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GRADUATE COLLEGE

# FAUNAL COMPOSITION, NON-MARINE VERTEBRATES, OF THE UPPER CEDAR MOUNTAIN FORMATION (CRETACEOUS: ALBIAN-CENOMANIAN), CENTRAL UTAH

A Dissertation

SUBMITTED TO THE GRADUATE FACULTY

In partial fulfillment of the requirements for the degree of

Doctor of Philosophy

By

PATRICIA GOLDBERG

Norman, Oklahoma

2000

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# FAUNAL COMPOSITION, NON-MARINE VERTEBRATES, OF THE UPPER CEDAR MOUNTAIN FORMATION (CRETACEOUS: ALBIAN-CENOMANIAN), CENTRAL UTAH

A Dissertation APPROVED FOR THE
DEPARTMENT OF ZOOLOGY

BY

# PREFACE

The following dissertation is organized into six chapters. The first is a general introduction and is not intended for publication. It serves to provide background information and context for the reader unfamiliar with the Cretaceous period. Chapters 2 and 3 are intended for independent publication. Chapter 2 provides an overview of the Mussentuchit fauna from an ecological perspective and examines the role of taphonomy in evaluating ecological patterns. Chapter 3 demonstrates sampling completeness. Chapters 4 through 6 are intended for publication as a set, in collaboration with R. Cifelli. Some redundancy between chapters necessarily follows. Chapter 4 demonstrates similarities and differences in faunal composition among sites, Chapter 5 examines taphonomic similarity among sites, and Chapter 6 examines faunal distributions from an ecological perspective. Format style in all chapters follows publication guidelines for submission to Paleobiology.

# ACKNOWLEDGMENTS

This dissertation was very much a community effort and drew from the strengths and knowledge of many people. In particular I thank my committee members, Richard Cifelli, Nick Czaplewski, Gary Schnell, Mike Kaspari, and Bruce Hoagland, each of whom contributed significant guidance, support, and knowledge in their respective fields. Every last one of them made time for me when I showed up at their doorway.

This study is based on data and specimens collected over a 10 year period by R. Cifelli and crews from the Sam Noble Oklahoma Museum of Natural History at an enormous cost in time, energy, and money. R. Cifelli provided me with access to specimens, databases, field notes, maps, unpublished manuscripts, and research materials and facilities. He was greatly instrumental in helping me get support in the manner of grants and scholarships for this work. In addition, he personally took me to all the microsites analyzed in this paper, taking care of permits, paperwork, and even arranging for the assistance of the Utah state geologist. Needless to say, this dissertation simply never would have happened without him.

Jim Kirkland spent two days in the Utah desert patiently sharing his geological knowledge with a novice (me). Rick Lupia came to the museum my last year in residence, and provided a great deal of assistance with (and enthusiasm about) paleoecological statistics. Coral McCalister drafted figures 3 (Chapter 1) and 1 (Chapters 2 and 3), saving me a lot of headache and doing a better job than I could. My fellow graduate students, Cindy Gordon, Randy Nydam, Kent Smith, Julian Hilliard, and Matt

Wedel, provided invaluable discussion and moral support. Arthur Harris, my former professor, has always very quietly provided encouragement in my goals and confidence in my abilities.

Funding for much of this work was provided through research and travel grants from the University of Oklahoma Graduate Student Senate and the University of Oklahoma Department of Zoology, as well as scholarships from the Alfred and Rose Miniaci Scholarship Fund (Dinamation International Society) and Blanche and Francis Adams Scholarship Fund. National Science Foundation grants (BSR 8906992, DEB 9401094, and DEB 9870173) and National Geographic grants (4761-91 and 5021-92) to R. Cifelli funded all the work to generate the data used in the first place.

Finally, I would like to thank my family. My parents prodded me to go to college and encouraged my interest in nature. My husband has been my partner, advocate, and friend. He has tolerated all the demands and complications that have arisen along the way with good humor. Lastly, I thank my son, Raymond, who sacrificed time with his mom this past year with a maturity, thoughtfulness, and sense of humor way beyond his years.

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# ABSTRACT

This project describes the faunal composition of the upper Cedar Mountain Formation (Mussentuchit Member: Albian-Cenomanian, Cretaceous) in Emery County, Utah, based on fossils and associated data from twelve microvertebrate fossil localities.

First, the Mussentuchit fauna was examined from an ecological perspective. Raw abundances were corrected for differences in preservation potential between families, using a weighted abundance of elements method. Biases in preservation strongly favored fishes and crocodiles. These groups were consequently over-represented in the record, distorting ecological patterns. The terrestrial fauna, particularly the microfauna, is extremely well represented, once correction factors are considered. Trophic structure approached realistic proportions, with 3% carnivores and 47% herbivores, once correction factors were applied. Body-size distribution of the terrestrial fauna suggest an open-woodland habitat.

Next, sampling issues were examined. Species-accumulation curves were plotted by adding sites and also by adding taxa over time at a single site through sampling over multiple years. Estimators of abundance were calculated to estimate the number of families and the number of mammal species as yet undiscovered. While several families are probably still undiscovered in the fauna, nearly all mammal species appear to have been found. Sampling in this member has reached the point of diminishing returns; finding any new taxa would probably require processing a very large volume of matrix.

The 12 sites were found to vary significantly in faunal composition using principal components analyses and Pearson's correlation coefficients. These techniques were used at five different taxonomic levels (higher-level taxa [ubertaxa], families, crocodile families, squamate species, and mammal species), and groupings of sites varied with the taxonomic level used to characterize their composition. The best resolutions of taxonomic distinctness occurred at the inclusive family level and at the mammal species level.

Eleven of the sites were relocated and examined for sedimentary structures in order to determine depositional environment and energy. Since the system was very fine-grained, thin sections were made to aid in interpretation. Specimens were weighed to determine the average weight of each taxon recovered, as well as the average weight of all fossils in a given site. These results were used to determine which sites were depositionally similar. Similarity based on geology did not correspond with similarity based on taxonomy at any level, using Mantel tests and Kendall's tau. Depositional processes, while altering the overall faunal composition in the Mussentuchit Member, apparently operated in a similar manner among sites.

Finally, taxonomic associations were examined using correspondence analyses at the ubertaxa, family, and mammal species level. Monte Carlo simulations were performed to determine which taxa were significantly abundant (or absent) at each site. Each family and most mammal species were found to occur in one or more sites in greater than expected abundances; distributions were significantly patchy and not even or random across the sites. Additionally, many families were significantly absent from some sites. Each site had a unique composition of animals, but some sites shared general patterns of association. Ubertaxa and families were found to form three loose associations; a terrestrial assemblage and two distinct aquatic assemblages. Correspondence analyses on taxa based on habitat, diet, and thermoregulation were all significantly non-random, suggesting an ecological basis for the patterns in faunal distribution among sites.

# Introduction

Goals.—The medial Cretaceous was a time of great importance in the history of life. Flowering plants had recently appeared and begun to radiate. The supercontinent Pangaea was rifting and the continents were drifting apart, carrying their endemic floras and faunas with them. This movement of the continents was causing changes in climate and the earth began getting wetter and warmer. Not surprisingly, the faunal composition of the earth during the Early Cretaceous is very different from that of the Late Cretaceous, but little is known of the fauna during the transitory period, the medial Cretaceous. One fauna of this key period, the Mussentuchit local fauna, is studied from an ecological perspective herein.

The goal of this project is to characterize the fauna of the Mussentuchit Member (Albian-Cenomanian) of the Cedar Mountain Formation, Emery County, Utah. The first chapter describes the taxa found in this fauna and reviews their biology. The Mussentuchit local fauna is described and characterized as a whole. The effects taphonomic processes have on community composition are discussed and an attempt is made to correct these biases. Next, modern ecological methods are applied to the fossil record in order to estimate the number of undiscovered taxa in the Mussentuchit Member, and an estimate of sampling effort required to recover them is made. Then I examine variability in taxonomic composition among 12 microvertebrate sites and characterize the composition of these sites. Variability in depositional environment and transport energies between sites are addressed in the following chapter. These data on geological similarity are compared with the data on taxonomic similarity in order to determine how much of the latter is explained by physical processes after death. Finally, the faunas of individual sites within the Mussentuchit Member are compared from an ecological perspective, demonstrating that small-scale ecological differences may play a role in the composition of fossil assemblages constrained in time and space.

Relevant background information is provided to inform the reader on the general state of the world during the Cretaceous Period, as well as to introduce technical terminology used throughout this dissertation.

Geologic time.—The Cretaceous Period spans about 79 million years, from 145 Mya to 65.5 Mya. It is divided into early and late epochs, with the division occurring at 98.5 mya (Gradstein et al. 1995). These epochs are further divided into a total of 12 stages, ranging from 2 Ma to 11.5 Ma in span (Fig. 1). The term "mid-Cretaceous" refers to the two ages (Albian and Cenomanian) bordering the division between early and late epochs.

Global geography.—The changing geography of the earth has been summarized and illustrated in Beherensmeyer et al. (1992), Smith et al. (1994), and Scotese (2000). The following synopsis draws from these sources. Throughout much of the early history of terrestrial vertebrates all land masses were fused into one large continent, Pangaea. Pangaea formed in the Permian with the fusion of the northern land masses, Laurasia, and the southern land masses, Gondwana. This supercontinent persisted through much of the Jurassic, with maximum consolidation during the middle to Late Triassic. By the Late Jurassic, Pangaea began to rift significantly. The North Atlantic began to open, separating North America from Eurasia. Meanwhile, western Gondwana

(Africa and South America) rifted from eastern Gondwana (Australia, Antarctica, and India). During the Early Cretaceous, the South Atlantic opened and expanded, slowly separating South America and Africa. India rifted from Australia/Antarctica around the same time and drifted northward until finally colliding with Asia in the Paleocene, forming the Himalaya Mountains. The dissociation of Gondwana was complete by the Eocene when Antarctica split from Australia. Around the mid-Cretaceous, the northern and southern continents had drifted far enough apart to establish a circum-equatorial seaway. North America was located 10° further south in the mid-Cretaceous than it is today, drifting northwest as the Atlantic Ocean spread and the Pacific Ocean shrank (Fig. 2).

Sea levels have fluctuated widely over time, as a function of global temperature (ice caps) and tectonics (for summaries see Vail et al. 1977, Hallam 1992, and Haq et al. 1987). During the Permian through Jurassic, when Pangaea was consolidated, sea levels were relatively low (but still higher than today). Sea levels rose throughout the Cretaceous as Pangaea rifted, peaking near the end of the period. This was the last major transgression of epieric seas, and culminated in the highest sea level stand of the Phanerozoic. During this time much of the interior of central North America was flooded (for details, see Elder and Kirkland 1993). The overall trend of rising sea level was not even and smooth, however, and the trend was interrupted in the mid-Cretaceous, at the Albian/Cenomanian boundary, when a moderate regression occurred (Fassel and Bralower 1999).

During the Early Cretaceous eastern North America was in close proximity to Europe, up through 120 Mya, but by 80 Mya the separation between the two continents was broad and complete (Hay et al. 1999). Western North America was linked intermittently to Asia via Beringia during the Late Cretaceous (Parrish 1987), particularly during the rarer periods of low eustacy. The Western Interior Seaway separated eastern North America from western North America during much of the Late Cretaceous when sea levels were high. During the period of interest in this study (98 Mya) North America and Europe were in the process of separating, the circum-equatorial current was being established, and the overall trend of rising sea level (flooding the interior of the central United States) was interrupted by a significant regression.

Global climate.—The fusion of land masses in the Triassic and Jurassic had several climatic consequences (summarized in Beherensmeyer et al. 1992). With the large interior area and small perimeter exposed to the ocean, much of the Pangaean continent was arid. In addition, rain shadows were abundant, caused by uplifted sutures. Dry air causes high diurnal temperature variation, but the well-mixed global ocean resulted in minimal latitudinal variation. Precipitation, however, was variable with three latitudinal belts: arid equatorial, seasonally wet, and polar moist temperate. In the summer months, hot dry land heated the air above, causing it to rise. Cool, moist air from the ocean was then drawn over the continent, creating a monsoonal climate. The breakup of Pangaea during the Cretaceous caused an overall warming, wetting trend that culminated in the Eocene. Seasonal variation decreased and maritime climates increased as coastal areas expanded. The arid equatorial belt shrunk and eventually disappeared as the seasonally wet and temperate moist bands expanded and shifted equatorward. The circum-equatorial seaway shunted warm equatorial waters 40° north, between north Africa and Europe, making that region unusually warm and wet (Beherensmeyer et al. 1992).

Compared to today, the Cretaceous world was warm, with moderate precipitation, and little latitudinal or seasonal variation (Parrish 1987, Frances and Frakes 1993, Fassell and Bralower 1999, Frakes 1999). Upchurch and Wolfe (1987) estimated mean annual temperatures at 30° latitude to be 21-22°C during the mid-Cretaceous and 23-25°C during the Late Cretaceous. These data correspond with Fassell and Bralower's (1999) estimates of 23-29°C at 25° latitude and 10-13°C at 60° S during the late Albian. Temperatures decreased poleward, but latitudinal temperature gradients were less than modern day. Poulson et al. (1999) suggested that this was caused by the opening of the Western Interior Sea, which warmed the northern polar region. In addition, seasonal variability in temperature was less than today, with the mean temperature varying 5°C at the equator and 10°C at the poles over the course of a year (Upchurch and Wolfe 1987).

The structure of wood and leaves has been used to make estimates on precipitation in western North America during the Cretaceous (Upchurch and Wolfe 1987, Wolfe and Upchurch 1987). The small size of leaves, lack of drip-tips, and other evidence led to the conclusion that annual precipitation was low to moderate (< 165 cm/year). In addition, wood structures showed a lack of seasonality, and the variability in precipitation over the year was probably less than 10 cm.

During the Albian-Cenomanian, western North America was relatively warm, with little seasonality in temperature (Upchurch and Wolfe 1993). The megathermal-mesothermal vegetation boundary, indicating a mean annual temperature of around 20°C, was located across Kansas. Moisture levels were subhumid but aseasonal, based on tree-ring evidence (Upchurch and Wolfe 1993). However, the moisture gradient in the United States was geographically reversed from the situation today; the southeast was drier and the west was wetter.

Vegetation.—The angiosperms made their first appearance in the early Cretaceous, near the Barremian-Aptian boundary in northern Gondwana, although they remained a minor part of the vegetation for much of that epoch (Saward 1992). Upchurch and Wolfe (1987), Crepet and Friis (1987), and Beherensmeyer et al. (1992) have traced the evolution of vegetation throughout the Cretaceous and the following summary follows these sources. Angiosperms diversified in the Early Cretaceous at low latitudes and spread rapidly, so that by the Aptian and Albian they were locally dominant, although regionally they accounted for no more than 20% of the flora. At this point they were restricted to early successional species, occurring as small herbs or thickets in disturbed areas, especially coastal plains (Retallack 1986, Nesterova et al. 1992). These early angiosperms had small diaspores within apocarpous fruits (Wing and Tiffney 1987). They underwent a tremendous radiation during the Albian-Cenomanian (Ligard and Crane 1988) and expanded into late successional communities, as understory trees and shrubs. By the late Cenomanian they comprised up to 40% of the flora and had spread to the mid-latitudes. Angiosperms diversified in physiognomic forms extensively by the Campanian and Maastrichtian, dominating successional forests and brackish habitats and representing 50-80% of the species present (reviewed in Beherensmeyer et al. 1992, but see Wing et al. 1993). This period represents a second major radiation. Fruits also diversified during this period, with fleshy drupes and hard nuts appearing in the Campanian and berries appearing in the Maastrichtian.

Productivity during the Cretaceous was highest in the mid- and high latitudes, where the rainfall was concentrated (Spicer et al. 1993). Early Cretaceous plant communities were diverse, with about 30% cycads, 30% ferns, 20% conifers, and the remaining 20% split among Gnetales, lycopods, and sphenopsids (Beherensmeyer et al. 1992). Brenner (1976) characterized four floristic provinces for the mid-Cretaceous on the basis of pollen: northern Laurasia (those areas now above 60°N); southern Laurasia (southern North America, Europe, and Asia); northern Gondwana (northern Africa and South America); and southern Gondwana (southern Africa, southern South America, Australia, Antarctica, and India [which was in the southern hemisphere during this time]). These regions correlate broadly with northern and southern tropical and temperate climatic belts.

Until the end of the Cretaceous Period, conifers were physiognomically dominant, forming the largest trees. In the Early Cretaceous, Cheriolepidiaceae, Araucariaceae, and, in the south, Podocarpaceae occurred in the drier tropical belt with an understory of ferns and shrubby cycadophytes. Ferns would sometimes form a savanna or plain, similar to grasslands today (Beherensmeyer et al. 1992). Lycopods and horsetails occurred along poorly drained coastal areas. In the temperate regions, deciduous Pinaceae ancestors, cycadophytes, and Ginkgoales dominated.

With the rapid diversification and expansion of angiosperms during the Late Cretaceous, cycads, Gnetales, and ginkgos (whom the angiosperms most closely resembled) were decimated, being reduced to small relict groups disjunct in distribution. Ferns were also reduced in abundance, though not so completely as the other groups (Lidgard and Crane 1988). Angiosperms spread from herbaceous forms living in disturbed banks and coastal plains in the low latitudes, to riparian shrubs and trees, and eventually to canopy trees in mid-latitude climax communities during this period (Retallack 1986). Conifers maintained their diversity and abundance, mostly through dominance in high-latitude communities and well-drained inland soils (Retallack 1986). The Cheriolepidaceae declined in the tropical regions, while Taxodiaceae and Pinaceae increased in the temperate belt (Saward 1992).

In much of North America, an open woodland habitat predominated during the Late Cretaceous (Upchurch and Wolfe 1987). The landscape was mostly dominated by conifer or ginkgo trees and shorter ferns and treeferns. However, conditions varied locally, providing much variation in habitat and vegetation. By the Cenomanian, canopied and multistratal forests occurred locally. Open dry areas were colonized by Schizaceae and Glecheniaceae ferns less than 2 m tall, while swampy environments with tall conifers and an understory of ferns were not uncommon (LaPashe and Miller

1984). Wetlands often were still dominated by horsetails and club mosses (Upchurch and Wolfe 1987).

Fauna.—The Cretaceous saw the first appearance of several insect groups including butterflies (Lepidoptera), aphids (Homoptera/Aphidoidea), short-horned grasshoppers (Orthoptera/Acridoidea), and gall wasps (Hymenoptera/Cynipidae). Termites (Isoptera), ants (Formicidae), and eusocial bees appear in the Late Cretaceous (Beherensmeyer et al. 1992). The radiation of many of these taxa may be linked to the radiation of angiosperms occuring around the same time through coevolutionary processes (Scott et al. 1992). However, Labandeira and Sepkoski (1993) asserted that any increase in insect diversity linked to flowering plants occurred at the genus or species level. While these groups may have been new at this point in time, insect pollination and dispersal were not. Insect pollination is thought to date back to the Carboniferous and occurred in many plants including Bennettitales, Gnetales, and cycads, while animal facilitated dispersal occurred as early as the Late Permian in conifers, pteridosperms, Bennetitales, Gnetales, and cycads (Beherensmeyer et al. 1992).

By the Early Cretaceous the large sauropods and armored stegosaurs that had been so prevalent in Jurassic faunas declined in North America. The ornithopods, especially iguanodonts and particularly hadrosaurs, radiated and diversified during the Cretaceous, increasing in dental complexity for grinding vegetation and dominating the fauna (Wing and Tiffney 1987). Heavily armored ankylosaurs became somewhat more prevalent. In addition, ceratopsians made their first appearance in the Early Cretaceous and one group, the Neoceratopsia, radiated in the Late Cretaceous. Similarly, pachycephalosaurs appeared in the Early Createaceous and became somewhat more diverse and abundant over time. Overall, however, they remained a relatively minor component of the fauna. Ornithomimids, dromeosaurs, and tyrannosaurs also diversified, preying upon the abundant herbivorous forms, though the ornithomimids may have been partly herbivorous.

Multituberculate mammals dominated the small herbivore/omnivore guild, radiating into a variety of forms during this period (Kielan-Jaworowska et al. in press). The dentition of many multituberculates trended toward a form suited for seed and fruit eating in the Late Cretaceous and Paleocene (Wing and Tiffney 1987). Two primitive mammalian groups, triconodonts (which were insectivorous to carnivorous depending on their size) and symmetrodonts (probably insectivorous), dwindled. Marsupials and eutherians made their first appearance, eutherians in the Early Cretaceous and marsupials in the mid-Cretaceous. Marsupials increased in abundance in North America during the Late Cretaceous, while eutherians remained relatively rare and in fact disappear from the record until the Campanian (Kielan-Jaworowska et al. in press).

Local geography.—This study focuses on the vertebrate fauna of the upper Cedar Mountain Formation in central Utah. This geologic unit extends from the Wyoming-Utah state line in the north, to the Henry Mountains in the south, and the Sanpete-Sevier Valley in the west. To the east, the Cedar Mountain Formation grades into the Burro Canyon Formation around the Utah-Colorado border (Tschudy et al. 1984). The formation is well exposed along the San Rafael Swell, a large anticline 18 by 46 km in size, located in Emery County, Utah (Stokes 1987). Consequently, much work has focused in this area. At the time of deposition, Emery County was positioned along the eastern edge of the Wasatch Line. The Sevier Orogeny was causing uplift to the west, while the foreland basin to the east was subsiding, providing accommodation space necessary for deposition of sediments. East of the line the terrain was mostly flat, with many rivers draining the uplifted mountains to the west (Stokes 1987), providing the sediment. Paleocurrent data (Currie 1998), as well as the geometry of the formation, supports a transport direction northeastward. During the mid-Cretaceous, seas were in a generally transgressive phase but the region around Emery County was west of the shore at the time of deposition (Elder and Kirkland 1993; Fig. 3).

Geology.—The Cedar Mountain Formation was deposited in eastern and central Utah during the early and mid-Cretaceous. It lies between the Brushy Basin Member of the Morrison Formation (below) and the Dakota Formation (above). Initially, the Cedar Mountain Formation was described as consisting of two members, the lower Buckhorn Conglomerate and an upper unnamed shale (Stokes 1944, 1952). The Buckhorn Conglomerate is composed of chert pebbles and has been variously interpreted as representing a winnowed sheet flood (Stokes 1944, 1952) to a Valanginian braided fluvial deposit (Currie 1998) to a Barremian high energy system (Kirkland et al. 1997). This member is thickest in the west and pinches out in the east, being absent in much of the area in which the formation outcrops. The shale member has been recently studied and divided into four members by Kirkland et al. (1997). The two lowest members are present only in the east (Fig. 4). The Yellow Cat Member is thought to be Barremian in age, possibly contemporary with the Buckhorn Conglomerate in the west. It is composed of mudstone with calcareous nodules, interbedded with sandstone, representing a regional floodplain in a semi-arid environment. Above this lies the Poison Strip Member, a fine- to medium-grained sandstone with chert pebbles, representing a meandering river of presumed Aptian-Albian age. The Ruby Ranch Member overlies the Buckhorn Conglomerate in the west and the Poison Strip Sandstone in the east. The Ruby Ranch Member is primarily composed of drab mudstones (paleosols) with abundant carbonaceous nodules and ribbon channel sandstones. Calcareous nodules suggest a semi-arid, monsoonal environment during the Albian. The youngest member, the late Albian to early Cenomanian Mussentuchit, is the focus of my study. Present only in the west, it thins toward the east. Also composed of mudstone, this member lacks caliche nodules and is highly smectitic. The environment was wetter than during the deposition of previous members and vulcanism in the southwest contributed ash to the clay.

Young (1960) first used invertebrate faunas and plant macrofossils to date the Mussentuchit Member of the formation as Aptian or Albian. Tschudy et al. (1984) refined this estimation using palynomorphs and dated the upper part of the formation as late Albian. Cifelli et al. (1997) used $^{40}Ar/^{39}Ar$ techniques to analyze an ash layer directly above two of the fossil sites, high in the Mussentuchit Member. An age of $98.39 \pm 0.07$ million years was determined, right at the Cenomanian-Albian (Early-Late Cretaceous) boundary.

Vegetation.—Unfortunately, studies on the vegetation of the Cedar Mountain Formation have been limited. Macrofossils are confined to carbonaceous lenses and palynomorphs are poorly preserved. Angiosperm dicot woods and conifer woods have been recovered and described (Thayne et al. 1983, 1984, 1985) within 10 m from the overlying Dakota Sandstone, apparently within the Mussentuchit Member. In addition, a comprehensive palynomorph study was performed by Tschudy et al. (1984), also from the upper mudstone member. Taxa found are listed in Table 1. A high proportion (35%) of pollen and spores was not identifiable, but of those identified, nearly one-quarter (24%) was bisaccate conifer pollen and one quarter (26%) was tricolpate angiosperm pollen. Another 17% was undifferentiated monosulcate pollen (primitive angiosperms and gymnosperms), 12% trilete spores (Pteridophytes), 11% Corollina (a large conifer), 6% Taxodiaceaepollenites (conifer), and 4% Liliacidites (monocot). Conifers dominated in abundance (41%), followed by angiosperms (30%) and ferns (12%), with 17% being a mixture of angiosperms and gymnosperms. While ferns may have been less abundant they were diverse; 28 species of Pteridophytes, 17 species of gymnosperms, and 16 species of angiosperms were found in the pollen analysis.

Mussentuchit local fauna.—The vertebrate remains recovered from the Mussentuchit Member of the Cedar Mountain formation have been extensively studied by many workers over the past 10 years, and the fauna is summarized in Cifelli et al. 1999. The fauna is diverse and includes various cartilagenous fish, bony fish, salamanders, frogs, turtles, lizards, crocodiles, dinosaurs, birds, and mammals. The functional morphology of many taxonomic groups has been well studied, and this immense body of work provides insight into the biology of many of the vertebrates found in this member.

Chondrichthyan morphology and biology is summarized in Welton and Farish (1993), Cappetta (1987), and Compagno (1990). The evolution, morphology, and biology of fish in general is discussed in Carroll (1988) and Maisey (1996). The following summary draws from these sources. Cappetta (1987) described five main tooth morphologies, reflecting diet or feeding strategies: clutching (three blunted cusps), tearing (one elongated main cusp with or without lateral cusps), cutting (broad triangle with serrations), crushing (massive and blunt), and grinding (hexagonal batteries). His study provides a basis for inferring diet in extinct sharks. Distinct tearing, cutting and grinding morphologies are absent in the Mussentuchit fauna, but clutching and crushing morphologies, grading into other morphologies, are represented in multiple taxa.

The sharks of the Mussentuchit fauna fall into two evolutionary grades, hybodonts and neoselachians. Two families of primitive (hybodont) sharks are represented: Hybodontidae and Polyacrodontidae. Freshwater hybodonts were tiny in general, with one of the few fully preserved specimens attaining an adult length of only 15 cm (Maisey 1996). The Hybodontidae are represented by one genus, Hybodus. Hybodus had a clutching dentition in a subterminal mouth. The Polyacrodontidae are the most abundant chondrichthyan family in the fauna, with two genera: Lissodus and Polyacrodus. Both genera had crushing teeth probably used for crushing molluscs or crustaceans (Capetta 1987). Modern elasmobranchs (neoselachians) are represented by five families, all more or less bottom-dwellers. All five families have extant members with morphologies and presumably ecologies that have changed little over the last 100 million years. Myliobatoidea (eagle rays) are common at some sites. Extant eagle rays are large (1 m or more in diameter), pelagic animals, with durophagous teeth for feeding on molluscs. Rhinobatoidea (guitarfish) are primitive rays found in tropical to subtropical seas or freshwater today. They are bottom-dwellers, as reflected in their dorso-ventrally flattened bodies (1-2 m in length) and enlarged pectoral fins. Their teeth are bulbous and used for crushing the small crustaceans and molluscs upon which they feed (Compagno 1990). Similarly, the Squatinidae (angel sharks) are small- to medium-sized (1-2.5 m), dorso-ventrally flattened sharks with enlarged pectoral fins. Their teeth are triangular to cone-shaped (cutting to crushing), adapted for eating invertebrates and fish (Compagno 1990). The Sclerorhynchidae (extinct sawfish) are another group of bottom-dwelling sharks with unique morphologies and habits. The elongated rostrum is edged with pointed teeth, which are sometimes used in extant sawfish (Pristidae) to slash through schools of fish. Stunned or injured individuals are then consumed. Alternatively, the rostrum can be used to probe and sift through the sandy bottom for molluscs or crustaceans, that are crushed with durophagous teeth in the jaw (Compagno 1990). The Orectolobididae (nurse sharks, wobbegongs) are only slightly flattened but spend much time sitting on the substrate. They are able to swim well in the water column. Their teeth have a blunted, tricuspid form, better adapted for holding or clutching than tearing as in most sharks, and they too feed on crustaceans and molluscs (Compagno 1990).

Bony fish are represented by five families of actinoptergygians (of two grades) and one dipnoan specimen. The most numerous taxon in the Cedar Mountain Formation is the Lepisosteidae, represented by scales and teeth. Lepisosteidae (gars) are a holostean group that first appeared in the Cretaceous. Their bodies are covered in heavy, durable ganoid scales, which accounts for the abundance of remains. Extant gars are elongate ambush predators that live in shallow, weedy freshwater and brackish habitats (Carroll 1988).

The Semionotidae are an extinct group of holostean fish ranging from the Late Permian to the mid-Cretaceous. Semionotidae had fusiform bodies with heavy ganoid scales (Maisey 1996). Their body form suggests that they were active swimmers.

Pycnodontidae range from the Late Triassic to the Early Tertiary. They too had heavy scales, but their bodies were deep and laterally compressed, resulting in a form adapted for maneuverability (Maisey 1996). Many modern reef fish possess this body form, which gives them the maneuverability to pluck food from the coral. The dentition of pycnodonts was durophagous, and they possibly feed on crustaceans or molluscs (Carroll 1988).

Amiidae are an extant group that appeared in the Early Triassic. They are typically placed in the holostean grade, but are considered closely related to teleosts (Carroll 1988). Today they are restricted to sluggish, clear freshwater systems rich in vegetation, but they were much more wide ranging in the past (Grande and Bemis 1998). Adults and larger juveniles feed mainly on fish, but small juveniles feed on insects and microcrustaceans.

Enchodontidae are an extinct family of teleosts with fusiform bodies, large heads, and elongate teeth, apparently adapted for eating small fish (Dixon et al. 1988). Although teleosts appeared in the Late Triassic, they did not undergo significant diversification until the mid-Cretaceous, then again in the Late Cretaceous with the radiation of the Perciiformes (Dixon et al. 1988).

Given their small size, amphibians are particularly well represented in the Mussentuchit local fauna, which includes five families of salamanders (or salamander-like taxa) and two grades of frogs. The biology and ecology of modern amphibians is reviewed thoroughly in Duellman and Trueb (1986), Stebbins and Cohen (1995), and Zug (1993). The following summary follows these sources. Except for their planktivorous tadpoles, amphibians feed overwhelmingly on invertebrates, although some salamanders are known also to eat plant or fungal material at times. Several species are also know to scavenge, eating detritus or rotting animals. All require moist conditions, at least to lay their eggs. Extant salamanders prefer cool temperatures and, consequently, are mainly a temperate group. Most are small, less than 15 cm long, but one aquatic form reaches lengths over 1.5 m. They are primarily nocturnal and range in habits from being fully aquatic to fully terrestrial, living under rocks, rotting logs, or leaf litter. Most are opportunistic feeders, eating whatever is abundant, usually insects and annelids for terrestrial species and crustaceans and fish for aquatic species.

Of the five families present in the Cedar Mountain Formation, three were fully aquatic. Sirenoidea are an extant group of fully aquatic, eel-like forms which lack hind limbs and retain gills as adults. Prosirenidae also were elongate, suggesting an aquatic lifestyle. Scapherpetontidae are represented by two taxa, Lisserpeton and Piceroeton. This group was paedomorphic and thus also fully aquatic (Cifelli et al. 1999).

The extant Salamandridae are diverse in size, shape, and habits, but all have well developed limbs so a more terrestrial niche is open to this group. Albanerpetontidae are an extinct family represented in the Cedar Mountain fauna by two taxa, divergent in size (Cifelli et al. 1999; Gardner 1999a). Albanerpetontidae were generally small with well-developed limbs and tough skin. The placement of the group within or as a sister group to salamanders is currently being debated (summarized in Gardner 1999b; McCord 1999). Albanerpetontidae were probably highly terrestrial (McGowan and Evans 1995), possibly burrowing (Gardner 1999c) amphibians that are presumed to have fed on active or tough prey (Gardner 1999c; McCord 1999).

Frogs are the most successful amphibian group today, generally ranging in size from 1 cm to 20 cm in body length (although a few species are bigger still). While tied to moisture for reproduction, they occupy a variety of habitats. Most are semi-aquatic, living in or near permanent water sources. Some live in leaf litter and many, especially in the tropics, are arboreal. Most frogs are generalist nocturnal insectivores (Duellman 1990) found in greatest abundance and diversity in the tropics.

Three turtle families are present in the Mussentuchit local fauna: Glyptopsidae, Pleurosternidae, and Trionychidae. Extant softshell turtles (Trionychidae) are aquatic ambush predators. They sit at the bottom of muddy rivers or lakes and eat insects, crustaceans, molluscs, amphibians, and fish. They also eat vegetation on occasion (Ernst and Barbour 1989). Hutchison and Archibald (1986) suggested that the

Baenidae, within which glyptopsids are sometimes included, were also fully aquatic bottom-dwellers and preferred stream habitats, based on their shell morphology and occurrence as fossils in sandstone channels. One intact shell measured 30 × 35 cm (Gaffney 1979), a bit larger than the cooters or sliders found in North American ponds today.

Crocodilians are represented by five families classified on the basis of tooth morphology: Teleosauridae, Pholidosauridae, Goniopholodidae, Atoposauridae, and Bernissartiidae. All range from the Late Jurassic to Late Cretaceous in age (Carroll 1988). Tooth morphologies and feeding guilds of marine reptiles were examined by Massare (1987). She identified a variety of reptilian tooth morphologies and correlated them with evidence of diet to establish seven feeding guilds: crush (feeding on molluscs), crunch (armored fish and crustaceans), smash (soft molluscs), pierce (fish), cut (large vertebrates), and general. Pomes (1988) followed her work in his interpretation of the diet of the crocodilies found in the Mussentuchit Member, which Hilliard (2000) has since updated.

Hilliard showed that many modern crocodilians are heterodont and use different regions of the jaw for different purposes. Most are opportunistic feeders and will eat whatever they can catch and overcome, with juveniles eating insects, crustaceans, molluscs, and fish. As crocodiles mature and grow, vertebrates of increasing size are taken. There are some specialists however, like the gavial which feeds primarily on fish. Hilliard (2000) also demonstrates that tooth morphologies were more diverse in the Cedar Mountain Formation than they are today, particularly the crushing tooth type.

Teleosaurs were a primarily marine group, probably fully aquatic (or nearly so) (Neill 1971). Individuals were large, attaining lengths up to 3 m (Dixon et al. 1988). Forelimbs were short and the tail laterally compressed for swimming (Carroll 1988). The snout was elongate with long, slender teeth, presumably for catching slippery fish or squid (Neill 1971). Pomes (1988) suggested that adults traveled up rivers to lay eggs and that the few teeth that have been found are tiny, probably representing juveniles.

Pholidosaurs had a long snout, but their dentition was generalized (Neill 1971), with long, thin teeth, perhaps allowing them to feed on the unarmored fish. Atoposaurs were small, semi-aquatic crocodiles, a little over 0.3 m in length as adults (Neill 1971). Their small teeth resemble blunted cones, a form within Massare's (1987) crunch guild. They may have fed on armored fish (like gars) or crustaceans. Goniopholidids were large, semi-aquatic forms; all large teeth recovered are from this group. Teeth are shaped like blunted cones adapted for crunching. Bernissartiids were moderately sized (0.6 m, Dixon et al. 1988) semi-aquatic forms with massive, durophagous teeth, similar to the mosasaur teeth Maasare (1987) used to characterize the crush guild. Like the mosasaurs, they may have eaten molluscs.

The lizard fauna of the Mussentuchit Member includes seven genera and five families. In addition, one snake is present. The lizard fauna of the Cedar Mountain Formation is discussed in detail by Nydam (in review [a]). Making any worthwhile deductions about diet or ecology based on teeth can be difficult because lizards are primarily generalized insectivores and because their teeth are generalized. Some notable exceptions occur in this fauna, however.

Primaderma is a new genus in the Monstersauria, a group including Helodermatidae and fossil relatives. Primaderma was a large lizard, slightly larger than the modern Gila monster (Heloderma suspectum; 330 mm average snout-vent length) with a blunt, rounded snout and long, serrated, recurved teeth (Cifelli and Nydam 1995, Nydam 2000). Most likely it included a substantial proportion of vertebrate prey in its diet, as the related and morphologically similar helodermatids do today.

Polyglyphanodontinae are represented by one specimen of Dicothodon. Polyglyphanodontines are a group of primitive teiid lizards, large in body size with massive heads (Nydam 1999). Because they are so distinct in size and morphology from other Teiidae, they are considered separately here. Dicothodon is the second largest lizard in the fauna, much smaller than Primaderma, but significantly larger than the others (Nydam, personal communication May 2000). In Dicothodon the teeth are transversely oriented and laterally expanded with a central ridge.

Another genus, possibly within the Polyglyphanodontinae, is present. Bicuspidon is the most numerous lizard fossil recovered in the Mussentuchit local fauna. The dentition in Bicuspidon is heterodont, with recurved teeth in the front grading into caniniform teeth and finally transverse, bicuspid teeth in the rear (Nydam in review [b]). Furthermore, juveniles apparently undergo an ontogenetic change in tooth form, possibly but not necessarily reflecting a shift in diet. Many nearly complete dentaries were recovered allowing estimates of body size to be calculated (Nydam et al. in prep). Size estimates for the species range from 53 mm to 110 mm snout-vent length (SVL) and 3 to 34 g in mass.

One other genus of Teiidae is present, Harmodontosaurus, as is one genus of Paramacellodidae, Pseudosaurillus. Enough of the dentary was intact in one specimen of Harmodontosaurus to estimate the SVL (102 mm) and mass (27 g). Two other genera of scincomorphs are present, Dimekodontosaurus (Scincoidea) and Bothriagenys (family indet.). Most, if not all of these, were probably insectivorous.

Predatory dinosaurs in the Mussentuchit local fauna include Dromaeosauridae, Troodontidae, Tyrranosauridae, and Oviraptorsauridae. One sauropod, a brachiosaurid, is present. Four families of herbivorous dinosaurs are present: the abundant Hadrosauridae, and the rare Pachycephalosauridae, Nodosauridae, and Ceratopsidae. Size and mass estimates were compiled from Carroll (1988), Dixon et al. (1988), Peczkis (1994), and Weishampel et al. (1990).

Dromaeosaurs were a group of moderate-sized predators, presumably very intelligent based on brain size (Carroll 1988). Typical members were around 2 m long and 40-70 kg in mass, but the genus present in the Cedar Mountain fauna, Ricardoestesia, is described as small (Cifelli et al. 1999). Troodon (Troodontidae) was another large-brained predator, around 1.75 m in length and weighing 10-40 kg. Alectrosaurus is described as a small- to medium-sized member (0.6-0.9 metric tons) of the Tyrannosauridae, a generally large-bodied group of predatory dinosaurs. Tyrannosaurs are characterized as feeding on other, herbivorous, dinosaurs.

The Oviraptorsauridae are group of small, bipedal dinosaurs, about 1.8 m in length and 10-40 kg in mass. Their small edentulous skulls initially were thought to have been used for preying on eggs, as the name suggests. More recently, however, their diet has been considered to be more broad, and similar to the ornithomimids, including insects, small vertebrates, and plant material. Barsbold (1990) suggested that the jaw mechanics and therefore diet differed between the two groups. He proposed that Oviraptoridae were durophagous and fed on molluscs.

Brachiosauridae are a group of gigantic high-browsing dinosaurs that probably used gut processing (gastroliths and fermentation) to process vegetation, presumably cycad fronds. Most had disappeared from North America by the Cretaceous and the Mussentuchit specimens represent the last of the group in this region (Cifelli et al. 1999). The specimens are described as being very small, and probably represented adults of small stature (Cifelli et al. 1999).

