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CONTENTS

Taphonomy and Paleoecology of a Microvertebrate Assemblage from the Morrison Formation (Upper Jurassic) of the Black Hills, Crook County, Wyoming

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ABSTRACT

The Little Houston Quarry in northeastern Wyoming preserves a diverse assemblage of vertebrates in an abandoned channel deposit in the Upper Jurassic Morrison Formation. Along with dinosaurs, the site contains abundant microvertebrate fossils in two thin layers within one of the excavations at the quarry (and in pockets of the other excavation). The quarry serves as a model defining one of two microvertebrate taphofacies for the Morrison Formation. A survey of the microvertebrate elements and taxa collected from the site indicates that the deposit likely represents a broad local community and is only moderately time-averaged. There is a higher diversity of terrestrial taxa than of aquatic or semi-aquatic forms, though, probably for taphonomic reasons, semi-aquatic taxa are more abundant. Larger taxa are also more abundant, though, as in most modern communities, the smaller mass categories contain the most diverse assemblage of animals. Feeding mode guilds are fairly evenly filled, though the highest diversities occur among invertivore/carnivores and omnivores, and omnivorous turtles dominate numerically. This microvertebrate fauna provides a basis for comparison with other small-vertebrate faunas of the Morrison Formation and, in conjunction with other Morrison sites, with those of Late Jurassic deposits in Europe, Asia, and Africa.

INTRODUCTION

The Little Houston Quarry in the Morrison Formation of the Black Hills in northeastern Wyoming has produced a variety of Late Jurassic dinosaur genera. During quarry operations over the past several field seasons, however, many specimens of small, non-dinosaurians have been recovered. Most small bones from the quarry are fragmentary and not diagnostic, but the good specimens demonstrate that this locality is the most diverse vertebrate paleofauna in the Jurassic of the Black Hills region. Non-dinosaurian vertebrates from the site include: actinopterygian fish, lungfish, a frog, two types of turtles, a lizard, a sphenodontian, a choristodere, a crocodilian, and four types of mammals. Dinosaur genera that have been found at the Little Houston Quarry include the theropod *Allosaurus*, the sauropods *Apatosaurus*, *Camarasaurus*, and *Diplodocus* (or *Barosaurus*), the ornithopods *Othnielia* and *Dryosaurus*, and the thyreophoran *Stegosaurus*.

The first reported occurrence of Late Jurassic vertebrates in the Morrison Formation of the Black Hills was Marsh's (1890) description of the sauropod *Barosaurus*. This type specimen was found near Piedmont, South Dakota, in 1889. In 1935, several partial sauropods were collected from a quarry high in the Morrison northeast of Spearfish, South Dakota. During a stratigraphic survey of the western Black Hills in Wyoming, Loomis (1902) noted fragmentary dinosaurian remains in the Morrison Formation. Since the mid-1970's several additional dinosaur localities in the Morrison Formation of both South Dakota and Wyoming have been found by crews from the Museum of Geology at the South Dakota School of Mines & Technology in Rapid City. The most productive of these localities is the Little Houston Quarry, which was first excavated in 1991 (Foster and Martin, 1994).

The Morrison Formation at the site lies above the Upper Jurassic marine Sundance Formation and below the Lower Cretaceous fluvial deposits of the Lakota Formation. Almost 14 meters of the Morrison Formation are exposed at the Little Houston Quarry, and most of the rock consists of gray, brown, maroon, and green-gray non-smectitic mudstones. Two thin, crossbedded sandstone units occur in the middle of the exposure. The quarries are located in a two-meter-thick unit just above the lower channel sandstone. The bone-bearing lithosome is a light greenish-gray, finely laminated siltstone with thinly interbedded claystones.

The Morrison Formation in the northwestern Black Hills is fairly thin compared to other regions (Mapel and Pillmore, 1963). Stratigraphic correlation with other areas is very difficult due to the apparent pre-Lakota erosion of the upper parts of the Morrison in northeastern Wyoming, the lack of the clay change boundary used to position quarries further south, and the distance of the Black Hills from other Morrison outcrops (Turner and Peterson, 1999). Recent work on the relative stratigraphic positions of Morrison dinosaur quarries indicates, however, that the Little Houston Quarry may be at a level approximately equivalent to the lower Brushy Basin Member near the contact with the underlying Salt Wash Member (Turner and Peterson, 1999). If this relative stratigraphic position is correct, then the quarry would be slightly older than the Dry Mesa Quarry and the Marsh-Felch Quarry, both in Colorado.

Though several of the Black Hills localities have produced non-dinosaurian vertebrates, none yielded the numbers or diversity of the Little Houston Quarry. The taphonomic characteristics of the quarry were studied during field excavation and are described in this paper. The taphonomy of the site is of interest because of the paucity of microvertebrate quarries in the formation, and description of this site allows comparison with the other sites. A survey of all sites in the Morrison Formation has already indicated some possible trends in the microvertebrate deposits (Foster, 1998; Foster and Trujillo, 2000), and these will be discussed in a following section.

In addition to the taphonomic description, a survey of approximately 400 microvertebrate elements and paleoecological categorizations of the represented taxa are used here to determine the relative abundance and diversity of different vertebrate guilds. These are compared with another microvertebrate locality in the Morrison Formation (Quarry 9 at Como Bluff), and the taphonomy of the Little Houston Quarry site is examined to determine the nature of its microvertebrate accumulation. The composition of the microvertebrate fauna from the Little Houston locality is important for comparison with other Morrison Formation microvertebrate localities such as Quarry 9, as well as others such as the Fruita Paleontological Area in Colorado, and Rainbow Park in Dinosaur National Monument, Utah.

With an understanding of the paleoecology of the microvertebrate fauna of the Morrison Formation, we can compare the range of paleoecological characteristics to those represented in the Late Jurassic vertebrate faunas worldwide. There are vertebrate genera common to the Late Jurassic vertebrate faunas of North America, Europe, and Africa, as well as taxa unique to each region. The variation in paleoecological characteristics of the microvertebrate faunas between these regions may lead to a better understanding of the global history and biogeographic distribu-

tion of vertebrate feeding mode, locomotion, and body mass guilds during the Late Jurassic. The paleoecological part of this study, then, begins to characterize the paleoecology of the microvertebrate fauna of the Morrison Formation in North America, as represented by one locality.

The term "microvertebrates" for this study will include medium-sized animals such as turtles, crocodilians, and small dinosaurs, as their remains are small, individual bones preserved alongside the truly microscopic elements of very small animals.

Specimens from the Little Houston Quarry are part of the collections of the Museum of Geology, South Dakota School of Mines & Technology, Rapid City. Abbreviations used include: AMNH–American Museum of Natural History, New York; CMNH–Cleveland Museum of Natural History, Cleveland; DNM–Dinosaur National Monument, Jensen; FMNH–Field Museum of Natural History, Chicago; LACM–Natural History Museum of Los Angeles County, Los Angeles; SDSM–Museum of Geology at the South Dakota School of Mines & Technology, Rapid City; USNM–National Museum of Natural History, Washington, D.C.; YPM–Yale Peabody Museum, New Haven.

LOCALITY

The Little Houston Quarry lies approximately 20 km west of the town of Sundance in southern Crook County, Wyoming, just north of Little Houston Creek (Fig. 1). The Little Houston Quarry locality actually consists of two separate but neighboring excavations, both in the same bone-bearing channel deposit: the Main Quarry (SDSM locality V9138) and the Mammal Quarry (V941), the latter of which will be the main focus of this study. The Main Quarry contains remains of numerous individual dinosaurs. The Mammal Quarry is located approximately 75 m north of the Main Quarry. The Mammal Quarry (LHMQ) has been known and worked occasionally since 1991 but was only excavated extensively beginning in 1994. During the 1994 season, it was discovered that in addition to many small bones, the Mammal Quarry contained an articulated to partly disarticulated series of caudal and dorsal vertebrae of the sauropod dinosaur *Camarasaurus*.

METHODS

Collection of Specimens

The taxa considered in this study include fish, a frog, a lizard, a sphenodontian, the choristodere *Cteniogenys*, and several mammals, but also larger vertebrates such as crocodilians, turtles; small theropods, and the small ornithopods *Othnielia* and *Dryosaurus*. These taxa are all included because the taphonomic mode of preservation for all these forms is similar; all are represented by isolated, disarticu-
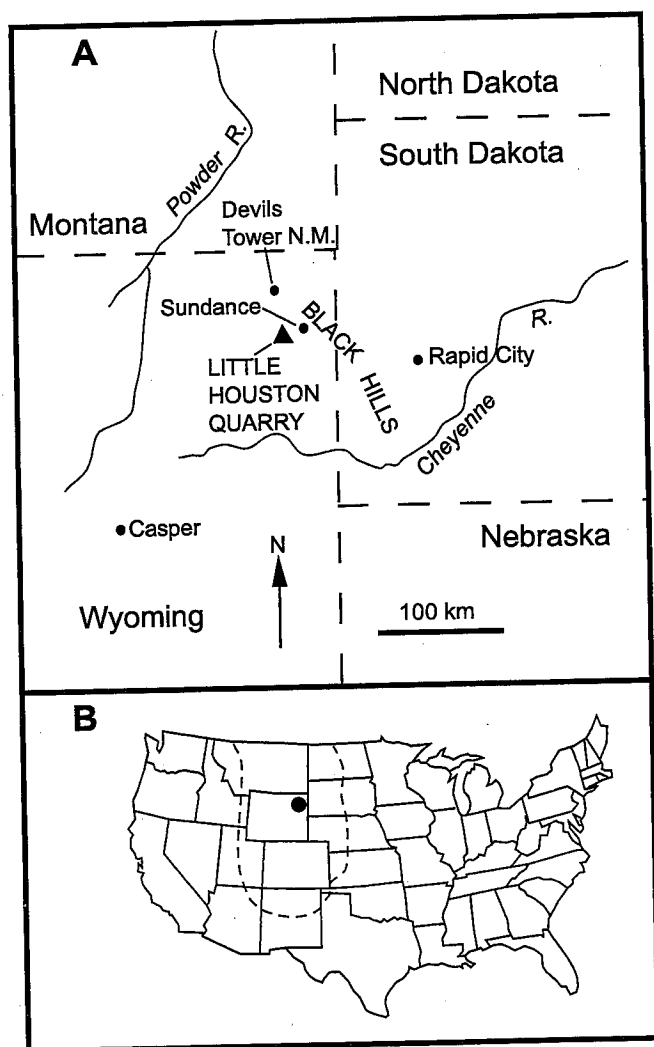
Figure 1. (A) Location of the Little Houston Quarry in northeastern Wyoming, west of the town of Sundance and south of Devils Tower National Monument. (B) Site in relation to the known distribution of the Morrison Formation (dashed line).

were particularly delicate and thus were prepared as far as possible but left in the matrix.

Larger bones in the quarry were mapped and photographed before removal, and some particularly important specimens (e.g. mammal jaws) that were too small to be drawn on the map simply had their approximate areas of collection mapped to within ~10 cm. Taphonomic notes on specimens and quarry layers were recorded in the field as well.

All but two specimens included in this study were from the LHMQ; jaw fragments of a multituberculate and a sphenodontian, taxa not known from the LHMQ, were found in the Main Quarry. Other Main Quarry microvertebrate material was not included in this study because the specimens have not been identified nor prepared from the blocks in which they were collected. Most Main Quarry microvertebrates occurred in pockets among the dinosaur material.

