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SHORT-TERM EVOLUTION OF PRIMARY SEDIMENTARY SURFACE TEXTURES (MICROBIAL, ABIOTIC, ICHNOLOGICAL) ON A DRY STREAM BED: MODERN OBSERVATIONS AND ANCIENT IMPLICATIONS

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ABSTRACT: **A wide variety of sub-ripple-scale sedimentary surface textures are known from bedding planes in the sedimentary rock record. Many of these textures were traditionally ascribed an abiotic origin (e.g., due to rain drop impact, adhesion, etc.), but in recent decades the role of microbial mats and biofilms in sculpting and mediating some forms has become increasingly recognized. Microbial sedimentary textures are now well-described and understood from modern tidal environments and biological soil crusts, but descriptions from fluvial settings are less common, despite their known occurrence in ancient alluvium. This paper reports a suite of primary sedimentary surface textures which were observed forming in discrete bodies of standing water in the lower reaches of the ephemeral Murchison River, Western Australia. Microbial sedimentary signatures included bubble impressions (burst and intact) and roll-ups, in addition to reduced horizons. Many of these features exhibited rapid temporal evolution of their morphology in the dry days following an interval of heavy rain. Significantly, these microbial features were witnessed in close spatial proximity to other abiotic and biotic sedimentary surface textures including raindrop impressions, adhesion marks, desiccation cracks, and vertebrate and invertebrate traces. Such proximity of abiotic and microbial sedimentary surface textures is rarely reported from bedding planes in the rock record, but these modern observations emphasize the fact that, particularly in non-marine environments, such structures should not be expected to be mutually exclusive. An appreciation of the fact that primary sedimentary surface textures such as these develop during intervals of stasis in a sedimentation system is crucial to our understanding of their significance and diversity in the rock record.**

INTRODUCTION

The contribution of microbial mats and biofilms towards shaping textures on siliciclastic bedding planes in the geological record has been the focus of much research in recent decades (e.g., Krumbein 1994; Hagadorn and Bottjer 1997; Pflüger 1999; Gerdes et al. 2000; Schieber et al. 2007; Noffke 2010; Seckbach and Oren 2010; Noffke and Chafetz 2012) and many such textures can be considered 'microbially induced sedimentary structures', or 'MISS' (Noffke et al. 2001). Fossilized examples of such features have commonly been explained through analogy with modern textures that can be seen forming under a microbial influence (e.g., Grazhdankin and Gerdes 2007), and modern MISS are well-documented from mats forming in tidal (e.g., Gerdes and Klenke 2007; Cuadrado et al. 2014), ephemeral lacustrine (e.g., Beraldi-Campesi and Garcia-Pichel 2011), and desert (biological soil crust) settings (e.g., Beraldi-Campesi et al. 2014). Significantly, where records of ancient MISS have been reported, it is only rarely that they have been recorded as co-occurring with abiotic textures such as adhesion marks or raindrop imprints, despite this association being common in modern settings (Davies et al. 2016). They are more frequently reported in association with current-related structures—e.g., Noffke (1998), Heubeck (2009), and Gerdes and Klenke (2007). A more holistic approach, considering MISS alongside abiotic textures as characteristics of bedding planes, is desirable in order to promote a more rounded understanding of their significance in ancient successions.

In a recent paper, Davies et al. (2016) emphasized the fact that MISS are actually one subset of an umbrella group of 'sedimentary surface textures', which also includes non-microbial and problematic textures. When observed on bedding planes in the rock record, such textures may exhibit substantial morphological variability in part due the palimpsesting of microbial and non-microbial signatures, but also due to post-depositional processes (such as loading), and later effects of diagenesis and weathering (Davies et al. 2016). Herein we emphasize an important distinction between primary sedimentary surface textures (formed *in situ* by contemporaneous processes on a depositional substrate, and sometimes preserved in the rock record) and secondary sedimentary surface textures (arising from post-depositional processes). In this paper we focus solely on the former.

The purpose of this short paper is to describe modern examples of primary sedimentary surface textures (microbial, neoichnological, and abiotic) co-occurring and actively forming in drying pools of water in the Murchison River of Western Australia (Table 1). Although ancient alluvial MISS have been documented throughout the Precambrian and Phanerozoic (e.g., Prave 2002; Davies et al. 2006; Sheldon 2012; Prescott et al. 2014), their modern counterparts are comparatively under-reported, and the Murchison River examples described here present an opportunity to survey recurring primary sedimentary surface textures from an active ephemeral stream setting. The co-existence of microbial and abiotic sedimentary surface textures, plus neoichnological signatures, is emphasized in order to inform interpretations made from the rock record. The microbial textures were observed to exhibit morphological change as the standing water bodies evaporated during a spell of hot and dry weather, while most of the abiotic textures exhibited little variation. We discuss how considering this rapid temporal variation in morphology may be used to explain the great diversity of primary microbial textures in the rock record (see Davies et al. 2016), and use the modern observations to provide a conceptual model

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TABLE 1.—*Details of primary sedimentary surface textures observed in the Murchison River. "Coverage" pertains to the spatial coverage of a particular feature in the locations in which said feature is observed, ranging from isolated to pervasive. "Classification" divides features into three categories (microbial, neoichnological and abiotic) dependent on mode of formation. "Formation" provides some discussion on the mode and time scale of formation of the textures. Note that while abiotic and neoichnological features are commonly the product of an event, microbial surface textures are frequently due to development over an extended time interval.*

Feature	Figures	Dimensions	Coverage	Classification	Formation
Raindrop impressions	2E, 2G, 4A–4D	2–10 mm diameter 1–25 mm^2 area	Pervasive	Abiotic	Individual or multiple precipitation events
Smoothed raindrop impressions	2F, 4C, 4D	2–10 mm diameter 1–25 mm^2 area	Locally pervasive	Abiotic	Individual or multiple precipitation events
Bubble impressions	2B, 2H, 2I, 4B–4H	1–3 mm diameter 0.25–2.25 mm^2 area	Pervasive	Microbial	An interval of prolonged microbial photosynthesis
Elongate bubble impressions	2C, 4A, 4B	0.2×1–0.7×5 mm^2 area	Locally pervasive	Microbial	An interval of prolonged microbial photosynthesis, followed by functional collapse of the microbial community
Branching burrow	2F, 2H, 3	3–10 mm width	Isolated	Neoichnological	Arthropod burrowing, possibly in multiple stages over the time interval during which the organism was domiciled
"*Cochlichnus*"	2F, 2I	0.2–0.4 mm width	Isolated	Neoichnological	Movement of an invertebrate across the sediment, in a single event
Biofilm/mat fragment	2H, 3, 4C–4F	11×15–26×35 mm^2 area	Isolated	Microbial	Singular event associated with physical decay and drying of a microbial film
Desiccation cracks	2A, 2B, 2E, 2F, 2I, 4A–4H	0.2–6 mm width 11×13–143×204 mm^2 plate area	Pervasive	Abiotic	Progressively developed during an interval of drying
Vertebrate tracks	3, 4C, 4D	140 mm × 70 mm length × width (individual footprint, bird) 19 mm × 16 mm length × width (footprint pair, mammal)	Isolated	Neoichnological	Movement of a vertebrate across the sediment, in a single event
Tepee structures	3	1–7 mm crest width	Locally pervasive	Abiotic	Progressively developed during an interval of drying
Adhesion marks	3, 6B	2–5 mm width	Pervasive	Abiotic	Punctuated episodes of accretion arising from aeolian transport of sediment over a damp substrate
Wrinkle marks	3	1–5 mm crest width	Locally pervasive	Microbial	Developed during interval of microbial activity