In contrast, hadrosaurs were low-level browsers with complex dental batteries for oral processing of vegetation. Many authors postulate that they fed on the low-growing angiosperms (Bakker 1986; Carroll 1988), however the only physical evidence of diet thus far indicated conifers were eaten (Kräusel 1922; Taggart and Cross 1996). Hadrosaurs averaged 9-10 m in length, and 1.0-3.6 metric tons in mass. Eolambia (Hadrosauridae) is the most abundant dinosaur in the fauna, and juveniles are well represented (Cifelli et al. 1999).

Pachycephalosaurs were small herbivorous dinosaurs averaging 2.0-3.5 m in length and 70-100 kg in mass. The most distinguishing feature of this group is the thickened skull. The dentition is comprised of unspecialized, leaf-shaped teeth, used to browse at mid-levels in the vegetation.

Nodosaurs were heavily armored, quadrapedal dinosaurs. The specimens represented in the Mussentuchit Member were small, perhaps 2 m in length and 50 kg in mass. The teeth were also small and leaf shaped in this group. They were used, along with a narrow, horny beak, to pluck and process vegetation (Fastovsky and Weishampel 1996). Their heavily armored body probably limited them to relatively low-level browsing.

Finally, the neoceratopsians were a group of moderately sized herbivores, typically 6 m in length and 7 metric tons in mass, although the taxon found in the Musentuchit local fauna is small, probably somewhere around 3 m in length. Neoceratopsians had a complex battery of cheek teeth and a horny beak for cropping and processing vegetation.

Based on fossil tracks, fossil nesting grounds, and monospecific bone accumulations, both the hadrosaurs and the ceratopsians are thought to have been herding animals. Multiple dromaeosaurs have been recovered around isolated herbivore carcasses (Maxwell and Ostrom 1995) and may have been "pack" hunters.

Little is know of the birds that are found in the Mussentuchit local fauna. Remains are restricted to isolated teeth and identification is limited to the level of "Aves". Avian bones are unlikely to be found because of their fragile, light-weight structure. With only teeth it is impossible to estimate the size, diet, or habits of the birds found here.

Early mammal morphology and ecology are summarized in various chapters in Lillegraven et al. (1979). Mesozoic mammals were insectivorous for the most part, with the largest species possibly including vertebrate prey in their diets. These suppositions are based on morphological similarity with modern insectivorous mammals, as well as their small size combined with homeothermy, which requires high energy foods.

The mammals of the Mussentuchit local fauna include a diverse mix of primitive groups (triconodonts and symmetrodonts), a highly diverse and derived extinct group (multituberculates), and stem members of modern groups (therians of metatherian-eutherian grade, marsupials). The Mussentuchit local fauna supported three species of triconodonts (described in Cifelli and Madsen 1998) and four or more species of symmetrodonts (Cifelli and Madsen 1999). The triconodonts include Astroconodon delicatus, Corviconodon utahensis, and Jugulator amplissimus. Cifelli and Madsen noted that these three taxa differ greatly in size and estimated body masses of 317, 523, and 749 g, respectively. Moreover, they suggested that tricondonts were opportunistic feeders, based on tooth morphology, and that smaller species probably fed on insects while the larger species may have fed on small vertebrates. Slaughter (1969) and Sigogneau-Russell (1995) have suggested that triconodonts were piscivores, based on tooth morphology and association with fish fossils (but see Jenkins and Crompton 1979; Cifelli and Madsen 1998).

The multituberculates were probably the first group of herbivorous mammals, with a unique dentition similar to that of rodents and some extant small herbivorous marsupials (Lillegraven et al. 1979). Jaw and tooth structure of this group has been studied extensively to determine diet; conclusions vary widely. Many authors consider them omnivores (Krause 1982, 1986; Wall and Krause 1992; Gambaryan and Kielan-Jaworowska 1995), while others have proposed granivory or frugivory (Del Tredici 1989; Weishampel and Norman 1989). The multituberculate radiation in the Cretaceous (Clemens and Kielan-Jaworowska 1979) corresponds with the radiation of angiosperms (Ligard and Crane 1988). Because of their high energetic requirements, multituberculates must have feed on fruits and seeds (or other high-energy foods), the very plant parts that were diversifying and becoming more common with the spread of flowering plants, rather than bulk vegetation (Krause 1982).

Multituberculates are the only non-therian mammalian group to survive into the Tertiary, besides the extant monotremes. Multituberculates are the most abundant and diverse mammal group in the Mussentuchit local fauna, with as many as 11 species (Eaton and Cifelli, in review).

Therians are also found in the Mussentuchit local fauna, but except for one marsupial, Kokopellia juddi (Cifelli and de Muizon 1997), they have not yet been formally described. Nevertheless, Cifelli (unpublished data) has tentatively divided the therians into four species of metatherian-eutherian grade and four species of marsupials.

Summary.—The study sites I have analyzed are located in the Cedar Mountain Formation, a body of rock deposited in central Utah about 98 million years ago, during the mid-Cretaceous. At that time eastern North America was close to Europe, the North Atlantic Ocean being young and narrow. A large inland sea covered much of central North America, with Utah being close enough to experience a maritime climate. The climate overall was relatively warm and moderately wet year-round. The timing of deposition coincided with the diversification and spread of flowering plants. The Cedar Mountain sites had a relatively high proportion of angiosperms, probably because the sites represented disturbed habitats along a river. The larger area was still dominated numerically (and probably physiognomically) by gymnosperms.

The vertebrate fauna was diverse and included a variety of large, herbivorous dinosaurs and some large predatory dinosaurs. Mammals and lizards were also abundant and diverse. A variety of crocodiles and fish shared the stream channels and oxbows with turtles, frogs, and salamanders.

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FIGURE 1. Geologic time scale showing eras and periods for Phanerozoic Eon, and epochs and ages for Cretaceous Period. Space scaled with time. Numbers are millions of years before present (Gradstein et al. 1995).

FIGURE 2. Global geography during mid-Cretaceous, 94 Mya. Modified from C. R. Scotese (2000).

FIGURE 3. Regional geography of western United States during mid-Cretaceous, showing epieric sea and mountain ranges.

FIGURE 4. Geology of Cedar Mountain formation. The five members of Cedar Mountain Formation and overlying Dakota Formation indicated in cross-section. Location of sites used in this study shown with arrow. Redrawn from Kirkland et al. (1997).

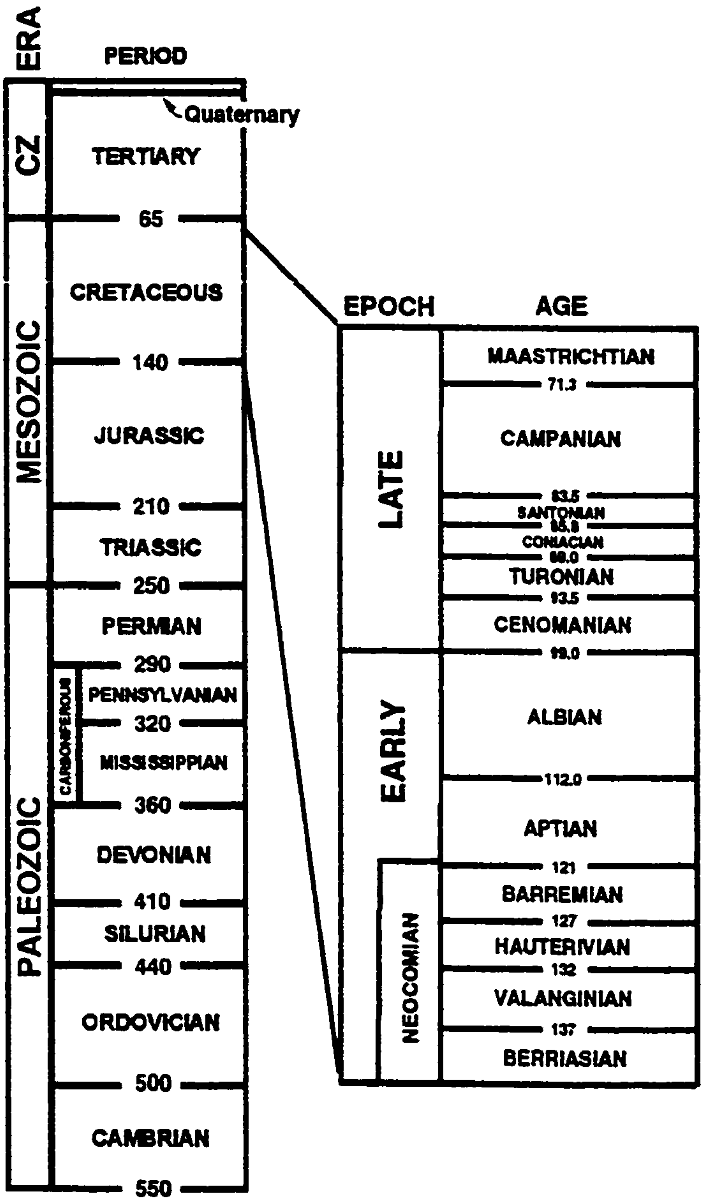
ERA
PERIOD
Quaternary
CZ
TERTIARY
65
MESOZOIC
CRETACEOUS
140
JURASSIC
210
TRIASSIC
250
PALEOZOIC
PERMIAN
290
CARBONIFEROUS
PENNSYLVANIAN
320
MISSISSIPPIAN
360
DEVONIAN
410
SILURIAN
440
ORDOVICIAN
500
CAMBRIAN
550
EPOCH
AGE
LATE
MAASTRICHTIAN
71.3
CAMPANIAN
83.5
SANTONIAN
85.8
CONIACIAN
89.0
TURONIAN
93.5
CENOMANIAN
99.0
EARLY
ALBIAN
112.0
APTIAN
121
NEOCOMIAN
BARREMIAN
127
HAUTERIVIAN
132
VALANGINIAN
137
BERRIASIAN

FIGURE 1

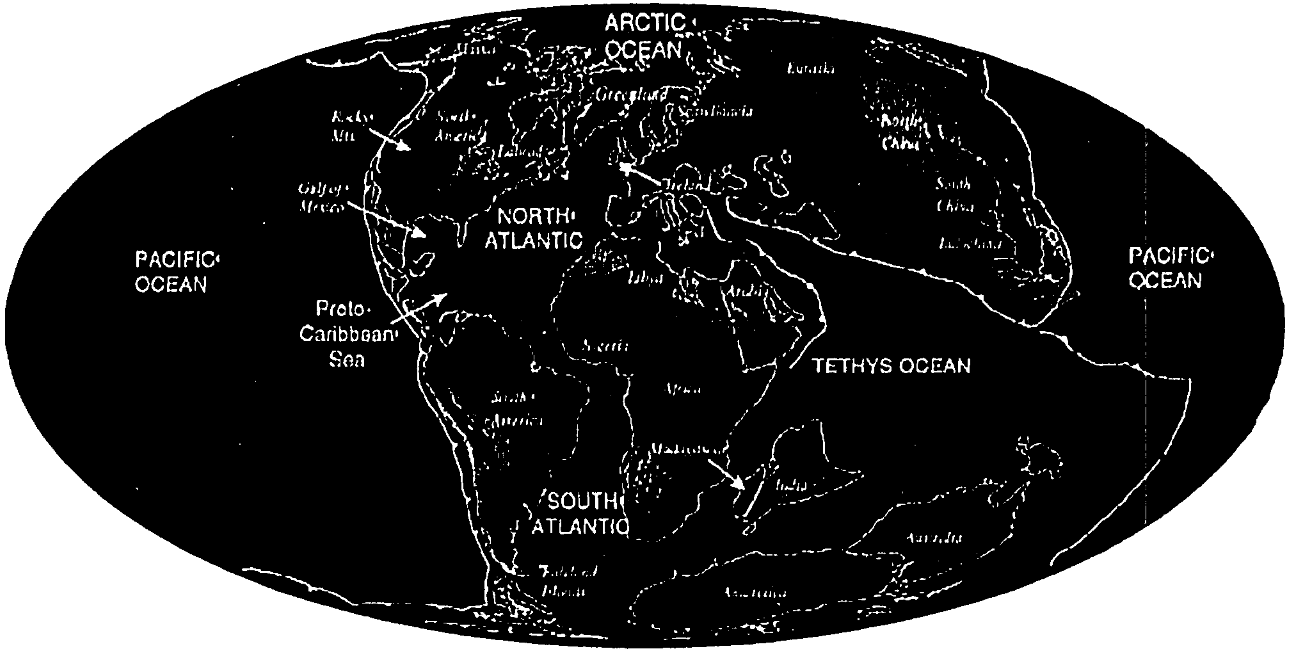

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FIGURE 2

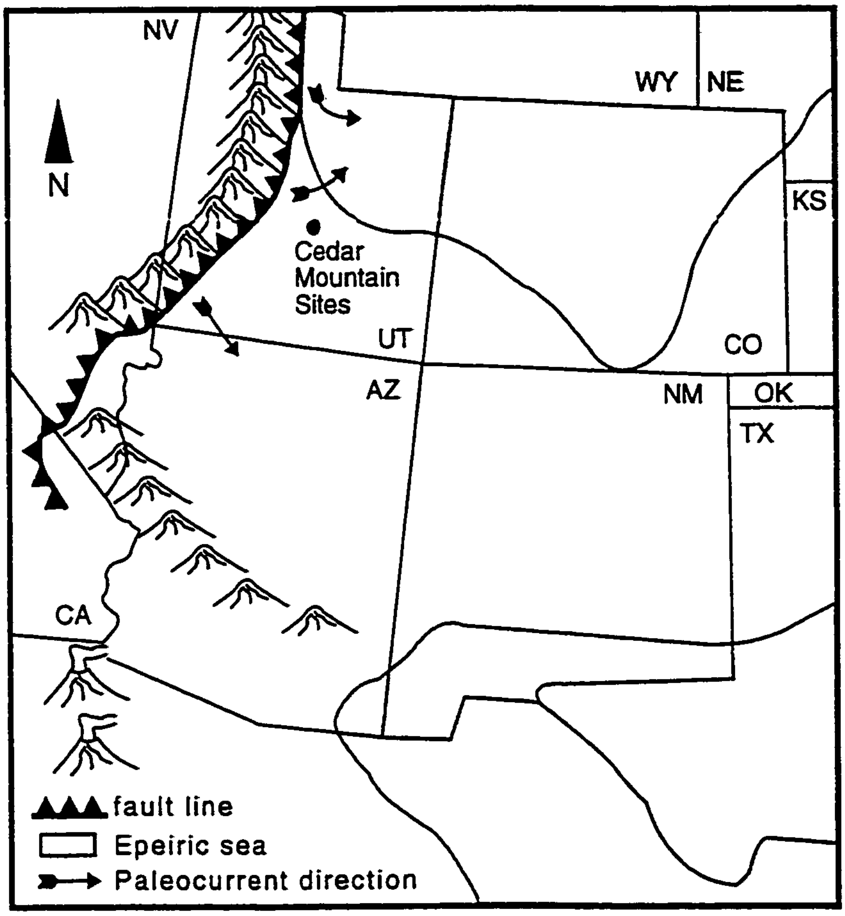
NV
WY
NE
N
KS
Cedar Mountain Sites
UT
CO
AZ
NM
OK
TX
CA
fault line
Epeiric sea
Paleocurrent direction

FIGURE 3

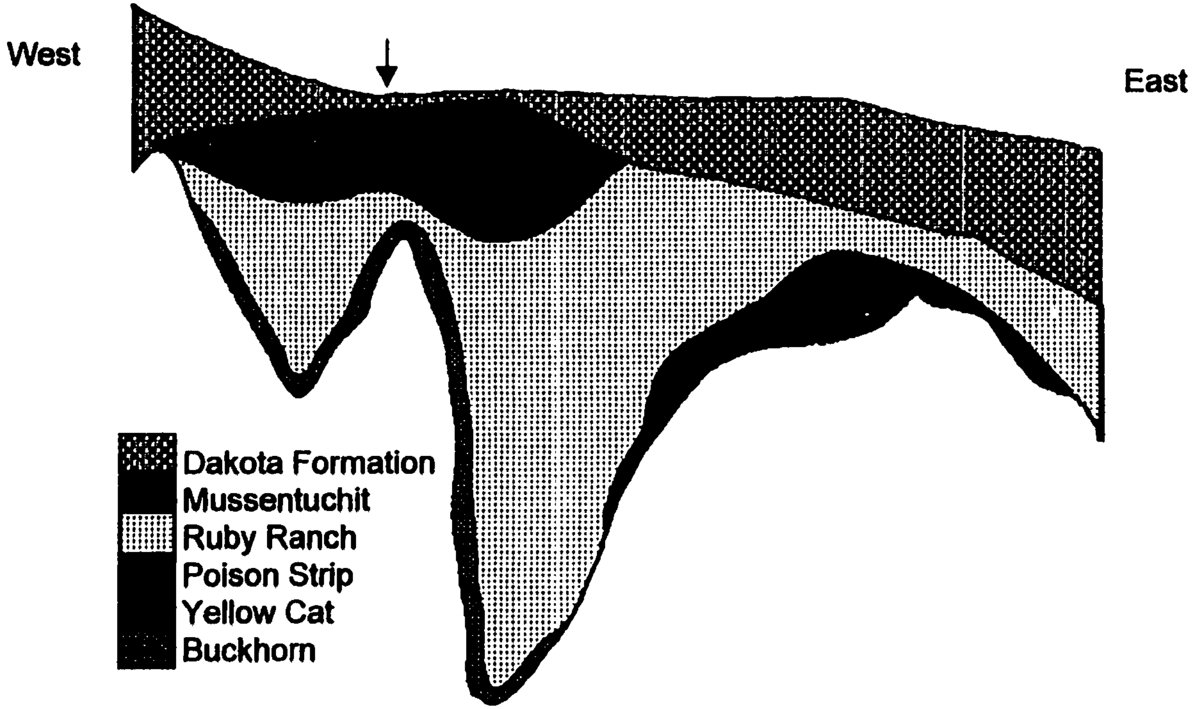
West
East
Dakota Formation
Mussentuchit
Ruby Ranch
Poison Strip
Yellow Cat
Buckhorn

FIGURE 4

TABLE 1. Diversity and abundances of Cedar Mountain palynomorphs, compiled from Tschudy et al. (1984). Diversities (number of species) of various groups indicated on left, with relative abundances of groups on right.

| Diversity | |
|---|---|
| Pteridophytes | 25 species |
| Psalixochlaenaceae (2) | |
| Dicksoniaceae (2) | |
| Osmundaceae (2) | |
| Gleichenaceae (1) | |
| Schizaceae (18) | |
| Gymnosperms | 18 species |
| Pteridosperm (1) | |
| Cycadophyte (3) | |
| Ginkgophyte (2) | |
| Conifer (12) | |
| Angiosperms | 16 species |
| Primitive monosulcate (2) | |
| Monocot (2) | |
| Dicot (12) | |

| Abundance | |
|---|---|
| Conifers | 27% |
| Angiosperm | 20% |
| Pteridophytes | 8% |
| Monosulcate | 11% |
| Unidentified | 34% |

# The effect of taphonomy on ecological patterns and faunal composition of the Mussentuchit local fauna

Patricia Goldberg

RRH: TAPHONOMY AND ECOLOGICAL PATTERNS

LRH: PATRICIA GOLDBERG

Abstract.—The Mussentuchit fauna of the Cedar Mountain Formation in central Utah is a diverse, well-studied assemblage occurring at a poorly represented and ecologically critical period, the medial Cretaceous. Herein, this fauna is examined in an ecological context. Taphonomic effects altering the death assemblage are discussed, and the relative abundances of organisms are corrected using weighted abundance of elements. Differences in preservation potential greatly alter the abundances of taxa present and, consequently, skew ecological patterns. In the Mussentuchit fauna, crocodiles and fish are over-represented, creating the appearance of an abundance of aquatic and semi-aquatic predators. Once corrected, the microterrestrial community is seen as being well-represented, particularly the herbivorous-omnivorous multituberculates.

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## Introduction

Ecological interactions and characterizations arguably have been among the most intensely studied topics in biology over the past 50 years. The application of general principles of ecology, such as trophic structure, body size patterns, and habitat partitioning, to fossil asemblages has largely been confined to Cenozoic faunas. Herein, I examine ecological patterns in a Mesozoic fauna from a little known time period (Albian-Cenomanian, Cretaceous).

Ecology is critical in understanding the causal forces behind large-scale phenomena such as evolution and biogeography. Unfortunately, it is one of the most difficult topics to interpret from the fossil record. Soft anatomy, physiology, and behavior are not typically preserved, but can sometimes be inferred. Organisms tend to be similar for one of two reasons: similar history (relatedness) or similar lifestyles (convergence). Where known, the ecology of closely related, extant taxa can be used as a model for extinct groups. In addition, the morphology of extinct taxa can be compared with extant taxa of similar form, and function inferred through analogy. Comparisons, however, become increasingly difficult as one reaches farther back in time.

The ecological interpretation of fossil assemblages is confounded by the physical processes that lead to the deposition and preservation of remains. Alterations in composition may occur at every stage in preservation, in addition to spatial and temporal averaging (Beherensmeyer et al. 1992). Individuals may be transported away from the death site, or subjected to scavenging, trampling, and other destructive processes (Behrensmeyer 1978; Beherensmeyer et al. 1979).

Elements typically become separated and scattered. Different taxa have different numbers of elements in their skeletons, and individuals with more hard parts will have a better chance of being preserved in the fossil record. Individual elements vary in hardness, size, durability, and, therefore, differ in preservation rate. Smaller elements, mostly representing smaller species, are more easily destroyed and, hence, underrepresented in the preserved assemblage. However, the sites used in this study were chosen for their abundance of small remains and hence are biased toward small species. Finally, some parts of some species are more easily identified than others, altering further the relative abundances of the taxa as represented in a collection database. Once recognized, however, these biases can be considered and in some cases compensated for when interpreting a fossil assemblage.

Abundances in fossil assemblages often are tabulated using the number of identified specimens (individual teeth or scales) (e.g. Case 1996; Badgley et al. 1998), if abundances are considered at all. In many studies describing faunas, only species lists or presence/absence data are given (e.g. Gangloff 1998; Milner and Evans 1998). Abundances in living communities are tabulated based on individuals. For reasons stated above, fossil abundances do not simply reflect the abundance of individuals, but the number of hard parts and the distinctness of those parts in each individual. A few paleontological studies focusing on ecology convert specimen numbers into minimum number of individuals (MNI; e.g. Breithaupt 1982; Gunnell 1994). Holtzman (1979) compared methods for correcting fossil abundances and determined that the weighted abundance of means (WAE) calculation was best in most situations. This measure can be obtained by dividing the number of identified specimens obtained by the number of recognizable hard parts in that species.

The Cedar Mountain Formation is a well-studied body of rock deposited in the medial Cretaceous in central Utah. The mudstones of the Mussentuchit Member were deposited by a meandering river system (Nelson and Crooks 1987, Pomes 1988, Currie 1990) around 98.39 million years ago (Cifelli et al. 1997). Over the past 10 years crews from the Oklahoma Museum of Natural History have recovered nearly 13,000 fossils representing 48 families from over 30 sites in this member. This fauna was summarized in Cifelli et al. (1999) and a faunal list is provided in Table 1.

The Mussentuchit fauna is a diverse, well-sampled assemblage of vertebrates. Remains are confined stratigraphically, and hence temporally, being deposited in the upper part of a single member. In addition, the remains are confined geographically; sites are all located within a single county. This assemblage thus represents a group of animals that are reasonably interpreted as having lived together and interacted with one another. The goal of this paper is to examine the Mussentuchit fauna from an ecological perspective and examine the effects of taphonomy on faunal composition. The importance of taphonomic processes on ecological patterns is shown by comparing composition based on raw specimen numbers with composition based on corrected numbers. Trophic structure and body size distributions in the fossil assemblage should fit patterns established by modern ecological studies better using corrected numbers.

## Methods

Abundances for each community were corrected using a weighted-abundance-of-elements (WAE) method (Holtzman 1979) to provide a more accurate picture of faunal composition. In this method, the number of specimens belonging to a particular taxon is divided by the number of recognizable elements in that taxon. This reduces biases caused by taxa having different numbers of hard parts and differences in identifiability. The number of identifiable elements was determined by first noting which elements were preserved in the deposit. Many taxa were represented only by teeth (the skeleton deteriorated or was only recognizable at a high taxonomic level), while others were represented by jaws with teeth (where isolated teeth could not be identified to the family level). The number of teeth, tooth-bearing bones, or other identifiable elements for each taxon was determined or estimated through data available in the literature, mainly Carroll (1988).

Comparisons between abundances based on number of specimens and number of individuals were then made for large-scale taxonomic categories (Chondrichthyes, Osteichthyes, Anura, Urodela, Chelonia, Crocodilia, Sauria, Dinosauria, Aves, and Mammalia) using simple frequency histograms. Next, the composition of four different communites (aquatic, semi-aquatic, microterresrial, and macroterrestrial) were compared in the same manner. Animals were categorized as aquatic if they spent all or most of their time submerged in the water (chondrichthyans, osteichthyans, and fully-aquatic salamanders). The semi-aquatic community was defined as the group of taxa that spent significant amounts of time (either daily or over the course of their lifetime) both in the water and on land. This group was comprised of amphibians (except for the fully-aquatic salamanders), chelonians, and crocodilians. The remaining taxa were considered to be terrestrial, and this group was divided into a microterrestrial component, made up of taxa less than 1000 g (lizards and mammals) and a macroterrestrial component, made up of taxa greater than 10,000 g (dinosaurs). Birds were not included, since data on their diet and habits were not available.

Additionally, the fauna was characterized based on the diet of the component members. Taxa were characterized as herbivores (ornithischian and brachiosaurid dinosaurs, Polyglyphanodontinae, and multituberculate mammals), omnivores (turtles), faunivores-invertebrates (chondrichthyans excepting Sclerorhynchidae, Pycnodontidae, anurans, lizards excepting Polyglyphanodontidae and Monstersauria, Bernissartiidae, and mammals excepting multituberculates), indiscriminant faunivores (Sclerorhynchidae and urodeles), and faunivores-vertebrates (bony fish excepting Pycnodontidae, Monstersauria, Aniliidae, crocodilians excepting Bernissartiidae, and theropod dinosaurs). Ecological features used in analyses are given in Table 2.

## Results and Discussion

Differences in composition using raw specimen numbers and corrected WAE numbers with higher level taxonomic categories can be seen in Figure 1. Each taxon is represented in a uniquely disproportionate level in the fauna. While the weighted abundance of elements is a good correction factor for two biases (number of hard parts and distinctness/identifiability of parts), estimates should be considered rough. Some clear and important patterns emerge, however. Fish, particularly bony fish, are over-represented in the fauna, as are crocodiles. Many lizards and salamanders are under-represented because only fragile, intact jaws are recognized. Similarly, mammals, recognizable only by molars, are under-represented. Multituberculates, the most abundant mammals in the sample, have few identifiable teeth and, hence, a relatively low preservation potential. Dinosaurs fall between these two extremes. Differences in the proportion of the fauna each taxon represents using raw numbers versus corrected numbers are provided in Table 2.

### Ecological Groupings

The fauna overall is divided here into four major habitat-preference categories (aquatic, semi-aquatic, microterrestrial, and macroterrestrial) and three major diet types (herbivores, invertebrate feeders, and carnivores), with gradients inbetween. Each of the broad-scale habitats is considered separately.

Aquatic guild.—The aquatic vertebrate guild is made up of six families of chondrichthyans, five families of osteichthyans, and three families of aquatic salamanders. The sharks in the Mussentuchit Member were all bottom dwellers, possessing a clutching/crushing dentition, and most likely ate molluscs or crustaceans rather than fish (Cappetta 1987; Welton and Farish 1993; Compagno 1990). In addition, they all were very small. The hybodontids were very small-bodied as a group and the neoselachians are represented by tiny specimens of small-to medium-bodied groups. The sharks varied somewhat in the presumed extent of flattening of their bodies and the robustness of their teeth. This group was very diverse in the number of species, but lacked the typical fusiform body of piscivorous column-dwellers. Except for the Polyacrodontidae and Myliobatoidea, chondrichythians were very rare elements of the fauna, both before and after correction factors were considered.

The pattern was very different for bony fish. The majority of remains recovered from the Mussentuchit Member belong to Lepisosteidae, but remains of Semionotidae and Amiidae are also very common. Extant species of Lepisosteidae and Amiidae prefer vegetated habitats in slow-moving backwaters (Carroll 1988; Grande and Bemis 1998). Moreover, both groups are able to respire by gulping air from the surface (Helfman et al. 1997). All three families were piscivorous, but differed in body form and presumably hunting methods. The elongated and heavily armored gars are ambush predators (Carroll 1988), impaling prey, while the lighter fusiform Amiidae are more active hunters and gape-and-suck feeders (Grande and Bemis 1998). The heavily armored but fusiform Semionotidae may have followed yet another strategy. Pycnodont fishes are not common numerically. These armored fishes probably fed on molluscs or crustaceans, like the chondrichthyans (Carroll 1988). This family is characterized as being marine, with laterally compressed bodies adapted to reef environments (Maisey 1996), so finding them at the majority of the freshwater Cedar Mountain localities may be notable. Finally, the rare Enchodontidae are an important component of the fauna because they are the only teleosts present and, as such, represent a group of fish with a highly derived and efficient feeding mechanism.

One lungfish toothplate was also recovered. This fossil, along with the abundance of air-gulping Lepisosteidae and Amiidae, suggests that some poorly aerated or ephemeral (in the case of the lungfish) ponds were present. Climate and vegetation reconstructions suggest the area was a warm, moderately dry, open woodland (Upchurch and Wolfe 1987; Wolfe and Upchurch 1987; Upchurch and Wolfe 1993). Seasonal drought or heat would dry up smaller reservoirs of water and might cause others to become oxygen-depleted.

Chondrichthyans and osteichthyans differ greatly in preservation potential. Furthermore, families within the bony fish group also vary greatly in the kinds of parts and number of parts that can be preserved. Except for teeth, shark remains are rare in the fossil record. The shark skeleton remains unossified throughout adulthood and deteriorates rapidly after death. However, teeth are very resistant to destruction, and sharks are prolific producers of teeth. In sharks, teeth may function for only days to weeks before being shed, the duration varying with species and position in the jaw (Maisey 1996). One estimate places the number of teeth shed in a lifetime at 10,000 for a lemon shark (Negaprion brevirostris) and 30,000 for a great white shark (Carcharodon carcharias), but replacement rates are slower in species with crushing dentitions such as those found in this assemblage (Maisey 1996). Moreover, individual shark teeth typically can be identified to a low taxonomic level. Consequently, sharks have the potential to contribute many identifiable remains to the fossil record over the course of their lifetime.

The scales of bony fish fall into three main types - cosmoid, ganoid, and elasmoid (Hildebrand 1988) - of which ganoid (Lepisosteidae, Semionotidae, Pycnodontidae) and elasmoid (Amiidae, Enchodidae) types occur in this fauna. Ganoid scales are covered by very thick layer of enamel (ganoine), while elasmoid scales are covered by a very thin layer of a different type of enamel. As a result ganoid scales, like teeth, preserve very well but elasmoid scales are lost. The number of scales in an individual fish is fixed and fairly conservative within species (Helfman et al. 1997). Scales typically grow as the fish grows and are not shed, but species vary in how easily scales may be lost when abraded. Fossil scales were identified to the family level for Lepisosteidae and Semionotidae, and a typical gar may have 1600 scales on its body. This represents a tremendous input in the fossil record for these groups. In addition to ganoid scales, fish teeth are commonly preserved. Many fish have a very high number of tiny teeth covering their palate and gill arches in addition to larger, marginal teeth in the jaws, which may or may not be replaced (Helfman et al. 1997). A typical Amia skull has over 1350 teeth, not including those on the gill arches. In contrast, lungfish only have up to six sets of toothplates, which are not shed (Carroll 1988). All of these structures are very hard, so preservation potential is good. Like the shark teeth, scales and teeth from bony fish recovered in the Mussentuchit Member are very small in size.

Finally, fully-aquatic salamanders are represented by three rare and localized families. Each family is represented by five or fewer specimens and each is restricted to a single locality. Individual teeth are not distinct enough to place in a family, and identified remains are restricted to marginal tooth-bearing elements (6) and unique vertebrae (15-65) per individual. These elements are large relative to fish teeth and scales, but are less resistant to destruction.

Scaling abundances with the number of elements per individual provides a somewhat different picture of the aquatic guild from that shown by the raw data (Figure

2a). Lepisosteidae are still the most abundant component, but comprise less than 50% of the fauna. Semionotidae and Prosirenidae are moderately abundant, as are Amiidae, Ceratodontidae, Pycnodontidae, and Scapherpetontidae. Polyacrodontidae, Myliobatoidea, and Sirenidae are uncommon, while the Hybodontidae and Rhinobatoidea are rare. Finally, Orectolobididae, Squatinidae, Sclerorhynchidae, and Enchodidae are all very rare. Although this is a very rough estimate, these proportions probably reflect the living community much better than raw numbers of specimens.

Some general patterns about fish assemblages can be outlined based on research in modern stream ecology. Important factors influencing community structure in river systems include flow rate, temperature, and dissolved oxygen. Food webs in streams often originate with detritus which is fed upon by many of the abundant invertebrates (Allan 1995). Horowitz (1979) found that an average of 55% of fish species prey primarily on these invertebrates. Another 16% are mainly piscivores and only 10% of fish species are herbivores or detritivores. Fish guilds are characterized not only by the food eaten, but also by the foraging position in the water column and the foraging strategy (Allan 1995).

Aquatic herbivorous vertebrates were absent in this assemblage and are relatively rare in modern aquatic ecosystems. Individuals in this assemblage are all small, and perhaps the channels they lived in were small and unable to support larger fish. As with any species, juveniles would be much more abundant and suffer higher mortality than full-grown adults, so these specimens may also represent young fish.

Overall, the aquatic component of the Mussentuchit fauna was fairly diverse with guilds largely following taxonomic lines. The ray-finned fishes were small, column-dwelling piscivores, except for Pycnodontidae, varying in feeding strategy. The chondrichthyans were small, bottom-dwelling invertebrate feeders, except for the Sclerorhynchidae, varying slightly in body form. The aquatic salamanders were probably generalists, feeding on either invertebrates or small vertebrates (such as tadpoles and little fish), whichever happened to be available (Duellman and Trueb 1986; Stebbins and Cohen 1995).

Semi-aquatic guild.— The semi-aquatic guild is represented by two families of semi-aquatic salamanders, two grades of frogs, three families of turtles, and five families of crocodilians. One of the families of terrestrial salamanders, Salamandridae, is represented by a single specimen while members of the other, Albanerpetontidae, are moderately abundant, being the most common of the five salamander families in the Mussentuchit local fauna. Frogs are the most common amphibians, though still not abundant compared to other groups. Similarly, turtles are moderately represented by three families: Glyptopsidae, Trionychidae, and Pleurosternidae.

The semi-aquatic community is dominated numerically by crocodilians. The marine Teleosauridae are rarest, represented by only 11 teeth, followed by Pholidosauridae, which are only moderately abundant. Atoposauridae, Goniopholididae, and Bernissartiidae were all very common. Together they represent the vast majority of recovered remains at many localities, around the same abundances of Lepisosteidae.

Most of the crocodile teeth are tiny, and the few large teeth found belong to Goniopholididae.

As discussed previously, the paucity of salamander remains is explained by the rarity and fragility of the elements required for identification: toothed jaws or vertebrae. Consequently, few salamanders became fossilized. Frogs are represented by individual elements and fragments. Their skeletons are made up of 45 larger, recognizable elements and many smaller elements that typically are not recovered. Many of the frog bones in the Mussentuchit Member have a slightly ornamented appearance, allowing even fragments to be identified as "frog," although classification rarely extends beyond this point. Both salamanders and frogs are represented by moderately sized specimens, since elements rather than individual teeth are preserved and recognized.

Turtles are represented by individual scutes and typical turtles possess 50 scutes between the carapace and plastron. These bony scutes are thick, flattened, interlocking pieces of spongy bone. Like frog bones, they are readily recognizable in a broad sense as "turtle shell". The three families represented in this fauna each have a unique ornamentation pattern on their shell that allows fragments to be identified to the family level. The shell of Naomichelys (Pleurosternidae) is covered with tiny raised bumps and is often described as "pustulate" (Cifelli et al. 1999), while the shell of Glyptops is only slightly bumpy and contains many fine crevasses. Member of Trionychidae have fenestrated shells that are reduced in thickness. Turtle shell fragments are the largest and heaviest specimens recovered from the fauna, except for the rare dinosaur bone, although their flat shape and low density may allow transport.

Although some crocodilian scutes have been recovered, they are not identifiable beyond this broad level. Crocodiles shed identifiable teeth (but for a cautionary note see Hilliard 2000) continuously over the course of their lifetimes. Hilliard (2000), in a summary of the literature, indicated that tooth replacement in crocodiles shifts from once a month to once a year as individuals mature. Each tooth position is probably replaced 50 times, and each individual has approximately 80 tooth positions, totaling on the order of 4000 shed teeth in a lifetime. Therefore, it should come as no surprise that they are well represented in the fossil record.

Scaling abundances based on available hard parts alters the composition dramatically (Fig. 2b). Anurans are the most common element of the community, being twice as abundant as the very common albanerpetontid salamanders and pleurosternid turtles. Bernissartiid, atoposaurid, and goniopholidid crocodiles are moderately common, as are the remaining turtle families, Glyptopsidae and Trionychidae. Salamandrid salamanders and pholidosaurid crocodiles are rare while marine teleosaurid crocodiles are very rare.

Anurans and salamanders probably formed a nocturnal insectivore guild, and both groups were probably opportunistic in their feeding, as are modern members (Duellman and Treub 1986; Stebbins and Cohen 1995). Turtles are also very opportunistic, but are active during the day. Moreover, they feed on larger prey items in addition to vegetation, at least as adults (Ernst and Barbour 1989). Crocodiles were diverse taxonomically, but may have partitioned food only moderately (Neill 1971; Hilliard 2000), with juvenile teleosaurids specializing on fish or insects and small bernissaritiids specializing on crushing invertebrates. Juveniles and small adults (atoposaurids) may have fed on invertebrates, including small vertebrates with increasing size. Pholidosaurids had a dentition that would have allowed them to feed on fish, while the rare large-bodied goniopholidids may have fed on tetrapods.

In summary, most of the members of the semi-aquatic guild probably spent much of their time in the water or adjacent to the water. They were most likely opportunistic in feeding, eating each other, fish, invertebrates, and in turtles possibly vegetation. The body sizes of semi-aquatic organisms seem roughly equivalent with those of modern representatives in salamanders, frogs, and turtles. Crocodile remains, however, belonged mostly to small-bodied adults or juveniles. Few large individuals were present.

Microterrestrial guild.—The microterrestrial vertebrate guild is comprised of two distinct groups, squamates and mammals. Squamates are diverse, represented by at least four families and two other taxonomic groups: Polygyphanodontinae, Teiidae, Paramacellodidae, Monstersauria, Scincidae, and Aniliidae (Nydam in review [a]). Polyglyphanodontinae, Scincidae, and Bothriagenys (family indet.) are rare. Dimekodontosaurus (family indet.) is a little more abundant, with six specimens, while Paramacellodidae and Monstersauria are both moderately abundant, with 16 specimens each. Finally, Teiidae are common lizards, represented by at least two species and 131 specimens. The sole snake, cf. Coniophis (Aniliidae), is rare.

Mammals in general were abundant and widespread. The primitive triconodonts are represented by 61 teeth from three species. One advanced family of the primitive symmetrodont group of mammals is represented by 255 teeth from three species.

Tribotheria are found at all sites with 317 specimens representing four species, although the vast majority of those specimens were not identified beyond "tribotheria." Marsupialia are also moderately diverse with four species, but they are rare (58 specimens). Finally, multituberculates dominated the microvertebrate community, with 852 teeth from as many as 11 species.

