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Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem—a synthesis

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Abstract

A synthesis of recent and previous studies of the Morrison Formation and related beds, in the context of a conceptual climatic/hydrologic framework, permits reconstruction of the Late Jurassic dinosaurian ecosystem throughout the Western Interior of the United States and Canada. Climate models and geologic evidence indicate that a dry climate persisted in the Western Interior during the Late Jurassic. Early and Middle Kimmeridgian eolian deposits and Late Kimmeridgian alkaline, saline wetland/lacustrine deposits demonstrate that dryness persisted throughout the Kimmeridgian. Tithonian-age coal reflects lower evaporation rates associated with a slight cooling trend, but not a significant climate change.

With a subtropical high over the Paleo-Pacific Ocean and atmospheric circulation generally toward the east, moisture carried by prevailing winds "rained out" progressively eastward, leaving the continental interior—and the Morrison depositional basin—dry. Within the basin, high evaporation rates associated with the southerly paleolatitude and greenhouse effects added to the dryness. Consequently, the two main sources of water—groundwater and surface water—originated outside the basin, through recharge of regional aquifers and streams that originated in the western uplands. Precipitation that fell west of the basin recharged aquifers that underlay the basin and discharged in wetlands and lakes in the distal, low-lying part of the basin. Precipitation west of the basin also fed intermittent and scarce perennial streams that flowed eastward. The streams were probably "losing" streams in their upstream reaches, and contributed to a locally raised water table. Elsewhere in the basin, where the floodplain intersected the water table, small lakes dotted the landscape. Seasonal storms, perhaps in part from the Paleo-Gulf of Mexico, brought some precipitation directly to the basin, although it was also subjected to "rain out" en route. Thus, meteoric input to the basin was appreciably less than groundwater and surface water contributions.

The terrestrial Morrison ecosystem, which can be likened to a savannah, expanded with the northward retreat of the Late Jurassic Western Interior Seaway. The ecosystem was a complex mosaic, the components of which shifted through time. Riparian environments probably were the most diverse parts of the ecosystem, where a multi-storeyed canopy supported a diverse fauna, from insects to dinosaurs. Equable conditions also existed in wetlands, lakes, and elsewhere on the floodplain when seasonal rainfall brought an herbaceous groundcover to life. Eolian environments and alkaline, saline wetlands were inhospitable to life.

Large herbivorous dinosaurs were adapted to this semi-arid landscape. Their size was an adaptive asset based on considerations of food requirements associated with a low metabolism and was also an advantage for migration during drought. Some of the large sauropods were adapted to browsing the higher vegetation associated with riparian environments; others to grazing the herbaceous groundcover on the floodplain and charophytes in the wetlands. The

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extensive distal wetlands may, in fact, have been refugia for some of these herbivores during the dry season and droughts. Extended periods of drought account for some of the dinosaur death assemblages; yet, the ecosystem could also sustain the most unusual life forms that ever roamed the Earth.

Keywords: Morrison Formation; Upper Jurassic; Ecosystem reconstruction; Western Interior USA

1. Introduction

The Upper Jurassic Morrison Formation of the Western Interior region of the United States (Fig. 1) is known world-wide for its dinosaur remains, particularly the large herbivorous sauropods. Although the dinosaurs have been studied extensively, less is known about the ecosystem in which they lived. The earliest effort to understand the Morrison Formation of the entire region is that of Mook (1916) although even earlier authors, most notably Hatcher (1903), attempted syntheses for more localized areas. The most recent and most thorough synthesis of knowledge about the ecosystem was by Dodson et al. (1980a,b). Since this latest synthesis, new research has contributed significantly to our understanding of the formation. Recently published reports summarize many of the new findings (Carpenter et al., 1998; Gillette, 1999). In addition, a joint U.S. Geological Survey–U.S. National Park Service project to reconstruct the Late Jurassic ecosystem in the Western Interior of the United States has recently been completed, and the results of the individual studies are presented in this volume. Attempted here is a synthesis of all available information, based on integrating the new findings with the work of previous authors.

A large and varied flora and fauna has been recovered from the Morrison Formation over the years, most recently tabulated by Chure et al. (1998). The most significant addition since then is the considerable variety of other organisms recorded by trace fossils (Hasiotis, this volume), particularly insects, which may well represent the principal small herbivores in the Morrison ecosystem (Engelmann et al., this volume). Taphonomic implications of the flora (Parrish et al., this volume) complement earlier taxonomic studies and increase our understanding of climate in the Morrison ecosystem. Isotopic studies of Morrison floodplain carbonate nodules, dinosaur teeth, and eggshells (Ekart, written communication, 1999) lend support to climate models that infer a warm and dry climate for the Morrison Formation (Valdes and Sellwood, 1992; Moore et al., 1992). Similarly, new studies of the paleosols (Retallack, 1997; Demko et al., this volume), bivalve mollusks (Good, this volume), and carbonate wetland/lacustrine deposits (Dunagan, 1998; Dunagan and Turner, this volume) further refine our understanding of the ecosystem.

Because water plays an important role in any ecosystem, paleohydrology is seen as a key to understanding the Late Jurassic ecosystem. Although paleoclimatic aspects are often addressed in geologic studies, paleohydrologic considerations are equally important, as the amount and distribution of water across the landscape is the primary control on the distribution of habitats within the ecosystem.

To reconstruct the Morrison ecosystem, we first describe the formation and place it in the context of the broader tectonic and global climatic settings, based on paleogeographic reconstructions and models. We then summarize climatic interpretations derived from the geologic evidence from the Morrison Formation, and establish a conceptual climatic/hydrologic framework for the depositional basin. This conceptual framework provides the basis for understanding the distribution of environments of deposition and their associated biotic communities, so that the ecosystem can be understood as a complex landscape mosaic, the components of which shifted through time. A series of paleogeographic maps illustrates some of these major shifts during Morrison deposition. Reconstruction of the ecosystem and its changes through time then provide the context for evaluating biostratigraphic trends and how the inhabitants of the Morrison ecosystem, especially the dinosaurs, lived and died.

2. Stratigraphy

The Morrison Formation extends from central New Mexico to Montana, and equivalent strata extend farther north into Alberta and British Columbia in southwestern Canada, where they have been assigned different names. The formation is best known stratigraphically in the Colorado Plateau

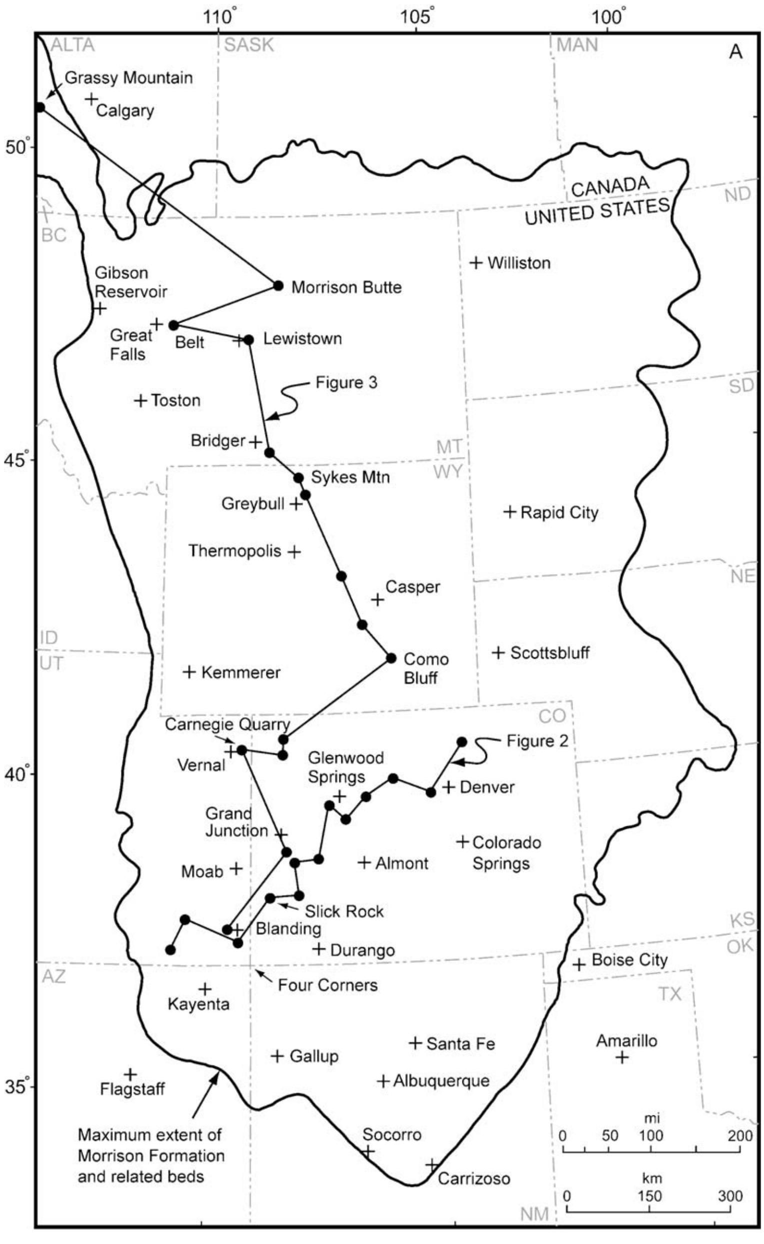


Fig. 1. Index maps showing lateral extent of the Morrison Formation and related beds in the Western Interior of the United States and adjacent Canada. (A) Index map showing lines of facies sections (Figs. 2 and 3). (B) Subsidiary Index map showing structural elements that were active during the Late Jurassic. CCU, Circle Cliffs uplift; DU, Defiance uplift; HB, Henry basin; KB, Kaiparowits basin; MU, Monument upwarp; UU, Uncompahgre uplift; ZU, Zuni uplift. After Merriam (1955), Peterson (1957, 1994), Peterson (1986, 1994), and Turner and Fishman (1991).

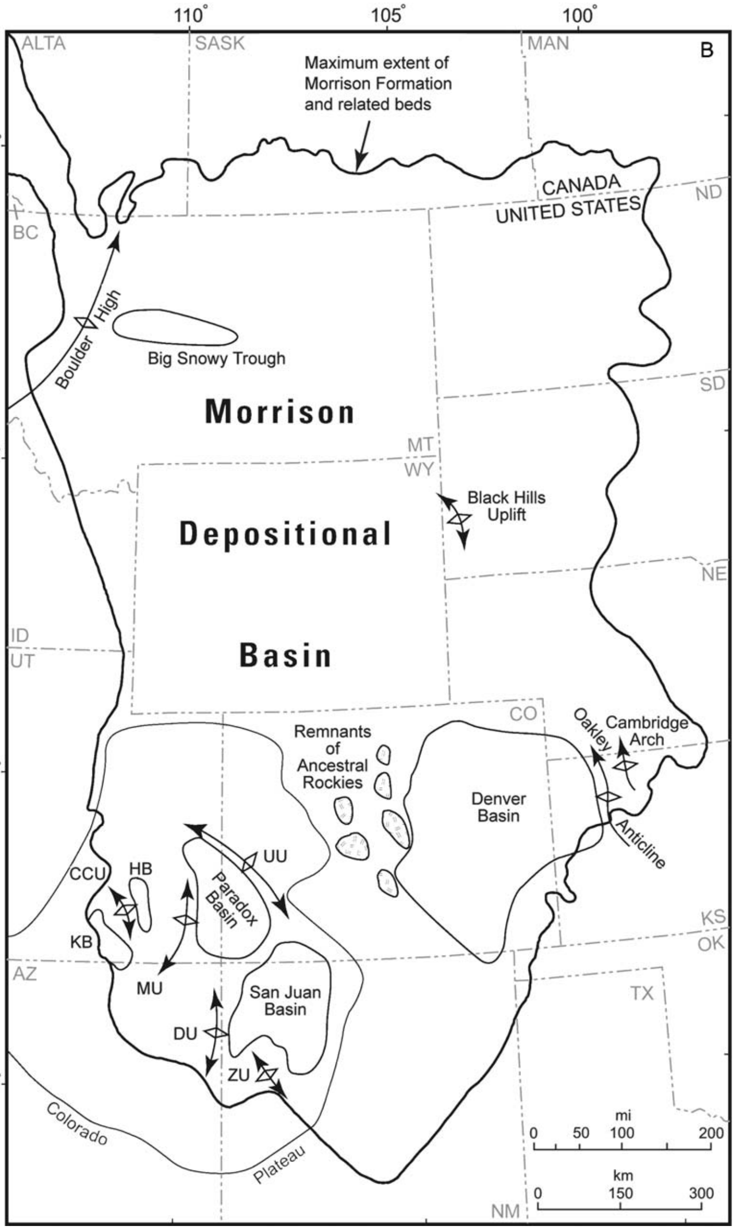


Fig. 1 (*continued*).

region, where it has been divided into ten formally named members. It is largely undifferentiated farther north and east, although two other formally named members are recognized in Wyoming and South Dakota, and several informal members also are locally recognized. The regional stratigraphic and facies relationships of the Morrison Formation and related beds are shown in Figs. 2 and 3. The formation consists largely of strata deposited in terrestrial environments, although it also includes marginal marine beds at the base from northern Utah and Colorado northward.

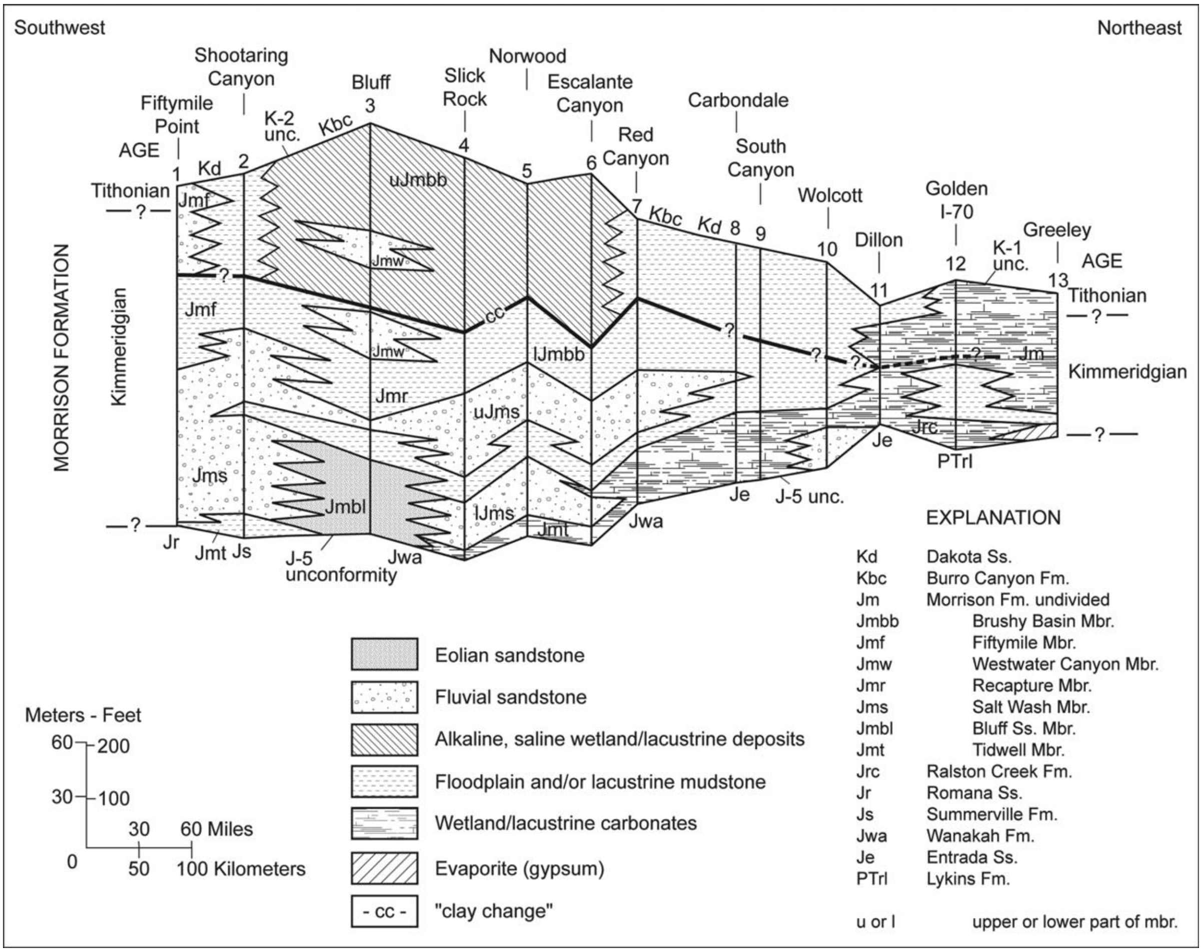


Fig. 2. Southwest-to-northeast facies section across the southern part of the Western Interior basin showing distribution of the principal facies in the Morrison Formation and related beds.

The vertical sequence of members at or near the Four Corners, where the states of Utah, Colorado, Arizona, and New Mexico meet, is fairly representative of the formation on the Colorado Plateau and consists of the following, generally from oldest to youngest, although there is extensive interfingering between some of these units: Tidwell, Bluff Sandstone, Junction Creek Sandstone, Salt Wash, Recapture, Westwater Canyon, and Brushy Basin Members (Figs. 2 and 3). The Junction Creek Sandstone Member of southwestern Colorado (O'Sullivan, 1997) is merely a different name for the Bluff Sandstone Member of southeastern Utah. The Fiftymile Member is recognized at the top of the formation in south-central Utah, and the Jackpile Sandstone Member is at the top of the formation in the southern San Juan basin of northwestern New Mexico.

Farther north in northern Utah, northern Colorado, Wyoming, and South Dakota, the Windy Hill Member is the lowest unit of the Morrison Formation. Regional relationships suggest that it is the equivalent, or at least the homotaxial equivalent, of the upper part of the Swift Formation in Montana. In western South Dakota, the Unkpapa Sandstone Member is recognized at the base of the formation (Szigeti and Fox, 1981).

