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MICROBIAL STRUCTURES AND DINOSAUR TRACKWAYS FROM A CRETACEOUS COASTAL ENVIRONMENT (DAKOTA GROUP, COLORADO, U.S.A.)

NORA NOFFKE,[1] JAMES HAGADORN, [2] AND SAM BARTLETT[3]

[1]*Department of Ocean, Earth & Atmospheric Sciences, Old Dominion University, Norfolk, Virginia 23529, U.S.A.*
[2]*Department of Earth Sciences, Denver Museum of Nature & Science, Denver, Colorado 80205, U.S.A.*
[3]*Friends of Dinosaur Ridge, 16831 West Alameda Parkway, Morrison, Colorado 80465, U.S.A.*
e-mail: nnoffke@odu

ABSTRACT: **Microbially induced sedimentary structures may help preserve unique glimpses of ancient shoreline habitats, but are little known from Mesozoic epicontinental settings. To help fill this knowledge gap, we describe a diverse suite of microbial structures from the Upper Cretaceous "J" Sandstone (South Platte Formation, Dakota Group) that are spectacularly exposed at Dinosaur Ridge in Morrison, Colorado, USA. Structures include "tattered" bed surfaces and ferruginous sand chips in supratidal flat facies. A large over-flip structure is preserved in a channel locally known as Crocodile Creek. In upper-intertidal facies, multidirectional ripple marks occur. Perhaps the most well-known microbial structures are exposed on extensive bedding surfaces known as "Slimy Beach," where lower supratidal-flat facies are dominated by decimeter-scale erosional remnants and pockets. Morphologies and superposition of the structures allows identification of three generations of erosional pockets. Generation A of these erosional pockets exhibit size similarities to ornithomimid, sauropod, and ornithopod dinosaur tracks from adjacent bedding planes, raising the question of whether initial disturbance of the mat-bound surface could have been from track making. Generation B erosional pockets are older and record continuous erosion of the initial pockets until they were eventually overgrown and sealed by microbial mats. Generation C pockets are the oldest ones, exposing wide areas of barren sediment that could not be overgrown by microbial mats anymore. In concert, the microbial structures point to seasonally variable meteorological conditions along the coastline of the Western Interior Seaway and indicate that the "Slimy Beach" bedding plane represents a multi-year record of dinosaur locomotion.**

INTRODUCTION

Large bedding planes representing facies deposited along the margins of epicontinental seas are rare, yet such exposures can provide key insights into the characteristics and paleontology of ancient coastal habitats. Dinosaur Ridge is one of the best-known examples of such a record for the Cretaceous. This National Park Service National Natural Landmark is recognized for its spectacular exposures of Jurassic to Cretaceous strata that bear dinosaur bones, trackways, fossil plants, ashes, and sedimentary structures (e.g., LeRoy 1946; MacKenzie 1963; Weimer et al. 1972; Lockley 1993; Hunt et al. 2002). In this succession, the "J" Sandstone is of particular interest because it includes a little-known suite of microbially induced sedimentary structures (MISS) that, in association with trace fossils and bedforms, preserves a snapshot of Earth history when ornithomimid, sauropod, and ornithopod dinosaurs ambled along the ancient shores of the Western Interior Seaway.

In these types of clastic settings, MISS are formed syndepositionally by benthic microbial communities (e.g., Schieber 1986; Gerdes and Krumbein 1987; Hagadorn et al. 1999; Gerdes et al. 2000; Schieber et al. 2007a; Noffke 2010). Such microbial structures are preserved in a variety of shallow marine, coastal, fluvial, and lacustrine environments. Comparative analyses with modern examples can help constrain ancient paleoenvironmental conditions. At Dinosaur Ridge, microbial structures have a long history of study. MacKenzie (1972) hypothesized that odd-shaped ripple patches occurring in Unit 21 (Weimer and Land 1972) at Dinosaur Ridge were deposited in a tidal flat dominated by "algal" mats. This microbial interpretation was later corroborated by Reineck (1979) and validated by Schieber (2007b).

Microbial communities like these are important because they can foster preservation of dinosaur-track-bearing surfaces, by enhancing bedding-plane cementation, and altering sediment rheology. For example, Kvale et al. (2001) noted erosional remnants and pockets comparable in size to those at Dinosaur Ridge (see also Lockley et al. 1986) at a tracksite formed on a Middle Jurassic tidal flat in Wyoming. Cariou et al. (2014) observed similar phenomena in a Late Jurassic tracksite of the Jura Mountains, France, and Marty et al. (2007, 2010, 2013) in the Jura Mountains in Switzerland and the High Atlas Mountains in Morocco. In an Early Cretaceous sauropod–theropod tracksite in Sichuan, China (Xing et al. 2016), desiccation of mat-overgrown tracks and early carbonate cementation catalyzed by microbial mats is thought to have stabilized tracks (*sensu* Marty et al. 2009; Cuadrado et al. 2011).

Microbes have also been invoked as catalysts for enhanced track formation. For example, microbial processes are hypothesized to have enhanced the formation of Early Cretaceous ornithopod tracks in clastic strata of Qijiang, China, by maintaining sub-mat sediment pliability while simultaneously reducing the sediment's proclivity to collapse from

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formation of deep tracks (Dai et al. 2015). In an Early Jurassic carbonate tidal flat from Italy, Avanzini et al. (1997) inferred that cyanobacterial mats helped sediments to behave plastically to semi-elastically, fostering formation of better-defined sauropod and theropod footprints.

To help refine our understanding of the paleoenvironments and preservational conditions represented by the "J" Sandstone at Dinosaur Ridge, we mapped and analyzed previously known and new MISS from the succession. We describe these structures below and suggest how their distribution, mode of preservation, and association with trace fossils contributes to our understanding of the paleoenvironment and dinosaur activity.

STUDY AREA

The Dakota Group contains a transgressive succession including facies thought to reflect transition from fluvial systems (channels and floodplains of the Lytle Formation) to swamps, marshes, and tidal flats (Plainview Sandstone Member). These facies are overlain by delta-plain and shallow-bay marine facies (Skull Creek Member). A subsequent shallow deltaic facies (Kassler Sandstone) is capped by tidal flat and channel ("J" Sandstone) facies that locally may be overtopped by marsh, swamp, and beach facies (Lane 1963; MacKenzie 1968, 1972; Weimer 1970; Chamberlain 1976; MacMillan and Weimer 1976).

Studied outcrops are in the "J" Sandstone Member of the South Platte Formation (Dakota Group), exposed along a roadcut on the eastern flank of Dinosaur Ridge (e.g., Weimer 1970) (Fig. 1). These sandy strata were deposited at approximately 45° north paleolatitude (see synthesis in van Hinsbergen et al. 2015) along the coastline of an epeiric sea that blanketed much of western North America during the Late Cretaceous (e.g., Waage 1955; Weimer and Haun 1960; MacKenzie 1965; Kaufman 1984). Our observations of the sedimentary characteristics of the succession are consistent with those of previous workers, and with the hypothesis that the upper part of the "J" Ss was deposited in a shallow, tidally dominated marine setting composed of a mosaic of intermittently emergent sand flats, tidal channels, and swampy to estuarine paleoenvironments.

To facilitate comparison with field guides by MacKenzie (1968), Lockley and Marshall (2014), and others, we have organized our contribution into a stratigraphic framework comparable to theirs. We key our graphic log in Figure 1 and our descriptions to Weimer and Land's (1972) unit numbers, which indicate well-known outcrops along West Alameda Parkway at Dinosaur Ridge.

METHODS

For this study, we conducted a lithological facies analysis of a 27-m-thick stratigraphic section from the upper Kassler Sandstone to the lower Mowry Shale, with detailed focus on the bedding planes on which we observed microbial structures (Fig. 1). Under permit by Jefferson County Open Space, samples from seven rock beds were taken for thin-sectioning to search for microbial textures. Petrographic examination showed that the rocks are too oxidized to bear carbonaceous laminae, but hematite-rich textures may occur. The distribution of structures on a large ($\sim$ 150 m^2) bedding surface at "Slimy Beach" (22.4 m in Fig. 1) and at a smaller exposure at "Crocodile Creek" (18.7 m in Fig. 1) were gridded, mapped, and photographed with the aid of a drone.

RESULTS

Stratigraphy and Facies

There are six main units in the "J" Sandstone at Dinosaur Ridge, known from bottom to top as Units 19 to 24 (Fig. 1). Strata are described in detail by Weimer and Land (1972), MacKenzie (1968, 1972), and MacMillan and Weimer (1976), and trace fossils are discussed in Chamberlain (1976). At the base of our studied succession is Unit 19, which is interpreted to have been deposited in a supratidal flat. It is characterized by very fine-grained sandstone that bears a variety of symmetrical, current, and interference ripples, vertical and horizontal bioturbation, local ferruginous crusts and woody and leafy plant debris, and clay laminae that are locally thicker and bear polygonal cracks. Unit 20 is thought to have been deposited in estuary-tidal or distributary channels and consists of medium- to fine-grained sandstone that fines upward, locally has local mud clasts at channel bases, and contains abundant tabular and trough cross-stratification, ripple cross stratification, leaf and stick impressions, *Diplocraterion*, and other vertical burrows. Unit 21 likely represents an upper-intertidal flat and is dominated by thin-bedded fine-grained sandstone that bears a diverse array of ripple cross stratification and a variety of trace fossils. Unit 22 is hypothesized to represent deposition in a tidal channel that incised supratidal flats, and is characterized by medium- to fine-grained sandstone that fines upward with trough cross stratification and ripple cross stratification, with rare impressions of plant debris and vertical bioturbation. Unit 23 is thought to represent deposition in lower-supratidal-flat and swamp settings, and is dominated by very fine to fine sandstone with minor siltstone and shale, trough and ripple cross stratification, channels, root marks, logs/branches, and sticks, and a variety of horizontal and vertical trace fossils including *Diplocraterion*. Unit 24 may represent a channeled tidal flat and is trough cross stratified fine- to medium-grained sandstone with thin, polygonally cracked shale beds, capped by a thin conglomeratic sandstone. Unit 24 is overlain by gray marine mudstones of the Mowry Shale.