Specimen Counts

Badgley (1986) reviewed common methods for counting relative numbers of individuals for mammalian assemblages. Regardless of the method used, there are always difficult aspects of the counting process for fossils that cannot always be entirely solved (e.g. Gilinsky and Bennington, 1994; Blob and Fiorillo, 1996; Blob, 1997). Among the methods reviewed by Badgley (1986) are minimum number of individuals (MNI), number of identified specimens (NISP), and minimum number of elements (MNE). For reasons discussed later, the number of indentified specimens is nearly equal to the minimum number of elements at the LHMQ. Thus, the main counting methods to be chosen between in this case are MNI and NISP. Badgley (1986) indicated that the MNI method is best suited to deposits in which there has been limited transport and in which the probability of association of elements is medium to high. The NISP method, on the other hand, works best for sites that show evidence of current transport of bones prior to burial and where the probability of association of elements is low. Nearly all microvertebrate specimens from the quarry are isolated individual elements, and there is very little association and no articulation; the quarry is also in a channel deposit. The material appears to have been transported at least a short distance, and, from the disarticulation of the material, the probability of association of the elements is considered low. Thus, the relative abundances of taxa were estimated using the NISP method. Specimens rather than elements are counted in the study (cf. Lyman, 1994); complete elements are less common in the LHMQ and tallies of these would limit the size and diversity of the dataset.

lated, individual elements in a high-density deposit of small bones. In addition, all theropod and ornithopod elements pertain to small individuals.

Specimens were collected by hand quarrying of siltstone matrix. In some cases, concentrated pockets of small bones were worked with needles, and occasionally, very small specimens were found via microscopic examination of the matrix. The matrix was not screen-washed because the matrix softens but does not completely breakdown in water, and because the bones were significantly more fragile than the matrix. Most specimens were prepared under a microscope, using a needle to remove matrix and small amounts of glue to repair cracks. Many specimens

In using the NISP method, it is valuable to have a similar possibility of preservation of the included taxa (J. Damuth, pers. comm., 1997). For this reason, larger taxa (medium and large dinosaurs) were not included in the analysis. Most small taxa from the quarry are assumed to have had an equal chance of preservation, except for the turtles and crocodilians, whose shell material and teeth, respectively, are probably more resistant to destruction during transport than most other elements. Crocodilian teeth are harder than bone and turtle shell fragments are generally thicker and less delicate than many microvertebrate elements.

Teeth are the most common remains of theropod dinosaurs and crocodilians in the sample. These elements were included in the count although one animal produces and sheds many teeth in its lifetime. Furthermore, these animals have substantially more teeth per individual than mammals. It is assumed, however, that few of these teeth belonged to the same individual. Counting all teeth may overestimate the abundances of theropods and crocodilians, but exclusion of teeth entirely would underestimate the abundances. Similarly, it was felt that doing a MNI count for turtle shell material would underestimate abundance more than including the material would overestimate it.

Ecological Categorizations

The specimen counts were used to determine relative abundances of the taxa, and each taxon was categorized by main habitat, feeding mode, and approximate weight in order to facilitate comparisons of the relative abundance of each group. Relative abundances and diversities of the ecological categories are compared with those of Morrison Formation microvertebrates in general. The likelihood of preservation of each species in the deposit is assumed to be roughly equal, and the accumulation appears to be in an abandoned channel. This paleoenvironmental interpretation suggests that the relative abundance counts would be dominated by aquatic and semi-aquatic species and by lighter-weight species (< 1 kg).

Habitat—Aquatic species are those that spend their lives entirely within bodies of water. Semi-aquatic species are those which either spend much of their time in water and some of it on land or are dependent on water sources for reproductive parts of the life cycle. Species in the terrestrial category are not dependent on water except for drinking and include all theropod and ornithopod dinosaurs, as well as mammals and lizards. This category does not differentiate scansorial, fossorial, or arboreal forms, which may have existed at least among the mammals and lizards.

Feeding mode—For the purposes of this study, species of the carnivore category are those that eat mainly other vertebrate forms. The herbivorous species possess teeth specialized for feeding on plants. The invertivore/carnivore category consists of small species that needed high-energy food and were small enough to feed mainly on adult insects and larvae, worms, and other soft-bodied invertebrates. Most of these species probably also fed on other microvertebrates occasionally, as some modern insectivorous and even herbivorous lizards and salamanders sometimes ingest other small vertebrates (Evans, pers. comm., 1999). Omnivorous species fed on plant material as well as invertebrates and possibly vertebrates.

Mass—The mass categories are here defined for animals <1 kg, 1–10 kg, and 10–100 kg. In this quarry, most of the larger species are represented by individuals under 100 kg. Weights of ornithopod dinosaurs and crocodilians and turtles were partly based on estimates in Dodson et al. (1980). Most other taxa are, based on size, similar to modern species that weigh less than 1 kg.

TAPHONOMY

The microvertebrate material is in a laminated siltstone. The siltstone occurs just above a convex-bottomed channel sandstone, which contains rounded bone fragments and calcium carbonate clasts, particularly at the base. To the south, the channel cuts into and across several layers of gray to red mudstone on either side. The fossiliferous unit consists of light greenish-gray, finely laminated siltstone beds 3–20 cm thick, thinly interbedded with dark greenish-gray to grayish-olive claystones 1–4 cm thick (Fig. 2). Some layers within the siltstones contain abundant rounded, green mudclasts up to about 10 mm in diameter. The matrix is interbedded with, and is eventually overlain by, green claystone and higher up is overlain by another channel sand. The siltstone quarry matrix often is laminated and consists of light gray silt and green clay layers, most less than 1 mm thick. Abundant carbonized plant material occurs in some layers, mostly within the siltstone beds. Invertebrates collected from the quarry include common casts and impressions of bivalves and gastropods. In addition, several charophyte gyrogonites were found in the Main Quarry.

To the south of the LHMQ, at the Main Quarry, the rocks demonstrate the same fining-upward trend, and the overlying sand can also be seen. About 1 m above the top of the bone layer, in the claystone, a single root cast was observed.

Quarrying operations at the mammal excavation demonstrate that the microvertebrate material occurs in two layers, each approximately 10 cm thick, separated by 10–15 cm. The thickness of each layer varies and is as thin as 1 cm. The top of the deposit is undulatory, sometimes dropping or rising 5–7 cm in the space of less than a meter laterally.

Dark greenish-gray claystone

Light tan fine- to very fine-grained sandstone; some crossbeds

Dark greenish gray, grayish-olive, and maroon claystone; rootcast

Light greenish-gray (5GY 8/1) to light olive gray (5Y 6/1) laminated siltstone and very fine-grained sandstone interbedded with dark greenish-gray (5GY 4/1) to grayish-olive (10Y 4/2) claystone; siltstone layers approximately 3-20 cm thick; claystone layers approximately 1-4 cm thick; abundant greenish-gray clay clasts in some siltstone layers; laminations in siltstones are planar to wavy; abundant carbonized plant remains in some siltstone layers; two microvertebrate layers (M) up to approximately 10 cm thick in lower part of unit, containing abundant disarticulated but well-preserved bones

M

M

Light tan, fine- to very fine-grained sandstone; moderately well sorted and rounded grains; 1-5 cm planar tabular and trough crossbeds; rounded clasts of calcium carbonate and clay common near base and center of channel; some well-rounded bone fragments near base; minor amount of recognizable turtle shell and crocodilian teeth

1 m
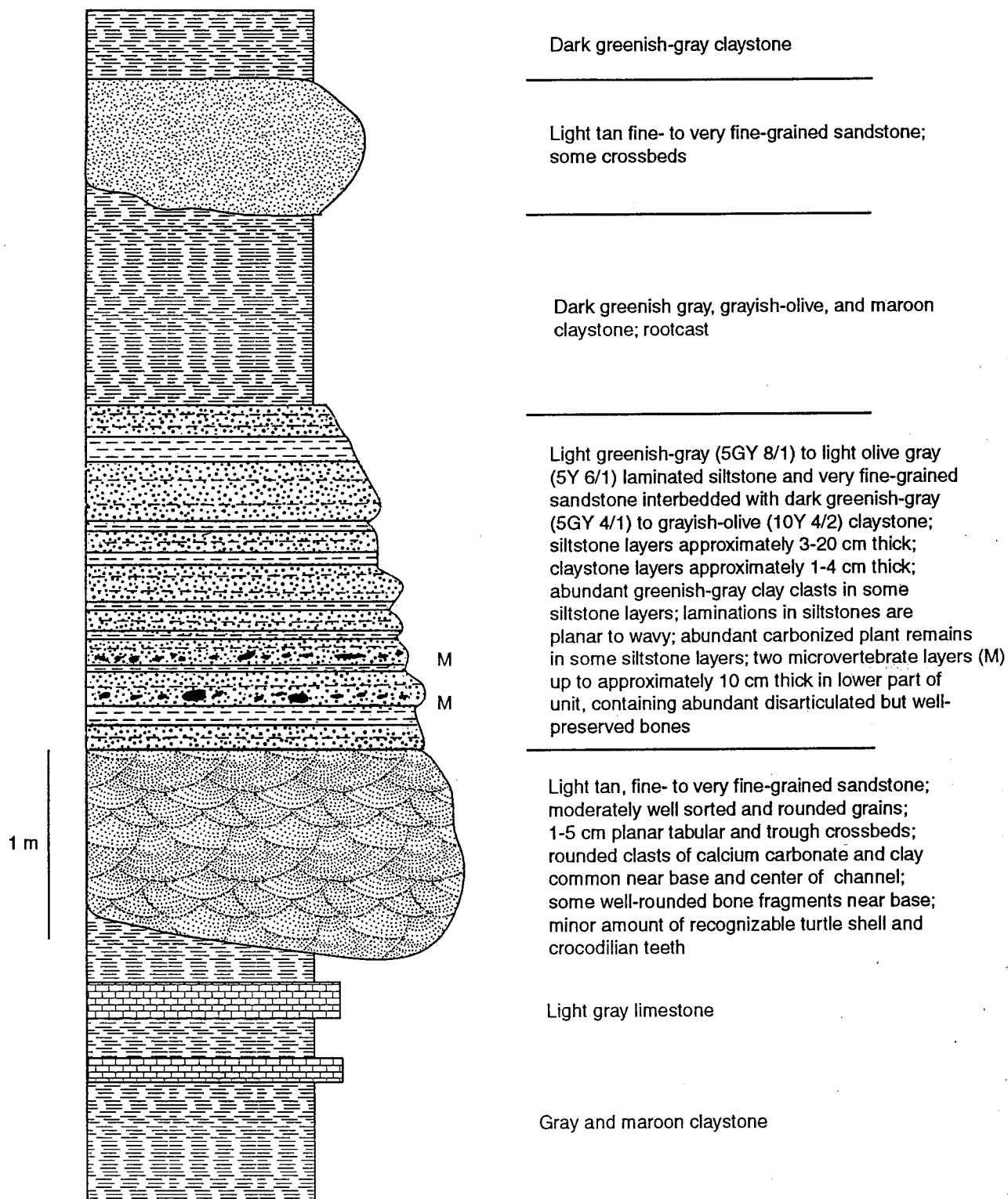
Light gray limestone

Gray and maroon claystone

Figure 2. Generalized stratigraphic section of the Little Houston Quarry exposure showing position of the microvertebrate layers (M) in a unit of interbedded siltstones and claystones above a channel sandstone. Section covered above and below; quarry is in the upper middle part of the Morrison Formation.

The microvertebrate remains are abundant in the fossiliferous layers, with up to several thousand bones and bone fragments per square meter (Fig. 3). Most are tiny, indeterminate fragments. The 400 or so bones from the LHMQ surveyed in this study were collected from an area of approximately 17 m² and thus had an approximate bone density in the quarry of 24/m² (for elements that can be identified at least to a major taxonomic vertebrate group).

