LIFE IN AN ANCIENT SEA OF SAND: TRACE FOSSIL ASSOCIATIONS AND THEIR PALEOECOLOGICAL IMPLICATIONS IN THE UPPER TRIASSIC/LOWER JURASSIC NUGGET SANDSTONE, NORTHEASTERN UTAH

by

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STATEMENT OF THESIS APPROVAL

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ABSTRACT

The Nugget Sandstone is a Triassic/Jurassic eolianite in western North America. It represents a portion of one of the largest dune environments to have ever existed in the geologic record. Paleontological interest in the Nugget Sandstone has grown in recent years upon numerous discoveries of vertebrate and invertebrate body fossils, trace fossils, and plant fossils. Invertebrate trace fossils in the Nugget Sandstone near Vernal, Utah, are identified, described and highlighted in this study, with an overview of past fossil discoveries in the Nugget and Navajo sandstones. Invertebrate trace fossils in this area include *Entradichnus meniscus*, *Entradichnus* isp., *Planolites beverleyensis*, *Taenidium* isp. “A,” *Taenidium* isp. “B,” *Skolithos* and *Planolites* isp., ‘burrow clusters’, ‘large oblique burrows’, ‘flared burrows’, *Paleohelcura,* and *Octopodichnus.* Arthropods, such as insects and arachnids, are considered possible trace makers. Vertebrate trace fossils of this same area include *Brasilichnium, Grallator*, *Eubrontes*, *Brachychirotherium, Pseudotetrasauropus, Tetrasauropus,* and *Otozoum*. Possible sphenophytes, cycads, and algal build-ups comprise the evidence for primary production in the ecosystem.

Sediment moisture must have played a key role in the production and preservation of all trace fossils in the Nugget Sandstone. Because of this, these trace fossils indicate that moisture was important for supporting such complex ecosystems, and that extended wet climatic intervals must have persisted intermittently between arid intervals. With fossil

evidence for primary production, herbivorous insects, and carnivorous arachnids provided in this thesis, as well as indirect evidence for environmental moisture content during deposition of the Nugget Sandstone, a more complete picture of the paleoecology of this ancient sea of sand can be constructed.

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CHAPTER 1

INTRODUCTION

The Triassic/Jurassic Nugget Sandstone, along with the correlative Glen Canyon Group (Wingate, Kayenta, and Navajo Sandstones) and Aztec Sandstone, represents one of the largest eolian environments to have ever existed. Paleontological studies of this unit in the literature are sparse, despite the richness and abundance of fossils (discussed in this thesis) in what must have been, at least intermittently, a surprisingly tolerable environment. In addition to the economic significance of the Nugget Sandstone as a hydrocarbon reservoir (Picard, 1977a), paleoenvironmental and paleoclimatic interest in the Nugget and Navajo sandstones has grown in recent years. Most of these studies, however, examine only the Navajo Sandstone of southern Utah, with little attention to invertebrate trace fossils. This study discusses the occurrences and diversity of trace fossils and their possible producers in the Nugget Sandstone, and explores their role in aiding interpretations of the paleoenvironment and paleoclimate of the Late Triassic/Early Jurassic in northeastern Utah.

1.1 Geologic Setting of the Nugget Sandstone

1.1.1 Tectonic Setting

The famous Colorado Plateau eolian deposits, including the Triassic/Jurassic Nugget Sandstone along with the Jurassic Aztec Sandstone and parts of the Glen Canyon Group (Wingate Sandstone/Moenave Formation, Kayenta Formation, and Navajo Sandstone), represent the remains of an expansive erg larger in scale than the Sahara Desert today (Kocurek and Dott, 1983; Milligan, 2012). These Late Triassic/Early Jurassic deposits are exposed in eight states – Idaho, Wyoming, Utah, Colorado, Nevada, California, Arizona and New Mexico – with a total area of about 370,000 km^2 (230,000 mi^2), and an estimated coverage of 1,370,000 km^2 (850,000 mi^2) during deposition (Kocurek and Dott, 1983; Milligan, 2012; Figure 1).

When the early Mesozoic American continent was pushed over a portion of the East Pacific Rise, a subduction zone and corresponding Andean-type volcanic arc were born in the western United States (Marzolf, 1986). Though still debated (Rowe et al., 2007), current paleolatitude estimates of the Colorado Plateau during the Late Triassic/Early Jurassic are generally accepted to be somewhere between 20° and 30° north of the equator (Kent and Irving, 2010), placing it roughly near the current global 30° high pressure zone of desert formation. The Nugget dune field of northeastern Utah and western Wyoming was deposited in a continental retro-arc foreland basin east of this volcanic arc in an increasingly arid climatic regime following a wet, fluvial and lacustrine environment as represented within the Triassic Chinle Formation below. This gradual transition to the arid climate of the latest Triassic may have been caused either by a northern tectonic migration away from the paleoequatorial region, and/or the termination of monsoonal conditions due to the breakup of Pangea (Dubiel, 1994; Kent and Tauxe, 2005). However initiated, the arid climate and northerly winds of northeastern Utah produced an extensive area of large sand dunes preserved as tall sets of sweeping cross-beds (up to 30 ft.) of fine- to medium-grained quartz sandstone interrupted only by thinner intervals that indicate relatively humid conditions. Thin layers of horizontal, laterally continuous sand or carbonate beds signify these wetter climatic periods between the characteristic eolian crossbeds, and they are increasingly less abundant toward the top of the formation. In northeastern Utah, the Nugget Sandstone is exposed near the city of Vernal in northeastern Utah, due to Laramide orogeny uplift of the east-west trending Uinta Mountains, and subsequent exhumation by river drainage.

1.1.2 Nomenclature of the Nugget Sandstone

The nomenclature of the eolian unit in northeastern Utah has changed through the years and remains somewhat controversial, although recent publications favor the term Nugget Sandstone over the other previously used terms, Glen Canyon Sandstone or Navajo Sandstone (Chambers et al., 2011; Chure et al., in press; Doelger, 1987; Engelmann et al., 2012; Jensen, 2005; Lockley et al., 2011; Peterson and Schenk, 1992; Sprinkel et al., 2005; Sprinkel et al., 2011). The Late Triassic/Early Jurassic eolian unit in northeastern Utah has been correlated with the Nugget Sandstone type locality in southwestern Wyoming (Veatch, 1907) by means of lithologic similarities and systematic interpretation of well logs (Sprinkel et al., 2011). As employed in this study, the Nugget Sandstone is currently defined as “strata that lie between the Ankareh-Chinle formations and Jurassic formations where the Kayenta Formation is not recognized” (Sprinkel et al., 2011). The term Glen Canyon Sandstone has been discontinued for the Late Triassic/Early Jurassic eolian units in the regions of northeastern Utah and northwestern Colorado, since they are situated stratigraphically between the Late Triassic Chinle Formation and the Early Jurassic Carmel Formation (Gregson and Chure, 2000; Sprinkel et al., 2011; Figure 2), and hence the term Nugget Sandstone is used herein.

According to Sprinkel et al. (2011), the Nugget Sandstone of the Uinta Basin correlates with the entire Glen Canyon Group of the Colorado Plateau, which includes the Wingate Sandstone/Moenave Formation, Kayenta Formation, and Navajo Sandstone, as was first suggested by Poole and Stewart (1964). Sprinkel et al. (2011) suggest that the Kayenta Formation either pinches out or transitions from fluvial to eolian beneath the southern Uinta Basin, where well logs indicate only the Nugget Sandstone between the Triassic Chinle Formation and the Jurassic Carmel Formations (Figure 2). It has commonly been noted that the Nugget Sandstone is the northern equivalent of the Navajo Sandstone in southern Utah. Because of this, the Nugget Sandstone is frequently compared to the Navajo Sandstone throughout this thesis. Although the precise relationship between these two formations remains controversial, they are at least clearly similar which is a sufficient basis for comparison between to two. However, it is important to emphasize that the correlation of Sprinkel et al. (2011) and the conformable nature of the Nugget upon the Chinle indicate that at least the lower third of the Nugget is laterally equivalent to the Wingate Sandstone, which is significantly older than the Navajo Sandstone.

1.1.3 Age of the Nugget Sandstone

The age of the Nugget Sandstone is often assigned as Triassic/Jurassic, because it is situated between the Triassic Chinle Formation and the Middle Jurassic Carmel Formation. Sprinkel et al. (2011) argue for a Triassic age in at least the lower portion of the Nugget Sandstone based on *Brachychirotherium* trackways (Lockley et al., 1992a) near the base of the formation. However, while the presence of trackways thought to have been produced by Late Triassic aetosaurs (Lucas and Heckert, 2011) supports a Late Triassic age, using these trackways as stand-alone evidence for a Late Triassic age is inconclusive. Recent discoveries of drepanosaurs, early archosauromorphs elsewhere known only from Middle to Late Triassic deposits, from the Nugget Sandstone in northeastern Utah is more conclusive evidence for a Late Triassic age of at least the lower portion of the Nugget Sandstone (Engelmann et al., 2012). Additional support for a Triassic age for the lower Nugget Sandstone includes a transitional contact between the Chinle Formation and basal Nugget Sandstone and the absence of a regional Triassic-Jurassic unconformity, leaving the Triassic-Jurassic boundary likely within the Nugget Sandstone.

1.1.4 Sedimentology and Stratigraphy of the Nugget Sandstone

The Nugget Sandstone is one of the best exposed formations in the Dinosaur National Monument area, where it is a light-colored, often bleached, prominent ridge former varying in thickness from about 180-200m (Gregson and Chure, 2000). Petrologic characteristics of the Nugget Sandstone in this area vary, but the formation is described as very fine- to medium-grained, moderately well-sorted, subangular to round, subarkose to quartz arenite (Doelger, 1987; Picard, 1977a). The Nugget Sandstone is dominated by large-scale, high-angle, trough-cross bedded sandstone, although flat, finer-grained, thin, wavy or irregular beds are not uncommon, and are interpreted as interdune deposits (Doelger, 1987).

The Nugget Sandstone in northeastern Utah previously was split into two informal members: a lower Bell Springs Member and an unnamed upper member. The Bell Springs Member was named for a sequence of sandstones, siltstones and shales in southern Wyoming (Pipiringos, 1968), and was correlated with previous workers' interpretations of the Upper Member of the Chinle Formation in northeastern Utah (Kinney, 1955; Poole and Stewart, 1964). Usage of the term Bell Springs Member in northeastern Utah was proposed by Jensen (2005) based on the interpretations of High et al. (1969), although the distinction of the proposed contacts between the Chinle Formation and the lower Bell Springs Member, and the upper Bell Springs Member and the unnamed Upper Member of the Nugget Sandstone is unclear and has not been generally accepted. The confusion over contact placement between the Chinle Formation and Nugget Sandstone can be explained by the transitional contact between the two formations.

The interbedded fluvial and lacustrine siltstones and mudstones of the upper Chinle Formation transition into thin-bedded sandstones, which further transitions into the eolian cross-bedded upper portion of Nugget Sandstone. This succession indicates a general drying trend toward the upper Nugget Sandstone. High and Picard (1975) identified this trend in northeastern Utah by distinguishing sedimentary cycles of red mudstones, siltstones and sandstones that formed during wet-dry climate fluctuations culminating in the domination of eolian dune deposition in the upper portion of the Nugget Sandstone. The migration rate of the cross-bedded dunes in the Navajo are estimated at 0.5 to 3 m/yr, so a similar migration rate is assumed for Nugget dunes (Eisenberg, 2003; Hummel and Kocurek, 1984). The Middle Jurassic Carmel Formation, composed of dark-red shallow-marine shales, siltstones and mudstones, sits unconformably above the Nugget Sandstone at the J-1 unconformity (Pipiringos and O'Sullivan, 1978) in this area.

1.2 Previous Work

1.2.1 Paleontology of the Nugget and Navajo Sandstones

The depositional environments represented by the Nugget Sandstone and its proposed southern eolian equivalents, the Navajo and Wingate sandstones, are often thought of as harsh, arid and lifeless, and until recently these formations have received little paleontological attention. However, over many years of fossil discovery (many of which incidentally resulted incidentally from nonpaleontological research and exploration) a significant diversity of fossil occurrences sheds light on the richness of species that once persisted. Still, the Wingate Sandstone provides few glimpses into its paleontological history, including only *Entradichnus*-like traces and other unnamed invertebrate burrows, and *Grallator*, *Eubrontes*, and other unnamed trackways (Clemmensen and Blakey, 1989; Dubiel et al., 1989; Hamblin and Foster, 2000; Hunt et al., 1953; Lockley et al., 1998; Riggs, 1904). Because of this, only the Nugget and Navajo sandstones are discussed in detail in this section. For a full list of described trace fossils, body fossils and plant fossils from the Nugget and Navajo eolianites, see Tables 1-6.

1.2.1.1 Trace Fossils

Trace fossils are the most abundant fossil type in the Nugget and Navajo sandstones, and a surprisingly large variety has been described since their first reports in the early 1900s. Many of the reports are cursory, mentioned only in passing as part of studies unrelated to ichnology, whereas most other reports describe surficial trackways and trails, with a large emphasis on dinosaur trackways.

In the same paper that described the type locality of the Nugget Sandstone in southwest Wyoming, "perforations" in the sandstones were suggested as the only evidence of organic remains (Veatch, 1907). The first irrefutable report of trace fossils are trackways from the Heber, Utah area (Buss, 1921). Although neither the formation name nor fossil names were provided by Buss, recent evaluation of specimens from that locality suggest that Buss' specimens are *Paleohelcura* and *Brasilichnium* from the Nugget Sandstone (Chure et al., in press). Similar specimens, presumably from the same quarry, were described in more detail by Albers (1975) and re-evaluated by Chure et al. (in press). Photographs, collected specimens, and casts from Albers (1975) preserve evidence of a diversity of traces, including tetrapod trackways (*Brasilichnium* and "lacertoid" tracks), arachnid trackways (*Octopodichnus* and *Paleohelcura*), and invertebrate burrows (*Entradichnus*; Chure et al., in press). In the few decades subsequent to the Buss (1921) reports only a few sporadic reports of trace fossils are mentioned in the literature, including unidentified markings resembling footprints in the Nugget Sandstone of southeast Idaho (Mansfield, 1927) and dinosaur trackways in the Navajo Sandstone of Arizona (Baker et al., 1936).

More reports of trace fossils transpired in the 1950s and 60s. The first and most comprehensive of these reports includes “lacertoid” tracks, *Brasilichnium*, *Paleohelcura*, *Octopodichnus*, and unidentified trails described from the Nugget Sandstone of northeastern Colorado (Faul and Roberts, 1951), a near identical assemblage to that described by Albers (1975; Chure et al., in press). A curious trace fossil was described from the top of the Nugget Sandstone in central Wyoming (Wroble, 1953). This single specimen is nearly 15cm long and 2cm wide and bilobed, consisting of pairs of curved ridges along a central ridge. It was later referred to *Gyrochorte*, a feeding trace (Donald W. Boyd *in* Knapp, 1976). Vertebrate trackways in the Nugget Sandstone of northeastern Utah are discussed by Stokes (1957, 1959) and in central Wyoming by Kayser (1964), and “organic trails” in central Wyoming were mentioned by Jordan (1965).

Economic and environmental interest in the Nugget and Navajo sandstones was strong in the 1970s, resulting in a number of trace fossil occurrence reports, in addition to detailed trace fossil descriptions. Vertebrate trackways received attention beginning with Iguanodon-like trackways (Marzolf, 1970), the *Brasilichnium*-related trackways *Bipedopus* and *Semibipedopus* (Haubold, 1971), possible pterosaur tracks (Stokes, 1973) and dinosaur tracks (Sanderson, 1974), all occurring within the Navajo Sandstone of southern Utah. Vertebrate trackways received the most attention from Albers (1975) and Stokes (1978), who noted both vertebrate and invertebrate trace fossil localities from five states containing Nugget and Navajo eolianites.

Invertebrate trace fossils received passing notice by other Nugget and Navajo workers. “Burrow structures” were reported from Navajo of eastern Utah (Stanley et al., 1971), meniscate burrows were noted and photographed from the Nugget of northern

Utah (Albers, 1975), "invertebrate trails" were reported from the Nugget of northwest Colorado (Knapp, 1976), small "vertical and horizontal burrows" were reported from the Nugget of western Wyoming and northern Utah (Pacht, 1976), and small vertical and horizontal burrows were reported from the Nugget and Navajo sandstones of Wyoming and Utah (Dott, 1979).

In the Nugget Sandstone in Wyoming, Doelger (1981) described meniscate burrows as 4mm wide, up to 50mm long, and visible when "layers of clean white sand alternate with layers of red clay-coated sand." The described traces resemble *Taenidium* isp. "A" as described in the present thesis. Doelger (1981) also mentions that "a number of other burrow types, as well as a variety of more enigmatic features which might be related to plant or animal activity were also observed."

In the 1990s Martin Lockley and others began detailed studies of vertebrate trackways in the Navajo Sandstone. They identified the vertebrate trackways *Brasilichnium, Eubrontes, Grallator, Otozoum, Brachychirotherium*, *Eosauropus*, and *Anomoepus,* in addition to the invertebrate trackways *Octopodichnus* and *Paleohelcura,* mostly in the Navajo Sandstone of southern Utah (Lockley, 1990, 1991; Lockley et al., 1991, 1992a; Lockley et al., 1992b; Lockley et al., 1992c; Lockley et al., 1994; Lockley and Hunt, 1995; Lucas et al., 2006b). Subsequent trackway descriptions include *Brasilichnium* and a crocodylomorpha trackway, *Batrachopus,* from the Navajo of southern Utah (Rainforth, 1997), *Eubrontes* and *Grallator* in the Nugget of northeastern Utah (Hamblin and Bilbey, 1999; Hamblin et al., 2000), *Brasilichnium* and *Octopodichnus* from the Nugget of northern Utah (Sanders and Picard, 1999), and *Grallator* and *Brasilichnium* from the Navajo of southern Utah (Loope et al., 2004a;

Loope and Rowe, 2003). Another *Brasilichnium* surface was reported from the Nugget of northeastern Utah (Engelmann et al., 2010), and a diversity of trackways was reported from the Nugget of southeastern Idaho and includes *Grallator*, *Otozoum*, *Batrachopus*, *Brasilichnium*, *Octopodichnus*, *Paleohelcura* and *Diplichnites* (Lockley et al., 2011).

In addition to trackways, large (possibly vertebrate) burrows have received attention. Casts of large burrows, reaching 20cm in diameter, were described from the Navajo of southeastern Utah and interpreted as mammal and therapsid burrows (Lucas et al., 2006a; Odier, 2006; Riese et al., 2011). Other large (possibly vertebrate or large invertebrate) burrows were reported from the Nugget in northeastern Utah (Engelmann et al., in press), and these also are discussed in the present thesis.

Invertebrate burrows in the Nugget and Navajo eolianites also began receiving significant attention. *Taenidium*, *Entradichnus* and *Beaconites* burrows were described in detail, in addition to the trackway *Octopodichnus,* from the a cross-bedded interval of the Nugget Sandstone in Northern Utah, near the outcrops studied by Albers (1975) (Sanders and Picard, 1999). Invertebrate burrows and bioturbation zones from the Navajo Sandstone also were discussed in detail in southern Utah and northern Arizona (Loope and Rowe, 2003). These unnamed burrows are unlined, 5mm in diameter, horizontal to subvertical, and occur in clusters within grain-flow strata and wind-ripple laminae. Ekdale et al. (2007) described seven invertebrate trace fossils in the Navajo Sandstone in southern Utah. These include *Planolites*, *Palaeophycus*, *Skolithos*, *Arenicolites*, *Entradichnus*, *Taenidium* and *Digitichnus*. In addition to describing trace fossils, paleoclimatic implications were made based on the trace fossils, which were shown to aid in the interpretation of a monsoonal climate. The latest report of invertebrate burrows from these eolianites is of *Planolites* described from the Navajo of southeastern Utah (Wilkens, 2008).

1.2.1.2 Animal Body Fossils

The Nugget and Navajo Sandstones have yielded very few body fossils, further stressing the importance of the more abundant trace fossils. Vertebrate body fossils from the Navajo Sandstone in Arizona were reviewed by Irmis (2005). These include a single tritylodont (Winkler et al., 1991), three crocodylomorph specimens (Galton, 1971; Rinehart et al., 2000; Rinehart et al., 2001), sauropodomorphs (Brady, 1935; Galton, 1971), a theropod partial skeleton and tooth of *Segisaurus* (Camp, 1936; Carrano et al., 2005; Winkler et al., 1991), and an indeterminate tibia (Winkler et al., 1991).

A quarry in northeastern Utah (Figure 3) has yielded thousands of bones and bone fragments (Britt et al., 2010; Britt et al., 2011; Chambers et al., 2011; Engelmann et al., 2011; Engelmann et al., 2012). Most of these bones belong to a new ceolophysoid theropod, characterized by a “lightly-built foot with a splint-like metatarsal II fused proximally to metatarsal III” (Chambers et al., 2011). Also recovered from this quarry are articulated partial skeletons of multiple drepanosaurs, a small diapsid reptile characterized by bizarre and distinctive features throughout the skeleton (Engelmann et al., 2012). Drepanosaurs are known only from Triassic strata, suggesting that at least the lower portion of the eolian member of the Nugget Sandstone is Triassic in age (Engelmann et al., 2012; Renesta et al., 2010). Other body fossils from the same quarry include teeth from a moderately-sized theropod and a small sphenodontid (Chambers et al., 2011). From the Navajo Sandstone of southern Utah, a partially articulated skeleton of *Seitaad ruessi*, a new basal sauropodomorph, has also been described (Sertich and Loewen, 2010).

A few invertebrate body fossils have also been reported from Nugget and Navajo Sandstones. The first reports of invertebrates are freshwater ostracodes similar to *Candona* sp. and clam shrimp *Lioestheria* aff. *L. ovata* from the upper part of the Navajo Sandstone in northeastern Arizona (Harshbarger et al., 1957). The same clam shrimp also were described from the same area (Lewis et al., 1961). Ostracodes have been reported from central Wyoming (Doelger, 1981; Doelger and Steidtmann, 1982), northeastern Arizona (Winkler et al., 1991), southern Utah (Wilkens, 2008), and southeastern Utah where they occur with brown algae (Dorney and Parrish, 2009). Additionally, imbricated deposits of freshwater clam of the family Unionidae occur at two localities from the Navajo Sandstone in southern Utah (Wilkens, 2008), and few small gastropod impressions have been discovered in interdune carbonates near Dinosaur National Monument (Figure 4).

1.2.1.3 Plant Body Fossils

Despite the low preservational potential of primary producers, a few occurrences of plant remains have been reported from the Nugget and Navajo sandstones, and all occur within interdune deposits. The first report of plant material is of fern and wood fragments associated with *Equisetum* remains in the Navajo Sandstone of northeastern Arizona (Harshbarger et al., 1957), followed by reports of unidentified plant fragments in southeastern Idaho (Oriel, 1959). *Equisetum* were reported from the Navajo Sandstone of southeastern Utah (Gilland, 1979). *Equisetum*, a member of the vascular plant group commonly known as “horsetails,” are also referred to as sphenophytes in the literature (Loope et al., 2004a; Winkler et al., 1991). Silicified conifer stumps and trunks, including some in growth position, were reported from southeastern Utah near Moab (Loope, 1979; Stokes, 1991) and were discussed in most detail in Parrish and Falcon-Lang (2007). These stumps indicate several decades of growth, and when found in growth position they occur in interdune lake deposits rooted in the eolian sandstone below. The most comprehensive paleobotanical report is by Wilkens (2008), who studied interdune deposits in the Navajo Sandstone of southern Utah. Findings include possible cycadeoid wood, *Araucarites* cone scales, seed molds resembling modern araucarian seeds, leaf molds resembling cycadeoids, and unidentified branch casts and rhrizocasts. Other possible cycadeoid impressions were reported in association with body and trace fossils at the Saints and Sinners Quarry in northeastern Utah (Britt et al., 2010; Chambers et al., 2011). Sphenophyte remains with nodes, internodes, intermodal ridging, and a whirl of thin elongate leaves (Figure 5) have also been identified from the Nugget Sandstone of northeastern Utah within Dinosaur National Monument (Daniel Chure, written communication, 2012).

1.2.2 Paleoclimate and Paleoenvironment

Considerable research has attempted to reconstruct the paleoclimate and paleoenvironments of the Nugget Sandstone and its potential equivalents (Bryant, 2011; Chan and Archer, 1999, 2000; Chandler et al., 1992; High and Picard, 1975; Loope and Rowe, 2003; Loope et al., 2001; Loope et al., 2004b; Picard, 1977b; Wilkens, 2008). Climate is one of the dominant factors in controlling nonmarine sedimentary deposits, and subsequent changes in sedimentation reflect climatic changes. Climatic fluctuation, such as monsoonal regimes, have been interpreted from climate-sensitive Jurassic eolian deposits (Chan and Archer, 1999, 2000; Loope and Rowe, 2003; Loope et al., 2001; Loope et al., 2004b). In addition to sedimentology, general circulation models (GCMs) have also proven useful in interpreting Pangaean climate controls, providing details such as climate and ocean circulation patterns, precipitation, and wind direction (Chandler et al., 1992; Loope et al., 2004b; Rowe et al., 2007).

Sedimentary cycles with periodicities ranging from annual to tens of thousands of years have been interpreted in the Nugget and Navajo sandstones.

Long-term paleoclimate fluctuations were deciphered from the Nugget Sandstone in northeastern Utah by identifying sedimentary cycles consisting of facies representing small lakes, inland sebkhas, mudflats and eolian dunes (High and Picard, 1975). This study identified seven wet-dry climatic cycles for the production of sedimentary cycles below the cross-bedded eolian deposits that dominate the upper strata of the formation, signifying a shift to a dominantly arid climate.

Decadal scale climate cycles were interpreted from the Navajo Sandstone in southeastern Utah (Chan and Archer, 1999). Harmonic analysis on cycles of grainfall and wind-ripple laminae reveals 30- and 60-year periodicities, interpreted as the product of climatic oscillations, solar variability, or seasonal precipitation.

Annual cycles and slumping were interpreted from the Navajo Sandstone in Arizona (Loope et al., 2001). Cyclic packages of grainflow beds and wind-ripple laminae indicate an annual shift in wind direction, and slumped slipfaces indicate heavy rains interpreted as seasonal monsoons.

Paleoenvironments have also been interpreted from Nugget and Navajo Sandstone deposits by numerous workers (Bryant, 2011; Doelger, 1981, 1987; Eisenberg, 2003; High and Picard, 1975; Loope et al., 2004a; Loope and Rowe, 2003; Stokes, 1991; Wilkens, 2008; Winkler et al., 1991). Most of these studies document evidence for the presence of water, the presence of ancient life, and wet environmental conditions.