Squamates are represented primarily by their jaws (two dentaries, two premaxilla, and two maxilla), except for Bicuspidon. Other elements were generally not preserved or recognized at the family level. Squamates shed their teeth but as a new tooth grows into place, the majority of the old tooth is resorbed, leaving a small, generally nondescript crown (Edmund 1969). Bicuspidon has a unique tooth structure, allowing shed crowns to be identified. Lizard teeth are shed about every six months (Edmund 1969). Small lizards are variable in life expectancy, ranging from less than a year to over a decade. Bicuspidon was heterodont, with 62 teeth in its maxillae and dentaries, 36 of which were of the distinct bicuspid morphology. Moreover, tooth morphology changed ontogenetically, and isolated juvenile teeth may not be recognized (Nydam in review [b]). The number of bicuspid teeth in the jaws is used as a rough estimate of recognizable elements for the species.

Mammals, in contrast, are often described on the basis of isolated cheek teeth, which tend to be distinctive. Mammals vary in the number of teeth in their jaws, but the number is conservative within groups, with total cheek teeth counts of 36 for triconodonts, 40 for symmetrodonts, and 28 for both therians of metatherian – eutherian grade and Marsupialia (Carroll 1988). Multituberculates vary more in the number of teeth, with cheek teeth reduced to a total of 12 in some groups (Carroll 1988). Premolars in symmetrodonts and tribotherians are not as distinctive as in other groups, reducing the number of identifiable elements to 16 (4 molars/jaw) in these groups, when used at the genus level. Similarly, only the 12 molars of multituberculates are distinctive at this level.

Mammals have a higher preservation potential than lizards, based on the number of identifiable elements in the skeleton and the durability of those elements (teeth vs. jaws). However, this difference is minor compared to differences in preservation potential among taxa in other guilds. Both squamates and mammals have a low preservation potential relative to most of the aquatic guild and the semi-aquatic guild. Adjusting abundances increases the dominance of multituberculates from one-half to two-thirds of the fauna (Fig. 2c). Tribotherians are second in abundance (12%), followed by symmetrodonts (7%). These three mammal taxa account for the vast majority of the fauna. Among the lizards, teiids remain most abundant (6%), although their relative importance is greatly diminished after accounting for the fact that they are the only lizard taxa identifiable based on isolated teeth. The second most abundant lizard is also the largest (Monstersauria). This might reflect a preservation bias, since larger organisms, particularly carnivores, tend to have larger ranges and smaller populations than smaller insectivores. Consequently, larger animals are expected to be less abundant than smaller ones in general.

Modern lizard assemblages and guilds have been studied extensively. Many studies have shown that lizard diversity is influenced mainly by habitat complexity and heterogeneity (e.g. Heatwole and Taylor 1987; Pianka 1993; James 1994; Vitt and deCarvalho 1995). Lizards partition niches by space and food, and occasionally by activity period. While some lizards have specialized diets (particularly ants and termites in several groups), most are diurnal generalist insectivores, eating whatever they are able to overpower (Pianka 1993). As a result, larger species eat larger prey on average, but small prey is also taken when available. Food partitioning is thus mainly a consequence of differences in body size, especially among active foragers. Sit-and-wait predators partition resources primarily based on microhabitat, and diet varies as a consequence (Vitt and Caldwell 1994; Vitt 1995).

Pough (1973) demonstrated that herbivory, uncommon in reptiles, is also correlated with size. He found that, except for the carnivorous Helodermatidae and Varanidae, lizards weighing more than 300 g are herbivorous while those less than 50 g are insectivorous. Furthermore, herbivorous lizards are typically insectivorous as small juveniles.

In the Mussentuchit local fauna, the Monstersauria are the largest lizards (around 330 mm estimated snout-vent length [SVL]) followed by Polyglyphanodontinae. The two teiid species overlap in size, averaging over 100 mm SVL as adults (using methods in Nydam et al. in prep). Estimates for body size could not be calculated for the remaining taxa. Although body sizes were estimated for only three of the seven species, there seems to be a variety of sizes, implying a variety in diet and niche partitioning, as expected in a diverse assemblage.

Studies by Legendre (1986, 1989) have characterized the physiognomy of fossil localities based on the structure of the mammal community. Fuentes (1976) found that two taxonomically unrelated extant lizard communities living under similar physiognomic conditions also converged in structure. It would be useful to try to characterize this relationship between lizard community structure and physiognomy further and apply it to Cretaceous faunas, where mammal community structure is distinctly different from today.

The overall small body sizes in both groups and homeothermy in mammals restrict this guild to feeding on high-energy food sources. Both groups evolved and diverisified before the angiosperms with their high-energy fruits, flowers, and seeds. Both were mainly insectivorous at this time (Carroll 1988), with squamates probably active during the day (being small ectotherms) and mammals hunting at night (as most modern analogous mammals do). Interesting deviations from mainstream insectivory occurred in both of these groups, however. In addition to the snake, one other squamate was almost certainly carnivorous (Monstersauria) and one group was probably herbivorous (Polyglyphanodontinae). The two teiids were of a body size that is below what Pough (1973) considered to be the transition zone from insectivory to herbivory. The bicuspid teeth of Bicuspidon and the ontogenetic change that occur in their morphology are consistent with the hypothesis that these animals may have been omnivorous, but their body size was probably too small for herbivory.

Mammals may have also had a carnivorous species in the fauna (Triconodonta: J. amplissimus [Cifelli and Madsen 1996]). Multituberculates made up the majority of species, specimens, and individuals in this community. They were also the most widespread group, occurring at all sites. The diet of this group of mammals has been much debated with some conservatively calling them omnivorous (Krause 1982, 1986; Wall and Krause 1992; Gomburyan and Kielan-Jaworowski 1995) and others arguing that they were granivorous or frugivorous (Del Tredici 1989; Weishampel and Norman 1989). Evidence for herbivory in multituberculates includes jaw and tooth structure (Del Tredici 1989; Weishampel and Norman 1989), an evolutionary radiation concurrent with the radiation and spread of angiosperms (Clemens and Kielan-Jaworowska 1979), and extinction of the group concurrent with the radiation and spread of rodents in the Cenozoic.

Macroterrestrial guild.—The macroterrestrial guild is composed entirely of dinosaurs. Nine families are represented: four carnivorous and five herbivorous. Most of these taxa are rare. Two (Troodontidae and Neoceratopsia) are represented by single specimens and two others (Brachiosauridae and Pachycephalosauridae) by two specimens. Tyrannosauridae are represented by five specimens, all from a single locality. Oviraptoridae specimens are more abundant (but may represent a single individual). They are restricted to macrovertebrate localities because of their lack of teeth. Nodosauridae are modestly represented by six specimens from three sites. Two families, Hadrosauridae and Dromaeosauridae, dominate the fauna. Dromaeosaurids are represented by 108 teeth at seven sites, while 338 hadrosaur teeth were identified at 10 sites.

Most dinosaurs are identified on the basis of isolated teeth, especially at the microvertebrate localities. However, because of their large size and concomitant resistance to destruction, bone is not uncommon, although typically recovered from different sites. Like crocodiles, dinosaurs replaced their teeth. The problem of estimating preservation potentials becomes more difficult in dinosaurs because replacement rates and life expectancies are unknown. Taxa varied in the number of teeth in the jaw as well, and estimates in tooth count were taken from Carroll (1988). Brachiosaurids and pachycephalosaurs had as few as 30 teeth in their skulls at any given time, while nodosaurs and neoceratopsians had around 80. Carnivorous dinosaurs had a number in between (around 60 in dromaeosaurids and 56 in tyrannosaurids). Hadrosaurids produced the most teeth, with complex dental batteries up to five rows deep. Kirkland (1994) estimated that Eolambia, of the Mussentuchit local fauna, had 124 teeth in its jaws.

After scaling abundances to reflect preservation potential (Fig. 2d), hadrosaurids still account for more than half the fauna in the macroterrestrial community. Dromaeosaurs increase in relative abundance, and the other taxa remain very rare. Like the members of the microterrestrial fauna, taxa varied in preservation potential, but not greatly.

Community structure and habitat.—Many of the remains recovered were small, from chondrichthyans, osteichthyans, crocodilians, to many of the dinosaurs, either reflecting a community of small individuals, a collecting bias, a transportational bias, or some other preservational bias. Many of the taxa (most of the chondrichthyans and crocodilians, many of the anurans) are restricted to or most diverse in the tropics today (Compagno 1990; Duellman 1990; Neill 1971). Others, like the salamanders, prefer temperate regions (Duellman and Trueb 1986). During the time of deposition, western North America was warm and subhumid, with little variation in temperature or rainfall over the course of the year. Moreover, there was less latitudinal variation in temperatures (Upchurch and Wolfe 1993). Many species tend to be limited in their distributions by climate, at least on the poleward side of their range (Macarthur 1972). This type of climatic equability may lead to high-diversity communities with a mix of organisms which do not co-occur under other conditions.

### Other Ecological Patterns

Body size. The open woodland habitat present in much of North America (Wolfe and Upchurch 1987) may have promoted a bimodal distribution in organism size, as found by Legendre (1986). This physiognomy favors either small animals that could hide within the brush, eating insects and seeds, or very large organisms that require open space to move, while feeding on either bulk vegetation or on other large animals. The terrestrial Mussentuchit fauna is very clearly divisible into a vertebrate microfauna and megafauna. As environments become more and more closed the number of medium-sized animals increases (Legendre 1986).

Legendre's (1986) work focused on mammals since mammals have come to dominate the terrestrial macrofauna following the extinction of non-avian dinosaurs, and interact with the environment at a macroscopic scale. In the Cretaceous, the terrestrial fauna was divided taxonomically into a microfauna that included mammals and a macrofauna comprised of dinosaurs. Even though these two groups differed in biology, the patterns of body-size distributions between them may still reflect physiognomy, although this has not been studied. Large animals, whether dinosaur or mammal, cannot easily manuever through dense forest. Distributions should become increasingly bimodal as habitat opens.

Legendre (1986) determined "threshold" body sizes and categorized mammals as being small (< 500 g), medium (500 g to 8 kg), and large (> 8 kg). In open woodland and grassland habitats today and in the early Cenozoic, the medium-sized animals are rare. This size category is also poorly represented in the Mussentuchit local fauna, based on the limited information available (Fig. 3). Mammals in the "medium" size range are rare, and even the largest species, such as J. amplissimus, are relatively small (749 g; squirrel-sized). There are no dinosaurs in the medium size category. The smallest dinosaurs, such as Troodon, weighed 10-40 kg (wolf-sized). Very large dinosaurs are absent in this fauna, however. The distinctness of size categories was probably even greater in the Jurassic, when sauropods were common and the climate was drier. Differences in metabolism between mammals and dinosaurs, habits and lifestyles that could be adopted for predator avoidance, and preservational issues all complicate the issue, but the idea may warrant further investigation.

Habitat representation.—The degree to which each community is represented in the fossil record is altered dramatically once abundances are scaled to preservation potential (Fig. 4a). Most of the specimens are from aquatic organisms, mainly fish, followed by semi-aquatic organisms, mainly crocodiles. These are the two groups that produce the most remains per individual. The terrestrial community appears better represented once this is considered. In fact, the microterrestrial community overwhelmingly dominates the fauna when weighted abundance of elements is used as a measure of abundance.

Small organisms tend to have smaller ranges, larger populations, shorter life expectancies, faster reproductive rates, and larger litter sizes relative to large animals (Hickman et al. 1984; Eisenberg 1990). In any given area and period of time one would expect many more remains to accumulate from small animals compared to large animals. Although the sites studied were worked because of the accumulation of small fossils, the teeth of larger animals are small enough to be found in these accumulations. In addition, the correction method counts only the small identifiable teeth from larger animals in preservation potential, so the collection bias against large dinosaurs is accounted for. Even with the size bias prevalent in preservation, with smaller remains destroyed at faster rates, the prolific number of individuals in small species may still be detected.

Trophic structure.—Trophic structure varied among guilds, with herbivores absent in the aquatic and semi-aquatic component. A replacement of insectivores (faunivores-invertebrates) with carnivores (faunivores-vertebrates) occurred between the terrestrial microfauna and macrofauna. Omnivores were rare overall, as they are in most modern systems (Rosenzweig 1995) if one considers multituberculates as herbivores. Herbivores dominated the fauna in overall abundance. However, this is not readily seen unless correction factors for preservation potential are applied (Fig. 4b). Once correction factors were applied the trophic structure approached a realistic pattern with 47%

herbivorous and 3% carnivorous, close to the 10:1 ratio expected between levels (Elton 1927). Omnivores comprised only 1% of the fauna, with the remaining 49% evenly split between invertebrate feeders and small opportunistic feeders that took both invertebrates and small vertebrates. There is a large bias in the fossil record toward vertebrate feeders, mainly crocodilians and fish.

Summary.—Ecological patterns are interpretable only after specimen numbers have been translated into individuals. Correction factors are particularly important when differences in preservational potential among taxa are high, as they are between mammals and fish or crocodiles. Even with all of the taphonomic biases, enough community structure is preserved in the Mussentuchit fauna to find patterns in trophic structure and body size. Thus, in an assemblage that existed 98 million years ago it appears possible to discern meaningful ecological patterns.

### Comparison with a Late Cretaceous fauna

Breithaupt (1982) reviewed the fauna of the Late Cretaceous Lance Formation in Sweetwater County, Wyoming. He collected over 2700 specimens through the processing of 2000 kg of matrix, so his fauna is less completely sampled compared to the 13,000 specimens from 49,000 kg of matrix analyzed here. The Lance Formation, like the Mussentuchit Member, was deposited by a large, lowland river. However, the Lance Formation was closer to the coast and was deposited about 30 my after the Mussentuchit Member. The Mussentuchit fauna is more diverse than the Lancian fauna (see Table 3), but at least some of this is probably due to differences in sampling. The large number of chondrichthyans and crocodilians in the Mussentuchit fauna accounts for much of the difference in the number of families.

Notable appearances in the Late Cretaceous Lance fauna include Sciaenidae (an advanced teleost within the perciformes), Crocodylidae (the modern eusuchian family of modern crocodiles and alligators), and two orders of eutherian mammals, Insectivora and Condylarthra. These groups are absent in the Mussentuchit fauna or any other fauna pre-dating the Late Cretaceous. Conversely, several groups present in the Mussentuchit fauna disappear and are not found in later faunas. These groups include triconodont and symmetrodont mammals, as well as the "therian of metatherian-eutherian grade" grouping of mammals. The distribution of at least two families present in the Lance fauna but absent in the better-sampled Mussentuchit, Acipenseridae (sturgeons) and Champsosauridae (a reptile convergent with gavials), cannot be explained by evolution and extinction. Many modern sturgeons spawn in freshwater, but spend the majority of their time at the mouths of large rivers, or in brackish estuaries or nearshore in the ocean. The Lance fauna was probably closer to the ocean shore at the time of deposition. Champsosaurs from the Lance fauna were similar in morphology and presumably ecology to the teleosaurids found in the Mussentuchit fauna. The presence of one may exclude the other, or teleosaurids may be mis-identified.

The relative abundances of taxa present also varied between the two faunas (Table 3). Using raw specimen numbers, both faunas were dominated by bony fish, the Lance much more so than the Mussentuchit. Crocodiles were nearly as abundant as fish in the Mussentuchit fauna, but were a distant third in abundance in the Lance fauna.

The raw specimen numbers were adjusted differently in the two faunas. In Breithaupt's study of the Lance fauna, specimens were converted to minimum number of individuals (MNI), while weighted abundance of elements (WAE) was used in this study. Both methods had the effect of reducing the dominance of fish and increasing the importance of tetrapods. Urodeles, mammals, and bony fish were nearly equally dominant in abundance in the Lance fauna, while mammals overwhelmingly predominated in the Mussentuchit fauna. Squamates and dinosaurs placed a distant second and third in dominance in the Mussentuchit fauna, suggesting the Mussentuchit fauna represents a more terrestrial grouping of animals than does the Lance material examined by Breithaupt.

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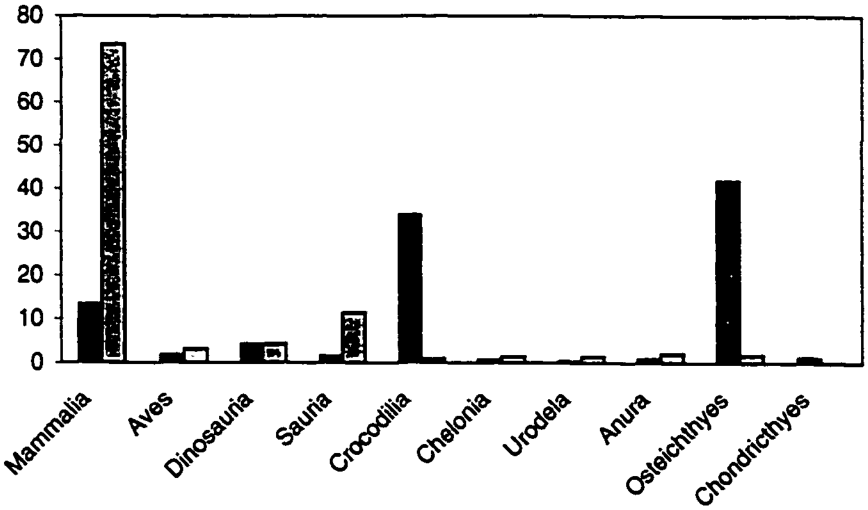
FIGURE 1. Percent abundance of Mussentuchit ubertaxa based on raw specimen numbers (black) and adjusted specimen numbers (WAE, gray).

FIGURE 2. Percent abundances of each family based on raw specimen numbers (black) and adjusted specimen numbers (WAE, gray) for (A) aquatic guild, (B) semi-aquatic guild, (C) microterrestrial guild, and (D) macroterrestrial guild.

FIGURE 3. Body size distributions (percent abundances) for families in the terrestrial guilds of the Mussentuchit local fauna based on raw specimen numbers (black) and adjusted specimen numbers (WAE, gray).

FIGURE 4. Percent abundance of taxa based on (A) habitat and (B) diet using raw specimen numbers (black) and adjusted specimen numbers (WAE, gray).


80
70
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30
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10
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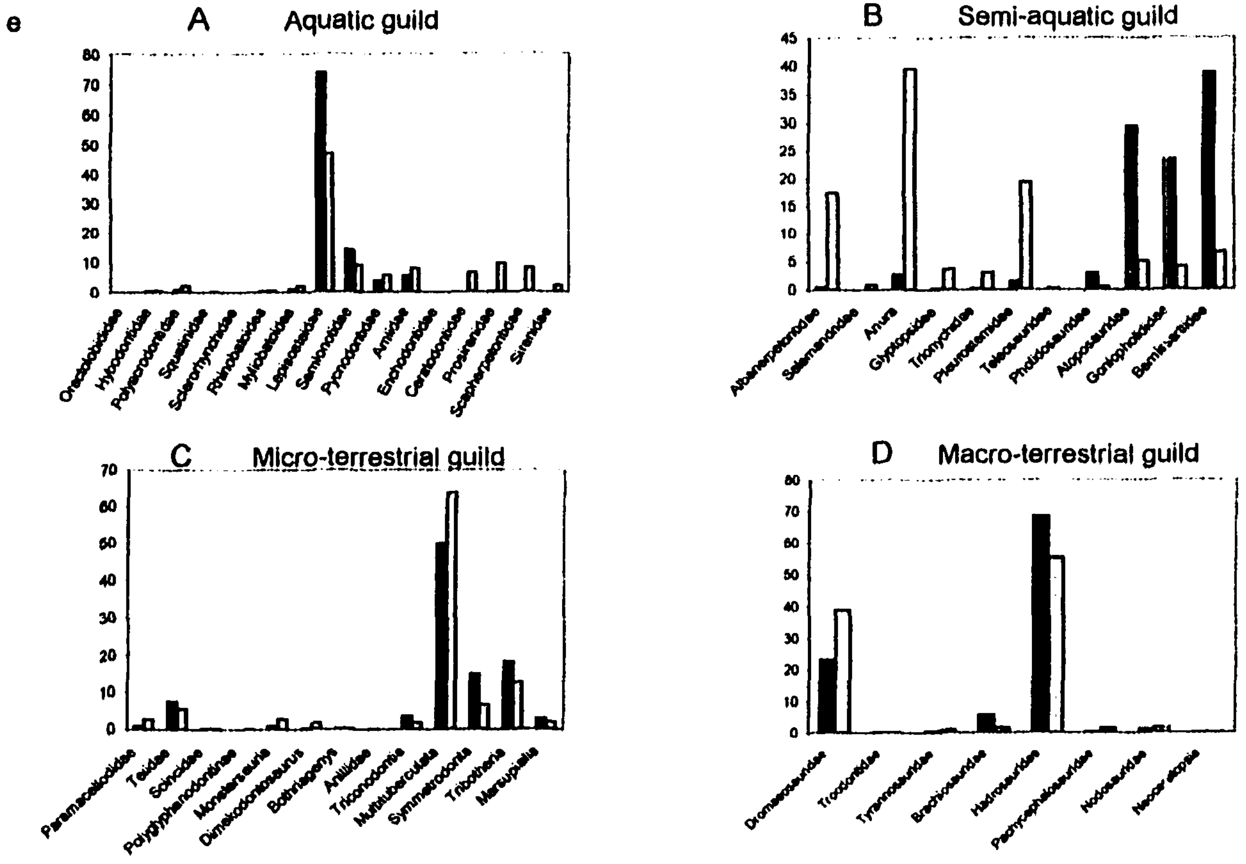
Mammalia
Aves
Dinosauria
Sauria
Crocodilia
Chelonia
Urodela
Anura
Osteichthyes
Chondricthyes

FIGURE 1


e
A Aquatic guild
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50
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10
0
Orectolobidae
Hybodontidae
Polyacrodontidae
Squatinidae
Sclerorhynchidae
Rhinobatoidae
Myliobatoidae
Lepisosteidae
Semionotidae
Pycnodontidae
Amiidae
Enchodontidae
Ceratodontidae
Prosirenidae
Scapherpetontidae
Sirenidae
B Semi-aquatic guild
45
40
35
30
25
20
15
10
5
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Albanerpetontidae
Salamandridae
Anura
Glyptopsidae
Trionychidae
Pleurosternidae
Teleosauridae
Pholidosauridae
Atoposauridae
Goniopholididae
Bernissartidae
C Micro-terrestrial guild
70
60
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30
20
10
0
Paramacellodidae
Teiidae
Scincidae
Polyglyphanodontinae
Monstersauria
Dimekodontosaurus
Bothriagenys
Aniliidae
Triconodontia
Multituberculata
Symmetrodontia
Tribotheria
Marsupialia
D Macro-terrestrial guild
80
70
60
50
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20
10
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Dromaeosauridae
Troodontidae
Tyrannosauridae
Brachiosauridae
Hadrosauridae
Pachycephalosauridae
Nodosauridae
Neoceratopsia

FIGURE 2

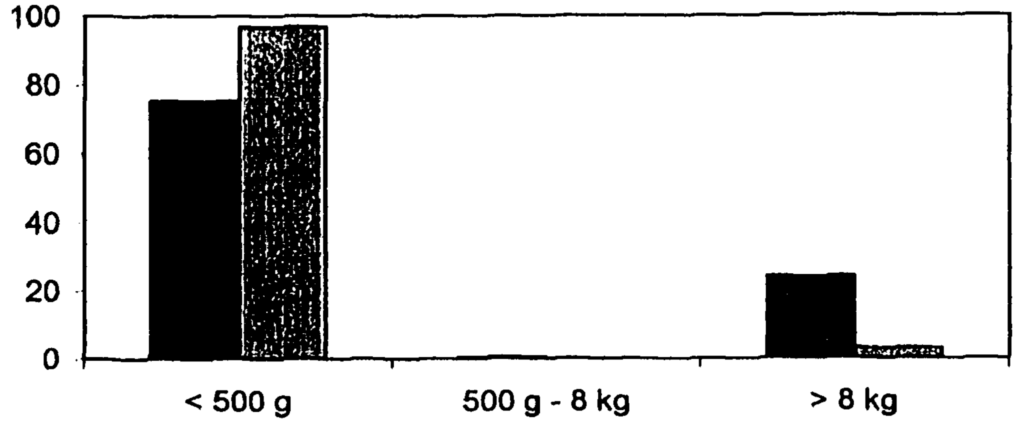
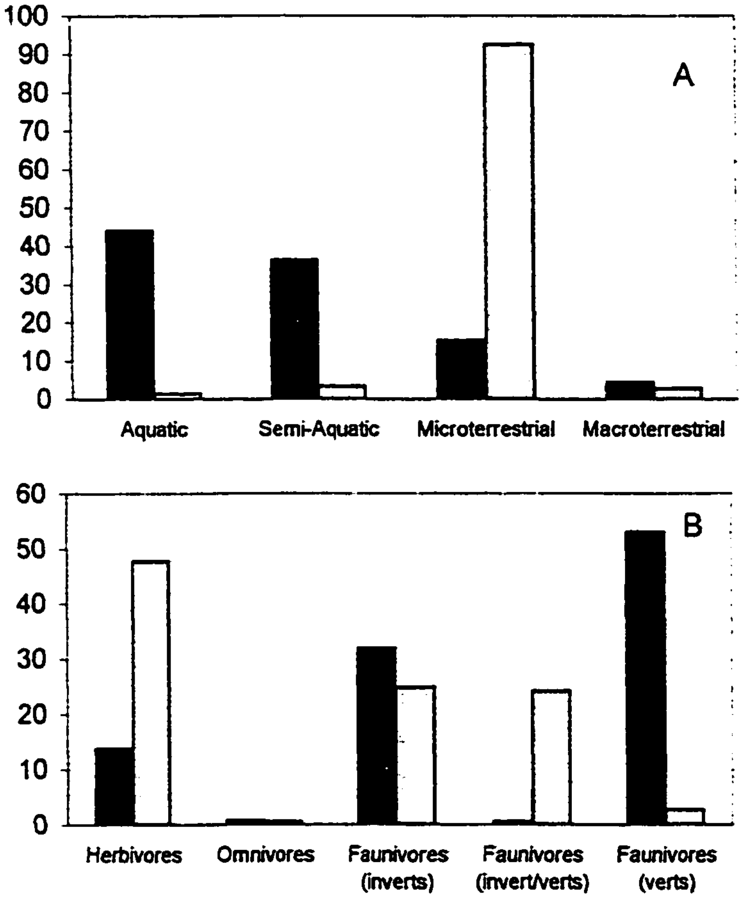


Figure 3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A
Aquatic
Semi-Aquatic
Microterrestrial
Macroterrestrial
60
50
40
30
20
10
0
B
Herbivores
Omnivores
Faunivores (inverts)
Faunivores (invert/verts)
Faunivores (verts)

FIGURE 4

TABLE 1. A list of taxa comprising the Mussentuchit local fauna.

- **Chondrichthyes**
  - Hybodontidae
    - *Hybodus*
  - Polyacrodontidae
    - *Lissodus* sp.
    - *Lissodus anitae*
    - *Polyacrodus parvidens*
  - Orectolobidae
  - Squatinidae
  - Sclerorhynchidae
    - *Ischyrhiza texana*
  - Rhinobatoidea
    - *Pseudohypolophus*
  - Myliobatoidea
- **Osteichthyes**
  - Lepisosteidae
  - Semionotidae
    - *Lepidotes*
  - Pycnodontidae
  - Amiidae
  - Enchodontidae
    - *Enchodus*
  - Ceratodontidae
- **Urodela**
  - Prosirenidae
  - Albanerpetontidae
    - *Albanerpeton*
  - Scapherpetontidae
    - *Lisserpeton*
    - *Picerpeton*
  - Salamandridae
  - Sirenidae
- **Anura**
- **Chelonia**
  - Glyptopsidae (*Glyptops*)
  - Trionychidae
  - Pleurosternidae (*Naomichelys*)

TABLE 1. Continued.

**Squamata**

- Paramacellodidae
  - *Pseudosaurillus* sp.
- Teiidae
  - *Harmodontosaurus emeryensis*
  - *Bicuspidon numerosus*
- Polyglyphanodontidae
  - *Dicothodon moorensis*
- Scincidae
- Monstersauria
  - *Primaderma nessovi*
  - *Dimekodontosaurus madseni* (Family indet.)
  - *Bothriagenys mysterion* (Family indet.)
- Serpentes
  - Aniliidae
    - *Coniophis* sp.

**Crocodylia**

- Teleosauridae
- Pholidosauridae
- Atoposauridae
- Goniopholididae
- Bernissartiidae

**Theropoda**

- Dromaeosauridae
- Troodontidae
  - *Troodon*
- Tyrannosauridae
  - *Alectrosaurus*
- Oviraptoridae

**Sauropoda**

- Brachiosauridae

**Ornithischia**

- Hadrosauridae
  - *Eolambia caroljonesa*
- Pachycephalosauridae
- Nodosauridae
- Neoceratopsia

TABLE I. Continued.

**Aves**

**Mammalia**
- Triconodontidae
  - *Astroconodon delicatus*
  - *Corviconodon utahensis*
  - *Jugulator amplissimus*
- Multituberculata
  - *Janumys erebos*
  - *Paracimexomys perplexus*
  - *Paracimexomys* cf. *perplexus*
  - *Paracimexomys* cf. *robisoni*
  - *Ameribaatar zofiae*
  - *Bryceomys intermedius*
  - *Bryceomys* cf. *intermedius*
  - *Cedaromys bestia*
  - *Cedaromys* cf. *bestia*
  - *Cedaromys parvus*
  - *Cedaromys* cf. *parvus*
- Symmetrodonta (Spalacotheriidae)
  - *Spalacolestes cretulablatta*
  - *Spalacolestes inconcinnus*
  - *Spalacotheridium noblei*
- Tribotheria
  - Picopsidae species A
  - Picopsidae species B
  - Family indet. species A
  - Family indet. species B
- Marsupialia
  - *Kokopellia juddi*
  - Species A
  - Species B
  - Species C

TABLE 2. A summary of ecological features of Mussentuchit families. The difference in relative abundance based on weighted abundance of elements and relative abundance based on raw specimen numbers is given in the second column.

| Taxon | WAE-raw | Habitat-broad | Habitat-narrow | Diet |
|---|---|---|---|---|
| Hybodontidae | -0.12 | aquatic | benthic | faunivores (invert.) |
| Polyacrodontidae | -0.44 | aquatic | benthic | faunivores (invert.) |
| Orectolobididae | -0.01 | aquatic | benthic | faunivores (invert.) |
| Squatinidae | -0.02 | aquatic | benthic | faunivores (invert.) |
| Sclerorhynchidae | -0.01 | aquatic | benthic | faunivores (vert./invert.) |
| Rhinobatoidea | -0.12 | aquatic | benthic | faunivores (invert.) |
| Myliobatoidea | -0.43 | aquatic | benthic | faunivores (invert.) |
| Lepisosteidae | -31.71 | aquatic | column | faunivores (vert.) |
| Semionotidae | -6.11 | aquatic | column | faunivores (vert.) |
| Pycnodontidae | -1.57 | aquatic | column | faunivores (invert.) |

TABLE 2. Continued.

| Taxon | WAE-raw | Habitat-broad | Habitat-narrow | Diet |
|---|---|---|---|---|
| Amiidae | -2.22 | aquatic | column | faunivores (vert.) |
| Enchodontidae | -0.03 | aquatic | column | faunivores (vert.) |
| Ceratodontidae | 0.08 | aquatic | column | faunivores (invert.) |
| Prosirenidae | 0.10 | aquatic | benthic | faunivores (vert./invert.) |
| Albanerpetontidae | 0.40 | semi-aquatic | nocturnal | faunivores (vert./invert.) |
| Scapherpetontidae | 0.08 | aquatic | benthic | faunivores (vert./invert.) |
| Salamandridae | 0.02 | semi-aquatic | nocturnal | faunivores (vert./invert.) |
| Sirenidae | 0.02 | aquatic | benthic | faunivores (vert./invert.) |
| Glyptopsidae | 0.03 | semi-aquatic | | omnivores |
| Trionychidae | 0.02 | semi-aquatic | | omnivores |
| Pleurosternidae | 0.14 | semi-aquatic | | omnivores |
| Paramacellodidae | 1.35 | microterrestrial | diurnal | faunivores (invert.) |

TABLE 2. Continued.

| Taxon | WAE-raw | Habitat-broad | Habitat-narrow | Diet |
|---|---|---|---|---|
| Teiidae | 1.89 | microterrestrial | diurnal | faunivores (invert.) |
| Scincidae | 0.17 | microterrestrial | diurnal | faunivores (invert.) |
| Polyglyphanodontinae | 0.08 | microterrestrial | diurnal | herbivores |
| Monstersauria | 1.35 | microterrestrial | diurnal | faunivores (vert.) |
| *Dimekodontosaurus* | 0.78 | microterrestrial | diurnal | faunivores (invert.) |
| *Bothriagenys* | 0.17 | microterrestrial | diurnal | faunivores (invert.) |
| Aniliidae | -0.02 | microterrestrial |  | faunivores (vert.) |
| Teleosauridae | -0.10 | semi-aquatic |  | faunivores (vert.) |
| Pholidosauridae | -1.03 | semi-aquatic |  | faunivores (vert.) |
| Atoposauridae | -10.54 | semi-aquatic |  | faunivores (vert.) |
| Goniopholididae | -8.40 | semi-aquatic |  | faunivores (vert.) |
| Bernissartiidae | -13.90 | semi-aquatic |  | faunivores (invert.) |

TABLE 2. Continued.

| Taxon | WAE-raw | Habitat-broad | Habitat-narrow | Diet |
|---|---|---|---|---|
| Dromaeosauridae | 0.05 | macroterrestrial | | faunivores (vert.) |
| Troodontidae | 0.00 | macroterrestrial | | faunivores (vert.) |
| Tyrannosauridae | 0.00 | macroterrestrial | | faunivores (vert.) |
| Oviraptoridae | -0.05 | macroterrestrial | | faunivores (vert./invert.) |
| Brachiosauridae | -0.21 | macroterrestrial | | herbivores |
| Hadrosauridae | -1.46 | macroterrestrial | | herbivores |
| Pachycephalosauridae | 0.02 | macroterrestrial | | herbivores |
| Nodosauridae | -0.01 | macroterrestrial | | herbivores |
| Ceratopsidae | 0.00 | macroterrestrial | | herbivores |
| Triconodontidae | 1.35 | microterrestrial | nocturnal | faunivores (invert.) |
| Multituberculata | 52.72 | microterrestrial | nocturnal | herbivores |
| Symmetrodonta | 4.92 | microterrestrial | nocturnal | faunivores (invert.) |

TABLE 2. Continued.

| Taxon | WAE-raw | Habitat-broad | Habitat-narrow | Diet |
|---|---|---|---|---|
| Tribotheria | 10.85 | microterrestrial | nocturnal | faunivores (invert.) |
| Marsupialia | 1.55 | microterrestrial | nocturnal | faunivores (invert.) |

Table 3. Comparison of abundances and diversities of major taxa from the Lance Formation and the Mussentuchit Member (Cedar Mountain Formation). Adjusted abundances for the Lance have been converted to percent based on minimum number of individuals (MNI) while those for the Mussentuchit have been converted to percent based on weighted abundance of elements (WAE). Data on Lance Formation modified from Breithaupt 1982.

| | Abundance (raw %) | | Abundance (adjusted %) | | Diversity (families) | |
|---|---|---|---|---|---|---|
| Taxon | Lance | Mussentuchit | Lance | Mussentuchit | Lance | Mussentuchit |
| Chondrichthyes | 2.67 | 1.24 | 2.60 | 0.08 | 3 | 7 |
| Osteichthyes | 78.94 | 42.68 | 18.26 | 1.10 | 4 | 6 |
| Anura | 2.49 | 0.28 | 3.48 | 1.33 | 2 | 2 |
| Urodela | 0.25 | 0.94 | 24.35 | 0.89 | 4 | 5 |
| Chelonia | 1.14 | 0.68 | 6.96 | 0.87 | 4 | 3 |
| Squamata | 9.24 | 1.57 | 15.65 | 7.34 | 5 | 6 |
| Crocodilia | 3.3 | 34.54 | 4.34 | 0.55 | 3 | 5 |
| Dinosauria | 1.1 | 4.25 | 4.34 | 2.76 | 8 | 10 |
| Mammalia | 0.84 | 13.79 | 20.00 | 85.17 | 3 (22 sp.) | 5 (26 sp.) |

# An evaluation of sampling effectiveness in a vertebrate fossil assemblage using ecological techniques

Patricia Goldberg

RRH: SAMPLING IN A FOSSIL ASSEMBLAGE

LRH: PATRICIA GOLDBERG

Abstract. – The Mussentuchit Member of the Cedar Mountain Formation in central Utah has been sampled extensively for microvertebrate fossils. The completeness of sampling was examined by constructing randomized accumulation curves (with increased sampling) at the vertebrate family and mammal species levels. The accumulation curve for families did not plateau, but the one for mammal species did. The completeness of sampling was quantified by estimating the total number of families and species present using three different techniques: abundance-based coverage, Chao's abundance-based estimate, and a jacknife estimate. These three estimators produced similar results, suggesting an average of 61 vertebrate families and 27 mammal species estimated to be present. So far, 48 families and 26 mammal species have been recovered. The amount of effort required to recover new taxa was estimated through extrapolation of the accumulation curve and found to be 6500 kg of matrix for a new vertebrate family and 6630 kg for a new mammal species. Sampling at this site has been extensive and has reached the point of diminishing return.

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## Introduction

Much work in biology and palaeontology involves finding and describing new species and cataloging faunas. With limited resources in both time and money, choices have to be made in determining which sites should be studied, how they should be sampled, and how much effort should be spent on them. Most of the time researchers have relied on intuition and educated guesses, which sometimes are fairly reliable. With the advent of conservation ecology much work has gone into devising methods of evaluating these questions quantitatively, allowing more accurate and economic decisions to be made.

The relationship between area and species richness is one that has been long known (e.g. Gleason 1922), and many studies have quantified and applied it for extant taxa (e.g. Preston 1960; Wilson 1961; Rosenzweig and Abramsky 1993). Rosenzweig (1995) reviewed this relationship over the spectrum of scales to which it can be applied and discussed the various underlying causal factors. In most communities, a few species are present in abundance, while most species are rare. A species-area curve rises steeply initially then flattens, mainly as sampling becomes adequate and includes most of the rare taxa present. In ecological inventory studies, sampling adequacy can be assessed by plotting an accumulation curve and determining if richness has plateaued (Longino and Colwell 1997). Other methods are available for determining total richness, based on multiple samples from a given site. In addition, methods are available to determine the sampling effort necessary to recover a specified number of species.

These same techniques can be applied to fossil assemblages in cases where sampling effort can be quantified. The Mussentuchit Member of the Cedar Mountain Formation is a mudstone deposited by a meandering river in the mid-Cretaceous (Nelson and Crooks 1987; Pomes 1988; Kirkland et al.1997; Currie 1998). It has been accurately dated at 98.39 + 0.07 m.a. (Cifelli et al. 1997) and has been well-sampled for microvertebrates (Cifelli et al. 1999). Moreover, records of sampling effort are available. Thus, it provides a suitable body of data to which ecological-assessment techniques can be applied and evaluated. The main goal of this study is to determine how well-sampled this particular fauna is by 1) examining the relationship between sampling effort and taxon accumulation, 2) estimating the number of vertebrate families, mammal species, and lizard species present in the assemblage, and 3) quantifying the amount of sampling effort required to retrieve new taxa in this member.

## Methods

Over 5000 specimens of vertebrate fossils from the Mussentuchit Member of the Cedar Mountain Formation have been collected over a period of 10 years by crews from the Sam Noble Oklahoma Museum of Natural History (OMNH). A total of 31 sites has been located and either quarried for macrovertebrates or processed for microvertebrates, using bulk matrix collection and wet-screening techniques described in Cifelli et al. (1996) and Madsen (1996). Washed matrix was dried, sorted, and picked for fossils under a dissecting scope. All specimens of all taxa were collected, identified, and catalogued into the OMNH database. Each element was counted as a separate specimen, unless obviously associated. A matrix of abundances of each taxa at each locality was constructed using these data.

An estimate of sampling efforts at each site for each year is available in field notes kept by R. Cifelli. Matrix was collected in burlap sacks, with each full sack weighing approximately 45 kg. The number of sacks collected each year from each site was noted. All matrix processed from a given site was pooled each year, so sub-sample data were not available.

