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Jurassic "savannah"—plant taphonomy and climate of the Morrison Formation (Upper Jurassic, Western USA)

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Abstract

The Morrison Formation contains six plant taphofacies: Wood, whole-leaf, leaf-mat, root, common carbonaceous debris, and rare carbonaceous debris. None of these taphofacies is common in the Morrison; particularly striking is the paucity of wood, even in more reducing environments. The flora of the Morrison Formation is distinct in the Kimmeridgian and Tithonian parts of the section. The plant taphofacies are consistent with a predominantly herbaceous vegetation. Evidence from the plant taphofacies, floras, and sedimentology of the Morrison is consistent with a warm, seasonal, semi-arid climate throughout, changing from dry semi-arid to humid semi-arid from the Kimmeridgian to the Tithonian parts of the formation.
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1. Introduction

The Morrison Formation consists of a suite of dominantly terrestrial deposits of Late Jurassic (Kimmeridgian and Tithonian) age that was laid down in a broad band stretching from northern Arizona and New Mexico into Montana (Fig. 1). Marine and terrestrial sedimentary equivalents are known from an even broader region extending into the Gulf Coast region to the southeast and into Canada to the north. The unit is remarkable for its dinosaur fossils, which are locally abundant throughout the region. For this reason, as well as for its significant uranium resources, the Morrison Formation has been intensively studied for many decades.

Despite the attention paid to it, the Morrison Formation remains controversial with respect to interpretation of the climate under which it was deposited. Much of the controversy derives from differences between interpretation of the flora and interpretation of the sedimentology of the formation. The Morrison and equivalent Upper Jurassic strata in the Western Interior of the United States and Canada have yielded a flora that has considerable value in interpreting the Late Jurassic climate and environment of the region. In a paper reviewing the Morrison flora, Tidwell (1990a) argued that the plants indicate a humid climate that was non-seasonal in the lowlands and seasonal in the uplands. This argument was based on a combination of the diversity of the plants, the climatic tolerances of their nearest living relatives, the occurrence of many Morrison plant taxa in purported

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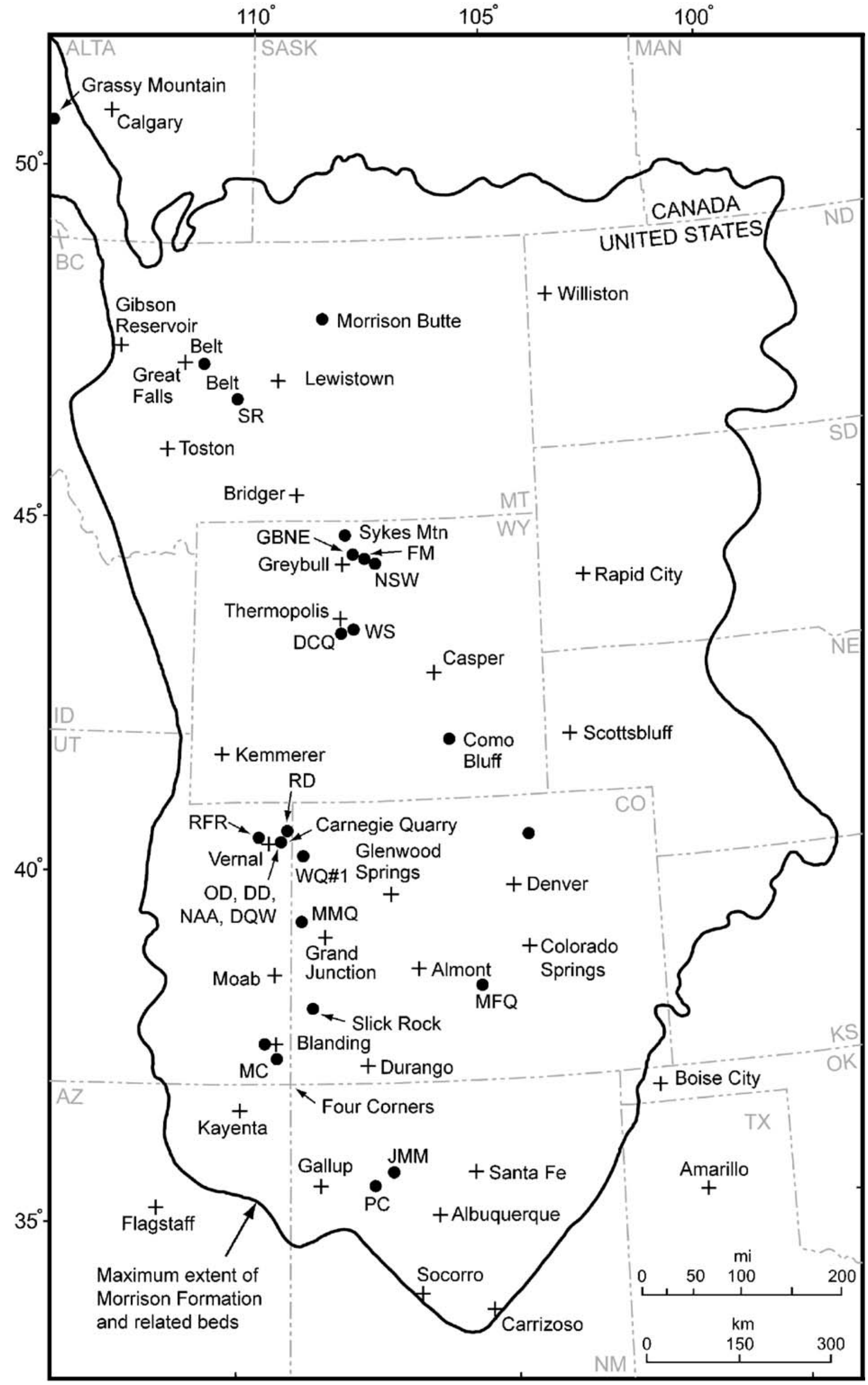

Fig. 1. Map showing the distribution of the Morrison Formation and plant localities examined for this study.

humid-climate floras in other parts of the Jurassic world, the presence of growth rings in some woods and not in others, and the inferred need for abundant vegetation to support the herbivorous dinosaurs. In contrast, the suite of sedimentary rocks in the Morrison is indicative of a climate that was semi-arid or arid. These rocks include fluvial and floodplain deposits that contain calcareous, vertic paleosols (Demko et al., this volume), eolian sandstone, bedded gypsum, and lacustrine deposits that formed in a large, saline–alkaline lake (Turner and Fishman, 1991).

The principal purpose of this paper is to describe and analyze the taphonomy of the Morrison floras and revise taxonomy-based paleoclimatic interpretations of the unit. Although climatic inferences from the taxonomic composition of floras are common in the literature, the method has its pitfalls. Among other problems is the tendency, in using plant taxa, to relate the climatic tolerances of the taxa to the nearest living relatives. This can result in erroneous interpretations, both because of the problems of attributing extinct taxa to modern groups and because of the implicit assumption that the plants have not evolved with respect to their tolerances (Dorf, 1970; Collinson, 1986; Spicer, 1986; Wolfe, 1971, 1993). We demonstrate, as has been demonstrated by many other studies (e.g., Ferguson, 1985; Gastaldo, 1986; Spicer and Greer, 1986; Spicer, 1989, 1991; Demko et al., 1998), that how the plant fossils occur in the depositional environment is at least as important for interpreting the paleoclimatic significance of the flora as the taxonomic composition.

To distinguish biogeographic variability from stratigraphic differences in plant assemblages, it is necessary to know the stratigraphic positions and relative ages of the plant collections from the Morrison Formation and equivalent strata. With recent advances in understanding stratigraphic and age relationships of these rocks, it is now possible to evaluate the paleogeographic and stratigraphic distribution of the plant assemblages in the Morrison Formation and equivalent strata. In this paper, we provide a revised and updated megaflora database. We then use this database to evaluate paleoclimatic interpretations based on taxonomy. These taxonomic interpretations are then used in conjunction with taphonomic considerations to develop a more complete paleoclimatic interpretation for the Morrison. Stratigraphic analysis of plant distributions in the Morrison Formation has not been attempted in the past, partly because of poor understanding of stratigraphic and age relationships and partly because of an assumption by previous workers that plant fossils recovered from the Morrison and equivalent formations in any single geographic area and any stratigraphic position are representative of the flora throughout the entire geographic and stratigraphic extent of the formation. We found this not to be the case.

Understanding the floras requires an understanding of the stratigraphy of the Morrison Formation and its equivalents, so we first discuss the stratigraphy and distribution of the formation itself. Following that, we describe the biogeography of the plants of the Morrison Formation and its equivalents, document the plant taphofacies, and summarize the sedimentologic information that bears on the climate of the Morrison. We conclude with an interpretation of the vegetation and climate of the Morrison Formation.

2. Stratigraphy

The Morrison Formation extends from central New Mexico to Montana, and equivalent strata extend into Canada, where they are assigned different names. The Morrison is best known stratigraphically on the Colorado Plateau, where it contains nine formally named members. The formation is largely undifferentiated farther north and east, although informal members are locally recognized. The Morrison Formation consists largely of strata deposited in terrestrial environments, although it also includes marginal-marine beds at the base of the formation in northern Utah, northern Colorado, and farther north.

For the purposes of understanding the geographic and stratigraphic distribution of the megafloral assemblages, the vertical sequence of members that is present at or near the Four Corners is most helpful. There, the sequence of members, roughly from oldest to youngest, is the Tidwell, Bluff Sandstone, Salt Wash, Recapture, Westwater Canyon, and Brushy Basin Members. These members are all conformable and some grade into others laterally. Most of the megaflora localities of the Colorado Plateau region are in the Salt Wash and Brushy Basin Members. The Salt Wash consists largely of fluvial sandstone complexes, and the Brushy Basin consists largely of lacustrine and overbank floodplain claystone–mudstone beds and scarce channelized fluvial sandstone beds.

An important stratigraphic horizon, called the "clay change", occurs in approximately the middle of the formation in much, but not all, of the depositional basin. The vertical change from dominantly non-smectitic clays below the clay change to dominantly smectitic clays above reflects an abrupt increase in altered volcanic ash in the upper part of the Morrison Formation. On the Colorado Plateau, where it is most readily recognized, the clay change defines the boundary between the lower and upper parts of the Brushy Basin Member. The dominantly non-smectitic (chiefly illite) clays below the marker horizon are non-swelling, whereas the dominantly smectitic clays above the change are swelling clays and weather to rounded slopes that exhibit "popcorn" weathering. This clay change can be recognized easily as far north as north-central Wyoming, but it is not recognized in north-eastern Wyoming, South Dakota, or farther north.