illustrating how microbial, ichnological and abiotic primary sedimentary surface textures may become preserved in the sedimentary rock record.

LOCATION OF STUDY

The observations described here were made at sites spaced along approximately 40 km, within gorges of the lower reaches of the Murchison River near Kalbarri, Western Australia (Fig. 1). The main observations were made in a series of drying puddles in a small entrenched tributary of the Murchison River at Stonewall and other observations were made from the main channel of the river at The Loop and Four Ways. The lower Murchison River was dry during the interval of study, with only scattered perennial pools of standing water along its length. The observations were made in autumn, following a four-month period in which the nearest weather station (Kalbarri) had recorded a near-average 48.9 mm of rain (compared to a mean rainfall of 46.3 mm for the same months in the years 1970–2015; Australian Government Bureau of Meteorology 2016). The first visit to the sites at Stonewall was made on 28 April 2016, following 9.7 mm of rain in the preceding 48 hours, including 0.6 mm in the preceding 24 hours. The preceding month was dry, except for 16.7 mm rainfall on 11–13 April. The second visit was made on 10 May 2016, after an interval of dry weather in which 0.2 mm rain fell (on May 8). The mean daily maximum temperature between the two visits was 25.9 °C. The first visit to the site at Four Ways was made on 27 April 2016, with subsequent visits made on May 9, 16, and 23. The final visit was preceded by 5.2 mm of rain, which fell on 22 May. During the period from 8 May to 21 May no rain fell. The only visit to the site at The Loop was made on 5 May 2016, following eight days without rainfall.

SEDIMENTARY SURFACE TEXTURES IN THE MURCHISON RIVER

The active sedimentary substrates of the Murchison River present an opportunity to study the short-term development of primary sedimentary surface textures, unaffected by secondary post-depositional processes,

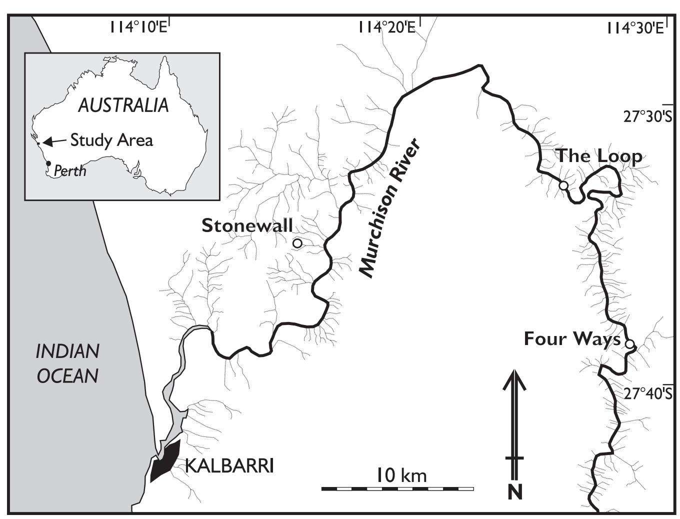


FIG. 1.—Location map of the lower Murchison River, Western Australia, showing sites at Stonewall, The Loop, and Four Ways.

