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Source: Journal of Vertebrate Paleontology, 36(2)

Published By: The Society of Vertebrate Paleontology

URL: http://www.bioone.org/doi/full/10.1080/02724634.2015.1071265

Journal of Vertebrate Paleontology e1071265 (12 pages)

DOI: 10.1080/02724634.2015.1071265

ARTICLE

VERTEBRATE PALEONTOLOGY OF THE CLOVERLY FORMATION (LOWER CRETACEOUS), II: PALEOECOLOGY

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ABSTRACT—Vertebrate microfossil assemblages in terrestrial formations are a promising source of data on the structure of fossil metacommunities. However, the degree to which these deposits capture true, metacommunity-level samples is unknown. Individual deposits may be biased in ways that limit their utility for intra- and inter-formation comparisons. This study describes the composition of ten vertebrate microfossil assemblages collected from the Lower Cretaceous Cloverly Formation in Montana and Wyoming, U.S.A., and evaluates whether the assemblages are sufficiently similar to suggest the presence of a single Cloverly metacommunity, or 'paleocommunity type.' The assemblages appear to be biased by factors related to the preferential incorporation and preservation of different taxa and skeletal element types, which compound with decreasing locality sample size. Less productive localities lack whole taxonomic groups, especially small, fully terrestrial vertebrates. Only the two vertebrate microfossil bonebeds approach the known formation richness. High individual tooth counts overrepresent particular species, especially the crocodylians. Despite these biases, the multiple assemblages nevertheless yield statistically similar taxon abundance rank orders, suggesting the presence of a single, formation-wide paleo-metacommunity, which bears resemblance to a viable metacommunity. The aggregate assemblage exhibits an 'Eltonian pyramid' trophic hierarchy for both terrestrial and aquatic taxa. Comparing the multiple assemblages synoptically also reveals possible landscape-scale abundance patterns for particular species. Taken together, microvertebrate assemblages offer insight into regional paleo-metacommunities and provide samples for inter-formational comparisons at this level.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Carrano, M. T., M. P. J. Oreska, and R. Lockwood. 2016. Vertebrate paleontology of the Cloverly Formation (Lower Cretaceous), II: Paleoecology. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2015.1071265.

INTRODUCTION

The Early Cretaceous witnessed several important ecological and evolutionary transitions, including radiations and niche diversification among mammals and birds (e.g., Zhou et al., 2003; Luo, 2007), a shift from sauropod- to ceratopsian- and ornithopod-dominated terrestrial herbivore faunas in North America (D'Emic and Foreman, 2012), and the emergence of many modern vertebrate clades (Evans, 2003; Benson et al., 2013). The resulting global faunal turnover is discernable in the fossil record over multiple temporal stages (e.g., Gates et al., 2010; Benson et al., 2013) but is less apparent at finer spatiotemporal scales. As a result, it has not been well studied at the scales on which most ecological drivers (such as competition and climate change) likely acted. Identifying such potential drivers behind major faunal transitions requires a better understanding of community structure variation, including relative taxonomic abundances, at regional scales and below (e.g., Barnosky, 2001; Blois and Hadly, 2009).

A few studies have attempted metacommunity-level analyses with fossil vertebrates, generally by aggregating occurrences in collection databases to assemble regional samples (e.g., Davis, 2005; Mitchell et al., 2012; Darroch et al., 2014). This aggregation can mask important collection effort sampling biases, particularly in the vertebrate fossil record, which is dominated by individual specimen occurrences. Furthermore, there might not be enough individual specimen occurrences to confidently assess assemblage relative abundances (Moore et al., 2007). One solution is to utilize vertebrate microfossil deposits, which provide more suitable samples by preserving large, diverse specimen assemblages that formed under restricted taphonomic, temporal, and geographic regimes.

Most hypotheses about how these deposits form assume a degree of postmortem mixing and time averaging, processes that might result in taxonomically more complete samples of the paleocommunity (e.g., Rogers and Kidwell, 2007; Palmqvist and Arribas, 2009; Terry, 2009; Rogers and Brady, 2010). Some vertebrate fossil concentrations possibly represent lag deposits (Rogers and Kidwell, 2000), but many others are found in channels (Eberth, 1990) and likely formed through re-deposition of reworked material (Rogers and Brady, 2010; meandering stream migration though existing fossiliferous deposits can exhume and transport material to new accumulation sites; e.g., Scasso et al., 2012). These processes may concentrate fossils from multiple communities in a single deposit, but they also introduce taphonomic biases that complicate comparisons, even within similar taphofacies (Moore, 2012). Hydraulic sorting during transport

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results in concentrations biased by specimen size, shape, and density (Blob and Fiorillo, 1996) and preferential element incorporation and loss.

Brinkman et al. (2005) noted that vertebrate microfossil deposits have already been used to make formational (e.g., Estes, 1964; Sahni, 1972) and intra-formational paleoecological comparisons (e.g., Estes and Berberian, 1970). In both cases, individual assemblages are sometimes assumed to represent a formation-wide 'paleofauna,' despite potential biases (e.g., Blob and Fiorillo, 1996). However, Eberth (1990) surveyed 24 Judith River Formation microfossil localities and concluded that many appeared to represent localized samples. Therefore, the degree to which vertebrate microfossil localities record a formation-wide ancient metacommunity remains uncertain.

Most studies have not attempted to determine the size of the paleocommunity contributing to a locality or whether individual localities provide representative samples of a formation-wide 'paleofauna.' A few studies have attempted to identify a subset of taxa at sites from a proximal community, following Shotwell's (1955) relative completeness index (e.g., Estes and Berberian, 1970), but this metric can be subjective for poorly known taxa represented by few elements. Other attempts to identify discrete paleocommunities include subdivisions based on presumed life-habit (Brinkman, 1990). Finally, only a few studies have noted apparent stratigraphic trends within a formation, including changes in the relative abundance of vertebrate groups consistent with changes in paleoenvironment over time (Brinkman, 1990; Garrison et al., 2007).

Here we determine the relative abundances of Cloverly species, identify regionally abundant taxa, and establish taxon trophic linkages in order to illuminate the paleoecology of individual Cloverly species. By partitioning recovered specimens according to guilds, we compare apparent metacommunity-level structure with the hypothesis that assemblages should exhibit an 'Eltonian pyramid'—potential prey species should outnumber consumers at each successive trophic level (Elton, 1927). For example, we might expect an inverted pyramid if the depositional settings coincided with areas where predators congregated, a flattened pyramid if the assemblage formed as a coprocoenosis (e.g., Fisher, 1981), or no pattern if body size bias was significant.

This study also evaluates whether observed biases preclude the use of Cloverly Formation vertebrate microfossil assemblages as samples from the ancient metacommunity. We consider whether site assemblages exhibit compositional variability attributable to real biological differences that would imply faunal and paleoenvironmental heterogeneity on the landscape during the time of deposition. Successfully assembling a metacommunity-level sample for the Cloverly Formation would provide a useful example for similar efforts in more fossiliferous formations.

(PALEO-) COMMUNITIES AND METACOMMUNITIES

The relationships between paleoecological concepts and their potential neoecological counterparts have been extensively discussed (e.g., Miller, 1990; Bennington and Bambach, 1996; Tomasovych and Kidwell, 2010) and are not reviewed in detail here. However, it is important to establish some conceptual limits to the terminology employed here and to relate them, as far as possible, to the samples at hand.

At the smallest scale, a neoecological 'community' is limited to taxa that cooccur in a given place at a given time (often defined as interacting within a habitat patch; Leibold et al., 2004). The 'metacommunity' refers to local communities linked by the "dispersal of multiple potentially interacting species" (Leibold et al., 2004:603). Although the concept is primarily spatial (cf. Hanski and Gilpin, 1991), the focus on dispersal allows neoecologists to account for compositional changes in individual communities over time.

Paleoecological parallels exist for both terms, although neither is exact or enjoys complete consensus. A 'paleocommunity' refers to a set of fossil taxa in an assemblage, but because of time-averaging and other impacts of fossilization, it may not represent a single original 'community' (Bennington and Bambach, 1996). Likewise, the 'paleocommunity type' refers to aggregations of similar paleocommunities (and local paleocommunities), which approximates the concept of a metacommunity (Bennington and Bambach, 1996) and can therefore also be termed a 'paleo-metacommunity.'