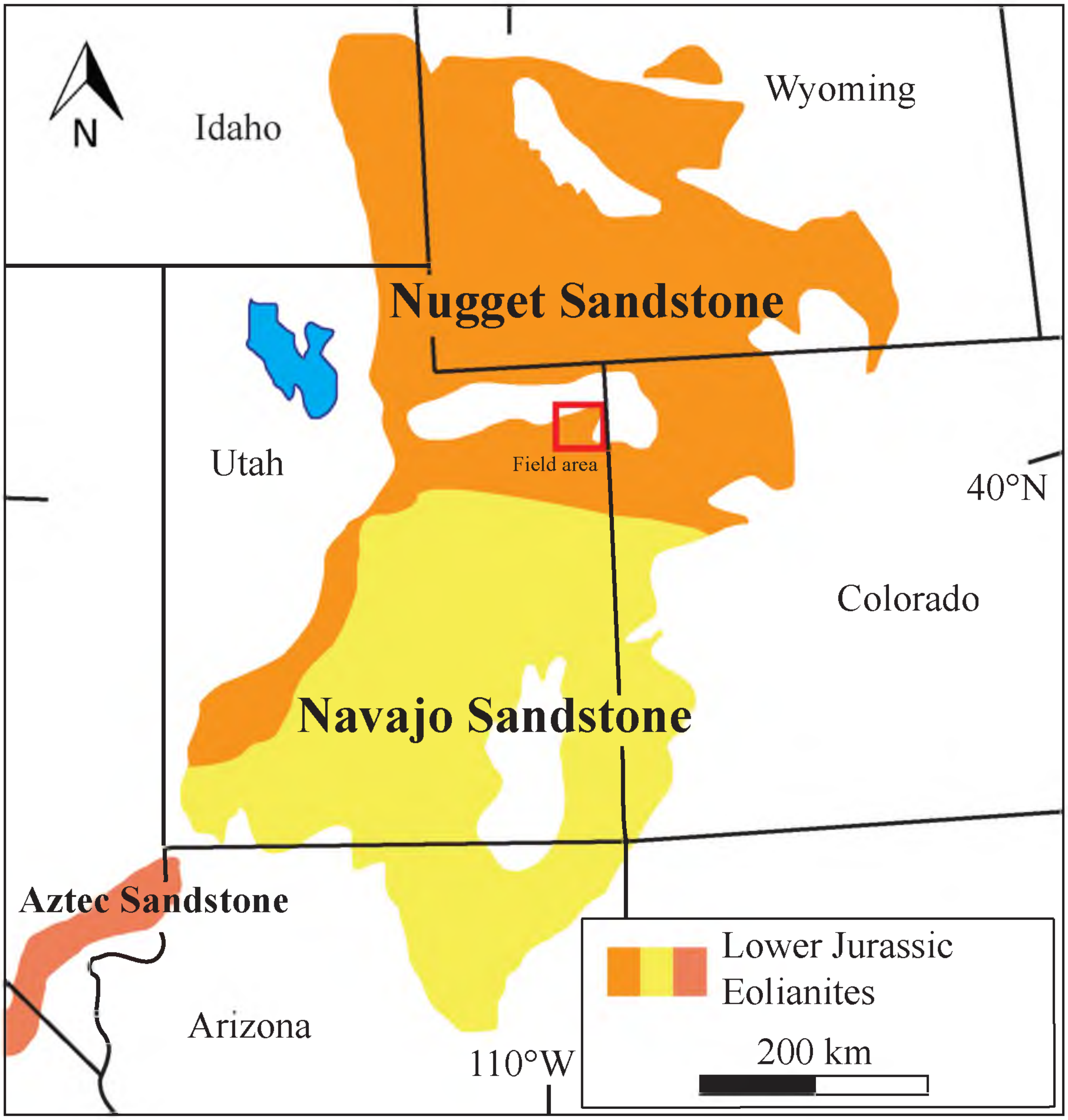


Figure 1. Map of the extent of the Nugget Sandstone, including subsurface. Also shown are the Navajo and Aztec sandstones, which are correlative with part of the Nugget. Inset field area shown in Figure 6. Modified from Stanley et al. (1971), Peterson (1972) and Sprinkel et al. (2011).

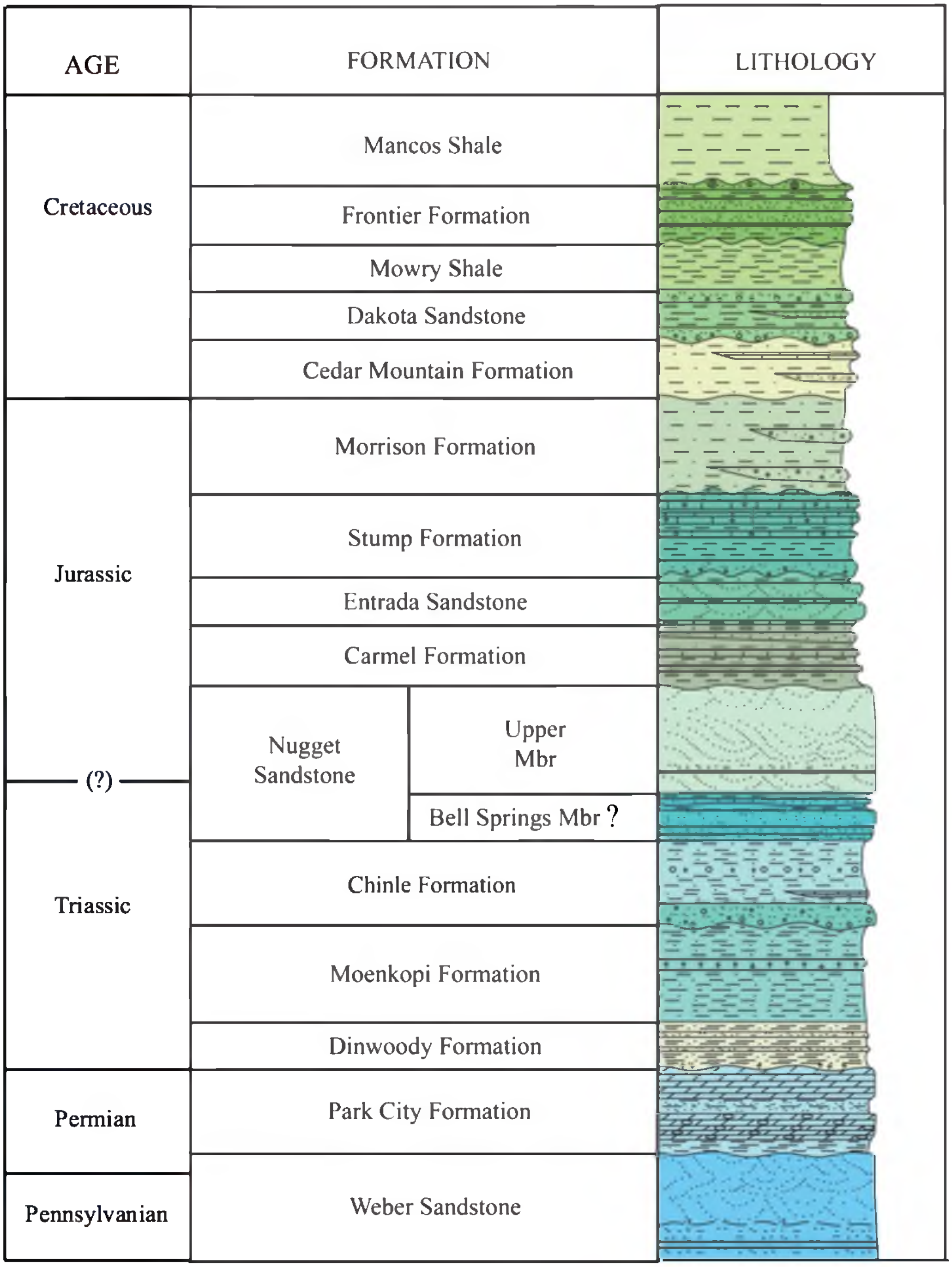


Figure 2. Stratigraphic section from northeastern Utah showing the Upper Triassic/Lower Jurassic Nugget Sandstone bounded by the Triassic Chinle Formation below and the Jurassic Carmel Formation above. Modified from Jensen (2005), this section shows the proposed distinction of a lower Bell Springs Member and Upper Member of the Nugget Sandstone, though this distinction has not been generally accepted and is not referred to in this study.

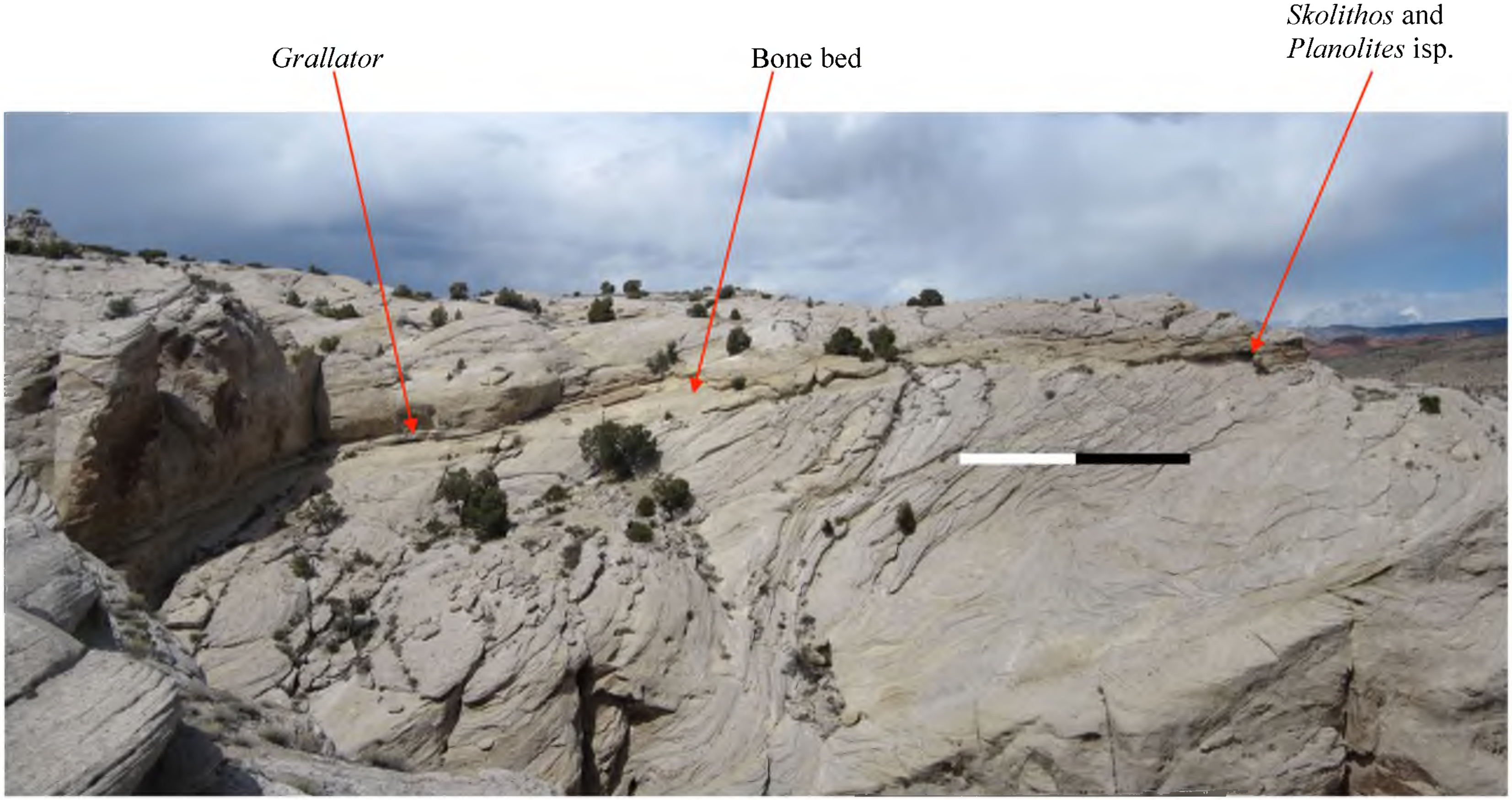


Figure 3. Saints and Sinners Quarry (BYU 1442) indicating the location of a bone bed and associated trace fossils within planar interdune beds. Scale bar units ~ 5m.

Figure 4. Small gastropod body fossils (external molds) preserved both (A) within interdune carbonate rock and (B) within carbonate-cemented sand directly below interdune carbonates. Scale bar units = 1mm.

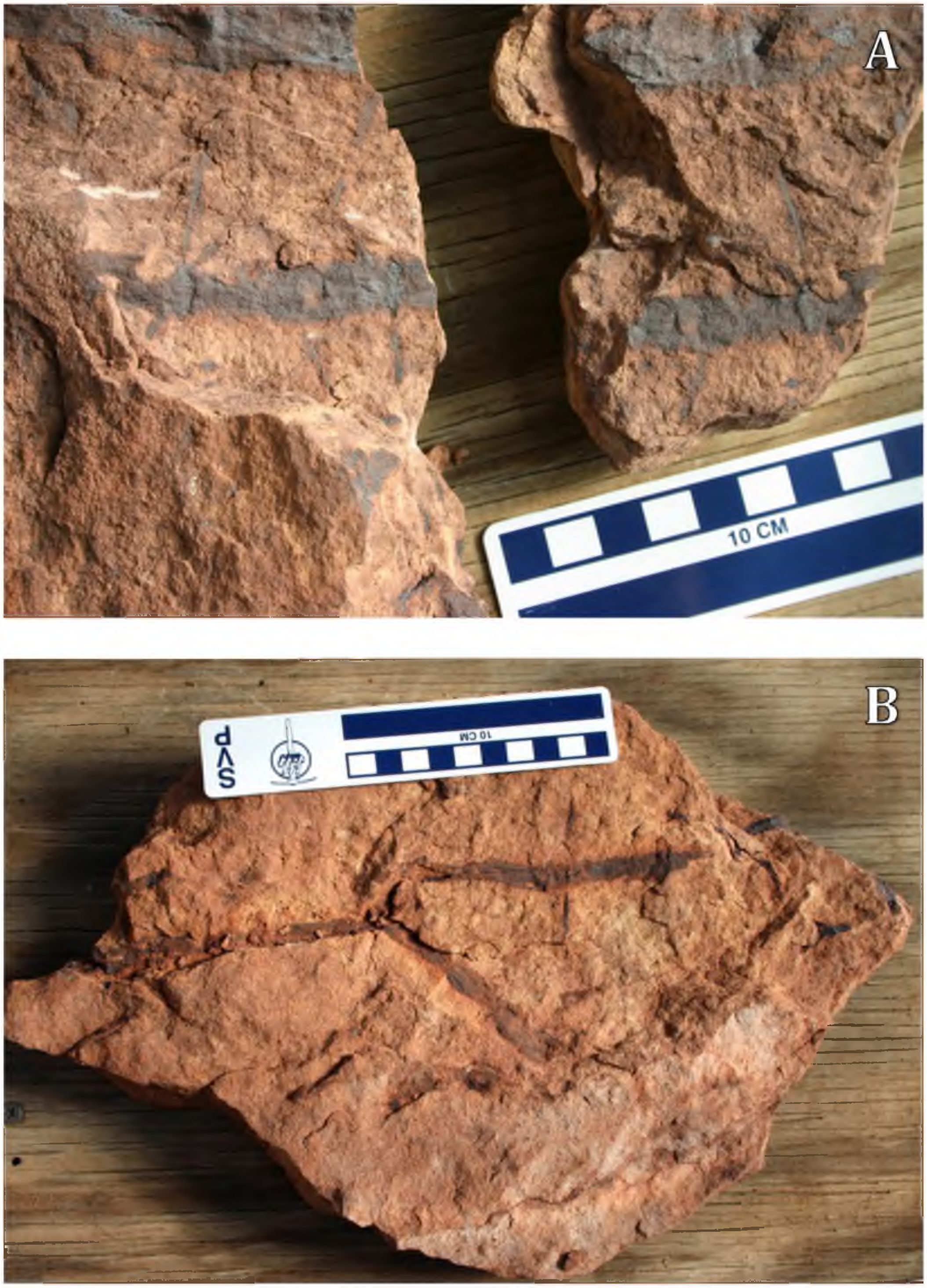


Figure 5. Sphenophyte plant fossils from an interdune deposit in the Nugget Sandstone within Dinosaur National Monument. (A) Nodes and internodes and (B) either rhizomes or above-ground foliage is preserved. Photos courtesy of Dan Chure, NPS. Scale bar units = 1cm.

Table 1. Trace fossils in the Nugget Sandstone

Trace Fossils in the Nugget Sandstone

Fossil	Area or Formation	Reference
Trackways (Later named *Paleohelcura(?)* and *Brasilichnium by* Chure et al., in press)	N Utah	Buss, 1921
Trackways and burrows (Lacertoid tracks, *Brasilichnium, Paleohelcura, Octopodichnus*, Undescribed trails)	NW Colorado	Faul and Roberts, 1951
Bilobed trail (Later named *Gyrochorte* by Picard, 1975; Knapp, 1976)	C Wyoming	Wroble, 1953
Small vertebrate trackways	NE Utah	Stokes, 1957, 1959 (from Picard, 1977a)
Possible vertebrate track	C Wyoming	Kayser, 1964 (from Doelger, 1987)
"Organic trails"	C Wyoming	Jordan, 1965 (from Picard, 1977a)
"Burrow structures"	E Utah	Stanley et al., 1971
Trackways and burrows (Later named *Brasilichnium,* Lacertoid tracks, *Paleohelcura, Octopodichnus, Entradichnus*, by Chure et al, (in press))	NE Utah	Albers, 1975
Invertebrate trails	NW Colorado	Knapp, 1976
Small vertical and horizontal burrows	W Wyoming, N Utah	Pacht, 1976
Dinosaur and reptilian trackways, invertebrate burrows and trails	Wyoming, Utah, Colorado, Idaho	Stokes, 1978
Small vertical and horizontal burrows	Wyoming, Utah	Dott, 1979
Meniscate burrows	C Wyoming	Doelger, 1981
Eubrontes, Grallator	NE Utah	Hamblin and Bilbey, 1999
Trackways and burrows (*Brasilichnium*, *Octopodichnus, Taenidium, Entradichnus, Beaconites*)	N Utah	Sanders and Picard, 1999
Dinosaur tracks (*Brachychirotherium*, *Grallator, Eosauropus cimarronensis, Otozoum, Pseudotetrasauropus, Tetrasauropus*)	NE Utah	Lockley et al., 1991; Lockley et al., 1992a-c; Lockley et al., 2001; Lucas et al., 2006b
Brasilichnium	NE Utah	Engelmann et al., 2010
Cheirothere tracks (*Brachychirotherium*)	NE Utah	Anderson, 2011
Large burrows	NE Utah	Engelmann et al., in press
Entradichnus, *Planolites, Taenidium, Skolithos*, 'burrow clusters', and 'flared burrows'	NE Utah	This study

Table 2. Trace fossils in the Navajo Sandstone

Trace Fossils in the Navajo Sandstone

Fossil	Area or Formation	Reference
Undescribed trackways	SE Idaho	Mansfield, 1927 (From Doelger, 1987)
Dinosaur tracks	? (Navajo Ss)	Baker et al., 1936 (From Doelger, 1981)
"Iguanodon-like trackway" and single dinosaur track	SE Utah	Marzolf, 1970 (from Picard, 1977)
Bipedopus and *Semibipedopus*	? (Navajo Ss)	Haubold, 1971 (from Lockley, 2011)
"Tracks of Pterosaurs and tracks of about 10 different other animals"	SE Utah	Stokes, 1973 (from Picard, 1977)
Dinosaur tracks	SE Utah	Sanderson, 1974
Dinosaur and reptilian trackways, invertebrate burrows and trails	Utah, Arizona	Stokes, 1978
Brasilichnium, *Eubrontes*, *Grallator*, *Otozoum*, *Anomoepus*, *Brachychirotherium, Eosauropus, Paleohelcura, Octopodichnus*	Navajo Ss	Lockley, 1990, 1991; Lockley *et al*., 1994, and Lockley and Hunt, 1995
Brasilichium, Batrachopus (Crocodylomorpha tracks)	? (Navajo Ss)	Rainforth, 1997 (From Irmis, 2005)
Large burrow casts and rhizoliths	SE Utah	Lucas et al., 2006a; Odier, 2006; Riese et al., 2011
Trackways and burrows (*Grallator, Brasilichnium,* vertical and horizontal burrows)	S Utah	Loope and Rowe, 2003
Invertebrate traces (Planolites, Palaeophycus, Skolithos, Arenicolites, Entradichnus, Taenidium, Digitichnus)	S Utah	Ekdale et al., 2007
Eubrontes, Anchisauripus, Grallator, and sauropodomorph tracks	N Arizona	Seiler and Chan, 2008
Planolites burrows	SE Utah	Wilkens, 2008
Grallator, Otozoum, Batrachopus, Brasilichnium, Octopodichnus, Paleohelcura and *Diplichnites*	SE Idaho	Lockley et al., 2011

Table 3. Plant body fossils in the Nugget Sandstone

<table>
<tr><th colspan="3">Plant Body Fossils in the Nugget Sandstone</th></tr>
<tr><td>Fossil</td><td>Area or Formation</td><td>Reference</td></tr>
<tr><td>Foliage impressions, possibly cycadeoid</td><td>NE Utah</td><td>Britt et al., 2010; Chambers, 2011</td></tr>
<tr><td>Sphenophytes</td><td>NE Utah</td><td>Daniel Chure, personal communication</td></tr>
</table>

Table 4. Plant body fossils in the Navajo Sandstone

<table>
<tr><th colspan="3">Plant Body Fossils in the Navajo Sandstone</th></tr>
<tr><td>Fossil</td><td>Area or Formation</td><td>Reference</td></tr>
<tr><td>Fern and wood fragments, and <i>Equisetum</i></td><td>NE Arizona</td><td>Harshbarger et al., 1957 (From Knapp, 1976)</td></tr>
<tr><td>Unidentified plant fragments</td><td>SE Idaho</td><td>Oriel, 1959 (From Doelger, 1987)</td></tr>
<tr><td>Plant impressions comparable to <i>Equisetum</i></td><td>SE Utah</td><td>Gilland, 1979</td></tr>
<tr><td>Conifers in growth position, likely araucarians</td><td>SE Utah</td><td>Loope, 1979; Stokes, 1991; Parrish and Falcon-Lang, 2007</td></tr>
<tr><td>Wood and logs, cone scales, seed molds, leaf molds, branch casts, rhizocasts, and cycadeoids</td><td>S Utah</td><td>Wilkens, 2008</td></tr>
</table>

Table 5. Animal body fossils in the Nugget Sandstone

Animal Body Fossils in the Nugget Sandstone		
Fossil	Area or Formation	Reference
Ostracodes, genus *Darwinula*	C Wyoming	Doelger, 1981; Doelger and Steidtmann, 1982
Coelophysoids, Theropod teeth, Sphenodontians, Protosuchians, Drepanosaurs	NE Utah	Britt, 2010, 2011; Chambers, 2011; Engelmann, 2012
Small gastropod impressions	NE Utah	Present thesis

Table 6. Animal body fossils in the Navajo Sandstone

Animal Body Fossils in the Navajo Sandstone		
Fossil	Area or Formation	Reference
Sauropodomorph	NE Arizona	Brady, 1935
Segisaurus halli (Theropod)	NE Arizona	Camp, 1936
Freshwater Ostracods, Clam shrimp *Lioestheria* aff. *L. ovata*	NE Arizona	Harshbarger et al., 1957 (From Picard, 1977)
Clam shrimp, *Lioestheria* aff. *L. ovata*	NE Arizona	Lewis et al., 1961 (From Picard, 1977)
Crocodylomorph, Suaropodomorph	NE Arizona	Galton, 1971
Ostracodes, tritylodontid synapsid, tibia of small dinosaur, theropod tooth	NE Arizona	Winkler et al., 1991
Crocodylomorphs	N Arizona	Rinehart et al., 2000; 2001
Ostracodes	SE Utah	Parrish and Falcon-Lang, 2007
Freshwater clams of family Unionidae, ostracodes	S Utah	Wilkens, 2008
Ostracods and brown algae	SE Utah	Dorney and Parrish, 2009
Sauropodomorph	S Utah	Sertich and Loewen, 2010
Protosuchids (Crocodylomorphs)	S Utah	Bryant, 2011

CHAPTER 2

METHODS AND LOCALITIES

2.1 Methods

Field work for this study included site reconnaissance, fossil identification and sample collecting within the field area in the vicinity of Dinosaur National Monument, northeastern Utah. Additional time was spent in modern dune environments of Utah to examine modern analogue settings. Lab work included thin section microscopy, QEMSCAN (**Q**uantitative **E**valuation of **M**inerals by **SCAN**ning electron microscopy) analysis, and fossil identification.

2.1.1 Field Methods

Field work was conducted during 2011 and 2012. Investigation of outcrops included sedimentary and stratigraphic interpretation and identification of trace fossils and their stratigraphic and lateral extent. Some localities were discovered prior to this study during National Park Service surveys of the Nugget Sandstone during 2009, 2010 and 2011.

Field investigation of modern dune environments was performed at three Utah locations: Little Sahara Recreation Area (BLM), Sand Hollow State Park, and Coral Pink Sand Dunes State Park in 2012. Dune field investigation included exploration of dune formation and processes and identification of modern trackways and burrows, and tracemaker behavior and preferences.

2.1.2. Lab Methods

Lab work consisted of thin section, QEMSCAN and sample analysis. Eight thin sections of representative types of sediment and trace fossils were examined. QEMSCAN analysis was conducted on two samples of trace fossils, a *Planolites beverleyensis* and a *Taenidium* isp. "A." Collected specimens of trace fossils were used to help classify ichnogenera.

2.2 Locality Information

All sites discussed herein occur in and around Dinosaur National Monument (about 10 miles east of Vernal) and north of Vernal along US Route 191 near Steinaker and Red Fleet reservoirs (Figure 6). Over 30 localities containing trace fossils in this area were identified during the course of this study. Most of these sites contain few trace fossils of a single ichnotaxon, and only a small number of sites contain many trace fossils of several ichnotaxa. All site information, including GPS data points and brief descriptions, are available upon request in the University of Utah Ichnology Collection (UUIC), and those with Dinosaur National Monument are also on file with the NPS. Five sites that are particularly notable for various reasons are described below and depicted in Figure 6.

2.2.1 Site 21 - Orchid Draw

This locality is at the terminus of a large drainage named Orchid Draw within the western boundary of Dinosaur National Monument. Part of the access cuts through private property, and permission to cross it is required. This locality consists of a series large, trough-cross bedded into planar bedded, medium- to fine-grained sandstone (Figure 7). The section of interest exposes high angle paleo-surfaces of lower slipfaces that merge tangentially into vertical outcrops of more distal, though contemporaneous, dune toe deposits. These interdune deposits consist of fine-grained, red and yellow, wind ripple laminations. A thin layer of desert varnish covers slipface surfaces, which aids in the visibility of *Brasilichnium* and *Paleohelcura* trackways. This section is bounded above and below by similarly cross-bedded sets of sandstone, though the vertical nature of these exposures limits access.