All of the members 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 marine sequence that appears to become 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, Canada (Pocock, 1964, 1972). The Windy Hill, Swift, and Morrissey Formations therefore represent the marine equivalent of a large part of the nonmarine Morrison Formation farther south. The marine parts of the Tidwell Member represent a short transgressive phase in the overall regressive sequence.

In southwestern Canada, nonmarine strata that correlate with the Morrison Formation are included in the Mist Mountain Formation of the Kootenay Group (Gibson, 1985). All of the plant collections from the Kootenay Group that pertain to this study came from the Upper Jurassic part of the Mist Mountain Formation.

3. Age

Palynomorphs indicate that most of the Morrison Formation is Kimmeridgian in age and that the uppermost part of the formation is early Tithonian (Litwin et al., 1998). This is supported by studies of charophytes and ostracodes (Schudack et al., 1998). The formation ranges from 155 Ma at the base to 148 Ma at the top, as determined by single-crystal and plateau ^{40}Ar/^{39}Ar age determinations on sanidine separates from bentonite beds (Kowallis et al., 1998). Because the Jurassic–Cretaceous boundary is currently thought to be at about 141 Ma (Bralower et al., 1990), a significant portion of the later part of the Tithonian Age is not represented in the Morrison.

On the Colorado Plateau, the Morrison Formation is mostly Kimmeridgian in age, although it might contain some Tithonian strata at the top, as suggested by isotopic dates. Age-diagnostic microfossils (palynomorphs, ostracodes, and charophytes) that have been recovered from the lower and middle parts of the formation on the plateau indicate Kimmeridgian ages (Litwin et al., 1998; Schudack et al., 1998). Charophytes and ostracodes of possible Tithonian age have been recovered from high in the formation at Dinosaur National Monument (Schudack et al., 1998), but age-diagnostic fossils have not yet been recovered from the uppermost part of the formation on the Colorado Plateau. The isotopic age of the Kimmeridgian–Tithonian boundary has not been determined accurately for the global standard. However, most recently published time scales would include the youngest date from uppermost Morrison strata on the Colorado Plateau (148.1 Ma, Kowallis et al., 1998) within the Tithonian (Harland et al., 1990; Gradstein et al., 1995; Palfy et al., 2000).

Similarly, the Morrison in southern Montana is largely Kimmeridgian in age; however, carbonaceous beds at the top of the formation in southern Montana have yielded palynomorphs that indicate an early Tithonian age (Litwin et al., 1998). Farther north, Morrison strata in the Little Rocky Mountains of north-central Montana are thought to be slightly younger than the carbonaceous uppermost Morrison of southern Montana, perhaps as young as middle Tithonian. This is supported by palynomorph studies of Pocock (1972) in nearby southern Alberta that indicate a late Kimmeridgian or Tithonian age (his J3^{3} zone) for marine strata of the Swift Formation, which lies directly beneath the Morrison in the Little Rocky Mountains. In Wyoming, a thick interval consisting largely of black carbonaceous mudstone in the uppermost Morrison is inferred to be equivalent in age to the Tithonian carbonaceous beds in Montana based on physical stratigraphy.

Strata in British Columbia and Alberta that correlate with or are slightly younger than the Morrison are dated by palynomorphs (Zieglar and Pocock, 1960; Pocock, 1962, 1964, 1972) and marine fossils (Stott, 1967; MacLeod, 1991; Macleod and Hills, 1991) as Kimmeridgian and Tithonian in age. The position of the Kimmeridgian–Tithonian boundary in Canada is somewhat uncertain, but it appears to be roughly at the contact between the Morrissey and Mist Mountain Formations of the Kootenay Group, judging from the available fossil evidence. Unlike the Morrison Formation farther south, the Canadian strata include uppermost Tithonian beds, based on a continuous sequence of beds from the Jurassic into the Cretaceous parts of the Canadian section and recovery of Tithonian and latest Tithonian fossils from east-central and northern British Columbia, respectively (Zieglar and Pocock, 1960; Macleod and Hills, 1990; MacLeod, 1991).

In southeastern British Columbia and southwestern Alberta, it was once thought that the entire Kootenay Formation of Gussow (1960, now the Kootenay Group) was Late Jurassic in age. Subsequent revision of the age of the Kootenay Group by Gibson (1985) demonstrated that the Jurassic–Cretaceous boundary is low in the Mist Mountain Formation of the Kootenay Group. The Jurassic part of the Mist Mountain Formation most likely is Tithonian in age although the basal beds could, conceivably, be as old as late Kimmeridgian (Pocock, 1972).

The Mist Mountain Formation has yielded the plant material that is of interest to this study. Because we are concerned only with Late Jurassic plant fossils, we recognize that some of the fossils included in earlier studies of the Kootenay flora (Ash and Tidwell, 1998) actually came from the Cretaceous part of the Mist Mountain Formation. Accordingly, we reevaluated the entire Mist Mountain (Kootenay) flora and eliminated those plant fossil collections that came from the Cretaceous part of the formation.

4. Distribution of plants in the Morrison Formation

Paleoclimatic interpretations require both taxonomic and taphonomic analysis of the megaflora. A critical analysis of the existing taxonomic database is important for several reasons. In previous work, paleoclimate interpretations for the Morrison were based on the combined flora from the entire Morrison Formation and equivalent beds in Canada. Thus, no attempt had been made to distinguish stratigraphic and geographic differences among the plant collections. With recent revisions in the stratigraphy and age of both the Morrison and equivalent beds in Canada, it became clear that sorting the taxa stratigraphically and geographically was possible and desirable. Moreover, paleoclimatic interpretations require that differences in the floras through time be distinguished from differences in space in order to fully evaluate the paleoclimatic implications of the flora. Finally, we recognized that some floras included in previous analyses were from rocks that were misidentified as belonging to the Morrison Formation.

4.1. Methods

An important problem concerning plant collections from the Western Interior of the U.S. and Canada is that the geographic and stratigraphic positions of many of the collections are known to be incorrect based on our attempts to locate them in the field (Jensen Quarry, UT, of Ash and Tidwell, 1998) or are poorly known (Grand County, UT, site of Tidwell and Ash, 1990; Potter Basin, CO, and Yellowcat, UT, sites of Ash and Tidwell, 1998)—or in some cases unknown—because the material was received from amateur collectors who did not report the exact locations (Blanding, UT, area of Tidwell et al., 1998; Escalante, UT, area of Ash and Tidwell, 1998; southeastern Utah area of Tidwell and Ash, 1990). The geographic locations of some of the collections, particularly those made in the early 1900s, are so poorly documented that one cannot determine if they actually came from Upper Jurassic strata (Black Hills, WY, site of Ward, 1905; Black Hills, SD, sites of Wieland, 1906; south rim of Bighorn Mountains, WY, site of Wieland, 1906; Boulder, CO, site of Ward, 1900a; Wieland,1906), and in several cases, they are now known to have come from Lower Cretaceous rocks (Black Hills, WY, site of Ward, 1900b; Morrison, CO, site of Knowlton, 1920). Some more recent collections identified as being from Jurassic rocks but actually from Lower Cretaceous strata were obtained by amateur collectors or others who were not familiar with the criteria that help to identify the upper contact of the Morrison Formation. These Cretaceous collections were also excluded.

Recent attempts to compile a comprehensive list of plant collection localities from Upper Jurassic beds (Tidwell, 1990a; Ash and Tidwell, 1998) are helpful but not sufficiently critical to eliminate poorly located collections. Thus, for this study, we undertook a critical review of the quality of the plant database for Morrison taxa. To accomplish this, we completely reexamined the literature and critically analyzed both the geographic locations and the stratigraphic positions of all published collections in an attempt to make the revised fossil plant list as accurate as possible.

The true stratigraphic positions of some collections made by amateur collectors remains in doubt. However, to eliminate all collections made by amateurs would eliminate many of the collections and reduce the list of Morrison plants from the Colorado Plateau to a mere handful. Accordingly, we decided to accept those collections that appear to have been obtained from the Morrison according to information available in the literature and/or personal communication with W.D. Tidwell (written commununication, 1998) and to reject those collections that are poorly located.

4.2. Results

The result of our critical evaluation of the literature is a revised list of Late Jurassic megaflora fossils from the Western Interior (Table 1). A detailed list of the collections with pertinent information about their locations, fossils, literature citations, and other notes will be presented in a web site.

4.2.1. Stratigraphic occurrence of megaflora

The majority of collections reported in the literature have come from a few stratigraphic intervals in the Morrison and equivalent strata. Most of the plant collections in the southern and central parts of the Western Interior (New Mexico to Wyoming) came from above the clay change, either in the upper part of the Brushy Basin Member or in correlative strata farther north in Wyoming, where the clay change is still identifiable but where formally named members are not recognized. The plant localities in the Brushy Basin occur in the smectitic interval of the upper part of the Brushy Basin Member, although not in the uppermost beds of that unit. Several collections came from the Salt Wash Member and one collection came from the Tidwell Member. All of the collections from the Colorado Plateau and Wyoming area are considered Kimmeridgian in age.

The megaflora collections in Montana are from the uppermost beds of the Morrison Formation in strata that are Tithonian in age and are younger than any of the collections farther south. Similarly, in Canada, the flora was recovered from strata that are equivalent to the uppermost Morrison beds in Montana or slightly younger Jurassic beds and are all Tithonian in age. It is important to note that many of the Canadian plant localities in the earlier compilations of Late Jurassic megaflora had to be eliminated in the revised compilation (Table 1) because of revisions in the age of the Kootenay Group in Canada.

4.2.2. Comparison of Kimmeridgian and Tithonian megafloral assemblages

In order to compare the Kimmeridgian and Tithonian floras, we limited our counts to leaves to avoid duplication, since different organs from the same plant usually have different taxonomic names; the one exception was *Equisetites*, which we did include, even though it commonly is found only as stems. Our list of megaflora for the Morrison Formation and equivalent strata (Table 1) shows 11 leaf form genera (12 form species) from Kimmeridgian strata and 21 leaf form genera (35 form species) from Tithonian strata. Of these leaf form taxa, only seven genera are common to both intervals, and most of these are different species (only two form species are shared).