Almost all elements of microvertebrates are completely disarticulated, and there are few occurrences of associated elements. Remains of animals from all habitat modes (terrestrial, semi-aquatic, and aquatic) are equally disarticulated; fish and turtle remains are disarticulated just as are terrestrial animals. The small bones do not show any preferred orientation. Although many bones are fragmented, few are worn or polished, and many preserve delicate laminae, processes and spines. Some bones are complete and undistorted, such as small hypsilophodontid femora with intact fourth trochanters, but there are also rare occurrences of highly worn and rounded, unrecognizable, fragments of larger bones. The amount of wear and rounding on most bones is low, although the degree of fragmentation is high, and few bones are entirely complete. The partial sauropod specimen from the LHMQ is articulated except for the distal parts of the tail and some of the anterior dorsal vertebrae (Fig. 4).

Behrensmeyer (1975) proposed a tooth/vertebra ratio as an index of fluvial winnowing for mammalian deposits. Since the tooth/vertebra ratio in a live mammal skeleton is often close to 1 (Badgley, 1986), the higher the ratio is, the more winnowed the deposit. Because vertebrae are easily transported and teeth difficult to move, the teeth would represent a lag deposit. Badgley (1986) found that Miocene channel deposits from Pakistan had ratios of about 3.3 and floodplain facies about a 1.7 ratio. With a greater component of reptilian taxa in a Jurassic deposit, the expected ratio should be somewhat different. The number of vertebrae in most small Jurassic reptiles would probably be somewhat greater than in many Cenozoic mammals, but the number of teeth would likely be much greater. Not only do many reptiles have more teeth per jaw than mammals, but they also continuously shed and replace teeth so that each individual can contribute many teeth to a deposit. We would thus expect the unwinnowed tooth/vertebra ratio of a Jurassic deposit to be somewhat higher than 1.

Interestingly, the ratio for the LHMQ is in fact lower. There are 88 vertebrae of microvertebrates in the sample and 53 isolated teeth (excluding a single very small fish tooth). This gives a tooth/vertebra ratio of 0.602. Including the 13 jaw fragments in the tooth sample, the ratio is 0.795. This suggests that the deposit is relatively unwinnowed.

Behrensmeyer (1988) described the taphonomic characteristics of two different modes of channel deposits for

vertebrates; these are the channel-lag and channel-fill modes. Channel-lags accumulate near the bases of active channels, while channel-fill deposits occur in abandoned channels. A range of intermediate types of deposits occurs between these two. Based on the characteristics for each listed by Behrensmeyer (1988), the Little Houston Quarry appears to represent an abandoned channel-fill deposit. Channel-fill deposit characteristics of the Little Houston Quarry are: occurrence in the upper part of the channel, above basal lags; lithology of mudstone, silt, clay, and fine sands; edges of bones usually fresh; fairly complete bones; wide range of body sizes preserved; and variable alignment of bones. The rareness of associated skeletal parts is more characteristic of channel-lag deposits, and even though some sauropod partial skeletons are articulated in both the Main and Mammal quarries, many of the bones of the smaller dinosaurs are disarticulated and unassociated.

The fact that the siltstone is laminated, and that the microvertebrate remains occur in two distinct layers of disarticulated elements within the siltstone, may indicate that the deposit was an abandoned, but occasionally reactivated, channel and that the bones were deposited during major flooding events. Features of the deposit indicate an abandoned channel, but not the extreme case in which the channel is cut off suddenly and gradually infilled with fine-grained sediments and buries articulated skeletons from nearby. Rather, the channel appears to have been gradually abandoned and to have gone through a period of reactivation during several flooding events before finally being completely cut off and eventually infilled. This would account for the bone deposit having some characteristics of a channel-lag. Similar conclusions about the nature of the Little Houston Quarry deposit were reached in a preliminary study of the Main quarry by Pagnac and DiBenedetto (1998).

A comparison of quarries containing microvertebrates in the Morrison Formation indicates some trends in the taphonomic preservation and that at least two microvertebrate taphofacies can be preliminarily defined (Table 1). These taphofacies are defined by the characteristics of the

Figure 3. (3.1) Photo of the Little Houston Mammal Quarry with bone layer exposed; bones and carbonaceous plant material are black to dark gray; unfossiliferous underlying layer is visible in lower right of photo above shadow; compass in lower left points north; labeled bones are of small ornithopod or theropod dinosaurs: (a) femur; (b) tibia; (c) metatarsal; (d) caudal vertebra; (e) phalanx; (f) small serrated, unrecurved theropod tooth. (3.2–3.6) Specimens of microvertebrates from the Little Houston Mammal Quarry: (3.2) Actinopterygian fish, skull fragment (maxilla?); (3.3) Frog, distal half of humerus; (3.4) Scincomorph? lizard, right dentary; (3.5) Othnielia, tooth; (3.6) Dryolestid mammal, left dentary with six teeth.
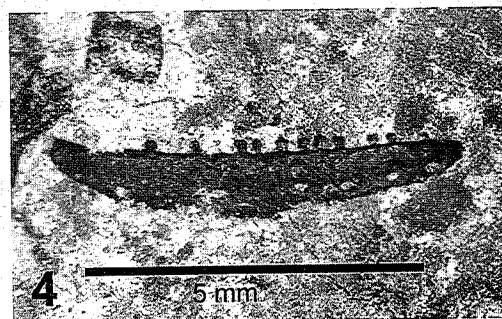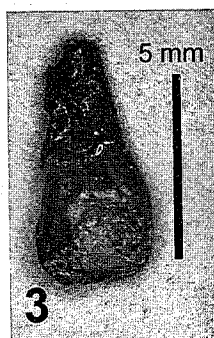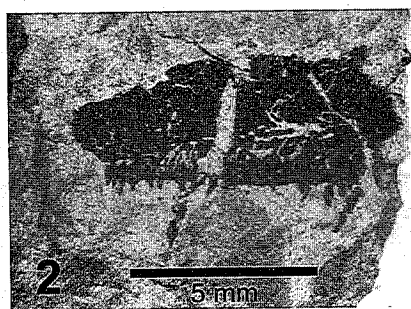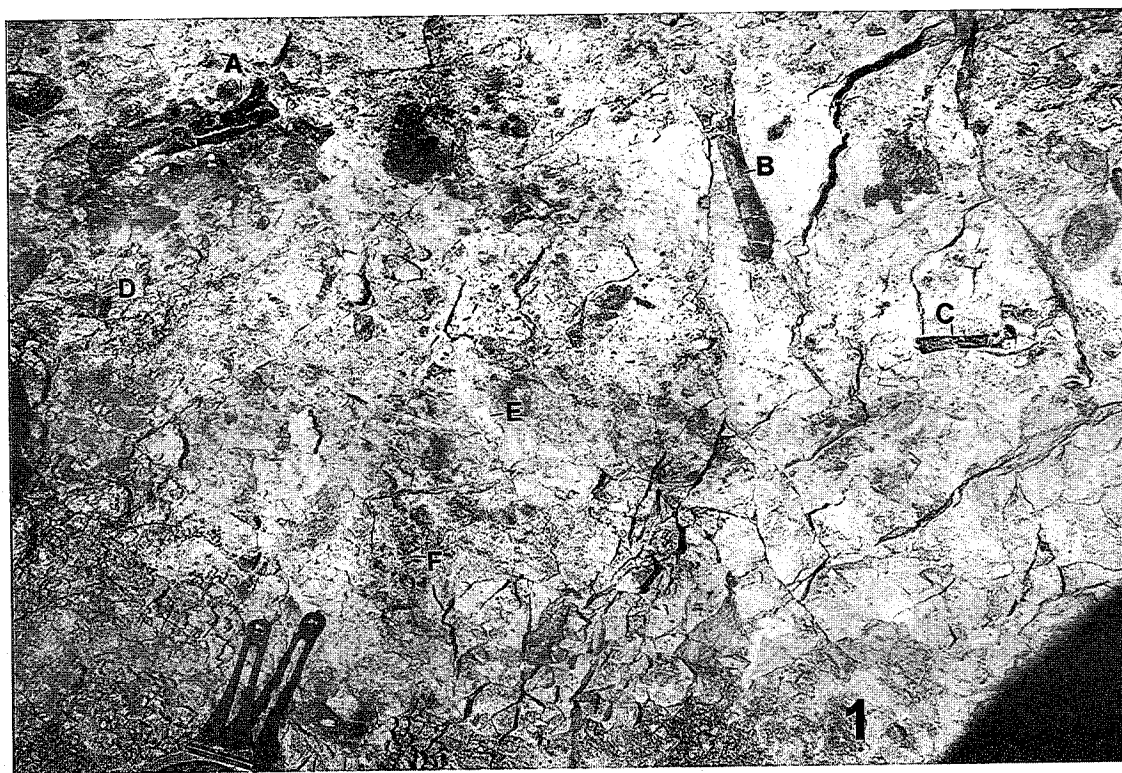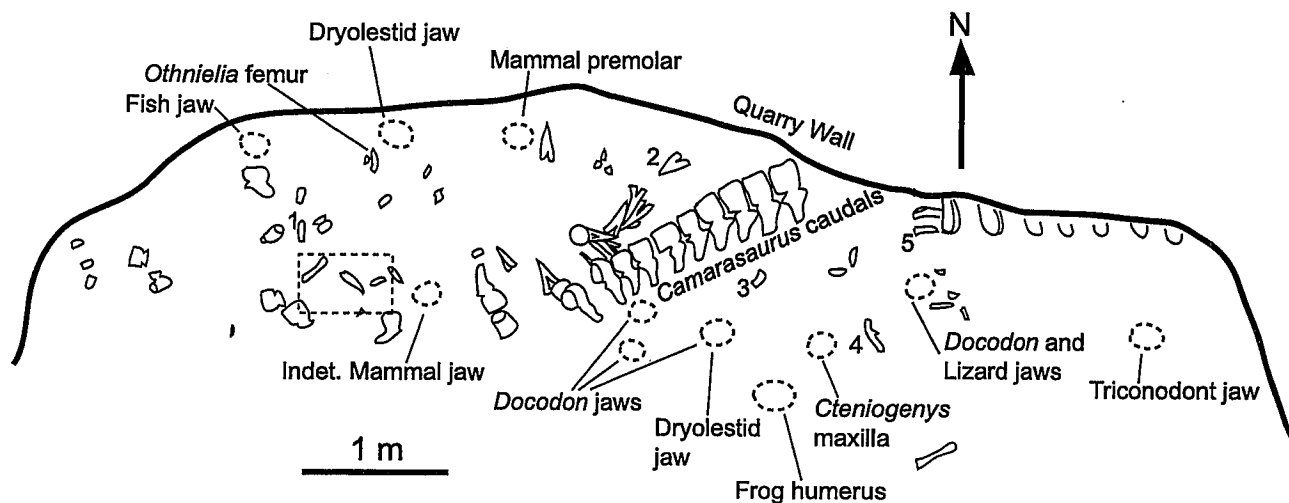
Figure 4. Map of the Little Houston Mammal Quarry as of 1996, showing Camarasaurus *vertebrae and distributions of other material; dashed circles indicate approximate positions of microvertebrate material as labeled. Numbered specimens are as follows: (1) ornithopod dinosaur humerus; (2)* Camarasaurus *chevron; (3) proximal half of ornithopod dinosaur femur; (4) complete femur of* Othnielia; *(5) ornithopod dinosaur metatarsal. Dashed rectangle indicates area of quarry shown in Figure 3.1.*

vertebrate fossil preservation and sedimentology of the quarries and are independent of the types of taxa they preserve. The Type I microvertebrate taphofacies is typified by the LHMQ deposit and this section has provided a description of its characteristics. The Type II taphofacies is based on sites at the Fruita Paleontological Area, in western Colorado, and differs from the LHMQ deposit in that the matrix is often slightly finer, rarely laminated, and more gray in color; it is also different in that microvertebrate remains are less densely accumulated than at the LHMQ and include articulated skeletons and partial skeletons. The LHMQ also preserves more aquatic and semi-aquatic taxa than do the quarries at Fruita, which include mainly terrestrial animals. The Fruita sites have been interpreted as overbank crevasse-splay deposits (Kirkland et al., 1990) and this probably accounts for many of the differences between these quarries and the abandoned channel LHMQ deposit.

