

ICHTNOFOSSILS FROM GARDEN PARK PALEONTOLOGICAL AREA, COLORADO: IMPLICATIONS FOR PALEOECOLOGIC AND PALEOCLIMATIC RECONSTRUCTIONS OF THE UPPER JURASSIC

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Ichnofossils preserved in the Felch Quarry (#1) Sandstone in the upper part of the Upper Jurassic Morrison Formation represent the organism–substrate relationships of crayfish, bees, beetles, termites, and plants, as well as their relationship with each other. These ichnofossils document the first descriptions of these invertebrates in Jurassic continental deposits. Because of their sensitive nature to environmental conditions, they allow for more precise and detailed paleoecological reconstructions of Late Jurassic ecosystems in which some of the world's most famous dinosaurs lived.

Keywords: Ichnofossils; Arthropods; Paleocology

INTRODUCTION

Compared to studies of Jurassic marine ichnofossils and their environmental significance, studies of Jurassic continental ichnofossils have been nearly non-existent, except for dinosaur footprints and trackways. Very little is known of the invertebrate fauna except for the snails and clams (Evanoff and others, this volume). Although the Jurassic Morrison Formation is justifiably well-known for its dinosaur fauna, extremely little is known about

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its abundant and diverse ichnotaxa. Some of these little-known ichnofossils are currently under study in deposits near the Felch Quarry (#1) in the Upper Jurassic Morrison Formation in Garden Park Paleontological Area (GPPA), Canon City, Colorado. The unit in which the ichnofossils are preserved is within fluvial deposits equivalent with the Brushy Basin Member of the Morrison Formation (Fig. 1).

This report is a preliminary description of a few of the ichnofossils present in the fluvial deposits of the Morrison Formation at GPPA. The Morrison at Felch Quarry (#1) contains at least five distinct ichnotaxa reported here for the first time that represent the behavior of various invertebrates, plants, and their interactions with each other.

STRATIGRAPHIC SETTING

The Morrison Formation in the area of Garden Park is a 100 m thick succession of sandstone, mudstone, and thin limestones (Brady, 1969; Johnson, 1991). The traces occur in a yellow-brown, cross-bedded, medium to coarse-grained sandstone (herein informally termed the Felch Quarry Sandstone) approximately 50 m above the base of the Morrison Formation (Fig. 2). This interval is immediately below the level in the Morrison in which the clay mineralogy of the mudstones changes from non-smectitic clays below

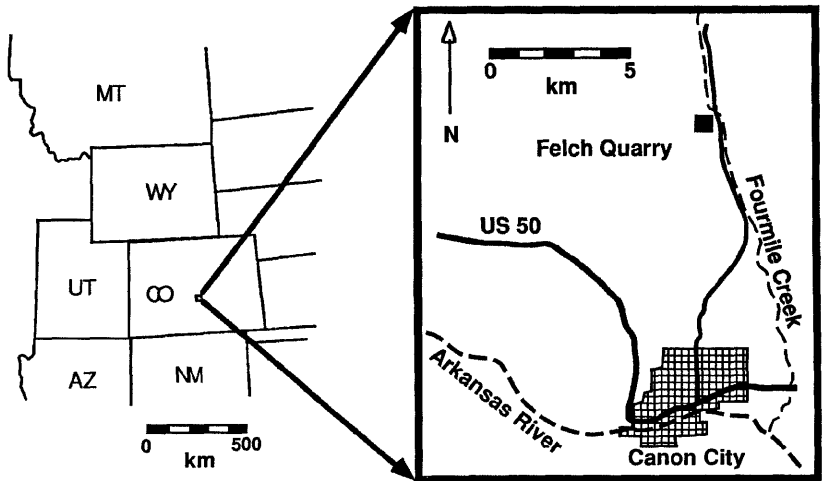


FIGURE 1 Locality map of the Felch Quarry in Garden Park Paleontological Area (GPPA) near Canon City, Colorado.