Weimer and Land (1972) suggest that these units were generally sourced from the west and deposited in a broad, shallow delta complex. Microbial structures are preserved in all of the non-channelized parts of these Units 19–24. Considered together, they represent the most diverse suite of microbial structures yet known from dinosaur tracksites, and are described below.

Microbially Induced Sedimentary Structures

Observation of Multidirected Ripple Marks.—Two large bedding planes of fine-grained hematitic sandstone of Unit 21 bear patches of ripple marks of various directions (Figs. 1, 2). The basal bed is 9.5 cm thick and bears ripple-mark cross stratification, in vertical section made visible by hematite-rich laminae. It overlies a 85-cm-thick, cross-stratified fine-grained sandstone. The upper bed is 3–5 cm thick and has rare ripple cross stratification. These beds are locally incised by meter-scale channels of the overlying rock unit.

The upper surfaces of both sandstone beds are covered by asymmetrical ripple marks (Fig. 2A). The basal bed has an average ripple index of 10.5 (4 to 16) whereas the upper bed has an average ripple index of 8.5 (4 to 12).

The ripple marks on the lower bedding plane surface are widely exposed on the left portion of the outcrop (Fig. 2A). They are arranged into decimeter-sized patches where each patch includes a group of ripples of the same direction. However, the ripple directions between the patches vary. In a representative study area (Fig. 2B) three main directions, labeled as a, b, and c, can be distinguished (Fig. 2C). The ripple valleys of each patch group show a different degree of infill (leveling).

Interpretation of Multidirected Ripple Marks.—Such multidirected ripple marks can result from the interference of episodic strong flood currents with microbial-mat development on a sandy tidal surface (Noffke 1998, 2010) (Supplemental Fig. 1). In the Dinosaur Ridge example illustrated in Figure 2, the sharply defined ripples of suite "c" cover the largest part of this representative study area. The relative large surface part occupied by those ripples and their unaltered morphologies suggests that they represent the youngest generation of ripples on the overall bedding plane. The ripples merge with those of ripple suite "b," which are

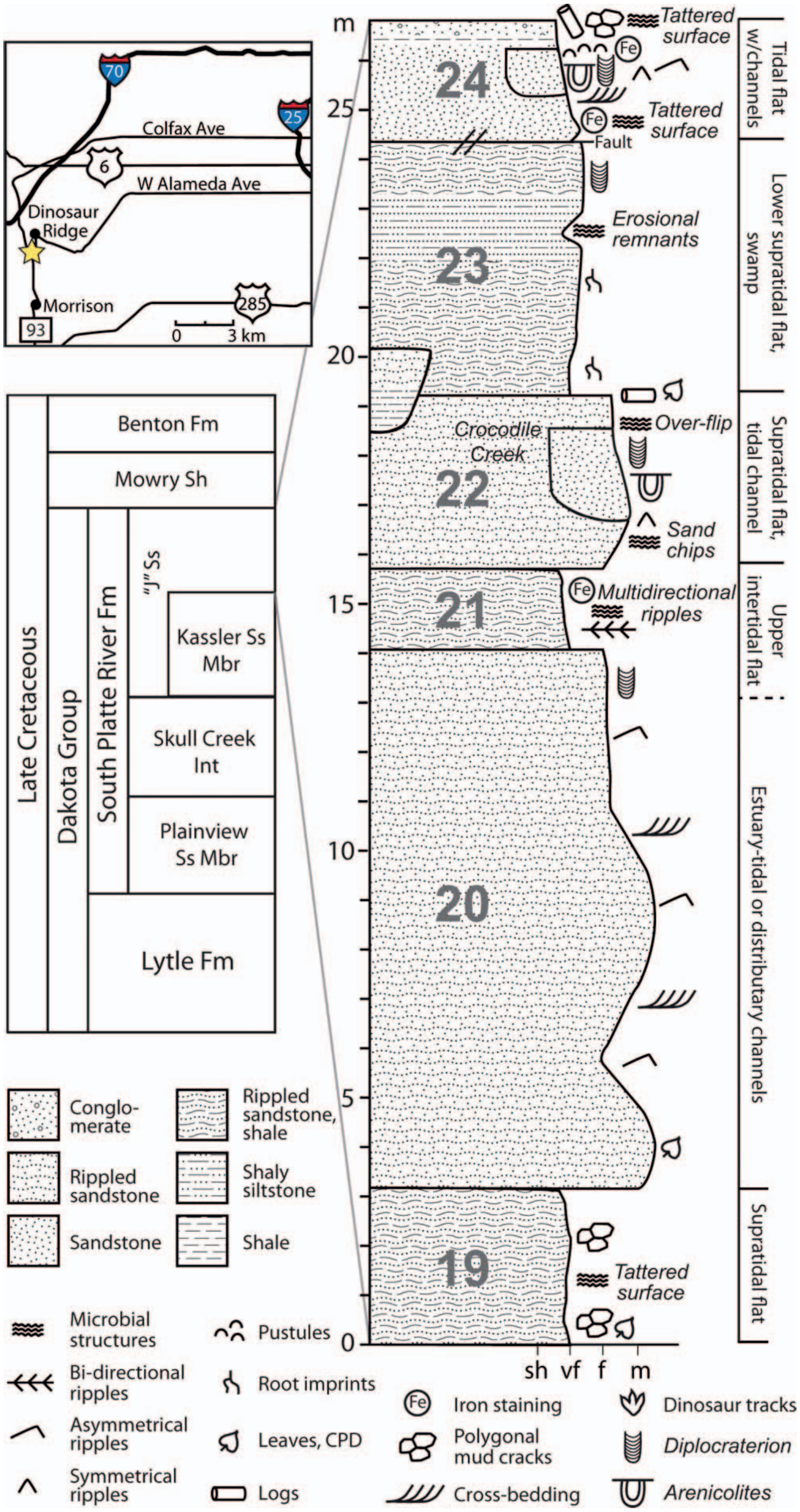

FIG. 1.—Location and stratigraphy of the study site (star), West Alameda Parkway, west of Denver, Colorado, USA. Here the "J" Sandstone Member of the South Platte Formation is dominated by sedimentary structures and fossils common to tidally influenced shallow to emergent marine settings. The "J" Sandstone is dominated by carbonate-cemented sandstones and very minor gravel, siltstone, and mudstone. Hematite or limonite-rich cement may occur (Fe). Although ripple marks and dinosaur footprints are common (Lockley and Marshall 2014; Lockley et al. 2016), not all occurrences are here noted. Trace fossils are abundant, especially towards the upper part of the section. The gray numbers denote units of Weimer and Land (1972), whose stratigraphy and paleoenvironmental bracketing we modified. CPD is comminuted plant debris.

interpreted to represent an older generation of ripples. Finally, ripple suite "a" covering the smallest area of the bedding plane, is inferred to be the oldest. The valleys of suite "a" ripples are filled in almost entirely by ancient mat coverage (Noffke 1998).

Water depths and current velocities inferred from ripple indices are internally consistent with these interpretations. For example, the basal bed's mean ripple index (10.5) suggests that it experienced current ripples formed in water depths of 20–100 cm, and under maximum current