A high diversity of trace fossils is occur at this locality, including *Brasilichnium*, *Paleohelcura, Taenidium* isp. “A,” ‘burrow clusters’, ‘flared burrows’, and a ‘large burrow’.

2.2.2 Site 15 - Large Mounds

The Large Mounds locality is located near Jensen, UT, south of Dinosaur National Monument and southeast of Chew Ranch. It is accessed by a jeep trail off of Blue Mountain Road. This locality is situated high on the east side of a canyon, and it is part of a carbonate complex that is likely related to carbonate beds on the west side of the canyon. It consists of convoluted fine- to very fine-grained sand capped by mounds of carbonate (Figure 8). The carbonates consist primarily of a calcite matrix supporting quartz grains, though in outcrop, masses of sandstone are mottled within the carbonate texture. Primary sedimentary structures are absent below the carbonate cap, though swaths of red sand orient themselves upward toward the carbonates. This red sand is calcite cemented and consists mostly of very fine, angular quartz grains though few large, well-rounded grains are present. The white sand that forms the majority of the outcrop below the carbonates consists of calcite-cemented, fine, subangular to rounded quartz. Further east on the outcrop the carbonates become thin and laminated. This carbonate contains abundant calcite grains with quartz dense layers defining the laminations. Associated carbonates on the other side of the canyon contain snail impressions (Figure 4).

The interval of interest is situated directly below the carbonate mounts on the southeast side of the outcrop. This interval consists of calcite-cemented, fine-grained, angular to subangular, well-sorted quartz. A *Taenidium* ichnofabric including few discrete *Taenidium* isp. “A” burrows occur within this interval.

2.2.3 Site 11 - Saints and Sinners

The Saints and Sinners Quarry (Brigham Young University locality number BYU 1442) is located south of the Utah portion of Dinosaur National Monument just north of US Highway 40. The outcrop consists of a three-meter thick set of planar beds bounded on top and bottom by tall sets of high angle, trough-cross bedded sandstone (Figure 3). Planar bedding is laterally limited, and it represents an interdune environment with standing water and oscillatory wave motion (Britt et al., 2011). This particular interval is of interest, having recently produced the largest collection of vertebrate fossils from the

Nugget Sandstone and its equivalents. These include skeletal remains of coelophysoid dinosaurs and small reptiles, including sphenodontians, protosuchians, and drepanosaurs (Britt et al., 2011; Britt et al., 2010; Chambers et al., 2011; Engelmann et al., 2012; Engelmann et al., 2011).

Grallator trackways are on interdune surfaces, and the burrowed interval is on the northernmost margin of this interdune deposit. The deposit is concretionary, and it comprises fine-grained, subangular quartz sand. The only *Skolithos* and *Planolites* isp. burrows from the area are at this locality.

2.2.4 Site 17 - Sounds of Silence

The Sounds of Silence locality is north of Blue Mountain Rd/Hwy 149 and east of the popular Sounds of Silence hiking trail in Dinosaur National Monument. At this locality the Nugget Sandstone beds are nearly vertical. The outcrop consists of fins of trough-cross bedded, fine-grained quartz sandstone protruding from the ground (Figure 9). These surfaces represent a lower slipface environment, and what would be associated planar interdune deposits are likely buried below. Both bottom and top surfaces of the slipface layers are covered in thin laminations of very fine-grained red sand that aids in high-resolution preservation of the burrows.

Well-preserved specimens of *Entradichnus meniscus*, *Entradichnus* isp., *Planolites beverleyensis*, and a *Taenidium* ichnofabric are present here.

2.2.5 Site 26 – Cub Creek Spire

The Cub Creek Spire locality is located just north of the road that leads to the historical site of Josie Morris' Ranch just after it forks off Blue Mountain Road. The outcrop at this locality consists of distal trough-cross and planar bedded, wind-ripple, fine-grained quartz sand that has been eroded into the shape of a spire (Figure 10). The wind-ripple laminations are thin, alternating red and yellow in color, and aid in the visibility of burrows. The spire is nearly 10m tall and contains two bounding surfaces in the upper half, each of which abruptly transitions the depositional environment from proximal lower slipface to more distal, dune toe deposits.

The outcrop surface is covered in burrows, most of which are attributed to *Taenidium* isp. "B."

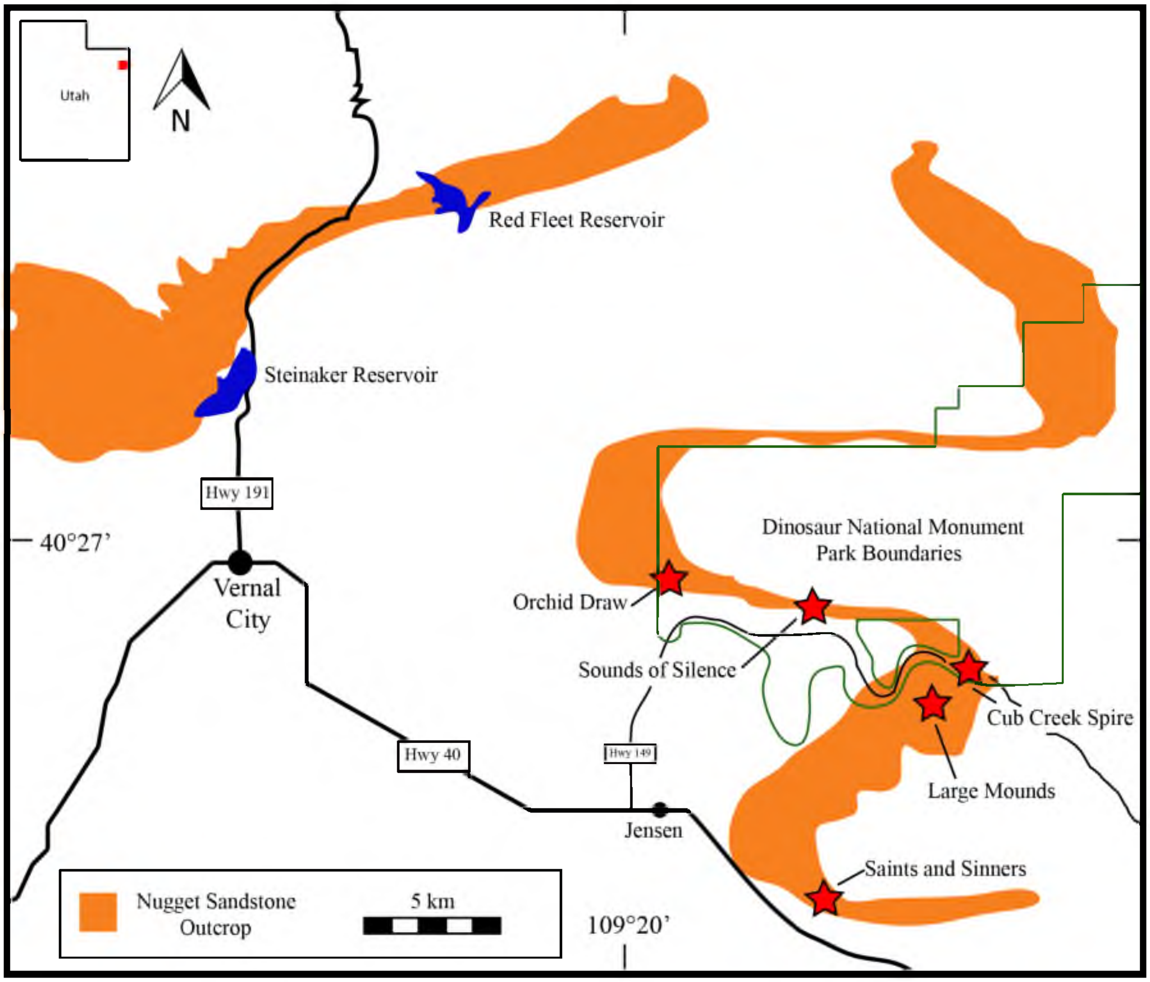


Figure 6. Area map showing outcrops of the Nugget Sandstone and five study localities investigated in this project.

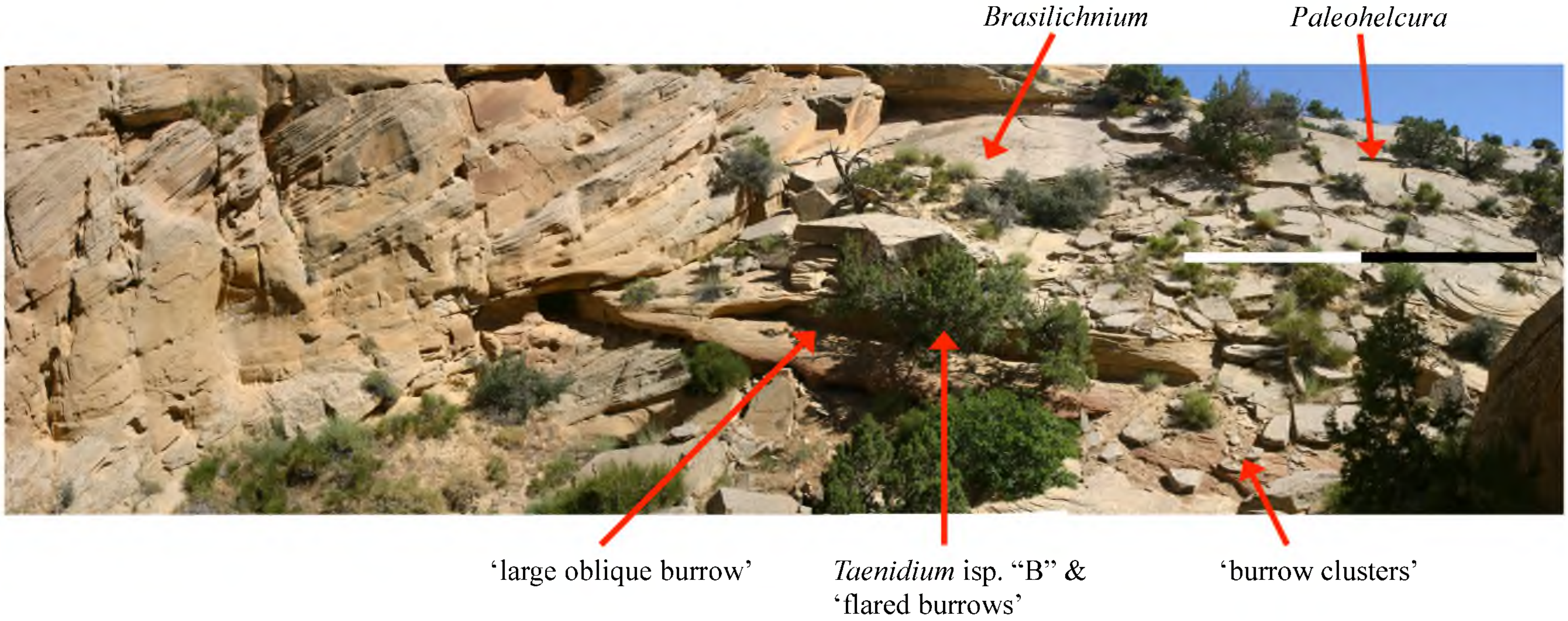


Figure 7. Orchid Draw locality showing the location of trace fossils on and within ancient dune. *Brasilichnium* and *Paleohelcura* are located on lower paleo-slipface surfaces, while the others occur on vertical or oblique cross section surfaces of a more distal, though contemporaneous, slipface environment. Photo courtesy of NPS. Scale bar units ~ 5m.

Taenidium isp. “A”
& *Taenidium*
ichnofabric

Figure 8. Large Mounds locality showing the location of *Taenidium* isp. “A” within a *Taenidium* ichnofabric. A mounded carbonate layer caps convoluted sandstone textures. Scale bar units ~ 5m.

Figure 9. Sounds of Silence locality showing large surface containing a dense population of *Entradichnus meniscus* and *Entradichnus* isp. in hyporelief.

Figure 10. Cub Creek locality spire containing abundant *Taenidium* isp. “B” in dune toe deposit. Scale bar units ~ 1m.

CHAPTER 3

TRACE FOSSILS IN THE NUGGET SANDSTONE OF NORTHEASTERN UTAH

3.1 Identification of Trace Fossils

Trace fossils in the Nugget Sandstone of northeastern Utah near Vernal, Utah, are described and discussed in this section. New fossil occurrences from this area include *Entradichnus meniscus*, *Entradichnus* isp., *Planolites beverleyensis*, *Taenidium* isp. "A," *Taenidium* isp. "B," *Skolithos* and *Planolites* isp., 'burrow clusters', 'large oblique burrows', 'flared burrows', *Paleohelcura,* and *Octopodichnus*. Previously described traces from this area include the small vertebrate trackways *Brasilichnium* and large vertebrate trackways *Grallator*, *Eubrontes*, *Brachychirotherium, Pseudotetrasauropus, Tetrasauropus,* and *Otozoum* tracks. References to original descriptions are found within. Figure 11 is an idealized sketch showing the spatial and facies relationships of the ichnotaxa and body fossils of the Nugget Sandstone in this area. Possible tracemakers are discussed in the following section, 'Identity of Trace Makers', and Table 7 outlines the interpreted dune facies, tracemakers, and sediment moisture content at time of production for each trace fossil.

Classification of some traces presents certain challenges due to ambiguity in the literature, particularly with invertebrate meniscate burrows. Some confusion probably emerges from a lack of a comprehensive protocol for a hierarchy of ichnotaoxobases, i.e., criteria that constitute the primary grounds for classification: geometry, internal morphology, orientation, size, presence or absence of a wall, or host sediment. These morphological features reflect behavioral qualities of the tracemaker, but according to the literature on terrestrial ichnology no single feature in particular is more apt to dictate an ichnotaxonomic identification than any other. This ambiguity is manifested in the literature, where some seemingly indistinguishable traces have been classified with different ichnogeneric names (D'Alessandro and Bromley, 1987).

3.1.1 *Entradichnus meniscus*

Entradichnus meniscus is a long, horizontal, unwalled, unbranched meniscate trail created by burrowers moving in straight or gently curved lines on the lower dune slip face (Ekdale and Picard, 1985). *Entradichnus* in the Nugget Sandstone in northeastern Utah range from 3-10mm in width (typically ~5mm) and up to over 50cm in length (Figure 12). The burrows show a well-developed meniscate backfill, contain no lining, and are generally parallel to the foreset laminae of the cross-bedded strata. No true branching is observed, although crossovers are frequent. *E. meniscus* commonly is in close association with other burrows in local abundance, including *Planolites beverleyensis* and *Entradichnus* isp. No preferential orientation is discerned, but a few examples show clusters of *Entradichnus* radiating from a central area (Figure 12b), such as can be observed in the *Entradichnus meniscus* of the Navajo Sandstone of southern Utah (Ekdale et al., 2007). Unlike all other reports of *Entradichnus* elsewhere, *E. meniscus* in the Nugget are preserved both in negative and positive hyporelief and epirelief, and sometimes they are preserved without discernable relief, seen by a contrasting color to the surrounding sediment. A majority of the horizontal, unwalled, unbranched traces in this area, which include *Entradichnus* isp. and *Planolites beverleyensis* are preserved in hyporelief. Grouping of menisci is observed in the best-preserved specimens, a feature referred to as "megamenisci" by Frey et al. (1984).

E. meniscus was first named from the Upper Jurassic Entrada Sandstone of southern Utah (Ekdale and Picard, 1985), and has since been identified in the Upper Triassic/Lower Jurassic Wingate Sandstone of northern Arizona (Clemmensen and Blakey, 1989), Upper Triassic/Lower Jurassic Nugget Sandstone of northern Utah (Sanders and Picard, 1999), Lower Jurassic Navajo Sandstone of southern Utah (Ekdale et al., 2007), Upper Cretaceous Djadokhta Formation at Tugrikiin Shiree in southern Mongolia (Seike et al., 2010), and from a specimen in Lower Permian Coconino Sandstone in the Raymond M. Alf Museum in Claremont, CA (see figure 35.8 in Ekdale, 2007). Ekdale et al. (2007) interpret *Entradichnus* as formed when "the animal pushed small packets of sand behind itself as it moved through the sediment across the slip face." They are essentially identical to the plowing trails of modern crane fly larvae (Ahlbrandt et al., 1978). *Entradichnus meniscus* is often associated with both *Entradichnus* isp. and *Planolites beverleyensis.*

Previous reports of *E. meniscus* are described as being preserved exclusively in epirelief, which has been considered a diagnostic feature of this ichnogenus (Ekdale et al., 2007; Ekdale and Picard, 1985; Seike et al., 2010). However, observations of *E. meniscus* topotypes from the University of Utah Ichnology Collection (UUIC-1728; UUIC-1730) reveal burrows in positive hyporelief, as well as in epirelief, suggesting that a particular preserved location within the bed does not reflect any distinguishing behavioral tendencies. The manner of preservational relief no longer should be considered a diagnostic feature of the ichnogenus.

Entradichnus differs from *Taenidium*, which is described as a branching tunnel, cylindrical in cross section, which incorporates ingested (or at least distinctly different) backfill. *Taenidium* typically does not strictly follow bedding planes, and usually is shorter and less straight than *Entradichnus*. Some *Taenidium* ichnospecies have been described with exceptions to these generally accepted characteristics (D'Alessandro and Bromley, 1987). However, *Entradichnus* is differentiated from *Taenidium* in this study on the basis of the combined set of characteristics that are fundamentally different from traditional and general diagnostic features of *Taenidium*.

3.1.2 *Entradichnus* isp.

Entradichnus isp. exhibits similar characteristics to *Entradichnus meniscus* and *Planolites beverleyensis,* but it is distinguished by its internal structure. The backfill consists of a “feather stitch” pattern, where the “stitches” are alternating at a nearly perpendicular orientation to each other and 45° to the direction of movement (Figure 13). *Entradichnus* isp. is ~5mm wide and up to 20cm long. It has no lining, is unwalled and unbranched. *Entradichnus* isp is observed in negative and positive hyporelief (Figure 13a), and also with no relief as a contrasting color to the surrounding sediment (Figure 13b). *Entradichnus* isp. is rarer than both *Entradichnus meniscus* and *Planolites beverleyensis*, but multiple specimens occur at two localities. One occurrence shows the “feather stitch” backfill transition into the meniscate backfill of *Entradichnus meniscus* within the same burrow (Figure 14).

Entradichnus isp. occurs in association with both *Planolites beverleyensis* and *Entradichnus meniscus* at two localities, of which one is the Sounds of Silence locality (Figure 9). One particular burrow displays the backfill of *E.* isp. transition into the backfill of *E. meniscus* (Figure 14), indicating that the same tracemaker is capable of producing two types of backfill.

A similar type of backfill in burrows in the Nugget Sandstone was described by Sanders and Picard (1999) as "asymmetrical, appearing as alternating wedge-shaped projections from the burrow wall," however no samples were collected nor photographs taken. With exception to this brief note, no other burrow of this type has been described from any setting – eolian or otherwise – though a similar backfill has been described from within the ornamented walls of *Scoyenia gracilis* in the fluvial Upper Triassic Malmros Klint Member of the Fleming Fjord Formation fluvial near Carlsberg Fjord, Greenland (Figure 15b; Bromley and Asgaard, 1979).

This "feather stitch" backfill may be the result of an adult arthropod pushing the sediment around its body with alternating appendage motion, or a larval-stage arthropod transporting sediment behind its side-alternating posterior. *E.* isp. contrasts with *E. meniscus*, which is produced as sediment is pushed around the body with simultaneous appendage motion, or somehow transported behind the animal evenly.

3.1.3 *Planolites beverleyensis*

Planolites beverleyensis contains no internal structure, but it is otherwise identical to, and almost always associated with, *Entradichnus meniscus* (Figure 16). *P beverleyensis* constitutes the majority of the horizontal, unwalled, unbranched traces in this area, along with *Entradichnus meniscus* and *Entradichnus* isp. Occurrences of *P. beverleyensis* range from dense (hundreds of burrows per m^2) to highly sparse (only one or two observed in a single locality). When preserved in dense populations they are not only grouped on single surfaces, but also in lateral depositional dip sections reaching as much as 30m.

Planolites occurs in a wide spectrum of depositional environments, and eolian deposits are no exception. *Planolites beverleyensis* is the most commonly observed trace fossil in the area, and it always occurs on lower slip-face surfaces of ancient dunes, including those at the Sounds of Silence locality (Figure 9). Its close association with *Entradichnus* suggests that *P. beverleyensis* was produced by the same tracemaker. In this area the preservation of internal structure in horizontal traces ranges from not preserved to very well preserved. The ichnogenus name *Planolites* is reserved for those traces that do not exhibit internal structure, while *Entradichnus meniscus* and *Entradichnus* isp. encompass those traces that contain, even faintly, internal backfill structure.

Rose diagrams were created based on three particularly dense *P. beverleyensis* surfaces to determine a preferred orientation (Figure 17). *P. beverleyensis* in this area are considered to be poorly preserved *Entradichnus* burrows, which in other formations have been observed to exhibit a preferred orientation parallel to the depositional dip of the cross-stratified laminae with a downward burrowing direction (Ekdale et al., 2007; Ekdale and Picard, 1985; Seike et al., 2010). Preferred burrowing orientations cannot be ascertained from *P. beverleyensis* burrows.

Surfaces A and C indicate a preferred orientation parallel to the depositional dip direction, although many burrows are at variance with this preference. Surface 2 shows the opposite, with burrows oriented in nearly every direction other than parallel to the depositional dip direction. This discrepancy in orientation preference indicates that downward or upward burrowing is preferred only sometimes. No ichnotaxonomic or environmental significance can be attributed to the burrow orientations. Four specimens of *P. beverleyensis* have been catalogued in the UUIC (UUIC 3335, 3338, 3339, 3340).

3.1.4 *Taenidium* isp. “A”

Taenidium isp. “A” is a tightly packed meniscate burrow that ranges from 4 to 10mm wide and is traceable up to 10cm long, although the true length of the burrow is obscured by outcrop surfaces (Figure 18a, b). *T.* isp. “A” has no lining, does not branch, is variably oriented as straight to sinuous, and is circular in cross section. Individual menisci alternate between red and yellow-stained quartz grains, though grain size remains constant. Thin section analysis shows that darker menisci in the backfill contain more clay in the space between quartz grains. Lighter menisci contain more calcite cement between quartz grains.

T. isp. “A” burrows are locally abundant and densely spaced, though regionally sparse. They commonly are associated closely with carbonate beds well within the Nugget Sandstone, or near the contact with the underlying Chinle Formation. Where *T.* isp. “A” occurs, primary bedding typically is completely obscured, presumably due to intense bioturbation. With the exception of a few well-exposed burrows at each site, a majority of the *T.* isp. “A” surfaces are viewed as a dense ichnofabric rather than a collection of distinct burrows. This texture is referred to as the *Taenidium* ichnofabric and is viewed as iron-stained, mottled surfaces containing faint outlines and occasional meniscate fills of *T.* isp. “A” (Figure 18c).

Taenidium isp. “A” is rarely associated with other trace fossils. They often occur in subaqueously deposited sediment, such as at the Large Mounds locality where they are closely associated with interdune carbonates (Figure 8), although sometimes this sedimentologic interpretation is hindered due to poor outcrop exposure. At the Sounds of Silence locality (Figure 9), T. isp. “A” is adjacent to beds containing abundant *Entradichnus* and *P. beverleyensis* in lower slipface deposits. Neoichnological experiments show that similar traces have been produced in moist, cohesive sand (Counts and Hasiotis, 2009).

T. isp. “A” burrows are similar to “adhesive meniscate burrows,” or AMB (Bown and Kraus, 1983; Hasiotis and Dubiel, 1994; Smith et al., 2008) in that they cannot be easily removed as individual specimens. They do not weather differentially in outcrop, and they have thin menisci alternating between oxidized and unoxidized grains aiding in visibility. However, these burrows do not contain ellipsoid-shaped packets, and there is no relationship between grain size and burrow size. Therefore, the term AMB does not apply to these traces. The name *Taenidium* isp. “A” is used here because this trace fossil does not fit into any preexisting *Taenidium* ichnospecies. A specimen of *T.* isp. “A” has been catalogued in the UUIC (UUIC 3332).

3.1.5 *Taenidium* isp. “B”

Taenidium isp. “B” is a meniscate, unbranched, thinly lined or unlined, vertical to subvertical (up to 15°) burrow. These burrows range from 5mm to 1cm wide and can reach up to 25cm long (Figures 19, 20). *T.* isp. “B” contain menisci oriented either concave up or concave down. *T.* isp. “B” always occurs within thin, wind-ripple laminae that alternate between red and yellow in color. When present, the thin lining is composed of fine-grained, red sand. Within the burrow the menisci displace primary laminae downward or upward by about 1cm (Figure 20).

When in cross section on bedding planes, these burrows appear as red, iron-oxidized rings (Figure 19b). *T.* isp. “B” occurs at three localities and occurs in local abundance in low densities. Discrete burrows are common, and overlap occurs only when multiple burrows form clusters (Figure 20c). The vast majority of *T.* isp. “B” do not weather out in relief, and they are visible due to coloration within the outcrop.

Taenidium isp. “B” is associated with ‘large oblique burrows’, ‘burrow clusters’, and ‘flared burrows’ at the toes of dunes where the slip face transitions into the interdune. It is most abundant at the Cub Creek locality (Figure 10). These associations may represent trophic interactions, since the producer of the ‘large oblique burrows’ may have been an insectivorous scorpionid or vertebrate, possibly preying on the producers of the smaller burrows.

The orientation of the menisci represents direction of movement, where concave-up reflects upward movement and concave-down reflects downward movement (Figure 20a, b). These traces were likely pascichnia, produced by grazing organisms in moist, organic-rich sediment. Because of this, there is no preference for burrowing either upward or downward, though there seems to be very little horizontal burrowing.

When *T.* isp. “B” burrows cross through prominent primary laminae in the sediment, these laminae are displaced inside the burrow. The distance between the primary laminae and the displaced laminae represents the length of the organism, about 1cm. Since these laminae are displaced only once, it is unlikely that these burrows were ever open or reburrowed.

T. isp. “B” burrows are sometimes clustered together (Figure 20c). These clusters may represent hatching sites and subsequent dispersal by grazing larvae, or possibly organic-rich areas exploited by multiple organisms.

The name *Taenidium* isp. “A” is used here because this trace fossil does not fit into any preexisting *Taenidium* ichnospecies.

3.1.6 *Skolithos* and *Planolites* isp.