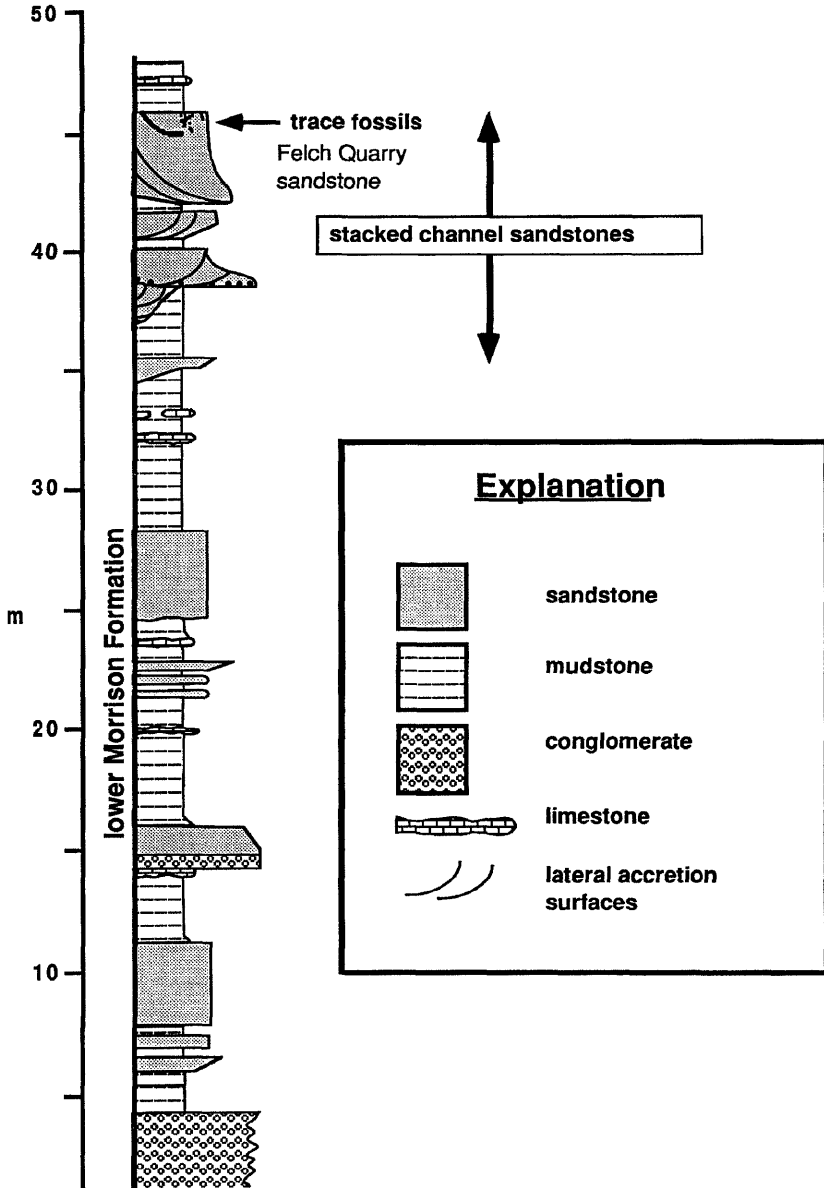


FIGURE 2 Stratigraphic section of the lower part of the Brushy Basin Member of the Upper Jurassic Morrison Formation at the Felch Quarry in the GPPA. The trace fossils studied occur in the uppermost sandstone (termed the Felch Quarry Sandstone) of the stacked channel sandstones in the quarry.

to smectitic clays above. The sandstone is the uppermost in a series of four vertically-stacked sand bodies (Fig. 2) (see also Evanoff and Carpenter, this volume). These stratigraphic units are equivalent to the lower Brushy Basin Member on the Colorado Plateau.

The Felch Quarry Sandstone is a lenticular body that ranges from 0 to 5 m thick. The sandstone fines upward from medium- to coarse-grained at the base to fine- to medium-grained at the top. The basal contact, with a greenish-gray to gray mudstone, is a sharp, erosional contact with up to 0.5 m of relief. There is a basal lag below the thicker portions of the sandstone that contain mudstone rip-up clasts, wood fragments, and pedogenic carbonate nodules in a coarse- to granular sandstone matrix. The upper contact, with a purple-gray mudstone, is also sharp. The sandstone is characterized by small- and medium-scale trough cross-beds, soft-sediment deformation structures, and large-scale lateral-accretion surfaces. Paleocurrent directions taken from trough beds indicate flow to the southwest. Lateral-accretion surfaces dip to the southeast indicating channel migration in that direction. Brady (1969), Dodson and others (1980), and Johnson (1991) all interpret the interval in which the Felch Quarry Sandstone occurs to have been deposited within a meandering stream and overbank floodplain environment. The four stacked sand bodies in the Felch Quarry area are probably part of the same channel belt, and record channel migration and floodplain aggradation (also E. Evanoff, personal communication, 1994).

Distinctive traces interpreted as Jurassic termites, bcc, beetle, and crayfish burrows and nests occur in the channel and levee sandstones and mudstones within Felch Quarry (#1). The ichnofossils of these invertebrates record their physiologically-constrained behavior with respect to the environmental setting in which they lived. Their ichnofossil tiering relationships also record the paleohydrologic and paleoecologic settings of the substrate, and will be discussed later.

ICHTHOLOGY

Five distinct types of Jurassic continental trace fossils are described here. The trace fossils at this locality are briefly described morphologically and are discussed with respect to the paleoecological and paleohydrologic significance of their architects. Identification of the burrow architect is of utmost importance in understanding the organism-substrate relationships portrayed by continental trace fossils. Both burrow architect and burrow are inherently related to each other and should not be viewed as separate

entities, especially when the burrow morphology can be attributed to an architect with relatively good confidence.

**Type 1. *Camborygma araioklados* Hasiotis and Mitchell, 1993
(Fig. 3(A) and (B))**

Diagnosis. The architectural morphology is moderately complex, with at least one entrance, a main shaft with a few corridors, and little chamber development. The surficial morphology exhibits a combination of transverse grooves, vertical scratches, knobby/hummocky textures, linings of mud and gravel, rounded striations, and body impressions. Differs from other quasi-vertical, tubular structures by the association of these architectural and surficial burrow morphologies; other types contain none of the elements above.