In southwestern Canada, Upper Jurassic rocks considered equivalent to and slightly younger than the Morrison Formation include, from oldest to youn-

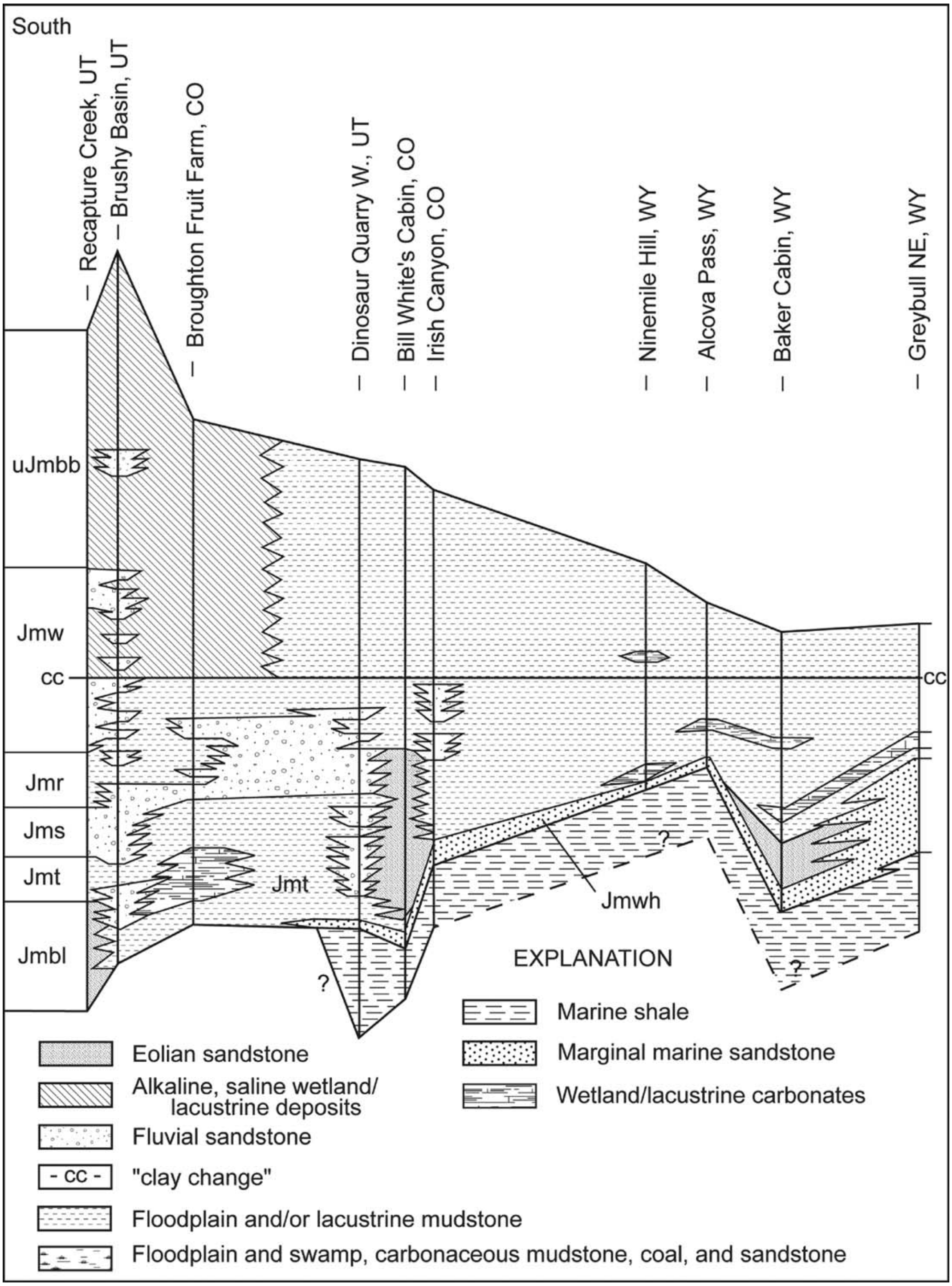
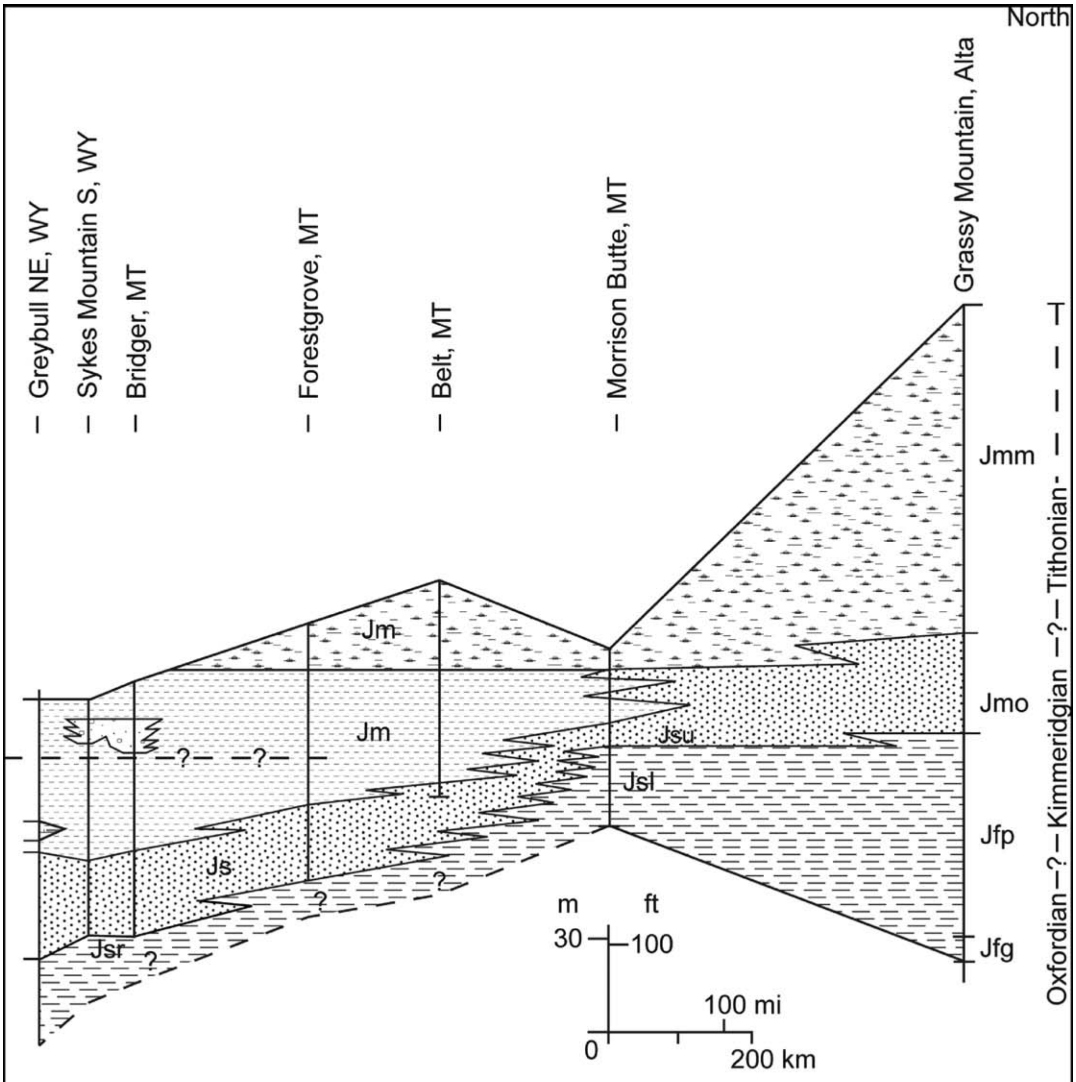


Fig. 3. South-to-north facies section across the Western Interior basin showing distribution of the principal facies in the Morrison Formation and related beds.



Jm	Morrison Formation undivided	Jmm	Mist Mountain Formation
	Brushy Basin Member:	Jmo	Morrissey Formation
uJmbb	Upper part		Fernie Formation:
lJmbb	Lower part	Jfp	Passage Beds
Jmw	Westwater Canyon Member	Jfg	Green Beds
Jms	Salt Wash Member		Sundance Formation:
Jmr	Recapture Member	Jsr	Redwater Shale Member
Jmt	Tidwell Member	Js	Swift Formation:
Jmbl	Bluff Sandstone Member	Jsu	Upper member
Jmwh	Windy Hill Member	Jsl	Lower member

Fig. 3 (*continued*).

gest, most of the Passage Beds at the top of the Fernie Formation, the Morrissey Formation, and the lower part of the Mist Mountain Formation (Fig. 3). The Morrissey and Mist Mountain Formations are included in the Kootenay Group, which was thought to be entirely Cretaceous or entirely Late Jurassic in age by earlier workers (Bell, 1946, 1956; Gussow, 1960). However, the Mist Mountain Formation is now thought to contain the Jurassic–Cretaceous boundary based on palynological evidence (Gibson, 1985).

All of the members of the Morrison Formation on the Colorado Plateau are nonmarine in origin with the exception of the Windy Hill Member and parts of the Tidwell Member. The Windy Hill is part of a regressive marginal marine sequence that becomes progressively younger to the north, becoming the upper part of the Swift Formation in Montana and the Morrissey Formation in southwestern Alberta and southeastern British Columbia (Pocock, 1964, 1972). These three units (Windy Hill, Swift, and Morrissey) were deposited during an overall northward marine regression and represent the marine equivalents of most of the nonmarine Morrison Formation farther south (Fig. 3). The marine parts of the Tidwell Member were deposited during one or more very brief transgressive phases in the overall regressive sequence.

Reliable stratigraphic markers are rare in the predominantly terrestrial deposits of the Morrison Formation, but, for the most part, correlations can be made by use of marker zones. Some of the marker zones may not be precisely isochronous or are of limited geographic extent, but they are adequate to identify the regional stratigraphic relationships of the various parts of the Morrison Formation and related beds (Turner and Peterson, 1999).

An important stratigraphic horizon called the "clay change" is approximately in the middle of the formation in much, but not all, of the depositional basin (Figs. 2 and 3). The vertical change from dominantly illitic mixed-layer clays in mudstones below, to dominantly smectitic mixed-layer clays in mudstones above, reflects an abrupt increase in altered volcanic ash in the upper part of the Morrison Formation (Owen et al., 1989). Calderas from which the ash erupted were southwest of the depositional basin, and the pattern of distribution of volcanic ash in the Morrison reflects the east to northeast dispersal pattern by paleowinds. On the Colorado Plateau, the clay change separates the lower and upper parts of the Brushy Basin Member. Elsewhere, the clay change can be identified in eastern New Mexico, eastern Colorado, and as far north as north-central Wyoming. It becomes increasingly difficult to recognize in northeastern Wyoming and South Dakota or farther north in Montana and Canada, which were all apparently beyond the limits of the major ashfalls. As a result, crystallites used to date the Morrison by radiometric techniques are difficult to find in the northern and eastern parts of the basin. Because the clay change reflects an abrupt increase in volcanic ash delivered to the depositional basin from its source area in central-eastern to southeastern California, it is thought to mark an isochronous or nearly isochronous surface and, because it is fairly widespread, it therefore constitutes the best marker horizon within the formation.

Recent work has resulted in some modifications of previous ideas concerning Morrison stratigraphy. The base of the formation is marked by the J-5 unconformity in the southern part of the region (Pipiringos and O'Sullivan, 1978), but recent work (Demko and Hasiotis, oral communication, 1996; Demko et al., this volume) indicates that the beds become conformable from northern Utah and Colorado northward, where marginal marine beds in the lower Morrison (Windy Hill Member) are gradational with underlying marine beds of the Redwater Shale Member of the Sundance Formation (Fig. 3). The Ralston Creek Formation in east-central Colorado lies above the J-5 unconformity and interfingers with the Morrison Formation. Based on this relationship and other regional correlations, the Ralston Creek Formation is considered part of the Morrison depositional package (Peterson and Turner, 1998).

Paleosols are recognized at various horizons within the Morrison Formation and, in some cases, are thought to be significant enough to be used for correlation purposes. One of these paleosol horizons occurs in the lower part of the Brushy Basin Member slightly above the Salt Wash Member on the Colorado Plateau and is thought by some workers to represent a regional unconformity (Demko et al., 1996, this volume; Hasiotis et al., 1997) or at least a considerable slowing of sedimentation. Reddish argillic Calcisols are particularly well developed at this horizon (Demko et al., this volume). Abundant termite nests and galleries mark the top of the Salt Wash Member locally and may record the same paleosol horizon (Demko et al., this volume). This particular paleosol horizon is significant because it clarifies the stratigraphic relationships of two of the members. Thus, the Salt Wash Member lies below this paleosol whereas the Westwater Canyon Member lies above it. Therefore, these members cannot correlate, as was suggested by Anderson and Lucas (1995). In other cases, the relationship between this paleosol horizon and other marker beds is less clear. For example, the ''Boundary Caliche'', a series of paleosols in Wyoming, in beds thought to be equivalent to the lower Brushy Basin Member (Allen, 2000), appears to be somewhat higher stratigraphically than the paleosol horizon within the lower Brushy Basin Member on the Colorado Plateau. In addition, extensive termite nests appear to occur at several stratigraphic levels in the formation, and thus the relationship between extensive termite nests and the various paleosol horizons is not clear.

A well-developed paleosol complex marks the upper contact between the Upper Jurassic Morrison and overlying Cretaceous beds in places. Although it may be absent (possibly by erosion) or difficult to identify at some localities, where well preserved it is a distinctive paleosol complex (Demko et al., this volume). Interpreted as a redoximorphic Gleysol, it formed under dominantly saturated soil moisture conditions with periodic drying, in contrast to the paleosols within the Morrison that indicate drier soil conditions (Demko et al., this volume).

Recognition of a paleosol complex as the upper contact of the Morrison has also contributed to a rethinking of the upper Morrison contact in Wyoming. In Wyoming, a thick interval of smectitic mudstones is present at the top of the Morrison Formation and is overlain by a similar thick smectitic mudstone interval in the Lower Cretaceous Cloverly Formation. As discussed by Winslow and Heller (1987), some workers assign all of these smectitic mudstones to the Cloverly Formation (Moberly, 1960; Furer, 1966). In contrast, we recognize the upper Morrison paleosol complex, in places well developed, within the smectitic mudstone interval. We thus assign the smectitic mudstones that underlie the paleosol complex to the Morrison Formation, and the smectitic beds above the paleosol complex to the Cloverly Formation. This suggested revision is also based on recognition of the mid-Morrison 'clay change' at the base of the lowest thick smectitic mudstone interval in Wyoming. This smectitic mudstone interval, in turn, overlies a palesol horizon similar to the one in the lower Brushy Basin Member on the Colorado Plateau. Thus, the proposed revision of stratigraphic relationships in this interval in Wyoming is consistent with the stratigraphic relationships seen on the Colorado Plateau, where the units are well dated (Figs. 2 and 3). From this we conclude that the lower part of the thick smectitic interval in Wyoming, the part that underlies the upper Morrison paleosol (as, for example, at Greybull, Wyoming), is Late Jurassic in age and equivalent to the upper part of the Brushy Basin Member of the Morrison Formation on the Colorado Plateau (Fig. 3; Turner and Peterson, 1999).

The Morrison Formation and equivalent beds represent a variety of terrestrial and marine depositional environments. Large fluvial complexes are included in the Salt Wash, Westwater Canyon, Fiftymile, and Jackpile Sandstone Members. These fluvial complexes are composed of vertically stacked, amalgamated fluvial sandstone packages that form sheet-like sandstone bodies, with little overbank mudstone preserved (Peterson, 1980a,b, 1984; Tyler and Ethridge, 1983a,b; Turner-Peterson, 1986; Miall and Turner-Peterson, 1989; Cowan, 1991; Godin, 1991; Robinson and McCabe, 1998). Eolian erg deposits characterize the Bluff Sandstone, Junction Creek Sandstone, and Unkpapa Members, and the lower part of the Recapture Member (O'Sullivan, 1980b, 1997; Szigeti and Fox, 1981; Condon and Peterson, 1986; Peterson, 1988a,b). The Windy Hill Member of the Morrison Formation as well as the Swift and Morrissey Formations are typically marginal marine sandstone units (Cobban, 1945; Gibson, 1985; F. Peterson, 1994), whereas the Fernie Formation consists of offshore marine mudstone, siltstone, and shale (Gibson, 1985). The Mist Mountain Formation and the uppermost parts (Tithonian) of the Morrison in the northern parts of the region are characterized by coal swamp and marsh environments (Harris, 1966; Walker, 1974; Gibson, 1985) . Mixed terrestrial environments characterize the remainder of the Morrison Formation. Overbank, lacustrine, and minor fluvial environments make up most of the Tidwell Member and Ralston Creek Formation (F. Peterson, 1994). The Recapture

Member includes a variety of depositional environments, including fluvial, overbank, eolian, and lacustrine units. The Brushy Basin Member is similarly characterized by a mixture of environments, including fluvial and overbank, as well as wetland and alkaline, saline–lacustrine deposits (Turner and Fishman, 1991; Dunagan and Turner, this volume).

In this report, we use stratigraphic relationships that are based on our work (F. Peterson, 1994; Peterson and Turner, 1998; Turner and Peterson, 1999) and the detailed stratigraphic work of O'Sullivan (1978, 1980a,b, 1981, 1997), Condon (1985a,b), Condon and Huffman (1994), and Huffman and Condon (1994). These stratigraphic relationships are consistent with the current understanding of age relationships in the Morrison, based on isotopic (Kowallis et al., 1998) and paleontological ages (Litwin et al., 1998; Schudack et al., 1998). In a series of reports, Anderson and Lucas (1992, 1994, 1995, 1996, 1998) depart from these stratigraphic relationships. Much of the disagreement concerns the stratigraphy and age of the lower part of the Morrison and its relationship to the underlying Middle Jurassic San Rafael Group. The stratigraphic relationships of Anderson and Lucas are not consistent with the current understanding of the age relationships and therefore are not used in this report.

3. Age

The age of the Morrison Formation and related beds is now fairly well understood. Palynological studies by Litwin et al. (1998) indicate that the Morrison Formation is largely Kimmeridgian in age and that only the uppermost part is early Tithonian in age. Palynomorphs from the Windy Hill Member at the base of the formation yielded a somewhat uncertain age; they indicate an age no older than latest Oxfordian but more likely early Kimmeridgian. Calcareous microfossils (charophytes and freshwater ostracodes) examined by Schudack et al. (1998) yielded essentially the same age for the formation as the palynomorphs. No freshwater calcareous microfossils are present in the brackish-water to marine beds of the Windy Hill Member and thus offer no information on the age of that member. The freshwater calcareous microfossils from the remainder of the formation, with the exception of the uppermost beds, indicate a Kimmeridgian age; those recovered from the uppermost beds demonstrate that those beds are not Cretaceous in age, but these microfossils, unlike the palynomorphs, were not sufficiently diagnostic to distinguish between the Kimmeridgian and Tithonian Ages.

Isotopic dates on sanidine separates from volcanic tuffs, usually smectitic tuffs, were dated by $^{40}Ar/^{39}Ar$ single crystal methodology (Kowallis et al., 1998). They indicate that the formation was deposited over a period about 7 million years, from 155 to 148 Ma. The end of the Jurassic Period is dated at about 141 Ma (Bralower et al., 1990), so the 148 Ma date from the top of the Morrison Formation indicates that the youngest part of what is preserved of the formation is about 7 million years older than the end of the Jurassic Period.