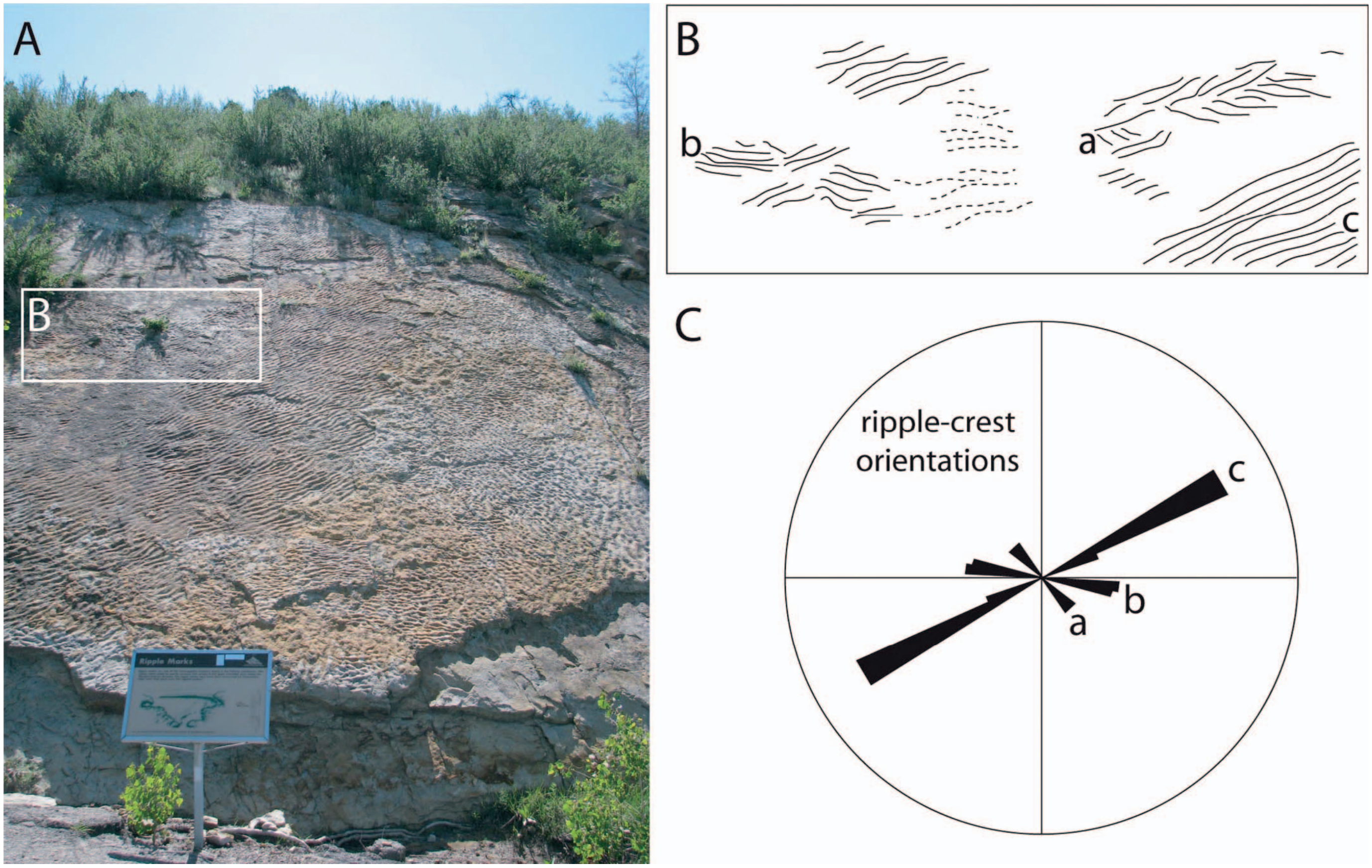

FIG. 2.—**A)** Overview of outcrop bearing ripple marks on red hematite-rich sandstone beds in Unit 21. White rectangle marks area where measurements of ripple-mark directions in Parts B and C were taken. **B)** Sketch of inset in Part A, illustrating twelve rippled patches. Seven patches are dominated by ripple-crest orientation "c," oriented toward present-day northeast–southwest; two patches show ripple-crest orientation "b" (present-day east–west); and two patches include orientation "a" (southeast–northwest). One patch includes ripple marks that are too poorly preserved to assign them to a specific orientation. **C)** Orientation of ripple marks a, b, and c, plotted as bidirectional azimuths. Compare also with Supplemental Figure 1.

velocities of 30–50 cm/s. The upper bed's ripple index (8.5) suggests it experienced water depths of 10–20 cm and maximum current velocities of 15–20 cm.

In modern tidal flats, multidirectional ripple marks form in a stepwise fashion over the course of weeks (Noffke 1998). At first, the surface of freshly deposited, ripple-marked sand is colonized by benthic microorganisms forming a thin biofilm within a few hours. Such initial growth stages of microbial mats tend to form patches instead of extensive sheets. The microbial patches protect the underlying sandy substrate against erosion, and the ripple marks (analogous to those of generation "a" at Dinosaur Ridge) are also protected against reworking compared to areas not yet colonized by microbenthos. Subsequently, the barren areas surrounding the mat-stabilized patches are reworked again by subsequent currents. Here, a second generation of ripple marks is formed (analogous to generation "b" at Dinosaur Ridge) that may have a different direction than the older ripple marks of the established mat patches. Over time, the initially established mat patches expand laterally and now stabilize the second generation of ripple marks as well. A third reworking event affects the remaining, still barren sedimentary surface, and a third generation of ripple marks forms. This last generation of ripple marks would be analogous to those of generation "c" at Dinosaur Ridge. The older a microbial mat is, the thicker it may become. Mature, epibenthic microbial mats may fill in ripple valleys. The ripple marks that were formed at first therefore have levelled ("smooth") valleys, filled in by a mature microbial mat, whereas younger ripples show unmodified ("sharp") valley-crest morphologies.

Observation of Sand Chips.—Two exposed bedding planes in Unit 22 display flat clasts scattered across the surfaces of heavily bioturbated, silty fine- to medium-grained quartz sandstones (Figs. 1, 3A). The chips are 3 to 12 cm long and 3 to 4 mm thick, and have unusual, irregular shapes with rounded margins that contain many lobes and embayments. They are composed of carbonate-cemented, fine-grained quartz sand. Their burnt yellow to rusty red color is caused by limonite staining (Fig. 3B).

Interpretation of Sand Chips.—These sand chips are interpreted as fossil fragments of ancient microbial mats (sand chips; Pflueger and Gresse 1996). Microbial sand chips observed in modern shoreline settings have distinct lobed shapes like the examples from Dinosaur Ridge (Fig. 3C).

Their shapes can be described using two indices (Noffke 2010). Index 1 is the longest axis of a chip divided by the axis, which runs through the central point of the long axis at a 90° angle.

Index 2 is the length of the circularity of the chip divided by the longest axis. In outcrop, four representative chips were measured; they have an index 1 of ~ 1.8, and an index 2 of ~ 0.31.

Examples of modern microbial sand chips show similar index 1 values of ~ 1.75 and index 2 values ~ 0.53 (Noffke 2010).

Microbial sand chips originate by erosive water currents undermining the edges of a microbial mat and removing the substrate beneath. After

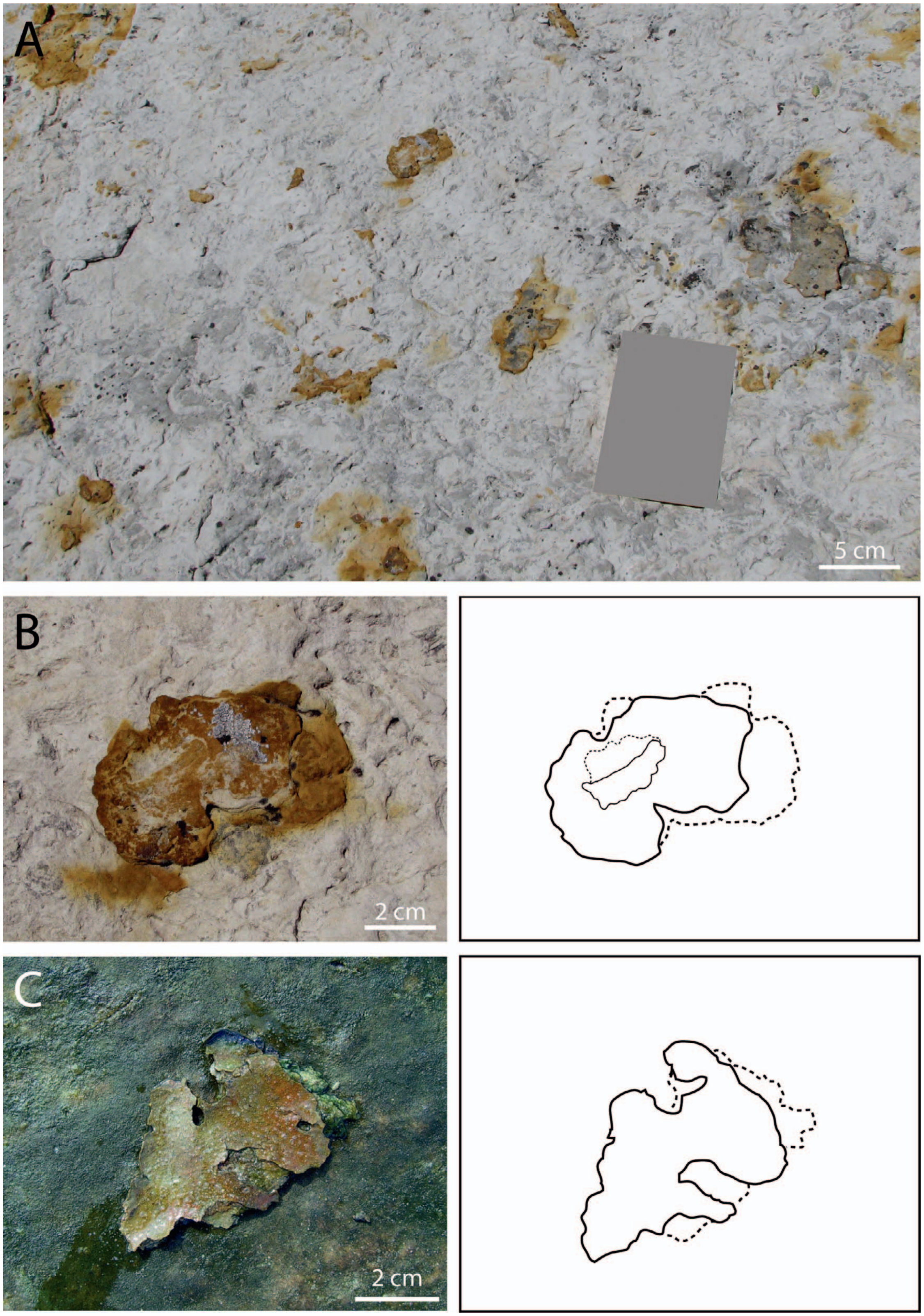

FIG. 3.—Microbial sand chips from Unit 22 and modern analogues. **A)** Chips are scattered across the ancient tidal surface. **B)** Close-up view of a sand chip. The outline of this chip is composed of lobes and embayments. The ancient chip is built up of several laminae; the stippled line in the sketch outlines laminae beneath the topmost lamina. **C)** Close-up of a modern microbial-mat chip, which shows the same characteristic outline of lobes and embayments. The stippled lines in the sketch outline the basal laminae of the mat, which are covered by the overlying mat layer. The modern mat chip appears rusty in color due to *in situ* pyrite-mineral precipitation and oxidation, analogous to coloration of chips in Parts A and B.

some time, the edge of the microbial mat hangs down like a tissue and becomes fringed. Eventually, centimeter-scale pieces of microbial mat are ripped off their parent site from the mat margin and then transported and redeposited at sites of lower current velocities. In modern tidal flats of Mellum Island, Germany, the transport distance of centimeter-scale chips commonly is less than 200 m from the point of their origin (Noffke 2010). These field measurements are consistent with boundary conditions observed for experimentally produced chips (Hagadorn and McDowell 2012).