Description. The burrows are characterized by a main shaft 4 cm in diameter that curve at depth to become a lateral corridor continuing into the outcrop. The total burrow depth is 90 cm (Fig. 3(A)). The top of the main shaft contains two entrances, each 3–4 cm in diameter forming a Y-intersection with an obtuse angle between the entrance corridors. The surficial morphology exhibits cm-scale transverse ridges (scrape marks), and portions of the burrow walls contain knobby/hummocky textures, and cm-scale wall-packed material (mud-liners).

These burrows represent the burrowing behavior of crayfish. They suggest that crayfish lived in-land along the shores of point bars of the fluvial channel (for lithofacies see Stratigraphic Setting). The surficial morphology of the burrow preserves the results of the burrowing mechanism of the architect, reflecting typical crayfish behavior and functional morphology (Hasiotis and Mitchell, 1993; Hasiotis and others, 1993). The chelae (claws) produced the transverse scrape marks visible at the cm scale, while the pereopods (walking legs) produced the knobby, hummocky textures on the burrow wall. The mud-liners preserve burrow wall-linings produced by the crayfish that packed the walls during burrow excavation and maintenance. This behavior also limited the number of dumping-trips to the surface. These recurring trips to the surface would have created a behavioral pattern visible to potential predators. This behavior is also common in modern burrowing crayfish in North America (e.g., Hasiotis and Mitchell, 1993).

The architectural morphology and overall crayfish burrow depth reflected the maximum drop of the water table in that particular area during the Late Jurassic (e.g., Hasiotis and Mitchell, 1993; Hasiotis and Dubiel, 1993; 1994). Therefore, the vertical depth of the crayfish burrows marked

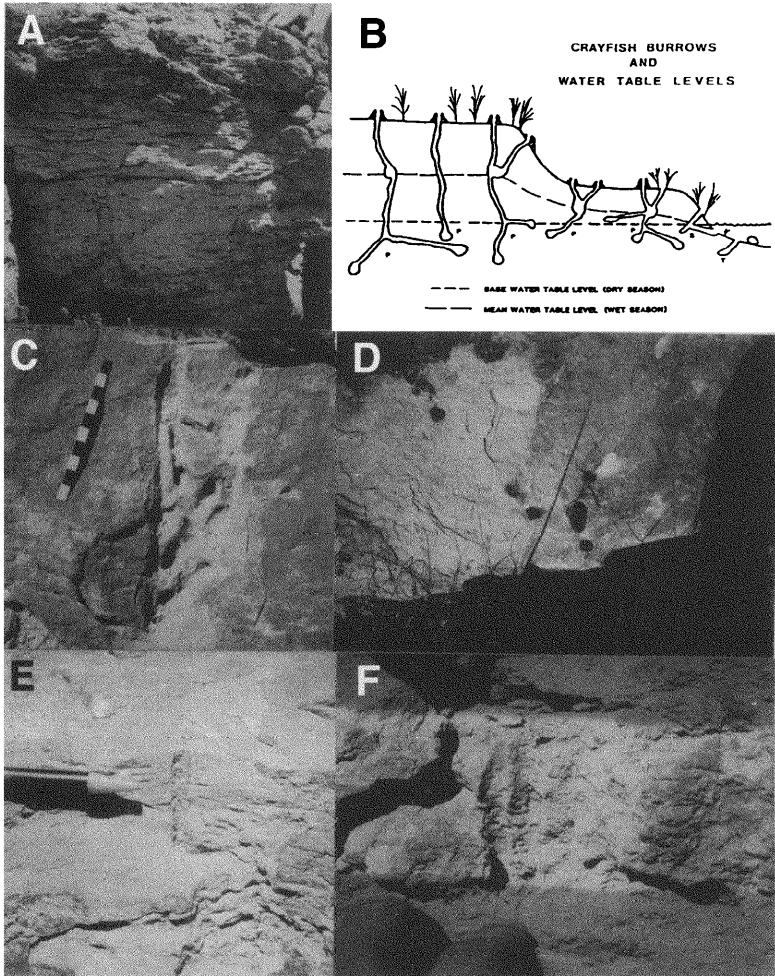


FIGURE 3 Ichnofossils from the Felch Quarry Sandstone. (A) Crayfish (*Astacidea*, *Cambaridae*?) burrows in point bar deposits. (B) Relationship between crayfish burrows and the water table. Modified from Hasiotis and Mitchell (1993). (C–D) Primitive social bee (*Hymenoptera*, *Apoidea*) cells that compose nests. (E–F) Vertical tube-shaped burrows constructed by coleopterans similar to Tiger Beetles (*Coleoptera*, *Cicindelidae*). Area with burrows highlighted in F.

the ground water table depth of nearly 80 cm, or the point at which the burrows changed from vertical to horizontal with respect to the bedding plane (Fig. 3(B)). The water table would have been located above this point, with the remaining 10 cm of the burrow below the water table.

Crayfish are excellent indicators of paleohydrologic and sedimentologic conditions and perturbations, and represent the largest invertebrate in the Jurassic food web. Crayfish burrows are unique interpretational tools because their behavior and burrow constructions, like many other infaunal and epifaunal invertebrates, record the moisture conditions conducive to their physiology (e.g., Hasiotis, and Bown, 1992). Crayfish played an important role as omnivores. They probably ate vegetation (primary consumer), pursued prey of equal or smaller size (secondary consumer), and dispatched of detritus and carcasses (decomposer). Their behavior was very similar to extant crayfish in similar settings (e.g., Saffrin and Barton, 1993; Momot, 1994; Hasiotis, unpublished data).

