A FUNCTIONAL FAUNA NETWORK ANALYSIS OF THE MORRISON FORMATION

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Abstract—Although a great diversity of vertebrate taxa are known from the Late Jurassic Morrison Formation, the structure of the ecological relationships between taxa remains unclear. Herein, we conducted a bipartite network analysis on the Morrison Formation fauna using ecomorphological traits of vertebrates: size class (mass), dietary guilds, and habitual tiering. Our results support local environments and habitat diversity as the driving cause of functional fauna disparity, but dinosaurian functional fauna throughout the formation was stable. These results support heterogeneity within the Morrison Formation, where a mosaic of similar yet separate local paleoenvironments was a major driver of species diversity. Our findings suggest that the Morrison Formation was a stable ecosystem throughout geological time, with different species undertaking similar functional roles despite taxonomic turnover. Utilizing a functional fauna approach for paleoecology allows for the study of ecosystems over time and can assess the distinction between faunal turnover and ecosystem functional changes.

INTRODUCTION

Western North America's Morrison Formation is a well-sampled and understood Late Jurassic terrestrial ecosystem. Over a century of collecting, particularly from highly productive quarries has provided a wealth of vertebrate fossil material as such, the Morrison has become the subject of many studies over the past 150 years regarding geology and depositional conditions (e.g., Mook, 1916; Stokes, 1944; Keller, 1953; Moberly, 1960; O'Sullivan, 1984; Demko and Parrish, 1998; Turner and Peterson, 1999; Myers et al., 2014; Owen et al., 2015), paleobotany (Brown, 1972; Brown, 1975; Miller, 1987; Tidwell, 1990; Ash and Tidwell, 1998; Tidwell et al., 1998; Chure et al., 2006; Foster et al. 2023; Gee, 2023a; Gee, 2023b; Hotton and Baghai-Riding, 2023), and vertebrate paleontology (Foster, 2003; Foster and Lucas, 2006; Foster, 2020; Hunt-Foster, 2024). The Morrison Formation extends over 1.2 million km^2 of the western United States and was deposited over 7-9 million years, from the uppermost Oxfordian to the Tithonian Stages of the Late Jurassic (~155-148 Ma; Turner and Peterson, 1999; Woodruff, 2019; Maidment and Muxworthy, 2019). The Morrison Formation has a diverse fossil vertebrate fauna, comprised of dinosaurs (Madsen, 1976; Britt, 1991; Madsen and Welles, 2000; Carpenter et al., 2005; Lovelace et al., 2007; Tschopp et al., 2015; van der Linden et al., 2024; Boisvert et al., 2024; Danison et al., 2024; Boisvert et al., 2025), pterosaurs (Padian, 1998), crocodylomorphs (Yoshida et al., 2021), testudines (Chure et al., 2006), lepidosaurs (Evans and Chure, 1998; Chure et al., 2006; Brownstein et al., 2022; Meyer et al., 2023), mammaliaformes (Chure et al., 2006; Davis et al., 2018; Davis et al., 2022), osteichthyans (Kirkland, 1998; Chure et al., 2006), and lissamphibians (Evans et al., 2005; Gardner and DeMar, 2013). Furthermore, ichnofossils, including invertebrate traces, small reptilian swim tracks, tubes and burrows, putative termite nests, invertebrate traces in bone and wood, dinosaur and pterosaur trackways related to these taxa have been described from the Morrison Formation (Hasiotis, 2004; Britt et al., 2008; Lockley and Gierlinski, 2014). The diverse community of vertebrates preserved in the Morrison Formation and its large depositional range make it ideal for investigating broad-scale ecological connections and laying the groundwork for applications in other Mesozoic ecosystems (e.g., Carpenter et al., 2005; Chure et al., 2006; Wings, 2014; Drumheller et al., 2020; Lei et al., 2023; Bivens et al., 2025). However, the ecosystems of the Morrison Formation, like modern ecosystems, have high complexity through abiotic and biotic component interactions, affecting the overall composition of this relatively well-understood rock unit (Woodruff, 2019).

The capacity to have stable, diverse megafaunal communities (*sensu* Martin, 1973, and Galetti et al., 2018) in Morrison Formation ecosystems has been called into question before (Whitlock et al., 2018; Woodruff, 2019; Maidment, 2024). Faunal communities would be expected to be uniform across the Morrison Formation if stable community structures existed, matching early interpretations of the Morrison Formation (Dodson et al., 1980; Foster, 2000; Foster and Chure, 2006). However, more recent Morrison Formation exploration has conversely suggested heterogeneous vertebrate diversity in the Morrison Formation, making stable community structures difficult to interpret (Foster et al., 2016; Foster and McMullen, 2017; Whitlock et al., 2018; Maidment, 2024). Regardless of gradients, the biota of the Morrison Formation inherently must have been subject to similar climatic changes, the effects from migration of new species, and changes in habitat composition due to their existence as a regional biota as defined by Patzowsky (2017), as all fauna within a single depositional basin. One way in which this could be reconciled would be identification of mosaic paleoenvironments within the Morrison Formation, which has been supported via paleobotanical evidence (Gee et al., 2014; Gee et al., 2019; Richmond et al., 2019; Foster et al., 2022; Foster et al., 2023; Hotton and Baghai-Riding, 2023; Xie et al., 2024), and additional corresponding faunal analyses pertaining to paleoecology and biodiversity (Foster, 2003; Good,

2004; Turner and Peterson, 2004; Noto and Grossman, 2010; Foster and McMullen, 2017; Whitlock et al., 2018; Maidment, 2024). The floral and faunal aspects of the Morrison Formation paleoenvironments were likely dictated by latitudinal climate differences, with semi-arid conditions persisting throughout, but increased precipitation and commonplace perennial streams occurring in northern regions of the depositional basin (Good, 2004; Parrish et al., 2004; Turner and Peterson, 2004). Therefore, the disparity between different Morrison Formation quarries remains unresolved due to the juxtaposition of dominant homogeneous taxa (e.g., *Camarasaurus* spp. and *Allosaurus* spp.; see Woodruff and Foster, 2017; Whitlock et al., 2018; Maidment, 2024) and the presence of generally heterogeneous paleoenvironments and their regionalized taxa (Whitlock et al., 2018, fig. 2).