Data were analyzed using EstimateS version 5.0 (Colwell 1997). Accumulation curves were constructed for families, lizard species, and mammal species. The order in which the data were entered into the curve was random and the calculations were repeated many times, randomizing the order in which the sites were added. This procedure removed the effects of variability in sampling effort and diversity among sites, producing a smooth curve and averaging the effort and diversity characteristic of each site. Additionally, collecting methods (multiple sites vs. multiple years at one site) were compared. Next, three estimates of actual richness were computed: abundance-based coverage estimator (Chao, Ma, and Yang 1993), Chao's estimator (Chao 1984), and a jacknife estimator (Burnham and Overton 1978, 1979). Derivations of the formulae used are provided in their respective papers, with overviews and comparisons in Colwell (1997) and Colwell and Coddington (1994). Abbreviations common to all include:

$\underline{S}_{abun}$ = number of abundant species (>10 individuals)

$\underline{S}_{rare}$ = number of rare species (<10 individuals)

$\underline{S}_{obs}$ = total number of species observed

$F_1$ = number of species with exactly 1 individual

$F_2$ = number of species with exactly 2 individuals

$Q_1$ = number of species occuring in exactly 1 sample (site)

$m$ = total number of samples (sites)

$N_{rare} = \Sigma F_i^{10}$

The abundance-based coverage estimator is calculated as:

$$S_{ace} = S_{abun} + S_{rare}/C_{ace} + F_1/C_{ace}\gamma^2_{ace},$$

where $C_{ace} = 1\text{-}F_1/N_{rare}$ and $\gamma^2_{ace} = \max\{(S_{rare}/C_{ace})(C_{ace}N_{rare}[N_{rare}\text{-}1]\}$.

Chao's abundance-based estimator is calculated as:

$$S_{chao} = S_{obs} + F_1^2/2F_2.$$

The jacknife estimator is calculated as:

$$S_{jack} = S_{obs} + Q_1([m\text{-}1]/m).$$

Finally, I calculated the average amount of matrix that would have to be processed to find a new family, a new lizard species, and a new mammal species in the Mussentuchit Member using non-linear regression in Statistica version 5.1 (StatSoft 1996).

## Results

The accumulation curves for families, mammal species, and lizard species are provided in Figure 1. All three curves rise with initial steepness. The mammal curve, however, flattens after eight sites were added, while the family and lizard accumulation curves continue to rise. The three richness estimators provided very similar results, with the total number of families estimated at 61.0, 59.5, and 61.7 with the abundance-based estimator, Chao's estimator, and the jacknife estimator, respectively (Fig. 2a,b,c). Similarly, the number of mammal species was estimated at 25.9, 26.0, and 28.7 with the same three methods (Fig. 2d,e,f). Estimates for the number of lizard species were more variable: 14.0, 12.5 and 10.8 (Fig. 2g,h,i).

Curves based on sampling multiple sites versus sampling the same site over multiple years differ little (Fig. 3). Finally, the amount of matrix required to find addition taxa is estimated by fitting a nonlinear regression equation to the curve. This model predicts that an additional 6500 kg of matrix would need to be processed in order to recover a new family, 6630 kg to recover a new mammal species, and 6300 kg to recover a new lizard species.

## Discussion

The species-accumulation curves and richness estimators demonstrate that the mammal fauna has been nearly completely sampled, but suggest that 17% of the families and 33% of lizard species have yet to be found. Wolff (1975) estimated only 55% of mammal species had been recovered from the Pleistocence Rodeo fauna in California, and this is considered a "best-case" assemblage for ecological analysis by Damuth (1982). The Mussentuchit local fauna can therefore be considered exceptionally well-sampled.

The effort required to adequately sample a locality varies from taxon to taxon and also with taxonomic level. The three richness indicators used provided similar estimates.

The jacknife estimate, as well as others not employed in this paper (see Colwell 1997), can be used with presence/absence data from multiple sites. The highest variation in estimates occurred with the data on lizard species. Lizards are relatively rare, with only 8 species recovered compared to the 26 mammal species and 48 families. Estimates may be less precise with rarer taxa. The shape of the estimation curves, however, indicated that the calculations are stabilizing and that the estimates are fairly accurate. The mammal species curves are flattened, showing a stabilized estimate, while the family curves continue to rise. The total number of families present may be underestimated.

The results of sampling completeness for vertebrate families and mammal species may seem counterintuitive at first glance. Even though the family level is more inclusive than the species level, the analysis based on families includes not just mammals, but all vertebrate families. Mammals were chosen for analysis at the species level because they are the only group from which many species have been identified and studied. The recovery of this group of animals was the primary goal of the excavations in the first place. Rare taxa include several families of chondrichthyans, two urodeles, and a few dinosaurs. These groups are either poorly sampled or poorly represented, and it is within these taxa that accumulation curves would show many undiscovered species.

Under these conditions, mammal species would be expected to be more completely sampled than vertebrates overall. The number of mammal species present is relatively large and suggests that the sample may not be local. Modern mammalian quadrupeds vary in diversity from 30-85 species (depending on latitude) within a 240 by 240 km plot (Rosenzweig 1995). However, diversity is generally higher in tropical environments (see review Rosenzweig 1995). North America was further south during this time and the climate was warm and equable (Parrish 1987; Frances and Frakes 1993; Smith et al. 1994).

The amount of effort required to attain some given number of taxa can be estimated after fitting an equation to the curvilinear relationship between sampling effort and richness. De Capraiis (1976) originally examined this problem from a slightly different angle; he calculated the volume of matrix necessary to recover all taxa. For his data, this value was far beyond what had actually been collected and accuracy is questionable. The advantage to using a non-linear regression is that effort estimates can be calculated for any number of taxa. This may be useful in determining which sites should be sampled further, and how much equipment or time will need to be devoted to the project. At some point either the fauna will be sampled completely or the cost of recovering new taxa becomes prohibitive, and determining this beforehand allows time and resources to be maximized.

Wolff (1975) estimated that 5000 to 10,000 kg of matrix would have to be processed to recover all mammal taxa in the Pleistocene Rodeo fauna. While this number will vary widely from site to site, nearly 49,300 kg has been processed from the Mussentuchit Member and this further supports the contention that it can be considered exceptionally well-sampled. Another 6630 (for a total of 55,930 kg) would have to be processed for complete sampling.

The shape of the accumulation curves for the different sampling strategies varied little. The curve for sampling accumulation over the first year's collection at multiple sites is very similar in shape, but slightly lower than the curve for all data (much matrix is recovered from sampling different sites just once). Some sites thought to be particularly rich were sampled over multiple years, until the recovery of new taxa ebbed. The accumulation curve for V695 (sampled over four years) lies above the other two, showing that more taxa have been recovered from this site than is typical. However, this curve appears to be flattening more rapidly than the others, suggesting that many of the taxa present there have already been recovered. Sampling all sites at least once and productive sites repeatedly appear to provide a good strategy, balancing exploring diversity among sites with assessing diversity within sites.

Summary – Ecological techniques used to determine sampling effectiveness and total richness in inventory studies of modern communities can be applied to fossil assemblages. These techniques are readily available and easy to use, providing a quantitative method of determining how many taxa are present in an assemblage and how much effort will be required to retrieve a particular proportion. If matrix is divided into subsamples and processed separately, these same methods can evaluate individual sites after a single season of collecting.

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FIGURE 1. Rarefaction curves for (A) all families, (B) mammal species, and (C) lizard species. Numbers on x-axis indicate the number of sites added. Y-axis is number of families (A) or species (B,C) recovered. Whiskers indicate one standard deviation.

FIGURE 2. Estimation curves for the number of Mussentuchit families (A-C), mammal species (D-F), and lizard species (G-I) using abundance-based coverage (left column), Chao method (middle column), and jacknife methods (right column). Numbers on x-axis indicate number of sites considered. Y-axis is estimated number of taxa. Whiskers show one standard deviation.

FIGURE 3. Sampling accumulation curves for families from Mussentuchit Member. Numbers on the x-axis indicate number of sites added, and y-axis indicates number of families recovered.

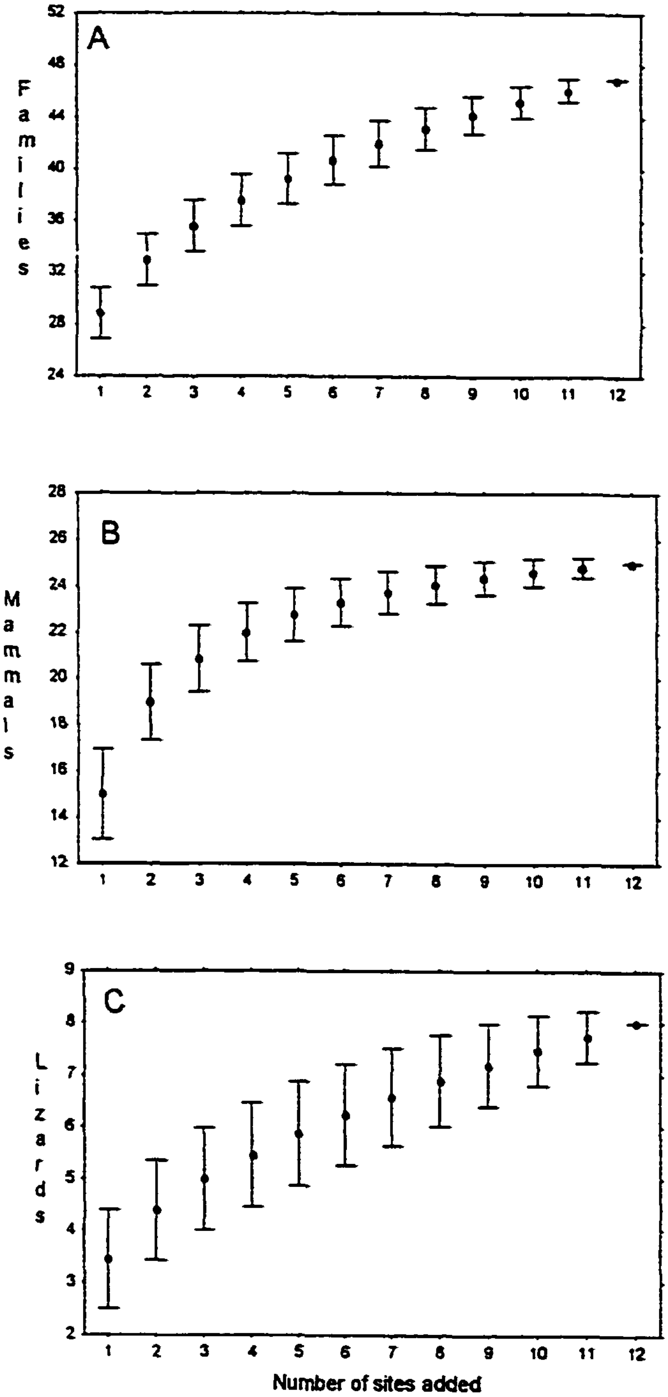
A
Families
24
28
32
36
40
44
48
52
B
Mammals
12
14
16
18
20
22
24
26
28
C
Lizards
2
3
4
5
6
7
8
9
1
2
3
4
5
6
7
8
9
10
11
12
Number of sites added

FIGURE 1

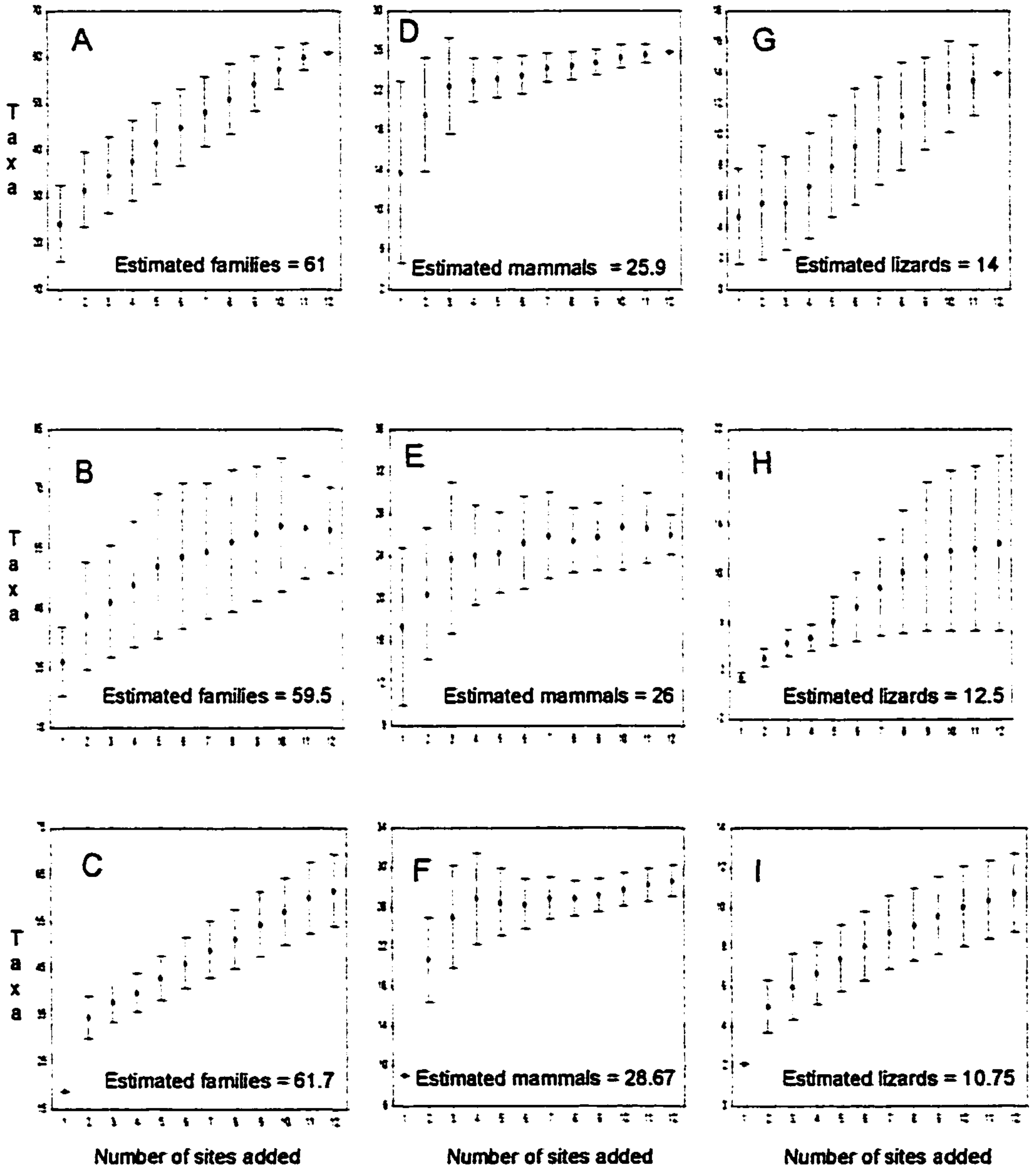
A
Estimated families = 61
D
Estimated mammals = 25.9
G
Estimated lizards = 14
B
Estimated families = 59.5
E
Estimated mammals = 26
H
Estimated lizards = 12.5
C
Estimated families = 61.7
F
Estimated mammals = 28.67
I
Estimated lizards = 10.75
Taxa
Taxa
Taxa
Number of sites added
Number of sites added
Number of sites added

FIGURE 2

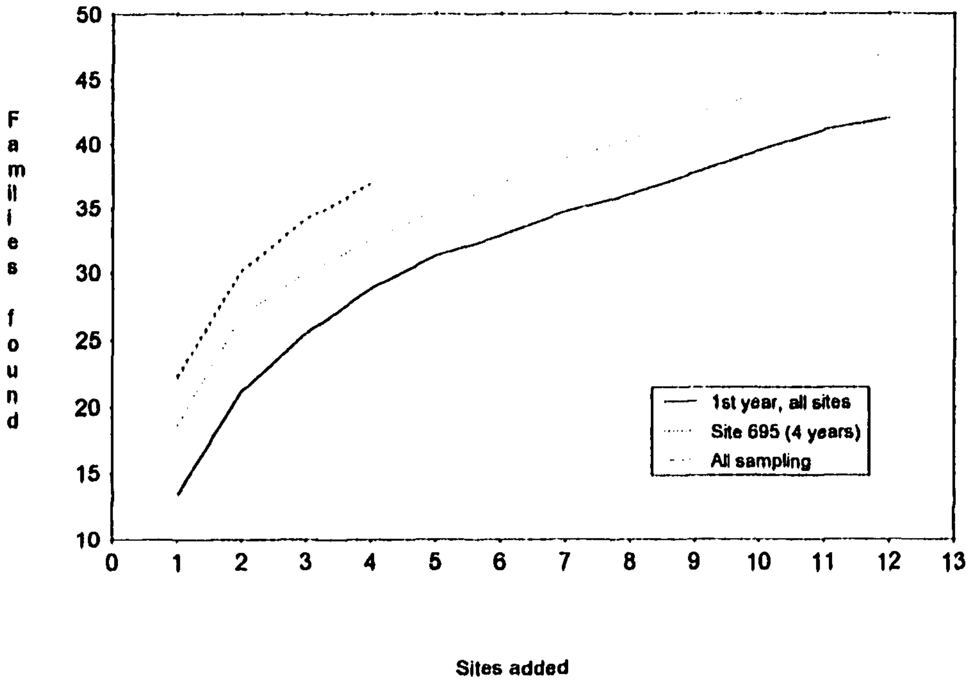
Families found
50
45
40
35
30
25
20
15
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
Sites added
1st year, all sites
Site 695 (4 years)
All sampling

FIGURE 3

# Taxonomic patterns among microvertebrate sites in the Mussentuchit Member of the Cedar Mountain Formation

Patricia Goldberg

RRH: FAUNAL PATTERNS IN THE MUSSENTUCHIT

LRH: PATRICIA GOLDBERG

Abstract. – The Cedar Mountain Formation in Emery Co., Utah, provides a unique opportunity to examine variation in faunal composition in the fossil record at a small scale. Twelve microvertebrate sites from the Mussentuchit Member have been well sampled over the past 10 years. These sites, constrained in time and space, were evaluated to determine which differed significantly in composition, using principal components analyses and Pearson's correlation coefficients. These analyses were performed over five taxonomic groupings: higher-level taxa (ubertatxa; generally class or order level), families (all taxa), crocodile families, lizard species, and mammal species. Projections of principal components showed the grouping of sites based on faunal similarity. The sites grouped differently when analyzed using different taxonomic levels, but ubertaxa-projection plots were similar to family-projection plots. Taxonomic distinctness among sites was best seen using the inclusive family-level analysis. The fauna in one cluster of sites was composed mainly of crocodilians (mostly Atoposauridae, Goniopholididae, and Bernissartiidae) and bony fish (primarily Lepisosteidae), while that in the other large cluster of sites had a higher proportion of terrestrial animals (mammals and dinosaurs). One site stood apart from the rest, with a fauna composed of otherwise rare cartilagenous fishes and dinosaurs, but little else. Pearson's correlation coefficients showed that some sites were statistically indistinguishable in composition, while other pairs of sites differed significantly. Most pairs of sites, however, were neither significantly different nor identical. These relationships are reflected in the distance between sites projected on principal components. Variability among sites of a local fauna

is rarely documented, and may indicate either taphonomic differences within the system or variability in the biological community across space and through ecological time.

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## Introduction

Inferences about the effects of taphonomy, ecology, and evolutionary trends are often made by comparing faunas of different formations or different members within a formation, thus varying in ages and locations. Sites are most often separated widely in space or time or both. Many interesting and useful studies have resulted, mostly focusing on biogeography, large-scale ecology/climatic differences, or faunal turnover (e.g. Olson 1952; Breithaupt 1982; Lehman 1987, 1997; Bryant 1989; Kirkland et al. 1997).

Rarely are abundant data from multiple sites in one stratum and geographic area of one formation available. Such sites would not be subject to the large-scale effects of climate, biogeography and evolution. Rather, they would differ because of small-scale ecological effects on life assemblages, the taphonomic effects on the fossil assemblages present in the rock, or both. Much work has been done on determining the role taphonomy plays in altering the character of death assemblages (Beherensmeyer 1978, 1982, 1988; Beherensmeyer et al. 1979; Beherensmeyer and Kidwell 1985; Aslan and Beherensmeyer 1996; Badgley et al. 1998; Fiorillo 1998). However, few studies have examined the effects of small-scale variability due to local ecology or changes in the environment in ecological time. One of the difficulties is that taphonomy and ecology are interrelated such that separating their effects is difficult and sometimes may not be possible.

The Cedar Mountain Formation is a Cretaceous unit located in central Utah. Twelve microvertebrate sites from the Cedar Mountain Formation have been well-sampled and are both stratigraphically and geographically confined (Fig. 1). These sites are located in the upper (Mussentuchit) Member, dated at 98.39 ± 0.07 million years (Cifelli et al. 1997). In addition, all are located within 80 km of one another in Emery Co., Utah, most along a 15-km stretch southwest of the San Rafael Swell. Thus, they provide a rare opportunity to study faunal differences in the fossil record at a local scale.

The fossil faunas of these 12 sites are described and then analyzed, using principal components analyses and Pearson's correlation coefficients, to determine if composition varies significantly among them. If sites so confined in time and space vary significantly in composition, then either differences in the living communities represented or differences in the processes leading to deposition are suggested. If such sites are the same in composition, then taphonomic processes among sites were most likely similar. Furthermore, either the community was stable over the area of the study and duration of deposition or taphonomic processes spatially and temporally averaged remains, obscuring differences.

## Methods

Fossils from these 12 microvertebrate sites have been collected by crews from the Oklahoma Museum of Natural History (OMNH), University of Oklahoma, for over 10 years (since 1990). Sites were first identified (by prospecting along the outcrop) then mapped. Bones were quarried from macrovertebrate sites, while bulk matrix was collected from microvertebrate sites. Some sites, such as OMNH locality V695, were both quarried and sampled with bulk-matrix techniques.

Matrix was processed either in the field or back at the museum using concentration and recovery techniques described in Cifelli et al. (1996) and Madsen (1996). Wet-screening techniques were employed for all sites, though some sites required additional processing. In each case, all remaining particles (fossil and debris) were rinsed, dried, and set aside for picking. The concentrate was examined through a dissecting scope, and fossils were picked, collected, identified, and catalogued.

All recognizable specimens of all taxa were collected, enabling abundance information to be analyzed. Any bias in specimen recognizability can be assumed to have acted equally on the entire assemblage. Specimens were then entered into the OMNH database along with all relevant associated data. Information in the database was used as a starting point for this study. Curated specimens were examined and lot sizes counted. Associated material was counted as one specimen when it represented parts of an individual skeleton, but lot size was used to indicate the number of specimens in unassociated material. Given the age of the deposit and the nature of the fossil assemblage, it was assumed that each bone originated from a different individual unless obviously associated. Although using the raw number of specimens is not reflective of proportions in the living community, corrections were not necessary when comparing and contrasting composition among sites. Sampling effort was estimated by using the mass of the matrix processed. Field notes were examined to determine the number of burlap sacks of matrix removed from each site each year, with each sack estimated to have the same mass (ca. 45.5 kg, R. Cifelli, personal communication 1999).

I tabulated the number of specimens at varying levels of the taxonomic hierarchy for each site (Appendix A). Taxonomy follows Cifelli et al. (1999) in general, Cifelli and Madsen (1998) for triconodont mammals, Eaton and Nelson (1991) and Eaton and Cifelli (in review) for multituberculate mammals, Cifelli and Madsen (1999) for symmetrodonts, Cifelli (unpublished notes) for tribotherians, and Nydam (in review) for lizards. Only specimens identifiable to at least the family level (slightly higher grouping in mammals) were included.

Analyses were performed at five taxonomic levels: (1) ubertaxa (Chondricthyes, Osteichthyes, Urodela, Anura, Chelonia, Squamata, Crocodilia, Theropoda, Ornithischia, Aves, and Mammalia); (2) all families; (3) crocodilian families only; (4) lizard species only; and (5) mammal species only (see Appendix A for details). These grouping were chosen for a several reasons. Most work has focused on the mammals and lizards and individual fossils can be recognized at the species level. Consequently, they are the only two groups from which multiple species have been accurately identified. Crocodiles are diverse, with five families, and very well represented in the fauna. Identification beyond the family level is problematic however. The family level was the finest level of taxonomic resolution possible for many specimens, and analyses at this level include most of the fauna. Finally, ubertaxa were analyzed to complete the nested sequence and determine if any of the patterns were iterative.

Ubertaxa groups include both classes (Chondrichthyes, Osteichthyes, Aves, and Mammalia) and orders (Urodela, Anura, Chelonia, Sqamata, and Ornithischia), as well as one suborder (Theropoda). The class Amphibia was broken into the two orders because of the morphological and ecological distinctness of the two groups. In addition, anurans are not identified to the family level and hence are not included in subsequent analyses. The class Reptilia is a large, paraphyletic taxon which includes many morphologically and ecologically distinct groups. This taxon is therefore divided into component orders (or suborders) and the taxa used in analyses represent good, monophyletic groups.

The groups used in the family-level analyses are mainly families, with a few exceptions. Polyglyphanodontinae are a subfamily of teiids, but are morphologically distinct and warrant a separate category. The categories used within the Mammalia are for the most part above the family level. The taxonomy and relationships of early mammals are poorly understood. Teeth can be readily recognized as belonging to more inclusive taxa, such as triconodonts, symmetrodonts, tribotherians, or multituberculates, however. The triconodonts belong to a single family, Triconodontidae, while the others are comprised of many families. The symmetrodonts in this fauna all belong to a single family, Spalacotherididae, but the multituberculates belong to more (Plagiaulacidae, and many taxa of dubious familial affinities). The taxonomy becomes even more complicated for tribotherians. Those belonging in the therian of maetatherian-eutherian grade include two Picopsidae species and two species of indeterminate families. In addition, there are four species belonging within the Marsupialia. For convenience and necessity, larger taxononmic groupings are used for mammals in the family-level analyses.

First, frequency histograms of faunal composition were constructed for each site at each taxonomic level. These were used to visualize differences in faunal composition between sites and aid in the description of each site.

Using NTSYS-pc version 2.02 (Rohlf 1999), five sets of principal components analyses were performed to group the sites based on similarities in taxonomic abundances. Principal components were calculated on the basis of standardized raw abundance (with a mean of 0 and standard deviation of 1). A correlation matrix, using Pearson's correlation coefficients, was constructed and used to determine the principal components axes. The number of components used was determined by comparing percent variability explained in the actual analysis to the expected variability explained in a broken-stick model (Joliffe 1986). A broken-stick model divides the variability by "breaking" the total variability in "pieces," thereby providing an estimate of the variability expected to be explained by chance at each level. Finally, projections of standardized data were plotted.

Significance in similarity (or dissimilarity) was evaluated by calculating Pearson's correlation coefficients for each pair of sites using abundance data standardized by site. Pearson's correlation coefficients reflect overall patterns regardless of sample size, so that the shared absence of rare taxa in poorly sampled sites does not result in positive correlations. Bonferroni corrections were applied to compensate for multiple comparisons (Sokal and Rohlf 1996).

## Results

A total of 13,036 specimens identifiable to the family level was recovered by processing 49,295 kg of matrix. Sites varied greatly in the amount of sampling effort, ranging from 775 to 14,580 kg of matrix processed (mean = 3935, standard deviation = 4240). Site V695 was the most heavily sampled, followed by V794, while site V213 was the least heavily sampled. Sites V236 and V696 were also relatively poorly sampled. Taxa also varied greatly in abundances. Nine of the 48 families present were represented by single specimens, and 11 others were represented by fewer than 10 specimens. A small number of taxa produced the vast majority of remains. Over one-quarter of the specimens (3667) came from a single family, Lepisosteidae (Osteichthyes). Five other families accounted for 41% of the fauna (see Appendix A for details): Bernissartiidae (Crocodilia), 1599; Atoposauridae (Crocodilia), 1212; Goniopholididae (Crocodilia), 966; Multituberculata (Mammalia), 865; and Semionotidae (Osteichthyes), 706.

Ubertaxa.—Differences in composition among sites at the ubertaxa level are shown in Figure 2. Sites V235 and V694 were mainly composed of crocodilians (50-65%) followed by bony fish (19-21%). Theropods and mammals were also an important component of the fauna. The vertebrate fossil assemblage found at sites V696 and V794 were similarly composed, with abundances of crocodiles (37-40%) and bony fish (28-36%) being more even. Again, theropods and ornithischians were abundant, followed by mammals and birds. Faunas of sites V240 and V695 were composed mainly of bony fish (57-65%). Site V240 retained the main pattern, with a large number of crocodiles (22%) followed by theropods. There were more frogs than mammals at this site however. Site

V695 has comparatively few crocodiles (<10%), but theropods, ornithischians, and mammals were abundant. Site V801 was composed of nearly 90% crocodiles followed by nearly 10% mammals. Sites V236, V239, and V868 formed a second group characterized by few fish (0, 4, and 8% respectively). Faunas of sites V239 and V868 were nearly equally composed of crocodiles and mammals followed by theropods, while V236 was comprised mostly of mammals, then nearly equal shares of the two types of dinosaurs, followed by crocodiles. This latter site also had a very large proportion of birds (14%) and turtles (3%). Site V868 had a large proportion of lizards (7%) with fairly high proportions of salamanders and frogs. Similarly, site V239 had a relatively high proportion of lizards. Site V234 was overwhelmingly composed of ornithischian dinosaurs (47%) followed by mammals (31%) then urodeles (9%). Site V213 included many dinosaurs (theropods 19%; ornithischians 28%), but had the highest proportion of cartilaginous fish of any site (30%). Bony fish were also prevalent (14%), as were mammals (8%).

The first four principal components were significant and accounted for 86.6% of the variability. Individual character loadings are provided in Table 1. Sites were very scattered on the projection plots (Fig. 3a), but reflected the general patterns in similarity described based on the frequency histograms. V694 and V235 were most similar, followed by V794 and V696, and then V240 and V695. These six sites along with V801 formed one large group. Sites V868, V239, and V236 formed another large group with V234 possibly being included. Site V213 was distinct from all the other sites (Fig. 3a).

Along the first axis sites abundant in large, terrestrial animals (theropods and ornithischians) are placed toward the back of the plot, while those abundant in anurans and chelonians are located toward the front. The position along the second axis is influenced by what I interpret to be a gradient in wetness, with those sites high in bird and mammal abundances on the right and those with high bony fish or cartilagenous fish abundances on the left. Similarly, sites abundant in crocodiles plot toward the bottom of the third axis, while those high in ornithischian dinosaurs and urodeles plot high. Position along the fourth axis is influenced mainly by the relative abundances of the rarer members of the microterrestrial fauna, birds and lizards.

Pearson's correlation coefficients show that three pairs of sites are positively associated at the (corrected) 0.05 level: V234 with V801, V235 with V794, and V694 with V794. Three pairs are negatively associated: V239 and V696, V694 and V695, and V695 and V794.

Families.—Frequency histograms showing differences in composition among sites at the family level are provided in Figure 4. Sites V695 and V240 had a large proportion of Lepisosteidae (50 and 68%, respectively). The remaining specimens were spread over many different families. Sites V694 and V794 had fewer Lepisosteidae (20-30%) with more of an emphasis on crocodiles of all families (75 and 50%, pooled, respectively). Both sites had some chondricthyans, but V794 also had a high diversity and abundance of other bony fish and mammals. Site V696 was intermediate between these two groups, with a high abundance of atoposaurid crocodiles (49%) and lepisosteid fish (35%). Sites V235, V236, V239, and V801 were characterized by a paucity of fish, especially the otherwise common Lepisosteidae. Sites V239 and V801 were composed mostly of the three common families of crocodiles, with V239 also having an abundance of multituberculates. Site V236 was mostly composed of mammals, mainly multituberculates, followed by goniopholidid crocodilians. In addition, this site also had an abundance of hadrosaurs and pleurosternid turtles. Site V235, like many of the sites, was composed mostly of the three abundant crocodile families. This site, however, also contained a diversity of bony fish, totaling around 25% of the fauna. Site V234 was characterized by a scarcity of fish and crocodiles (5%). This site was unique in having abundant triconodont and tribotherian mammals (otherwise rare), and albanerpetontid salamanders. Site V868 was similar to the others at a broad taxonomic scale, being composed nearly equally of bony fish, crocodiles, and mammals; however, the proportions of families within these groupings are unique. Semionotidae contributed more to the abundance of the bony fish than Lepisosteidae, while bernissartiid crocodiles (usually the abundant crocodilian group) are relatively rare. Multituberculate mammals are abundant, but so are symmetrodonts and tribotherians. Moreover, this site also has a significant teiid and paramacellodid lizard component. Finally, site V213 is very different from all other sites at the family level, as it is at higher taxonomic levels. This site is composed mostly of six families of cartilaginous fishes, although two families of bony fishes are also well represented. Curiously, crocodiles are relatively rare but dinosaurs are common, especially hadrosaurs.

The first three principal components from the analysis of these 48 families accounted for 77.1% of the variability. Only two axes were significant using the broken-stick model; however, the third axis had a high eigenvalue (4.53) and those data are included here. Loadings for all families are provided in Table 2. Clustering of sites on the projection plot conformed with faunal similarity as described based on the frequency histograms. Site V213 was distinct from all others. Sites V240, V695, V696, V794, and V694 formed one group, with V236, V239, and V801 forming another. Sites V234 and V235 are intermediate and link these two groups together. Finally, site V868 stood slightly apart from this latter group (Fig. 3b).

Site position along the first axis was overwhelmingly influenced by rare taxa, with 16 families, mostly tetrapods, having very high negative loadings (<- 0.95) and eight families of cartilagenous fishes and herbivorous dinosaurs having moderately high positive loadings (>0.55). Sites with rare chondrichthyans (Orectolobididae, Squatinidae, Sclerorhychidae, and Rhinobatoidea) and high proportions of dromaeosaurs plot on the left of the projection, while those sites with many common lizards (Paramacellodidae and Teiidae) and symmetrodont mammals plot to the right. Sites seem to follow a gradient in habitat, from wet to dry, along the third axis. Marsupials, triconodonts and tribosphenic mammals, along with albanerpetontid salamanders, had high positive loadings, causing sites to plot high on the third axis. Sites in which bony fish (Lepisosteidae, Semionotidae, and Pycnodontidae) predominate plot low.

Because site V213 was so different from the others, another principal components analysis was performed excluding this site to determine if it had a large influence on the groupings of the other sites. In addition, since this level of analysis seemed most prone to sampling bias, with many families represented by fewer than five specimens, the principal components analysis was redone omitting 17 groups (i.e. families represented by five or fewer specimens), both with and without site V213. In the analysis excluding the rarest taxa, the 12 sites plotted in an identical pattern compared to the original plot. In the analyses excluding site V213, the remaining 11 sites plotted in similar positions relative to one another, so the analyses are robust.

Pearson's correlation coefficients indicate only one positive association (V694 with V696) and one negative association (V213 and V695). Five other negative associations were significant before Bonferoni corrections were applied.

Crocodilians.—Except for the poorly represented sites (V213 and V234, with one bernissartiid each, and site V236 with 10 goniopholidids), sites were similar compositionally (Fig. 5). Sites V695 and V868 were most similar, with 42% atoposaurids, 38-48% goniopholidids, and 11-12% bernissartiids, while sites V794, V235, and V239 had higher proportions of bernissartiids: 45% bernissartiids, 20-25% goniopholidids, 22-32% atoposaurids, and 1-2% pholidosaurids. Sites V240, V696, and V801 varied in proportions of atoposaurids, goniopholidids, and bernissartiids, and were intermediate in composition compared to the two groups described above. Site V696 was unique in being composed overwhelmingly of atoposaurids (over 95%).

Almost all variability (99.8%) was accounted for by the first three principal components, with loadings provided in Table 3. Sites V213 and V234 plotted on the same point; both sites have only one bernissartiid specimen. Sites V695 and V868 cluster closely in one group with large and equal proportions of atoposaurids and goniopholidids, while V235, V239, and V794 cluster together in another group, with nearly equal amounts of bernissartiids, atoposaurids, and goniopholidids. All other sites are scattered among these groups (Fig. 3c).

Sites scattered along the first axis based mainly on the relative proportions of two moderately common families to the two rare families. Sites with high abundances of atoposaurids and goniopholidids plot toward the front of the graph, while those more abundant in teleosaurids or pholidosaurids plot toward the back. Sites with high proportions of the common bernissartiids plot to the left on the second axis and those with low proportions of this taxon plot on the right. The relative proportions of atoposaurids and goniopholidids is sorted on the third axis, with sites more abundant in atoposaurids plotting high and sites more abundant in goniopholidids plotting low.

Pearson's correlation coefficients show three positively associated sites: V213 with V234, V213 with V236, and V234 with V236. Three negative associations are also indicated: V235 and V236, V240 and V801, and V695 and V794.

Squamates.— Many sites had very few (1 or 2) or no lizard remains; only six sites are considered here (Fig. 6). Sites V695 and V794 were similar in that both included mainly Bicuspidon numerosus: V794 was entirely B. numerosus and V695 was 75% B. numerosus, with the remaining 25% of the fauna split among five other species. Sites V235, V239, and V868 also were composed mostly of B. numerosus (45%), but in addition had high proportions of Harmodontosaurus emeryensis (ca. 35%) and Primaderma nessovi (ca. 10%). Site V240 had an equal distribution of these three species (33% each).

With only six lizard species and one snake species, a large amount of variability (69.0%) was captured in the first axis of the PCA. Only the first axis was significant using the broken-stick model, but the second had an eigenvalue greater than one and is also included in the interpretation (Table 4). The six sites analyzed fell into three distinct clusters: V794 and V695; V239, V868, and V235; and V240 alone (Fig. 7).

The relative abundance of B. numerosus, the most common lizard species in the fauna, influences the position of sites along the first axis (with a loading of 0.99). Sites with the highest proportion of this species plot on the left, while those with lower proportions of B. numerosus, and relatively high proportions of H. emeryensis, plot on the right. Position along the second axis was influenced by the proportions of the other, rarer taxa. Sites with higher abundances of Dicothodon moorensis and Dimekodontosaurus madseni plotted high, while those more abundant in P. nessovi, Bothriagenys mysterion, and Coniophis sp. plotted low.

Pearson's coefficients indicate six positive correlations: V234 with V239, V235 with V240, V235 with V868, V239 with V868, V240 with V868, V695 with V794, and V695 with V868.

Mammals.—Sites V868, V794, V235, and V695 were characterized by high diversity, with Spalacolestes cretulablatta being the most abundant species. Spalacotheridium noblei, Paracimexomys perplexus, and marsupial species "C" were also relatively abundant. Sites V696 and V801 were both poorly represented by six and four specimens, respectively. However, both sites contained Astroconodon delicatus and Spalacotheridium noblei. The remaining sites seemed to have little in common (Fig. 8).

Four specimens were recovered from site V694, three of *Paracimexomys perplexus* and one of *Ameribaatar zofiae*. Site V213 contained only one mammal specimen identified to the species level, a therian of metatherian-eutherian grade. Site V236 similarly contained only two mammal specimens identified to the species level, both of which were *Kokopellia juddi*. Site V239 contained 62 specimens belonging to 16 species, but was overwhelmingly dominated by *Cedaromys parvus*. Sites V240 and V234 were poorly represented with seven specimens each, scattered over five and six (different) species, respectively.

Over two-thirds of the variability (70.1%) in mammal composition was captured in the first four principal components. Loadings for the 25 species used in the analysis are provided in Table 5. Points were very scattered and formed only loose clusters, with sites V868, V794, V235, and V695 forming one, sites V213, V236, V239, and V240 forming another (although with little in common), and sites V696 and V801 forming a third. Site V694 plotted inbetween these three groups, while V234 plotted alone (Fig. 3d).

Sites with high proportions of the rarest species, *Paracimexomys* cf. *perpleuxs*, *Paracimexomys* cf. *robisoni*, *Cedaromys* cf. *bestia*, and Picopsidae species "A", plotted to the front, while those with high proportions of *Bryceomys intermedius* and *Spalacolestes cretulablata* are found to the back of the first axis. *Cedaromys* cf. *parvus* and *Jugulator amplissimus* had high negative loadings for the second axis (with sites plotting to the right), while marsupial species "A", *Ameribaater zofiae*, and *Spalacolestes inconcinnus* had high positive loadings, causing sites to plot to the left. Only one species, Astroconodon delicatus, had a high loading value for the third axis (0.87), and sites with high proportions of this taxon plotted high. Ameribaater zofiae, Bryceomys intermedius, and Picopsidae "A" had the highest negative loadings (-0.42, -0.42, and -0.43), and sites with high proportions of these taxa plot low. Finally, sites plot along the fourth axis based on the abundances of Spalacotheridium noblei and Picopsidae "A" relative to the abundances of the therian of metatherian-eutherian grade "B" and Paracimexomys perplexus.