Type 2. *Celliforma spirifer* Brown, 1934 (Fig. 3(C) and (D))

Diagnosis. The architectural morphology of individual cells is flask-shaped; with or without caps that enclosed the cells. They occur as quasi-vertically separate or tightly clustered cells. Surficial morphology of the cells is smooth or slightly rough where linings have weathered away. Differ from *Teredolites* and other club-shaped cells, which are clavate, irregular, and are found in wood substrates that were afloat in seawater.

Description. Individual cells are flask-shaped, occur as either individual or tight clusters of cells ($n=10$), each about 0.5–0.7 cm in diameter and 1–2 cm in length (Fig. 3(C)). The cell walls are smooth and the opening of the cell is slightly constricted. The cells are associated with narrow shafts and corridors, approximately 0.7 cm in diameter that form U-shapes of 10–20 cm in depth (Fig. 3(D)).

These traces resemble brood cells constructed by hymenopterous insects most closely related to sweat bees, and are tentatively placed in the ichnotaxon *Celliforma spirifer*. Although the earliest known fossil bees (Michener and Grimaldi, 1988) and wasps (Darling and Sharky, 1990) are from the Late and Early Cretaceous, respectively, hymenopterous nests indicative of primitive bees have recently been described from Upper Triassic continental rocks of Arizona (Hasiotis and others, 1995; Hasiotis, 1997). Thus, the occurrence of bee brood cells in the Upper Jurassic Morrison Formation is realistic and significant. The overall morphology of the bee cells are similar to the Holocene stingless bee families Anthophoridae and Halictidae (sweat bees). These extant bees construct individual cells in groups varying in number depending on the ontogenetic stage of the nest during the reproductive season and the suitability of the nest locality (Sakagami and Michener, 1962; Michener, 1974).

The Morrison bee brood cells represent pre-social or primitive social behavior in hymenopterans that began at least in the Triassic, and before the evolution and radiation of angiosperms (Hasiotis and others, 1995; Hasiotis, 1997). As with many modern stingless and stinging bees, nest construction reflects variable amounts of task-sharing and specific labor tasks. In the Anthophoridae and Halictidae, for example, females may work with one another to construct a communal nest for which they take turns guarding the entrance and fetching provisions for each brood cell constructed (e.g., pre-social behavior). Offspring hatched from these nests may leave to establish new nests. Alternatively, they may stay and help construct, guard, and provision the new cells of the nest, while the founding female becomes the “queen” and lays all the eggs for the cells in the nest (e.g., social behavior) (Michener, 1974).

These traces are tentatively placed in the *calichnia* behavioral category for constructed structures that are modified from the substrate for breeding purposes. Calichnia is the sub-category of *aedificichnia* that represents ichnofossils constructed from materials extraneous to the substrate. These types of behavioral characteristics in continental trace-making organisms have yet to be synthesized into hierarchical relationships similar to the those of marine trace-making organisms.

Type 3. *Cylindricum antiquus* Linck, 1949 (Fig. 3(E) and (F))

Diagnosis. The architectural morphology is vertical, test tube-shaped, and at least three-times as long as wide. The burrows occur individually or in groups of 2 to 4. The surficial morphology exhibits various scratches or quasi-vertical striations. They differ from other vertical traces like *Celliforma*, which is flask-shaped with a tapered neck.

Description. The burrows occur in groups of 2 to 4, and sometimes alone (Fig. 3(E)). Each burrow is approximately 0.3–0.5 cm in diameter and 2–3 cm in length and nearly vertical in orientation (Fig. 3(F)). The burrow walls are relatively smooth with local diagonal scratches constituting the surficial morphology.

The architectural and surficial morphologies reflect burrow construction most similar to tiger beetles of the family Cicindelidae (e.g., Chamberlain, 1975) and are tentatively placed in the ichnotaxa *Cylindricum antiquus* Linck, 1949. All of these burrows appear to have originated at one particular paleosurface in the upper part of the point bar sandstone proximal to the shoreline. Today, tiger beetles and their larvae construct vertical, tube-shaped dwelling and shelter burrows in subaerial portions of the shorelines

of point bars, and in mid- and lateral-channel point-bars of meandering and braided fluvial channels (Chamberlain, 1975; Hasiotis and Bown, 1992). The architecture of the modern burrows reflect the lower level of the water within and along the channel such that the capillary fringe of the water table does not attain the surface. These beetles will also construct their burrows in areas away from open waters in substrates with moderate soil water (e.g., Milne and Milne, 1980). The surficial morphology of the ancient burrows preserves remnants the burrowing mechanism and general anatomy interpreted to represent cicindelid beetles. The beetles are relatively long and narrow, and their larvae are S-shaped with curved, gripping hooks on the fifth abdominal segment (Milne and Milne, 1980). The hooks may account for the diagonal scratches on the burrow walls.