Today, large herbivores alter the spatial and taxonomic patterning in the African Savannah, a warm semi-arid environment like the Jurassic Morrison Formation. Among large African herbivores, the most applicable functional analogs approaching the colossal sauropods of the Morrison Formation are the African bush elephant (*Loxodonta africana*) and African forest elephant (*Loxodonta cyclotis*). Studies of elephant impacts across Africa showed that while elephants have an impact on tree abundance, they do not have a negative effect on other animals that share space with them (Coverdale et al., 2016; Guldemond et al., 2017; Poulsen et al., 2017; Cardoso et al., 2019). Additionally, elephant foraging has even been shown to promote the diversity of understory species, since branches damaged during feeding decrease the frequency of herbivory and provide refuge for palatable plant species (Coverdale et al., 2016). Elephant browsing on savannah woodlands in Hwange National Park, Zimbabwe, showed that high elephant densities altered woody plant abundance according to height layer, where the number of tall plants decreased and the number of short plants increased (Ferry et al., 2021). These megaherbivore changes in the structure of vegetative communities may have knock-on effects on other aspects of savannah ecology. In the Sabi Sand Wildtuin in South Africa, the increase in elephant density and its associated landscape modifications drove a decline in the abundance of medium-sized browsers and favored the dominance of grazers and megaherbivores (de Boer et al., 2015). The more open landscapes elephant foraging produces may also affect the relationship between predators and prey, altering the "landscape of fear" for prey and altering cover for both predator and prey (Fležar et al., 2019). In Hwange National Park, lion (*Panthera leo*) kill sites were characterized by higher levels of elephant impact than random, supporting the notion that the megaherbivores may affect predator-prey interactions in their ecosystems (Ferry et al., 2020). Given the historic impact of two extant species of elephant across multiple biomes on the African continent, we must consider the browsing of several species of sauropods, which equalled or exceeded the mass of an elephant, as a major element affecting the structure of communities in the Jurassic west.

The history of the African Savannah is also important to consider. The step-wise aridification of Eastern Africa in the Plio-Pleistocene produced a mosaic of wooded and more open habitats, which drove the evolution of the modern assemblage seen today (deMenocal, 2004; Bibi & Cantalapiedra, 2023; Rowan et al., 2024). The rich fossil record of Plio-Pleistocene Africa may provide a useful comparison due to interpretations of similar mosaic paleoenvironments in the Morrison Formation (Augustine, 2003; Gillson, 2004; Murwira and Skidmore, 2005; Bakker et al., 2015; Marston et al., 2019; Trepel et al., 2024). Recent analyses also indicate that taxonomic change is commonly independent of ecosystem functionality (Vandewalle et al., 2010; Mlambo, 2014; Jarzyna and Jetz, 2018; Baker et al., 2021), as determined by their ecomorphological traits (Barr, 2018; Blanco et al., 2021; Bateman and Larsson, 2025) when interpreting selective mammalian-dominated communities (Dunne et al., 2014; Oliveira et al., 2016; Lacher et al., 2019; Blanco et al., 2021; Fricke et al., 2022; Hedberg et al., 2022; Bibi and Cantalapiedra, 2023) and other vertebrate and invertebrate dominated communities (Foster and Twitchett, 2014; Dineen et al., 2014; Dunhill et al., 2017; Cribb et al., 2023; Huang et al., 2024).

Modern understanding of taxonomic composition is defined by diagnosable taxa, whilst functional fauna is defined by the role taxa have in ecosystem structure, independent of taxonomic status. Ecological functional units (EFUs) determine functional fauna and are contingent upon ecomorphological traits, where network analysis has been used in recent studies to investigate the disparity or stasis of faunal assemblages throughout time (Blondel et al., 2008; Lozano et al., 2016; Blanco et al., 2021; Blanco et al., 2025). EFUs are defined within each study by combinations of three or more ecomorphological traits, such as size, dietary guild, with Blanco et al. (2021) utilizing locomotion, whereas Cribb et al. (2023) used tiering (i.e., the occupied ecospace, such as aquatic or arboreal, a taxon occupies within an ecosystem).

Using EFUs, Blanco et al. (2021) investigated mammalian assemblages of the Iberian Peninsula over a 20-million-year duration to assess the stability or change of the functional fauna of these mammalian assemblages. This method allows for the assessment of ecosystem functionality, independent of taxonomic composition, and takes into account when different taxa that may be closely related or not fulfill similar ecological functional roles. When this occurs, that function in the ecosystem is maintained even with a taxonomic turnover, with that EFU persisting through time. Blanco et al. (2021) found there were three main functional faunas for a 20-million-year duration, which included multiple different taxa fulfilling the same ecological functional unit; hence, this function persisted through time. The three functional fauna shifts occurred in a wider context of climatic shifts. Such a method would allow for functional fauna stability or change of the Morrison Formation to be assessed independently of the taxonomic composition.

The limited fossil record impacts paleoecological reconstruction methodologies more than in extant ecosystem analyses, attempting to recognize ecosystem structure in deep time. For the Morrison Formation fauna, due to the diverse faunal assemblages across multiple dinosaur-bearing quarries, we can begin to test the ecosystem dynamics of these different quarries through time. In this study, we aim to determine ecosystem similarity and disparity across space and time within the Morrison Formation. This paper analyzed different Morrison Formation quarries using network analysis to study the disparity of the functional fauna of the Morrison Formation. Ultimately, the goal of this study is to determine if there are differences and/or stability across multiple functional faunas in the Morrison Formation based on ecomorphological similarities (Lucas and Heckert, 2000; Button et al., 2014; Whitlock et al., 2018; Tschopp et al., 2019; Foster et al., 2020; Richmond et al., 2020).

