

Paleoecology of the Quarry 9 vertebrate assemblage from Como Bluff, Wyoming (Morrison Formation, Late Jurassic)

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Received 9 May 2005; received in revised form 16 November 2005; accepted 18 November 2005

Abstract

Quarry 9 is among the richest microvertebrate localities in the Morrison Formation, having thus far produced the remains of dozens of Late Jurassic taxa. Because this lenticular claystone deposit records such a high diversity of contemporaneous species, it provides an exceptionally detailed view of their paleoecology and local paleoenvironment. In this study, we reexamined the entire Quarry 9 collection, totaling more than 3700 specimens, and developed a revised faunal list that was used to determine taxonomic and ecological diversities. Comprehensive abundance data were collected as well, revealing significant discrepancies between the most diverse and most abundant groups. Amphibious taxa (crocodilians and turtles) were very abundant, and seemed to fill an important ecological role as “connectors” between the terrestrial and aquatic food webs. In contrast, small terrestrial taxa (small theropods, mammals, and small reptiles) were very diverse, highlighting their central placement within the terrestrial food web. Lithologically and sedimentologically, the deposition of Quarry 9 occurred in a low-energy pond or swamp, an interpretation supported by the available taphonomic data.

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Keywords: Dinosaurs; Paleoenvironment; Taphonomy; Food web; Mammals

1. Introduction

The Morrison Formation is one of the richest dinosaur-bearing strata in the world (e.g., [Dodson et al., 1980a,b, 1983; Foster, 2003](#)), and as such has provided a wealth of data on Late Jurassic dinosaur morphology, evolution, and paleoecology. The wide-ranging Morrison depositional paleoenvironment largely represents semi-arid fluvio-lacustrine floodplains ([Dodson et al., 1980a,b; Demko and Parrish, 1998; Turner and Peterson, 2004](#)) that were host to a diverse assemblage of

dinosaurs, crocodylians, mammals, and other vertebrates. Indeed, Morrison dinosaurs and mammals are among the best-known members of their respective clades known from any Late Jurassic formation anywhere in the world.

The paleoecology of this environment was complex ([Dodson et al., 1980a,b; Foster, 2003; Engelmann et al., 2004](#)), and in some ways remains puzzling. In part this is due to the overwhelming bias of most Morrison sites toward very large animals, especially sauropods (whose diversity testifies to how well-sampled these large herbivores are in the formation) (cf. [Turner and Peterson, 1999; Foster, 2003](#)). Smaller vertebrates, including amphibians, lepidosaurs, and fishes, have received less attention due to their relative infrequency, probably

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resulting in an underestimation of their diversity. This is unfortunate because such taxa can be important indicators of temperature, salinity, and other environmental factors; indeed, these smaller vertebrates are largely restricted to the wetter facies of the Morrison (Foster, 2003; Engelmann et al., 2004). Such taxa bring the added possibility of inferring biological data from potentially similar extant relatives.

Most information on Morrison microvertebrates comes from a limited number of sites, including Nine-mile Hill (Trujillo, 1999; Foster and Trujillo, 2000), Dinosaur National Monument (Chure et al., 1989; Henrici, 1998; Chure and Evans, 1998; Evans and Chure, 1999; Evans et al., 2005), the Little Houston Quarries (Martin and Foster, 1998; Foster, 2001), and Quarry 9, at Como Bluff (Simpson, 1926a,b; Prothero, 1981; Ostrom and McIntosh, 1999). Thankfully, more recent dinosaur quarry work has also focused on collecting associated microvertebrate remains, although study is still in progress for many such sites, especially in the Fruita Paleontological Area (e.g., Kirkland et al., 1990; Small and Carpenter, 1997). In the context of more general Morrison Formation sampling (e.g., Turner and Peterson, 1999), microvertebrate localities probably account for less than 10% of all sites, although this is only a qualitative assessment. This is in contrast with (e.g.) the microvertebrate-rich Judith River and Hell Creek Formations of the Late Cretaceous.

Within the Morrison, Quarry 9 contains the richest and best-known microvertebrate sample to date. William Reed discovered the site in 1879 while working for O.C. Marsh along the Como Bluff anticline (Fig. 1; Ostrom

and McIntosh, 1999). The locality soon yielded many important specimens of Late Jurassic mammals (Marsh, 1880, 1887) and other small vertebrates (Simpson, 1926a). Since then, most work has focused on the diverse mammalian assemblage (e.g., Simpson, 1925a,b,c, 1927, 1928; Prothero, 1981; Martin, 1999), which represents the majority of mammalian diversity—and most of the specimens—known from Jurassic North America (Prothero, 1981). The remaining Quarry 9 fauna includes dinosaurs, fishes, rhynchocephalians (Gilmore, 1909; Simpson, 1926b) and other lepidosaurs (Prothero and Estes, 1980), as well as amphibians (Evans and Milner, 1993), crocodylians (Ostrom, 1971), and turtles. Because it has received less study, the non-mammalian vertebrate material likely conceals additional data on the lower-level diversity of these groups.

Only Simpson (1926a) attempted a paleoecological reconstruction of the Quarry 9 assemblage, outlining hypothetical food chains of the aquatic and terrestrial components. His work was largely qualitative and focused on taxonomic diversity, ignoring important data from relative taxonomic abundances. To this date, no study has obtained complete abundance data from the Quarry 9 assemblage. This is problematic in mammal-rich assemblages, because mammalian fossils tend to be more closely studied (resulting in finer taxonomic resolution) and more specifically identified (resulting in more accurate counts of individuals) than taxa from other clades.