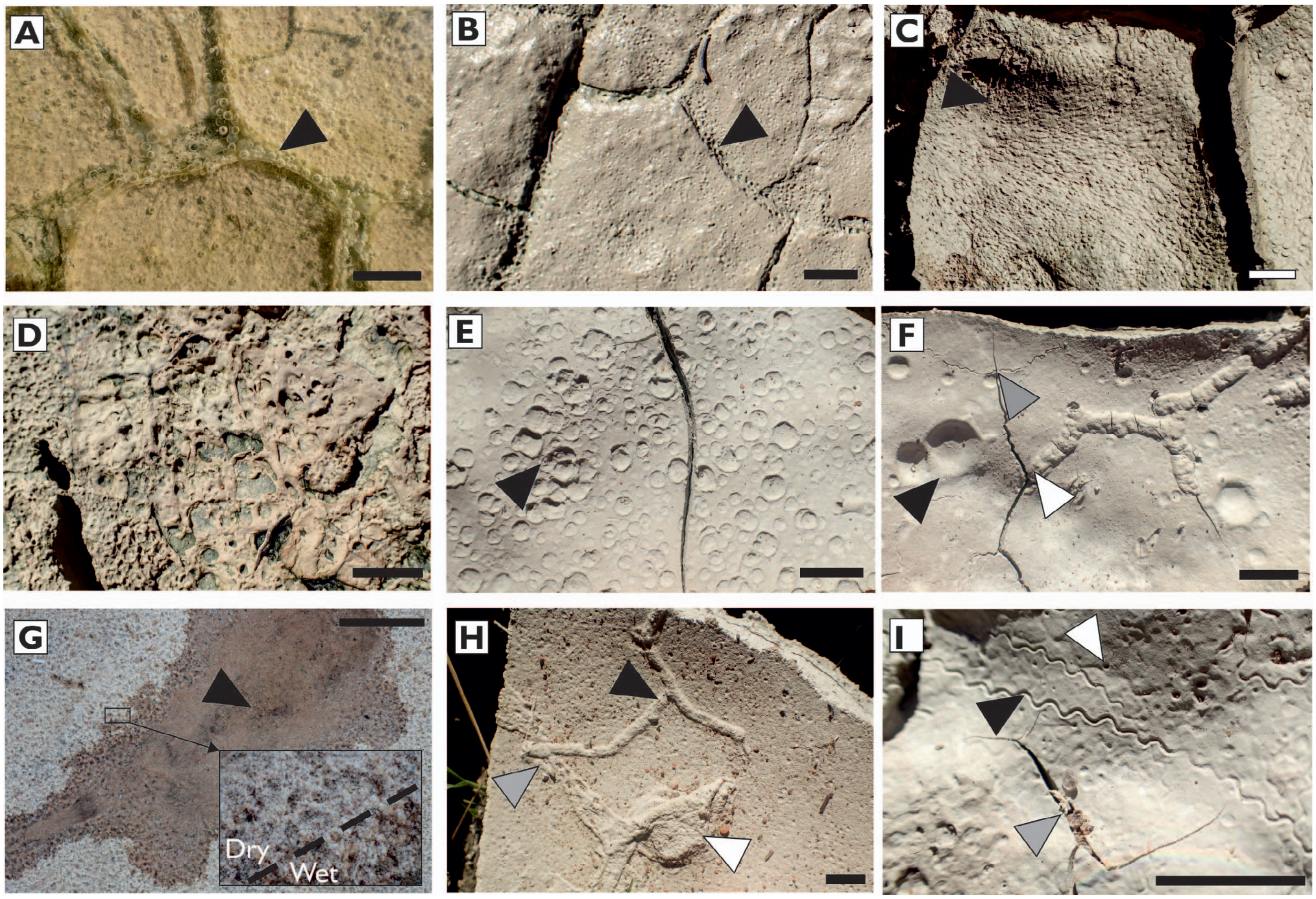


FIG. 2.—Microbial and abiotic sedimentary surface textures in the Murchison River. Images A–F and H–I from ponds at Stonewall, scale bar = 1 cm. Image G from alluvial sand at Four Ways, scale bar = 5 cm. See Online Supplemental File 1 for high-resolution, zoomable images. **A**) Submerged biofilm with oxygen bubbles. Arrow indicates how a thicker, filamentous microbial community has developed along the edge of a submerged desiccation crack and acts as a locus for a greater density of bubbles. **B**) Dried equivalent of A, where cavities left by bubble have been left in clay film. Arrow points to greater density of bubble marks along desiccation crack. **C**) Elongate bubble impressions in dried clay on slope slightly inclined in direction of arrow. Arrow indicates how ellipsoidal bubble marks are aligned downslope, presumably due to retreat as water dried, and show convergence and divergence of bubble tracks around an obstacle—in this instance a small raised mound of sediment. **D**) Dried biofilm on clay substrate demonstrating original organic material with cavities from burst bubbles aligned in direction of water retreat. **E**) Raindrop impressions in dried clay. Impressions formed when clay was wet; they have greater dimensions, overlap one another, and display crater rims (arrow), which distinguish them from bubble marks. **F**) Neoichnological, microbial, and abiotic sedimentary surface textures in close association. Raindrop impressions formed on a substrate with a veneer of water at the time of precipitation have wider dimension than those in damp sediment, and less pronounced rims, although craters still exhibit interference with one another (black arrow). Branching insect burrow superimposed by small biofilm bubble marks (white arrow), which also occur on sediment away from burrow. Small "*Cochlichnus*"-type trail, formed when sediment had a thin film of water, has been offset by later desiccation cracking (gray arrow). **G**) Raindrop impressions in sand, stabilized by salt crust. Water was poured onto the impressions from a bottle, but the impressions were only destroyed when they were directly under the poured stream (arrow). Where sediment was dampened, salt crust preserved original morphology (inset). **H**) Branching insect burrow (black arrow) and rolled up preserved biofilm (white arrow). Superimposition of the former onto the latter indicates that it post-dated the degradation and roll-up of the biofilm (gray arrow). **I**) Sinusoidal trail ("*Cochlichnus*") likely made by insect larva or worm in thin veneer of water on sediment (Metz 1987) (black arrow). Close association with both microbial bubble marks (white arrow) and partial desiccation crack (gray arrow).

which have implications for analogous features that may be seen in the rock record (see later discussion). Sedimentary surface textures were observed which arose from microbial, abiotic, and neoichnological processes: three distinct classes of origin, within which multiple different processes or organisms may have operated (e.g., raindrop impressions and adhesion (abiotic), vertebrate and invertebrate tracemakers (neoichnological), or cyanobacteria and other microbes (microbial). The term 'abiotic' is used here to describe those sedimentary structures and textures that can be observed (in nature or experimentally) to form in the absence of biological influences. While we emphasize that interstitial micro-, meio- and macrofauna may be present within most naturally occurring sediment on Earth today, sedimentary structures and textures are here considered abiotic when the presence of such organisms is not a prerequisite for their physical formation, based on current understanding.

Microbial Sedimentary Surface Textures

Subsequent to the development of the Murchison River ponds as they filled with meteoric water, biofilm communities had established within a matter of hours. Microbial communities containing EPS-secreting cyanobacteria (observed to be oxygenic) were seen to have developed across the substrates, but were thicker and more filamentous in locally deeper water, along the margins of relict, submerged desiccation cracks (Fig. 2A). The predominant visible effect of these biofilms on the substrate arose from their production of bubbles of oxygen via photosynthesis, which developed across

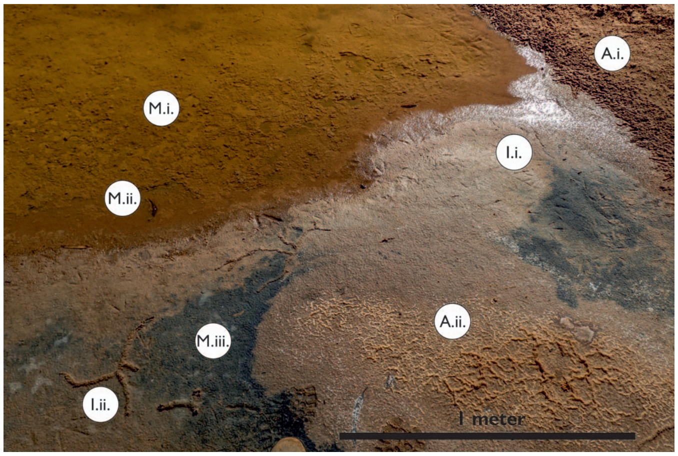


FIG. 3.—Margin of deep pool of standing water on dry river bed of the Murchison River, west of The Loop. Image shows close spatial proximity of sedimentary signatures developed by abiotic (A), microbial (M) and ichnological (I) means. Abbreviations: A.i. = adhesion marks developed on the bottomset of a 1.5 m-tall fluvial sand bar; A.ii. = tepee structures developed in salt crust; M.i. = wrinkled surface developed on top of 0.5 cm-thick microbial mats; M.ii. = rolled-up and curled fragments of microbial mat in shallower water; M.iii. = reduced layer of black sediment exposed where mats were previously active; I.i. = bird footprints; I.ii. = branching insect burrow developed in thin layer of oxidized sediment underneath salt crust, does not penetrate into reduced sediment.

the biofilm, but particularly in areas where the biofilms were thicker (Fig. 2A). Following drying, and the subsequent disappearance of the biofilms, impressions of these bubbles could be seen across muddy substrates and were distinguishable from raindrop impressions by their smaller diameter (Table 1), lack of raised rims, and clustering along the margins of desiccation cracks, where biofilms had produced more bubbles (Fig. 2B).