Skolithos and *Planolites* isp. are short, unlined, unbranched burrows with no internal structure and rounded burrow terminations (Figure 21). *Skolithos* and *P* isp. typically are 5mm to 8mm wide and can reach 7cm long, though true length is obscured by outcrop surfaces. Burrow fill is darker than the matrix, but grain size remains constant. Vertical to subvertical burrows are referred to as *Skolithos*, and less common horizontal to subhorizontal burrows display the same characteristics, and they are referred to as *Planolites* isp. *P*. isp. burrows often show gentle vertical undulation (Figure 21b), and sometimes they are connected with vertical *Skolithos* burrows. Some surfaces contain a high density of mostly *Skolithos*, although individual burrows are distinct with rare crossovers. *Planolites* isp. is differentiated from *Planolites beverleyensis* in that it can be seen in vertical cross section, has a contrasting sediment fill to surrounding matrix, occurs in subhorizontal orientations, and sometimes displays an undulatory form.

Skolithos and *P* isp. occur in beds with an abundance of iron oxide concretions. When preserved on bedding surfaces, *Skolithos* appears as dark circles that could be confused for small concretions (Figure 21b).

Skolithos and *Planolites* isp. are associated with *Grallator* trackways and numerous vertebrate body fossils, and these trace fossils occur exclusively at the Saints and Sinners locality (Figure 3). The horizontal beds containing these fossils are interpreted as shallow lacustrine interdune deposits (Britt et al., 2011; Engelmann et al., 2011). *Skolithos linearis* are common in the Navajo Sandstone in southern Utah as short, unlined, vertical shafts perpendicular to dipping foreset laminae (Ekdale et al., 2007). No *Skolithos* burrows occur within cross-bedded eolian sand in the Nugget Sandstone.

Skolithos and *Planolites* isp. in the Nugget sandstone show no internal structure, which may be an artifact of preservation. Few examples could be interpreted as having faint meniscate fill, in which case they could be classified as *Taenidium*. Additionally, few occurrences superficially appear as discontinuous U-shaped *Arenicolites* burrows, but this habit is not conspicuous or typical. *Skolithos* and *Planolites* isp. are described together here because they display the same distinguishing characteristics, were likely produced by the same tracemaker employing the same ethology, and occur together at only one locality. The name *Planolites* isp. is used in the present thesis to differentiate it from *Planolites beverleyensis*. Although *P isp.* is similar to *P beverleyensis*, it differs in being undulatory, preserved in vertical section, and found only within interdune facies. The *Skolithos* and *Planolites* isp. specimen shown in Figure 21b has been catalogued in the UUIC (UUIC 3333).

3.1.7 ‘Burrow Clusters’

‘Burrow clusters’ consist of hundreds of circular to elliptical burrows that are consistently about 1cm wide and have a red, fine-grained lining (Figure 22). The lining ranges from thin, <1mm, to quite thick, >1cm – sometimes half the width of the burrow – even within the same burrow. ‘Burrow clusters’ occur on vertical and oblique surfaces in wind ripple sediment consisting of thin red and white laminae. ‘Burrow clusters’ form clusters that are dense with overlapping burrows in the centers that become less dense with more individually discrete burrows farther out from the centers. No internal structure can be discerned within the burrows, and only a few are expressed as a longitudinal burrows.

These enigmatic traces are present at two localities and are associated with *Taenidium* isp. “B” and ‘large oblique burrows’ at both, in addition to ‘flared burrows’ at the Orchid Draw locality (Figure 7). These features are not rhizoliths (plant root structures) based on their clustering habit, invariability in size, and tendency to overlap. They are also not considered open chambers due to common overlapping.

It is tempting to associate such a clustering of burrows to colonial eusocial behavior. However, social insects do not have a body fossil record until the Cretaceous Period (Grimaldi and Engel, 2005). Although complex trace fossils interpreted as social insect structures have been described from as far back as the Late Triassic Period (Bordy et al., 2004, 2005; Hasiotis, 2003), these reports are controversial at best (Genise, 2004, 2005; Lucas et al., 2010; Tapanila and Roberts, 2012). Instead, these clusters probably represent hatching centers, much like the clustering of *Taenidium* isp. “B.” This close association and similar size distribution of *T.* isp. “B” with the burrows in the ‘burrow clusters’ begs the interpretation of production by the same tracemaker. However, clusters of *T.* isp. “B” differ from ‘burrow clusters’ in that they are vertical to subvertical burrows with internal structure.

These burrows cannot readily be assigned to an ichnogenus. Clustering cannot be a diagnostic feature, because the burrows spread into isolation. Presence and preservation of iron cement precipitation cannot be a diagnostic feature, because it is a secondary feature. True morphology is indiscernible, and what few vertical burrows are closely associated are assignable to *Taenidium* isp. “B.” These traces remain enigmatic and unnamed. Future discoveries hopefully will lead to a more complete interpretation.

3.1.8 ‘Large Oblique Burrows’

‘Large oblique burrows’ are 4-6cm wide and up to a meter long, making them the largest burrows in the area. ‘Large oblique burrows’ are straight to gently curved, cylindrical, unbranching, unlined, and preserved at low angles to the bedding surface (Figures 23, 24). When burrows intersect the outcrop surface circular cross sections are observed (Figure 23b). Internal structure is only preserved rarely, but a few show inclined laminae along wall margins (Figure 24c). Fill usually consists of sand similar to the surrounding matrix, but it does not include laminations. One burrow has weathered out in relief (Figure 24a), but most are not preserved in relief. No evidence of bioglyphs or scratches is seen, which may be an artifact of preservation or the low resolution offered by medium-grained sand. These burrows are preserved in outcrops with irregular surfaces (Figure 23a) making true lengths and morphology nearly impossible to construe. Because of this, many of the preserved features are likely a portion of an even larger structure.

These particular burrows have been described by Engelmann et al. (in press).

'Large oblique burrows' are present at three localities in northeastern Utah, and are associated with *Taenidium* isp. "B," 'flared burrows', and 'burrow clusters', all of which occur exclusively in dune toe deposits, such as those in the Orchid Draw locality (Figure 7). As explained by Engelmann et al. (in press), these features are differentiated from inorganic water escape structures for multiple reasons: 1) water escape structures would be subvertical, not subhorizontal; 2) water escape structures generally form tabular dikes instead of cylindrical structures indicated by the preserved circular cross sections (Figure 23b); 3) water escape structures would have variable widths and morphologies, not uniform; 4) water escape structures would show deformation along feature margins, such as drag or deflection of laminae, not sharp contacts; 5) rare occurrences of inclined laminae are easier to attribute to burrow excavation than fluidized flow. Similar structures in the Triassic and Jurassic are interpreted as vertebrate burrows (Krapovickas et al., 2012; Loope, 2008).

Lack of internal structure indicates that these were once open burrows, possibly used for protection, reproduction, or thermoregulatory purposes. The few examples of inclined laminae at burrow margins (Figure 24c) could be attributed to the passive infilling of sediment by wind or water, but these features also can be produced biogenically as the burrow excavator throws sediment out of the burrow (Hembree et al., 2012). A discussion of the identity of the possible tracemakers can be found in Engelmann et al. (in press) and in the 'Burrow tracemakers' section of this chapter.

3.1.9 ‘Flared Burrows’

‘Flared burrows’ are vertical to subvertical, 15 to 20cm long, unlined structures that widen up to 10cm at the bottom of an upper shaft that reaches only up to 1.5cm wide (Figures 25, 26). The internal structure of the lower flare is convoluted, but it generally consists of broad, sweeping, slightly concave-up patterns. The upper shaft has no organized internal structure and is visible only because it disrupts the surrounding laminated sediment. Four ‘flared burrows’ occur at two localities within wind-ripple sediment consisting of thin red and white laminae.

‘Flared burrows’ are associated with *Taenidium* isp. “B” ‘burrow clusters’, and a ‘large burrow’, all of which occur in wind-ripple, dune toe deposits. These burrows are the most perplexing of the traces described from this area, because nothing like them has been described from any environment – ancient or modern. It is unclear if the wide lower portion was an open chamber, or just a broader disruption of the sediment possibly for feeding purposes. Close association with *T.* isp. “B” could indicate production by the same tracemaker given that the shaft width of ‘flared burrows’ are similar to burrow widths of T. isp. “B.”

3.1.10 *Paleohelcura*

Paleohelcura, originally described by Gilmore (1926), is a trackway consisting of two parallel rows of alternating groups of three to four leg impressions. Specimens range from 6cm to 10cm wide and have a 4cm to 6cm spacing between groups of impressions, with consistent spacing within a given trackway (Figures 27, 28). In the Nugget Sandstone, groups of impressions generally contain three linearly arranged imprints, and no evidence of body or tail drags is present. Trackways are preserved as filled or unfilled impressions in epirelief on lower slip face surfaces. Some trackways contain push-up rims on down-slope side of impressions. No preferred orientation is discernable, though only three specimens have been discovered in the area. A cast of a portion of the *Paleohelcura* specimen shown in Figure 27 has been catalogued in the UUIC (UUIC 3337).

Paleohelcura is associated with *Octopodichnus* and *Brasilichnium*. One location contains multiple *Brasilichnium* trackways associated with a large *Paleohelcura* trackway (Engelmann et al., 2010), and another occurrence shows all three ichnogenera occurring on one surface in close proximity (Figure 28). *Paleohelcura* also has been described in the Nugget Sandstone near Heber, UT (Albers, 1975; Chure et al., in press), and scorpionid trackways have been mentioned from the Nugget Sandstone near Dinosaur National Monument (Engelmann et al., 2010).

More complete preservation of one side of the trackway is a common feature in trackways of the Nugget Sandstone. This suggests that the animal was walking on a slope with less weight on the set of legs on the upper part of the slope, an explanation supported by the presence of push-up rims on the down-slope side of impressions.

3.1.11 *Octopodichnus*

Octopodichnus, originally described by Gilmore (1927), is a trackway with alternating patterns of four leg impressions in a triangular arrangement (Figure 29). Trackway sizes in this area show little variation, ranging from 7 to 8cm in width, and an 8 to 9cm stride. No evidence of body or tail drags is present.

Octopodichnus in the Nugget Sandstone, like *Paleohelcura,* is preserved as filled or unfilled impressions in epirelief on lower slip face surfaces. No preferred orientation is discernable, but only four specimens have been discovered in the area. One side of some trackways is poorly preserved or absent, and many of the impressions show push-up rims on the down-slope side (Figure 29a). One specimen of *Octopodichnus* was collected by Dinosaur National Monument staff (specimen DNM 0486), and one locality of another specimen has been noted, but not collected (locality DNM 0487). A cast of the *Octopodichnus* specimen shown in Figure 29b has been catalogued in the UUIC (UUIC 3336).

Octopodichnus is associated with *Paleohelcura* and *Brasilichnium*. One site (DNM 0475) preserves all three ichnogenera on the same surface crossing over one another (Figure 28). *Octopodichnus* has also been described in the Nugget Sandstone near Heber, UT (Albers, 1975; Chure et al., in press).

Many trackways in the Nugget Sandstone, including *Octopodichnus*, show one side preserved more completely. This suggests that the animal was walking on a slope with less weight on the set of legs on the upper part of the slope, an explanation supported by the presence of push-up rims on the down-slope side of impressions. The upper side of the *Octopodichnus* trackway on specimen DNM 0486 (Figure 29a) shows more complete preservation in addition to push-up rims that indicate a down-slope direction to the top of the photograph.

3.1.12 *Brasilichnium*

The ichnogenus *Brasilichnium* was described by Leonardi (1981). *Brasilichnium* tracks in the Nugget Sandstone are small, rounded impressions that contain push-up rims on down-slope sides and rarely reveal four toe impressions (Figure 30). They often include relatively smaller manus impressions in addition to the larger pes impressions that average 10mm in diameter. *Brasilichnium* tracks are present at three localities in this area, including those at the Orchid Draw locality (Figure 7) briefly discussed by Engelmann et al. (2010). *Brasilichnium* are preserved on slip face surfaces in epirelief as impressions sometimes filled with coarser sand. Visibility is aided by the presence of desert varnish on slipface surfaces.

Brasilichnium tracks are associated with *Paleohelcura* and *Octopodichnus*. At the Orchid Draw locality, *Brasilichnium* tracks occur with *Paleohelcura* on a dune surface contemporaneous to more distal, wind-ripple dune toe deposits containing 'burrow clusters', 'flared burrows', *Taenidium* isp. "B," and a 'large burrow'. These trackways indicate that the track makers preferentially travel up the slipface (Engelmann et al., 2010). *Brasilichnium* is a common trace fossil in Mesozoic eolian deposits, including the Nugget and its equivalents, and it is attributed to quadrapedal synapsids (Lockley et al., 1994).

3.1.13 Large Vertebrate Trace Fossils

A number of sites containing large vertebrate trackways have been described from the Nugget Sandstone near Vernal, Utah. These include the trace fossils *Grallator, Eubrontes,* *Brachychirotherium, Pseudotetrasauropus, Tetrasauropus,* and *Otozoum* tracks. Brief descriptions and site information are described in this section.

Grallator is an ichnogenus reserved for small tridactyl tracks of functional vertebrate bipeds, whereas *Eubrontes* is reserved for large tridactyl tracks (Hunt and Lucas, 2007). *Grallator* tracks that average 15cm from heel to toe and *Eubrontes* tracks that average nearly 40cm from heel to toe were described from horizontal beds in the Nugget Sandstone in northeastern Utah on the margin of Red Fleet Reservoir by Walker and Harms (1972). *Grallator* and *Eubrontes* were produced by two different species of theropod dinosaurs or by different age groups of the same species of theropod dinosaur (Hamblin et al., 2000; Olsen et al., 1998).

Other smaller tridactyl impressions referable to *Grallator* (Figure 31) occur at the Saints and Sinners locality (Figure 3) and are associated with the *Skolithos* and *Planolites* isp. burrows. These *Grallator* trackways occur on planar surfaces of an interdune lake closely associated with the bone beds within (Britt et al., 2011; Britt et al., 2010; Engelmann et al., 2012; Engelmann et al., 2011) and are attributed to theropod dinosaurs.

Otozoum, a trackway referable to basal sauropodomorphs, occurs with *Grallator* and *Eubrontes* near the top of the Nugget Sandstonenear the western visitor’s center in Dinosaur National Monument. Otozoum tracks are elongated and contain five short toe imprints on pes impressions (Figure 32; Rainforth, 2003).

Brachychirotherium (an aetosaur trackway (Lucas and Heckert, 2011)), *Pseudotetrasauropus,* and *Tetrasauropus* (sauropodomorph trackways (Lockley et al., 2001)) have been described in what was once considered Chinle strata, but is now considered to be the lower Nugget Sandstone, and they do not occur within eolian strata in the Nugget Sandstone (Lockley et al., 1992b; Lockley et al., 2001; Sprinkel et al., 2011). Previously described as the “Cub Creek” locality by Lockley et al., this site is now commonly referred to as the BD locality based on its proximity to Bourdette Draw. Because these horizontal beds of the Nugget Sandstone are similar to those of the Chinle Formation, these trackways were preserved before the climate was sufficiently arid to produce large dunes.

3.2 Identity of Tracemakers

Linking tracemakers with the trace fossils described in the previous section is facilitated by studying modern burrowers in similar environments. This is a worthwhile endeavor when attempting to understand the ecology of the ancient ecosystem. However, difficulties arise when comparing modern dune settings to the 200 million year old Nugget erg, primarily because there are no good modern analogues – environmental, ecologic, climatic, or sedimentologic. One reason for this is that the Nugget Sandstone predates the evolution of angiosperms, social insects, and eutherian mammals, all of which dominate modern desert environments today. Interpretations can also be muddled by the fact that many organisms can create the same type of burrow and that a single organism can produce several types of burrows. Further complicating matters, insects with multiple life stages may produce different structures during successive life stages. Additionally, body fossils of likely tracemakers of most of the burrows described are nonexistent. Nonetheless, this section provides a short exploration of possible tracemakers and their ecology in the Nugget erg.

Neoichnological studies of burrows in eolian settings are few and far between. Among the most comprehensive, Ahlbrandt et al. (1978) is often cited when assigning modern analogues (Bown and Kraus, 1983; Ekdale et al., 2007; Ekdale and Picard, 1985; Frey et al., 1984; Loope and Rowe, 2003; Retallack, 2001). More recently, other studies have addressed modern burrowers and burrow morphology in more detail (Counts and Hasiotis, 2009; Davis et al., 2007; Hembree, 2009; Hembree et al., 2012; Smith and Hasiotis, 2008; Smith et al., 2008; Tschinkel, 2002). These papers offer information about only a few existing modern burrowers, and they represent a growing research interest in continental neoichnology. Such neoichnological studies will prove valuable in interpreting trace fossils such as those described in this thesis. Numerous books offer extensive information on modern desert biology and ecology, but they provide little information on tracks and traces (Cloudsley-Thompson, 1996; Costa, 1995; Crawford, 1981; Heatwole, 1996; Louw and Seely, 1982; Punzo, 2000; Ward, 2009).

In order to cope with varying and unpredictable environmental conditions, desert organisms, including plants, tend to be opportunistic, and either generalists or specialists. Opportunistic generalists tend to be longer-lived and more mobile creatures that usually rely on a few types of food and resources but take advantage of episodic, more attractive alternatives. Opportunistic specialists, alternatively, tend to be shorter-lived and less mobile species that emerge after sufficient rainfall (Louw and Seely, 1982). Wet periods in deserts create an explosion of life in interdune ponds. Algae, bacteria, and protozoans multiply within hours, previously dormant small crustaceans and ephemeral plants appear within days (Louw and Seely, 1982), and specialized secondary consumers follow shortly thereafter.

It seems reasonable to conclude that fossils that occur exclusively within beds interpreted as wet interdune deposits – *Taenidium* isp. “A,” gastropod molds, *Skolithos*, *Planolites* isp., and possibly *Taenidium* isp. “B” and ‘burrow clusters’ – represent opportunistic specialism in the fossil record. This interpretation does not help to narrow the identification of the tracemakers, since closely related species can adopt contrasting techniques. For example, most tenebrionid beetles in the Namib Desert are long-lived generalists, while their close relative, *Eustolopus ocoseriatus*, is a highly specialized tenebrionid that occurs following adequate rainfall to feed on grasses, which may only occur once or twice in a decade (Louw and Seely, 1982).

Louw and Seely (1982) generalize that “most plants and animals survive in the desert because they do not live in the desert.” This suggestion alludes to physiological and behavioral traits that allow desert organisms to survive by avoiding harsh desert conditions. Among the many physiological and behavioral traits observed in modern desert animals, burrowing is common, and burrows of course have a high preservational potential.

Burrowing is a widespread habit in desert environments because of the ease of burrowing in a sandy substrate. Excavating loose sand requires fewer morphological and/or behavioral adaptations than excavating firmer substrates, thus allowing a wider variety of organisms to burrow.

Burrowing can be either permanent or temporary. Earthworms, moles and mole rats almost never leave their burrows, while many insects and arachnids are scavengers that spend part of their life outside their burrows (Costa, 1995). Some insects have subterranean larval phases, but as adults they adopt a subaerial behavior (Costa, 1995).

Burrows can be used for shelter, reproduction, aggregation, feeding, and locomotion. They also can create a thermally stable environment by providing shade and cooler temperatures, or they may act as a hiding place for predation, such as in the case of tiger beetles of southern Utah that wait beneath the entrance of their burrow for unsuspecting prey to pass overhead (Crawford, 1981). Some tenebrionid beetles dig trenches that could be confused with burrows on dune surfaces to collect moisture from fog (Seely and Hamilton, 1976). Fossil burrows with internal meniscate structure, such as the *Entradichnus* and *Taenidium* ichnospecies and 'flared burrows', probably represent locomotion (repichnia) or grazing (pascichnia) behavior. Possible open burrows in the Nugget Sandstone, such as the 'large oblique burrows', *Skolithos* and *Planolites* isp., could represent shelter (domichnia), reproduction or thermoregulatory behaviors.

In desert areas today, invertebrates include protozoans, nematodes, gastropods, isopods, arachnids, myriapods, and various insects of the clades Hymenoptera, Orthoptera, Diptera, Isoptera, Coleoptera, Blattodea, Thysanoptera, and Lepidoptera and Hemiptera. The large group of organisms in this list is not surprising, since small ectotherms are best adapted to the intense solar radiation and unpredictable supply of food and water offered by desert environments, and therefore they are most abundant (Crawford, 1981). This list can be narrowed to include only invertebrates that fit three criteria: they are known to burrow in desert environments, are of similar size to the described burrows, and are known to have evolved by the Late Triassic. This list includes gastropods (pulmonate snails), isopods, arachnids (spiders and scorpions), myriapods (millipedes and centipedes), and insects of the orders Hymenoptera (solitary wasps), Orthoptera (crickets), Diptera (flies), Blattodea (cockroaches), Coleoptera (beetles) and

Hemiptera (cicadas). There is little detailed information in the literature regarding modern burrow morphology for many of these taxa. With the exception of gastropods (present thesis), ostracodes (Doelger, 1981; Harshbarger et al., 1957; Winkler et al., 1991) and conchostracans (clam shrimp; Harshbarger et al., 1957; Lewis et al., 1961), no other invertebrate body fossils have been described in the Nugget or Navajo sandstones.

Gastropod burrows have received little attention in the literature. Ahlbrandt et al. (1978) refer to them as shallow burrowers in permanent and ephemeral interdune ponds. Interdune carbonates in the Nugget Sandstone contain few gastropod remains (Figure 4), but no burrows attributed to gastropods have been identified.

Desert isopods today can build 50cm deep vertical burrows with attached horizontal branches terminating in chambers (Shachak, 1980). This type of burrow morphology indicates socialism, a behavior not known to have existed during the Jurassic (Grimaldi and Engel, 2005), nor a behavior represented by structures identified in the Nugget Sandstone.

Modern arachnids, including scorpions and spiders, produce trackways similar to *Paleohelcura* and *Octopodichnus* as preserved in the Nugget Sandstone. *Paleohelcura* and *Octopodichnus* traditionally have been attributed to scorpionids and spiders, respectively (Brady, 1947, 1961; Faul and Roberts, 1951; Lockley et al., 1995), but recent work shows that either trackway could be produced by both spiders and scorpions (Davis et al., 2007; Sadler, 1993). Because of this, *Paleohelcura* and *Octopodichnus* are attributed to arachnids in general. Solfugids may produce these types of trackways, but no neoichnological studies have addressed them.

Arachnids are also known to burrow in eolian environments. Some spiders produce vertical, silk-reinforced open burrows on stoss sides of dunes (Ahlbrandt et al., 1978; Lubin and Henschel, 1990). No such burrows have been identified in the Nugget Sandstone. Some scorpions are known to be highly active burrowers, and studies have shed light on modern burrow morphologies (Harrington, 1978; Hasiotis and Bourke, 2006; Hembree et al., 2012). The 'large oblique burrows' in the Nugget Sandstone have been attributed to small therapsids or large scorpions (Engelmann et al., in press). Neoichnological studies (Hembree et al., 2012) show that modern burrow morphologies of scorpions are consistent with the 'large oblique burrows' in the Nugget Sandstone in several respects: 1) scorpion burrows typically are constructed at low angles to the surface and often are straight or slightly curved; 2) some scorpion burrows can reach 2m in depth; 3) scorpion burrows have no lining and reveal a sharp contact with the surrounding sediment; 4) scorpion burrows do not preserve bioglyphs; 5) scorpions can produce inclined laminae, as seen in a few 'large oblique burrows' (Figure 24c), by throwing sediment out of the burrow.

Some common characteristics of scorpion burrows are not observed in burrows in the Nugget, such as elliptical cross sections and helical, U-shaped or maze-like morphologies. Other characteristic features are not preserved, such as burrow openings. Evidence of small vertebrates is present in the Nugget Sandstone from this area from the Saints and Sinners Quarry (Britt et al., 2010; Britt et al., 2011; Chambers et al., 2011; Engelmann et al., 2011; Engelmann et al., 2012), so burrow production by small vertebrates cannot be ruled out.

The presence of carnivorous spiders and scorpions in this ecosystem obviously suggests the presence of prey. Scorpions can eat a wide range of organisms, some of which are known to burrow, including other scorpions, spiders, harvestmen, wood lice, myriapods, grasshoppers, crickets, mantids, cockroaches, earwigs, beetles, flies, butterflies, ants, and even small lizards and mice (Costa, 1995). This diversity of food preference by scorpions complicates the identification of other possible tracemakers based on trophic interactions.

Millipedes can produce horizontal meniscate burrows (Retallack, 2001), and they prefer wet sediments or soils. Retallack (2001) attributed Ordovician *Scoyenia* to millipedes. Neoichnological work by Hembree (2009) shows that millipedes construct open burrows by either compressing or excavating sediment. Their burrows range from horizontal to vertical and may contain a terminal chamber. No such traces have been identified in the Nugget Sandstone.

Wasps can create open vertical, subvertical or horizontal burrows depending on the burrow type, which include test, sleeping, nesting and false burrows (Ahlbrandt et al., 1978). Modern wasps are particular about texture and cohesiveness of the substrate (Ahlbrandt et al., 1978), and they typically prefer stoss sides of dunes (Loope and Rowe, 2003). *Skolithos* and *Planolites* isp. burrows could be attributed to wasps, although they are located in an interdune interval that is thought to have been deposited by standing water.

Crickets can create straight burrows, sometimes branching, oriented obliquely into damp, cohesive dune slopes on both stoss and lee sides (Ahlbrandt et al., 1978; Loope and Rowe, 2003). Some sections of the burrows may be backfilled, while others remain open. *Taenidium* isp. "B," *Skolithos* and *Planolites* isp. could be attributed to crickets.

Fly larvae burrow just beneath dune surfaces and produce meniscate filled burrows (Ahlbrandt et al., 1978). *Entradichnus meniscus* has been attributed to crane fly larvae (Ekdale et al., 2007; Seike et al., 2010). One locality in the Nugget Sandstone shows examples of *Entradichnus meniscus* that transition into *Entradichnus* isp., interpreted as being produced by alternations in appendage movement, within the same burrow. If larvae produce *Entradichnus meniscus* in the Nugget Sandstone, then *Entradichnus* isp. is more difficult to explain. A similar style of backfill described by Bromley and Asgaard (1979) is interpreted as alternations in the direction of the animal's anus as pulses of transported sediment are deposited, either by ingestion or peristalsis. Nonetheless, larvae remain suspect in the production of *Entradichnus* and *Planolites beverleyensis*, which is thought to be poorly preserved *Entradichnus*.

Both larval and adult cockroaches, like crane fly larvae, are known to burrow horizontally just beneath surfaces of sand dunes (Hawke and Farley, 1973). Similarly *Entradichnus meniscus*, *Entradichnus* isp. and *Planolites beverleyensis* could be attributed to cockroaches. Little is known about the morphology of cockroach burrows, but if adult cockroaches produce horizontal meniscate traces, it is possible that *Entradichnus meniscus* and *Entradichnus* isp. could be produced by simultaneous and alternating appendage motion, respectively, of cockroaches. This would help explain the two behaviors interpreted from within a single horizontal burrow in the Nugget Sandstone.