In this study, we utilize two scales of assemblages, equivalent to those described above. A 'paleocommunity' is the assemblage of taxa recorded at an individual Cloverly Formation locality. The aggregate of all taxa in the formation is the 'paleo-metacommunity'. We compare taxonomic composition between different paleocommunities and between these paleocommunities and the paleo-metacommunity. Formations provide convenient geographic and stratigraphic boundaries for defining paleo-metacommunities. By comparing multiple paleocommunities sampled throughout the Cloverly Formation, we evaluate whether they provide evidence for a single paleo-metacommunity at the regional scale. If so, vertebrate microfossil deposits could serve as replicate samples for inter-formational comparisons to help quantify differences between metacommunities.

METHODS

Quantifying Taxon Abundances

The data and methods for fossil collection and identification are as described previously (Oreska et al., 2013). A total of 29 vertebrate microfossil localities ('microsites,' sensu Brinkman et al., 2004, 2005) were found, 10 of which were productive enough to warrant bulk sampling. Bulk samples were wet-sieved using 0.5-mm mesh, revealing a range of productivity, from sites with near-background concentrations (<0.25 specimens per kilogram) to those with concentrations >1 specimen per kilogram. The richer USNM Locs. 42183 and 42222 yielded fossil concentrations >5 specimens per kilogram and are here considered 'vertebrate microfossil bonebeds' (=VMBs, sensu Rogers and Brady, 2010). Specimens were sorted and identified to the lowest possible taxonomic level and element type was noted. The most productive localities were more intensively sampled and, as a result, most specimens derived from a small number of localities (Oreska et al., 2013:table 1).

We aggregated specimen counts by taxon and sorted them into taxonomically nested sets. Faunal diversity was analyzed at 'class,' 'order,' and 'species' levels (the debate about strict equivalence across Linnean ranks need not be revisited here; these levels only need to be equivalent in their hierarchical relationships). Individual 'species'-level taxa represented unique 'operational species units' (OSU). These included forms that could only be diagnosed at higher taxonomic levels but that must have existed as species—and thus been taxonomically distinct from other faunal constituents (e.g., *Egertonodus* sp., Theropoda indet. A). Each OSU therefore represented a hierarchically consistent, lowest possible assignment (see systematic paleontology in Oreska et al., 2013). Higher taxonomic levels were similarly designated 'operational order units' (OOUs) and 'operational class units' (OCUs).

The mixed, fragmentary nature of vertebrate microfossil accumulations complicates abundance determinations (see discussions in Carrano and Velez-Juarbe [2006] and Oreska et al. [2013]). Our primary concerns are: (1) the comparability of different samples, which relies on obtaining a sufficient sample size (e.g., Jamnickzky et al., 2003) and applying appropriate comparative techniques (see Oreska et al. [2013] for rarefaction comparisons and details of Cloverly Formation samples) and (2) the relationship between the sample and the original fauna. The latter is a complex topic with no clear solution and requires multiple approaches—but rests on decisions of how to count specimens.

It is important to note that none of the localities studied here show evidence of fluvial deposition or extensive specimen transport, and therefore we do not consider hydraulic sorting to have been especially important in determining the nature of these assemblages. Rather, they appear to have been attritional accumulations that underwent minimal transport and predominately in situ mixing and postmortem winnowing. In addition, we found no evidence that any of the specimens were originally associated and so we consider each specimen to have been derived from a different once-living organism. Therefore, and unless otherwise noted, the following analyses used raw specimen counts—the total number of specimens (NS) assigned to a taxon (cf. Carrano and Velez-Juarbe, 2006). These NS counts provide a standard abundance baseline in assemblages dominated by isolated specimen occurrences (Badgley, 1986).

However, using NS certainly overcounts particular taxa. Specifically, continual tooth replacement allows one individual to contribute many teeth to a deposit, in addition to its final contribution at the time of death. Thus, the same individual could contribute to the biocoenosis and the taphocoenosis. The resulting bias favors fishes, amphibians, and (most) reptiles over mammals and turtles. (Further research is needed to accommodate potential taxonomic differences in tooth replacement rates.) To help mitigate these biases, we standardized isolated tooth counts according to the total number of teeth in an individual. For chondrichthyans, osteichthyans, crocodylians, dinosaurs, and avians we divided NS of isolated teeth by the expected number of teeth for an individual to give an adjusted tooth count (NS*). For example, individual bernissartid crocodylians had ~80 teeth (Buffetaut and Ford, 1979) and *Deinonychus* had ~70 teeth (Ostrom, 1969). Other estimates were based on comparisons with similar and/or related extant taxa, e.g., ~100 teeth in modern *Amia calva* (Grande and Bemis, 1998) for the Cloverly amiiforms. These methods were not applied to mammals (for which only deciduous teeth would impact NS) or teeth in jaws (which can only have entered the system through death of the individual).

OSUs were rank-ordered using both NS and NS*. For the latter, NS* tooth counts were added to counts of other element types for each taxon. We conservatively excluded material from the species level that might have originated from one of several OSUs. For example, crocodylian dermal scutes and vertebrae could not be definitively assigned to any one of the four crocodylian OSUs that were diagnosed by distinctive teeth. Likewise, indeterminate sauropod and large theropod specimens were not included in Titanosauria indet. or Tetanurae indet., respectively, if we could not formally refer these elements to those specific taxa. Numerous osteichthyan scales were also excluded from OSU comparisons but were included in OCU and OOU analyses along with OSU counts, which were sorted into taxonomically nested sets and aggregated at the higher levels.

Factors related to preferential element inclusion and taxon body size may have favored specimen preservation for particular taxa in the mixed fossil assemblages (e.g., Blob and Fiorillo, 1996; Palmqvist and Arribas, 2009; Brown et al., 2013). For example, taxa that contributed a greater diversity of element types might be better represented by individual specimens in deposits. We tested the degree to which biases were present by correlating the log-transformed NS abundance of vertebrate classes to the number of element types representing each class. It was not possible to rank species-level taxa by element diversity, because the majority of species were represented by only one type of element. We checked for a body size bias by looking for a correlation between a species' abundance (both NS and NS*) and its estimated body mass. Body mass estimates were obtained from the published literature or estimated using autecology (see Supplementary Data, Table S1). Estimated body mass was not normally distributed, so correlations were evaluated using Spearman's r_s and Kendall's τ. Both correlation tests were run on rank-order data obtained from the bulk-sampled localities ($N = 10$).

We determined whether certain taxa were consistently more abundant in vertebrate microfossil assemblages by applying the nonparametric Friedman test to NS abundance data for each taxon in the 10 bulk-sampled localities. Taxon abundance represented the 'treatment' and the localities served as 'blocks.' Our null hypothesis was that a taxon's abundance rank at a given locality would be independent from its rank at other localities. Under such a scenario, a taxon's abundance rank would appear to be random in each assemblage. We conducted Friedman tests on OCU-, OOU-, and OSU-level NS abundance data; it was necessary to assume that absences at localities represented true absences (this is justified for the VMB sample sizes but uncertain for the other localities; Jamniczky et al., 2003). We used post hoc sign tests between taxon pairs to determine whether particular taxa contributed to significant results. Plotting the average locality abundance of each taxon against its frequency of occurrence (the number of localities at which it occurred) allowed us to identify individual taxa that occurred with relatively high abundance across multiple localities, those that appeared to be locally abundant, and those that were consistently rare or absent—different occurrence patterns that influenced Friedman test results. Friedman tests and follow-up comparisons were run using the R Stats Package (R Core Team, 2012); correlation tests were run using the R ltm Package (Rizopoulos, 2012).

Comparing Assemblages

The total number of fossils varied greatly across localities. Given the practical difficulties in achieving similar sample sizes for all localities, we calculated the Simpson index of diversity ($1 - D$) and Pielou's J evenness at all three taxonomic levels for each bulk-sampled locality using the R Vegan Package (Oksanen et al., 2013) to compare assemblage diversity and evenness. Contrary to expectations, $1 - D$ appeared to increase with increasing sample size. Correlation tests on $1 - D$ and J and sample NS were used to look for sample size bias, with a strong correlation suggesting a sample size effect on index value. One locality, USNM Loc. 43416 was omitted from the correlation analyses because it had a richness of 1. A Pearson correlation test was run on log-transformed $1 - D$ and log-transformed NS. Spearman's rank correlation was used to evaluate a correlation between J and NS, because J values were not normally distributed and could not be transformed to meet the normality assumption. A linear regression model was used to evaluate the relationship between $1 - D$ and log-transformed sample size (R Stats Package; R Core Team, 2012).