AUTECOLOGIES OF TAXA

The following section details which taxa have been identified at the Little Houston Mammal Quarry and the characteristics of each regarding habitat, food preference, and weight category.

OSTEICHTHYES
ACTINOPTERYGII

Fish are represented in the Little Houston Mammal Quarry mainly by scales and jaw fragments, and occasional

skull fragments and teeth (Fig. 3.2). Fish known from the Morrison include Palaeonisciformes, Leptolepididae, Halecostomi, Pycnodontoidea, and Amiiformes (Kirkland, 1998). The identities of the fish from the LHMQ are unknown, but they are relatively small and most do not appear to be amioids.

All actinopterygian fish in the quarry were aquatic, and though some forms or individuals may have grown larger, the remains found here indicate that most were small and weighed <1 kg. Their small size suggests the fish ate invertebrates such as surface insects and worms as well as smaller fish. Modern freshwater fish sometimes ingest plant material, but since this is unlikely to be a major source of energy for fish of this size, the Morrison actinopterygians are classified as invertivore/carnivores.

DIPNOI
Ceratodus sp.

Lungfish are represented in the quarry by two tooth plates. The lungfish were probably several tens of centimeters long and weighed at least 1–2 kg but probably not more than 10 kg, based on comparisons with a modern lungfish with similar skull size. Some specimens of *C. robustus* weighed considerably more, but their tooth plates are much larger than those at the quarry. *Ceratodus* is assumed to have been fully aquatic, though it may have aestivated during dry periods. The teeth of lungfish from the Morrison indicate that the animals probably ate soft-bodied invertebrates when young and clams and other

Table 1. Characteristics of Taphofacies I and II for microvertebrate assemblages within the Morrison Formation of the western United States. Example quarries include main ones, on which characteristics are based, and other sites that are similar in parentheses.

Taphofacies	Lithology	Taphonomy	Example Quarries
Type I	Siltstone, claystone, fine sands; some lamination of siltstones; often green-gray; some small clay clasts; often just above or below channel sands	Relatively abundant disarticulated remains of small vertebrates; often in thin, distinct, high-density accumulations	Little Houston Mammal Quarry (Quarry 9; Small Quarry)
Type II	Siltstone, claystone, very fine sands; rare lamination; often gray; sometimes associated laterally with channel sands	Less abundant articulated to disarticulated remains of small vertebrates; low-density accumulations; less distinct bone layers than Type I	Quarry 4 and Tom's Place at Fruita Paleo Area (Wolf Creek Quarry)

harder shelled animals as adults (Kirkland, 1987). They may also have eaten some aquatic plant material and, when larger, some small fish and other vertebrates, as modern lungfish sometimes feed on these items. Thus, the *Ceratodus* specimens from the Little Houston Mammal Quarry are categorized as invertivore/carnivores.

AMPHIBIA
Anura indet.

A single frog specimen has been found in the quarry; it consists of the distal half of a humerus (Fig. 3.3). Evans and Milner (1993) noted that there were at least two families of frogs represented in the Morrison Formation, the Discoglossidae and the Pelobatidae, but that most material from the formation is undiagnostic below family level. Henrici (1998), however, documented pipoid frogs at Dinosaur National Monument in Utah. The new species *Enneabatrachus hechti* (Evans and Milner, 1993), a discoglossid, and *Rhadinosteus parvus* (Henrici, 1998), a pipoid, are currently the only valid species, as *Eobatrachus agilis* (Marsh, 1887) and *Comobatrachus aenigmatis* (Hecht and Estes, 1960) are considered *nomina dubia* (Evans and Milner, 1993). Humeri in particular are difficult to identify due to ontogenetic changes in the features of these elements; thus, the Little Houston Quarry specimen is simply identified as Anura indeterminate.

The small size of the humerus, and most Morrison frog material, indicates that the animals were less than 1kg in weight. Many small frogs are invertivores and eat mainly ants, termites, beetles, snails, and worms, most of which appear to have been present during Morrison times (Evanoff et al., 1998; Hasiotis and Demko, 1998). Jurassic frogs may have eaten some vertebrate material as well and are here considered as invertivore/carnivores. The mode of life classification used for this study will be semi-aquatic, due to the frogs' dependence on water sources and because many modern species live near lakes, swamps, marshes, and streams. Modern discoglossids and pelobatids, however, have varied habitat preferences ranging from aquatic environments, to near ponds and streams, to rather arid regions (Mattison, 1987).

REPTILIA
CHELONIA
Glyptops plicatulus

This species is represented entirely by carapace and plastron fragments. Other turtle elements could not be distinguished from *Dinochelys* and are thus identified as Chelonia indeterminate. The sculpted and ridged shell of this species is similar to *Uluops uluops* (Bakker et al., 1990) but is unlikely to belong to that form, as *Uluops* is so far only identified from two sites in the upper part of the Morrison. *Glyptops* is a semi-aquatic species and, based on its relatively small size probably weighed 1–10 kg. This species, along with all Morrison turtles, is classified as an omnivore, as modern chelonians eat insects, small fish and other vertebrates, as well as plant material, and vary their diet seasonally and/or as they grow (Alderton, 1988).

Dinochelys whitei

This turtle species is distinguished from *Glyptops* by its relatively smooth, unsculpted shell surface (Gaffney, 1979). It is more common at the quarry than *Glyptops*,

and is also only represented by carapace and plastron fragments. *Dinochelys* is similarly semi-aquatic, omnivorous, and approximately 1–10 kg in weight.

SPHENODONTIA
Opisthias?

A single sphenodontian jaw fragment was found in the Main Quarry. The fragment consists of a section of the posterior part of the dentary with three teeth. *Opisthias* was a small reptile, most likely weighing less than 1 kg, and was terrestrial and mainly insectivorous. The *Opisthias* feeding mode is here considered to be invertivore/carnivore, as the modern *Sphenodon* occasionally consumes small vertebrates.

SQUAMATA
Scincomorpha? indet.

The single lizard specimen from the quarry is a tiny (6 mm) right dentary with several relatively blunt teeth (Fig. 3.4). Generic identification is difficult, but the teeth are too blunt to be from an anguimorph (Hoffstetter, 1967; Evans, 1996). It is not referrable to either of the known Morrison scincomorphs, *Paramacellodus* or *Saurillodon* (Evans, pers. comm., 1996), but that lacertilian group may be the best tentative identification. The specimen is considered to represent a terrestrial form weighing less than 1 kg and is categorized as an invertivore/carnivore, as most small, modern skinks and anguids are largely insectivorous (Mattison, 1989) but some lizards may occasionally feed on small vertebrates (Evans, pers. comm., 1999).

CHORISTODERA
Cteniogenys sp.

This species was named by Gilmore (1928) as a probable lizard, based on elements from Quarry 9 at Como Bluff, but additional material from Europe has indicated that it is actually a small, early choristodere (Evans, 1989). It is represented at the quarry by vertebrae and dentary and maxilla fragments (Foster and Trujillo, 2000). It is a small animal, approximately 25 cm long (Evans, 1991), and weighed considerably less than 1 kg. Like turtles and crocodilians, it was probably semi-aquatic (Evans, 1990). Based on its small size, it probably ate insects and other small invertebrates, as well as small fish.

CROCODYLIA INDET.

Crocodilians are represented mainly by teeth, scutes, and a few jaw fragments that are too incomplete to allow more detailed identification. These crocodilians were semi-aquatic forms of moderate size, most likely *Goniopholis* or *Eutretauranosuchus*, traditionally referred to as goniopholids. The material is not identified here as belonging to that family, as *Eutretauranosuchus*, though related to *Goniopholis*, may be closer to the Dyrosauridae and Thalattosuchia than to *Goniopholis* (Clark, 1994). Additionally, there may be yet unidentified elements of cursorial crocodilians in the collection. Long-limbed cursorial crocodilians are known from the Morrison Formation in Utah and Colorado (Clark, 1985; Kirkland, 1994), but no positively identifiable elements of these taxa have been found in the Little Houston Quarry.

Preserved elements indicate animals of relatively moderate size and most probably weighed less than 100 kg. Dodson et al. (1980), based on Mook's (1925, 1942) descriptions, estimated the weight of *Goniopholis* as being up to 50–60 kg. *Eutretauranosuchus* (Mook, 1967) probably had a similar mass, as the type specimen (CMNH 8028) is slightly smaller than most known *Goniopholis* specimens and appears to be a relatively young individual. Although young crocodilians may feed largely on insects (Pooley, 1989), animals of the lengths indicated by the material from the quarry probably fed primarily on fish, but also on some small vertebrates. The modern crocodilian *Crocodylus niloticus*, at lengths similar to Morrison crocodilians (~2.5–3 m), feeds mostly on fish as well as some small mammals and reptiles, and occasionally ingests snails and shellfish (Pooley, 1989).

REPTILIA? INDET.

Most of the specimens from the Little Houston Quarry are bones, mostly vertebrate and limb elements, probably of small indeterminate reptiles. Many probably belong to turtles, crocodilians, and lizards.

DINOSAURIA
SAURISCHIA
Theropoda

Theropod dinosaurs are represented at the site mainly by teeth and some vertebrae and limb elements. Most of the specimens appear to be of small theropods, including juvenile *Allosaurus* and an unidentified form with laterally compressed but unrecurved teeth. The small theropods are included in this study because the size of their remains indicates that few were much larger than the ornithopod dinosaurs in the collection, and because the taphonomic mode of their preservation is similar to the other animals.

The theropods from the site are carnivorous. Based on their relatively small size, they fed on small reptiles and mammals and other small dinosaurs. Theropods are terrestrial, and those at the site were 100 kg or less.

It should be noted that while the remains from the LHMQ indicate relatively small theropods, the Main Quarry 75 m to the south does contains elements of larger theropods, including adult *Allosaurus*.

ORNITHISCHIA
ORNITHOPODA
Othnielia rex

This small ornithopod, named by Galton (1977), is represented in the LHMQ mainly by teeth (Fig. 3.5) and several femora. The LHMQ teeth include specimens with accessory ridges similar to *Drinker nisti* (Bakker et al., 1990), although these ridges are known from teeth of some specimens of *Othnielia* as well (R. Scheetz, pers. comm., 1998). The teeth of *Nanosaurus agilis* (Marsh, 1877) appear to be slightly different from those of *Othnielia*, but preservation of the dentary and teeth as an impression in matrix in the type specimen of *Nanosaurus* makes it difficult to satisfactorily compare the two. *Nanosaurus*, though considered valid by Galton (1983), is among the *nomina dubia* listed by Sues and Norman (1990), and that classification is followed here. The teeth in the Little Houston Quarry collection are referred to *Othnielia*.

Othnielia was a small ornithopod weighing between 3 and 30 kg, with a modal adult weight of approximately 12 kg (Dodson et al., 1980). It was undoubtedly terrestrial and a low-browsing herbivore that orally processed its food (Sues and Norman, 1990).

Dryosaurus altus

This species is represented by a small pubis of a juvenile. Interestingly, none of the ornithopod teeth in the quarry belong to this species. Dodson et al. (1980) gave the range of weights of *Dryosaurus* as less than 10 kg to about 300 kg with a modal size of 100 kg. The juvenile found at the LHMQ was less than 100 kg as a living animal. Like *Othnielia*, *Dryosaurus* was a terrestrial, low-browsing herbivore and probably possessed more efficient oral processing, because of its more advanced teeth.