Available paleomagnetic data is scant but, once reinterpreted, appears to be consistent with the paleontological data cited above. Steiner et al. (1994) had interpreted approximately the lower third of the Morrison as Oxfordian in age based on paleomagnetics, but this age is inconsistent with the more recent paleontologic information cited above. We therefore reject an Oxfordian age for most of these beds, with the possible exception of the Windy Hill Member, which is no older than latest Oxfordian but more likely early Kimmeridgian (Litwin et al., 1998). In reviewing the magnetic anomaly at the top of the Morrison in the Steiner et al. (1994) Slick Rock magnetostratigraphic section, it appears that this anomaly correlates best with the M-22 magnetochron in the marine magnetic anomaly sequence, based on the paleontologic determinations of Litwin et al. (1998) and Schudack et al. (1998). Because the Jurassic–Cretaceous boundary is at or very near the base of magnetochron M-18, the paleomagnetic studies suggest that about three of the youngest Jurassic magnetochrons are missing at Steiner's paleomagnetic section. A certain amount of uncertainty is involved in the interpretation of the age of the Morrison based on paleomagnetic results because paleomagnetics usually require other dating methodologies for their interpretation. Recent age determinations permit a more accurate interpretation of the paleomagnetic data. An important result from the integration of the paleomagnetics with the paleontology is that the top of the formation is appreciably older than the end of the Jurassic Period, which is consistent with the isotopic dates.

The age of the Morrison Formation has long been thought to be the same as most of the Tendaguru Formation of Tanzania in east-central Africa because of the similarity of dinosaur faunas recovered from both formations (Schuchert, 1918; Simpson, 1926). The Tendaguru Formation consists of six members, the lower five of which contain the dinosaurs as well as intercalated marine strata. Age determinations based on marine invertebrates recovered from these lower five members indicate Oxfordian, Kimmeridgian, and Tithonian(?) ages (Zils et al., 1995; Schudack, 1999a), which indicates that the Tendaguru is close to the age of most of the Morrison Formation.

4. Tectonic setting

The tectonic framework of the region south, southwest, and west of the Morrison depositional basin is important for determining the source of Morrison clastic sediment and the source of the abundant volcanic ash incorporated in Morrison deposits. A significant source of sediment for the Morrison Formation was from elevated rift shoulders associated with a magmatic arc that developed along the western edge of the continent (Fig. 4), as suggested by tectonic studies in the western US (Dickinson, 2001), and from provenance studies in the Morrison Formation and related beds. An eastward-dipping subduction zone that began during the Middle Triassic produced a magmatic arc along the western edge of the continent (Dickinson, 2001). Oblique right lateral subduction between the continent and the Paleo-Pacific plate resulted in an arc-graben depression within the part of the magmatic arc that stretched southeastward from east-central California through southern Arizona and into Mexico. The graben was the site of considerable magmatic activity, attested to by silicic ignimbrites and flows locally preserved within the rift (Busby-Spera, 1988; Saleeby and Busby-Spera, 1992; Dick-

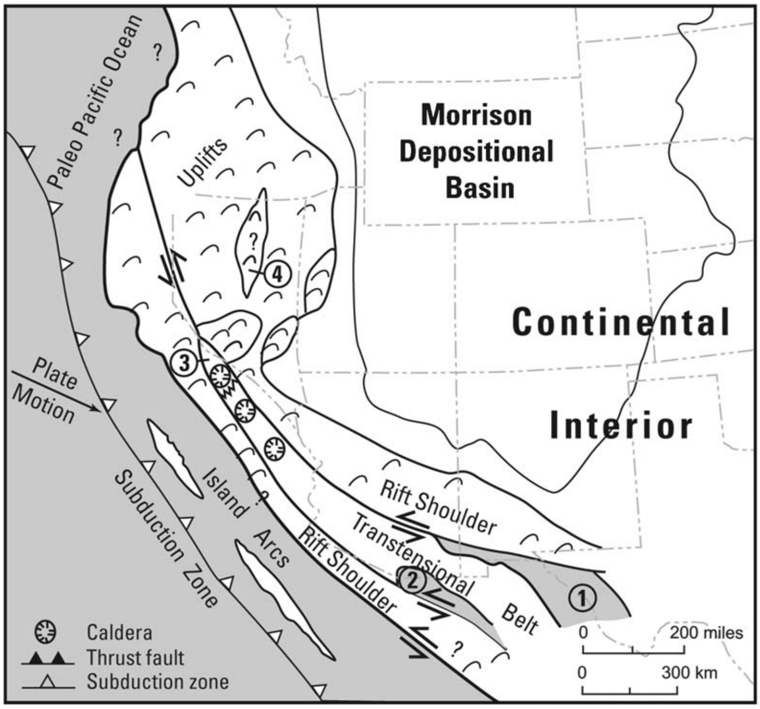


Fig. 4. Map of the western US showing the tectonic setting during Late Jurassic time. 1, Chihuahua trough; 2, Mar Mexicano; 3, Remnant of Middle Jurassic arc graben depression; 4, Remnant of Middle Jurassic Toiyabe uplift(?). Modified after Saleeby and Busby-Spera (1992, pl. 5F) and Lucas et al. (2001).

inson and Lawton, 2001). Where documented, it appears that the shoulders all along the rift were elevated by thermotectonic processes (Dickinson, 1981; Bilodeau, 1986; Lawton, 1994; Nourse, 1995; Lucas et al., 2001). These rift shoulders became source areas for some of the sediment brought into the Morrison depositional basin from the southwest during the early and middle Kimmeridgian, an interpretation that is consistent with provenance and paleocurrent studies of the predominantly fluvial Recapture and Westwater Canyon Members (Craig et al., 1955; Cadigan, 1967; Martinez, 1979; Hansley, 1986; Turner-Peterson, 1986).

By late Kimmeridgian time (about 150 Ma, May et al., 1989), most of the arc-graben depression evolved into a transtensional rift zone with thermotectonic shoulders (Bilodeau, 1986) that continued to be a source of sediment for streams that flowed northeastward toward the depositional basin. Fluvial deposits of the Brushy Basin and Jackpile Sandstone Members along the southwestern part of the Western Interior basin record this continued influx of detrital material (Moench and Schlee, 1967; Owen et al., 1984; Turner and Fishman, 1991). The transition to a transtensional rift zone occurred when the continent began rapid northwestward movement that resulted in sinistral (left-lateral) displacement along the western edge of the continent (Saleeby and Busby-Spera, 1992). By this time, only the northern end of the arc-graben depression remained.

In spite of the reduced areal extent of the arc-graben depression, considerable volumes of silicic volcanic ash and massive tuff breccias, locally preserved in the Sierra Nevada and nearby areas, attest to significant eruptive centers in or near the depression (Fiske and Tobisch, 1978; Tobisch et al., 1986; Stone et al., 2000). The chemistry and mineralogy of Morrison tuffs indicate that the ash originated from silicic magmas (dacitic or rhyolitic) that erupted from calderas (Christiansen et al., 1994). Based on paleocurrent studies of eolian deposits in the Morrison Formation, Late Jurassic winds blew from the southwest (Peterson, 1988b), which indicates that the large amount of ash that was incorporated in the upper part of the Brushy Basin Member of the Morrison Formation most likely originated in these eruptive centers (Christiansen et al., 1994). Interestingly, a major eruptive event occurred in the arc at about 155–148 Ma (Dunne et al., 1998), a time interval that coincides with the age of the entire Morrison Formation including the tuffaceous interval in the upper part of the Brushy Basin that is dated at 150–148 Ma (Kowallis et al., 1998). Similarly, most of the igneous activity in the arc is interpreted to have shut down by the time of emplacement of the Independence dike swarm at about 148 Ma (Chen and Moore, 1979, 1982; Coleman et al., 2000), a date that coincides with the age of the top of the tuffaceous interval in the Brushy Basin (148 Ma). The beginning of this major eruptive event is recorded in the Morrison Formation by the ‘clay change’ (Figs. 2 and 3) within the Brushy Basin Member because the smectitic clays above the ‘clay change’ formed by the alteration of volcanic ash from the eruptions farther west.

Throughout Morrison deposition, detritus was derived from uplands in the back arc region in the area of present-day eastern Nevada and western Utah, an area that would have been between the magmatic arc to the west and the depositional basin to the east (Fig. 4). For example, provenance studies of the Salt Wash Member of the Morrison Formation relate certain lithologies to specific source areas in this back arc region (Poole, oral communication, 1980; F. Peterson, 1994).

The nature and causes of the uplifts in the back arc region are controversial; the disagreements hinge on the time of thrusting. Most workers believe that Sevier thrusting did not occur during the Late Jurassic and, instead, began appreciably later toward the end of the Early Cretaceous (Heller et al., 1986; Thorman et al., 1992; Yingling and Heller, 1992; Lawton, 1994; Miller and Hoisch, 1995; Dickinson, 2001). In contrast, Currie (1997, 1998) proposed that a foreland basin developed during Morrison deposition as part of a Late Jurassic phase of the Sevier orogeny and that the foredeep was largely cannibalized by later thrusting. According to Currie’s (1997, 1998) hypothesis, the Morrison Formation, which exhibits no westward thickening indicative of foreland basin deposition, was deposited in a backbulge basin east of an inferred foreland basin. The inferred presence of a foreland basin implies that extensive regional thrusting occurred in eastern Nevada and (or) western Utah during the Late Jurassic, which is an opinion also shared by Taylor et al. (2000).

Although the controversy is not resolved, the bulk of the evidence indicates a lack of significant thrust activity during the Late Jurassic in western Utah and eastern Nevada. Local thrusting associated with emplacement of small plutons (Miller and Hoisch, 1995) had originally been thought to be Late Jurassic in age; however, more recent dating shows that the local thrusting occurred during the Middle Jurassic (Elison, 1995; Girty et al., 1995). In addition, geobarometry studies by Miller and Hoisch (1995) show that pluton emplacement and related minor thrust faults occurred at relatively shallow crustal levels in this region, not at the considerably greater crustal depths that would have occurred with massive overthrusts. Moreover, Miller et al. (1989) suggest that east–west extension, not compression, occurred in this region during the Late Jurassic. Thus, it appears that thrust fault movement was relatively minor and occurred earlier than Morrison deposition, whereas the regional thrusting associated with the Sevier orogeny began late in the Early Cretaceous, well after Morrison deposition.

Lack of extensive thrust faulting during the Late Jurassic is consistent with the timing of events within subduction cycles. Ward (1995) modeled subduction cycles, including one for the Jurassic of western North America. According to him, Morrison deposition occurred during a "chaotic tectonics" phase, near the end of a subduction cycle. This phase significantly postdated a phase of regional thrusting that is inferred to have occurred in Early Jurassic time during a phase of rapid subduction. Between the time of rapid subduction in the Early Jurassic, and the "chaotic phase" in the Late Jurassic (Morrison deposition) was a phase of batholith emplacement that occurred largely in the Middle Jurassic. Caldera development in the arc-graben depression during the middle Jurassic was related to emplacement of batholithic intrusions (Saleeby and Busby-Spera, 1992). Morrison deposition in the Late Jurassic was thus separated in time from significant thrust activity, which occurred largely during the Early Jurassic, and not again until late in Early Cretaceous time. Lack of evidence for extensive thrusting during the Late Jurassic in the western Morrison source area (western Utah and eastern Nevada) suggests that this region, which lies between the arc and the depositional basin, was elevated by other mechanisms.

The most reasonable explanation for tectonic uplift in the region between the arc and the depositional basin (that is, in eastern Nevada and western Utah) is upwelling of the asthenosphere in response to subduction farther west. The upwelling resulted in lithospheric thinning, deformation from intrusions, and thermal weakening of the crust in the area of the present-day Great Basin region (Elison, 1995; Dickinson, 2001). Thus, the highland areas that were source areas for some of the Morrison clastic sediment most likely were elevated topographically by thermal processes associated with asthenospheric upwelling rather than by extensive thrust faults.

Somewhat less is known about the source regions for Morrison deposition farther north. Paleocurrent studies in Wyoming and Montana demonstrate that the sediment came from highlands to the west (Winslow and Heller, 1987; Cooley, 1993), but Morrison rocks in these states have not yet been studied sufficiently to pinpoint the exact locations of the source areas. In Idaho and eastern Oregon and Washington, rocks of Late Jurassic age are not present and thus no record exists about the highland source regions that contributed to the Morrison depositional basin there. Saleeby and Busby-Spera (1992) suggest that this area was elevated during emplacement of superterranes farther west.

Minor uplifts and structural flexures also occurred within the depositional basin (Fig. 1B), but their importance derives mostly from their influence on facies distribution, not as source areas, as they only contributed sediment to the basin in rare instances. During deposition, these structures moved only slightly but enough to influence sedimentation patterns, local accommodation space, and, in some cases, the type of deposit. The Ancestral Rocky Mountains are the only uplift within the depositional basin known to have contributed significant amounts of sediment to the Morrison. Angular chert fragments and granitic debris in the Morrison of the eastern Front Range foothills in Colorado confirm that a relatively minor but distinctive source of clastic sediment was derived from the Ancestral Rockies, which were largely but not entirely buried beneath Morrison sediment at the time.

In contrast to the western conterminous United States, Late Jurassic foreland basin deposition occurred in southwestern Canada east of an active thrust belt. The thrust belt extended south to the international border or only slightly into the US (Gillespie and Heller, 1995). In British Columbia and Alberta, foreland basin subsidence resulted in accumulation of Oxfordian, Kimmeridgian, and Tithonian marine and continental rocks (upper Fernie Formation and lower Kootenay Group) that contain clastic material derived largely from the west (Gillespie and Heller, 1995). Foreland basin subsidence apparently began in British Columbia and Alberta during Oxfordian time: The Green Beds and overlying Passage Beds at the top of the Fernie Formation record the initiation of uplift of westward source areas that continued through deposition of younger beds in the Kootenay Group (Gillespie and Heller, 1995). The distribution of shoreface sandstone deposits on both the west and east sides of the seaway and the different composition of these sandstone deposits indicate that the sediment came from elevated areas west of the seaway as well from the Canadian Shield to the east (Rapson, 1965; Poulton, 1984; Stott, 1984; Monger, 1998).

In summary, the Morrison depositional basin was separated from the Paleo-Pacific Ocean by several highlands or mountain ranges, some of which contributed sediment to the depositional basin. Considerable volumes of volcanic ash were derived from calderas in the remnant of the arc-graben depression and in the transtensional rift zone that extended from southern Arizona to central eastern California. Prevailing winds in the Western Interior during the Late Jurassic blew toward the northeast, and the lack of any significant quantity of volcanic ash in the Morrison Formation of Montana and equivalent rocks of British Columbia and Alberta reflects the scarcity of volcanic centers north of about central California. Clastic sediment in the depositional basin was largely derived from highlands that extended from northern Mexico well up into British Columbia. The highlands were predominantly rift shoulders and uplifts in the back arc region. Highlands that may have been elevated by thrusting were restricted to the northernmost part of the region, in western Canada. A relatively minor amount of clastic material was derived from local topographic highs in the largely buried Ancestral Rockies and perhaps in other local areas farther north. The resulting picture of the regional tectonic framework of the western United States is more complicated than that of earlier models, in which a simple continental-margin Andean-type magmatic arc extended along the entire west coast of the conterminous United States.

5. Climate

The Morrison depositional basin and the uplands that shed sediment into the basin were part of a Late Jurassic North American continent that was both farther south and warmer than today. The Four Corners area (Fig. 1), which today is at latitude 37° north, was at about 32° north, or the present latitude of southern Arizona (Paleogeographic Atlas Project, 1984; Parrish and Peterson, 1988). North America was moving northward and was rotated clockwise relative to its present orientation so that the Paleo-North Pole was approximately northwest in terms of today's coordinates. The entire Earth was significantly warmer than today, as suggested by the appreciably higher carbon dioxide content of the atmosphere (Ekart et al., 1999).

Several reconstructions of the Late Jurassic global climate are based on reconciling numeric models with geologic paleoclimate data. Moore et al. (1992) assumed a CO_2 concentration in the atmosphere four times that of the pre-industrial age atmosphere of 280 ppm CO_2 and found that the simulations agreed reasonably well with the geologic data. They concluded that the Late Jurassic was a time of warmer overall global temperatures from an enhanced greenhouse effect and that the predicted winter and summer surface temperatures in the Western Interior region were approximately 20 °C (68°F) and 40–45 °C (about 104–113°F) respectively. They also found that the annual precipitation predicted from their models was less than 500 mm (< 20 in) for the Western Interior, and that evaporation appreciably exceeded precipitation. Somewhat different paleoclimate modeling by Valdes and Sellwood (1992), who did not use elevated CO_2 values, produced somewhat lower predicted winter and summer temperatures of 8 °C (46°F) and 24–28 °C (75–82°F), respectively, but similarly indicated that the climate, at least throughout the southern United States, was dry. Recent studies by Ekart et al. (1999) suggest a considerably higher CO_2 content than that used by Moore et al. (1992). Ekart et al. (1999) found that the Late Jurassic atmosphere contained about 3180 ppm CO_2, which is on the order of 11 times that of the pre-industrial age atmosphere of about 280 ppm.

The high temperatures predicted by the model of Moore et al. (1992), which incorporates a high CO_2 content of the atmosphere, suggest that evaporation could have been significant year round, rather than only in summer (Parrish et al., this volume). Soil moisture, which is a measure of the balance between precipitation and evaporation, was included in the model by Valdes and Sellwood (1992). Later climate model results by Valdes (1993) did not include soil moisture, but are consistent with the results of Valdes and Sellwood (1992). The models indicate a semi-arid climate in the Western Interior. They also predict a lower latitudinal temperature gradient for the Morrison than today and slightly wetter conditions in the soil to the north, probably because of lower evaporation rates associated with slightly lower temperatures (Parrish et al., this volume).

The geologic evidence also indicates a dry climate throughout the Western Interior during the Late Jurassic. One of the geologic indicators of dryness is the presence of ergs in the lower part of the formation (below the 'clay change') in the southern part of the region in the Four Corners area (Figs. 2 and 3). Smaller eolian deposits occur in the lower Morrison as far north as north-central Wyoming (Peterson, 1988b) and southwestern South Dakota (Szigeti and Fox, 1981). Presence of an extensive alkaline, saline wetland/lake complex during deposition of the upper part of the formation, above the 'clay change' in the eastern Colorado Plateau region (Turner and Fishman, 1991; Dunagan and Turner, this volume), indicates that dryness continued during deposition of the upper part of the Morrison Formation. Alkaline, saline lakes and wetlands form in closed hydrologic basins where net evaporation exceeds precipitation and runoff (Jones, 1966; Garrels and MacKenzie, 1967; Hardie and Eugster, 1970; Surdam and Sheppard, 1978), conditions that occur in semi-arid to arid environments. Another indicator of dryness is the presence of evaporite minerals in the Morrison Formation. Bedded gypsum occurs at or near the base of the Morrison in the southern part of the region (O'Sullivan, 1992), and in northeastern Wyoming (Bergendahl et al., 1961; Pillmore and Mapel, 1963; Robinson et al., 1964; Pipiringos, 1968). External molds of a cubic mineral, most likely halite, were reported from basal Morrison beds in South Dakota (Bell and Post, 1971) and in northwestern Colorado (Pipiringos et al., 1969), and pseudomorphs of gypsum, halite, and trona, as well as minor magadi-type chert, occur locally in carbonate wetland/lacustrine deposits in east-central Colorado (Dunagan, 2000; Dunagan and Turner, this volume). In a unit defined as bed A at the base of the Morrison in the Colorado Plateau area (O'Sullivan, 1980a), casts of halite crystals occur locally. Evidence from paleosols in the Morrison also support the interpretation of a dry climate (Retallack, 1997; Demko et al., this volume). The dryness interpreted for the Morrison depositional basin is consistent with the tendency for dry air to occur at low mid-latitudes (Parrish and Curtis, 1982).