Beetle larvae can produce straight, vertical to subvertical burrows with densely packed meniscate fill (Counts and Hasiotis, 2009). These types of burrows are produced in subaerial, moist, sandy soil. Based on the interpretations and photographs of modern beetle larvae burrows (Counts and Hasiotis, 2009), *Taenidium* isp. "A" can be attributed to beetle burrows. Tiger beetle larvae create open, vertical burrows in moist interdune sand (Ahlbrandt et al., 1978), and adult chafer beetles use a sand-swimming motion to move through the substrate, creating collapsed burrows that, when vertical, contain chevron-shaped fill (Counts and Hasiotis, 2009). Neither of these structures is identified in the Nugget Sandstone.

Cicadas can also produce burrows similar to *Taenidium* isp. "A" (Smith and Hasiotis, 2008; Smith et al., 2008), though cicada burrows contain ellipsoid-shaped packets not seen in T. isp. "A." Cicada burrows typically occur in alluvial deposits and paleosols (Smith and Hasiotis, 2008; Smith et al., 2008).

Only some of the trace fossils described in this thesis have been attributed to the work of a particular group of organisms. Others, such as the 'flared burrows' and 'burrow clusters', remain completely cryptic. These enigmatic trace fossils could be the work of taxa that no longer exist, behaviors that no longer exist, or behavior that has yet to be described in modern settings.

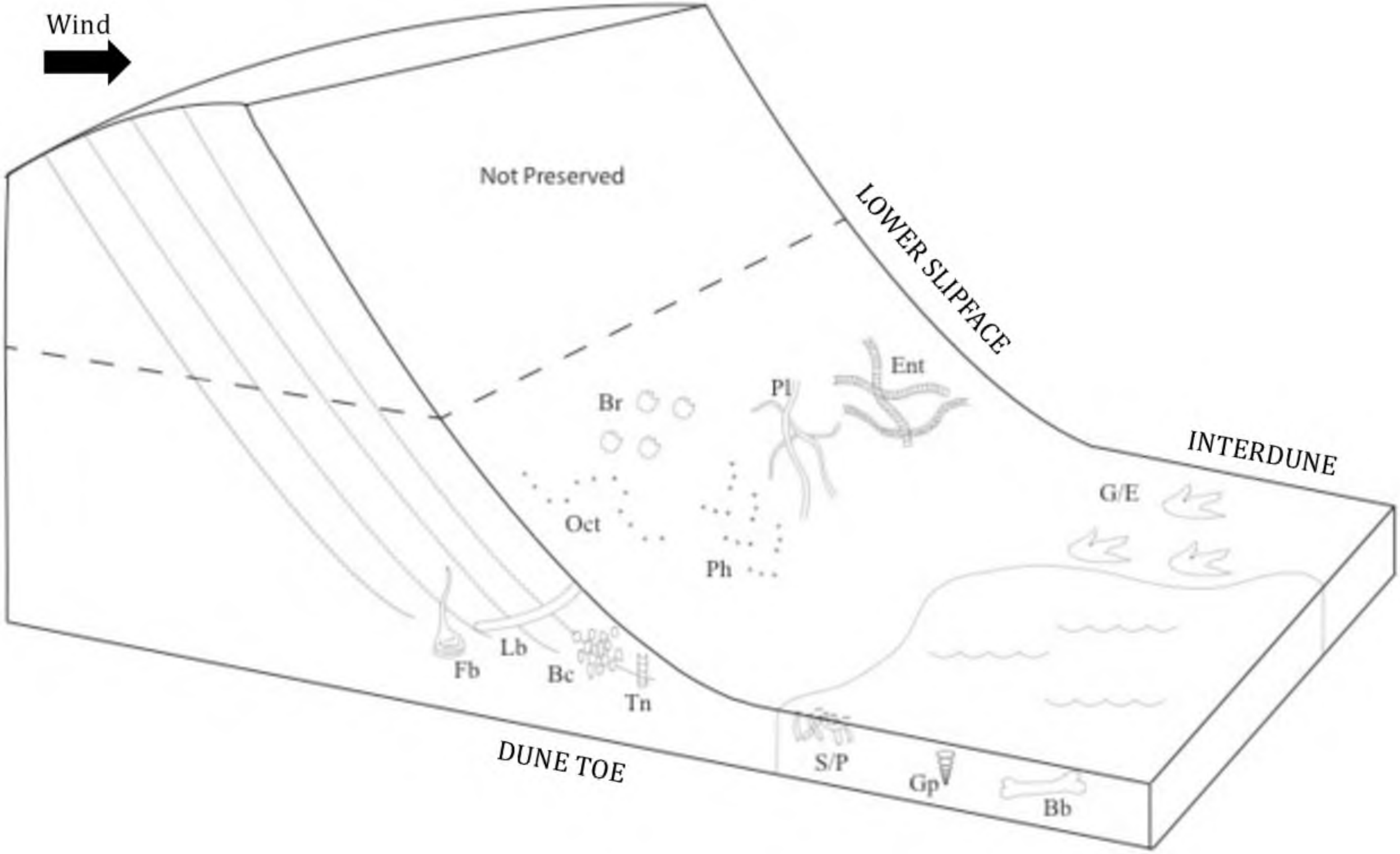


Figure 11. Idealized sketch of trace fossil and body fossil associations in the Nugget Sandstone of northeastern Utah. Bc, 'burrow clusters'; Br, *Brasilichnium*; Ent, *Entradichnus*; Fb, 'flared burrows'; G/E, *Grallator* and *Eubrontes*; Gp, gastropods; Lb, 'large oblique burrows'; Oct, *Octopodichnus*; Ph, *Paleohelcura*; Pl, *Planolites beverleyensis*; S/P, *Skolithos* and *Planolites* isp.; Tn, *Taenidium*; Bb, bone bed.

Figure 12. Entradichnus meniscus in hyporelief. *E. meniscus* in (A) is shown in (B) for context. Scale bar units = 1cm. (B) *Entradichnus meniscus* with *Planolites beverleyensis* in hyporelief. Black arrow indicates burrow shown in (A). Scale bar units = 1cm.

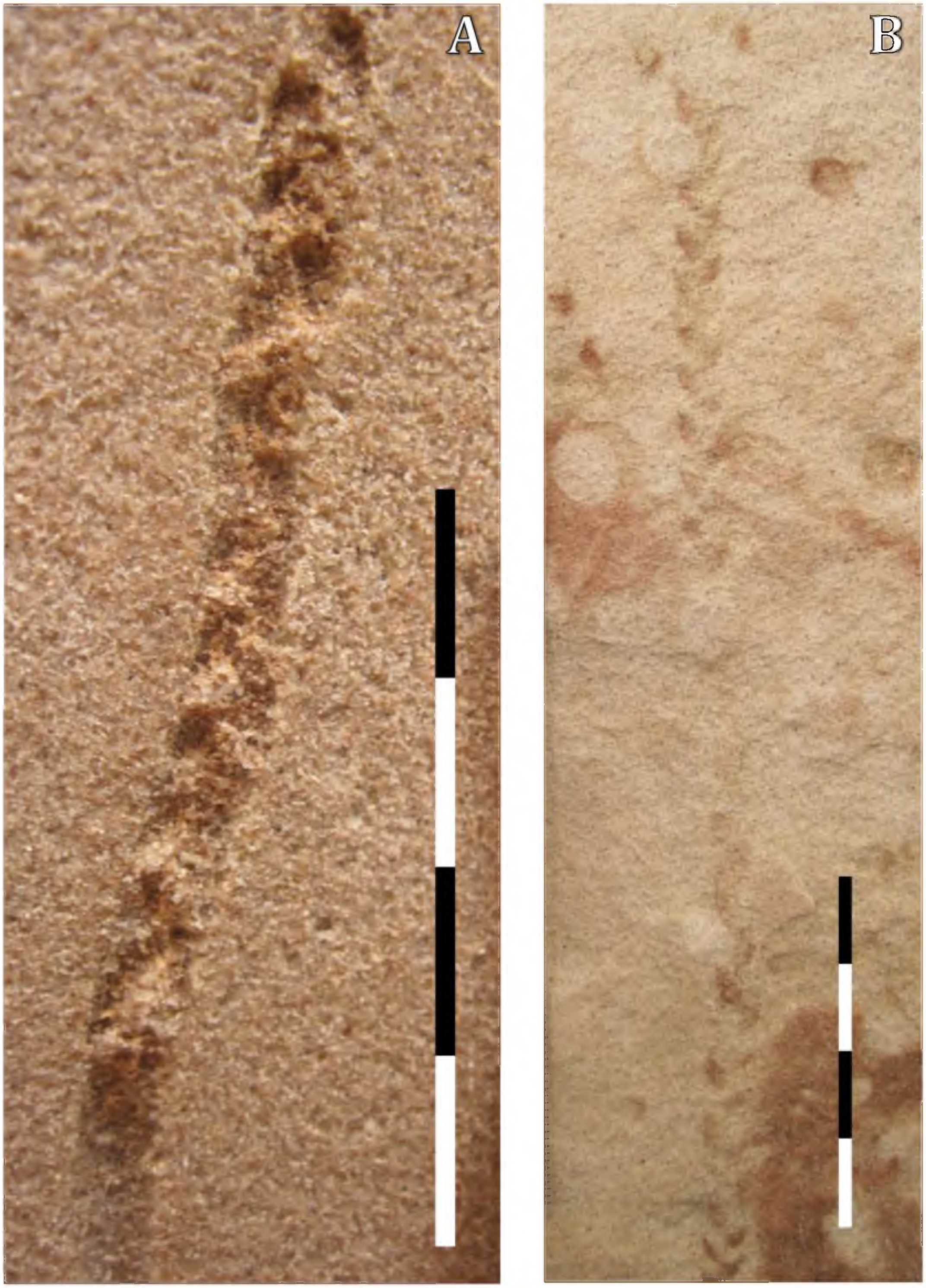


Figure 13. Entradichnus isp. displaying its characteristic "feather stitch" backfill. *E.* isp. is preserved in (A) negative hyporelief and (B) with no relief as a contrasting color to the surrounding sediment. Scale bar units = 1cm.

Figure 14. Entradichnus burrow containing characteristic meniscate backfill of *E. meniscus* to the right of the image, and characteristic “feather stitch” backfill of *E.* isp. to the left, with a transition zone between these two distinct backfills. Scale bar units = 1cm.

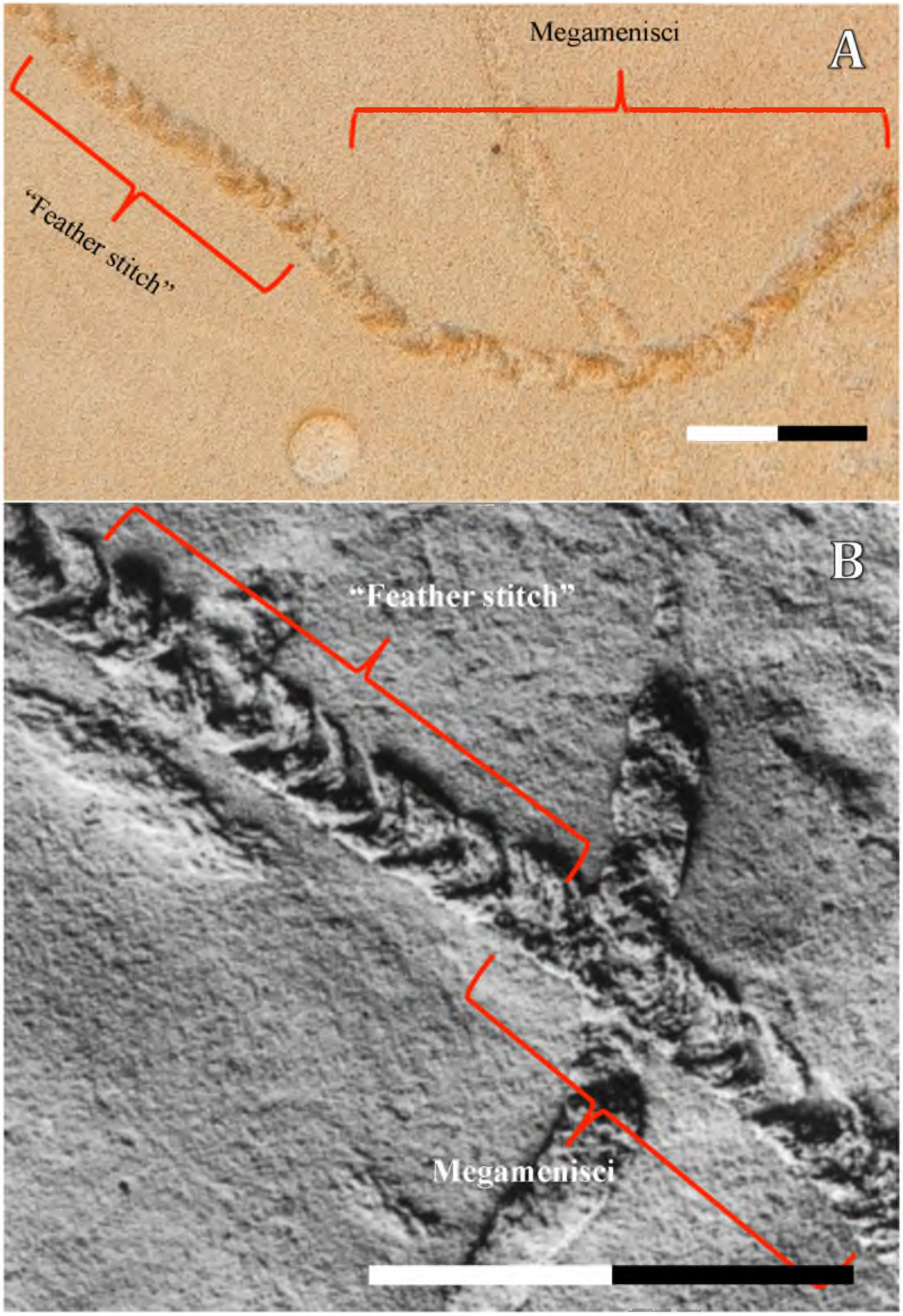


Figure 15. Backfill of (A) *Entradichnus* from the Nugget Sandstone compared to the backfill of (B) *Scoyenia gracilis* from a Triassic fluvial deposit in Greenland (Bromley and Asgaard, 1979). Scale bar units = 1cm.

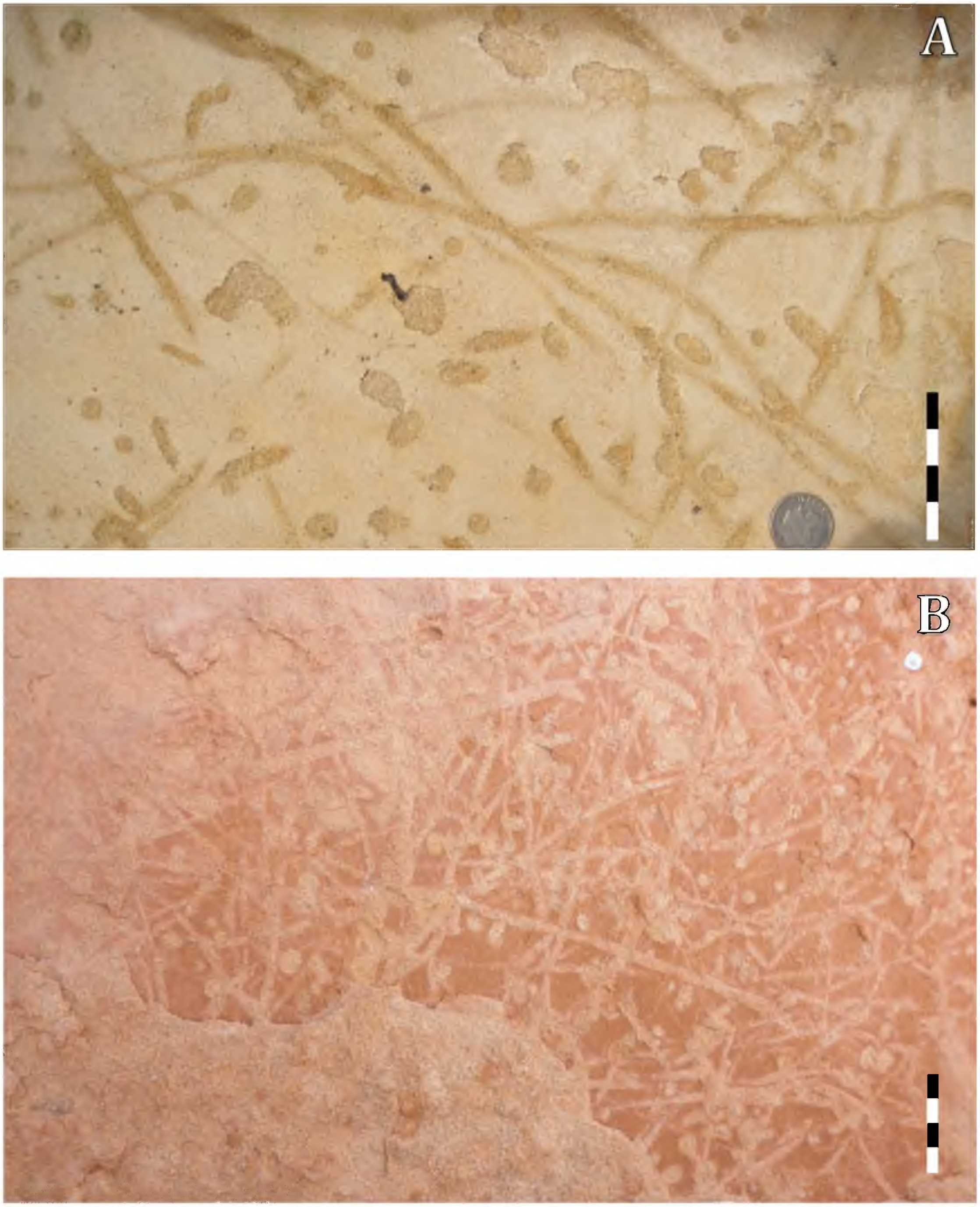


Figure 16. Planolites beverleyensis in preserved in hyporelief. (A) closely resembles specimens UUIC 3335, 3338, and 3341. Scale bar units = 1cm.

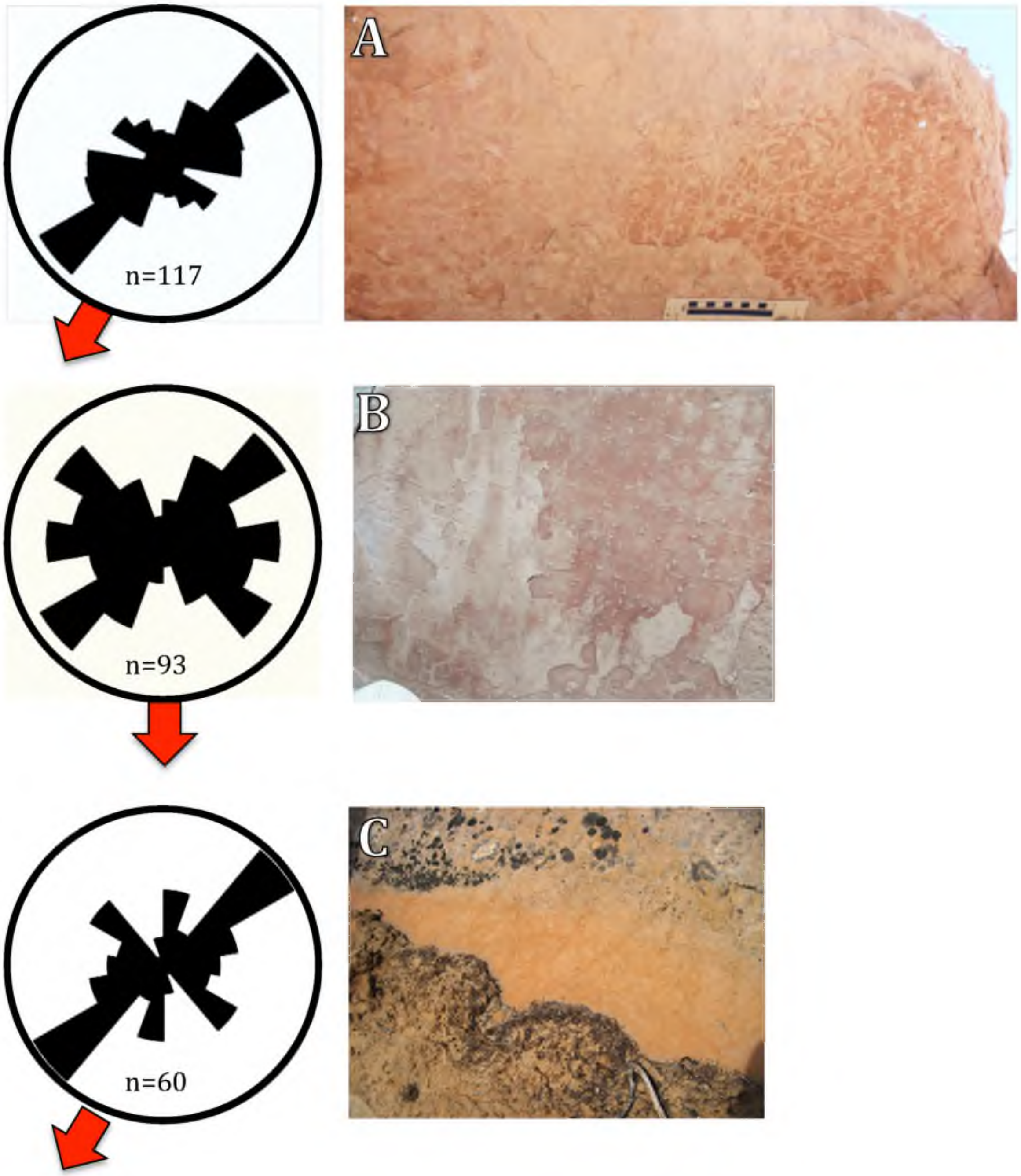


Figure 17. Rose diagrams of dense *Planolites beverleyensis* orientations and photos of their corresponding bedding surfaces. Photo orientation is the same as that of the rose diagrams. Burrow orientations were measured and placed into 20° bin increments in rose diagrams, and red arrows indicate dune foreset depositional dip directions. *P. beverleyensis* in this area are considered to be poorly preserved Entradichnus burrows.

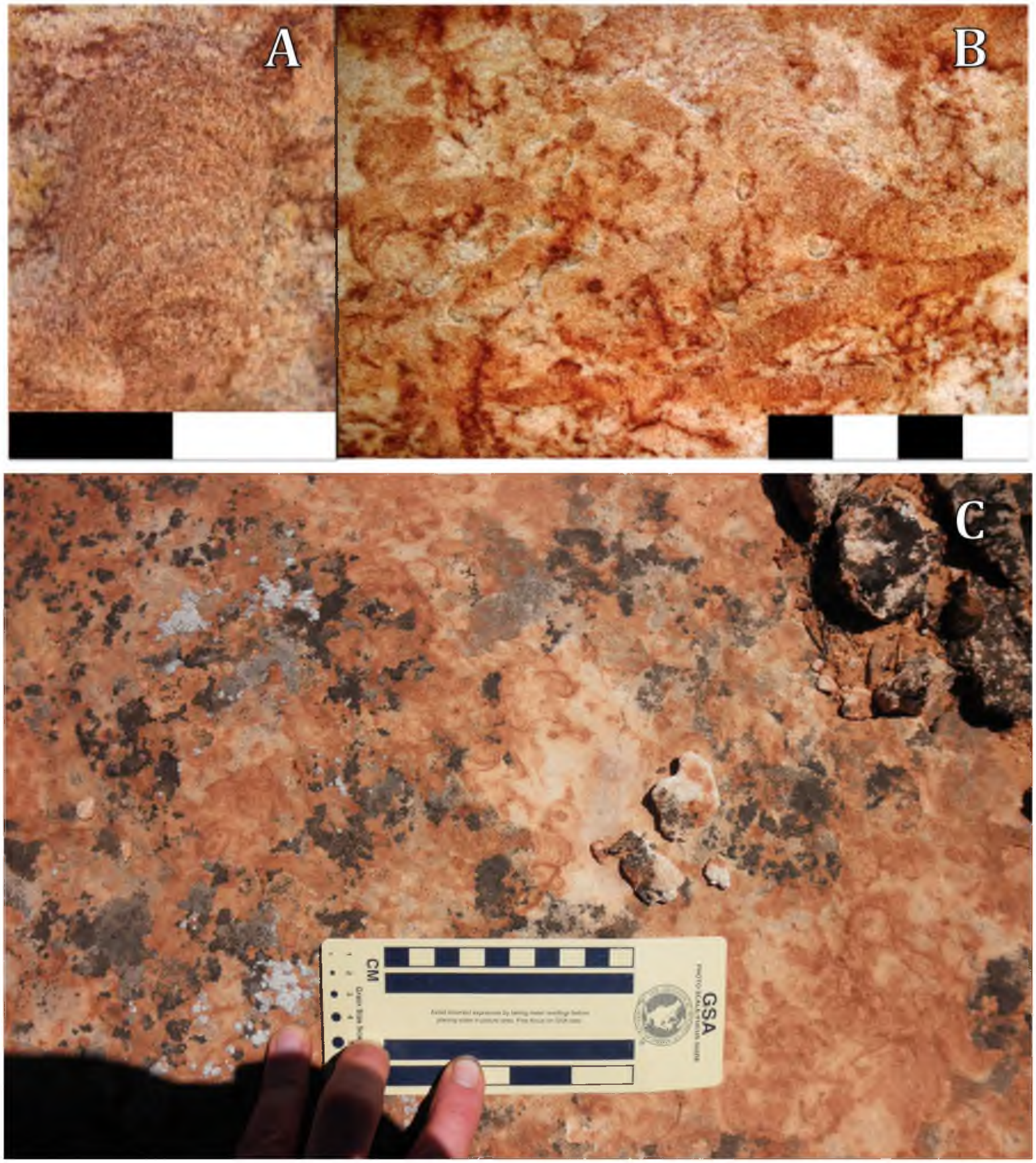


Figure 18. Taenidium isp. “A” preserved both (A) in relief and (B) with no relief as a contrasting color to the surrounding sediment. (C) *Taenidium* ichnofabric, viewed as iron-stained, mottled surfaces containing faint outlines and occasional meniscate fills of *T. isp. “A”. Specimen* UUIC 3332 contains *T.* isp. “A” and the *Taenidium* ichnofabric. Scale bar units = 1cm.

