

CONTINENTAL TRACE FOSSILS AS THE KEY TO UNDERSTANDING JURASSIC TERRESTRIAL AND FRESHWATER ECOSYSTEMS

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Jurassic paleoenvironmental and paleoecological reconstructions of continental depositional systems typically rely on vertebrate and plant fossils that are often deposited or reworked out of context of their original habitats (e.g., bone beds, plant hash, etc.). Such evidence alone creates unreliable reconstruction scenarios of ancient ecosystems. Trace fossils, however, preserve *in situ* evidence of organism–substrate relationships defined by the physiological characters of the organism and the physicochemical characters of the environment. Trace fossils, ichnocoenoses (communities of traces), and their tiering relationships more clearly define terrestrial and freshwater ecosystems of the Jurassic, as well as other Mesozoic continental depositional systems. Paleoclimatic effects on these ancient systems can be measured by integrating paleobiologic and paleohydrologic interpretations of the trace fossils, as well as from vertebrate, invertebrate, and plant fossils to produce more holistic reconstructions of Jurassic ecosystems.

Keywords: Ichnofossils; Ichnocoenoses; Terrestrial; Freshwater ecosystems

INTRODUCTION

In order to sufficiently understand the paleoecological settings of any continental or marine deposit, a great deal of information must be extracted from a combination of vertebrate, invertebrate, and plant body and trace fossils. For example, vertebrate fossils and invertebrate ichnofaunas have been well-documented in Jurassic marginal-marine and marine deposits, and are often used for neritic and benthic community and ecosystem reconstructions and their interactions (e.g., Crimes and Harper, 1970; Fursich, 1974; Heinberg and Birkelund, 1984; Pienkowski, 1985, and

references therein). In comparison, the Upper Jurassic Morrison Formation and other Jurassic continental deposits are well known for their magnificent dinosaur fossils (e.g., Weishampel and others, 1990; Carpenter and others, 1994), but almost nothing is known of the ichnofauna, except for dinosaur footprints (e.g., Gillette and Lockley, 1989; Lockley and Hunt, 1994).

Documentation of trace fossils in continental deposits is important because they represent the activity of different types of invertebrates, vertebrates, and plants, and record the interactions of each community element with each other. Since trace fossils are almost invariably found *in situ*, understanding their presence and distribution allows for more refined and accurate paleoecological interpretations (Hasiotis and Bown, 1992). Invertebrate traces are the most useful environmental and ecological indicators because they are physiologically-constrained to specific moisture and substrate conditions, and salinity ranges. These constraints are reflected in their behavioral relationship with the substrate (e.g., tiering) and with other organisms (e.g., associations – food web) (Hasiotis and Bown, 1992; Hasiotis and Dubiel, 1994). For example, the interactions between plants and invertebrates most often are preserved as tissue damage to plants (e.g., Scott, 1992) both above and below ground, allowing reconstruction of plant/animal/substrate ecological associations. On the other hand, large vertebrates and their traces, such as dinosaur footprints and trackways, are relatively useless as environmental and ecological indicators. The physiological make-up of large terrestrial vertebrates allowed them to interact with numerous moisture and substrate conditions, and a wide range of salinity. Also, dinosaur ecology is not well understood (Weishampel and others, 1990; T.M. Bown, personal communication, 1995). Thus, terrestrial life-styles of the Jurassic dinosaurs enabled them to cross areas characterized by different environmental conditions and ecological settings (e.g., Lockley and Hunt, 1994; Lockley and others, 1994). This scenario would be analogous to the distribution of humans over nearly every available environment on the planet today (e.g., deserts, polar regions, mountains, shallow and deep oceans, etc.), thus, rendering us (e.g., especially our footprints) useless as ecologically-sensitive indicators. Ichnofacies based on footprints would be disastrous! For example, our footprints occur nearly everywhere on earth and also on the Moon's surface, which is under extremely different atmospheric and gravitational forces, but would be part of a *Homo sapien* ichnofacies!

ICHNOFOSSIL APPLICATIONS TO JURASSIC ROCKS

Continental invertebrate, vertebrate, and plant ichnofossils have the potential to contribute to existing understanding of a stratigraphic unit's depositional history, its biologic composition and interaction with the environment, and its paleoecosystem reconstructions. The following categories and examples outline the utility of continental ichnofossils described from other Mesozoic and Cenozoic deposits. They have been used to more fully reconstruct the biological and ecological character of continental deposits like the Upper Jurassic Morrison Formation, about which we know very little except for its vertebrate fauna and ichnofauna. The identification of trace fossils in the Morrison Formation would greatly enhance existing knowledge of Jurassic invertebrates, vertebrates, rooting strategies of plants, and their paleohydrologic and paleoecologic interactions.