Pearson's correlation coefficients show four positive associations: V213 with V234, V234 with V240, V236 with V694, and V696 with V801.

## Discussion

Compositional differences among sites confined in space and time are unusual or at least poorly documented in vertebrate faunas. Estes (1964) compiled data from 41 sites in the Lance Formation of eastern Wyoming, six of which were well-sampled. He found that these six sites were faunally similar and went on to infer climate and ecology for the entire group of sites. Similarly, Case (1996) looking for differences related to fine scaled biostratigraphy, found no differences among sites in an Eocence penguin assemblage. Badgley et al. (1998) compared the small-mammal faunas from the Miocene of the Chinji Formation and, again, no differences were found.

Even though the 12 microvertebrate sites examined were deposited over a relatively short period of time and within close geographic proximity of one another, they vary in faunal composition. Either the processes leading to the deposition of fossils varied among sites (e.g. Blob 1994), with different biases altering the composition of the fossil assemblages at different sites, or the ecological conditions varied spatially or temporally among sites (as found in Wing 1984). Sites vary in composition at multiple taxonomic levels; however, the clustering of sites varies with the taxonomic level used to characterize them.

The principal components projections for the family analysis and the ubertaxa analyses produced similar clusters. Site V213 seemed to have been deposited under very different conditions and/or at a very different time than the others, with a high diversity and proportion of otherwise rare cartilagenous fish. This site stands alone as an outlier in the ubertaxa and family-level projection plots, reflecting its distinct composition. Sites V240, V695, V794, and V696 clustered together with high numbers of bony fish (mostly Lepisosteidae) in all of them. Sites V234, V236, V239, and V868 all lacked fish and were high in abundances of crocodiles, mammals and dinosaurs, suggesting a more terrestrial influence. The positions of sites V801 and V235 shifted in the ubertaxa projection compared to the family-level projection. The fauna at site V801 was mostly crocodiles, with no fish. Site V235 was mostly composed of fish and crocodiles, but Lepisosteidae fish were balanced by Semionotidae and Pycnodontidae fish.

The analysis of lizard species also produced clusters similar to those obtained in the ubertaxa- and family-level analyses. However, the analysis using crocodile families produced a projection with unique clusters. Finally, mammal species also produced unique clusters representing the microterrestrial fauna.

Pearson's correlation coefficients indicated that some sites were compositionally the same, others were significantly different, and many did not differ from random, at least using conservative statistics with corrections for Bonferroni inequalities. These relationships differed when looking at different taxa and when looking at specimens at different taxonomic levels. In general, similarities and differences are reflected in the distances between points on the projection plots derived from the principal components analyses. These results suggest that the sites are not temporally and spatially averaged to the point where they are homogenized. Some sites differ and some causal factor, either different depositional processes or different ecological conditions, appears to be responsible. Conversely, the few sites that have the same composition may either be isotaphonomic or similar in ecological conditions, or, probably, both.

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APPENDIX. Nested abundances (number of specimens) of Mussentuchit local fauna by site. Values for ubertaxa and totals in bold.

| Taxon | Site | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 | Total | Other sites | Grand total |
| **Chondrichthyes** | **11** | **0** | **11** | **0** | **2** | **1** | **8** | **10** | **4** | **86** | **0** | **3** | **136** | **5** | **141** |
| Hybodontidae | 4 | 0 | 1 | 0 | 1 | 0 | 7 | 1 | 4 | 1 | 0 | 0 | **19** | 0 | **19** |
| *Hybodus* sp. | 4 | 0 | 1 | 0 | 0 | 0 | 7 | 0 | 3 | 0 | 0 | 0 | **15** | 0 | **15** |
| Polyacrodontidae | 3 | 0 | 5 | 0 | 0 | 0 | 1 | 0 | 0 | 39 | 0 | 0 | **48** | 5 | **53** |
| *Lissodus* sp. | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | **12** | 4 | **16** |
| *Lissodus anitae* | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 31 | 0 | 0 | **34** | 0 | **34** |
| *Polyacrodus parvidens* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **2** | 1 | **3** |
| Orectolobididae | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **1** | 0 | **1** |
| Squatinidae | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **1** | 0 | **1** |
| Sclerorhynchidae (*Ischyrhiza texana*) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | **1** | 0 | **1** |
| Rhinobatoidea (*Pseudohypolophus* sp.) | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 9 | 0 | 2 | 0 | 0 | **14** | 0 | **14** |
| Myliobatoidea | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 44 | 0 | 3 | **52** | 0 | **52** |
| **Osteichthyes** | **5** | **0** | **294** | **0** | **21** | **525** | **120** | **2288** | **104** | **1395** | **2** | **61** | **4815** | **13** | **4828** |
| Lepisosteidae | 4 | 0 | 139 | 0 | 18 | 502 | 116 | 1736 | 101 | 989 | 0 | 54 | **3659** | 8 | **3667** |
| Semionotidae | 1 | 0 | 76 | 0 | 2 | 12 | 2 | 461 | 0 | 150 | 1 | 0 | **705** | 1 | **706** |
| *Lepidotes* sp. | 1 | 0 | 63 | 0 | 2 | 1 | 0 | 459 | 0 | 122 | 0 | 0 | **648** | 0 | **648** |

APPENDIX. Continued.

| Taxon | Site | | | | | | | | | | | | Total | Other sites | Grand total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 | | | |
| Pycnodontidae | 0 | 0 | 68 | 0 | 0 | 8 | 2 | 51 | 2 | 47 | 1 | 6 | 185 | 2 | 187 |
| Amiidae | 0 | 0 | 10 | 0 | 1 | 3 | 0 | 39 | 1 | 209 | 0 | 1 | 264 | 0 | 264 |
| Enchodontidae (*Enchodus* sp.) | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 3 |
| Ceratodontidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| **Urodela** | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 10 | 1 | 0 | 6 | 10 | 32 | 0 | 32 |
| Prosirenidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 5 | 0 | 5 |
| Albanerpetontidae (cf. *Albanerpeton arthria* | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 5 | 1 | 0 | 0 | 10 | 21 | 0 | 21 |
| Scapherpetontidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 4 | 0 | 4 |
| *Lisserpeton* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Piceerpeton* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Salamandridae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Sirenidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| **Anura** | 0 | 0 | 4 | 0 | 4 | 30 | 1 | 47 | 3 | 5 | 0 | 10 | 104 | 3 | 107 |
| **Chelonia** | 0 | 0 | 1 | 2 | 3 | 5 | 0 | 49 | 0 | 10 | 3 | 1 | 74 | 4 | 78 |
| Glyptopsidae (*Glyptops* sp.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 1 | 0 | 11 | 0 | 11 |
| Trionychidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 9 | 0 | 9 |

APPENDIX. Continued

| Taxon | Site | | | | | | | | | | | | Total | Other sites | Grand total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 | | | |
| Pleurosternidae (*Naomichelys* sp.) | 0 | 0 | 1 | 2 | 3 | 5 | 0 | 30 | 0 | 10 | 2 | 1 | 54 | 4 | 58 |
| **Squamata** | 0 | 0 | 12 | 0 | 14 | 7 | 0 | 73 | 0 | 12 | 3 | 53 | 174 | 4 | 178 |
| Paramacellodidae | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 5 | 0 | 0 | 0 | 8 | 16 | 0 | 16 |
| *Pseudosaurillus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Teiidae | 0 | 0 | 10 | 0 | 9 | 4 | 0 | 56 | 0 | 12 | 2 | 38 | 131 | 0 | 131 |
| *Harmodontosaurus emeryensis* | 0 | 0 | 5 | 0 | 4 | 2 | 0 | 5 | 0 | 0 | 0 | 14 | 30 | 0 | 30 |
| *Bicuspidon numerosus* | 0 | 0 | 5 | 0 | 5 | 2 | 0 | 41 | 0 | 7 | 2 | 18 | 80 | 0 | 80 |
| Polyglyphanodontinae | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Dicothodon moorensis* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Scincidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 2 |
| Monstersauria (*Primaderma nessovi*) | 0 | 0 | 1 | 0 | 1 | 2 | 0 | 5 | 0 | 0 | 1 | 4 | 14 | 2 | 16 |
| *Dimekodontosaurus madseni* (Family indet.) | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 6 | 0 | 6 |
| *Bothriagenys mysterion* (Family indet.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 2 |
| Serpentes (Aniliidae, *Coniophis* sp.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 3 |
| **Crocodylia** | 1 | 1 | 703 | 10 | 298 | 184 | 406 | 312 | 144 | 1421 | 189 | 217 | 3886 | 21 | 3907 |
| Teleosauridae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 2 | 0 | 0 | 11 | 0 | 11 |

APPENDIX. Continued.

| | Site | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 | Total | Other sites | Grand total |
| Pholidosauridae | 0 | 0 | 12 | 0 | 2 | 4 | 45 | 11 | 1 | 43 | 0 | 1 | 119 | 0 | 119 |
| Atoposauridae | 0 | 0 | 234 | 0 | 83 | 88 | 97 | 132 | 139 | 323 | 21 | 88 | 1205 | 7 | 1212 |
| Goniopholididae | 0 | 0 | 136 | 10 | 79 | 37 | 16 | 120 | 2 | 356 | 94 | 105 | 955 | 11 | 966 |
| Bernissartiidae | 1 | 1 | 321 | 0 | 134 | 55 | 248 | 40 | 2 | 697 | 74 | 23 | 1596 | 3 | 1599 |
| **Dinosaur predators** | 7 | 5 | 99 | 6 | 64 | 22 | 58 | 417 | 56 | 312 | 0 | 105 | 1151 | 57 | 1208 |
| Theropoda, Family Indet. | 5 | 5 | 94 | 6 | 61 | 21 | 57 | 323 | 50 | 312 | 0 | 105 | 1039 | 44 | 1083 |
| Dromaeosauridae | 2 | 0 | 4 | 0 | 3 | 1 | 1 | 91 | 6 | 0 | 0 | 0 | 108 | 7 | 115 |
| Troodontidae (*Troodon* sp.) | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Tyrannosauridae (cf. *Alectrosaurus* sp.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 3 |
| Oviraptoridae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 6 |
| **Dinosaur herbivores** | 10 | 21 | 95 | 14 | 56 | 15 | 12 | 260 | 19 | 223 | 1 | 22 | 748 | 32 | 780 |
| Ornithischia | 5 | 21 | 61 | 8 | 50 | 5 | 9 | 109 | 12 | 135 | 1 | 15 | 431 | 73 | 504 |
| Brachiosauridae | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 |
| Hadrosauridae | 4 | 0 | 33 | 5 | 4 | 10 | 3 | 146 | 7 | 88 | 0 | 6 | 306 | 32 | 338 |
| *Eolambia caroljonesae* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 20 | 21 |
| Pachycephalosauridae | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 |

APPENDIX. Continued.

| Taxon | Site | | | | | | | | | | | | Total | Other sites | Grand total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 | | | |
| Nodosauridae | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 6 | 0 | 6 |
| Neoceratopsia | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| **Aves** | 0 | 0 | 32 | 9 | 2 | 1 | 7 | 21 | 13 | 84 | 0 | 11 | 180 | 37 | 217 |
| **Mammalia** | 3 | 15 | 161 | 23 | 231 | 18 | 20 | 492 | 20 | 329 | 14 | 217 | 1543 | 17 | 1560 |
| Triconodontidae | 0 | 8 | 4 | 0 | 15 | 3 | 0 | 14 | 1 | 11 | 4 | 1 | 61 | 0 | 61 |
| *Astroconodon delicatus* | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 6 | 0 | 6 |
| *Corviconodon utahensis* | 0 | 1 | 2 | 0 | 4 | 2 | 0 | 1 | 0 | 3 | 0 | 0 | 13 | 0 | 13 |
| *Jugulator amplissimus* | 0 | 1 | 2 | 0 | 4 | 0 | 0 | 5 | 0 | 1 | 0 | 0 | 13 | 0 | 13 |
| Multituberculata | 2 | 1 | 92 | 16 | 169 | 7 | 13 | 296 | 13 | 171 | 8 | 64 | 852 | 13 | 865 |
| *Janumys erebos* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 17 | 0 | 3 | 1 | 3 | 25 | 0 | 25 |
| *Paracimexomys perplexus* | 0 | 0 | 11 | 0 | 6 | 0 | 3 | 18 | 1 | 18 | 0 | 2 | 59 | 1 | 60 |
| *Paracimexomys* cf. *perplexus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 2 |
| *Paracimexomys* cf. *robisoni* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 3 |
| *Ameribaatar zofiae* | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 5 | 0 | 6 | 17 | 0 | 17 |
| *Bryceomys intermedius* | 0 | 0 | 4 | 0 | 1 | 0 | 0 | 8 | 0 | 8 | 0 | 6 | 27 | 1 | 28 |
| *Bryceomys* cf. *intermedius* | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 4 | 0 | 4 |

APPENDIX. Continued.

| | Site | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 | Total | Other sites | Grand total |
| *Cedaromys bestia* | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 21 | 2 | 3 | 0 | 2 | 29 | 0 | 29 |
| *Cedaromys* cf. *bestia* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |
| *Cedaromys parvus* | 0 | 0 | 2 | 0 | 15 | 0 | 0 | 8 | 0 | 2 | 1 | 1 | 29 | 0 | 29 |
| *Cedaromys* cf. *parvus* | 0 | 1 | 0 | 0 | 4 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 7 | 0 | 7 |
| Symmetrodonta (Spalacotheriidae) | 0 | 0 | 26 | 0 | 7 | 4 | 6 | 108 | 1 | 42 | 1 | 60 | 255 | 3 | 258 |
| *Spalacolestes cretulablatta* | 0 | 0 | 12 | 0 | 2 | 1 | 0 | 40 | 0 | 16 | 0 | 19 | 90 | 0 | 90 |
| *Spalacolestes inconcinnus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 5 | 0 | 5 |
| *Spalacotheridium noblei* | 0 | 0 | 6 | 0 | 3 | 2 | 0 | 16 | 1 | 9 | 1 | 9 | 47 | 0 | 47 |
| Tribotheria | 1 | 5 | 33 | 5 | 33 | 4 | 1 | 62 | 4 | 89 | 1 | 79 | 317 | 1 | 318 |
| Picopsidae species A | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 7 | 0 | 7 |
| Picopsidae species B | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Family indet. species A | 1 | 2 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 9 | 0 | 9 |
| Family indet. species B | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 4 | 0 | 6 | 0 | 0 | 14 | 0 | 14 |
| Marsupialia | 0 | 1 | 6 | 2 | 7 | 0 | 0 | 12 | 1 | 16 | 0 | 13 | 58 | 0 | 58 |
| *Kokopellia juddi* | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 7 | 0 | 2 | 0 | 0 | 13 | 0 | 13 |
| Species A | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 4 | 0 | 4 |

APPENDIX. Continued.

| | Site | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 | Total | Other sites | Grand total |
| Species B | 0 | 0 | 2 | 0 | 3 | 0 | 0 | 1 | 1 | 4 | 0 | 2 | 13 | 0 | 13 |
| Species C | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 4 | 0 | 10 | 0 | 8 | 28 | 0 | 28 |
| **Total specimens** | 37 | 46 | 1413 | 64 | 695 | 808 | 632 | 3979 | 364 | 3877 | 218 | 710 | 12843 | 193 | 13,036 |
| Mass of matrix processed (kg) | 775 | 1825 | 4690 | 910 | 1960 | 1915 | 3645 | 14,580 | 955 | 11,390 | 1820 | 2780 | 47,245 | 2050 | 49,295 |
| Number of families | 14 | 4 | 26 | 7 | 25 | 21 | 15 | 38 | 16 | 21 | 15 | 21 | 48 | 22 | 50 |

FIGURE 1. Location of Mussentuchit microvertebrate localities. Localities in bold are the well-sampled sites used in formal analyses. Redrawn from Cifelli et al. (1997).

FIGURE 2. Percent abundances of Mussentuchit ubertaxa.

FIGURE 3. Principal component projections for Cedar Mountain sites based on (A) higher-level taxa, (B) all families, (C) crocodile families, and (D) mammal species.

FIGURE 4. Percent abundances of Mussentuchit families: 1) Orectolobididae, 2) Hybodontidae, 3) Polyacrodontidae, 4) Squatinidae, 5) Sclerorhynchidae, 6) Rhinobatoidae, 7) Lepisosoteidae, 8) Semionotidae, 9) Pycynodontidae, 10) Amiidae, 11) Albanerpetontidae, 12) Pleurosternidae, 13) Paramacellodidae, 14) Teiidae, 15) Pholidosauridae, 16) Atoposauridae 17) Goniopholididae, 18) Bernissartiidae, 19) Dromaeosauridae, 20) Brachiosauridae, 21) Iguanodontidae, 22) Hadrosauridae 23) Triconodontidae, 24) Multituberculata, 25) Spalacotheriidae, 26) Tribotheria.

FIGURE 5. Percent abundance of crocodilian families.

FIGURE 6. Percent abundances of lizard species.

FIGURE 7. Principal component projections for six Cedar Mountain sites based on abundances of lizard species.

FIGURE 8. Percent abundances of mammal species: 1) *Astroconodon delictus*, 2) *Corviconodon utahensis*, 3) *Jugulator amplissimus*, 4) *Janumys erebos*, 5) *Paracimexomys perplexus*, 6) *P*. cf. *perplexus*, 7) *P*. cf. *robisoni*, 8) *Ameribaatar zofiae*, 9) *Bryceomys intermedius*, 10) *B*. cf. *intermedius*, 11) *Cedaromys bestia*, 12) *C*. cf. *bestia*, 13) *C*. *parvus*, 14) *C*. cf. *parvus*, 15) *Spalacolestes cretulablatta*, 16) *S*. *inconcinnus*, 17) *Spalacotheridium noblei*, 18) Picopsidae "A", 19) Picopsidae "B", 20) therian of metatherian-eutherian grade "A", 21) therian of metatherian-eutherian grade "B", 22) *Kokopellia juddi*, 23) marsupial "A", 24) marsupial "B", 25) marsupial "C" .

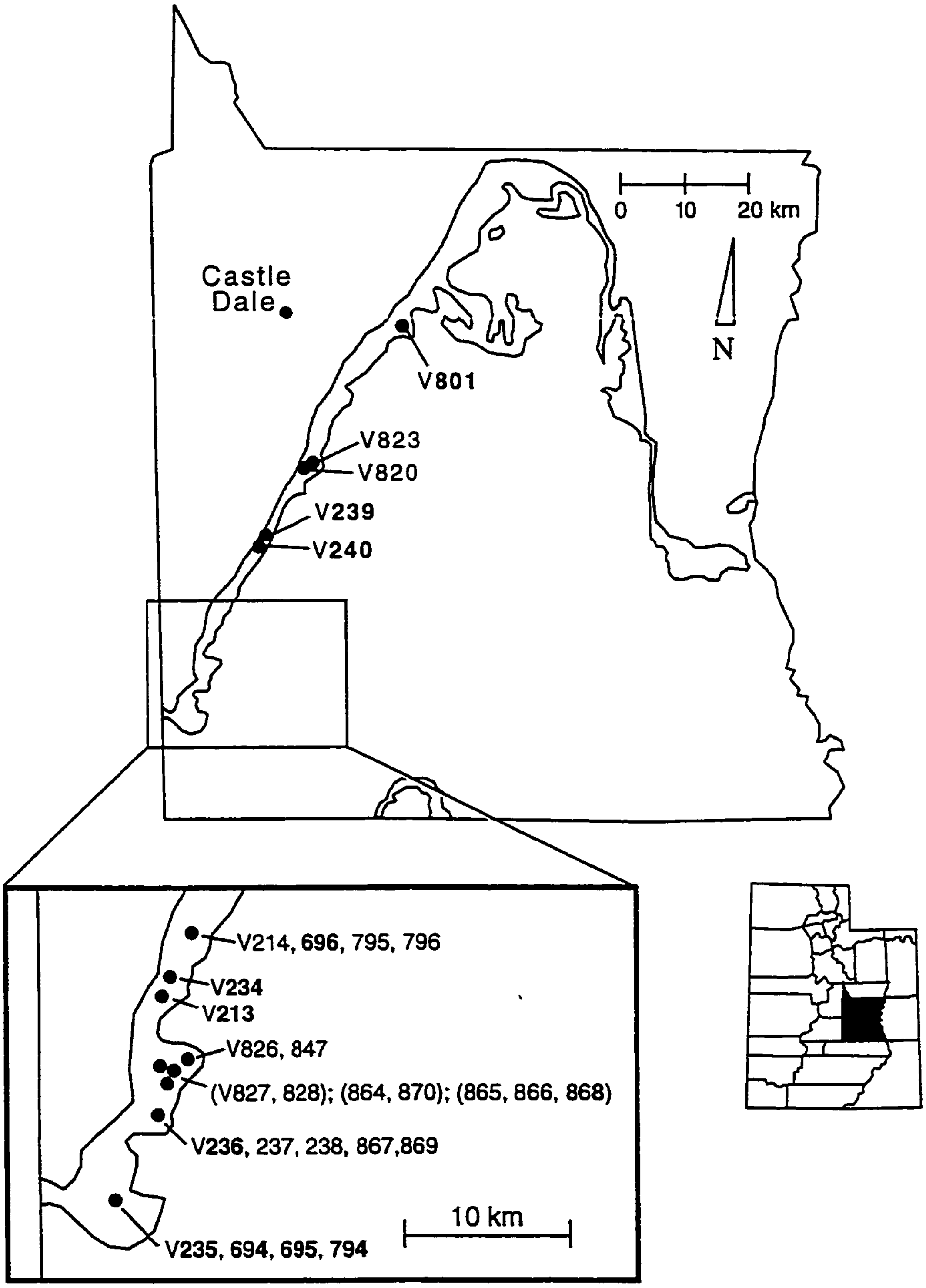
0 10 20 km
N
Castle Dale
V801
V823
V820
V239
V240
V214, 696, 795, 796
V234
V213
V826, 847
(V827, 828); (864, 870); (865, 866, 868)
V236, 237, 238, 867,869
V235, 694, 695, 794
10 km

FIGURE 1

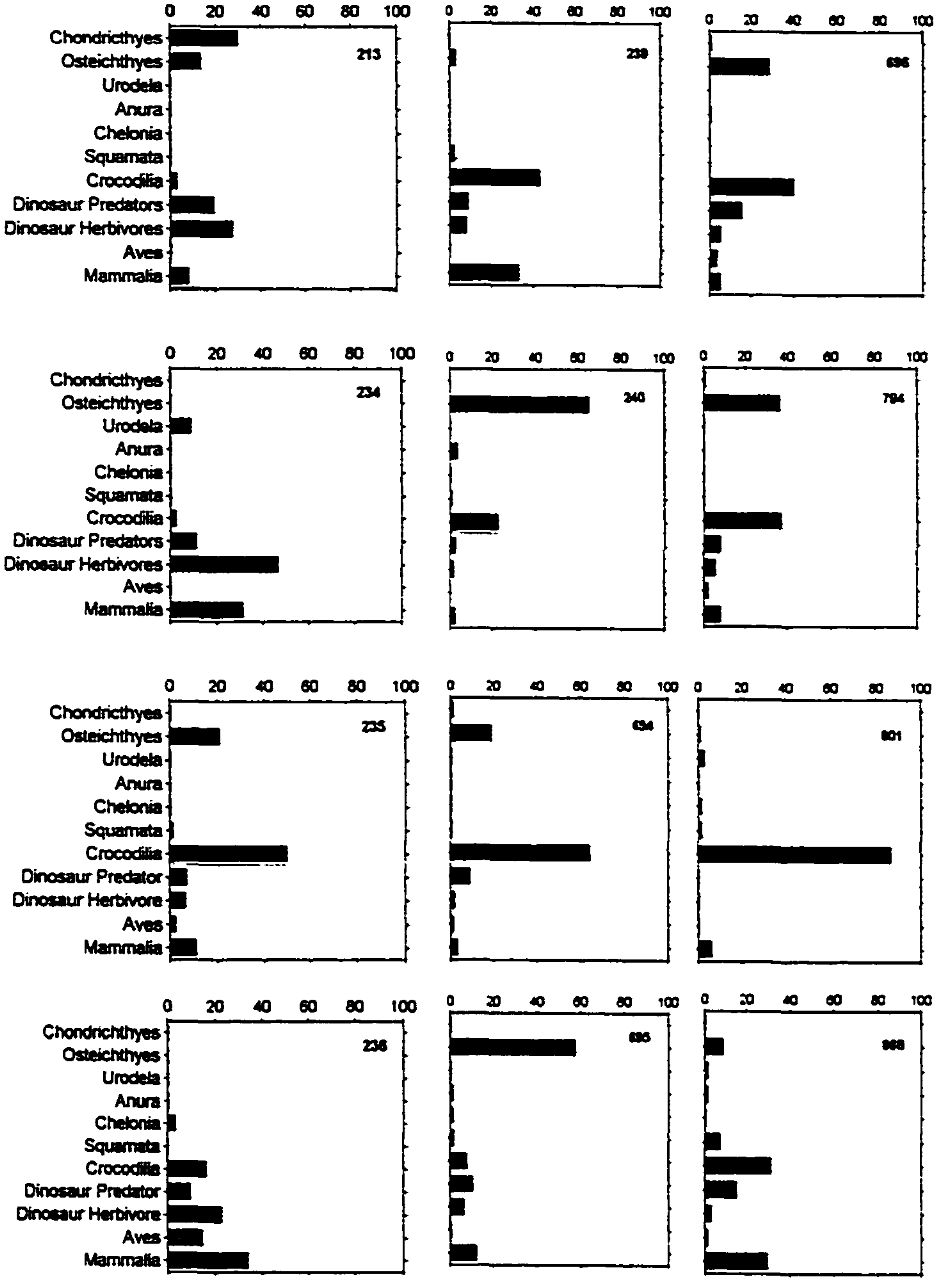
0 20 40 60 80 100
Chondricthyes
Osteichthyes
Urodela
Anura
Chelonia
Squamata
Crocodilia
Dinosaur Predators
Dinosaur Herbivores
Aves
Mammalia
213
239
696
234
240
794
Dinosaur Predator
Dinosaur Herbivore
235
634
801
Chondrichthyes
236
695
888

FIGURE 2

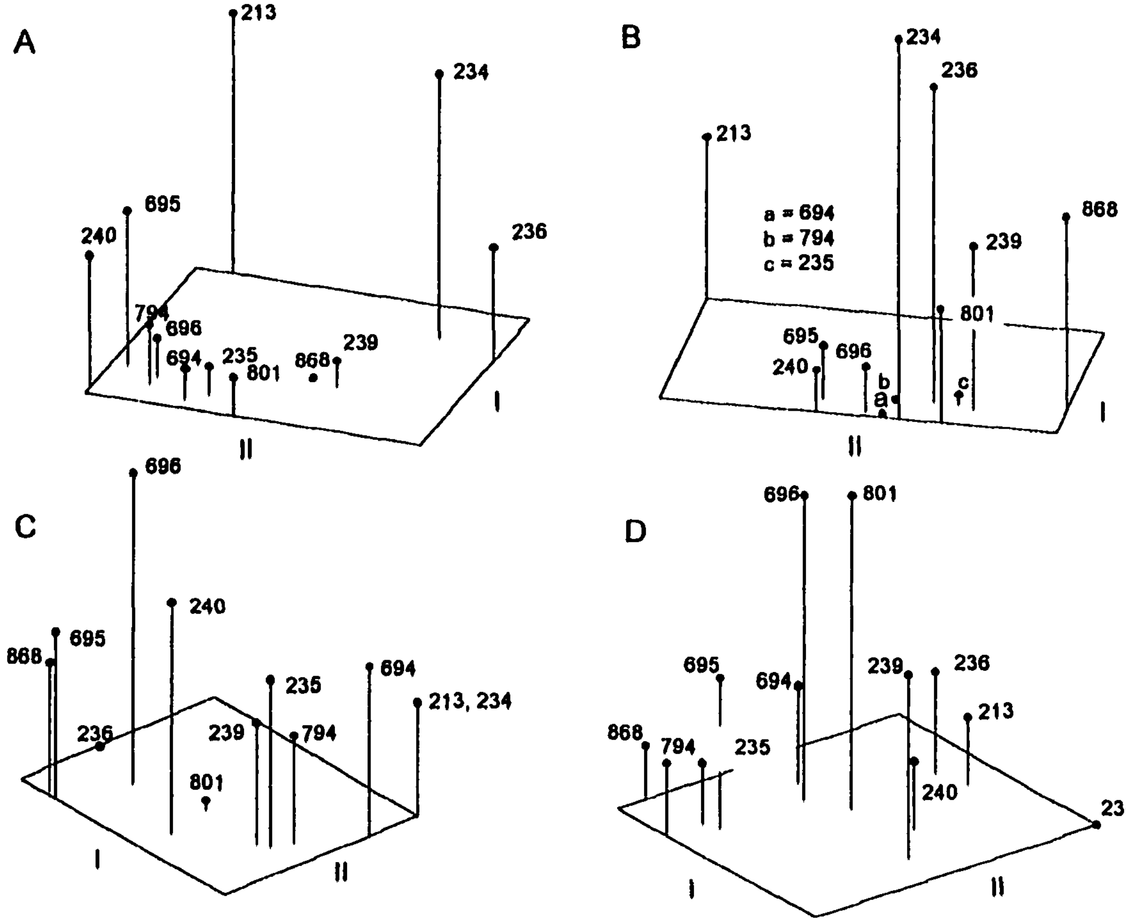
A
213
234
695
240
236
794
696
694
235
801
868
239
II
I
B
234
236
213
a = 694
b = 794
c = 235
868
239
801
695
696
240
b
a
c
II
I
C
696
240
695
868
235
694
213, 234
236
239
794
801
I
II
D
696
801
695
694
239
236
213
868
794
235
240
234
I
II

FIGURE 3

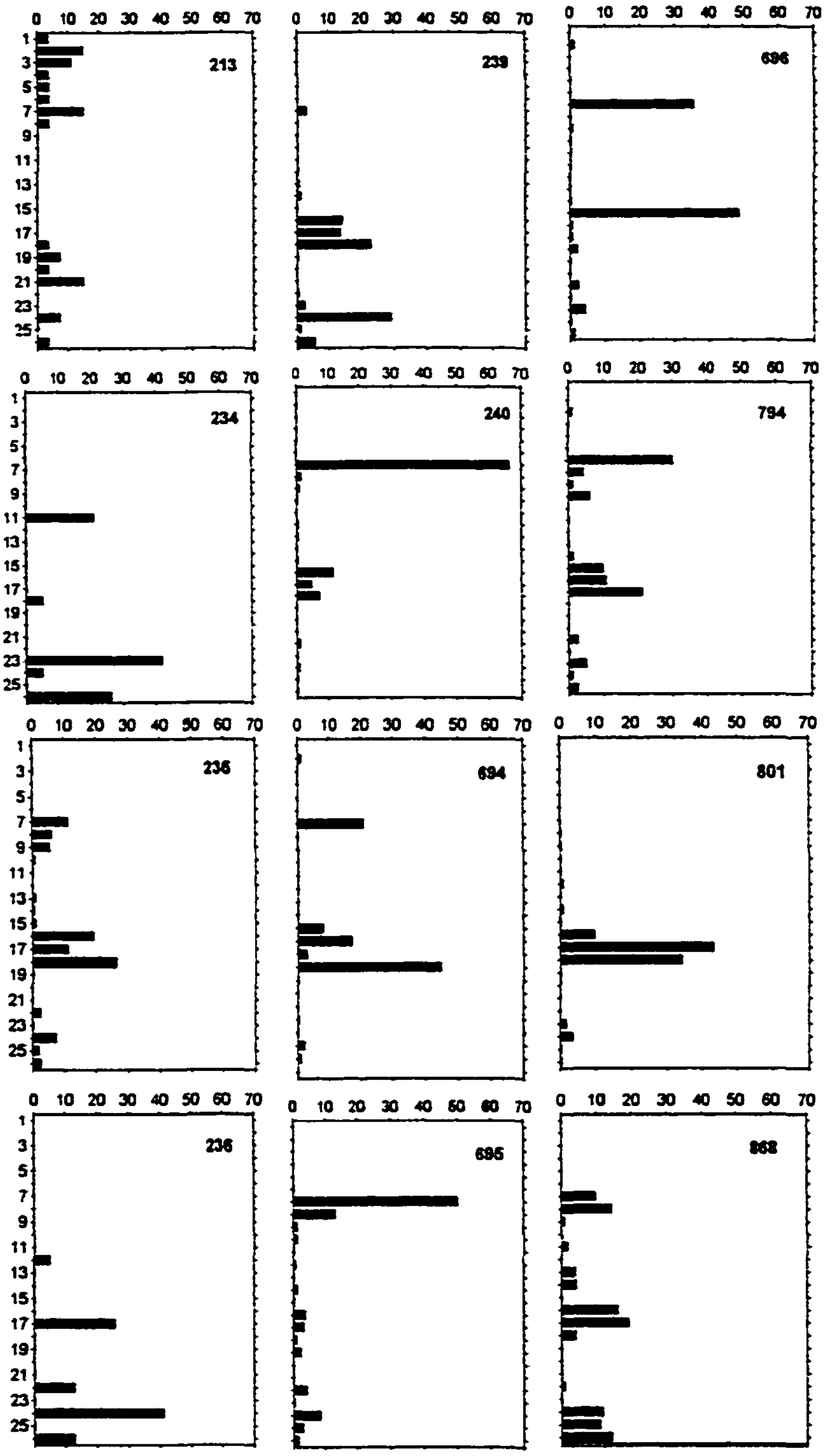
0 10 20 30 40 50 60 70
1 3 5 7 9 11 13 15 17 19 21 23 25
213
239
696
234
240
794
236
694
801
236
695
868

FIGURE 4

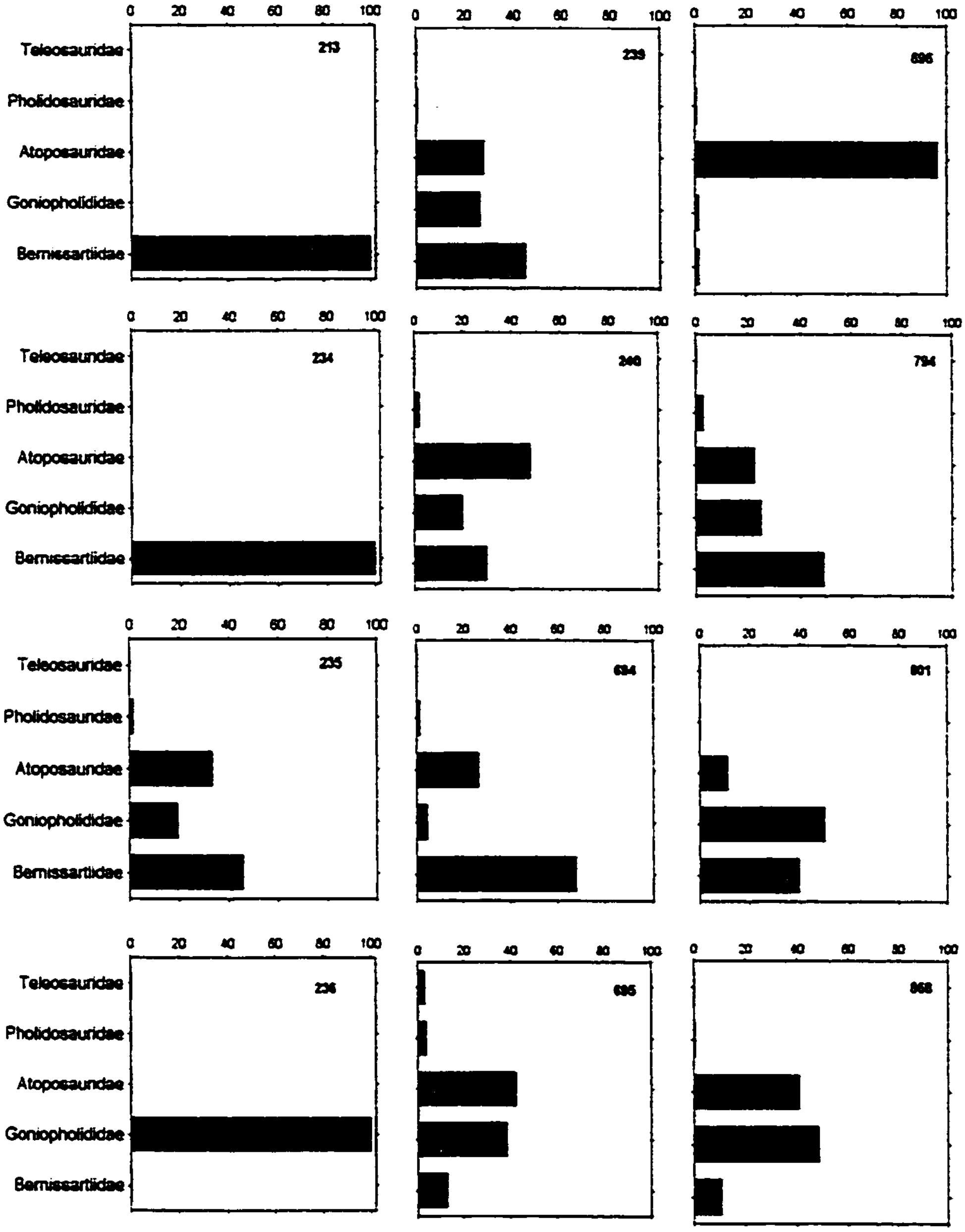
0
20
40
60
80
100
Teleosauridae
Pholidosauridae
Atoposauridae
Goniopholididae
Bernissartiidae
213
239
896
234
240
794
235
694
801
236
695
868

FIGURE 5

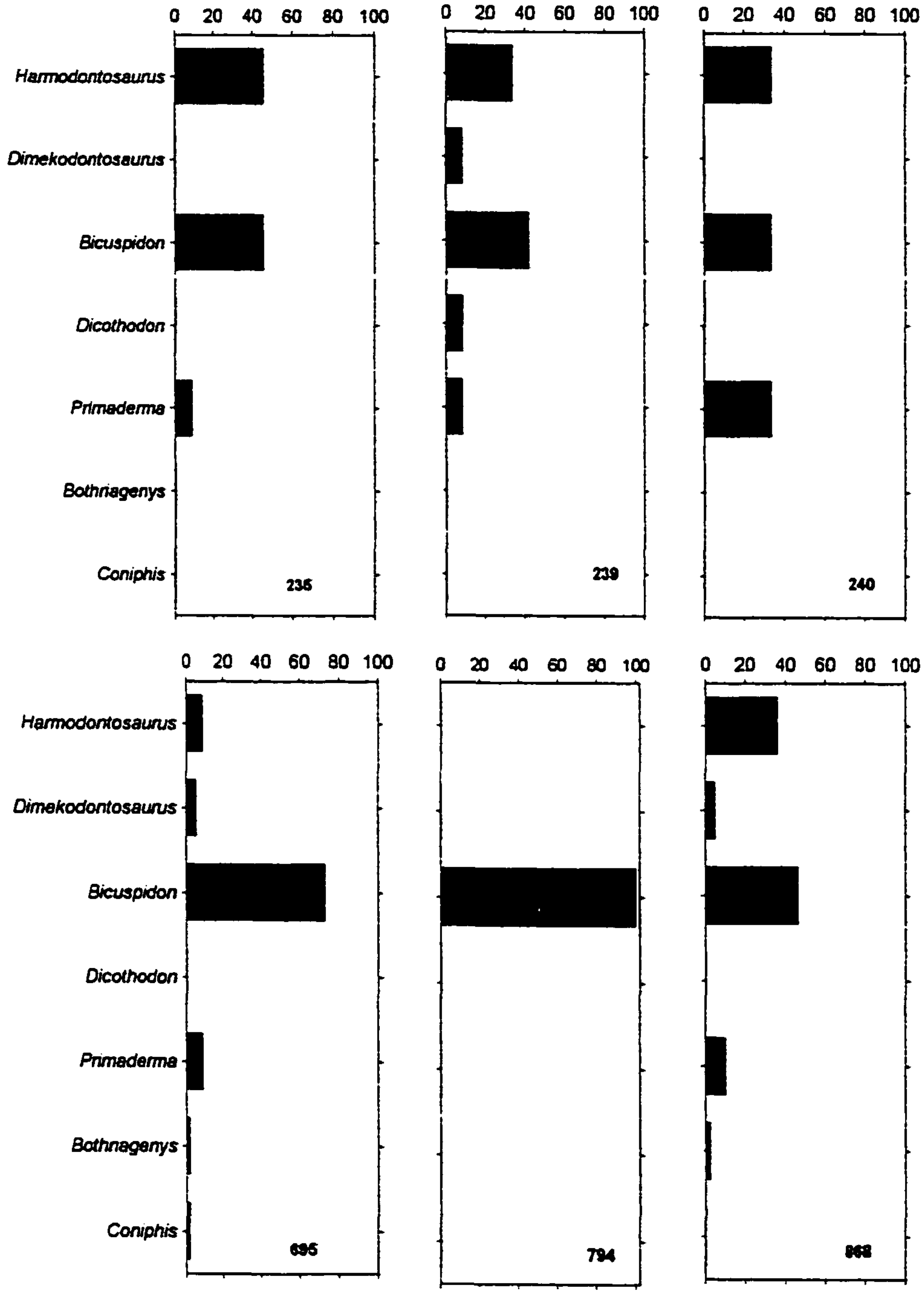
0 20 40 60 80 100
Harmodontosaurus
Dimekodontosaurus
Bicuspidon
Dicothodon
Primaderma
Bothriagenys
Coniphis
236
239
240
695
794
868