METHODS

Defining Morrison Formation Functional Fauna Units

Using Foster (2020), we gathered taxonomic data, selecting quarries with ≥6 taxa present, providing us with 48 quarries in total from the Morrison Formation. Quarries with six or more taxa present were selected, similar to Blanco et al. (2021), to try to represent a relatively complete faunal assemblage. We assigned three broad ecomorphology metrics to each taxon: a size class group (Table 1), dietary guild category, and habitual tiering to investigate the functional diversity of fauna to produce the EFUs as similar to Blanco et al. (2021) and Cribb et al. (2023). To account for discrepancies in the current chronostratigraphical

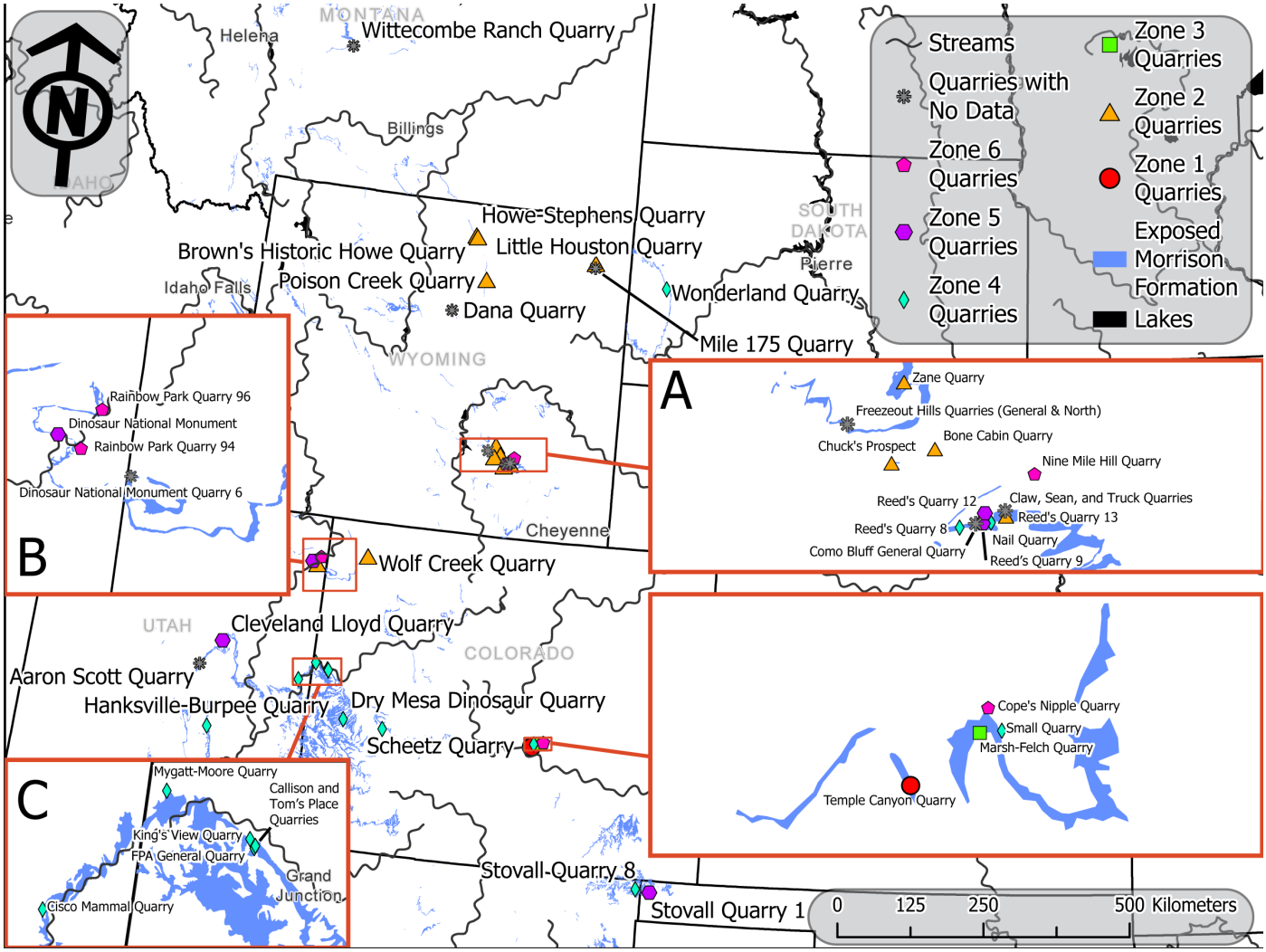

FIGURE 1. Map overview of all quarries utilized, binned by Foster's time zones (Foster, 2003; 2020; J. Foster, personal commun. 2025), mapped to Morrison Formation exposures. Panels represent a high density of quarries in a single subsection: **1A**, Como Bluff study area, **1B**, Dinosaur National Monument, and Rainbow Park study area. **1C**, Fruita Paleontological Area study area. **1D**, Colorado Springs-Cañon City study area. All quarry locations were roughly approximated from literature or instead sourced from the PaleoBiology Database, possibly not representative of the true quarry location. Mapping resources taken from Natural Earth, ESRI, TomTom, Garmin, FAO, NOAA, USGS, BLM, NPS, USFWS, METI/NASA, and the Nebraska Game & Parks Commission.

metrics, when assessing potential changes through time, we used: Stratigraphic Levels (Foster, 2020), Dinosaur Faunal Zones (Turner & Peterson, 1999), and System Tracts (Maidment & Muxworthy, 2019). We include indeterminate remains at specific quarries on a case-by-case basis; if no higher taxonomic occurrence was present for that clade (i.e., an indeterminate diplodocoid would be included if there were no diplodocoid taxa and only generic macronarians present, but would be excluded if a named diplodocoid taxon were present).

Further new taxonomic assessments were outside the scope of this paper. Due to each category correlating to a number in the analysis, taxa that functioned as identical EFUs would result in having the same number as well as the same descriptor (e.g., 151 as giant (1) ground dwelling (5) ground height browser (1) in the analysis).

Quantifying Size Class

We followed a modified size class system from Holtz (2021) using information and comparison with Sander et al. (2011), Rauhut et al. (2011), and D'Emic (2023) (Table 1). Mass estimates used were largely based on femoral circumference (Campione et al., 2014; Benson et al., 2014; Benson et al., 2018; Campione and Evans, 2020), while size classes were assigned to animals in the analysis by comparing derived mass estimates to each other. As some of these specimens may represent juveniles, using size classes that encompass a range of masses to account for variation helped avoid skewing data, where the formulated size classes successfully separated the largest taxa from the smallest taxa with sufficient disparity.

