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Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses

Stephen T. Hasiotis*

Department of Geology, University of Kansas, 1475 Jayhawk Boulevard, 120 Linley Hall, Lawrence, KS 66045-7613, USA

Abstract

Seventy-five types of ichnofossils documented during a four-year reconnaissance study in the Upper Jurassic Morrison Formation demonstrate that highly diverse and abundant plants, invertebrates, and vertebrates occur throughout most of the Morrison or equivalent strata. Invertebrate ichnofossils, preserving the most environmentally and climatically sensitive in situ behavior of Morrison organisms, are in nearly all outcrops. Terrestrial ichnofossils record biotic processes in soil formation, indicating soil moisture and water-table levels. Freshwater ichnofossils preserve evidence of water depth, salinity, and seasonality of water bodies. Ichnofossils, categorized as *epiterraphilic*, *terraphilic*, *hygrophilic*, and *hydrophilic* (new terms), reflect the moisture regime where they were constructed. The ichnofossils are vertically zoned with respect to physical, chemical, and biological factors in the environment that controlled their distribution and abundance, and are expressed as surficial, shallow, intermediate, and deep.

The sedimentologic, stratigraphic, and geographic distribution of Morrison ichnofossils reflects the environmental and climatic variations across the basin through time. Marginal-marine, tidal to brackish-water ichnofossils are mainly restricted to the Windy Hill Member. Very large to small termite nests dominate the Salt Wash Member. Similar size ranges of ant nests dominate the Brushy Basin Member. Soil bee nests dominate in the Salt Wash, decreasing in abundance through the Brushy Basin. Deeper and larger insect nests indicate more seasonal distribution of precipitation and rainfall. Shallower and smaller insect nests indicate either dry or wet substrate conditions depending on the nest architecture and paleopedogenic and sedimentologic character of the substrate. Trace–fossil indicators of flowing or standing water conditions are dominant in the Tidwell Member and in fluvial sandstones of the Salt Wash and Brushy Basin Members. Large communities of perennial, freshwater bivalve traces are abundant in the Tidwell and Brushy Basin Members but to a lesser extent in the Salt Wash Member. Shallow crayfish burrows, indicating a water-table level close to the surface (< 1 m), are restricted to channel bank and proximal alluvial deposits in the Salt Wash, Recapture, and Brushy Basin Members. Sauropod, theropod, pterosaur, and other vertebrate tracks occur throughout the Morrison Formation associated with alluvial, lacustrine, and transitional-marine shoreline deposits.

Ichnofossils and co-occurring paleosols in the Morrison reflect the local and regional paleohydrologic settings, which record the annual soil moisture budget and were largely controlled by the climate in the basin. Contributions to near-surface biologic systems by groundwater from distant sources were minor, except where the water table perennially, seasonally, or ephemerally intersected the ground-surface. The Jurassic Morrison Formation in the southern portion of the basin experienced a mosaic of

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* Fax: +1-785-864-5276.
E-mail address: hasiotis@ku.edu (S.T. Hasiotis).

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seasonal climates that varied from a drier (Tidwell/Windy Hill deposition) to a wetter (lower and middle Salt Wash deposition) and slightly drier (upper Salt Wash deposition) tropical wet–dry climate, returning to a wetter tropical wet–dry climate near the end of Morrison deposition (Brushy Basin deposition). The northern part of the basin experienced similar trends across a mosaic of Mediterranean climate types. The range and mosaic pattern of wet–dry Morrison climates is analogous to the range of climates (and their seasonal variability) that dominates the African savanna today.

Keywords: Ichnofossils; Invertebrates; Vertebrates; Continental; Jurassic; Rocky Mountains; Paleoecology; Paleohydrology; Paleoclimate

1. Introduction

This paper summarizes the results of a four-year reconnaissance investigation of ichnofossils in the Upper Jurassic Morrison Formation. To date, 75 ichnofossil morphotypes documented in the Morrison provide new information on the paleoenvironments, paleoecology, and paleoclimatic settings previously unreported from alluvial, lacustrine, eolian, and continental–marine transitional deposits. Although several brief contributions on Morrison ichnofossils have recently appeared in the literature (e.g., Hasiotis and Demko, 1996, 1998; Hasiotis and Kirkland, 1997; Hasiotis et al., 1998a,b, 1999a,b; Engelmann and Hasiotis, 1999), the bulk of the ichnofossil evidence is presented here.

Trace fossils throughout the Morrison Formation (from New Mexico to Montana) represent such invertebrates as ants, bees, beetles, caddisflies, crayfish, flies, horseshoe crabs, gastropods, mayflies, bivalves, soil bugs, and termites. Associated with the invertebrate traces are those of plants (rhizoliths and stump steinkerns) and vertebrates (tracks, trackways, and burrows). These and other trace fossils make excellent proxies for presence of organisms in terrestrial and freshwater deposits. Body fossils of terrestrial and freshwater organisms are not often preserved in continental deposits because of oxidizing conditions, consumption of the remains by other organisms, and the reworking of near-surface sediment where bodies may be buried (e.g., Behrensmeyer et al., 1992; Hasiotis and Bown, 1992). When they are preserved, continental body fossils are often deposited outside their original environmental context.

Morrison ichnofossils indicate (1) the presence of a large number of invertebrates and vertebrates whose body fossils are absent or taphonomically reduced; (2) in situ evidence of food web relations between fossorial, terrestrial, and freshwater communities; (3) soil moisture and water-table levels; and (4) precipitation and its seasonality for a specific climatic setting. This study, although preliminary and still in progress, provides baseline information on ichnofossils necessary to interpret the Morrison deposits. These interpretations are critical for resolving accurately the Morrison paleoenvironments, as well as deciphering its paleoecology and paleohydrology across intracontinental sedimentary environments that reflect the paleoclimatic settings across the basin.

2. Study area and geologic setting

The Morrison Formation was deposited throughout the Rocky Mountain region (Fig. 1A), stretching from Montana to New Mexico (Peterson, 1994). The Morrison ranges in thickness across the Colorado Plateau from 0 to 150 m along the Front Range of Colorado and 0 to 300 m in the Four Corners (Arizona, Colorado, New Mexico, and Utah) area (Peterson, 1994). These deposits range in age from latest Oxfordian (?) or early Kimmeridgian (~ 155 Ma) to early Tithonian (~ 148 Ma) (Kowallis et al., 1998). Morrison stratigraphy is relatively complex because it contains many sedimentary facies and because the nomenclature changes from east to west and north to south across the depositional basin. Generally, in the Colorado Plateau area the Morrison includes the Tidwell, Salt Wash, and Brushy Basin Members (Fig. 1B). The Tidwell Member interfingers with the Bluff Sandstone and Junction Creek Sandstone Members in the Four Corners region, whereas the lower Brushy Basin and Salt Wash Members grade into and interfinger with the Recapture and Westwater Canyon Members in the same area (Peterson and Turner-Peterson, 1989; Peterson, 1994). In northern Colorado and northern Utah,

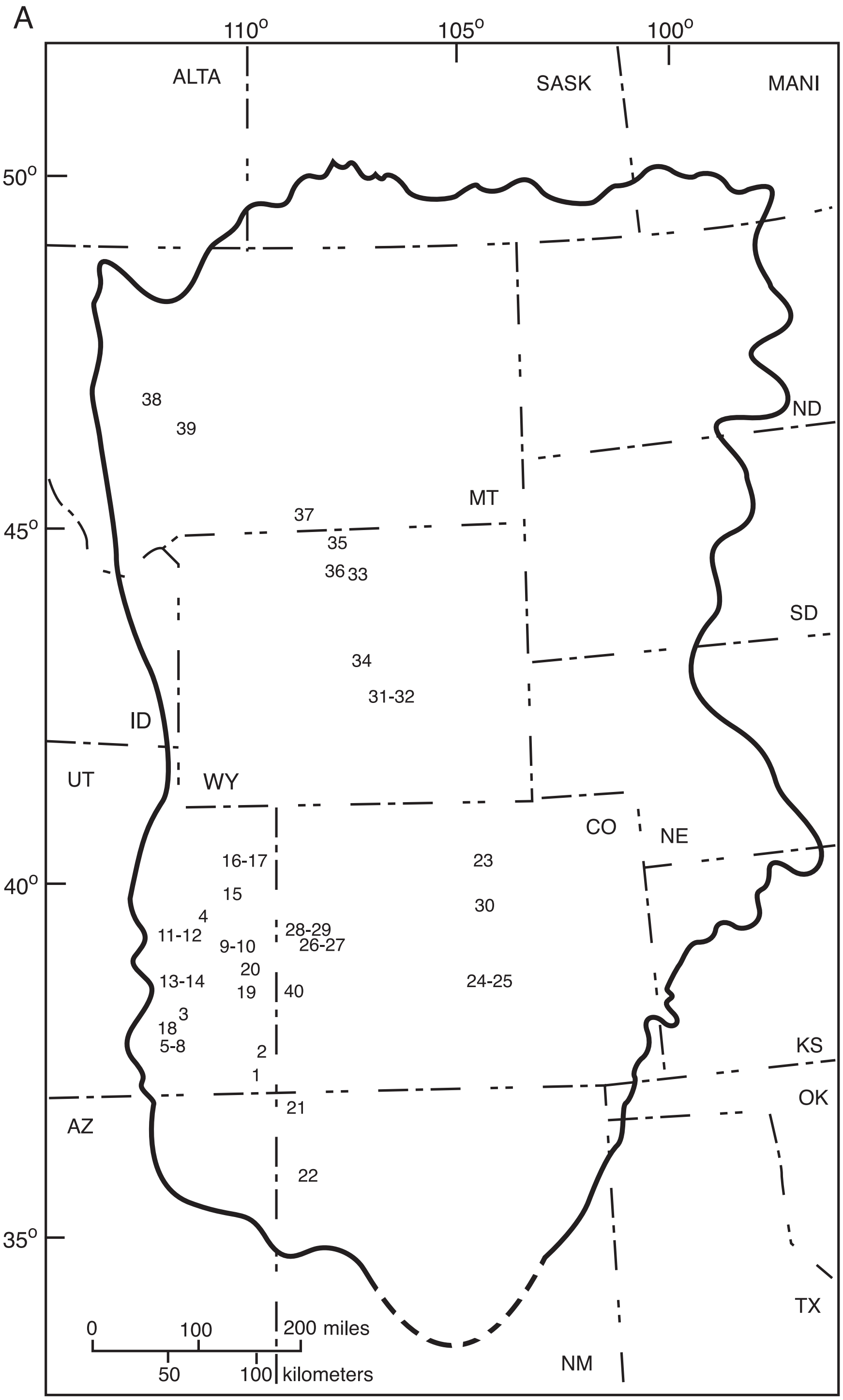


Fig. 1. (A) Sites in the Rocky Mountain region examined in the reconnaissance study of the Upper Jurassic Morrison Formation. Numbers 1 to 40 correspond to localities listed in Appendix A. (B) Generalized stratigraphic correlation chart of Middle and Upper Jurassic units associated with the Morrison Formation across the study area. Modified from Peterson (1994).

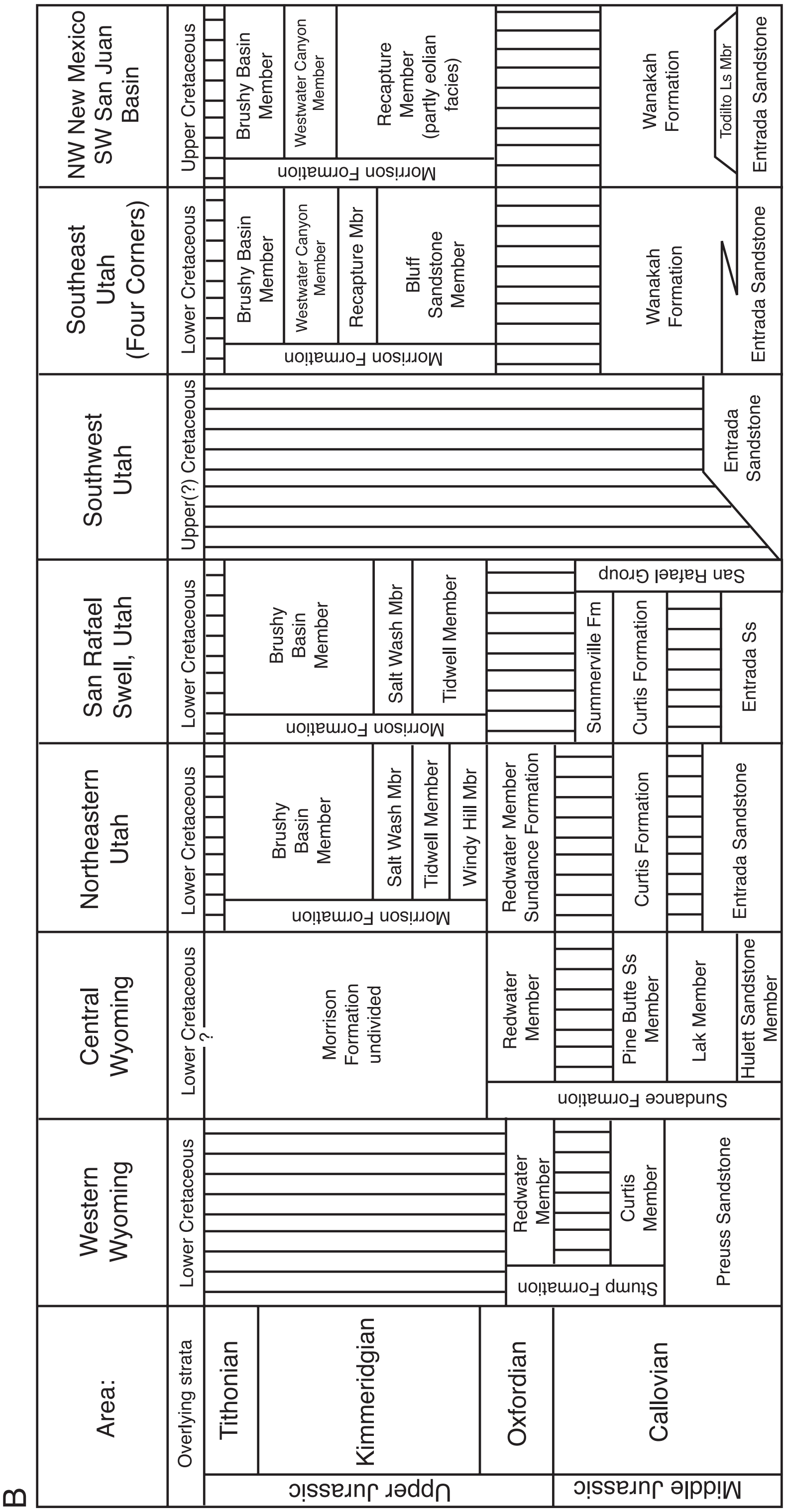


Fig. 1 (*continued*).

the Windy Hill is the basal unit in the Morrison Formation and interfingers with the Tidwell Member (Turner and Peterson, 1992; Peterson, 1994). Off the Colorado Plateau, the Morrison is largely undivided or divided into informal units. The Windy Hill Member, however, occurs at the base of the formation from northern Utah and Colorado northward to Wyoming and into western South Dakota. The Unkpapa Member lies at the base or just above the Windy Hill in the eastern foothills of the Black Hills in western South Dakota (Peterson, 1994; Turner and Peterson, 1999). For recent, detailed discussions on the stratigraphy of the Morrison, see O'Sullivan (1992), Turner and Peterson (1992, 1999), and Peterson (1994).

The Morrison Formation is composed of successions of conglomerate, sandstone, siltstone, mudstone, mudrock, limestone, and evaporites that were deposited in alluvial, lacustrine, eolian, and continental–marine transitional environments (e.g., Brady, 1969; Dodson et al., 1980; Peterson and Turner-Peterson, 1989; O'Sullivan, 1992; Peterson, 1994; Merkel, 1996; Dunagan, 1998; Turner and Peterson, 1999). The lowest portion of the Morrison Formation near Dinosaur National Monument and the San Rafael Swell records interbedded mudstone and sandstone, and bedded gypsum deposition in a marginal-marine and tidal sequence (Peterson, 1994). In the Four Corners area, the Bluff Sandstone and Junction Creek Members represent localized eolian deposits composed of fine-grained, well-sorted sandstones that interfinger with the fluvial and lacustrine deposits of the Tidwell Member (Peterson, 1994). The Salt Wash and Westwater Canyon Members represent major fluvial and overbank complexes composed of vertically stacked and laterally amalgamated sandstones and interbedded mudstones in the lower and middle parts of the Morrison Formation. In various places on the Colorado Plateau (i.e., Kaiparowits Plateau, UT; Grand Junction, CO), the lacustrine siltstones and limestones of the Tidwell interfinger with the sandstones, siltstones, and mudstones of Salt Wash Member (Peterson, 1994). Across most of the study area, the upper part of the Morrison is represented by the Brushy Basin Member, which is dominated by swelling clays, composed mainly of smectite in its upper part. The Brushy Basin Member also contains interbedded sandstones, mudstones, mudrocks, tuffs, and some thin limestones deposited by alternating alluvial and lacustrine systems. Highly variegated orange and green tuffaceous beds represent early diagenesis in the saline alkaline lake environments of Lake T'oo'dichi' (Turner and Fishman, 1991; Turner, 1992). Lacustrine deposition in Lake T'oo'dichi', which extended across a large part of the southeastern Colorado Plateau, was interrupted by brief episodes of fluvial deposition and pedogenesis (Turner and Fishman, 1991). Many of the alluvial, lacustrine, palustrine, and eolian deposits throughout the Morrison Formation were modified by some degree of pedogenesis after deposition, producing weakly to highly variegated units.

3. Approach and method

Modern organisms are distributed vertically and laterally in a depositional environment according to their physiological needs or tolerance to water, soil moisture, salinity, ecological associations with other organisms, and ultimately by climate (Wallwork, 1970; Whittaker, 1975; Hasiotis and Bown, 1992; Hasiotis, 1997a, 2000). Identifying and interpreting traces in deposits like the Morrison Formation can increase our understanding of ancient environments and the mechanisms that influenced them. Terrestrial and aquatic organisms have different requirements for water or soil moisture, substrate consistency at the water–substrate interface, and the degree of ionic concentration and salinity within the water or substrate. Continental organisms may be terrestrial in habitat (above, on, and below the soil but above the water table), amphibious (restricted to shorelines), freshwater-aquatic (e.g., below the water table, rivers, lakes, and capillary water around grains), or hypersaline-aquatic (e.g., playa lakes).

Invertebrates and their traces are useful in delineating hydrologic profiles and ecological partitions (Hasiotis and Bown, 1992; Hasiotis, 1997a, 2000). Most invertebrates belong to insects in the Isoptera, Hymenoptera, and Coleoptera, of which the first two construct the most elaborate and distinctive structures of all continental (as well as all marine) trace-making organisms (Wilson, 1971; Milne and Milne, 1980). Chamberlain (1975), Ratcliffe and Fagerstrom (1980), Hasiotis and Bown (1992), and Buatois et al. (1998) published comprehensive overviews of the different types of invertebrates inhabiting terrestrial and aquatic environments. These include: (1) insects and arachnids, including ants (Hymenoptera: Formicidae), termites (Isoptera), bees and wasps (Hymenoptera: Aculeata), crickets (Orthoptera), earwigs (Dermaptera), antlions (Neuroptera), spiders (Arachnida), caddisflies (Trichoptera), mayflies (Ephemeroptera), true flies (Diptera), terrestrial and water-loving beetles (Coleoptera); (2) soft-bodied annelids, including terrestrial and aquatic earthworms (Oligochaeta), leeches (Annelida), nematodes (Nematoda); (3) mollusks, including terrestrial and aquatic gastropods, mussels, clams; and (4) terrestrial and aquatic crustacea, especially crayfish, shrimp, and crabs (Decapoda), conchostracans (Branchiopoda), sow bugs (Isopoda), scorpions (Scorpionida), ostracodes (Ostracoda), and amphipods (Amphipoda).

Vertebrates (Voorhies, 1975; Martin and Bennet, 1977) and plants (Klappa, 1980; Wing et al., 1995) are also useful in delineating environmental conditions, especially in conjunction with invertebrates and their traces. Vertebrates and their traces are of popular interest because of work with dinosaur trackways and comparative ichnologic experiments with modern reptiles and birds (e.g., Hitchcock, 1858; Sarjeant, 1983; Gillette and Lockley, 1989; Lockley, 1991; Lockley and Hunt, 1995). They are limited in scope and utility, however, as specific environmental and ecological indicators because vertebrates generally are not preserved as in situ indicators of environment, vertebrates are not as sensitive as invertebrates to environmental conditions (e.g., Wallwork, 1970; Hole, 1981), and their behavioral traits preserved as traces (e.g., trackways) cross environments with different physicochemical characteristics.

Root patterns reflect the behavior of plants with respect to water absorption, nutrient collection, and substrate consistency (Pfefferkorn and Fuchs, 1991). As roots grow and regrow through the life of the plant, they push their way through the sediment into cracks and follow preexisting burrows, taking the path of least resistance and reacting to changes in soil moisture, chemistry, and consistency (e.g., Aber and Melillo, 1991; Pfefferkorn and Fuchs, 1991). Rhizoliths, although not plant-specific, are useful for environmental interpretation, particularly when they are associated with traces of terrestrial and aquatic invertebrates, which used them for shelter, food, and burrowing pathways.

Based on the distribution of extant organisms and their physiological requirements for water, a four-part division of burrowing behavior was created to categorize ichnofossils into behavioral groups that reflect different space and trophic use as well as moisture zones of the groundwater profile (Hasiotis, 2000; Fig. 2). Organisms living above the water table in the uppermost parts of the soil–water profile down to the upper part of the vadose zone construct *Terraphilic* traces. These organisms have low tolerance for areas of prolonged high moisture levels, can tolerate short periods of 100% soil moisture, and can live in areas with relatively little available water. This category also includes surface-dwelling and trackway-making organisms whose traces are termed *Epiterraphilic*. Organisms living within the upper, intermediate, and lower portions of the vadose zone with specific physiological and reproductive soil moisture requirements construct *Hygrophilic* traces. This category includes organisms living aboveground but that burrow to this level for reproduction. These organisms obtain oxygen from the soil atmosphere rather than from groundwater or soil moisture; however, soil moisture is likely to have been a physiologic requirement (Hasiotis, 2000). *Hydrophilic* traces are constructed by organisms that live below the water table within a soil and below the substrate in open bodies of water where the water table intersects the land surface (e.g., rivers and lakes); these organisms obtain oxygen from the water. They can also use high levels of soil moisture to keep their gills wet for short periods of time (e.g., Hasiotis and Mitchell, 1993). This category includes those organisms that burrow to depths below the water table and maintain the burrow's entrance at the surface.

Although the position of the ancient water table is not preserved in the rock record, its position can be approximated through ichnologic, sedimentologic (primary and secondary sedimentary structures), and paleopedologic (mottling, ped structure, micromorphology, texture, and soil geochemistry) evidence. For example, both insects and crustaceans exhibit burrowing behaviors unique to specific subaqueous or subaerial portions of terrestrial and aquatic environments. The depths of these traces, their crosscutting relationships with other traces (e.g., tiering), and their decrease in abundance within a profile approximate the position of the ancient soil moisture zones and the

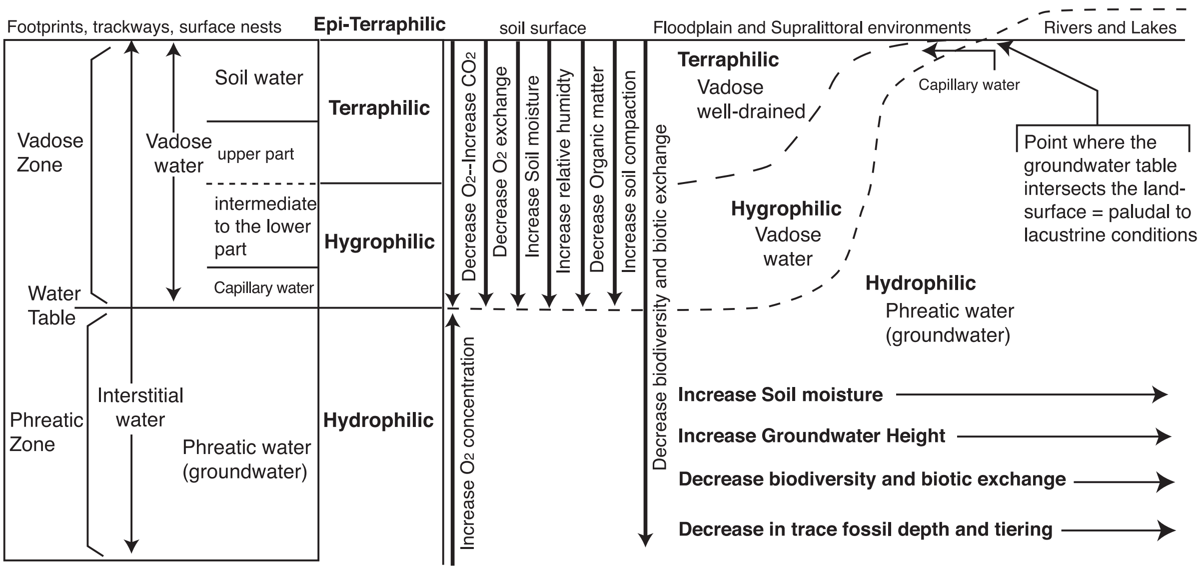


Fig. 2. Ichnofossils categorized into behavioral groups, epiterraphilic, terraphilic, hygrophilic, and hygrophilic, which indicate use of specific moisture zones, space and trophic resources. These zones can be compressed or expanded depending on the amount of soil moisture and the level of the water table. Moisture zones and, thus, behavioral and reproductive strategies in floodplain and supralittoral environments are upwardly compressed as they approach an area where the groundwater table intersects the land surface to form rivers and lakes. The spatial and temporal variation in the hydrologic system controls the distribution of trace-making organisms in terrestrial and freshwater environments. Modified from Hasiotis (1997a).

water table. These traces occur in deposits whose primary and secondary sedimentary structures or pedogenic features preserve characteristics of the environment in which the organism was burrowing. Integration of physical, biogenic, and chemical evidence provides information about the paleohydrology. In turn, ichnologic evidence is integrated with other physical and geochemical evidence to interpret the climate at a particular time and place (Hasiotis and Dubiel, 1994; Hasiotis, 2000).

In modern continental environments, climate controls the formation of soil types, the distribution of above- and below-ground biodiversity, and net primary productivity (NPP) of the ecosystem (Whittaker, 1975; Lydolph, 1985); biologic activity is one of the soil-forming factors identified by Jenny (1941), and thus links soil ecosystems to climate. Climate can also be expressed by the water balance of soils and is controlled by the relation between annual precipitation inputs, soil moisture changes, evapotranspiration losses, and solar radiation (Thornthwaite and Mather, 1955). Soil ecosystems (soils and their trace-making organisms) are expressions of these climatic elements, and when integrated with other climatic indicators, such as faunal and floral diversity, pedosedimentary characteristics, geochemical signatures, and isotopic fractionations represent the totality of climate (i.e., Thornthwaite and Mather, 1955; Whittaker, 1975; Lydolph, 1985; Aber and Melillo, 1991). As a result, patterns of vegetation, aboveground organisms, soils, and soil organisms are largely controlled by local variations in precipitation, solar radiation, and evapotranspiration (i.e., climate). Distant sources of overland flow (i.e., sheet wash or runoff), regional groundwater aquifer flow (i.e., hydrogeologic sources), and stream flow (i.e., hydrologic sources) have little or no control on the distribution of NPP. Steam flow and overland flow from external sources have very localized effects limited to the most proximal area of fluvial channels (e.g., Thornthwaite and Mather, 1955; Lydolph, 1985), and regional groundwater aquifers are very deep to contribute significant amounts of moisture to the ecosystem, except where it intersects the surface (as in lakes, swamps, and springs; Driscoll, 1986; Fetter, 1994). In the Morrison Formation, the information from trace fossils (morphology, depth, interpretation of the tracemaker), when integrated with the type and distribution of paleosols (maturity, degree of weathering, leaching, etc.), the biodiversity (plants, palynomorphs, invertebrates, vertebrates, and their physiological characteristics), and other physical and chemical data (from paleolatitude reconstructions of continents to pCO_2 and the fractionation of carbon and oxygen isotopes), yields interpretations that represent the totality of the Late Jurassic paleoclimates across the depositional basin.

4. Ichnology

Seventy-five morphotypes of ichnofossils identified from the members of the Morrison Formation and equivalent strata from 40 localities (Appendix A) are described below and listed in Table 1 with their environments of occurrence and paleosol associations. Localities of trace fossils described in each section are listed as a number within parentheses [i.e., (23)—Park Creek Reservoir, CO]. The trace fossils are presented as 51 types, with some types containing one or more related patterns of morphology (—morphotypes); the interpreted tracemaker, if known, is identified in the heading. Each type contains a concise discussion of its (1) description, (2) occurrence, (3) tracemaker, and (4) interpretation. The latter includes the paleoenvironmental and paleohydrologic significance of the structure. Table 2 lists these ichnofossils with their moisture relations and tiering strategies, and Table 3 lists their possible taxonomic affinities. These interpretations are supported by comparing the architecture of the ichnofossil to traces produced by extant organisms observed in the field or from the literature. The ichnotaxonomy of many of these traces is very lengthy to discuss here and will appear in other reports in the future.

4.1. Type 1—adhesive meniscate burrows (AMB), Fig. 3A,B

Description: Predominantly vertical to oblique burrows are identified by characteristic backfill menisci and thin to absent burrow walls (Bown and Kraus, 1983). Burrow walls exposed in the matrix are commonly smooth. Enlarged rounded parts of the burrow occur at or within the path or at the termination. Although a burrow wall may be present, it is not physically distinct as those of *Camborygma*, *Scoyenia*, or *Ancorichnus*. Burrows are 0.3–2 cm in diameter and are 1–8 cm long. Their path through the outcrop face obscures the true length of the burrows. Menisci are thin, ungraded, fine-grained, and often stained with alternating zones of oxidized and unoxidized iron compounds. Mottling and reduction halos help to accentuate the traces. The burrows are termed *adhesive* because they do not weather differentially from the rock matrix and cannot be removed easily as an individual entity.

Occurrence: These burrows often occur in great abundance within very fine grained sandstone, siltstone, and mudrock interpreted as alluvial levee and floodplain deposits in the Tidwell, Salt Wash, and Brushy Basin Members. They often obliterate all bedding, rendering the unit homogeneous, and are the most abundant compared to other forms. These traces tend to co-occur with fine rhizoliths and pedogenically modified substrates.

Tracemaker: Based on comparisons to modern continental burrows, AMB are most likely to have been constructed by soil bugs (Insecta: Hemiptera) and less likely by the larvae of ground beetles (Coleoptera: Carabiidae) and scarab beetles (Coleoptera: Scarabaeidae). More work is necessary on the burrows of these extant insects to document the differences in burrow morphologies.

Interpretation: AMB were constructed in levee and floodplain sediments after deposition in subaerial conditions. The trace is hygrophilic, and the co-occurrence of AMB with rhizoliths and the upper parts of crayfish burrows reinforces this interpretation. Based on the burrow morphology and comparison to similar extant structures (Willis and Roth, 1962; Hasiotis and Bown, 1992; Hasiotis and Demko, 1996), the burrows are thought to have been constructed in sediment undergoing pedogenesis with moisture levels of 10–37%. Their occurrence in the bioturbated upper portions of depositional sequences with other traces and pedogenic structures suggests they were part of the A and uppermost B soil horizons (Fig. 3A,B).

4.2. Type 2—cf. Ancorichnus isp. Fig. 3C,D

Description: Mainly horizontal burrows characterized by distinct walls and discrete backfill menisci

Table 1
Lithologic and stratigraphic distribution of Morrison ichnofossils

Type	Trace Fossil	Members						Lithologies						Environments										Paleosols				
		WH	TW	SW	RE	WW	BB	SS	SLT	SH	MR	LS	WD	CH	LV	OX	PF	DF	PL	DL	TI	ES	EO	EN	VT	AL	CA	SP
1	Adhesive meniscate burrows		x	x			x	x	x		x				x		x	x	x					x	x	x	x	
2	cf. *Ancorichnus* isp.			x	x		x	x	x						x		x											
3a	Ant nest—dispersed system		x	x	x		x	x	x								x	x						x		x		x
3b	Ant nest—concentrated system			x			x	x			x						x	x										
3c	Ant nest—low concentrated system			x			x	x			x						x	x										
4a	*C. litonomos*		x	x				x						x	x				x					x				
4b	*C. eumekenomos*				x		x				x						x	x									x	
4c	*C. airioklados*			x			x				x			x	x				x					x				
5a	cf. *Celliforma*—solitary		x	x			x	x			x				x		x	x						x		x		x
5b	cf. *Celliforma*—gregarious		x	x				x																x				
5c	cf. *Celliforma*—social			x			x	x									x	x						x				
5d	cf. *Rosellichnus* isp.			x				x									x	x						x				
6a	Cocoons—large			x				x	x								x							x				
6b	Cocoons—small			x				x	x								x							x				
7a	*Steinichnus* isp.		x	x				x	x						x				x									
7b	*Steinichnus* isp.—branched		x	x			x	x	x						x				x									
8	cf. *Cylindrichum* isp.		x	x			x	x	x					x	x				x					x				
9	cf. *Scoyenia* isp.						x	x	x						x									x				
10a	*Coprinisphaera* isp.—large			x				x	x								x	x						x				x
10b	*Coprinisphaera* isp.—small			x				x	x								x	x						x				x
11	J-shaped burrow		x	x				x						x	x													
12	Vertical burrows—vari.diameter			x	x		x	x							x		x							x				
13	*Paleobuprestis* isp.			x			x						x				x											
14	*Paleoscolytus* isp.			x									x				x											
15	Irregular cavities in wood			x			x						x				x	x										
16	Smooth cavities in wood			x									x															
17	Teeth marks in dinosaur bone						x	x			x			x			x	x										
18	Circular borings in dinosaur bone						x	x			x			x			x	x										
19	cf. *Phycodes* isp.	x	x?					x				x										x						
20	Pustulose marks	x						x														x						
21	Stromatolites	x	x						x			x							x			x						
22	Borings in top of stromatolites	x	x						x			x							?			x						
23	*Lockeia* isp.	x	x					x													x							
24	*Lingulichnus* isp.	x						x													x							
25	*Arenicolites* isp.	x						x													x							

(continued on next page)

Table 1 (*continued*)

Type	Trace Fossil	Members						Lithologies						Environments										Paleosols				
		WH	TW	SW	RE	WW	BB	SS	SLT	SH	MR	LS	WD	CH	LV	OX	PF	DF	PL	DL	TI	ES	EO	EN	VT	AL	CA	SP
26	*Conichnus* isp.	x						x													x							
27	*Palaeophycus* isp.	x	x					x		x												x						
28	*Scolicia* isp.	x						x													x							
29	"*Terebellina*" isp.	x						x		x											x	x						
30	Patterned surface trail—large	x						x													x							
31	Escape traces	x						x													x							
32	*T. kollospilas*						x				x						x											
33a	Bivalve trace—dwelling		x	x			x	x	x					x														
33b	Bivalve trace—locomotion			x			x	x	x					x														
33c	Bivalve trace—escape		x				x	x	x					x														
34a	Rhizoliths—small diameter	x	x	x	x	x	x	x	x		x	x				x	x	x	x			x	x	x	x	x	x	x
34b	Rhizoliths—large diameter			x	x	x	x	x	x		x						x	x						x	x	x	x	x
34c	Tree trunk steinkerns			x	x			x	x								x						x	x				
35	*Fuersichnus* isp.		x	x				x	x							x	x		x									
36a	*Kouphichnium* isp.—resting		x					x											x									
36b	*Kouphichnium* isp.—locomotion		x					x											x			x						
37a	Gastropod feeding trace		x	x			x	x						x					x									
37b	Gastropod crawling trail		x	x			x	x						x					x									
38a	Termite nest—very large/deep				x	x?		x	x									x										x
38b	Termite nest—rhizolith specific			x	x	x?	x	x	x						x		x	x						x		x		
38c	Termite nest—rhizolith engulfing			x	x	x?	x	x	x								x	x						x		x		
38d	Termite nest—spherical			x	x			x			x						x	x						x				
38e	Termite nest—ramps			x	x			x			x						x	x						x				
38f	Termite nest—concent. galleries			x	x			x			x						x	x						x				
39a	Shallow U-tubes—reinforced		x					x											x									
39b	Shallow U-tubes—ghosts		x					x											x									
40	cf. *Planolites* isp.		x					x						x		x	x	x	x	x	x	x	x	x				x
41	Horizontal U-tubes		x	x				x						x					x									
42	Vertical Y-tubes			x				x						x														
43a	*Cochlichnus* isp.—small diam.		x					x											x									
43b	*Cochlichnus* isp.—large diam.		x					x											x									
44a	*Pterichnus* isp.—tracks	x	x					x		x									x		x	x						

Table 1 (*continued*)

Type	Trace Fossil	Members						Lithologies						Environments										Paleosols				
		WH	TW	SW	RE	WW	BB	SS	SLT	SH	MR	LS	WD	CH	LV	OX	PF	DF	PL	DL	TI	ES	EO	EN	VT	AL	CA	SP
44b	*Pteraichnus* isp.—feeding traces	x	x					x		x									x		x	x						
45	Small reptile swimming tracks		x					x											x									
46	Sauropod tracks	x	x	x			x	x	x	x	x	x		x	x		x		x		x	x		x				
47a	Ornithopod tracks	x	x	x			x	x	x	x	x	x		x	x		x		x		x	x		x				
47b	Theropod tracks	x	x	x				x	x	x	x	x		x	x		x		x		x	x		x				
48	Reptilian? burrow			x				x	x						x		x							x				
49	Mammal? burrows			x					x		x						x							x	x	x		
50	Horizontal striated burrow			x	x	x	x	x	x		x				x		x	x					x	x	x	x	x	
51	Quasi-vertical striated burrow		x	x	x		x	x	x		x				x		x	x						x	x	x	x	

Abbreviations are as follows. Members of the Morrison Formation: WH, Windy Hill; TW, Tidwell; SW, Salt Wash; RE, Recapture; WW, Westwater Canyon; BB, Brushy Basin. Lithologies: SS, sandstone; SLT, siltstone; SH, shale; MR, mudrock; LS, limestone and marl; WD, wood substrates. Environments: CH, channel; LV, levee; OX, oxbow lake; PF, proximal floodplain; DF, distal floodplain; PL, proximal lacustrine; DL, distal lacustrine; TI, tidal; ES, estuarine; EO, eolian. Paleosol occurrence: EN, entisol; VT, vertisol; AL, alfisol; CA, calcisol; SP, spodosol.

(Frey et al., 1984a). Burrow diameter is 0.5–1.0 cm, and burrow length is 3–15 cm. The burrow wall is a thin mantle of sediment in which the menisci overlap and merge into the wall. Menisci seem to be texturally sorted into fine-grained and coarser-grained menisci. These burrows differ from AMB in that cf. *Ancorichnus* does not exhibit high density of menisci, has no enlarged or bulbous features within or at the terminus of the trace, exhibit a well-defined wall, and is mainly horizontal in orientation.

Occurrence: Burrows are found predominantly in ripple- to planar-laminated sandstones and, to a lesser extent, in poorly sorted siltstones interpreted as levee, splay, and proximal floodplain deposits in the Salt Wash, Recapture, and Brushy Basin Members. These traces tend not to obliterate the bedding and are associated mostly with desiccation cracks and a few shallow penetrating rhizoliths.

Tracemaker: Based on comparisons with modern continental burrows, cf. *Ancorichnus* is interpreted as an insect burrow, most likely a beetle (Insecta: Coleoptera). Because of the distinct burrow walls and menisci, the burrower must have had fairly well-scleratized exoskeleton and appendages.

Interpretation: cf. *Ancorichnus* was constructed by adult arthropods (probably beetles) living at or just below the sediment–air interface in levee, extrachannel splay, and proximal floodplain sediments that were very moist to saturated (50–100% pore water). Such high moisture levels in these settings signify the proximity of the capillary fringe and the water table. This hygrophilic trace is often associated with fluventisols—alluvial deposits that are very little to weakly modified by pedogenesis. Because of their proximity to the channel, high flow or floodwaters often inundated these sediments.

4.3. Type 3a–c—interconnected polydomal chambers and galleries—ant nests, Fig. 4A–F

Description: Interconnected oblate to hemispherical chambers (several forms occurring together) and galleries spatially distributed as:

(a) Concentrated systems—hundreds to thousands of chambers and galleries (Fig. 4A–D).
(b) Dispersed systems—10–25 dispersed polydomal chambers and galleries (Fig. 4E).
(c) Low concentrated systems—10–30 closely spaced chambers and galleries (Fig. 4F).

As in the concentrated and dispersed systems, the architecture and distribution of the chambers and galleries changes with the depth of the nest (e.g., Fig. 4E–F). Very large nests tend to obliterate sedimentary structures, whereas small nests have minimal impact on the surrounding sedimentary structures.

Table 2
Interpreted moisture and tiering strategies represented by Morrison ichnofossils

Type	Ichnofossil	Epit	Terr	Hygro	Hydro	Surf	Shallow	Intermediate	Deep	V. deep
1	Adhesive meniscate burrows			x			x	x		
2	cf. *Ancorichnus* isp.			x			x			
3a	Ant nest—dispersed system		x				x	x		
3b	Ant nest—concentrated system		x				x	x	x	
3c	Ant nest—low concentrated system		x				x	x		
4a	*C. litonomos*				x		x			
4b	*C. eumekenomos*				x				x	
4c	*C. airioklados*				x		x	x		
5a	cf. *Celliforma*—solitary		x				x			
5b	cf. *Celliforma*—gregarious		x				x			
5c	cf. *Celliforma*—social		x				x	x		
5d	cf. *Rosellichnus* isp.		x				x			
6a	Cocoons—large		x				x			
6b	Cocoons—small		x				x			
7a	*Steinichnus* isp.			x		x	x			
7b	*Steinichnus* isp.—branched			x		x	x			
8	cf. *Cylindrichum* isp.		x				x			
9	cf. *Scoyenia* isp.			x			x	x		
10a	*Coprinisphaera* isp.—large		x				x			
10b	*Coprinisphaera* isp.—small		x				x			
11	J-shaped burrow		x				x			
12	Vertical burrows—vari. diameter		x				x			
13	*Paleobuprestis* isp.		x				x			
14	*Paleoscolytus* isp.		x				x			
15	Irregular cavities in wood			x					x	
16	Smooth cavities in wood		x						x	
17	Teeth marks in dinosaur bone	x					x			
18	Circular borings in dinosaur bone	x					x			
19	cf. *Phycodes* isp.				x		x			
20	Pustulose marks				x		x			
21	Stromatolites				x	x				
22	Borings in top of stromatolites				x	x				
23	*Lockeia* isp.				x		x			
24	*Lingulichnus* isp.				x		x			
25	*Arenicolites* isp.				x		x			
26	*Conichnus* isp.				x		x			
27	*Palaeophycus* isp.				x		x			
28	*Scolicia* isp.				x	x				
29	"*Terebellina*" isp.				x		x			
30	Patterned surface trail—large			x		x				
31	Escape traces				x		x			
32	*T. kollospilas*				x	x				
33a	Bivalve trace—dwelling				x		x			
33b	Bivalve trace—locomotion				x	x				
33c	Bivalve trace—escape				x		x			
34a	Rhizoliths—small diameter			x			x	x		
34b	Rhizoliths—large diameter			x			x	x		
34c	Tree trunk steinkerns		x			x	x			
35	*Fuersichnus* isp.				x		x			
36a	*Kouphichnium* isp.—resting				x	x				
36b	*Kouphichnium* isp.—locomotion				x	x				
37a	Gastropod feeding trace				x		x			
37b	Gastropod crawling trail				x	x				

Table 2 (*continued*)

Type	Ichnofossil	Epit	Terr	Hygro	Hydro	Surf	Shallow	Intermediate	Deep	V. deep
38a	Termite nest—very large/deep		x							x
38b	Termite nest—rhizolith specific		x				x	x		
38c	Termite nest—rhizolith engulfing		x					x		
38d	Termite nest—spherical		x					x		
38e	Termite nest—ramps		x				x	x		
38f	Termite nest—concentrated galleries		x				x	x		
39a	Shallow U-tubes—reinforced				x		x			
39b	Shallow U-tubes—ghosts				x		x			
40	cf. *Planolites* isp.				x		x			
41	Horizontal U-tubes				x		x			
42	Vertical Y-tubes				x		x			
43a	*Cochlichnus* isp.—small diam.				x	x				
43b	*Cochlichnus* isp.—large diam.				x	x				
44a	*Pteraichnus* isp.—tracks	x				x				
44b	*Pteraichnus* isp.—feeding traces	x				x				
45	Small reptile swimming tracks				x	x				
46	Sauropod tracks	x				x				
47a	Ornithopod tracks	x				x				
47b	Theropod tracks	x				x				
48	Reptilian? burrow		x				x			
49	Mammal? burrows		x					x	x	
50	Horizontal striated burrow		x				x	x		
51	Quasi-vertical striated burrow		x				x	x		

Moisture regimes are epiterraphilic (epit), terraphilic (ter), hygrophilic (hygro), and hydrophilic (hydro). Tiering depths are surface (surf), shallow (1 to 100 mm), intermediate (100 to 500 mm), deep (500 to 5000 mm), and very deep (>5000 mm). The latter category is only for those traces whose architectural morphology ranges to extreme depths.