The dryness during Morrison deposition can be attributed to a subtropical high-pressure cell that was positioned over the eastern Paleo-Pacific Ocean that migrated between about 25° and 35° north latitude over the course of a year (Parrish and Curtis, 1982). This high-pressure cell dominated atmospheric circulation in the Western Interior during the Late Jurassic. The northern edge of the high-pressure cell produced warm westerly winds that carried Pacific moisture eastward toward the continent. "Rain out" progressively inland depleted the air mass of moisture. This left the continental interior to the east—including the Morrison depositional basin—dry. Paleocurrent studies of eolian sandstone beds in the Morrison Formation confirm that winds blew toward the northeast (present coordinates) across the Colorado Plateau region, or approximately due east in terms of Late Jurassic paleocoordinates (Parrish and Peterson, 1988; Peterson, 1988b).

A dry continental interior is also indicated by stable isotope studies. Calcareous nodules from Morrison floodplain deposits are highly depleted in ^{18}O. $\delta^{18}O$ values for these nodules range from -6.5‰ to -12‰ PDB (Ekart, written communication, 1998). These are typical for values developed in either a rain shadow or in a dry continental interior (Ekart, written communication, 1999). A rain shadow interpretation would imply limited drainages on the lee side of the mountain ranges, which seems unlikely given the large fluvial complexes in the Morrison Formation that drained these mountain ranges. Development of a dry continental interior, caused by progressive "rain out" of moisture west of the depositional basin, is the preferred explanation, as sufficient moisture would then have been available to supply eastward draining streams, which better explains the large Morrison fluvial complexes. Additional seasonal moisture from the Paleo-Gulf of Mexico would have "rained out" in a similar fashion before reaching the Western Interior depositional basin. Thus, moisture carried eastward by prevailing winds from the Paleo-Pacific Ocean, and northwestward from the Paleo-Gulf of Mexico, probably were similarly depleted in ^{18}O.

Although a warm, dry climate is inferred for Morrison deposition, some workers suggest slight temporal and latitudinal trends in temperature and/or moisture regimes. Analysis of warm-water charophytes and oxygen isotopes in certain ostracodes suggest that the Western Interior climate became slightly cooler with time and also that the temperature decreased slightly from south to north (Schudack, 1999b). The temporal cooling trend may reflect the northward migration of the continent, and the slight latitudinal cooling may reflect a normal northward decrease in temperature in the northern hemisphere (Schudack, 1999b). A possible underlying cause for the temporal trend is the inferred slight decrease in the carbon dioxide content of the atmosphere during the Late Jurassic (Ekart et al., 1999).

The proposed slight cooling with time is consistent with interpretations of the coal and associated carbonaceous mudstone beds in the uppermost beds of the Morrison in central Montana. The cooler temperatures resulted in lower evaporation rates and thus more moisture was retained in the sediments, but still in a fairly dry climate (Parrish et al., this volume). The high ash and high sulfur content of the coal is consistent with deposition in peat mires in a relatively dry climate and a high water table (Parrish et al., this volume). The continued dryness is also attested to by the presence of cheirolepids, which are considered indicators of a dry climate (Alvin, 1982; Vakhrameyev, 1982). Cheirolepids are found throughout the Morrison Formation, including the coal-bearing beds. Thus, the climate change from Kimmeridgian to Tithonian could not have been dramatic (Parrish et al., this volume).

The well-developed unconformity paleosol complex that defines the top of the Morrison Formation may not represent conditions at the end of Morrison deposition but, instead, may represent an episode of soil formation that occurred entirely in Early Cretaceous time, in which case, inferences concerning the Late Jurassic climate from the palesol complex are not warranted. The paleosol is a redoximorphic Gleysol that formed under "wetter" conditions than other paleosols in the Morrison (Demko et al., this volume). Strata from the earliest stages of Cretaceous deposition are missing in the Western Interior, so that it is difficult to determine when the unconformity paleosol developed. Additional Morrison strata may have accumulated on top of what is now preserved of the Morrison Formation, and some Lower Cretaceous strata may have been deposited and eroded before the paleosol developed on the top of the preserved parts of the Morrison Formation. Thus, the paleosol may represent the last event recorded before net accumulation of Lower Cretaceous strata in the Western Interior, but most likely it is not related to the climate during deposition of the uppermost part of the Morrison Formation.

Another aspect of Morrison climate is the degree of seasonality. The most conclusive evidence for seasonality is from freshwater bivalves. Good (this volume) noted annual growth bands in thin-shelled unionid bivalves recovered from lacustrine beds in the Salt Wash and Brushy Basin Members. The growth bands indicate seasonally fluctuating temperatures and (or) precipitation. Unionid bivalves recovered from pond deposits in the Tidwell Member, however, do not exhibit annual growth bands, which may reflect a uniform optimum habitat that resulted from proximity to the Late Jurassic Western Interior seaway, rather than a lack of seasonality. In lowlands near the coastline, the water table would have been consistently high year round, and the air temperatures would have been moderated by proximity to the seaway, thereby tempering any seasonal climatic fluctuations. The presence of crayfish burrows throughout the Morrison, including the Tidwell Member, suggests that seasonality prevailed (Hasiotis, this volume) even though it was not recorded by the unionids in the Tidwell Member.

Two species of conifers from the Morrison Formation exhibit annual growth rings, whereas other species do not (Medlyn and Tidwell, 1979; Tidwell et al., 1998). Tidwell and Medlyn (1993) suggested that those exhibiting growth rings grew in upland regions that experienced seasonality and floated down river during floods, whereas those without growth rings grew in the depositional basin where, according to their interpretation, no seasonal changes occurred. Because we now have evidence from annual growth bands in bivalves that seasonal changes did occur within the depositional basin, another explanation for the presence or absence of growth rings in the fossil trees may be offered. The conifers that lack growth rings may have grown near perennial sources of water and those with growth rings may have grown where water was only seasonally available.

Some evidence exists to suggest that moisture varied over time periods longer than the seasonal cycles indicated by growth bands in the bivalves and growth rings in the trees, but the nature of this longer-term variation is unclear. Within the depositional basin, distinguishing between greater precipitation and a higher water table is not readily accomplished, as higher water tables can result from changes in basin dynamics as well as changes in precipitation in the recharge area. A good example is Lake T'oo'dichi', which was an alkaline, saline wetland/lake complex that experienced at least one episode of fresh water lake deposition. In the Four Corners area, a dark, laminated, lacustrine mudstone unit as much as 2 m thick occurs within a thick clinoptilolite-rich interval in the alkaline, saline wetland deposits. The lacustrine mudstone interval contains a variety of megaplant remains, including leaf mats of ginkgophytes (Ash and Tidwell, 1998; Parrish et al., this volume). The lake developed when sufficient surface water was available to form a lake in the same lowland that was more often occupied by a groundwater-fed alkaline, saline wetland. Given that longer-term climatic variations are known to occur, it is likely that any cyclic variations are obscured in the Morrison Formation by the shifting sedimentation patterns in the dominantly terrestrial environments.

In summary, the bulk of the evidence indicates that a warm, dry climate predominated during the Late Jurassic in the Western Interior. With atmospheric circulation predominantly toward the east, much of the moisture carried by prevailing westerly winds from the Paleo-Pacific Ocean, and from the Paleo-Gulf of Mexico during seasonal storms, was "rained out" en route to the depositional basin. Moreover, the basin experienced high net evaporation rates, enhanced by greenhouse effects and the southerly paleolatitude, adding to the overall dryness of the interior basin.

6. Paleohydrology

The paleohydrology during Morrison deposition is intimately related to the paleoclimatic interpretations and is essential to understanding the distribution of life in the ancient ecosystem. Although it is impossible to reconstruct the paleohydrology in detail, a conceptual hydrologic model can provide a framework for integrating the available data and observations.

6.1. Conceptual model

Determining the availability of the various sources of water—surface, ground, and meteoric—is key to the paleohydrologic interpretation of the Morrison ecosystem. Our conceptual paleohydrologic model is based on reasonable implications of the paleoclimatic setting, tectonic setting, and the geologic evidence. Moisture carried eastward by prevailing winds "rained out" in the uplands west of the basin. This gave rise to a situation in which the water that reached the continental interior basin, in which the Morrison was deposited, did so largely through groundwater and surface water that originated outside the basin, and to a lesser extent from direct meteoric precipitation in the basin. Precipitation in the uplands west of the depositional basin infiltrated and recharged aquifers that underlay the depositional basin, and also fed intermittent and scarce perennial streams that flowed eastward toward the basin. Aquifers would have been Paleozoic and lower Mesozoic sandstone and limestone units (Sanford, 1994). The perennial or intermittent nature of the streams probably was related to the size of the drainage basin. Meteoric precipitation in the depositional basin was scarce, and was largely seasonal in nature, delivered partly by storms that carried moisture from the Paleo-Gulf Coast. The interpretation of Morrison hydrology as largely a groundwater system, supplemented by surface water in the form of predominantly intermittent streams, and limited meteoric water, provides the best way to explain the combination of geologic features that indicate a warm, dry landscape (ergs; alkaline, saline wetland/lacustrine deposits; and evaporites) and those that indicate the availability of water (fluvial systems, groundwater-fed carbonate wetlands and lakes in the distal part of the basin, and floodplain ponds).

6.2. Regional groundwater system

Discharge of regional aquifers that carried groundwater from the uplands to the downstream regions of the basin is evident from the presence of green mudstone and limestone beds that were deposited in groundwater-fed wetlands and lakes in the distal or eastern part of the depositional basin, extending north and south from the Denver basin (Fig. 1B; Dunagan and Turner, this volume). The carbonate wetlands/lake complex formed largely from spring seepage and discharge in the distal lowlands, where the regional water table intersected the landscape. The low variability in the $\delta^{18}O$ values for these carbonates reflects through flow of water and water lost by outflow in an open hydrologic setting rather than by evaporation (Dunagan and Turner, this volume). The resulting carbonate deposits are similar to those described by Quade et al. (1995) and by Quade et al. (2003), who reinterpret many carbonate deposits, once considered lacustrine, as largely spring-related wetland deposits. Those that formed in the distal lowland regions of the Morrison depositional basin exhibit similar attributes—open hydrologic characteristics and low variability in the isotopic values.

A paucity of shoreline or deltaic deposits within the distal carbonate/mudstone systems confirms that they were fed largely by groundwater, not by streams, which is consistent with a predominantly wetland interpretation (Dunagan and Turner, this volume). Lacustrine deltas in north-central Colorado (Jackson, 1979) and shoreline deposits in southeastern Colorado (Dunagan and Turner, this volume), although scarce, attest to periods of increased stream flow into the distal lowlands. During these episodes, surface water became a major component of water entering the lowlands, and lacustrine deposition occurred, although groundwater discharge continued to be a factor. Interbedding of wetland and lacustrine deposits in the distal lowland regions reflects the relative importance of groundwater and stream flow though time. The water level in the wetlands and lakes fluctuated, perhaps seasonally, so that the margins were intermittently exposed, resulting in significant pedogenic modification (i.e., palustrine features).

A wetland interpretation for many of the carbonates and mudstones deposited in the downstream reaches of the Morrison depositional basin is significant because it is likely that the depleted oxygen isotopic values in these distal limestone beds reflect the same depleted recharge values of the surface waters that drained the upland areas and fed the regional aquifers (Quade et al., 2003). The abundance and wide distribution of charophytes in the distal carbonate sequences is also consistent with a groundwater origin for many of these beds (Forester, oral communication, 2003). According to the groundwater model for these deposits, which best accommodates the geologic and isotopic data, the mountainous regions west of the basin were high enough to generate sufficient head for the water to flow through regional aquifers to distal regions of the depositional basin, where the water table intersected the landscape and discharged as springs to form wetlands.

Discharge of regional aquifers also occurred along the margins of the Late Jurassic Western Interior seaway. Here, evaporative basins as well as freshwater wetlands and lakes developed during the early stages of Morrison deposition as the seaway retreated northward.

6.3. Floodplain carbonate nodules and groundwater

Carbonate nodules in the floodplain deposits of the Morrison Formation also formed from water depleted in ^{18}O. Although originally interpreted as pedogenic in origin (Ekart, written communication, 1998), it is likely that some of these floodplain nodules formed from groundwater processes rather than from soil processes. This reinterpretation is suggested by both the lack of rhizoliths in some of the nodule-bearing horizons and the similarity between the oxygen isotope values of these floodplain carbonate nodules (-6.5‰ to -12‰, Ekart, written communication, 1999) and those for groundwater-fed limestones deposited in wetland environments in the distal regions of the basin (-8.26‰ to -12.99‰, Dunagan and Turner, this volume). Thus, instead of reflecting meteoric water composition, the isotopic composition of the floodplain nodules is more consistent with a groundwater origin. Other workers have similarly reinterpreted carbonate nodules in floodplain deposits in other geologic units as groundwater rather than pedogenic in origin (Goudie, 1983; Forester, oral communication, 2002). Formation of the floodplain nodules in the Morrison may have occurred where "losing" streams fed the local water table. The isotopic composition of these nodules is similar to that of the distal limestones because the same surface waters that fed Morrison streams also entered aquifers in the upstream reaches and flowed toward points of regional discharge in the distal reaches in the eastern part of the basin. Morrison streams drained uplands west of the depositional basin where "rain out" had already depleted the ^{18}O. The oxygen isotopic values thus reflect depletion of the heavy isotopes that occurred west of the depositional basin.

6.4. Role of evapotranspiration

The ratio between precipitation and evapotranspiration is more important than the amount of precipitation in an ecosystem. Meteoric water was only seasonally a major source of water in the Morrison ecosystem; at other times, "rain out" to the west, as well as high net evaporation rates in the warm, southerly latitudes, enhanced by greenhouse effects, kept the airmass dry over the depositional basin. Evapotranspiration would thus have been a major factor in the hydrology, just as it is today in semi-arid to arid regions. Some estimates indicate that about 30% of the world's precipitation evaporates; in arid regions, the rate is considerably higher (Stannard, oral communication, 2002).

6.5. Local closed basin hydrology

Discharge of shallow groundwater and high net evaporation rates played critical roles in the development of a large, alkaline, saline wetland/lake complex (Lake T'oo'dichi') in the area west of the ancestral Uncompahgre uplift (Turner and Fishman, 1991). Formation of an alkaline, saline wetland/lake complex requires a hydrologically closed basin, with no surface outlets, in which evaporation exceeds precipitation and runoff (Jones, 1966). The ancestral Uncompahgre uplift formed a barrier to shallow, eastward-flowing groundwater and surface waters, which led to the formation of a hydrologically closed basin on the west side of the uplift. The streams that emptied into the closed basin were probably characterized by intermittent flow, flowing only during floods and diminishing to sub-stream flow beneath dry washes at other times. This inference is based on the lack of deltaic deposits or reworking of sands in the nearshore zones and the presence of rip-up clasts of lacustrine tuffs at the base of fluvial sandstones (Turner and Fishman, 1991). The apparent lack of shoreline and deltaic deposits supports the idea that this system was fed largely by groundwater, not surface water, and thus is best interpreted largely as an alkaline, saline wetland. High net rates of evaporation in the dry climate concentrated the pore waters in the wetland/lake basin considerably. A critical factor in development of the alkaline, saline pore waters was the addition of silicic volcanic ash to the sediments of the closed basin. The ash originated in calderas to the west (Christiansen et al., 1994) and was carried to the basin by prevailing westerly winds. Alteration of the ash resulted in a highly alkaline and saline pore water chemistry, which led to the formation of zeolites and other authigenic minerals (Turner and Fishman, 1991). The relatively high density of the pore waters was sufficient to generate a downward flux into underlying sediments, which resulted in alteration of detrital grains and precipitation of cements (Hansley, 1986; Turner and Fishman, 1998). Rare episodes of increased surface water input are indicated by gray, laminated lacustrine mudstones. These lacustrine episodes reflect intervals when a greater component of surface water than groundwater entered the wetland/lake basin.

6.6. Floodplain ponds and lakes

Small lakes and ponds developed in low-lying areas of the Morrison floodplain, where the water table associated with shallow aquifers intersected the landscape, or where regional aquifers discharged along faults or fractures. These lakes are represented by gray mudstones that are locally laminated, and rare thin limestone beds.

6.7. Nature of streams

Although significant fluvial systems drained the upland regions, it appears that many, if not most, of the streams that flowed eastward across the depositional basin were intermittent in nature, although some perennial streams were also present. Admittedly, perennial and intermittent streams are difficult to distinguish in the geologic record, but some clues exist. For example, eolian deposits of the Bluff–Junction Creek erg are preserved downwind of the Salt Wash fluvial deposits and locally interfinger with them. When the streams were dry, prevailing winds from the west carried sand from the streambeds eastward, which was deposited in dunefields in the lee of the ancestral Monument upwarp. In addition, the scarcity of deltaic and shoreline deposits in the distal carbonate wetland/lacustrine complexes and in the more localized alkaline, saline wetland/lacustrine complex attests to the intermittent nature of many Morrison streams.

The intermittent nature of Morrison streams is compatible with what might be expected in semi-arid to arid landscapes and with the inferred seasonality for the Morrison depositional basin. Typically, upstream reaches of streams in arid or semi-arid regions are "losing streams", because they lose water downward to the water table (Fig. 5). Intermittent streams in the Morrison may have run seasonally for several months a year and during storms. When the amount of surface water was insufficient to sustain flow above the streambed, the stream sank below the surface as substream flow. Water holes formed where deep scours in the streambed locally intersected the substream flow when the water was not far below the surface of the streambed.

Perennial streams were also present in the depositional basin, as indicated by the occurrence of unionid bivalves in some of the fluvial sandstone beds (Good, this volume). Unionids undergo a larval stage and the larvae attach themselves to the gills of fish. This obligate parasitism indicates that fish had to have been present. The fish, in turn, require perennial streams. Unionids have been found in only a few fluvial deposits which suggests that there were few perennial streams.

The size of the drainage area probably was a major factor in determining whether streams were perennial or intermittent. Larger watersheds probably sustained the perennial streams that entered the depositional basin, whereas smaller watersheds may not have collected enough surface water to sustain year-round flow, which resulted in intermittent stream flow. At times, surface waters sustained flow in intermittent streams for periods longer than the usual seasonal flow, and, conversely, during times of extreme drought, perennial streams went dry.