Several elements of indeterminate ornithopods have been found in the deposit also, and these most likely belong to one of the two above species.

MAMMALIAFORMES
Docodon victor

This docodont is represented by five jaw fragments and one partial molar. Though several species of *Docodon* have been named, Gingerich (1973) noted that all are probably referrable to *D. victor*. This species was less than 1 kg and terrestrial. Docodonts are believed to have been omnivorous (Simpson, 1933) but may have relied more on small invertebrates than on plant material. The multiple cusps of docodonts have numerous shearing surfaces, which would be useful in processing small, soft-bodied invertebrates and adult insects, but the teeth overall have relatively shorter, blunter cusps and greater occlusal surface area than most other Jurassic mammals, other than multituberculates. These features probably allowed for docodonts to include small seeds and other plant material in their diet.

MAMMALIA
Multituberculata
Psalodon marshi

This plagiaulacid multituberculate was found in the Main Quarry 75 m south of the LHMQ and near a series of *Camarasaurus* caudal vertebrae. *Psalodon marshi* was named by Simpson (1929) for lower jaws and teeth that were larger than the other Morrison multituberculate known at the time, *Ctenacodon*. Simpson (1929) noted that this form probably belonged to *Psalodon potens*, which is based on upper teeth and maxillae, but that he could not be certain. The specimen from the Little Houston Quarry (SDSM 26912) is referred to *P. marshi*, as it consists of a dentary fragment with p4 and m1 that is closer in size to the type specimen of that species (USNM 2684) than to lower jaws and teeth of *Ctenacodon* (Martin and Foster, 1998).

Morrison multituberculates were small and almost certainly weighed less than 1 kg. Though some multituberculates may have been scansorial, there is no evidence of any being fossorial or aquatic (Clemens and Kielan-Jaworowska, 1979), so those of the Morrison are classified as terrestrial, with no differention made for further specializations. The diet of multituberculates has been debated, though it is generally agreed that they were herbivorous to some degree. Simpson (1926) concluded that plagiaulacoid and ptilodontoid multituberculates were largely herbivorous, while Clemens and Kielan-Jaworowska (1979) preferred an omnivorous interpretation of the multituberculate diet. Krause's (1982) study of *Ptilodus* indicated that this genus (and ptilodontoids generally) was probably omnivorous. *Ptilodus* is not much larger than the Morrison multituberculate taxa, and though it has a single, larger blade-like p4, *Ptilodus* has a fairly similar lower dention to *Ctenacodon* and *Psalodon*, which have four, smaller, interlockling blade-like premolars. Krause (1982) also noted that ptilodontoids were probably too small to be entirely folivorous. It is likley, then, that *Psalodon* and other Morrison multituberculates were omnivorous and ate a variety of plant material and seeds as well as insects and other small invertebrates.

Triconodonta indet.

A single, poorly preserved maxilla fragment with one molar is the only evidence of this group found at the LHMQ. The specimen may belong to either *Priacodon* or *Trioracodon*. Triconodonts were most likely terrestrial and weighed less than 1 kg. Early triconodonts were probably insectivorous and later forms most specialized to become partly carnivorous (Jenkins and Crompton, 1979). Since almost no contemporaneous vertebrates were smaller than the mammals, it is likely that the diet of the triconodonts of the Morrison Formation consisted of insects, soft-bodied invertebrates such as slugs and grubs, and possibly small vertebrates.

Dryolestidae indet.

This family is represented by two specimens at the Little Houston Mammal Quarry. The first is a partial jaw with six teeth (Fig. 3.6); it is closest in molar morphology to *Dryolestes priscus* but has a reduced number of molars and may be a juvenile (see T. Martin, 1999). The second Little Houston specimen is a jaw fragment of an indeterminate form, and, as no teeth are preserved, it is identifiable as a dryolestid only because of the characteristically unequal root structure of the alveoli.

Dryolestids had high, pointed cusps and were best suited for feeding on insects and other small invertebrates (Simpson, 1933). The dryolestids were, like the other mammals mentioned here, small and terrestrial. A postcranial skeleton of a paurodontid from Portugal, however, suggests that some members of the order Dryolestida may have been arboreal (Krebs, 1991).

RESULTS AND DISCUSSION

The numbers of elements of each taxon observed in the survey are summarized in Table 2. The habitat, feeding mode, and weight category distributions are summarized in Tables 3–5. The terrestrial habitat category is most diverse, along with the <1kg weight category. Fairly high diversities occur within the invertivore/carnivore feeding mode guild, although the distribution among the other three guilds is fairly even; a relatively even diversity across guilds is a pattern common to many modern communities as well (Gotelli and Graves, 1996). The high diversities in the terrestrial, <1 kg, and invertivore/carnivore ecological categories appear to be significant, even considering the numbers of specimens of each guild in the sample.

Approximately one-third of the specimens in the sample belongs to indeterminate vertebrates (Fig. 5A). Almost all of these are small elements, mainly vertebrae and limb elements, probably belonging to turtles, small crocodil-

ians, lizards, amphibians, and small archosauromorphs such as *Cteniogenys*. Another third of the sample is composed of turtles and crocodilians. The turtle sample consists of *Glyptops, Dinochelys,* and indeterminate turtle remains. Turtles and more specifically *Dinochelys* are the most common identifiable taxa preserved. Ornithopods, theropods, and actinopterygian fish are all roughly similar in abundance and together comprise about a quarter of the sample. Rarer elements of the fauna include mammals, *Cteniogenys, Ceratodus,* frogs, sphenodontians, and lizards. Among these, mammals are represented by the most elements (17), and *Cteniogenys* specimens (6) outnumber the single specimens of frogs, sphenodontians, and lizards.

A census of collections of microvertebrates from other Morrison sites (at the YPM, AMNH, USNM, FMNH, LACM, and DNM) demonstrates that in Quarry 9 at Como Bluff, *Cteniogenys* and sphenodontian specimens each outnumber the lizards significantly (nearly twice and three times as many specimens as lizards, respectively), whereas at the Dinosaur National Monument sites (including Rainbow Park), lizards and sphenodontians are nearly equally common and there is only a single *Cteniogenys* jaw fragment (Chure and Evans, 1998). At the Fruita Paleontological Area in western Colorado, lizard specimens outnumber sphenodontians 3:2 (Foster, 1998), but no specimens of *Cteniogenys* are known, and at Ninemile Hill, north of Como Bluff, *Cteniogenys* specimens are relatively common among a collection also including mammals, lizards, and fish (Trujillo, 1999). These data suggest possible biogeographic patterns in the microvertebrate faunas of the Morrison Formation, particularly the more abundant occurrence of *Cteniogenys* in, and perhaps its restriction to, northern areas of Morrison distribution, (Chure and Evans, 1998; Foster and Trujillo, 2000). Also, the sample from Quarry 9, along with those from Dinosaur National Monument and Fruita, indicates that sphenodontians may have been more common relative to lizards in northern areas; thus, more data are needed from other microvertebrate sites in northern areas.

The occurrence of *Docodon* as the most common mammaliform genus at the Little Houston Quarry is also interesting in that this genus still seems to be restricted mainly to eastern localities (Engelmann and Callison, 1998). It is also known from Quarry 9, Ninemile Hill, and from the Marsh-Felch Quarry and the Small Quarry at Garden Park, Colorado. At all but one of these sites, *Docodon* is the most common mammaliform genus in the sample (the Marsh-Felch Quarry produced one jaw each of *Docodon* and *Kepolestes* [= *Amblotherium* in T. Martin, 1999]), but it is still unknown from western sites such as Rainbow Park and the Fruita Paleontological Area. The occurrence of

Table 2. Specimen counts by taxon and element for the Little Houston Quarry assemblage.

Actinopterygii	Jaw fragments		12	*Dryosaurus altus*	Pubes	1
	Skull fragments		5		Total:	1
	Scales		14	*Othnielia rex*	Teeth	11
	Teeth		1		Femora	3
		Total:	32		Total:	14
Ceratodus sp.	Tooth plates		2	Ornithopoda indet.	Teeth	3
		Total:	2		Limb elements	4
Anura	Humeri		1		Vertebrae	14
		Total:	1		Pect/Pelv girdle elements	2
Glyptops plicatulus	Shell fragments		7		Total:	23
		Total:	7	Reptilia? indet.	Limb elements	66
Dinochelys whitei	Shell fragments		45		Ribs	11
		Total:	45		Vertebrae	59
Chelonia indet.	Shell fragments		25		Total:	136
	Limb elements		14	*Psalodon marshi*	Jaw fragments	1
	Vertebrae		1		Total:	1
	Pect/Pelv girdle elements		11	*Docodon victor*	Jaw fragments	5
		Total:	51		Molars	1
Opisthias?	Jaw fragments		1		Total:	6
		Total:	1	Triconodonta	Maxilla fragments	1
Scincomorpha?	Jaw fragments		1		Total:	1
		Total:	1	Dryolestidae	Jaws	1
Cteniogenys sp.	Jaw fragments		3		Jaw fragments	1
	Maxillae		1		Total:	2
	Vertebrae		2	Mammalia indet.	Jaw fragments	1
		Total:	6		Premolars	3
Crocodylia	Teeth		11		Molars	1
	Scutes		21		Canines	1
	Jaw fragments		3		Incisors	1
	Limb elements		3		Total:	7
		Total:	38			
Theropoda	Teeth		19		Total Sample:	410
	Vertebrae		12			
	Limb elements		4			
		Total:	35			

Docodon in a variety of lithologies suggests that this distribution is not necessarily a result of paleoenvironmental or preservational bias.

More than half of the identifiable microvertebrate specimens from the Little Houston Quarry are semi-aquatic forms (Fig. 5B). Together, semi-aquatic and aquatic taxa make up about two-thirds of the sample, the remaining third being composed of various terrestrial forms (indeter-

minate reptiles? were not included). Behrensmeyer (1975) noted that aquatic depositional environments increase the abundance of aquatic and semi-aquatic taxa relative to terrestrial taxa, but that the numerical representation of terrestrial taxa should be similar to what would be seen in terrestrial deposits. That terrestrial forms are less common in a channel deposit is not surprising. Fully aquatic species, however, seem to be less common than expected.

Table 3. Habitat category assignments for taxa known from the Little Houston Quarry.

Aquatic	Semi-Aquatic	Terrestrial
Actinopterygii	Anura	Scincomorpha?
Ceratodus sp.	*Glyptops plicatulus*	Theropoda
	Dinochelys whitei	*Othnielia rex*
	Chelonia indet.	*Dryosaurus altus*
	Cteniogenys sp.	Ornithopoda indet.
	Crocodylia	*Psalodon marshi*
		Docodon victor
		Triconodonta
		Dryolestidae
		Mammalia indet.
		Opisthias?

This may be a result of a truly more diverse and numerous population of semi-aquatic forms in the region or of a taphonomic bias against the preservation and/or easy recognition of aquatic forms. The relative rareness of *Ceratodus* tooth plates may stem from a low population density in the original environment, but actinopterygian fish elements, which are much smaller and more easily destroyed, are less likely to be preserved or are not easily recognized. On the other hand, Dodson et al. (1980) noted that the microvertebrate component of the Morrison, particularly aquatic forms, was low-density and "background" in nature, perhaps a result of the seasonal to semi-arid climate that appears to have been prevalent. A number of newly-found microvertebrate sites in the Morrison, which contain abundant remains of fish and other aquatic taxa, suggest, however, that these forms were not as rare as previously supposed.