Occurrence: These nests occur in coarse- to very fine grained sandstone and mudrock in the Tidwell, Salt Wash, Recapture, and Brushy Basin Members.

Tracemaker: Based on comparisons to modern continental burrows, these variably complex structures are interpreted to have been constructed by ants (Hymenoptera: Formicidae; e.g., Wheeler, 1910; Hutchins, 1967; Wilson, 1971).

Interpretation: The different types of nests probably represent different genera of ants similar to *Formica*, *Atta*, *Pogonomyrmex*, and *Myrmex* (e.g., Wheeler, 1910; Hutchins, 1967) constructed in bank or levee and proximal and distal floodplain sediments. These ichnofossils represent the earliest known fossil evidence of ants and predate body fossils in amber by 50 million years (e.g., Wilson et al., 1967; Hölldobler and Wilson, 1990). The composite nature of these terraphilic ichnofossils indicates social behavior between nest mates via cooperation in nest construction and maintenance and a likely division of labor, similar to that of modern ants (e.g., Wilson, 1971; Hölldobler and Wilson, 1990). Nests were constructed in subaerial conditions where the ants lived in the upper vadose zone. Deeper nests signify lower soil moisture and water-table levels. Shallower, smaller nests, like those constructed in braided river deposits along active channel complexes, represent higher moisture and water-table levels.

4.4. Type 4—Camborygma isp. [4a: Camborygma litonomos Hasiotis and Mitchell (1993), 4b: Camborygma eumekenomos Hasiotis and Mitchell (1993), 4c: Camborygma araioklados Hasiotis and Mitchell (1993)]—crayfish burrows, Fig. 5A–G

Description: Burrows with 2–10 cm diameters with simple to complex architectures that vary among:

(a) A single vertical or U-shaped tubes < 50 cm long (Fig. 5A).

(b) Quasivertical burrows < 50 cm long with one or more openings culminating in a shaft or chamber with or without a lower shaft (Fig. 5B,F–G).

Table 3
Interpreted possible taxonomic diversity represented by Morrison terrestrial, freshwater, and transitional marine ichnofossils

Type	Ichnofossil	Constructor(s)	Class or order	Superfamily/family
1	Adhesive meniscate burrows	soil bugs/beetles	Hemiptera/Coleoptera	
2	cf. *Ancorichnus* isp.	beetles	Coleoptera	
3a	Ant nest—dispersed system	ants	Hymenoptera	
3b	Ant nest—concentrated system	ants	Hymenoptera	
3c	Ant nest—low concentrated system	ants	Hymenoptera	
4a	*C. litonomos*	crayfish	Decapoda	Cambaridae
4b	*C. eumekenomos*	crayfish	Decapoda	Cambaridae
4c	*C. airioklados*	crayfish	Decapoda	Cambaridae
5a	cf. *Celliforma*—solitary	soil bees	Hymenoptera	Apoidea
5b	cf. *Celliforma*—gregarious	soil bees	Hymenoptera	Apoidea
5c	cf. *Celliforma*—social	soil bees	Hymenoptera	Apoidea
5d	cf. *Rosellichnus* isp.	soil bees	Hymenoptera	Apoidea
6a	Cocoons—large	wasps	Hymenoptera	Sphecidae?
6b	Cocoons—small	wasps	Hymenoptera	Sphecidae?
7a	*Steinichnus* isp.	mole crickets	Orthoptera	Gryllotapidae?
7b	*Steinichnus* isp.—branched	mud-loving beetles	Coleoptera	Heteroceridae?
8	cf. *Cylindrichum* isp.	tiger beetles	Coleoptera	Cicindelidae?
9	cf. *Scoyenia* isp.	beetle/fly larvae	Coloeptera/Diptera	
10a	*Coprinisphaera* isp.—large	dung beetles	Coleoptera	Scarabaeidae
10b	*Coprinisphaera* isp.—small	dung beetles	Coleoptera	Scarabaeidae
11	J-shaped burrow	rove beetles	Coleoptera	Staphylinidae
12	Vertical burrows—vari. diameter	wasps?	Hymenoptera?	Sphecidae?
13	*Paleobuprestis* isp.	bark beetles	Coleoptera	Buprestidae?
14	*Paleoscolytus* isp.	engraver beetles	Coleoptera	Scolytidae?
15	Irregular cavities in wood	fungus	Fungi[a]	
16	Smooth cavities in wood	wood-boring insects		
17	Teeth marks in dinosaur bone	dinosaur-carnivore?	Dinosauria	Allosauridae?
18	Circular borings in dinosaur bone	carian beetles	Coleoptera	Dermestidae
19	cf. *Phycodes* isp.	polychaete worm?	Annelida[b]	
20	Pustulose marks	polychaete worm?	Annelida[b]	
21	Stromatolites	cyanobacteria	Monera[a]	
22	Borings in top of stromatolites	insect larva or clams		
23	*Lockeia* isp.	clams		
24	*Lingulichnus* isp.	finger nail clams	Brachiopoda[b]	Lingulidae
25	*Arenicolites* isp.	polychaete worm	Annelida[b]	
26	*Conichnus* isp.	anenome		
27	*Palaeophycus* isp.	annelid?	Annelida?[b]	
28	*Scolicia* isp.	snail? echinoid?		
29	"*Terebellina*" isp.	polychaete? annelid?		
30	Patterned surface trail—large	snails? crabs?		
31	Escape traces	bivalves?		
32	*T. kollospilas*	caddisflies	Trichoptera	Limnephilidae?
33a	Bivalve trace—dwelling	clams	Pelecypoda	Unionidae
33b	Bivalve trace—locomotion	clams	Pelecypoda	Unionidae
33c	Bivalve trace—escape	clams	Pelecypoda	Unionidae
34a	Rhizoliths—small diameter	roots	Plantae[a]	Gymnosperms
34b	Rhizoliths—large diameter	roots	Plantae[a]	Gymnosperms
34c	Tree trunk steinkerns	tree	Plantae[a]	Gymnosperms
35	*Fuersichnus* isp.	mayfly	Ephemeroptera	
36a	*Kouphichnium* isp.—resting	horseshoe crab	Merostomata	
36b	*Kouphichnium* isp.—locomotion	horseshoe crab	Merostomata	
37a	Gastropod feeding trace	snail	Gastropoda	
37b	Gastropod crawling trail	snail	Gastropoda	

Table 3 (*continued*)

Type	Ichnofossil	Constructor(s)	Class or order	Superfamily/family
38a	Termite nest—very large/deep	termites	Isoptera	Macrotermitidae?
38b	Termite nest—rhizolith specific	termites	Isoptera	Kalotermitidae?
38c	Termite nest—rhizolith engulfing	termites	Isoptera	Rhinotermitidae?
38d	Termite nest—spherical	termites	Isoptera	Termitidae?
38e	Termite nest—ramps	termites	Isoptera	Termitidae?
38f	Termite nest—concent. galleries	termites	Isoptera	Macrotermitidae?
39a	Shallow U-tubes—reinforced	midge	Diptera	Chironomidae?
39b	Shallow U-tubes—ghosts	larva	Diptera?	Chironomidae?
40	cf. *Planolites* isp.			
41	Horizontal U-tubes	mayflies	Ephemeroptera	
42	Vertical Y-tubes	caddisflies?	Trichoptera?	Polycentropodidae?
43a	*Cochlichnus* isp.—small diam.	nematod? ins. larva		
43b	*Cochlichnus* isp.—large diam.	aquatic worm	Annelida[b]	
44a	*Pteraichnus* isp.—tracks	pterosaur		
44b	*Pteraichnus* isp.—feeding traces	pterosaur		
45	Small reptile swimming tracks	crocodile? turtle?		
46	Sauropod tracks	sauropods		
47a	Ornithopod tracks	ornithopods		
47b	Theropod tracks	therapods		
48	Reptilian? burrow	reptile		
49	Mammal? burrows	mammal		
50	Horizontal striated burrow	insects? larvae?		
51	Quasi-vertical striated burrow	cicada nymph?	Homoptera?	

[a] Denotes kingdom.

[b] Denotes class.

(c) Vertical tubes 50–100+ cm long with or without multiple openings terminating in a chamber or laterally branching tunnels (Fig. 5C–E).

The surficial morphology of all these burrows have scrape marks (transverse ridges, cm scale), scratch marks (quasilongitudinal, mm scale), knobby and hummocky textures (cm scale), and mud and lag liners (wall-packed material, cm scale; Hasiotis and Mitchell, 1993). In general, the burrow density is low, with no more than five burrows observed within a square meter.

Occurrence: Burrows occur in fine-grained sandstone, siltstone, and mudrock in the Tidwell, Salt Wash, Recapture, and Brushy Basin Members.

Tracemaker: Burrows were constructed probably by freshwater and terrestrial crayfish (Decapoda: Cambaridae) (Hasiotis and Mitchell, 1993).

Interpretation: Architecture and depth of the hydrophilic burrows reflect the depth and fluctuation of the ancient water table (Hasiotis and Mitchell, 1993). *C. litonomos* was constructed in sediments deposited in channel, levee or bank, and proximal lacustrine environments that were episodically subaerially exposed. *C. eumekenomos* was constructed in mainly proximal floodplain environments in subaerially exposed sediments with water tables 100–150 cm in depth. *C. araioklados* was constructed in sediments deposited in channel, levee or bank, and proximal lacustrine environments that were often subaerially exposed.

4.5. Type 5a–c—cf. Celliforma isp.—bee nests, 5d—cf. Rosellichnus isp., Figs. 6A–H, 7A–B

Description: Large aggregations (50 or more individuals; Fig. 6A–C), small clusters (Fig. 6D,G,H), to solitary (Fig. 6E,F) smooth-walled, flask-shaped cells (e.g., Brown, 1934), each approximately 0.5–0.7 cm wide and 1–2 cm long. Some cells have extended necks (Fig. 6F), whereas others may or may not have spiral caps. Cells may or may not be associated with narrow shafts and tunnels as much as 0.7 cm wide that form U-shaped to multiply branched networks from 10 cm to more than 40 cm in depth. A rare configuration of cells contains clusters that share adjacent

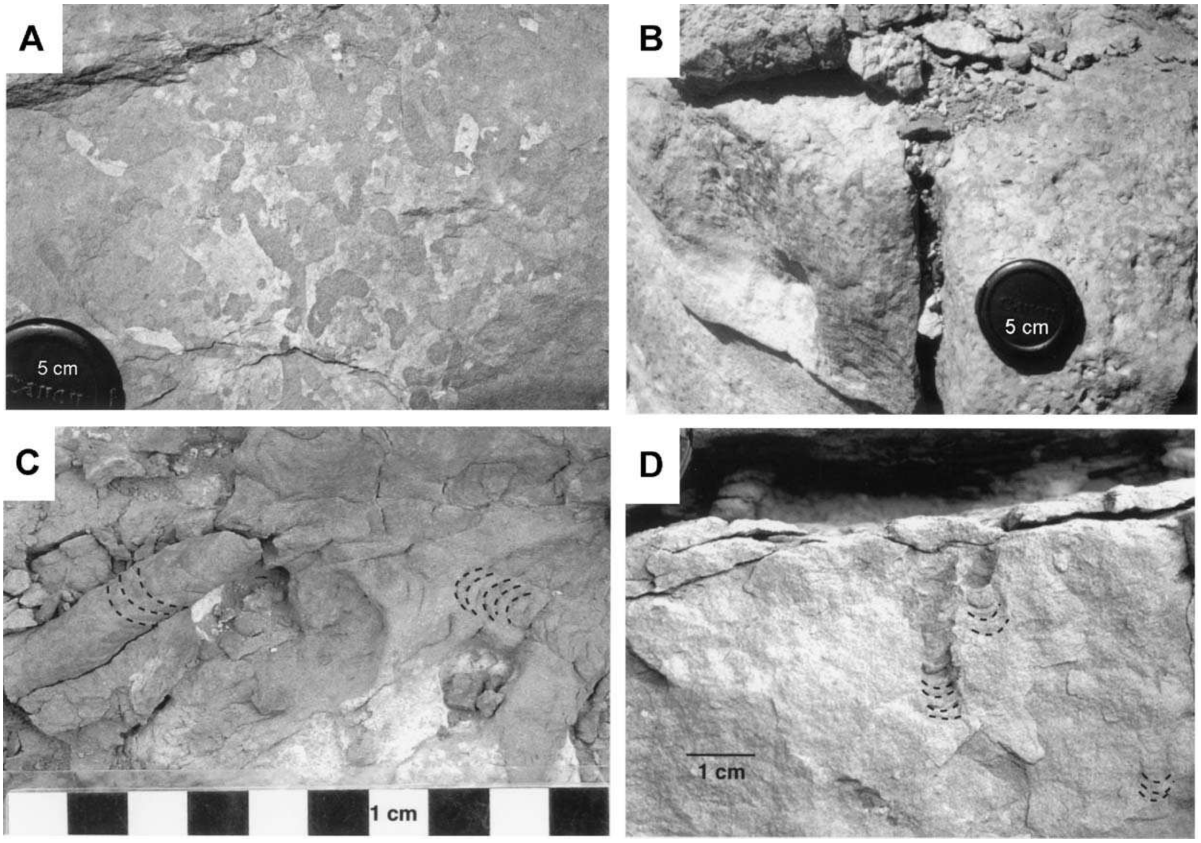


Fig. 3. Typical occurrence of adhesive meniscate burrows (AMB): (A) Salt Wash Member, Shootaring Canyon, UT; (B) Brushy Basin Member, Salt Valley Anticline, UT; (C–D), Examples of cf. *Ancorichnus* isp. that show external and internal backfill patterns (C), upper Morrison Formation, Fox Mountain, WY (33), and discrete backfill in heavily bioturbated sandstone (D), Brushy Basin Member, Moore Cut-off Road, UT (4). Dashed lines show the position of the backfilled sediment.

cell walls occur with as few of 3 cells to as many as 10 cells, (e.g., Genise and Bown, 1996). In general, cells may obliterate partly to completely the sedimentary structures of the beds.

Occurrence: These traces occur in fine-grained sandstone and mudrock deposits in the Tidwell, Salt Wash, and Brushy Basin Members. Wall-sharing cell clusters occur only in the Salt Wash Member.

Tracemaker: These traces resemble most closely the brood cells constructed in shallow to deep subterranean nests of ground-dwelling bees (Hymenoptera: Apoidea). Individual cells (Type 5a) and closely spaced individual cells (Type 5b) are the nesting grounds of solitary bees. Tightly packed individual cells to small clusters of cells associated by shafts and tunnels (Type 5c) are nests of primitively social ground-dwelling bees (e.g., Michener, 1974). Cell clusters that share walls (Type 5d) are tentatively assigned to *Rosellichnus* isp.; these traces may be the work of one female (e.g., Genise and Bown, 1996).

Interpretation: The terraphilic ichnofossil nests are various forms of behavior likely of anthophorid and halictid bees (Sakagami and Michener, 1962) constructed in proximal and distal floodplain sediments undergoing varying degrees of pedogenesis. In general, the number of cells in these nests indicates short-term to long-term usage over one or more breeding seasons (e.g., Michener, 1974). For example, few cells suggest that the nest was relatively new, whereas greater numbers of cells suggest that the nest was used for a much longer period of time.

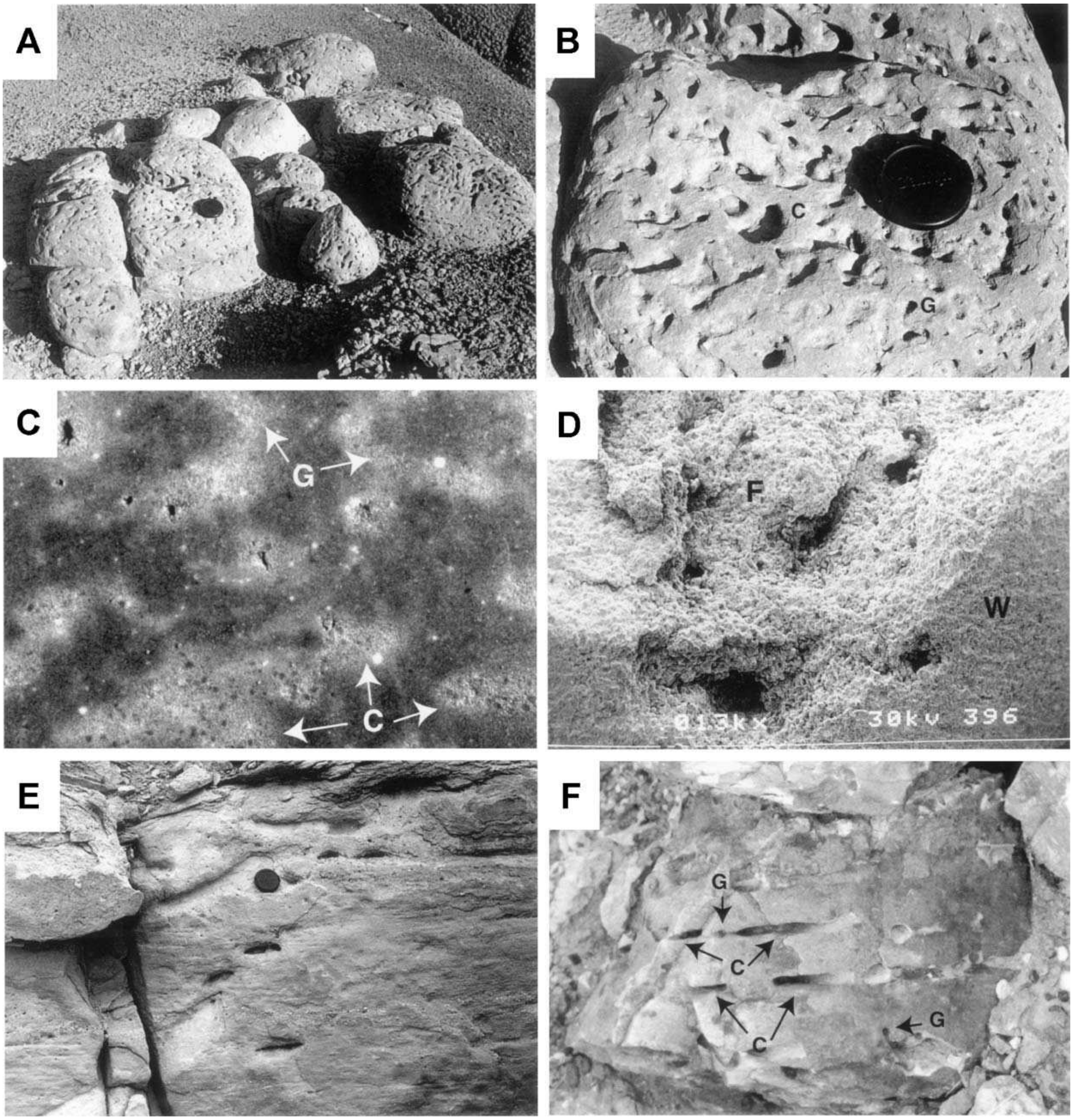
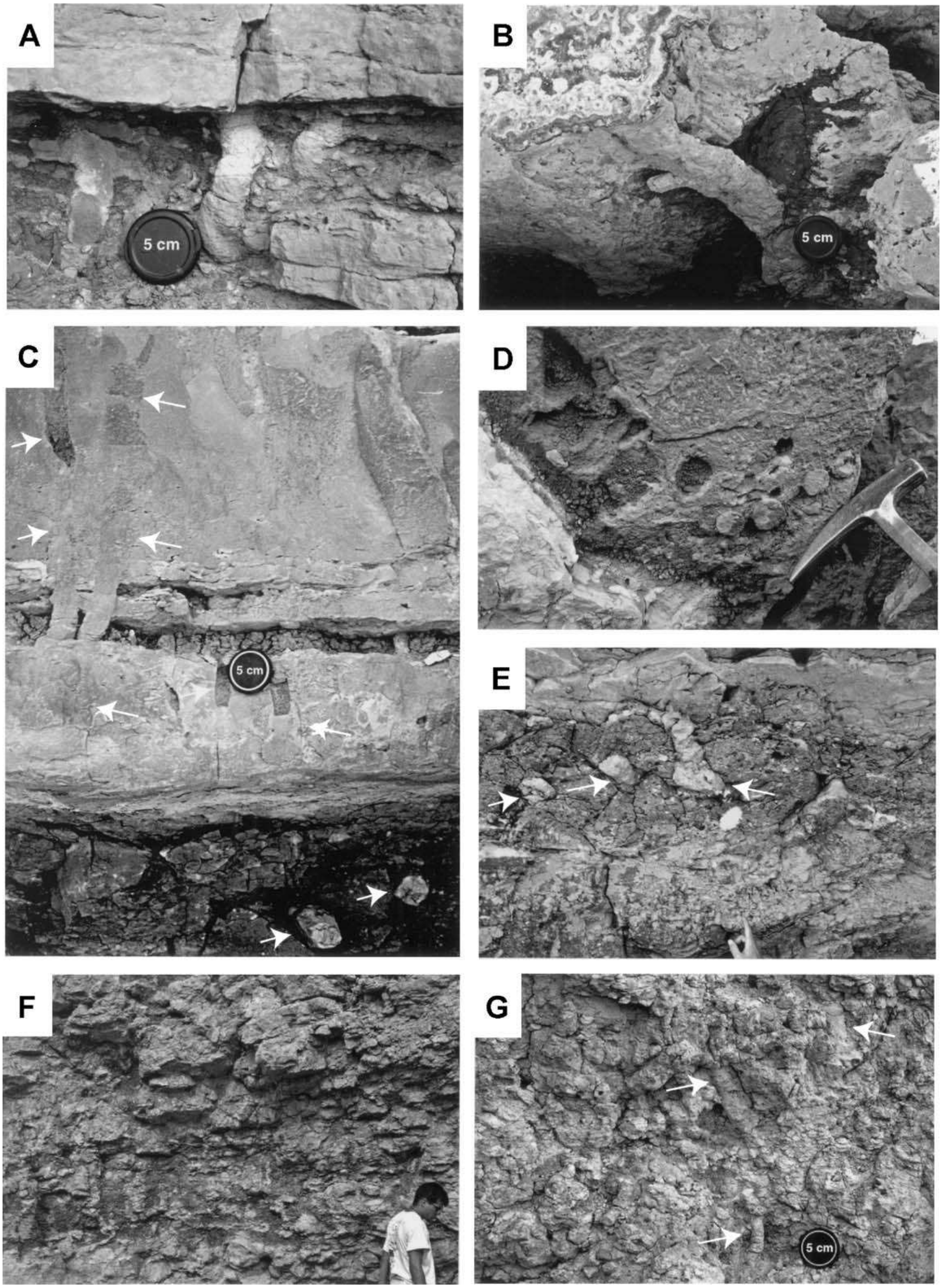


Fig. 4. Dispersed and concentrated chamber and gallery systems interpreted as ant nests. Concentrated chamber–gallery system, lowermost Brushy Basin Member, Hanksville (3). (A) Outcrop and (B) close-up of nest. (C) Rock polished section through part of the nest showing the internal distribution of chambers (labled with a C) and galleries (labled with a G). (D) SEM photo of area between a chamber and surrounding matrix. The walls (labled with a W) of the chambers appear compacted, while the fill (labled with an F) is not compacted. The photo is about 1 mm wide. (E) Dispersed chamber–gallery system, lowermost Salt Wash Member, Hatt Ranch, UT (14). Lens cap for scale = 5 cm. (F) Lower part of concentrated chamber–gallery system containing horizontal flattened chambers (labled with a C) and few galleries (labled with a G), middle Brushy Basin Member, Moore Cut-Off Road (4); the figure is about 40 cm wide.


A
5 cm
B
5 cm
C
5 cm
D
E
F
G
5 cm

Sedimentary structures associated with nests of fewer cells are encompassed by a small amount of disturbed sediment compared to larger nests where no sedimentary structures are preserved. Shallow cells and nests reflect higher soil moisture levels, whereas deeper cells imply lower soil moisture levels because the bees must burrow deeper to reach suitable cell construction sites (e.g., Michener, 1974). The number of cells and the overall amount of bioturbation increased with greater duration of subaerial exposure of that environment.

The earliest known bee body fossil comes from Cretaceous amber (Michener and Grimaldi, 1988) dated 90–110 million years old. These Jurassic Morrison bee nests are not unusual because older bee nests have been interpreted in Triassic rocks in Petrified Forest National Park, Arizona (Hasiotis et al., 1995, 1996; Hasiotis, 1997b), while similar traces interpreted as bee nests have been described from the Cenomanian (lowermost part of the Upper) Cretaceous in Arizona (Elliot and Nations, 1998).

Also present in the Morrison Formation, particularly in the friable sandstone units in the Salt Wash and Brushy Basin Members, are nests of extant species of bees attributed to the Adrenidae (Fig. 7A,B) which were constructed sometime in the Holocene. These nests represent the only known hard ground continental burrowers described to date (e.g., Mikulas and Cilek, 1998; Hasiotis, unpublished data) and can be mistaken easily for trace fossils constructed in the Upper Jurassic sediments.

4.6. Type 6a and b—spindle- to tablet-shaped cocoons (small, large)—wasp nests, Fig. 8A,B

Description: Small clusters of 4 to 10 individual spindle- to tablet-shaped casts and molds 10–35 mm long and 0.3–1.5 cm in diameter are interpreted as cocoons (Fig. 8A,B). The surficial morphology of the best-preserved portions of the cocoons has a woven, threadlike pattern.

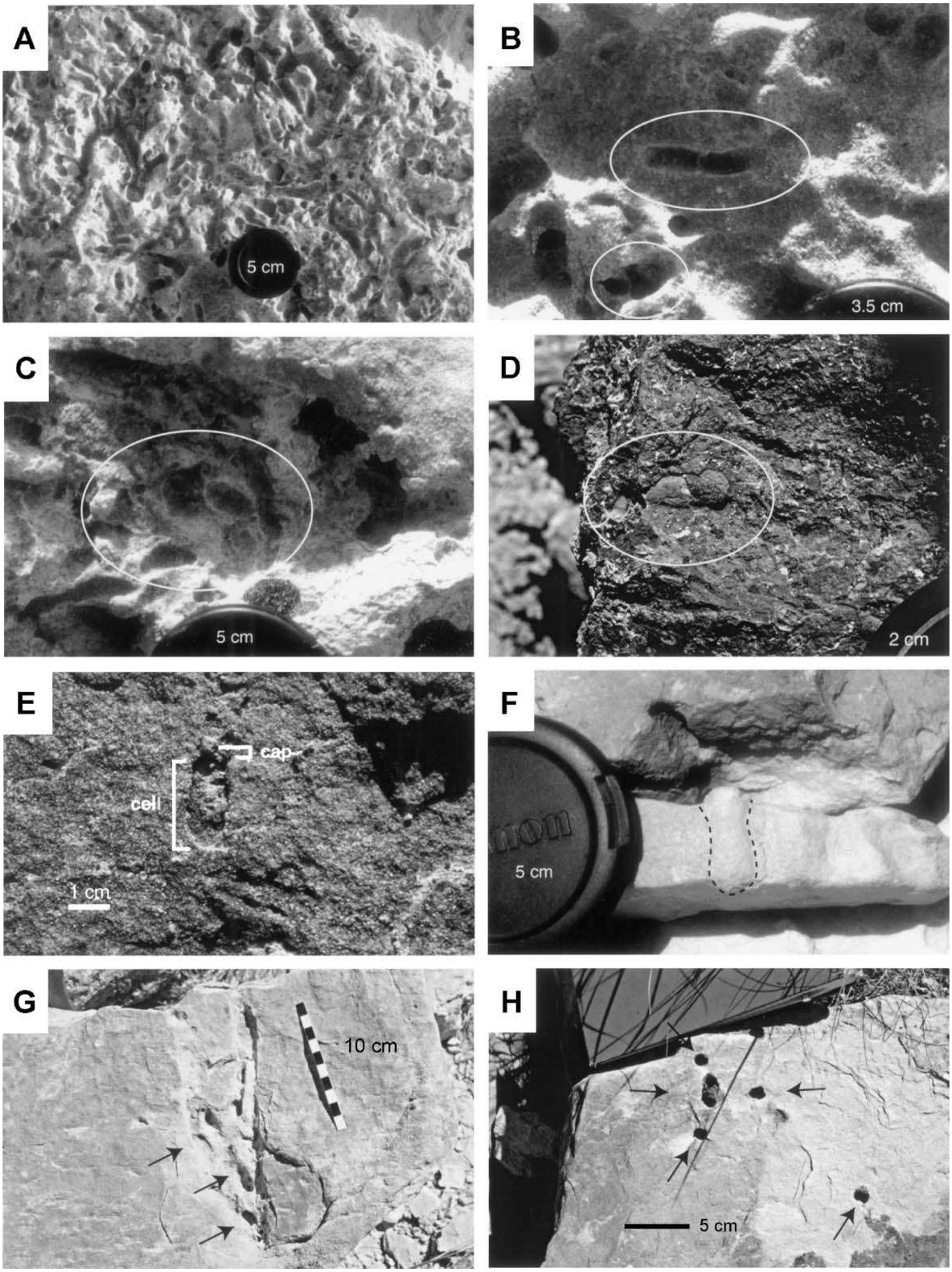
Occurrence: These traces occur in fine-grained sandstone and siltstone deposits of the Salt Wash Member.

Tracemaker: Cocoon morphology and configurations strongly resemble nests of gregarious sphecid wasps (e.g., Evans, 1963), which nest in close proximity to one another, construct nests with of 4 to 20 cells, and whose larvae spin cocoons with a sturdy silk. The clusters of small and large cocoons most likely represent different genera of sphecid wasps or variably provisioned cells of the same species (e.g., Evans and Eberhard, 1970).

Interpretation: The terraphilic wasp nests were constructed in proximal and distal floodplain sediments undergoing varying degrees of pedogenesis. The depth of the cocoons (nests) reflects the relative position of the upper vadose zone. Shallow cells and nests (Fig. 8A,B) indicate higher soil moisture levels, whereas deeper cocoons imply lower soil moisture levels because wasps must burrow deeper to reach suitable construction sites (e.g., Evans, 1963).

The earliest known wasp body fossils come from Lower Cretaceous lacustrine deposits (e.g., Darling and Sharkey, 1990; Rasnitsyn et al., 1998) dated 110 million years old. The occurrence of Jurassic Morrison cocoons are not unusual because older traces interpreted as wasp cocoons occur in Triassic rocks in Petrified Forest National Park, Arizona (Hasiotis et al., 1995, 1996; Hasiotis, 1997b), and similar traces interpreted as wasp cocoons have been described also from the Upper Cretaceous (Hasiotis et al., 1996). Although no wasp body fossils have been found in Triassic or Jurassic deposits, the morphology of the traces suggest the existence of wasps earlier than their earliest known body fossil record. Darling and Sharkey (1990) are convinced that the fossil record of these, other higher taxa Aculeata, and the Hymenoptera are much older than their known body fossil records, based on the derived morphological characters possessed by many of the body fossils described to date and their diversity by the Early Cretaceous.

Fig. 5. *Camborygma* isp. interpreted as crayfish burrows. (A) *C. litonomos*, a U-shaped burrow in interbedded sandstone and siltstone levee deposit, Salt Wash Member, Shootaring Canyon, UT. (B) *C. litonomos* in a muddy channel deposit, Salt Wash Member, Shootaring Canyon, UT. (C) *C. eumekenomos* (arrows) in a proximal siltstone floodplain deposit, with view of the burrows (D) from the bottom of the burrow-bearing bed, Recapture Member, Aneth, UT. (E) *C. eumekenomos* terminating in a chamber and associated with lateral components (arrows) of vertical burrows (C) and (D) from above. (F) *Camborygma* isp. in a calcrete (calcic vertisol), with burrow examples (arrows) located to left and above the lens cap (G), Brushy Basin Member, Ruby Ranch, UT.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4.7. Type 7a (unbranched) and b (branched)—Steinichnus isp., Fig. 9A–E

Description: Horizontal burrows 1–2 cm in diameter and 5–25 cm long with false Y- and T-shaped intersections (Fig. 9D), formed by burrows that crosscut another burrow and follow the previous path (e.g., Bromley and Asgaard, 1979). Some burrows exhibit true branching patterns (Fig. 9E). Both types of burrows may have sections of expanded diameters. Textures of burrow fill range from backfill menisci to massive to vuggy. The surficial morphology ranges from transverse crescentic, crosscutting ridges (Fig. 9A,B) to knobby markings (Fig. 9D).

Occurrence: These traces occur in thin to thick, interbedded fine-grained sandstones and siltstones in the Tidwell, Salt Wash, and Brushy Basin Members.

Tracemaker: Burrow architecture and surficial morphology are similar to burrows constructed by mud-loving beetles (Heteroceridae) and mole crickets (Gryllotalpidae) (Chamberlain, 1975; Metz, 1990). Mole crickets may have constructed nonbranching burrows, whereas mud-loving beetles probably constructed the branching burrow systems.

Interpretation: *Steinichnus* isp. was constructed in water-saturated sediments at the sediment–water–air surface in shoreline settings of channel–levee and proximal lacustrine environments. These hygrophilic traces are associated with bedding surfaces that exhibit locally ripple marks and desiccation cracks whereas others lack desiccation cracks, suggesting brief periods of subaerial exposure that allowed construction of burrows. Unbranched and branched varieties of *Steinichnus* isp. rarely occur together. Unbranched varieties of *Steinichnus* isp. are associated predominantly with lacustrine environments, whereas branched varieties are associated mostly with channel–levee environments.

4.8. Type 8—cf. Cylindrichum isp.—tiger beetle burrow (Coleoptera), Figs. 9E, 10A,B

Description: The burrows are vertical straight tubes (e.g., Linck, 1949). They occur individually or in groups of two to four. Burrows are 0.3–0.5 cm in diameter and 2–3 cm long (Figs. 9E, 10A,B). Burrow walls are irregular but relatively smooth with few diagonal scratches constituting the surficial morphology.

Occurrence: The burrows occur in fine-grained sandstone and siltstone deposits in the Tidwell, Salt Wash, and Brushy Basin Members.

Tracemaker: The burrow morphologies indicate construction most similar to the burrows of tiger beetle larvae of the Cicindelidae (e.g., Chamberlain, 1975).

Interpretation: The possible Jurassic tiger beetle burrows were constructed in channel–levee alluvial environments as well as in proximal lacustrine environments. The larvae constructed vertical, straight tube dwelling and shelter burrows in subaerial portions of point bars and in mid- and lateral-channel bars. In lacustrine siliciclastic systems, the larvae constructed vertical burrows in subaerial portions of distributary channel bars, crevasse–splay sands, and shoreline sands. The architecture of the terraphilic burrow reflects lower water levels within and along the channel and shoreline such that the capillary fringe is close to the sediment surface but does not reach it.

4.9. Type 9—cf. Scoyenia isp.—insect larvae (Coleoptera? and Diptera?), Fig. 9F

Description: Slender burrows having ropelike surficial morphology. Burrow diameters are from 0.5–1.0 cm and up to 10 cm long. Burrows are unbranched and horizontal. They sometimes are thickened and

Fig. 6. Simple to complex arrangement of flask-shaped cells and gallery systems interpreted as bee (Hymenoptera: Apoidea) nests. (A), (B), and (C): Shallow distribution of smooth-walled, flask- to capsule-shaped cells of a laterally constructed series with cells constructed in series, upper part of the Salt Wash Member, Shootaring Canyon, UT (6). Some cells appear isolated (C) but clearly show the smooth wall, flask-shaped construction. (D) Isolated cell (circle) from a simple vertical nest with only four individual cells identified, middle part of the Brushy Basin Member, Montezuma Creek, UT (2). (E) Isolated cell from a simple vertical nest with only two cells identified, middle part of the Salt Wash Member, Blue Mesa, CO (40). Triangular cap clearly visible. (F) Isolated cell showing flask-shaped construction (inside dashed line) from a simple, shallow nest, lower part of the Salt Wash Member, Shootaring Canyon, UT (6). Cross-section (G) and plan-view section (H) through simple nests with up to 6 cells (arrows), Marsh quarry area, lower part of the Brushy Basin Member, Cañon City, CO (2).

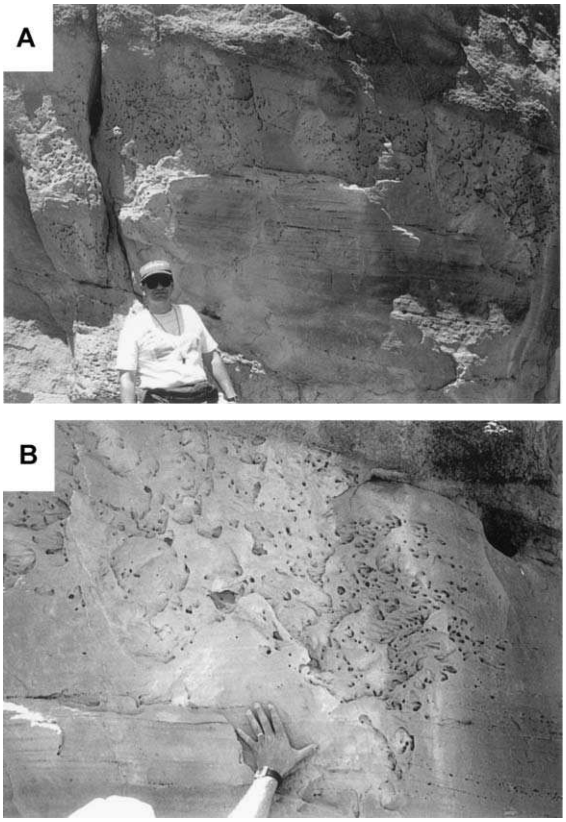


Fig. 7. Modern communal nests excavated in friable channel sandstone by bees belonging to the Andrenidae and represent hard ground borers. (A) Lateral extent to which these nests are constructed by many individuals and cover up to 8 m^2 or more. (B) Close-up of nest architecture and shallow construction of galleries and cells.

thinned locally along their length. The burrow interior is composed of meniscate backfilling.

Occurrence: These burrows were found at only one locality in interbedded fine-grained sandstone and siltstone in the upper part of the Brushy Basin Member, Skyes Mountain, WY.

Tracemaker: The surficial morphology suggests that deposit-feeding insect larvae, probably beetles (Coleoptera) or craneflies (Diptera), produced the burrows.

Interpretation: These hygrophilic burrows were constructed in point bar and levee sediments. The sediments were partially bioturbated and then rapidly buried by the next levee-building sedimentation event. The burrow thickening and thinning suggests that the organism moved and pushed itself through the sediment using peristaltic muscle expansion and contractions. Exterior ornamentation (scratches) implies that the limb morphology or protuberances on the body of the organism was adapted for gripping to the burrow walls to enhance the peristaltic burrowing technique. The presence of the fine-scratch pattern suggests that the burrows were constructed in moist, compact substrates such as silty clay (e.g., Hasiotis and Bown, 1992; Hasiotis and Dubiel, 1993). The mode of occurrence (sediment package and burrow morphology) suggests that this trace is indicative of very high soil moisture approaching 100% saturation of freshwater.

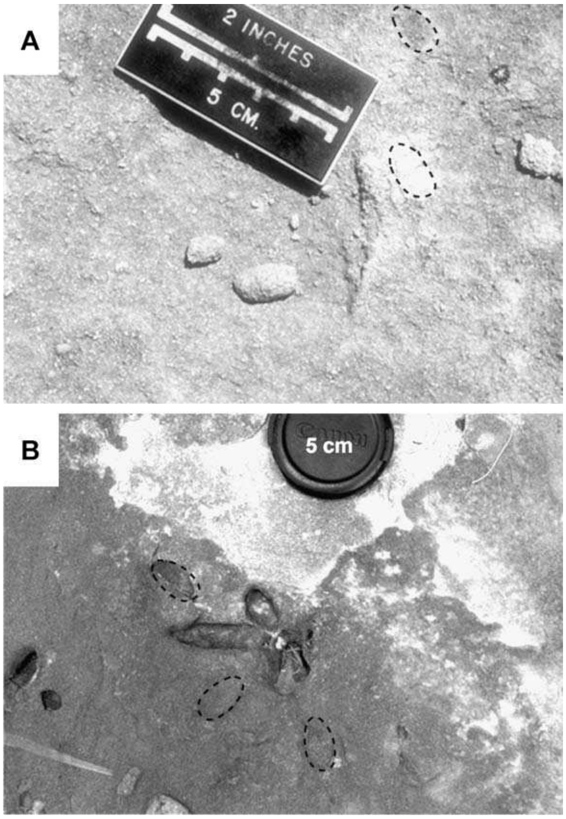


Fig. 8. Cocoons and nests interpreted as various types of wasp nests used for reproduction. (A) Several cocoons weathered from the outcrop and still within the outcrop (dashed lines), upper part of the Salt Wash Member, Green River, UT (9). (B) Natural outcrop cross-section through a nest that exhibits several cocoons (dashed lines) associated with partially preserved tunnels (center of the photo), Naturita, CO (39).