Notwithstanding these differences, some similarities exist between the older and younger parts of the Morrison Formation. Most striking is the presence of *Classopollis* in Kimmeridgian beds of the Morrison Formation and also in Tithonian beds in Canada (Pocock and Jansonius, 1961; *Corallina* of Litwin et al., 1998). *Classopollis* is known to be the pollen of conifers of the family Cheirolepidiaceae (Alvin et al., 1978, 1981), to which the leaf form, *Brachyphyllum*, which occurs in the Kimmeridgian part of the Morrison, also belongs (Alvin, 1982; Tidwell, 1990a). Another significant similarity between the two intervals is the presence of *Czekanowskia* leaf mats. These similarities are important for the interpretation of the climate of the Morrison Formation, and will be discussed in that section at the end of the paper.

Table 1
Kimmeridgian and Tithonian leaf taxa from the Morrison Formation and its equivalents[a]

TAXA	Kimmeridgian	Tithonian
Bryophyta		
Thallites(?) sp.	X[1]	
Marchantites sp.		X[2]
Sphenophyta		
Equisetum sp.	X	
E. cf. *E. burchardtii*	X[1]	
E. laterale		X[2]
E. lyelli		X[4b]
Filicophyta (Ferns and Fern Allies)		
Hausmannia fisheri		X[2]
Coniopteris brevifolia		X[2b]
C. hymenophylloides	X[1]	X[3]
Adiantites montanensis		X[2]
Cladophlebis alberta		X[2]
C. heterophylla		X[3]
C. virginiensis		X[3]
Sphenopteris cordai		X[2b]
S. latiloba		X[3b]
Pteridospermophyta (Seed Ferns)		
Sagenopteris elliptica		X[2]
Cycadophyta		
Nilssonia sp.		X
N. cf. *N. compta*		X[2]
N. parvula		X[4b]
N. schaumburgensis	X[1]	X[4b]
N. tenuicaulis		X[4b]
Zamites arcticus		X[2]
Otozamites sp.	X[1]	
Cycadolepis sp. A (of Brown, 1972)		X[2]
Cycadolepis sp. B (of Brown, 1972)		X[4]
Cycadolepis sp. C (of Brown, 1972)		X[4]
Cycadolepis(?) sp.	X[1]	
Weltrichia(?) sp.		X[2]
Ptilophyllum arcticum		X[2b]
P. (*Anomozamites*) *montanense*		X[4b]
Pterophyllum bellii		X[2b]
Ginkgophyta		
Baiera cf. *B. furcata*		X[2b]
Ginkgoites cascadensis		X[2]
Ginkgo sp.	X	
Ginkgo(?) sp.	X[1]	
G. pluripartita		X[2]
G. huttoni		X[4b]
Czekanowskia sp.	X	X
C. turneri	X[1]	
C. cf. *C. rigida*		X[2b]
Coniferophyta		
Cupressinocladus(?) sp.	X[1]	
Coniferophyta		
Podozamites sp.		X
P. corbinensis		X[2b]
P. lanceolatus		X[4]
Pityophyllum lindstromi		X[2]
P. nordenskiöldii		X[4]
Brachyphyllum sp.	X	
Brachyphyllum sp. A (of Tidwell et al., 1998)	X[1]	
B. rechtenii	X[3]	
Pagiophyllum sp.	X[1]	X[2]

[1] and [2] indicate listings counted as 1 genus and 1 species in the Kimmeridgian and Tithonian, respectively. [3] and [4] indicate listings counted as one species in the Kimmeridgian and Tithonian, respectively (genus already counted).

[a] Leaf taxa only; full taxonomic list available from authors. Data from Arnold (1962); Ash (1994); Ash and Tidwell (1998); Bass (1964); Bell (1956); Brown (1972, 1975); Chandler (1966); Delevoryas (1960); B. Dower, personal communication; Knechtel (1959); Knowlton (1907); LaPasha (1984, and oral commununication, 1998); MacLeod (1991); Medlyn and Tidwell (1975a,b 1979, 1992); Tidwell (1990a,b, 1994); Tidwell and Ash (1990); Tidwell et al. (1998); Tidwell and Medlyn (1992, 1993); Tidwell and Rushforth (1970); and Ward (1900a). Does not include plant fossils listed as "Yet to be published" by Ash and Tidwell (1998). The numbers in superscript indicate how the taxa were counted for Kimmeridgian and Tithonian taxonomic diversity (see text).

[b] Indicates taxa reported only in Morrison equivalents in Canada.

Some of the differences in the floras are undoubtedly stratigraphic, particularly at the species level. However, a climatic difference is also suggested by some of the genera. *Podozamites* and *Pityophyllum*, for example, tend to be humid-climate genera during the Jurassic and Cretaceous (Macleod and Hills, 1991; see Discussion). A higher diversity of fern taxa, as occurs in the Tithonian flora, is also suggestive of a wetter and/or cooler climate or higher water tables.

5. Plant taphonomy of the Morrison Formation

5.1. Methods

In July and September 1998 and August 1999, we visited 22 localities of the Morrison Formation in Utah, New Mexico, Colorado, Wyoming, and Montana that were known or reported to bear plant remains

(Fig. 1). Our sampling in the Morrison Formation was intentionally biased toward finding plant remains; no attempt was made to do representative sampling of the unit as a whole. The reason for this is that the Morrison Formation covers an enormous area, and plant fossils—even carbonaceous debris—are rare in the context of the entire unit. The many years of work on the Morrison Formation, including scores of detailed measured sections and previous searches for carbonaceous, pollen-bearing beds are likely to have revealed many of the potential plant localities. Thus, we regard our samples as representative of plant occurrences in the Morrison.

Where necessary, trenches were dug both vertically and laterally to provide the freshest surfaces possible and to provide samples of lateral variation, if any, in the taphofacies. In addition, at some sites, multiple trenches were dug along strike to provide a larger view of lateral variation. Hand samples were collected of representative occurrences of plants and carbonaceous debris and examined with a binocular microscope.

Based on field observations, the occurrences of plant material were divided into taphofacies using the methods of Behrensmeyer (1991) and Demko (1995). The taphofacies are listed in Table 2, along with the lithologies in which each characteristically occurs,

Table 2
Taphofacies in the southern portion of the Morrison Formation

Taphofacies	Description	Lithology	Associated features	Localities
Wc	coalified wood	claystone to pebbly sandstone	laminated or massive	DNM-NAA, GBNE, *WQ#1*, *RFR*, *MC*, *PC*, *FM*, **B1**, **WS**
Ws	silicified wood	siltstone to pebbly sandstone	cross beds	DNM-DD, *WQ#1*, *DNM-RD*, *PC*, *DCQ*
Wch	charcoal, abraded	siltstone	cross beds, low-flow-regime parallel lamination	DNM-DQW, *MC*, *FM*, *NSW*
Wi	wood impressions	sandstone	overbank, low-flow-regime parallel lamination, massive	*DCQ*
LM	leaf mats	claystone to very fine sandstone	laminated	MC, JM, **B1**, **SR**, **WS**
LW	macerated plant debris, occasional identifiable fragments of leaves	claystone to fine sandstone	low-flow-regime parallel lamination, massive, or laminated; sometimes associated with rootlets and peds	DNM-DQW, *DNM-OD*, *MC*, *DCQ*, **B1**, **B2**, **SR**, **WS**
R	rootlets or rhizomes	claystone to siltstone	root mottled, massive, or faintly laminated	GBNE, *MC*, *MMQ*, *MFQ*, **B1**, **SR**
UCC	macerated, degraded plant debris, common to abundant (10–90% grain density), no identifiable plant remains	siltstone to very fine sandstone	massive	*MMQ*, *MC*, *NSW*
UCR	macerated, degraded plant debris, rare (< 10% grain density), no identifiable plant remains	silty claystone to sandstone	massive, bioturbated, laminated	GBNE, *RFR*, *MFQ*, *FM*, *NSW*, WS

Abbreviations of localities: DNM, Dinosaur National Monument, UT (all sites were in Utah): DD, Douglass Draw; OD, Orchid Draw; DQW, Dinosaur Quarry section; NAA, Not-an-allosaur site; RD, Rainbow Draw. MC, Montezuma Creek, UT: RFR, Red Fleet Reservoir, Vernal, UT; MMQ, Mygatt–Moore Quarry, CO; WQ#1, Witherell Quarry #1, CO; MFQ, Marsh Felch Quarry, Cañon City, CO; PC, Poison Canyon Mine, NM; JM, Johnny M Mine, NM; WS, near Warm Springs oil field, Thermopolis, WY; DCQ, Dinosaur Center Quarry, Thermopolis, WY; GBNE, northeast of Greybull, WY; FM, Fox Mountain, WY; NSW, North Sheldon Wash, WY; B1, Belt, MT; B2, Belt, MT; SR, Scholtztown Ranch, MT. Locality abbreviations in normal type are from the Salt Wash Member and its equivalents, in italics from the Brushy Basin Member and its equivalents, and in bold from Tithonian or presumed Tithonian rocks (see text for further explanation).

associated features, and the localities at which the taphofacies were observed.

5.2. Results

We identified six taphofacies for plant remains in the Morrison Formation. All were in the Brushy Basin and Salt Wash members of the Morrison of the Colorado Plateau and the undivided Morrison Formation in Wyoming and Montana (Fig. 1; Table 2). These localities are projected onto the stratigraphic section roughly parallel to latitude. All but one of the taphofacies are illustrated in Figs. 2–6. The specimens illustrated are predominately from the Montezuma Creek locality because the contrast between the plant material and matrix is greatest there, making them easiest to photograph.

5.2.1. Taphofacies W

Taphofacies W consists of small pieces of wood in high concentrations or isolated large pieces of wood. We divide this taphofacies into four groups, consisting of coalified wood (taphofacies Wc), charcoal (taphofacies Wch), silicified wood (taphofacies Ws), and wood impressions (taphofacies Wi). Coalified wood (Wc) is the most prevalent. Coalified wood occurs in claystone, siltstone, sandstone, or pebbly sandstone and in rocks that are laminated or massive. Charcoal (Wch; Fig. 2) is found in siltstone or sandstone with small-scale cross beds or low-flow-regime parallel lamination, commonly in very high concentrations, on partings parallel to bedding in grain densities as high as 90%. In this taphofacies, and in other taphofacies in which charcoal fragments are scattered, the fragments are subrounded to well rounded by abrasion during transport. The sizes of the wood fragments in Wc and Wch tend to correlate, ranging from < 1 cm in the finer sandstone to >10 cm in the coarsest ones, but most wood fragments are smaller than 5 cm in length. The environments of deposition for both Wc and Wch were lacustrine or fluvial, close to the lake margin based on associated facies both laterally and vertically.