Proxies for Fossil Occurrences

Trace fossils make excellent proxies for documenting the presence of organisms in continental deposits (e.g., Hasiotis and Bown, 1992; Hasiotis and Mitchell, 1993; Hasiotis and Dubiel, 1995a,b). Body fossils of terrestrial and freshwater organisms are not often preserved in continental (as well as marine) depositional systems because of poorly-skeletonized bodies, oxidizing conditions, consumption of the remains by other organisms, and reworking of upper layers of sediments where remains may be buried (Hasiotis and Bown, 1992). When they are preserved, body fossils are often reworked, removing them from their original environmental context.

The geologic ranges of many higher taxa have recently been documented and extended by the identification of their trace fossils in various depositional environments. Crayfish body and trace fossils were described from Triassic fluvial deposits of the Colorado Plateau (Hasiotis and Mitchell, 1993; Hasiotis and others, 1994), extending their fossil record roughly 170 million years in North America and 100 millions in Eurasia. Termites and their eusocial behavior were documented in Triassic fluvial overbank deposits through description of their nests and galleries in alluvial paleosols, extending their fossil occurrence nearly 120 million years (Hasiotis and Dubiel, 1995). Primitive-social bees and gregarious wasps are currently being described from numerous paleosols and wood substrates from the Triassic Chinle Formation, extending their fossil occurrence nearly

140 million years. Their identification is based on the distinct flask-shaped, nest-forming cells and the spindle-shaped cocoons (Hasiotis and others, 1995; Hasiotis, 1997). Many other insects, like coleopterans and tricotterans, as well as plants, have been identified in other Triassic continental deposits by the presence of their traces (Hasiotis and Dubiel, 1993a,b; 1994; 1995a,b). These organisms were once thought to have originated in the late Mesozoic or early Cenozoic, but their trace fossil occurrences in Triassic deposits shows they should almost certainly be found in Jurassic deposits as well.

Moisture/Water Table Indicators

The morphology and tiering of continental trace fossils have been shown to reflect the original hydrologic characteristics of the substrate, as well as burrowing efficiencies, and term-usage of constructed habitations (e.g., Chamberlain, 1975; Ratcliffe and Fagerstrom, 1980; Hasiotis and Bown, 1992; Hasiotis and Mitchell, 1993; Hasiotis and others, 1993; Hasiotis and Dubiel, 1993a,b; 1994; 1995a). The morphology of a burrow often preserves the remnants of the burrowing mechanism, in many cases permitting the identification of the trace-maker (e.g., Hasiotis and Mitchell, 1993; Hasiotis and others, 1993). Once a trace-maker is identified, its physiological interaction with the substrate can be inferred not only from the burrow morphology and substrate, but also from architect/burrow comparisons to modern analogs and homologs to better understand the structure and function of the burrow (Hasiotis and Mitchell, 1993; Hasiotis and others, 1993). Where numerous burrows occur together throughout a deposit, vertical and lateral tiering relationships can be studied with respect to the environment represented by the deposit (Hasiotis and Bown, 1992; Hasiotis and Dubiel, 1994).

The tiering relationship of continental traces reflects not only spatial and temporal variations in soil moisture and water table fluctuations, but also the physiological and ecological interactions between organisms (e.g., competition, food chain interaction, etc.) and the organisms and the substrate (Hasiotis and Dubiel, 1994). For example, crayfish are ecologically dispersed by their interaction with the water table and its expression with the geomorphic surface. They can be found in lentic, lotic, and terrestrial environments where their burrow architecture and length reflects the depth and fluctuations of the water table (Hasiotis and Mitchell, 1993; Hasiotis and Dubiel, 1993a; Hasiotis and others, this volume). Termite nests, on the other hand, reflect well-drained paleosols of various stages of maturity

with specific amounts of soil moisture, delineating the A and upper B horizons (e.g., Hasiotis and Bown, 1992; Hasiotis and Dubiel, 1995). Invariably, the soil moisture and water table of a region recorded by ichnofossils are controlled by seasonal and annual precipitation and temperature, and thus, trace fossils provide insights in paleoclimatic settings.

Environmental Gradients

The occurrence and distribution of trace fossils within and between fluvial, lacustrine, and eolian depositional environments in continental and marginal-marine settings allows reconstruction of specific environmental gradients. These gradients act directly upon the physiological characteristics of the trace-making organisms, particularly infaunal invertebrates (Hasiotis and Bown, 1992). These organisms and their traces can be used to infer the proximal and distal impacts of the depositional energy (e.g., degree of scouring, flooding, etc.), sedimentation rates, salinity, water table, soil moisture, oxygenation, substrate texture, paleosol maturity, photic zone, circulation patterns, and food web interactions (Hasiotis, 1994). Environmental gradients are unique to specific depositional systems, as well as the organisms that inhabit those environments. All of these ecological settings (organisms and environments) are controlled by local variations in temperature, precipitation, and sedimentation rate, which are in turn controlled by regional climate and tectonics (Hasiotis and Dubiel, 1994). Rocks are inter-connected by definition, but these inherent principles are often not applied to the reconstruction of paleoecosystems or the interpretation of ichnological enigmas (e.g., Hasiotis and Bown, 1992).