Cicindelid beetle larvae and adults play an important role in the food chain of modern terrestrial and freshwater-aquatic ecosystems (e.g., Milne and Milne, 1980). They most likely had equal importance in the Jurassic Morrison ecosystem. Both modern adults and larvae are aggressive carnivores and feed on various insects smaller than themselves. They, in turn, serve as a food source for larger insects and arthropods, and other organisms. Thus, they would have served as intermediates on a food pyramid between small energy sources and larger consumers in the Jurassic (e.g., Aber and Melillo, 1991).

The vertical nature of the Morrison cicindelid burrows and their overall depth record the local paleohydrologic settings in that channel at that time in the Late Jurassic. The 3-cm-long burrows of the tiger beetle larvae preserve the relative lowering of water in the channel, and hence, lowering of the water table in that particular area adjacent to the channel. This condition would have been stable over a period of time long enough for larval growth and pupation to adult form. The Jurassic burrows could have also recorded the shelter-burrowing behavior of the adult beetles. Like modern beetles, the adults probably constructed vertical burrows to escape large temperature extremes that occurred during the day or night (e.g., Chamberlain, 1975; Milne and Milne, 1980).

Type 4. Rhizoliths (see Fig. 4(A–C))

Diagnosis. The architectural morphology is tubular and oriented vertically in the outcrop. The diameter and length of each structure is variable, but proportionate to each other. They typically exhibit ratios of 1–10 and 1–20 (width to length). They are quite distinct from vertical burrows because rhizoliths taper downward in size and branch downward.

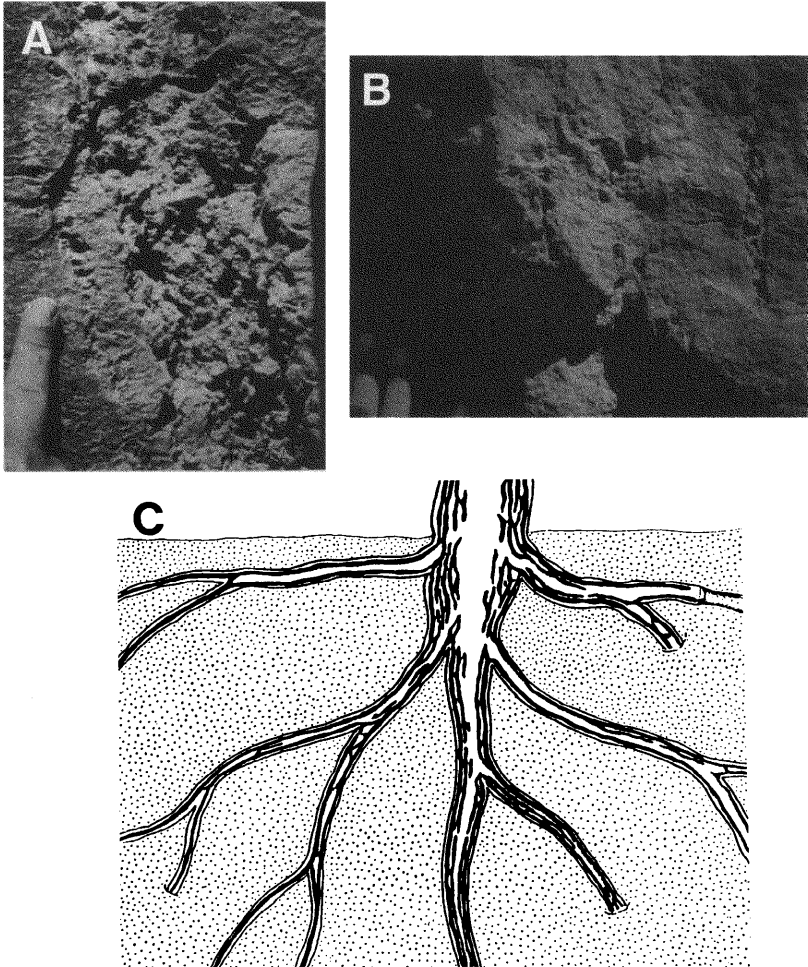


FIGURE 4 (A–B) Interconnected and anastomosed galleries of termite (Isoptera: Kalotermitidae?) nests constructed in dying or dead roots of woody and fibrous plants. (C) Reconstruction of rhizoliths with termite galleries excavated within the root system.

Description: These structures are 1–10 cm in diameter and spherical to elliptical in cross-section. They taper in size downwards and commonly exhibit downward and lateral branches of lesser diameter, which also taper along their lengths. The overall vertical length ranges from 30 to 40 cm and 50 to 60 cm. The tubular structures generally occur in groups with individuals spaced at variable distances from each other, but they were not observed closer than 10 cm to each other. Nearly all of these structures

terminate in a taper or as filamentous traces. The surfaces of these traces are well-defined, and they range from smooth to filamentous.

The architectural and surficial morphology confirm that these traces are roots of woody plants (rhizoliths) with primary and secondary branches (e.g., Hasiotis and Dubiel, 1994). Filamentous structures along the margins and at the ends of the rhizoliths represent root hairs that grew from the primary and secondary roots. In modern plants, these filamentous hairs are used to increase water and mineral absorption from the substrate. Associated with these rhizoliths, particularly within the rhizolith architecture, are traces of an extensive gallery system composed of anastomosing and interconnected tubes 0.2–0.5 cm in diameter. These structures within the rhizoliths are most similar to modern termite nests constructed in dead or dying root systems of woody plants. The interpretation of the termite nest ichnofossils will be discussed later.