FIGURE 6

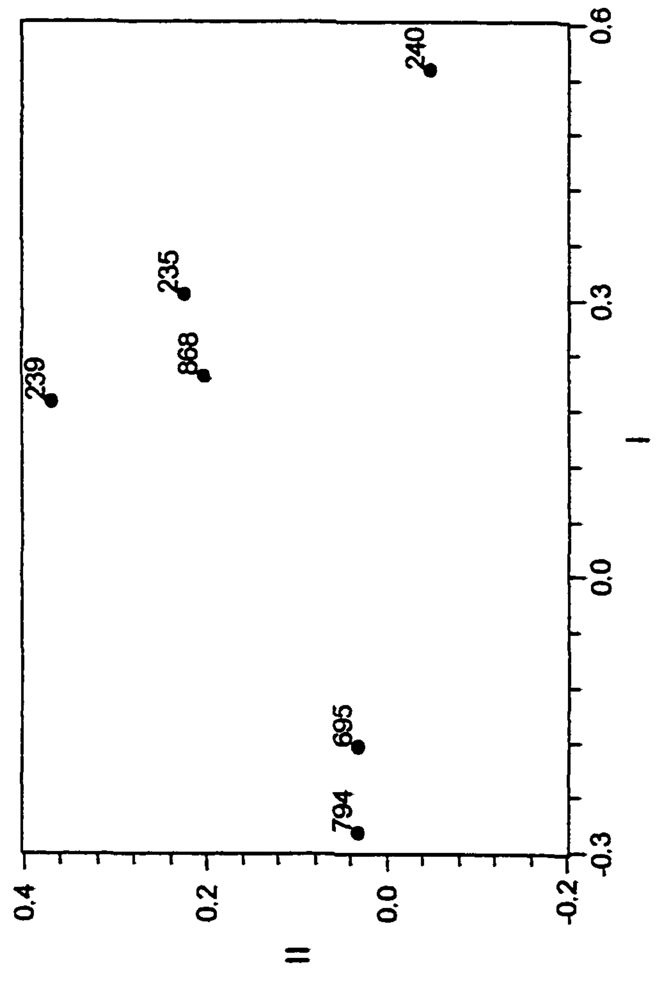

FIGURE 7

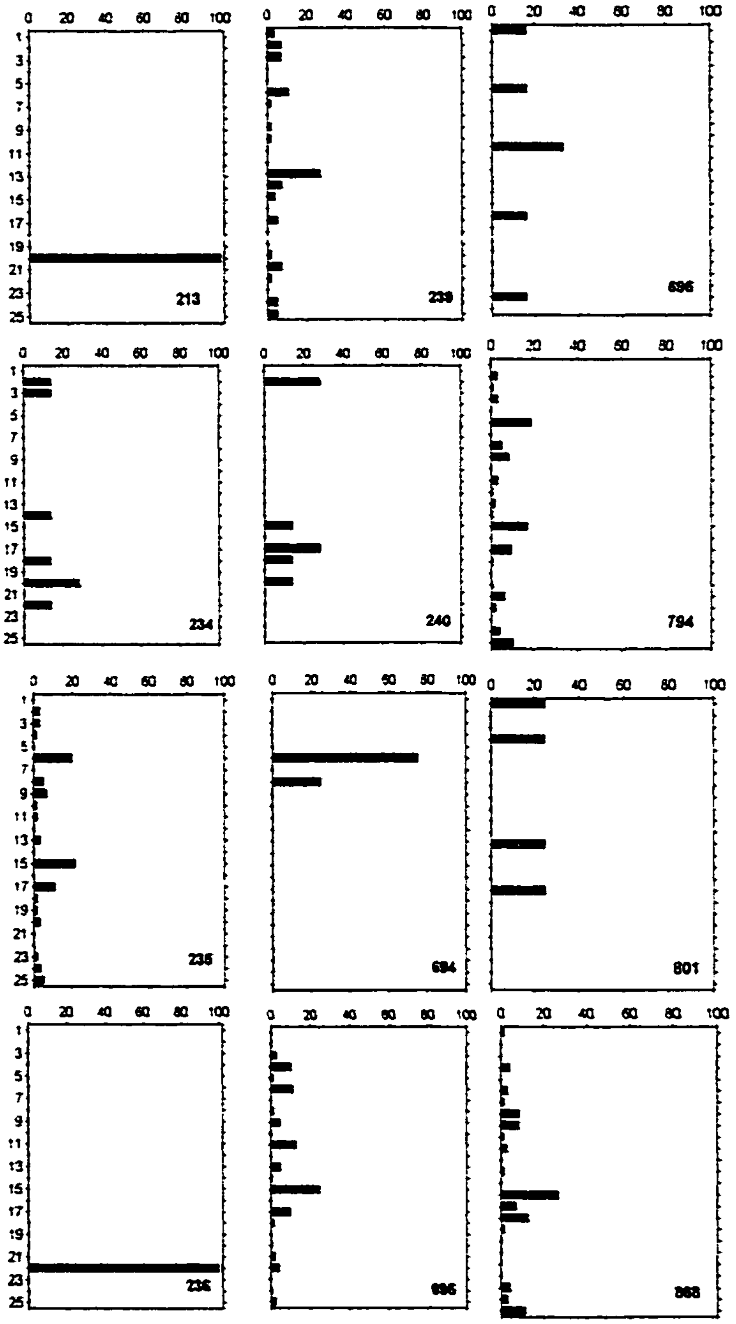
0 20 40 60 80 100
1 3 5 7 9 11 13 15 17 19 21 23 25
213
239
696
234
240
794
236
694
801
236
696
868

FIGURE 8

TABLE 1. Loadings for ubertaxa based on abundances at 12 microvertebrate localities. Numbers in bold indicate relatively high absolute values.

| | Principal component | | | |
|---|---|---|---|---|
| Taxon | I | II | III | IV |
| Chondricthyes | 0.58 | 0.53 | 0.32 | 0.05 |
| Osteichthyes | -0.34 | **0.68** | 0.06 | 0.40 |
| Urodela | -0.47 | -0.22 | **0.69** | -0.42 |
| Anura | **-0.90** | 0.20 | 0.31 | -0.05 |
| Chelonia | -0.78 | -0.31 | 0.36 | 0.29 |
| Squamata | -0.64 | 0.07 | -0.21 | **-0.64** |
| Crocodilia | -0.56 | -0.03 | **-0.64** | -0.09 |
| Theropoda | **0.84** | 0.32 | -0.16 | -0.23 |
| Ornithischia | 0.68 | -0.35 | **0.64** | -0.05 |
| Aves | -0.05 | **-0.73** | -0.15 | **0.62** |
| Mammalia | 0.36 | **-0.76** | -0.19 | -0.34 |
| Eigenvalue | 4.11 | 2.27 | 1.74 | 1.40 |
| Percent variance explained | 37.4 | 20.6 | 15.8 | 12.8 |

Table 2. Loadings for families based on relative abundances at 12 microvertebrate localities. Numbers in bold indicate relatively high absolute values.

| | Principal component | | |
|---|---|---|---|
| Taxon | I | II | III |
| Orectolobididae | 0.56 | **0.80** | 0.12 |
| Hybodontidae | 0.76 | 0.62 | 0.08 |
| Polyacrodontidae | 0.77 | 0.62 | 0.06 |
| Squatinidae | 0.56 | **0.80** | 0.12 |
| Sclerorhychidae | 0.56 | **0.80** | 0.12 |
| Rhinobatidae | 0.55 | **0.81** | 0.11 |
| Lepisosteidae | -0.06 | 0.32 | **-0.59** |
| Semionotidae | 0.17 | 0.22 | **-0.51** |
| Pycnodontidae | -0.16 | -0.33 | **-0.55** |
| Amiidae | -0.21 | -0.08 | -0.44 |
| Enchodontidae | **-0.96** | 0.28 | -0.01 |
| Prosirenidae | -0.80 | 0.24 | -0.01 |
| Albanerpetonidae | -0.23 | -0.05 | **0.62** |
| Scapherpetontidae | **-0.95** | 0.29 | 0.00 |
| Salamandridae | **-0.96** | 0.29 | 0.01 |

TABLE 2. Continued.

| Taxon | Principal component I | II | III |
|---|---|---|---|
| Sirenidae | **-0.95** | 0.28 | 0.00 |
| Glyptopsidae | **-0.94** | 0.29 | -0.01 |
| Trionychidae | **-0.95** | 0.29 | -0.01 |
| Pleurodontidae | -0.57 | 0.12 | 0.40 |
| Paramacellodidae | -0.12 | **-0.75** | 0.13 |
| Teiidae | -0.12 | **-0.77** | 0.06 |
| Polyglyphanodontinae | **-0.96** | 0.27 | 0.02 |
| Scincidae | **-0.96** | 0.29 | 0.01 |
| Monstersauria | **-0.93** | -0.03 | 0.05 |
| *Bothriagenys* | **-0.97** | 0.21 | 0.03 |
| Aniliidae | **-0.96** | 0.29 | 0.01 |
| Teleosauridae | **-0.95** | 0.29 | -0.02 |
| Pholidosauridae | -0.41 | 0.09 | -0.39 |
| Atoposauridae | -0.16 | -0.40 | -0.48 |
| Goniopholididae | -0.11 | -0.55 | 0.11 |
| Bernissartiidae | -0.05 | -0.21 | **-0.57** |

TABLE 2. Continued.

| | Principal component | | |
|---|---|---|---|
| Taxon | I | II | III |
| Dromaeosauridae | 0.65 | **0.72** | 0.04 |
| Troodontidae | **-0.96** | 0.28 | -0.01 |
| Tyrannosauridae | **-0.96** | 0.29 | 0.00 |
| Brachiosauridae | 0.56 | **0.80** | 0.11 |
| Hadrosauridae | 0.70 | 0.54 | 0.22 |
| Pachycephalosauridae | -0.72 | 0.20 | 0.36 |
| Nodosauridae | **-0.96** | 0.19 | 0.03 |
| Neoceratopsia | **-0.96** | 0.29 | 0.01 |
| Triconodontidae | -0.22 | 0.02 | **0.60** |
| Multituberculata | 0.17 | -0.28 | 0.47 |
| Spalacotheriidae | 0.13 | **-0.80** | 0.01 |
| Tribosphenida, inc. sed. | 0.14 | -0.47 | **0.80** |
| Marsupialia | -0.38 | -0.32 | **0.81** |
| Eigenvalue | 20.35 | 9.03 | 4.53 |
| Percent variance explained | 46.3 | 20.5 | 10.3 |

TABLE 3. Loadings for crocodile families based on abundances at 12 microvertebrate localities. Numbers in bold indicate relatively high absolute values.

| | Principal component | | |
|---|---|---|---|
| Taxon | I | II | III |
| Teleosauridae | **0.89** | 0.45 | 0.09 |
| Pholidosauridae | **0.90** | 0.40 | 0.15 |
| Atoposauridae | -0.57 | 0.22 | **0.79** |
| Goniopholididae | -0.44 | 0.59 | **-0.67** |
| Bernissartiidae | 0.41 | **-0.90** | -0.14 |
| | | | |
| Eigenvalue | 2.29 | 1.57 | 1.13 |
| Percent of variance explained | 45.8 | 31.4 | 22.6 |

TABLE 4. Loadings for squamate species based on abundances at 12 microvertebrate localities. Numbers in bold indicate relatively high absolute values.

| | Principal component | |
|---|---|---|
| Taxon | I | II |
| *Harmodontosaurus emeryensis* | 0.86 | 0.38 |
| *Dimekodontosaurus madseni* | -0.84 | 0.46 |
| *Bicuspidon numerosus* | **-0.99** | 0.01 |
| *Dicothodon moorensis* | -0.71 | **0.53** |
| *Primaderma nessovi* | 0.71 | **-0.54** |
| *Bothriagenys mysterion* | -0.83 | -0.50 |
| *Coniophis* sp. | -0.84 | -0.50 |
| | | |
| Eigenvalue | 4.83 | 1.42 |
| Percent variance explained | 69.1 | 20.3 |

Table 5. Loadings for mammal species based on abundances at 12 microvertebrate localities. TMEG = therians of metatherian - eutherian grade. Numbers in bold indicate relatively high absolute values.

| | Principal component | | | |
|---|---|---|---|---|
| Taxon | I | II | III | IV |
| *Astroconodon delicatus* | 0.20 | 0.09 | **0.88** | 0.16 |
| *Corviconodon utahensis* | 0.23 | -0.61 | -0.31 | 0.41 |
| *Jugulator amplissimus* | 0.31 | **-0.76** | -0.27 | -0.21 |
| *Janumys erebos* | -0.13 | 0.18 | 0.49 | 0.36 |
| *Paracimexomys perplexus* | -0.39 | 0.21 | -0.03 | **-0.57** |
| *Paracimexomys* cf. *perplexus* | **0.85** | 0.32 | 0.15 | 0.00 |
| *Paracimexomys* cf. *robisoni* | **0.83** | 0.31 | 0.07 | -0.23 |
| *Ameribaatar zofiae* | -0.14 | **0.70** | -0.42 | -0.25 |
| *Bryceomys intermedius* | -0.75 | 0.41 | -0.42 | -0.08 |
| *Bryceomys* cf. *intermedius* | 0.76 | 0.40 | -0.01 | -0.22 |
| *Cedaromys bestia* | -0.15 | 0.14 | 0.58 | 0.06 |
| *Cedaromys* cf. *bestia* | **0.80** | 0.34 | 0.07 | -0.13 |
| *Cedaromys parvus* | -0.09 | -0.38 | 0.45 | -0.34 |
| *Cedaromys* cf. *parvus* | 0.44 | **-0.73** | -0.22 | -0.24 |

Table 5. Continued.

| | Principal component | | | |
|---|---|---|---|---|
| Taxon | I | II | III | IV |
| *Spalacolestes cretulablata* | -0.78 | 0.27 | -0.38 | 0.25 |
| *Spalacolestes inconncinus* | 0.26 | **0.68** | -0.26 | 0.18 |
| *Spalacotheridium noblei* | -0.45 | 0.09 | 0.36 | **0.71** |
| Picopsidae "A" | 0.44 | -0.47 | -0.43 | **0.55** |
| Picopsidae "B" | **0.81** | 0.39 | 0.01 | -0.03 |
| TMEG "A" | 0.60 | -0.26 | -0.35 | 0.14 |
| TMEG "B" | -0.23 | -0.36 | 0.10 | **-0.69** |
| *Kokopellia juddi* | 0.53 | -0.01 | -0.15 | -0.18 |
| Marsupial "A" | 0.44 | **0.75** | -0.27 | 0.16 |
| Marsupial "B" | -0.14 | 0.09 | 0.52 | -0.32 |
| Marsupial "C" | -0.70 | 0.29 | -0.39 | -0.25 |
| Eigenvalue | 6.90 | 4.64 | 3.34 | 2.66 |
| Percent of variance explained | 27.6 | 18.6 | 13.4 | 10.7 |

# Geology of 11 Mussentuchit microvertebrate sites in the Cedar Mountain Formation: taphonomic implications

Patricia Goldberg

RRH: GEOLOGY OF MICROVERTEBRATE SITES

LRH: PATRICIA GOLDBERG

Abstract. – The geology and taphonomy of 11 fossil microvertebrate sites from the Cedar Mountain Formation in Emery County, Utah, were examined to determine the nature and extent to which abiotic features influence taxonomic distribution according to site. Two measures of energy level were examined using thin sections obtained from hand samples: maximum clast size and percent clasts (relative to mud). The average mass of fossil specimens from each site was also determined and used as an estimate of energy. Additionally, depositional environments were determined based on sedimentary features. A correlation matrix based on these geological features was calculated and compared to correlation matrices previously calculated based on taxonomic similarity for ubertaxa, families, crocodile families, and mammal species. The matrix based on geologic similarity did not correlate with any of the matrices based on taxonomic similarity. The rankings of sites based on each of the different geological features were compared with rankings derived from loadings from the principal components analyses on taxonomic similarity using Kendal's tau. Only one of these comparisons corresponded with statistical significance. Taxonomic groupings between sites do not appear to be related to taphonomic processes in this case.

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## Introduction

Taphonomy is the study of factors and processes that affect an organism from death until recovery from the fossil record. Many studies in paleoecology attempt to reconstruct communities as they existed in life. Taphonomic processes can greatly distort how the life assemblage is represented in the fossil assemblage (Behrensmeyer and Kidwell 1985). At least three major biases result from taphonomic processes: differential loss of species and elements, spatial averaging, and temporal averaging.

Small species are commonly under-represented in fossil assemblages through differential loss. Small bones are destroyed faster by weathering processes, trampling, and scavenging (Behrensmeyer 1978; Behrensmeyer et al. 1979). In addition to losing species completely, the relative abundance of species is altered, with abundance becoming increasingly biased and under-represented as size decreases (Behrensmeyer et al. 1979; Damuth 1982). Differential loss of elements within a species also occurs because smaller and more fragile elements are more readily destroyed (Behrensmeyer 1978). Of small vertebrate specimens, often only the hardest elements, typically teeth and heavily plated scales, remain in abundance.

Spatial averaging occurs through transport of remains. Carcasses and elements may be transported away from the death site and deposited in aggregations of fossils that do not accurately represent life assemblages (Behrensmeyer 1988). If the scale at which this occurs is large, associations and habitats cannot be inferred directly. Finally, slow deposition, over the course of hundreds to thousands of years, along with reworking of older fossils, causes temporal averaging (Beherensmeyer 1982; Alsan and Behrensmeyer

1996). This also may cause difficulties in interpreting relative abundances and associations.

Many fossil assemblages are subject to all of these biases, some more than others. In general, higher-energy systems exacerbate most of these problems. Fossil localities may differ compositionally simply because the abiotic processes responsible for burial differed, rather than because any biological differences were actually present. Differences in faunal composition between sites can be interpreted as being biologically significant with greater confidence when sites are isotaphonomic (Behrensmeyer et al. 1992).

The Mussentuchit local fauna (Cifelli et al. 1999) is one assemblage that lends itself to a study of this kind. Confined in space to a single county and confined in time to the upper part of a single member, it has been extensively sampled (Goldberg 2000) at multiple sites. The faunal composition of 12 microvertebrate sites from the Mussentuchit Member of the Cedar Mountain Formation has been characterized previously (Goldberg 2000). These assemblages have been found to vary significantly among sites, even though the sites are geographically and stratigraphically confined. The geology and taphonomy of these microvertebrate localities are examined herein to determine if postmortem abiotic processes can account for the patterns seen in the fossil record.

The Cedar Mountain Formation was deposited in eastern and central Utah during the Early and mid-Cretaceous. Stokes (1944, 1952) originally described the Cedar Mountain Formation, dividing it into two members, the lower Buckhorn Conglomerate and an upper, unnamed shale. The shale member has recently been divided into four members (Kirkland et al. 1997): the Yellow Cat, Poison Strip, Ruby Ranch and Mussentuchit (from oldest to youngest). Of the four, only the Ruby Ranch and Mussentuchit Members are present in the study area in Emery County, Utah. Both rock bodies consist predominantly of mudstones, but they are easily distinguished based on the presence of calcareous nodules in the Ruby Ranch. The Mussentuchit Member lacks these nodules and is highly smectitic. Cifelli et al. (1997) have dated this member at 98.39 + 0.07 Ma using $^{40}$Ar/$^{39}$Ar techniques, placing it on the Albian-Cenomanian boundary (Gradstein et al. 1995).

The depositional environment of the Mussentuchit Member was interpreted as an aggradational meandering river system (Harris 1980; Nelson and Crooks 1987; Pomes 1988; Currie 1998). The majority of the rock is overbank (floodpain) deposit consisting of laminated mudstone and claystone with backswamps of carbonaceous shales, but other environments are present. Point bars of silty sandstone along the curving margin of the sandstone stream channels are evident, and natural levees of laminated coarse siltstone and slickenside crevasse splays also occur. Other depositional environments include lacustrine deposits of nodular limestone and terrestrial paleosols.

If differences in taphonomic processes (size sorting, spatial and temporal averaging) among sites was a significant factor in determining the composition of the fossil assemblages, then similarity in taxonomic composition will be reflected in similarity in geologic features. If geologic similarity does not correspond with taxonomic similarity, then other factors must be responsible for differences among sites.

## Methods

The Cedar Mountain Formation in Emery County, Utah was visited in the summer of 1999 in order to collect geologic data related to taphonomy. Eleven of the 12 well-sampled microvertebrate sites characterized in Goldberg (2000) were relocated. Ten sites were located with absolute confidence (V234, V235, V239, V240, V794, V694, V695, V696, V801, V868) and one (V236) with moderate confidence by R. Cifelli and R. Nydam (Fig. 1). Site V213 was not located. An attempt was made to place as many of the sites as possible in relative order in the stratigraphic column. Four of the 11 sites were placed in sections previously characterized by Cifelli et al. (1999), and another five were tentatively added in this study.

The rock face and hand samples from each site were examined in the field for sedimentary features that might provide clues to depositional environment. Sites were then characterized as representing fluvial oxbow, floodplain, splay, or channel deposits. In addition, hand samples were brought back to the museum and thin-sectioned to aid in the interpretation of depositional environment and energy. These sections were cut by the thin-section laboratory at the Department of Geology, University of Oklahoma, and examined under a compound microscope. Standard geologic terminology is used to describe clast size: silt, < 0.062 mm; very fine sand, 0.062-0.125 mm; fine sand, 0.126-0.250 mm; and medium sand, 0.251-0.500 mm.

Finally, an attempt was made to characterize taphonomic features of the fossil assemblages by site and by taxa. Three measures were used to reflect transport energy: maximum clast size, amount of clasts in the deposit, and average mass of fossils collected from the deposit. Clast sizes and amounts were determined by examination of the thin-sections. Average fossil mass was included because it was possible that the river had the potential to carry larger particles, but none were available in the system. The microvertebrate fossils were for the most part tiny, disarticulated, and isolated, suggesting that they had been transported as clasts in the river. If so, they might reflect energy better than the fine sand and mud.

Around 20 kg of matrix was collected and processed from each site. All fossils, including unidentifiable bone pebbles, were picked. These were weighed and an average mass per specimen was calculated. An average mass of specimens also was calculated for each family, using catalogued specimens available in the collections at the Oklahoma Museum of Natural History. Very large specimens were not included in the calculations because their rarity combined with small sample sizes would create a large bias. In addition, specimens embedded in matrix, coated or impregnated with glue, or mounted on pins were excluded from the analysis. This resulted in the exclusion of 12 of the 48 families in which all specimens were unavailable for weighing.

These data were combined and used to construct a similarity matrix among sites based on geologic features related to taphonomy. Subenvironments were ranked from lowest to highest energy, with the oxbow being 1, floodplain 2, splay 3, and channel 4. Similarly, maximum clast sizes observed in the thin-sections were ranked, with silt being 1, very fine sand 2, fine sand 3, fine-medium sand 4, and medium sand 5. Additionally, the amounts of clasts in the thin sections were ranked from lowest to highest. Finally, the average fossil mass at each site was incorporated into the matrix. Correlation coefficients were calculated for each pair of sites.

Four correlation matrices based on faunal similarity among sites were constructed using standardized abundance data on the same taxonomic levels as in Goldberg (2000): ubertaxa (Chondrichthyes, Osteichthyes, Anura, Urodela, Chelonia, Squamata, Crocodilia, Theropoda, Ornithischia, Aves, and Mammalia); all families; crocodile families; and mammal species.

Each of these matrices was then compared with the correlation matrix based on geologic similarity using a Mantel test (Sokal and Rohlf 1995) to determine whether sites similar in geology were also similar in taxonomic composition. In Mantel tests, the correlation between two independent similarity or dissimilarity matrices is calculated by summing the products of each pair of corresponding cells in the matrices. The significance of this value is determined by constructing a probability distribution based on randomizing one of the matrices and calculating the coefficient many times (500 in this case).

Mantel tests may show no overall correlation between two matrices even when correlations between individual variables exist, if those correlations are swamped by variables that do not correlate. To test for this, correlation in rankings among each of the geologic variables (the three measures of energy [clast size, clast amount, and fossil mass], stratigraphic position, and depositional environment) and loadings from prinicpal components analyses at each taxonomic level (ubertaxa, families, crocodile families, and mammal species) were calculated using Kendal's tau (Sokal and Rohlf 1995). Because faunal composition and average fossil mass may have been interrelated, the average mass of the ubiquitous crocodile teeth was calculated for each site. Rankings based on this measure were compared to taxonomic similarity at each level.

## Results

Stratigraphic relationships.—Determining the relative positions of sites in the column was complicated by the terrain and distance between some of the sites. In addition, the Mussentuchit Member is composed of smectitic muds. The infrequent rains cause erosion and swelling of the muds on the sides of the hill, obscuring bedding within the member. However, one marker bed is available, the ash layer used to date the sites. Sites V235, V694, and V794 are located at nearly the same level above the ash (Plate 1) while V695 (Plate 1) and V868 (Plate 2) are located immediately below the ash layer. The two sites near Short Canyon are located in different horizons of the Mussentuchit Member. Site V239 is near the top of the unit, just below the Dakota Formation (Plate 3), and locality V240 is near the base of the Mussentuchit Member, adjacent to the contact with the Ruby Ranch Member (Plate 4). These two sites are located 30 km from the main cluster, and it is difficult to evaluate how the two groups relate stratigraphically, given local variation in unit thickness. Similarly, V234 (Plate 5) and V801 (Plate 6) are isolated, but both are near the bottom of the Mussentuchit Member. Sites V236 and V696 could not be placed within the column, because of their isolation from other sites and lack of markers. Sections were measured previously by Cifelli et al. (1999);

however, only four of the 11 microsites in my analysis (V235, V694, V695, and V794) were placed within those sections.

Sedimentary structures.— Sites V236 and V239 were identified as channel deposits due to the presence of relatively large (pebble-sized) clasts. Site V239 also has a pebble lag at its base and a brown sandstone lateral to the site. Sites V794 and V868 were identified as either channel deposits or splays. Both have abundant clay balls within the mudstone. Sandy areas are intermingled with the fine mudstone at site V868 while site V794 is relatively coarse overall. The latter site also has a large amount of plant debris.

Sites V235 and V696 were identified as splays. The deposit at V235 is coarse, blocky, and amorphous. In addition, plant debris is present. Site V696 contains clay clasts and is located approximately 10 m from a small channel. Site V240 may also have been deposited in a splay event. This site contains sandy areas and clayballs, but also slickensides from repeated wetting and drying.

Site V234 was interpreted as a floodplain or splay, and is located proximal to a large east-west flowing channel with adjacent pointbar (Plate 5). The deposit is fine grained and without structure. Sites V694 and V695 also were interpreted as floodplain deposits based on fine grain size and faint laminae. Site V694 contains slickensides and is heterogenous in grain size with sandy areas. Site V695 lacks these features. Because of water and ash accumulation, this site was interpreted as a low spot on the floodplain. In addition, plant activity (rooting, mottling) is lacking, and some fossils remain articulated.

Site V801 was interpreted as an abandoned channel (oxbow). Stacking channel sands are located under this site and many fossils were found articulated, including several turtle shells. Freshwater invertebrates are abundant, and the mottled coloration indicates a high amount of biological activity. Subenvironments are summarized in Table 1.

Thin sections.—Clast size and proportion of mud to sand was readily observable using thin-sections of rock from the 11 sites investigated (Fig. 2). Hand samples from sites V695 and V868 were variable in coarseness, so the single small thin-sections described herein must be interpreted with caution. Overall, the thin-sections were fine grained with a high mud content.

Site 868 was the coarsest, with the largest clasts being medium sand grains. Clasts comprised approximately 35% of the rock, and mud matrix filled the space between the grains. Grains varied from subangular to well-rounded and were poorly to moderately sorted. Site V236 contained the second largest clasts, again medium sand grains. Grains were moderately sorted, subrounded in shape, and comprised 30% of the rock. Site V794 also was relatively coarse, with fine to medium sand clasts making up 15% of the rock and dark mud filling the remainder. Grains were subangular and moderately sorted.

Sites V235 and V239 were very similar, with the thin sections composed mostly of moderately to poorly sorted subangular to subrounded clasts. Fine to medium sand clasts filled 20% of the rock at site V235 and very fine sand clasts comprised 35% of the rock at site V239. Mud filled the space between grains.

Sites V240, V694, V695, and V696 were predominantly mud with very poorly sorted subangular to subrounded clasts sprinkled within the matrix. Clast content varied from 15% at site V240 to 10% at site V694 to 5% at sites V695 and V696. Maximum clast size varied little between these sites, with site V240 containing a few medium-sized sand clasts while V694, V695, and V696 contained fine sand grains.

Site V234 was composed mostly of mud with only very small clasts (very fine sand) included. These clasts were moderately sorted subangular to subrounded grains comprising 30% of the rock, the remaining 70% being mud. Finally, site V801 was entirely mud without clasts. Clasts sizes and amounts are summarized in Table 1.

Taphonomic analysis.—Site V239 contained the largest fossil specimens, with an average mass of 41.1 mg. This was three times as great as site V236, which had the second largest specimens (mean = 14.9 mg). Sites V868 and V696 also had relatively large fossils, (mean = 8 and 6.1 mg, respectively). Sites V240 and V694 had moderately sized particles (ca. 4 mg), while sites V235 and V794 had smaller fossils (ca. 2 mg). Sites V801, V695, and V234 had the smallest fossils, averaging less than 2 mg. Average specimen masses are provided in Table 1.

A scatterplot (Fig. 3) was constructed to group the sites based on geologic similarity, using maximum clast size, clast amount, and fossil mass. Sites V694, V695, and V696 formed a tight group, while sites V235 and V794 formed another cluster nearby. Sites V236 and V868 plotted together, forming a close pair. Sites V234, V239 and V801 stood apart from other sites.

The average mass of specimens varied greatly by taxon, over four orders of magnitude. Pycnodontid teeth were smallest, averaging 0.596 mg, while pleurosternid shell fragments were largest, averaging 3394 mg per specimen. The mean mass was 0.4064 mg ±1.012 (standard deviation). A complete listing of average specimen mass for each family is provided in Table 2.

Four matrix comparisons were done: correlations among sites based on geologic similarity were compared to taxonomic correlation at the levels of ubertaxa, families, crocodile families, and mammal species. None of these comparisons were significant: mammal species ($\underline{p} = 0.38$), family ($\underline{p} = 0.75$), crocodile families ($\underline{p} = 0.29$), and ubertaxa ($\underline{p} = 0.90$; Fig. 4).

The analyses using Kendal's tau demonstrate that many of the geologic features correlate with one another. Clast amount correlates with clast size ($\underline{p} = 0.01$) and depositional environment ($\underline{p} = 0.01$). Environment also correlates with fossil mass ($\underline{p} = 0.003$). Faunal composition does not appear to correspond with these geologic features, however. The loadings of the principal components for site distributions of ubertaxa, families, crocodile families, and mammal species did not correspond with any of the geologic features (clast amount, clast size, depositional environment, fossil mass, crocodile specimen mass), with one exception (Table 3). The average mass of crocodile specimens corresponded with ubertaxa loadings. This may be a significant relationship, but 1 of the 24 comparisons is likely to have a significant value through chance alone.

## Discussion

In many paleontological studies, differences in faunal composition among sites are correlated with the position of the sites in the stratigraphic column. Directional environmental or climatic changes, such as warming, cooling, wetting, or drying, may produce a directional change in floral and faunal composition over time scales ranging from ecological succession in an abandoned channel (Wing 1984) to range-shifts associated with glacial advances and retreats (e.g., Davis 1976). Over even longer time scales evolution and extinction produce changes in fossil assemblages that can be traced through the stratigraphic column. This is the basis of the entire field of biostratigraphy. These types of changes are particularly well documented in Cenozoic mammal communities (MacFadden and Cerling 1996; Webb 1983) and across extinction boundaries (Archibald and Bryant 1990). Taphonomic or ecological differences occurring at smaller scales, patchy in time, will not be correlated with stratigraphic position.

The relative position of 9 of the 11 sites in the stratigraphic column was determined, but this seemed to be unrelated to taphonomy and taxonomy. There was no trend in grain size, clast amount, or fossil mass moving up the column. In addition, there was no correlation between stratigraphic position and taxonomy at the level of ubertaxa, family, crocodile family, or mammal species. This lack of directional change in faunal composition suggests that the time scale represented is too short to detect evolutionary turnover, and that differences in faunal composition among sites are not due to long-term, directional ecological changes.

Energy level is key to interpreting the extent by which the composition of an assemblage has been altered. The energy available for transport is related to the degree of spatial averaging. Higher-energy environments carry remains farther away from the site of death (Beheresmeyer et al. 1992). In addition, higher-energy environments favor the deposition of larger elements and species. These environments are able to transport larger particles and may either destroy or winnow smaller, more fragile specimens. Different subenvironments have different characteristic energy levels, but the processes involved in depositing sediment affect faunal composition in other ways as well (Beherensmeyer et al. 1992).

However, matrix comparisons showed no significant correlation between geologic features related to deposition and any of the taxonomic groupings at the Mussentuchit sites (Fig. 4). This can also be seen by comparing the scatterplot of sites based on geologic features (Fig. 3) with the principal components projection plots based on taxonomic composition at each level (Goldberg 2000). Moreover, only 1 of the 24 comparisons between geologic variables and taxonomic groups using Kendal's tau were significant (even without Bonferonni corrections): crocodile specimen mass and ubertaxa. This provides strong negative evidence suggesting that taphonomic processes are not causing the variability in taxonomic composition seen between sites. Geological variables are interrelated as expected, and the data and methods used to evaluate relationships appear sound.

Finally, there are significant differences in size of specimens among taxa (Table 2), which almost certainly results in the death assemblage being inaccurately represented in the fossil record. However, these processes seem to be working in similar ways among the 11 sites, so comparisons between sites should be valid. Composition in this case is unrelated to depositional energy and specimen size. This is shown in a plot of the proportion of specimens in each family, arranged in ascending order by mass (Fig. 5), at each site. Different sites are compositionally different (with different sites peaking at different taxa), but all sites contain a variety of taxa of different sizes (the peaks for any given site are not confined to a particular size range). Site V234, which is by measures used here a low-energy site, contains the remains of moderately sized Albanerpetontidae and Bernissartiidae, as well as small mammal teeth. Sites V236 and V868 are both high-energy systems, but have abundant small mammal teeth in addition to large crocodile teeth and turtle shells.

While there are differences in the geology among sites, the differences are relatively minor and appear not have affected faunal composition. Clasts are all small and the deposits predominantly mud; gravel, pebbles, and even coarse sands are not found at any of the sites, except as lag in channels. The angularity of the sand grains varied greatly, even within sites, and sorting was typically poor to moderate, suggesting that sediment load exceeded the capacity of the river to carry it. The energy of the entire system and all of its subenvironments overall is low, so that small or light fossils were carried and deposited with minimal damage. It is unlikely even in the highest energy environments (small- to medium-sized channels) that fossils were transported on a regional scale. The faunal composition seems to have been altered in the same way among sites, and explanations for differences in faunas need to be sought elsewhere.

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APPENDIX. Color plates of selected microvertebrate localities in the Mussentuchit Member of the Cedar Mountain Formation, Emery County, Utah.

PLATE 1. Sites V695, V235, V794, and V694, from left to right.

PLATE 2. Site V868.

PLATE 3. Site V239.

PLATE 4. Site V240.

PLATE 5. Site V234 with pointbar and channel.

PLATE 6. Site V801.