6.8. Summary of hydrology for the Morrison ecosystem

The Morrison depositional basin received most of its water from groundwater and surface water, with lesser contributions from meteoric water. Much of the moisture was "rained out" in the upstream reaches of the basin, although sufficient water was available to

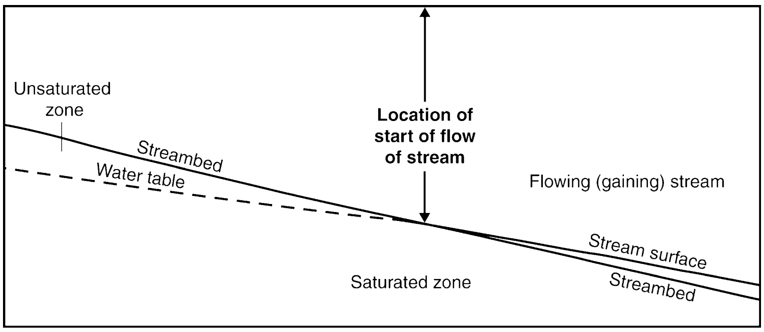


Fig. 5. Idealized regional hydrograph showing the position of the water table with respect to the ground surface in an upstream-to-downstream direction. The general distribution of environments and many sedimentary features within the Morrison Formation can be interpreted in terms of this regional hydrograph. After Winter et al. (1998).

recharge regional aquifers, and to feed intermittent and scarce perennial streams that flowed across the basin. A hydrograph for the Morrison depositional basin would have been similar to that shown in Fig. 5. The water table probably was at greater depths upstream than downstream, and the streams in the upper reaches were most likely losing streams that contributed to the groundwater table.

The regional water table intersected the land surface downstream in the low-lying, distal parts of the basin and discharged through seeps and springs, which resulted in the formation of wetlands and lakes where carbonates precipitated in an open hydrologic setting. The edge of the alluvial plain typically is a zone of discharge and mixing of shallow local and deeper regional flow (McLean, 1970; Duffy and Al-Hassan, 1988; Straw et al., 1990). When sufficient surface water reached the distal lowlands, they became sites of lacustrine deposition. When surface water input was low or non-existent, groundwater was the predominant source of water in the lowlands, and carbonate wetlands formed.

According to Toth (1962, 1963), shallow flow may discharge farther upslope. Lake T'oo'dichi', an alkaline, saline wetland/lacustrine complex, formed farther upslope in the Morrison depositional basin, where shallow groundwater was ponded within a hydrologically closed basin. The closed-basin hydrology of Lake T'oo'dichi' contrasted with the open hydrologic setting of the wetlands in the more distal regions of the basin. In addition, a large component of silicic volcanic ash contributed to the alkaline, saline nature of the Lake T'oo'dichi' wetland complex, in contrast to the fresh water carbonate environments that predominated in the distal wetlands. The distal wetlands were farther from the source of the volcanic ash, so fewer ash falls reached them.

Freshwater ponds formed in floodplain regions of the Morrison depositional basin, where the local water table reached the surface or where regional aquifers discharged along faults or fractures. Seasonal precipitation moistened the remainder of the floodplain.

The three sources of water in the Morrison depositional basin—surface water, groundwater (both local and regional), and direct precipitation in the basin—played a role in defining habitats and in governing the nature, abundance, and adaptations of plant and animal life. One of the challenges in interpreting the amount of moisture available to life in the basin is distinguishing among the three types of water delivered to the basin.

It is important to distinguish, as much as possible, the potential sources of moisture in the sediment within the basin and to differentiate between moisture from intrabasinal and extrabasinal sources. Sediment can have a high-moisture content even when the overlying airmass is relatively "dry". 'Wet' conditions in sediment can be caused by a high water table or by flooding of streams that receive their water largely from precipitation that fell in the upland regions. Thus, sediment can become 'wet' in the absence of direct precipitation of meteoric water in the basin. Climatic indicators for the Morrison suggest a relatively dry air mass over the depositional basin much of the time, but this does not preclude the availability of moisture from both surface runoff and groundwater from the upland regions to the west. Seasonal meteoric water was also important, particularly on the floodplain, but appears not to have been a major overall source of water compared to the extrabasinal sources of water.

7. The landscape mosaic

The Morrison ecosystem was a complex mosaic of environments that developed largely in response to the availability of water. The ecosystem was the sum of many different communities where life adapted to the conditions associated with different depositional environments. Interpretations of Morrison climate and hydrology outlined earlier are further refined and constrained by evidence from the various communities that thrived on the Morrison landscape. Life in the Morrison depositional basin and the upland regions that lay to the west can be broadly related to the basin hydrograph, and different communities can be described in terms of depositional environment, local and regional hydrology, and associated life forms. Although they are described separately, the communities are complexly interrelated.

7.1. Uplands

Moisture that fell in the uplands west of the depositional basin probably supported a vegetated terrain. Vegetated slopes would have contributed to a slowing of runoff during storms as well as greater infiltration into the aquifers and steadier surface runoff into streams that drained toward the depositional basin. It is reasonable to suppose that parts of these upland terrains served as refugia for dinosaurs during dry seasons or periods of extreme drought in the lowlands.

7.2. Streams

Morrison streams hosted a variety of life forms, some of which are preserved in the fossil record. Fish remains, although found in the lacustrine beds (Kirkland, 1998), have not been reported from the fluvial beds of the Morrison, probably because of the intermittent nature of many of the streams and the low preservation potential of the delicate bones in fluvial strata. Thick shelled unionids, in contrast, are preserved locally in scarce perennial stream deposits because their thick shells resist abrasion. Turtle and crocodile remains also occur in stream deposits of the Morrison and probably lived in the streams. The turtles from the Morrison are typical of present-day aquatic turtles, and the larger crocodiles were aquatic as well (Chure, oral communication, 2002). The turtles and crocodiles also could have lived in ponds. Caddisfly cases that occur in ponds near stream channels may have been constructed in the fluvial channels and then washed over into ponds during floods (Hasiotis, this volume). Morrison streams were an important part of the ecosystem because animals would have frequented the perennial streams and waterholes in intermittent streambeds for water. Water holes formed in intermittent streambeds where deep scours locally intersected the substream flow; therefore, even along intermittent streams, animal life often had access to water.

7.3. Riparian environments

Adjacent to the streams were riparian environments that preserved more evidence of life forms than the streambeds. Riparian environments include stream bank, levee, splay, and proximal floodplain environments, each represented chiefly by sandstone. Body and trace fossils attest to the abundance and diversity of life that found suitable habitat adjacent to the streams. The equable environment was largely created by trees that lined stretches of the river where they could tap the water table that was at shallower depths than on the adjacent floodplain (Fig. 6). The larger rhizoliths that occur in the Morrison are in deposits associated with riparian environments (Hasiotis, this volume). In contrast, medium and small rhizoliths are more widespread, and are associated with deposits that were riparian in origin as well as those deposits associated with more distal parts of the floodplain (Hasiotis, this volume). The confinement of larger vegetation, chiefly conifers (Ash and Tidwell, 1998), primarily to the riparian areas suggests that an understory and groundcover of shrubs and smaller plants flourished there, where evapotranspiration rates were somewhat lower due to the cooler temperatures in the shade of the trees. The understory and groundcover probably consisted of the ginkgophytes, cycads, tree ferns, horsetails, and a variety of ferns that have been reported from the formation (Ash and Tidwell, 1998; Chin and Kirkland, 1998). Riparian environments provided water, shade, food, and shelter for a variety of life forms. Camarasaurs, brachiosaurs, and perhaps other herbivorous dinosaurs that could reach higher food sources probably browsed extensively in the riparian regions. Various dinosaur tracks (sauropod, ornithopod, and theropod) occur in the riparian environments (Hasiotis, this volume). Underfoot were numerous small animals, such as mammals, sphenodonts, and lizards (Chure et al., 1998).

Along both perennial and intermittent streams, the water table was higher in riparian environments than in most of the floodplain areas. The depth of the water table controlled the distribution of many of the life forms that inhabited the region. The interpretation that

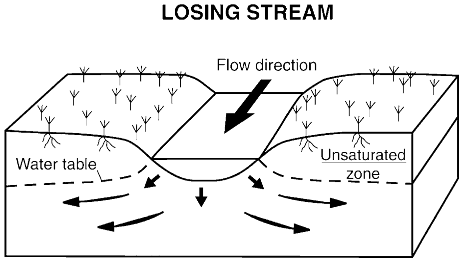


Fig. 6. Diagram that illustrates how water from a ‘losing’ stream flows into the groundwater, locally raising the water table. After Winter et al. (1998).

Morrison streams were losing streams in their upstream reaches is consistent with evidence from crayfish burrows. The occurrence of these burrows in channel and proximal floodplain deposits implies that the streams were at least seasonally losing (Hasiotis, this volume). Intermittent flooding by streams probably helped maintain some of the riparian vegetation, which may have depended upon flooding for reproduction, much like some of the riparian vegetation adjacent to modern-day streams. The Morrison contains evidence of life forms that dwelled below the water table (for example, crayfish), some that lived in the vadose zone (termites), and some that lived in soil zones above the water table (ground-dwelling bees; Hasiotis, this volume). Close proximity to the water table in the proximal overbank environments provided suitable habitat for crayfish, who burrow down to the water table, and termites, who burrow into the moist capillary fringe above the water table. Crayfish were restricted to these proximal overbank areas, which is typical of the distribution of crayfish in drier environments (Hasiotis, this volume). In humid environments, crayfish will be distributed across the floodplain because of the greater availability of water. Additional evidence for riparian dwellers in the Morrison includes termite nests, insect larvae, bee nests, various beetle burrows, ant nests, wasp nests, and cricket traces (Hasiotis, this volume). The abundance of insects ensured a ready food source for other elements of the biota, such as the terrestrial lizards, which had sharp teeth suitable for eating insects (Chure, oral communication, 2002). Additional trace fossils have been attributed to such things as mayflies; various reptiles such as crocodiles, sphenodonts, and turtles; and mammals (Hasiotis, this volume).

7.4. Distal floodplain

Beyond the riparian zones associated with the proximal floodplain environments were the more distal floodplain environments. These parts of the floodplains received finer-grained sediment, chiefly mud that was altered to varying degrees by soil-forming processes. Most of the paleosols developed in alternating wet and dry conditions (Demko et al., this volume). The alternating wet and dry conditions may relate to seasonal precipitation in the depositional basin, but the record is probably complicated by flooding of streams at times of increased runoff caused by storms either in the upland regions or occasionally within the depositional basin.

A question has often been, what, if anything, occupied the niche of present-day grasses on the Morrison floodplain? Recent studies suggest that the floodplain hosted low, herbaceous vegetation that prevented excessive erosion during storm events, and also provided additional edible vegetation for the herbivores (Parrish et al., this volume). This conclusion was partly reached by reconciling the megafloral record with the palynoflourule record. Plant material preserved as megaflora is generally scarce throughout the Morrison Formation. About 32 leaf form species of megaflora have been reported in the Morrison (Parrish et al., this volume), whereas over 225 fossil pollen and spore types have been recovered (Litwin et al., 1998). The appreciable difference between the quantity of plant life recorded by the abundant palynomorph flora compared to the relatively meager amount of megaplant remains is intriguing. Some of the palynomorphs undoubtedly came from the uplands; however, many of the palynomorphs likely came from herbaceous plants, many of which do not leave a megaplant fossil record (Parrish et al., this volume). Ferns account for many of the taxa in the palynological record of the Morrison Formation (Litwin et al., 1998). The scarcity of megaplant remains, limited occurrences of fossil wood, small shallow root impressions (even on well-developed paleosols), and the high ratio of palynomorph types to megafloral taxa throughout the Morrison are a strong indication that the entire Morrison flora was dominated by herbaceous plants and small-statured woody plants (Parrish et al., this volume).

The floodplain probably was the predominant ecological niche for the herbaceous plants, much like the niche occupied by grasses in modern savannahs (Parrish et al., this volume). The larger shrubs and trees appear to have been restricted to stretches along the streams, based on the presence of large rhizoliths only in areas adjacent to the streams (Hasiotis, this volume). The herbaceous plants, which are opportunists and thus capable of enduring stressed environments that might be inhospitable to other plant types, would have been able to occupy the niche provided by the floodplain, even if precipitation was only seasonal. The small rhizoliths reported from floodplain environments (Hasiotis, this volume) probably reflect the growth of the herbaceous plants. The herbaceous plants could be some of the "unrecognizable organic matter" found in dinosaur coprolites (Chin and Kirkland, 1998). Medium-size rhizoliths in the floodplain deposits probably indicate that shrubs also lived there, at least locally.

Various types of animals spent much of their lives on the floodplains. Some of the smaller Morrison crocodiles were cursorial and thus were more terrestrial than aquatic (Chure, oral communication, 2002). These crocodiles may have inhabited the floodplains, along with various lizards and small mammals. Trace fossils that record evidence of life that lived in the distal floodplain regions include beetle burrows, ant nests, termite nests, bee nests, and wasp nests (Hasiotis, this volume). Crayfish burrows, which occur in the proximal floodplain environments of the Morrison Formation, are not present in the distal floodplain environment, which is consistent with the dry climate (Hasiotis, this volume).

7.5. Eolian environments

Conditions hostile to most life in the Morrison ecosystem were found in the various eolian dune fields that developed during the early part of Morrison deposition. The larger ergs developed in the southern part of the region, in the upstream reaches of the depositional basin, where the water table was lower than in the downstream reaches. The sand to build the dune fields was derived from adjacent upwind dry streambeds, as indicated by interfingering between intermittent stream and eolian deposits. Farther north, smaller dune fields apparently were sourced from exposed shoreline deposits at the edge of a receding seaway. The presence of eolian deposits reflects the dryness that prevailed in the depositional basin.

Termite nests occur in thick eolian dune deposits in northwestern New Mexico, but they appear to originate in a paleosol that developed at the top of the eolian deposits and most likely were not part of the eolian habitat (Hasiotis, this volume). Similarly, fossil tree stumps were found in growth position in dune deposits of central Wyoming, but they appear to have begun their growth before they were enveloped by the eolian dune field and thus do not necessarily reflect an eolian habitat. Other trees occur in growth position in the Salt Wash Member in Colorado (Shawe et al., 1968). The occurrence of trees in growth position is additional proof that trees grew in the depositional basin as well as in the upland regions. For the most part, eolian deposits lack evidence of bioturbation, a reflection of the inhospitable environment (Hasiotis, this volume).

7.6. Floodplain lakes and ponds

Morrison floodplain lacustrine deposits, characterized by gray mudstones that may be laminated and local thin limestone beds, locally contain thin-shelled unionids, fish, gastropods, *Botryococcus* sp. (a lacustrine alga), salamanders, frogs, turtles, crocodiles, aquatic lizards, charophytes, ostracodes, and conchostracans (Chure et al., 1998; Evanoff et al., 1998; Schudack et al., 1998; Good, this volume). Some of these water bodies may have been perennial but many probably were ephemeral ponds, particularly those that contain conchostracans, which typically inhabit ephemeral water bodies. Two types of gastropods occur in Morrison lacustrine deposits. The prosobranchs, or gill-breathers, inhabited well-oxygenated, perennial clear or fairly clear water bodies whereas the pulmonates, or lung-breathers, could have tolerated more ephemeral and muddier water bodies. The thin-shelled unionids in the lacustrine deposits exhibit annual growth bands that provide evidence for seasonality (Good, this volume). Pseudoannual growth bands, which are less regular than those related to seasonality, are attributed to the response of the bivalves to stress, such as drought or a sudden influx of volcanic ash (Good, this volume).

A close association between many of the fossil remains and the lacustrine deposits suggests that the animals (or plants) described above lived in these lakes (Chure, oral communication, 2002). In some cases, the adaptations of the various animals or known affinities also support this interpretation (fish, larger aquatic crocodiles, turtles, salamanders, frogs, charophytes, ostracodes, and conchostracans). It is possible, however, that some of the remains were washed in, as in the case of rare egg shell fragments that occur in lacustrine deposits. Modern frogs, for example, are typically aquatic, but some species require water bodies only for the laying and hatching of their eggs.

Thus, inferences from modern fauna must be made with caution.

A variety of other organisms inhabited the floodplain lakes. Trace fossils associated with the margins of some of these floodplain lakes include traces of horseshoe crabs, bivalves, gastropods, beetles and crickets, medium and smaller rhizoliths, insect larvae (including those of caddisflies), trails of nematode worms, and possibly mayfly burrows (Hasiotis, this volume). Evidence that larger animals frequented the shorelines of these same lakes is provided by pterosaur tracks and small reptile swimming tracks (possibly from crocodiles or turtles), and sauropod, ornithopod, and theropod tracks (Hasiotis, this volume). In the subaqueous parts of the lakes are tubes produced by insect larvae, and traces of gastropods that suggest feeding, hiding, crawling, and grazing behaviors (Hasiotis, this volume).

Plant remains (in addition to charophytes) locally occur in floodplain lake and pond deposits because of the favorable conditions for preservation. Abundant palynomorphs preserved in these gray lacustrine mudstones help to infer an herbaceous origin for much of the vegetation in the Morrison Formation.

7.7. Wetland/lacustrine carbonate environments

The wetland and lacustrine carbonates that formed in the distal lowlands contain microbialites (stromatolites), charophytes, ostracodes, thin-shelled unionids, sponges, and gastropods (Dunagan, 1998). Conchostracan-bearing beds attest to more ephemeral water bodies. The distribution of charophyte- and ostracode-bearing limestone and calcareous mudstone deposits suggests that although this environment was particularly well developed in the downstream lowlands of the depositional basin (Dunagan and Turner, this volume), conditions on the overbank floodplains were locally conducive to development of similar water bodies throughout much of the depositional basin (Peck, 1957; Schudack et al., 1998). Abundant dinosaur tracks in the distal lacustrine limestone beds attest to the idea that the distal lowland water bodies were good sources of water (Lockley et al., 1986). Tracks occur in at least four layers of limestone and shale in a large track site in southeastern Colorado. At this locality, more than 1300 tracks have been recorded from a single limestone bed in the Morrison Formation, representing the trackways of more than 100 animals. Fossil organisms associated with the tracks include charophytes, horsetails, crustaceans, gastropods, bivalves, and fish (Lockley et al., 1986).

The abundance of tracks in the succession of limestones indicates that dinosaurs revisited the water body through time. The lakes and wetlands were sources of freshwater, and also, perhaps, sources of food for grazing sauropods, as the charophytes that grew in the wetlands and lakes would have been available to them. In New Zealand, subaqueous charophyte "meadows" form a lush vegetative carpet along some modern lake bottoms, and their abundance, as shown in photographs (http://www.thekrib.com/Plants/Plants/NZ/meadow.jpg), suggest that they might have provided a reasonable source of food for the Morrison sauropods. Because the range of their neck movements permitted *Diplodocus* and *Apatosaurus* to graze below the level of their feet (Stevens and Parrish, 1999), charophytes that grew in the lakes and wetlands may have served to supplement their diets. That charophytes were a possible food source for the "grazing" dinosaurs is suggested by the fact that charophytes are the main diet for modern-day coots (Forester, oral communication, 2003).

7.8. Alkaline, saline wetland/lake environments

In contrast to the habitat provided by the distal carbonate wetlands and lakes, the highly alkaline nature of the wetlands that formed upstream, associated with the tuffaceous units of Lake T'oo'dichi' (Fig. 9), made these wetlands inhospitable to most life. Fossil remains are rare in these deposits. Abundant small unidentified burrows, largely of one type, were found in the tuffs, suggesting the low diversity typical of highly stressed environments (Hasiotis, oral communication, 1994). Small rootlets, similar to those found elsewhere in the Morrison, indicate episodes of exposure of the wetland sediments. Laminated, fresh water lacustrine deposits that are interbedded with the alkaline, saline wetland deposits contain various megaplant remains (Ash and Tidwell, 1998; Parrish et al., this volume).