5.2.2. Taphofacies (Ws)

Silicified wood of taphofacies (Ws), although sometimes found in beds as fine grained as siltstone, more commonly occurs in sandstone to pebbly sandstone that is usually crossbedded. The environments of deposition were fluvial, although one poorly silicified specimen was found in siltstone that was likely deposited in a channel cut-off. The sizes of the wood specimens in the Ws taphofacies ranged from 8 to 10 cm to more than a meter in length. Only one sample, which occurred in a pebbly sandstone in Rainbow Draw, showed evidence of abrasion, probably after petrifaction, based on the relationship of the abraded surfaces to silicified tissue that showed evidence of pre-petrifaction decay. No other specimens from the same bed showed evidence of abrasion.

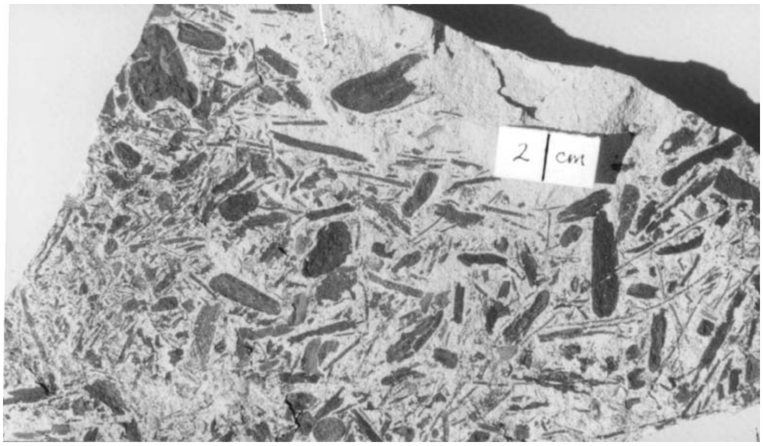

Fig. 2. Taphofacies Wch from Montezuma Creek, UT. The large, rounded pieces and the thicker elongated pieces are charcoalified wood. The charcoalified wood is mixed in this specimen with linear plant compressions, probably fragments of *Czekanowskia turneri* leaves.

5.2.3. Taphofacies LM

This taphofacies consists of leaf mats. These are dense accumulations of whole leaves or large fragments of leaves that cover bedding planes, usually several bedding planes within several decimeters of section. The taphofacies was observed at five localities. One was in a clinoptilolite-rich mudstone in the Brushy Basin Member at Montezuma Creek, Utah, and the leaves were exclusively those of *Czekanowskia* (Ash, 1994; Fig. 3). We found no evidence of fragmentation of the leaves. Some of the leaves could be traced for more than 20 cm along a bedding plane. All terminuses were where the sample was truncated. The second LM occurrence was in several horizons in claystone or siltstone near Belt, MT. These horizons consisted of dense mats of small, strap-like leaves, probably *Czekanowskia*, which has been identified at that locality by B.L. Dower (personal communication). One bed consisted of cuticle, and the accumulation was so dense that it was impossible to segregate or trace individual leaves. At "Scholtztown" Ranch, southwest of Windham, MT, the LM facies consists of similar strap-like leaves and small cycadophyte rachises, possibly *Ptilophyllum*. Based on a single sample, we also identified this taphofacies in a mud drape on sandstone from the Johnny M Mine in New Mexico; these leaves also appeared to be *Czekanowskia*, which is known from that locality (Ash, 1994). The fifth occurrence was from presumed Tithonian beds near the Warm Springs oil field near Thermopolis, WY. This occurrence was in claystone in which one interval approximately 5 cm thick contained dense mats of small, strap-like leaves; these were identical to *Czekanowskia*, although that genus has not been reported previously from Wyoming.

The LM taphofacies occurs in claystone to very fine-grained sandstone. At each locality, the environment of deposition was a lake margin.

5.2.4. Taphofacies LW

Taphofacies LW consists of degraded and/or macerated plant material (carbonaceous debris) with occasional identifiable parts of leaves or stems. Most of the Morrison plant taxa are found in this taphofacies, including several genera of ferns (Fig. 4), cycads, ginkgoes, the conifer *Brachyphyllum*, and the horsetail *Equisetites*.

Taphofacies LW occurs in claystone to fine-grained sandstone. The beds are massive or laminated, with low-flow-regime parallel laminations in the coarser beds. Taphofacies LW may be associated with rootlets and weakly developed peds (paleosol textures). The

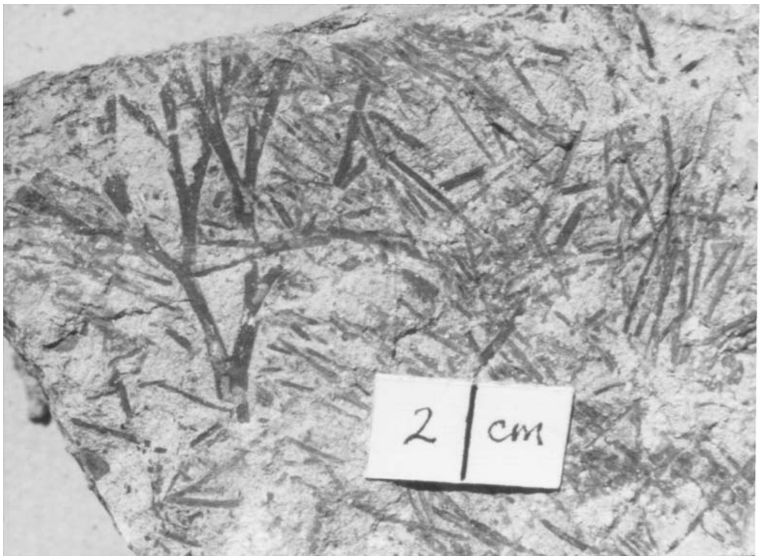

Fig. 3. Taphofacies LM from Montezuma Creek, UT. The leaves are *Czekanowskia turneri*. This is a relatively less dense leaf mat; the more typical mats are much denser and photograph poorly.

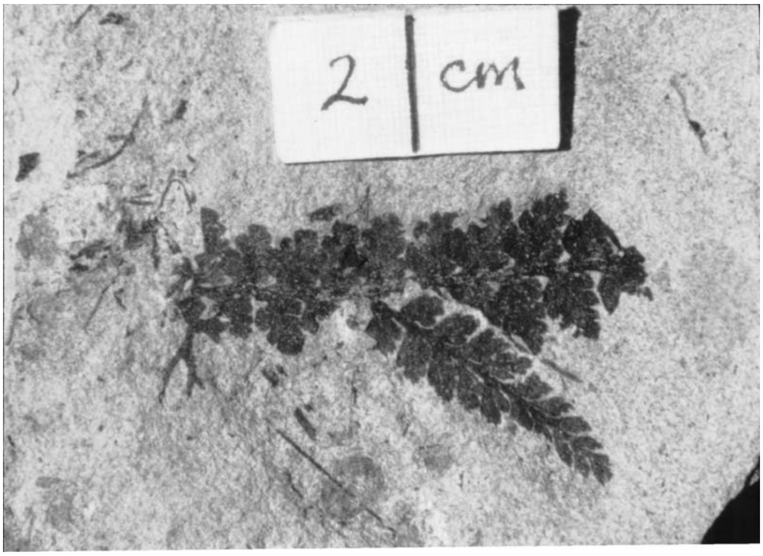

Fig. 4. Taphofacies LW from Montezuma Creek, UT. Fragment of fern leaf and unidentifiable small fragments of plant material.

environments of deposition are mostly lake margin. However, at Belt, MT, the taphofacies occurs not only in lake-margin sediments but also in a distal crevasse-splay siltstone, where it forms a monospecific assemblage of *Nilssonia*. At DQW in Dinosaur National Monument, an assemblage of *Czekanowskia* fragments (Ash, 1994) forms this taphofacies in a fluvial sandstone.

5.2.5. Taphofacies R

Taphofacies R consists of rootlets and/or rhizomes (Fig. 5). The preserved rootlets are usually very small, $\ll$1 mm in diameter and $<$2 cm long, usually considerably shorter. This taphofacies occurs in massive, faintly laminated, or root mottled claystone to siltstone deposited in marsh or lake-margin environments or in palustrine and, more rarely, lacustrine limestone (Dunagan, 1998, 2000). Root traces in the latter environments are occasionally >2 cm long and thicker than 1 mm.

5.2.6. Taphofacies UCC

Taphofacies UCC consists of macerated and/or degraded plant material (carbonaceous debris) that is

Fig. 5. Taphofacies R from Belt, MT.

common to abundant, that is, in grain densities ranging from 10% to 90%, although usually less than 60% (Fig. 6). Unlike taphofacies LW, taphofacies UCC contains no identifiable plant remains, with the exception of fragmented and decayed cuticular material that is most likely individual, scale-like leaves of *Brachyphyllum*. This taphofacies occurs in massive siltstone to very fine-grained sandstone and is probably the most common taphofacies in the Morrison, although we documented more localities of taphofacies LW because of our sampling strategy. The environments of deposition most likely were at lake margins.

5.2.7. Taphofacies UCR

Taphofacies UCR consists of rare macerated and/or degraded carbonaceous debris in grain densities less than 10%. No identifiable plant remains occur in this taphofacies. UCR occurs in massive or bioturbated siltstone to sandstone in lacustrine sediments, possibly well away from the shoreline, although this could not be documented with certainty. This taphofacies is also relatively common in the Morrison Formation.

Short shoots occur as replacements by calcite, silica, or iron oxide in localities near Cañon City, CO, and, according to the literature, near Greybull, WY. We attempted to characterize this taphofacies near Cañon City, but were unsuccessful because the remains were found in rock, apparently mudstone, that was reworked by slumping. We do not treat this possible taphofacies here, but future work may reveal the need to establish it as an additional taphofacies.