The overall morphology and depth of the rhizoliths record the local paleohydrologic settings and seasonal fluctuations from the period of growth to death of the plant. The two groups of depths described above may represent periods of old and new growth of the same type of plant, or may represent two different types of moisture-tolerant plants. The shallower rhizoliths may have recorded the area of the paleo-soil profile with moisture levels similar to the upper vadose zone, whereas deeper roots would have recorded the depth of the intermediate vadose zone of the groundwater (e.g., Bown, 1982; Hasiotis and Bown, 1992).

The exact cause of death of these Jurassic woody plants, whether from old age or something else, can never be known for sure. However, the excellent preservation of the interior and exterior rhizolith morphology and the lack of organic debris suggests that the death of these woody plants was probably simultaneous, and due to several factors. The water table may have risen to the point of “drowning” the roots. This could be substantiated by the lack of sediment homogeneity and preservation of sedimentary structures that would have been destroyed by subaerial (e.g., above the water table) bioturbation (e.g., Hasiotis and Bown, 1992). The plants may also have died due to the combination of feeding effects of large herbivores and/or the infestation of insects. This scenario could be substantiated by the occurrence of herbivorous dinosaur bones in the quarry (e.g., Dodson and others, 1980 and references therein) and the occurrence of insect traces within the roots. Another likely scenario includes a lower water table that reached the point of the permanent wilting point of the plants, but this is not substantiated by any desiccation-related primary sedimentary structures (e.g., mud cracks).

Type 5. Termite Nests in Rhizoliths (Fig. 4(A–C))

Diagnosis. The composite architectural morphology of trace fossils is confined to the configuration of the rhizoliths in which they occur. They rarely extend further outward than the diameter of a particular rhizolith. The burrows of the composite structure exhibit variable sizes, but mostly mm-scale. They differ from other associated groups of burrows in that these termite galleries are interconnected to each other with variations of T- or Y-intersections and are part of the same structure.

Description. Within the primary and secondary branches of the rhizoliths are hundreds of horizontal and vertical, anastomosed and interconnected burrows. The burrow diameters range from 0.15 to 0.5 cm, but are predominantly 0.2–0.3 cm in diameter (Fig. 4(A–B)). Individual burrows can be traced from approximately 1.0 to 10 cm in length that either terminate or join other burrows (Fig. 4(B)). The burrows are filled mostly with sand and silt, and mud from the deposits above. The overall surficial morphology of the burrows range from smooth to highly textured and pustulose. However, it is often difficult to determine specific details of the surficial morphology due to the anastomosing nature of the burrows and the coarse texture of the matrix that contains these structures. Their architectural and surficial morphologies are the most unique yet identified in the Felch Quarry sandstone.

The anastomosing and interconnected morphology of the small-diameter burrows and the close relationship to the form of the whole burrow complex and rhizolith architecture suggests that these traces represent galleries of termite nests (Fig. 4(C)). These are the first reported occurrences of ichnofossil termite nests in Jurassic continental deposits and second report of nest ichnofossils of this antiquity, preceded only by ichnofossil nests from Triassic continental deposits in Petrified Forest National Park, Arizona (Hasiotis and Dubiel, 1995). The earliest known termite body fossils, on the other hand, are known from Lower Cretaceous rocks (Jarzembowski, 1981; Krishna, 1990). The Jurassic ichnofossil nests are most similar to nests of Holocene termites belonging to the families Porotermitidae, Kalotermitidae, Stolotermitidae, and Mastotermitidae, all of which attack and construct nests in either living, dead or dying, and dry or damp woody tissues (Krishna and Weesner, 1970). The nest architectures of these Holocene families include interconnected and anastomosing galleries of various diameters in the roots, stems, and branches of trees and shrubs. At this time in the study the Jurassic termite nests have not been designated to a specific family nor designated to an ichnotaxa.

These nest ichnofossils are not the nest systems of ants (Hymenoptera: Formicidae) for several reasons. Ants form similar gallery patterns in wood, but they are not as elaborate or highly constructed as those of termites (e.g., Krishna and Weesner, 1970). Ants typically will hollow-out the interior of vascular plants, but will seldom modify or construct elaborate burrow systems within them (e.g., Wheeler, 1925). Ant nests have been tentatively identified in the Brushy Basin Member of the Morrison Formation elsewhere on the Colorado Plateau (Hasiotis, unpublished data).

The antiquity of the Morrison nests is not surprising since the evolutionary radiation of the families mentioned above were thought to have occurred in the Triassic and Jurassic, hypothesized by vicariance biogeographic reconstructions (Boullion, 1970). This theory is further supported by the occurrence of hodotermitid or mastotermitid termite nests in the Late Triassic (Hasiotis and Dubiel, 1995). The morphology of the Morrison nests also preserves the results of eusocial behavior in termites and their niche diversification. The intricate nature of the nest within the rhizoliths implies that 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, 1974).