PLATE 1

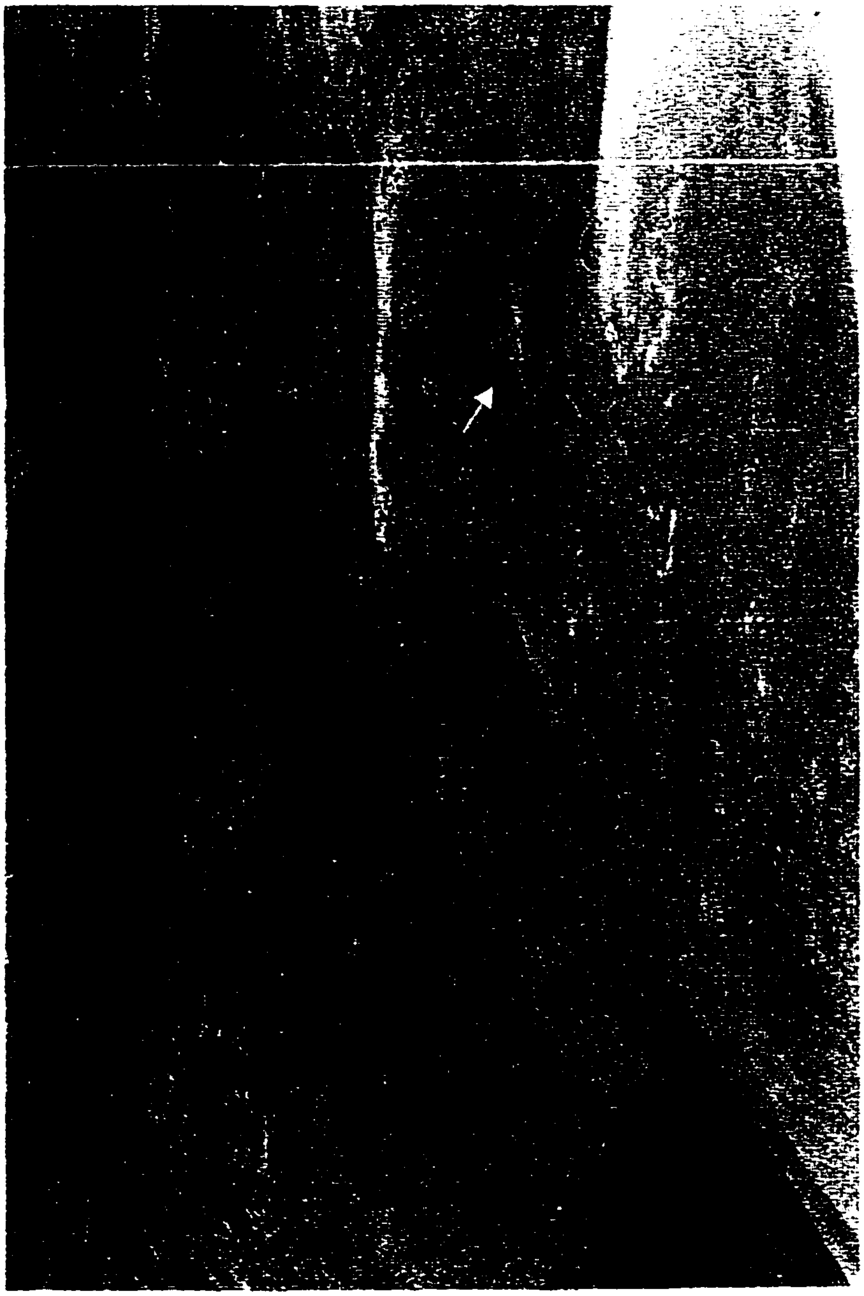


PLATE 2

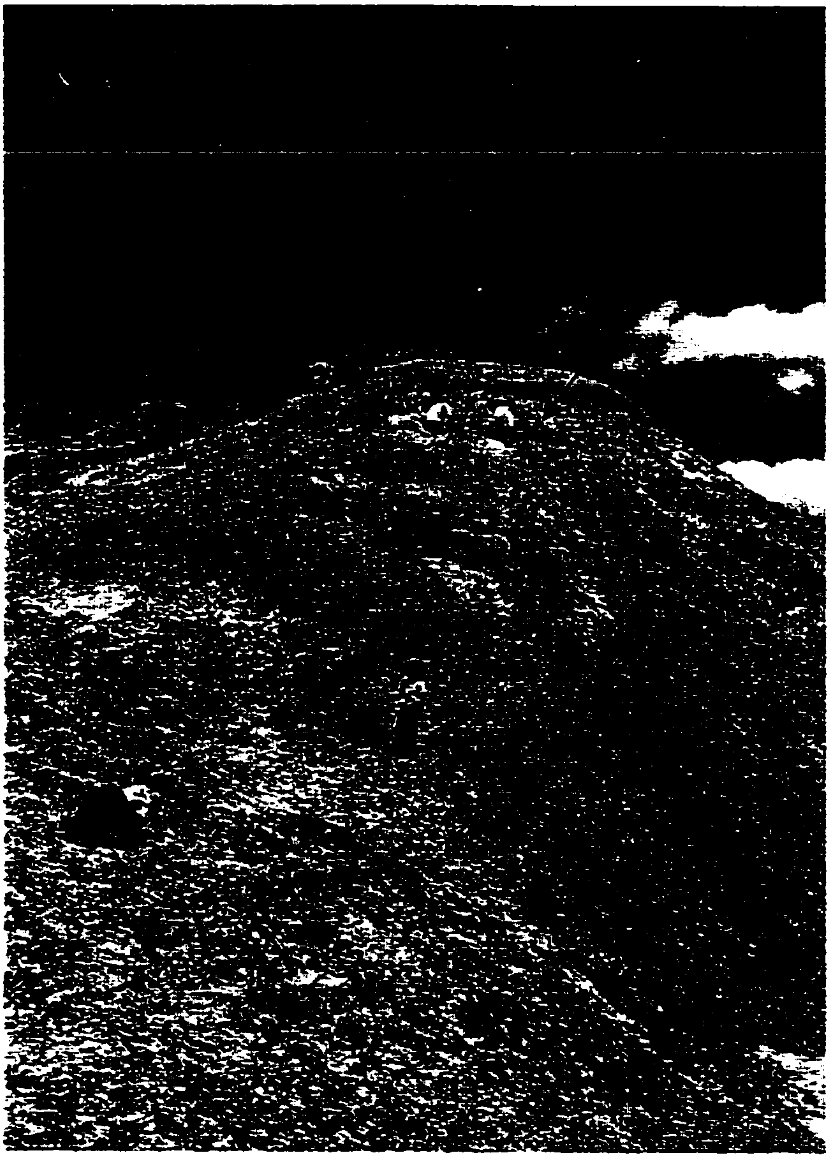
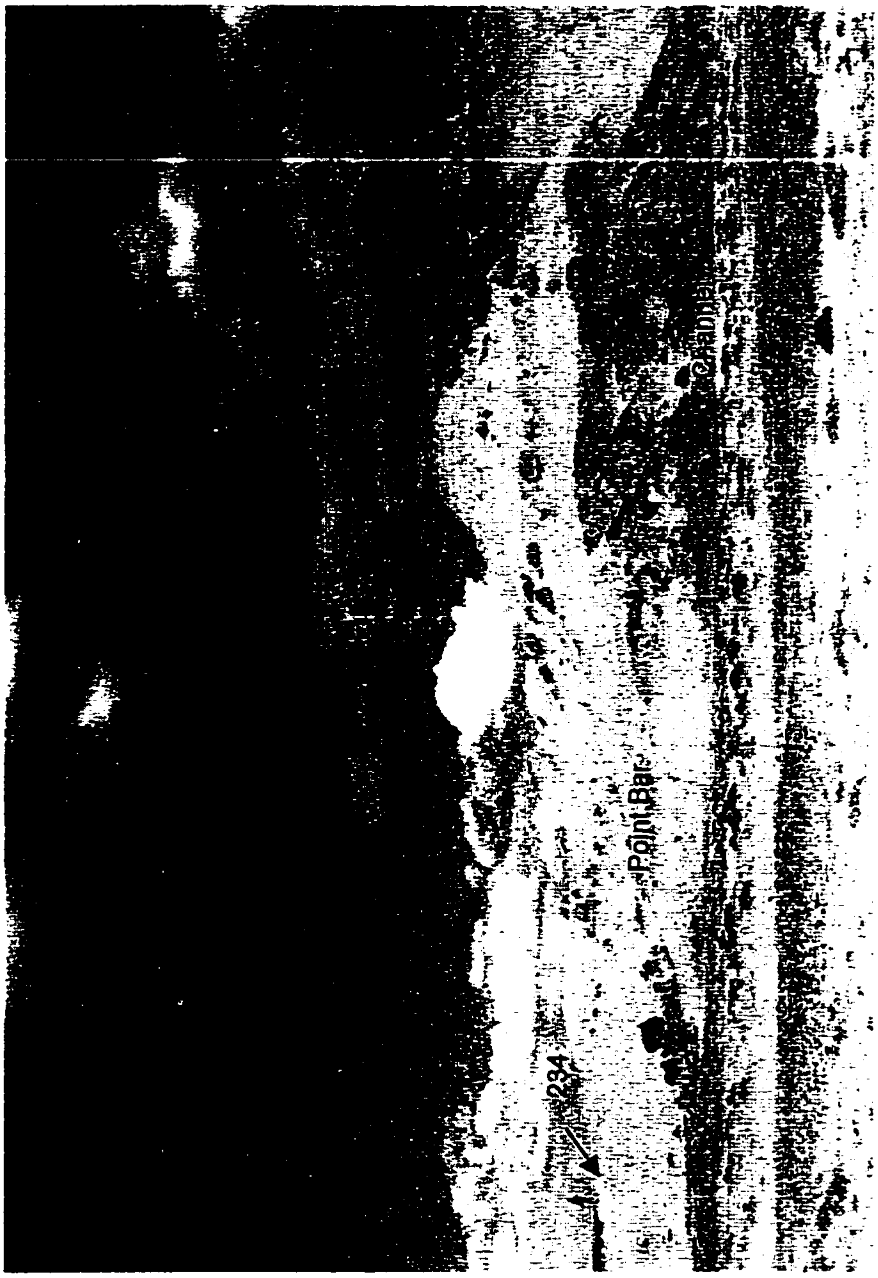


PLATE 3

PLATE 4



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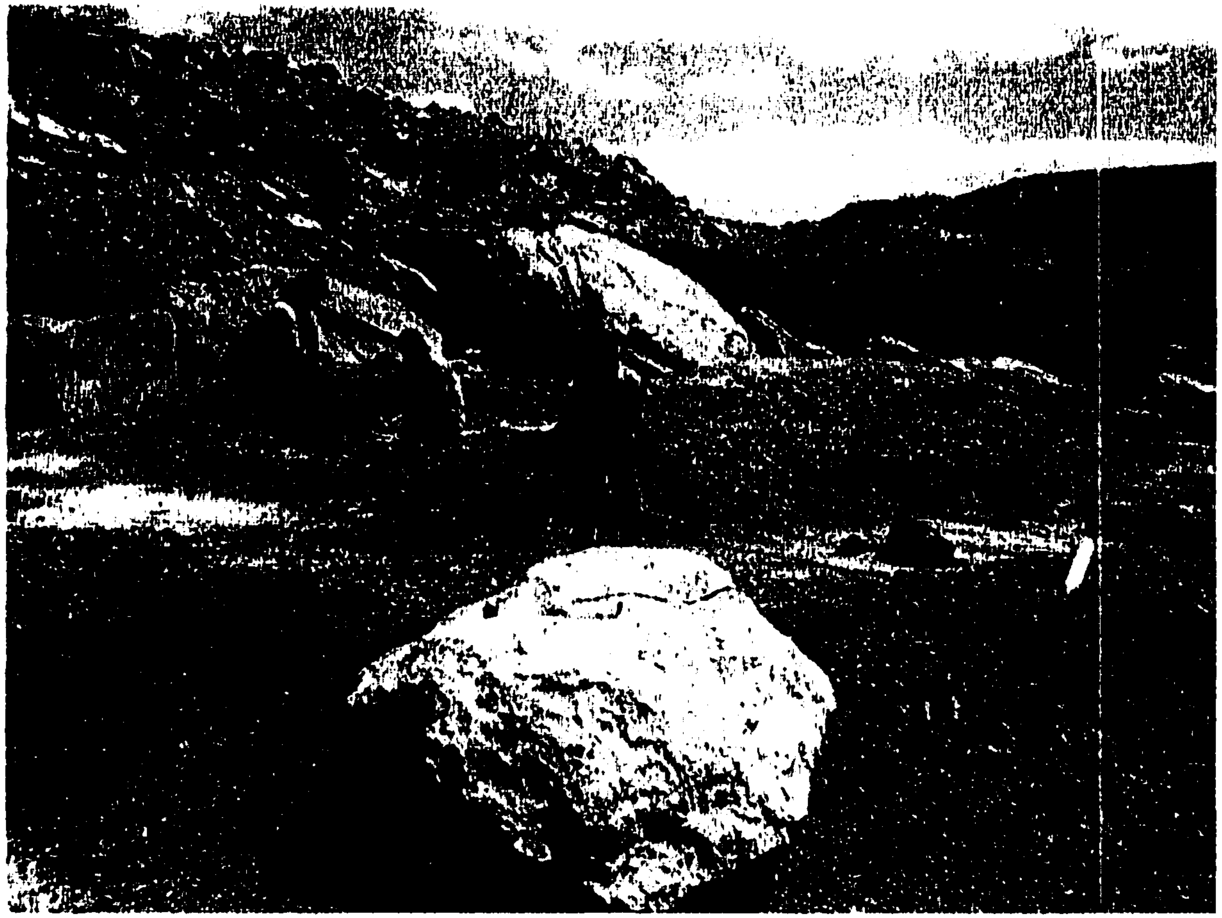

Plate 6

FIGURE 1. Map of microvertebrate localities, from the Mussentuchit Member of the Cedar Mountain Formation, analyzed in this study.

FIGURE 2. Thin-sections from 11 microvertebrate sites from the Mussentuchit Member of the Cedar Mountain Formation. Clayballs in 695 and 240 are roughly 0.75 mm in diameter.

FIGURE 3. Scatterplot of Cedar Mountain fossil localities based on geologic charateristics related to deposition. Z-axis represents fossil mass.

FIGURE 4. Scatterplot of Pearson's correlation coefficients (calculated for each pair of sites) based on geologic similarity vs. taxonomic similarity of (A) ubertaxa, (B) families, (C) crocodile families, and (D) mammal species.

FIGURE 5. Percentages of specimens in each family-level group at each site arranged in ascending order, by average mass: 1) Pycnodontidae, 2) Tribotheria, 3) Spalacotheriidae (Symmetrodonta), 4) Polyglyphanodontinae, 5) Orectolobididae, 6) Rhinobatoidae, 7) Sclerorhynchidae, 8) Triconodontidae, 9) Multituberculata, 10) Amiidae, 11) Squatinidae, 12) Semionotidae, 13) Hybodontidae, 14) Lepisosteidae, 15) Teiidae, 16) Albanerpetontidae, 17) Atoposauridae, 18) Bernissartiidae, 19) Paramacellodidae, 20) Teleosauridae, 21) Aves, 22) Pholidosauridae, 23) Anura, 24) Nodosauridae, 25) Theropoda, 26) Brachiosauridae, 27) Goniopholididae, 28) Hadrosauridae, 29)

Pachycephalosauridae, 30) Monstersauria, 31) Dromaeosauridae, 32) Trionychidae, 33) Pleurosternidae, 34) Glyptopsidae.

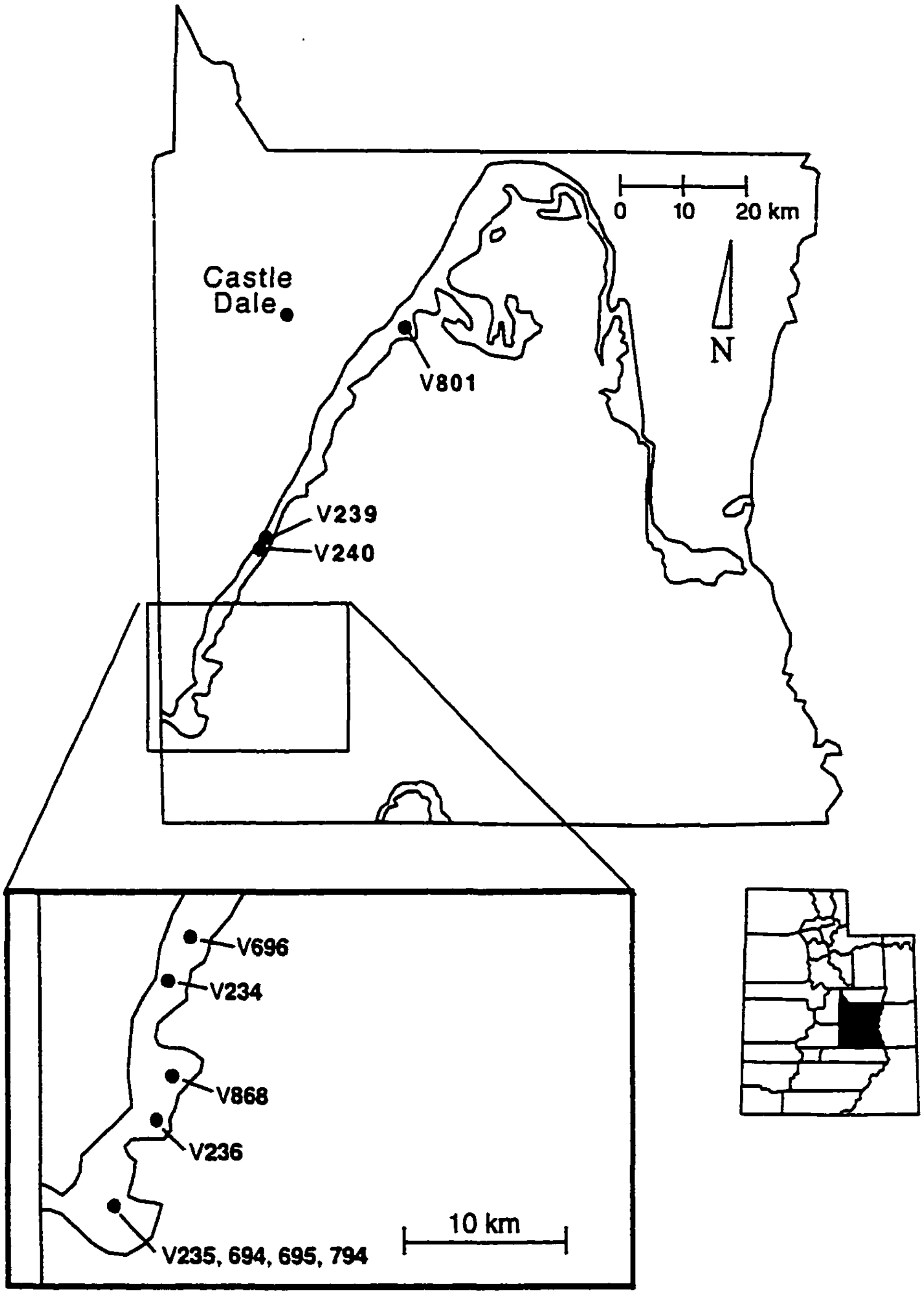
0
10
20 km
N
Castle Dale
V801
V239
V240
V696
V234
V868
V236
V235, 694, 695, 794
10 km

FIGURE 1

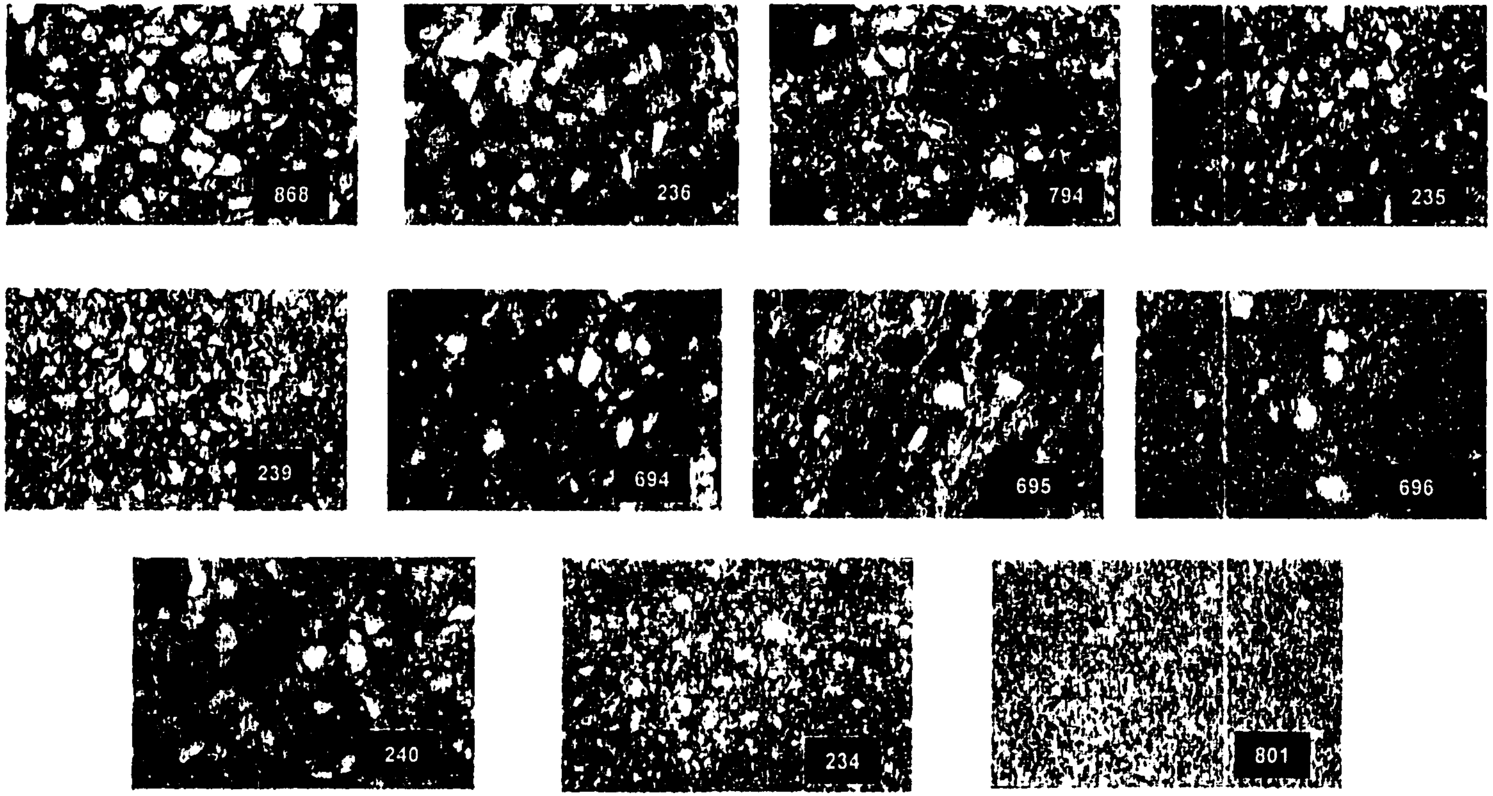

FIGURE 2

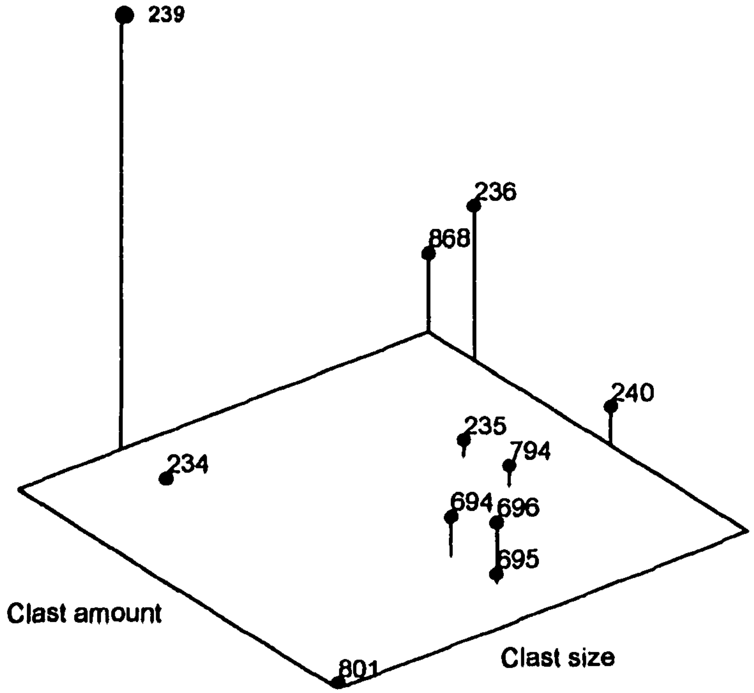
239
236
868
240
235
794
234
694
696
695
Clast amount
801
Clast size

FIGURE 3

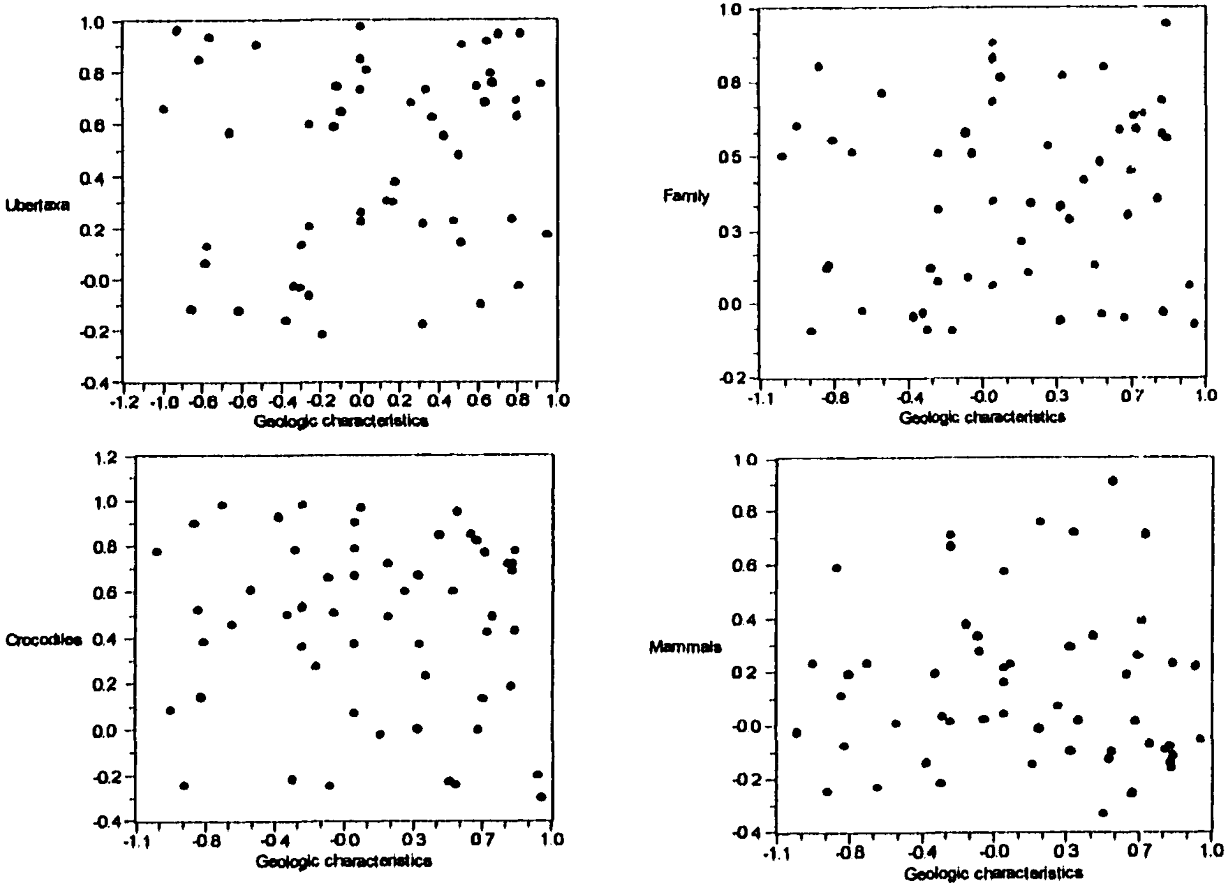
Ubertaxa
1.0
0.8
0.6
0.4
0.2
-0.0
-0.2
-0.4
-1.2 -1.0 -0.8 -0.6 -0.4 -0.2 0.0 0.2 0.4 0.6 0.8 1.0
Geologic characteristics
Family
1.0
0.8
0.5
0.3
0.0
-0.2
-1.1 -0.8 -0.4 -0.0 0.3 0.7 1.0
Geologic characteristics
Crocodiles
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-1.1 -0.8 -0.4 -0.0 0.3 0.7 1.0
Geologic characteristics
Mammals
1.0
0.8
0.6
0.4
0.2
-0.0
-0.2
-0.4
-1.1 -0.8 -0.4 -0.0 0.3 0.7 1.0
Geologic characteristics

FIGURE 4

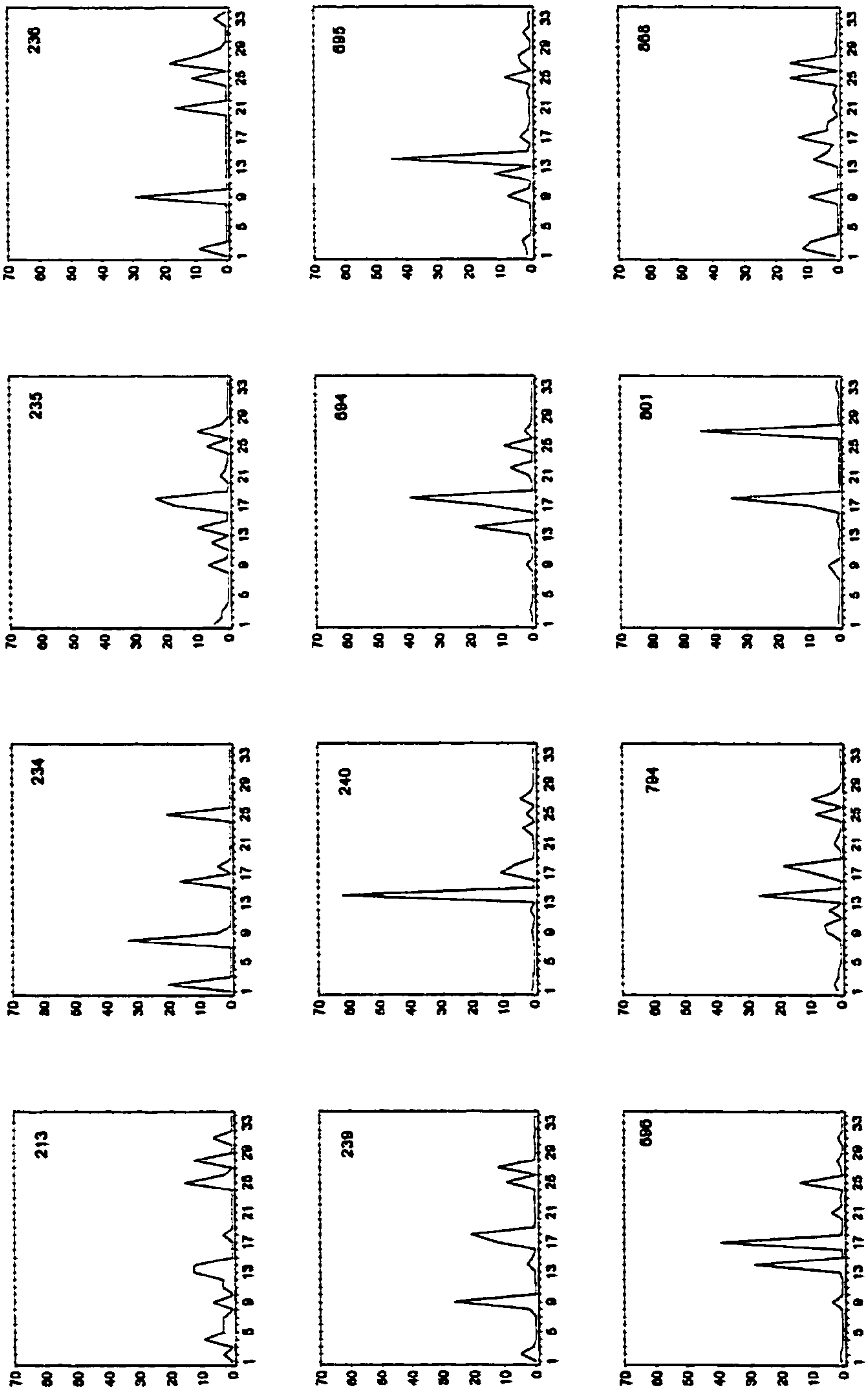
213
234
235
236
239
240
694
695
696
794
801
868
0
10
20
30
40
50
60
70
1
5
9
13
17
21
25
29
33

FIGURE 5

TABLE 1. Summary of geologic features related to taphonomy at 11 Cedar Mountain sites.

| | Field observations | | Thin sections | | Average fossil mass (mg) |
|---|---|---|---|---|---|
| Site | Position in column | Subenvironment | Maximum clast size | Percent clasts | based on matrix samples |
| 234 | low | splay/floodplain | very fine sand | 30 | 0.64 |
| 235 | above ash | splay/floodplain | fine-medium sand | 20 | 2.05 |
| 236 | ? | channel | medium sand | 30 | 14.90 |
| 239 | high | channel | very fine sand | 35 | 41.10 |
| 240 | low | splay | medium sand | 15 | 4.28 |
| 694 | above ash | floodplain | fine sand | 10 | 4.00 |
| 695 | below ash | floodplain | fine sand | 5 | 1.47 |
| 696 | ? | splay | fine sand | 5 | 6.08 |
| 794 | above ash | channel/splay | fine-medium sand | 15 | 2.35 |
| 801 | low | oxbow | silt | 0 | 1.13 |
| 868 | below ash | channel/splay | medium sand | 35 | 7.96 |

TABLE 2. Average specimen mass (mg) and standard deviations for each family (NA = not available).

| Family | Mean | Standard deviation | Elements preserved |
|---|---|---|---|
| Orectolobididae | 1.00 | NA | teeth |
| Hybodontidae | 2.20 | 0.829 | teeth |
| Polyacrodontidae | 0.95 | 0.660 | teeth |
| Squatinidae | 2.00 | NA | teeth |
| Sclerorhynchidae | 1.49 | 0.893 | teeth |
| Rhinobatoidea | 1.31 | 0.972 | teeth |
| Lepisosteidae | 3.05 | 1.823 | teeth, scales |
| Semionotidae | 2.13 | 0.727 | teeth, scales |
| Pycnodontidae | 0.60 | 0.064 | teeth |
| Amiidae | 1.80 | 1.350 | teeth, vertebrae |
| Enchodontidae | NA | NA | teeth |
| Prosirenidae | NA | NA | jaw fragments |

TABLE 2. Continued.

| Family | Mean | Standard deviation | Elements preserved |
|---|---|---|---|
| Albanerpetontidae | 4.50 | 4.950 | jaw fragments |
| Scapherpetonidae | NA | NA | jaw fragments |
| Salamandridae | NA | NA | vertebrae |
| Sirenidae | NA | NA | jaw fragments |
| Anura | 44.22 | 82.664 | skeletal fragments |
| Glyptopsidae | 4756.00 | 5118.039 | carapace and plastron fragments |
| Trionychidae | 1264.00 | NA | carapace and plastron fragments |
| Pleurosternidae | 3394.43 | 2365.266 | carapace and plastron fragments |
| Paramacellodidae | 14.67 | 8.959 | jaw fragments |
| Teiidae | 4.38 | 6.599 | teeth and jaws |
| Scincidae | NA | NA | jaw fragments |
| Polyglyphanodontidae | NA | NA | teeth |

TABLE 2. Continued.

| Family | Mean | Standard deviation | Elements preserved |
|---|---|---|---|
| Monstersauria | 1109.50 | 1556.342 | skull and jaw fragments, vertebrae |
| Aniliidae | NA | NA | jaw fragments |
| Teleosauridae | 25.00 | NA | teeth |
| Pholidosauridae | 40.04 | 106.565 | teeth |
| Atoposauridae | 8.68 | 5.639 | teeth |
| Goniopholididae | 147.58 | 161.316 | teeth |
| Bernissartiidae | 12.69 | 20.595 | teeth |
| Theropoda | 110.41 | 313.362 | teeth |
| Dromaeosauridae | 1152.50 | 1612.911 | post crania |
| Troodontidae | NA | NA | teeth |
| Tyrannosauridae | NA | NA | teeth |
| Brachiosauridae | 134.00 | NA | rib and tooth |

TABLE 2. Continued.

| Family | Mean | Standard deviation | Elements preserved |
|---|---|---|---|
| Hadrosauridae | 634.33 | 328.765 | teeth |
| Pachycephalosauridae | 808.00 | NA | teeth |
| Nodosauridae | 107.50 | 94.045 | teeth |
| Neoceratopsia | NA | NA | teeth |
| Aves | 25.63 | 24.545 | teeth |
| Triconodontidae | 1.50 | NA | teeth and jaws |
| Multituberculata | 1.50 | 1.414 | teeth and jaws |
| Spalacotheriidae | 0.70 | 0.700 | teeth and jaws |
| Tribotheria | 0.60 | 0.153 | teeth and jaws |
| Marsupialia | NA | NA | teeth and jaws |

Table 3. $P$-values for pair-wise comparisons of geologic variables and taxonomic similarity using Kendal's Tau and $P$-values for matrix comparisons between geologic similarity and taxonomic similarity using Mantel tests.

| Taxon | Clast size | Clast amount | Fossil mass | Crocodile mass | Environment | Mantel test |
|---|---|---|---|---|---|---|
| Ubertaxa | 0.80 | 0.57 | 0.81 | 0.97 | 0.74 | 0.90 |
| All families | 0.44 | 0.22 | 0.93 | 0.43 | 0.51 | 0.75 |
| Crocodile families | 0.44 | 0.93 | 0.93 | 0.68 | 0.87 | 0.29 |
| Mammal species | 0.44 | 0.16 | 0.39 | 0.81 | 0.87 | 0.38 |

# Faunal associations and compositional differences among sites in the Mussentuchit Member of the Cedar Mountain Formation

Patricia Goldberg

RRH: FAUNAL ASSOCIATIONS AND COMPOSITION

LRH: PATRICIA GOLDBERG

Abstract.—The Mussentuchit fauna of the Cedar Mountain Formation is a diverse, well-studied assemblage. Previous studies have shown that faunal composition varies among sites and that this variability does not correspond with geologic features related to transport. Associations between taxa at multiple taxonomic levels (ubertaxa [classes, mostly], all families, and mammal species), were first examined using correspondence analyses. The patterns of association at the family level and ubertaxa level were similar and showed that most sites were composed of a more terrestrial assemblage while the remaining sites were divided into two distinct aquatic assemblages. Monte Carlo simulations were done at the vertebrate family level and mammal species level to determine which taxa were present in higher than expected abundances at each site. Nearly all taxa were significantly over-abundant at one or more sites and significantly under-represented at other sites. Each site had a unique composition of relatively common and rare taxa. Finally, three separate correspondence analyses were performed on ecological groupings, based on diet, habitat, and endothermy/ectothermy. All analyses showed that sites were significantly non-random in the distribution taxa based on these characteristics.

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## Introduction

The paleontological record is notoriously spotty. Fossil localities rich in vertebrate remains generally are separated widely in space and/or time. As a consequence, much of the work that has been done comparing vertebrate faunas has focused on large-scale patterns such as evolutionary turnover and global biogeography (e.g. Lehman 1987, 1997; Kirkland et al. 1997). The few studies that have considered faunal variability at a smaller scale (within a sratigraphic member of a formation, for instance) have typically found sites to be the same (e.g. Estes 1964; Case 1996). Resolution may be higher for studies focusing on pollen or marine microfossils (e.g. Wing 1984) rather than vertebrates. Small-scale variability in faunal composition was found in the Mussentuchit Member (Cedar Mountain Formation) and the aim of this paper is to relate these differences to ecology.

One problem in looking for small-scale differences among sites in the fossil record is paucity of data. Oftentimes, sampling is restricted to, or dominated by, one or two localities (e.g. Estes 1964; Lillegraven 1969; Archibald 1982; Breithaupt 1982) so that comparisons simply cannot be made. Moreover, collections of bones can be altered dramatically by the processes involved in transport and burial. These processes may create biologically irrelevant differences among sites through sorting, or conversely homogenize different assembleges through averaging (Behrensmeyer 1982, 1988; Behrensmeyer et al 1992; Aslan and Behrensmeyer 1996).

The Cedar Mountain Formation is a well-studied body of rock deposited in the Cretaceous of Utah. Kirkland et al. (1997) have described four members within this formation. The youngest member, the Mussentuchit, was deposited by a meandering river (Nelson and Crooks 1987; Pomes 1988; Currie 1990) around 98.39 million years ago (Cifelli et al. 1997). An extensive collection of microvertebrates has been made from this member and is summarized in Cifelli et al. (1999).

The faunal compositions of 12 of the best-sampled microvertebrate sites were examined previously and found to vary significantly (Goldberg 2000). These taxonomic differences did not correspond with differences in geology, so although geologic processes have altered the assemblage as a whole, they have apparently operated in a similar way among sites. Differences in faunal composition among sites may be related to local ecology or changes in conditions over ecological time. The goal of this paper is to examine differences in the Mussentuchit fauna from an ecological perspective, looking for interactions among taxa.

## Methods

Data were compiled from the Oklahoma Museum of Natural History (OMNH) database. Specimens were collected from the Mussentuchit Member over the past 10 years by crews from OMNH using bulk matrix techniques described in Cifelli et al. (1996) and Madsen (1996). All specimens of all taxa were collected, allowing the use of abundance data. Specimens were identified to the finest taxonomic level possible and entered into the database along with relevant associated data.

Data from the 12 best-sampled microverebrate localities were used to construct three data matrices, each at a different taxonomic level. Abundances of higher-level taxa (ubertaxa; Chondrichthyes, Osteichthyes, Anura, Urodela, Chelonia, Crocodilia, Squamata, Theropoda, Ornithischia, Aves, Mammalia) at each of the 12 sites formed one such matrix. Another included abundances of each of the 48 families found in the fauna by site. The third matrix tabulated abundances of the 26 mammal species found at the 12 microvertebrate localities.

Multiple taxonomic levels were analyzed because taxonomic resolution varied, with many taxa identified only to the family level. Some important taxa could only be identified to a higher-level category (e.g., Anura, Aves). The family-level analysis balanced inclusion of the majority of the specimens with taxonomic resolution. Species-level analyses were restricted to mammals because this is the best studied group in this fauna, and the only group where a large number of species has been identified.

Associations among taxa were examined using correspondence analyses at all three taxonomic levels in NTSYS-pc version 2.02 (Rohlf 1999). Correspondence analysis is an ordination technique that allows the examination of relationships among taxa and the relationships among sites simultaneously. A $\chi^2$ coefficient is used, as it is an appropriate statistic for contingency tables. Additionally, the $\chi^2$ distance reduces problems associated with differences in sampling effort, such as shared absence of taxa in poorly sampled sites. Taxa are plotted in multidimensional space based on their abundances at each site and much of the variability in the distributions of taxa can be captured and visualized in just a few axes. Additionally, a probability of independence of rows and columns (in this case, taxa and sites) is given.