Plant/Insect Interactions

Traces in wood, leaves, and roots best record the ecological interactions between plants and insects via stem and leaf galls, leaf feeding, leaf and blotch mining, bark and wood galleries, spore and seed feeding, and various penetrations in roots (e.g., Scott, 1992; Hasiotis and others, 1995). These traces are produced by the activities of insects for temporary and permanent shelter, feeding, and reproduction. There are a wide variety of insect-plant interactions involving numerous insect groups that are commonly specific to family taxonomic levels. Many examples of these interactions have been said to be rare and less frequent in the past (e.g., Scott, 1992), but this may be an artifact of non-recognition in many fossil examples. For example, studies of Triassic plant fossils in the Petrified Forest

National Park, Arizona, have revealed abundant amounts of tissue damage to plants by scolytid and buprestid beetles, hodotermitid and stotermitid termites, and other beetles and insects yet to be taxonomically determined (Hasiotis and others, 1994; Hasiotis, unpublished data; S. Ash, personal communication, 1994; Ash and Hasiotis, 1996).

These and other plant-substrate (Hasiotis and Dubiel, 1994; Wing and others, 1994) and plant-insect interactions yield much paleoecological information not found in body fossils. The soil moisture content, water table depth, and water salinity also play a role in controlling not only root depths and plant type, but nature of predation on various plant tissues as well. For example, ichnofossils of flank-buttress trees in late Eocene coastal-plain deposits suggest either a high water table or saline groundwater, and poor substrate conditions for anchoring roots (Wing and others, 1995).

NEW MORRISON FORMATION TRACES

Trace fossils recently described from the Morrison have already been used to extract paleohydrologic and paleoecologic information from specific localities previously unavailable (papers by Hasiotis and others, this volume). For example, the presence of crayfish, termites, bees, beetles, caddisflies, and low-lying plants in the Morrison is based on their trace fossils rather than body fossils. Their burrows have been used to estimate burrowing efficiencies, short-term vs. long-term habitation, and ecologic interactions with each other. Their burrow architecture and tiering relationships have been used to estimate soil moisture levels, water table depths, and their relative fluctuations with respect to the paleoclimatic setting.

Reconnaissance expeditions to assess the Morrison's trace fossil potential in other regions of the Colorado Plateau have already lead to the discovery of more than 50 types of traces (Hasiotis, unpublished data; Hasiotis and others, unpublished data). Many of these new trace fossils record the presence and activity of different types of crayfish (Decapoda), snails (Gastropoda), isopods (Isopoda), termites (Isoptera), bees and ants (Hymenoptera), beetles (Coleoptera), soil bugs (Hemiptera), caddisflies (Tricoptera), chironomids (Diptera), and stoneflies (Ephemeroptera), all of which require further study. Undoubtedly, these and other studies will illustrate the immense ichnodiversity that has gone undetected in the Morrison and in other Jurassic continental rocks since the initiation of their study.

SUMMARY

The organism–substrate relationships of trace fossils can be inferred from Jurassic continental traces, thus, allowing ichnological research to closely approximate various soil moisture and water table levels at specific locations during specific periods in the Jurassic for the first time. These trace fossils can also be used to reconstruct the lower and often the most important portions of food webs that once supported the existence of larger terrestrial and aquatic reptiles, amphibians, and fishes.

The presence of particular organisms in continental deposits of Late Triassic age suggests that their traces should also be found in fluvial and lacustrine deposits of the Upper Jurassic Morrison Formation, as well as in other Jurassic and younger continental deposits. Because Jurassic deposits are younger, despite the end-Triassic mass extinctions, many groups of vertebrates and invertebrates further diversified and the potential for new trace-makers and traces may be even greater in Jurassic deposits.

In summary, continental ichnology is a dynamic interpretational tool for understanding terrestrial and freshwater ecosystems through integration of paleobiologic, paleoecologic, sedimentologic, and paleopedologic analyses of trace and body fossils. Suites of trace fossils and body fossils can be used to differentiate: (1) soil moisture and water table regimes, (2) salinity gradients, (3) depositional energies and sedimentation rates, (4) habitat energy flow, (5) other physico-chemical gradients, (6) overall environmental stability, (7) major paleoecosystem types, and (8) paleoclimatic changes and trends.

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