In this paper, we present the results of a reanalysis of the Quarry 9 assemblage. We examined the entire collection from the original Quarry 9 site, with the

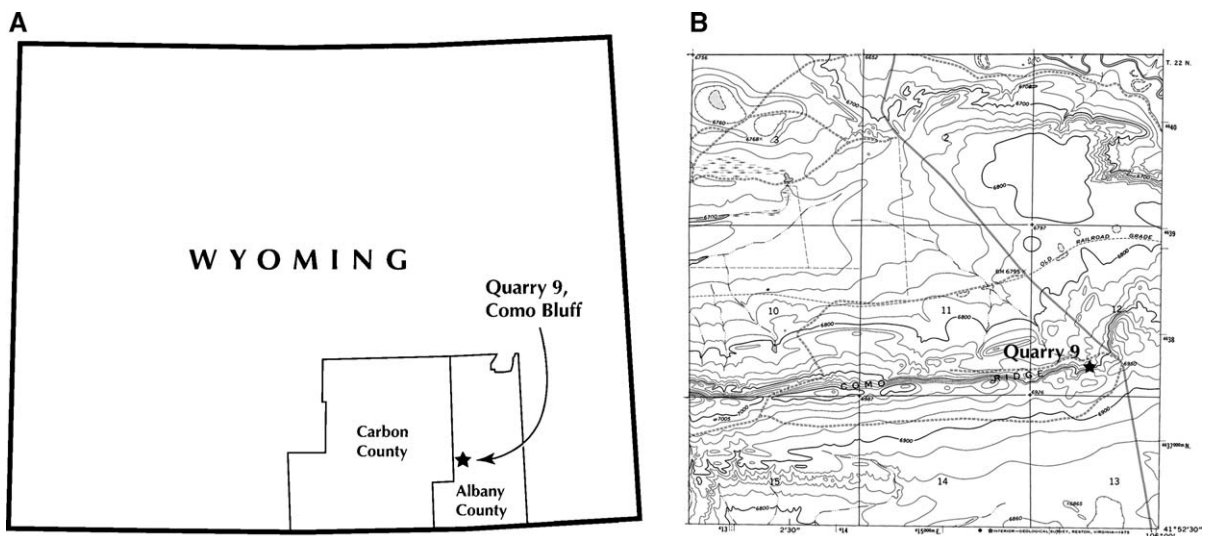


Fig. 1. (A) Map of Wyoming showing the location of Como Bluff and the Quarry 9 site, Albany County. (B) Topographic map showing a portion of the Aurora Lake quadrangle and the approximate location of Quarry 9.

goal of identifying as many individual specimens as possible and thereby generating comprehensive diversity estimates. In addition, we collected data on taphonomy and depositional environment, based on specimens and existing blocks of matrix from the original excavation. Ecological data were inferred directly from organismal morphology and indirectly based on extant relatives of Jurassic taxa. These data were synthesized to produce a new paleoecological reconstruction of the Quarry 9 paleoenvironment.

2. Materials and methods

Como Bluff and Como Ridge are topographic features that straddle the boundary between Carbon and Albany counties, Wyoming just north of US Route 30/287. Quarry 9 itself occurs in the SW 1/4 of section 12, T22N, R77W (Fig. 1; Ostrom and McIntosh, 1999), along the northern face of Como Ridge and toward its eastern end. The primary fossil collections were made by Yale University crews between 1879 and 1889, followed by the American Museum of Natural History in 1897. These collections were made prior to the advent of screenwashing techniques in vertebrate paleontology, and were obtained through surface collection and quarrying. Subsequently, a joint expedition by these two institutions reopened the quarry and made further collections (most via screenwashing) during 1968–1970 (Prothero, 1981). In the interim, a collection was also made from the site in the early 1960s by the Field Museum of Natural History (Foster, 2003).

The majority of Quarry 9 fossils are now part of the vertebrate paleontology collections at the National Museum of Natural History, Smithsonian Institution (USNM; Washington, DC), the Peabody Museum of Natural History, Yale University (YPM; New Haven, CT), and the American Museum of Natural History (AMNH; New York). We confined our study to the original Marsh collection and one subsequent AMNH collection from the same site (Prothero, 1981), because they represent excavations of a single depositional lens. Although other subsequent work has been done at the locality (cf. Prothero, 1981; Foster, 2003), those collecting efforts that did not sample the original bone producing layer are excluded from further consideration here.

We used a Zeiss Stemi SV 6 microscope and two digital cameras (Nikon D-100 and Kodak CX7430) for fossil examination. For non-mammalian vertebrates, museum identifications were noted but reconfirmed by direct examination. Mammalian identifications were accepted as stated or listed (e.g., Simpson, 1927), using the most recent synonymies for taxonomic

assignment (Kielan-Jaworowska et al., 2004). We obtained both numbers of taxa and numbers of specimens. We tallied both specific and generic diversity in order to minimize the inflating effects of the highly detailed methodology for identifying fossil mammalian taxa when compared to the quite general methods applied to other fossil taxa.

Many isolated theropod teeth are present in the collection. We were able to identify some of these teeth based on comparisons with in situ specimens of *Ceratosaurus nasicornis* (USNM 4734) and *Allosaurus fragilis* (USNM 4735). We divided the remaining specimens into three morphological groups based on serration pattern (e.g., Currie et al., 1990; Fiorillo and Currie, 1994). Tooth type A had serrations along the entire mesial carina; type B had serrations on the apical portion of the mesial carina; type C lacked serrations on the mesial carina. All three types retained serrations along the entire distal carina. Next, we measured the fore-aft base length (FABL) and the number of serrations per millimeter along the distal edge. By plotting FABL versus serration density, we were able to identify morphometric “clusters” that likely represented discrete theropod taxa.

We used raw specimen counts to calculate abundances, but tallied associated or articulated materials as single specimens. Calculating modified census measures, such as minimum numbers of individuals (MNI), would have introduced several additional error factors, among them:

- (1) We could not reliably distinguish left and right for many non-mammalian jaw fragments because most were still embedded in matrix, leading to potential overcounting if all were included, or undercounting if only half were included;
- (2) Dividing non-mammalian tooth counts by the numbers of teeth per individual undercounts by failing to account for individuals of different sizes;
- (3) We could not identify the majority of reptilian vertebrae, and so could not determine numbers of taxa, nor therefore numbers of individuals for nearly one-quarter of all specimens;
- (4) MNI will exaggerate the mammalian sample by undercounting taxa (i.e., non-mammals) for which less specific anatomical and individual identifications can be made.