The relative abundances of taxa in each feeding mode category (Fig. 5C) indicate that the omnivores (turtles and two types of mammals) and carnivores (crocodilians and theropod dinosaurs) dominate, comprising two-thirds of the sample. The next most-common group (invertivore/carnivores) in the sample includes the two types of fish, the dryolestid and triconodont mammals, frogs, lizards, sphenodontians, and *Cteniogenys*, while the herbivores were ornithopod dinosaurs. The invertivore/carnivore category is the most diverse feeding mode (Table 4). The omnivores are fairly common and also reasonably diverse (Table 4). This is unusual, as most food webs have relatively few omnivorous species (Rosenzweig, 1995). Conceivably, the sampled community may have been significantly more diverse than is currently apparent, the omnivorous species may have been drawn from separate communities, or the assignment of some of the species to omnivorous habits

may be mistaken. The fact that the deposit combines taxa from both terrestrial and aquatic environments also probably accounts for some of the diversity and abundance among omnivores.

Dodson (1973) studied the transport potential of elements of microvertebrates and warned that, because of the ease with which these bones are carried downstream, it is risky to make paleoecological conclusions based on assemblages of microvertebrates. Dodson found that vertebrae are particularly quick to move and that jaws remain stationary the longest; he suggested that a common occurrence of vertebrae relative to jaws in a microvertebrate deposit may indicate a lack of selective winnowing. Vertebrae are reasonably common elements in the Little Houston Mammal Quarry sample, with more than three times as many vertebrae as jaws (Fig. 5D) and more vertebrae than teeth, as well. The abundance of vertebrae is a bit surprising, as other taphonomic characteristics of the deposit (layering of two microvertebrate layers; disarticulaton and disassociation; rare rounded bone fragments) indicate deposition during flood events. It is possible, however, that large amounts of bone material were transported a short distance into the abandoned channel rather quickly and little flow occurred after this, allowing the material to settle with no subsequent winnowing removing more easily transported elements. Thus it is possible that the specimens are from a local community. Hanson (1980), however, found little abrasion or other transport-related damage on bones that had been carried 2 km. How much communities on the Morrison floodplain would have varied in this distance cannot be determined.

As the fauna may represent a paleocommunity from the surrounding floodplain and not a mixture of proximal and distal communities, it will be interesting to compare other microvertebrate deposits of the Morrison Formation. A faunally and lithologically comparable site is Quarry 9 at Como Bluff, Wyoming, several hundred kilometers to the southwest of the Little Houston Quarry (see Ostrom and McIntosh, 1966). Quarry 9 also represents a Type I taphofacies (Table 1). All taxa known from the Little Houston site also occur at Quarry 9, but numerous other genera are known at the latter as well. Mammals are particularly diverse at Quarry 9 (Simpson, 1929). A preliminary survey of 870 specimens from Quarry 9 (from the collections at YPM, USNM, AMNH, and FMNH) and 193 from the Little Houston Quarry (excluding sauropods and larger theropods at both) reveals 38 genera from the former and 16 from the latter. Table 6 compares the relative abundance percentages of taxa from the Little Houston Quarry with those of Quarry 9. Some distinct differences are apparent. Fish are the most common taxon at Quarry 9, mainly due to a significant sample of amioid vertebrae, whereas at the Little Houston Quarry the turtle *Dinochelys* is most common.

Table 4. Feeding Mode category assignments for taxa known from the Little Houston Quarry.

Carnivores	Herbivores	Invertivore/Carnivores	Omnivores
Crocodylia	Othnielia rex	Actinopterygii	Dinochelys whitei
Theropoda	Dryosaurus altus	Ceratodus sp.	Glyptops plicatulus
	Ornithopoda indet.	Cteniogenys sp.	Docodon victor
		Psalodon marshi	
		Chelonia indet.	
		Anura	
		Scincomorpha?	
		Triconodonta	
		Dryolestidae	
		Opisthias?	

Table 5. Mass category assignments for taxa known from the Little Houston Quarry.

<1kg	1–10kg	10–100kg
Actinopterygii	Glyptops plicatulus	Theropoda
Anura	Dinochelys whitei	Othnielia rex
Cteniogenys sp.	Chelonia indet.	Dryosaurus altus
Scincomorpha?	Ceratodus sp.	Ornithopoda indet.
Psalodon marshi		Crocodylia
Docodon victor		
Triconodonta		
Dryolestidae		
Mammalia indet.		
Opisthias?		

Dinochelys is more common than Glyptops at the LHMQ, but the two turtles are about equally abundant at Quarry 9. Also, crocodilians are abundant at the Little Houston Quarry but are a minor component of the Quarry 9 fauna. Some of the differences in abundances and diversity between the two sites may be due to the drastically different sample sizes. Is the diversity at the Little Houston Quarry lower (or higher) than we should expect for a sample of approximately 190 specimens drawn from the same community as Quarry 9?

Rarefaction curves were calculated for each quarry in order to compare the relative generic diversities. These curves were calculated using the equations of Tipper (1979), which are in turn based on Hurlbert (1971) and Heck et al. (1975). The method of Sanders (1968) is simple to compute but consistently overestimates the expected number of species (Heck et al., 1975). It is important that samples compared using rarefaction are taxonomically similar, are from similar habitats (lithologically and taphonomically similar, in this case), and have been collected using similar techniques (Tipper, 1979; Gotelli and Graves, 1996). As stated above, the faunas, lithology, and taphonomy of the Little Houston Quarry and Quarry 9 are quite similar and both were collected mainly through hand quarrying of matrix. Rarefaction curves based on counts of vertebrates, in which the numbers of preservable elements are not always the same between different taxa, may vary slightly due to the necessarily less-reliable way these animals must be counted. However, this should not present much of a problem as long as the preservation potential of taxa remains the same between localities (e.g. Clyde and Gingerich, 1998).

The rarefaction curves for the LHMQ and Quarry 9 (Fig. 6) suggest that the samples were drawn from communities similar in species richness and that the LHMQ sample is not significantly less diverse than expected for the number of specimens known. The number of genera from the LHMQ is just below the 95% confidence interval of the expected value for a sample of similar size from Quarry 9. A sample of 190 specimens from Quarry 9 would
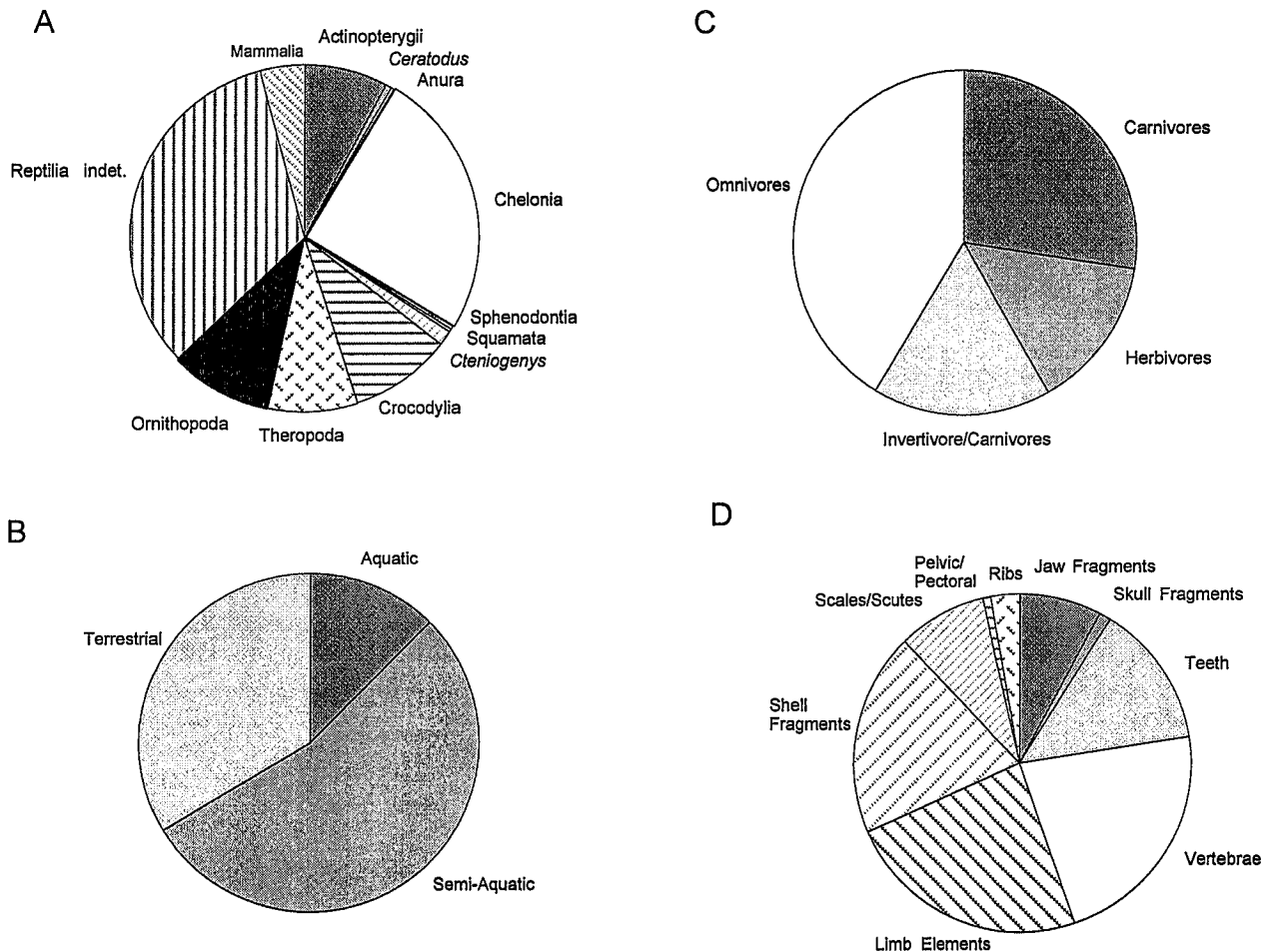
Figure 5. (A) Relative abundances of microvertebrate taxa in the sample from the Little Houston Mammal Quarry. N = 410. (B) Relative abundances of quarry specimens attributed to different habitat categorizations. N = 274. (C) Relative abundances of quarry specimens from each feeding mode category. N = 266. (D) Relative abundances of quarry microvertebrate elements. N = 399.

be expected to have about 24 genera represented, but the confidence interval allows a range of about 16 to 32 genera; the LHMQ has 16 genera known with 193 specimens. For sample sizes smaller than 190, the 95% confidence intervals of the two quarries' samples overlap. Thus, although the LHMQ sample may in fact be drawn from a taxonomically similar but less diverse paleocommunity than Quarry 9, these data cannot confirm that.

Most Morrison high-level vertebrate taxonomic groups are present in the Little Houston Quarry sample. The main groups missing are pterosaurs and symmetrodont and paurodont mammals. Thus, most of the missing generic diversity at the Little Houston Quarry is among these groups and in the range of taxa known among the crocodilians and dryolestid, triconodont, and multituberculate mammals at Quarry 9. Aside from the greater sample size at Quarry 9, the higher diversity there may also result

from that deposit perhaps being drawn from a greater geographic area within the Morrison floodplain. Also, it may have been time-averaged over a greater interval than the LHMQ; both of these factors would have increased the chances of preservation of rarer taxa, such as the crocodilian *Macelognathus*, known from a single specimen from Quarry 9 and nowhere else.

The degree to which the LHMQ sample may be time-averaged is difficult to precisely ascertain. Channel-fill deposits like the LHMQ should be drawn from shorter intervals (and from smaller areas) than channel-lags (Behrensmeyer and Hook, 1992). Estimates for the range of deposition of channel-fill accumulations are generally from 10s or 100s to 1000s of years (Kidwell and Behrensmeyer, 1993; Rogers, 1993), and the effects of time-averaging can include distortions of species richness and other characteristics of the fauna (Fürsich and Aberhan, 1990).