Particular groups of organisms were rare or absent at localities that yielded smaller sample sizes. We identified the taxonomic groups contributing to unusual occurrence patterns at localities by manually ordering the locality OCU specimen matrix according to predetermined factors: (1) specimen abundance per OCU; (2) locality occurrence frequencies per OCU; (3) total number of specimens per locality (productivity); and (4) total number of OCUs per locality (a measure of richness; Table 1). Rows and columns were ordered in decreasing magnitude, which allowed us to search for 'embedded absences' (sensu Leibold and Mikkelson, 2002) and expected rank-order reversals—deviations from

TABLE 1. Ordinated locality–taxon matrices of bulk-sampled localities by OCU. **A**, rows ranked by OCU specimen abundance (decreasing from top to bottom); columns ranked by USNM locality specimen abundance (decreasing from left to right); **B**, rows ranked by OCU occurrence frequency (number of localities decreases from top to bottom); columns ranked by USNM locality richness (number of OCUs decreases from left to right). Richness totals exclude indeterminate specimens.

A	42183	42222	42175	43420	43422	42146	43416	42225	43418	42159	Total
Osteichthyes	1,318	2,178	54	7	16	19	7	2			3,601
Crocodylia	1,188	839	136	42	7	1	2	5	2	1	2,223
Dinosauria	574	348	186	12	19	6	1	2	3	2	1,153
Amphibia	537	166	23	2		1					729
Testudinata	272	225	30	90	4	3	2	1	1		628
Chondrichthyes	264	21	14								299
Malacostraca	95	2	2								99
Mammalia	43	24	1								68
Squamata	24	15	1								40
Aves	3	2	1								6
Bivalvia							1				1
Gastropoda	1										1
Total	4,319	3,820	448	153	46	30	13	10	6	3	8,848

B	42183	42222	42175	43420	42146	43422	43416	42225	43418	42159	Freq.
Crocodylia	1,188	839	136	42	1	7	2	5	2	1	10
Dinosauria	574	348	186	12	6	19	1	2	3	2	10
Testudinata	272	225	30	90	3	4	2	1	1		9
Osteichthyes	1,318	2,178	54	7	19	16	7	2			8
Amphibia	537	166	23	2	1						5
Chondrichthyes	264	21	14								3
Malacostraca	95	2	2								3
Mammalia	43	24	1								3
Squamata	24	15	1								3
Aves	3	2	1								3
Bivalvia							1				1
Gastropoda	1										1
Richness	11	10	10	5	5	4	4	4	3	2	

aggregate sample trends at individual localities that might relate to paleoecological or paleoenvironmental signals (see Discussion for an explanation of observed patterns and how these patterns possibly relate to either taphonomic biases or genuine signals). Focusing on OCUs allowed us to maximize the number of included specimens.

Analyzing Trophic Structure

In order to investigate apparent Cloverly paleo-metacommunity trophic structure, we assigned each OSU a set of ecomorphological characteristics (cf. Matsukawa et al., 2006). These included basic skeletal structure (vertebrate vs. invertebrate), body mass, life habit (aquatic, amphibious, or terrestrial), and trophic habit (herbivore, omnivore, or carnivore). Life habit and trophic habit were identified from the published literature or inferred using autecology (see Supplementary Data, Table S2). Using these assignments, we organized Cloverly species into trophic guilds (e.g., large terrestrial herbivores) to infer a Cloverly paleo-metacommunity food web (Fig. 1). Taxa were also aggregated into ordered, canonical trophic levels (sensu Ulanowicz and Kemp, 1979). Carnivore trophic levels were defined using estimated body size (cf. Lindeman, 1942:fig. 2; see Supplementary Data, Table S2).

We hypothesized that taxa at higher trophic levels should have lower abundances than those at lower levels, and evaluated this by testing for a rank-order correlation between trophic level (= maximum number of trophic steps between a taxon and primary producers) and the NS (or NS*) assigned to each trophic level (i.e., the aggregate NS for each taxon grouped within each trophic level: see Supplementary Data, Table S3). For the most part, all constituents of individual guilds received the same trophic rank, but certain size discrepancies suggested the need for additional ranks within particular carnivore guilds (e.g., between larger and smaller crocodylians within the amphibious large-carnivore guild). Correlations between trophic level and specimen abundance were evaluated for each habitat type (terrestrial, amphibious, and aquatic) using Pearson tests. It was necessary to log-transform NS* counts for aquatic taxa and square root–transform NS* counts for amphibious taxa to meet normality assumptions.

RESULTS

Abundance and Distribution of Cloverly Taxa

Ranking Cloverly OSUs by their aggregate specimen abundance generated a highly concave rank-abundance curve (Fig. 2), in which abundant taxa outnumbered rare taxa by several orders of magnitude. A similar pattern has been observed at VMBs in other terrestrial formations (e.g., Jamniczky et al., 2003:table 1). The cf. atoposaurid was the most abundant OSU, followed by the cf. pholidosaurid. Both were represented entirely by isolated teeth. Other abundant OSUs included representatives from multiple taxonomic groups: *Naomichelys*, Titanosauria indet., '*Glyptops*' *pervicax, Albanerpeton, Deinonychus*, and the cf. bernissartid, in descending order. The most abundant osteichthyan was an indeterminate amiiform, also represented exclusively by isolated teeth. We recovered 71 osteichthyan centra (compared to 303 isolated teeth), but these were too weathered to permit OSU assignment. None of the 2,111 indeterminate scales could be related to a particular OSU, although the majority exhibited holostean characteristics and might derive from *Lepidotes*. Likewise, a large number of amphibian centra were recovered (262 specimens), but many were too poorly preserved to permit referral to a particular OSU (although most seem to pertain to either salamanders or albanerpetontids).

Among rare taxa, the indet. alticonodontine was the most abundant mammal (13 teeth in the aggregate assemblage),