More importantly, studies of the mammalian specimens have concluded that although many original taxa are now synonyms of one another (Kielan-Jaworowska

et al., 2004), few appear to belong to the same individuals. Because similar taphonomic processes were almost certainly at work on both the mammalian and non-mammalian taxa, this supports the inference that most specimens derive from distinct individuals. In practical terms, initial MNI calculations produced very similar proportions to those achieved with raw counts, especially with regard to the overall dominance of particular taxonomic groups and ecological categories.

3. Results

3.1. Stratigraphy, sedimentology and lithology

The original Quarry 9 deposit has been described as a “lens”, and indeed the later excavations may have approached at least one edge of it (Prothero, 1981). Although there are no photographs or detailed drawings that conclusively demonstrate the structure of the main quarry deposit, we accept its lenticular nature in the absence of contrary evidence. This lens was apparently beneath a sandstone layer, which was itself subjacent to a second fossiliferous layer that was sampled by the later AMNH/YPM excavations (Prothero, 1981; Foster, 2003).

Most of the USNM specimens from Quarry 9 were removed in small blocks, and many still remain in this state. As a result, some observations can be made on the sedimentology and lithology of the site, despite the fact that the original lens may have been depleted and can no longer be observed at the site.

Existing sediment blocks are primarily composed of a light olive gray (5Y 6/1), blocky mudstone (sandy claystone with minor silt component). The constituent grains are mostly quartz, but occasionally there are tiny, unidentifiable fragments of bone as well. These grains are poorly sorted and angular, embedded in a clay matrix that presumably was the primary component of the depositional lens. Within the rock, the distribution of sand grains is irregular, and likewise isolated mud clasts 2–5 mm in diameter are irregularly dispersed throughout.

Without a description of these rocks in situ in the original quarry, it is not possible to provide a detailed sedimentological description. However, it is worth noting that none of the extant blocks show evidence of fine scale (i.e., ≤ 5 mm) lamination or any other structural feature. This is apparently common for certain gray Morrison mudstone deposits (Dodson et al., 1980a,b; Foster, 2003), but laminations are present in other productive microvertebrate localities that share with Quarry 9 a “Type P” taphofacies (Foster, 2003).

3.2. Diversity

Based on our analysis, we revised the existing faunal list from Quarry 9 (Ostrom and McIntosh, 1999) to include several additional vertebrate taxa (Table 1). The mammalian diversity was revised downward to incorporate recent judgments of synonymy (Kielan-Jaworowska et al., 2004). The total vertebrate diversity now stands at 67 taxa. All non-mammalian genera appear to be monospecific within this assemblage.

Osteichthyan diversity appears to be low, but little taxonomic effort has been expended on the considerable materials from Quarry 9. The dipnoan specimens can all be assigned to *Ceratodus guentheri* (Kirkland, 1987). Actinopterygian materials include jaws and skull fragments of the amiiform *Ophiopsis*, as well as at least one non-amiiform of uncertain affinities.

Recent work (Evans and Milner, 1993) has resulted in an increase in recognized amphibian diversity at Quarry 9, including both frogs and salamanders. Anuran ilia, tibiofibulae, and humeri, as well as the limbs, vertebrae, and (possibly) jaws of salamanders suggest that several taxa were present (Moodie, 1912; Hecht and Estes, 1960; Evans and Milner, 1993). Unfortunately, the current impossibility of associating these disarticulated elements makes any diversity estimate uncertain.

Among non-archosaurian reptiles, the genus *Glyptops* was once assumed to comprise all of the Quarry 9 turtle specimens (Gilmore, 1909), but the more recently named *Dinochelys* is also present in the collection (Foster, 2003). Two rhynchocephalians, *Theretairus* and *Opisthias*, are moderately common and easily distinguished based on jaw morphology (Gilmore, 1909; Simpson, 1926a,b; Fraser and Wu, 1998). The lizards *Dorsetisaurus* and *Paramacellodus* are likewise known from a number of fragmentary jaws (Prothero and Estes, 1980), along with at least one other saurian taxon.

Crocodylian diversity remains unchanged, except for the reassignment of *Macelognathus* to this clade (Ostrom, 1971; Göhlich et al., 2005). Choristoderes are represented by *Cteniogenys* (Gilmore, 1928; Prothero and Estes, 1980; Evans, 1990), and pterosaurs by *Laopteryx* (although this is usually considered a nomen dubium). Isolated pterosaur teeth—slender, recurved, very slightly compressed, and bearing a rounded point—are present in the collection, but it is not clear whether they belong to *Laopteryx* or another form.

Six theropod taxa are present, including three forms that were identified based on tooth morphology. Theropod teeth of type A correspond to *Allosaurus* and

Table 1
Faunal list from Quarry 9, Como Bluff, Wyoming

Charophyta (1)
Charophyta indet.*
Mollusca (3)
Gastropoda
Valvatidae*
Planorbidae
cf. <i>Planorbis</i> sp.
Pelecypoda
<i>Unio</i> sp.
Osteichthyes (3)
Actinopterygii
Actinopterygii indet.*
Amiiformes
<i>Ophiopsis</i> sp.*
Sarcopterygii
Dipnoi
<i>Ceratodus guentheri</i>
Amphibia (6)
Anura (4)
<i>Comobatrachus aenigmatis</i> †
Discoglossoidea
<i>Enneabatrachus hechti</i>
Pelobatidae indet.
Pipoidea?
<i>Eobatrachus agilis</i> †
Caudata (2)
Caudata indet.
<i>Comoneurooides marshi</i>
Reptilia (22)
Testudines (2)
Amphichelydia
<i>Dinochelys whitei</i>
<i>Glyptops ornatus</i>
Squamata (2)
?Sauria indet.
Lacertilia
<i>Dorsetisaurus</i> sp.
<i>Paramacellodus</i> sp.
Rhynchocephalia (2)
<i>Opisthias rarus</i>
<i>Theretairus antiquus</i>
Choristodera (1)
<i>Cteniogenys antiquus</i>
Crocodylia (2)
Sphenosuchia
<i>Macelognathus vagans</i>
Mesosuchia
<i>Goniopholis</i> sp.
Saurischia (8)
Theropoda (6)
<i>Allosaurus fragilis</i>
<i>Ceratosaurus nasicornis</i>
<i>Coelurus fragilis</i>
<i>Ornitholestes hermanni</i> ?*
Tyrannosauroida
<i>Stokesosaurus clevelandi</i> ?*
Theropoda indet. (tooth type B)*
Sauropoda (2)
Macronaria indet.
Diplodocidae indet.