The remains of *Seismosaurus hallorum* were found in a fluvial sandstone bed that is underlain and overlain by clinoptilolite-bearing tuffs that formed in the alkaline, saline wetlands of Lake T'oo'dichi'. The sandstone represents an episode in which the wetland/lake complex was completely dry and flash floods delivered sand, as well as the carcass of *S. hallorum*, well out into the lake basin. Additional dinosaur remains and other fossils occur near the margins of the wetland/lacustrine complex, such as the numerous dinosaur and micro-vertebrate remains around the northern and eastern flanks of the Uncompahgre uplift in Colorado. One such accumulation of dinosaur remains is attributed to a mass mortality associated with extreme drought during a dry interval associated with the alkaline, saline wetland. The bones are thought to have been buried by a subsequent short-lived flash flood across the dry basin (Richmond and Morris, 1998).

7.9. Coal swamps and marshes

In the northern parts of the depositional basin, near the margins of the Late Jurassic Western Interior Seaway, coal swamps and marshes developed where the water table was high in low lying areas in Montana and Canada. These deposits are present only in the uppermost part of the formation in strata of Tithonian age in the US. In Canada, coal formation began earlier, during the Kimmeridgian, and persisted into the Early Cretaceous. Coals and gray to brown sandstones and mudstones were deposited in mires and associated rivers, floodplains, and lakes in Montana (Parrish et al., this volume). The high ash and sulfur contents of these coal beds are consistent with peat formation under seasonally dry climates in a region with a high water table (Cecil et al., 1981, 1982; Parrish et al., this volume).

Many of the taxa in the Late Jurassic Western Interior floral record came from the Tithonian age coal-bearing intervals in the Morrison and equivalent beds in Montana and Canada. The flora in the Tithonian is similar to that in the Kimmeridgian part of the formation, but includes some taxa that are consistent with slightly wetter sediment conditions (Parrish et al., this volume). These slightly wetter sediment conditions may have been caused by slightly greater amounts of precipitation or cooler conditions that led to lower evaporation rates (Parrish et al., this volume). A higher water table could also contribute to wetter conditions in the sediments. In spite of the indications that the sediments were slightly wetter, the climate remained relatively dry (Parrish et al., this volume).

7.10. Evaporative embayments

In low lying areas adjacent to the Late Jurassic Western Interior Seaway, hypersaline conditions prevailed within shallow marine embayments. In places, casts and external molds of halite attest to the high salinity that developed. Within the embayments, shallow marine water evaporated in the dry climate and formed beds of gypsum. Sulfur isotopes confirm a marine origin for these evaporites (Northrop, oral communication, 1987). The evaporite deposits tend to be overlain by lacustrine beds that represent the progradation of non-marine sedimentation during retreat of the seaway. The evaporative basins did not preserve any evidence of life, which was probably scarce in this environment.

7.11. Marine environments

The normal and brackish marine waters of the Late Jurassic Western Interior Seaway extended as far south as northern Utah and Colorado. The shoreline was characterized by low-energy deposition on a low gradient. Glauconitic sandstones are common, and thin deltaic sequences are locally present. Lagoonal gray to black laminated mudstones with finely comminuted plant debris, and thin-bedded sandstones locally overlie the marine sandstones and represent a transition to non-marine deposition.

A marine and brackish water fauna includes body and trace fossils of bivalves, oysters, lingulid brachiopods, crabs, gastropods, and polychaete worms (Hasiotis, this volume). Dinoflagellates have also been recovered from some of the marine deposits (Litwin et al., 1998). Pterosaur tracks as well as ornithopod and theropod dinosaur tracks also occur in the shoreline setting (Hasiotis, this volume). Scarce ammonites occur in these beds in Canada.

8. Paleogeographic reconstructions

Although the climate did not change significantly throughout Morrison deposition, the mosaic of environments and their associated communities, shifted considerably through time. Similarly, the water table seems to have been higher at some times than others. The distribution of environments and communities can be illustrated with a series of paleogeographic maps. Several time slices were selected to demonstrate major shifts in the regional paleogeography (Figs. 7–10). The maps show the maximum advance and subsequent retreat of the Late Jurassic Western Interior Seaway and evolution of the Morrison terrestrial ecosystem. Those time intervals selected were the early, middle, and late Kimmeridgian, as well as the early Tithonian.

Paleocurrent directions from fluvial beds are an essential part of the paleogeographic maps. There is a great deal of variability in the availability of paleocurrent data across the depositional basin, and thus, some of the stream flow is inferred. This is particularly true in the northern part of the basin. A limited number of measurements from fluvial strata in the Morrison of Wyoming and western to central Montana suggest a generally eastward to northeastward paleoflow (Walker, 1974; Winslow and Heller, 1987; Cooley, 1993). Inferred westward flow for streams in eastern Montana and North Dakota is based entirely on subsurface work (Peterson, 1957). Others have inferred a southwestward flow from the Canadian Shield toward the Late Jurassic Western Interior Seaway in Alberta and Saskatchewan, although no terrestrial rocks of this age are present on the east side of the seaway (Poulton, 1984; Stott, 1984; Smith, 1994). It seems reasonable that the streams in the northern part of the Morrison depositional basin, or on the Canadian Shield, would have emptied into the seaway, but no paleocurrent data exist to substantiate this.

Paleocurrent measurements in fluvial sandstone beds in the southeastern part of the basin (northeastern New Mexico, westernmost Oklahoma, and southeastern Colorado) indicate generally eastward-flowing streams, which most likely turned south in Oklahoma and Texas and emptied into the ancestral Gulf of Mexico. Farther north in Montana and Wyoming, proximity to the Late Jurassic seaway indicates that most stream flow in the lower part of the Morrison should have been toward the north, although fluvial sandstone beds are extremely rare in the lower part of the formation in that region and therefore few paleocurrent measurements exist.

Two major fluvial complexes that existed in the upstream reaches of the depositional basin are represented by the Salt Wash and Westwater Canyon Members (Figs. 2 and 3). These units have been studied extensively and have yielded the most reliable paleocurrent data and provenance information for the Morrison Formation. The streams that deposited both of these members emerged from the upland areas of the Morrison source areas and flowed eastward across the depositional basin (Craig et al., 1955; Turner-Peterson, 1986; F. Peterson, 1994).

8.1. Early Kimmeridgian

Deposition of the Morrison Formation and related beds began during maximum inundation of the Late Jurassic Western Interior Seaway (Fig. 7). The map shows the paleogeography during an early stage of Morrison deposition. Units represented are the Tidwell and Windy Hill Members and part of the Recapture Member of the Morrison Formation to the south; the Ralston Creek Formation in east-central Colorado; the Unkpapa Member of the Morrison in western South Dakota; the upper part of the Swift Formation in Montana and adjacent areas; and the upper Fernie, Morrissey, and lower Mist Mountain Formations in Alberta and British Columbia, western Canada.

Uplifts to the west established the eastward drainage pattern that continued throughout Morrison deposition. An alluvial plain of limited areal extent represents the first fluvial deposits in the Morrison (Fig. 7). Low hills that were remnants of the ancestral Rocky Mountains were present in central Colorado and contributed minor amounts of sediment eastward to the Denver basin. Westward-flowing drainage along the northeast side of the Morrison depositional basin is inferred from subsurface data by J.A. Peterson (1957). A shallow marine shelf occupied a large part of the Western Interior at this time. The seaway connected to the Paleo-Pacific Ocean in central to northern British Columbia (Imlay, 1980). Evaporative embayments developed in low-lying areas in the southern part of the region that were connected to the main seaway through narrow inlets. The marine water in the embayments was subjected to intense evaporation in the semi-arid to arid climate, resulting in the precipitation of gypsum and minor halite. The dry conditions also were conducive to development of extensive eolian dune fields (ergs) in the southern part of the region. The sand for dune formation was derived from intermittent streambeds during dry peri-

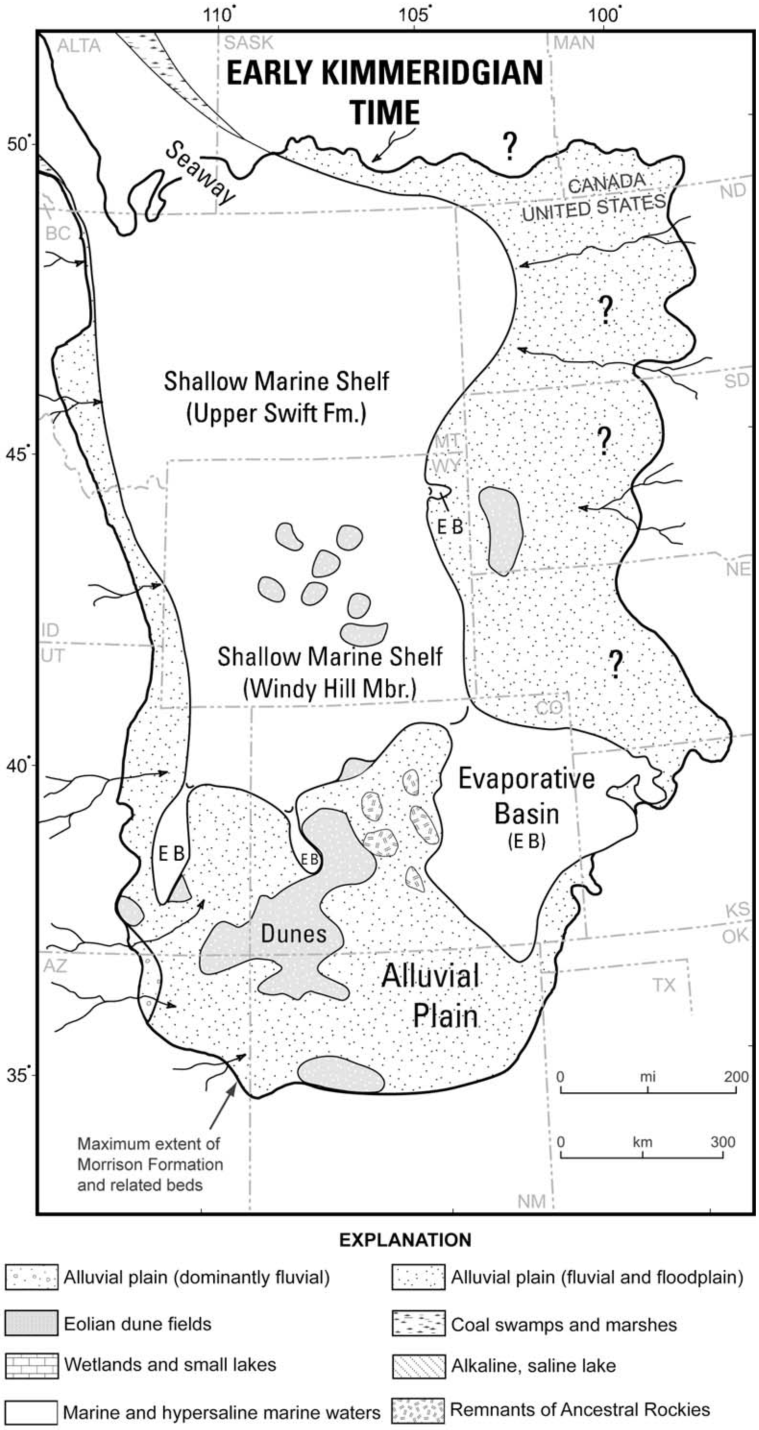


Fig. 7. Paleogeographic map of the Morrison depositional basin in early Kimmeridgian time during deposition of the Tidwell Member and correlatives. The explanation applies to this figure and Figs. 8–10. Except in Canada, the patterns are only shown within the depositional basin.

ods when deflation by prevailing southwesterly winds carried the sands downwind into depressions. This interpretation is based on interfingering relationships among the Bluff Sandstone, Tidwell, and Salt Wash Members (O'Sullivan, 1980b) as well as interfingering of fluvial and eolian deposits in the Recapture Member (Condon and Peterson, 1986). Dunes also developed locally on islands in the seaway during lowstands when marine sands of the Windy Hill Member were exposed to wind erosion.

During the earliest stages of Morrison deposition, the warm shallow seaway provided favorable conditions for a variety of marine organisms that could tolerate somewhat more brackish conditions than persisted in the earlier Sundance Sea when more open marine conditions existed. Pterosaur tracks at the margins of the seaway may indicate that the pterosaurs, some of which had teeth adapted for catching fish, lived at the edge of the seaway. Their tracks are also found considerably inland, which suggest that they may have fed on fish in floodplain ponds and in the rivers as well. The evaporative basins were more hostile to life, as were the dune fields on the adjacent landscape.

In the southern terrestrial part of the ecosystem (Tidwell Member), proximity to the shoreline of the Late Jurassic Western Interior Seaway (Fig. 7) ameliorated seasonal climatic fluctuations that typically characterize interior basins, as reflected in the lack of annual growth bands in unionid bivalves (Good, this volume). Weakly developed paleosols (argillic Calcisols) in the Tidwell Member (Demko et al., this volume) also formed marginal to the seaway, where a relatively high water table existed year round.

Early Kimmeridgian streams and their associated overbank deposits provided the initial environments for establishment of the various terrestrial communities. Aquatic and riparian fauna and flora, as well as overbank floodplains and ponds hosted the earliest Morrison life forms, including the first Morrison dinosaurs. Dinosaur remains are more scarce in the lower Kimmeridgian deposits than higher in the formation. A few bones of a stegosaur and a primitive diplodocid (Turner and Peterson, 1999), and rare dinosaur tracks, are the only indications of dinosaurs thus far obtained from this interval. A partial reason for the low recovery may be the limited extent of land during the maximum inundation by the Late Jurassic Western Interior Seaway.

8.2. Middle Kimmeridgian

As Morrison deposition continued into the middle Kimmeridgian, the Late Jurassic Western Interior Seaway retreated rapidly to the north, leaving behind a much larger alluvial plain in the depositional basin than existed during the early Kimmeridgian (Fig. 8). Units represented include part of the Recapture Member of the Morrison Formation in northern New Mexico; the upper part of the Salt Wash Member in eastern Utah and western Colorado; the Unkpapa Sandstone Member in southwestern South Dakota; part of the upper Swift Formation in northern Montana and parts of the Fernie, Morrissey, and lower Mist Mountain Formations in Alberta and British Columbia; and largely the lower-middle part of the Morrison Formation where it is undifferentiated.

Increased uplift in the source regions to the west produced large volumes of clastic sediment that were carried by largely intermittent eastward-flowing streams into the depositional basin (Craig et al., 1955; Turner-Peterson, 1986; Winslow and Heller, 1987; Cooley, 1993; F. Peterson, 1994). The Salt Wash Member represents an eastward prograding sequence of fluvial sandstones that reached its maximum eastward extent in the middle Kimmeridgian. The fluvial complex was characterized by a braid plain in which channels switched back and forth across the alluvial plain and deposited amalgamated (sheet-like) sandstone deposits. The streams were intermittent in nature and changed downstream to isolated, often straight, fluvial channels surrounded by overbank mudstone.

Progressively, in a downstream direction, streams of the Salt Wash Member were replaced by wetland/lacustrine environments that were pushed farther and farther eastward during Salt Wash deposition. For example, during early Salt Wash deposition, wetland/lacustrine beds (limestone, sandstone, and mudstone) were deposited in the area around Grand Junction, Colorado, whereas by middle Kimmeridgian time, wetland/lacustrine deposition was pushed farther eastward toward Glenwood Springs, Colorado. Wetland/lacustrine deposition also predominated east of

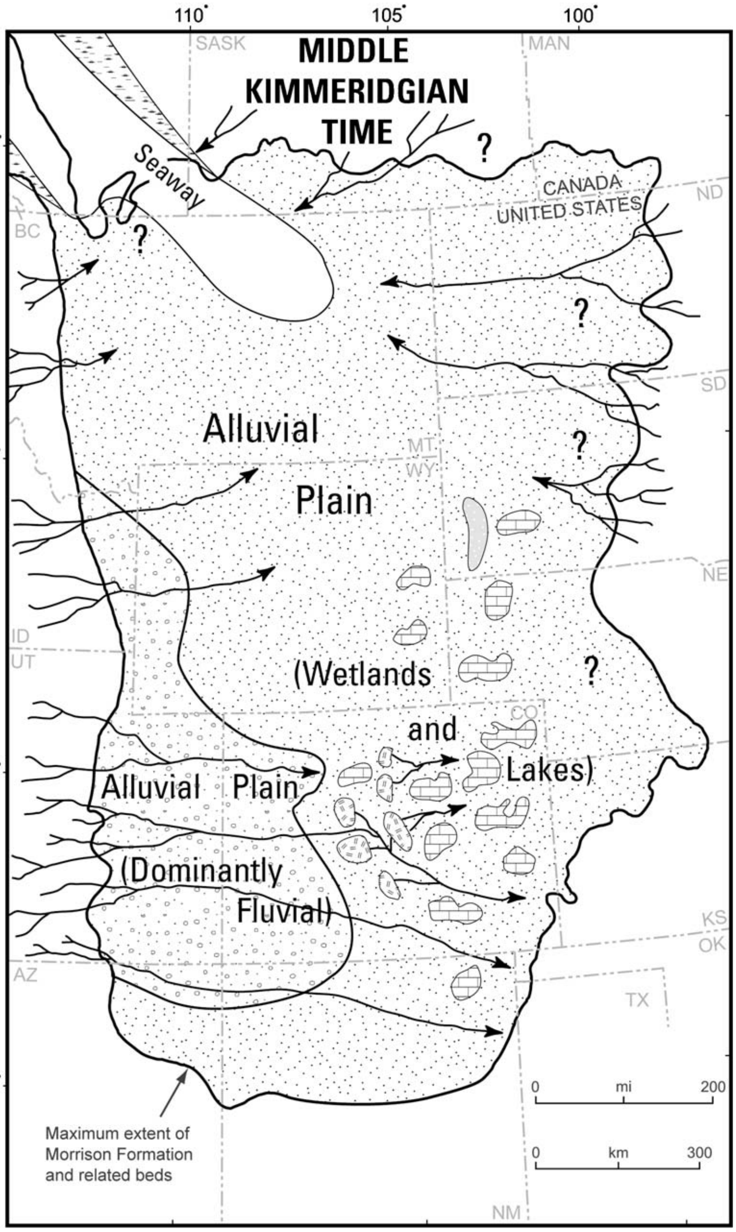


Fig. 8. Paleogeographic map of the Morrison depositional basin in middle Kimmeridgian time during deposition of the upper part of the Salt Wash Member and correlatives.

the ancestral Rocky Mountains (Dunagan and Turner, this volume), which were by now small, low-lying hills that provided little sediment to the depositional basin. Moreover, the ancestral Rockies apparently were not much of a barrier to drainage, as demonstrated by freshwater snails (particularly *Mesauriculstra* spp.), whose biogeographic distribution suggests a drainage system between remnants of the ancestral Rocky Mountains (Evanoff et al., 1998). Wetland and lacustrine deposition in east-central Colorado was characterized by open-hydrologic conditions, with the margins of the wetlands and lakes intermittently exposed to soil-forming processes, processes that led to formation of pseudomicrokarst, and brecciation, which produced palustrine deposits (Dunagan and Turner, this volume). Wetland and lacustrine deposition prevailed in the downstream reaches because of the reemergence of the regional water table in low-lying, distal parts of the depositional basin. A west to east trend in paleosols, from vertic Calcisols to palustrine Protosols and argillic Calcisols (Demko et al., this volume), reflects this inferred hydrograph.