Based on the ichnofossil evidence and the association of modern termites and vascular plants, the paleoecologic interactions between the termites and the plants can be reconstructed. The architecture of ichnofossil termite nests reflects not only the substrate conditions necessary for nest construction, but also the amount of moisture required by the termite colony (e.g., Krishna and Weesner, 1970; Hasiotis and Bown, 1992) and the trophic relationship between insects, plants, and the environment (e.g., Hasiotis and Dubiel, 1994; Genise and Bown, 1994). The construction of the Jurassic nests within the roots suggests that the termites were eating and constructing galleries in the roots and wood simultaneously. Because the galleries completely fill the rhizoliths, the upper portions of the woody plant must have been intact during nest construction suggesting that destruction of the plants occurred near or after death. Also, the appropriate amount of moisture probably existed in the substrate similar to well drained soils with moisture contents equivalent to the upper vadose zone or the upper most part of the intermediate vadose zone, ranging from approximately 5% to 35% in soil moisture (e.g., Hasiotis and Bown, 1992). Thus, the termite ichnofossil nests are evidence of nutrient cycling between the producers (plants) and the decomposers (termites). These decomposers (termites)

probably also served as a food source for secondary consumers living in the substrate.

ICHNOFOSSIL TIERING RELATIONS

Tiering or stratification is defined as the vertical partitioning of an animal and plant community with respect to the physical, chemical, and biological parameters delineated by the environment (Odum, 1975; Aber and Melillo, 1991). In marine ichnology, this concept has been applied to endobenthic communities where individuals employ different mechanisms of sediment processing at distinct levels beneath the ocean floor to produce complex biogenic sedimentary features (e.g., Seilacher, 1978; Bromley, 1990). Infaunal organisms and their burrows in both modern and ancient terrestrial and freshwater ecosystems are distributed ecologically in tiers based on their physiology, trophic needs, and environmental settings (e.g., Hasiotis and Dubiel, 1994). Therefore, the trace fossils of infaunal organisms in the Morrison Formation at GPPA represent paleoecological tiers based on their original organism–substrate and organism–organism interactions.

The Morrison fluvial deposits contain multiple, stacked tiers each of which would reflect the paleohydrologic character of the substrate and the paleoecologic interactions of the organisms based on the assemblage of ichnofossils. Cross-cutting, co-occurring, and conterminous relationships between the crayfish, bee, tiger beetle, termite, and plant ichnofossils and the substrate characters (e.g., texture, sorting) demonstrate that these organisms concurrently occupied different levels of the substrate. Their overlapping distribution was controlled by the vertical and lateral variation soil moisture percent dictated by the local paleohydrologic regime.

The tiering relationships interpreted from the ichnofossils preserved in the Felch Quarry (#1) sandstone suggest that four paleoecological tiers existed after the deposition of the sandstone body. Since the nature of tiering relations in all types of terrestrial and freshwater deposits are not well understood because of the infancy of this type of study, the tiers in the Felch Quarry sandstone are informally numbered I–IV. The shallowest tier (I) was represented by the bee brood cells and possibly by the tiger beetle burrows, which occurred between a few centimeters to possible 20 cm below the paleosurface. Tier I most likely represented the area of the substrate that underwent the greatest fluctuation of wetting and drying caused by evapotranspiration. The next deepest tiers (II and III) are represented by the rhizoliths and termite nests of 30–40 cm and 50–60 cm in

depth below the paleosurface. These tiers are difficult to differentiate from one another, but the rhizolith depths suggests differences imparted by the paleo-soil moisture levels.

The presence of the termite nests within the rhizoliths suggests that either the termites were tolerant of increasing soil moisture, or that the soil moisture level was nearly similar to the levels above. Further study and identification of other ichnofossils will allow further differentiation of these tiers. The deepest tier (IV) is represented by the crayfish burrows, which recorded the paleo-water table depth of 80 cm or greater. These crayfish would have been adapted to living in groundwater that was depleted in oxygen due to the minimal contact of the water with the open atmospheric cycling (e.g., Hobbs, 1981; Hasiotis and Mitchell, 1993). Like their Holocene counterparts, the Jurassic crayfish were probably omnivorous and fed on arthropods, plants and roots, and detritus in and around the burrow. Because this habitat was proximal to the channel, it probably experienced seasonal fluctuations in paleo-water table and soil moisture levels due to the river's varying flow regime. This is evidenced by the depth and architecture of the crayfish burrows and also by the close proximity of tiers II–IV, recording a narrow moisture range between the upper vadose zone and the phreatic zone (water table). Analogous tiering relationships of proximal fluvial environments are seen in other Mesozoic and Cenozoic environments similar to the one preserved in the Felch Quarry (e.g., Chamberlain, 1975; Hasiotis and Bown, 1992; Hasiotis and Mitchell, 1993; Hasiotis and Dubiel, 1994).