Table 1 (continued)

Ornithischia (4)
Ornithopoda (3)
Hypsilophodontidae
<i>Othnielia rex</i> *
<i>Dryosaurus</i> sp.
<i>Camptosaurus</i> sp.
Stegosauria (1)
<i>Siegosaurus</i> sp.
Pterosauria (1)
Rhamphorhynchoidea
<i>Laopteryx priscus</i> †
Mammalia (35)
Docodonta (5)
Docodontidae
<i>Docodon affinis</i>
<i>Docodon crassus</i>
<i>Docodon striatus</i>
<i>Docodon superus</i>
<i>Docodon victor</i>
Multituberculata (6)
Alloodontidae
<i>Ctenacodon laticeps</i>
<i>Ctenacodon scindens</i>
<i>Ctenacodon serratus</i>
<i>Psalodon fortis</i>
<i>Psalodon potens</i>
? <i>Psalodon marshi</i>
Triconodonta (7)
Amphilestidae
<i>Aploconodon comoensis</i>
<i>Comodon gidleyi</i>
Triconodontidae
<i>Priacodon ferox</i>
<i>Priacodon grandaevus</i>
<i>Priacodon lulli</i>
<i>Priacodon robustus</i>
<i>Trioracodon bisulcus</i>
Symmetrodonta (2)
Amphidontidae
<i>Amphidon superstes</i>
Tinodontidae
<i>Tinodon bellus</i> (incl. <i>T. lepidus</i>)
Dryolestida (15)
Dryolestidae
<i>Amblotherium gracilis</i> (incl. <i>A. debilis</i> , <i>Laodon elegans</i>)
<i>Dryolestes priscus</i> (incl. <i>Asthenodon segnes</i> , <i>Laolestes elegans</i> , <i>L. grandis</i> , <i>Herpetairus arcuatus</i> , <i>H. humilis</i> , <i>Stylacodon validus</i>)
<i>Dryolestes obtusus</i>
<i>Dryolestes vorax</i>
<i>Laolestes eminens</i>
<i>Laolestes (Melanodon) goodrichi</i>
<i>Laolestes (Melanodon) oweni</i> (incl. <i>Malthacolestes osborni</i>)
<i>Miccylyotyrans minimus</i>
Paurodontidae
<i>Araeodon intermissus</i>
<i>Archaeotrigon brevimaxillus</i>
<i>Archaeotrigon distagmus</i>
<i>Comotherium richi</i>

(continued on next page)

Table 1 (continued)

Mammalia (35)
Paurodontidae
<i>Euthlastus cordiformis</i>
<i>Paurodon valens</i>
<i>Tathiodon agilis</i> (incl. <i>Pelicipsis dubius</i>)

Taxa marked with an asterisk represent additions to previous lists (Simpson, 1926a; Ostrom and McIntosh, 1999; Foster, 2003); those marked with a dagger are currently considered nomina dubia but nonetheless can be identified to their respective higher taxa. Minimum numbers of taxa are indicated for each group within parentheses.

Ceratosaurus (already known from this locality), and the distinctive premaxillary teeth of both taxa are also present. Type B teeth cannot yet be assigned to any taxon, but appear to represent a distinct form; these teeth show a decrease in serration number as FABL increases, unlike those of the previously mentioned taxa. More comparative material from other Morrison theropod species is needed before anything more specific can be said concerning these teeth. Finally, type C teeth are tentatively assigned to *Ornitholestes hermanni* based on the characteristics listed by Ostrom (1969). Fragmentary premaxillary teeth from a tyrannosauroid are also present (H.-D. Sues, personal communication); these may be referable to *Stokesosaurus*.

Sauropods include a macronarian (either *Camarasaurus* or *Brachiosaurus*) and a diplodocid, while ornithischians are represented by *Stegosaurus*, *Campyosaurus*, *Dryosaurus*, and *Othnielia* (including material formerly referred to *Laosaurus*; Gilmore, 1909). Most of these genera are represented by teeth, although identifiable vertebrae, jaws, and limb bones are present from each of the ornithopods. The total dinosaur diversity of Quarry 9 includes 12 species.

Among the limited invertebrate collection from Quarry 9, we were able to identify several charophyte

oogonia and small valvate gastropod shells. Simpson (1926a) also indicated the presence of planorbid gastropods, and the bivalve *Unio*.

The majority of the species-level faunal diversity (52%) is composed of mammals, followed by dinosaurs (18%) amphibians (9%), and squamates (6%) (Fig. 2A). Crocodylians, turtles, and fishes each represent less than 5% of the fauna. A habitat distribution chart shows that the overwhelming majority (78%) of the organismal diversity is composed of terrestrial taxa, followed by amphibious forms (Fig. 4A). Fully aquatic and volant taxa are the least diverse. In general categorical terms, the insectivores/small carnivores dominate faunal diversity (70%), followed by herbivores, large carnivores, and finally omnivores (Fig. 3A).

Examining generic diversity somewhat alters these patterns by approximately halving mammalian diversity (from 35 species to 18 genera); no other vertebrate group shows any taxonomic reduction. As a result, mammalian genera account for only 38% of the total fauna, with proportional increases in other taxonomic groups (dinosaurs, 24%; amphibians, 12%; squamates, 8%) (Fig. 2B). Only slight alterations are apparent in the proportions of both insectivores/small carnivores and herbivores as components of the total faunal diversity (Fig. 3B), but terrestrial taxa decrease due to the reduction in mammalian diversity (Fig. 4B).