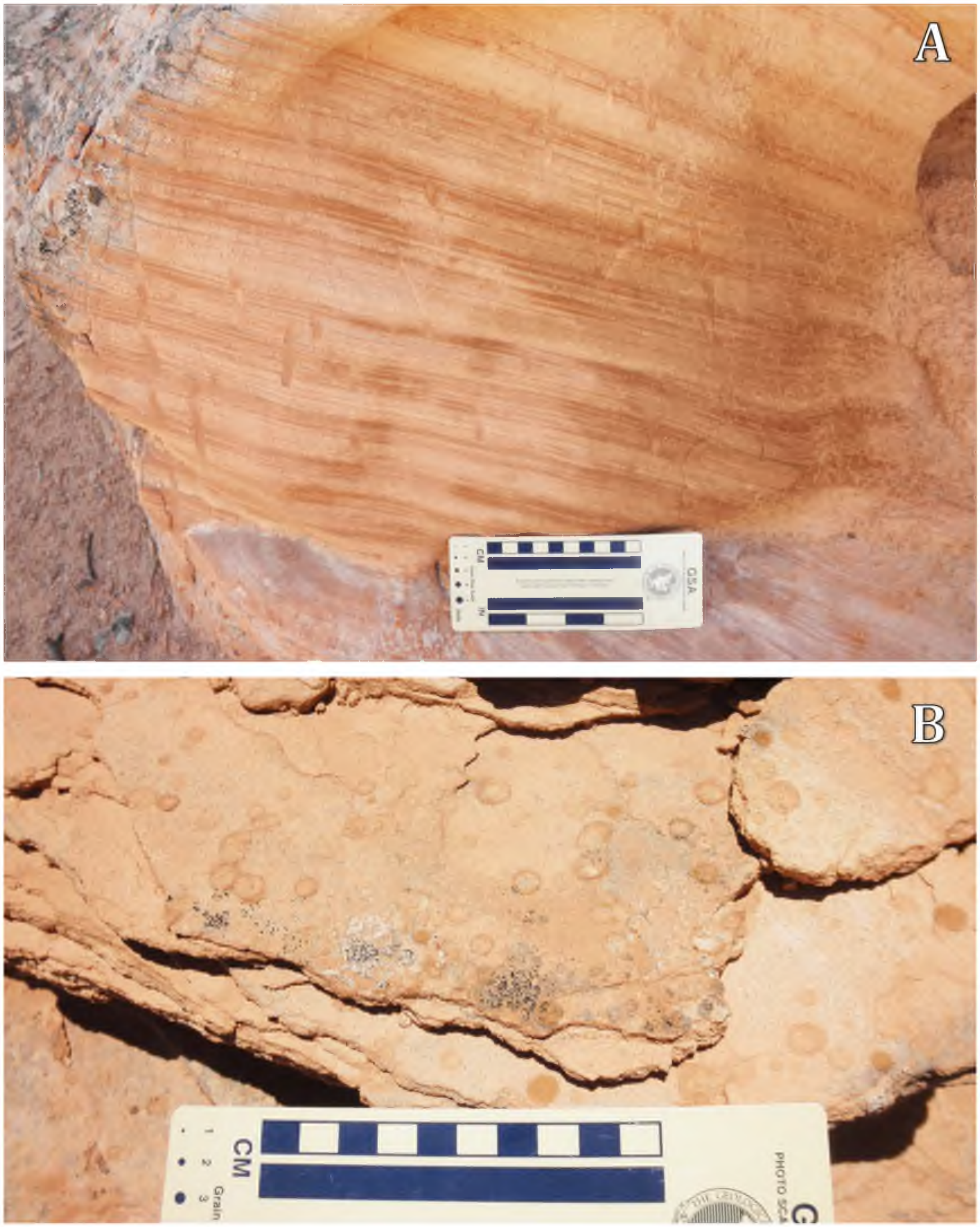


Figure 19. *Taenidium* isp. “B” at the Cub Creek locality preserved in (A) vertical cross section and (B) on bedding planes as red, iron-oxidized rings. Scale bar units = 1cm.

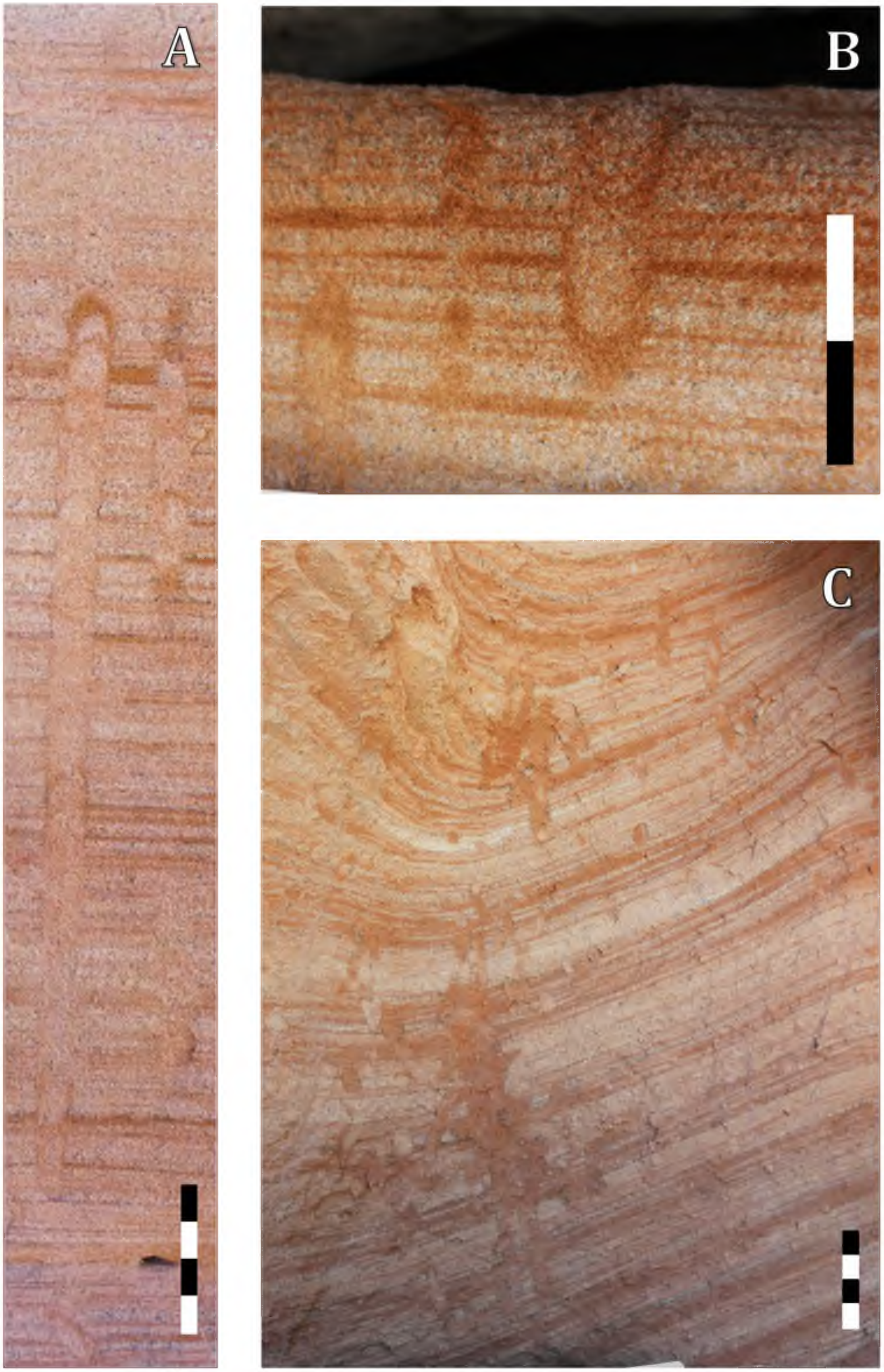


Figure 20. Taenidium isp. “B” preserved in vertical cross section in (A) concave-down (photo courtesy of NPS), and (B) concave-up orientations, and (C) clustered together. Scale bar units = 1cm.

Figure 21. Skolithos and *Planolites* isp. at the Saints and Sinners Quarry. (A) *Skolithos* and *P*. isp. clustered and overlapping in vertical cross section. (B) *P*. isp. with *Skolithos* on a bedding surface (UUIC 3333), bracket indicates *P.* isp. exhibiting common gentle vertical undulation. (C) *Skolithos*-dominant surface in vertical cross section. Scale bar units = 1cm.

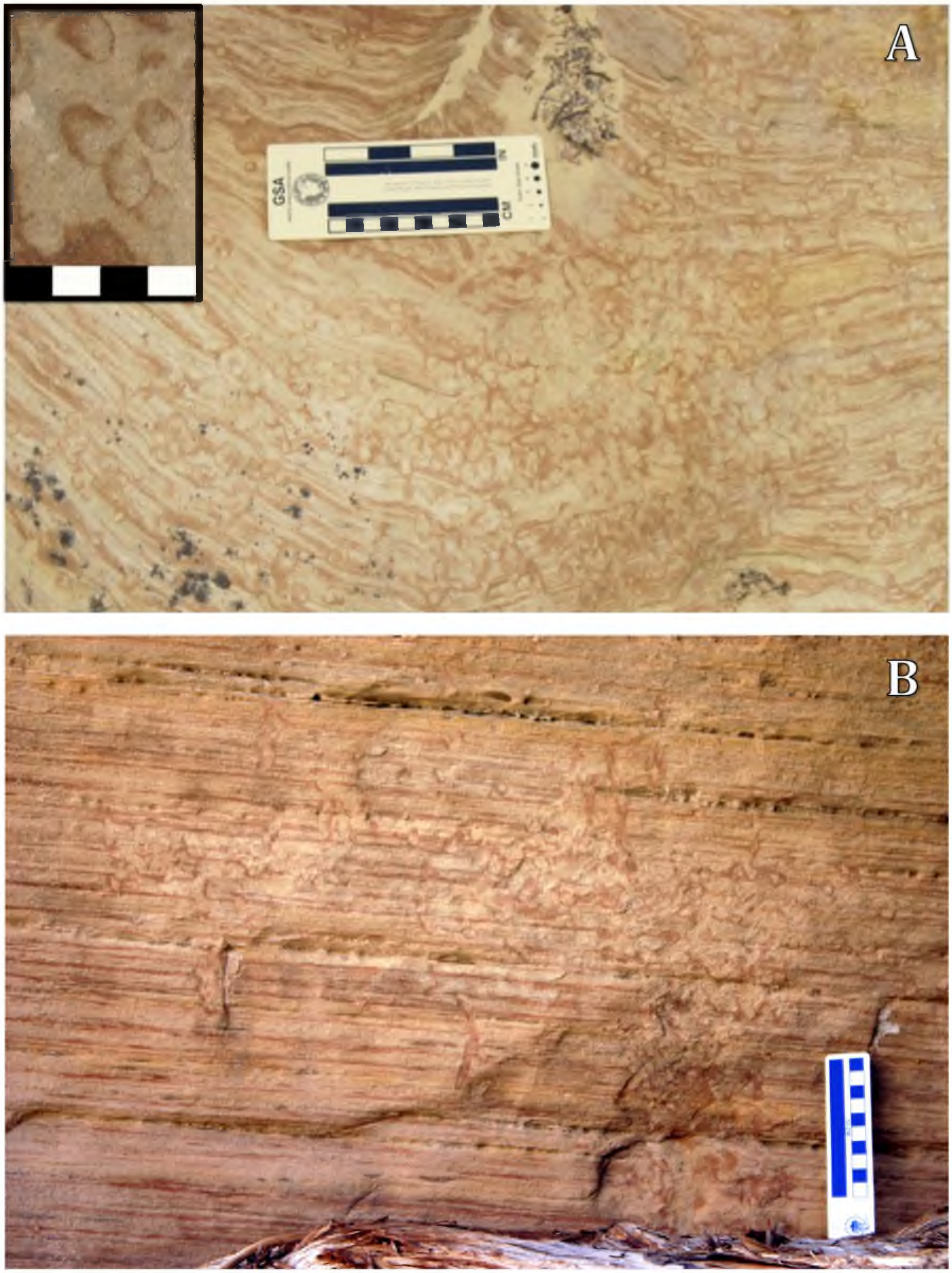


Figure 22. 'Burrow clusters' at Orchid Draw locality in (A) oblique section, inset shows close-up of lining, and (B) vertical cross section (photo courtesy of NPS). Specimen UUIC 3334 exhibits 'burrow clusters'. Scale bar units = 1cm.

Figure 23. 'Large oblique burrows' preserved on oblique outcrop surfaces. (A) Locality of dense associations of 'large oblique burrows'. Arrow indicates the location of burrow photographed in (C). (B) Photograph of vertical cross section view, taken at low angle on oblique outcrop surface of burrow cross section indicated by arrow in (C). Inset indicates outline of cross section in red. (C) 'large oblique burrow' and cross section, located on surface indicated by arrow in (A). Scale bar units = 10cm.

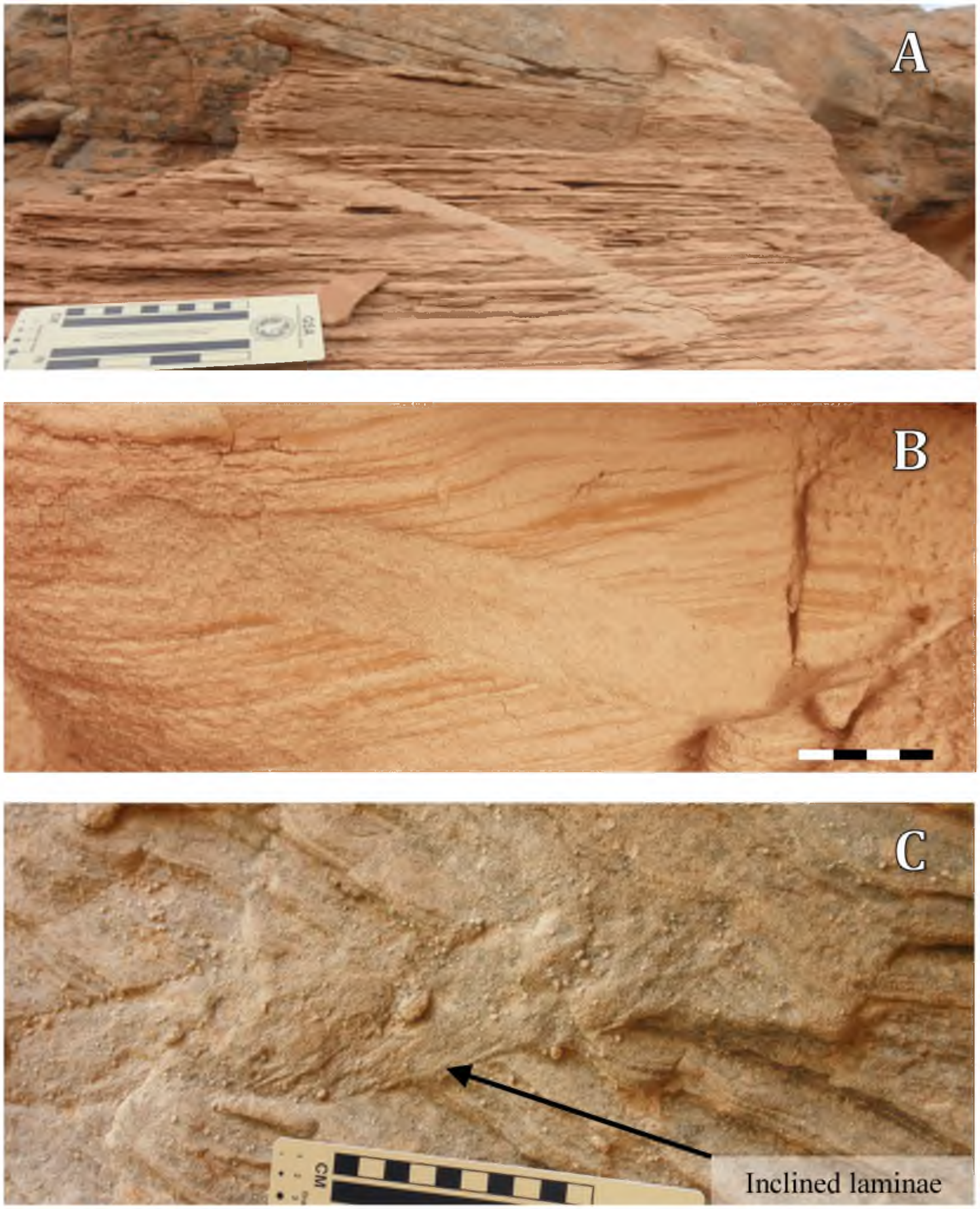


Figure 24. 'Large oblique burrows' at low angles preserved both (A) in relief and (B) with no relief as a contrasting color to surrounding sediment. (C) Inclined laminae are preserved along margin wall of a 'large oblique burrow'. Scale bar units = 1cm.

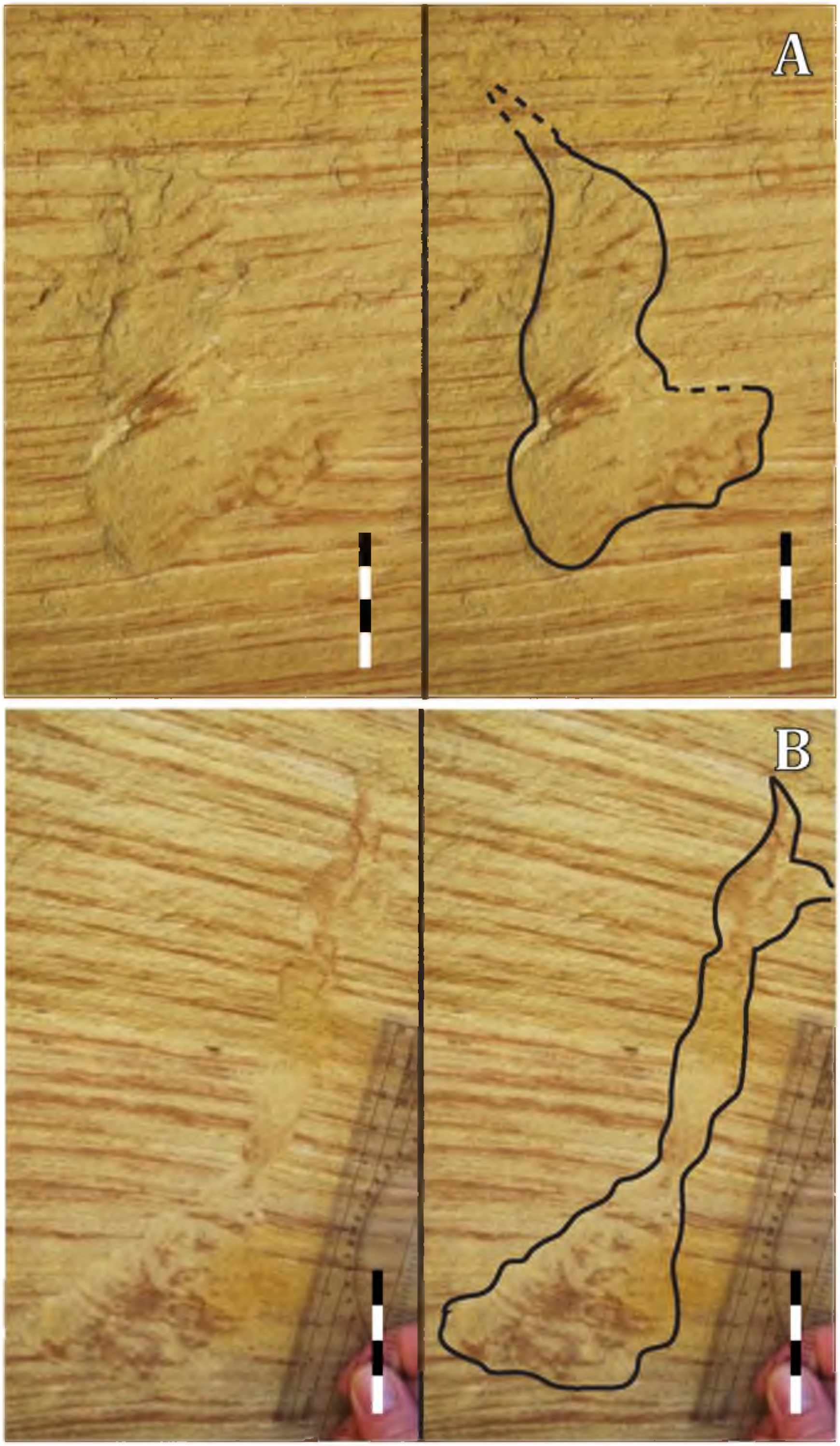


Figure 25. 'Flared burrows' in vertical cross section at the Orchid Draw locality. Interpreted burrow margins are outlined in duplicate photographs. Scale bar units = 1cm.

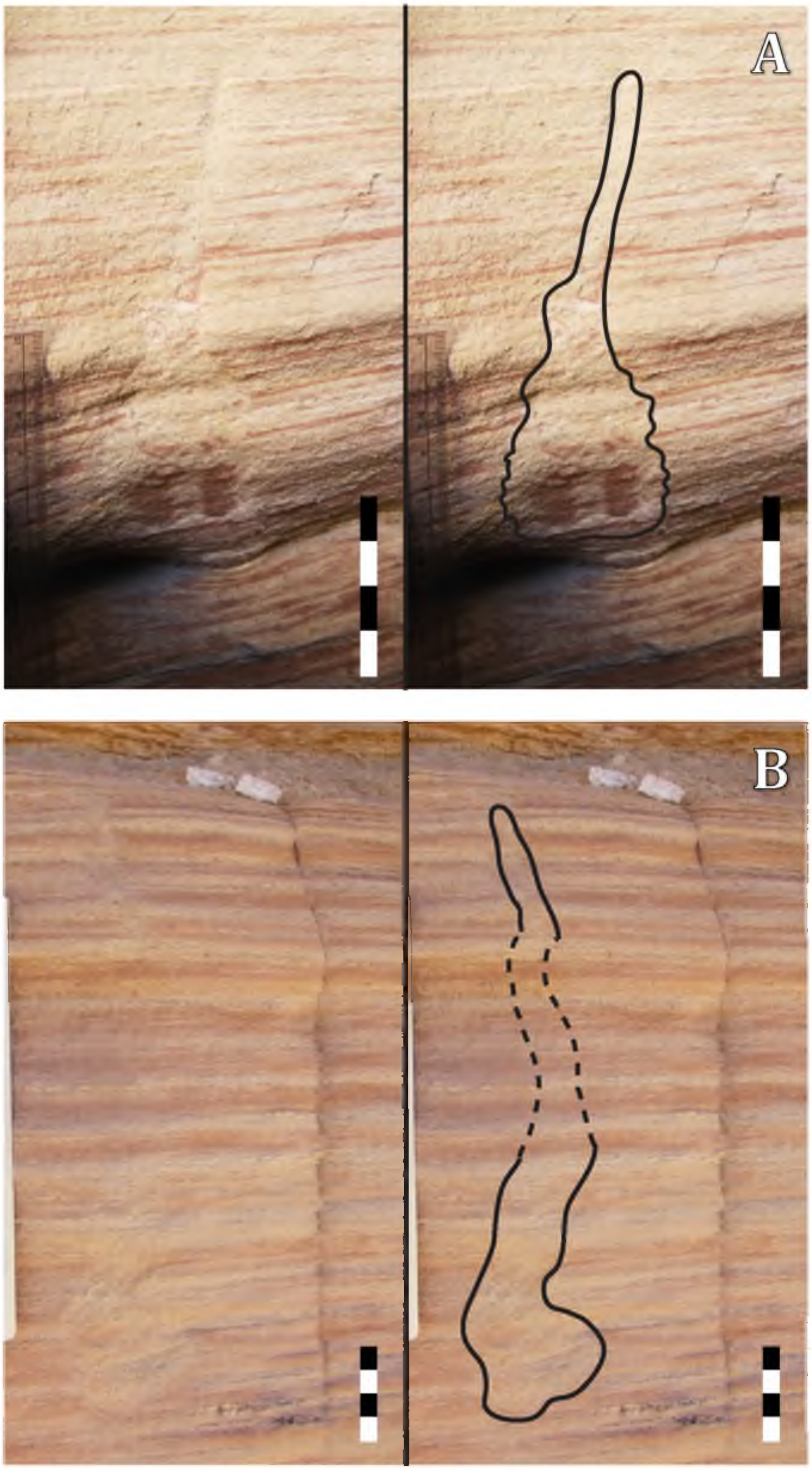


Figure 26. 'Flared burrows' in vertical cross section at the Orchid Draw locality. Interpreted burrow margins are outlined in duplicate photographs. (B) Photograph courtesy of Daniel Chure, NPS. Scale bar units = 1cm.

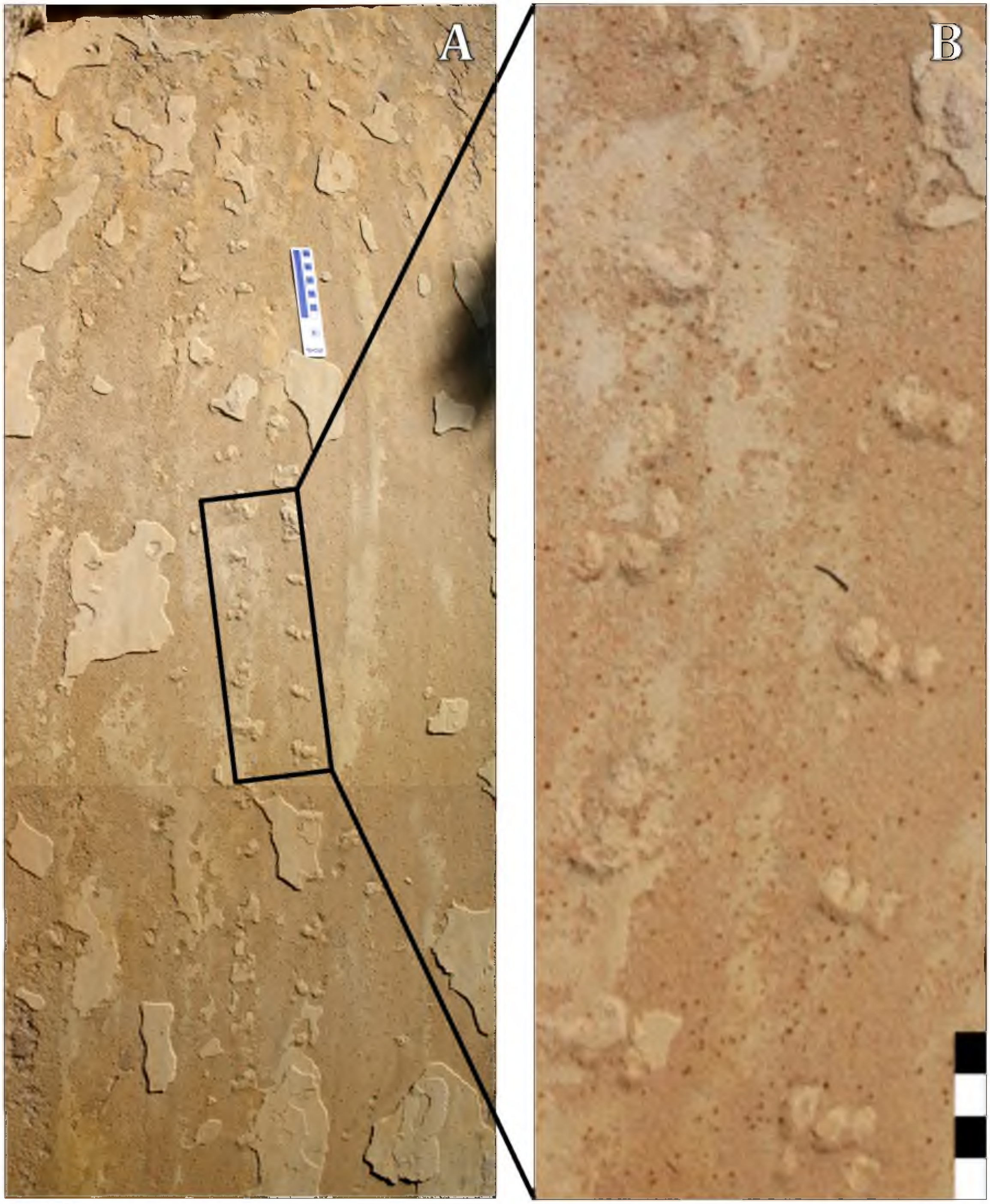


Figure 27. (A) *Paleohelcura* preserved in epirelief at the Orchid Draw locality with (B) close-up image. Specimen UUIC 3337 is a cast of a portion of this trackway. Photos courtesy of Daniel Chure, NPS. Scale bar units = 1cm.