5.3. Discussion of taphofacies

The most important observation about the distribution of taphofacies in the Morrison Formation is the paucity of plant remains of any kind, especially in the Kimmeridgian part of the formation. Very few beds in the Kimmeridgian part contain carbonaceous debris or horizons with obvious bioturbation by roots. In contrast, strata containing carbonaceous debris or plant remains are commonly found in the Tithonian part of the Morrison in Montana and are fairly common in equivalent beds in Wyoming. Thus, the overall taphonomy of the Morrison flora, like the taxonomic composition, differs between the two parts of the formation. In the following sections, we discuss the Kimmeridgian and Tithonian intervals separately.

5.3.1. Kimmeridgian

Most beds in the Kimmeridgian part of the Morrison Formation, even in the finer-grained facies, are barren of even the smallest fragments of carbonaceous debris. The possible explanations for this are (1) complete mechanical degradation of plant material in most environments, (2) complete oxidation of plant

Fig. 6. Taphofacies UCC from Montezuma Creek, UT. Although plant debris is abundant it is macerated, degraded, and unidentifiable.

material in most environments, and/or (3) a depauperate source of plant material in most environments.

Mechanical degradation must have been important in the channels represented by the Salt Wash Member sandstones and conglomerates, which is where the Ws facies is well developed. However, this explanation applies only to the fluvial-channel sediments. Mechanical degradation by bioturbators is possible in the finer-grained sediments, which is probably the case for the UCR taphofacies. Mechanical degradation by bioturbation or current action may also have played a role at the Mygatt–Moore Dinosaur Quarry and at the Dinosaur Center Quarry (Fig. 1). The carbonaceous debris in those rocks is commonly randomly oriented both vertically and horizontally, consistent with deposition from turbulent flow.

The sheer volume of fine-grained rock that contains no carbonaceous debris, combined with the color of much of the Kimmeridgian rock, suggests that oxidation played a major role in destroying carbonaceous material. Most rocks from the Morrison in this interval are light in color, predominately light greenish gray, light to medium gray, red, tan, or purple. Dark gray rocks are rare. However, even those more reducing lithofacies contain very little plant material.

Where identifiable plant material is preserved, it is usually as isolated fragments of leaves or shoots or more robust organs such as petrified short shoots, seeds, and wood (e.g., Tidwell et al., 1998). Although the shoots of *Brachyphyllum* are robust enough to have been transported short distances, most of the other leaf taxa are delicate and must be parautochthonous. The fact that most remains are isolated occurrences suggests that, even when conditions were favorable for preservation, few plants were preserved. This, in turn, suggests that the vegetation was not particularly dense or large-statured in most places. This is supported by the very small dimensions of the roots and rhizomes in the R taphofacies; evidence for deep rooting or large roots is rare in the Morrison Formation (Hasiotis and Demko, 1998).

The leaf mats of *Czekanowskia* are the one exception to the general scarcity of plant occurrences. That the leaf mats are monospecific and limited to narrow intervals suggests an ecology for this plant that is different from the other plants in the region, as suggested in the section later in this report on the distribution of the megaflora.

5.3.2. Tithonian

The sedimentologic and plant taphonomic environment in the Tithonian beds of central Montana was very different from that of the Kimmeridgian. The Tithonian-age rocks tend to be gray and brown, whereas the red, green, and light brown colors that characterize the Morrison elsewhere are lacking. This part of the formation also contains thin, high-ash, high-sulfur coal beds (Calvert, 1909; Fisher, 1909)[1] that were mined mostly between 1885 and 1955 (Silverman and Harris, 1967). The sedimentologic evidence indicates that the Morrison in central Montana was deposited in mires and associated rivers, floodplains, and lakes.

The taphonomy of the plants in this region is consistent with other coal-bearing units such as, for example, the Cretaceous Kogosukruk Tongue of the Prince Creek Formation in Alaska, which also contains thin coals. The Kogosukruk Tongue contains abundant carbonaceous debris with some leaf mats (Spicer and Parrish, 1987; Parrish and Spicer, 1988), similar in distribution to the taphofacies of the Morrison Formation near Belt, MT. A striking contrast with the Kogosukruk Tongue, however, is the lack of wood. Although the Wc taphofacies is present in Montana, it is rare and the wood fragments are small, < 12 cm long. The coal beds contain little vitrinite, based on field observations, indicating that the mire community was also depauperate in woody plants. This contrasts markedly with the Kogosukruk coals, which have abundant vitrinite (J.T. Parrish, personal observations, 1986).

Dark brown or gray mudstones at the top of the Morrison in some locations in Wyoming (near Warm Springs oil field east of Thermopolis and in the vicinity of Greybull) are presumed to be Tithonian in age on the basis of lithostratigraphic correlations with the Morrison Formation in Montana. These include the LM-, LW-, and Wc-bearing beds near the Warm Spring oil field near Thermopolis (Table 2). The mudstones were deposited in lakes and lake margins, but the site near Warm Springs is the only

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[1] Ash and sulfur contents from the coals at Lewiston, Montana, are 13.0% (average), range 8.1–22.5% and 4.46% (average), range 1.82–9.57%, respectively (Calvert, 1909) and from Great Falls, Montana, 18.0% (average), range 14.2–22.3% and 3.16% (average), range 1.71–4.46%, respectively (Fisher, 1909).

one with significant plant remains. Otherwise, the taphofacies in the presumed Tithonian part of the Morrison of Wyoming is limited to UCR.

The LW taphofacies is more common stratigraphically in the Tithonian than in the Kimmeridgian parts of the Morrison. In addition, the density of identifiable leaf remains on bedding planes is higher, quantified as common or abundant in most samples versus rare in most samples from the Kimmeridgian (leaf mats were quantified as "superabundant" in bedding-plane density, covering more than 90% of the bedding-plane surface).

The R taphofacies is also more common stratigraphically in the Morrison Formation in Montana compared with the other areas studied. Interestingly, however, the rootlets and rhizomes in Montana are the same small size as in the rocks elsewhere in the Morrison. This is consistent with the paucity of wood and the low vitrinite content of the coals in Montana.

6. Climate and vegetation of the Morrison Formation

Interpretations of the climate of the Morrison Formation must be able to explain all the data that provide information on paleoclimates (Parrish, 1998), including sedimentological, paleobotanical, taphonomic, and geochemical information. In this paper we concentrate on the plants and plant taphonomy, but in this section, we also refer to relevant information from climate-model results from the sedimentologic and geochemical record.

6.1. Climate-model results

Late Jurassic global circulation models have been produced by Valdes (1993). The model results show a Late Jurassic mean summer temperature difference of about 10 °C between southern Utah and western Montana and a mean winter difference of 14 °C. This is the opposite of the present situation, in which the summer gradient is higher (mean summer temperature difference 17 °C, mean winter temperature difference 9 °C). In addition, the model results indicate higher temperatures overall than today. The higher temperatures are consistent with the significantly higher CO_2 content of the atmosphere during the Jurassic as compared to the present (Ekart et al., 1999). This means that evaporation could have been significant year round, rather than only in the summer. According to the model, precipitation probably was low throughout the region in summer and had a gradient from < 1 mm/day in southern Utah to >2 mm/day in western Montana in the winter. Valdes (1993) did not provide model results for soil moisture, but soil moisture was shown by Valdes and Sellwood (1992). Soil moisture, which is a measure of the precipitation–evaporation balance, was higher in the winter in the region of Montana according to the model by Valdes and Sellwood (1992). This is consistent with the later model results (Valdes, 1993). In general, the models suggest a semi-arid climate in the Western Interior with a lower latitudinal temperature gradient than today and slightly wetter conditions to the north, probably because of lower temperatures and, thus, lower evaporation rates.

Rees et al. (1999) modeled Late Jurassic climates, specifically for the purpose of predicting biomes. Their models suggest a winterwet biome, similar to that now found in central California, central Chile, or southwestern Europe, for the Colorado Plateau region. Today, such biomes include grasslands, shrubs, and small-statured trees that favor wetter areas close to the water table. Because climate overall was warmer in the Late Jurassic than it is today, it is likely that the vegetation in a winterwet climate was more xerophytic (adapted for dry conditions) than the equivalent flora today. The biome modeled by Rees et al. (1999) for the region that has the northernmost extent of the Morrison Formation and its equivalents in Canada was warm temperate.

6.2. Sedimentology and geochemistry

In the Morrison Formation of the Colorado Plateau, early Kimmeridgian deposition is represented by the Tidwell, Bluff Sandstone, Salt Wash, and lower Recapture Members and their correlatives (Peterson, 1994). The Bluff consists of eolian sandstone that was deposited around the Four Corners area and is largely contemporaneous with another extensive eolian sandstone unit in the lower part of the Recapture Member farther south, in northwestern New Mexico (Peterson, 1994). In addition, other eolian sandstone deposits of similar age occur in the lower Morrison as far north as north-central Wyoming and western South Dakota. Most of these are relatively small eolian sandstone bodies, but eolian sandstone deposits of the Unkpapa Sandstone Member of the Morrison Formation extend along the entire east side of the Black Hills, SD, and an unknown distance farther east in the subsurface (Peterson, 1988).

The Tidwell Member consists of red or gray mudstone, buff-colored sandstone and, in places, thick beds of gypsum. The Tidwell was deposited in terrestrial environments and marginal-marine embayments of the Late Jurassic Western Interior seaway, which retreated to the north during deposition of the lower part of the Morrison Formation (O'Sullivan, 1992; Peterson, 1994).

The Salt Wash Member consists primarily of braidplain deposits. The Bluff Sandstone Member consists largely of eolian sandstone. The sand of the Bluff was derived from the Salt Wash braidplain during times when the streams went dry (Peterson, 1994).

Paleosols in the Tidwell and Salt Wash members are Aridisols and gypsic Entisols (Demko et al., this volume). These paleosols, the eolian sandstones, and the bedded gypsum are all consistent with dry climates. The presence of fluvial strata and pond or small lake deposits in parts of the Salt Wash, along with Calcisols and argillic Calcisols, suggests at least seasonal influx of rainfall or places where the land surface intersected the water table (Demko et al., this volume).