On parts of the substrate that exhibited relief—for example, the sloping margins of drying ponds—the bubble impressions were seen to be elongate, reflecting bubble trackways in biofilms that had retreated downslope as the ponds evaporated. In these instances, the bubble impressions also exhibited a tendency to diverge and converge around small undulations in the muddy sediment (Fig. 2C).

In addition to impressions left in the sediment, occasional organic remnants of dried biofilm were observed. These retained circular impressions of former bubbles that were often distorted, reflecting the contraction and shear of the biofilm as it dried out (Fig. 2D). Other features associated with dried preserved biofilms included isolated instances of curled and rolled fragments which were formed after the mat had become detached from the substrate and were thought to have ceased producing oxygen bubbles (Figs. 2H,4E, 4F).

Where biofilms were observed in deeper (up to 1 meter) ponds of water that pre-dated the most recent precipitation event, their prolonged activity on the sediment surface had led to the development of a prominent black horizon of anoxic sediment beneath the mat, possibly arising from the activity of microbial constituents (Fig. 3).

Abiotic and Neoichnological Sedimentary Surface Textures

Raindrop impressions, characterized by raised rims and occasionally overlapping craters of 2–10 mm diameter, formed during the precipitation event of 26–27 April, preferentially in damp muddy sediment adjacent to submerged pools (Figs. 2E, 4C). These impressions did not form in fully submerged sediment, where standing water acted as a buffer to impact. Some examples were seen which may have impacted substrates that had a thin film of water: in such instances, the raindrop impressions exhibited less defined crater rims and were seen in direct association with horizontal insect burrows and relict bubble impressions from former biofilms (Fig. 2F). Alternatively, these smoothed raindrop impressions may reflect leveling of the crater rims as the puddle levels rose and transgressed over the rain-pitted damp substrate following the precipitation event.

In sandy substrates, raindrop impressions were less well-defined in terms of crater rims, but were stabilized by salt such that they maintained their morphology even when they were artificially wetted (Fig. 2G). Where salt was more abundant, such as on the evaporated margins of larger pools of standing water, tepee ridges developed, although their microbial equivalents (petee ridges, Gavish et al. 1985) were absent. Other non-microbial textures in sandy substrates included adhesion marks formed by the accretion of wind-blown sand onto damp sediment (Kocurek and Fielder 1982) (Fig. 3).

Muddy substrates were also characterized by partial/incipient desiccation cracks that began to develop shortly after the precipitation event (Fig. 2F, 2I). These desiccation cracks became more pronounced and deep-penetrating during the subsequent dry interval, with many of the cracks having detached at a sandy layer below the muddy substrate twelve days later (Fig. 4C, 4D). The formation of some of the desiccated surfaces had clearly initiated during an interval of drying that preceded the precipitation of 26–27 April, apparent through their existence on both submerged and emergent substrates at the time of the first visit (Fig. 2A). Density of desiccation was greater (i.e., surface plates were smaller; Table 1) around pond margins where water was shallower and more rapidly evaporated, such that, during the interval of this study, the duration of subaerial exposure was longer.

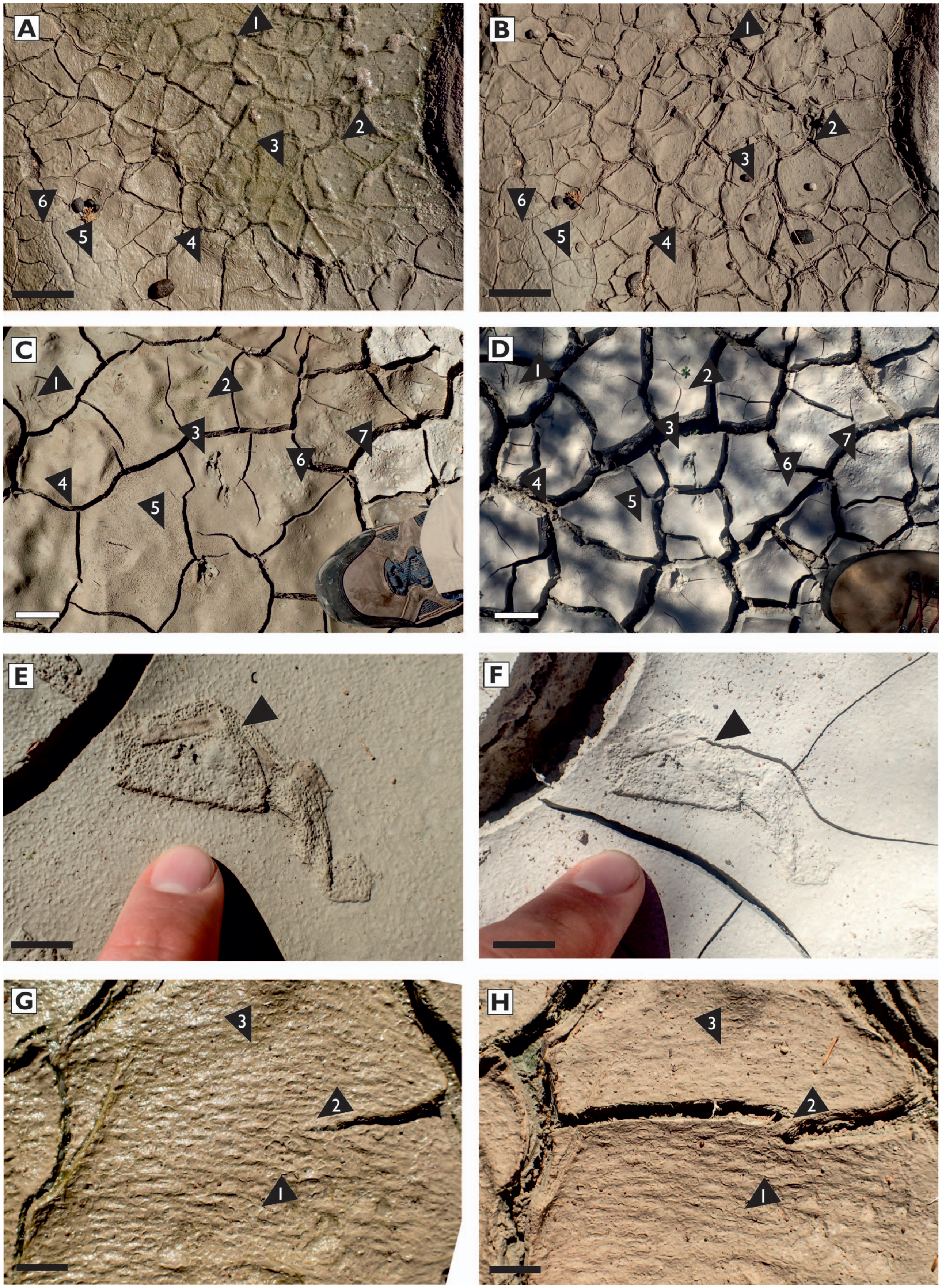
Neoichnological traces were also commonly observed in the Murchison River ponds, with vertebrate tracks (Fig. 3), branching burrows of insects (cf. Hasiotis 2002) (Fig. 2H) and sinusoidal trails ("*Cochlichnus*") likely made by annelids (cf. Hasiotis 2002) or insect larva (cf. Metz 1987) in a thin veneer of water on sediment (Fig. 2I). These tracks and trails corroborate observations made from modern tidal settings (e.g., Baucon 2008; Cuadrado et al. 2014) that MISS need not be exclusive of sedimentary evidence for co-existing metazoan life.