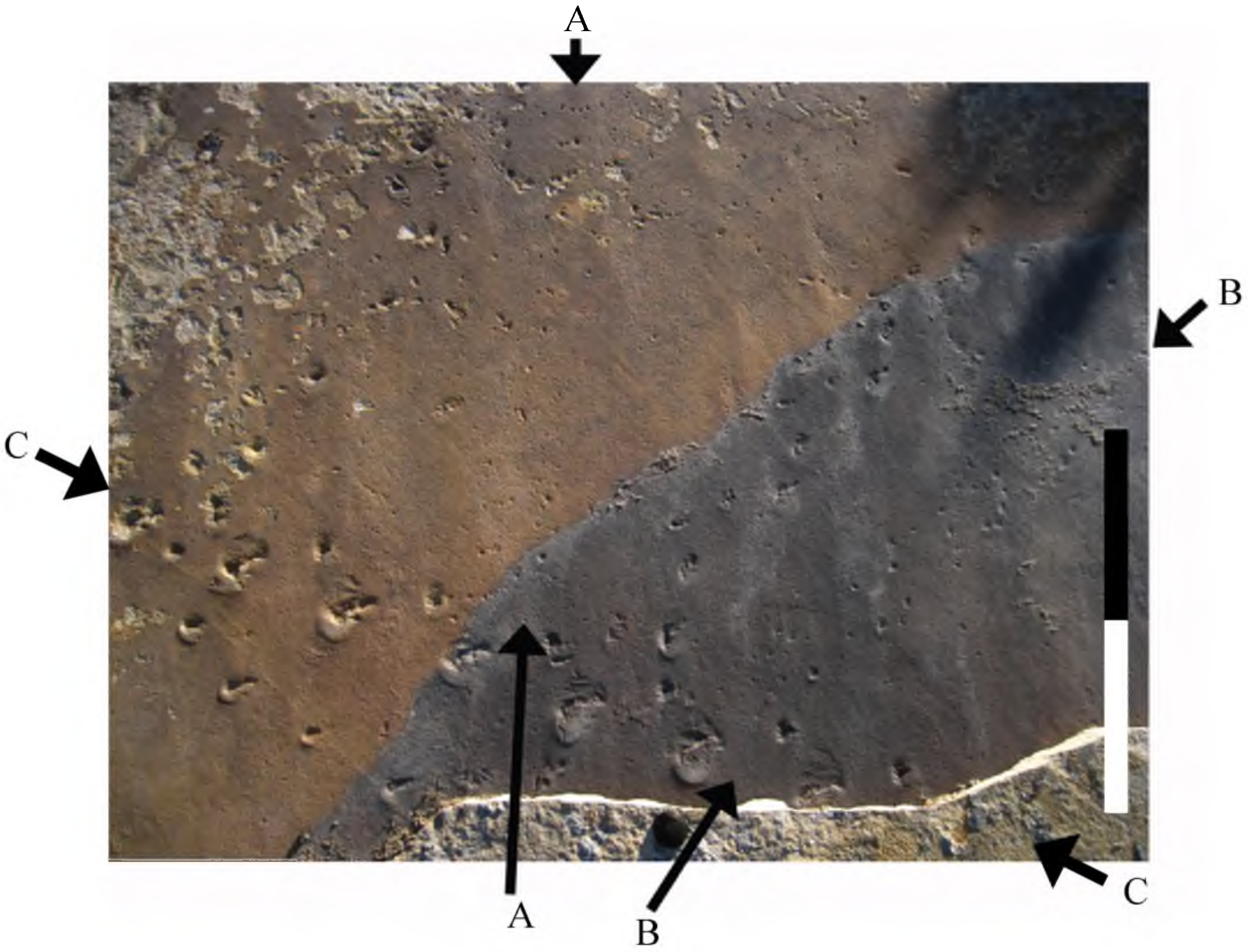


Figure 28. Three trackways preserved in epirelief in close proximity, including (A) *Paleohelcura*, (B) *Octopodichnus* and (C) Brasilichnium. Photo courtesy of Daniel Chure, NPS. Scale bar units = 10cm.

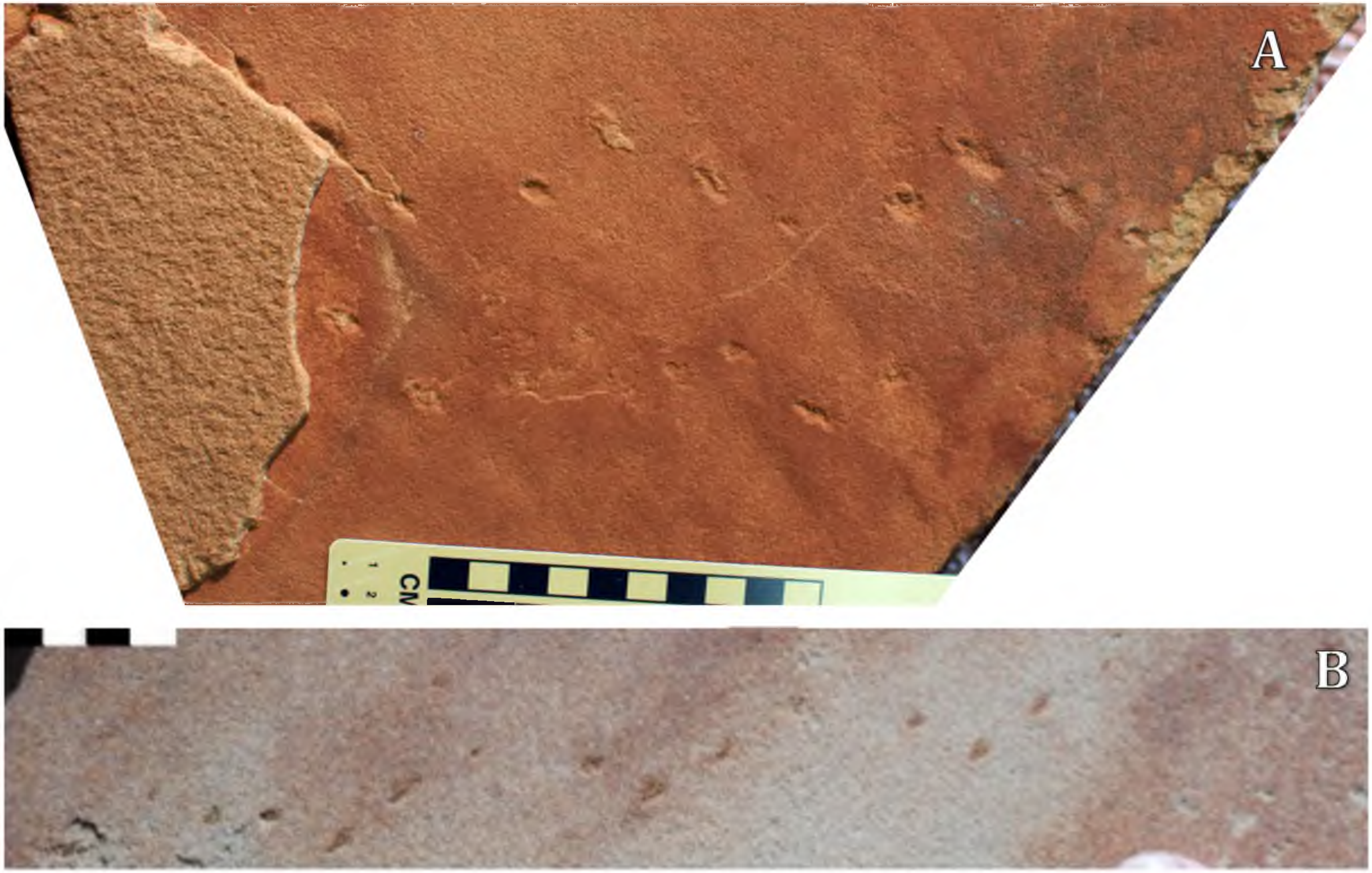


Figure 29. Octopodichnus in epirelief. (A) *Octopodichnus* specimen DNM 0486 (Dinosaur National Monument) showing a more complete preservation of the upper part of the trackway with push-up rims indicating a downs-slope direction to the top of the photograph (photo courtesy of Daniel Chure, NPS), and (B) *Octopodichnus* showing a more complete preservation of the lower part of the trackway with push-up rims indicating a down-slope direction to the bottom of the photograph. UUIC 3336 is a cast of specimen (B). Scale bar units = 1cm.

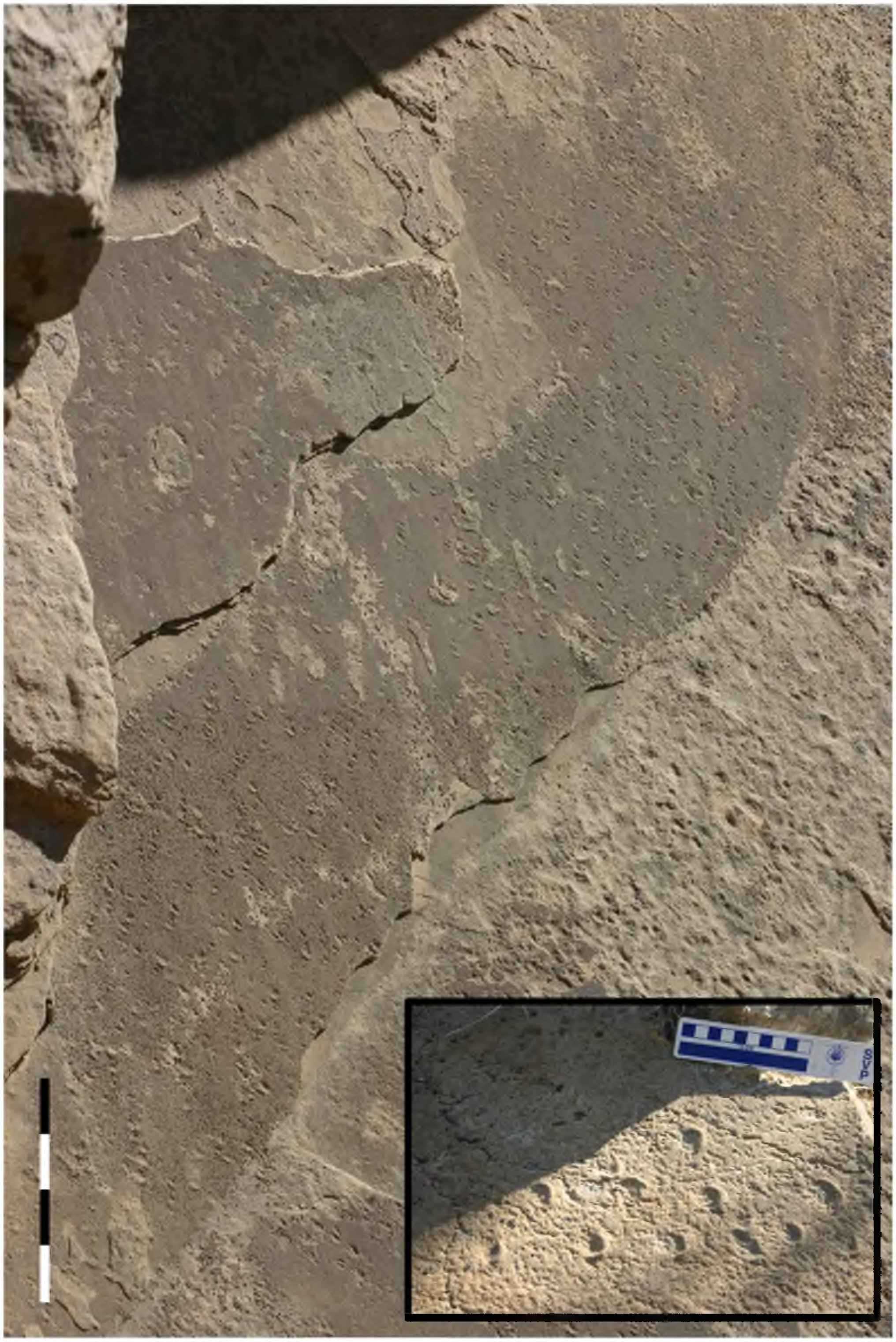


Figure 30. Hundreds of *Brasilichnium* impressions preserved in epirelief at Orchid Draw locality. Scale bar units = 10cm. Inset shows close-up of surface, revealing individual toe impressions and push-up rims. Scale bar units = 1cm. Photos courtesy of Daniel Chure, NPS.

Figure 31. Grallator preserved in epirelief at the Saints and Sinners Quarry. Scale bar units = 1cm.

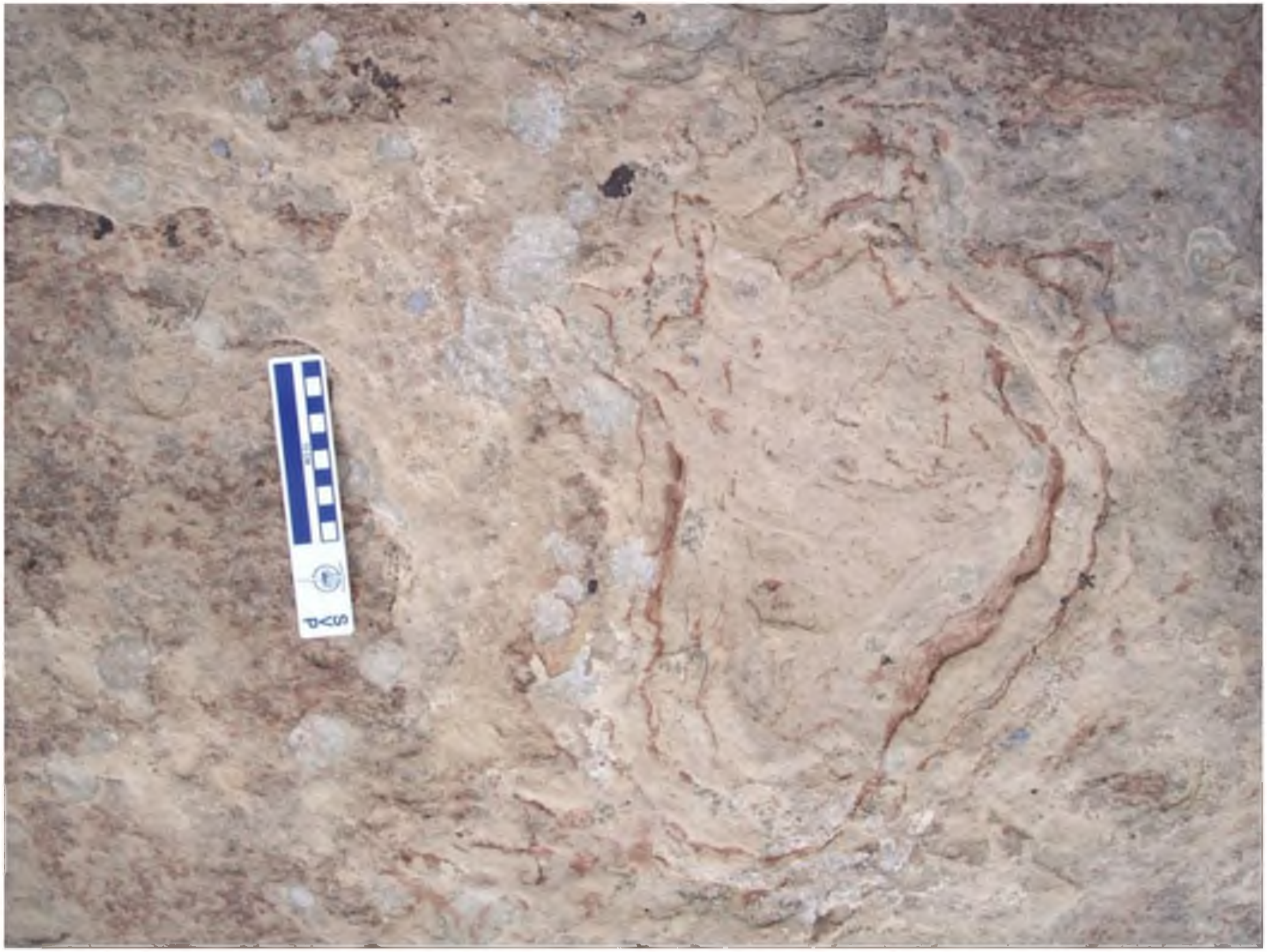


Figure 32. Otozoum track preserved near the top of the Nugget Sandstone, associated with *Grallator* and *Eubrontes*. Photo courtesy of Daniel Chure, NPS. Scale bar units = 1cm.

Table 7. Interpretations of invertebrate trace fossils in the Nugget Sandstone of northeastern Utah

Invertebrate Trace Fossil Interpretations

Invertebrate Trace Fossils	Facies	Possible Tracemaker	Sediment Moisture Content
Entradichnus meniscus	Lower slipface	Crane fly larvae; Cockroach adult or larvae; other insect larvae	Moist
Entradichnus isp.	Lower slipface	Crane fly larvae; Cockroach adult or larvae; other insect larvae	Moist
Planolites beverleyensis	Lower slipface	Crane fly larvae; Cockroach adult or larvae; other insect larvae	Moist
Taenidium isp. "A"	Dune toe; interdune	Beetles	Saturated
Taenidium isp. "B"	Dune toe	Crickets	Moist
Skolithos & *Planolites* isp.	Interdune	Wasps or crickets	Moist or Saturated
'Burrow clusters'	Dune toe	Insect hatching center?	Moist
'Large oblique burrows'	Lower slipface; dune toe	Scorpions; small vertebrates	Moist
'Flared burrows'	Dune toe	?	Moist
Paleohelcura	Lower slipface	Arachnids (spiders or scorpions)	Moist
Octopodichnus	Lower slipface	Arachnids (spiders or scorpions)	Moist

CHAPTER 4

PALEOECOLOGICAL, PALEOCLIMATIC, AND PALEOENVIRONMENTAL IMPLICATIONS OF NUGGET SANDSTONE FOSSILS

In addition to the paleobiological significance of fossils in the Nugget Sandstone, the fossil assemblage has implications for the paleoecology in this ancient erg system. Large tetrapod trackways in the Nugget and Navajo Sandstones have long been of interest to both scientists and the general public, and smaller trace fossils afford clues to the community structure and ecosystem that supported these carnivorous vertebrates.

These fossils also can provide insight into the paleoclimate and paleoenvironment during the Late Triassic and Early Jurassic. Some workers have attempted to reconstruct these two aspects, but there is no clear consensus on details of the climatic conditions during deposition of the Nugget and Navajo ergs or the environments that persisted within (Bryant, 2011; Chan and Archer, 1999, 2000; Chandler et al., 1992; Eisenberg, 2003; High and Picard, 1975; Loope and Rowe, 2003; Loope et al., 2001; Loope et al., 2004b; Picard, 1977b; Stokes, 1991; Wilkens, 2008).

This chapter explores how the presence and preservation of trace fossils and body fossils in the Nugget Sandstone can aid in paleoecologic, paleoclimatic and paleoenvironmental interpretations.

4.1 Role of Water in the Preservation of Eolian Trace Fossils

To anyone who has visited a modern dune field, traces in dry eolian sand seem to have little potential for preservation. Trackways produced during the night typically are blown away by midday, burrows constructed in loose sand immediately collapse unless reinforced biogenically, and meniscate burrows are nearly impossible to produce in truly dry sand due to lack of cohesion. Nevertheless, diverse trace fossil assemblages manage to appear in the fossil record of eolianites. Preservation, and probably even much of the production of organism traces, can be facilitated only by the presence of water in the environment of deposition.

Few studies of trace fossils in eolianites have addressed their method of preservation, and those that have consider only surficial trackways and impressions. Similar factors, however, must affect the preservation of shallow burrows, such as those described in this study. Two factors that enhance trace survivorship in eolian settings have been proposed: sufficient moisture content and sufficient clay content (Ahlbrandt et al., 1978; Davis et al., 2007; Loope, 1986; McKee, 1947; McKeever, 1991; Sadler, 1993; Stokes and Madsen, 1979; Walker and Harms, 1972). Regardless of the preservation method, if a trace can retain its shape long enough for burial, which occurs frequently in the high sedimentation rates of eolian settings, it has a good chance of preservation.

One method of preservation is cohesion of the substrate by increased moisture content and subsequent burial (Davis et al., 2007; McKee, 1947; McKeever, 1991; Sadler, 1993; Stokes and Madsen, 1979). Anyone who has walked on a sandy beach knows that sand becomes cohesive when moistened. However, there is an optimum moisture content level for cohesion, and after this point the sediment becomes less cohesive as saturation increases. In eolian environments, moisture in the sediment can result from precipitation, fog, dew, streams fed by adjacent highlands, or deep springs.

It has been previously suggested that moist, not saturated, sand must have been required to preserve trackways in eolian sandstone (McKeever, 1991; Stokes and Madsen, 1979). Stokes and Madsen (1979) conjectured that the trackway must have been covered by an immediate and gentle process to avoid desiccation of the sand and obliteration of the impression. McKeever (1991) suggested that sediment with more clay preserves trackways with higher resolution, and saturated sediment preserves trackways with little morphological detail.

Neoichnological experiments on reptile and arachnid trackway survivorship reveal that the best-preserved and most distinct trackways were made in damp sand that was covered shortly after by dry sand (McKee, 1947; Sadler, 1993). Additionally, experiments by Davis et al. (2007) indicate that invertebrate trackways persist significantly longer in moist sand than in dry sand when subjected to wind speeds of 5m/s, and that the relationship between moisture content and survival time is linear. They also pointed out that some ventral anatomical features of the invertebrates used in the experiments only appear in the trackway morphology in dry substrate conditions, and that these features are rare in the fossil record, suggesting that dry substrate conditions are unfavorable for trace fossil preservation.

Clay mineral content has been suggested as an agent of sand cohesion in eolian settings that can aid in preserving traces, a phenomenon attributed to electrostatic charges of the clay minerals (Nichols, 1999). Walker and Harms (1972) speculated that raindrop impressions in the eolian Lyons Sandstone in Colorado were formed on a thin layer of clay that settled from the atmosphere during calm conditions. According to this idea, clay helped protect the impressions until the surface was buried. Similarly, McKeever (1991) suggested that detrital clays helped preserve trackways in two Permian eolianites of Scotland. He cited the presence of clays, raindrop impressions and sun cracks as evidence for heavy showers or small floods that brought in the clays and gave the sediment sufficient competence for the preservation of trackways.

Based on observational and experimental studies in dune sands of Nebraska that contain up to 4% silt and clay, Loope (1986) suggested that increased clay content increases preservational potential. The clay exists as thin detrital coatings on the sand grains, which likely were deposited by water moving through the vadose zone. Loope (1986) identified abundant vertical-sided cattle tracks in cohesive wind-ripple dune sands with a moisture content of less than 1%. Davis et al. (2007) tested the clay content idea on invertebrate trackway survivorship by adding 0% to 4% of dry Kaolin 50, a mixture of 63% kaolinite, 28% mica, and 7% quartz, to fine grained sand. They found that the relationship between the percentage of Kaolin 50 and degradation time of the trackways is exponential, with 4% Kaolin 50 allowing for nearly two hours of trackway survival when exposed to a wind speed of 5 m/s, as opposed to only a couple minutes with 0% Kaolin 50. However, these tests were not subjected to burial.

Of the four studies suggesting that clay mineral content aids in trace preservation, two are directly correlated to raindrop impressions (McKeever, 1991; Walker and Harms, 1972). This indicates that a moist substrate, in addition to clay mineral content, also is likely an important factor in preservation. Experiments conducted by Davis et al. (2007) show that trackways in clay-enriched substrate are more resistant to wind, but are not subjected to burial. The study by Loope (1986) concerns only large vertebrate trackways that disrupt multiple laminae, making the effect of clay coatings on small burrows and trackways unclear.

QEMSCAN analysis was conducted on a representative sample of *Planolites beverleyensis* from the Nugget Sandstone (Figure 33). Results show a patchy distribution of kaolinite-filled pore spaces between quartz and feldspar grains, indicating that the clays are secondary, likely deposited by groundwater. There is no evidence of clay coatings on grains or any other primary clays, which would reveal a more regular distribution in the sample. A representative sample of *Taenidium* isp. "A" also was analyzed with QEMSCAN, and results showed a similarly patchy distribution of kaolinite-filled pore spaces. These analyses show that there was little or no clay at the time of deposition and production of traces in both interdune and lower slipface environments in the Nugget Sandstone. Instead, secondary groundwater processes likely deposited the preserved kaolinite. It should be noted that there is a possibility that some of the feldspar detected in the QEMSCAN analysis may represent some other types of clay, given limitations of the SIP (Species Identification Protocol) used for this analysis.

All studies described above concern surficial trackways and impressions exclusively. Burrows that penetrate through sediment layers and exist in the subsurface have a higher preservational potential, because they escape erosion by wind, rain or avalanche. For open or backfilled burrows to hold their structure, the sand must be cohesive unless they are biogenically reinforced, which is an uncommon characteristic of eolian burrows (Gwynne and Watkiss, 1975; Lubin and Henschel, 1990). Burrows in unconsolidated sand contain no structure, so sand grains collapse freely around the organism. Burrowing in unconsolidated sand is usually accomplished by a sand swimming motion that does not produce an open tunnel or an organized burrow morphology, and the burrows typically are recognized by a disruption of the sediment laminations (Counts and Hasiotis, 2009; Goldman and Hu, 2010; Hembree and Hasiotis, 2007). Sand swimming is not possible in consolidated sediments, and structures created by sand swimming have not been identified in the Nugget Sandstone.