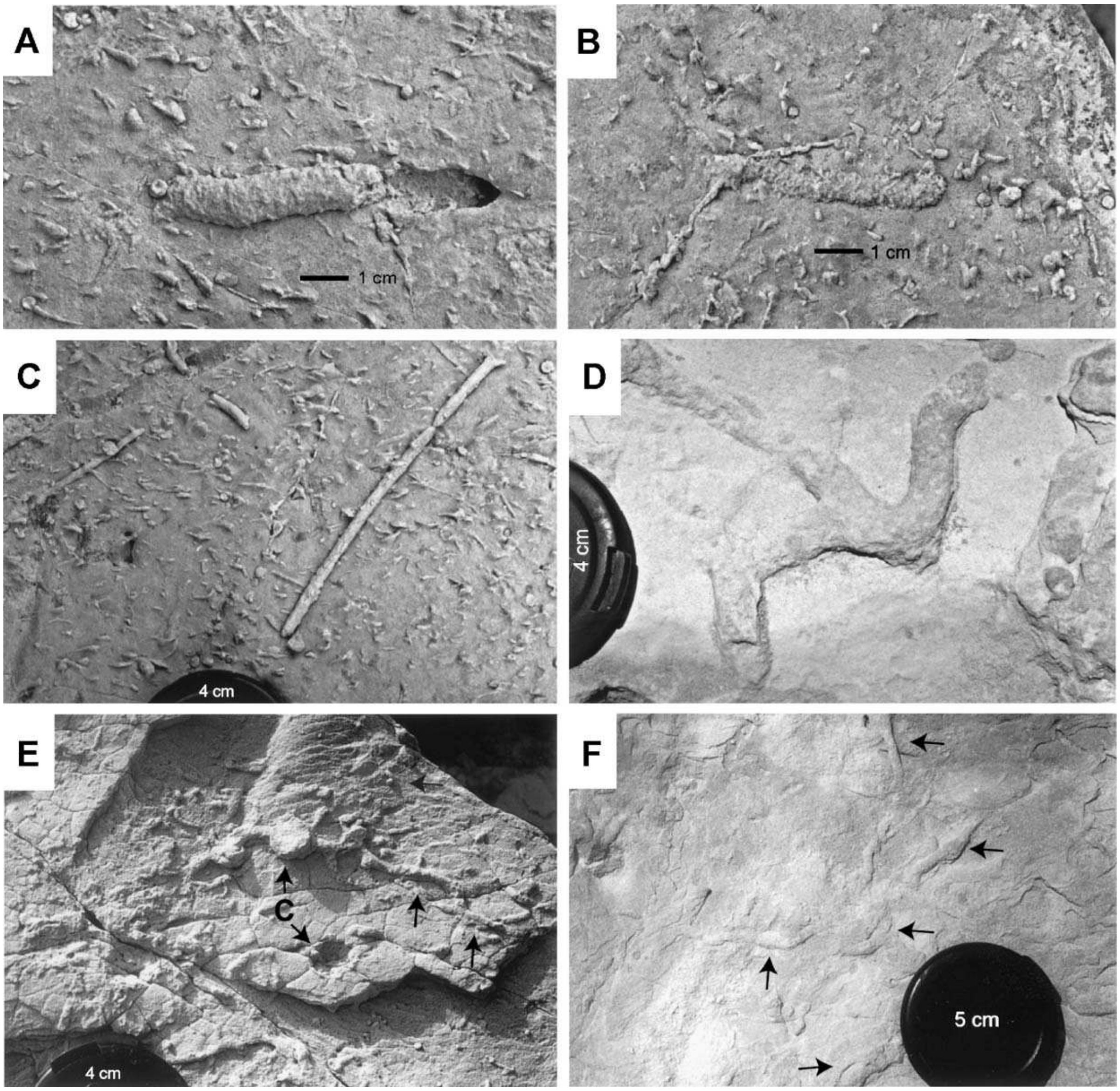


Fig. 9. Flattened horizontal and cylindrical vertical burrows interpreted as various types of beetle (Insecta: Coleoptera) burrows. A–C, *Steinichnus* isp. with transverse striations in laminated calcareous sandstone, lowermost part of the Tidwell Member, Hatt Ranch (A-13) and Shootaring Canyon, UT (B, C-6). (D) Interpenetrating *Steinichnus* isp., lower part of the Salt Wash Member, Shootaring Canyon, UT (6). (E) Small diameter, branching horizontal burrows (arrows), assigned to *Steinichnus* isp., penetrated by small to large diameter vertical burrows (labeled with a C), assigned to *Cylindrichum* isp. (labled with a C), upper part of the Brushy Basin Member, Cleveland–Lloyd Quarry, UT (12). (F) Slightly sinuous horizontal burrows with faint striations similar to *Scoyenia* isp., middle part of the Morrison Formation (undifferentiated), Sykes Mountain, WY (35).

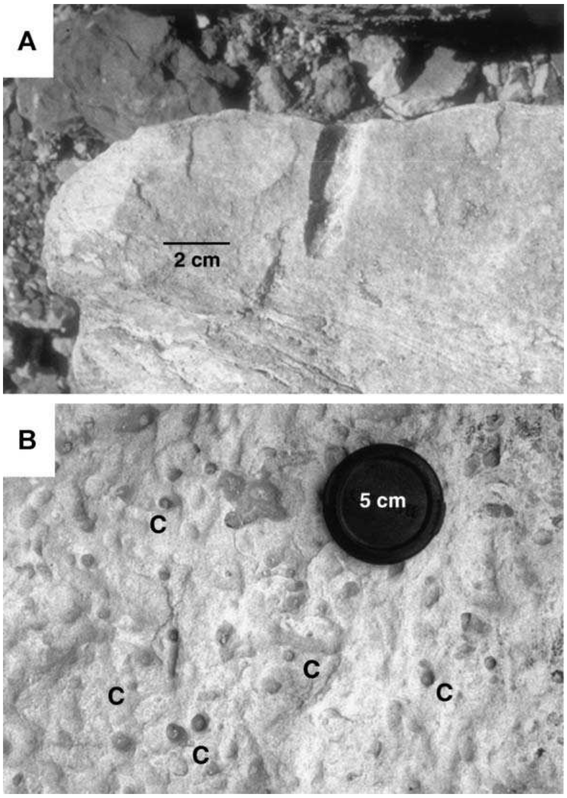


Fig. 10. Vertical, test-tube-shaped burrows assigned to cf. *Cylindrichum* and interpreted as tiger beetle burrows. (A) Cross-section through cf. *Cylindrichum*, lower part of the Salt Wash Member, Shootaring Canyon, UT (6); note that the upper portion of the bed is massive and likely to have been churned by several generations of bioturbation. (B) Bedding plane view of the openings to many individuals of cf. *Cylindrichum* (labled with a C), upper part of the Salt Wash Member, Shootaring Canyon, UT (6).

4.10. Type 10a (large) and b (small)—Coprinisphaera isp.—dung beetle nest (balls), Fig. 11A,B

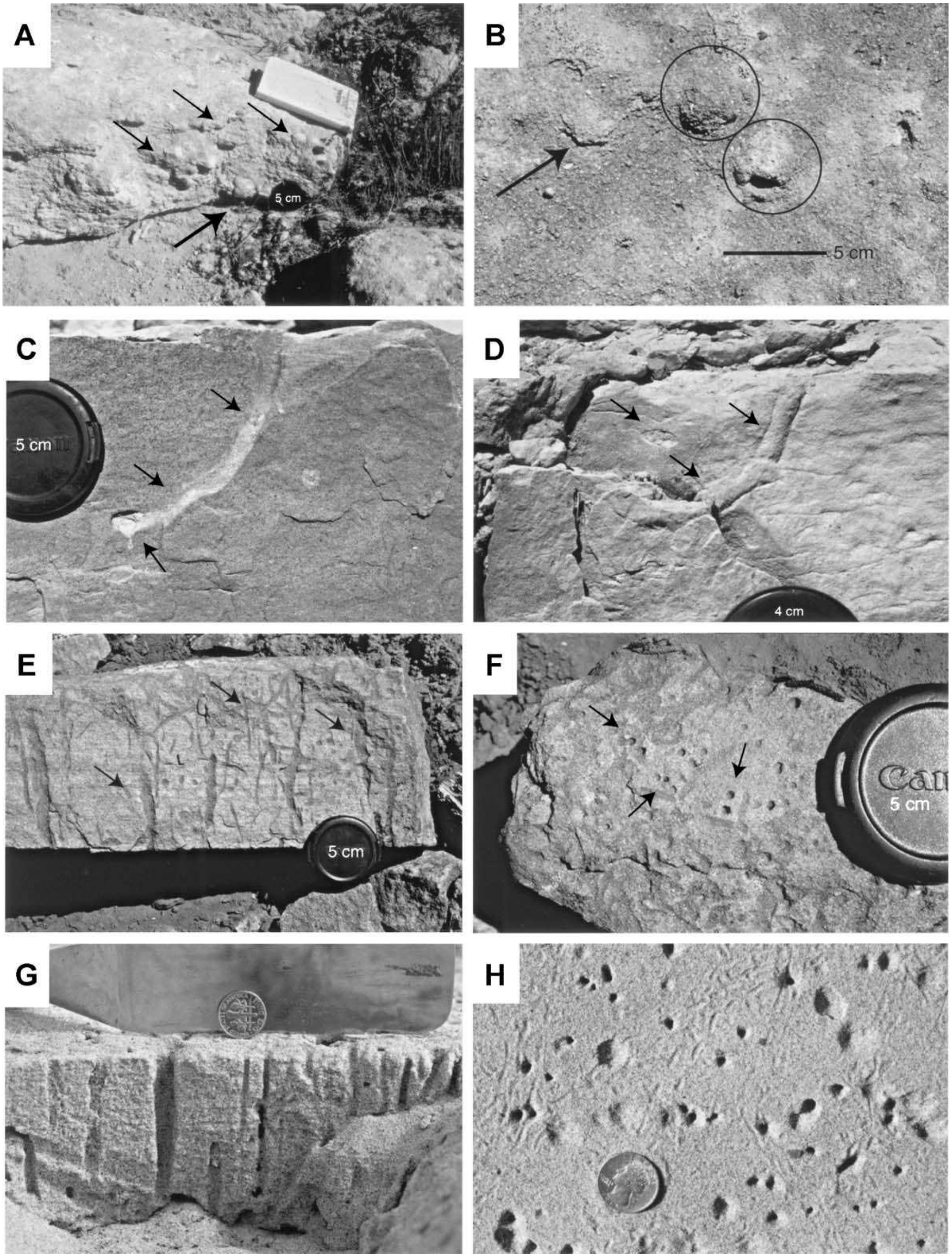
Description: Spherical to pear-shaped masses (a) 3–4 and (b) 5–6.5 cm in diameter with sediment-filled interiors. Some masses exhibit a small hole in the top, 0.2–0.5 cm in diameter. When broken open, the best-preserved masses have an external wall about 0.5–0.8 cm thick. Other masses contain a larger hole at the top or are missing the upper quarter to one-third of the spheroid.

Occurrence: These traces occur in isolated clumps in pedogenically modified, massive, very fine to medium grained sandstone and siltstone in the upper part of the Salt Wash Member. These units are associated with trough cross-stratified, ripple- and planar-laminated sandstone interbedded with siltstone and mudrock.

Tracemaker: These traces are most similar to nests constructed by extant dung beetles (Coleoptera: Scarabaeidae; e.g., Halffner and Edmonds, 1982).

Interpretation: The Salt Wash spheroids, which occur in alluvial proximal and distal floodplain environments, are similar to *Coprinisphaera* described by Genise and Bown (1994a) from Miocene alluvial paleosols in Argentina. Thus, these terraphilic traces represent the earliest known occurrence of *Coprinisphaera*. These Morrison traces are most abundant in proximal floodplain environments that include extrachannel deposits (outer levee, overbank) and occur in units that contain sauropod footprints and trackways. The Salt Wash *Coprinisphaera* are likely to represent dung beetles using the excrement of herbivorous dinosaurs feeding or traveling close to open water bodies. The beetles rolled balls of the partially digested plant material contained in the dung, which would also incorporate a large amount of sediment during the rolling process. The balls were later buried in a subterranean nest in relatively close proximity to the source of dung in sediment that was well aerated in the uppermost vadose zone. *Coprinisphaera* nests composed of relatively larger balls each may have contained three to four balls. Nests composed of smaller balls may have contained only two to three balls. In both cases, however, several mating periods

Fig. 11. Spherical traces (arrows) with and without a nipplelike structure at the top (circles) interpreted as dung beetle balls (i.e., Coleoptera: Scarabaeidae) and assigned to the ichnogenus *Coprinisphaera*; (A) uppermost part of Salt Wash Member, Ruby Ranch, UT (9); (B) upper part of Salt Wash Member, Shootaring Canyon, UT (6). (C) J-shaped burrow with small terminal chamber similar to staphylinid beetles, middle part of the Salt Wash Member, Blue Mesa, CO (40). (D) Same burrow architecture in the lower part of the Salt Wash Member, Shootaring Canyon, UT (6); note the same burrows coming out of the outcrop. Cross-section (E) and plan-view (F) of vertical burrows (arrows) of several diameter sizes in a fine-grained laminated sandstone bed, upper part of the Salt Wash Member, Blue Mesa, CO; note that the burrows are not U-shaped. Cross-section (G) and plan-view (H) of burrows constructed by digger wasps (Hymenoptera: Sphecidae) in a sand bar, Niobrara River, Nebraska; courtesy of J.A. Fagerstrom.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for dung beetles during one or more seasons are most likely present, so that the number of dung balls per nest is difficult to determine.

The occurrence of *Coprinisphaera* in Morrison outcrops is compelling evidence for detritivore nutrient cycling (e.g., Halffter and Matthews, 1966; Boucot, 1990) in Jurassic soil ecosystems. The dung of herbivorous dinosaurs likely provided new but temporary niches that were a food source and a reproductive medium for coprophages, carnivores, parasites, fungivores, and microphytic feeders (e.g., McKevan, 1962; Wallwork, 1970).

4.11. Type 11—J-shaped burrows—rove beetles (Coleoptera: Staphylinidae), Fig. 11C,D

Description: Burrows are 0.3–1 cm in diameter and 5–10 cm long, although many are incomplete because of their oblique orientation to the outcrop face. The burrows are vertically oriented to slightly inclined and J-shaped and may terminate in an oblate chamber. Burrow fillings vary in texture, lithology, and grain size, indicating both passive and active filling.

Occurrence: The burrows occur in fine- to very fine grained ripple- and planar-laminated sandstones interbedded with thin mudstones in the Tidwell and Salt Wash Members.

Tracemaker: The J-shaped burrow morphologies are most similar to modern burrows constructed by rove beetles (Coleoptera: Staphylinidae) but are constructed by such other insects as dung beetles and crickets (e.g., Chamberlain, 1975; Ratcliffe and Fagerstrom, 1980). Based on the grain size, sedimentary structures, and overall composition of the deposit, however, the best interpretation is that they are the burrows of rove beetle burrows.

Interpretation: Burrows were constructed in channel point bar and levee sediments. These terraphilic traces often occur in units that are intensely bioturbated (Fig. 11C,D), suggesting subaerial exposure for extensive periods of time in areas of high soil moisture and water-table levels. This interpretation is based on the paucity of desiccation cracks and rhizoliths, and, more importantly, the occurrence of partially to intensely bioturbated ripple-laminated sandstones at the tops of bar forms in which they are found.

4.12. Type 12—vertical tubes (variable diameter), Fig. 11E–H

Description: Vertical to quasivertical burrows varying in diameter from 0.2–1.0 cm. Burrow length ranges from 0.5–20+ cm, along which burrow diameter may vary slightly. Upper parts of burrows may be diagonal but become vertical a few centimeters below the paleosurface. Few burrows appear to branch upwards from about 5–10 cm below the surface; however, this may represent the intersection of two different burrows.

Occurrence: Burrows occur in fine-grained to very fine grained, planar-laminated sandstone with or without siltstone partings in the Salt Wash, Recapture, and Brushy Basin Members.

Tracemaker: Identification of the tracemaker is tentative and unsettled. Based on comparisons to modern traces and observations (Fig. 11G,H), these traces are interpreted to have been burrows made by extant digger wasps (J.A. Fagerstrom, 1996, personal communication). Further study of both the Jurassic traces and extant digger wasp (Hymenoptera: Sphecidae) burrows is necessary.

Interpretation: These terraphilic burrows were constructed in levee and extrachannel splay environments with weak and short-lived soil development (e.g., fluventisols) due to the frequency of depositional events. The upper parts of the units where these burrows are found also contain few rhizoliths. Based on the comparison to extant burrows in similar environments, the Jurassic burrows are interpreted as having been formed in subaerially exposed substrates with low to intermediate soil moisture levels (about 5–25%), which allowed the sediment to remain cohesive as the burrows were formed, probably by wasps. The greater intensity of bioturbation near the upper 5–10 cm of each sedimentary package interpreted as levee deposits (Fig. 11E,F) suggests that initial soil moisture levels were high but decreased over a short period that allowed deeper-burrowing organisms to enter this environment.

4.13. Type 13—Paleobuprestis isp.—beetle borings, Fig. 12A,B

Description: Circular to weakly elliptical borings and channels below the bark (not preserved) of fossil wood. The diameter of the borings range from 0.3–1 cm (Fig. 12A). Some opening are filled with what appears to have been frass or masticated wood (Fig. 12B). Channels range in length from 2–10 cm and are recognizable around the tree; however, most examples are poorly preserved.

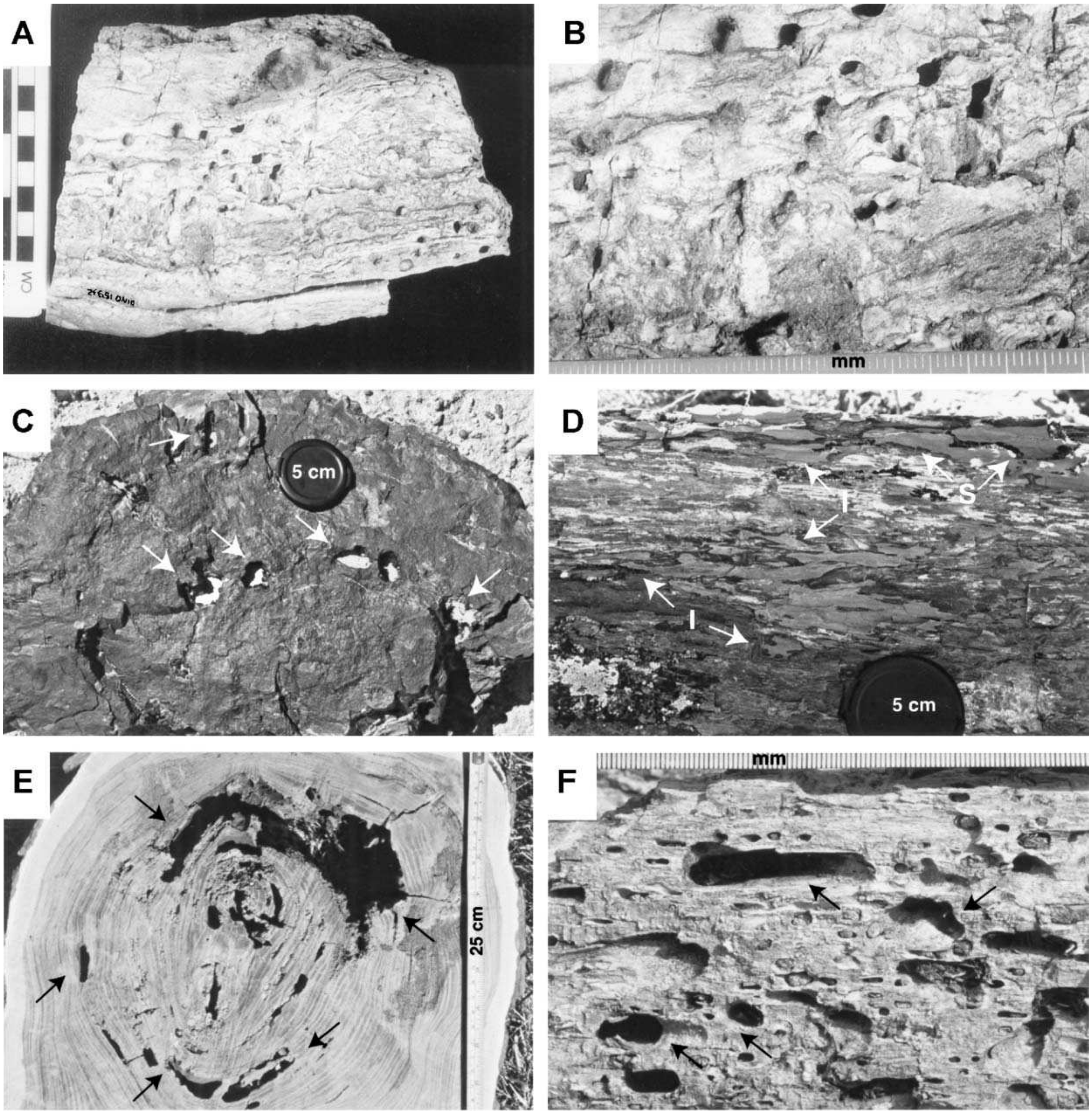


Fig. 12. Borings in Jurassic wood. (A–B): Borings assigned to *Paleobuprestis* isp. in petrified wood specimen DINO15932, Dinosaur National Monument, UT (17). (C) Irregular cavities (arrows) of varying volume in heartwood of recrystallized coniferous wood interpreted as fungal heartwood rot similar to those found in modern conifers (E). (D) Smooth to irregular walled chambers and galleries of several sizes visible in a cross-section of Jurassic conifer (arrows). Boring patterns (arrows) are also similar to those in modern conifers excavated by carpenter or wood ants (Hymenoptera) and termites (Isoptera) (F).

Occurrence: These borings occur in fossil conifer wood (DINO 15932) from the Brushy Basin Member. Others were identified in wood from outcrops in the Salt Wash Member.

Tracemaker: Jurassic beetles similar to those belonging to the extant Buprestidae are likely to have been produced these features.

Interpretation: The Jurassic wood with these types of borings were probably infested while standing. Most trees are attacked for reproductive purposes when they are alive by several types of wood-boring insects (e.g., Johnson and Lyon, 1991). The trace is terraphilic in terms of moisture affinity although the burrows are in xylic substrates. In modern environments, healthy trees are often susceptible to beetle infestation during episodes of stress brought on by drought, heat wave, or a combination of factors through time.

4.14. Type 14—Paleoscolytus isp.

Description: Mainly channels 0.2–0.7 cm in diameter, running in all directions along the surface of fossil wood that was presumably below the bark (which is not preserved). They are open and not filled with frass or other masticated material.

Occurrence: Examples of these borings were identified in fossil wood of conifers in outcrops of the Salt Wash Member.

Tracemaker: These borings were probably produced by Jurassic beetles similar to the extant Scolytidae (engraver beetles).

Interpretation: The presence of borings all around a tree trunk suggests that the Jurassic trees were infested while alive and co-occur with *Paleobuprestis* isp. The trace is terraphilic in terms of moisture affinity although the burrows are in xylic substrates. In extant environments, infestations typically occur in localized sections of forests. The activities of these beetles can kill trees if they are very weak to expel the invaders with sap. The trees will literally bleed to death and dry out. This type of boring behavior in wood likely killed the Jurassic conifers in a way similar to extant scolytid beetles.

4.15. Type 15—irregular cavities in wood, Fig. 12C–E

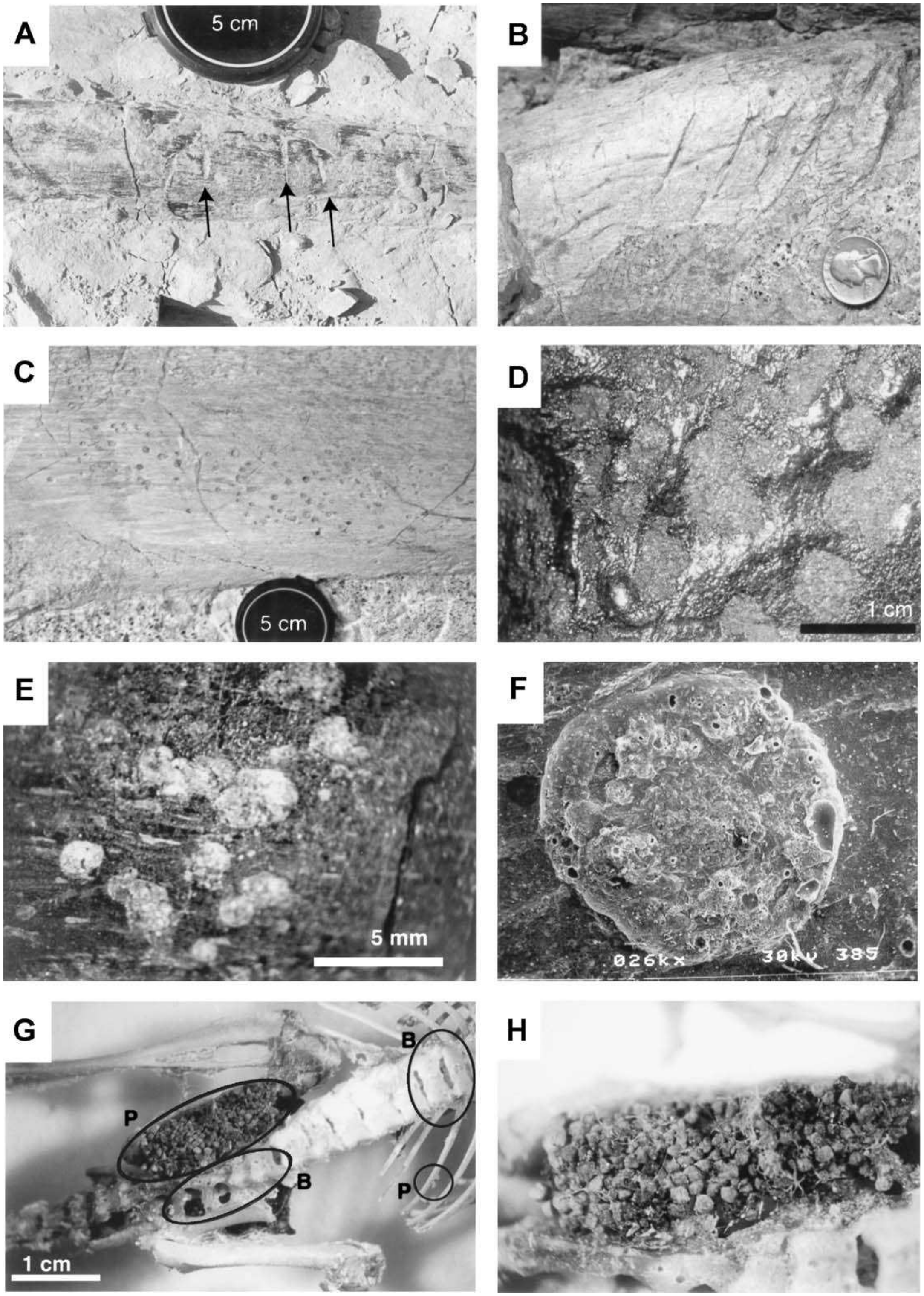
Description: Small to large cavities 1–5 cm in diameter, which occur in the heartwood of permineralized coniferous wood (Fig. 12C). Lengths vary from 5–20+ cm but are indeterminate due to poor examples of cross-sections of the logs. The cavities appear to follow the paths of old growth rings and then extend outward across the grain. The lengths and shapes are highly variable.

Occurrence: These cavities occur in outcrop examples of coniferous wood in the Salt Wash and Brushy Basin Members.

Tracemaker: From comparison to modern wood pathologies, these cavities were most likely produced by fungus that actively digested the heartwood (Sinclair et al., 1987). The result, commonly referred to fungal rot, is common in extant pine trees (Fig. 12E).

Interpretation: These structures suggest that the Jurassic trees were infested with fungal rot while upright. The trace is terraphilic but may represent higher moisture levels with hygrophilic affinities. In modern environments, although a tree may appear healthy from the outside, it can be destroyed from the inside out by the activity of diverse fungi. Often, trees are structurally weakened, eventually leading to death by breaking or the introduction of other pathogens (Sinclair et al., 1987). In other instances, once a tree has blown over or dies while upright, the fungal rot continues to digest the wood, resulting in cavities.

Fig. 13. Traces in dinosaur bones. (A) Rib of an unidentified sauropod with grooves (arrows) produced by the teeth of a scavenger, lower part of the Morrison Formation, Greybull, WY (36). (B) Scavenger bite marks at the end of scapula analogous in size and spacing to the teeth spacing of *Allosaurus*. (C) Small hemispherical borings on the surface of a femur of *Diplodocus* preserved in various stages of construction (17). (D) Large hemispherical borings on the surface of an *Allosaurus* femur (AMNH 699) with the fill intact (17). (E) Small hemispherical borings on the surface of a *Dryosaurus* bone with the fill intact, from the Carnegie Quarry, DNM (17). (F) SEM photograph of a boring, about 1 mm in diameter, from the bone in (C) cast with silicon gel. The surface of the boring preserves bite marks of the insect larva. (G) Skeleton of mouse cleaned of tissue by dermestid beetles and exhibiting pupal cases of the larvae (middle of photo); P, pupal cases; B, borings. (H) Close-up of pupal cases (cocoons) constructed in hardened skin and the surface of the pelvis. Note the borings that have penetrated parts of the vertebrae and the upper portion of the pelvis (bottom center of photo below cocoons).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4.16. Type 16—smooth cavities in wood, Fig. 12D,F

Description: Oval to strongly ellipsoidal cavities, 1–5 cm in diameter, that co-occurs with irregular cavities in the heartwood of permineralized coniferous wood. They are distinguished from irregular cavities by their smooth surface. Their observed maximum lengths range from 1–15+ cm, but the true lengths cannot be determined accurately due to the lack of cross-sections of the logs. In some examples of fractured logs (Fig. 12D), however, the smooth cavities are clearly visibly connected to irregular cavities and are often interconnected or crosscut by others.

Occurrence: Examples of these borings were identified in permineralized coniferous wood in outcrops of the Salt Wash Member.

Tracemaker: From comparison to modern wood pathologies, insects such as beetles, termites, or ants feeding on the fungus that digested the heartwood and created the cavities most likely produced these cavities. These cavities were actually the remains of digested wood (Fig. 12F).

Interpretation: These structures, similar to the irregular cavities produced by fungal rot, were likely produced by detritivorous insects. These traces are terraphilic but may have formed at higher moisture levels with hygrophilic affinities. Insects were attracted to fungus, as well as to the partially digested wood left behind by the fungus. Smooth walls resulted from the insects tunneling and eating the digested wood to the point where the rot ends (Fig. 12F). Today, trees are recycled in this very manner by the combination of fungal and insect activity. This explains the co-occurrence of the smooth and irregular cavities. The interconnected cavities were likely the result of the insects boring between cavities where the heartwood was weakened but not totally destroyed by the fungus.

4.17. Type 17—toothmarks in dinosaur bone, Fig. 13A,B

Description: Sets of relatively shallow grooves that are parallel to subparallel to each other in dinosaur bones. Grooves vary from 3–6 cm long and from 0.1–0.3 cm deep. They are typically shallow at one end with the deeper end slightly wider. The grooves occur predominantly in the long bones of sauropods.

Occurrence: These traces were observed in dinosaur bones in outcrops of the Brushy Basin Member in Utah and Wyoming.

Tracemaker: The grooves were most likely produced by the teeth of a theropod dinosaur through the combined action of biting and pulling.

Interpretation: The grooves in sauropod long bones (e.g., femur, tibia, fibula, and humerus) appear to have been inflicted during the scavenging of the carcass. These traces are terraphilic in that they were likely inflicted while the carcasses were in a terrestrial setting. The deeper end of the grooves reflects the initial bite site where the scavenger bit down firmly because this would have been the area of greatest force applied during the action of biting and tearing. The shallower end of the groove probably reflects the point from where the flesh was removed.

4.18. Type 18—circular to elliptical borings in dinosaur bone, Fig. 13C–H

Description: Predominantly circular to slightly elliptical in plan-view, the borings are preserved as molds and casts within the bone and are shallow hemispheres typically 0.01–4.0 mm deep. Some elliptical pits appear to be incomplete borings. The borings range from 0.5–1, 2.5–3, and 4–5.0 mm in diameter. Clusters of borings are random with no particular distribution between borings. Some skeletal elements contain both small and large borings, but one size always dominates the bone surface. Borings from different quarries have similar diameters, shapes, and distributions across bone surfaces. None of the dinosaur bones examined contain deep or fully penetrating holes or trails.

Occurrence: Dinosaur bone borings were observed in quarries in the Brushy Basin Member in Colorado, Utah, and Wyoming.

Tracemaker: The morphologies suggest that these borings were most likely produced by the larvae of carrion beetles (Coleoptera: Dermestidae) and are very similar to the traces of modern dermestids (Fig. 13G–H).

Interpretation: These borings resulted from the formation of cocoons during the pupation stage of dermestid beetles, a transitional phase in the metamorphosis from larva to adult. These traces are terraphilic because they were formed on carcasses above the substrate in subaerial conditions. Dermestid activity requires specific environmental conditions (Reed, 1958; Smith, 1986). The presence of these pupal chambers (borings) on the bones implies: (1) the skeletons must have been partially covered by dried flesh; (2) the carcasses were above water and dry (consistency of dried beef); and (3) carcasses had lain on the sediment surface long enough to allow dermestid infestation (e.g., Payne, 1965). During the period of infestation, the carcasses and the beetles lay on the floodplain for different amounts of time, as indicated by the densities of borings in the skeletal elements. Carcasses and their borings were later buried locally or transported and then buried in channel or floodplain sediments.

These ichnofossils not only represent the earliest evidence of dermestid beetles by nearly 120 million years but also record the recycling component of the food web and provide information about local paleoclimatic settings in Jurassic terrestrial ecosystems (e.g., Hasiotis et al., 1999a).

4.19. Type 19—cf. *Phycodes* isp., Fig. 14A,B

Description: Bundles of cylindrical tunnels in divergent pattern from a central point filled with fine-grained sandstone on the lower surfaces of beds (Fig. 14A,B). Some tunnels, especially those on the bottom and outside of the bundles, have transverse sculpture. Other tunnels occur one atop the other and separate downward and spiral outward.

Occurrence: These traces occur in interbedded fine-grained, ripple-laminated sandstone and mudstone in the Windy Hill Member (23) and in calcareous, very fine grained, ripple-laminated sandstone in the Tidwell Member (8).

Tracemaker: Cf. *Phycodes* was most likely constructed by the feeding behavior of a polychaete worm.

Interpretation: These traces occur in siliciclastic units interpreted as transitional marine environments most similar to bays and estuaries in the Windy Hill and Tidwell Members. The trace is hydrophilic. The designation of the appropriate member is based on lithologic descriptions and stratigraphic distribution of units (Peterson, 1994; F. Peterson, 1999, personal communication). The occurrence of cf. *Phycodes* in the Tidwell Member (8; collected by Deborah Michelson) suggests (1) that a freshwater organism with a feeding behavior as complex as marine organisms existed here, or (2) that a marine incursion into this area associated with the Windy Hill to the north (locality 18) occurred and was documented by these traces. The freshwater explanation would represent the first documentation of such behavior in freshwater systems in the Mesozoic, but these traces have not been reported in any other freshwater lacustrine deposits in the Morrison. The marine interpretation suggests that a high frequency, short-lived rise of sea level reached far into south-central Utah and created shallow-marine embayments with high evaporation rates that facilitated carbonate precipitation (e.g., limestones). Both scenarios are still under investigation, however.

4.20. Type 20—pustulose marks, Fig. 14A

Description: Small, shallow circular depressions with asterisklike impressions impressed into the walls ranging from 0.2–0.35 cm in diameter and from 0.1–0.25 cm in depth. They are found in high abundance and at several different intervals within a bed.

Occurrence: Associated with cf. *Phycodes* occurring in interbedded sandstone and mudstone of facies equivalent to the Windy Hill and Tidwell Members.

Tracemaker: The tracemaker is unknown. Based on the morphology and distribution of the traces, however, they are interpreted as having been produced by the probing behavior of polychaete worms.

Interpretation: These pustulose traces have not been previously recognized in the Morrison Formation. Investigation of the trace fossils recorded in the literature also has not revealed ichnites with similar morphology. Because these hydrophilic traces and marine invertebrates were found in interbedded sandstones and mudstones, cf. *Phycodes*, *Planolites*, and oysters likely represent burrowing marine invertebrates in such transitional marine environments as bays and estuaries. The asterisk pattern within the small depressions could have been produced by the probing behavior of polychaete worms in these marine environments.

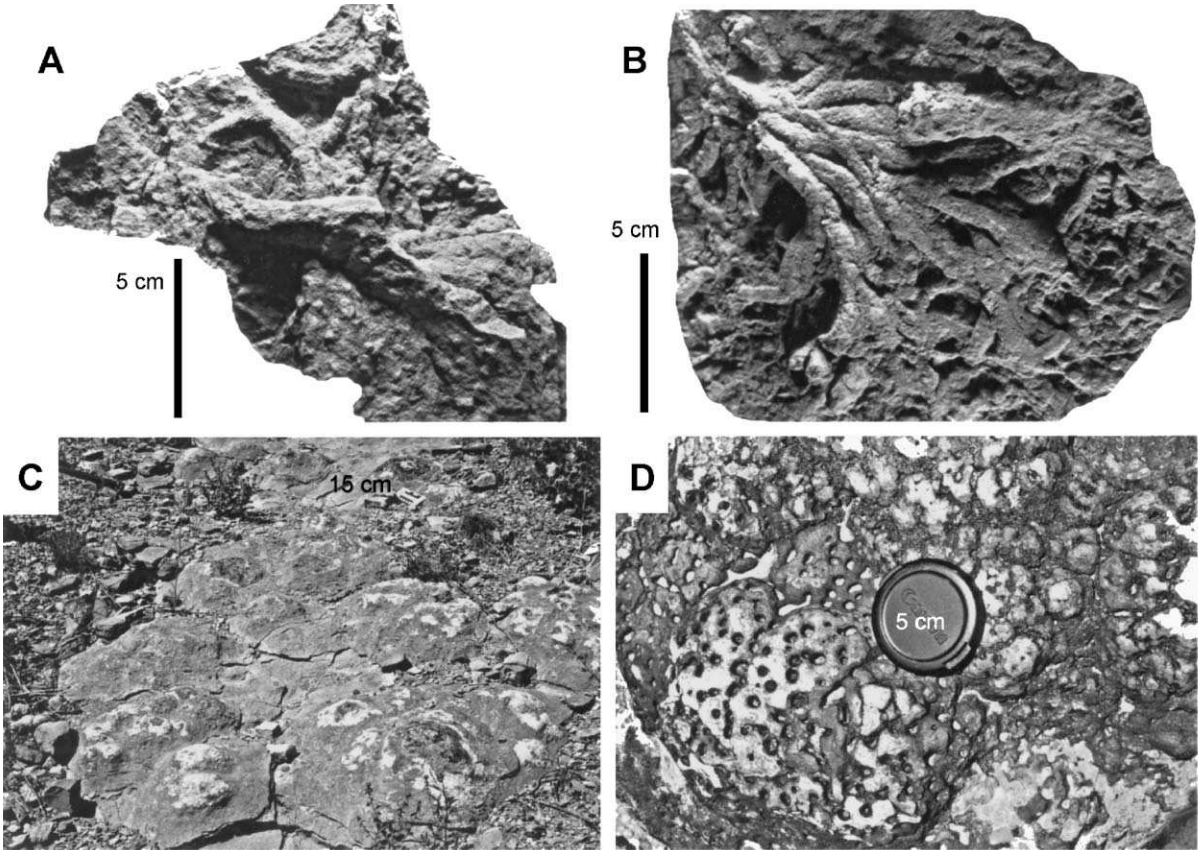


Fig. 14. (A) Downward spiraling burrow with fine, transverse scratches on the burrow walls, also associated with a pustulose texture and scratch patterns similar to those on the burrow walls, Tidwell Member equivalent, Park Creek Reservoir, CO (23). (B) Shallow, downward-branching burrow system exhibiting behavior similar to *Phycodes* and *Chondrites*, Tidwell Member, Shootaring Canyon, UT (6). (C) Stromatolites in calcareous fine-grained sandstone and siltstone, Tidwell Member equivalent, Park Creek Reservoir, CO (23). (D) Patches of the Stromatolites containing high densities of shallow, circular borings, Tidwell Member equivalent, Park Creek Reservoir, CO (23).

4.21. Type 21—stromatolites and algal laminates, Fig. 14C,D

Description: Sheetlike to domal structures composed of thin, relatively continuous couplets of light and dark calcareous laminae. Sheetlike laminates occur in an outcrop area of at least 50 m^2 or more. Individual laminae were traced several meters, and a series of laminae could be traced up to 5 m. Domal structures 20–30 cm thick have a high- to low-relief pattern that occurs over an area of 2.5 km^2.

Occurrence: These traces have been identified in calcareous units equivalent to the Tidwell Member in Colorado and Wyoming.

Tracemaker: The external and internal morphology of the sheets and mounds suggest construction by interwoven strands of cyanobacteria.

Interpretation: The hydrophilic stromatolites were built by cyanobacteria in lime-producing environments similar to freshwater lacustrine or coastal bay settings with fluctuating salinity that results in stressed conditions. Petrographic analysis has shown that the Park Creek Reservoir (Colorado) stromatolites were constructed by cyanobacterial filaments associated with freshwater ostracodes, charophytes, possible fish remains, and Magadi-type cherts (Dunagan, 1998, 2000, personal communication). Dunagan (2000) suggested that the stromatolites were constructed in open lacustrine systems that experienced periods of increased alkalinity. Algal laminates in Greybull, WY, are also associated with sauropod tracks in sedimentary units that can be interpreted similarly to those in Colorado. The units in Colorado and Wyoming are closely associated with marine estuarine and shoreface deposits, suggesting that freshwater lacustrine environments probably existed in coastal settings adjacent to marine environments.

4.22. Type 22—stromatolite borings, Fig. 14D

Description: Simple, cylindrical borings 0.3–0.5 cm in diameter and 0.2–0.5 cm deep. They occur in the upper portion of domal structures 20–30 cm thick that are interpreted as stromatolite mounds.

Occurrence: The borings are in the tops of stromatolites that occur in only one known locality (23) in the study area.

Tracemaker: The architect of these borings is unknown. Several organisms, like insect larva, gastropods, or small bivalves may have constructed these traces depending on the environmental setting. See discussion below.

Interpretation: Borings in the upper surfaces of stromatolites have not previously been reported from the Morrison or from Jurassic or older rocks. The traces are hydrophilic, and interpretation of the tracemaker poses a problem, unlike the identification of the stromatolites. No extant freshwater borers are currently known to bore into stromatolites or into hard grounds. Some species of extant bees are known to bore into friable sandstone (see discussion under Type 5a–d), and only type of insect larva bored into lacustrine substrate composed of chalk bedrock has been observed (J.I. Kirkland, 1994, personal communication). If the stromatolites were built in freshwater transitional (coastal) lacustrine settings, the borer may have been introduced from juxtaposed marine environments when the barrier between the two systems was breached. The newly introduced marine borers may have been bivalves, gastropods, or barnacles (e.g., Ekdale et al., 1984) that ravaged the stromatolites once salinity reached tolerable levels. But if the borings were made by freshwater organisms, then extant candidates are few: (1) well-scleratized insect nymphs, like mayflies, with the ability to scrape a hole into the mounds, and (2) acid-secreting insect larvae, like some caddisflies.

4.23. Type 23—*Lockeia* isp., Fig. 15A,D

Description: Small, oblong-shaped burrows in concave epirelief with pointed ends and narrow keels along the length. The burrows range from 0.7–1.2 cm in length and about 0.3 mm in width and 0.4 cm in depth.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstones in the Windy Hill (16) and Tidwell (18) Members.

Tracemaker: The morphology of the trace suggests they were constructed by shallow-infaunal small bivalves (Hantzschel, 1975).

Interpretation: These traces occur in transitional marine settings similar to tidal and estuarine environments and were formed as resting burrows of suspension-feeding marine bivalves. The trace is hydrophilic. They are associated in a succession of thin interbedded sandstone and mudstone with *Arenicolites*, *Conichnus*, *Lingulichnus*, *Planolites*, *Palaeophycus*, *Phycodes*, *Scolicia*, and “*Terebellina*”. At locality 16, the Windy Hill Member of the Morrison appears to rest conformably over the Redwater Member of the Stump Formation. These traces and their occurrence in sandstone-dominated interbedded units, however, suggest tidal deposits in small, incised valleys. Documenting the presence of such valleys at this locality is difficult because the units have been tilted upwards at a high angle (~ 60°). Future work is planned for this and other localities with the Windy Hill and Tidwell Members to provide evidence for incised valleys at the base of the Morrison.

4.24. Type 24—*Lingulichnus* isp.—lingula burrows, Fig. 15B–E

Description: Straight to slightly curved, slitlike structures, 0.7–1.0 cm in diameter, preserved in concave epirelief. Sometimes, the slits are connected to vertical burrows below them that are strongly elliptical in cross-section; however, they are often poorly preserved or missing.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstones in the Windy Hill Member (16). They are found in association with *Arenicolites*, *Conichnus*, *Lockeia*, *Planolites*, *Palaeophycus*, *Phycodes*, and *Scolicia*.