Establishing Tiering and Dietary Guild

Five tiering categories were used in the analysis: ground-dwelling, aerial, semi-aquatic, aquatic, and burrowing. These were assigned to taxa based on the literature. The six dietary guild categories used in the analysis were: ground height browser (eating foliage less than 1.5 meters from the ground), mid to high height browser (eating foliage greater than 1.5 meters off the ground), omnivore (consumption of producers and consumers), insectivore (carnivores primarily eating insects), as well as carnivore and hypercarnivore (see definition below). A comprehensive literature search was done to categorize each animal selected across the Morrison Formation quarries sampled

for this study.

For the purposes of this analysis, we defined hypercarnivores as consumers with a generalist diet of terrestrial tetrapods. This distinction was made to help differentiate the diets and roles of *Allosaurus* and *Torvosaurus* (Bakker and Bir, 2004) as it is hypothesized that *Allosaurus* predated primarily upon dinosaurian prey (Foth et al., 2015; Hone and Chure, 2018) whereas *Torvosaurus* may have predated upon more aquatic prey, including, fish, crocodylians, and turtles. *Torvosaurus* had a more sinuous body that has been suggested to be an adaptation of hunting in and around waterways and mesic-rich habitats (Bakker and Bir, 2004). Partitioning of *Allosaurus* and *Torvosaurus* is supported by anatomical morphological differences, rare stomach contents of fish within megalosaur fossils (Eudes-Deslongchamps, 1838), and the occurrence of megalosaurs in coastal deposits (Allain, 2005), evidence which is lacking across Allosauroidea. Phylogenetic bracketing may imply fish-eating as an ancestral behavior in Megalosauroidea, and present in both Spinosauridae and its sister clade Megalosauridae, though to a lesser extent (Farlow and Pianka, 2002; Bakker and Bir, 2004; Allain, 2005; Razzolini et al., 2016; Arden et al., 2019). For these reasons, *Torvosaurus* was coded as a carnivore rather than a hypercarnivore.

Functional Fauna Analysis

The bipartite networks were formed by the occurrences and the number of EFUs at different sites. This was then used to assess the similarity and disparity of the functional fauna of the 48 quarries (see Table 2). Subsequently, sites with the same depositional environments (i.e., floodplain, channel, lacustrine, and so on [as categorized by Foster, 2020]) or time zones (System Tracts 1-6, see Maidment, 2024; Dinosaur Faunal Zones 1-4, See Turner and Peterson, 1999; Stratigraphic Levels 1–6; see Foster, 2020 for applicable sites) were analyzed (Table 2, Tests 3-22). Further parameters include the total number of EFUs at a site and the number of dinosaurian EFUs. Sites with either or both at least 15 EFUs or five or greater dinosaurian EFUs were analyzed individually (see Table 2 for the full breakdown of all tests and parameters of the sites analyzed). The similarity and disparity of the sites in each test group were analyzed in R using Analysis of Variance (ANOVA) of the bipartite networks, to see if there was a significant p-value in the disparity using a simple linear model, for example, such as floodplain communities or communities in time Zone 4 (*sensu* Foster, 2020).

Limitations and Assumptions

Historically, vertebrate paleontology involves rigorous reconstruction of fossil faunal compositions and correlation between them across time and space (Tschopp et al., 2015; Foster et al., 2016; Whitlock et al., 2018). Well-constrained and documented locality data are required for placing faunal assemblages within the proper context to begin reconstructing trophic levels across an extinct ecosystem (Turner and Peterson, 1999; Dunne et al., 2014; Trujillo and Kowallis, 2015; Lozano et al., 2016). Despite detailed understandings of trophic structures, through approaches such as large-scale paleoecology energetics (Farlow and Pianka, 2002; Farlow et al., 2010; Cortés and Larsson, 2023; Farlow et al., 2023; Chiarenza, 2024; Ősi et al., 2024), faunal composition (Foster, 2003; Foster, 2013; Foster et al., 2016; Whitlock et al., 2018; Woodruff, 2019; Mannion et al., 2021; Farlow et al, 2023; Maidment, 2024), and food web reconstructions (Matsukawa et al., 2006; Codron et al., 2013; Dunne et al. 2014; Amiot et al., 2015; McHugh, 2018; Fuller et al., 2020; Wyenberg-Henzler, 2022), the lack of cohesion and incomplete nature of the fossil record makes our understanding limited. The Morrison Formation, being no exception, suffers from no consensus on a unified chronostratigraphic framework, and the knowledge of its vertebrate fauna is not synthesized in such a way that fully accounts for ecological diversity at this time (Woodruff, 2019).

TABLE 1. The upper and lower limits of each size class in mass (kg).

Size class group name	Lower limit (kg)	Upper limit (kg)
Tiny	>0	100
Small	101	500
Medium	501	2000
Large	2001	10000
Gigantic	10001	30000
Titanic	30001	100000

While transportation of remains was certainly a major part of the taphonomic processes in the Morrison Formation, we assume that the regional biota (the organisms living within a single depositional basin) (Patzkowsky, 2017) would have had interactions even if gradients or preferred habitats did exist. Populations along these gradients will experience different pressures within a single species' range, but still would experience gene flow between them on the basis of being the same species, making individual quarry populations insufficient for understanding the broader ecosystem the organisms lived in (Congreve et al., 2018). Interactions along gradients are supported by autochthonous and parautochthonous preservation at the Cleveland-Lloyd Dinosaur Quarry, indicating varied short-range transport despite being deposited in the same beds (Peterson et al., 2017). Variation in the Morrison Formation makes understanding each population's dynamics difficult to decipher. However, the gradient described in Patzkowsky (2017) and evidence from Dodson et al. (1980) indicates that dinosaur remains discovered in the Morrison Formation are largely autochthonous, meaning depositional facies reflect the environment of individual living specimens. For this study, an assumption was made that fauna found in different depositional environments lived in those environments before dying there rather than displaced organismal remains, which follows the expectations of regional biotas along a gradient (Dodson et al., 1980; Peterson et al., 2017; Patzkowsky, 2017).

For our purposes, there is an assumption that the preserved fauna is not too dissimilar to the ones that lived in the same environments and time averaging at specific sites is at a minimum. Therefore, the faunal assemblage preserved at a site is treated as a single faunal assemblage and not multiple faunal assemblages.