Eolian deposition during the middle Kimmeridgian was restricted to small Recapture dune fields in northwestern New Mexico, where stratal relationships suggest that the eolian sand, as in the early Kimmeridgian, continued to be derived from dry streambeds farther upwind (Condon and Peterson, 1986; F. Peterson, 1994), and southwestern South Dakota, where the sand apparently was derived from Windy Hill shoreface sands farther west. Marine deposition was restricted to the northwestern part of the depositional basin. Marginal to the marine trough in Canada were coal swamps of the Mist Mountain Formation (Fig. 8). The rest of the basin was a broad alluvial plain with isolated stream channels crossing an expansive floodplain. Well-developed annual growth banding exhibited by unionid bivalves from lakes that formed on the floodplain at this time provide the best evidence for seasonality in the Morrison (Good, this volume). The climate remained dry (semi-arid to arid), but there was at least seasonal precipitation.

Dinosaurs roamed throughout most of the vast alluvial plain that stretched from northern New Mexico to Montana during the middle Kimmeridgian. In low-lying distal parts of the basin in southeastern Colorado, dinosaur trackways demonstrate that the dinosaurs frequented the wetlands and lakes (Lockley et al., 1986). Charophytes that grew in these wetlands and lakes may have provided an additional source of food for the grazing diplodocids, who may have used their peg-like teeth to rake through the waters to consume these plants.

8.3. Late Kimmeridgian

An apparent decrease in the volume of detrital material delivered to the basin by Morrison streams, as indicated by the lack of large alluvial complexes in the upper Kimmeridgian, is contrasted with a significant increase in the volume of air-fall volcanic ash blown into the basin by prevailing westerly winds. Throughout a large part of the depositional basin, the beginning of the voluminous outpourings of volcanic ash is reflected by the "clay change" between the lower and upper parts of the Morrison (Figs. 2 and 3). Fig. 9 shows the paleogeography during this time. Units represented are the upper part of the Brushy Basin Member, correlative strata of the upper part of the Morrison where it is undifferentiated; and correlative parts of the Fernie, Morrissey, and lower Mist Mountain Formations in Alberta and British Columbia.

Streams at this time had fairly straight channels and are represented by ribbon-type fluvial channel sandstone beds. Stacked fluvial deposits are restricted to the southwesternmost area of the depositional basin; elsewhere single-channel deposits typify the interval. Volcanic ash may have choked the stream courses on occasion, causing them to overflow their banks. Fossil localities near Grand Junction, Colorado have been attributed to such flood events (Newell, 1997).

At this time, a structural low developed in the Four Corners area between the ancestral Monument and Defiance-Zuni uplifts to the west and southwest, and the Uncompahgre uplift to the east and northeast. A hydrologically closed basin formed in this structural low, fed by discharge of shallow groundwater on the upstream (southwest) side of the Uncompahgre uplift. The addition of air-fall volcanic ash to the wetland, coupled with high evaporation rates in the dry climate, created optimum conditions for development of an alkaline, saline wetland, which was part of the wetland/lacustrine complex named Lake T'oo'dichi' (Fig. 9; Turner and Fishman, 1991).

Farther downstream in the distal low-lying parts of the depositional basin in east-central Colorado, freshwater from regional discharge continued to feed wetlands and lakes, and carbonate deposition continued from the middle Kimmeridgian. Low hills of the ancestral Rocky Mountains were shedding little if any detrital material into these wetlands and lakes, and were not a sufficient barrier to groundwater flow to isolate the carbonate-precipitating water bodies from regional groundwater and intermittent surface flow (Evanoff et al., 1998).

The Late Jurassic Western Interior Seaway was receding slowly to the northwest during this time, and coal swamps persisted along the margins of the

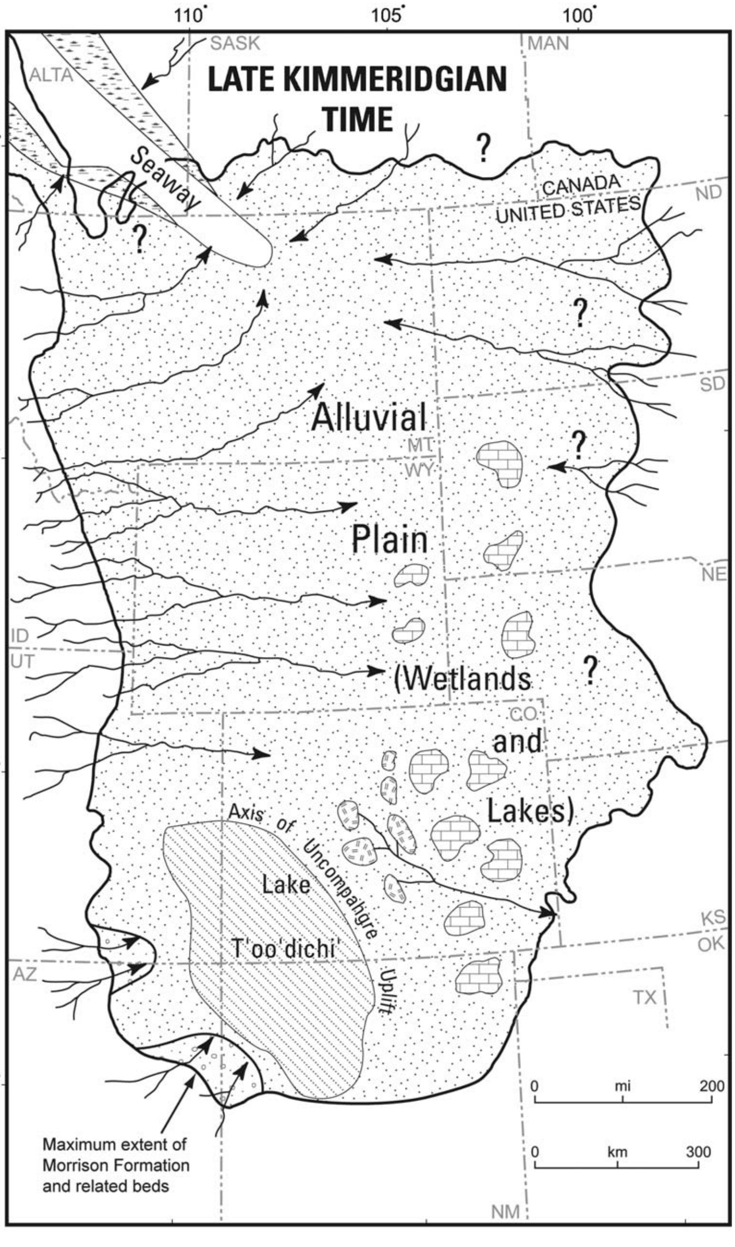


Fig. 9. Paleogeographic map of the Morrison depositional basin in late Kimmeridgian time during deposition of the upper part of the Brushy Basin Member and correlatives.

seaway, resulting in deposition of the coal beds in the Upper Jurassic part of the Mist Mountain Formation in Canada (Gibson, 1985).

Detrital lakes and ponds of various sizes, represented by gray to black mudstone and scarce limestone beds, dotted the landscape in the late Kimmeridgian. The high water table that led to formation of the lakes also resulted in relatively immature paleosol development, chiefly weakly to moderately developed floodplain Protosols and Calcisols (Demko et al., this volume) and weakly developed, noncalcareous marginal-lacustrine paleosols (Newell, 1997). The types of paleosols and their relative immaturity, coupled with the types of stream deposits and abundance of wetland and lacustrine deposits, are interpreted by Demko et al. (this volume) to represent a landscape characterized by sluggish, low-gradient streams and various types of intermittent and perennial water bodies. Mudstones deposited in the floodplain at this time contain little in the way of rhizoliths, and, in many places, the only evidence of the vegetation that lived there are shallow-penetrating filamentous rootlets (Demko et al., this volume). These probably reflect the roots of the small herbaceous plants that occupied this niche in the ecosystem (Parrish et al., this volume) whereas large trees and shrubs were confined mostly to the riparian regions.

Even though large volumes of volcanic ash were incorporated in the sediments, the air-fall ash events seem not to have significantly affected life forms more than temporarily. For example, Evanoff (oral communication, 2001) noted that prosobranch gastropods are more abundant in the upper Brushy Basin Member (upper Kimmeridgian) than the lower, which is characterized by more pulmonate gastropods. It might be expected that the volcanic ash in the late Kimmeridgian would have temporarily increased the turbidity in lakes, ponds, and wetlands, and thus made them inhospitable to prosobranch gastropods. Apparently, however, these gill-breathers were only temporarily affected by the air-fall ash events. The higher ratio of prosobranch to pulmonate gastropods at this time may also reflect a higher water table, which would have increased the likelihood of perennial wetland or lake environments. The presence of weakly developed annual growth bands in unionids from the late Kimmeridgian is also consistent with a higher water table for this time interval (Good, this volume). Turbidity associated with volcanic ash events may have caused some of the pseudoannual bands in these bivalves, although runoff from isolated storms may also have caused this type of growth banding (Good, this volume).

Eolian beds are not present in this time interval, in spite of the continued dry climate that is indicated by development of an alkaline, saline wetland/lacustrine complex (Fig. 9). Large fluvial complexes, from which earlier eolian deposits derived their sand, were lacking in the late Kimmeridgian, as were the associated actively moving structures that had promoted eolian sand accumulation. The higher water table may also have been a factor.

The reason for the high water table during the late Kimmeridgian is not clear. It may be that the Salt Wash Member and its correlatives, deposited earlier during the middle Kimmeridgian, provided a shallow, regional aquifer with continuous connectivity to sources of water. Water that infiltrated the upland regions and losing streams in the upstream reaches may have recharged the newly available sandstone aquifer, which provided a shallow water table for much of the depositional basin. Alternatively, there may have been more precipitation in the uplands during late Kimmeridgian time, providing greater recharge to regional aquifers.

As during the middle Kimmeridgian, dinosaurs lived throughout the extensive alluvial plain. The spectacular accumulation of dinosaur bones at the Carnegie Quarry at Dinosaur National Monument, Utah, are representative of the giant herbivores that lived during the late Kimmeridgian.

8.4. Tithonian and Tithonian(?)

Known Tithonian deposits occur in the northern part of the depositional basin. Toward the end of Morrison deposition, coal swamps and related depositional environments developed in central Montana and Canada (Fig. 10). These beds are dated by their megaflora (Brown, 1946) and palynomorphs (Gibson, 1985; Litwin et al., 1998). The abundant megaflora from these beds indicate equable conditions marginal to the seaway, although there was not a significant climate change from the late Kimmeridgian to the early Tithonian.

The regional extent of Tithonian age deposits to the south is poorly known, and based mostly on lithologic correlations and reasonable inference. Black mudstones, such as those that occur in the upper part of the Morrison Formation at Como Bluff, Wyoming, may be Tithonian in age. Similar black mudstones occur in the upper part of the Morrison as far south as Morrison, Colorado (Peterson and Turner, 1998). Fluvial sandstone beds locally occur above the coal beds in Montana, and below the regional paleosol that marks the end of

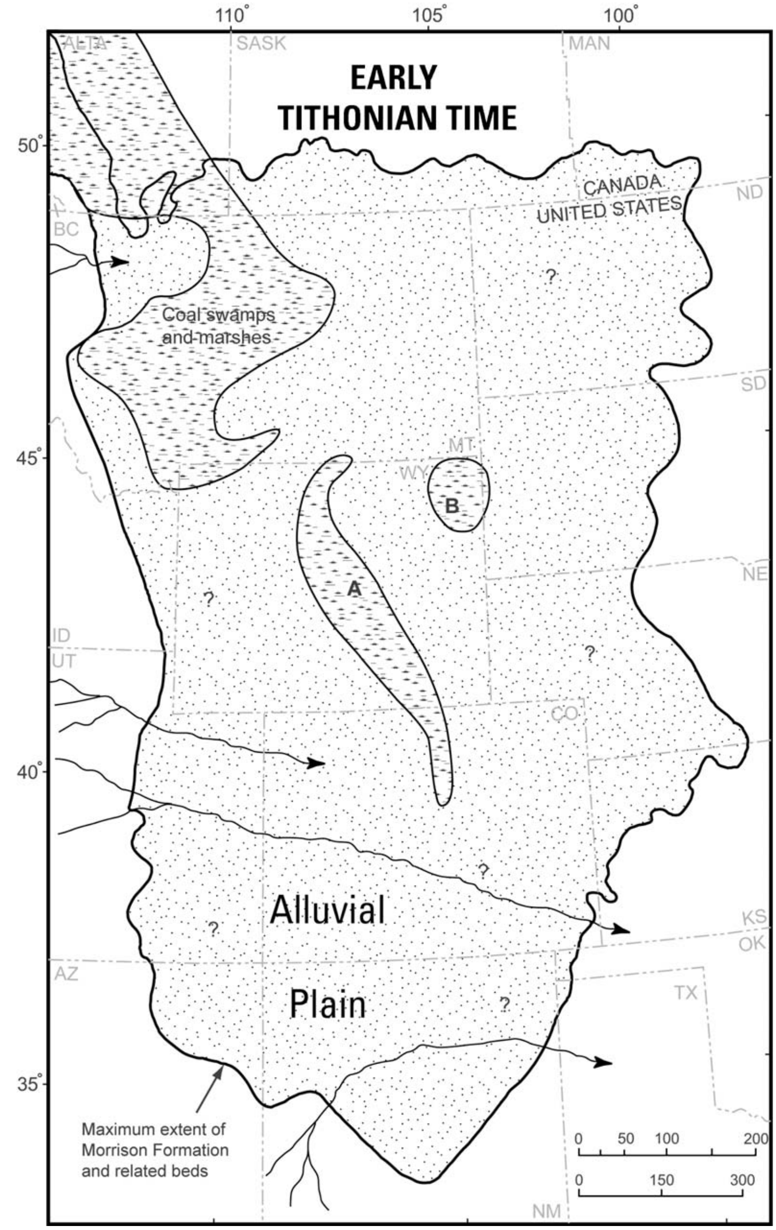


Fig. 10. Paleogeographic map of the Morrison depositional basin in early Tithonian and Tithonian(?) time during deposition of the uppermost beds of the Morrison Formation and correlatives. The interval is poorly dated. Coal swamps were only present in the northernmost area. Areas A and B include scattered marshes.

Morrison deposition (Demko et al., this volume). Similar fluvial sandstone beds are present at the top of the Morrison elsewhere in the depositional basin and may indicate a final fluvial episode in the basin.

Some of the earlier dinosaur quarries that yielded the first dinosaur bones in the Morrison Formation occur in beds stratigraphically high in the formation in beds of Tithonian(?) age. Recovery of large specimens of herbivores from these quarries indicates that the giant herbivores continued to thrive in the Morrison depositional basin.

9. Biostratigraphic trends

The paleogeographic maps for the various intervals of Morrison deposition (Figs. 7–10) illustrate some of the major shifts in depositional environments in the Morrison. Biostratigraphic studies indicate that the fauna may have responded to changes in the depositional basin that are not captured in the four paleogeographic time slices. For example, some of the changes in the diversity of the dinosaurs coincide fairly well with changes in diversity of charophytes and ostracodes (Schudack et al., 1998; Turner and Peterson, 1999). This suggests that some environmental changes that occurred at these times were sufficient to exert an influence on markedly different organisms (Turner and Peterson, 1999). Such significant changes in the fauna and flora suggest that the biota was responding to certain broad ecological changes. Although the nature of the widespread paleoecological changes cannot be determined, the biota apparently responded to stresses or changes within the ecosystem.

Interestingly, the mid-Morrison paleosol near the base of the lower part of the Brushy Basin Member does not seem to coincide with any significant changes in biota, even though an unconformity may be present at the top of the paleosol (Demko et al., this volume). The paleosol does, however, appear to coincide with a significant shift in paleomagnetic pole positions (Steiner and Helsley, 1975; May et al., 1989).

10. Life and death in the Morrison ecosystem

With the new understanding of the Morrison ecosystem, it is possible to evaluate the distribution of the flora and fauna across the landscape and also how the dinosaurs, especially the giant herbivores, flourished and succumbed on the vast Morrison alluvial plain. The diversity of the fauna recovered from the Morrison Formation (Chure et al., 1998) might appear, at first glance, to conflict with the climatic interpretations for the Morrison. Because the dinosaurs provide little help in refining interpretations of climate, Engelmann et al. (this volume) considered how the fauna could have adapted to the climatic conditions indicated by the geologic interpretations to see if the fauna could reasonably have been expected to thrive in the dry habitat. Morrison deposition occurred in a semiarid climate, with seasonal precipitation and longer intervals of dryness that sometimes resulted in extreme drought. Thus, through time, the ecosystem ranged from relatively equable habitats during wet seasons, to one characterized by small, widely separated refugia during periods of severe drought (Engelmann et al., this volume).

The distribution of communities within the ecosystem can be evaluated in terms of both the hydrologic landscape and the adaptations of the flora and fauna that allowed them to prevail. It appears that water reached the ecosystem largely through surface water in numerous intermittent streams and a few major perennial streams, and through groundwater that fed ponds on the floodplain and wetlands and lakes in the low-lying distal areas of the basin. Many of the animals inhabited the riparian and floodplain/lake environments, as indicated by the preponderance of body and trace fossil remains in these environments (Engelmann and Callison, 1998; Engelmann and Fiorillo, 2000; Engelmann et al., this volume; Hasiotis, this volume). Except during periods of extended drought, conditions in these local ecological niches remained favorable to a biota that depended upon continuous availability of water. An important aspect of the habitat is the depth of the water table. Availability of water determines the type and abundance of vegetation, and is also important to some animals. Estimates of the depth to the ancient water table can be obtained from termite and crayfish burrows. Termites are air breathers and must construct their underground nests above the water table whereas crayfish burrow down into the water table so they can moisten their gills (Hasiotis, this volume). Where they occur together and their burrows can be related to the paleoground surface, the termite burrows always terminate downward above the lowest depth of the crayfish burrows. In most cases, the termite burrows extend one or a few meters below the paleoground surface. Where they are present, the crayfish burrows suggest water-table depths of about 4 m (13 ft) or less from the surface (Hasiotis, this volume).

Seasonal flooding helped sustain the riparian communities, which probably was important for reproduction stages of many riparian plants. In modern environments, riparian vegetation often depends on fluctuating river levels and annual flooding for reproduction. Water available from perennial streams and groundwater-fed lakes on the floodplain was supplemented by at least seasonal rainfall, which brought moisture to the remaining floodplain areas and produced a carpet of herbaceous groundcover.