Association of Textures and Temporal Variation

Microbial, abiotic, and neoichnological textures co-occurred in the studied ponds, frequently in close proximity. Figure 3 illustrates an area of approximately 1.5 m^2 where living biofilms, with curled margins, have persisted in a standing body of water. In the immediately adjacent emergent areas, a tepee-ridged salt crust has developed on black sediment possibly indicating chemical reduction associated with a formerly submerged biofilm. The salt crust is disturbed by later bird footprints as well as branching burrows which formed at the interface between the salt layer and underlying reduced sediment. The pond also borders a relict sandy fluvial bar form, with abiotic adhesion marks developed on the damp bottomsets of the bedform and later stabilized by salt.

In shallower ponds of water, palimpsesting of features that developed during different stages of rapid wetting or drying were frequently observed. One example of this can be seen in the preferential development of bubble marks along the margins of submerged desiccation cracks (Fig. 2B). A further example can be seen in Figure 2H where microbial bubble marks are superimposed on an insect burrow, but are absent within the craters of raindrop impressions, permitting the order of the features' formation to be ascertained (burrow, bubble marks, raindrop impressions; see Online Supplemental File 1 for larger image).

These examples illustrate the fact that microbial and abiotic textures are not mutually exclusive. They also illustrate the potential for morphological change and palimpsesting over relatively short intervals of time. Figure 4 shows four examples of sedimentary surface textures, illustrating temporal evolution of the morphology of these features during the 12 days of drying that followed the precipitation event. With the exception of desiccation, which became more intense with time, the majority of the non-microbial features reflect individual events (e.g., rain impact or trackway formation)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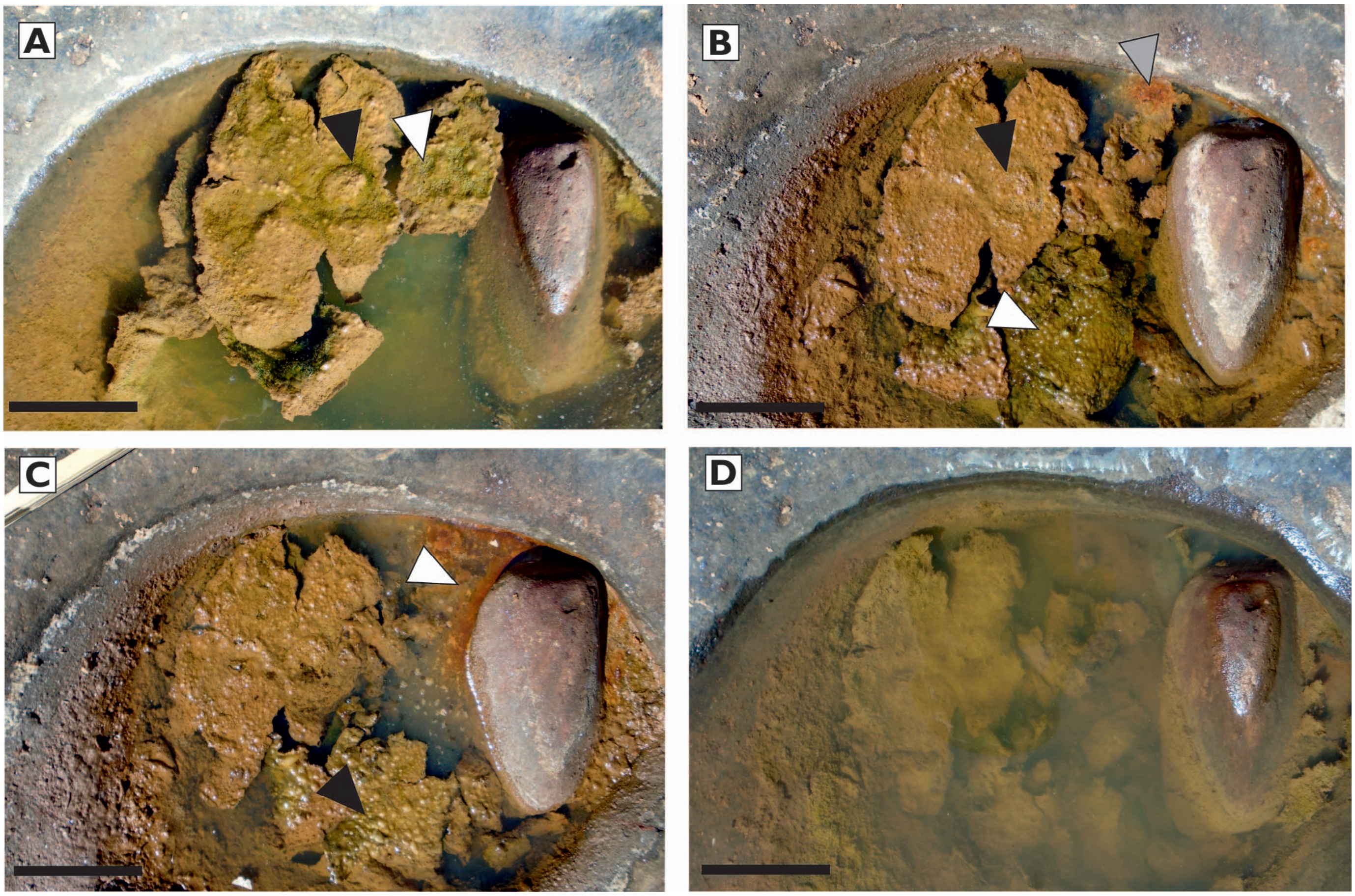