The Brushy Basin Member overlies the Salt Wash and consists primarily of mudstone with intercalated sparse, small, ribbon sandstone beds deposited by low-gradient streams. The member contains lacustrine rocks and weakly to strongly developed vertic and argillic Calcisols (Demko et al., this volume). On the east side of the Colorado Plateau, the upper part of the Brushy Basin was deposited in a broad saline–alkaline lake with characteristic zonation of authigenic minerals, including zeolites (Lake T'oo'dichi'; Turner and Fishman, 1991; Dunagan and Turner, this volume).

North and east of the Colorado Plateau, other lacustrine deposits occur throughout most of the Morrison Formation (including the Ralston Creek Formation in the foothills west of Denver; see Peterson and Turner, 1998) and consist of calcareous mudstone and/or limestone (Dunagan, 1998) with charophytes and ostracodes (Schudack et al., 1998), pulmonate and prosobranch gastropods (Evanoff et al., 1998), freshwater sponges (Dunagan, 1999), unionid bivalves (Evanoff et al., 1998), and stromatolites (Neuhauser et al., 1987; Dunagan and Turner, this volume), all of which indicate freshwater lakes. These freshwater lacustrine deposits are approximately equivalent to the Tidwell, Salt Wash, and Brushy Basin Members on the Colorado Plateau.

Evaporation rates must have been high during deposition of the upper part of the Brushy Basin Member, at least in the southern part of the Western Interior, to create the conditions for a saline–alkaline lake to form. The lack of a geochemical signature consistent with high salinity and alkalinity farther north and east probably reflects slightly lower evaporation rates and/or a slightly higher influx of freshwater there. However, this difference may have been quite small, as evidence exists for periodic freshening of the saline–alkaline lake and palustrine limestones in east-central Colorado have been reported to contain minor evaporites and Magadi-type cherts (Dunagan, 1998).

The large saline–alkaline lake, known as Lake T'oo'dichi', was surrounded by low uplifts that included the ancestral Uncompahgre uplift to the north and east, the Nacimiento uplift to the southeast, the Zuni uplift to the south, and the Defiance and Monument uplifts to the west. The hydrologically and hydrographically closed basin between these uplifts, along with the rain shadow that resulted in high evaporation rates and the influx of large quantities of volcanic ash, produced ideal conditions for the lake to form.

Paleosols in the lower part of the Brushy Basin Member, particularly in the southern and western portions of the Western Interior, are weakly to well-developed vertic and argillic Calcisols (Demko et al., this volume). In contrast, paleosols in the upper part of the member, particularly in the northern and eastern portions of the Western Interior and correlative rocks in Wyoming and Montana, are weakly developed Entisols and Calcisols (Demko et al., this volume). This difference is consistent with a slightly greater supply of moisture, either through higher groundwater levels, lower evaporation rates, and/or higher precipitation rates during deposition of the upper part of the Brushy Basin Member and correlative rocks elsewhere (Demko et al., this volume). Given that Lake T'oo'dichi', which is in the upper part of the Brushy Basin Member, has a mineral assemblage consistent with high evapotranspiration rates, the explanation of higher groundwater levels is the most likely.

Oxygen isotope geochemistry of lacustrine carbonates and ostracodes from the Morrison Formation shows a small gradient from south to north (D.D. Ekart, written communication, 1998; Schudack, 1999). $\delta^{18}O$ throughout the region is unusually light and indicates a rain shadow extending along the western margin of Morrison deposition and a rainout effect as the air masses were carried eastward by westerly winds (D.D. Ekart, written communication, 1998; Schudack, 1999). The gradient in $\delta^{18}O$ from south to north is consistent with a temperature gradient with slightly lower temperatures to the north (D.D. Ekart, written communication, 1998; Schudack, 1999). Lower temperatures would result in lower evaporation rates, which could account for the lack of saline–alkaline lake deposits in the northern portion of the Morrison Formation during deposition of beds equivalent to the Brushy Basin Member.

The uppermost beds of the Morrison Formation in Wyoming and Montana are Tithonian in age and were deposited in mires, lakes, and associated floodplain deposits. Lacustrine deposits in the Tithonian beds are mostly dark gray to black, whereas such deposits are rare in the Kimmeridgian part of the formation. This indicates that the Tithonian lakes were, by and large, more reducing. The paleosols are Gleysols and Histosols (Demko et al., this volume), which is consistent with slightly wetter climates and/or higher water tables compared to the Kimmeridgian. The Gleysols as well as the high content of ash and sulfur in the coals, however, suggest that the climate was nevertheless seasonal with respect to rainfall (Cecil et al., 1981, 1982).

6.3. Synthesis

There are three questions we endeavor to answer with the information present here: What was the climate of the Morrison Formation? Did the climate change during deposition of the Morrison Formation and its equivalents? What was the vegetation like?

6.3.1. What was the climate during deposition of the Morrison Formation?

The sedimentological evidence from the Kimmeridgian part of the Morrison Formation strongly suggests a climate that was on the dry side of semi-arid and seasonal with respect to rainfall. The evidence for semi-aridity includes evaporites, eolian sandstones, saline–alkaline lake sediments, palustrine limestones, and mature vertic and argillic Calcisols (Fig. 7).

Sedimentological evidence from the Tithonian part of the Morrison is more ambiguous. Coal is commonly considered characteristic of wet climates (e.g., Parrish et al., 1982; Scotese and Barrett, 1990) deposited in low-lying, groundwater-fed mires. However, although peat does not require abundant rainfall, it does require relatively constant rainfall, however slight, to prevent the top of the peat from drying and killing the swamp (Gyllenhaal, 1991; Lottes and Ziegler, 1994). Under conditions of high water tables, however, peats may even form in climates that are seasonal with respect to rainfall (Gyllenhaal, 1991). The high ash and sulfur content of the coal beds are consistent with peat formation under seasonally dry climates in a region with a high water table (Cecil et al., 1981, 1982). Similarly, paleosols respond as much to water-table levels as precipitation, so the Gleysols and Histosols are also not necessarily indicative of a wet climate.

Tidwell (1990a; see also Tidwell et al., 1998) and Ash and Tidwell (1998) interpreted the climate during deposition of the entire Morrison Formation as humid based on the plant fossil assemblages, analogy with modern relatives, floral assemblages elsewhere in the world, and on the assumed food requirements of dinosaurs. However, Tidwell (1990a) also acknowledged that many of the taxa are consistent with or permit a drier climate. In addition, even though he documented some of the geographic variations in the floras, for the purposes of paleoclimate interpretation, Tidwell (1990a) apparently considered the entire Morrison flora as a single vegetational unit. Instead, we distinguish between the Kimmeridgian and Tithonian floral assemblages, which differ considerably.

Although the Pangean monsoon had broken down by Late Jurassic time (Parrish et al., 1982; Parrish and Peterson, 1988; Parrish, 1993), rainfall

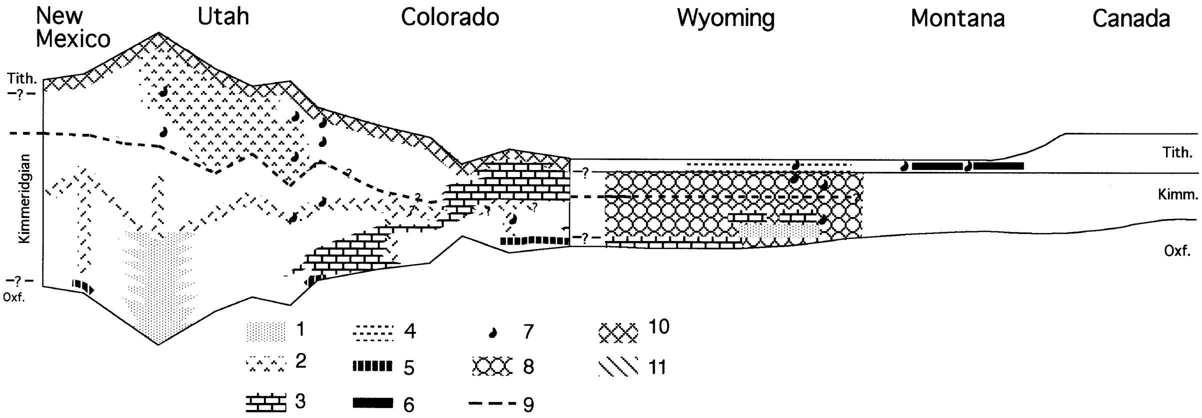

Fig. 7. Schematic cross-section of the Morrison Formation showing the paleoclimatically significant lithologies and the stratigraphic distribution of localities examined for this study. Lithologies and sample localities are projected onto the line roughly from the northwest and southeast, and some sample localities may not be found in the lithologies indicated on the diagram; consult Table 2 for the lithofacies in which the taphofacies occur. Some locality symbols represent more than one sample locality. Symbols: 1, eolian sandstone; 2, saline, alkaline lake deposits; 3, lacustrine calcareous mudstone and limestone; 4, carbonaceous mudstone; 5, evaporite (gypsum); 6, coal; 7, plant taphonomy sample locality; 8, general interval of poorly to moderately developed paleosols, including some caliche or silcrete, indicating seasonal climate (from Demko et al., 9, clay change; mature, well-drained paleosols indicating semi-arid and seasonal climate; 10, mature paleosols, commonly Vertisols, with hydroxymorphic overprint, gray where extrapolated (from Demko, et al., this volume, paleosol at top of Morrison); 11, calcic Vertisols and/or Aridisols, usually well developed, with termite nests and/or crayfish burrows indicating semi-arid and seasonal climate, gray where extrapolated (from Demko et al., this volume, top of Salt Wash Member and equivalents). Tith., Tithonian; Oxf., Oxfordian.

might have been seasonal by virtue of the continent's position in mid-latitudes and by analogy with modern mid-latitude continents (e.g., Rumney, 1968).

Climate models suggest that the Kimmmeridgian climate in the Morrison depositional basin was quite dry, < 1–2 mm/day in winter (December–February) and summer (June–August; Valdes and Sellwood, 1992; Valdes, 1993), and more seasonal north of about central Utah and Colorado. Evidence for seasonality of climate with respect to rainfall comes from the paleosols, particularly the vertic Calcisols and the co-occurrence of argillic and calcic horizons (e.g., Machette, 1985; Dubiel et al., 1991; Mack and James, 1994; Demko et al., this volume). Many of the trace fossil assemblages also are characteristic of seasonal climates and fluctuating water tables (Hasiotis, this volume). Further evidence of seasonality comes from seasonal growth bands in the freshwater bivalves from the Salt Wash Member and, to some extent, in the Brushy Basin Member (Good, this volume).