In modern settings, the behavior of cyanobacteria in MISS can be observed. If a mat chip flipped over so that its foremost top layer formed by photoautotrophic cyanobacteria now faces downward, the microbes move towards the new top of the chip in order to receive sunlight. Once the microbes deceased, their organic matter remains and is within hours diagenetically mineralized by heterotrophic bacteria that foster precipitation of pyrite (Noffke 2000; Schieber 2007b; Newman et al. 2016). This pyrite may later be oxidized to limonite. Such microbial behavior and subsequent diagenetic alterations may explain why the rims of some Dinosaur Ridge sand chips are stained by limonite.

Observation of Over-Flip Structure.—At least four discrete tidal channels (numbered 1–4 in Fig. 4A) occur in Unit 22 (Fig. 1). In all channels, only the stoss-sides are preserved. The sides are $> 45°$ steep. Such an angle is unusually high for unconsolidated sand, which commonly builds only up to 30° slope angles. Along the stoss side of channel 1, ripple marks (arrow "rm" in Fig. 5A) are oriented almost perpendicular to the inferred water line.

The stoss side of channel 1 displays a slump structure of 0.5 m length × 15 cm width resembling an "overturned fold" (Fig. 4A, arrow "over-flip"). The close-up in Figure 4B and sedimentological evidence reveal that the slump structure is a 1–1.5-cm-thick layer of sandy sedimentary rock. Along this same channel slope, scratch marks of crocodile claws are visible (Lockley 1993) (Fig. 4B, arrow "b").

Interpretation of Over-Flip Structure.—The morphological appearance of this structure is highly unusual for slumped beds of sand (Fig. 4B). First, it is unusual that an originally uncemented sand layer formed a wavy coherent sheet only a centimeter in thickness while having a relatively wide lateral extent. Second, whereas in a slump structure the apex of the "fold" normally would point downslope, this example here has an apex pointing uphill (Fig. 4B, marked with "a"). Therefore, we interpret this "slump" structure as a fossilized microbial mat that was flipped over (Fig. 4C). Such over-flip structures have been observed in other ancient deposits (e.g., Donaldson et al. 2002; Noffke et al. 2008), and a continuum of such flipped-over structures have been produced experimentally (Hagadorn and McDowell 2012). If the levee and stoss sides of the channels at Dinosaur Ridge were lined by a microbial mat, it would have stabilized the sandy slope sufficiently to support this steep angle of this channel slope. Crocodile scratch marks (marked with "b" in Fig. 4B) that are associated with this over-flip structure suggest a scenario in which a crocodile may have slid down into this channel and pulled some of the microbial-mat-bound lining with it.

Observation of Erosional Remnants and Pockets.—In Unit 23, a large, planar sandstone surface, known to park visitors as "Slimy Beach," displays an array of round to ellipsoidal depressions, many with irregular outlines (Figs. 1, 5). The depressions vary widely in size, ranging from ~ 10 cm to several meters wide. They are 1–4 cm deep with a ca. 20° to 90° steep slope all around. Their bottoms are often covered by ripple marks, and they cover about a third of the planar bedding surface. In thin section, the sandstone forming the planar surface area has more carbonate cement than the more hematite-rich depressions. The sedimentary surface is also littered with sand chips. Most sand chips are 1–5 cm wide, but some reach 30–40 cm in diameter, such as those in the lower right corner of the outcrop, close to the "Slimy Beach" interpretive sign (Fig. 5).

Interpretation of Erosional Remnants and Pockets.—Earlier studies noted these rippled depressions, referring to them as "patchy ripples" (MacKenzie 1972; Schieber 2007b), with Reineck (1979) comparing the morphological similarity of the surface bed with "erosional remnants and pockets." Such erosional remnants and pockets form in the lower supratidal zone of modern sand flats like those of Okracoke Island (North Carolina, USA) (Supplemental Fig. 2), and Mellum Island in the North Sea (Reineck 1979; Gerdes et al. 1985; Noffke 1999, 2010). Our 1:1 scale survey of the surface (Fig. 5) yielded no evidence inconsistent with interpreting these structures as "erosional remnants and pockets," as suggested by the earlier workers. The elevated, planar areas of the sandstone surface are interpreted as fossilized epibenthic microbial mats.

Monitoring the formation of modern erosional remnants and pockets in equivalent shoreline settings showed that a small obstruction or damage to the sediment-sealing microbial mat is sufficient for erosion to start. At this initial local spot of disturbance, water currents remove the substrate beneath the microbial mat to form an erosional dent. Starting from here, scouring continues to undercut the margins of the surrounding mat and a depression forms growing laterally over time (Noffke 1999; Hagadorn and McDowell 2012). Because the sand in such depressions is not bound by microorganisms, the grains remain loose and ripple marks may form. At Dinosaur Ridge, a similar paragenetic sequence is inferred (Supplemental Fig. 3).

Measurements of the geometry of the depressions allow the reconstruction of the direction of the tidal currents forming the topography. In general, erosional remnants and pockets in a tidal system derive from the energy-rich spring flood current ascending the tidal flat and deforming the sandy surface; the weaker ebb current drains the surface leaving fainter structures behind. The surface relief of this Dinosaur Ridge bedding plane records a dominant current directed north to south and a somewhat subordinate current of southwest to west direction (Fig. 6A, B). The ripple direction and the shape of the ripples (short ripple slope pointing landwards) suggest that the ancient shoreline at Dinosaur Ridge was located somewhere towards present-day southwest, which is towards the lower left edge of the outcrop (downdip and downhill of the exposure). Log impressions of mangrove tree trunks, presumably deposited with a receding tide or as flotsam along a strandline, support the interpretation of a nearby location of the shoreline (Fig. 5, Supplemental Fig. 4). Hypothetically, because two current directions are visible, the local shoreline could have been a small embayment causing reflection and separation of the incoming flood water into two currents. A similar situation is described from Mellum Island, Germany (Noffke 1999) (Fig. 6C).

Observations of Tattered Surfaces.—Two widely exposed bedding planes in Units 19 and 24 have a strongly weathered appearance (Figs. 1, 7A). The surfaces of the quartz-rich fine-grained sandstones display a pitted and "tattered" morphology. This appearance of these surfaces is caused by flat clasts that have highly irregular, ragged outlines (Fig. 7B). Most clasts are 1–2 mm thick, and their diameters range from 1 to 20 cm. Holes a few millimeters in diameter are common in the clasts. The clasts are light tan, whereas the remaining rock bed surface is dark brown. Many clasts are connected with each other, whereas others are solitary. The clasts seem to have been "shaved off," with many having only little contact with the underlying bedding plane (Fig. 7A, B). Some clasts overlie one another in such a way that they appear to have been transported or redeposited (Fig. 7D). Whereas surfaces with such a weathered appearance may be typical for fissile mudstone, the two rock beds are, however, sandstone.