3.3. Abundance

Our total sample from Quarry 9 comprised 3748 specimens (Table 2). When individual specimen counts are considered, it is clear the mammalian taxa no longer represent the majority of the Quarry 9 fauna, but are relegated to a mere 8% (282 specimens) (Fig. 5). The most common taxa are crocodylians (1016 specimens, 27%), bony fishes (571 specimens, 15%), dinosaurs

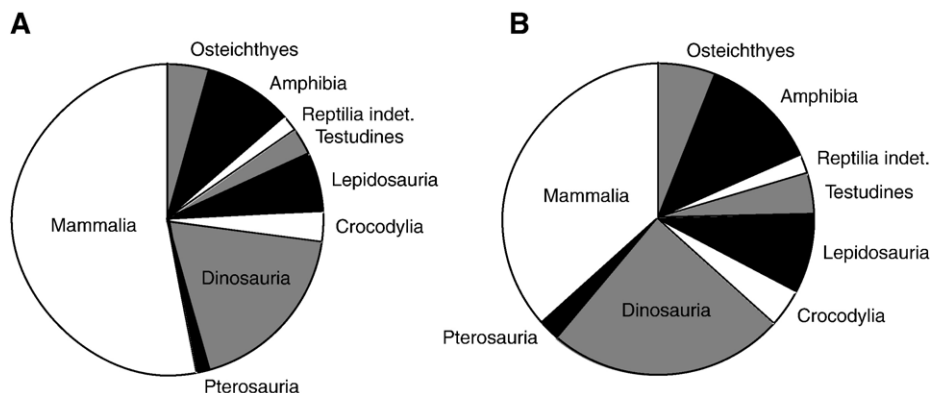


Fig. 2. Taxonomic diversity of the Quarry 9 assemblage. (A) Species-level diversity. (B) Genus-level diversity.

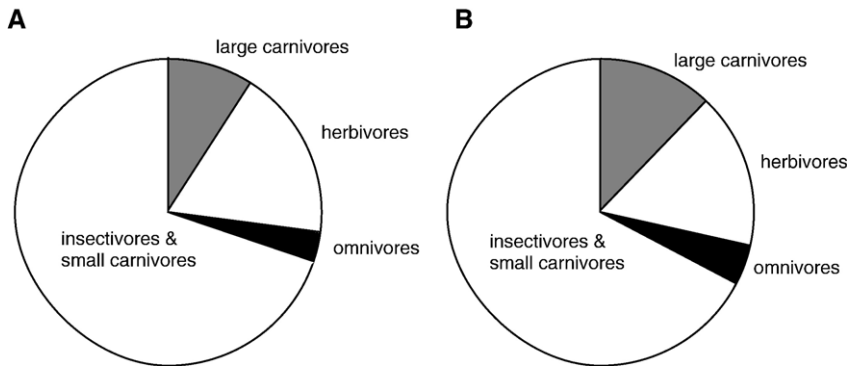


Fig. 3. Ecological diversity of the Quarry 9 assemblage. (A) Species-level diversity. (B) Genus-level diversity.

(494 specimens, 13%), and turtles (402 specimens, 11%), all of which are more abundant than mammals. Indeterminate reptiles form a large percentage of the collection (667 specimens, 18%), and further work on their identification will certainly add to both the diversity and abundance of lepidosaurs and other diapsids.

In contrast to the results of the diversity analysis, 50% of all specimens derive from amphibious organisms, especially turtles and crocodylians (Fig. 6). Indeed, crocodylians account for nearly half (49%) of the entire aquatic and amphibious species sample. Dinosaurs are the majority of terrestrial specimens (37%), with mammals contributing 22%. Due largely to the high numbers of dinosaurs and crocodylians, the large carnivores are now the majority (51%), whereas herbivores (primarily sauropods and ornithischians) are the smallest ecological category (5%) (Fig. 7).

3.4. Taphonomy

Based on their condition within extant sediment blocks from the original excavations, it is clear that

most of these specimens represent isolated individuals. Rare associated specimens (e.g., AMNH 11523; Prothero and Estes, 1980) make up less than 5% of the total. No articulated elements were found in the existing collection, and in fact most fossils are themselves only fragments of isolated skeletal elements.

The actual elements are generally well preserved, with few indications of subaerial weathering or hydraulic rolling. Bone surfaces are not etched or pitted, although some elements exhibit distinctive surface striations that tend to occur on juvenile bones. We could find no evidence of borings or other invertebrate damage on Quarry 9 bones.

Most remains derive from small-sized taxa (i.e., mammals, amphibians, and squamates), but larger organisms are also present (i.e., crocodylians and dinosaurs). However, even the latter are overwhelmingly represented by smaller (generally <5 cm) individual elements, including some that must have come from very juvenile individuals. The largest specimens include dinosaurian and crocodylian limbs, pelvic elements, vertebrae, jaw fragments, and braincases; none

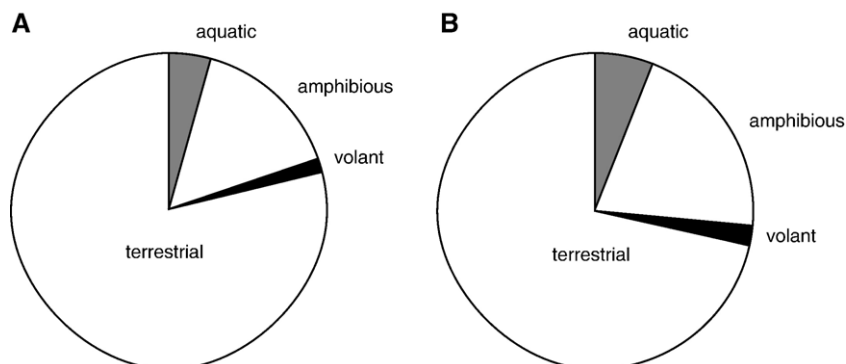


Fig. 4. Habitat diversity of the Quarry 9 assemblage. (A) Species-level diversity. (B) genus-level diversity.