The presence or absence of growth rings in conifers from the Morrison Formation leads to conflicting interpretations of the environment. The principal conflict is with interpreting the original ecological habitat of the trees now found as silicified logs in the Salt Wash and Brushy Basin Members. Tidwell and Medlyn (1993) and Tidwell et al. (1998) found growth rings in *Protopiceoxylon resiniferous* from the Salt Wash Member and *Protocupressinoxylon medlynii* from the Brushy Basin Member and a lack of growth rings in *Araucarioxylon hoodii* and *Mesembrioxylon carterii* both from the Brushy Basin Member, and *Xenoxylon morrisonense*, from the Salt Wash and Brushy Basin Members. They also reported a lack of definite growth rings in the short shoots of *Behuninia* and *Steinerocaulis*, both of which came from the Brushy Basin Member or correlative rocks. They reasoned that the trees with growth rings grew in uplands where seasonality prevailed, whereas the other plants grew in lowlands of the depositional basin where climate was less seasonal, and that the logs with growth rings were transported some considerable distance to the depositional site by streams.

Tidwell and Medlyn (1993) and Tidwell et al. (1998) reported no taphonomic evidence for greater transport distances of the specimens with growth rings. Given that the evidence presented here and by others demonstrates that seasonality did occur in the Morrison depositional basin, at least during deposition of the Salt Wash Member and probably during deposition of the Brushy Basin Member (Good, this volume), their explanation is untenable. We suggest three alternate explanations for the presence of co-occurring logs with and without growth rings in the Morrison. One explanation is that the small sample sizes resulted, by chance, in the specimens of one taxon having growth rings while the specimens of others did not, and that the presence or absence of growth rings was related to the depth of the water table where the individual trees grew. Environments farther from the channels would have been more sensitive to water-table fluctuation associated with periodic drought than those close to the channels, and this environmental sensitivity would have affected the trees. A similar distribution with respect to channels probably influenced growth-ring development in trees from the Upper Triassic Chinle Formation (J.T. Parrish, unpublished data). Alternatively, the Morrison trees might have been ecologically segregated such that the species with growth rings lived in habitats away from the channels and the species lacking growth rings lived in the riparian habitat. The trees living farther from the water courses would have been more sensitive to water-table fluctuations and thus more likely to produce growth rings. Finally, it is possible that seasonality was not strong enough to cause growth to cease during the dry season, and that the presence or absence of growth rings was genetically controlled. The available information from the Morrison samples does not permit distinguishing among these alternative explanations.

6.3.2. Did the climate change during deposition of the Morrison Formation and its equivalents?

The types of variations in deposition, flora, and plant taphonomy in the Morrison Formation and equivalents could have been brought about by variations in climate or the position of the water table, which are not necessarily linked, since water tables throughout the depositional basin might rise with a rise in sea level. The almost complete lack of information from the Kimmeridgian part of the Morrison in the northern part of the region and apparent paucity of Tithonian-age rocks in the southern part of the region makes distinguishing these two effects difficult. However, changes in the character of the mature paleosols suggest that, although water-table effects may explain part of the pattern, the climate during deposition of the Morrison Formation and its equivalents did become slightly wetter with time. This could have been brought about by slightly increased rainfall, a longer wet season, or lower temperatures. Evidence exists that temperatures became cooler through time, and this alone would make the climate wetter (Schudack, 1999). Alternatively, climate could have become slightly wetter through an increase in precipitation, either through a slight increase in rainfall or a longer wet season, or a combination of all these factors. The latitudinal effect on temperature (D.D. Ekart, written communication, 1998; Schudack, 1999) during the Kimmerdgian was small and presumably was also small in the Tithonian.

The cheirolepids are considered good indicators of dry climates (Alvin et al., 1981; Vakhrameyev, 1982), not only by their sedimentologic association and biogeography worldwide but by their thick-cuticled, microphyllous habit. The presence of cheirolepids throughout the Morrison and equivalent beds is thus interpreted to indicate that any gradient in moisture in either space or time was not strong. The cheirolepids are represented in the Morrison and equivalent beds by the pollen genus *Classopollis* and the leaf genus *Brachyphyllum*. *Classopollis* (= *Corollina*) has been recovered from the Kimmeridgian as well as the Tithonian parts of the Morrison Formation from the Colorado Plateau and Montana (Newman, 1972; Tschudy et al., 1981a,b, 1988a,b; Litwin et al., 1998). It has also been recovered from Tithonian strata of Canada (Zieglar and Pocock, 1960; Pocock, 1964). Thus far, *Brachyphyllum* has only been recovered from the Kimmeridgian part of the Brushy Basin Member on the Colorado Plateau (Tidwell and Medlyn, 1992; Ash and Tidwell, 1998; Tidwell et al., 1998). It is significant that in some of our samples (9807034 and 9807035, Orchid Draw, Dinosaur National Monument, Utah), nearly all the carbonaceous debris was cuticle of *Brachyphyllum* leaves, which is interpreted as an indication that the cuticle was so thick that it could withstand sedimentological processes more easily than other plant parts. The cheirolepids are represented in the Tithonian rocks only by the pollen *Classopollis*. Given the robustness of *Brachyphyllum*, it is somewhat surprising that it is not found among the leaf taxa described from Tithonian beds in the Western Interior (Table 1).

The presence of *Czekanowskia* in beds of both the Kimmeridgian saline–alkaline lake sequence on the Colorado Plateau and Tithonian coal-bearing beds in Montana is notable but perhaps of lesser paleoclimatic significance than the presence of cheirolepids. Ash and Tidwell (1998) argued that *Czekanowskia* was a water-loving plant based on general lithologic and paleontologic associations elsewhere in the world. If this is true, *Czekanowskia* might have been at the limits of its ecological range in Utah and thus confined to narrow paleoenvironments there. We speculate that these environments were those in which the water table was temporarily relatively high and that the plants were sensitive to changes in salinity, such that during a dry spell, they would shed their leaves quickly and enter dormancy, resulting in leaf mats. Even in Montana, the climate probably would not have been cold enough, even in the winter, to cause leaf fall in *Czekanowskia*. (e.g., Valdes, 1993). Thus, an increase in salinity during the dry season may have been the trigger for *Czekanowskia* leaf fall. Indeed, this is the only explanation that can account for *Czekanowskia* leaf mats in such different depositional environments. The presence of such leaf mats in the Tithonian, then, would be consistent with a dry season. An incursion of marine water can be ruled out on paleogeographic grounds as an explanation for salinity changes.

Although the presence of cheirolepids throughout the Morrison and the presence of *Czekanowskia* in Upper Kimmeridgian to Tithonian beds indicates that climate change during deposition of the Morrison could not have been dramatic, some change may be indicated in that much of the remaining flora does change significantly between the Kimmeridgian and Tithonian. However, the significance of the change is not clear. The Tithonian flora recovered from Montana and Canada has a higher diversity of ferns than the Kimmeridgian flora (Table 1), which might be indicative of wetter climates in the Tithonian. However, almost all of the plant fossils in the Tithonian part of the section came from strata immediately adjacent to coal beds and thus reflect the wet conditions of the mire-margin. For this reason, they are probably not as good for interpreting the paleoclimate as the paleosols.

While the change in species through time probably simply reflects evolution, the turnover in genera may reflect climatic change. Macleod and Hills (1991) listed a number of characteristics of the warm temperate, relatively humid-climate Siberian paleoflora of Vakhrameev (1966; Kimura (1988); this contrasts with Vakhrameev's arid-climate Indo-European flora (see also Kimura, 1980). Although many of the criteria Macleod and Hills (1991) used to interpret the relatively humid paleoclimate depended on abundance data that are not available for the Morrison, some features of the floras they described are suggestive for the Tithonian part of the Morrison. These include, in part, the abundance of *Nilssonia*, *Ginkgo*, *Baiera*, and *Czekanowskia*; the presence of *Nilssonia schaumbergensis*; the abundance of *Podozamites* and other leafy, as opposed to scaly, conifers; and the presence of *Cladophlebis* (see Macleod and Hills, 1991, for full list of criteria). Although *Ginkgo*, *Czekanowskia*, and *Nilssonia*, including *N. schaumbergensis*, occur in the Kimmeridgian part of the Morrison, they are also present in the Tithonian part of the Morrison and its equivalents, and both *Ginkgo* and *Nilssonia* are represented in the Tithonian by several species (Table 1). In addition, *Baiera*, *Podozamites*, the leafy conifer *Pityophyllum*, and *Cladophlebis* occur only in the Tithonian parts of the Morrison and its equivalents (Table 1). These similarities establish an affinity between the Tithonian flora of the Morrison and the humid, temperate Siberian paleoflora of Macleod and Hills (1991) and thus support a conclusion of slightly wetter climates. It is worth noting, however, that the Kimmeridgian flora of the Morrison also contains some elements of the Siberian paleoflora (see Table 1), suggesting that the change from the Kimmeridgian to the Tithonian in the Morrison Formation was not great.

Although higher base levels and/or higher local water tables could explain the apparent climatic differences between the Kimmeridgian and Tithonian parts of the Morrison, there are four reasons to believe that the differences are largely explained by climate. First, base level, as indicated by southward penetration of the sea from Canada, probably was higher during deposition of the lower members of the Morrison Formation, yet these deposits contain indicators of dry climates (Fig. 7). The bedded gypsum in places at the base of the Morrison Formation, the rather extensive eolianites around the Four Corners region in the lower Morrison below the clay change, and some aspects of the paleosols at the base could be consistent with a hyperarid environment. However, if the climate were hyperarid, then even more evidence of such a climate would be expected as sea level fell and lowered base level, but this is not seen. In addition, deposition of the lower members occurred on a gypsiferous unconformity paleosol (Demko, this volume); such a paleosol could not form in a hyperarid environment. Second, some of the Gleysols and Histosols in the Tithonian of Montana are mature and thus must have formed in the better-drained and longer-exposed parts of the system. They are thus good indicators of the climate under which they formed because soils formed where high water tables occur are never mature. Finally, stratigraphic and sedimentologic evidence suggests that none of the lakes in the Morrison was very deep, at most several meters (see references in Dunagan and Turner, this volume). Because shallow lakes are more sensitive to climate change than deeper lakes, the differences in lacustrine sedimentary rocks, from limestone or green or gray mudstone to black mudstone, is considered to be related to climate.