FIG. 5.—Changes to living microbial mat in response to environmental changes, within an isolated rain-fed pothole at Four Ways. Scale bar = 5 cm. See Online Supplemental File 3 for high-resolution, zoomable images. **A**) Detached mat containing oxygenic microbial community floating in pond and exhibiting doming (black arrow) and small surficial bubbles of oxygen (white arrow). Photograph taken on 27 April 2016, following 9.7 mm rain in the previous 24 hours. **B**) Same mat 12 days later (9 May 2016) with only 0.2 mm rain in intervening days. Pond has dried slightly. Mat dome has collapsed (black arrow) and mat has fragmented further. Fewer oxygen bubbles visible, but 'lizard-skin' domes (*sensu* Eriksson et al. 2007) have developed in separate mat fragment floating deeper under water (white arrow). New microbial community seen as reddened biofilm (gray arrow) has developed (possibly indicating a community of iron-oxidizing bacteria). **C**) Mat on 16 May 2016, following seven days without precipitation. No surficial oxygen bubbles. Lizard-skin lower mat now subaerially exposed at water-air interface, but maintaining form (black arrow). Red biofilm has expanded (white arrow). **D**) Mat on 23 May 2016, immediately after 5.2 mm precipitation. Pond has refilled, but mats have not yet 'caught-up' with new water level. Mats are apparently temporarily dormant with no evidence for active production of oxygen bubbles.

and remained 'frozen' in the cohesive muddy substrate with little degeneration of their morphology for days after their formation. This contrasts with areas formerly colonized by biofilm, the morphology of which clearly evolved as the biofilms expired and then degraded. Even greater short-term morphological variation could be seen within living microbial mats over similar time intervals, as microbial communities developed and responded to external environmental factors (Fig. 5).

IMPLICATIONS FOR PRIMARY SEDIMENTARY SURFACE TEXTURES IN THE ROCK RECORD

While sedimentary surface textures in the rock record may be complicated by the palimpsesting of post-depositional signatures, clear examples do exist where only primary sedimentary surface textures have been preserved (Fig. 6). The observations made on the diversity and short-

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FIG. 4.—Temporal variation in sedimentary surface textures at Stonewall between 28 April (following a 48-hour interval of 9.7 mm precipitation) and 10 May 2016 (following a 12-day interval of 0.2 mm precipitation). Scale bar = 5 cm in A–D and 1 cm in images E–H. See Online Supplemental File 2 for high-resolution, zoomable images. **A**, **B**) Partly submerged substrate which dried completely during the interval, showing: 1) complete desiccation and detachment of mud clasts formerly colonized by biofilm; 2) relict desiccation cracks (existing prior to filling of puddle in A) maintaining their form; 3) actively photosynthesizing mats creating bubbles in (A) that are preserved as bubble impressions in (B); 4) elongate bubble marks, the most pronounced of which are preserved over the period of study; 5) increased density of desiccation cracks; and 6) raindrop impressions in clayey substrate at margin of submerged area maintaining their form. **C**, **D**) Damp substrate which dried completely during the interval, showing: 1) biofilm roll-up maintaining form; 2) active biofilm (green) which left no trace; 3) vertebrate tracks degrading but largely maintaining form; 4) increasing depth and degree of desiccation; 5) preservation of bubble impressions; 6) preservation of subdued raindrop marks made in sediment that was submerged under a film of water during precipitation event; and 7) preservation of sharply defined raindrop marks made in subaerially exposed sediment during precipitation event. **E**, **F**) Microbial roll-up (arrow), containing bubble marks, maintaining form despite desiccation. **G**, **H**) Microbial mat composed of both sediment and filamentous microbiota drying from damp state, exhibiting: 1) preservation of burst bubble marks made while mat was photosynthesizing; 2) incomplete desiccation due to binding effect of filaments; and 3) raised, unburst bubbles which have developed longitudinal cracks during drying.

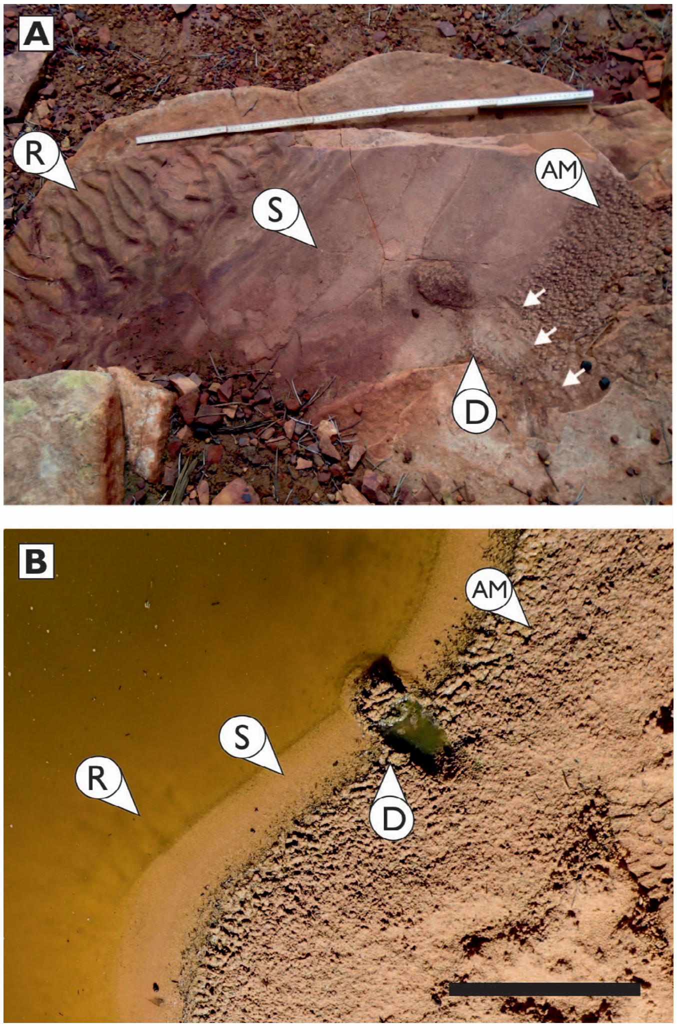

FIG. 6.—Evidence for preservation of primary sedimentary surface textures in the geological record, shown through comparison of ancient and modern surfaces. **A**) Bedding plane exposure of the Silurian Tumblagooda Sandstone, preserved in the wall of the Murchison River Gorge at The Loop. Ruler for scale is 1 meter. **B**) Modern pond of standing water in the Murchison River, west of The Loop. Scale bar = 20 cm. Both the modern and ancient examples reveal analogous substrate conditions, exhibiting ripple formation in deeper parts of a submerged pond (arrow R), a smooth substrate on the recently emergent drainage slope at the pond margin (arrow S), adhesion marks on the emergent margin of the pond (arrow AM), and a dislodged raft of adhesion marked sediment (arrow D). In the modern example, the raft was dislodged artificially, while in the ancient example it appears to have been dislodged by an arthropod; arthropod tracks are common in the formation and a series of grooves (small white arrows) at this location may be repichnial.

term preservation of microbial, neoichnological and abiotic textures on the stream bed of the Murchison River have implications for such instances in terms of their associations, diversity, preservation potential, and stratigraphic representation of time.