Although seasonal rainfall provided much-needed moisture to the floodplain, many of the animals may have had strategies that allowed them to survive extended periods of drought. Conchostracans, for example, are known to inhabit ephemeral water bodies (Lucas and Kirkland, 1998) and to go into the egg stage during dry periods, awaiting the next wet period. Some modern varieties of salamanders and frogs can sustain droughts up to 2 1/2 months (Martof, 1972). Modern lizards and insects inhabit a wide range of environments and many species are well adapted to semi-arid conditions (Engelmann et al., this volume). The turtles in the Morrison ecosystem seem more adapted to water than land, as were the larger crocodiles; however, some modern members of these groups can withstand even severe droughts (Engelmann et al., this volume). Similarly, some of the plants appear to have had strategies to survive periods of drought. Modern cycads all have 'contractile roots', which afford protection during drought and fires by drawing sensitive parts of the seedlings under the soil surface (Hill, 1998). Ferns can reproduce asexually in dry periods and can grow new fronds without water. If the Morrison cycads and ferns resemble those living today, they might have had the same adaptations. Therefore, even though Morrison plants preferred to live near water, they were probably adapted to survive periods of drought.

The dry climate inferred for the Morrison typically raises concerns about the herbivorous dinosaurs, whose food and water requirements are often thought to have been considerable. Ironically, the large size attained by these giant herbivores may have been an ideal adaptation to their environment (Engelmann et al., this volume). An inverse relationship between size and metabolism (Kleiber, 1961; Schmidt-Nielsen, 1984) suggests that their food requirements may have been lower than initially thought. Efficiency of dinosaurian digestive systems would also have made a difference in an environment where food resources may have been limited. Analogies with modern elephants, whose digestive systems are fairly inefficient, are probably not valid; instead, the digestive systems of the Morrison herbivores may have been much more efficient, like their modern descendants, the birds (Horner, oral communication, 1994). Evidence from dinosaur coprolites is equivocal on this point—much of the plant matter is unidentifiable, yet some of it is well preserved (Chin and Kirkland, 1998). An advantage of the large herbivorous dinosaurs may have been their ability to tolerate lower dietary quality than smaller animals (Owen-Smith, 1988), allowing the dinosaurs to use a broader resource base, which is important in times of drought (Engelmann et al., this volume). Because of their size, large herbivorous dinosaurs were free to travel from one favorable environment to another and to cover large distances in search of food in times of drought (Engelmann et al., this volume).

The distribution of vegetation in the Morrison—with shrubs and trees growing primarily along stream courses and herbaceous plants chiefly occupying the floodplains—is of interest when considering resource partitioning inferred from dental microwear patterns and range of movement studies in certain sauropods (Engelmann et al., this volume). Fiorillo (1998) concluded from microwear dental patterns that *Camarasaurus* consumed coarser vegetation than *Diplodocus*. Analysis of the range of movement of cervical vertebrae of *Diplodocus* and *Apatosaurus* indicate that their necks could not be raised much above the height of the shoulders (Stevens and Parrish, 1999). In contrast, *Brachiosaurus* has a skeletal structure in which the front legs are longer than the rear legs, which suggests that it ate the higher vegetation, and *Camarasaurus*, with a somewhat similar build, may also have eaten the higher vegetation. In addition, *Diplodocus* and *Apatosaurus* had peg-like teeth whereas *Camarasaurus* had blade-like teeth. All of this suggests possible resource partitioning, with *Diplodocus* and *Apatosaurus* grazing on the softer herbaceous plants on the floodplain, and *Brachiosaurus* and *Camarasaurus* browsing on higher and coarser woody vegetation in riparian areas. Although the studies on dental microwear patterns have only been done for a few species, those that were studied are among the most common species recovered from the Morrison Formation. Resource partitioning is a common adaptation in resource-limited environments and might be expected in the semi-arid to arid conditions experienced by the dinosaurs in the Morrison ecosystem (Engelmann et al., this volume).

That water was also a limited resource in the Morrison ecosystem has been established. Additional evidence for the limited availability of water comes from isotopic analyses of dinosaur teeth and eggshells. Analyses of $\delta^{18}O$ from Morrison dinosaur teeth suggest that these animals were eating plant material that was water-stressed; additionally, it appears that the dinosaurs met some of their need for water from ingested water from the plants (Ekart, written communication, 1999). Isotopic analyses of dinosaur eggshells also indicate that some of the ingested water came from water-stressed plants (Ekart, written communication, 1999).

Restriction of the low-grazing dinosaurs, such as the diplodocids, to the herbaceous vegetation on the floodplains might raise questions about resource availability during the dry seasons. The herbaceous groundcover may have been only seasonally abundant on the floodplain, as it most likely flourished during episodes of seasonal rainfall. However, ferns, which can regenerate fronds asexually when water is scarce, may have helped to replenish the food source on the floodplain during dry seasons. Ferns comprise a large percentage of the palynoflorules in the Morrison (Litwin et al., 1998) and thus were probably a major component of the floodplain vegetation.

An intriguing thought is that the carbonate wetlands and lakes that developed in the low-lying distal reaches of the depositional basin may have provided an additional food source for the herbivorous dinosaurs, particularly during the dry season when the floodplain may not have had a lush herbaceous flora. These distal wetlands and lakes were known to attract dinosaurs because of the numerous track sites associated with these deposits (Lockley et al., 1986). The dinosaurs probably found these environments to be good sources of fresh water. Charophytes flourished in the distal lowland water bodies (Schudack et al., 1998; Dunagan and Turner, this volume) and may have been an additional source of food for the large herbivores, particularly the diplodocids who had considerable neck flexibility that allowed them to lower their necks well below the level of their feet (Stevens and Parrish, 1999). Their neck mobility would have made it possible to stand at the edge of the water bodies and consume the charophytes without becoming mired down in the mud. Thus, even during dry periods on the floodplain, either seasonal or longer, the distal wetlands and lakes offered an interesting possibility as refugia. Some of the dinosaur population, particularly the grazers, may have included the distal wetlands and lakes as part of their territory. Others, particularly the browsers, may have depended more on riparian areas.

The uplands offer other possible refugia for the dinosaurs, considering that the uplands were most likely vegetated and received more precipitation than the lowlands. It is unclear how well the dinosaurs could migrate upstream, and if they did, they most likely stayed near stream courses rather than hillsides. The alluvial plain, however, was probably the preferred habitat for much of the year. The large herbivores probably could have traveled significant distances, when necessary, to reach widely separated resource patches (Engelmann et al., this volume).

In spite of the semi-arid to arid climate, the nutritional and water needs of the dinosaurs apparently were sufficiently met for them to find the alluvial plain of the Morrison ecosystem suitable for nesting and raising their young, at least some of the time. Nesting sites for dinosaurs occur in floodplain environments (Alf, 1998; Bray and Hirsch, 1998). In addition, embryonic remains of *Camptosaurus* (Chure et al., 1994), and juvenile remains of *Dryosaurus*, *Camarasaurus*, and *Stegosaurus* occur at Dinosaur National Monument (West and Chure, 2001). The occurrence of nesting sites, as well as embryonic and juvenile remains, indicate that the alluvial plain was suitable for the dinosaurs to bear and raise their young.

Accumulations of dinosaur bones offer clues to droughts that were more prolonged than the seasonal dryness inferred for the Morrison ecosystem. The fluvial sandstone bed that contains the spectacular death assemblage of dinosaur bones at the Carnegie quarry in Dinosaur National Monument, for example, illustrates the significance of perennial streams in the dry climate that characterized the Morrison ecosystem. Several lines of evidence help to determine the reasons that a large collection of diverse species of dinosaurs died there. Many of the bones in the quarry sandstone bed are only slightly disarticulated and are remarkable in the preservation of features that would not be preserved had the carcasses been subjected to significant transport. For example, a *Camarasaurus* skull is attached to its cervical vertebra, a rare occurrence because of the delicate nature of this joint. The skeleton of a juvenile *Camarasaurus* is also almost entirely preserved. Several long vertebral columns remain intact. Other dinosaur remains experienced somewhat greater degrees of dismemberment.

Other interesting features in the quarry provide clues to the demise of the dinosaurs. Numerous unionid shells are part of the basal conglomerate in the fluvial channel that contains many of the bones. Most of the shells show little evidence of abrasion and a few of the shells are in their original growth position (Good, oral communication, 1996). The presence of unionids indicates that when they were alive, stream flow was perennial, and the lack of serious abrasion suggests that the shells were not transported any significant distance (Good, this volume). The close spatial association between the unionids and many of the dinosaur bones in the lower part of the stream channel suggests that they were transported and deposited during the same event, and the evidence indicates that neither was transported far. Small borings produced by the larvae of dermestid beetles are present in many of the bones. Because the beetles and their larvae are air breathers, the bones in the streambed must have been exposed to air at the time the borings were made (Hasiotis, this volume).

Taken together, along with the interpretation that the Morrison Formation was deposited in a generally dry climate with more intermittent than perennial streams, the evidence suggests a scenario for the demise and burial of the dinosaurs at the Carnegie quarry. As in modern savannahs, during periods of extended drought, waterholes in intermittent streambeds serve as water sources until they too go dry. Dinosaurs would most likely head toward a more reliable water source—the nearest perennial stream—such as the one represented by the fluvial sandstone bed at the Carnegie quarry. As the drought continued, however, even the perennial streams on the Morrison alluvial plain went dry. The animals that had gathered at the perennial stream had no other water resources to draw upon and therefore died. The unionids would also have perished when the stream went dry. Remains of crocodiles and turtles are also associated with the quarry sandstone bed and are among the stream dwellers that suffered a fate similar to that of the unionids. Dermestid beetles ate the exposed carcasses of the dinosaurs in the dry streambed and their larvae created the borings (Hasiotis, this volume). The beetle-bored bones, along with the unionids, were slightly dislodged and tumbled to varying degrees when water began flowing in the stream at some later time, probably during the first rain that ended the drought. Sand entrained along the stream bottom and on mid-channel bars that migrated downstream eventually covered the remains, encasing and preserving them. The drought scenario for the Carnegie quarry sandstone may apply to some of the other death assemblages of dinosaurs within Morrison strata (Stokes, 1985; Richmond and Morris, 1998; Hasiotis, this volume). The Carnegie quarry has a great diversity of dinosaur genera, whereas 67% of the dinosaur localities in the Morrison Formation have only one or two dinosaur genera identified (Turner and Peterson, 1999), so a drought scenario might not explain all of the dinosaur death assemblages in the Morrison.

11. Summary and conclusions

In spite of changes in paleogeography through time, and corresponding shifts in depositional environments, it appears that the climate did not change significantly throughout Morrison deposition. It remained mostly warm and dry, but with at least seasonal precipitation. Warmth due to the greenhouse effect and the southerly position of the continent, combined with dryness associated with "rain out" of most of the moisture in uplands to the west and southwest of the basin, to create a high rate of net evapotranspiration, a major factor in Morrison climate. It appears that much of the moisture that reached the depositional basin was from extrabasinal surface and subsurface water delivered to the basin from uplands to the west and southwest. Surface runoff was delivered to the basin by streams, both perennial and intermittent, depending on the size of the drainage area. Subsurface water reached the basin through shallow, local groundwater flow, and through deeper, regional groundwater flow. The streams that crossed the basin were most likely ''losing'' streams in their upstream reaches and contributed to a raised water table in the riparian areas adjacent to them. The scarce perennial streams probably formed green ribbons of vegetation winding through the semi-arid landscape. During dry seasons, the amount of surface runoff that fed the intermittent streams was not sufficient to maintain flow above the level of the streambed, but may have been sufficient to maintain substream flow, which increased the potential for waterholes in the streambed and the ability to sustain vegetation along the banks. Seasonal precipitation moistened the floodplain areas not reached by stream flooding, bringing much needed moisture to the groundcover. Locally, ponds and lakes formed on the floodplain where low-lying areas intersected the water table. A seasonally fluctuating water table appears to have characterized most of Morrison deposition.

Throughout Morrison deposition, upstream to downstream trends can be related to position on an inferred hydrograph for the basin. Deeper, regional ground-water flow discharged in the low-lying distal parts of the depositional basin, contributing to the wetland and lake environments of east-central Colorado (Dunagan and Turner, this volume). Here, carbonate deposition occurred in wetlands and lakes that maintained hydrologically open and primarily freshwater conditions in the semi-arid climate due to replenishment by groundwater seepage and spring discharge. Local discharge of shallow groundwater farther upstream occurred during the late Kimmeridgian on the upstream side of the ancestral Uncompahgre uplift. Here, in the San Juan/Paradox basin, evaporative concentration of pore waters in the dry climate, and the alteration of volcanic ash produced an alkaline, saline lake within a hydrologically closed basin (Turner and Fishman, 1991). For the most part, however, drainages from west to east remained largely interconnected, as suggested by the biogeographic distribution of certain gastropods (Evanoff et al., 1998). Disruptions to shallow groundwater flow were caused by local intrabasinal structures (Peterson, 1986), and remnants of the ancestral Rocky Mountains. The ancestral Rockies were the only known internal source of sediment in the basin.

The hydrograph for the depositional basin also is expressed in the upstream to downstream changes in paleosols. Throughout Morrison deposition, paleosols in the upstream regions reflect drier soil moisture conditions than those of equivalent age farther downstream (Demko et al., this volume). An overall upstream to downstream change from vertic Calcisols to palustrine Protosols and argillic Calcisols (Demko et al., this volume) is consistent with a lower water table upstream than downstream.

Although the climate did not change appreciably during Morrison deposition, paleogeographic reconstructions record differences in the distribution of environments through time. Major eolian environments occurred throughout early and middle Kimmeridgian time, and an alkaline, saline lake environment existed throughout most of the late Kimmeridgian. Both environments require a dry climate, which constrains climatic interpretations for the Morrison ecosystem. What appear to be slightly wetter conditions in the Tithonian that led to deposition of coal and carbonaceous mudstone may, instead, reflect lower evaporation rates associated with a slight cooling trend and not a significant change in the overall climate (Parrish et al., this volume). A slight cooling trend is consistent with isotopic studies of the ostracodes (Schudack, 1999b). A possible underlying cause for the vertical trend is the inferred slight decrease in the carbon dioxide content of the atmosphere during the Late Jurassic (Ekart et al., 1999).

The major differences in the distribution of environments through time appear to reflect tectonic influences and withdrawal of the Late Jurassic Western Interior Seaway. Marginal marine environments in the early Kimmeridgian were replaced by alluvial plain deposition as the sea retreated to the northwest. By middle Kimmeridgian time, large fluvial complexes developed in the upstream reaches of the depositional basin, while wetlands and lakes developed where the regional water table discharged in low-lying areas farther downstream in the distal parts of the basin. Terrestrial environments persisted through the late Kimmeridgian, and a large alkaline, saline lake reflects continued high evaporation rates in the basin. The only strata of known Tithonian age are in Montana and reflect the development of extensive coal swamps and marshes at the edge of the Late Jurassic Western Interior

Seaway toward the end of Morrison deposition. Farther south, local fluvial deposits that may be correlative with known Tithonian beds to the north suggest the influx of more detrital sediment from the west and southwest.

Within the overall dry landscape, moisture was available in riparian environments adjacent to the major stream courses, in wetlands, in lakes and ponds, and more regionally during seasonal precipitation in the basin. Paleosols respond as much to water-table levels as precipitation (Parrish et al., this volume), and, because the climate did not change appreciably, changes in paleosol types through time probably reflect changes in depth to the water table. Evidence for seasonality is most apparent in unionids from the middle Kimmeridgian (Good, this volume). Lack of seasonal growth bands in early Kimmeridgian unionids (Good, this volume) probably reflects equable conditions caused by a high water table adjacent to the seaway, which reached its farthest extent southward at this time and provided the moderating influence of a coastal environment. Weakly developed growth banding in late Kimmeridgian unionids may be related to a higher regional water table. Changes in paleosols through time parallel the patterns of the unionids. Paleosols show evidence for drier soil moisture conditions in the middle Kimmeridgian than for both the early and late Kimmeridgian. Those in middle Kimmeridgian strata are better drained than those in either lower or upper Kimmeridgian strata, which exhibit weakly developed paleosols (Demko et al., this volume). The unionids and paleosols probably were influenced mostly by the position of the water table through time, as the climate and evaporation rates apparently remained similar throughout the Kimmeridgian. The water table is thus inferred to have been lower in the middle Kimmeridgian and higher in the early and late Kimmeridgian.

The Morrison landscape has been likened to that of a savannah (Parrish et al., this volume). Riparian environments, especially those associated with perennial streams, were among the lushest parts of the ecosystem and probably consistently supported a larger biotic community than elsewhere in the ecosystem. A gallery of conifer trees provided shade for an understory and groundcover of cycads, ginkgophytes, tree ferns, horsetails, and a variety of ferns. Life was fairly abundant in this ribbon-like oasis that wended its way across the alluvial plain. Beneath the "losing" streams that characterized the upper part of the alluvial plain, the water table probably was raised to a shallower level than the regional water table. In addition, flood events and seasonal variations in flow contributed to a fluctuating water table, creating habitats where life forms such as crayfish and termites could flourish (Hasiotis, this volume).

Equable conditions also existed in wetlands and lakes that formed in low-lying areas in the distal parts of the basin where the water table discharged, and in long-term lakes and ponds elsewhere in the depositional basin where the floodplain also intersected the water table. In the distal wetlands and lakes, food and water probably were available year round, making these distal water bodies excellent refugia. Elsewhere on the floodplain, resources to sustain life may have been only seasonally available due to seasonally restricted precipitation, but may have had high net productivity during the rainy season, as in modern grasslands (Parrish et al., this volume). Eolian and alkaline, saline wetland/lake environments were inhospitable to most life forms.

The streams and wetlands, as well as freshwater lakes and ponds, supported an aquatic fauna of crocodiles, turtles, lungfish, frogs, salamanders, fish, crayfish, bivalves, gastropods, ostracodes, charophytes, sponges, and microbialites (stromatolites). Conchostracans inhabited more ephemeral aquatic environments. A diverse assortment of insects (Hasiotis, this volume) may have been the dominant small herbivores in the ecosystem and most likely were a primary food resource for the small vertebrates (Engelmann et al., this volume). A cursorial fauna that included lizards, the smaller crocodiles, small dinosaurs, sphenodonts, and mammals probably stayed close to the favorable habitats of the riparian and lacustrine environments, but could extend their range depending on their size and water requirements (Engelmann et al., this volume).

In the floodplain environments, a herbaceous groundcover that came to life during seasonal rains may have been a staple in the diet of the giant herbivorous dinosaurs such as *Diplodocus* and *Apatosaurus*. They may have supplemented their diets by grazing charophytes in the wetlands and lakes. This left the coarser vegetation along the stream banks to the other herbivores, such as *Brachiosaurus* and *Camarasaurus*. As in all semi-arid environments, the Morrison ecosystem was vulnerable to extended periods of drought, which accounts for some of the death assemblages of the large vertebrates in the Morrison Formation. Although metabolic and migratory advantages associated with size were adaptive assets in the dry climate (Engelmann et al., this volume), the dinosaurs perished along with other inhabitants of the ecosystem during severe droughts. What is clear, however, is that the giant sauropod herbivores reached their largest body size during Morrison deposition, which suggests that the Morrison ecosystem sustained the most unusual form of life that ever roamed the planet.

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