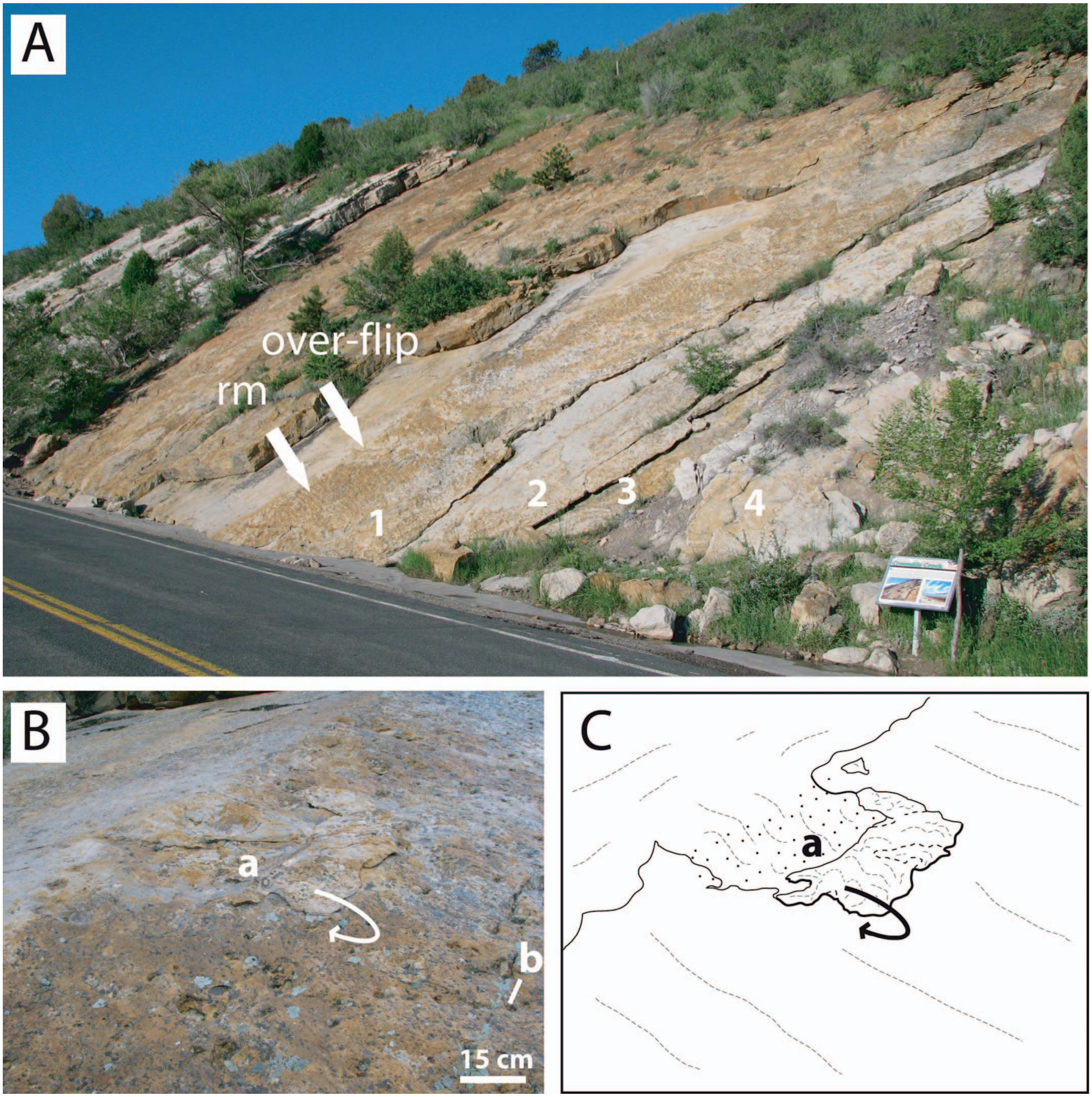

FIG. 4.—Over-flip structure and crocodile claw marks in Unit 22 at the top of the tidal channel complex known to park visitors as "Crocodile Creek." **A)** Overview of the outcrop. Four tidal channels are visible (1–4), but only the stoss sides of the channels are preserved. Channel 1 shows ripple marks (arrow "rm") that are oriented almost perpendicular to the water line of the channel; here an over-flip structure is preserved. **B)** Close-up of the over-flip structure. The apex "a" of the sediment "fold" points uphill, not downhill as it would be the case for an abiotic slump structure. The letter "b" points out one of the crocodile claw marks along the channel slope. **C)** Interpretive sketch of Part B.

Interpretation of Tattered Surfaces.—Comparable structures are known from modern sandy supratidal flats like those of Portsmouth Island, North Carolina, USA (Noffke 2010). Here cyanobacteria-dominated microbial mats start to decompose in early fall, when growth conditions become less favorable (Fig. 7C, E). The mats decompose and shed into jagged chips similar in morphology and size to the ones at Dinosaur Ridge. These modern examples exhibit the same type of embayments and lobes of their margins as well as perforation in their centers. In modern sites that contain such "shredded" mats, the mat chips are still connected to the parent mat, whereas others were ripped off completely by erosion, and then transported a few centimeters or decimeters before being redeposited. In light of the morphological similarities with the structures at Dinosaur Ridge, we suggest that these ancient bedding planes record such tattered surfaces during seasonal degradation of microbial mats.

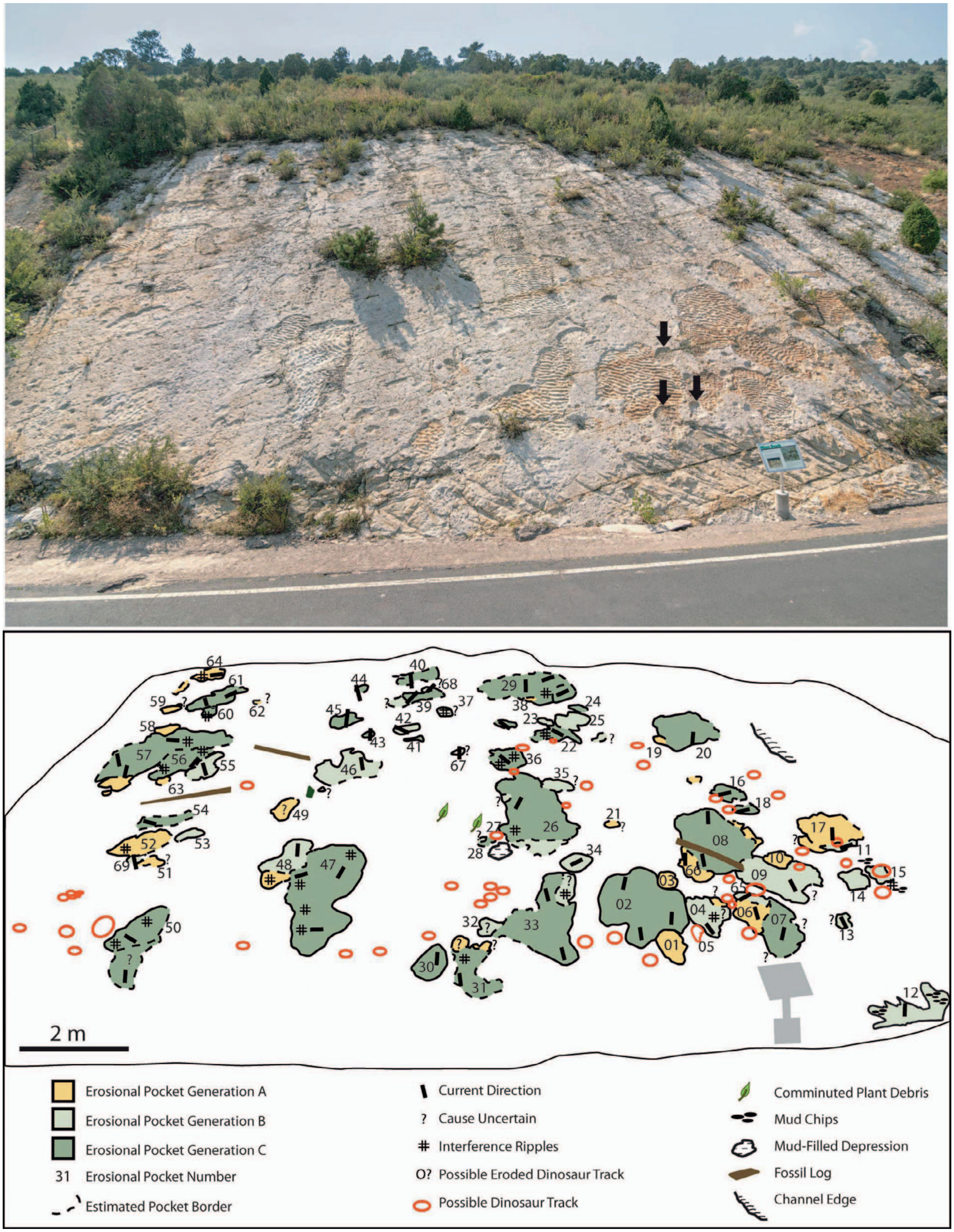

FIG. 5.—Erosional remnants and pockets on the bed surface in Unit 23, known to park visitors as "Slimy Beach." The planar parts of the bedding plane surrounding the deeper ripple-marked depressions are *in situ* preserved epibenthic microbial mat, or "erosional remnants." The depressions are called "erosional pockets." Here the sandy surface was originally barren. (See Supplemental Fig. 2 for modern–ancient comparisons of such mat-induced erosional remnants and pockets and Supplemental Figure 3 for the development of such erosional remnants and pockets.) The sketch documents the structures on the bedding plane shown in the photo, including interpretations of their stratigraphic superposition. Of 64 erosional pockets recognizable with certainty, three generations (A–C) are recognizable, including 14 belonging to Generation A, 17