Tracemaker: Based on the comparison to fossil and extant traces, they were most likely produced by lingulid brachiopods (Hakes, 1976).

Interpretation: *Lingulichnus* is interpreted to occur in tidal and estuarine environments (Hakes, 1976). These hydrophilic traces represent burrows of vertically oriented, suspension-feeding lingulids below the sediment surface. Although no body fossils of *Lingula* were found in the outcrop, the burrows are very similar to those of extant lingulids dwelling in tidal settings in the Gulf of California, Mexico (T.M. Demko, 1996, personal communication).

4.25. Type 25—Arenicolites isp., Fig. 15A,D,E

Description: U-shaped burrows without spreite where the tubes are perpendicular to the bedding plane. The bases of the burrows are not visible or are poorly preserved. The diameter of one of the tubes is larger than the other ranging from 0.2–0.3 and 0.3–0.4 cm for each tube. Spacing between the tubes varies from 0.6–1.0 cm. The very thin wall in the apertures suggests that the tubes are lined with mud.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstones in the Windy Hill Member (16). They are found in association with *Conichnus*, *Lingulichnus*, *Lockeia*, *Planolites*, *Palaeophycus*, *Phycodes*, and *Scolicia*.

Tracemaker: These traces were most likely constructed by polychaete worms similar to the extant *Arenicola* (Bromley, 1996).

Interpretation: *Arenicolites* is interpreted to have occurred in tidal environments in the lowest part of the Windy Hill Member. These hydrophilic traces represent dwelling burrows of detritus-feeding or deposit-feeding polychaete worms (e.g., Bromley, 1996). Based on the sedimentary units in which the burrows occur, it suggests that they were formed by detrital-feeding burrows.

4.26. Type 26—Conichnus isp., Fig. 15C–E

Description: Simple cone-shaped, vertically oriented structures that occur as single, isolated entities. They are 1.5 cm in diameter and 1.0–1.5 cm deep and taper downward to one-third the diameter, terminating in a sharply rounded base. The surficial morphology of the traces is smooth.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstones in the Windy Hill Member (16). They are found in association with *Arenicolites*, *Lingulichnus*, *Lockeia*, *Planolites*, *Palaeophycus*, *Phycodes*, and *Scolicia*.

Tracemaker: The morphology suggests that this trace was most likely made by an anemonelike invertebrate (Bromley, 1996).

Interpretation: *Conichnus* is interpreted to have occurred in tidal environments and is found in the lowest part of the Windy Hill Member. These hydrophilic traces represent dwelling burrows of suspension-feeding or carnivorous anemonelike organisms (e.g., Bromley, 1996).

4.27. Type 27—Palaeophycus isp., Fig. 15A,C

Description: Unbranched, cylindrical to subcylindrical, horizontal burrows 0.4–0.7 cm in diameter and 3–5 cm long that are distinctly lined. The smooth lining is a thin wall composed of the same sediment that surrounds and fills the burrow. These burrows are often discontinuous due to collapse.

Occurrence: The traces occur in fine-grained ripple-laminated sandstones in the Windy Hill (16) and Tidwell (23) Members. They are found in association with *Arenicolites*, *Conichnus*, *Lockeia*, *Planolites*, *Phycodes*, and *Scolicia*.

Tracemaker: These traces were most likely constructed by marine polychaetes as well as a host of other infaunal invertebrates that could have lined their burrows.

Interpretation: *Palaeophycus* is interpreted to have been constructed in estuarine and coastal bay environments. These hydrophilic traces represent dwelling and deposit-feeding burrows that were reinforced with a lining to prevent collapse in noncohesive sediment. The movement of the organism's body would have helped to mantle the interior of the burrow with processed material.

4.28. Type 28—Scolicia isp., Fig. 15E

Description: Slightly curved to sinuous, concave furrows in epirelief about 1 cm wide and 1 mm deep, with lateral, rounded ridges. In one instance (Fig. 15E), the trail beginning at a burrow aperture continues for nearly 9 cm, where it stops, and then continues until it is no longer recorded in the sediment.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstones in the Windy Hill Member (16). They are found in association with *Arenicolites*, *Conichnus*, *Lingulichnus*, *Lockeia*, *Planolites*, *Palaeophycus*, and *Phycodes*.

Tracemaker: Based on the morphology, the trail was most likely made by a gastropod, crustacean, or an echinoid (Bromley, 1996).

Interpretation: *Scolicia* is interpreted to have been constructed in tidal environments and occurs in the lowest part of the Windy Hill Member. These hydrophilic traces represent locomotion trails of an invertebrate similar to a gastropod, amphipod-like crustacean, or irregular echinoid. The furrows may represent the area to the edges of the trail pushed up by a shell as exhibited in the trails of many extant gastropods. If the substrate was somewhat soft, the detailed surficial morphology would not have been preserved, and positive identification of the tracemaker is difficult.

4.29. Type 29—“Terebellina” isp., Fig. 15C

Description: A subcylindrical, horizontal to oblique burrow that contains a thin pale-colored wall that may be faded in color but retains a distinct appearance. These structures are commonly crushed and incompletely filled.

Occurrence: These traces occur in fine-grained, ripple- and planar-laminated sandstones in the Windy Hill Member (16). They are found in association with *Arenicolites*, *Conichnus*, *Lingulichnus*, *Lockeia*, *Planolites*, *Palaeophycus*, *Phycodes*, and *Scolicia*.

Tracemaker: A tube-building invertebrate, possibly a polychaete or some other type of annelid, constructed the trace.

Interpretation: “*Terebellina*” is interpreted to have been constructed in the tidal environments and is found in the lowest part of the Windy Hill Member. This ichnotaxon is currently interpreted as a benthic foraminiferan, not a trace fossil (Miller, 1995); however, the Morrison trace fossil in question does not appear to be a foraminiferan but rather a partially cemented tube. These hydrophilic traces probably formed as dwelling tubes of annelids in noncohesive sediment. The tube occurs nearly at the sandstone–mudstone interface and appears to have continued into the mudstone. Thus, the tube was “anchored” or terminated in the sandstone, extending into the mudstone in which the organism likely made its living through deposit or detritus feeding.

4.30. Type 30—patterned surface trail (large), Fig. 15F

Description: A surface trail ranging in width from 2–3 cm that has several side trails of equal dimension. These side trails reunite with the main trail forming a mazelike network. The pattern itself is composed of shallow but well-incised rasping marks throughout the trail.

Occurrence: These traces occur in fine-grained, ripple-laminated sandstones in the Windy Hill Member (16). They are found in association with *Arenicolites*, *Conichnus*, *Lingulichnus*, *Lockeia*, *Planolites*, *Phycodes*, and *Scolicia*.

Tracemaker: The pattern is similar to those produced by rasping feeding patterns of gastropods and the feeding excavation patterns (minus the pellets) of fiddler crabs and other shoreface dwelling crabs (Frey et al., 1984b).

Interpretation: The patterned surface trail is interpreted as having occurred in the tidal environments and is found in the lowest part of the Windy Hill Member. The trace is hygrophilic. These traces most likely formed as the feeding patterns of a grazing gastropod or excavation and grazing patterns of shoreline-dwelling crabs. The rasping features suggest that the features were constructed while the surface was subaerially exposed and then later buried. Gastropods have rasping teeth that they use to graze on algae, organic material, or very small invertebrates growing and living within the thin veneer on the surface. Such decapods as fiddler crabs also graze newly exposed surfaces during low tide for bits of organic debris and algae by plucking the surface. The most likely constructor of this trace was a gastropod, although none has been found large enough to make the trail. Furthermore, the rasping marks of a gastropod would have to be deeper than the overall modi-

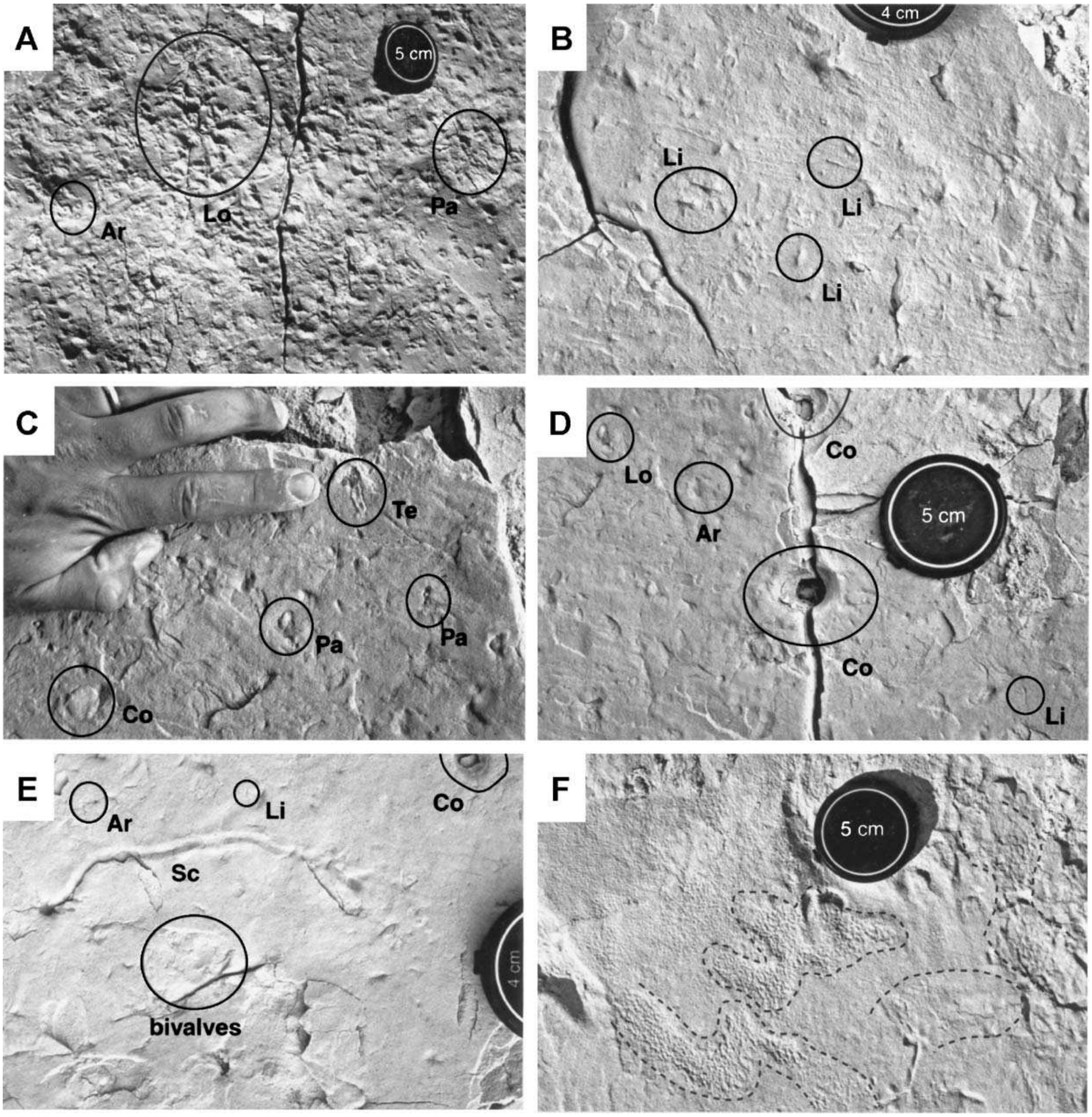


Fig. 15. Marine trace fossils from the Windy Hill Member, Dinosaur National Monument, UT (16). Note that circles highlight particular trace fossils and are associated with abbreviations: Ar, *Arenicolites*; Co, *Conichnus*; Li, *Lingulichnus*; Lo, *Lockeia*; Pa, *Palaeophycus*; Sc, *Scolicia*; and Te, *Terebellina*. (A) High density of shallow, lined, and paired tubes assigned to *Arenicolites* isp. associated with *Lockeia* isp., and *Palaeophycus* isp. (B) *Lingulichnus* isp. expressed on a surface exhibiting fine sets of scratches produced by currents dragging plant material. (C) Surface with *Conichnus* isp., *Palaeophycus* isp., and rare *Terebellina* isp. (D) Shallow circular structures assigned to *Conichnus* isp. (modified from Hasiotis, 2002) associated with *Lockeia* isp., *Arenicolites* isp., and *Lingulichnus* isp. (E) Short, thin slits assigned to *Lingulichnus* isp. (to the left of the lens cap) with a trail exhibiting raised ridges on the outer edges tentatively assigned to *Scolicia* isp.; also note the impressions of several marine bivalves (circle) as well as *Arenicolites* isp. and *Conichnus* isp. (modified from Hasiotis, 2002). (F) Surface grazing trails containing small rasping marks (outlined by dashed lines); modified from Hasiotis (2002).

fication of the sediment by the foot moving the gastropod forward. If a crab produced the trail, it would be the earliest evidence of this type of decapod in the fossil record. Body fossils of crabs have been reported from the Late Cretaceous (Glaessner, 1969).

4.31. Type 31—escape traces, Fig. 16A,B

Description: Vertical traces distinguished by their strong, downward deflections of adjacent laminations. Deflections are 1.5–3 cm in diameter and 2–15 cm long. Many of these structures occur together, originating from the same bedding plane but terminate at several levels.

Occurrence: These traces occur in fine-grained ripple-laminated sandstones in the Windy Hill Member equivalents (32) in central Wyoming.

Tracemaker: The escape traces were constructed by several kinds of invertebrates (Schafer, 1972).

Interpretation: Escape structures are commonly associated with rapid sedimentation events in which any organism living on or just below the surface was suddenly buried (Schafer, 1972). Downward-deflected laminations record attempted upward movement of an organism trying to escape burial by rapidly accumulating sediment. These hydrophilic escape traces occur in a tidal channel within an estuarine setting. In one part of the outcrop (Fig. 16B), the escape traces are clearly visible within the tidal bundles of climbing ripple laminations, approximately 10 cm thick, contained within a lenticular tidal channel. The organisms, either gastropods, bivalves, or anemone, moved upward through the sediment, disturbing the succession of ripple laminations. Escape traces can occur in continental or marine environments in which there are episodic rapid sedimentation events.

4.32. Type 32—*Tektonargus kollospilas* Hasiotis et al. (1998b)—caddisfly cases, Fig. 17A–D

Description: Cylindrical, tubular structures 0.4–0.6 cm in diameter and 1.1–1.4 cm long. They are constructed from subangular to subrounded, relatively coarse, brownish-red grains 0.05–0.3 cm in diameter. Each structure is composed of 30 to 40+ grains that are juxtaposed with one another and interlocked with the grains above and below. The exact number of grains and constructed layers is difficult to determine because of the interlocking nature of the material. The tubes are relatively straight and do not appear to taper at either end. The lack of tapering, however, may be a preservational bias due to transportation and burial (Fig. 17A–D).

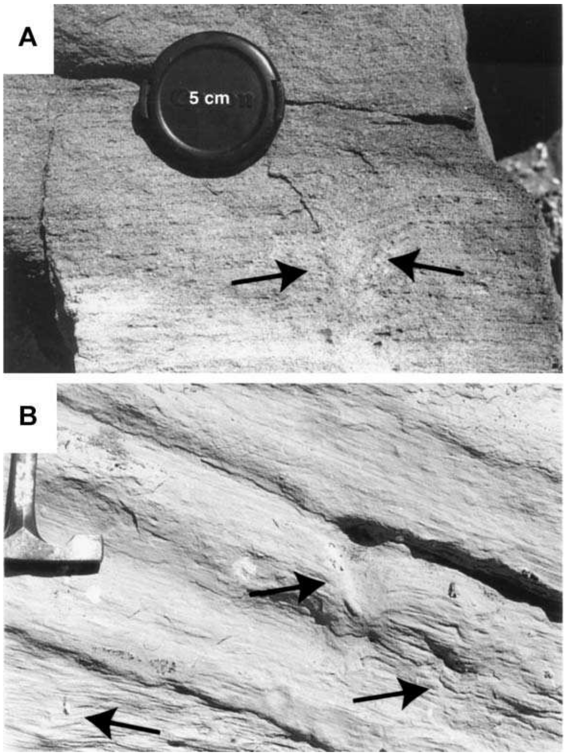


Fig. 16. Escape traces in planar laminations (A) and in climbing ripple laminations (B) associated with tidal channel deposits, Windy Hill Member, Grey Reef, Alcova, WY.

Occurrence: The traces occur in finely laminated, gray mudstone associated with sandstones and siltstones in the Brushy Basin Member, Fruita Paleontological Area, CO.

Tracemaker: These structures are most similar to modern larval tube-cases and saddle-cases constructed by caddisflies (Insecta: Trichoptera) of the families Limnephilidae and Glossosomatidae (Hasiotis et al., 1998b).

Interpretation: The larval tube-cases of the Limnephiloidea may be straight, tapered, or cornucopia-shaped (Wiggins, 1996). Saddle-cases of the Rhyacophiloidea are open at both ends from which the head, thorax, and anal prolegs protrude (Wiggins, 1996).

Today, both rhyacophilids and limnephilids include species whose larvae construct protective cases in fast-flowing streams and in standing pools of water. The finely laminated gray mudstones were deposited pond settings proximal to fluvial channels (Callison, 1987; Kirkland et al., 1990). The hydrophilic caddisfly cases were not constructed in ponds due to the lack of coarse-grained materials for making cases. Therefore, the cases are interpreted as having been constructed in channels where there was a source of coarser-grained material and then washed into the ponds during seasonal flooding of adjacent streams.

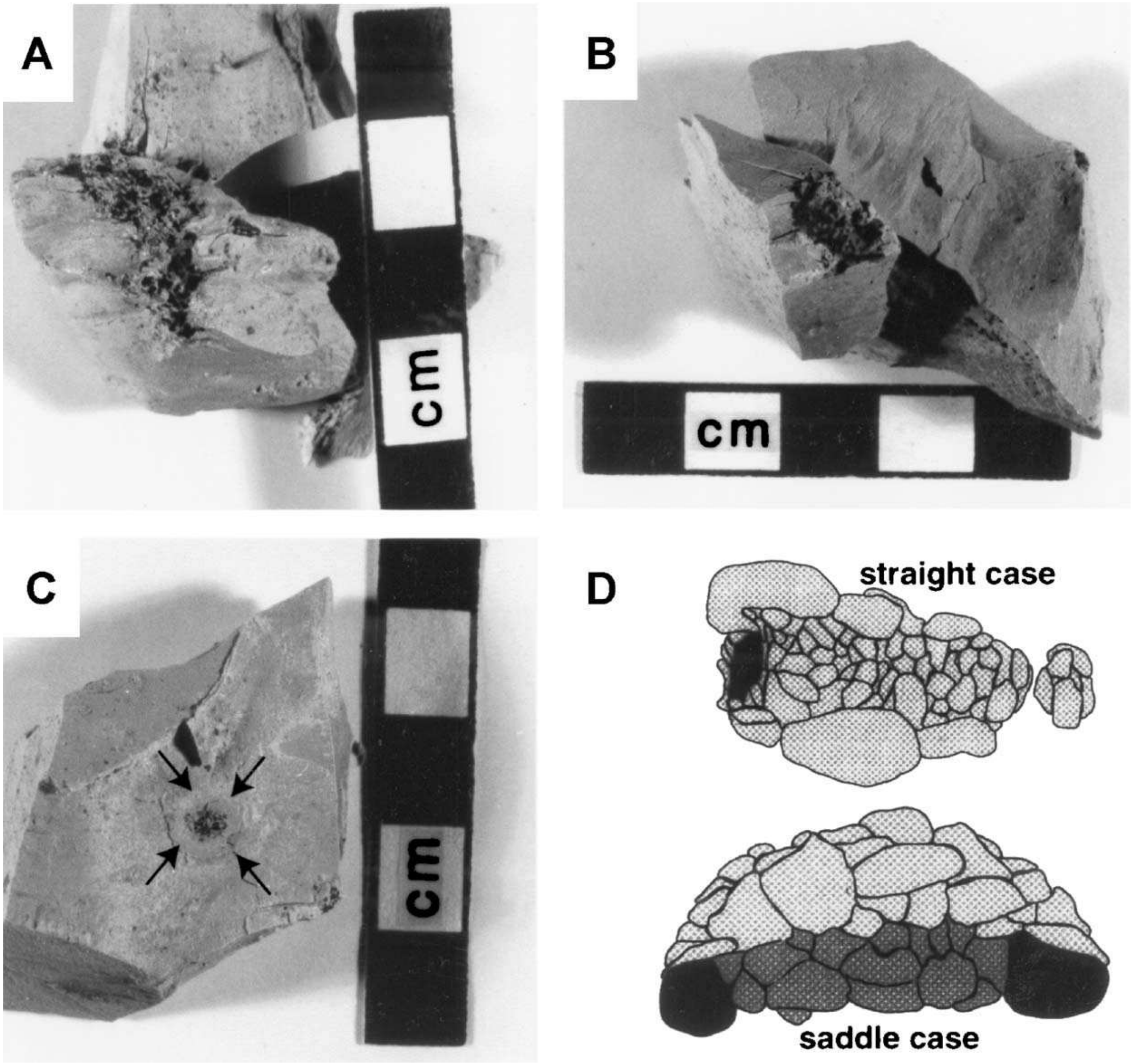


Fig. 17. *T. kollospilas*, caddisfly larval cases from the lower part of the Brushy Basin Member, Morrison Formation, Fruita Paleontological Area (FPA), Fruita, CO. (A) LACM 11348. (B) LACM 11349. (C) Raised nipple (arrows) of claystone around a caddisfly case reflecting settlement through the water column and emplacement into the substrate while it was very soft. (D) Examples of modern larval cases of the caddisfly families Limnephilidae (straight cases) and Glossosomatidae (saddle cases) that are most similar to the Morrison cases (modified from Hasiotis et al., 1998a,b).

Caddisfly larval cases in Jurassic deposits suggest that: (1) trichopterans were present in the Jurassic although no body fossils have been found in the Morrison or elsewhere in time-equivalent Jurassic rocks; and (2) they likely were an important component of Jurassic benthic communities that significantly contributed to the food web of Morrison freshwater ecosystems. Today, trichopteran larvae support small and large fish and amphibians (Cummins, 1973; Wiggins, 1984).

4.33. Type 33a (dwelling/resting traces), b (locomotion traces), and c (escape traces)—elliptical- to almond-shaped structures—bivalve traces, Fig. 18A–F

Description: Large elliptical- to almond-shaped trace preserved as convex hyporelief, concave epirelief, and in full relief, resembling bivalves. One end of the bivalve-shape is asymmetrical and wider, while the other is rounder. The trace is nearly perpendicular to the bedding but may also be at a greater angle to the bed. Several behavioral patterns are identified:

(a) Closely spaced vertical traces (1–100+) characterized by pronounced, downward-deflected laminae in the form of bivalves (Fig. 18A,B).
(b) Closely spaced individuals (1–100+; Fig. 18C,E), concave epireliefs of bivalve forms with tubes (Fig. 18F) extending upward from the outside edges to the bottom of the bed.
(c) Bivalve-shaped form at the end of a thin, uniform trail that is as wide as the form and preserved as an epirelief surface trail (Fig. 18D).

Their strongly bivalve-shaped form that is associated with the sediment disturbances suggests that these three forms be grouped together.

Occurrence: These traces occur within fine-grained sandstone often interbedded with siltstone or mudstone in the Tidwell (5, 13, 26), Salt Wash (6, 40), and Brushy Basin (12, 38) Members.

Tracemaker: Based on the form of these traces, they were most likely constructed by individuals or communities of freshwater unionid bivalves.

Interpretation: These hydrophilic traces represent three distinct behaviors: (a) dwelling–resting, (b) locomotion, and (c) escaping behavior. These Morrison forms do not fit the description of *Lockeia* (e.g., Hantzschel, 1975; Maples and West, 1989), an ichnogenus interpreted as a pelecypod trace, and thus, the Morrison traces likely require their own ichnogenera. Nevertheless, freshwater clams produced all of these organism–substrate interactions. Individual clams to large communities suspension-feeding from the water column formed dwelling–resting traces. Foot and siphon marks are also well represented in some of the traces. These traces preserve the subtle shifts of individuals within the community. Individuals moving through the substrate to different positions produced locomotion traces. The bivalve form is visible in several places within the trails where the individual stopped for some unknown time. At the end of these trails, the bivalve form is clearly visible along with a thin layer of disturbed sediment. This layer was likely caused by the repositioning of bivalves or by the upward movement of individuals to stay in equilibrium with the bottom as it slowly accreted. Large numbers of closely spaced escape traces record the upward movement of the clam community during an episodic sedimentation event.

The recognition of unionid bivalve trace fossils is important because they record specific environmental conditions. Like extant unionids, the presence of Morrison bivalves reflects conditions of perennially fresh, flowing-water conditions ((Evanoff et al., 1998; S.C. Good, 1999, personal communication; Good, this volume). Because body fossils of these organisms are not always preserved in every environment in which they lived, their trace fossils serve as excellent in situ proxies that document their presence in alluvial channel deposits.

4.34. Type 34a (small), b (large), and c (tree steinkerns)—rhizoliths, Fig. 19A–D

Description: Tubular structures with diameters that range from (a) 0.05–0.1, (b) 1–10, and (c) 50–100+ cm (Fig. 19A–D). The traces commonly reach depths of 1–100+ cm. The tubes commonly exhibit downward and lateral branches of lesser diameter that taper along their lengths. The largest traces, steinkerns of subaerial to subterranean structures, branch off laterally and downward and taper along their length. Nearly all of these structures taper to a point or grade into filamentous traces. Abundant but dispersed fila-

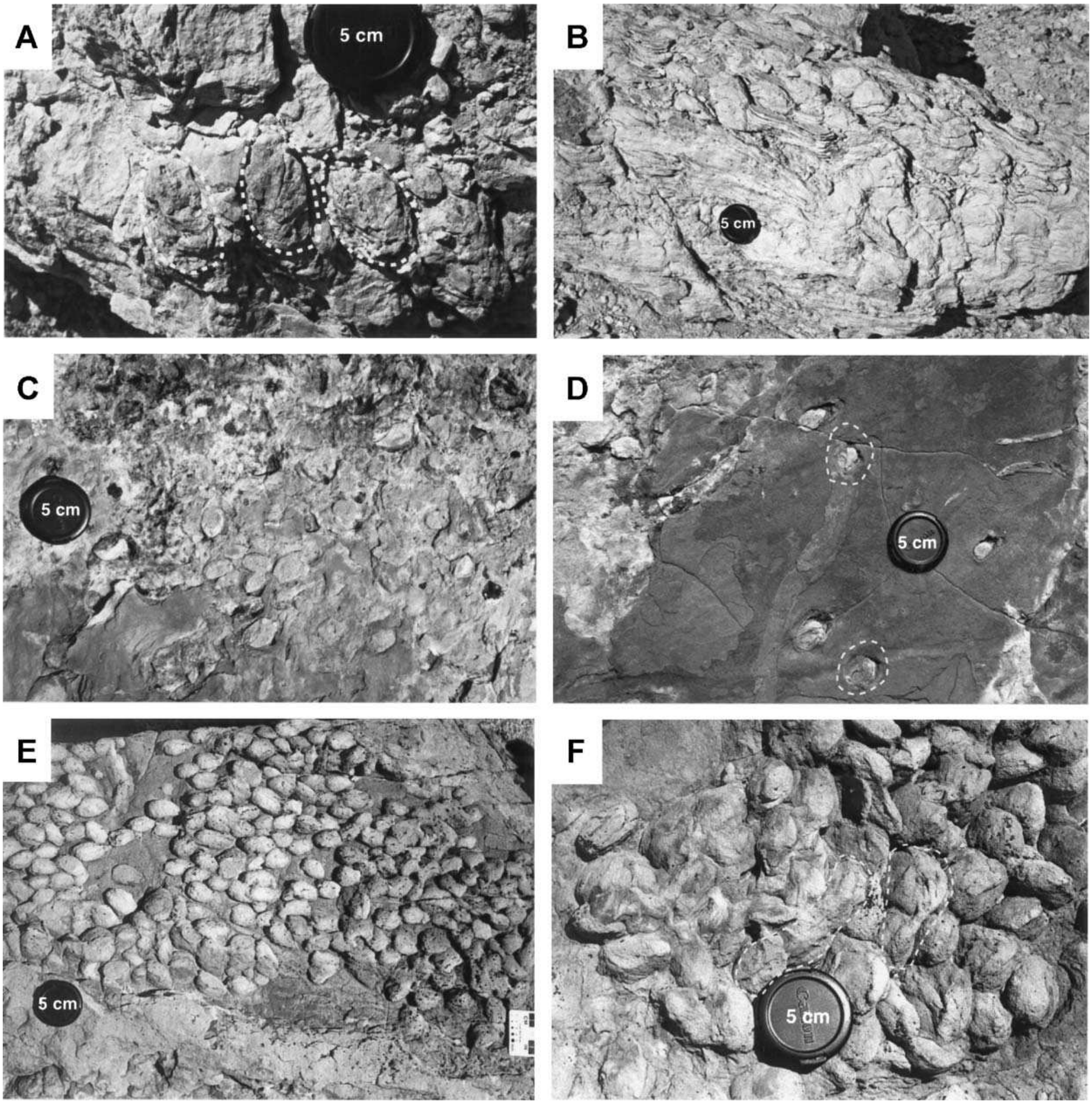


Fig. 18. Bivalve traces. Close up of a bed of escape traces (A) produced by the freshwater clam *Unio* sp. at the base of Bed A in the Tidwell Member at Hatt Ranch, UT; dashed lines outline several of the escape structures. (B) Portion of the unit showing an interior surface of the community composed of more than 100 individuals that produced the escape traces; note the elliptically shaped bodies. Dwelling (C) and locomotion (D) traces of freshwater bivalves (dashed lines) in the middle part of the Salt Wash Member, Blue Mesa, CO. Note that the dwelling traces (dashed lines) are at the end of the locomotion trails. (E) and (F): Dwelling traces of bivalves in the uppermost part of the Brushy Basin Member at the Cleveland–Lloyd Quarry, UT. Individual traces preserve lateral movements (dashed lines in middle of photo F) of the clams as well as foot impressions between some of the clams in the middle of the photograph.

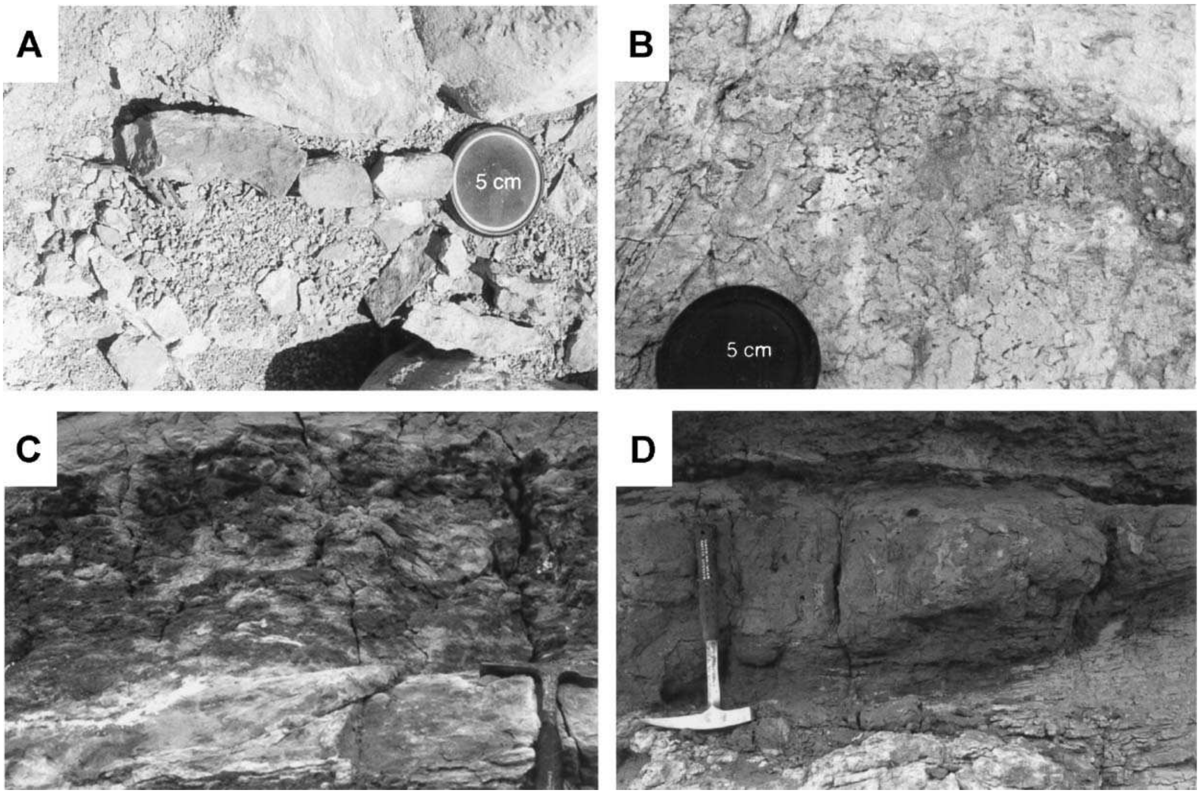


Fig. 19. Rhizoliths. (A) Horizontal rhizolith in silty mudstone interpreted as transitional swamp deposits in the coastal plain, Windy Hill Member, Grey Reef, Alcova, WY. (B) Dispersed, fine-textured rhizoliths (dark zigzagged lines) in interbedded sandstone and mudrock interpreted as pedogenically modified overbank floodplain, Salt Wash Member, Hatt Ranch, UT. (C) Rhizoliths as color mottles in mudrock; rock hammer for scale, Salt Wash Member, Shootaring Canyon, UT. (D) Close-up of pedogenically modified floodplain channel (pinches out to right of photo) with rhizoliths (light-colored mottles) and burrows (dark areas); rock hammer for scale.

mentous tubes 0.05–0.1 cm in diameter are common. The outer surfaces of the traces are relatively well defined and range from smooth to filamentous. These tubular structures occur generally in groups with individuals spaced at various distances from one another but not less than 10 cm.

Occurrence: These structures occur in every member of the Morrison.

Tracemaker: The architectural and surficial morphology demonstrate that these traces are plant roots or rhizoliths.

Interpretation: The overall morphology and depth of these rhizoliths record the local paleohydrologic settings and groundwater fluctuations during the life of the plant. These traces are mainly hygrophilic; however, hydrophilic plant traces exist (e.g., horsetail rhizomes). When rhizoliths of varying depth co-occur, the shallower rhizoliths record the area of the paleogroundwater profile with moisture levels similar to the upper vadose zone; deeper roots likely indicate the depth of the intermediate vadose zone. The depth of the rhizoliths also reflects the size of the plant, its shade tolerance, its anchoring mechanism (flankbuttress vs. deep roots), and variations in local soil water content, nutrient base, and soil maturity. The largest rhizoliths and trunk steinkerns were most likely riparian, based on their association with levee and proximal floodplain deposits. Abundant medium to small rhizoliths are common in proximal to distal alluvial floodplain and supralittoral and littoral lacustrine deposits. Large primary and secondary branches are most likely of woody plants based on morphology (e.g., Bown, 1982; Hasiotis and Dubiel, 1994). The filamentous traces at the ends and along the margins of the main rhizoliths represent root hairs that grew to increase water and mineral absorption from the substrate. Associated with these rhizoliths are the traces of extensive gallery systems most similar to termite nests.

Rhizoliths and associated ichnofossils that disrupt the bedding of alluvial and transitional lacustrine environments indicate that surfaces and their underlying substrates underwent pedogenesis. The most abundant in the Morrison are paleosols identified as fluvents (fluventisols), or entisols developed on fluvially deposited sediments. These are immature paleosols that delineate short durations of soil development interrupted by the deposition of new material, after which soil-forming processes worked on the new surface and underlying material.

4.35. Type 35—Fuersichnus isp.—mayfly? burrows, Fig. 20A–H

Description: Horizontal to subhorizontal burrows composed of retrusive, curved paths along an axis that were backfilled as each path was constructed (Fig. 20A–H). These structures differ from *Rhizocorallium* in that they lack an outer U-shaped tube with downward deflected spreiten filling between the tubes.

Occurrence: These structures occur in the upper surfaces of fine-grained, ripple-, and planar-laminated sandstones in the Tidwell and Salt Wash Members.

Tracemaker: Based on comparisons to extant burrow morphologies, this trace was most likely constructed by insect nymphs similar to extant mayflies or was constructed by caddisfly larvae (Ward, 1992).

Interpretation: These hydrophilic traces were constructed in alluvial channel, proximal floodplain, and proximal lacustrine environments. *Fuersichnus* occurs in a shallow-water alluvial deposit interpreted as a cutoff meander or oxbow lake in the Salt Wash Member. It also occurs in shallow-water lacustrine deposits interpreted as interdistributary bays or proximal, low-energy inlet shorelines in the Tidwell Member. *Fuersichnus* was the product of probing movements by a deposit-feeding organism working along a curved axis backfilling the path behind itself. If these burrows were constructed by mayfly (Ephemeroptera) or caddisfly (Trichoptera) insects (nymphs and larvae), then their traces indicate seasonal to perennial freshwater bodies. Extant reproductive forms of Ephemeroptera and Trichoptera typically require favorable water conditions in order to complete their reproductive life cycle. Stagnant and hypersaline water are detrimental to the reproduction of these insects (Ward, 1992).

4.36. Type 36a (resting) and b (locomotion)—Kouphichnium isp.—horseshoe crab traces, Fig. 21

Description: Four kinds of track imprints are common:

(1) Two chevronlike series of tracks, each with four oval to round holes or bifid V-shaped impressions or scratches (Fig. 21).
(2) One pair of digitate or flabellaie, toe-shaped imprints with or without a medial drag mark.
(3) Partial to complete, shallow, bell-shaped or cuspate impressions occurring in a linear series 5 to 10 cm or more in length.
(4) Other traces include bell-shaped anterior regions of impressions that sometimes have the outline of the midregion and posterior of a horseshoe crab.

Occurrence: These traces occur in calcareous sandstones in the lower part of the Tidwell Member in Colorado National Monument.

Tracemaker: These traces were produced by freshwater horseshoe crabs (limulids).

Interpretation: These horseshoe crab traces are interpreted to have been produced in perennial freshwater lacustrine environments and represent the geologically youngest known occurrence of freshwater limulids. These hydrophilic traces are preserved in deposits that were once firm and moist, and submerged in shallow water. Resting or hiding traces (a) preserve the whole outline of the body or mainly the cephalic shield of the limulid. Locomotion and feeding traces (b) preserve various parts of the crawling trails and shallow-feeding strategies of the limulids. Experiments with extant arthropods and various substrates demonstrated that arthropod surface traces are best preserved in moist, saturated, and firm substrate conditions (Brady, 1939).

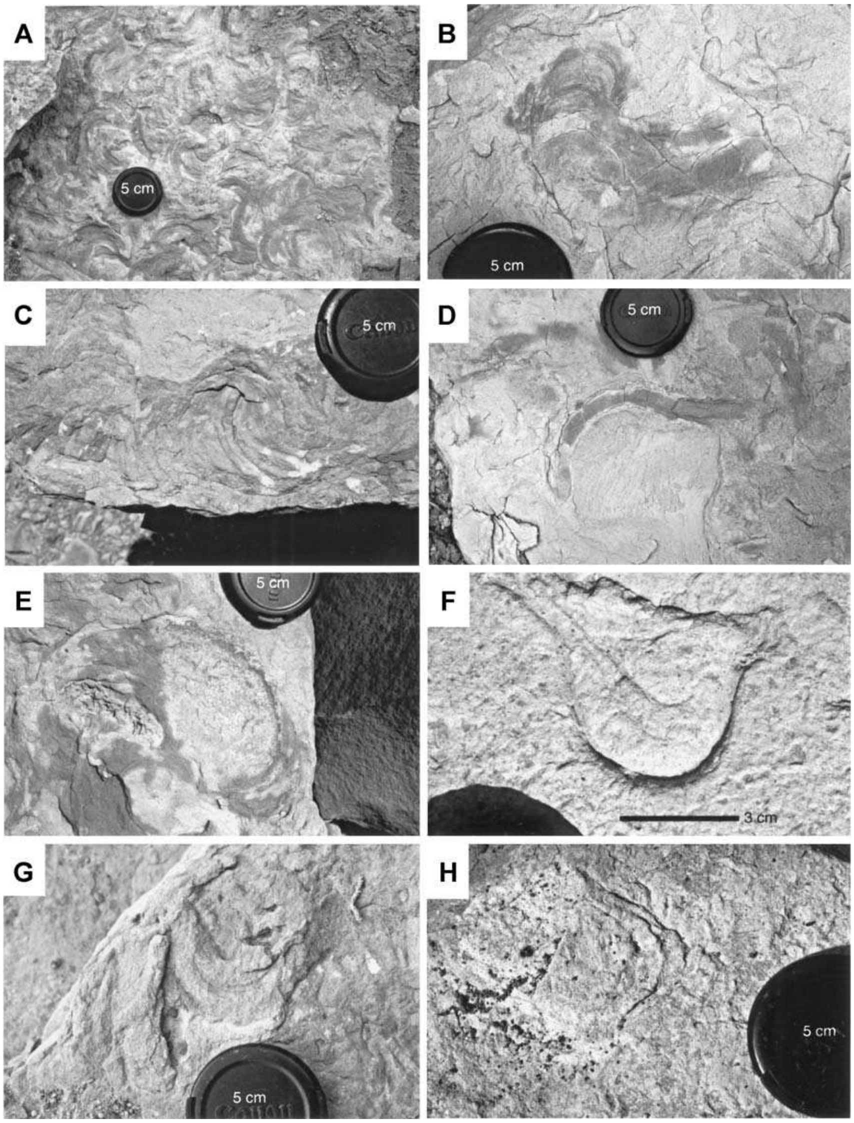


Fig. 20. Relatively shallow feeding structures assigned to *Fuersichnus* isp., Salt Wash Member, Blue Mesa, CO. (A) Bedding surface completely churned by crosscutting deposit-feeding structures assigned to *Fuersichnus* isp. (B) An isolated *Fuersichnus* isp. exhibiting a sharply curved pathway of the tracemaker with the end of the trace reflecting the retrusive feeding behavior. (C) An example of a well-formed *Fuersichnus* isp. without an external burrow wall bounding the spreite. (D) An example of a *Fuersichnus* isp. with an external burrow wall on one side of the spreite which is absent or poorly preserved near the terminus of the trace. (E) An example of *Fuersichnus* isp. that increases by over twice its initial width during construction. (F) *Fuersichnus* isp. exhibiting a well-formed outline with poorly defined internal spreiten; note that the trail is wider at the onset of feeding (modified from Hasiotis, 2002). (G) *Fuersichnus* isp. in hyporelief exhibiting consistently deeper mining of the substrate per each pass of the curved feeding path (modified from Hasiotis, 2002). (H) *Fuersichnus* isp. [similar to (F)] in epirelief but much wider and preserves several complete feeding paths (modified from Hasiotis, 2002).