Table 2
Abundance and ecological data for Quarry 9 vertebrates

Taxa	N	Trophic category	Habit
Osteichthyes	571	Small carnivores/insectivores	Aquatic
Actinopterygii	539	Small carnivores/insectivores	Aquatic
Dipnoi	32	Small carnivores/insectivores	Aquatic
Amphibia	110	Small carnivores/insectivores	Amphibious
Anura	13	Small carnivores/insectivores	Amphibious
Caudata	23	Small carnivores/insectivores	Amphibious
Testudines	402	Omnivores	Amphibious
Crocodylia	1016	Large carnivores	Amphibious
Lepidosauria	857	Small carnivores/insectivores	Terrestrial
Squamata	74	Small carnivores/insectivores	Terrestrial
Rhynchocephalia	116	Small carnivores/insectivores	Terrestrial
Dinosauria	494		Terrestrial
Large Theropoda	60	Large carnivores	Terrestrial
Small Theropoda	203	Small carnivores	Terrestrial
Sauropoda	30	Herbivores	Terrestrial
Stegosauria	11	Herbivores	Terrestrial
Small Ornithopoda	95	Herbivores	Terrestrial
Large Ornithopoda	50	Herbivores	Terrestrial
Pterosauria	15	Small carnivores/insectivores	Terrestrial
Mammalia	282		Terrestrial
Multituberculata	24	Herbivores	Terrestrial
Triconodonta	47	Small carnivores/insectivores	Terrestrial
Symmetrodonta	18	Small carnivores/insectivores	Terrestrial
Dryolestida	113	Small carnivores/insectivores	Terrestrial
Docodonta	59	Small carnivores/insectivores	Terrestrial

N=number of specimens. Note that smaller taxonomic category counts frequently sum to less than the total for their parent taxon due to the large number of indeterminate specimens.

are larger than a few centimeters in any dimension. The smallest elements are sub-millimeter sized teeth, phalanges, and charophytes.

Teeth (33% of all identified elements) and vertebrae (29%) are the most common elements in the assemblage (Fig. 8), followed by jaws (13%), limb elements (8%), and phalanges (6%), many of which are quite

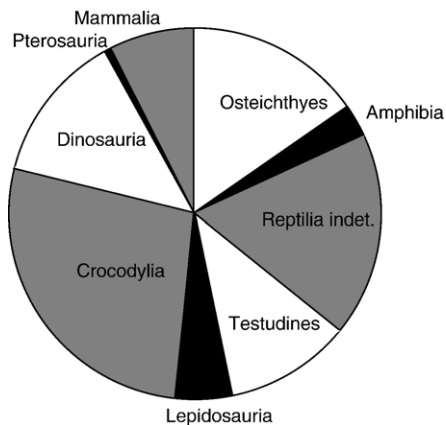


Fig. 5. Taxonomic abundance of the Quarry 9 assemblage. See Table 2 for abundances.

delicate. Flat and disc-shaped elements account for approximately 7% of the total, but most of these are turtle shell; fish scales and crocodylian scutes are comparatively rare. Conspicuously rare are braincases and girdle elements from smaller taxa, although at least parts of both are preserved for certain larger archosaurs. Crocodylian and theropod teeth are fairly common, and most appear to have been shed from living individuals.

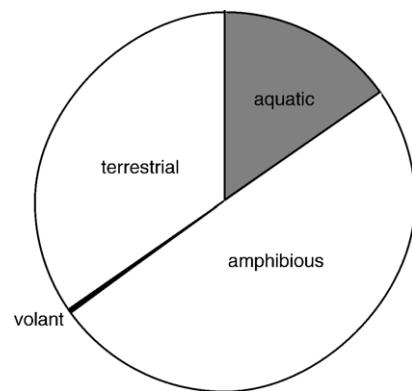


Fig. 6. Habitat abundance of the Quarry 9 assemblage. See Table 2 for abundances.

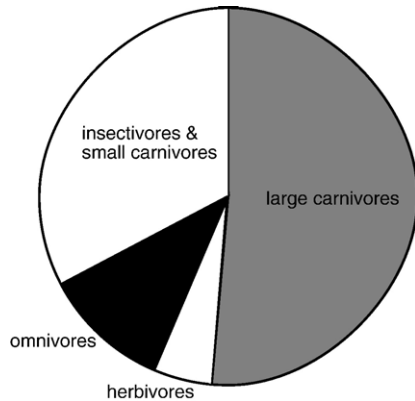


Fig. 7. Ecological abundance of the Quarry 9 assemblage. See Table 2 for abundances.

Both shed and complete ornithischian teeth are present, whereas most sauropod teeth are intact.

4. Discussion

4.1. Taphonomy

The sedimentology of Quarry 9 is indicative of a low-energy depositional environment in which little hydraulic sorting occurred, and the large size of most fossils relative to dominant grain size argues for their local origin. Together, these factors imply that the deposit records a genuine paleo-fauna rather than one with significant geographic or environmental “averaging”.

The near-total disarticulation and fragmentation of specimens is perhaps the most prominent taphonomic quality of the Quarry 9 assemblage, and in this it resembles a small number of other Morrison sites (Foster, 2003). Although this could have been caused by subaerial exposure of the skeletal remains after death, few elements show evidence of any extended weathering or decomposition. The lack of invertebrate borings suggests that bones were not exposed long enough to promote extensive infestation (Hasiotis et al., 1999).

One possibility is that disarticulation occurred in an aquatic or semi-aquatic environment, whereas fragmentation was primarily the result of subsequent bioturbation in the pond or lake bottom. The presence of small teeth with complete roots (commonly from small ornithopods), jaws with teeth, delicate tiny limb elements, and small vertebrae with intact processes points to disarticulation in a low-energy setting.

The high number of worn and shed predator teeth indicates that crocodylians and theropods were actively feeding in the environment. Similarly common shed herbivore teeth may also point to local feeding by

these animals. We note that the majority of shed herbivore teeth belong to ornithopods, whereas nearly all of the sauropod teeth have attached roots and were presumably dislodged from intact jaws upon the animals’ deaths. This may indicate particular habitat preferences for these taxa, with ornithopods and large predators as frequent visitors or inhabitants, in contrast to a more episodic sauropod presence.

The large proportion of isolated vertebrae, teeth, and phalanges probably reflects the high numbers of these elements in individual skeletons. In contrast, jaws appear to be over-represented; perhaps the dentigerous portions survived thanks to their increased durability. This may also explain the prevalence of teeth over other skeletal elements from the mammalian taxa. Given the large numbers of unidentifiable limb and rib fragments in the collection, it is unlikely that this represents a collecting bias.