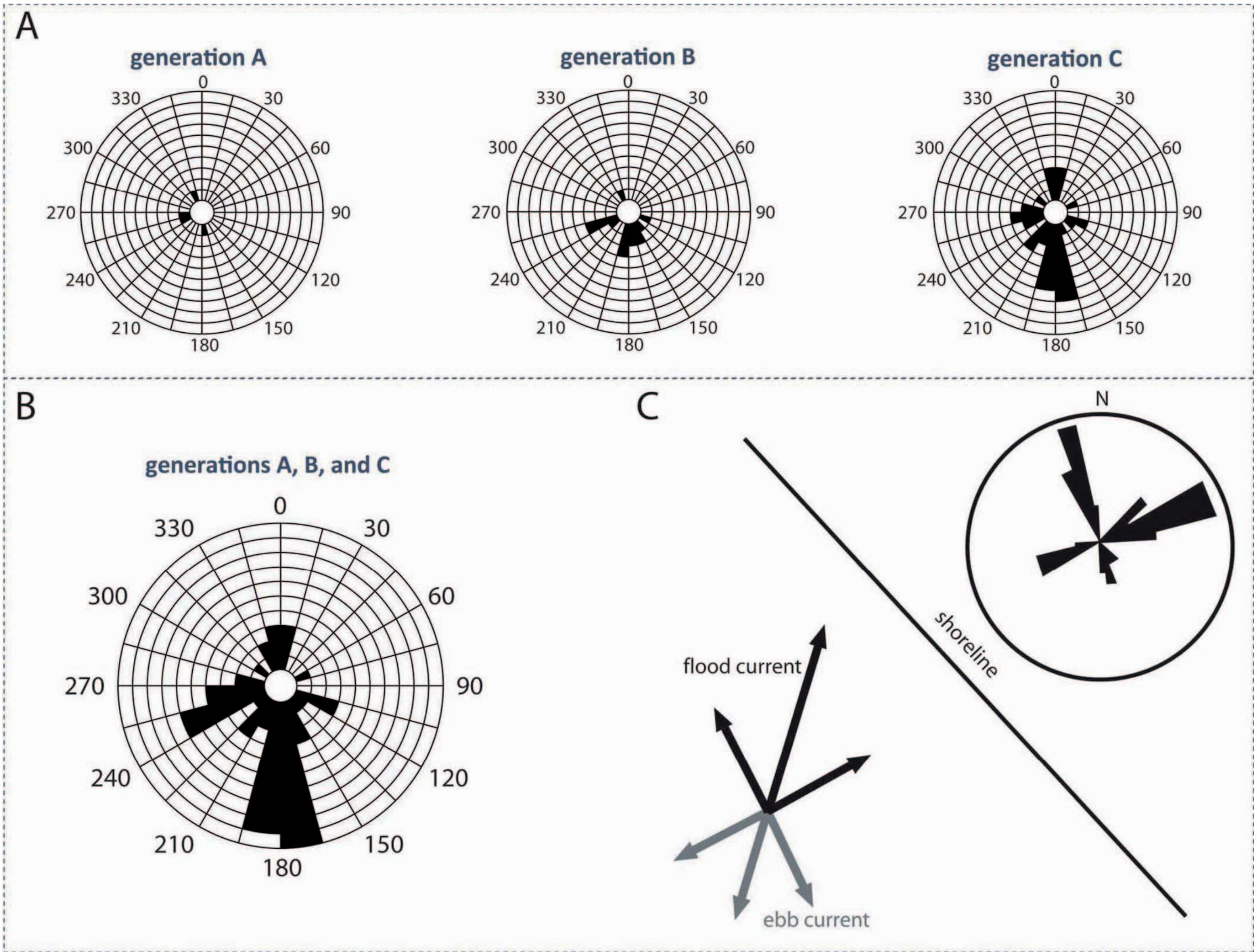

FIG. 6.—Directions of ancient currents as recorded by ripple marks in the erosional pockets, Unit 23. **A)** Shown are the flow directions of currents identified from ripples in the three different generations of erosional pockets, including Generation A (the youngest), B (intermediate), and C (oldest). The relative size of each orientation "petal" in the rose diagrams is proportional to the number of erosional pockets bearing current indicators of that orientation. **B)** The geometry of the directions records a flood current of almost north-to-south direction and the much weaker southwest–west ebb current. **C)** A similar current geometry documented from a modern supratidal flat in which reflection of flood currents (here: north-northeast) by the shoreline is occurring (Noffke 1999). The shoreline is located northeastwards of the rose graph with a strike of northwest to southeast.

DISCUSSION

Paleoenvironmental Implications

Microbial structures at Dinosaur Ridge not only enhance our understanding of the prevailing paleoenvironmental conditions that produced the "J" sandstone but also provide a useful analogue for understanding how other large dinosaur tracksites might have formed. For example, MISS help constrain the hydraulic conditions in which strata were deposited. Collectively, physical sedimentary structures and MISS suggest minimum depositional depths for the "J" Sandstone ranging from zero to a few decimeters deep for the facies represented by Units 19 and 22 (interpreted as having been produced in the lower-supratidal flats) and extending a meter to several meters in depth for Unit 20 (distributary channels). Dinosaur Ridge's erosional remnants and pockets point to a tidally dominated system with a dominant north–south oriented current and a subordinate southwest–west current, with a shoreline located toward present day southwest. Ripples suggest that current velocities at least ranged from 15 to 50 cm/s. In concert with ripple morphology in Unit 21, the tidal flats were probably ascending at first towards present day southeast (towards the lower-right edge of the outcrop). During the deposition of Unit 23, however, the shoreline must have been located in present day southwest (the lower left of the outcrop). Multidirectional

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corresponding to Generation, B, and 25 belonging to Generation C. Question marks indicate where we are uncertain about to which generation the erosional pocket belongs. The lines in the pockets indicate the axes of paleocurrents (deduced from ripple marks); these are summarized in Figure 6. Arrows in photo point to three examples of depressions in Generation A that are interpreted as dinosaur tracks that experienced minor erosion shortly after formation. Red-encircled depressions are possible small tracks, analogous in size to those from overlying horizons that have been inferred to be produced by small ornithopod dinosaurs.

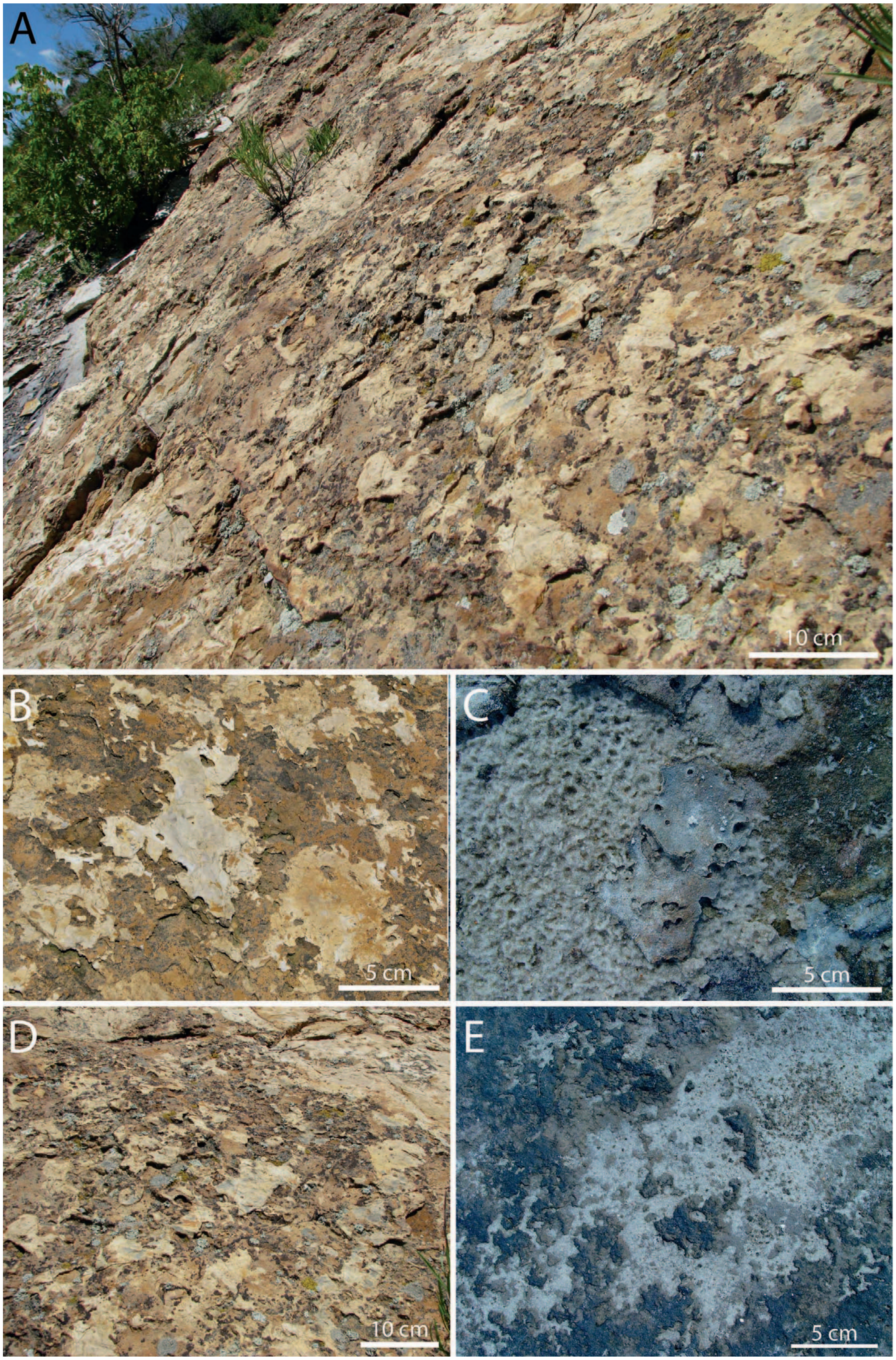

FIG. 7.—Tattered surfaces in Unit 24 and modern analogues. **A)** Oblique overview of a part of this bedding plane, illustrating that although its surface viewed from the distance appears generally planar, in close-up, its surface is quite irregular and composed of a multitude of tan-colored flakes peeling off the rock. **B)** One fragment with its typical, highly irregular outline of lobes and embayments. Like many clasts on this bed surface, small, round holes occur within its center. **C)** A microbial-mat chip on a sandy surface of a modern tidal flat in Portsmouth Island, North Carolina. Both fragments have irregular outlines composed of lobes and embayments and are perforated by small rounded holes. Compared to the still-living microbial mat visible in the upper right corner, which appears dark green, the ripped-off mat chip has dried and has a different

ripple marks and erosional remnants and pockets may have been products of episodic strong landward winds pushing flood currents far onto the intertidal and supratidal flats. The tattered bedding surfaces and the release of microbial sand chips point towards a seasonally variable ecosystem.