Morrison horseshoe crabs were primary consumers and served as nourishment for secondary and tertiary consumers inhabiting lentic (standing water) and lotic (flowing water) environments. The horseshoe crabs likely fed on algae, organic debris, and plant fragments. Such larger vertebrates as fish, reptiles, and

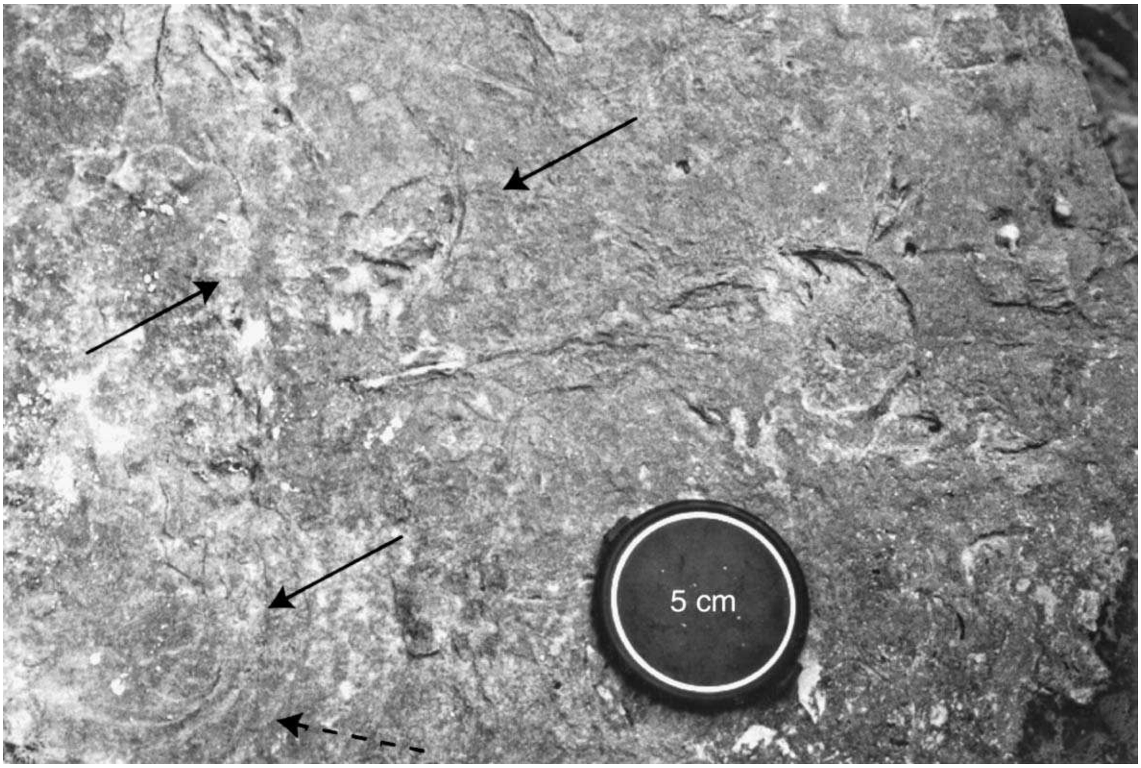


Fig. 21. *Kouphichnium* isp., Tidwell Member, Colorado National Monument, CO (modified from Hasiotis, 2002). Resting (center, above lens cap) and locomotion (arrows) traces of horseshoe crabs in carbonate cemented fine-grained sandstone interpreted as freshwater lacustrine deposits. These traces co-occur with freshwater ostracodes and charophytes.

dinosaurs may have fed on the horseshoe crabs in and along the shorelines of water bodies.

4.37. Type 37a (elongate, furrow—feeding–hiding trace) and b (furrow with striations—crawling–grazing trail)—gastropod traces, Fig. 22A,B

Description: Elongate depressions or furrows (a) of systematically decreasing diameter downward such that each level is commonly differentiated by a rim (Fig. 22A). Several thinner furrows at the same interval can be present, whereas others show bilateral symmetry. These traces are sometimes associated with trails 5–15 cm long or more, composed of a furrow with raised edges (b). Within the furrow are discontinuous, longitudinal striations that are deeply impressed closer toward the outside of the furrow (Fig. 22B). In some cases, the depressions occur within or along side the trail. This behavior is analogous to the relationship between *Cruziana* and *Rusophycus* (e.g., Ekdale et al., 1984; Bromley, 1996).

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstone in the Tidwell, Salt Wash, and Brushy Basin Members.

Tracemaker: These traces were most likely produced by a freshwater gastropod involved in two distinct and sometimes related behaviors.

Interpretation: These hydrophilic traces were formed by gastropods living in freshwater, subaqueous environments. The elongate furrows that form depressions most likely reflect a feeding or hiding behavior of a gastropod. The occurrence of several thinner furrows at the same interval, as well as others that show bilateral symmetry, show the morphology of the foot forcing itself downward.

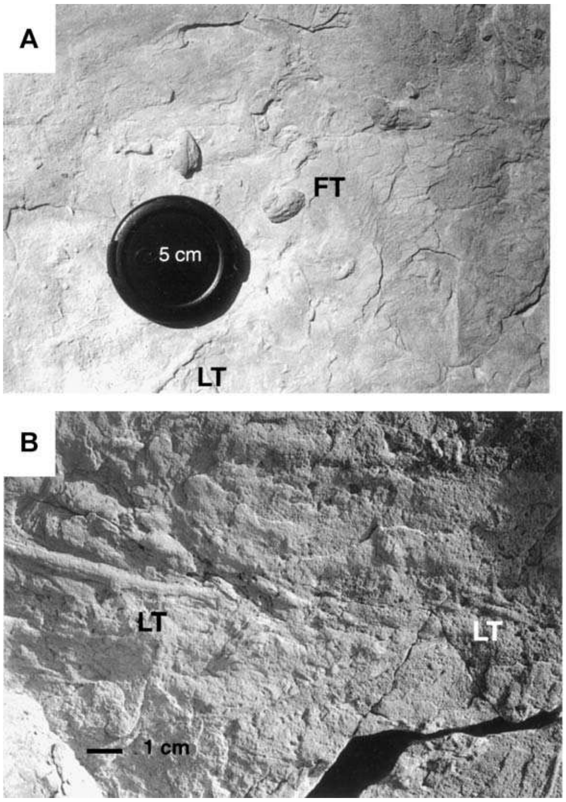


Fig. 22. Gastropod trails in the uppermost part of the Brushy Basin Member, Cleveland–Lloyd Quarry, UT. (A) Feeding traces (FT) in point bar sandstone bed composed of several crosscutting narrow paths attributed to feeding foot of gastropods. (B) Locomotion trails (LT) exhibiting discontinuous longitudinal scratches attributed to the shells of gastropods.

This motion may have formed while the gastropod was searching for some buried food source or pulling itself into the subsurface. Thus, the rims could imply a higher position of its shell and higher activity level of the gastropod pulling itself downward. The furrows with raised edges likely represent their crawling trails. Deeply impressed, discontinuous, longitudinal striations indicate the movement of the gastropod shell. Microtopography and microconsistency of the substrate would affect the overall pattern and morphology of the trail. Depressions within or alongside the trails reflect changes in the behavior of the gastropod from feeding to crawling or to possibly protecting itself from predators.

4.38. Type 38a (very large and deep), b (rhizolith-specific), c (rhizolith-engulfing), d (spherical), e (ramps), and f (concentrated galleries)—multiarchitectural, coterminous chambers and galleries—termite nests, Figs. 23A–D, 24A–E

Description: Architectural and surficial morphologies of these traces are highly variable and represent at least six types of nest architectures (Figs. 23A–D, 24A–E). The overall surficial morphology of the nests ranges from smooth to highly textured and pustulose.

(a) Very large and deep in size: Immense concentration of galleries (estimated *N*>100,000) and flattened to spherical chambers with the main portion spread over a small surface area (0.5–2 m^2) extending 10–40 m in depth. Nests contain an array of architectural elements found in other specific types of nests and may be associated with rhizoliths or tree steinkerns.

(b) Rhizolith-specific: Galleries and chambers confined to the morphology of roots and stumps, rarely extending much farther outward than the diameter of a particular rhizolith. Within the primary and secondary rhizolith branches are more than 100 horizontal and vertical, anastomosed and interconnected galleries occur with diameters from 0.15–0.5 cm but predominantly 0.2–0.3 cm in diameter; nest extends to the depth of rhizolith penetration. A few galleries, 0.2–0.3 cm in diameter, with thin wall linings radiate out from the nest.

(c) Rhizolith-engulfing: Engulfs the entire root system and the surrounding substrate of the root composed of anastomosed and interconnected galleries 0.15–0.5 cm in diameter, with chambers commonly within the main portion of the concentration; nest extends to the depth of rhizolith penetration.

(d) Spherical: Spherical arrangement of chambers and galleries 8–20 cm in diameter and depths from 40–100 cm. Some spheroids are preserved empty or with several dividers, while others contain visible layers of galleries and open spaces. Lesser numbers of galleries, 0.2–0.3 cm in diameter, with thin wall linings radiate out from the nest.

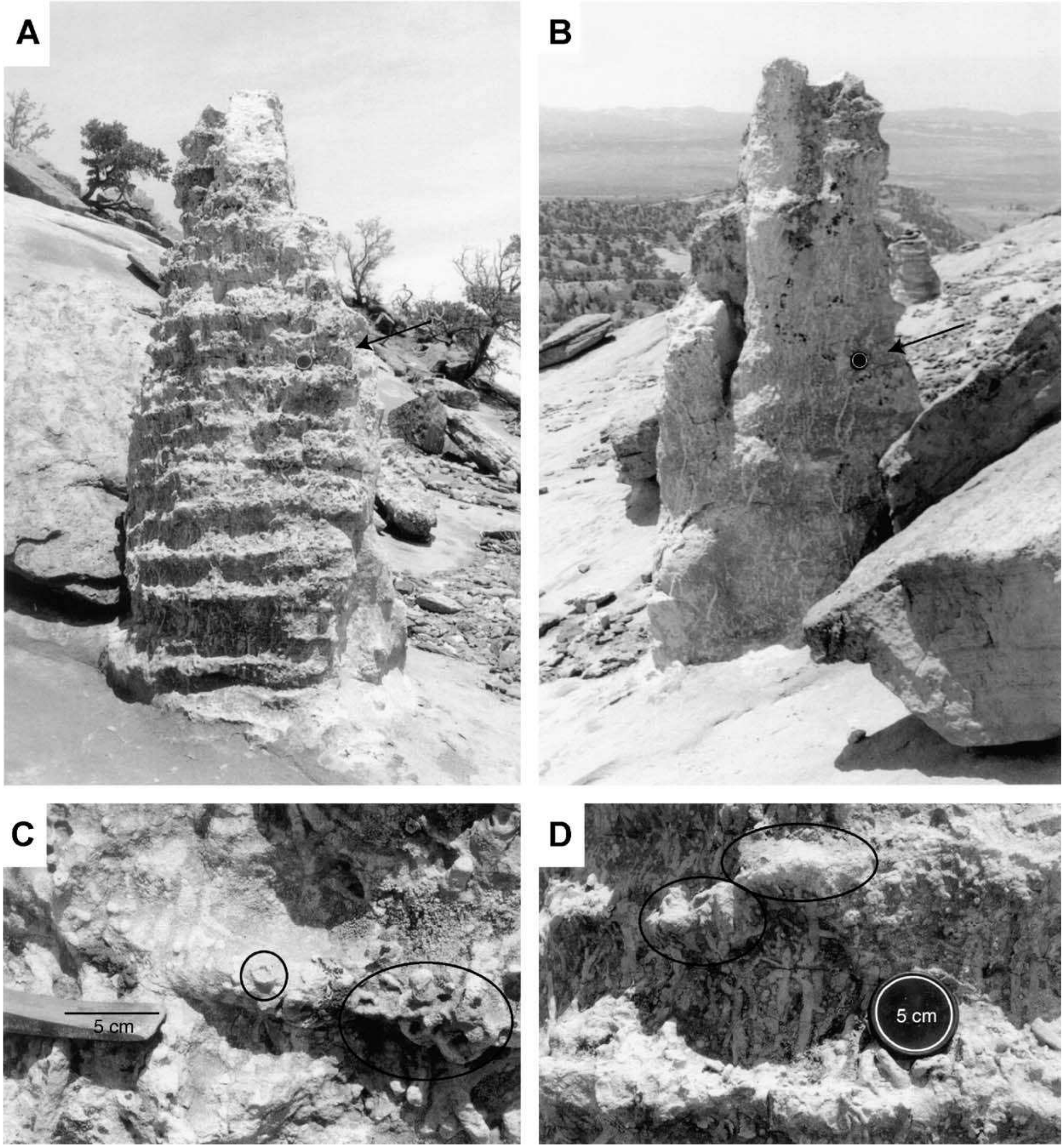


Fig. 23. Giant ichnofossils interpreted as termite nests in eolian facies of the upper part of the Recapture Member, Morrison Formation, Navajo Church, NM. Portion of a subterranean termite nest exhibiting different morphologies; front (A) with galleries intersecting thin, elongate perpendicular chambers and back (B) with mainly vertical and lateral galleries and small chambers. Lens cap (arrow) is 5 cm in diameter. (C) Close-up of galleries showing reinforced construction of tunnels (circled areas), as well as branching patterns in upper left and lower right of photograph. (D) Close-up of variations in gallery diameters and the high density of galleries associated with the thin, elongate perpendicular chambers (circled areas) that appear to coalesce at distinct intervals (bottom of photograph).

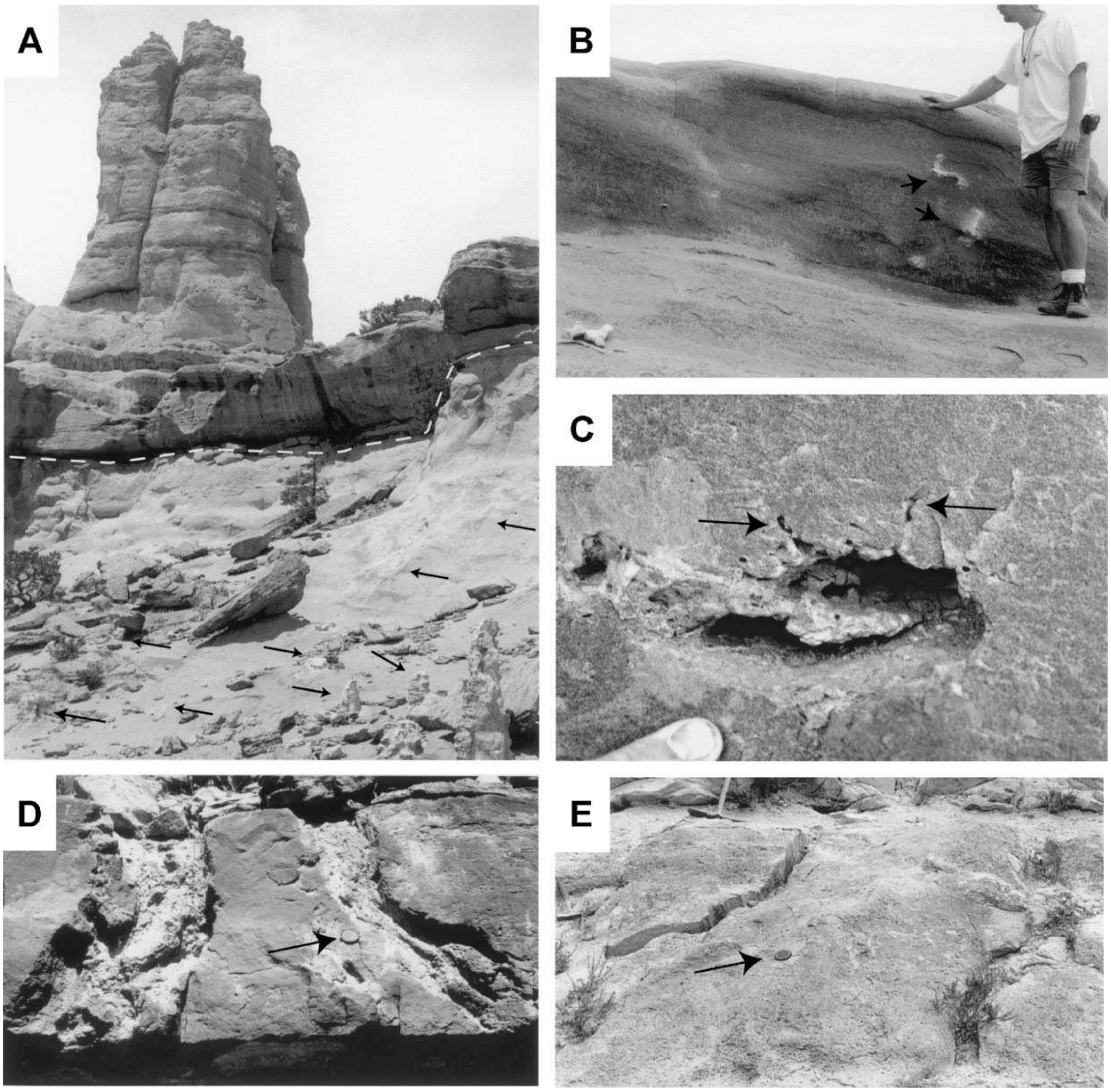


Fig. 24. Termite nests in the Recapture and Salt Wash Members of the Morrison. (A) Surface of origination for the termite nests in the Recapture Member (Jmr; Navajo Church, NM; 22) is at a sequence boundary (dashed line) with the fluvially deposited Westwater Canyon Member (resistant sandstone ledge in the upper part of the photograph) overlying the pedogenically modified sediments in the eolian facies of the Recapture Member; arrows denote nests in the outcrop. Nest in Fig. 23A located in lower right of photograph. (B) Eolian bedding nearly destroyed from intense bioturbation by termites and other insects; note the sections of termite nests adjacent to the left of person (arrows). (C) Close-up of spherical termite nest in the Recapture Member, Aneth, UT, exhibiting remnants of the internal structures and radiating galleries (arrows) from the nest. (D) Large termite nests constructed in large tree stump steinkerns, middle part of the Salt Wash Member, Shootaring Canyon, UT; note the patterns of galleries within and extending out of the main portions of the nests (area of arrow and lens cap). (E) Large, laterally extensive, subterranean termite nest composed of hundreds of thousands of galleries and smaller chambers in fluvially deposited sandstone, near Colorado National Monument, CO.

(e) Ramps: Contains 2–8 pancake-shaped inclined ramps 1–2 cm in thickness and 15–30 cm in length. Rarely are galleries found emanating from the ramps, most of which occur in the middle to lower portions of the nest.

(f) Concentrated galleries: Great concentration of galleries (estimated N>10,000) and nondistinct chambers that are spread over a large area surface (>2 m^2) and to a depth of 1–2.5 m.

These nest types contain similar components of interconnected single to compound galleries and flattened to spherical chambers. Galleries are similar to *Planolites* and *Palaeophycus*, whereas the chambers grossly resemble globular or lenticular concretions.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstone and small- to large-scale cross-bedded to massive sandstone and mudrock in the Tidwell, Salt Wash, Recapture, and Brushy Basin Members.

Tracemaker: Comparisons to nests of extant burrowing organisms suggest that these simple to very complex trace fossils were termite nests. They are most similar to extant termite nests belonging to the Porotermitidae, Kalotermitidae, Stolotermitidae, and Mastotermitidae (Krishna and Weesner, 1970).

Interpretation: The terraphilic Jurassic nest ichnofossils were constructed in association with vegetation growing in proximal to distal alluvial floodplains as well as in supralittoral lacustrine environments. All architectural morphotypes of the Jurassic termite nests are present in younger continental rocks of northern Africa, some of which are currently used by extant termites in northern and southern Africa (e.g., Krishna and Weesner, 1970; Sands, 1987; Genise and Bown, 1994b). The presence of termite nests in the Morrison was predicted by Hasiotis and Dubiel (1995) when they reported hodotermitid- or mastotermitidlike termite nests in the Upper Triassic Chinle Formation in northern Arizona. Furthermore, Boullion (1970) hypothesized through patterns in vicariance biogeography of extant termites that the evolutionary radiation of the families mentioned earlier most likely occurred in the Triassic and Jurassic.

The ichnofossil nests indicate the niche diversification of termites as detritivores. Many of the Jurassic termite nests are composed of interconnected and anastomosing galleries of various diameters that correspond to presence and size of roots, stems, and branches of trees and shrubs. It is interpreted that the Jurassic termites used these materials as their food source, digested through a symbiotic relationship with cellulose-digesting bacteria in their gut, similar to extant termites (Krishna and Weesner, 1970). The Porotermitidae, Kalotermitidae, Stolotermitidae, and Mastotermitidae attack and construct nests in living, dead or dying, and dry or damp woody tissues (Krishna and Weesner, 1970).

The Morrison nests also preserve eusocial behavior by Jurassic termites. The intricate nature of the nests imply that a high degree of cooperation was necessary in order to maintain the construction of hundreds of galleries (workers), defend the nest from invaders (soldiers), regulate and dispose of the nest waste products (workers), as well as egg rearing (nursery workers) and egg laying (queen) to produce more caste members and future kings and queens (elates; Wilson, 1971).

4.39. Type 39a (reinforced tops) and b (ghost traces)—compressed U-shaped tubes, Fig. 25A–B

Description: Shallow, compressed U-shaped burrows characterized by openings 0.8–1.0 cm apart from each other. In cross-section, the tubes do not appear to connect and only rarely is there evidence of connection.

(a) Reinforced tops: Upper portions of the U-tubes are well preserved and reinforced with a thin sediment lining.

(b) Ghost U-traces: Shallow U-shaped tubes are preserved as faint, contorted paths of the arms and base of the burrow without any reinforced tubes or wall linings above, at, or below the path of the paleosurface.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstone interbedded with mudstone in the Tidwell Member.

Tracemaker: These traces were most likely constructed by at least two different aquatic insect larvae of the (a) chironimids (Diptera) and (b) ephemeropterans (Ephemeroptera).

Interpretation: These hydrophilic, U-shaped tubes were constructed in proximal and shallow distal lacustrine environments similar to the littoral, sublittoral, and the proximal profundal zones in modern lacustrine settings. Chironomid larvae commonly construct temporary to long-term use U-shaped burrows. Some reinforce the openings of their tubes above the surface of the substrate, whereas others construct burrows during daylight hours for protection and leave them at dusk to feed in the water column (Chamberlain, 1975). Still others may ingest their way through the sediments or invariably feed on detrital organics within the sediments. Burrowing mayfly larvae are filter feeders, using the burrow as a shelter, whereas other larvae move through the sediment in search of prey (Ward, 1992).

4.40. Type 40—cf. Planolites isp., Fig. 25B

Description: Smooth, unornamented, cylindrical to subcylindrical, unlined burrows ranging from 0.3–0.6 cm in diameter. Burrows are slightly curved to sinuous and do not exhibit branching.

Occurrence: These traces occur in massive to fine-grained ripple- and planar-laminated sandstone interbedded with mudstone in all members of the Morrison.

Tracemaker: All invertebrates including those with and without rigid or flexible exoskeletons most likely constructed this type of trace.

Interpretation: These burrows are not distinctive to the tracemaker and occur in nearly every Morrison environmental setting. Often, poorly preserved horizontal burrows are assigned to this ichnotaxon. In continental settings, these hydrophilic burrows are, for the most part, not diagnostic of any environment. In the marine realm, *Planolites* has been used to suggest stressed environmental and oxygenation conditions (e.g., Ekdale et al., 1984). Similar types of burrows in freshwater lacustrine environments may also be suggestive of stressed conditions due to oxygenation and pH and Eh conditions.

4.41. Type 41—horizontal U-tubes—mayfly? burrows, Fig. 25C

Description: Horizontal U-shaped tubes where the distance between the tubes at the openings is less than or equal to the distance between the tubes at the base of the U. The burrow is within a few centimeters of the paleosurface.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstone interbedded with mudstone in the Tidwell and Salt Wash Members.

Tracemaker: The aquatic insect larvae of the Ephemeroptera most likely constructed these traces.

Interpretation: Mayfly burrows have been described as vertical to horizontal U-shaped tubes (e.g., Needham et al., 1935; Silvey, 1936; Chamberlain, 1975). These hydrophilic traces occur in alluvial channel deposits in the upper parts of planar cross-bedded sandstones (Fig. 25C) suggesting that the burrow was constructed during periods of nondeposition or sediment bypass. The burrow remained open during the larval phase of the insect's life cycle and was used for dwelling and filter feeding or collecting plant debris (Edmunds and Waltz, 1996). The larvae of mayflies commonly occupy bars and point bars in the actively flowing parts of streams and rivers.

4.42. Type 42—vertical, bent Y-tube, Fig. 25D

Description: Vertical U-shaped tubes where the angle of each tube is approximately 60–70° from the horizontal of the paleosurface. A shaft coming from the U-tube may extend deeper into the substrate. The opening originates along the accretionary surface of a bar within a planar cross-bed set. The walls of the tube seem smooth and unlined.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstone in the Salt Wash Member.

Tracemaker: The tracemaker is unknown; however, the burrow pattern is similar to that of aquatic insect larvae belonging to mayflies (Ephemeroptera), caddisflies (Trichoptera), or midges (Diptera).

Interpretation: Mayflies (Ephemeroptera), caddisflies (Trichoptera), and midges (Diptera) are known to construct several forms of U-shaped burrows, both horizontal and vertical to the bedding surface. U-shaped tubes of mayflies and midge larvae have been described above. Polycentropodid caddisflies construct retreats as Y-shaped burrows similar to those described in the Morrison. Extant species of *Phylocentropus* (Trichoptera: Polycentropodidae) living

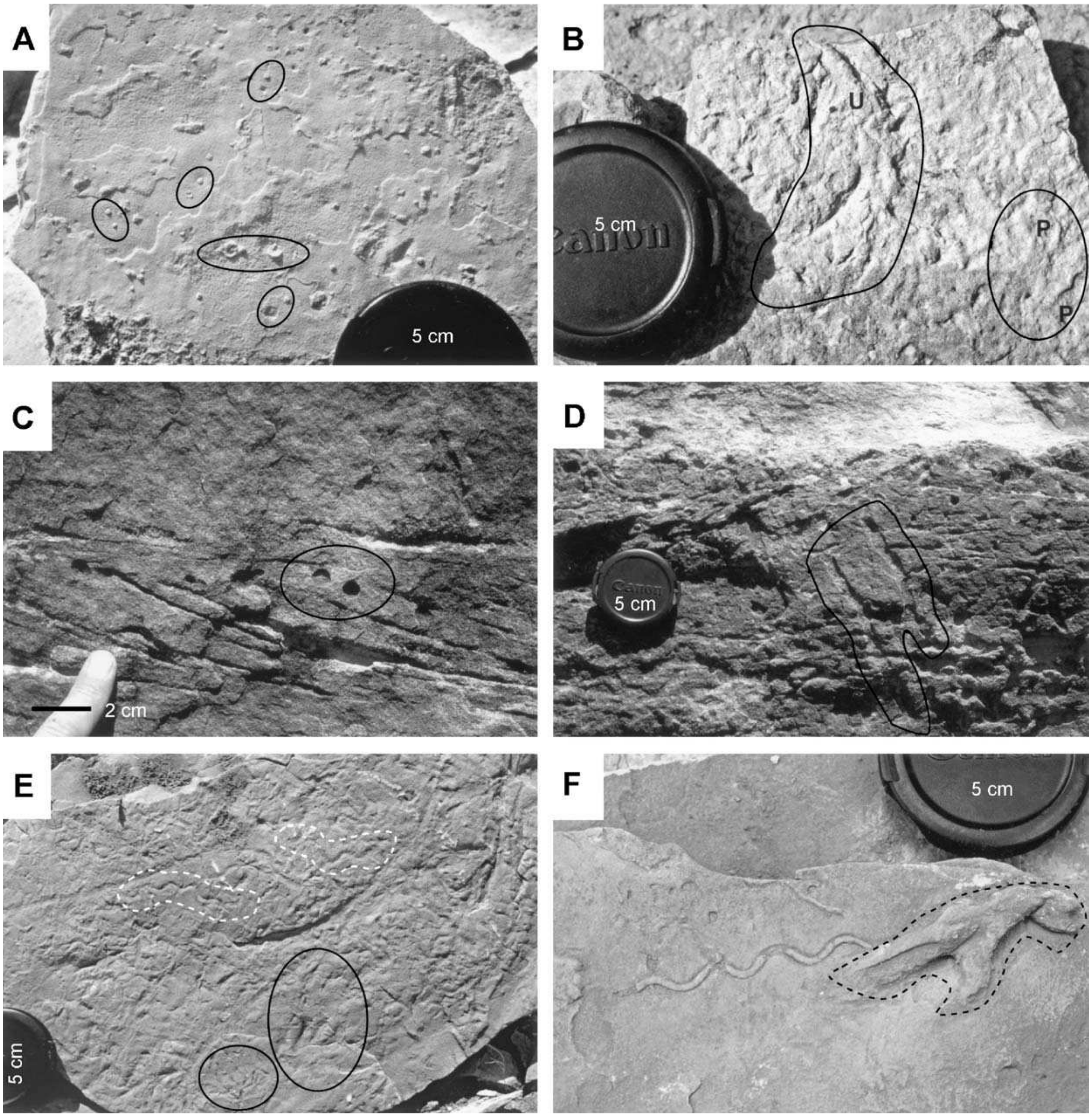


Fig. 25. Invertebrate trace fossils from lotic and lentic environments. (A) Top of a bed showing the upper reinforced parts of U-shaped tubes (paired tubes above bedding plane) constructed in very fine grained distributary sandstone splay deposits, upper part of the Tidwell Member, Blue Mesa, CO (modified from Hasiotis, 2002). (B) Top of bed with irregular texture produced by grazing invertebrates that excavated shallow U-shaped tubes (U) and shallow *Planolites*-like burrows (P), upper part of the Tidwell Member, Blue Mesa, CO. (C) Planar cross-bedded sandstone with horizontal U-shaped burrows attributed to mayflies, lower part of the Salt Wash Member, Blue Mesa, CO. (D) Vertical Y-shaped burrow in cross-section crosscutting older horizontal Y-shaped burrows (right of center in photograph), lower part of the Salt Wash Member, Blue Mesa, CO. (E) Bed surface with *Cochlichnus* and larger *Cochlichnus*-like trails attributed to oligochaetes (dashed line); both associated with *Pteraichnus* isp. and longitudinal scratches (circled areas) produced by dragging of the pes of *Pteraichnus* isp. (modified from Hasiotis, 2002). (F) Large *Cochlichnus*-like trail attributed to oligochaetes associated with the pes of *Pteraichnus* isp. (dashed line; modified from Hasiotis, 2002).

along the margins of sandy rivers construct Y-shaped tubes of silk covered with sand and small pieces of detritus with the upstream end extending above the substrate. It is within the side tube of the Y in which the caddisfly feeds on fine organic material and diatoms. The overall length of the single main tube can be up to 16 cm (Wallace et al., 1976). More work is necessary to determine the relationship of this hydrophilic burrow morphology and the extant Y-shaped burrows.

4.43. Type 43a (small diameter) and b (large diameter)—Cochlichnus isp., Fig. 25E,F

Description: Horizontal, smooth sinusoidal trails preserved in concave epirelief. Thin trails (a) are 0.5–1.0 mm in diameter and 5–15 cm long, retaining the same diameter. These trails are fairly abundant ranging from 5 to 15 individuals on a 25-cm^2 surface.

Large-diameter, smooth, roughly sinusoidal trails (b) are 0.2–0.35 cm in diameter and 10–20 cm long. One end of the trail tapers to a point, whereas the other end terminates in a slightly bulbous form that is slightly wider than the trail. These trails are less abundant than the thinner ones, with 1–3 individuals on a 25-cm^2 surface.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstone interbedded with mudstone in the Tidwell and Salt Wash Members.

Tracemaker: Comparisons to modern trails suggest that these sinusoidal traces were most likely made by nematodes, biting midge larvae, or by oligochaetes.

Interpretation: *Cochlichnus* isp. (small and large) was constructed in proximal lacustrine environments similar to the littoral zone of modern lakes. These traces are hydrophilic. Hitchcock (1858) originally attributed the trace to a worm, while Moussa (1970) attributed the tracemaker to a nematode. More recently, Metz (1987a) described extant trails of biting midge larvae constructing the sinusoidal trail (Diptera: Ceratopogonidae). Moreover, Metz (1987b) found that many other types of insects construct some form of sinusoidal to irregular trail in ephemeral puddles. The Morrison forms also reflect similar construction to those trails described above, suggesting that only a thin film of water covered the sediments. At least two or more types of invertebrates—insect larvae and annelids—constructed these trails based on size and amplitude of the sinusoidal traces. Further work is necessary to delineate specifically which invertebrates actually constructed the Morrison traces. Nevertheless, the narrow and broad sinusoidal trails reflect conditions related to subaqueous substrates in aquatic environments. Because many of these trails occur with footprints and feeding marks of pterosaurs, the water depth was probably less than 1 cm in order to get manus and pes impressions and scratch patterns.

4.44. Type 44a (tracks) and b (feeding traces)—Pteraichnus isp., Fig. 26A–C

Description: The tracks occur as surface impressions (concave epirelief) of the manus and pes of one or more individuals (Fig. 26A–C). The manus is represented by an asymmetrical three-toed print in a triangular to boomerang form. The pes is represented by an elongate triangular shape with four digits that contain impressions of pads and a claw on the end of each digit.

In certain bedding planes, pes impressions occur with shallow, elongate raking marks, roughly 4–10 cm in length, that have the same number of furrows as digits on the pes. In some instances, several scratch patterns occur together with four to nine furrows of relative completeness. Also associated with these traces are short claw impressions 0.2–0.5 cm in length that are abundant (>50) across the bed surface.

Occurrence: These traces occur in very fine to fine-grained ripple- and planar-laminated sandstone interbedded with mudstone in the Windy Hill and Tidwell Members.

Tracemaker: These features were produced by two behaviors of pterosaur: (a) locomotion and (b) feeding.

Interpretation: Pterosaur trace fossils were produced in proximal lacustrine environments similar to the epilittoral and littoral zones of modern lakes and transitional marine settings. These traces are hydrophilic and were produced in substrates at or just below the water surface. Pterosaur tracks have been described from the Morrison at several localities (e.g., Stokes, 1957; Logue, 1994; Lockley and Hunt, 1995; Lockley et al., 1996). Those described here are new, however. Similar raking traces were also discovered by Debra Mickelson at other Morrison localities (D. Mickelson, 1997, oral communication). We have interpreted independently these traces as

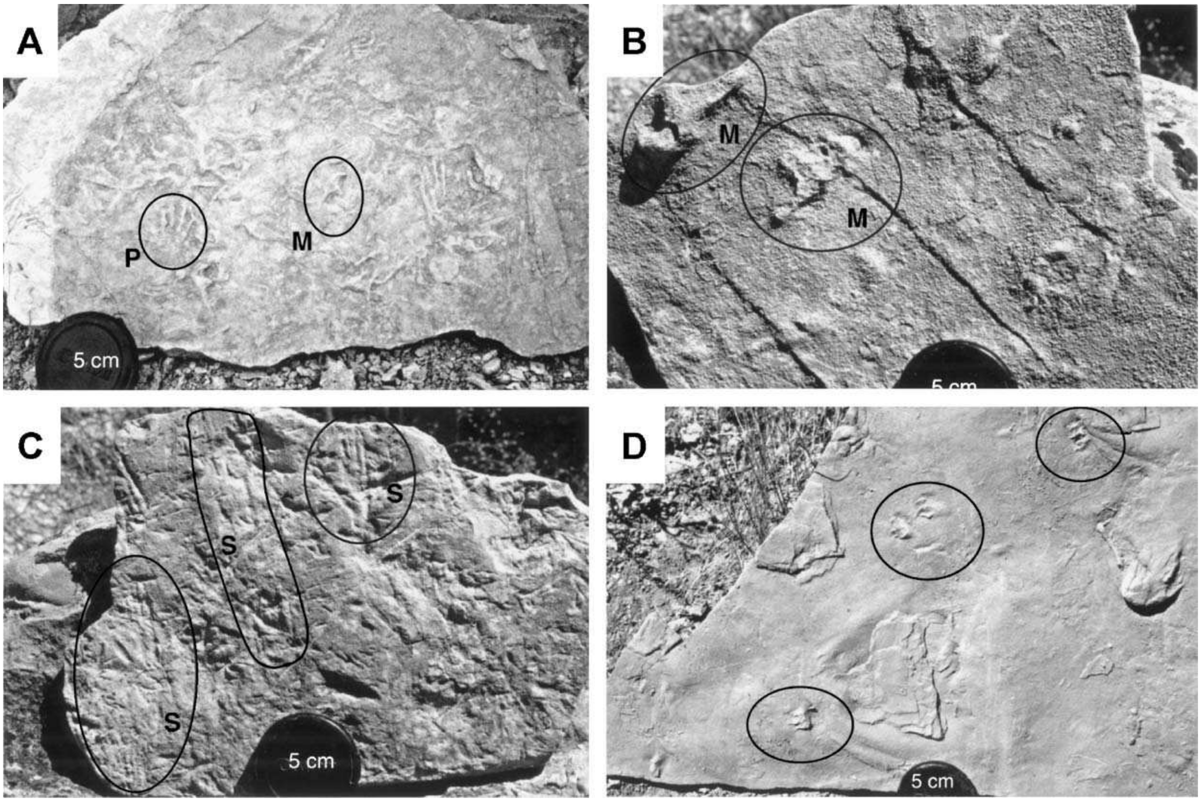


Fig. 26. Small vertebrate tracks, Tidwell Member, Blue Mesa, CO. (A) *Pteraichnus* isp., manus (labeled with an M) and pes (labeled with a P) impressions associated with invertebrate locomotion and dwelling traces in lacustrine sandstones. Underside (B) and top (C) surface of a sandstone bed with *Pteraichnus* isp. (modified from Hasiotis, 2002); note that the tracks in (B) are larger than those in (C). Scratch marks (labeled with an S) are also visible in (C). (D) Swimming tracks of an unidentified reptile.

pterosaur feeding tactics, where these reptiles raked the sediment along the shoreline of a lake or tidal flat to reveal annelids or insect larvae hidden just below the surface.

4.45. Type 45—small reptile swimming tracks, Fig. 26D

Description: Tracks preserved in concave epirelief that form a discontinuous trackway. Small tridactyl prints, about 1.5 cm wide and 0.7 cm long, that exhibit shallow but distinct digit traces with or without slightly deeper posterior impressions. Most tracks do not contain the posterior part but only the impressions of the digits. Still other tracks appear to be two or three sets of short scratches (0.4–0.7 cm) representing the digits.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstone interbedded with mudstone in the Tidwell Member.

Tracemaker: A swimming reptile, perhaps a crocodile or a turtle, most likely produced these tracks (Foster et al., 1999).

Interpretation: These tracks were produced in proximal lacustrine environments similar to the littoral zone of modern lakes. They are epiterraphilic but constructed in hydrophilic settings; they were produced below the water surface. The paleosurface contains several layers of tracks: (a) offset trackway with individual tracks showing toe scrapes and palm slippage produced on the surface and co-occurring aquatic invertebrate traces, and (b) larger, undertrack impressions (center of photo) made by a bigger vertebrate on a higher surface. The combination of features described in (a) supports observations that the tracks were made in an aquatic environment. The pattern of the smaller tracks suggests the that body was buoyed up in the water and that the discontinuous tracks were produced while the organism swam and pushed off the bottom at intervals between 10 and 20 cm apart. Because only the front parts of the manus and pes are preserved, this probably reflects partial placement of the appendage against the substrate for pushing off. This interpretation is supported by observation of tridactyliform claw impressions preserved in the bottom.

4.46. Type 46—large circular depressions—sauropod tracks, Fig. 27A–E

Description: Large tracks from 20 cm to more than 100 cm in diameter and from 10 cm to more than 60 cm deep that resemble pillow or load structures and contain impressions of digits and striations on the vertical surface of the impression (Fig. 27A–E). The best preserved tracks reveal five digits, whereas more poorly preserved tracks display one to four digits of various quality for the same size and shape print. Cross-section shapes vary from lobate to asymmetrical lobate. They occur as partial trackways (several isolated tracks found together) or as tens to hundreds of impressions. Many of the tracks are visible in cross-section, whereas others weather out and accumulate in the talus below the outcrop.

Occurrence: These traces occur in fine-grained, trough-cross-stratified, ripple- and planar-laminated sandstone interbedded siltstone and mudstone in all the members of the Morrison with the exception of the Westwater Canyon. These tracks occur by the hundreds in ooid grainstone (limestone) in the Purgatoire River area of southeastern Colorado (Lockley et al., 1986; Dunagan, 1998).

Tracemaker: The form and depth of the tracks suggests that sauropods produced them.

Interpretation: Sauropod tracks and trackways forming trampled grounds were produced in an array of environments including alluvial channel, levee, and floodplain, proximal lacustrine, and transitional marine environments. Organisms living in terrestrial environments produced these traces, but their tracks are best preserved in substrates suitable for hygrophilic and hydrophilic organisms. The most abundant trampled grounds or dinoturbation occur in alluvial environments, followed by proximal lacustrine environments. Dinoturbation (sensu Lockley, 1991) is particularly abundant in transitional lacustrine environments where the Tidwell and Salt Wash interfinger with one another.

The distribution of dinosaur tracks and trackways across the continental and transitional marine environments (e.g., Lockley and Hunt, 1995; Lockley et al., 1994, 1999) demonstrates that the use of traces of large reptiles for paleoenvironmental interpretations is limited in scope and utility as specific environmental, ecological, and ichnofacies indicators. Terrestrial vertebrates, as a whole, are not sensitive environmental indicators, and their tracks occur in habitats with different physical and chemical environmental characteristics. They do serve as indicators of their presence in a particular area, in situ evidence of their feeding, hunting, and migration domains. The presence of tracks and trackways in deposits interpreted as riparian settings places the dinosaurs in areas where they obtained water and nutrients, which in turn, explains the presence of large herds of sauropods and other herbivores in an area, resulting in trampled grounds.

4.47. Type 47(a) ornithopod and (b) theropod tracks, Fig. 27F

Description: Tridactyl prints occur as individual tracks or in partially exposed trackways, many of which are poorly preserved or not clearly visible in the outcrop. Tridactyl broad-toed impressions are generally symmetrical and may occur with other prints that are posteriorly narrow, tridactyliform impressions with elongate digits.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstone interbedded with mudstone in the Windy Hill, Tidwell, Salt Wash, and Brushy Basin Members.

Tracemaker: Tridactyl broad-toed symmetrical impressions are attributed to large ornithopods (a). Tridactyliform impressions with elongate digits that narrow posteriorly with claw marks are attributed to theropods (b).