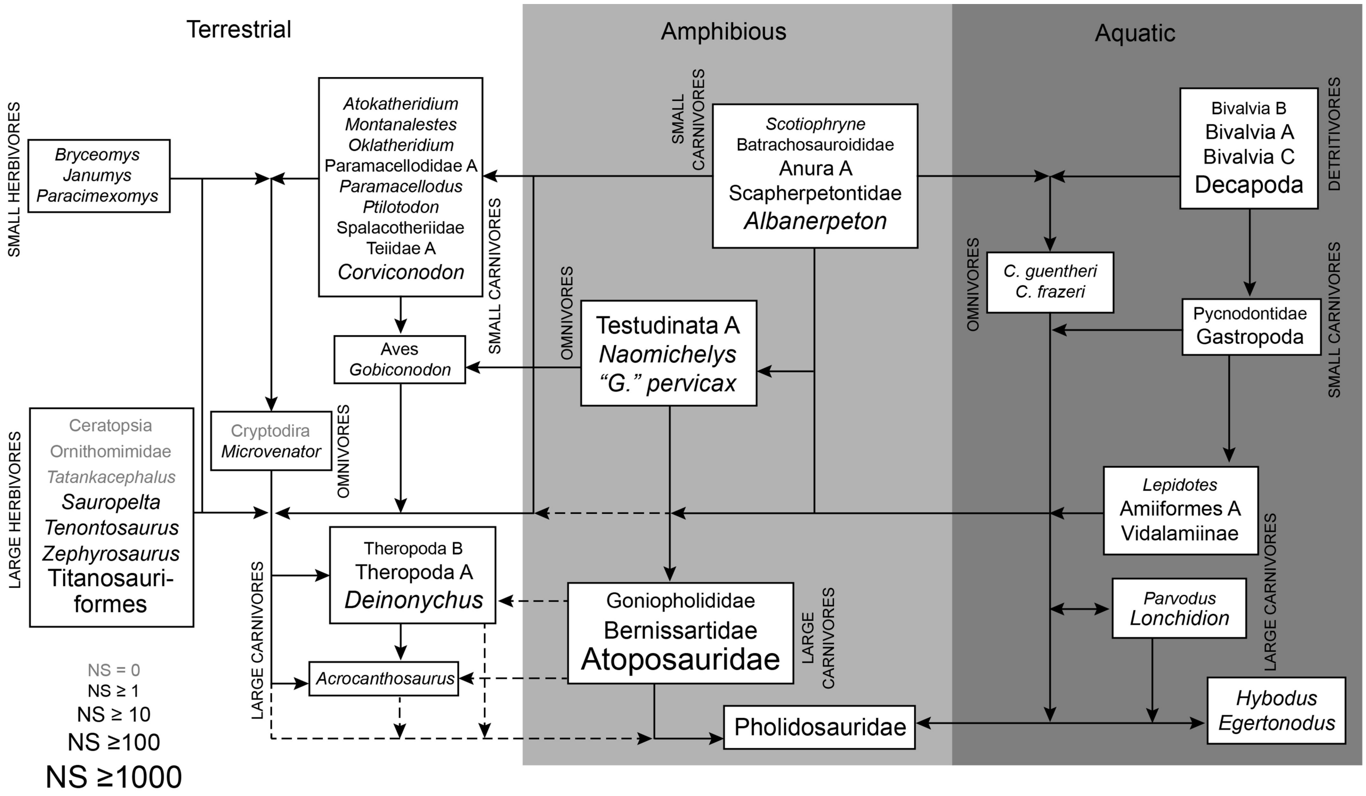

FIGURE 1. Hypothesized trophic web for Cloverly Formation fauna. Arrows indicate direction of energy transfer, and dashed lines represent tentative linkages that were not used in the trophic correlation analysis. Taxon name sizes correspond to the number of specimens for that taxon in the aggregate assemblage; identification qualifiers (e.g., 'cf.,' 'aff.') have been omitted for space; possibly synonymous indeterminate taxa are referred to known taxa (e.g., indet. alticonodontines are all listed as *Corviconodon montanensis*).

but ?*Paracimexomys* was also relatively abundant (seven teeth). The remaining mammalian taxa, *Microvenator*, all lizard taxa, and *Parvodus* were represented by fewer than five specimens apiece. With the exception of *Microvenator*, these rare OSUs only occurred at the VMBs. Three previously reported Cloverly OSUs appeared to be definitively absent from our samples: the myliobatoid *Pseudohypholophus, Aquilaceratops*, and an ornithomimid. Another two OSUs appeared absent—*Tatankacephalus* and Ostrom's (1970) Cryptodira indet.—but might be represented by indeterminate material not referable to an OSU.

These relative abundance results possibly reflect a real paleoecological signal, in addition to expected assemblage biases. Different taxa were disproportionately represented by different element types in the aggregate assemblage. Those OCUs represented by a greater number of element types also tended to be more abundant (Fig. 3); this partly reflects our ability to include a greater variety of element types at higher levels of taxonomic assignment (e.g., crocodylian femora, dermal scutes, and vertebrae could be added to the OSU-level teeth). The number of element types per OCU was significantly positively correlated with the log-transformed abundance of each OCU (log NS), according to the Pearson test ($r = 0.752$, $N = 9$, $p = 0.019$). The number of element types per OCU was normally distributed according to the Shapiro-Wilk test ($W = 0.921$, $N = 9$, $p = 0.399$). Log-transformed NS abundances were also normally distributed ($W = 0.936$, $N = 9$, $p = 0.537$).

Because of difficulties assigning OSU-indeterminate material, most taxa were identified based on only one element type (typically teeth), but such specimen counts are likely biased in favor of particular taxa. The high relative abundances for the cf. atoposaurid, titanosauriform, and *Deinonychus* may be attributable to the fact that individuals exhibited continual tooth replacement and had a large number of teeth at any given time. Calculating NS* tooth counts and using the adjusted counts to recalculate the relative abundance of all taxa yielded a different rank order (Fig. 4). Turtles and amphibians replaced crocodylians, the titanosauriform, and *Deinonychus* as the most abundant taxa. *Naomichelys* rose from rank 3 to become the most abundant OSU, followed by '*G.*' *pervicax. Albanerpeton* rose from rank 6 to rank 3. The titanosauriform fell from rank 4 to rank 18. Likewise, *Deinonychus* fell from rank 7 to rank 17.

Body size also likely creates biases among taxa, but our results are ambiguous. Estimated body mass was significantly positively correlated with NS according to Spearman's rank correlation ($r_s = 0.326$, $N = 45$, $p = 0.029$) but not significantly correlated according to Kendall's τ ($\tau = 0.198$, $N = 45$, $p = 0.061$). The five most abundant OSUs by NS all had estimated body masses ≥1 kg, although the two crocodylians and the titanosauriform were represented exclusively by isolated teeth. Estimated body mass was also significantly correlated with NS* abundance—using both Spearman ($r_s = -0.357$, $N = 45$, $p = 0.016$) and Kendall ($\tau = -0.245$, $N = 45$, $p = 0.020$)—but the correlation coefficients were negative for NS* comparisons.

Despite possible differences in rank abundance attributable to counting method, the relative abundance of taxa appeared broadly consistent across localities. According to the Friedman test, certain taxa were regularly more abundant than others in the individual bulk-sampled assemblages (Table 2A). However, differences in the specific rank order of taxa among localities

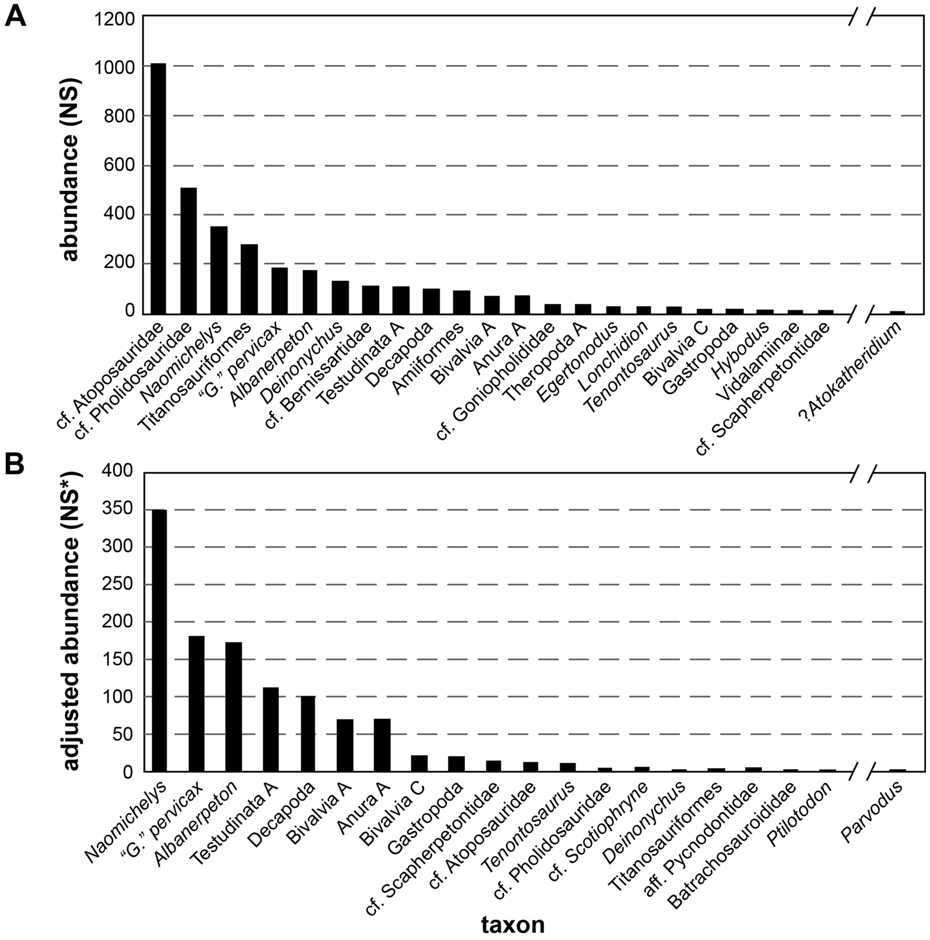

FIGURE 2. Rank abundances of Cloverly Formation OSUs. **A**, rank abundances according to NS abundance in the aggregate sample; **B**, adjusted aggregate rank abundances; counts represent NS* for isolated teeth + NS for other specimens; indeterminate specimens at the OSU level (e.g., indet. actinopterygian teeth) were excluded. **Abbreviations**: **NS***, adjusted number of specimens; **NS** = number of specimens.