The tiering relationship of the epifaunal and infaunal burrows in this fluvial sandstone deposit strongly suggest that the distribution of the burrowers was likely controlled in part by the annual and seasonal fluctuations of paleo-soil moisture and the depth and fluctuations of the paleo-water table. The depth and distribution of these organisms was also controlled by their relationships with their energy sources and the general function of the burrow with respect to the behavior of the organisms (Fig. 4). The Felch Quarry sandstone ichnofossils likely reflect four paleoecological tiers that occupied explicit 3-dimensional space. Tier I occupied the first 25–30 cm (paleosurface to 30 cm depth) with high fluctuations of moisture input and evapotranspiration. Tier II occupied depths approximately 30–35 cm (base of tier I to 60–65 cm) with more stable moisture contents and less moisture loss than from evapotranspiration than tier I. Tier III probably occupied a 30 cm zone (base of tier II to 90 cm deep) and suffered few fluctuations in soil moisture loss and gain. Tier IV occupied the subsurface defined by the phreatic zone (90 + cm

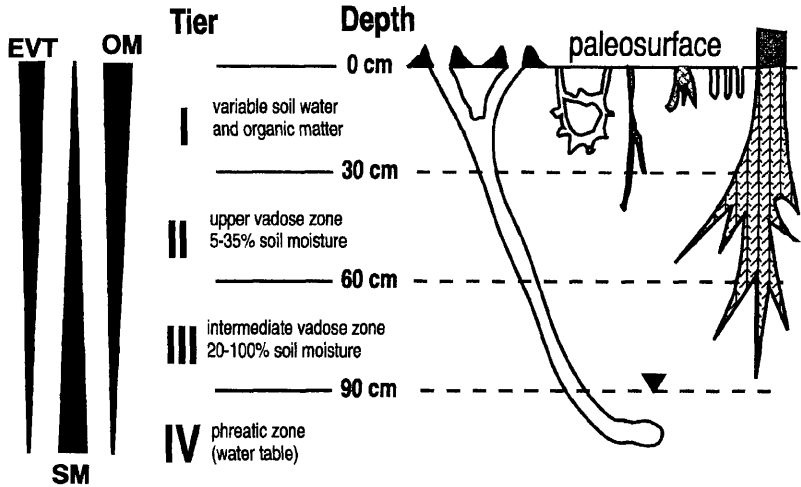


FIGURE 5 Schematic of tiering relationship between the burrowing organisms preserved in the Felch Quarry Sandstone and the hydrologic regime at the time of their emplacement during the Late Jurassic. From the top of a paleosol to the paleo-water table evapotranspiration (EVT) decreases, soil moisture (SM) increases, and organic matter (OM) decreases in content. Traces from left to right: crayfish burrow (to 90+ cm), bee nest (to 25 cm), termite nests in short rhizoliths (10–35 cm), beetle burrows (<5 cm), termite nests in large rhizoliths (to 70 cm).

deep) where organisms such as crayfish are adapted to living at or below the air/water interface with 100% soil moisture and relatively lower oxygen content than the atmosphere and open water bodies.

SIGNIFICANCE

Jurassic continental ichnofossils are important because they are *in situ* evidence of ancient life interacting with the environment and with each other, and therefore, represent interactions between producers, consumers, and decomposers. Large, woody plants and smaller shrubs (Tracheophyta: Gymnosperms) were probably the primary producers of the riparian setting, which converted raw materials and sun light into sugars, carbohydrates, cellulose, and other materials. Primitively-social bees (Hymenoptera: Apoidea) were likely consumers (herbivores) that collected pollen and resin from the trees and shrubs in the riparian setting. Eusocial termites (Isoptera: Kalotermitidae?) probably acted as decomposers of dying and dead woody and fibrous plants. To a lesser degree, the termites may have

also utilized any fungus growing on these items. Tiger beetle adults and larvae (Coleoptera: Cicindelidae) probably acted as carnivores (2nd or 3rd order consumers) that could have fed upon the eggs, larvae, pupae, and adults of other insects. Crayfish (Astacidea: Cambaridae?) were macro-invertebrates that probably acted as herbivores, carnivores, and scavengers (omnivorous) of plants, insects, and carrion in their immediate environments. The trace fossils of all these organisms provide evidence that the lower portions of the Late Jurassic food web was preserved in the geologic record. They played an active part in supporting the higher vertebrates like those dinosaurs found in the Felch Quarry Sandstone.

The inferred paleobiologic characters of these invertebrate and plant trace fossils contributes new information for the reconstruction of local paleoecological settings in the Morrison. The amounts and fluctuations of the paleo-soil moisture and the position of paleo-water table can be inferred from the burrow and nest morphology and the identification of the trace-maker within a deposit. The effectiveness of the interpretation of a trace fossil's paleohydrologic signature is multiplied through the comparison of these ancient burrows and their inferred trace-makers to the behavior of burrowing homologs and analogs in similar environments in the Holocene.

Regional Morrison paleoecosystem reconstructions can now incorporate interpretations of the relative spatial and temporal levels and amounts of paleo-soil moisture and paleo-water table. This type of information can be used to facilitate paleoclimatic interpretations for various paleogeographic regions during the Late Jurassic. As with Holocene soil water profiles and hydrologic settings, paleo-groundwater profiles were regulated by seasonal and annual precipitation and temperature, which directly influenced the distribution and tiering of burrowing organisms. These tiering relationships in turn are controlled by regional and global climatic cycles that vary with respect to orographic effects, latitude, and the proximity to coastal areas. Thus, identifying and understanding continental ichnofossils and their architects, and their tiering relations can lead to greatly enhanced paleoecologic and paleoclimatic reconstructions in the future.

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