RESULTS

Similarity in Functional Fauna across Depositional Environments

Channel, floodplain, and overbank deposits with few microvertebrate sites had no statistically significant result (p-value greater than 0.05) with these tests (see Tests 3,4, and 6 in Table 2), supporting the view that the functional faunas within these depositional environments were ecologically stable and similar throughout the duration of the Morrison Formation deposition. These environments (see Tests 3,4, and 6 in Table 2) did not preserve many EFUs in the small or tiny size classes and were therefore not treated as microvertebrate sites, following the definition from Foster (2020). Depositional environments classified as lacustrine and overbank deposits with microvertebrates preserved had multiple EFUs in tiny and

TABLE 2. The bipartite network and ANOVA results of the functional fauna analysis of the Morrison Formation, based on different quarry parameters (i.e., depositional environment, time zone, and so forth).

Test Type	Test Number	Quarry parameters being compared	Number of sites (n)	p-value (One-Way ANOVA)
All Sites (with Temple Canyon)	1	All	48	Less than 0.0001
All Sites (without Temple Canyon)	2	All	47	0.0359
Environmental	3	Channel	9	0.9322
Environmental	4	Floodplain (dry and wet)	15	0.4248
Environmental	5	Overbank with dense microvertebrates	6	0.0083
Environmental	6	Overbank with few microvertebrates	4	0.3613
Environmental	7	Lacustrine (All)	4	Less than 0.0001
Environmental	8	Lacustrine (No Mammalians)	3	0.0238
Stratigraphic	9	Stratigraphic Levels Zone 1 (only one quarry met our criteria)	1	n/a
Stratigraphic	10	Stratigraphic Levels 2	8	0.0932
Stratigraphic	11	Stratigraphic Levels Zone 3 Foster (only two quarries met our criteria)	1	n/a
Stratigraphic	12	Stratigraphic Levels Zone 4	13	0.0053
Stratigraphic	13	Stratigraphic Levels Zone 5	5	0.6166
Stratigraphic	14	Stratigraphic Levels Zone 6	3	0.6718
Stratigraphic	15	Dinosaur Faunal Zones 2	16	0.0117
Stratigraphic	16	Dinosaur Faunal Zones 3	10	0.4594
Stratigraphic	17	Dinosaur Faunal Zones 4	4	0.6718
Stratigraphic	18	System Tract 3 (only one quarry met our criteria)	1	n/a
Stratigraphic	19	System Tract 4	12	0.0317
Stratigraphic	20	System Tract 5	10	0.019
Stratigraphic	21	System Tract 6	10	0.6761
Stratigraphic	22	All known Stratigraphic Level quarries (excluding zone 1, as just fish preserved)	31	0.0188
Ecological functional units	23	Minimum 15 ecological functional units	11	0.4604
Ecological functional units	24	Minimum 15 ecological functional units, excluding Reed's Quarry 9, as primarily microvertebrates	10	0.6741
Ecological functional units	25	Minimum of 5 dinosaurian ecological functional units	31	0.4221

small size classes that were additionally from non-dinosaurian clades. These environments had statistically significant results (p-value less than 0.05) in the disparity of their functional faunas within these categories (see Tests 5,7, and 8 in Table 2). These sites often, but not exclusively, lacked EFUs in the larger size classes (medium or large classes) in addition to diverse EFUs of non-dinosaurian clades. Mammals had diverse dietary ecologies within the Morrison Formation (Foster, 2020), where such variation is likely the cause of the disparity of the EFUs, hence generating a significant result within lacustrine and overbank deposits within microvertebrates. In addition to being a more aquatic-based ecosystem than floodplains, lakes possessed greater preservation potential within the Morrison Formation for smaller vertebrates compared to other depositional environments (Foster, 2020). Aquatic and terrestrial functional faunas would be different, for example, due to the presence or absence of fishes. The reduction of the dinosaurian-EFU presence, the increased preservation of the small and tiny size class EFUs, and the differences in the environments are likely the causes of the significant result of the p-value in sites where microvertebrates or small vertebrate taxa are preserved (i.e., Table 2, Tests 5, 7, and 8). Due to channel, floodplain, and overbank deposits with few microvertebrates categories having no statistically significant result with regard to their functional fauna and containing sites that are not co-eval (including sites where calibration has not been completed), suggests that the functional fauna, at least within these environments, were not significantly different temporally and were ecologically functionally stable.

Similarity in Functional Fauna across Time Zones

Analyzing the sites by co-eval time metrics (see Tests 9 to 22, Table 2) resulted in five (Tests 12, 15, 19,20, and 22) having a significant p-value, whereas the other co-eval time metrics did not. It should be noted that these all represent a single co-eval time metric from one of the three different chronostratigraphy metrics (i.e., Stratigraphic Level 4, Dinosaur Faunal Zones 2, and System Tract 4). This implies that the diverse depositional environments and selective preservational biases of smaller taxa are driving the significant differences in the p-value. Analyzing all known time zones in Stratigraphic Levels (see Test 22, Table 2) while excluding sites that predominantly contain organisms from the tiny size class, found that there was still a significant result in the p-value. However, these sites have great variation in their depositional environments, preservation from tiny to titanic size classes, and in the number of ecological functional units, varying from 7 to 20+. The observed disparity, as highlighted by the statistically significant result, is likely the result of the variable preservation of the fossil record, meaning it is not representative of a genuine pattern due to the large discrepancy in the dataset being compared.

Ecological Functional Units Occurrence in the Morrison Formation

Our results support the significant impact of selectively preserved small animals (size classes tiny and small) on the functional fauna. Taphonomic biases against small animals make them less likely to be preserved, as documented in the Hell Creek and Lance Formations (Brown et al., 2022), and this preservational bias was detected by our model, with the presence or absence of small and tiny size classes at different sites with diverse ecomorphologies driving disparity in the functional fauna. These changes are unlikely to be genuine differences in functional fauna due to preservational biases (Table 2, Tests 5,7,8). Therefore, to represent sites that preserved a greater proportion of their ecosystem and thus functional fauna, sites with a minimum of 15 ecological functional units were analyzed. Applying this constraint, no significant p-values were found (Table 2, Tests 23, 24). This was also true for sites that had a minimum of 5 dinosaurian EFUs (Table 2, Test 25).