Considered together with previous studies of carbonate cements (Grotzinger and Knoll 1999; Dupraz et al. 2009; Noffke 2010; Warden et al. 2016) and ferruginous staining like that found in sand chips and erosional remnants at Dinosaur Ridge, microbially bound strata were deposited along a shallow to intermittently emergent coastline that fostered carbonate mineral and hematite precipitation.

Given the diversity of microbial structures at Dinosaur Ridge and the paucity of such large bedding plane exposures in the region (i.e., a near prerequisite to recognition of such structures) it is possible that they are more prevalent in the "J" sandstone elsewhere. If so, it is worth considering that microbial mats may have been prevalent in the upper-intertidal to lower-supratidal zones elsewhere in the Western Interior Seaway, along which the "J" Sandstone was deposited.

Formation and Taphonomy of Dinosaur Tracks

Microbial communities, like those that are inferred for the "J" Sandstone, may have fostered the preservation of dinosaur tracks at Dinosaur Ridge. Track preservation can be supported initially by increased plasticity of the fresh sediment, followed by continued growth of mats and microbe-mediated mineral cementation during consolidation of track-bearing surfaces. Evidence for multiple generations of post-dinoturbation microbial growth in the lower-supratidal-flat facies (Unit 23) at Dinosaur Ridge (Fig. 5) is consistent with these processes. Interestingly, such enhanced preservation is also known from lacustrine to palustrine facies in Early Cretaceous strata from Cuenca, Spain, including from a site that bears crocodilian tracks akin to those at Dinosaur Ridge's "Crocodile Creek" (Moratalla et al. 2017).

Based on thicknesses of sand chips and tattered surface fragments, Dinosaur Ridge's microbial mats were at least 1 to 4 mm thick. They episodically became desiccated based on their occurrence in intermittently emergent facies—a change that altered sediment elasticity and saturation of the underlying sediment with water. Such changes in the tensile strength of comparable modern sandy mats (e.g., Amos et al. 2004; Schieber 2007c; Friend et al. 2008; Noffke 2010; Hagadorn and McDowell 2012) allow for the possibility that Dinosaur Ridge's mats could have actually inhibited formation of small tracks and subdued the details of some trackmaker's anatomy (*sensu* Marty et al. 2009, 2010; Cariou et al. 2014).

Conversely, some of the observed microbial structures, such as the erosional pockets, may have actually been triggered by animal behavior, such as dinosaurs walking across the "J" sandstone tidal flat. Kvale et al. (2001), for example, illustrated comparable modern ripple patches from Pine Island, Florida, whose formation was triggered by animals walking across the tidal flat. To assess this possibility, we evaluated the paragenetic sequence represented by the erosional remnants and pockets in Unit 23 (Fig. 5; Supplemental Fig. 5). There are three generations: (i) small, round erosional pockets 10 to 50 cm in diameter (Generation A) of which some show an about $\sim$ 1-centimeter-high rim. The bottom of these pockets may include structures akin to deformed and broken-up microbial mats. The large clasts near the interpretive sign "Slimy Beach" may have been mat fragments ripped off their substrate and dragged upward by a dinosaur foot until falling back onto the surface. (ii) Larger, mostly ellipsoidal erosional pockets that reach 50 to 1.20 m diameters and that display ripples of well-preserved morphology, sometimes with a reddish color (Generation B); and (iii) very large (up to several meters in diameter) erosional pockets with a highly irregular outline (Generation C) that have ripple marks with rounded crests and valleys; sometimes a multidirected ripple pattern exists on the bottoms of those erosional pockets. The rounded crests and valleys point to an exposure of the originally loose sand to wind erosion and desiccation. The irregular outer shape of these depressions was caused through the continuing lateral erosion of the original pockets until neighboring depressions finally became connected with each other. Smaller depressions that are very shallow and of smooth morphology can be interpreted as footprints that were overgrown by microbial mats before any further erosive destruction (Supplemental Fig. 5). The crosscutting relationships, lateral arrangements, and sizes of the depressions lead to the suggestion that the different generations of erosional pockets record a temporal succession of individual events of dinosaurs crossing this tidal flat area; each event may have been several weeks or months apart from the next. The reasons for this hypothesis are that erosional remnants and pockets in modern supratidal flats are flooded only on occasion, when strong landward winds support a spring high tide, and that microbial mat regeneration takes a few months.

Other sites, such as the Lower Cretaceous ripple-patch-bearing tracksites of the Sousa Basin (Carvalho et al. 2013) might be amenable to such inquiry, and could help to test these hypotheses. Sedimentological studies of geologically "young" shallow to emergent dinoturbated strata is growing, and many marginal lacustrine and marginal marine Cretaceous and Jurassic strata bear signs of microbial influence (Silvia Filho 2009; Porchetti et al. 2016). Integrating data from sites like Dinosaur Ridge with the growing body of work on modern and ancient trackmaker–microbial interactions (e.g., Marty et al. 2009; Cuadrado et al. 2011; Carvalho et al. 2013) offers a direct path for deconvolving the paragenetic and taphonomic history of ancient tracksites.

CONCLUSIONS

The "J" Sandstone at Dinosaur Ridge bears a diverse array of clastic microbial structures. The rock succession includes typical MISS like microbial sand chips, erosional remnants and pockets, tattered surfaces, multi-directed ripple marks, and over-flips. These structures help constrain local hydraulic conditions, identify the location of the paleoshoreline, and refine our understanding of the amount of time represented by Dinosaur Ridge's bedding planes.

Sedimentological studies of these types of dinoturbated strata are growing, illustrating that many marginal lacustrine and marginal marine Cretaceous and Jurassic strata were microbially influenced.

SUPPLEMENTAL MATERIAL

Supplemental files are available from the SEPM data archive: https://www.sepm.org/supplemental-materials.

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color. **D)** Light-tan-colored fragments with highly irregular outlines cover the otherwise brown rock bed surface. **E)** In this modern example of a decomposing microbial mat from Portsmouth Island, many fragments of the mat have been released, and the fragments are distributed at random, sometimes overlapping, sometimes deposited individually, sometimes still connected to each other—morphologies analogous to those observed at Dinosaur Ridge.

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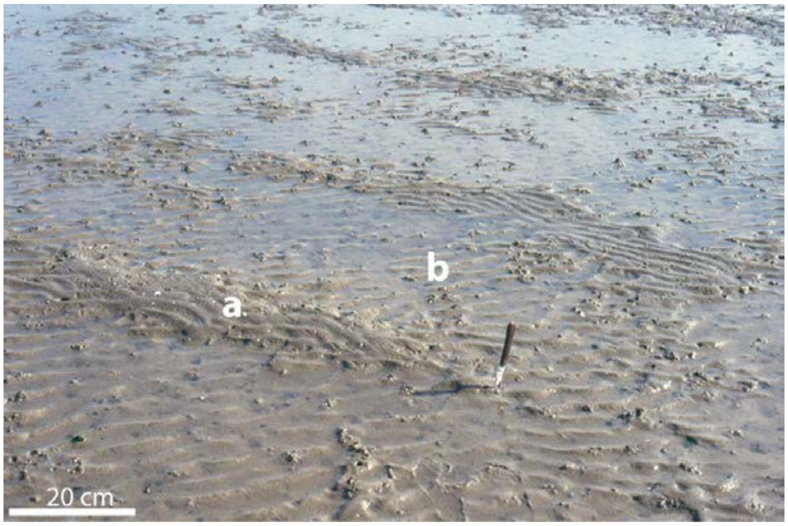
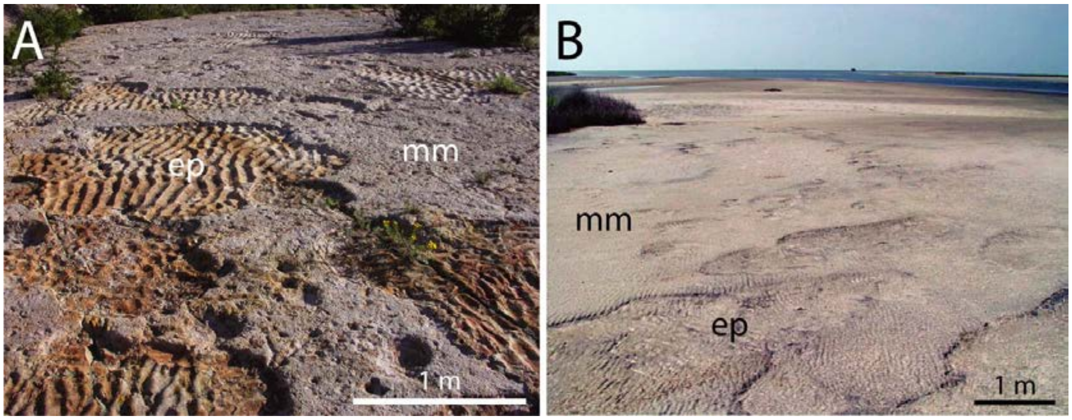
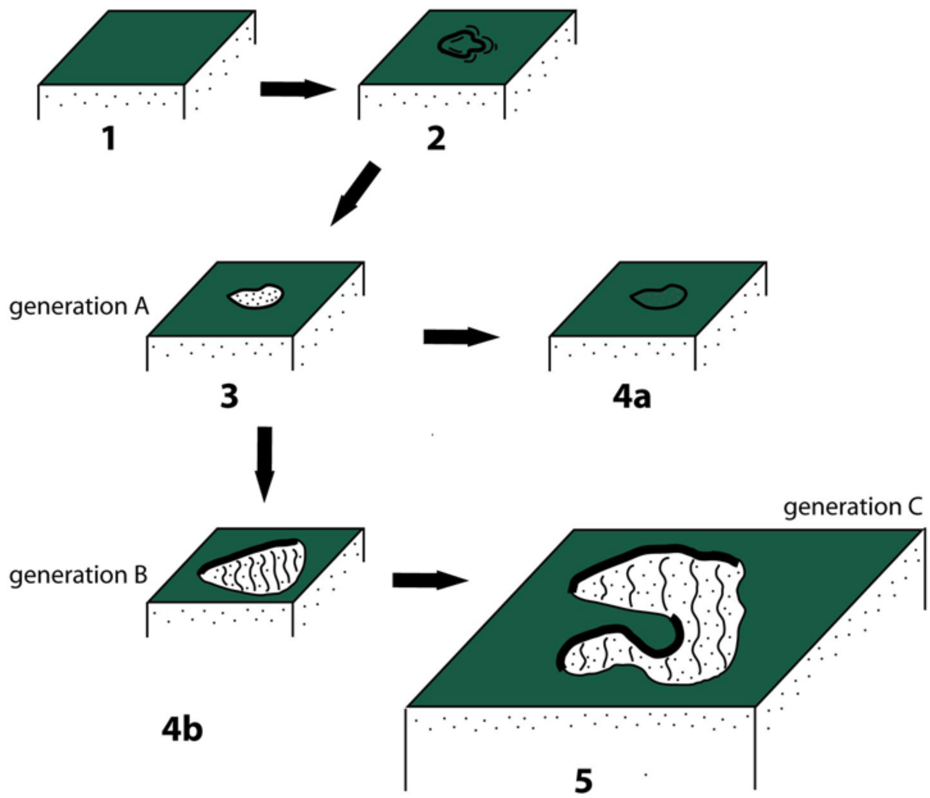