limited our ability to definitively identify which taxa contributed to significant results. Follow-up tests did not identify statistically significant abundance differences between taxon pairs (Table 2B). None of the OCU-level pairwise comparisons were significant at the Bonferroni-adjusted alpha ($\alpha' = 0.0008$), nor were pairwise comparisons between OOUs ($\alpha' = 0.0002$) or OSUs ($\alpha' = 0.00003$). However, among these follow-ups the lowest p-values resulted from comparisons between Titanosauriformes indet. (represented in this analysis only by isolated teeth) and individual rare OSUs ($p \approx 0.008$). The titanosauriform occurred frequently and relatively abundantly: an average of 28 titanosauriform teeth were found at 10 out of 27 localities (Fig. 5). The cf. pholidosaurid was another widespread (eight localities) and reasonably abundant (avg. $N = 63$ specimens) OSU. Rare taxa found only at the VMBs consistently ranked last at localities and likely also helped drive Friedman test significance.

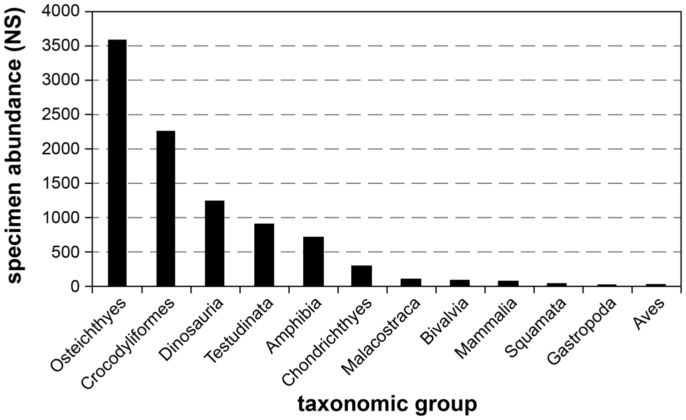

FIGURE 3. Rank abundances of OCU-level taxa in the aggregate sample. **Abbreviation**: **NS**, number of specimens.

Other occurrence patterns were also noteworthy, because they appeared to defy consistent biases either for or against specimens. Certain OSUs were locally abundant, whereas others occurred across the formation but at relatively low specimen concentrations. The cf. atoposaurid occurred at only 6/27 localities (Fig. 5), with specimen counts ranging from one tooth (USNM Loc. 42146) to 604 teeth (USNM Loc. 42183). The average number of cf. atoposaur specimens was 168, but the median specimen count was also high ($N = 50$). *Albanerpeton* and Amiiformes indet. A also had high average specimen abundance but were restricted to three and two localities, respectively. In comparison, '*Glyptops*' *pervicax* was found at the most localities (16), but only a modest number of specimens were recovered at any one locality (avg. $N = 11$). *Deinonychus*, Testudinata indet. A, and *Naomichelys* also occurred relatively frequently but with low average specimen abundance.

Differences between Assemblages

The aforementioned occurrence patterns highlight the need to consider differences between individual assemblages. The total number of specimens recovered from different localities varied

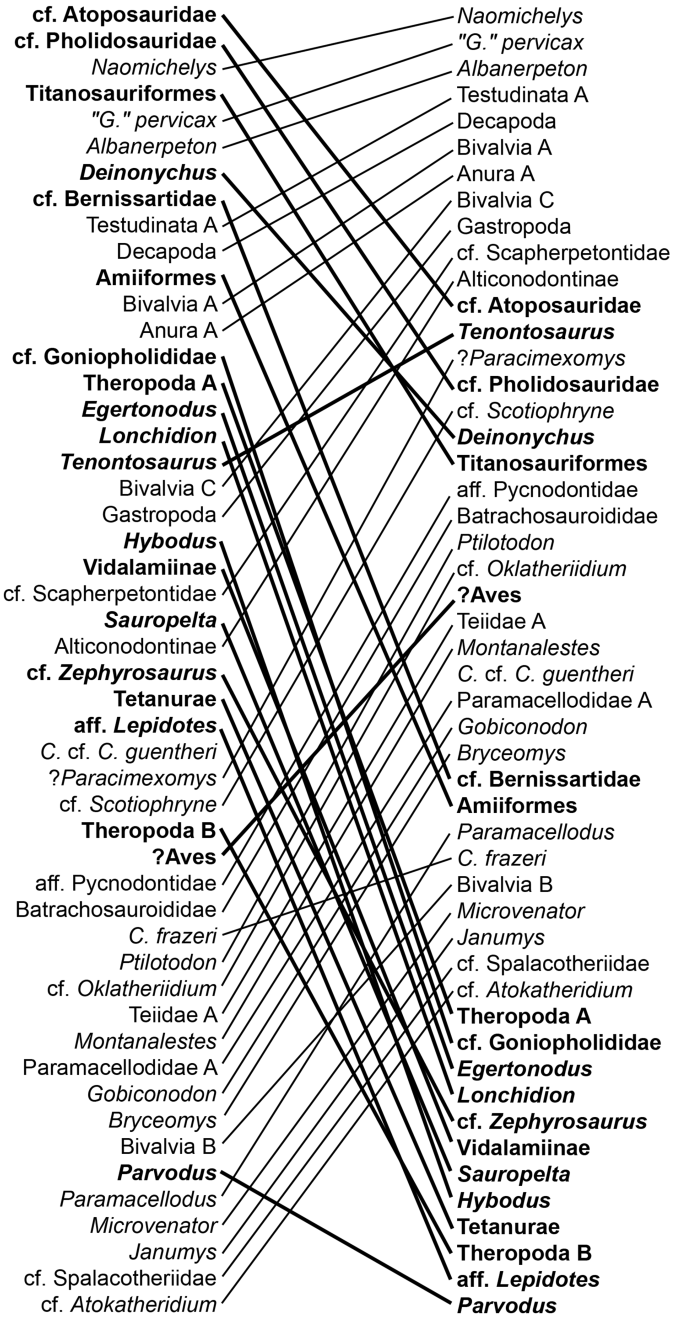

FIGURE 4. Comparison between rank abundances of Cloverly Formation species. Left, rank abundances according to NS abundance; right, adjusted aggregate rank abundances. Lines show changes in rank order for listed taxa. Names and lines in bold represent taxa for which NS* was applied.

considerably, with the two VMBs alone contributing 89.1% of the aggregate sample. Calculating diversity and evenness index values for each locality allowed us to compare assemblages (Table 3) and revealed some noteworthy differences. For example, bulk sampling USNM Loc. 43420 produced a reasonably large fossil sample (152 class-level specimens) but one that exhibited lower apparent vertebrate diversity ($1 - D = 0.55$) than some less-productive bulk-sampled localities (e.g., USNM loc. 42146) and surface collections (e.g., USNM loc. 42179). The two VMBs, however, exhibited the highest specimen count, richness, and $1 - D$ diversity index values.

TABLE 2. Friedman test results for bulk-sampled localities ($N = 10$). **A**, standard results. **B**, follow-up pair-wise comparisons between selected OSUs (Bonferroni-adjusted $\alpha' = 0.00003$).