DISCUSSION

Overall, the implications of a stable functional fauna across the Morrison Formation are a testament to how diverse megafaunal assemblages interacted and reinforces the hypothesis of heterogeneous paleoenvironments in the Morrison Formation. However, the discrepancy of the differential preservation bias across the Morrison Formation, in addition to how all quarries relate to one another, needs to be addressed. For instance, small-bodied theropods of the Morrison Formation are relatively more rare than the larger megatheropods (theropods greater than 1000 kg), which dominated their ecosystems (Dodson et al., 1980; Schroeder et al., 2021). Microvertebrate sites within the Morrison Formation are rare despite being crucial for paleoecological reconstructions (Foster, 2001; Carrano and Velez-Juarbe, 2006). The paleoenvironmental setting in which these vertebrates lived both contributed to their paleoecology (Foster, 2003; Foster et al., 2016; Foster and McMullen, 2017), as well as their subsequent preservation. Additionally, the

quarries which preserve these vertebrates, while constrained to a single rock unit they relate to, may be temporally and spatially disparate, which is important to consider when reconstructing functional fauna over millions of years, as this underpins our analysis.

Challenges regarding Dating and Correlation of Morrison Formation Quarries

Resolving the poor temporal resolution of the Morrison Formation is an active field of study (Turner and Peterson, 1999; Foster, 2003; Trujillo and Kowallis, 2015; Maidment and Muxworthy, 2019; Foster, 2020; Kirkland et al., 2020), as a reliable chronostratigraphic framework will aid in assessing the Morrison Formation's biodiversity across time to distinguish evolutionary patterns (Woodruff, 2019). The Morrison Formation on the Colorado Plateau is largely represented by the Tidwell, Salt Wash, and Brushy Basin Members, yet they become undifferentiated or absent when outside this geographic province despite rock units which are roughly lithologically and/or stratigraphically equivalent (Kirkland et al., 2020; Boisvert et al., 2025; J. Foster, personal commun. 2025). Currently, with exception to select regions adjacent or proximal to the Colorado Plateau (Anderson and Lucas, 1995; Kirkland et al., 2020; J. Foster, personal commun. 2025), without further fieldwork efforts and dating the presence of these three Colorado Plateau members outside the Colorado Plateau seem currently unfit for use in the working Morrison Formation chronostratigraphic framework despite prior reports (e.g., Salt Wash Member present in Montana; Myers and Storrs, 2007; J. Foster, personal commun. 2025). Morrison Formation exposures off the Colorado Plateau have been poorly correlated with those on the Colorado Plateau (Stokes, 1944; Szigeti and Fox, 1981; Owen et al., 1984; Cowan, 1991; Peterson and Turner, 1998; Holland and Wright, 2020) although ongoing work may temporarily resolve some of these issues (see Allen et al., this volume).

Various studies have aimed to correlate stratigraphic sections within a temporal framework, with early works by Kowallis et al. (1998) and Turner and Peterson (1999) being among the first attempts to correlate prolific quarries. However, these attempts have since been questioned due to unreliable stratigraphic markers (e.g., the "clay change"; see Trujillo et al., 2006). Specific studies (e.g., Foster, 2003, 2020; Whitlock et al., 2018) have continued to use curated data gathered in Kowallis et al. (1998) and Turner and Peterson (1999) to avoid using the clay change as a stratigraphic marker in assessing the temporal distribution of the Morrison Formation biota. The first official proposal for a Morrison Formation time-calibrated stratigraphic framework was produced by Maidment and Muxworthy (2019), which found the temporal bounds of the Morrison Formation largely in general agreement via corroborating radiometric dating and magnetostratigraphy by looking across the entirety of the rock unit (Kowallis et al., 1998; Trujillo and Kowallis, 2015, Whitlock et al., 2018). Despite this, the discordance of interpretations on the Morrison Formation in past literature overall renders its working chronostratigraphic framework still unresolved, leaving room for error in assessing faunal assemblages. However, the historical time zones that have been refined over time at the least demonstrate a baseline for understanding faunal assemblages in the Morrison Formation (Turner and Peterson, 1999; Foster, 2003; 2020), indicative that there's an ecological signal of functionally stable fauna recovered in our results based on this linear model.

Stability and Drivers of Change in Morrison Formation Paleoenvironments

Rapid vegetation growth may have been necessary to support the diverse herbivorous fauna of multiple size classes. However, the presence of oxidized sediments and calcretes alongside a noticeable lack of coals and aquatic vertebrates suggests that water was seasonally rare across the formation and through time (Dodson et al., 1980; Good, 2004; Dunagan and Turner, 2004; Turner and Peterson, 2004). Fossil woods also vary in the presence of growth rings. *Protocupressinoxylon medlynii* preserves growth rings consistently, *Xenoxylon mooreei* occasionally preserves distinct rings, and *Mesembrioxylon carterii* lacks growth rings, despite all co-occurring at the Mygatt-Moore Quarry (Tidwell et al., 1998). Tidwell et al. (1998) hypothesized that trees with distinct growth rings may have been spatially partitioned from those without due to climatic differences, although they do not preclude other factors causing the differences in tree ring preservation. Additional evidence of varied growth bands in unionid bivalves found by Good (2004) at other localities provides evidence for climatic differences temporally within the Morrison Formation. Evidently, there is a complex relationship between sedimentological, paleontological, and paleobotanical evidence regarding the broad-scale temporospatial climate patterns in the Morrison Formation, illustrating the rigorous aspects of work conducted, currently in progress, along with still needed to characterize Morrison Formation paleoenvironments (Turner and Peterson, 2004; Jennings et al., 2011; Owen et al., 2015). Geological events (e.g., mountain building and transgression-regression cycles from the Sundance Sea; Woodruff, 2019; Maidment and Muxworthy, 2019) are demonstrated to alter