Association of Primary Sedimentary Surface Textures in the Rock Record

The close association of multiple different abiotic and microbial sedimentary surface textures in the Murchison River pools emphasizes that instances of primary MISS identified in the rock record should be expected to co-occur in the same or adjacent bedding planes as abiotic textures, such as raindrop impressions or adhesion marks, and trace fossils. The relative paucity of such published records may suggest that some occurrences of abiotic textures have been misinterpreted as being microbially induced in instances where they have been seen in close association with more convincing MISS (Davies et al. 2016). In future studies, a concerted effort to describe abiotic textures with as much attention to detail as associated MISS will shed new light into the processes and products of ancient sedimentary substrates.

Preservation of Primary Sedimentary Surface Textures in the Rock Record

It has been suggested that certain features of ancient substrates in the rock record, such as setulfs and multi-directed ripple marks, must have been stabilized by biofilms or mats in order for them to have been preserved (e.g., Eriksson et al. 2010; Sarkar et al. 2011; Petrov 2015). However, the temporary preservation of delicate textures in the Murchison River examples lends support to the contention that such biofilm stabilization does not need to be invoked (Davies et al. 2016). For example, the majority of microbial sedimentary surface textures in the pools reflect the formation of bubbles by biofilms, but such structures are most evident in the sediment once the biofilms have degraded away. In this instance, the subsequent (temporary) preservation of these bubble marks was reliant on the fact that they had developed in cohesive sediment. This observation emphasizes that factors other than biofilms (e.g., clay or salt) may stabilize sedimentary surface textures prior to their interment in the sedimentary record, whether they are microbial or abiotic. Fundamentally, providing that the next sedimentation event lacks the erosional capacity to destroy pre-existing sedimentary surface textures (regardless of whether they are stabilized or not), there is the potential for that substrate (and its surficial signatures) to enter the rock record.

The Importance of Stasis in the Development of Sedimentary Surface Textures

The observations of short-term morphological evolution of sedimentary surface textures in the Murchison River ponds were made over an interval of a few days, on substrates which remained otherwise stable, with no net removal or addition of sediment. Appreciating that microbial sedimentary surface textures may exhibit continual evolution of morphology, without interment or erosion, is crucial for understanding why their ancient counterparts exhibit such variation in the geological record. Sedimentation systems can be considered as being in a state of deposition, erosion, or stasis (each with or without transportation) (e.g., Tipper 2015). Primary sedimentary surface textures develop when the local sedimentation system is in stasis, such as in the dried fluvial interval in which the ephemeral Murchison River was studied, with the negligible removal or addition of sediment meaning that the substrate remains a stable 'canvas' onto which they may be imparted. Many abiotic and ichnologic sedimentary surface textures develop during individual events in that interval of stasis (Table 1). For as long as the local sedimentation state remains in stasis, these textures may persist on substrates as relict records of their formative event (though they may degrade or become palimpsested as the interval of stasis proceeds).

Sedimentary stasis is even more important for microbial sedimentary surface textures as microbial mats require time to grow, uninterrupted by sedimentation (e.g., Gerdes 2010). However, in contrast to physical textures, microbial sedimentary surface textures may exhibit rapid morphological variation reflecting the inception of colonization, growth and changes in constituent species, response to environmental factors, functional collapse, decay, and degradation. If it is accepted that each moment of time during stasis is potentially an instant of interment (i.e., stasis cessation and the onset of deposition), then the morphological