In general, large numbers of easily transported elements (e.g., phalanges, metapodials, vertebrae, and rib shafts) are present in the quarry (Voorhies, 1969), suggesting that little winnowing has occurred. This interpretation is consistent with hydrodynamic studies on small mammals (Dodson, 1973) and reptiles (Blob, 1997; Blob et al., 1997), and may mitigate certain transport-induced biases (Blob and Fiorillo, 1996).

4.2. Paleoenvironment

Based on lithological and sedimentological evidence, Dodson et al. (1980a,b, 1983) referred Quarry 9 to their “lithofacies C”: drab mudstones deposited in the reducing environments of swamps, small lakes, and

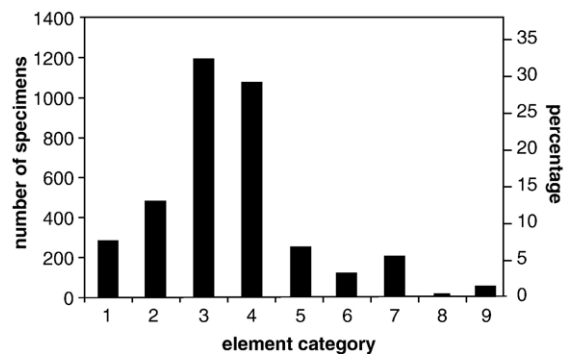


Fig. 8. Frequency distribution of skeletal elements in the Quarry 9 assemblage. Total frequencies (numbers of specimens) are shown on the left axis; relative frequencies (percent of total) are shown on the right. Element categories: 1=long bones (ribs, limbs); 2=jaws; 3=teeth; 4=vertebrae; 5=flat bones (scutes, shell, scales); 6=skull pieces; 7=phalanges (including claws); 8=carpals and tarsals; 9=girdle elements.

shallow ponds. These occurred within broad floodplains and alluvial plains that were characterized by a high water table, apparently common in the Late Kimmeridgian and Early Tithonian (Dodson et al., 1980a,b, 1983; Turner and Peterson, 2004). The available data from existing Quarry 9 sediment samples suggest a low-energy depositional environment within a distinct physical structure, such as a pond or oxbow lake.

The taphonomic evidence is also supportive of this interpretation. In particular, the prevalence of small and delicate skeletal elements that show little abrasion indicate a low-energy depositional system with little unidirectional flow. The lack of large elements is interpreted as a constraint imposed by the small size of the preserving lens (and perhaps of the original body of water), rather than the effects of direct hydraulic winnowing. Although disarticulated, skeletal elements show little evidence for digestive etching or other indicators of carnivore-induced accumulation. Bioturbation could account for the high degree of disarticulation, as well as the lack of planar lamination in the sediments.

This scenario is consistent with the abundance of turtle and crocodylian remains, as well as the occurrence of charophyte oogonia (Ross, 1960), valvatid and planorbid gastropods, and unionid bivalves. Remains of frogs, salamanders, and fishes provide further evidence that freshwater conditions were prevalent in the Quarry 9 depositional environment.

Thus, the Quarry 9 pond or lake provided a host environment for aquatic (fishes, invertebrates, and charophytes) and amphibious (amphibians, crocodylians, and turtles) organisms. It also provided a necessary water source for terrestrial organisms, in addition to an abundant supply of potential prey items, which would have been particularly enticing in the semiarid Morrison climate (Parrish et al., 2004; Englemann et al., 2004).

4.3. Paleoecology

Simpson (1926a,b) provided a reconstruction of the paleoecology of Quarry 9, in which he divided the environment into terrestrial and aquatic cenobiotas. Due to the lack of plant fossils and relatively poor invertebrate fauna, Simpson was forced to make generalized inferences about the lower trophic levels in this food web. His terrestrial cenobiota brought energy to top predators (certain mammals, small theropods) from “land plants” via small ornithopods, multituberculates, and a variety of mammals and small reptiles that fed on herbivorous insects. The aquatic cenobiota led from “water plants” through aquatic microbes and inverte-

brates to fish and amphibians, and finally to the predatory turtles and crocodylians. The two biotas were connected primarily via crocodylian and turtle predation on terrestrial vertebrates, as well as via amphibian and fish predation on terrestrial invertebrates.

As an outline of faunal interactions, Simpson's scheme is probably generally accurate, but (admittedly) omits certain important details that may now be included. It is important to note that the revised web presented here (Fig. 9) is no more quantitative than Simpson's, and should be viewed as a schema rather than an explicit ecological hypothesis. In particular, it certainly underestimates the true connectedness of the Quarry 9 organisms, and relies primarily on inferences, not direct evidence, to reconstruct interactions. However, it provides a convenient graphic demonstration of several broad but important aspects of this Late Jurassic paleoenvironment.

Among the most significant new inclusions are the large terrestrial predatory theropods (e.g., *Allosaurus*, *Ceratosaurus*) and herbivorous sauropods. The theropods add another trophic level at the top of the terrestrial cenobiota, while the sauropods create an additional energy “loop” between the land plants and these predators.

The inclusion of abundance data highlights the relative energetic contributions of each faunal component (Fig. 9). In this view it becomes clear that crocodylians served a critical faunal role as a top predators in (and therefore acted as a major link between) both the terrestrial and aquatic cenobiotas. Amphibians and turtles also provided key links between these systems. These two groups, along with small reptiles, small theropods, actinopterygians and carnivorous mammals, were also highly abundant. Their strong connectedness to other organisms highlights the central roles of these taxa within the Quarry 9 food web.

The low abundances of terrestrial herbivores suggests that they were frequenting this environment as a water source, rather than feeding on aquatic vegetation. Certainly the aquatic herbivores were incapable of exploiting terrestrial plant resources, and as a result the primary connections between the terrestrial and aquatic cenobiotas were amphibious predators. Thus Quarry 9 illustrates an environment with two autotrophic levels (land and water plants) that are integrated only subsequently through various heterotrophic connections.