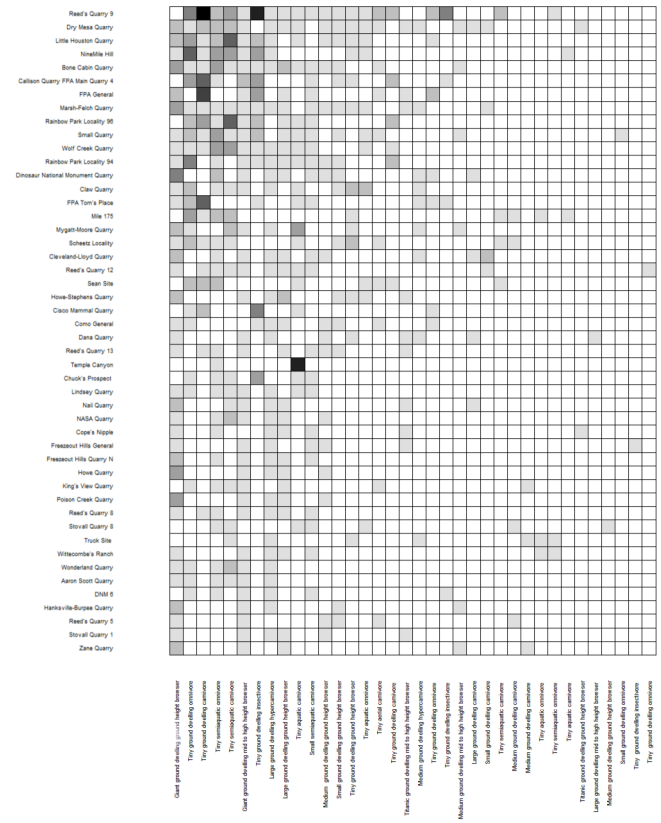

FIGURE 2. Representation of the ecological functional units (EFU) present at the 48 different quarries used in the analysis. The EFUs are on the x-axis, and the quarry names are on the y-axis. A white square represents an absence of an EFU at a quarry, whereas darker squares represent an increased number of taxa occupying an EFU at a given quarry.

climatic processes (e.g., increasing precipitation, high elevation freeze-thaw cycles, and chemical weathering) and thereby raise or lower depositional rates (Turner and Peterson, 2004). These changes then would contribute to how the mosaic paleoenvironments that supported dinosaurian functional fauna were structured (Turner and Peterson, 2004; Demko et al., 2004; Parrish et al., 2004; Whitlock et al., 2018; Richmond, 2023), which in turn supports our results due to the stable and speciose ecological diversity recovered. This is not to say that these mosaic environments were static throughout time, but instead their mosaic features changed over time (Owen et al., 2015; Maidment and Muxworthy, 2019; Kirkland et al., 2020), which could have then led to faunal turnover, which may have resulted in changes to the functional fauna (Woodruff, 2019; Kirkland et al., 2020; Kirkland et al., 2024).

Cenozoic mammalian communities show remarkable structural stability in the face of climate change (Blois and Hadly, 2009). Abiotic events only rarely interrupt this stasis (Blanco et al., 2021; Blanco et al., 2025). An example, in the Neogene of Europe, shows maintained trophic structure, despite taxonomic turnover in terrestrial mammalian communities (Jernvall and Fortelius, 2004; Blanco et al., 2021). Additionally, in Neogene Europe, large herbivore species did not persist for long periods of time; however, their abundance remained the same across time (Jernvall and Fortelius, 2004). During the same time interval in the Iberian Peninsula, trophic networks were gradually restructured by the decline of medium-sized herbivores (Nascimento et al., 2024). Predators who depended on these medium-sized herbivores showed greater extinction risk, suggesting that prey species richness shapes patterns of extinction among predators (Nascimento et al., 2024). Functional turnover occurs when evolutionary and ecological processes alter community traits, even when holding the number of species constant (Blois and Hadly, 2009). Among Cenozoic mammals, these responses include changes in body-size distribution (Bown et al., 1994; Croft, 2001), increases in tooth crown height (hypsodonty) (Flynn et al., 2003; Fortelius et al., 2002; Janis et al., 2004; Jernvall and Fortelius, 2004; Pascual, 2006), and locomotor mode changes such as greater cursoriality or fossorial adaptations (Janis, 2008; Vizcaíno et al., 2006).

Such functional shifts due to environmental changes could have occurred during the deposition of the Morrison Formation. For instance, there is a paleoenvironmental change induced by shifts in paleoclimate toward the top of the Morrison Formation within Foster's Zones 5 and 6, which were deposited during the Late Jurassic (Parrish et al., 2004; Demko et al., 2004; Turner and Peterson, 2004). Here, the paleoclimate is one driving factor identified in the Morrison Formation, which could explain the apparent reduction of *Haplocanthosaurus*, *Camarasaurus*, and other sauropods across quarries from Zone 5 to Zone 6 (Woodruff, 2019; Boisvert et al., 2025). Changes in fauna which could influence our understanding of the functional ecology of the Morrison Formation should be placed into context of a resolved Morrison Formation chronostratigraphic framework (Woodruff, 2019; J. Foster, personal commun. 2025), and additionally must be configured with respect to paleobotanical and geological proxies for characterizing Morrison Formation fauna to determine how functional fauna in the Morrison Formation may have deviated from stability during the latest Jurassic into the Early Cretaceous.

Influence of Small Tetrapods and Fishes in Morrison Formation Paleoecology

It is also important to consider the presence of smaller vertebrates (<100 kg herein) and their place as ecological components in the Morrison Formation. Such animals found within Morrison Formation strata include: small-bodied dinosaurs (Marsh, 1877; Madsen, 1974), pterosaurs and other reptiles (DeMar et al., 2022) including an early snake (Caldwell et al., 2015); fishes, with ray-finned fishes (Kirkland, 1998) being one of the most abundant Morrison Formation vertebrate groups (Foster, 2020), and mammals (Foster, 2020). The fossil record exhibits a strong bias for the preservation of large animals, including the sauropods, although they are often disarticulated due to their large size and difficulty in becoming buried in a single event (Cashmore et al., 2020). This is despite large animals being typically less abundant than small animals when observed in extant ecosystems (Behrensmeyer et al., 1979; Peters and Wassenberg, 1983; Cotgreave, 1993; Foster, 2020). Regarding formations for comparison to the Morrison Formation, Brown et al. (2022) found evidence for taphonomic size biases against small-bodied taxa (studying mammals and dinosaurs) within the Hell Creek and Lance Formations. Given this bias, it can be difficult to ascertain if the relative rarity of small-bodied taxa is due to selective preservation or indicative of genuine rarity in Morrison Formation ecosystems. An example of fewer occurrences suggesting genuine rarity exists for large-bodied Morrison Formation ankylosaurs. Despite being over 100 kg, the first Morrison Formation ankylosaur, *Mymoorapelta maysi* (Kirkland and Carpenter, 1994), was not described until 1990, over 100 years after the first Morrison Formation fossils were discovered, and only *Gargoyleosaurus parkpinorum* (Carpenter et al., 1998) has been described since, suggesting that ankylosaurs may have been rare within Morrison Formation ecosystems. Analysis of microvertebrate fossils can reveal the presence of small taxa previously not identified at a particular site, as well as provide some indication of abundance, such as ray-finned fishes being the most abundant microvertebrate fossils found at some sites (Foster, 2020). While microvertebrate assemblages provide a snapshot of smaller fauna, these fossils are also only selectively preserved and limited in their use in representing the number of individuals within any taxon present. Further use of vertebrate microfossils in paleoenvironmental and ecological reconstruction have become prolific in the Norian-Rhaetian Chinle Formation (Stocker et al., 2019; Kligman et al., 2023) and Campanian Judith River Formation (Rogers and Brady, 2010; Woodruff et al., 2025), and such techniques could be applied to increase our understanding of the Morrison Formation microvertebrate fauna in the future.