Comparisons	χ^2	p
A		
OCUs across formation	$\chi^2(11) = 85.9$	<0.001
OOUs across formation	$\chi^2(22) = 134.4$	<0.001
OSUs across formation	$\chi^2(54) = 186.4$	<0.001
B		
Titanosauriformes vs. *Paramacellodus*	$\chi^2(1) = 7$	0.008
Titanosauriformes vs. *Atokatheridium*	$\chi^2(1) = 7$	0.008
Titanosauriformes vs. cf. Bernissartidae	$\chi^2(1) = 4.5$	0.034
Titanosauriformes vs cf. Atoposauridae	$\chi^2(1) = 1$	0.317
Titanosauriformes vs. cf. Goniopholidae	$\chi^2(1) = 3.6$	0.059
Titanosauriformes vs. cf. Pholidosauridae	$\chi^2(1) = 0$	1
Titanosauriformes vs. *Deinonychus*	$\chi^2(1) = 2.7$	0.103
Deinonychus vs. *Tenontosaurus*	$\chi^2(1) = 4$	0.046

Assemblage $1 - D$ diversity was positively correlated with locality NS. The Pearson correlation between log-transformed NS and log-transformed $1 - D$ index values for bulk-sampled localities was highly significant ($r = 0.832$, $N = 9$, $p = 0.005$). Both log-transformed NS ($W = 0.926$, $N = 9$, $p = 0.446$) and log-transformed $1 - D$ index values ($W = 0.883$, $N = 9$, $p = 0.168$) were normally distributed according to the Shapiro-Wilk test. Bulk-sampled localities that yielded fewer specimens exhibited significantly lower $1 - D$ (Table 3). Locality $1 - D$ index values increased linearly with log-transformed locality specimen counts ($y = 0.102x + 0.473$, $R^2 = 0.719$, $F_{1,7} = 17.88$, $p = 0.004$).

These same lower-sample localities also lacked one or more (typically rare) OCUs, which was confirmed by ordination of the locality–taxon matrix by OCU abundance and locality specimen productivity (Table 1A). Chondrichthyes, Squamata, Aves, Mammalia, and decapod crustaceans were restricted to the two VMBs and USNM Loc. 42175, and amphibians were absent at five out of six localities with the lowest NS productivity. However, some common taxa were also absent at these localities. Osteichthyes was the most abundant OCU in the aggregate sample, and osteichthyan specimens occurred frequently—at eight out of ten bulk-sampled localities. Given these factors, the absence of osteichthyan remains at USNM Locs. 43418 and 42159 represent 'embedded absences' in the ordered matrix. The absence of amphibians at USNM Loc. 43422 was another 'embedded absence,' given the presence of a lissamphibian dentary at (less productive) USNM Loc. 42146.

Assemblage evenness differed among productive bulk-sampled localities but was not significantly correlated with locality sample size ($r_s = -0.657$, $N = 6$, $p = 0.175$). The four least-productive localities all yielded J values of 1. Although the abundance rank-order of taxa was broadly consistent across localities, according to the Friedman test, actual relative abundance varied among localities and between individual localities and the aggregate sample. Locality–taxon matrix ordination revealed possibly noteworthy abundance deviations for particular taxa at particular localities. Locality USNM 42175 had a much lower percentage of osteichthyan specimens (12.1%) than did USNM Locs. 42183 (30.5%) and 42222 (57.0%). This discrepancy was further underscored by the fact that Loc. 42175 yielded a comparable percentage of chondrichthyans (3.1%) to Loc. 42183 (6.1%), but the percentage at Loc. 42222 was considerably lower (0.6%). Other examples were also evident. At USNM Loc. 42183, amphibians were more abundant than turtles, but the latter were more abundant in the aggregate assemblage. Dinosaurs had a higher abundance rank at USNM Locs. 42175 (41.1%) and 42146 (20.0%) than at the VMBs (13.2% for USNM Loc. 42183 and 9.1% for USNM Loc. 42222).

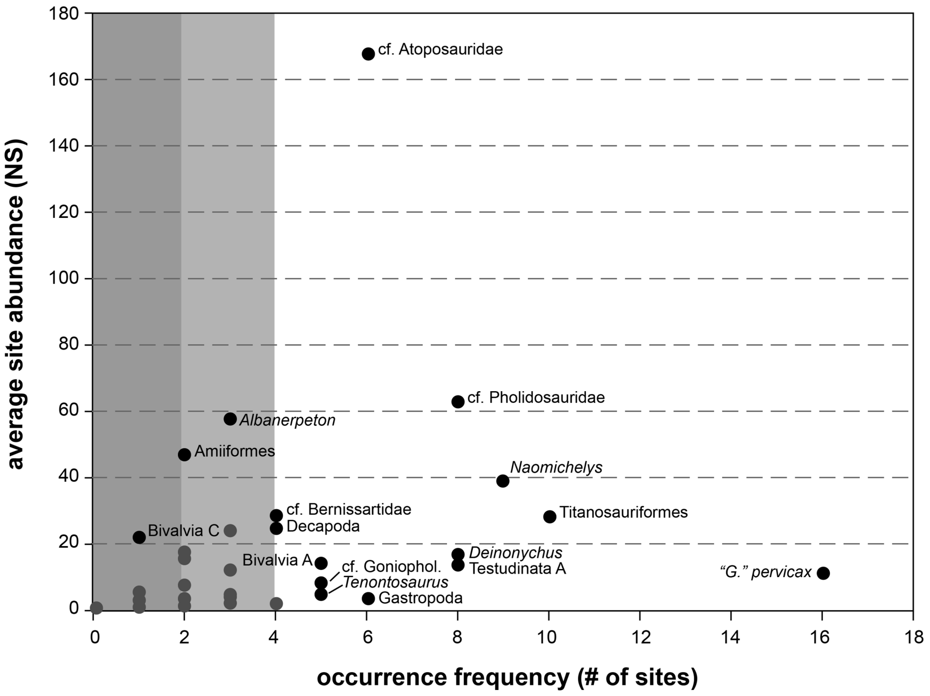

FIGURE 5. Occurrence frequencies of Cloverly Formation taxa compared with their average abundances. Points that fall within the dark gray zone include taxa only found at the two VMBs; points within the light gray zone include taxa only found at the VMBs plus USNM Locs. 42175 and 43420. **Abbreviations**: **Goniophol.**, Goniopholididae; **NS**, number of specimens.

Ordering the locality–taxon matrix by specimen occurrence frequency, rather than by abundance, further underscored the fact that particular assemblages were biased against less common taxa (Table 1B). Occurrence frequency ordination yielded no 'embedded absences,' in part because taxon rank order was not influenced as heavily by the VMB contributions. Using the frequency approach, however, the two VMBs and USNM Locs. 42146 and 43416 produced more osteichthyan specimens than expected, because Osteichthyes had a lower frequency rank relative to Crocodylia, Dinosauria, and Testudinata. The four most prominent OCUs were all widely distributed, but osteichthyan abundance fluctuated to a greater extent among localities.

TABLE 3. Diversity and evenness statistics for 22 Cloverly Formation localities using NS for OSUs. Specimens that could not be identified to OSU were excluded, along with seven localities whose specimens could be identified to OSU. Bulk-sampled localities are underlined. **Abbreviations**: **NA**, not applicable; **NS**, number of specimens.

USNM locality	NS	Richness	Simpson ($1 - D$)	Pielou's J
42159	2	2	0.50	1.00
42175	164	15	0.84	0.79
42179	25	8	0.81	0.88
42183	1,627	43	0.83	0.64
42146	3	3	0.67	1.00
42153	8	2	0.22	0.54
42222	1,270	31	0.85	0.67
43416	1	1	0.00	NA
43418	2	2	0.50	1.00
43420	111	7	0.55	0.55
43421	10	3	0.34	0.58
43422	12	3	0.65	0.98
42225	3	3	0.67	1.00
42233	11	2	0.17	0.44
42244	40	4	0.59	0.80
42245	2	2	0.50	1.00
43627	1	1	0.00	NA
43628	3	3	0.67	1.00
43629	6	1	0.00	NA
43632	59	7	0.63	0.67
43635	2	1	0.00	NA
43638	5	4	0.72	0.96
Aggregate	3,367	45	0.86	0.65

Metacommunity Trophic Assessment

Cloverly taxa represented a variety of trophic guilds, from aquatic detritivores to large, terrestrial carnivores. Most terrestrial guilds showed high species diversity but low specimen abundance per species (Fig. 6). In comparison, the small, amphibious carnivore guild had fewer species, but most of these occurred at higher specimen abundance. The terrestrial omnivore guild showed low abundance and diversity, but many taxa listed as small, terrestrial carnivores might have been omnivorous. Aquatic guilds did not exhibit the highest diversity or abundance, despite the fact that most specimens in the aggregate assemblage were deposited in the two lacustrine VMBs (Fig. 6; see Oreska et al. [2013] for locality lithologies).