In summary, the best evidence for a climate change from the Kimmeridgian to the Tithonian parts of the Morrison comes from the change in the taxonomic composition of the flora at the generic level and changes in the types of mature paleosols; changes in the nature of the lacustrine deposits may also be significant. That the climate change was not drastic, and might have been enhanced by a rise in water tables, is suggested by the presence of cheirolepids throughout the Morrison and its equivalents, the presence of *Czekanowskia* leaf mats through about the upper half of the Morrison and equivalent strata, the ambiguity in the environmental occurrences of the ferns, and affinities with the Siberian paleoflora that are stronger in the Tithonian but present in the Kimmeridgian as well. Further evidence against a large change in climate is discussed in the following section.

6.3.3. What was the vegetation like during deposition of the Morrison Formation?

Coupled with the recognition that the Kimmeridgian and Tithonian parts of the Morrison Formation and its equivalents in Canada contain taxonomically distinct floras, the taphonomy of the plants provides a much more comprehensive and representative picture of the vegetation than can be inferred from previously published taxonomic lists. In this section, we propose that the vegetation of the Morrison Formation consisted largely of herbaceous (that is, non-woody) plants, perhaps mixed with low-growing woody shrubs, and that the arboreal component was mostly limited to the riparian habitats.

The limited occurrences of the W taphofacies in the Morrison suggest that large-statured, woody plants were a small component of the flora, except perhaps locally in the Salt Wash and Westwater Canyon Members. The Wc, Wch, and Wi taphofacies are all characterized by small fragments of wood. From our observations and from information in the literature, the Ws taphofacies is predominantly in the Salt Wash Member and includes most of the large conifer wood specimens and silicified manoxylic stems of cycads; however, these remains are not common even there. Root traces of trees have been observed in paleosols from that interval of the Morrison (Hasiotis, this volume). The Salt Wash braidplain near active stream channels probably was vegetated, at least locally, with conifer trees and an understory of cycads. The flora probably included other plants as well, but the relatively high energy of the fluvial system would not have favored preservation of more delicate plants. The Ws taphofacies also occurs in the Westwater Canyon Member of the Morrison but the silicified wood in this member has not yet been studied. Although slightly younger, Westwater Canyon vegetation presumably occurred in habitats similar to those of the Salt Wash Member.

Most striking is the very local and minor presence of the W taphofacies in the Brushy Basin Member and, especially, in Tithonian rocks, even in the coal beds, and the small sizes of the wood specimens that are preserved. The occurrences of taphofacies W listed in Table 2 are from single beds or very narrow (< 1 m) intervals. This is additional evidence against an appreciable change in climate between the Kimmeridgian and Tithonian parts of the Morrison. If climate in general became substantially wetter, one would expect to see more fossils of large-statured plants. One possible explanation is that the mire environment in Montana was, for some unknown reason, inimical to the growth of trees, such that the only trees in the ecosystem were in the better-drained environments where the Gleysols formed. By virtue of the advanced pedogenesis, it is less likely that plant remains, even wood, would be preserved in the Gleysols. In addition, it is possible that the limited exposures of the Morrison Formation in Montana restrict the chances of finding the remains of large plants there.

Root impressions are generally small and shallow in the Morrison Formation (R taphofacies and unpublished observations), even on well-developed paleosols. Root traces observed in this study were rarely longer than a few centimeters and much narrower than a millimeter in diameter, except in the lacustrine limestones, where they are larger but still consistent with an herbaceous habit. Hasiotis and Demko (1998) described root traces as long as 60 cm in beds equivalent to the lower part of the Brushy Basin Member near Cañon City, CO; these root traces are consistent with a shrubby habit, but not with trees.

All of these observations, combined with the sparse megaplant remains in most of the Morrison and the scarcity of vitrinite in the coal beds lead us to the interpretation that the entire Morrison flora was dominated by herbaceous and small-statured woody plants. Ecologically, such a flora would have been equivalent to modern tropical savannah grasslands, which are composed of grasses and scattered shrubs and trees, with a higher density of shrubs and trees along the water courses. Grasses, of course, did not exist in the Late Jurassic, but we interpret that herbaceous plants occupied the same ecological niche as grasses in the Morrison savannahs LePage and Pfefferkorn (2000). The semi-arid climate that is interpreted from sedimentological information in the Kimmeridgian part of the formation is entirely consistent with savannah-like vegetation. The slightly wetter but still seasonal climate interpreted from the sedimentology of the Tithonian part of the Morrison is consistent with a marshy, herb-dominated vegetation. Thus, based on our data, we interpret the overall climate of the Morrison Formation to have been semi-arid, with a change from dry semi-arid to wet semi-arid from the Kimmeridgian to Tithonian.

Additional work by others supports our interpretation. The interpretation of the Morrison flora as dominantly herbaceous is supported by the large ratio of palynomorph taxa to megafloral taxa throughout the Morrison. Thirty-two (32) leaf form species (18 genera) have been identified from the Morrison Formation proper (Table 1, excluding taxa found only in Canada). In contrast, Litwin et al. (1998) identified more than 225 pollen and spore taxa from the Morrison Formation of the Western Interior U.S. (they did not study palynomorphs in Canadian equivalents). A similar discrepancy between the diversities of the megafloras and palynofloras was found in the Late Cretaceous Prince Creek Formation of Alaska (Spicer and Parrish, 1990). Spicer and Parrish (1986) and Parrish and Spicer (1988) documented a drastic reduction in the diversity of megafloral forms through the Late Cretaceous in Alaska, culminating in the Kogosukruk Tongue of the Prince Creek Formation, and interpreted this and other data as indicating a strong cooling trend. This decrease in diversity of the megaflora was accompanied by an increase in the diversity of the palynoflora (May and Shane, 1985; Frederiksen et al., 1988). The cooler climates of the Prince Creek Formation would have favored herbaceous plants (Spicer and Parrish, 1990), which tend to be opportunistic. That is, they are able to respond more quickly to environmental perturbations than woody plants, which grow more slowly. Opportunistic herbaceous plants would have been similarly better adapted than woody plants to the seasonal, arid to semi-arid climates we suggest for the Kimmeridgian beds of the Morrison.

The presence of apparently water-loving plants, that is, *Czekanowskia*, in the Kimmerdigian part of the Morrison (Tidwell, 1990a; Ash and Tidwell, 1998) is not inconsistent with a semi-arid climate. Preservation of leaves occurs predominantly in wetter areas anyway, regardless of the regional climate. This was strikingly demonstrated by Demko (1995) and Demko et al. (1998) in the Chinle Formation, in which most of the preserved plants are found in incised-valley fills. The water table in the Chinle was confined between the valley walls and remained above the ground surface in the valleys, even during dry seasons, thereby enhancing preservation of plant material. A similar variation in plant preservation could occur on a lower-gradient landscape, such as that envisioned for much of the Morrison Formation, even in a climate less seasonal than that of the Chinle. In the Morrison, groundwater fluctuation could have been great enough to leave a paleosol record at sites well above the water table but not great enough to completely dry out all the lakes and streams; total topographic relief in such a landscape need not be more than a few meters.

We now return briefly to the argument made by Tidwell (1990a) that the Morrison vegetation must have been lush in order to support the abundant dinosaur fauna. Although dinosaur fossils are abundant in the Morrison Formation, as shown by Turner and Peterson (1999), it does not follow that at any given point in time, the density of dinosaurs on the landscape was high, and in fact they might have been migratory (Dodson et al., 1980). In addition, although Tidwell (1990a) acknowledged that grasses are sufficient for large grazers today, he did not appear to consider the possibility of a substantive herbaceous component to the Morrison flora except along the water courses, nor did he consider the possibly lower metabolic rates for dinosaurs (Coe et al., 1987). He argued that the dinosaurs would have devastated such limited vegetation, and that they must, therefore, have relied on a lush woody vegetation for food, and such a vegetation could grow only in a wet climate. However, if the vegetation were predominantly herbaceous, with woody plants limited to the riparian environments, that would have been a situation comparable to modern environments that support large grazers. In addition, grazing is a potentially advantageous strategy for large animals in that herbaceous plants can grow much more quickly than woody plants and are thus able to recover faster from both grazing and from growth-disrupting environmental conditions. For example, modern tropical grasslands have net primary productivities (new biomass added) of 200–2000 g/m^2/year, which substantially overlaps the forest values of 600–3500 gm/m^2/year (Lieth, 1975) for modern forest types analogous to those proposed by Tidwell (1990a).

Finally, Stevens and Parrish (1999) have shown that the neck morphology of two of the largest dinosaurs from the Morrison Formation, the sauropods *Diplodocus* and *Apatosaurus*, was adapted for a grazing and low browsing habit. Some other dinosaurs in the Morrison Formation were capable of browsing on vegetation no higher than about 3 m (Coe et al., 1987). A grazing or low-browsing habit for at least some of the animals is supported by studies of dinosaur coprolites, which contain volcanic glass shards and sand grains that most likely were ingested during browsing on low vegetation, and plant fragments identified as derived from cycadeoids that tend to be fairly short (Chin and Kirkland, 1998). The plant material in these coprolites shows a fragmentation and digestion pattern similar to that of modern grazers (Chin and Kirkland, 1998).

7. Conclusions

We arrived at three important conclusions as a result of this study.

(1) The flora of the Morrison Formation was predominantly herbaceous and, in the Kimmeridgian part of the formation, resembled that of modern savannahs in which trees are not abundant and are most common in the riparian environments. Although the vegetation in the Tithonian part of the Morrison was still predominantly herbaceous, it included elements that are consistent with a slightly more humid climate. We propose that the climate was slightly wetter in the Tithonian because either precipitation was higher or cooling led to lower evaporation rates, or both.

(2) The climate in the Morrison depositional basin was warm, semi-arid, and seasonal and became slightly wetter through time, progressing from dry semi-arid in the Kimmeridgian part of the formation to humid semi-arid in the Tithonian.

(3) The taxonomic composition of the floras in the Kimmeridgian and Tithonian parts of the Morrison Formation is strikingly different, and it is therefore misleading to consider the flora of the entire formation as a single vegetational unit.

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