Table 6. Comparison of the relative abundances of taxa in the Little Houston Quarry and Quarry 9 microvertebrate assemblages.

Taxon	Little Houston Quarry Percent of Sample	Quarry 9 Percent of Sample
Dinochelys	23.3	8.7
Crocodylia	19.7	3.5
Theropoda	18.1	1.0
Actinopterygii	16.6	29.2
Othnielia	7.3	0.73
Glyptops	3.6	11.5
Cteniogenys	3.1	3.8
Docodon	3.1	6.1
Ceratodus	1.0	3.1
Dryolestidae	1.0	12.7
Dryosaurus	0.5	0.44
Anura	0.5	0.58
Psalodon	0.5	1.5
Triconodonta	0.5	3.4
Scincomorpha?	0.5	1.9
Sphenodontia	0.5	5.3
Ctenacodon	—	2.3
Caudata	—	0.15
Pterosaur	—	0.30
Symmetrodonta	—	2.4
Paurodontidae	—	1.7
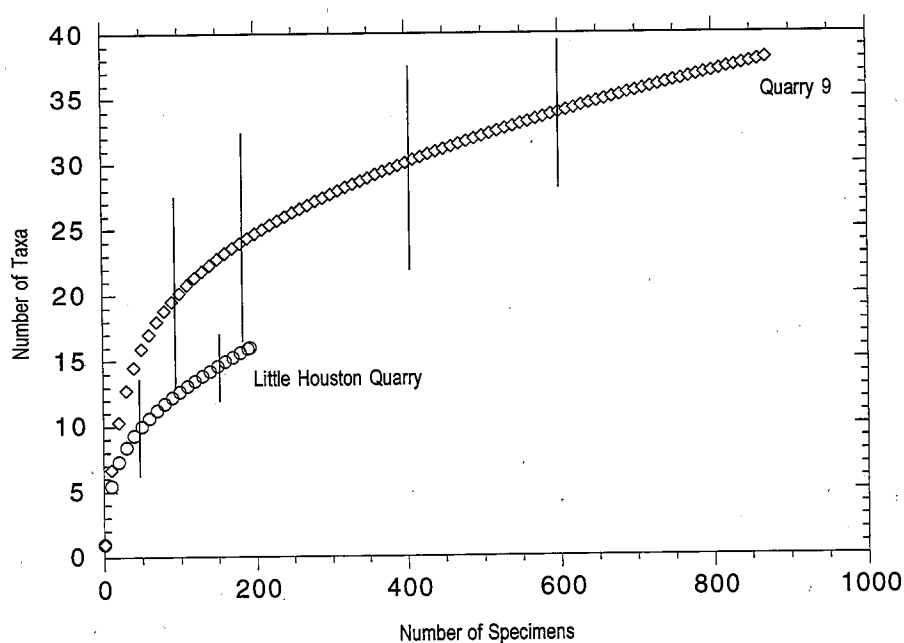
Figure 6. Rarefaction curves for microvertebrate material from the Little Houston Mammal Quarry and Quarry 9, showing expected number of taxa at smaller sample sizes. Vertical lines indicate 95% confidence interval.

A

B
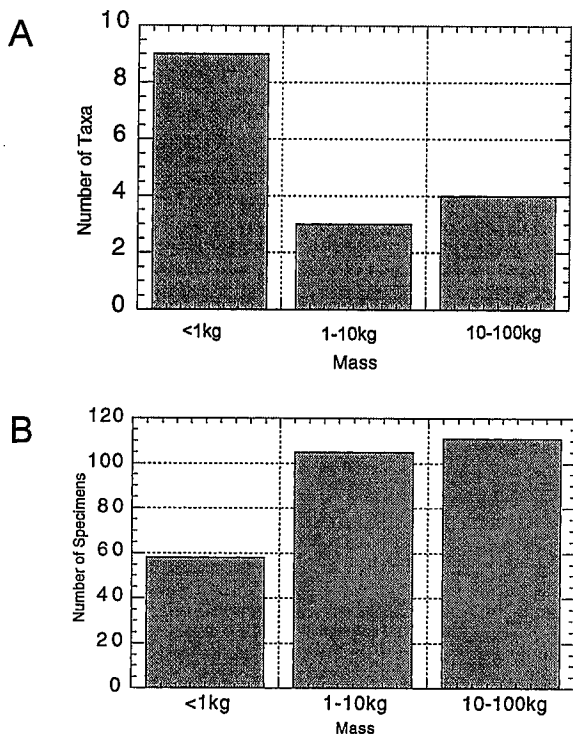
Figure 7. (A) Taxonomic diversity within mass categories for the Little Houston Mammal Quarry sample. (B) Numeric abundance within mass categories.

However, advantages of moderate time-averaging include the filtering out of minor fluctuations in the environment that may affect populations and ecosystem dynamics; this would result in the record reflecting the long-term average composition of the fauna (R. Martin, 1999). Also, analyzing the composition of the fauna through ecological characterizations (e.g. feeding and habitat modes) appears to be less prone to distortion than other attributes (Fürsich and Aberhan, 1990).

The sample from the Little Houston Quarry resembles the Morrison Formation in general, and most modern communities, in preserving a higher diversity of animals of small body size than of larger sizes (Fig. 7A). However, there is still a greater abundance of specimens of larger-bodied animals in the sample (Fig. 7B), indicating that, despite the great range of body sizes preserved at the quarry and the relative abundance of small animals compared to many quarries in the Morrison Formation, there still is a preservational bias in favor of larger skeletal elements. Alternatively, the fact that many of the smallest elements from the quarry are taxonomically indeterminate, and thus cannot be assigned to a specific weight category, may have lowered the abundance of taxa with a body mass less than 1 kg in Figure 7B.

CONCLUSIONS

The Little Houston Quarry microvertebrate fossils are preserved in an abandoned channel deposit. The fossiliferous layers were likely deposited fairly quickly with well-preserved vertebrate material, derived from nearby, mixed with a very minor component of rounded bone fragments, apparently transported a significant distance. Preservation of a wide variety of microvertebrate elements in good condition, including vertebrae and other more easily transported elements, suggests a lack of significant winnowing of the deposit.

The paleofauna represents a mixture of the local aquatic, semi-aquatic, and terrestrial communities. Because of the aquatic environment of deposition, the semi-aquatic taxa are most abundant, though the terrestrial animals have a greater overall diversity. As with most other communities, the smaller-bodied weight categories were more diverse than larger ones and feeding mode guilds were fairly evenly filled. Numerically, however, identifiable small-bodied animals are less abundant, and the omnivore feeding mode (mostly turtles) dominates; both of these abundance patterns are products of the taphonomy of the site and not true paleoecological patterns unique to the area. In fact, these abundance patterns are characteristic of the Morrison Formation as a whole. Smaller-bodied animals must have been far more abundant and ecologically important than their known record indicates.

The microvertebrate fauna at the LHMQ is taxonomically similar to Quarry 9, and the generic-level diversity is apparently within the range expected for its smaller sample size. In addition to its larger sample size, the greater diversity at Quarry 9 may be a result of greater time averaging within the deposit or from having a greater area from which the material was drawn in the original ecosystem. If biogeographic patterns of diversity change within the vertebrate fauna of the Morrison Formation are found, the patterns would not likely be a result of temporal differences between sites, as the expected vertebrate generic diversities for the Morrison Formation as a whole do not seem to have changed significantly through time (Foster, 1998). North-south microvertebrate diversity and biogeographic distribution patterns within the formation, if present, could be related in part to an observed trend toward more humid conditions in the more northern parts of Morrison deposition (Miller, 1987).

Patterns of occurrence and abundance of *Cteniogenys*, lizards, sphenodontians, and other animals at the Little Houston Quarry and other microvertebrate sites in the Morrison Formation suggest biogeographic distributions that are more varied than those of some larger-bodied species (Foster, 2000). The choristodere *Cteniogenys* and the mammaliform *Docodon* are known mainly from northern

and eastern localities, respectively, and these distributions seem to be independent of sample size (Chure and Evans, 1998; Engelmann and Callison, 1998; Foster and Trujillo, 2000). Each occurs in its respective region at large and small sites and is nearly absent from other areas even in large sample sizes.

Our understanding of paleobiogeographic distribution and abundance patterns will improve with the discovery and analysis of new microvertebrate sites and with continued analysis of those already known. Comparison of the faunas and collections of the microvertebrate localities will help determine in which groups the differences between the quarries are greatest. Finding whether these differences are due to species biogeography, paleocommunity patterns, or some other factor, will require a better understanding of all microvertebrate localities within the Morrison Formation.

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REFERENCES CITED

Alderton, D., 1988, Turtles and Tortoises of the World: Facts on File, New York, 191 p.

Badgley, C., 1986, Counting individuals in mammalian fossil assemblages from fluvial environments: Palaios, v. 1, p. 328–338.

Bakker, R.T., Carpenter, K., Galton, P., Siegwarth, J., and Filla, J., 1990, A new latest Jurassic vertebrate fauna, from the highest levels of the Morrison Formation at Como Bluff, Wyoming, with comments on Morrison biochronology: Hunteria, v. 2, n. 6, p. 1–19.

Behrensmeyer, A.K., 1975, The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya: Bulletin of the Museum of Comparative Zoology, v. 146, p. 473–578.

_____, 1988, Vertebrate preservation in fluvial channels: Palaeogeography, Palaeoclimatology, Palaeoecology,v. 63, p. 183–199.

Behrensmeyer, A.K., and Hook, R.W., 1992, Paleoenvironmental contexts and taphonomic modes: In A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichele, R. Potts, H.-D. Sues., and S.L. Wing (eds.), Terrestrial Ecosystems Through Time: University of Chicago Press, Chicago, p. 15–136.

Blob, R.W., 1997, Relative hydrodynamic dispersal potentials of soft-shelled turtle elements: implications for interpreting skeletal sorting in assemblages of non-mammalian terrestrial vertebrates: Palaios, v. 12, p. 151–164.

Blob, R.W., and Fiorillo, A.R., 1996, The significance of vertebrate microfossil size and shape distributions for faunal abundance reconstructions: a Late Cretaceous example: Paleobiology, v. 22, p. 422–435.

Chure, D.J., and Evans, S.E., 1998, A new occurrence of Cteniogenys, with comments on its distribution and abundance: Modern Geology, 23, 49–55.

Clark, J.M., 1985, A new crocodilian from the Upper Jurassic Morrison Formation of western Colorado: Unpublished master's thesis, University of California, Berkeley, 102 p.

_____, 1994, Patterns of evolution in Mesozoic Crocodyliformes: In N.C. Fraser and H.-D. Sues, In the Shadow of the Dinosaurs–Early Mesozoic Tetrapods: Cambridge University Press, Cambridge, p. 84–97.

Clemens, W.A., and Kielan-Jaworowska, Z., 1979, Multituberculata: In J.A. Lillegraven, Z. Kielan-Jaworowska, and W.A. Clemens, Mesozoic Mammals–the First Two-Thirds of Mammalian History: University of California Press, Berkeley, p. 99–149.

Clyde, W.C., and Gingerich, P.D., 1998, Mammalian community response to the latest Paleocene thermal maximum: an isotaphonomic study in the northern Bighorn Basin, Wyoming: Geology, v. 26, p. 1011–1014.

Dodson, P., 1973, The significance of small bones in paleoecological interpretation: Contributions to Geology, University of Wyoming, v. 12, p. 15–19.

Dodson, P., Behrensmeyer, A.K., Bakker, R.T., and McIntosh, J.S., 1980, Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation: Paleobiology, v. 6, p. 208–232.

Engelmann, G.F., and Callison, G., 1998, Mammalian faunas of the Morrison Formation: Modern Geology, v. 23, p. 343–379.