Interpretation: These tracks were produced in alluvial channel, levee, floodplain, proximal lacus-

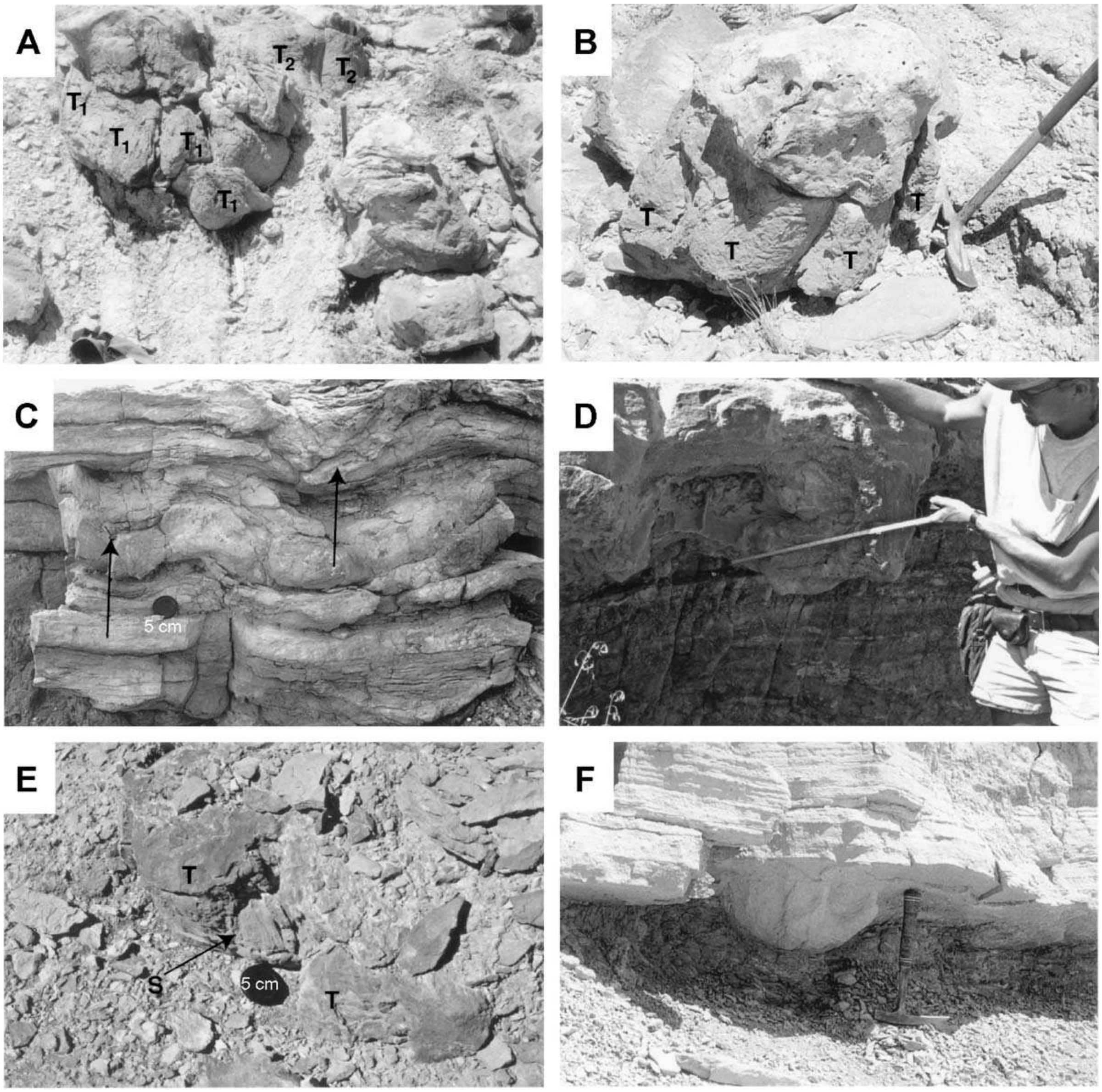


Fig. 27. Dinosaur footprints and solemarks. Salt Wash Member: Sand-filled sauropod tracks in fluvial overbank deposits near Colorado National Monument (CO) that exhibit (A) the morphology of toes (T; numbers denote each foot); (B) close-up of scratch marks and expansion cracks due to track formation. (C) Several layers of bed deformation in the upper part of the Brushy Basin Member (Cleveland–Lloyd Quarry, UT) due to dinosaur trackways, with individual tracks (arrows) visible in the center and upper part of the photograph. (D) Sand-filled sauropod tracks in overbank mudrock that was weakly modified by pedogenesis after track emplacement, lower part of the Brushy Basin Member near Arches National Park, UT. (E) Sand-filled casts of sauropod tracks in overbank splay deposits, Bighorn Canyon National Recreation Area, WY, showing partial morphology of the toes (labeled with a T) and striations (labeled with an S) made by the withdrawal of the pes from the bed. (F) Well-preserved ornithopod track in the bottom of a tidal channel sandstone, Windy Hill Member of the Morrison Formation, Grey Reef, WY.

trine, and transitional marine environments. Organisms living in terrestrial environments produced these traces, but their tracks are best preserved in substrates suitable for hygrophilic and hydrophilic organisms. The tracks of other types of ornithopods and theropods are also not useful ichnofacies indicators because they are limited in scope and utility as specific environmental and ecological indicators. Their tracks cross many different types of environments, including those along transitional marine environments. Their presence in such environments, however, indicates that they also played a role in the ecologic web of coastal regions.

4.48. Type 48—simple large-diameter, inclined burrows—reptilian? burrows, Fig. 28A–C

Description: Gently inclined (10–25°), subcylindrical burrows 15–40 cm in diameter and 0.75–1.0+ m long (Fig. 28A–C). They are commonly filled with fine- to coarse-grained sandstone and conglomerate. Surficial morphology of the burrows includes low to high densities of longitudinal scratches varying from 0.5–2 to 15–25 cm long. The lateral walls and floors of the narrower burrows contain very high densities of scratches.

Occurrence: The burrows are found in interbedded sandstone and siltstone, and in mudrocks of the lower, middle, and upper parts of the Salt Wash Member.

Tracemaker: Based on comparisons to extant burrow morphologies, these burrows were most likely constructed by vertebrates most similar to crocodiles, sphenodontids, and turtles. The burrow sizes are more similar to those of crocodiles or sphenodontids (e.g., Voorhies, 1975).

Interpretation: These burrows were constructed in alluvial levee and proximal floodplain environments. These terraphilic burrows are similar to extant burrows excavated by alligators, crocodiles, turtles, and sphenodonts. These modern reptiles ordinarily constructed burrows with gently dipping tunnels that eventually open into a large spherical den or form a T-intersection with another tunnel. They did not construct complex burrow systems like those of mammals, insects, or such large crustaceans as crayfish. The morphology and filling of the Jurassic burrows indicates that they were open and constructed in firm substrate that was subaerially exposed. Their association with channel and levee deposits suggests that they lived close to open bodies of water.

4.49. Type 49—complex, large-diameter burrows—mammal? burrows, Fig. 28D–F

Description: Burrows consist of U- or Y-shaped openings, with shallow to steeply dipping shafts leading to low-angle, diagonal, or spiraling tunnels. Burrow diameter is 5–20 cm. Chamber dimensions are variable; with the largest measuring 60 (l) × 40 (w) × 30 (h) cm. Burrow length is 100–400+ cm; vertical depth is 50–150+ cm. The burrows are preferentially cemented with carbonate and, in most cases, seem nodular. Burrow walls contain short to elongate scratch patterns when not covered by carbonate precipitation.

Occurrence: The burrows are found in mudrocks of the lower, middle, and upper parts of the Salt Wash Member.

Tracemaker: Based on these comparisons to fossil and modern burrows (e.g., Voorhies, 1975; Hasiotis et al., 1999a,b; Groenewald et al., 2001; Miller et al., 2001), these Jurassic structures are interpreted as mammal burrow systems (Hasiotis and Wellner, 1999).

Interpretation: These burrows are associated with entisols, alfisols, and vertisols developed in overbank alluvial deposits. On the basis of size, morphology, and occurrence, these terraphilic ichnofossils may represent fossorial behavior in early mammals (e.g., Voorhies, 1975). Fossil evidence of mammals dates back to the Late Triassic; however, there is no pre-Cenozoic evidence of their burrowing behavior. These Late Jurassic ichnofossils exhibit architectural elements also found in the burrow systems of (1) Permian and Triassic mammal-like reptiles, (2) Neogene canines and rodents, and (3) modern fossorial marsupial and placental mammals (e.g., Voorhies, 1975; Hasiotis et al., 1999a,b). Morphologies suggest communal or subsocial behavior and that the burrows were designed for long-term use: residence, raising young, storage and disposal of food and wastes, and coping with episodic inundation by water (Hasiotis and Wellner, 1999).

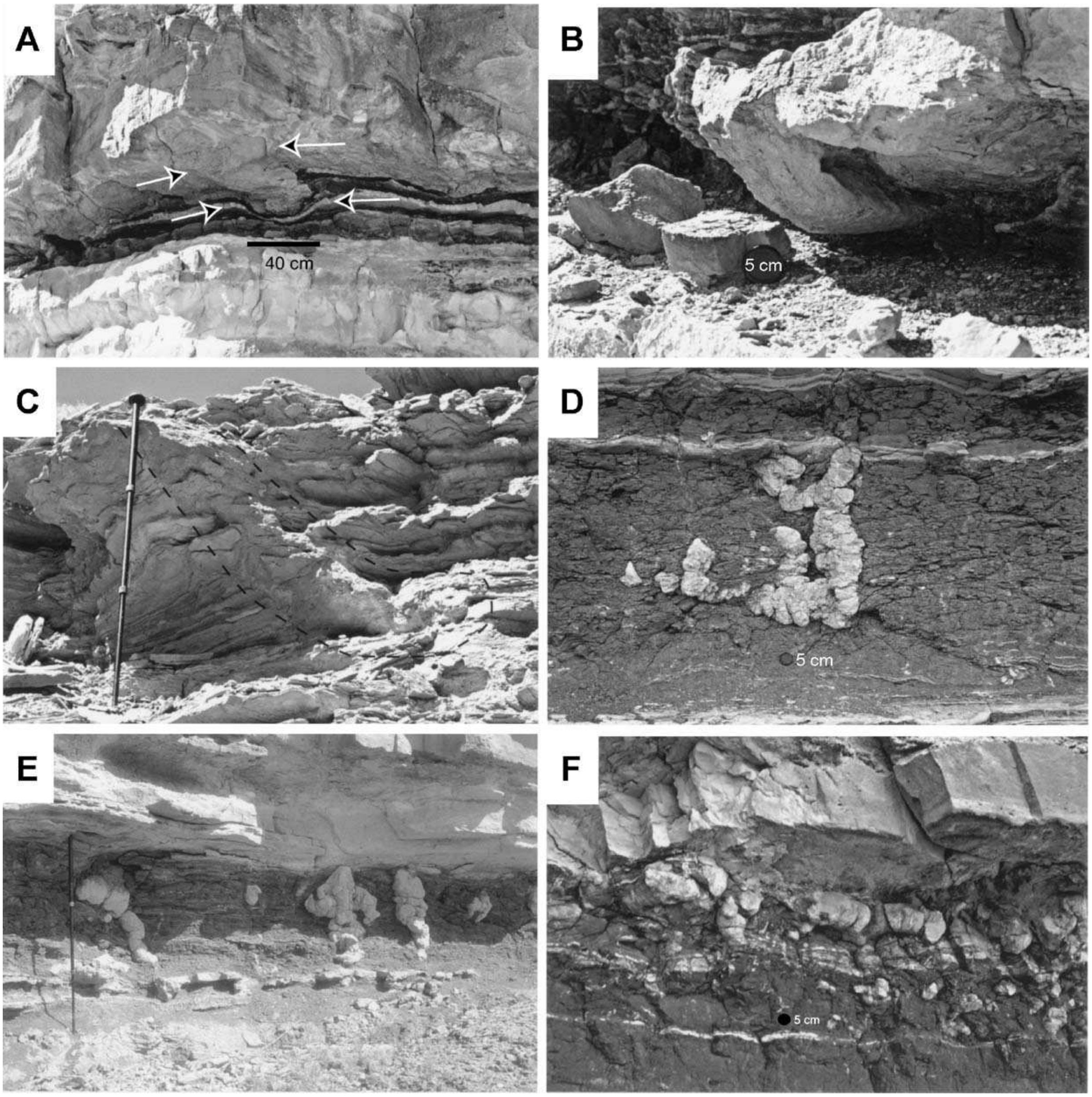


Fig. 28. Large-diameter burrows interpreted as subterranean vertebrate burrows. (A) Very large diameter sand and gravel-filled, low-angle-inclined burrow (arrows) in proximal overbank deposits attributed to crocodiles or sphenodontids; middle part of the Salt Wash Member, Shootaring Canyon, UT. (B) Sand-filled, low-angle inclined burrow attributed to sphenodontids in proximal overbank deposits filled with younger floodplain deposits, Salt Wash Member, Trachyte Ranch, UT. (C) Diagonal burrow (dashed line) in overbank deposits penetrating older lacustrine deposits, upper part of Tidwell Member, Shootaring Canyon, UT. (D), (E), and (F) Complex burrow systems attributed to primitive subsocial mammals in pedogenically modified overbank mudrocks (entisols to vertisols), upper part of Salt Wash Member, Shootaring Canyon, UT. Note the variations in burrow diameters, architecture, and depth. Jacob's staff is 1.5 m long.

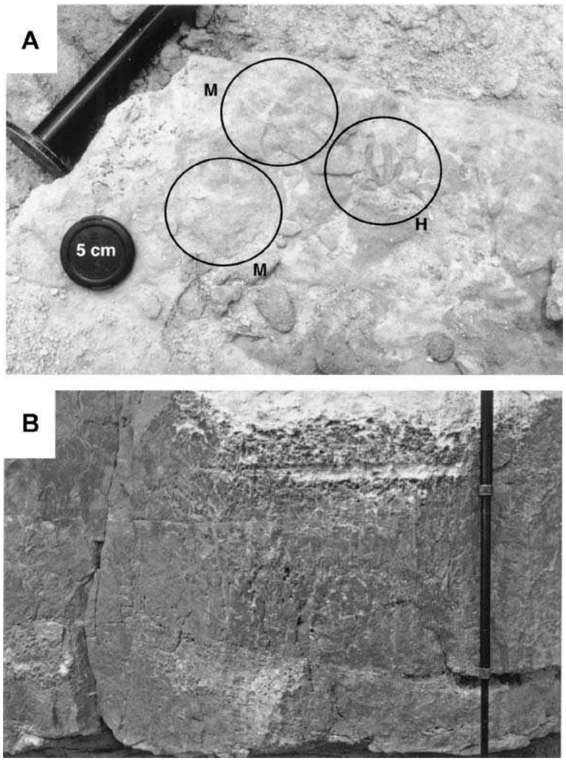


Fig. 29. (A) Sandstone bed with horizontal striated burrows (labeled with an H) in the Tidwell Member, Hatt Ranch, UT; churned areas by these burrows produced a mottled texture (labeled with an M). (B) Quasivertical striated burrows that commonly occur in high density in the lower part of the Brushy Basin Member, Salt Valley Anticline, UT; Jacob's staff is 30 cm long.

4.50. Type 50—horizontal striated burrow, Fig. 29A

Description: Horizontal, subcylindrical to cylindrical burrows 0.5–1 cm in diameter and 2–20+ cm long that usually occur in abundance (N >50 per 15 cm^2), often crosscutting one another (Fig. 29A). The burrows may be longer because their complete lengths are obscured in the outcrop. The surficial morphology exhibits fine to coarse longitudinal scratch patterns that are randomly distributed along the burrow.

Occurrence: These traces occur in massive to fine-grained ripple- and planar-laminated sandstone interbedded with mudstone in the Tidwell, Salt Wash, and Brushy Basin Members.

Tracemaker: These burrows resemble structures produced by adult or larval insects similar to ground-dwelling beetles (Carabiidae), crickets (Gryllidae), craneflies (Tipulidae?), and other true flies (in the Diptera).

Interpretation: Striated horizontal burrows were produced in proximal extrachannel and floodplain environments, including those associated with splays. These hygrophilic traces are also found in transitional and proximal lacustrine environments. They most likely represent relatively stable substrates that are at the sediment–water–air interface. It is difficult to assess the significance of these burrows, with the exception that they typically occur as monospecific assemblages and that they nearly always obliterate the sedimentary fabric of the beds in which they occur. The striated burrow walls reflect relatively firm substrates. Other horizontal burrows within the same bed, however, show only few or no striations that may be due to moister substrates or burrow degradation. In some instances, striated burrows crosscut nonstriated burrows, whereas, in other examples, nonstriated burrows crosscut striated burrows. This relationship shows short-term changes in moisture content and substrate consistency.

4.51. Type 51—quasivertical striated burrow, Fig. 29B

Description: Cylindrical, quasivertical burrows 1–1.5 cm in diameter and 15–45 cm in length. The burrows have sharply defined walls and weak to strong ornamentation with massive to vuggy filling.

Occurrence: These traces occur in fine-grained ripple- and planar-laminated sandstone interbedded with mudstone in the Salt Wash and Brushy Basin Members.

Tracemaker: Based on morphology of extant burrows, these traces were most likely constructed by insects similar to extant cicada nymphs (Insecta: Homoptera).

Interpretation: These vertical burrows are abundant in levee and proximal floodplain environments including those associated with splays. These hygrophilic traces commonly co-occur with rhizoliths in oxidized, weakly modified substrates. They also typically occur as monospecific assemblages (excluding rhizoliths), and they nearly obliterate the sedimentary fabric of their beds. The burrows are often filled with finer-grained material, demonstrating that they remained open. The striations on the burrow walls imply firm substrates. The close association of the burrows and rhizoliths reinforces the interpretation that the cicada-like nymphs were probably feeding on the roots within the soil substrate as they matured. Extant cicada nymphs occur in soils ranging in depth from 7–37 cm and feed very little by little on the roots of trees and shrubs by sucking fluids from them (Johnson and Lyon, 1991).

5. Discussion

Ichnofossils in alluvial, lacustrine, eolian, and transitional continental–marine deposits of the Morrison Formation preserve information that is invaluable for interpreting the environmental, ecologic, hydrologic, and climatic settings across the Western Interior during the Late Jurassic. The abundance and aerial extent of these ichnofossils that record in situ terrestrial and aquatic ichnocoenoses reflect a greater diversity and abundance of community members in Jurassic ecosystems than previously thought. Within these communities, the invertebrates are most sensitive to physical, chemical, and biological components in their environment. Comparison of structures produced by trace-making organisms in extant terrestrial and freshwater communities aids in interpreting the structures and the significance of the Morrison continental ichnofossils.

Ichnofossils record biodiversity not represented by body fossils within the Morrison. At least 14 orders, 23 families, and 37 behaviors are recorded by ichnofossils of unknown taxonomic affinities from Morrison rocks (Table 3). Of the invertebrates ascribed to the ichnofossils, only the gastropods, bivalves, and crayfish are represented by body fossils (e.g., Yen, 1952; Hasiotis and Kirkland, 1997; Hasiotis et al., 1998a,b; Evanoff et al., 1998). Although freshwater snails and clams are well represented in the Morrison, they are rarely preserved in life position. Their ichnofossils locate specifically where they occurred as either isolated individuals or as whole communities. Similarly, vertebrate ichnofossils also reduce taphonomic biases by preserving the exact places where ornithopods, sauropods, and theropods spent time feeding (hunting or scavenging), drinking, reproducing (based on nests and egg shells [not true trace fossils]), and traveling (e.g., Horner, 1982, 1984; Lockley, 1991; Lockley and Hunt, 1995; Martin and Hasiotis, 1998). Additional information on dinosaurian distribution is bolstered by the recognition of various types and intensities of dinoturbation that was once interpreted as physical soft-sediment deformation. Most of our knowledge comes from vertebrate bones in various degrees of articulation collected from quarries or time-averaged deposits (e.g., Turner and Peterson, 1999). Vertebrates interpreted to have been burrowers based on Morrison traces, such as fossorial mammals and sphenodontid reptiles, are also newly but informally described. Although mammals and crocodilians have been described from the Morrison (e.g., Engelmann, 1999; Engelmann and Callison, 1999), burrowing representatives of these groups have yet to be described. The abundance of rhizoliths from nearly every member of the Morrison with the exception of the Westwater Canyon Member, in general, signifies a larger biomass of groundcover plants than may be preserved as body fossils (e.g., Ash and Tidwell, 1998; Tidwell et al., 1998; Parrish et al., this volume). These ichnofossils are found in numerous assemblages or ichnocoenoses that represent a simultaneous occupation of an aboveground or belowground fossorial community.

5.1. Distribution of ichnofossils in transitional, alluvial, lacustrine, and eolian units

The sedimentologic and stratigraphic distribution of ichnofossils reflects the various environmental settings during Morrison deposition (see lithologic descriptions in Study area and geologic setting). In most instances, the ichnofossils support previous interpretations of depositional environments. In others, newly discovered or reinterpreted ichnofossils add another dimension to the paleoenvironmental interpretations. Ichnofossils may even suggest high frequency sea-level changes and associated environmental changes that may not be recognized or preserved by invertebrate body fossils or sedimentary packages. In general, ichnofossils are distributed within distinct intervals of the Morrison. Many of these ichnofossils occur as intensely bioturbated horizons rather than isolated specimens (e.g., Hasiotis and Demko, 1996; Engelmann, 1999).

5.1.1. Continental-marine transitional environments

Marginal-marine, tidal to brackish-water ichnofossils are restricted mainly to the Windy Hill Member, with rarer examples occurring in some places in the lower part of the Tidwell Member (Fig. 30). The presence and position of marine trace fossils or marine invertebrate fossils previously undescribed in multiple stratigraphic successions from several localities suggests short-term, high-frequency sea-level changes that created brackish to marine intervals in the predominantly fluvial–lacustrine units of the Tidwell Member (Appendix A, Table 1). For example, localities in eastern Colorado (23) and central Utah (18) (see Appendix A) contain marine trace fossils in thin carbonate-cemented sandstones interbedded with mudstone in fluvial–lacustrine units of the Tidwell. Samples from the Tidwell Member at Dinosaur National Monument contain dinoflagellates (locality 16; R. Litwin, 2000, personal communication) and several types of marine trace fossils. In another example of indirect evidence of sea-level fluctuations, a dinosaur-trampled stromatolite-bearing carbonate unit at locality 23 also contains freshwater charophytes, ostracodes, and part of a crocodile jaw, suggesting freshwater deposition. These stromatolites, however, were bored by an unidentified tracemaker that is probably a marine organism because no known freshwater organism similar to the boring size is known with this behavior. Furthermore, interbedded sandstone and mudstone directly overlying the carbonates contain oysters (*Gryphaea* sp.), *Phycodes*, and pustulose marks likely made by deposit-feeding polychaete worms. At this locality, the interbedded freshwater lacustrine and marine estuarine deposits could have been produced by (1) high frequency sea-level changes or (2) by large storm events that breached barriers separating freshwater from marine environments. Because these different trace–fossil-bearing units occur in stratigraphic succession, the first scenario is the most likely interpretation of the ichnologic, sedimentologic, and stratigraphic relations at locality 23.

Ichnocoenoses that are found in estuarine and tidal environments in the lowest parts of the Morrison were supported by productivity generated from autotrophic bacteria and algae, as well as from terrestrial inputs as fine particulate organic matter (FPOM) and coarse particulate organic matter (CPOM; e.g., De Santo, 1978). The communities contain suspension- and deposit-feeding organisms making their living from FPOM and CPOM. In turn, such surface-grazing or surface-feeding organisms as decapods and gastropods preyed on algae and shallow infaunal burrowing organisms. During low tide, such flying organisms as pterosaurs likely fed on shallow-burrowing benthic organisms. Areas containing algal laminates and stromatolites that may include sauropod and theropod trackways were either hypersaline, restricted marine, or alkaline freshwater, and thus did not contain any grazing or nektonic organisms.

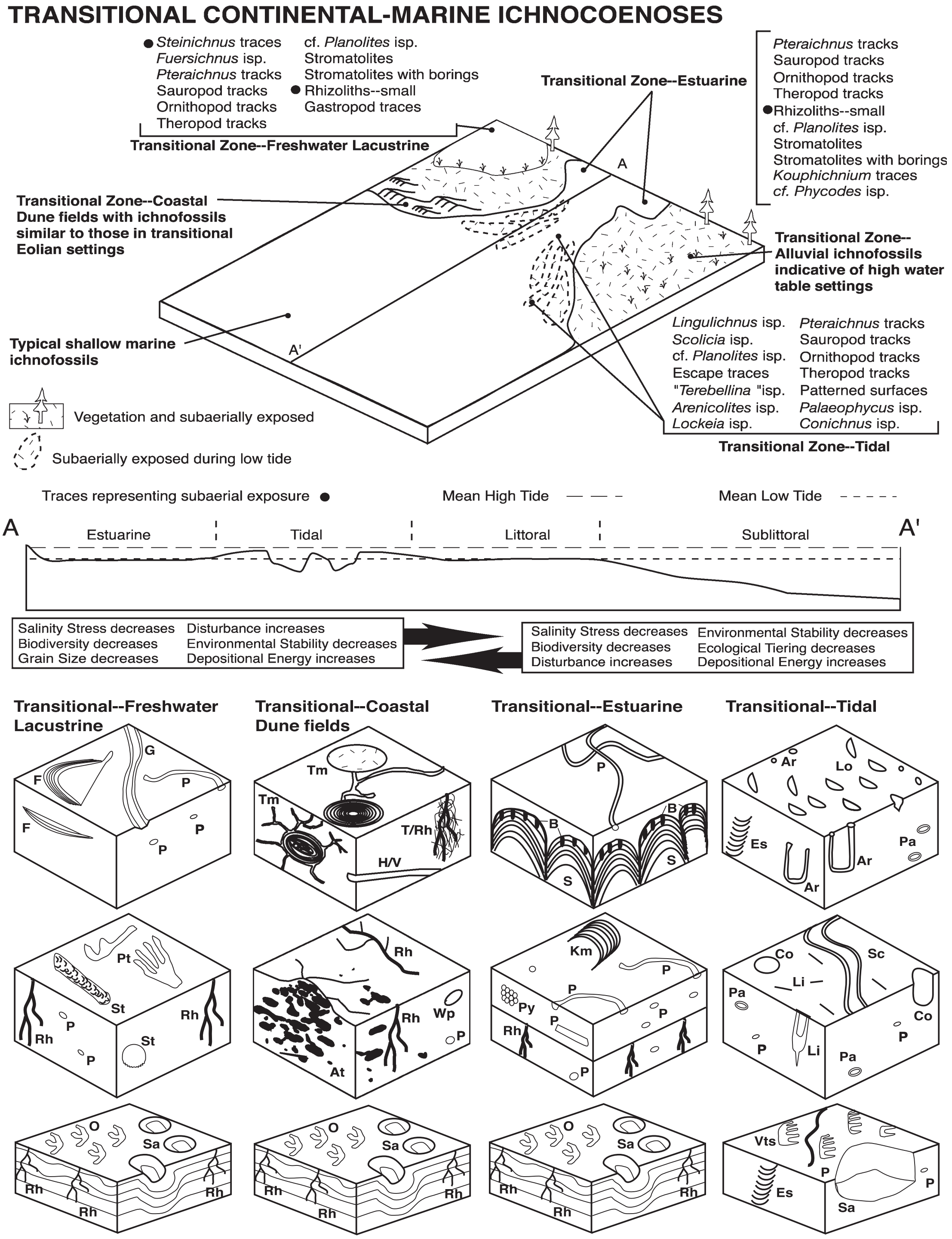
5.1.2. Alluvial environments

Channel, levee or bank, crevasse or splays, and proximal and distal floodplain environments contain several types of ichnocoenoses dominated by one or more types of organisms (Fig. 31). Although each environment is interpreted from vertically and laterally related sedimentary units with distinct sedimentary structures, many of the trace fossils were constructed in these units under different environmental and hydrologic conditions (see Tables 1 and 2). Alluvial ichnocoenoses will be different before, during, and after a crevasse or an avulsive, or anastomosed depositional event(s). Ichnocoenoses present during or shortly after an extrachannel depositional event will record water-table levels at or above the surface with turbid to clear-water conditions. Depending on the frequency and magnitude of the extrachannel event affecting the landscape, the original trace-making communities may be displaced by communities with greater numbers of hygrophilic and hydrophilic behaviors due to higher overall soil moisture and water-table levels subsequent to the event(s) (i.e., Hasiotis, 2000). In another example, abandoned or buried channels, levees, and splays generally contain burrows constructed by organisms living in proximal or distal floodplain environments directly overlying these older deposits. Oftentimes, when sand, silt, and mud are deposited in braided, anastomosed, avulsive, or meandering alluvial systems, areas that are no longer active due to channel switching or stream capture will behave depositionally and hydrologically like a proximal or distal floodplain. These environmental characteristics also explain the apparent lack of dinoturbation in distal floodplain environments. This is likely to be due to better-drained conditions existing away from open bodies of water, resulting in much firmer substrates that preclude footprint impressions. Hence, ichnocoenoses are interpreted as varying for a specific type of paleoenvironmental setting due to the hydrologic conditions and the frequency and magnitude of events affecting the alluvial system. Within each subenvironment, the ichnofossils are vertically tiered with regard to their hydrologic and ecologic affinities (see Table 2, Fig. 2).

Alluvial ichnocoenoses preserve remnants of very complex terrestrial and freshwater food webs founded on plants (primary producers), built and interwoven mainly with invertebrates and, to a lesser extent, vertebrates as primary, secondary, and tertiary consumers (herbivores and carnivores), and balanced by those organisms acting as recyclers (detritivores and saprovores). These food webs are complex because they involve fluvial and overbank depositional processes that control the availability of nutrients and water. Ferns and fern allies, seed ferns, ginkgoes, cycads, and gymnosperms, and, to a lesser extent, bryophytes and sphenophytes (Ash and Tidwell, 1998; Tidwell et al., 1998; Parrish et al., this volume) were the autotrophs in most of these environments. Primary consumers, such as insects (and other arthropods) and large herbivores, fed directly on plants. Fungi, a major saprovore in extant habitats (Wallwork, 1970), contributed less to aboveground consumers but is likely to have played a major role as additional productivity used in the detritivore nutrient cycle of soil ecosystems that supported vast communities of terraphilic, hygrophilic, and hydrophilic organisms (e.g., Hasiotis, 2000).

Freshwater ecosystems in rivers were supported by nutrients generated from terrestrial inputs as CPOM, FPOM, dissolved organic matter (DOM), and, to a lesser extent, photosynthetic bacteria and algae (e.g., De Santo, 1978; Ward, 1992). The food web in Morrison rivers was based on detritivores and autotrophs. The detritivores were supported by CPOM and FPOM, and the autotrophs (e.g., bacteria, algae, and plants) were supported by photosynthesis and by DOM (e.g., Ward, 1992). Freshwater communities were probably composed of a highly diverse group of shredders, grazers, collectors, and predators that were recorded in the Morrison sediments by their various types of burrowing behaviors related to suspension

Fig. 30. Schematic diagrams of large-scale ichnocoenoses found in transitional continental–marine environments preserved in the Windy Hill and Tidwell Members (and equivalent strata) of the Morrison Formation. Cross-section A–A′ illustrates relations between the physicochemical and physiological controls active in the transitional zone and the general abiotic and biotic trends that shape the ichnocoenoses. Text in the box adjacent to the flattened end of each arrow is a summary of the physical, biologic, and ecologic characteristics and trends that operate in the direction of the arrow. Box diagrams depict examples of ichnocoenoses that are found in those environments. Abbreviations are as follows: AMB—Adhesive meniscate burrows, An—*Ancorichnus*, Ar—*Arenicolites*, At—Ant nests, B—Borings, Bv—Bivalve traces, Ca—*Camborygma*, Ce—*Celliforma*, Ck—*Cochlichnus*, Cl—*Cylindrichum*, Co—Conichnus, Cp—*Coprinisphaera*, Es—Escape traces, F—*Fuersichnus*, G—Gastropod trail, Hb—Horizontal burrows, Hu—Horizontal U-shaped burrow, Jb—J-shaped burrow, Km—*Kouphichnium*, Li—*Lingulichnus*, Lo—*Lockeia*, O—Ornithopod and theropod tracks, P—*Planolites*, Rh—Rhizoliths, Pa—*Palaeophycus*, Pt—*Pteraichnus*, Pts—Pterosaur scratch marks, Py—*Phycodes*, Rl—*Rosellichnus*, S—Stromatolites, Sa—Sauropod tracks, Sc—*Scolicia*, So—*Scoyenia*, St—*Steinichnus*, Tm—Termite nest, T/Rh—Termite nests in rhizoliths, Ut—Ghost U-shaped tubes, Uts—Shallow U-shaped tubes, Vb—Quasivertical burrows, Vtb—Vertebrate burrows, Vts—Vertebrate swimming tracks, Wp—Wasp nest/cocoons, Yt—Y-shaped vertical burrow. Trace fossil illustrations and box diagrams are not to scale. Abbreviations are also applicable for Figs. 31–33.


TRANSITIONAL CONTINENTAL-MARINE ICHNOCOENOSES
● Steinichnus traces
Fuersichnus isp.
Pteraichnus tracks
Sauropod tracks
Ornithopod tracks
Theropod tracks
cf. Planolites isp.
Stromatolites
Stromatolites with borings
● Rhizoliths--small
Gastropod traces
Transitional Zone--Freshwater Lacustrine
Transitional Zone--Estuarine
Pteraichnus tracks
Sauropod tracks
Ornithopod tracks
Theropod tracks
●Rhizoliths--small
cf. Planolites isp.
Stromatolites
Stromatolites with borings
Kouphichnium traces
cf. Phycodes isp.
Transitional Zone--Coastal Dune fields with ichnofossils similar to those in transitional Eolian settings
A
Transitional Zone--Alluvial ichnofossils indicative of high water table settings
Typical shallow marine ichnofossils
A'
Lingulichnus isp.
Scolicia isp.
cf. Planolites isp.
Escape traces
"Terebellina "isp.
Arenicolites isp.
Lockeia isp.
Pteraichnus tracks
Sauropod tracks
Ornithopod tracks
Theropod tracks
Patterned surfaces
Palaeophycus isp.
Conichnus isp.
Transitional Zone--Tidal
Vegetation and subaerially exposed
Subaerially exposed during low tide
Traces representing subaerial exposure ●
Mean High Tide — — –
Mean Low Tide - - - - -
A
Estuarine
Tidal
Littoral
Sublittoral
A'
Salinity Stress decreases
Biodiversity decreases
Grain Size decreases
Disturbance increases
Environmental Stability decreases
Depositional Energy increases
Salinity Stress decreases
Biodiversity decreases
Disturbance increases
Environmental Stability decreases
Ecological Tiering decreases
Depositional Energy increases
Transitional--Freshwater Lacustrine
Transitional--Coastal Dune fields
Transitional--Estuarine
Transitional--Tidal
F
G
P
F
P
P
Tm
Tm
T/Rh
H/V
P
B
B
S
S
Ar
Lo
Es
Pa
Ar
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feeding, deposit feeding, temporary and semipermanent dwelling, and prey searching. Communities in the deeper, high-energy portion of alluvial channel environments were depauperate and likely to have been detritivore based. Shallow infaunal, simple deposit-feeding strategies dominated shallow, slack-water, and shoreline environments (submerged and exposed bars and upper parts of lateral accretion surfaces), an interpretation that is based on the ichnofossils.

Although sauropods, iguanodontids, stegosaurs, and other herbivorous dinosaurs (see Engelmann et al., this volume) were quite large, they were undoubtedly outnumbered and outweighed by the insects and other soil arthropods in the food pyramid (e.g., Odum, 1971; De Santo, 1978). Some dinosaurs interpreted as herbivores, such as stegosaurs and ankylosaurs (e.g., thyreophores), may not have been exclusively plant-eaters but rather omnivores with a large part of their diet consisting of insects such as termites and ants. Evidence in the form of morphologic features of these dinosaurs, including the size and arrangement of teeth, smooth palate, morphology of the snout and cranium, arrangement and morphology of the spine and hips, and body armor and physical defenses, are similar to those of extant mammals (Walker, 1996) that feed on solitary, gregarious, and social insects. The hypothesis of insects as food for smaller dinosaurs is not unreasonable because termites and ants can have large populations per nest, and each nest can produce large numbers of highly nutritious individual reproductives per mating season (e.g., Behnke, 1977; Redford, 1987).

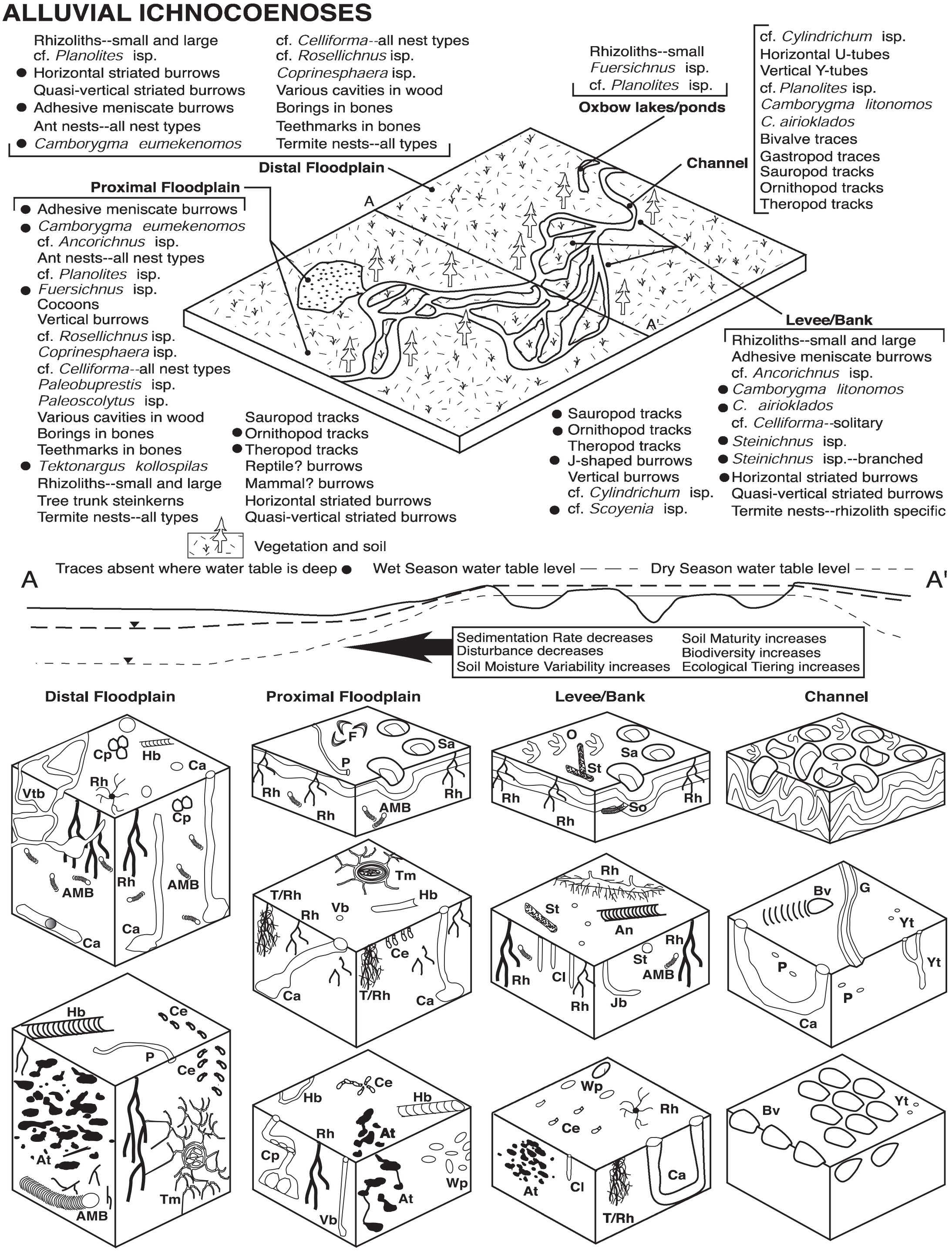
Many insects probably indulged in some form of food hoarding (e.g., Vander Wall, 1990) used in their reproductive strategies as food reserves for individual eggs buried in constructed cavities (e.g., solitary bees, wasps, beetles). Such social insects as termites, ants, and bees likely collected and stored large amounts of plant material and other food (e.g., insects, carrion) in their nests to feed the members of their colony as well as cultivating fungus for food. Food hoarding is likely to have occurred above- and belowground in association with feeding and reproductive behavior in nearly every continental environment in the Morrison.

Food hoarding, coprophagy, and necrophagy behaviors also played an important role in Jurassic detritivore nutrient recycling. Extant ants and termites, in particular, are known to collect and eat dead plant material. The size and morphology of the Jurassic nests suggest that these insects, particularly the termites, were behaving in like manner. These insects would have been attracted also to sauropod and ornithopod dung for several reasons. For termites, the quest was for the partially digested plant material. For ants, trips to the dung pile were for food in the form of other insects and their larvae, including fly maggots, termites and dung beetles. The latter two insects also used the material for their nests. A whole, virtually unrecorded detritivore-based food pyramid would have existed around the dung.

Another practically unrecorded detritivore-based food pyramid in the Morrison probably occurred around vertebrate carcasses. Ichnologic evidence on dinosaur bones shows scavenging by other dinosaurs and such insects as dermestid beetles. Besides scavenging animals and birds, modern forensic studies demonstrate that there is a succession of necrophilous (dead-flesh eating) and saprophagous (feeding on dead or decaying material) insects throughout the stages of decay on carcasses (e.g., Smith, 1986). An ecological succession of insects results from changes in the attractive nature of a carcass leading to the complete decomposition of the animal (e.g., Reed, 1958; Payne, 1965). This process was also likely a dominant recycling mechanism during the Late Jurassic (Hasiotis et al., 1999a,b).

The overwhelming diversity of ichnofossils in alluvial and marginal lacustrine environments in the Morrison Formation (Fig. 31) could occur in any one of the proposed *Scoyenia*, *Termitichnus*, and *Coprinisphaera* ichnofacies based on their broad and ambiguous definitions (see summaries of basic features and environmental significance by Buatois and Mángano,

Fig. 31. Schematic diagrams of large-scale ichnocoenoses found in alluvial (fluvial and overbank) environments preserved in the Tidwell, Salt Wash, Recapture, Westwater Canyon, and Brushy Basin Members (and equivalent strata) of the Morrison Formation. Cross-section A–A′ illustrates relations between the physicochemical and physiological controls active in the alluvial settings and the general abiotic and biotic trends that shape the ichnocoenoses. Text in the box adjacent to the flattened end of each arrow is a summary of the physical, biologic, and ecologic characteristics and trends that operate in the direction of the arrow. Box diagrams depict examples of ichnocoenoses that are found in those environments. See Fig. 30 for explanation of abbreviations.