In general, specimen abundance decreased with trophic level within each habitat type as one might expect. Correlation coefficients for all comparisons were negative, except for the comparison between NS abundance and amphibious trophic level, which was not statistically significant (Table 4). The NS abundance comparisons for the terrestrial and aquatic communities were negative but not statistically significant.

However, correlations between NS* abundance and trophic level in the terrestrial and aquatic communities were statistically significant and highly negative, especially the aquatic NS* correlation ($r = -0.993$, $N = 5$, $p = 0.001$). In comparison, the square root–transformed NS* appeared to be uncorrelated with amphibious trophic level ($r = -0.109$, $N = 5$, $p = 0.861$).

DISCUSSION

To What Extent Are These Fossil Assemblages Biased?

Certain biases were consistent across localities. Small terrestrial taxa were generally rare or absent, including lizards, birds, and mammals—consistent with predicted taphonomic and

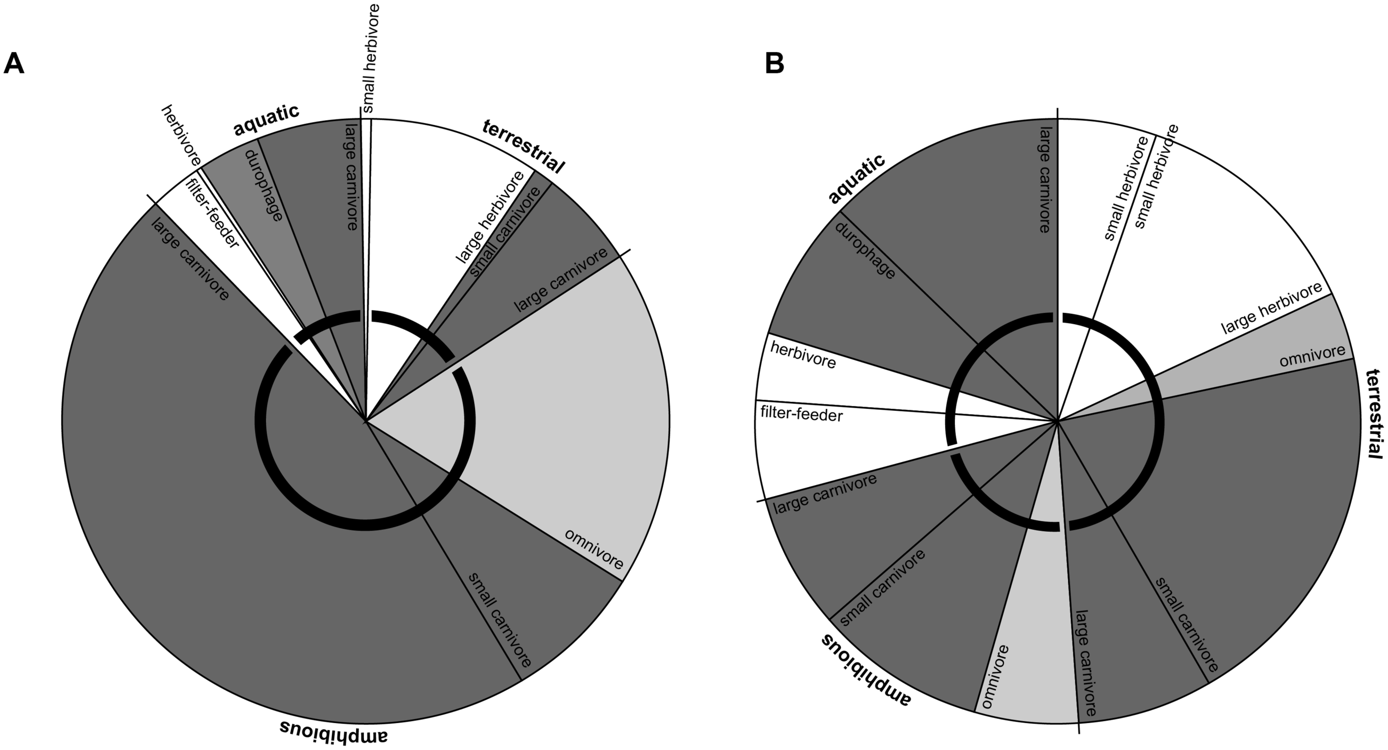

FIGURE 6. Taxonomic distributions within Cloverly trophic guilds. **A**, percentage abundances; **B**, percentage diversities.

proximity biases against these groups. Conversely, the high relative abundance and occurrence frequencies of crocodylians and turtles were unsurprising, considering their probable aquatic or amphibious life habits and fairly durable elements. The positive, significant correlation between the number of element types per OCU and its NS favored Osteichthyes, Crocodylia, and Amphibia, consistent with Shotwell's (1955) suggestion that element diversity in deposits increases with proximity of life habit to the site of deposition.

Separate from this possible proximity bias, different elements were also consistently rare to absent in deposits. Vertebral, pelvic, and appendicular elements were all rare, suggesting preferential loss. Fish centra were surprisingly rare, given the large number of isolated scales in some localities. Amphibian vertebrae were occasionally present but typically lacked diagnostic characters, which prevented more specific assignment. In comparison, isolated teeth tended to be common, relatively well preserved, and diagnostic. Consequently, tooth counts factored heavily in species-level relative abundance determinations—a clear bias against edentulous taxa, such as *Microvenator*, and a possible bias against taxa with relatively few teeth, such as dipnoans and avians. The OSU-level analyses consequently included this taxonomic bias, in addition to apparent taphonomic biases.

The role of a possible body size bias was less clear. The difference in the direction of the correlation between body mass and abundance depending on counting method (NS versus NS*) further illustrates the fact that element type and specimen entry mode might significantly bias abundance counts. A separate body size bias that favored large taxa seems unlikely, however, given the nature of the deposits. All recovered specimens were relatively small, and NS counts for certain large organisms were likely overestimates. Furthermore, had we been able to specifically refer isolated fish scales and indeterminate amphibian postcranial material, both of the NS and NS* body mass correlations might have been significant and negative.

Other biases were apparently locality specific. Particular assemblages exhibited notable differences in taxonomic richness, composition, and abundance relative to the aggregate assemblage. These might have derived from differences in either taphonomic regime or paleocommunity at localities (or both). Examples included the 'embedded' absence of fishes at USNM

TABLE 4. Pearson correlation test results for trophic-level abundance comparisons. **Abbreviations**: **NS**, number of specimens; **NS***, adjusted number of specimens; **sqrtNS***, square root of NS*.

		Shapiro-Wilk normality		Correlation test	
Habitat	Count	W	*p*	*r*	*p*
Terrestrial	NS	0.809	0.095	−0.568	0.318
	NS*	0.84	0.165	−0.896	0.040
Amphibious	NS	0.983	0.948	0.727	0.164
	sqrtNS*	0.867	0.254	−0.109	0.861
Aquatic	NS	0.891	0.362	−0.331	0.587
	LogNS*	0.988	0.971	−0.993	0.001

Locs. 43418 and 42159 and the relatively low percentage of fishes at USNM Loc. 42175. Taphonomy at the first two localities likely precluded the preservation of fish fossils; they produced only a few specimens, all relatively robust crocodylian, dinosaur, or turtle remains. In comparison, the relative absence of fishes at USNM Loc. 42175 might be due in part to a difference in paleoenvironment between this and other localities. Given the high osteichthyan abundance in the aggregate sample, one might have predicted this locality to have more osteichthyan specimens than dinosaur and crocodylian specimens. In addition to this discrepancy, it yielded proportionally more dinosaur remains than would be expected based on the aggregate sample, suggesting a terrestrial signal. These four localities all occur at slightly different stratigraphic levels, but the absence of a diverse, otherwise abundant group such as Osteichthyes is unlikely to represent a paleo-metacommunity change over time.

How Were Cloverly Vertebrate Microfossil Localities Derived from the Paleo-metacommunity?