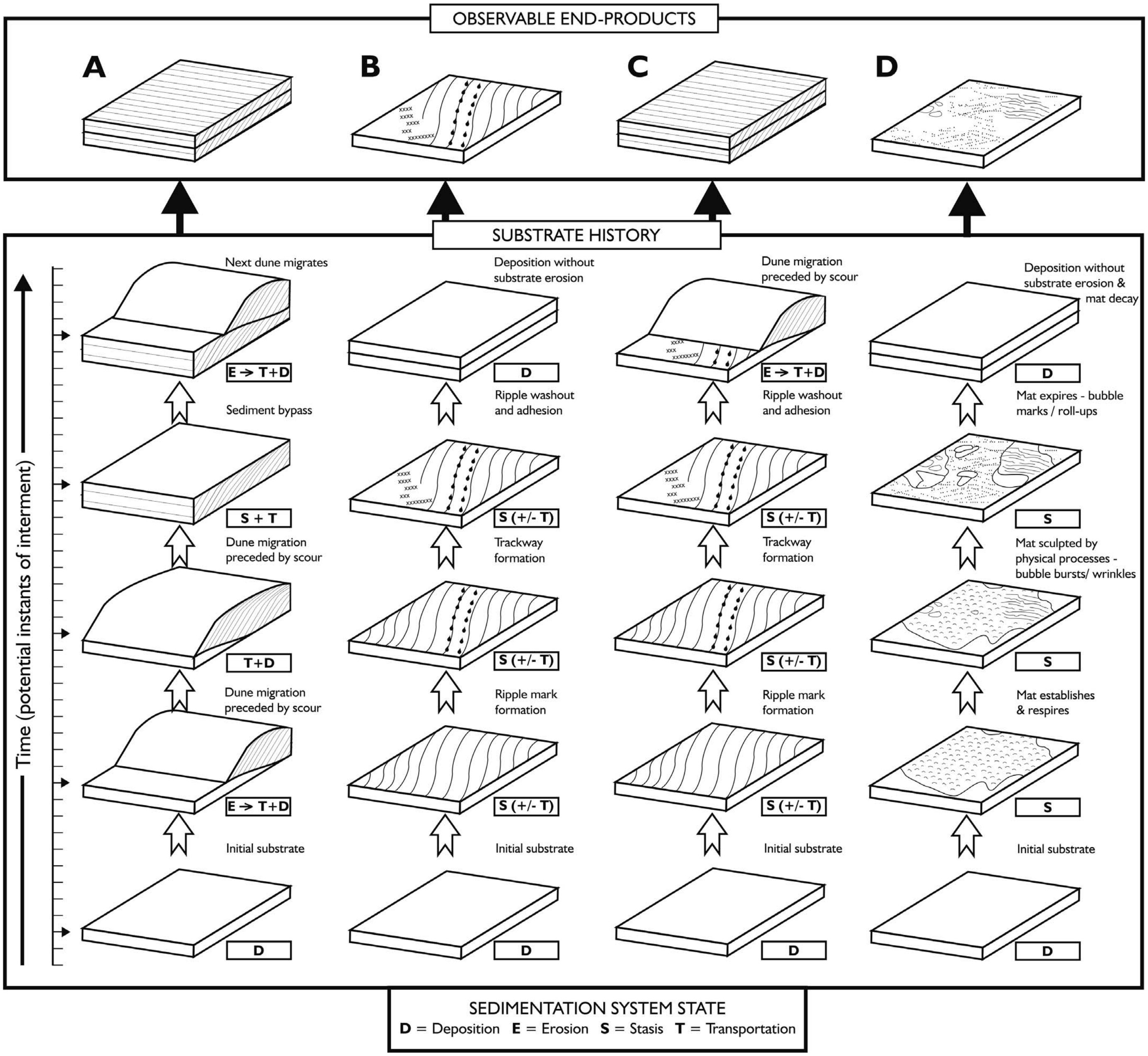

FIG. 7.—Conceptual model illustrating how sedimentary surface textures in the rock record reveal features developed during stasis, how they differ from hydrodynamic bedforms deposited during stasis, erosion, deposition and transport, and how the potential morphology of their signatures may vary significantly depending on the instant of interment. Time scale on left is representative only, but all four examples could be considered discrete components of the same deposystem. **A**) Hydrodynamic bedforms, developed during erosion, deposition, stasis, and transport. **B**) Abiotic and ichnologic sedimentary surface textures developed as events during stasis. **C**) Abiotic and ichnologic sedimentary surface textures developed as events during stasis, but later destroyed by erosion and deposition. **D**) Microbial sedimentary surface textures developed as ongoing morphological evolution during stasis, with resultant greater potential variability. Note that if the observable end-products B or D are seen in the rock record, then they must be a palimpsested record of multiple events during an interval of sedimentary stasis.

variety of microbial sedimentary surface textures, across multiple substrates buried following random durations of stasis, will far exceed that witnessed in most abiotic textures (Fig. 7). Abiotic features which develop slowly, such as desiccation cracks, may be a partial exception to this rule, but even in these instances the variable outcomes of physical morphological change are more predictable and limited (Bohn et al. 2005) than for a living microbial colony and its morphological responses. This partially explains the high level of variation of ancient microbial textures (Davies et al. 2016): the preserved microbial sedimentary surface textures in the rock record were interred at different instants of the inception, growth, living responses, and degradation of different colonies.

The variety of microbial textures in Precambrian and Phanerozoic rocks is further broadened by factors such as the exact nature and life habits of ancient microorganism species responsible (some of which may be extinct and unknowable, without modern counterparts), their potentially non-actualistic interactions with environmental factors (e.g., Fedorchuk et al. 2016), and post-depositional development of secondary sedimentary surface textures.

The primary sedimentary surface textures of the Murchison River substrates can be considered a short-term historical record of sedimentary stasis, comprised of a palimpsest of (1) temporally variable microbial sedimentary textures and (2) abiotic textures that developed during discrete events.

Ancient Primary Sedimentary Surface Textures as a Representation of Time

The fact that primary sedimentary surface textures on substrates are imparted during intervals of sedimentary stasis means that they present a fundamentally different representation of time than other sedimentary structures observed in the rock record (Fig. 7). For example, in temporal terms, a cross-bedded sedimentary unit effectively consists of an amalgam of multiple 'snapshots' taken during the hydrodynamic evolution of an ancient bedform—each foreset being a formerly active lee slope of a migrating dune. Thus, such forms record a prolonged interval of time, in which the sedimentation state could variably have been depositional, erosional, transportational, or stasic (e.g., a dune actively migrating, plus potentially ceasing and reactivating migration). A further characteristic of such structures is that they often cannot be taken to record a true likeness of the geomorphic element in which they formed, as in many instances the deposition of hydrodynamic bedforms (by waning flow) is preceded by the erosional scour of underlying sedimentary bedforms. By contrast, the existence of ancient primary sedimentary surface textures in the rock record is inherent proof that a true representation of an ancient substrate has been preserved to some degree (Fig. 6). In instances where such features are observed, the succeeding sediment must have been deposited from a fluid which lacked the capacity to erode the underlying substrate (not necessarily requiring 'protection' of the substrate), and post-depositional and diagenetic alteration must have had a negligible effect on surface features. The bedding plane itself records only the moment of interment, whereas the surficial textures on the bedding plane also record a preceding interval of sedimentary stasis, during which multiple palimpsested textures were imparted to the sediment. Such ancient primary sedimentary surface textures thus provide valuable windows into events in ancient deposystems during localized intervals of sedimentary stasis.

CONCLUSIONS

The development and persistence of standing ponds of water during sedimentary stasis in the Murchison River gorge, Western Australia, has permitted the opportunity to observe associations of microbial and non-microbial primary sedimentary surface textures in a modern ephemeral stream setting. These included microbial bubbles, roll-ups and distorted biofilms, abiotic raindrop impressions, desiccation and adhesion marks, and both vertebrate and invertebrate tracks and burrows. The observations emphasize that both microbial and non-microbial forms are closely associated in modern settings and that ancient substrates in the rock record should also be expected to demonstrate such a signature. Future studies of ancient substrates will benefit if an equal amount of emphasis is placed on the description and detail of abiotic sedimentary surface textures as is commonly placed on microbially induced sedimentary structures. Where bedding planes in the rock record represent ancient substrates, they preserve a palimpsested record of multiple events during an interval of sedimentary stasis, some of which may be microbial and some of which may not.

When they were wet, microbial mats in the Murchison River exhibited morphological variation reflecting the life histories and responses of colonies of living organisms. The subsequent drying of the ponds led to further morphological evolution of the microbial textures associated with decay and degradation, but less contemporaneous variation was witnessed in non-microbial textures. Considering that preserved substrates in the rock record represent interment after variable durations of stasis, it should be expected that microbial sedimentary signatures can exhibit more intra-structure morphological variety than their abiotic counterparts.

Both microbial and abiotic sedimentary surface textures in the Murchison River section were stabilized because of a muddy substrate or salt, suggesting that it is not necessary to invoke biofilm stabilization as a means for preserving primary sedimentary surface textures in the rock record.

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SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: http://www.sepm.org/pages.aspx?pageid=332.

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