Monte Carlo simulations were performed using the family level and mammal species matrices to determine the sites at which each taxon was present in greater than expected abundances (Sokal and Rohlf 1995). An urn was constructed with the total abundance of each family from all 12 sites using Resampling Stats version 5.0.2 (Simon 1999). The total number of specimens (identified at the family level) recovered from the first site was determined, and this number of "specimens" was drawn at random from the urn. The abundance of each family in this sample fauna was noted. This process was repeated 1000 times. A probability value for each family was determined by dividing the number of random trials in which the abundance equaled or exceeded the actual value by 1000. The same method was used for the remaining 11 sites, drawing the number of specimens recovered from each locality. The entire process was repeated using the total abundances of mammal species, to evaluate the distribution of mammals among sites.

Three other correspondence analyses were also performed by grouping families into ecological categories (based on Goldberg 2000): habitat, diet, and thermoregulation. First, a broad-level habitat was attributed to each family. The abundances of aquatic, semi-aquatic, microterrestrial, and macroterrestrial organisms at each of the 12 microvertebrate localities was tabulated and analyzed. Next, each family was placed in a diet category: herbivore, omnivore, invertebrate feeder, invertebrate/vertebrate feeder, or vertebrate feeder. Abundances of organisms in each of these diet categories at each of the 12 sites were tabulated and analyzed. Finally, organisms were grouped based on thermoregulatory abilities. Three groups were used: endotherms, ectotherms, and dinosaurs. Dinosaurs were placed in a separate group based on the controversy surrounding their metabolism (e.g. Thomas and Olsen 1980; Bakker 1986). These data were analyzed in the same manner.

## Results

Associations.—Correspondence analysis at the ubertaxa level shows a distinct grouping of some aquatic taxa (chelonians, anurans, and osteichthyans) on the left side of the first axis and a distinct grouping of terrestrial taxa (sqamates, mammals, and dinosaurs) toward the center of the first axis (Fig. 1). The right side of the first axis is comprised of an eclectic grouping of crocodilians, chondrichthyans, and aves, with urodeles separating from the group on the second axis.

This pattern is repeated in the correspondence analysis at the family level (Fig. 2). Here, four of the five families of crocodilians (Pholidosauridae, Bernissartidae, Goniopholididae, Atoposauridae) plot together on the left side of the first axis, along with two of the three most common chondrichthyans (Hybodontidae, Polyacrodontidae). Three less common bony fish families plot toward the middle of the axis (Amiidae, Pycnodontidae, Enchodontidae), while the two commonest families (Semionotidae, Lepisosteidae) plot on the right. Exceptions to these general patterns include the placement of Teleosauridae (Crocodilia) on the far right of the plot, beyond the bony fish, with dromaeosaurs and glyptopsid turtles. Similarly, Rhinobatoidea (Chondrichthyes) are placed away from the main chondrichthyan group but together with the common bony fish. Mammals and lizards form a cluster toward the center of the primary axis, and apart from the aquatic groups on the second axis. Within the mammal cluster, triconodonts plot furthest away from the other mammalian groups, while tribosphenids and marsupials form a tight pair. Polyglyphanodontinae (Squamata) plot to the left of the other lizard families. The families of herbivorous dinosaurs represented in the fauna (mainly ornithischians) form a loose cluster toward the center of the primary axis, while the two most common families of predatory theropods plot on opposite ends of the axis.

A plot of the correspondence analysis showing the distributional relationships among mammal species is provided in Figure 3. The distribution of species along the primary axis is unrelated to body size, with species of a variety of sizes toward the center. It is also independent of relatedness. While the three species of triconodonts are close to one another on the plot, the marsupials, tribotherians, and multituberculates can be found all along the primary axis. Seven species form a loose cluster (S. cretulablatta, S. noblei, C. cf. bestia, Bryceomys intermedius, Paracimexomys cf. robisoni, Marsupial C, and Picopsidae B), with three other species separated from this group along the second axis (Paracimexomys perplexus, Paracimeomys cf. perplexus, C. bestia). The probability of independence of sites and taxa (at all three levels; ubertaxa, families, and mammal species) was less than 0.001.

Monte Carlo Simulations.—Families found in abundances greater than expected by random chance and families found in abundances less than expected by chance are summarized for each site in Table 1. Each site has at least one family that is significantly over-represented, and all but V213 have at least one family that is conspicuously under-represented or absent. Each site has a unique faunal composition that differs significantly from all other sites. Few general patterns emerge. Site V213 is distinct from all others, with an abundance of all chondricthyan families. In addition, brachiosaurs and dromaeosaurs are found here in high abundances. While the lack of fish of the family

Lepisosteidae and the common families of crocodiles is not significant at the 0.05 level using a two-tailed value, the probabilities are very low and may be meaningful. Sites V235, V239, V694, V794, V801, and V868 are similar in their lack of common bony fish coupled with an abundance of crocodiles. Site V801 differs from the others in its abundance of turtles (Glyptopsidae), salamanders (Prosirenidae and Sirenidae), and mammals (triconodonta). Sites V868 and V239 also share an abundance of multituberculates, tribotherians, and marsupials, while sites V694, V794, and V801 conspicuously lack multituberculates and symmetrodonts.

The Monte Carlo simulations using mammal species produced similar results. Each site had at least one mammal species present in significantly high abundances. However, only three sites were notably lacking particular species (Table 2). No distinct groups emerged in this analysis; each site is unique in composition.

Ecological analyses.—Correspondence analysis performed by assigning families to one of four communities resulted in a distribution of communities along the first axis in a gradient, with the macroterrestrial community to the far left, followed by the microterrestrial community, the semi-aquatic community, and finally the aquatic community to the right (Fig. 4). This first axis captured 67.1% of the variability in the data, and the second axis captured another 19.9%. The probability of independence between community and site was less than 0.001. This analysis shows that the microterrestrial fauna predominates at a few sites (V234, V236, and V239), the macroterrestrial fauna predominates at two sites (V695 and V696), and the semi-aquatic community at most of the remaining sites (V235, V240, V694, V801, and V868). The aquatic community predominates at V794 and V213 although these two sites are very distinct in actual composition from one another.

The correspondence analysis performed after assigning each family to a diet category resulted in a distribution along the primary axis roughly reflecting a gradient in food preference (Fig. 5). The first axis captured 56.4% of the variability and the second another 29.9%. From left to right along the primary gradient, diet categories were vertebrate feeders, invertebrate feeders and invertebrate/vertebrate feeders, omnivores, and finally herbivores. Invertebrate and invertebrate/vertebrate feeders were separated widely along the second axis. Again, the p-value for independence of feeding category and site was less than 0.001. Here, vertebrate feeders were concentrated mainly at sites V694, V794, and V868. Invertebrate feeders predominated at most of the sites (V213, V235, V240, V695, and V696), while invertebrate/vertebrate mixed feeders and omnivores were most abundant at V801 and V234. Sites V239 and V236 had high proportions of herbivores.

The correspondence analysis using thermoregulatory categories produced an unusual distribution. The primary axis captured 67.7% of the variability, with the remaining variability reflected on the second axis. Ectotherms were located on the left of the primary axis, endotherms toward the middle/right, and dinosaurs along the far right (Fig. 6). The p-value for independence between thermoregulatory abilities and sites was once again less than 0.001.

## Discussion

### Associations

Ubertaxa.—Associations at the ubertaxa level seem to be correlated with habitat at a broad scale, and demonstrate that analyses at this level may produce ecologically meaningful patterns. Mammals, lizards, ornithischians, and theropods formed one group, with the two groups of dinosaurs forming a close pair. This pairing of dinosaur taxa may reflect an ecological interaction (e.g. habitat requirements or a trophic relationship) or a taphonomic phenomenon. The latter explanation is unlikely because, while both were large-bodied in life, the sizes of the remains recovered are distinct (Goldberg 2000). Most of the remains of fossil theropods are small teeth, whereas most of the fossils of ornithischians are relatively large hadrosaur teeth. Both kinds of dinosaurs would have required an open habitat and an abundance of bulk vegetation, either directly (ornithischians) or indirectly (theropods) through feeding on the herbivores (Fastovsky and Weishampel 1996).

Similarly, mammals and lizards are small animals, but the fossils recovered are distinct in size, with mammals represented mainly by isolated teeth and lizards recognizable only with partial jaws. However, both animals benefit from an environment that provides small hiding places and both (in general) feed on insects (Lilligraven et al. 1979; Pianka 1993). Sites must have varied in habitat at the time of deposition, with any particular site being suitable for some animals but not others. Differences in faunal composition among sites may reflect these habitat preferences. At the broadest scale, all the terrestrial animals tend to be found together.

Interestingly, not all the aquatic animals are found together. Turtles, frogs, and bony fish tend to co-occur, but not with crocodilians or chondrichthyans. The joint presence of turtles, frogs, and bony fish may reflect a quiet stream community. Chondrichthyans are localized in their distribution and the one site at which they are found in abundance may have been nearer the sea than the others. While several chondrichthyan families are represented, all are bottom-dwellers to some extent and most have a durophagous dentition (Cappetta 1987; Compagno 1990; Welton and Farish 1993). They were probably limited by similar habitat requirements, either through diet or physiology.

The disjunction of crocodiles and bony fish is more difficult to interpret. Within a river system, it would be reasonable to expect these two groups to co-occur. Crocodilians have the ability to move across land easily and may use ephemeral ponds, unlike fish. Moreover, their eggs are laid on the dry banks of rivers rather than in the water. Small juveniles probably fed mainly on insects; fish and tetrapods are not a significant component of the diet of modern crocodiles until they reach relatively large sizes (Neill 1971; Hilliard 2000). The majority of crocodilian remains recovered are tiny teeth, most likely from juveniles. Research on modern crocodiles has revealed that juveniles are the most abundant component of the population and habitat segregation by size classes occurs in at least some species (Hutton 1989; Da Silveira et al. 1997). The fossils recovered from the Mussentuchit Member may represent mortality or shed teeth of juveniles living in smaller, isolated bodies of water with abundant invertebrates but not fish.

Families.—Several associations occurred at the family level, but the biological meaning, if any, behind the associations was often unclear. All six chondrichthyan families and Brachiosauridae were significantly abundant at V213, a relatively poorly sampled site. Three chondrichthyan families occurred only at this site: Orectolobididae, Squatinidae, and Sclerorhynchidae. All were durophagous, bottom-dwelling sharks, although their body forms differed. This group was clustered toward the top of the second axis on the canonical plot and represents a unique assemblage at a single site. This site must have been distinct from others in some aspect of its ecological conditions, possibly in proximity to the coast at the time of deposition.

Two salamander families, Prosirenidae and Sirenidae, were associated on the left side of the primary axis. Both of these fully aquatic taxa are found in significant abundances at V801. Site V801 was interpreted as an oxbow lake (Goldberg 2000) and these two salamanders may have preferred this very quiet, vegetated habitat as is the case for many modern salamanders (Stebbins and Cohen 1995).

Also clustered toward the left side of the first axis were four of the five crocodile families (Pholidosauridae, Goniopholididae, Bernissartiidae, and Atoposauridae). In general, they were significantly abundant at V235, V239, and V801, while being significantly under-represented at V240 and V695. This suggests that they had similar habitat requirements. While dentition and presumably diet varies among these families (Massare 1987; Pomes 1988), all were semi-aquatic and the juveniles presumably faced the same predators and fed on the same prey. Also plotting amongst this group were the triconodont mammals. Previous studies have suggested triconodonts were semi-aquatic and may have been piscivorous, based on tooth structure and associations with fish fossils (Slaughter 1969; Sigogneau-Russell 1995). While I did not find these particular triconodonts associated with fish, they did co-occur with the semi-aquatic crocodiles more than with other terrestrial families, suggesting that they may have preferred a wetter habitat.

On the right side of the primary axis, another fully aquatic salamander of the family Scapherpetontidae was found associated with members of the terrestrial Salamandridae, as well as with certain semi-aquatic turtles (Trionychidae), snakes (Aniliidae), species of the family Scincidae, and a dinosaur group (Neoceratopsia). Families of marine crocodiles (Teleosauridae), theropods (Dromaeosauridae), and another turtle group (Glyptopsidae) are also found on the far right of the diagram. The two common bony fish (Lepisosteidae and Semionotidae) along with pleurosternid turtles were also found toward this end of the axis. This, more specifically, is the composition of the "typical" aquatic community described earlier. All but Lepisosteidae were found at highly significant abundances at V695 and few were significantly abundant elsewhere. Some associations (e.g. the turtles, salamanders, and fish) are probably ecologically significant, reflecting animals with similar habitat requirements. Others might be incidental, providing a cautionary note in interpreting interactions based on association. The placement of dromaeosaurs with aquatic taxa raises the possibility that one species may have been specialized for feeding on shallow-water vertebrates, however more data (taxonomic resolution, diet preference revealed by isotopes) is required to test this idea.

Points near the center of the primary axis represent mainly terrestrial taxa: dinosaurs, mammals, and lizards. Two fish families (Amiidae and Enchodontidae) occur in this otherwise terrestrial grouping. The placement of these two families away from other fishes is unusual because both are thought to have fed mainly on fish (Grande and Bemis 1998; Dixon et al. 1998), especially the Enchodontidae which have elongated teeth. Within this broad grouping of terrestrial animals, three distinct subgroups appear. Tribosphenids, marsupials, and paramacellodids form one such group, to the left near the crocodile and triconodont group. Monstersauria, Anilidae, Teiidae, Nodosauridae, Symmetrodonta, and Enchodontidae form another group clustered to the right near the gars. Finally, Amiidae and multituberculates form a third group between these other two. This further supports the idea that two distinct aquatic habitats existed, with the terrestrial fauna associated with the margins of these habitats differing.

Mammal species.—Associations among mammal species show some interesting patterns. By comparing the canonical analysis with the results from the Monte Carlo simulations, four groups of mammal species appear to be distinct and meaningful. One symmetrodont, Spalacolestes inconcinnus, was associated with a marsupial (species "A") and a multituberculate (Ameribaatar zofiae). Cifelli and Madsen (1999) postulated that S. inconcinnus was specific in habitat requirements, based on its distribution within the member, mainly at site V868. Both and A. zofiae and marsupial species A were also found in greater than expected abundances at this site, and may have shared these limitations. These three species plot together on the far left of the primary canonical axis.

*Paracimexomys* cf. *perplexus* and marsupial B are both localized at V696. *Astroconodon delicatus* is also found in high abundances at this site, but also V801. These three species, a marsupial, a multituberculate, and a triconodont may have preferred some habitat characteristic present at site V696.

Three multituberculates, *Paracimexomys* cf. *perplexus*, *Cedaromys bestia*, and *Janomys erebos* were also found to co-occur. All plotted toward the left end of the primary axis and high on the secondary axis and all were found in very high abundances at site V695.

Finally, therian A, *Corviconodon utahensis*, and *Cedaromys* cf. *parvus* all plotted toward the right of the primary axis and all were abundant at V234 and either V239 or V240. If these three species shared similar habitat limitations, then sites V234, V239, and V240 should have been similar in this regard at the time of their deposition. These three sites differed in depositional environments (Goldberg 2000), but to date no analysis of vegetational differences has been done at this scale.

*Cedaromys parvus* and *Cedaromys* cf. *parvus*, were both found in high abundances at V239. The taxonomy implies they are very similar, so it is curious that they should be found positively associated. Typically, closely related and similar species are disjunct in distribution (e.g. Bowers and Brown 1982; Brown and Lomolino 1998) or distinct in habitat (e.g. Vaughan 1967). *Cedaromys* cf. *parvus* may be a morphological variant of *C. parvus*.

Other sites seemed to be unique in composition and other taxa unique in distribution. Fourteen mammal species plotted near the center of the primary axis, but appear to have little in common.

Summary

The primary factor in the distribution of taxa among sites seems to be habitat preference, the influence of which is apparent when looking at the distribution of taxa in the correspondence analyses. This seems to be the most common ecological pattern detected in the fossil record (e.g., Lehman 1987, 1997). In this case at least, statistically meaningful relationships exist between the distribution of taxa among sites and other ecological characteristics of the taxa, such as diet and metabolism. These other factors may be obscured by interpretations relating to habitat and remain undetected if not looked for specifically.

Each site was unique in its composition of taxa. However, some sites shared general patterns of association. Sites similar in mammal species composition were different from sites similar in overall vertebrate composition at higher taxonomic levels. Sites V868 and V694 were similar in mammal species, as were sites V240, V239, and V234. Site V236 was distinctive.

Overall, sites V801 and V213 were distinct in vertebrate composition and presumably habitat. Site V801 was the only productive oxbow in the Mussentuchit Member (Goldberg 2000), a habitat very different from the rest of the river system. Unfortunately, geologic data are not available for site V213. Sites V695 and V240 are similar in composition as are sites V234, V239, and V694. The others are more difficult to interpret, but V868 and V236 form one similar pair and sites V794 and V696 another. The differences in faunas are significant and could not be linked with depositional environment or taphonomy (Goldberg 2000). The hypothesis that the faunal composition of sites is mainly influenced by habitat differences could be evaluated by examining the plant or invertebrate composition of those sites. The idea would be supported if similarities and differences in composition coincide.

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FIGURE 1. Plot of Mussentuchit ubertaxa on first two correspondence analysis axes based on their distribution at 12 microsites.

FIGURE 2. Plot of Mussentuchit families on first two correspondence analysis axes based on their distribution at 12 microsites. Numbers correspond as follows: 1) Polyglyphanodontinae; 2) Troodontidae; 3) Bernissartiidae; 4) Pholidosauridae; 5) Goniopholididae; 6) Polyacrodontidae; 7) Triconodontidae; 8) Albanerpetontidae; 9) Atoposauridae; 10) Tribotheria, Marsupialia, Paramacellodidae; 11) Amiidae; 12) Multituberculata, Pycnodontidae; 13) Monstersauria; 14) Nodosauridae; 15) Spalacotheriidae; 16) Teiidae; 17) Enchodontidae; 18) Bothriagenys; 19) Pachycephalosauridae; 20) Hadrosauridae; 21) Pleurosternidae; 22) Lepisosteidae; 23) Semionotidae; 24) Rhinobatoidea; 25) Teleosauridae; 26) Glyptopsidae; 27) Dromaeosauridae; 28) Ceratopsidae, Aniliidae, Scapherpetontidae, Salamandridae, Trionychidae, Scincidae.

FIGURE 3. Plot of Mussentuchit mammal species on first two correspondence analysis axes based on their distribution at 12 microsites. Mammal species are: 1) Spalacolestes inconcinnus; 2) marsupial A; 3) Ameribaatar zofiae; 4) Bryceomys intermedius; 5) Spalacolestes cretulablatta; 6) Janumys erebos; 7) Cedaromys bestia; 8) Paracimexomys cf. perplexus; 9) marsupial C; 10) picopsid B; 11) Cedaromys cf. bestia; 12) Spalacotheridium noblei; 13) Paracimexomys perplexus; 14) Bryceomys cf. intermedius; 15) marsupial B; 16) Paracimexomys cf. robisoni; 17) Astroconodon delicatus; 18)

therian of metatherian-eutherian grade B; 19) picopsid A; 20) *Jugulator amplissimus*; 21) *Cedaromys parvus*; 22) *Corviconodon utahensis*; 23) therian of metatherian-eutherian grade A; 24) *Cedaromys* cf. *parvus*; 25) *Kokopellia juddi*.

FIGURE 4. Plot of Mussentuchit fauna grouped by habitat on first two correspondence axes, based on their distribution at 12 microvertebrate sites.

FIGURE 5. Plot of Mussentuchit fauna grouped by diet on first two correspondence axes based on their distribution at 12 microvertebrate sites.

FIGURE 6. Plot of Mussentuchit fauna grouped by metabolism on first two correspondence axes based on their distribution at 12 microvertebrate sites.

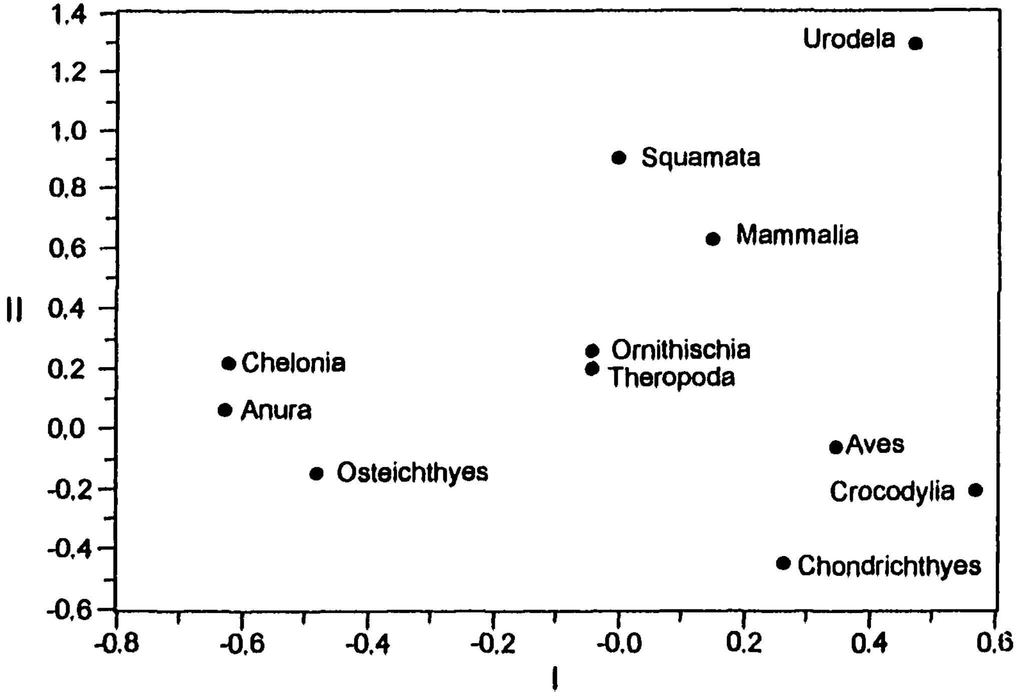
Urodela
Squamata
Mammalia
Ornithischia
Theropoda
Chelonia
Anura
Osteichthyes
Aves
Crocodylia
Chondrichthyes
II
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-0.6
-0.4
-0.2
-0.0
0.2
0.4
0.6
I

FIGURE 1

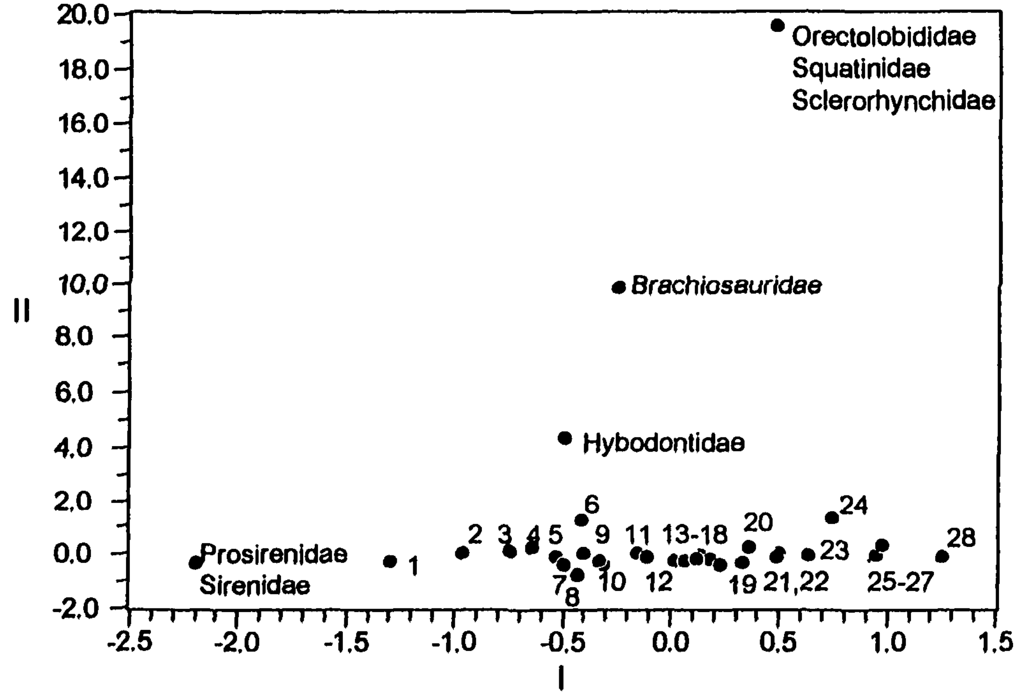
Orectolobididae
Squatinidae
Sclerorhynchidae
Brachiosauridae
Hybodontidae
Prosirenidae
Sirenidae
1
2
3
4
5
6
7
8
9
10
11
12
13-18
19
20
21,22
23
24
25-27
28
II
20.0
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
-2.0
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
I

FIGURE 2

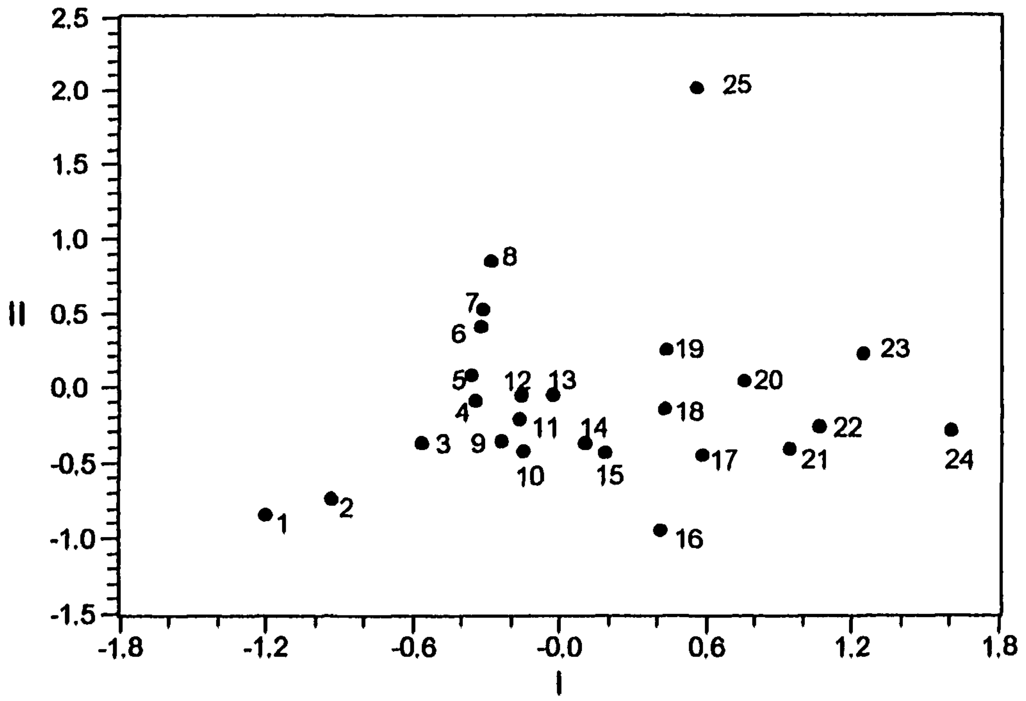
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
II
-1.8
-1.2
-0.6
-0.0
0.6
1.2
1.8
I
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

FIGURE 3

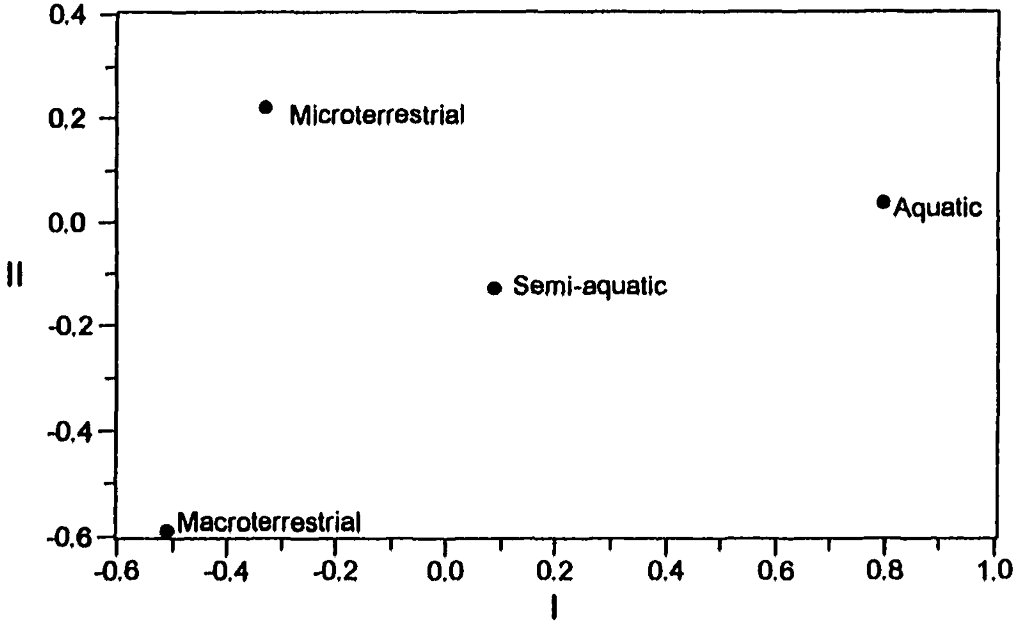
Microterrestrial
Aquatic
Semi-aquatic
Macroterrestrial
0.4
0.2
0.0
-0.2
-0.4
-0.6
II
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
I

Figure 4

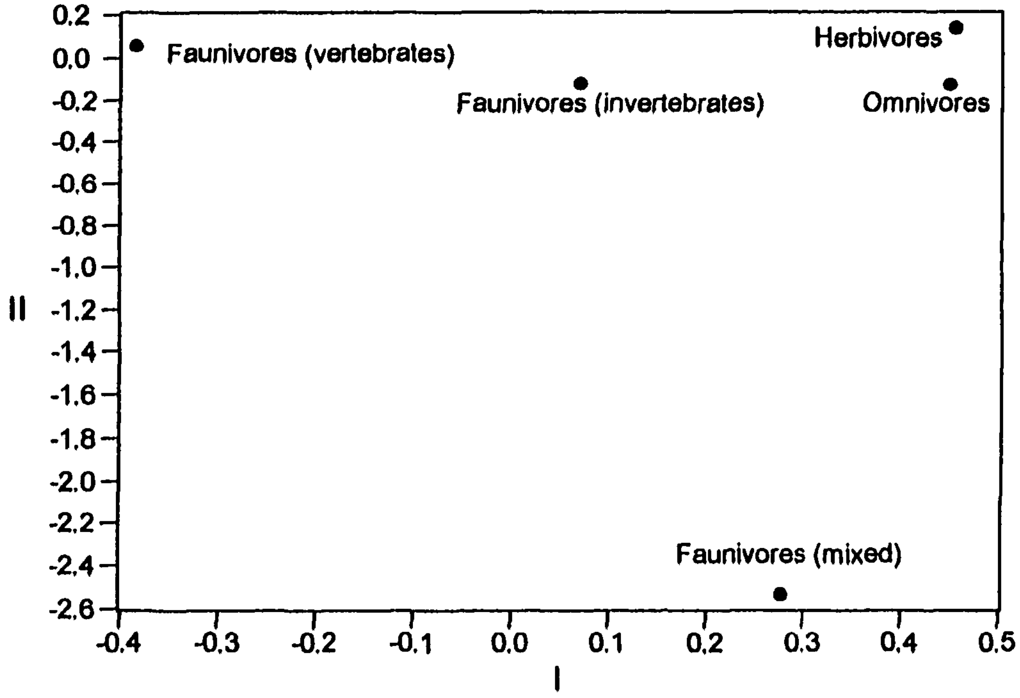
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
-1.4
-1.6
-1.8
-2.0
-2.2
-2.4
-2.6
II
-0.4
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
I
Faunivores (vertebrates)
Faunivores (invertebrates)
Herbivores
Omnivores
Faunivores (mixed)

FIGURE 5

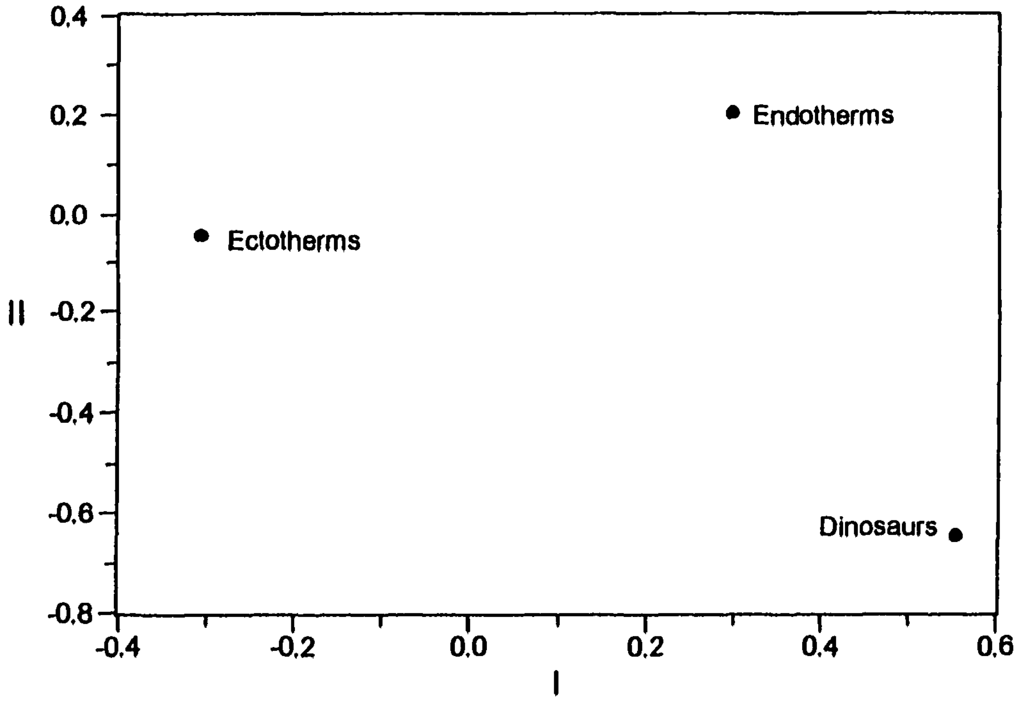
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
II
-0.4
-0.2
0.0
0.2
0.4
0.6
I
Endotherms
Ectotherms
Dinosaurs

FIGURE 6

TABLE 1. Summary of distribution of Mussentuchit families among 12 microvertebrate sites. A "+" indicates actual abundance greater than expected at p=0.025 level, ++ at p=0.005 level. Similarly, a "-" indicates abundance less than expected at p=0.025 level, -- at p=0.005 level.

| Taxon | Site | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 |
| Hybodontidae | ++ | | | | | | ++ | -- | ++ | -- | | |
| Polyacrodontidae | ++ | | | | | | | -- | | ++ | | |
| Orectolobididae | ++ | | | | | | | | | | | |
| Squatinidae | ++ | | | | | | | | | | | |
| Sclerorhynchidae | ++ | | | | | | | | | | | |
| Rhinobatoidea | ++ | | | | | | | | | | | |
| Lepisosteidae | | -- | -- | -- | -- | ++ | -- | | | -- | -- | -- |
| Semionotidae | | | | | -- | -- | -- | ++ | -- | -- | -- | -- |
| Pycnodontidae | | | ++ | | -- | -- | - | -- | | | | |
| Amiidae | | | -- | | -- | -- | -- | -- | - | ++ | - | -- |
| Enchodontidae | | | + | | | | | | | | | |
| Prosirenidae | | | | | | | | | | | ++ | |
| Albanerpetontidae | | ++ | | | | | | | | -- | | ++ |
| Scapherpetontidae | | | | | | | | ++ | | | | |

TABLE 1. Continued.

| Taxon | Site | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 |
| Salamandridae | | | | | | | | ++ | | | | |
| Sirenidae | | | | | | | | | | | ++ | |
| Glyptopsidae | | | | | | | | ++ | | | + | |
| Trionychidae | | | | | | | | ++ | | | | |
| Pleurosternidae | | | - | + | | | | ++ | | | | |
| Paramacellodidae | | | | | | | | | | – | | ++ |
| Teiidae | | | | | | - | – | ++ | | – | | ++ |
| Scincidae | | | | | | | | ++ | | | | |
| Polyglyphanodontinae | | | | | ++ | | | | | | | |
| Monstersauria | | | | | | | | | | - | | ++ |
| Aniliidae | | | | | | | | ++ | | | | |
| Teleosauridae | | | | | | | | ++ | | | | |
| Pholidosauridae | | | | | | | ++ | – | | | | – |
| Atoposauridae | | | ++ | - | ++ | | ++ | – | ++ | – | | ++ |
| Goniopholididae | | | ++ | ++ | ++ | – | – | – | – | ++ | ++ | ++ |
| Bernissartiidae | | | ++ | – | ++ | – | ++ | – | – | ++ | ++ | – |
| Dromaeosauridae | ++ | | – | | | – | - | ++ | + | – | | - |

TABLE 1. Continued.

| Taxon | Site | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 |
| Troodontidae | | | ++ | | | | | | | | | |
| Tyrannosauridae | | | | | | | | ++ | | | | |
| Brachiosauridae | ++ | + | | | | | | | | | | |
| Hadrosauridae | | | | ++ | — | - | — | ++ | | | — | — |
| Pachycephalosauridae | | | | ++ | | | | | | | | |
| Nodosauridae | | | | | ++ | | | + | | | | |
| Neoceratopsia | | | | | | | | ++ | | | | |
| Triconodontidae | | ++ | | | ++ | | | | | - | ++ | |
| Multituberculata | | | | ++ | ++ | — | — | ++ | | — | - | ++ |
| Symmetrodonta | | | | | | — | - | ++ | - | — | | ++ |
| Tribotheria | | ++ | | ++ | ++ | — | — | | | | - | |
| Marsupialia | | ++ | | ++ | + | - | | | | | | |

TABLE 2. Summary of distribution of Mussentuchit mammals among 12 microvertebrate sites. A "+" indicates actual abundance greater than expected at p=0.025 level, ++ at p=0.005 level. Similarly, a "-" indicates abundance less than expected at p=0.025 level, -- at p=0.005 level.

| Taxon | Site | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 |
| *Astroconodon delicatus* | | | | | | | | | ++ | | ++ | |
| *Corviconodon utahensis* | | + | | | + | ++ | | | | | | |
| *Jugulator amplissimus* | | + | | | + | | | | | | | |
| *Janumys erebos* | | | | | | | | ++ | | | + | |
| *Paracimexomys perplexus* | | | + | | | | ++ | | | + | | -- |
| *Paracimexomys* cf. *perplexus* | | | | | | | | ++ | | | | |
| *Paracimexomys* cf. *robisoni* | | | | | | | | | | | | |
| *Ameribaatar zofiae* | | | | | | | + | | | | | ++ |

TABLE 2. Continued.

| Taxon | Site | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 |
| *Bryceomys intermedius* | | | | | | | | | | | | |
| *Bryceomys* cf. *intermedius* | | | | | | | | | | | | |
| *Cedaromys bestia* | | | | | - | | | ++ | + | | | |
| *Cedaromys* cf. *bestia* | | | | | | | | | | ++ | | |
| *Cedaromys parvus* | | | | | ++ | | | | | | + | |
| *Cedaromys* cf. *parvus* | | + | | | ++ | | | | | | | |
| *Spalacolestes cretulablatta* | | | | | -- | | | + | | | | + |
| *Spalacolestes inconcinnus* | | | | | | | | | | | | ++ |
| *Spalacotheridium noblei* | | | | | | | | | | | | |
| Picopsidae A | | + | | | | | | | | | | |
| Picopsidae B | | | ++ | | | | | | | | | |

TABLE 2. Continued.

| Taxon | Site | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 213 | 234 | 235 | 236 | 239 | 240 | 694 | 695 | 696 | 794 | 801 | 868 |
| TMEG A | ++ | ++ | | | | ++ | | | | | | |
| TMEG B | | | | | + | | | | | + | | |
| *Kokopellia juddi* | | + | | ++ | | | | | | | | |
| Marsupial A | | | | | | | | | | | | ++ |
| Marsupial B | | | | | | | | | + | | | |
| Marsupial C | | | | | | | | - | | + | | + |