None of the localities yielded the paleo-metacommunity gamma diversity (i.e., total formation richness), and only the two VMBs and USNM Loc. 42175 produced a full complement of known vertebrate OCUs. The $1 - D$ diversity of assemblages increased linearly with exponentially increasing sample size, supporting the concern that large sample size discrepancies affect apparent diversity among vertebrate microfossil localities. Larger samples should exhibit lower $1 - D$ diversity, all other factors being equal. Instead, increasing the sample size greatly increased OSU richness. Smaller assemblages also lacked particular vertebrate groups entirely, including lizards, birds, and mammals. In comparison, the richness at USNM Locs. 42183 and 42222 approached the gamma richness, suggesting that the VMBs approach true metacommunity-level samples. This is consistent with the suggestion that lacustrine VMBs capture a time-averaged picture of their surrounding paleocommunities (Rogers and Brady, 2010). The size of this composite paleocommunity (i.e., local or regional) likely depends on the size of the catchment supplying the deposit over time.

The evenness results suggest that the vertebrate microfossil localities do not accurately record a single, uniform paleo-metacommunity. If all of the localities had accurately recorded the same paleo-metacommunity, then the assemblages should exhibit the same evenness. However, the discrepancies do not lend themselves to easy interpretation. If there had been a strong positive correlation between evenness and sample size, then larger samples might average out to a single paleo-metacommunity abundance distribution. Assuming that the true paleo-metacommunity evenness was fairly moderate, and that all of the localities recorded the same paleo-metacommunity, a strong negative correlation might have indicated that disproportionately many specimens of common taxa and more specimens for rare taxa would be accumulated by increasing the size of the fossil deposits. This might be evident at the two VMBs, which appeared less even than certain low-sample localities. The lack of a significant correlation with sample size suggests that these signals are either mutually confounding or broadly inconsistent across localities. The localities might have accurately recorded different paleocommunities with different relative abundance distributions or recorded the same paleo-metacommunity but with different biases for different taxa or a combination of local paleocommunity and paleo-metacommunity signals.

There are, however, reliable paleo-metacommunity signals in the data set, as evidenced by abundance patterns among localities. The Friedman test results suggest that bulk samples from productive microvertebrate localities do approximate replicate samples of a single, formation-level metacommunity, albeit with variation among samples. Some absences were apparently due to taphonomy (i.e., were not true absences), but the occurrence of rare taxa at unproductive localities would likely not have altered the relative rank order of taxa across localities to a significant degree. However, the observed rank abundance consistency might derive from either the paleo-metacommunity or from relative taphonomic effects acting semi-uniformly across all localities. Unusual occurrence patterns for particular OSUs suggest that some relative abundance patterns might be genuine paleoecological signals: for example, the low abundance/high frequency distribution of ‘*G.*’ *pervicax* across localities. And despite possible element preservation bias, the most abundant OSUs are not necessarily those represented by the greatest element diversity. If high element diversity indicates a life habit proximal to the site of deposition, this proximity does not automatically confer an overwhelming abundance advantage. Unlike fishes and amphibians, titanosauriforms are only represented in the lacustrine VMBs by teeth, but these teeth outnumber many individual fish and amphibian OSU samples, suggesting that titanosauriforms were fairly abundant on the Cloverly landscape and/or visited the depositional sites frequently. This was perhaps also true for *Deinonychus*, which is abundantly represented by both teeth and other elements.

Does Apparent Community Structure Reflect the Original Paleo-metacommunity?

It is difficult to evaluate the hypothesized trophic web presented in Fig. 1, in the absence of more information about the paleoecology of individual taxa and a better sense of how taphonomy and other factors might have biased assemblage specimen counts. The paleo-metacommunity picture suggested by the aggregate vertebrate microfossil assemblage nevertheless appears reasonably consistent with expectations for an actual metacommunity. The correlation analyses provide very coarse support for the ‘Eltonian pyramid’: taxa from lower trophic levels generally outnumbered those from higher trophic levels in both aquatic and terrestrial paleocommunities. The absence of a correlation for amphibious taxa is due in part to the very high number of crocodylian teeth present in deposits, likely attributable to the aforementioned preservation biases. This bias is partially mitigated by the use of NS* counts. It is worth noting, however, that Elton (1927) and later studies (Lindeman, 1942) based the ‘pyramid of numbers’ concept on the assumption that predators are always larger than their prey at each canonical trophic level. The ‘Eltonian pyramid’ observed for the terrestrial paleo-metacommunity is supported in large part by a high abundance of sauropods in the first trophic level.

We also note that the canonical trophic levels used to assess metacommunity structure might not accurately reflect actual paleo-metacommunity trophic chain lengths. The higher δ^{15}N enrichment of dromaeosaurid fossils relative to large tyrannosaurid fossils in the Judith River Formation suggests a longer trophic chain for the former (Ostrom et al., 1993). The δ^{15}N enrichment for the tyrannosaurid appeared to be about one trophic step above that of the large herbivores in the formation. In our analysis, we placed *Deinonychus* in the fourth trophic level and the large tetanuran (*Acrocanthosaurus*) in the fifth, due to its larger size, to conform with canonical expectations about potential energy flow (Lindeman, 1942). However, if *Acrocanthosaurus* only consumed larger herbivores, it would have been part of a much shorter, two-step trophic chain.

Our picture of the paleo-metacommunity is surely incomplete. Some ecological guilds were absent from the vertebrate microfossil deposits. No obligate amphibious herbivores, grazers, or detritivores were recovered. Insects and other small invertebrates might have occupied this niche, or certain Cloverly amphibians might have been omnivorous. The productive vertebrate microfossil localities nevertheless provide samples reflecting an ecologically diverse fauna, consistent with a functional metacommunity inhabiting an interconnected patchwork of terrestrial and freshwater habitats.

CONCLUSIONS

The Cloverly Formation records evidence of a diverse regional vertebrate community in which titanosauriform sauropods and particular amphibious taxa predominated. Proximity of life habit to depositional sites and durable diagnostic elements probably enhanced the fossil abundance of many amphibious taxa, especially the large crocodylian. However, other taxa (e.g., titanosauriform sauropods and *Deinonychus*) were likely genuinely abundant in the original paleo-metacommunity. Differences between localities are relatively small but may represent genuine paleocommunity variation (i.e., beta diversity) across the Cloverly landscape.

More generally, life habit, element diversity, and taphonomy can be seen as separate ‘filters’ that combine to influence the specimen abundance of a fossil taxon in a vertebrate microfossil assemblage. It is difficult to determine the magnitude of discrepancies between any single vertebrate microfossil assemblage and the original metacommunity from which it derived, which limits our ability to quantify some aspects of these paleocommunities. Nevertheless, apparent abundance distortions in Cloverly vertebrate microfossil deposits are consistent with expected biases and appear to vary predictably depending on the characteristics of the locality. For example, crocodylians were particularly abundant in most localities, consistent with their probable proximity to the original depositional sites and their ability to contribute many shed teeth to a single deposit.

New analytical approaches are ultimately needed to constrain these biases, such that different assemblages can be standardized for comparison. But even in the absence of such approaches, vertebrate microfossil deposits provide information on paleo-metacommunity structure that can, in the future, be used to attempt more detailed intra- and inter-formational comparisons. As detailed elsewhere (Oreska et al., 2013), the most robust comparisons can be made with VMB assemblages, but the present work shows that less productive localities can also provide a useful perspective on the landscape-scale distribution of fossil taxa within a formation.

ACKNOWLEDGMENTS

We thank S. Jabo, P. Kroehler, G. Wesley-Hunt, and all of the participants of the 2004–2010 field expeditions, during which the materials used in this study were collected. We also thank C. Manuel, R. Manuel, and E. Kvale for their invaluable advice, support, and hospitality during that time. F. Grady picked most of the fossils from the matrix. This research was supported by the Smithsonian Institution through a Walcott Grant and two Small Grants, as well as the NMNH Equipment Fund, and by the National Science Foundation through NSF EAR-1052673 (to MTC). Much of this project was completed as part of a senior undergraduate honors thesis in geology at the College of William and Mary by MPJO. We are especially grateful to the Bureau of Land Management in Wyoming and Montana for their cooperation and permission to collect the materials studied herein (under permits PA03-WY-102, PA05-WY-133, PA07-WY-150, PA07-WY-151, PA07-WY-152, and M 100511 to MTC). Finally, the article was substantially improved thanks to the careful and thoughtful reviews provided by R. Rogers, D. Brinkman, and R. Butler.

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Submitted January 13, 2015; revisions received June 1, 2015;
accepted June 28, 2015.
Handling editor: Richard Butler.