Field studies in modern dunes at Little Sahara Recreation Area (BLM) and Coral Pink Sand Dunes State Park revealed that fossorial desert organisms prefer to excavate moist sediment over dry sediment. Burrow openings occurred only in lower slip-face sediments and interdunes where there was moist sediment only a few centimeters below the surface. Further evidence for a moisture preference in modern burrowers was observed when a burrow had been excavated where camp wastewater had been discarded the previous night (Figure 34).

Based on results from the studies referenced above, the argument for clay content as a sole factor in preserving small burrows and trackways, such as those discussed in this thesis, is insufficient. It should be noted that the effects of both moisture content and clay mineral content are not mutually exclusive; together they can create the most cohesive sediments. Therefore, it is assumed that the presence of water was a requirement for the preservation of all burrows and trackways described and discussed in this thesis, and sediment moisture probably served as a preference for burrowers. Water may have been present at the time of burrow production, as was likely the case for *Entradichnus*, *Taenidium*, *Planolites*, and *Skolithos* in this study. For small trackways, moisture that was introduced subsequent to trace production remains a possibility.

4.1.1 Similarity of *Entradichnus* to Subaqueous Traces

Entradichnus in the Nugget Sandstone shows a resemblance to traces that commonly occur in aquatic environments, such as shallow lacustrine or fluvial (Bromley and Asgaard, 1979; Buatois and Mángano, 2011; D'Alessandro and Bromley, 1987; Frey et al., 1984; Stanley and Fagerstrom, 1974). Traces with similar meniscate fill, such as *Scoyenia* and *Taenidium*, are characteristic of lake margins, including closed lakes where high salinity and rapidly fluctuating shorelines create stressful ecosystems (Buatois and Mángano, 2011), such as could have been the case in the Nugget interdunes. These comparisons point to the production of *Entradichnus* under moist or saturated conditions within the Nugget Sandstone. No sedimentologic evidence of standing water is associated with *Entradichnus* in the Nugget Sandstone, possibly due to subsequent erosion of water-lain sediments or lack of sediment deposition of short-lived ephemeral water or precipitation.

There is a resemblance between the meniscate structure of *Entradichnus* and the backfill of *Scoyenia gracilis* from Carlsberg Fjord, East Greenland (Figure 15; Bromley and Asgaard, 1979). These Triassic traces, from in the upper Malmros Klint Member of the Fleming Fjord Formation, were produced under very shallow aquatic conditions and resubmerged in fine sediments that allow for high-resolution preservation of burrow morphology. Where the burrow wall is preserved, characteristic *Scoyenia* wall scratchings can be seen. The backfill consists of “megamenisci,” or groups of menisci that can also be observed in the Nugget *Entradichnus meniscus* (Figures 14,15). The most significant resemblance occurs where the “megamenisci” fill transitions into the “feather stitch” fill, a backfill also characteristic of the Nugget Sandstone *Entradichnus* isp. This “feather stitch” backfill has not been described elsewhere in the literature from any environment. Also worth noting is that the *Scoyenia gracilis* of Greenland are commonly preserved on the same bedding planes as conchostracan (clam shrimp) body fossils. Conchostracan fossils have been discovered in the Navajo Sandstone in northeastern Arizona (Harshbarger et al., 1957; Lewis et al., 1961). Clam shrimp are known to dig burrows for depositing eggs (Zucker et al., 2002) and possibly for deposit feeding (Martin and Cash-Clark, 1993), though little is known of the clam shrimp burrow morphology. A glaring difference between the two traces, however, lies in the absence of a burrow wall in the Nugget *Entradichnus*. Burrow walls are built to prevent burrow collapse within soupground or softground substrates (Bromley, 1996). In the case of the Nugget *Entradichnus*, it may be that the substrate texture did not require the production of a burrow wall, or that because of unknown diagenetic reasons a wall was not preserved, or that these burrows and tracemakers are unrelated, and *Entradichnus* producers never produced wall linings. Regardless, these uncanny resemblances of internal burrow morphology, conchostracan affiliation, and possible ethologic and environmental association are worth considering.

4.1.2 ‘Large Oblique Burrows’ Produced in Cohesive Sediment

The ‘large oblique burrows’, discussed in Chapter 3 and in Engelmann et al. (in press), provide insights into the moisture content of the ancient dune toe in which they are preserved. These burrows are preserved within a 2m stratigraphic interval bound on top and bottom by similar, crossbedded intervals, one of which contains a few remnants of *Planolites beverleyensis*. The interval containing the ‘large oblique burrows’ contains the distal foreset laminae of which the associated interdune deposits have been eroded. Hence, nonexistent interdune deposits cannot give sedimentologic clues, such as carbonate deposition or thin, fine-grained beds, to the nature of the surrounding environment in which the burrows are preserved that would indicate the presence of water in the interval containing the 'large oblique burrows'.

The margins of the 'large oblique burrows' always contain a sharp contact with the surrounding matrix (Figure 23, 24). This requires that the surrounding sand was cohesive, because experiments with animals in loose, dry sand create soft-sediment deformation while burrowing (D. Hembree, written communication, 2013). Assuming an air-breathing burrow producer, such as a scorpion or small tetrapod, the presence of sharp contacts on burrow margins indicate a moist, unsaturated substrate. Because the burrows are observed to transect nearly 1m or more of section, possibly more, this indicates that at least 1m of sediment was moist at the time of burrow production. This amount of moisture probably would result only from recharge by heavy, possibly monsoonal, rain, or ephemeral rivers sourced in the adjacent highlands.

4.2 Periods of Increased Moisture

Short periods of increased sediment moisture are interpreted based on fossil evidence in the Nugget Sandstone. *Entradichnus meniscus* and *Planolites beverleyensis* most often occur in dense populations on slipface surfaces the Nugget Sandstone. Where outcrop availability allows, these surfaces can be traced to laterally and stratigraphically adjacent surfaces containing identical fossil assemblages. These stratigraphic associations are traceable up to 10m, while lateral depositional dip sections can reach up to 30m, although outcrop availability generally prohibits these extensive associations.

For reasons previously discussed, *E. meniscus* and *P. beverleyensis* are interpreted as shallow burrows produced in cohesive sediments on lower slipface surfaces. The necessary moisture to allow for production and preservation could have resulted from rainfall associated with summer monsoon seasons or other unrelated climate intervals, or the formation of dew during daily periods of increased atmospheric moisture. It has been suggested that monsoons developed during deposition of the Navajo Sandstone in southern Utah (Chan and Archer, 1999; Chandler et al., 1992; Loope and Rowe, 2003; Loope et al., 2001), but the idea of dew production in the Nugget and Navajo erg has not been entertained in the literature, perhaps because dew alone would not produce distinguishable sedimentologic features.

Because burrows are preserved in thick lateral sections, dune migration must have been active during these moist intervals. Grainflows can originate when dry sand accumulates in the cornice, which eventually fails, producing an avalanche that buries the lower slipface where the burrows are preserved. Given that the stoss side of dunes is subjected to more wind and direct sunlight than lee sides, desiccation, transport and avalanche could occur before complete desiccation of lower slipface sediments during a hiatus in moisture input, allowing the shallow burrows to retain their morphology in moist sediment for burial.

It has been suggested that dune migration occurred during wet intervals in the Navajo Sandstone. Cycles of slumped foresets from northern Arizona indicate the migration of dunes during monsoonal rain (Loope et al., 2001), and the interfingering of dune and interdune deposits indicate either a fluvial input from higher, wetter sources, or dune migration in spite of heavy rainfall (Bryant, 2011). Modern dunes typically are stabilized to some degree by vegetation, such as grass and other angiosperms, preventing dune migration during wet periods. The Jurassic dunes were barren of this type of stabilizing vegetation, which appeared in the Cretaceous, and the dunes therefore could migrate freely if sufficient drying intervals allowed for desiccation of at least the stoss and crests sands of the dunes (Glennie and Evamy, 1968; Loope, 1988; Marzolf, 1988).

There is also paleontological evidence for long-term wet intervals in the Nugget Sandstone. Discovery of the Saints and Sinners bone bed has shed light on the diverse assortment of vertebrates that once occupied the interdunes of the Nugget Sandstone in northeastern Utah, including coelophysoid theropods, sphenodontians, protosuchians, and drepanosaurs (Britt et al., 2011; Britt et al., 2010; Chambers et al., 2011; Engelmann et al., 2012). Similar assemblages of vertebrates have been discovered in the Navajo Sandstone to the south (Tables 2,4,6). Winkler et al. (1991) pointed out that these vertebrate fossils from the Navajo are similar to taxa that occur in the older, underlying Kayenta and Moenave formations of the Colorado Plateau, and they conjectured that none were adapted to the extreme arid environment generally associated with the Navajo Sandstone. In a study of Navajo interdunes, Wilkens (2008) indicated the occurrence of widespread climatic events during the deposition of the Navajo Sandstone. He suggested that these climate intervals created long-term mesic conditions, at least long enough for large conifers to grow without seasonal variation of wood growth, and he further suggested that mesic-adapted vertebrates occupied interdunes during these intervals. Millennial-scale wet climate intervals in the Navajo Sandstone also were interpreted based on sedimentologic evidence (Loope and Rowe, 2003), and giant stromatolites provide evidence for plentiful water and stable dunes for intervals of thousands of years in the Navajo Sandstone (Eisenberg, 2003).

The presence of mesic-adapted organisms in the Nugget Sandstone indicates that at least one similar climate oscillation period occurred during deposition, though there were likely more, signified by the presence of thick carbonate interdune deposits. The diversity of small vertebrates at the Saints and Sinners Quarry, such as the drepanosaurs and sphenodontians, indicate the long-term presence of the interdune lake they were deposited in (Daniel Chure, written communication, 2012). This is because small vertebrates lack the vagility required to migrate opportunistically across extensive erg environments during short intervals to reach isolated and laterally restricted wet areas. They were more likely inhabitants of a permanent, productive ecosystem afforded by a long-term shift in climate.

In addition to vertebrate fossils, small and variably oriented invertebrate burrows such as *Taenidium* isp. “B” and *Skolithos* occur within lacustrine interdune deposits. Because of this, these burrows were likely produced in saturated sediment, and producers of such burrows are considered to be mesic-adapted organisms. Unlike the vertebrates discovered in the Nugget Sandstone, the invertebrates that produced *Taenidium* and *Skolithos* may have been capable of dormancy, such as aestivation or diapause. Desert environments favor the evolution of invertebrates capable of some form of dormancy, since tolerable conditions are often separated by long, intolerable periods in desert environments. As soon as conditions are tolerable, burrowing organisms capable of dormancy reactivate or hatch within hours or days (Crawford, 1981; Louw and Seely, 1982). Because invertebrates capable of dormancy would not have needed time to migrate into habitable interdune environments, such as small vertebrates would have, long-term climate intervals were not needed to allow for the activity of such invertebrates within the erg.

This conclusion is supported by the presence of variably oriented burrows, such as *Taenidium*, in deposits resulting from long-term wet intervals in addition to deposits that would otherwise be interpreted as dry lower slip-face or interdune facies. The *Taenidium* ichnofabric is preserved on surfaces where overlying strata have been eroded and underlying strata are not exposed or are poorly exposed (Figure 18c). At these locations it would be reasonable to assume that the sediment was saturated and situated beneath standing water during the time of bioturbation.

4.3 Paleoecology of the Nugget Sandstone

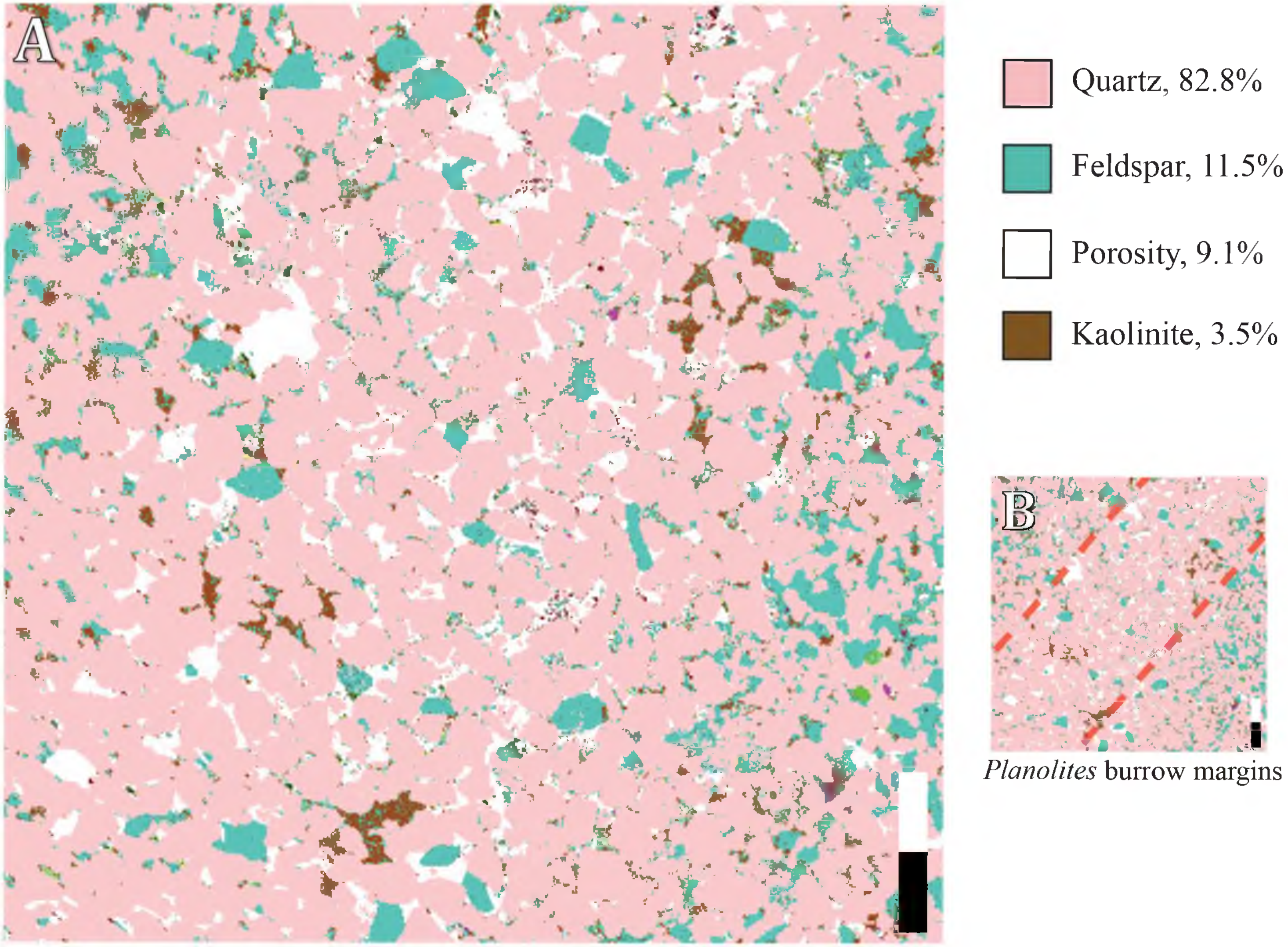
The wide diversity of trace fossils, including trackways and burrows, as well as thousands of bones and possible plant remains, provides a clear picture of the paleoecology of the Nugget Sandstone. Although sufficient fossil evidence is available to reconstruct a functioning food web, gaps and biases in the fossil record inhibit a full reconstruction. An attempt to model energy flow in the Navajo Sandstone in southern Utah was made by Shibata et al. (2006) based on net primary productivity, transfer efficiency including consumption, assimilation, and production efficiencies, and the estimated energy intakes for the known taxa. Their calculations were based mainly on measurements of vertebrate trackways. Results of their study are speculative, because initial estimates of type and abundance of primary productivity and values for animal energy intake are widely varying and not well constrained for Early Jurassic taxa.

Based on current correlations (Sprinkel et al., 2011), the Nugget Sandstone was deposited over tens of millions of years, leaving few traces of life within its various stratigraphic levels. Intervals containing fossil evidence are limited in lateral extent and nearly impossible to correlate with other specific intervals, making it difficult to demonstrate that uncorrelated fossil occurrences contain taxa and ichnotaxa that existed at exactly the same time. High diversities of fossils within the same interval, such as those at Orchid Draw (Figure 7), provide evidence for interactions between trace fossil producers. Also, for reasons discussed previously in this chapter, fossil preservation in the Nugget Sandstone indicate that most animal productivity occurred during wet climatic intervals, and thus the organisms and their behaviors were preserved during similar climates. Because of this, it is assumed that most of the known taxa and ichnotaxa from various intervals likely inhabited the dune and interdune environments contemporaneously.

Primary productivity is essential for supporting any ecosystem. Although the preservational potential of plant remains in the Nugget Sandstone is extremely low, some evidence for the types of plants that persisted in these ancient ergs is available (Tables 3, 4). Two types of plant remains have been discovered in the Nugget Sandstone. Foliage impressions from the Saints and Sinners Quarry have been interpreted as cycadeoid (Britt et al., 2010; Chambers et al., 2011), and sphenophyte remains have been located near Orchid Draw in Dinosaur National Monument (Figure 5). Other plant fossils in the Navajo Sandstone of Arizona, Idaho and southern Utah include horsetails (*Equisetum*), conifers (araucarians), and cycads (Gilland, 1979; Harshbarger et al., 1957; Loope, 1979; Oriel, 1959; Parrish and Falcon-Lang, 2007; Stokes, 1991; Wilkens, 2008). Because conifer fossils occur in the Navajo Sandstone, the partially correlative similar environment represented by the Nugget Sandstone to the north may have harbored conifers as well, in addition to the ferns and cycads already preserved there. Additionally, various types of algae, including brown algae, and stromatolites also have been described in the Navajo Sandstone, adding to the list of potential primary producers in the Nugget Sandstone (Dorney and Parrish, 2009; Eisenberg, 2003; Loope et al., 2004a; Stokes, 1991). Possible algal buildups identified in this study are preserved near the Large Mounds locality (Figure 35).

With sufficient numbers of primary producers in the Nugget Sandstone, primary consumers (herbivores) flourished and supported a complex food chain. Primary consumers included insects and other small herbivorous and detritivorous invertebrates that produced the smaller trace fossils described in this study. Larger herbivores, such as the basal sauropodomorph dinosaurs that produced *Otozoum* trackways in the upper Nugget Sandstone, and ornithischian dinosaurs that produced *Anomoepus* trackways in the Navajo Sandstone, and possible tritylodonts that produced *Brasilichnium***,** would have aided in energy transfer from primary producers to the top predators. Arachnids, such as those that produced *Octopodichnus* and *Paleohelcura,* presumably were insectivorous. Drepanosaurs, sphenodontians and synapsids may have consumed both insects and arachnids, although sphenodontians and synapsids may have been herbivorous. Apex predators would have included theropods, represented by the ichnotaxa *Grallator* and *Eubrontes*, as well as theropod teeth and coelophysoid body fossils from Saints and Sinners (Figure 3). These top predators may have fed on large arthropods or small vertebrates, such as sphenodontians and synapsids.

The complex trophic structure of the Nugget ecosystem would have required an adequate amount of water in the form of substrate moisture and even standing water in the form of ephemeral interdunes or streams. Because the Nugget erg persisted in an arid climate, as evidenced by its large, cross-bedded dune deposits, populations of at least the large vertebrates were likely transient, inhabiting the erg only during sufficiently wet and lengthy climatic intervals, and leaving the smaller herbivorous, insectivorous, and more desert-adapted animals to persist during dryer intervals. In this way, organism diversity and food web complexity was increased during wetter climatic conditions, and they decreased during more arid conditions.



Planolites burrow margins

Figure 33. False-color QEMSCAN of a representative sample of *Planolites beverleyensis* showing a patchy distribution of sparse kaolinite between the well-sorted quartz grains. Scale bar units = 1mm

Figure 34. Modern burrow (arrow) excavated in moist sand indicating a moist substrate preference in modern desert burrowers at Little Sahara Recreation Area. Hammer is 30cm long.

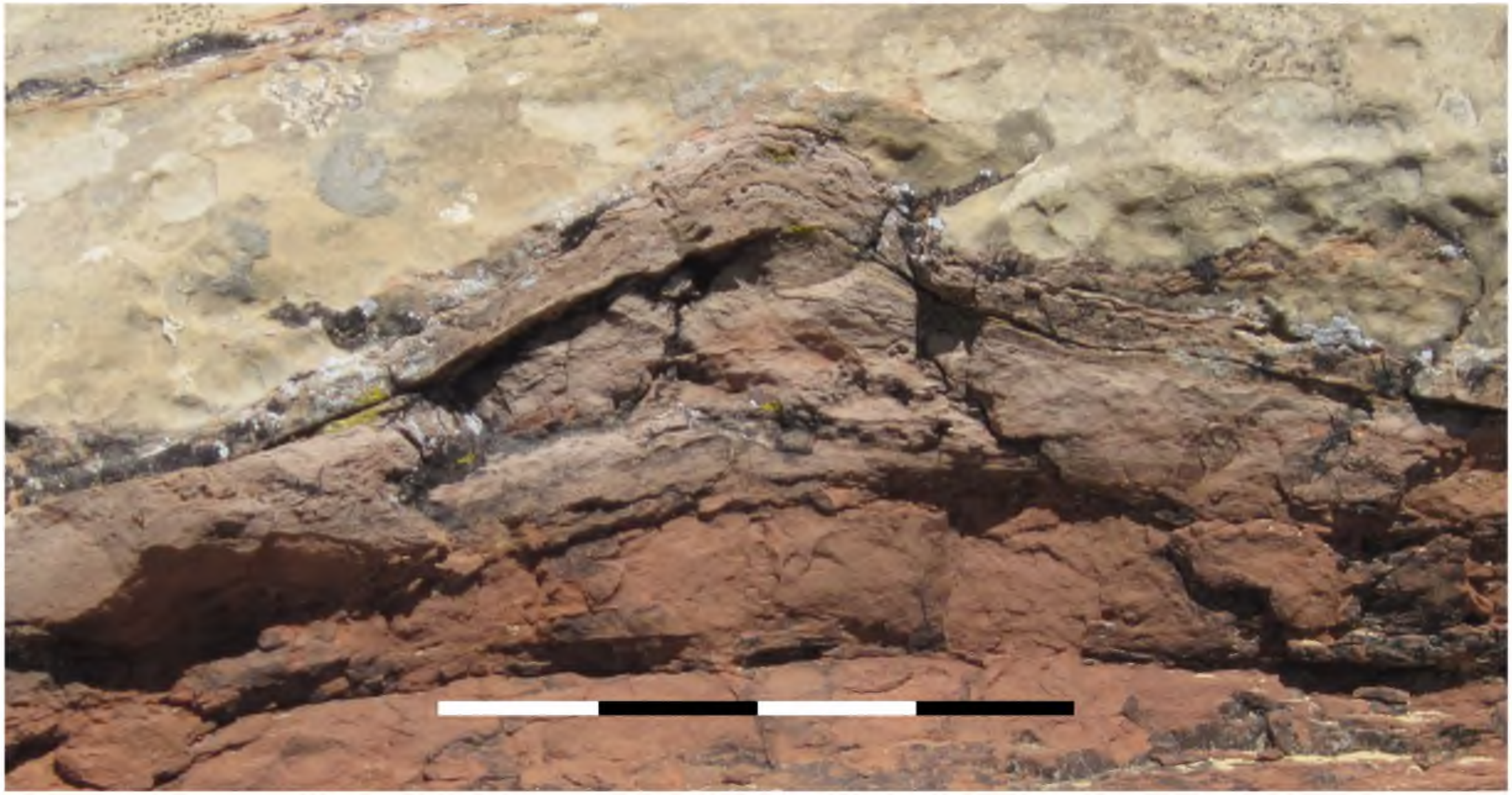


Figure 35. Possible algal buildup (vertical view) preserved in carbonate layer near Large Mounds locality. Scale bar units = 10cm.

CHAPTER 5

SUMMARY AND CONCLUSIONS

The Upper Triassic/Lower Jurassic Nugget Sandstone represents a portion of a vast inland erg of eolian sand dunes that were populated by a diverse assemblage of taxa, including both vertebrates and invertebrates, which are represented in the geologic record primarily by their trace fossils. A comprehensive list of all trace, body and plant fossils from the Nugget Sandstone and the partially correlative Navajo Sandstone was compiled to highlight the biologic diversity (Tables 1-6). Body fossils from these eolianites are extremely rare, making the trace fossil record essential for deciphering the paleoecology of this ancient dune system.

This thesis describes 12 types of invertebrate trace fossils from 30 sites in the Nugget Sandstone of northeastern Utah. Five particularly notable sites were described in detail (Orchid Draw, Large Mounds, Saints and Sinners, Sounds of Silence, and Cub Creek Spire). Many of the invertebrate trace fossils are described in the Nugget Sandstone for the first time, and all are new to the field study area. These trace fossils include *Entradichnus meniscus*, *Entradichnus* isp., *Planolites beverleyensis*, *Taenidium* isp. “A,” *Taenidium* isp. “B,” *Skolithos* and *Planolites* isp., ‘burrow clusters’, ‘large oblique burrows’, ‘flared burrows’, *Paleohelcura* and *Octopodichnus*. Possible tracemakers include arachnids and insects, and production of the traces was controlled by the dune facies (lower slipiface, dune toe, or interdune) and sediment moisture content (Table 7).

Small invertebrate burrows require at least some sediment cohesion for both burrower preference and preservation. Multiple lines of evidence support the hypothesis that moisture provided sediment cohesion in the Nugget Sandstone: 1) no evidence of clay grain coatings or other primary clays was detected in QEMSCAN analyses of Nugget burrows, indicating that electrostatic charges between clay particles were not the agent for substrate cohesion; 2) modern burrowers in Utah eolian environments show a preference for moist sediment; 3) meniscate burrows in the Nugget Sandstone resemble fluvial or shallow lacustrine burrows, such as *Scoyenia* and *Taenidium,* indicating production in similarly moist sediment.

Extended periods of increased moisture are interpreted from trace and body fossils in the Nugget Sandstone. Preservation of *Planolites beverleyensis* in a lateral depositional dip sections reaching as much as 30m indicates a steady moisture input for hundreds to thousands of years, with active dune migration during this time. Additionally, the body fossils of small vertebrates from the Saints and Sinners Quarry represent organisms not adapted to extreme arid environments, suggesting that at least one (and probably more) long-term wet climatic interval occurred during deposition of the Nugget Sandstone.

With findings from this study, evidence for all parts of a functional food web is now available in the Nugget Sandstone. This includes primary production by plants, primary consumption by insects and other large herbivores, secondary consumption by arachnids and small vertebrates, and tertiary consumption by theropods, as the apex predators.

Trace fossils, such as those discussed in this thesis, play a critical role in interpreting the paleoecology of the ancient dune environment represented by the Nugget Sandstone. Future studies in neoichnology will help refine interpretations of possible tracemakers in ancient ergs, and comparative studies of other Early Mesozoic eolianites will provide a more complete understanding of the spatial and temporal extent of their life habits.

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