CONCLUSIONS

The dinosaurian functional fauna appears to be stable throughout the Morrison Formation, with no statistically significant result in disparity, temporally or spatially. The mosaic paleoenvironment of the Morrison Formation appears to have a greater impact on the vertebrate functional fauna, yet preservational bias against small-bodied taxa makes it difficult to assess the ecomorphological differences throughout the formation (i.e., fish, mammals, and small reptiles). With this in mind, using a functional fauna approach would enable us to assess ecosystem structure and stability in other well-sampled fossiliferous formations through time, and investigate the differences between faunal turnover and ecosystem functional change.

ACKNOWLEDGMENTS

We thank Natalie Cooper from the Natural History Museum in London for help with statistical method inquiries, John Foster and Dean Lomax for their assistance with numerous different inquiries pertaining to the geology and paleoecology of the Morrison Formation, and Sergey Krasovskiy for the paleoart for this paper. We additionally thank Danielle O'Callaghan, who has supported Ezekiel O'Callaghan throughout this project. We give special thanks to John A. Whitlock, Kenneth Carpenter, and John Foster for their reviews that greatly improved the manuscript. We thank John Foster and Kelli Trujillo for the invitation to this

special volume and their editorial work managing this special Morrison Volume.

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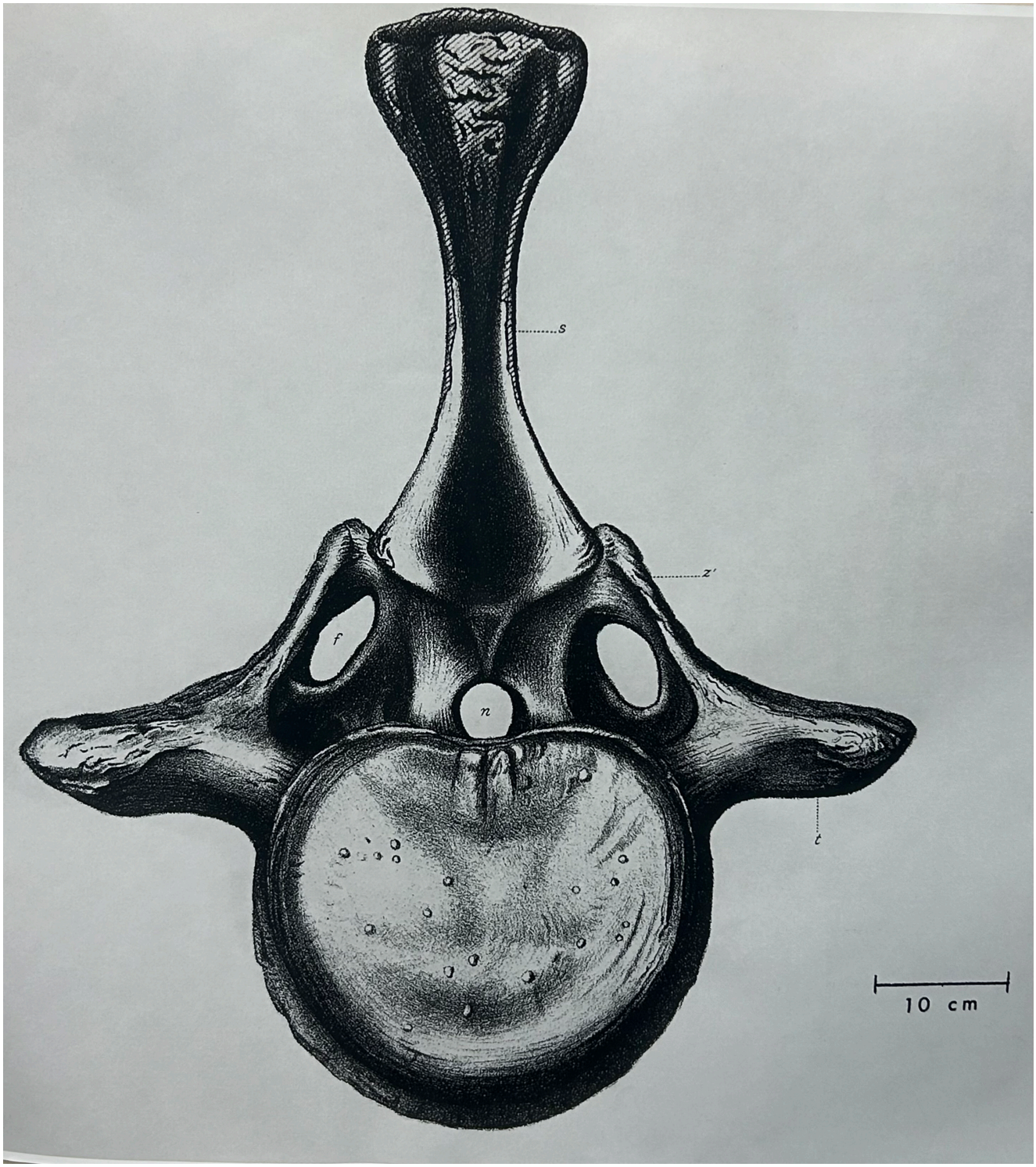

Apatosaurus caudal. (From Ostrom and McIntosh, 1966)