VP14128 are reminiscent of the co-occurring camarasaurid condition. If these characters represents recapitulation, we could hypothesize that dietary generalization is the more basal condition and increasing specialization the more derived.

**Possible dwarfism?** Instead of a juvenile, CMC VP14128 could represent an unknown Morrison Formation dwarf taxon. Two separate investigations of age determinant histology and morphology of the MDQ material produced different results. The bone tissue types in the first analysis indicate average sized immature diplodocids with typically expressed tissues, yet many of the specimens of the second analysis exhibit tissues indicating skeletal maturity. In comparing histology, this is not simply the case of incorrect tissue interpretations – the varying tissue morphologies indicate a more complex story for the MDQ.

The regional geology does not support the presence of an island depositional system – an extensive marine unit with localized terrestrial deposits. Nevertheless, regional geography or environment could explain a possible size difference. In the case of stegosaur specimens from the northern extent of the Morrison Formation, larger overall size (*Stegosaurus*) appears correlated with arid environments, and smaller size with wetter climates (*Hesperosaurus*). Based on the coastal setting adjacent to the Sundance Seaway, this trend in stegosaur size was hypothesized to be environmentally correlated. A similar pattern might hold true for the MDQ diplodocids.

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**Figure 5.** Life reconstruction of CMC VP14128. Note the cranial morphologies interpreted to denote differing feeding strategies: in CMC VP14128 the narrow snout with posteriorly elongated and morphologically varied tooth row for bulk feeding vs. the widened snout with anteriorly restricted peg-shaped teeth for ground-level browsing in adults. Also note the camouflaged ontogenetic color change suggesting young diplodocids may have sought forested refuge. Reconstruction by A. Atuchin.
Other Morrison Formation localities in Montana record more typical sized specimens of Apatosaurus and Diplodocus\(^{2,3}\). This regional size difference, and size difference within the MDQ\(^{11}\), may represent regional variation. Such regional differences are present in a modern group of herbivores, cervids. The North American coastal White-tailed Deer (Odocoileus virginianus) have an average body mass of 77 kg, while their interior counterparts have an average body mass in excess of 100 kg\(^{22}\). The smallest sub-species, the Key Deer (Odocoileus virginianus clavium) represents an example of island dwarving has an average body mass of 34 kg\(^{27}\). Therefore, these size differences between localities may indicate variably-sized regional diplodocid populations. In spite of these findings CMC VP14128 is almost certainly not a regional dwarf because it lacks autapomorphies. The morphologies we assigned to ontogeny could hypothetically be used to erect autapomorphies, however we strongly caution that the onus is on such an analysis to demonstrate that no attributes are related to ontogenetic variation as proposed herein. Alternatively, opposed to the dwarf morphotype observed by Waskow et al\(^{41}\), CMC VP14128 may represent the larger morph present at the site.

**Conclusions**

Within Dinosauria, there are small bodied taxa that display basal and derived characters and occupy unusual basal phylogenetic positions. The validity and position of such taxa has been disputed\(^{11–26,68,69}\), and regarding sauropodomorph phylogeny, we would advocate that the combination of basal and derived characters and basal phylogenetic recovery should be recognized as an indicator of an immature ontogimorph – instead of a distinct taxon. In light of the current wealth of information pertaining to dinosaur ontogeny, we can no longer assume that all morphological differences correspond with phylogenetic distinctiveness. Accounting for ontogeny could prove as test for our phylogenies. Recognizing the ontogenetic age of immature specimens provides important insights into the life history of these animals. The immature Diplodocus specimen CMC VP14128 extends our understanding of the ontogeny of the genus and the evolution of diplodocoids into new areas, where:

1. The combination of basal and derived characters in the juvenile is broadly congruent with the phylogenetic transition from eusauropods to diplodocoids.
2. The pleiomorphic tooth morphology is retained in immature Diplodocus and lost with maturity, and we predict this growth pattern will be seen in all other diplodocoids.
3. As first proposed by Whitlock et al\(^{3}\), tooth and skull morphology indicate that during growth Diplodocus inhabited different trophic levels/niches, where juveniles were generalists (i.e., browsers; Fig. 5) and more mature individuals were specialists (i.e., ground-level browsing), a pattern that we predict is ancestral for Diplodocidae.

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Author Contributions
G.W.S. collected the specimen, D.C.W. described the specimen, D.C.W., T.D.C., G.W.S., K.W., J.B.S., K.K.N. and J.P.W. wrote the manuscript, T.D.C. and K.K.N. created and analyzed the phylogenetic models, J.B.S. created the transformation grid, J.P.W. photographed the specimen and created the photogrammetric models.

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