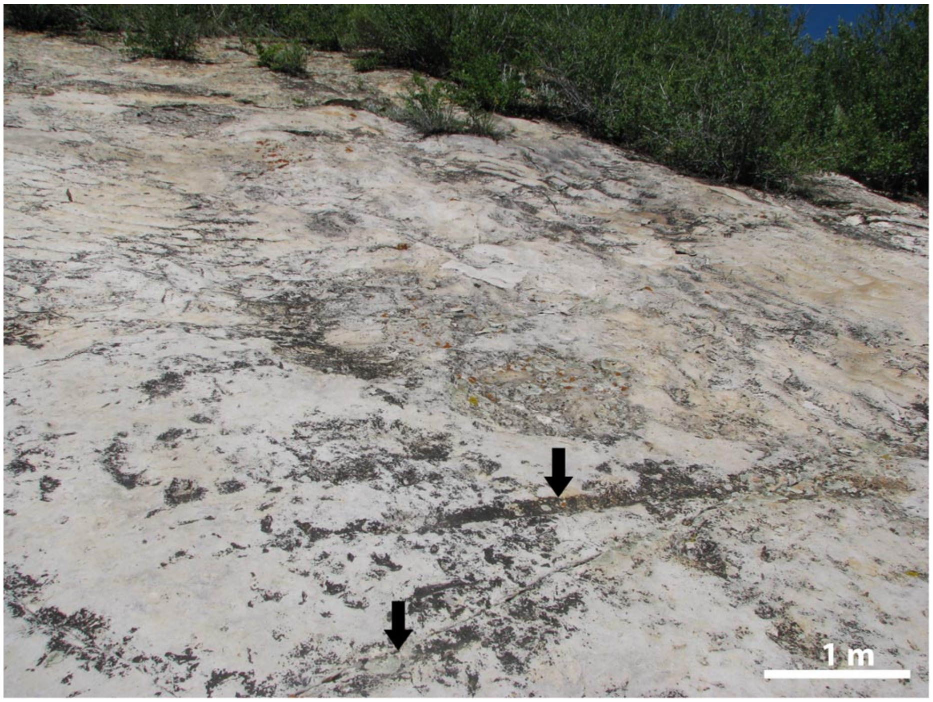
SUPPLEMENTARY FIGURE 1 - Multidirected ripple marks from modern tidal flats on Mellum Island, Germany. Two ripple mark directions, including an older generation (a) and a younger generation (b) were formed by sequential reworking events that interrupted microbial mat development. The ripple patches of generation (a) are slightly elevated because they are biostabilized by an endobenthic microbial mat.



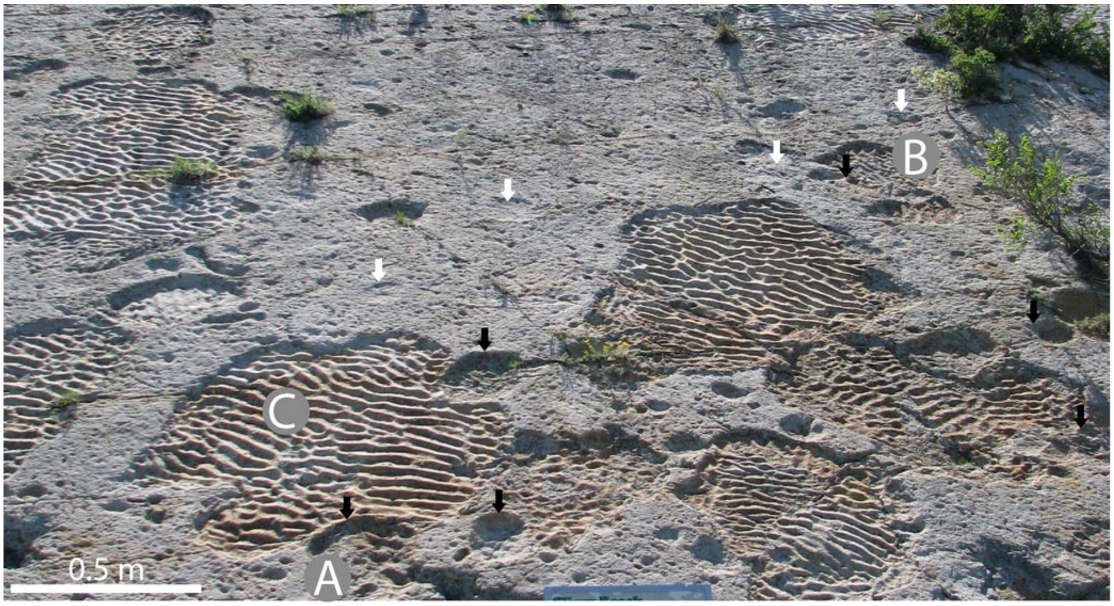
SUPPLEMENTARY FIGURE 2 - Erosional remnants and rippled erosional pockets from Unit 23 (A) and a modern tidal flat from Okracoke Island, North Carolina, USA (B). Such depressions are called erosional pockets (ep); the microbial mat (mm) forms the planar surface surrounding the depressions. The planar 'mesas' are called erosional remnants.



SUPPLEMENTARY FIGURE 3 – Steps of formation of erosional remnants and pockets at Dinosaur Ridge. (1) The tidal flat surface is covered by a microbial mat and stabilized against erosion. (2) A dinosaur footprint causes a local disturbance of the mat's integrity. (3) Erosion starts and removes the microbial mat cover that was disturbed. An erosional pocket starts to form (Generation A). Ripple marks are not yet present. (4a) The microbial mat regrows and 'heals' the eroded spot. The disturbance is now less visible (compare features shown in Fig. 11, white arrows). (4b) In this example, however, erosion continues and ripple marks form at the bottom of the erosional pocket (Generation B). (5) Lateral expansion by continuing erosion causes several small erosional pockets to join. Large erosional pockets with irregular outlines form (Generation C). Ripple marks are now exposed to aerial erosion, which reduces the contours of the ripple crests and valleys.



SUPPLEMENTARY FIGURE 4 - Upper portion of the "Slimy Beach" outcrop in Unit 23, illustrating some of the log imprints (arrows). The logs were from mangrove-like forests that colonized nearby swamps. If the logs accumulated at the ancient shoreline, they suggest shallow depositional conditions consistent with ripple, channel, and paleocurrent data.



SUPPLEMENTARY FIGURE 5 - Annotated photograph of a portion of the erosional pockets and dinosaur tracks in Unit 23. This close-up shows erosional pockets of Generations A, B and C. Small depressions with steep slopes are interpreted as individual dinosaur tracks. Note the elevated rims (black arrows) around some examples, perhaps sediment squeezed out from beneath the foot. White arrows point to shallow depressions that may represent much older dinosaur tracks that have been overgrown ('healed') by microbial mats and therefore are more diffuse in their morphological details.