Evanoff, E., Good, S.C., and Hanley, J.H., 1998, An overview of the freshwater mollusks from the Morrison Formation (Upper Jurassic, Western Interior, USA): Modern Geology, v. 22, p. 423–450.

Evans, S.E., 1989, New material of Cteniogenys (Reptilia: Diapsida; Jurassic) and a reassessment of the phylogenetic position of the genus: Neues Jarhbuch für Geologie und Paläontologie, v. 1989, p. 577–589.

_____, 1990, The skull of Cteniogenys, a choristodere (Reptilia: Archosauromorpha) from the Middle Jurassic of Oxfordshire: Zoological Journal of the Linnaean Society, v. 99, p. 205–237.

_____, 1991, The postcranial skeleton of the choristodere Cteniogenys (Reptilia: Diapsida) from the Middle Jurassic of England: Geobios, v. 24, n. 2, p. 187–199.

_____, 1996, Parviraptor (Squamata: Anguimorpha) and other lizards from the Morrison Formation at Fruita, Colorado: The Continental Jurassic, Museum of Northern Arizona, Bulletin 60, p. 243–248.

Evans, S.E., and Milner, A.R., 1993, Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America: Journal of Vertebrate Paleontology, v. 13, p. 24–30.

Foster, J.R., 1998, Aspects of vertebrate paleoecology, taphonomy, and biostratigraphy of the Morrison Formation (Upper Jurassic), Rocky Mountain region, western United States: Unpublished Ph.D. dissertation, University of Colorado, Boulder, 405 p.

_____, 2000, Paleobiogeographic homogeneity of dinosaur faunas during the Late Jurassic in western North America: In S.G. Lucas and A.B. Heckert (eds.), Dinosaurs of New Mexico: New Mexico Museum of Natural History and Science, Bulletin 17, p. 47–50.

Foster, J.R., and Martin, J.E., 1994, Late Jurassic dinosaur localities in the Morrison Formation of northeastern Wyoming: Wyoming Geological Association, 44th Annual Field Conference Guidebook, p. 115–126.

Foster, J.R., and Trujillo, K.C., 2000, New occurrences of Cteniogenys (Reptilia, Choristodera) in the Late Jurassic of Wyoming and South Dakota: BYU Geology Studies, v. 45, p. 11–18.

Fürsich, F.T., and Aberhan, M., 1990, Significance of time-averaging for paleocommunity analysis: Lethaia, v. 23, p. 143–152.

Gaffney, E.S., 1979, The Jurassic turtles of North America: American Museum of Natural History, Bulletin 162, p. 95–135.

Galton, P.M., 1977, The ornithopod dinosaur Dryosaurus and a Laurasia-Gondwanaland connection in the Upper Jurassic: Nature, v. 268, p. 230–232.

_____, 1983, The cranial anatomy of Dryosaurus, a Hypsilophodontid dinosaur from the Upper Jurassic of North America and east Africa, with a review of Hypsilophodontids from the Upper Jurassic of North America: Geologica et Palaeontologica, v. 17, p. 207–243.

Gilinsky, N.L., and Bennington, J B., 1994, Estimating numbers of whole individuals from collections of body parts: a taphonomic limitation of the paleontological record: Paleobiology, v. 20, p. 245–258.

Gilmore, C.W., 1928, Fossil lizards of North America: Memoirs of the National Academy of Sciences, v. 22, n. 3, p. 1–169.

Gingerich, P.D., 1973, Molar occlusion and function in the Jurassic mammal Docodon: Journal of Mammalogy, v. 54, p. 1008–1013.

Gotelli, N.J., and Graves, G.R., 1996, Null Models in Ecology: Smithsonian Institution Press, Washington, 368 p.

Hanson, C.B., 1980, Fluvial taphonomic processes: models and experiments: In A.K. Behrensmeyer and A.P. Hill (eds.), Fossils in the Making: Vertebrate Taphonomy and Paleoecology: University of Chicago Press, Chicago, p. 156–181.

Hasiotis, S.T., and Demko, T.M., 1998, Ichnofossils from Garden Park Paleontological Area, Colorado: implications for paleoecologic and paleoclimatic reconstructions of the Upper Jurassic: Modern Geology, v. 22, 461–479.

Hecht, M.K., and Estes, R., 1960, Fossil amphibians from Quarry Nine: Postilla, n. 46, p. 1–19.

Heck, K.L., Jr., van Belle, G., and Simberloff, D., 1975, Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size: Ecology, v. 56, p. 1459–1461.

Henrici, A.C., 1998, A new pipoid anuran from the Late Jurassic Morrison Formation at Dinosaur National Monument, Utah: Journal of Vertebrate Paleontology, v. 18, p. 321–332.

Hoffstetter, R., 1967, Coup doeil sur les sauriens (= lacertiliens) des couches de Purbeck (Jurassique Supérieur d'Angleterre): Probléms Actuels de Paléontologie (Évolution des Vertébrés), Colloques Internationaux du Centre National de la Recherche Scientifique, v. 163, p. 349–371.

Hurlbert, S.H., 1971, The nonconcept of species diversity: a critique and alternative parameters: Ecology, v. 52, p. 577–586.

Jenkins, F.A., Jr., and Crompton, A.W., 1979, Triconodonta: In J.A. Lillegraven, Z. Kielan-Jaworowska, and W.A. Clemens, Mesozoic Mammals-the First Two-Thirds of Mammalian History: University of California Press, Berkeley, p. 74–90.

Kidwell, S.M., and Behrensmeyer, A.K., 1993, Summary: estimates of time-averaging: In S.M. Kidwell and A.K. Behrensmeyer (eds.), Taphonomic Approaches to Time Resolution in Fossil Assemblages: Paleontological Society Short Courses in Paleontology, n. 6, p. 301–302.

Kirkland, J.I., 1987, Upper Jurassic and Cretaceous lungfish tooth plates from the Western Interior, the last dipnoan faunas of North America: Hunteria, v. 2, n. 2, p. 1–16.

_____, 1994, Predation of dinosaur nests by terrestrial crocodilians: In K. Carpenter, K.F. Hirsch, and J.R. Horner, Dinosaur Eggs and Babies: Cambridge University Press, Cambridge, p. 124–133.

_____, 1998, Morrison fishes: Modern Geology, v. 22, p. 503–533.

Kirkland, J.I., Mantzios, C., Rasmussen, T.E., and Callison, G., 1990, Taphonomy and environments; Fruita Paleont. Resource Area, Upper Jurassic, Morrison Formation, W. Colorado (abs.): Journal of Vertebrate Paleontology, v. 10, supplement n. 3, p. 31A.

Krause, D.W., 1982, Jaw movement, dental function, and diet in the Paleocene multituberculate Ptilodus: Paleobiology, v. 8, p. 265–281.

Krebs, B., 1991, Das Skelett von Henkelotherium guimarotae gen. et sp. nov. (Eupantotheria, Mammalia) aus dem Oberen Jura von Portugal: Berliner Geowissenschaftliche Abhandlungen, v. 133, 110 p.

Loomis, F.B., 1902, On Jurassic stratigraphy on the west side of the Black Hills-second paper on American Jurassic stratigraphy: American Museum of Natural History Bulletin v. 16, p. 401–407.

Lyman, R.L., 1994, Relative abundances of skeletal specimens and taphonomic analysis of vertebrate remains: Palaios, v. 9, p. 288–298.

Mapel, W.J., and Pilmore, C.L., 1963, Geology of the Inyan Kara Mountain quadrangle, Crook and Weston counties, Wyoming: United States Geological Survey, Bulletin 1121, p. M1–M15.

Marsh, O.C., 1877, Notice of some new vertebrate fossils: American Journal of Science, (ser. 3) v. 14, p. 249–256.

_____, 1887, American Jurassic mammals: American Journal of Science, v. 33, p. 327–348.

_____, 1890, Description of new dinosaurian reptiles: American Journal of Science, (ser. 3) v. 39, p. 81–86.

Martin, R., 1999, Taphonomy: A Process Approach: Cambridge University Press, New York, 508 p.

Martin, T., 1999, Dryolestidae (Dryolestoidea, Mammalia) aus dem Oberen Jura von Portugal: Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, v. 550, p. 1–119.

Martin, J.E., and Foster, J.R., 1998, First Jurassic mammals from the Black Hills, northeastern Wyoming: Modern Geology, v. 23, p. 381–392.

Mattison, C., 1987, Frogs and Toads of the World: Facts on File, New York, 191 p.

_____, 1989, Lizards of the World: Facts on File, New York, 192 p.

Miller, C.N., 1987, Terrestrial vegetation in the northern Rocky Mountains before the appearance of flowering plants: Annals of the Missouri Botanical Gardens, v. 74, p. 692–706.

Mook, C.C., 1925, A revision of the Mesozoic Crocodilia of North America: American Museum of Natural History Bulletin, v. 51, p. 319–432.

_____, 1942, Skull characters of Amphicotylus lucasii Cope: American Museum Novitates, v. 1165, p. 1–5.

_____, 1967, Preliminary description of a new Goniopholid crocodilian: Kirtlandia, v. 2, p. 1–10.

Ostrom, J.H., and McIntosh, J.S., 1966, Marsh's Dinosaurs: Yale University Press, New Haven, 388 p.

Pagnac, D.C., and DiBenedetto, J.N., 1998, A preliminary report on the taphonomy of the Little Houston Quarry (Upper Jurassic), northeastern Wyoming (abs.): The 5th Conference on Fossil Resources, 1998, Partners Preserving Our Past, Planning Our Future. Sponsored by National Park Service, United States Department of Agriculture–Forest Service, Bureau of Land Management, South Dakota School of Mines & Technology, and North Dakota Geological Survey.

Pooley, A.C., 1989, Food and feeding habits: *In* C.A. Ross (ed.), Crocodiles and Alligators: Facts on File, New York, p. 76–91.

Rogers, R.R., 1993, Systematic patterns of time-averaging in the terrestrial vertebrate record: a Cretaceous case study: *In* S.M. Kidwell and A.K. Behrensmeyer (eds.), Taphonomic Approaches to Time Resolution in Fossil Assemblages: Paleontological Society Short Courses in Paleontology, n. 6, p. 228–249.

Rosenzweig, M.L., 1995, Species Diversity in Space and Time: Cambridge University Press, Cambridge, 436 p.

Sanders, H.L., 1968, Marine benthic diversity: a comparative study: The American Naturalist, v. 102, p. 243–282.

Simpson, G.G., 1926, Mesozoic Mammalia. IV, The multituberculates as living animals: American Journal of Science, (ser. 5), v. 11, p. 228–250.

———, 1929, American Mesozoic Mammalia: Memoirs of the Peabody Museum Yale University, v. 3, p. 1–171.

———, 1933, Paleobiology of Jurassic mammals: Palaeobiologica, v. 5, p. 127–158.

Sues, H-D., and Norman, D.B., 1990, Hypsilophodontidae, *Tenontosaurus*, Dryosauridae: *In* D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria: University of California Press, Berkeley, p. 498–509.

Tipper, J.C., 1979, Rarefaction and rarefiction—the use and abuse of a method in paleoecology: Paleobiology, v. 5, p. 423–434.

Trujillo, K.C., 1999, Vertebrate paleontology, stratigraphy, and sedimentology of new microvertebrate localities in the Morrison (Upper Jurassic) and Cloverly (Lower Cretaceous) formations, Ninemile Hill, Carbon County, Wyoming: Unpublished master's thesis, University of Wyoming, Laramie, 90 p.

Turner, C.E., and Peterson, F., 1999, Biostratigraphy of dinosaurs in the Upper Jurassic Morrison Formation of the Western Interior, USA: *In* D.D. Gillette (ed.), Vertebrate Paleontology in Utah: Utah Geological Survey Miscellaneous Publication 99-1, p. 77–114.