ALLUVIAL ICHNOCOENOSES
Rhizoliths--small and large
cf. Planolites isp.
● Horizontal striated burrows
Quasi-vertical striated burrows
● Adhesive meniscate burrows
Ant nests--all nest types
● Camborygma eumekenomos
cf. Celliforma--all nest types
cf. Rosellichnus isp.
Coprinesphaera isp.
Various cavities in wood
Borings in bones
Teethmarks in bones
Termite nests--all types
Distal Floodplain
Proximal Floodplain
● Adhesive meniscate burrows
● Camborygma eumekenomos
cf. Ancorichnus isp.
Ant nests--all nest types
cf. Planolites isp.
● Fuersichnus isp.
Cocoons
Vertical burrows
cf. Rosellichnus isp.
Coprinesphaera isp.
cf. Celliforma--all nest types
Paleobuprestis isp.
Paleoscolytus isp.
Various cavities in wood
Borings in bones
Teethmarks in bones
● Tektonargus kollospilas
Rhizoliths--small and large
Tree trunk steinkerns
Termite nests--all types
Sauropod tracks
● Ornithopod tracks
● Theropod tracks
Reptile? burrows
Mammal? burrows
Horizontal striated burrows
Quasi-vertical striated burrows
Rhizoliths--small
Fuersichnus isp.
cf. Planolites isp.
Oxbow lakes/ponds
Channel
cf. Cylindrichum isp.
Horizontal U-tubes
Vertical Y-tubes
cf. Planolites isp.
Camborygma litonomos
C. airioklados
Bivalve traces
Gastropod traces
Sauropod tracks
Ornithopod tracks
Theropod tracks
A
A'
Levee/Bank
Rhizoliths--small and large
Adhesive meniscate burrows
cf. Ancorichnus isp.
● Camborygma litonomos
● C. airioklados
cf. Celliforma--solitary
● Steinichnus isp.
● Steinichnus isp.--branched
● Horizontal striated burrows
Quasi-vertical striated burrows
Termite nests--rhizolith specific
● Sauropod tracks
● Ornithopod tracks
Theropod tracks
● J-shaped burrows
Vertical burrows
cf. Cylindrichum isp.
● cf. Scoyenia isp.
Vegetation and soil
Traces absent where water table is deep ●
Wet Season water table level — — —
Dry Season water table level - - - -
A
A'
Sedimentation Rate decreases
Disturbance decreases
Soil Moisture Variability increases
Soil Maturity increases
Biodiversity increases
Ecological Tiering increases
Distal Floodplain
Proximal Floodplain
Levee/Bank
Channel
Cp Hb Ca Vtb Rh Cp AMB Rh AMB Ca Ca
F P Sa Rh Rh Rh AMB
O Sa St Rh Rh So Rh
T/Rh Tm Hb Vb Rh Ce Ca T/Rh Ca
Rh St An Rh St AMB Rh Cl Rh Jb
Bv G Yt Yt P P Ca
Hb Ce P Ce At Tm AMB
Ce Hb Hb Rh At Cp At Wp Vb
Wp Rh Ce At Cl Ca T/Rh
Bv Yt

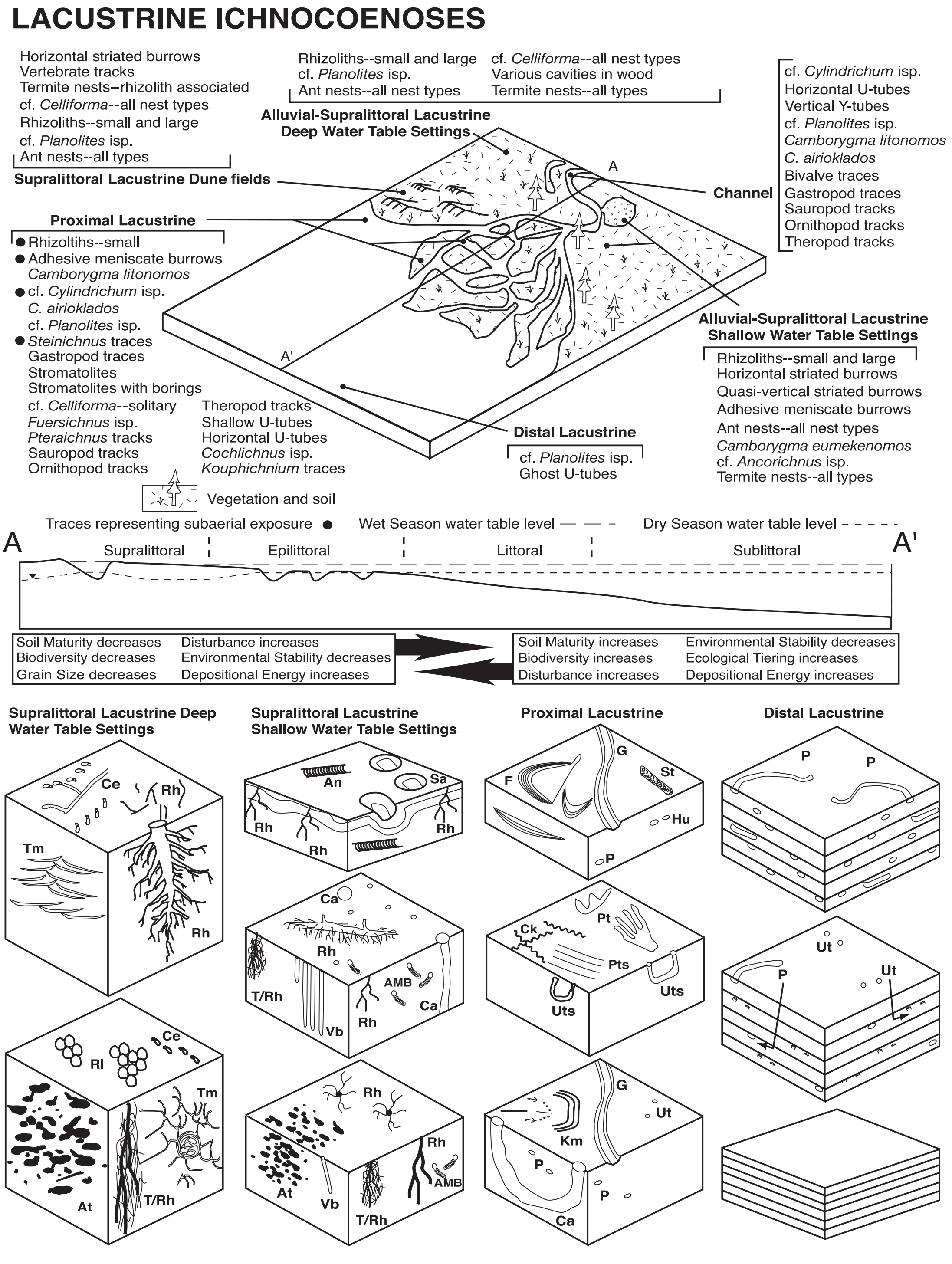
1995; Buatois et al., 1998; Genise et al., 2000). For example, some Morrison alluvial subenvironments contain termite nests, bee nests, crayfish burrows, beetle burrows, other insect traces, dinosaur trackways, and rhizoliths in close proximity to each other in weakly modified channel–levee and proximal floodplain deposits. These represent dwelling, breeding, locomotion, and feeding structures that fit readily into any of the three subaerial ichnofacies. If the *Coprinisphaera* ichnofacies is excluded based on the lack of soil maturity and angiosperm-based grassland vegetation and the *Termitichnus* ichnofacies is excluded because of the lack of closed forests (interpretation-based constraint), then the traces belong to the *Scoyenia* ichnofacies. This ichnofacies, however, is defined as ''intermediate between fully aquatic to nonaquatic environments'' (Buatois and Mángano, 1995), and thus the Morrison traces would not be assigned to this ichnofacies. Besides, most alluvial settings contain subenvironments that exhibit hydrologic conditions that are episodically or periodically and seasonally or ephemerally intermediate between fully aquatic and nonaquatic (Bown and Kraus, 1987; Aber and Melillo, 1991; Hasiotis, 2000). Furthermore, many of the components typical of each of these proposed ichnofacies, very numerous to list here, are absent from the Morrison deposits.

5.1.3. Lacustrine environments

Proximal and distal lacustrine environments and their associated transitional settings (alluvial–lacustrine, eolian–lacustrine) contain ichnocoenoses dominated by one or more types of organisms (Fig. 32). The diversity and abundance of ichnofossils in these environments is less than that in alluvial environments. Organisms living in proximal lacustrine environments (epilittoral and littoral zones) contend with higher depositional energy and greater hydrologic variability due to seasonal fluctuations in water availability (e.g., Ward, 1992; Hasiotis, 2000). Distal lacustrine environments (sublittoral and profundal zones) are less frequently affected by depositional events associated with shorelines and shallower water and are more hydrologically stable (Wetzel, 1983). The configuration of the lacustrine basin, however, with either ramplike or shelflike margins will impact the bathymetric zonations and degree of water-level fluctuations in the lake. In shallow lakes, slight changes in water level expose extensive areas of shoreline. Because of the shallow nature of most lakes, they are typically stratified with respect to physicochemical properties. Stratified lakes typically have anoxic or alkaline waters that rarely, if ever, mix with water from above. For example, Turner and Fishman (1991) reported that the highly variegated orange and green tuffs deposited in lacustrine settings resulted from early diagenesis in a saline alkaline lake that likely did not overturn its water.

Morrison lacustrine ichnocoenoses differ in composition due to the hydrologic conditions and greater benthic ichnodiversity within proximal settings. These results are consistent with benthic diversity data from modern lakes (e.g., Wetzel, 1983; Ward, 1992), demonstrating that the profundal zone contains fewer species to the point where tubificid annelids or chironomid larvae are the only organisms present. Ichnofossils are vertically tiered with regard to behavior, substrate requirements, and ecologic affinities within proximal and distal lacustrine environments (see Table 2). In general, tiering in lacustrine environments (e.g., hydrophilic behavior; see Fig. 2) is quite shallow and can be subtle. For example, some distal Morrison lacustrine deposits composed of thin bedded, very fine-grained sandstone, siltstone, and mudstone did not contain any evidence of bioturbation (localities 19, 21, and north of Ft. Collins, CO; see Appendix A). The lack of bioturbation is likely to indicate anoxic bottom conditions or high sedimentation rates. In some instances, however, bioturbation was at the laminae-scale and produced no macroscopic traces of burrowing organisms but mixed sediments at the micro- and

Fig. 32. Schematic diagrams of large-scale ichnocoenoses found in lacustrine (including palustrine) environments preserved in the Tidwell and Brushy Basin Members (and equivalent strata) of the Morrison Formation. Cross-section A–A′ illustrates relations between the physicochemical and physiological controls active in the lacustrine settings and the general abiotic and biotic trends that shape the ichnocoenoses. Text in the box adjacent to the flattened end of each arrow is a summary of the physical, biologic, and ecologic characteristics and trends that operate in the direction of the arrow. Box diagrams depict examples of ichnocoenoses that are found in those environments. Boxes with no bioturbation reflect environmental settings in which no bioturbation occurred in that subenvironment; in some cases, bioturbation was at the laminae scale and produced no macroscopic trace fossils but mixed sediments at the mesoscopic and macroscopic scale. See Fig. 30 for explanation of abbreviations.


LACUSTRINE ICHNOCOENOSES
Horizontal striated burrows
Vertebrate tracks
Termite nests--rhizolith associated
cf. Celliforma--all nest types
Rhizoliths--small and large
cf. Planolites isp.
Ant nests--all types
Rhizoliths--small and large
cf. Planolites isp.
Ant nests--all nest types
cf. Celliforma--all nest types
Various cavities in wood
Termite nests--all types
Alluvial-Supralittoral Lacustrine Deep Water Table Settings
Supralittoral Lacustrine Dune fields
Proximal Lacustrine
● Rhizoltihs--small
● Adhesive meniscate burrows
Camborygma litonomos
● cf. Cylindrichum isp.
C. airiokladus
cf. Planolites isp.
● Steinichnus traces
Gastropod traces
Stromatolites
Stromatolites with borings
cf. Celliforma--solitary
Fuersichnus isp.
Pteraichnus tracks
Sauropod tracks
Ornithopod tracks
Theropod tracks
Shallow U-tubes
Horizontal U-tubes
Cochlichnus isp.
Kouphichnium traces
A
Channel
cf. Cylindrichum isp.
Horizontal U-tubes
Vertical Y-tubes
cf. Planolites isp.
Camborygma litonomos
C. airiokladus
Bivalve traces
Gastropod traces
Sauropod tracks
Ornithopod tracks
Theropod tracks
Alluvial-Supralittoral Lacustrine Shallow Water Table Settings
Rhizoliths--small and large
Horizontal striated burrows
Quasi-vertical striated burrows
Adhesive meniscate burrows
Ant nests--all nest types
Camborygma eumekenomos
cf. Ancorichnus isp.
Termite nests--all types
A'
Distal Lacustrine
cf. Planolites isp.
Ghost U-tubes
Vegetation and soil
Traces representing subaerial exposure ●
Wet Season water table level — — —
Dry Season water table level - - - - -
A
Supralittoral
Epilittoral
Littoral
Sublittoral
A'
Soil Maturity decreases
Biodiversity decreases
Grain Size decreases
Disturbance increases
Environmental Stability decreases
Depositional Energy increases
Soil Maturity increases
Biodiversity increases
Disturbance increases
Environmental Stability decreases
Ecological Tiering increases
Depositional Energy increases
Supralittoral Lacustrine Deep Water Table Settings
Supralittoral Lacustrine Shallow Water Table Settings
Proximal Lacustrine
Distal Lacustrine
Ce
Rh
Tm
Rh
An
Sa
Rh
Rh
Rh
F
G
St
Hu
P
P
P
Ca
Rh
T/Rh
AMB
Ca
Vb
Rh
Ck
Pt
Pts
Uts
Uts
Ut
Ut
P
Rl
Ce
Tm
At
T/Rh
Rh
Rh
AMB
At
Vb
T/Rh
G
Ut
Km
P
P
Ca

mesoscopic scale (localities 5, 19, 21, and 26; see Appendix A).

Like modern lacustrine ecosystems (e.g., Odum, 1971; De Santo, 1978; Ward, 1992), Morrison siliciclastic and carbonate lacustrine ecosystems were probably supported by primary productivity generated by autotrophs, such as plankton, algae, charophytes, and plants, which had little or no fossil record in the Morrison but are likely to have been present and from terrestrial inputs as CPOM, FPOM, and DOM. Here, the food web was detritivore and autotroph based, the detritivores supported by CPOM and FPOM and the autotrophs supported by DOM and photosynthesis. Communities in proximal settings were probably composed, at least in part, of a highly diverse group of shredders, grazers, collectors, and predators that would have left a record in the sediment of various types of burrowing behaviors such as suspension feeding, deposit feeding, temporary and semipermanent dwelling, and prey searching (Ward, 1992; Saffrin and Barton, 1993; Momot, 1994). Communities in distal lacustrine settings were apparently depauperate and were detritivore based. Shallow infaunal, simple deposit-feeding strategies dominated in proximal lacustrine settings based on the ichnofossils.

Lacustrine ichnocoenoses should be distinctly different from marine ichnocoenoses (Hasiotis, 1997a), which are dominated by vast bodies of water with environments of geologically long duration and with regional circulation patterns that distribute nutrients, larvae, and heat from one place to another. Lacustrine environments are geologically short-lived (~ 100,000 years) and highly variable, with fluctuations in lake level, depth, subaerial exposure, salinity, and temperature (Wetzel, 1983; Ward, 1992). Relatively short-lived ponds and lakes did not exist for a sufficient amount of time for the development of burrowing and feeding innovations by epifaunal and infaunal freshwater organisms that are similar to such marine organisms that have complex feeding and mining strategies as *Chondrites*, *Helminthopsis*, *Thalassinoides*, *Zoophycus*, and *Paleodictyon*. Furthermore, if distal deep-water lacustrine organisms did develop specialized complex feeding behaviors, their innovations would have been lost because these short-lived environments are evolutionary dead-ends (Hasiotis, 1997a). Organisms with complex feeding and grazing behaviors would have been constrained from readapting and competing with shallow-water organisms over short spans of time, and thus likely prohibited these specialized organisms from migrating to other lakes via rivers. Simple horizontal, vertical, and U-shaped feeding and burrowing traces similar to *Planolites*, *Palaeophycus*, *Arenicolites*, *Skolithos*, and the like should be present in lacustrine ichnocoenoses given the appropriate conditions.

Morrison trace fossils in supralittoral, littoral, and sublittoral lacustrine settings do not fit the definition of the *Mermia* ichnofacies, which is characterized by *Mermia*, *Gordia*, *Undichna*, *Helminthoidichnites*, *Helminthopsis*, *Vagorichnus*, *Treptichnus*, *Lockeia*, *Tuberculichnus*, *Maculichnia*, *Circulichnus*, and *Palaeophycus* (Buatois and Mángano, 1995; Buatois et al., 1998). Many of the Morrison traces reflect relatively firm substrates and shallow water with intermittent subaerial exposure. Deeper water environments also do not show any of the diversity expected for the purported *Mermia* ichnofacies; only *Planolites* and simple ghost U-tubes are present in Morrison sublittoral deposits. Furthermore, many of the components typical of this ichnofacies are absent from Morrison lacustrine deposits, with the exception of *Cochlichnus* and cf. *Planolites* which occur in littoral environments. Other lacustrine units examined in Mesozoic and Cenozoic outcrops in the Rocky Mountain region (e.g., Moussa, 1970; Hasiotis et al., in review; Hasiotis, unpublished data) do not show the ichnodiversity and behavioral variability described in purported lacustrine deposits in Carboniferous and Permian strata where the *Mermia* ichnofacies was defined (Buatois and Mángano, 1995; Buatois et al., 1998).

5.1.4. Eolian environments

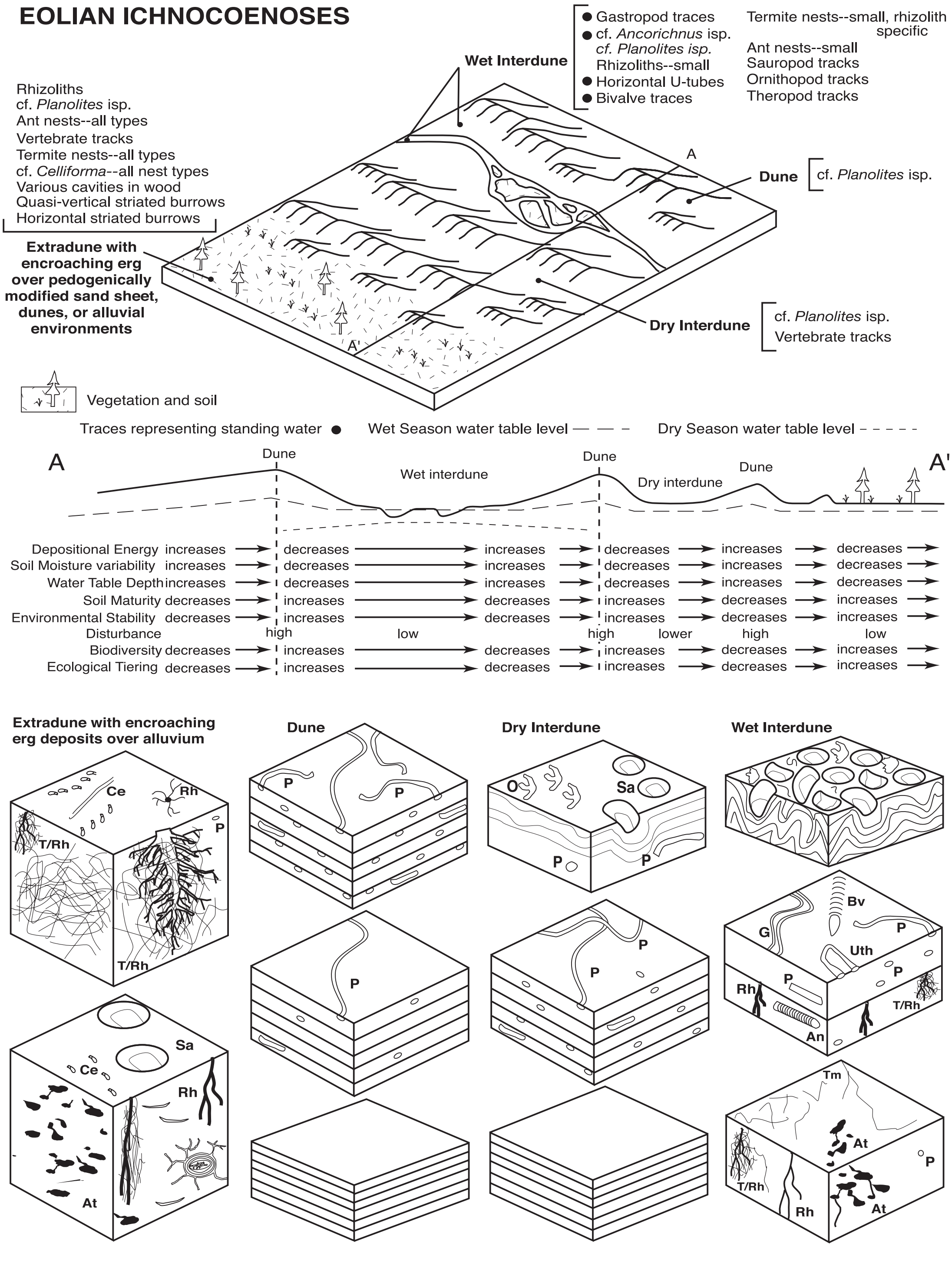
Although most of the eolian units in the Morrison (e.g., Bluff Sandstone Member) were not examined in detail, data supporting the ideas described below were collected from outcrops of the eolian facies of the Recapture Member near Gallup, NM (22), aerially restricted eolianites at or near the base of the formation at Alcova, WY (31), at Hanna, UT (15), and at Dinosaur National Monument, UT (16). Dune, dry interdune, wet interdune, and encroaching dune environments contain several types of sparsely diverse ichnocoenoses dominated by one or more types of organisms (Fig. 33). For the most part, dune and dry interdune deposits lack any notable bioturbation. Most evidence of bioturbation was found in deposits interpreted as vegetation-stabilized dune deposits, wet interdune environments, and encroaching dune fields on alluvial, marginal lacustrine, and transitional continental–marine environments.

The most bioturbation observed in Morrison eolian units is in the upper 35 m of the eolian facies of the Recapture Member near Gallup, NM (22). The organism activity and pedogenesis in these units, however, was due to a different paleoclimatic setting from that which occurred during deposition of the eolian facies of the Recapture Member (see also Demko et al., this volume). Large, complex, and deeply penetrating termite nests occur in reddish-pink eolian sandstones containing faint, bioturbated, pinstriped eolian cross-bedding in a single bed set over 25 m thick (Condon, 1985; Condon and Peterson, 1986). At Gallup, alluvial sandstone deposits of the Westwater Canyon Member unconformably overlie the Recapture Member (also see Demko et al., this volume). The uppermost part of the Recapture, which is from where the termite nests originated, was eroded by Westwater Canyon alluvial systems (mostly, the fluvial components are preserved but there are very few overbank deposits), yet ample evidence is still preserved in the highly bioturbated and pedogenically modified uppermost part of the Recapture to reconstruct the successive paleoenvironmental and paleoclimatic changes.

A paleosol developed on the uppermost surface of the Recapture before deposition of the Westwater Canyon. The termite nests are part of the paleosol that formed during deposition of the uppermost Recapture and represents a long duration of surface and subsurface modification by pedogenic processes (see also Demko et al., this volume), including organism activity. The termite nests and paleosol were not constructed during the eolian phase of the Recapture but at a later time under different conditions. The presence of these gigantic nests suggests that ample vegetation was present, there was enough water in the local hydrologic system to support vegetation and other organisms necessary to promote their growth above and below the surface, and environmental and ecological conditions were favorable to allow a depth of 20 to 35 m of substrate modification. The high level of bioturbation (ichnofabric index (Droser and Bottjer, 1986) = 3 to 5; 5—completely burrowed by several generations) of the eolian beds and their characteristic pinkish to light-reddish color could not have been possible if the environmental and climatic conditions were similar to those conditions represented by most of the eolian deposits. The climate shifted from arid to at least semiarid with strongly seasonal precipitation, while the environment became similar to today's partially wooded savanna with ferns, herbs, and some coniferous trees as Jurassic counterparts of modern-day grasses and other angiosperms (see Demko et al., this volume).

The degree of bioturbation in Morrison eolianites and in the example described above warrants a brief review of the relationship between eolian depositional settings, precipitation (P), evapotranspiration (E), potential evapotranspiration (PE), and biodiversity. Eolian environments represented by vast erg deposits bear evidence of little or no life due to the lack of available water and food (Crawford, 1981, 1991; Louw and Seely, 1982) in an arid climate. Arid is defined as $P/E < 1$ with $P < 1/2$PE and is also expressed as >25 cm of precipitation/year (Lydolph, 1985; Christopherson, 2000). Where small dune systems or edges of vast ergs encroach on environments that have ample water and nutrients to support life, traces of organisms can be preserved relative to the biodiversity present. This is analogous to modern deserts, or places with semiarid to arid climates ($P > 1/2$PE but < PE; also expressed as 25–50 cm precipitation/year; Lydolph, 1985), as well as those on the border of dry–humid climate regimes (e.g., Oliver, 1973; Lydolph, 1985; Goode's World Atlas, 2000). These environments support life that has evolved to deal with water loss, limited nutrient supplies, and fluctuating temperatures (Crawford, 1981, 1991; Louw and Seely, 1982). Although many modern deserts have meager vegetation cover, areas with constantly shifting surface materials driven by winds (e.g., supralittoral dune fields and coastal deserts) also have little or no vegetation (e.g., Lydolph, 1985).

For the most part, cursory ichnologic and paleopedologic analysis of the Morrison eolian deposits indicates that low diverse ichnocoenoses were due to constantly shifting substrates in aerially restricted settings associated with eolian, transitional marine, marginal lacustrine, and lowland alluvial environments in the Bluff, Windy Hill, Tidwell, and Recapture Members. Preliminary analysis suggests that the lower to upper part of the Bluff Sandstone was likely to have


EOLIAN ICHNOCOENOSES
Wet Interdune
● Gastropod traces
● cf. Ancorichnus isp.
cf. Planolites isp.
Rhizoliths--small
● Horizontal U-tubes
● Bivalve traces
Termite nests--small, rhizolith specific
Ant nests--small
Sauropod tracks
Ornithopod tracks
Theropod tracks
Rhizoliths
cf. Planolites isp.
Ant nests--all types
Vertebrate tracks
Termite nests--all types
cf. Celliforma--all nest types
Various cavities in wood
Quasi-vertical striated burrows
Horizontal striated burrows
Extradune with encroaching erg over pedogenically modified sand sheet, dunes, or alluvial environments
A
A'
Dune
cf. Planolites isp.
Dry Interdune
cf. Planolites isp.
Vertebrate tracks
Vegetation and soil
Traces representing standing water ●
Wet Season water table level — — —
Dry Season water table level - - - - -
A
Dune
Wet interdune
Dune
Dry interdune
Dune
A'
Depositional Energy increases → decreases → increases → decreases → increases → decreases →
Soil Moisture variability increases → decreases → increases → decreases → increases → decreases →
Water Table Depth increases → decreases → increases → decreases → increases → decreases →
Soil Maturity decreases → increases → decreases → increases → decreases → increases →
Environmental Stability decreases → increases → decreases → increases → decreases → increases →
Disturbance high low high lower high low
Biodiversity decreases → increases → decreases → increases → decreases → increases →
Ecological Tiering decreases → increases → decreases → increases → decreases → increases →
Extradune with encroaching erg deposits over alluvium
Ce
Rh
T/Rh
P
T/Rh
Sa
Ce
Rh
At
Dune
P
P
P
Dry Interdune
O
Sa
P
P
P
P
Wet Interdune
Bv
G
P
Uth
P
Rh
P
T/Rh
An
Tm
At
P
T/Rh
Rh
At

been deposited in a local climate where $P < 1/2\text{PE}$ (~ < 25 cm precipitation/year), possibly with a very short and meager wet season. The edges of the Bluff eolian system interfingered with the Salt Wash alluvial and Tidwell lacustrine environments that are interpreted to have likely been deposited in wetter conditions (25–100 cm precipitation/year), based on paleontologic, ichnologic, paleopedologic and sedimentologic evidence. The lower, middle, and upper parts of the eolian facies of the Recapture were deposited in a climate similar to that of most of the Bluff. The uppermost part of the Recapture modified by bioturbation and pedogenesis (30–40 m), however, represents a wetter climate where seasonally delivered precipitation ranged from $P > 1/2\text{PE}$ but $< \text{PE}$ to $P/E < 1$, with an overall deficit of precipitation (~ 25 to 100 cm precipitation/year).

The bioturbation and paleosol formation are key pieces of evidence that record subtle but important information for the interpretation of the climate change near the end of deposition of the Recapture Member. The stratigraphic occurrence of this evidence and noninterfingering nature of the Recapture with the paleosol sequence argues against a gradational progradation of the Westwater Canyon alluvial system from the southwest. Comparisons of climates and ecosystems in Namibia and Egypt to the upper part of the Recapture also fail to support an arid climate. For example, the precipitation in the Namib Desert (~ 20° to 25°S latitude) ranges from less than 15 to 19 mm/year from the coast to 87 to 89 mm/year near the eastern escarpment inland (Lancaster, 1989). Across this gradient, the vegetation is either absent (dominated by migrating dunes), or sparse and clumped grasses and dwarf shrubs are common (Louw and Seely, 1982; Lancaster, 1989). These areas also receive fog precipitation of 34 mm/year at the coast to 184 mm/year inland, dropping off to 15 to 31 mm/year to the east; relative humidity also ranges from 87% near the coast to 37% inland (Lancaster, 1989). The Namib Desert has retarded soil development that ranges from entisols to aridisols with sparse infaunal components (Oliver, 1973; Louw and Seely, 1982; Lydolph, 1985; Goode's World Atlas, 2000). In order to have partial or complete stabilization of the Namib dunes with vegetation and increased soil development, total precipitation (rainfall + fog contributions) would have to increase by at least two to three times the present amount (Lancaster, 1989). The Sahara Desert has similar characteristics, even in the area of the Nile River (Louw and Seely, 1982; Lydolph, 1985; Lancaster, 1989; Goode's World Atlas, 2000). The Sahara Desert is the most extensive dry area on Earth with most places receiving no rainfall, while portions of the interior receive less than 2 to 5 mm/year (Lydolph, 1985). In the eastern part of the Sahara where the Nile River flows through, precipitation is aseasonal, and water stress occurs throughout the year. These conditions are also indicated by the limited vegetation and biota along from the river (Louw and Seely, 1982; Lydolph, 1985). Little to no life or soil development occurs at relatively short distances away from the Nile without irrigation. Although termites and vegetation occur in both of these deserts, the termite nests are diminutive, and vegetation is very limited (Louw and Seely, 1982). The physical and biologic–pedogenic evidence in the upper part of the Recapture strongly suggests much more precipitation and net primary productivity (NPP; vegetation and animals) than would have occurred in an arid climate, based on inferences drawn from data from the Namib and Sahara Deserts. Likewise, comparison of the Recapture data to that of the semiarid climates of the modern Four Corners area also suggests that the latest Recapture was wetter with greater NPP, soil development, and biodiversity than what is present today in the Four Corners. Ultimately, further work is necessary to evaluate the degree and type of bioturbation in the Bluff Sandstone and Recapture Members and its equivalents to understand better and to determine the degree and range of aridity in the

Fig. 33. Schematic diagrams of large-scale ichnocoenoses found in eolian (and eolian-influenced) environments preserved in the Bluff and Recapture Members (and equivalent strata) of the Morrison Formation. Cross-section A–A′ illustrates relations between the physicochemical and physiological controls active in the eolian settings and the general abiotic and biotic trends that shape the ichnocoenoses. Text in the box adjacent to the flattened end of each arrow is a summary of the physical, biologic, and ecologic characteristics and trends that operate in the direction of the arrow. Box diagrams depict examples of ichnocoenoses that are found in those environments. Boxes with no bioturbation reflect environmental settings in which no bioturbation occurred in that subenvironment due to substrate and other physicochemical factors that prevented successful habitation of the substrate. See Fig. 30 for explanation of abbreviations.

paleoclimate in which the eolian units of the Morrison were deposited.

5.2. Traces and paleosols

Numerous trace fossils identified in the Morrison Formation are associated with sedimentary successions that contain weakly to well-developed paleosols (Table 1). Paleosols are not deposits; rather, they are the result of postdepositional modifications of deposits within alluvial, lacustrine, eolian, and transitional environments. This is contrary to the approach taken by other ichnologists (e.g., Ekdale et al., 1984; Bromley, 1990; Buatois and Mángano, 1995; Buatois et al., 1998; Genise et al., 2000) who treat paleosols as a separate kind of environment or ichnofacies. Consequently, paleosols cannot be used as a subdivision or potential ichnofacies. Pedogenesis modifies nearly all surficial deposits. It occurs at different rates and with different results based on the magnitude and frequency of depositional events, distance from sediment source, parent material, position and fluctuation of groundwater profile, inherent local topography, composition of biotic communities, and the climatic setting with regard to temperature and precipitation (Bown and Kraus, 1987; Kraus, 1987; Hasiotis and Bown, 1992; Hasiotis, 2000). The broad range of soil types and conditions in continental environments produces a high degree of spatial heterogeneity, resulting in juxtaposed microcosms, each with unique physical, chemical, and biological properties (i.e., Cloudsley-Thompson, 1962; Wallwork, 1970; Richards, 1974; Birkeland, 1984; Retallack, 1990).

The effect of macroscopic organisms can be observed in soil-profile development and used to measure the role of organisms' activity in soil-forming processes in modern continental environments. Organisms affect soils by mounding, mixing, forming voids, backfilling voids, forming and destroying peds; by regulating soil erosion, regulating water, air movement, plant litter, animal litter, nutrient cycling, and biota; and by producing special constituents (e.g., Thorpe, 1949; Hole, 1981).

Ichnofossils can also be used in the same manner to identify and characterize the role of organisms in soil formation during the Late Jurassic. Many of the organisms represented by ichnofossils (Table 3) in terrestrial and transitional-aquatic environments participated in producing different soil types (Table 2) shaped by the duration of subaerial exposure, frequency and magnitude of depositional events, and the amount of material deposited or removed by a flooding event. Plant and animal ichnofossils reflect that these organisms operated in relatively aerated, well-drained, and environmentally stable conditions to often saturated conditions with frequent accumulation of new sediment. Many Morrison paleosols are associated with alluvial deposits in highly aggradational systems. Soils have little time to mature, and thus have biologic and pedogenic characteristics typical of entisols or inceptisols (relatively immature soils). Other paleosols in the Morrison contain highly smectitic clays that exhibit large pseudoanticlines with other subparallel fractures formed by expansion and contraction due to wetting and drying. Distinct ichnofossil components, many of which are not preserved due to the destructive, expanding and contracting nature of the clays, indicate the alternating wet and dry conditions in which these paleosols formed. These paleosols are typically referred to as vertisols and a few have been identified in the Morrison (also see Demko et al., this volume). Other paleosols have relatively high-clay content (e.g., mudrock) and contain an assortment of ichnofossils of fossorial insects, crayfish, and some mammals. They also have carbonate nodules of varying abundance associated with them, in some cases, forming around rhizoliths and burrows; these are classified as Bk horizons. These paleosols are also referred to as alfisols or calcisols, depending upon the amount of calcium carbonate associated with them. Plant and animal ichnofossils in these paleosols also suggest that the carbonate reflects the depth of wetting during infiltration and reprecipitation during evapotranspiration. The calcium carbonate may have been enhanced by synformational or postburial groundwater based on interpretations of the character of many of these horizons (see Demko et al., this volume).

The density of burrowing, the amount of soil turnover, and nutrient contributions illustrate the role of organisms in soil formation. Invertebrates, particularly insects, are known for turning over millions of tons of soil per year (Thorpe, 1949; Hole, 1981). In several intervals within the Salt Wash, Recapture, and Brushy Basin Members, beds of intense bioturbation record the burrowing activity of many generations of termites, ants, beetles, soil bugs, crayfish, and other arthropods that redistributed and destroyed most evidence of pedogenic horizonation. In these situations, soil-forming bioturbation outpaced soil-forming pedoturbation. Bioturbation was most intense near the surface of the paleosol and decreased downward through the substrate, reflecting a decrease in pedogenic activity with depth. Similar bioturbation patterns have been observed in Mesozoic and Cenozoic alluvial soil studies (Wallwork, 1970; Hasiotis and Dubiel, 1994; Thackery, 1994; Bown et al., 1997; Lavelle et al., 1997; L.P. Wilding, 1999, personal communication; W. Miller, 1999, personal communication; Hasiotis and Honey, 2000).

In modern continental ecosystems, aboveground and belowground organisms such as earthworms, termites, and beavers are referred to as ecosystem engineers (Jones et al., 1994; Lavelle et al., 1997) because their physicochemical activities modify the environment and regulate nutrients to biota above and below them in the trophic pyramid. The intensity and distribution of bioturbation in the Morrison paleosols suggest that some invertebrates played major roles as ecosystem engineers. The activity of Morrison termites, ants, and crayfish modified the local environment, controlled subsurface air and moisture constituents, mixed and formed soil aggregates, and regulated nutrients to biota that were above and below them in the trophic pyramid. Burrowing and track-making mammals, amphibians, and reptiles have a lesser impact on soil formation in alluvium (e.g., Thorpe, 1949; Voorhies, 1975; Hole, 1981; Meadows and Meadows, 1991). These types of traces are also reported from the Morrison (Table 1) and suggest mixing of substrates to a lesser degree; nevertheless, they were part of the pedogenic process.

In Morrison paleosols, burrows and nests with the greatest preservation potential are those that are constructed and reinforced rather than merely excavated. Reinforced and constructed burrows and nests contain organic material altered during pedogenesis and later by diagenesis, preferentially preserving the structure of the burrow or nest (Hasiotis and Bown, 1992; Hasiotis and Mitchell, 1993; Hasiotis and Dubiel, 1995; Hasiotis et al., 1993a,b; Genise and Bown, 1994a). This type of preservation is abundant in the Morrison Formation, from the elaborate and detailed morphology of termite and ant nests, the architecture and depth of crayfish burrows, to the preservation of spheroids and adhesive meniscate burrows produced by beetles and soil bugs. Each type of ichnofossil is excavated and reinforced in varying degrees, but this demonstrates the presence of temporary to long-term fossorial organisms in pedogenically modified terrestrial deposits.

5.3. Morrison trace fossils: continental ichnocoenoses vs. proposed ichnofacies models

Over the last decade, several attempts have been made to erect archetypal ichnofacies models or ichnofacies assemblages that recur for continental depositional environments (e.g., Frey and Pemberton, 1987; Buatois and Mángano, 1995; Buatois et al., 1998; Genise et al., 2000). Currently, only the *Scoyenia* ichnofacies (Seilacher, 1967) is accepted as a valid archetypal assemblage of continental environments; yet, it is broadly defined and poorly constrained. Proposed ichnofacies, including the amended *Scoyenia* and *Termitichnus* ichnofacies, the *Coprinisphaera* ichnofacies, and the *Mermia* ichnofacies (Buatois and Mángano, 1995; Buatois et al., 1998; Genise et al., 2000), were erected to represent moist to wet, low-energy environments (from alluvial to wet-interdune environments), paleosols developed in closed forests (alluvial environments), terrestrial herbaceous (angiosperm) communities (alluvial environments), and noncohesive, well-oxygenated, fine-grained sediment in permanent subaqueous zones (deep to shallow lakes and fjords), respectively (Buatois and Mángano, 1995; Buatois et al., 1998; Genise et al., 2000). Yet, these redefined and newly erected ichnofacies are broadly and poorly defined and constrained.

The ichnofossil–ichnofacies problem is due to the pervasive overuse of archetypal ichnofacies models that for several reasons are flawed with respect to facies and behavioral interpretations. Goldring (1995) listed 13 reasons, including insufficient ichnofacies resolution, the lack of relationships between the sediment and the ichnofossil, the absence of the name-bearing ichnotaxon from the ichnofacies, the inability to identify ichnofacies in highly bioturbated sediments, the inability to identify important facies changes, and wide distribution of similar trace fossil morphologies in marine to continental deposits. A major problem that is often overlooked is the improper interpretation of behavior from architectural and surficial morphologies of a burrow (Hasiotis and Bown, 1992; Hasiotis and Mitchell, 1993); morphology is not behavior but a consequence of a behavior that is subjective rather than objective and must be interpreted. This problem is compounded when an ichnofossil or ichnofossil suites are used to define behavioral (ichno-) facies based on the types of trails or burrows occurring in a substrate and sedimentary facies that are never part of the scheme to interpret behavior or the tracemaker. A critical assessment by Byers (1982) of the ichnofacies models showed that they were generalizations that linked trace fossils of the rock record to the current understanding of ocean sediments. More importantly, Byers (1982) noted that the ichnofacies focused on the distribution of the trace fossils rather than on the marine organisms that constructed them and the conditions under which they were formed. Although Buatois and Mángano (1995), Buatois et al. (1998), and Genise et al. (2000) attempted to erect viable archetypal continental ichnofacies, the occurrence and distribution of the Morrison ichnofossils do not support such models for reasons described herein; they also have problems similar to that of other archetypal ichnofacies (Byers, 1982; Hasiotis and Bown, 1992; Goldring, 1995).

The ichnofossils in alluvial, lacustrine, and eolian environments of the Morrison are most appropriately treated as traces of biological community assemblages or ichnocoenoses. An ichnocoenosis is a localized remnant of the above- and belowground soil (or substrate) community and should be named for the most abundant or most pedoecologically modifying behavior in that part of the subenvironment. Generally, a high degree of spatial heterogeneity exists in alluvial and supralittoral environments that result in a mosaic of juxtaposed microcosms or biotopes, each with unique physical, chemical, and biologic properties (e.g., wide range of soil types and substrate conditions). Thus, a uniform sedimentary package in the Salt Wash or Recapture Member may laterally exhibit juxtaposed crayfish, beetle, and termite ichnocoenoses that are readily interpreted to reflect a deepening of the water table away from a channel–levee complex toward the proximal floodplain. The emphasis is on the community structure as it changes from areas dominated by omnivory (many crayfish burrows) in relatively oxygen-deprived, high water-table conditions to areas dominated by detritivory (large or numerous termite nests) in variably elevated CO_2, low soil moisture, and deep water-table conditions.

5.4. Continental sequence-stratigraphic implications

Intervals with high densities of ichnofossils, like the termite nests at the top of the Recapture Member, are excellent stratigraphic markers of discontinuity surfaces in the Morrison Formation with possible sequence-stratigraphic significance in continental environments (Hasiotis and Honey, 2000; also see Demko et al., this volume). Morrison trace fossils also represent surfaces of varying degrees of environmental stability. Burrowed intervals described from the Tidwell, Salt Wash, Recapture, Westwater Canyon, and Brushy Basin Members reflect surfaces of nondeposition, local to extensive subaerial exposure, and pedogenesis of varying duration. Because the burrowed beds are part of pedogenic intervals representing short to long duration of subaerial exposure, some may also have regional to basinal extent (also see Demko et al., this volume). Local subaerial exposure surfaces of short duration are plentiful in the Morrison. They are represented by surface and shallow, low to high densities of trace fossils in channel, bar, point bar, levee, and other proximal deposits as well as proximal lacustrine deposits. The intensity of bioturbation is determined by the length of exposure, the suitability of the environment for occupation, and the hydrologic setting. Local to regional surfaces of long duration representing extensive subaerial exposure and pedogenesis sometimes contain high densities of trace fossils like crayfish burrows, rhizoliths, adhesive meniscate burrows, and nests of ants, bees, wasps, and termites. For example, at locality 22, the high density of termite nests in the eolian facies of the Recapture Member can be traced from Church Rock to Pyramid Rock, over a distance of nearly 2 km at about the same stratigraphic position. The beds between the two points cannot be walked out because a valley separates them, but it is clear that they occur at the same level. This interval may also have regional significance if it can be traced outside of the Gallup, NM, area.

Trace fossils, such as AMB (1; Appendix A), ant and bee nests (3a–c; Appendix A), vertical and horizontal burrows (12, 49, 50; Appendix A), crayfish burrows (4a–c; Appendix A), mammal and reptilian burrows (47–48; Appendix A), and dinosaur-trampled grounds (44–45; Appendix A) are also indicators of subtle changes in mudrock on mudrock and sandstone on sandstone facies and local base level. Greater densities of burrows within an interval indicate longer periods of surface stability due to sediment bypass at or nearing local base level or during incision. Lower burrow densities indicate greater sedimentation rates or higher water tables, as well as chemically inhospitable substrates directly adjacent to or in evaporative lakes. Where high water tables and standing water persist for long periods of time with little or no terrigenous input, then palustrine carbonates (see Dunagan and Turner, this volume) or peat swamps (coals) form like those in the northern part of the Morrison depositional basin in Montana and Canada. Relatively higher sedimentation rates and high, standing water tables (or areas where the water table intersects the surface) produce thick intervals of lacustrine mudstones and siltstones and very thin sandstones with very little bioturbation (Fishman and Turner, 1991; see Dunagan and Turner, this volume). For example, the near lack of bioturbation in the lacustrine deposits of the Brushy Basin Member is attributed to high rates of sedimentation and alkalinity of the water, and bottom sediments where volcanic ash was a major source of sediment (Bell, 1986; Turner and Fishman, 1991; Turner, 1992). The occurrence of mottled, quasihorizontal burrows (locality 19; Appendix A) and shallow, dense rhizoliths (locality 21; Appendix A) in thin sandstones within these lacustrine deposits, however, probably represents temporary episodes of local freshening of the alkaline waters that allowed infaunal organisms and shallowly rooted plants to occupy the substrate in proximal lacustrine environments.

Burrowed intervals and paleosols, indicating environmental stability, represent potential surfaces of sequence-stratigraphic significance when used in conjunction with sandstone and mudrock successions to identify alluvial stacking patterns in the Morrison (Currie, 1997, 1998; also see Demko et al., this volume). These surfaces are analogous but not genetically related to surfaces and sequences in marine settings (Van Wagoner et al., 1988, 1990). Similar observations have been made in younger continental deposits in the Washakie, Great Divide, Hanna, Piceance, and Wind River basins in Wyoming and Colorado (Hasiotis and Honey, 2000). Alluvial units characterized by channel–levee complexes composed of increasingly better-developed, more mature paleosols with higher bioturbation intensity imply lower sedimentation rates, base level, and accommodation space. In basin lowlands, these Morrison units are characterized by thinner alluvial deposits that change facies into lacustrine deposits dominated by carbonates (Peterson, 1994; Dunagan and Turner, this volume). Toward the basin lowlands, depositional sequences contain less well-developed paleosols with slight to moderate bioturbation. Successions of alluvial, lacustrine, and eolian units are bounded by surfaces or sequence boundaries (Currie, 1997, 1998) marked by well-developed and bioturbated paleosols (Demko et al., 1996; Demko et al., this volume) and fluvial channels contemporaneous with those surfaces. Stratigraphic successions delimited by these sequence boundaries define an alluvial sequence (e.g., Hasiotis and Honey, 2000). These boundaries should reflect the local environmental, hydrologic, and climatic conditions in a subbasin, with boundary characteristics varying across the depositional basin. Thus, within or between Morrison members, several continental sequences will exhibit stratal patterns of overall high aggradation, low aggradation, or degradation. This pattern will also vary in a basinward direction and are likely to record relative aggradation, retrogradation, or progradation of sequences across the Morrison basin.