In this light, the high diversity of the Quarry 9 mammals becomes explicable, because these taxa occupied multiple differentiated roles within the fauna. We therefore predict that a comparable diversity of

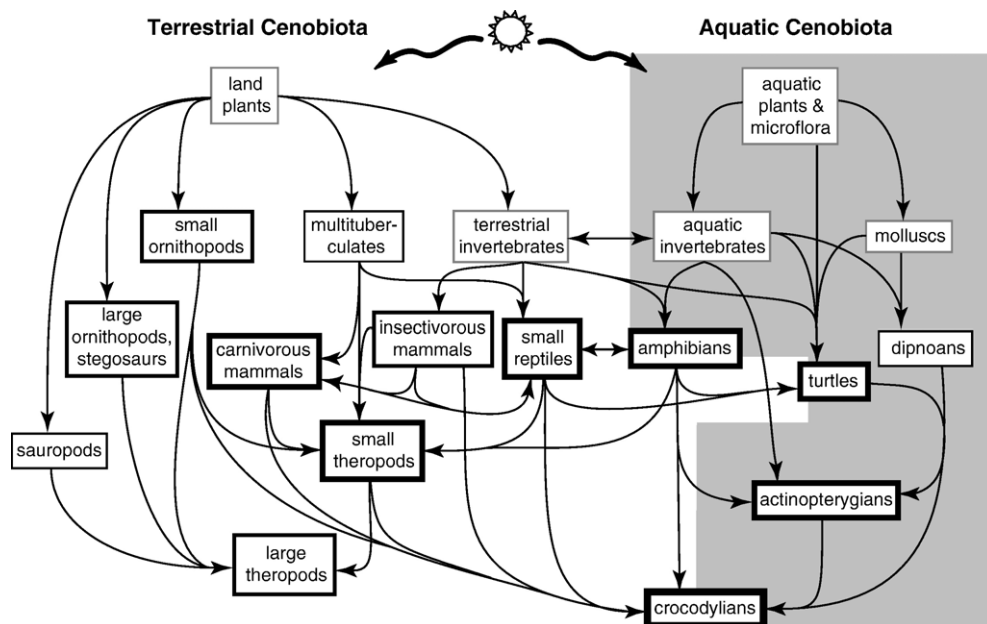


Fig. 9. Paleoecology of the Quarry 9 depositional environment. Known and inferred components of the Quarry 9 paleoenvironment are placed into a reconstructed food web, segregated into terrestrial and aquatic (gray background) cenobiotas. Connections are inferred from body size, taxonomic membership, and ecological abilities, and are not based on direct evidence. Four taxon-abundance levels are illustrated by the thickness of the box outlines surrounding each name: 0–50 specimens (1-point line), 50–100 specimens (2-point line), 100–1000 specimens (3-point line), and 1000+ specimens (4-point line). Gray outlines indicate groups for which no abundance data are available. See Table 2 for abundance data.

small reptiles and amphibians may also have existed, and may be revealed by further study (e.g., Evans and Chure, 1999). This is contrasted by the lower diversity (but high abundance) of turtles and crocodylians. Turtles may have taken advantage of a more generalized ecological role, and thus show less specialization (and therefore less differentiation), whereas crocodylians sustained their high abundances thanks to the lower energetic demands of ectothermy on such top predators. Without articulated specimens, subtler ecological distinctions within each group cannot be made.

Quarry 9 may also inform the respective ecological roles of sauro pods and large theropods in Morrison environments more generally. Both groups were diverse in the Morrison, and could be locally common (Turner and Peterson, 1999). Large theropods almost certainly served as top terrestrial predators, but in doing so were probably direct predators of comparatively few taxa. Many of the most numerous and diverse terrestrial vertebrates—small reptiles, amphibians, and mammals—were not likely prey items of large theropods. With the limited number of prey taxa available (primarily larger ornithopods, sauro pods, and thyreophorans), any niche partitioning in theropods must have relied at least partly on paleoenvironmental and behavioral differentiation, including variations in home range size and overlap.

Sauro pods, on the other hand, seem to have been disconnected from most other Morrison taxa in the food web. As herbivores, they would have been primary consumers, and as enormous vertebrates they would have been subjected to predation only by large theropods (if at all). Thus they formed part of a discrete energetic “loop” between plants and decomposers, involving at most one other trophic step (large theropods). The ability of Morrison environments to support a high diversity of these large herbivores may be partly tied to the fact that this “loop” would have cycled energy back into the environment at a relatively high rate, because few, if any, additional steps existed at which energy could have been lost.

5. Summary

The present study reports the results of an extensive review of the vertebrate collections from the Late Jurassic Quarry 9 site, in the Morrison Formation at Como Bluff, Wyoming. The faunal composition of this site is revised to include several additional vertebrate taxa, providing a refined view of taxonomy diversity. In addition, comprehensive abundance data form the basis for a new paleoenvironmental interpretation.

The high abundances of fishes, crocodylians, and turtles, along with the presence of charophytes and

other invertebrates, indicate that Quarry 9 was deposited in a freshwater environment. Lithological and sedimentological evidence, along with the fragile but disarticulated nature of most of the fossil remains, indicate that the site accumulated under low-energy conditions, perhaps a pond or abandoned channel situated on one of the many Morrison floodplains. A reconstructed food web underscores the central ecological roles of small reptiles, dinosaurs, and mammals (hence their high diversities), and the critical connective roles of amphibious forms such as crocodylians and turtles (hence their high abundances).

Thus, the results of this study provide insight into the paleoenvironment of the most productive microvertebrate-bearing quarry of the Morrison Formation. Furthermore, it emphasizes the importance of using microvertebrates in site-specific interpretations, particularly in widespread, complex depositional paleoenvironments such as the Morrison.

Acknowledgments

The authors would like to acknowledge the National Science Foundation's Research Experiences for Undergraduates program for funding this project through a grant awarded to the NMNH Research Training Program, Award Number DBI-0243512. We thank J. Young, K. Moreno, H.-D. Sues, and J. Head (NMNH) for helpful comments and assistance in identifying specimens, J. Foster and K. Trujillo for discussions, and W. Joyce (Peabody Museum of Natural History) for facilitating examination of the Quarry 9 specimens at the YPM. The comments of two anonymous reviewers were extremely helpful and greatly improved the final manuscript; their efforts are much appreciated. Finally, we acknowledge M. Rosen, D. Steere, and the Smithsonian Institution Libraries for their help in obtaining several important references. This project was conducted while the second author was participating in the Research Training Program of the Smithsonian Institution during the summer of 2004.

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