5.5. Paleoecologic significance of the morrison ichnofossils

The spatial and vertical distribution of Morrison ichnofossils (see Fig. 2) attests to adaptation of terraphilic, hygrophilic, and hydrophilic burrowing organisms to localized and widespread hypoxic (O_2 deprived) and hypercarbic (elevated CO_2) conditions due to inundation and competition for O_2 with nearby microbial decomposers. Belowground atmospheric conditions differ from those in aboveground habitats because O_2 concentrations decrease with depth, and CO_2 levels are elevated in the soil profile or substratum (Villani et al., 1999). Water infiltration, however, inhibits diffusion and can drastically reduce O_2 levels (Glinski and Lipiec, 1990). The concentration of soil gases is dependent on abiotic (soil structure, texture, and moisture) and biotic factors (amount of decaying organic matter, root density, soil animal density). Behavioral responses of Morrison soil fauna to these problems include lateral or vertical movement through the soil pores by burrowing or moving to more favorable conditions through preexisting burrows of other organisms or tunnels of decomposed plant roots (e.g., Willis and Roth, 1962; Hole, 1981; Marinissen and Bok, 1987; Cherry and Porter, 1992). Undoubtedly, the larvae of many Morrison insects (e.g., Coleoptera, Diptera, and Lepidoptera?) used a plastron or physical gill through morphology or by a combination of behavior and physiology (e.g., Villani et al., 1999) as an adaptation to substrate inundation from precipitation and flooding. Ventral body flattening and hydrofugic (i.e., water shedding) hairs on the bodies of insect larvae, construction of temporary cavities, and formation of cocoons is likely to have provided exchange surfaces for renewal of O_2 and loss of CO_2 while discouraging the osmotic influence of water through permeable cuticle (Eisenbeis and Wichard, 1987; Villani et al., 1999).

The diversity and abundance of ichnofossils in the Morrison Formation demonstrate the presence of highly evolved terrestrial and aquatic ecosystems that contained all the major components of detritivore-based food webs shaped by the physical–chemical environment in which they occur (see Tables 2 and 3; Figs. 30–33). The food pyramids of Morrison ecosystems contained the infrastructure of energy pathways and niches that linked detritivores (saprophagous, coprophagous, and necrophagous roles), herbivores, omnivores, and carnivores. As in extant soil ecosystems (Wallwork, 1970), the greater part of organic matter fixed by higher plants in the Morrison was likely to have returned directly to the soil via the producer–decomposer pathway (mainly, insects and other arthropods). The material and energy for these ecosystems were provided by green plants (autotrophs) in the form of dead and decaying leaves, fruits, woody stems, and roots (e.g., Wallwork, 1970; Aber and Melillo, 1991; Parrish et al., this volume). The primary consumers in the soil ecosystems, however, were the detritivores, whereas, aboveground, the herbivores occupied this role (e.g., Wallwork, 1970; Richards, 1974). The presence of macrofaunal trace fossils in the Morrison is a direct indicator of the presence of the mesoscopic and microscopic fauna and flora (including bacteria, fungi, algae, and protozoa) that formed the major part of the detritivore food web. As in aboveground ecosystems, the primary consumers were preyed on by carnivores or secondary consumers that, in turn, were preyed on by the larger carnivores or tertiary consumers (Wallwork, 1970). Although soil-dwelling predators played no direct role in the transformation of organic litter into humus, they helped maintain detritivore populations and the balance between primary and secondary consumers.

Some of the ichnofossils preserve remnants of coprophagous, necrophagous, and saprophagous feeding and nesting soil organisms that were part of the detritivore-based nutrient dynamics in terrestrial and aquatic Morrison ecosystems. Those insects that used dung in subsurface nests, like the beetles that constructed *Coprinisphaera* and backfilled burrows, also adapted elevated tolerances to hypoxia (O_2 deprived) and hypercarbia (elevated CO_2) brought on by decomposing dung within and above the nests (e.g., Holter, 1994). The presence of *Coprinisphaera*, backfilled burrows interpreted to have been formed by ground beetles, adhesive meniscate burrows, and the large number of herbivorous dinosaur fossils (Engelmann, this volume) suggests that Morrison dung piles were likely to have provided new, temporary niches as a food source and a reproductive medium for coprophages, carnivores, parasites, fungivores, and microphytic feeders (e.g., McKevan, 1962; Wallwork, 1970). This interpretation is based on modern studies of dung as ecological units (e.g., Mohr, 1943). The dung piles were useful for arthropod immigration from one region of the Morrison depositional basin to another by following their food source (e.g., McKevan, 1962; Waterhouse, 1974)—the locally and regionally migrating herds of herbivorous and predatory dinosaurs (Gillette and Lockley, 1991; Lockley, 1991; Lockley and Hunt, 1995).

The feeding and nesting behavior of necrophagous and saprophagous invertebrates is represented by small hemispherical borings in Jurassic dinosaur bones in Wyoming, Utah, and Colorado (Laws et al., 1996; Hasiotis and Fiorillo, 1997; Hasiotis et al., 1999b). These traces most likely represent the puparia of carrion beetle larvae (Coleoptera: Dermestidae) associated with the dry decay stage in carrion decomposition (e.g., Hasiotis et al., 1999b). The borings indicate that previous successions of necrophagous and saprophagous invertebrates were present at the carcass to bring it to the stage occupied by the dermestids. The decaying bodies of Morrison dinosaurs, evidenced by the dinosaurian fossil record, fed and moved entire communities of necrophagous and saprophagous insects to new geographic ranges, opened up specific niches under favorable climatic conditions, trapped moisture, and provided shelter for other soil organisms (e.g., Reed, 1958; Payne, 1965; Coe, 1978). The ecologic function of megafaunal carrion in Morrison terrestrial ecosystems is analogous to that of whale carcasses on deep ocean basin floors used for dispersion of larva (e.g., Smith, 1985; Allison et al., 1991) by providing pathways for the immigration and emigration of soil arthropods from one habitat to another, particularly during an extended dry season. These ichnofossils provide excellent evidence for the coevolution of vertebrates, invertebrates, and the detritivore nutrient cycle in Mesozoic soil ecosystems (Hasiotis, 2000).

The complex burrow structures in the Morrison interpreted as termite, ant, and possibly bee nests preserve unique solutions to fossorial life through social cooperation (e.g., Wilson, 1971; Villani et al., 1999). Insect societies of termites (Isoptera), ants (Hymenoptera), and the higher bees and wasps (Hymenoptera: Aculeata) cooperated to construct and maintain the nest, collect and grow food supplies, feed nest members, protect the nest from invaders, and care for the young (e.g., Evans and Eberhard, 1970; Lee and Wood, 1971; Wilson, 1971; Michener, 1974). Large numbers of individuals worked together to maintain and alter the nest architecture to bring appropriate atmospheric and climatic conditions to the subterranean community, as well as to avoid hypercarbic and hypoxic gas levels ordinarily caused by large numbers of insects respiring in close proximity (e.g., Luscher, 1961). During Morrison wet seasons that produced heavy rainfalls and flooding, termite, ant, and bee nest members are likely to have barricaded nest entrances and sealed off galleries and chambers where water began to accumulate (e.g., Krishna and Weesner, 1970; Wilson, 1971). During the Morrison dry season, the temperature and atmospheric conditions in social insect nests were likely to have been regulated through the combined effort of individuals to generate airflow in the nest by reorganizing tunnels, opening passages to fungal gardens, and the strategic distribution of individuals throughout the nest (e.g., Evans and Eberhard, 1970; Wilson, 1971; Michener, 1974).

5.6. Paleohydrologic and paleoclimatic significance of the Morrison ichnofossils

The tiering of epifaunal and infaunal burrowing organisms in sandstone and mudrock deposits indicates that their distribution was controlled in part by annual and seasonal fluctuations of soil moisture and water-table depth and fluctuations (see Table 2, Fig. 2). The local and regional climatic setting at the time the ichnofossils were constructed, in turn, controlled these groundwater features. The relationship between an organism's energy sources (e.g., food) and the general function of their burrow with respect to behavior also controlled the depth and distribution of organisms. Infaunal organisms and their burrows are distributed ecologically in tiers based on their physiology, trophic needs, and environmental settings. Therefore, the ichnofossils of infaunal organisms represent paleoecological tiers based on their original organism–substrate and organism–organism interactions that operated under specific hydrologic and climatic conditions (e.g., Hasiotis and Dubiel, 1994). This information, combined with other paleontologic, sedimentologic, stratigraphic, isotopic, and paleogeographic data, is used herein to reconstruct the Morrison paleoclimate from the bottom–up. This is accomplished by piecing together detailed physical, biological, and chemical climatic data from various regions of Morrison outcrops to produce a semiquantitative interpretation of the paleoclimate at the continental to hemispheric scale.

The different local climatic and environmental settings during deposition of the Morrison controlled soil formation and the abundance and distribution of the fauna, flora, and soil biota. Traces of crayfish, termites, ants, bees, beetles, soil bugs, and plants are the preserved products of the water balance in paleosols that record the relation between annual precipitation inputs, solar radiation, evapotranspiration losses, and soil moisture changes during the Late Jurassic. Continental trace fossils can be used to determine these parameters because the distribution of organisms that construct traces in terrestrial and aquatic environments is controlled by climate (e.g., McKevan, 1962; Wallwork, 1970; Aber and Melillo, 1991; Hasiotis and Bown, 1992; see also Approach and method). The ancient soil–water budget also should have reflected the above-ground net primary productivity in an ecosystem as biomass produced in terms of vegetation and the organisms that are supported in the system (i.e., Whittaker, 1975).

The limited depth, restricted distribution, and low abundance of crayfish burrows in the Salt Wash and Recapture Members suggest that the rivers were above the local water table. Burrow depths of 1 to 2 m occur close to paleochannels and in very proximal extrachannel environments that were weakly modified by pedogenesis. Distal floodplain settings devoid of crayfish burrows likely had water-table levels in excess of 3 m deep and did not support hydrophilic organisms. The seasonal precipitation was probably very low to support vast populations of floodplain-dwelling crayfish that depended on groundwater levels at least within 4 m from the surface (e.g., Hobbs, 1981; Hasiotis and Mitchell, 1993; Hasiotis et al., 1993a,b). There was, however, enough water flowing in rivers to support open-water crayfish populations (Hasiotis and Kirkland, 1997; Hasiotis et al., 1998a). Crayfish burrows in the lower to upper parts of the Brushy Basin Member have an increasingly broader distribution in pedogenically modified proximal extrachannel and floodplain environments. This distribution suggests less strongly seasonal water-table fluctuations with overall widely distributed and higher water-table levels, implying that seasonal precipitation was greater compared to that of the rest of the Morrison Formation.

Termite nests, from less than 1 m to more than 30 m in depth, reflect shallow to deep water tables in proximal to distal alluvial and eolian-derived deposits in the Salt Wash, Recapture, and Brushy Basin Members. Most nests occur in the shallow subsurface in well-drained and oxygenated substrates weakly modified by pedogenesis, with fewer and fewer galleries and chambers (fungal gardens, storage, and waste disposal) found deeper in the paleosols. The deepest galleries typically extended down to the nearest source of water that includes either a perched water table or the phreatic zone. The shallowest nests were found in highly aggradational alluvial proximal and distal environments that were weakly modified by pedogenesis in the Brushy Basin and Salt Wash Members; the deepest nests are in the eolian facies of the Recapture Member, and these substrates are strongly modified by pedogenesis. The presence of these small to large trace fossils also provides indirect evidence of low-lying plants to relatively large trees that would have co-occurred in the area of the nests and provided organic material for the termites to eat.

Several beds of coalified or petrified logs occur in the proximal alluvial deposits in the lower and upper part of the Salt Wash Member. The petrified logs, up to 15 m long and some of which contain insect and fungal borings, occur locally in abundance (more than 100 logs/1000 m^2), and many contain root boles, suggesting that they were deposited nearly in situ. The abundance and distribution of logs do not appear to be strictly confined to the wettest margin of riparian watercourses, and the logs do not appear to have been transported from elsewhere. The number of individual trees is suggestive of open forests or mixed wooded savanna (mixed refers to patches of groundcover vegetation and trees). Rhizoliths in mostly immature paleosols (see Demko et al., this volume) farther away from the river courses in proximal to distal floodplain deposits suggest communities of riparian open-canopy forests, decreasing to relatively small woody and herbaceous plants with often abundant, low-lying vegetation in more distal locations. This pattern suggests that, at least seasonally, rivers fed the phreatic zone that deepened away from river systems during the dry season. Modern climate analogs where mixed forests are found suggest that these Morrison forests represented seasonally delivered precipitation between 750 to 1000 and 1000 to 1500 mm/year, depending on the amount of evapotranspiration and solar radiation for this area during the Late Jurassic (Oliver, 1973; Lydolph, 1985; Aber and Melillo, 1991). Because the area of the Salt Wash where the logs grew was at around 30°N latitude and under a greenhouse climate with globally warmer temperatures than today, the rainfall amount probably ranged from around 1000 to 1500 mm/year delivered under conditions $P/E \sim 1$ (e.g., Oliver and Hidore, 1984; Lydolph, 1985).

These and other Morrison organisms dwelling in alluvial and lacustrine environments were also adapted to the wet and dry seasons such that, during the wet seasons, the soils (substrates) were saturated and the rivers were fed by groundwater, followed by dry seasons without any appreciable precipitation and the rivers locally fed the groundwater. Dwelling and hiding, resting, and feeding traces of freshwater clams and snails in alluvial and lacustrine deposits of the Tidwell, Salt Wash, and Brushy Basin Members imply the perennial flow of mostly sediment-free freshwater in rivers and lakes. Unionid bivalves are sensitive to the freshness and clarity of the water they inhabit (Evanoff et al., 1998; see Good, this volume). Morrison clam and snail communities attest to perennial sources of water flowing through various parts of the basin without severe losses due to dry-season water deficits, although many higher-order rivers are likely to have flowed intermittently, while smaller lakes became unfit for survival or possibly dried up in some instances. Morrison bivalves have growth bands that indicate relatively optimum conditions in the Tidwell, to seasonal variability in the Salt Wash, and mixed conditions in the Brushy Basin (Good, this volume), an interpretation that is corroborated by the large number of bivalve ichnofossils. Dermestid beetle borings in bones of several types of dinosaurs at several different occurrences in the Salt Wash and Brushy Basin Members reflect insect successions on moist-to-dried carcasses that were being eaten and bored by the beetles while the bones were exposed to the air on the ground-surface, presumably during the dry season prior to burial by fluvial processes during the following wet season. Modern dermestids occur in environments with a wide range of seasonally wet–dry climates, but these beetles are absent to rare in extremely dry and extremely wet climates. Hymenopteran (bees, wasps, and ants) and coleopteran (dung beetle) nests also indicate well-drained substrates in the Salt Wash and Brushy Basin Members with weakly to moderately developed paleosols in proximal alluvial and supralittoral lacustrine settings. The presence of large and diverse nests of gregarious and social insects (bees, ants, termites) in the Salt Wash, Recapture, and Brushy Basin Members implies ample and accessible sources of dead vegetation and equivalent amount of live material and groundwater. Several types of aquatic insect nymphs and larval dwelling and feeding structures in the Tidwell, Salt Wash, and Brushy Basin Members indicate a range of seasonal to perennial sources of water that allowed them to complete their life cycles.

The ichnocoenoses, body fossils, types of paleosols, and the sedimentary packages indicate a mosaic of seasonal to strongly seasonal climates across the Morrison depositional basin with dominant wet and dry seasons during the year. An analogous range of climates today occurs in savannas or steppes dominated by grasses (i.e., groundcover) and mixed woodlands (e.g., Lydolph, 1985; Goode's World Atlas, 2000). This interpretation is also based on the following: (1) paleolatitude positions of the Morrison depositional basin during the Late Jurassic (Four Corners area—30°N; Zeigler et al., 1983; Paleogeographic Atlas Project, 1984 at the University of Chicago); (2) the proximity of the basin to the Late Jurassic Western Interior seaway, the Laurasian coast, and the presence of coastal embayments as a potential moisture source; (3) expanded climate zones during a greenhouse period; (4) potential orographic effects from highlands and mountain ranges along the western and southern boundaries of the basin; (5) initial isotopic evidence across the basin (e.g., Ekart et al., 1999); and (6) plant, invertebrate, and vertebrate body and trace fossil evidence indicating appreciable biodiversity (e.g., Peterson, 1994; Morales, 1996; Carpenter et al., 1998; Chure et al., 1998; Litwin et al., 1998; Parrish, 1998; Parrish et al., this volume). The biodiversity of the Morrison is comparable to extant patterns in biodiversity and net primary productivity (NPP) associated with the nature of modern tropical wet–dry climates (e.g., Whittaker, 1975; Oliver and Hidore, 1984; Lydolph, 1985; Olff et al., 2002). The term "tropical" here is used in a continental biogeographical sense, meaning the lack of a cold season and not just a zone bounded by latitude lines (Neill, 1969). Wet–dry is indicative of a climate where precipitation (P) exceeds evapotranspiration (E) during one period of the year ($P/E>1$), while the reverse is true during a second season ($P/E<1$) (Oliver, 1973; Lydolph, 1985). Savannas and steppes have NPP values ranging from 200–2000 g/m^2/year with a mean of 900 g/m^2/year (Whittaker, 1975), while seasonal (wet–dry) tropical forests have NPP values ranging from 1000–2500 g/m^2/year with a mean of 1600 g/m^2/year (Whittaker, 1975). A similar combination of these types of tropical wet–dry ecosystems with analogous NPP values likely shaped Morrison environments and supported the biota.

During the Late Jurassic, climate zones in the Morrison depositional basin reflected the greenhouse climate that was likely to have been brought on by a sixfold (Moore et al., 1992) to as much as an 11-fold increase in CO_2 (Ekart et al., 1999) and the configuration of continents, among other things (e.g., Moore et al., 1992; Valdes, 1992, 1993). Changes in the Earth's equator-to-polar temperature gradient leads to a modification of the general circulation pattern and results in changes in precipitation patterns (e.g., Oliver and Hidore, 1984). In the Northern Hemisphere, during a greenhouse period, the location of the jet stream and equatorward limit of the Rossby region, which serves as a function of cooling and warming trends, moves poleward. This would expand the tropical climate zones, including the intertropical convergence zone (ITC), northeast trades, and subtropical highs, and, in effect, widen them. Nicholson and Flohn (1980) discussed analogous changes in the ITC for central and northern Africa during the warming trends in the latest Pleistocene and Holocene, which, in effect, widened its range and distributed greater precipitation across the Sahara to about 30°N latitude. In the Sahara, during the Pleistocene, summer–wet and winter–dry precipitation patterns are likely to have existed. Furthermore, during Morrison deposition, the subtropical high-pressure belt was likely to have migrated poleward from its typical location at 30°N latitude and distributed more moisture above this latitude while creating arid conditions farther northward of present day settings (about 40° to 45°N). Associated with this pattern would have been hotter summers and strongly seasonal precipitation delivered in winter (December–March) months by the ITC (e.g., Oliver and Hidore, 1984; Moore et al., 1992) to the northern part of the Morrison depositional basin (i.e., Mediterranean climate-type). This produced a tropical wet–dry climate with seasonal delivery of precipitation.

The modern tropical wet–dry climatic environment contains large herds (elephants, rhinoceros, wildebeests, zebra, and gazelle), predators (several types of cats, hyenas, and wild dogs) and flocks of vertebrates (various birds), perennial freshwater organisms (fish, clams, and snails), vast numbers of insects, and a variety of plants. This biodiversity must be shaped by a climate that can support the total biomass through a nutrient and energy cycle robust enough to maintain the ecosystem (e.g., Odum, 1971; De Santo, 1978; Aber and Melillo, 1991; Martinez et al., 1999). Arid regions ($P < 1/2$PE with $P < 250$ mm/year), where, by definition (Lydolph, 1985), evapotranspiration exceeds precipitation ($P/E < 1$) throughout the year, do not and could not support such biomass. The annual water deficit means that contributions of moisture from the groundwater do very little to support the local biomass (e.g., Lydolph, 1985; Aber and Melillo, 1991; Goode's World Atlas, 2000). A transitional semiarid zone ($P > 1/2$PE but $<$PE with $P = 250$ to 500 mm/year) occurs between the arid and wet–dry regions. In these regions, precipitation exceeds evapotranspiration ($P/E < 1$) during a very short wet season, and, for the rest of the year, evapotranspiration exceeds precipitation, creating a major water deficit (Thornthwaite and Mather, 1955; Lydolph, 1985).

Long-term water deficits create deserts that could not support a biodiversity and biomass (NPP; Whittaker, 1975) similar to that recorded by the Morrison ichnofossils, body fossils, and palynomorphs (e.g., Chure et al., 1998; Litwin et al., 1998; and papers in this volume). Based on their sheer size alone, sauropods, ornithopods, and theropods (see Engelmann, this volume) would require fairly large amounts of water and nutrients to maintain metabolic and thermoregulation systems (assuming that dinosaurs were homeotherms) as in extant Serengeti vertebrates for example (e.g., Louw and Seely, 1982; Owen-Smith, 1988; Aber and Melillo, 1991; Alexander, 1998). Extant vertebrates migrate seasonally to follow growth and maturity of food sources and water supplies driven by the wet–dry seasonal cycle (e.g., Sinclair and Norton-Griffiths, 1979; Aber and Melillo, 1991; Olff et al., 2002). Megaherbivores, such as elephants, rhinoceros, hippopotamus, and giraffe, through their lifetimes move over home ranges of several hundred square kilometers per year (elephants and giraffes) to 10 to 100 km^2 (rhinoceros) or less (hippopotamus) (Owen-Smith, 1988). The greatest densities of individuals (megaherbivores) occur in the tropical savannas and forests, while the lowest number of individuals is in semiarid steppes and thorn–shrub desert environments (Owen-Smith, 1988; Aber and Melillo, 1991; Olff et al., 2002). More importantly, these megaherbivores cover only 10% of their home range in the dry season and tend to remain near known water holes, while greatest dispersal occurs during the wet season and away from permanent water bodies (Owen-Smith, 1988).

However, the requirements are much the same for smaller herbivores, such as migratory antelope and wildebeest; they cover 500 to 20,000 km^2 annually (Owen-Smith, 1988; Aber and Melillo, 1991). The megaherbivores also ingest roughly 1% of their body mass daily with a fairly rapid (as seen in elephants) to long (as seen in hippopotamus) turnover rate of dung production, and thus require a large amount of vegetation where the number of individuals is high (Owen-Smith, 1988). The Late Jurassic Morrison dinosaurs were also thought to have seasonally migrated to locate preferred feeding habitats and avoid temperature and moisture extremes (e.g., Moore and Ross, 1994; Lockley and Hunt, 1995). Although there is no direct measure of dinosaur activity for their lifetime, examples from the modern Serengeti are used herein to hypothesize that Jurassic megaherbivores were more likely to have had relatively smaller home ranges with seasonally ample vegetation to support large numbers of individuals and tended to frequent areas with permanent sources of water. Relatively smaller Jurassic megaherbivores may have had larger home ranges in which they migrated, but the metabolic costs of locomotion relative to body maintenance for large vertebrates may have been very great for extreme coverage of distances. This is also true for extant vertebrates in Africa and Asia (i.e., Owen-Smith, 1988).

A recent study of the global distribution of vertebrates by Olff et al. (2002) demonstrated that precipitation, soil fertility, and plant nutrient content control the diversity and abundance of small and large herbivores. Such areas with seasonal but abundant rainfall as the tropics and savannas have the greatest diversity of small and large herbivores. Seasonality in precipitation was shown to increase nitrogen content in plants, and thus its quality. Olff et al. (2002) also found that the occurrence of large herbivores increased with greater precipitation and was relatively independent of plant quality. In contrast, the occurrence of small herbivores decreased with increasing precipitation because they require a higher quality of plants. Assuming that Jurassic herbivores and megaherbivores had basic nutrient requirements and ranges of feeding behaviors proportional to their size and physiology akin to those of extant African herbivores, then the diversity and distribution of all Jurassic herbivores would likely have been comparable under analogous ecologic and climatic settings.

The preponderance of paleontologic, ichnologic, paleopedologic, isotopic, and sedimentologic data suggests clearly that the spatial and temporal variations of Morrison climates were similar to the range of tropical wet–dry climates of today (e.g., Oliver and Hidore, 1984; Lydolph, 1985). Totals for seasonally delivered precipitation for Morrison strata below the clay change in the Brushy Basin Member are here estimated to have ranged from: (1) less than 250 mm/year to 250 to 500 mm/year in the southwestern portion of the Morrison basin (Bluff Sandstone and equivalent eolian strata); (2) 700 to 1500 mm/year from the southeastern to central portion of the Morrison basin (Tidwell, Salt Wash, uppermost part of the Bluff and Recapture, and equivalent strata); to, (3) for strata above the clay change, an increasingly wet seasonal climate with summer maximum precipitation from 800 to 1500 mm/year near the end of Morrison deposition (Brushy Basin and equivalent strata). The annual amount of precipitation across the Morrison basin (see Fig. 1A) decreased to the north which is evidenced by an increase in the amount of carbonate in units interpreted as paleosols and groundwater-fed, palustrine settings below the clay change (see Demko et al., this volume; Dunagan and Turner, this volume); lower amounts of precipitation would not have flushed the carbonate from the system.

These Late Jurassic settings were analogous to climates that dominate the African savanna today from about 14°N to 5°N latitude and 2°S to 22°S latitude. This interpretation is also supported by the occurrences of coalified and petrified trees in the lower and upper part of the Salt Wash Member in southeastern Utah (6; Appendix A), which are excellent indicators of the amount of precipitation. Based on modern analogs and their climatic settings, the logs in the Salt Wash suggest seasonally delivered precipitation between 1000 to 1500 mm/year, depending on the amount of evapotranspiration and solar radiation (Oliver, 1973; Lydolph, 1985; Aber and Melillo, 1991). The expanded climate zones were likely to have placed the Late Jurassic Laurasian coastal regions, including the northern part of the Morrison depositional basin (Wyoming and Montana), in slightly more arid conditions where $P/E < 1$. This area of the basin had a wet–dry climate with precipitation amounts similar to the winter maximum precipitation delivery in the present day Mediterranean (about 400 to 800 mm/year). The severity and timing of seasonal drought would have determined the amount and timing of plant growth that, in turn, determined the carrying capacity and seasonal distribution of herbivorous and predatory dinosaurs. The timing and duration of feeding, food hoarding, and reproductive activities of aboveground and belowground soil organisms were also controlled by the tropical wet–dry seasonal climate cycle.

6. Conclusions

Trace fossils in the Morrison Formation are useful interpretational tools for understanding physical, chemical, and biologic systems that operated in the Western Interior during the Late Jurassic. Continental, transitional, and marine ichnofossils represent the activities of different types of invertebrates, vertebrates, and plants that are not commonly preserved as body fossils and may erroneously be considered to have been absent. Based on the architectural and surficial burrow and trail morphologies, members of the Annelida (nematodes), Brachiopoda (lingulids), Bivalvia (freshwater clams, marine pectin), Gastropoda (marine and freshwater snails), Merostomata (horseshoe crabs), Isoptera (termites), Trichoptera (caddisflies), Hemiptera (including the Homoptera; soil bugs, cicadas), Ephemeroptera (mayflies), Orthoptera (crickets, mole crickets), Coleoptera (rove, tiger, dung, dermestid, wood-boring, and ground beetles), and Hymenoptera (bees, ants, wasps) are represented by simple to complex burrows and nests that contain unique features most commonly seen in a particular taxonomic class, order, or family (see Table 3). Ichnofossils interpreted to be the work of ants (Hymenoptera: Formicidae), soil bees (Hymenoptera: Apoidea), sphecid wasps (Hymenoptera: Aculeata), termites (Isoptera: Mastotermitidae?, Kalotermitidae?, Hodotermitidae?), and dermestid beetles (Coleoptera: Dermestidae) are older than their respective body fossils by 50 to 120 million years (e.g., Wilson et al., 1967; Jarzemboski, 1981; Michener and Grimaldi, 1988; Darling and Sharkey, 1990; Krishna, 1990). Crayfish (Crustacea: Decapoda) body fossils occur only at two localities in Colorado (28, 29; see Appendix A), yet their burrows are found at many more localities and beds across the Morrison depositional basin (New Mexico, Colorado, Utah, Wyoming). The earliest known body fossils of burrowing crayfish were recently discovered in the Upper Triassic Chinle Formation in southeastern Utah (Hasiotis and Mitchell, 1993), yet their presence was first identified by the burrow morphology. These and other ichnofossils in Morrison terrestrial and aquatic ecosystems represent hidden biodiversity because the traces represent members of the paleocommunity that have not been previously recognized.

Morrison ichnofossils also record the interactions of biotic elements with one another and the physical and chemical systems of their environment. The presence of dung beetle balls (in nests) indicates the presence of herbivorous dinosaurs and vegetation that the dinosaurs had eaten locally. The occurrence of petrified logs with fungal rot and insect borings suggests several successions of infestations of saprovores that fed on fungus, degraded wood, and other insects and their larvae prior to burial. Dinosaur bones containing beetle borings indicate a previous succession of carcass degradation under specific environmental and climatic conditions that had to take place prior to the boring event, which was prior to burial. Because trace fossils are found in situ, understanding their presence and distribution allows more refined and accurate interpretations and reconstructions of Late Jurassic paleoecosystems (see Figs. 30–33). Invertebrate trace fossils are the most useful environmental and ecological indicators because they are physiologically constrained to specific substrate texture, sediment moisture, depth and fluctuation of the phreatic zone, and salinity conditions of their environment. For instance, crayfish burrows delineate the depth of the freshwater table, whereas, in contrast, dinosaur tracks and trackways cut across alluvial channel and levee, supralittoral to littoral lacustrine, and transitional marine settings with different depositional energies, salinity, substrate, and hydrologic conditions. *Arenicolites*, *Lingulichnus*, *Palaeophycus*, *Conichnus*, *Lockeia*, *Scolicia*, *Terebellina*, patterned surface trails, and pustulose markings represent the behaviors of intertidal dwelling organisms in the Windy Hill and Tidwell Members. Their presence supports the interpretation of a transitional continental–marine environment for the Windy Hill and also provides new evidence of these environments in the Tidwell. Suspension-feeding, detritus-feeding, and predatory mayflies, nonbiting flies, caddisflies, mud-loving beetles, oligochaetes, and nematodes ate CPOM, FPOM, and prey and passed nutrients upward through the food web to crayfish, fish, amphibians, pterosaurs, small dinosaurs, and other reptiles, which continued upward to much larger vertebrates. Fossorial mammals burrowed in the proximal to distal floodplain in well-drained soils and were likely have fed on gregarious and social insects. These mammals were indirectly in competition with omnivorous dinosaurs that also preyed on these insects from the surface, hypothetically.

The integration of data sets collected from Morrison trace fossils, paleosols, and sedimentary environments provides new interpretations and reconstructions of the paleohydrologic, paleoecologic, and paleoclimatic settings during the Late Jurassic. The patterns of vegetation, epigeal animals, and temporary to permanent fossorial invertebrates and vertebrates in the Morrison Formation, integrated with data from paleosols and other physical and chemical parameters, suggest spatial and temporal variations ranging from a tropical wet–dry climate in the southern part of the depositional basin to a mediterranean climate in the northern part of the basin close to or at the edge of the Late Jurassic seaway. Throughout the Morrison depositional basin, the tropical wet–dry and mediterranean climates fluctuated likely between seasonally drier and wetter years, as do climates today (Oliver, 1973; Lydolph, 1985). This included extreme years with either extended periods of drought or precipitation (or $P/E>1$), the latter reflected in higher NPP. Locally, the members of the Morrison record high spatial heterogeneity that produced a mosaic of microclimates coupled with environments that included migrating dune fields in transitional marine, alluvial, and lacustrine landscapes (Windy Hill, Tidwell, Bluff, and Recapture Members), rapidly aggraded to topographically dissected mixed alluvial landscapes (Salt Wash, Westwater Canyon, Brushy Basin Members), and freshwater and alkaline lacustrine systems (Tidwell and Brushy Basin Members). Consequently, within a relatively short distance across the Morrison landscape from any one position at any given time, the ichnofossils, body fossils, sedimentary facies, paleosols, and geochemical and isotopic signatures of the sediments reflected drier to wetter environmental, hydrologic, and climatic settings.

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Appendix A. Upper Jurassic Morrison Formation trace fossil localities

Upper Jurassic Morrison trace fossil localities visited in the reconnaissance study. Included in the table are trace fossil associations, stratigraphic occurrence, and 7.5′ quadrangle locations. For ichnofossil types, see Table 1.

#	Locality	1/4 Section	Sec	Tnsp	Range	County	7.5′ Quadrangle	Member	Trace fossil associations	Stratigraphic occurrence and sedimentologic association
1	Aneth, UT	SW, NW, NW, SW	25	T41S	R25E	San Juan	Aneth	Recapture	3a; 4a; 34a; 38d, e	upper part of section, 30 m below the top of the Recapture Member in red fine-grained homogenous ss
2	Montezuma Creek (north), UT	SE, SW, SE, NW	7	T40S	R24E	San Juan	Montezuma Creek	Brushy Basin	1; 2; 5a; 34a	upper part of section; in purple paleosol composed of mudrock
3	Hanksville (west), UT	SE, NW, SW, NE, SW	13	T28S	R10E	Wayne	Steamboat	Brushy Basin	3b; 34a	~ 1 m above the Salt Wash; in pedogenically modified mr dominated by v.fine-grained ss
4	Moore Cut-off Road, Moore, UT	C, SW, NW, NW, SE	6	T22S	R8E	Emery	Short Canyon	Brushy Basin	3a, b; 34a; 38d	upper part of section; in fine-grained ss interbedded with slt and ms
5	Shitamaring Canyon, UT	SE1/4	16	T35S	R11E	Grand	Copper Creek Benches	Tidwell	2; 4a; 5a, c; 7a, b; 44a	above "bed A" of O'Sullivan (1992) and Peterson (1994); in thin to thick fine-grained ss interbedded with ms
6	Shitamaring Canyon, UT	SE1/4	16	T35S	R11E	Grand	Copper Creek Benches	Salt Wash	1–3a, c; 4a, c; 5; 10; 13–16; 34; 38b–d; 46–51	from base to top of Salt Wash; in pedogenically modified ss, slt, mudrock deposits
7	Shitamaring Canyon, UT	SE1/4	16	T35S	R11E	Grand	Copper Creek Benches	Brushy Basin	1; 3b; 10b; 34a; 38d	lower part below the clay change; in pedogenically modified thick bedded ss interbedded with mudrock
8	Shitamaring Canyon, UT	SE1/4 Lost Spring—N	16	T35S	R11E	Grand	Copper Creek Benches	Summerville Fm.	26; 40	upper most part; in lower fine-grained sandstone interbedded with ms
9	Ruby Ranch-1, UT	SE, SW, SW, SW, NW	1	T23S	R17E	Emery	Green River	Salt Wash–Brushy Basin	1; 2; 4a, b; 34a, b; 50; 51	upper part of section 0–12 m below the Jr–K boundary; calcretized mudrock interbedded with ss, slt

10	Ruby Ranch-2, UT	C–N, SE, SE, SW, NW	1	T23S	R17E	Grand	Dee Pass	Brushy Basin	3b, c; 50; 51	upper part of section; in pedogenically modified, mudrock dominated by fine-grained ss and slt
11	Cleveland–Lloyd, UT	C–NE, SW, SW, SE, SE	21	T17S	R11E	Emery	Cow Flats	Brushy Basin	17; 18	in the quarry section—bones from within the quarry; pedogenically modified murock
12	Cleveland–Lloyd, UT	C–NE, SW, SW, SE, SE	21	T17S	R11E	Emery	Cow Flats	Brushy Basin	7a, b; 32a, b; 36a, b; 39; 46; 47	uppermost part to the base of the Cretaceous Cedar Mountain Fm.; ss interbedded with thin ss, slt, and ms
13	Hatt Ranch, UT	SE, NW, SW, SE	27	T22S	R14E	Emery	Horse Bench West	Tidwell	7a; 33; 40; 46	at the base of bed A and above in ∼ 3 m thick interval; med. to fine-grained ss, interbedded with thin ms
14	Hatt Ranch, UT	SE, NW, SW, SE	27	T22S	R14E	Emery	Horse Bench West	Salt Wash	3a, c; 33a; 46	base of the Salt Wash in the first thick (∼ 3 m) coarse- to fine-grained ss and in contorted interbedded ss, ms
15	Meat-Packing Plant, Hanna, UT	SE, NW, SW, NW	11	T1S	R8W	Duchesne	Hanna	Tidwell	40; 44	∼ 1 m above the Windy Hill and just below reworked eolian sandstone; interbedded thin ss, ms
16	Dinosaur National Monument (DNM), UT	NW, NW, NW, SW	26	T4S	R23E	Uinta	Dinosaur Quarry	Windy Hill	23–31	above the Red Water Formation (ss?) and below the Tidwell; thin ripple-bedded ss interbedded with ms
17	Dinosaur National Monument (DNM), UT	C, W, NE, SW	26	T4S	R23E	Uinta	Dinosaur Quarry	Brushy Basin	17; 18	in Carnegie Quarry sandstone; many major elements—scapula, femur, humerus, ribs, etc.
18	Trachyte Ranch, UT	SW, NW, SW, NE	6	T33S	R12E	Garfield	Cass Creek Pass	Tidwell/Windy Hill	23; 40; 47	∼ 4 m above base; in thin ss interbbedded with ms; footprints in thicker bedded ss above other traces

(continued on next page)

Appendix A (*continued*)

#	Locality	1/4 Section	Sec	Tnsp	Range	County	7.5′ Quadrangle	Member	Trace fossil associations	Stratigraphic occurrence and sedimentologic association
19	Courthouse Draw, UT	NE, SE, SE, NE	11	T24S	R20E	Grand	Merrimac Butte	Brushy Basin	1; 40	5 m interval, ~ 15 m below top of the Brushy Basin; in thin ss interbedded with modified ash beds
20	Salt Valley Anticline, UT	C, SE, SW, NE	30	T22S	R20E	Grand	Klondike Bluffs	Salt Wash, Brushy Basin	1; 2; 4a, c; 34a, b; 46; 47	in upper part of Salt Wash; rhizoliths, backfilled burrows, and paleosols in upper part to J/K boundary
21	Beclabito Dome, NM	NW, NW, SW, NW	17	T30N	R20W	San Juan	Rocky Point	Brushy Basin	4a; 34a, b; 38b, c; 50; 51	in bioturbated thick sandstones and in thin bedded ss/ms interbedded facies
22	Gallup (east), NM	C, NE, SE	2	T15N	R17W	McKlinley	Church Rock	Recapture	?34a, b; 38a; 50; 51	0–35 m below base of Westwater; eolian ss modified by long-term pedogenesis; uppermost part removed by Westwater
23	Park Creek Reservior, CO	SE, NE	18	T10N	R69W	Larimer	Livermore	Windy Hill/ Tidwell	19–22; 46; ?47	Ralston Creek equiv., 0–4 m above base; silty lms w/chert replacement; sand-filled spiral burrows in ms
24	Canon City-1, CO	C–S1/2, SE, SE, SE	28	T17S	R70W	Freemont	Cooper Mountain	Brushy Basin	5a, c	20–30 m interval above base; thin to thick ss interbedded thick bedded mudrock
25	Canon City-2, CO	C–N1/2, SW, NE, SE	28	T17S	R70W	Freemont	Cooper Mountain	Brushy Basin	4b; 5a; 8; 34a, b; 38b, c	35–45 m interval above base; in fine-grained heterolithic, inclined strata and interbedded ss–ms
26	Colorado National Monument (CNM)-1	SW, NW, SE, NW	30	T11S	R101W	Mesa	CNM	Tidwell/Salt Wash	36; 46	Artist Point trailhead; in thin bedded limy sandstone; sauropod tracks in contorted ss—ms interbeds
27	Colorado National Monument (CNM)-2	NE, SW, NE, NE	26	T11S	R101W	Mesa	CNM	Brushy Basin	38f	Riggs Hill, uppermost part of section; in thin to thick bedded fine-grained ss, with coarse interbeds
28	Fruita Paleontological Area (FPA), CO	NE, SW, NE, NW	24	T1N	R3W	Mesa	Mack	Brushy Basin	4a; 32; 34a, b; 38b, c	FPA–Dryosaur locality; in thin interbedded ss–ms; massive gray ms;

29	Rabbit Valley, CO	C, SW, NW, NE	20	T10S	R104W	Mesa	Bitter Creek Well	Brushy Basin	2; 4a; 34b	above clay change; in thin planar- to ripple-laminated ss interbedded with thin ms
30	Alameda Parkway, CO	SE, NE, SE, NW	26	T4S	R70W	Jefferson	Morrison	Brushy Basin equivalent	1; 2; 34b; 46	in uppermost red paleosol at Jr–K boundary; pedogenically modified mudrock with columnar morphology
31	Alvoca Lake–Campground, WY	NW, SW, NE, SE	35	T30N	R83W	Natrona	Alcova	Tidwell/Windy Hill	23; 27; 40; 44a; 47	from base of unit to below large eolian dune; in thin interbedded ss—ms
32	Alvova Lake–Grey Reef, WY	SE, NW, NE, SW	18	T30N	R82W	Natrona	Alcova	Tidwell/Windy Hill	?4a; 27; 31; 34a, b; 40	lower part of section; lenticular fine-grained, planar- to ripple-laminated ss in contorted and mottled mudrock
33	Termite Gulch (Fox Mountain), WY	SW, NW, SW, NE	14	T52N	R92W	Big Horn	Manderson NE	Brushy Basin equivalent	38b, c; 50; 51	lower to middle part; pedogenically modified interbedded ss—mudrock; egg shells in thick section of variagated mudrock
34	Baker Cabin, WY	NE, SW, SE, NW	25	T39N	R86W	Natrona	Three Buttes	Tidwell equivalent	14; 34c; 44a	lower part of section; in thin, fine-grained ss interbedded with ms; tree trunks buried by eolian ss
35	Sykes Mountain, WY	NW, SW	2	T57N	R95W	Big Horn	Sykes Spring	lower Morrison	2; 9; 34a, b; 40; 46	lower part of section; in ripple-laminated ss interbedded with ms
36	Greybull, WY	NW, SW	35	T53N	R93W	Big Horn	Greybull North	lower Morrison	17; 18; 21; 40; 46; 50	lower part of section; in thin bedded, ripple- and planar-laminated ss—ms units
37	Mother's Day Quarry, MT	NE, NW, SE, NW	19	T7S	R24E	Carbon	Wade	Windy Hill/ Tidwell equivalent	23; 27; 36b; 40; 46; 47	lower part of section; in interbedded ss—ms and thick bedded ss, below quarry interval
38	Gibson Reservoir, MT	NW, NW, NE, SW	4	T21N	R9W	Teton	Patricks Basin	Morrison	33a; 37b; 40	lower part of section; in thin bedded, ripple-laminated ss interbedded with ms
39	Belt, MT	W1/2, NE, SE,	26	T19N	R6E	Cascade	Belt	upper Morrison	1; 2; 34a, b	uppermost part; pedogenically modified fine-grained ss, slt, mudrock
40	Blue Mesa, CO	SW, SE, SE, NE	3	T48N	R18W	Montrose	Red Canyon	Tidwell–Salt Wash	1; 2; 5a–b; 8; 12; 33; 35; 38–47	various localities within the Tidwell, Salt Wash, and Brushy Basin Members in ss, slt, ms, and mr

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