A LARGE COLLECTION OF WELL-PRESERVED THEROPOD DINOSAUR SWIM TRACKS FROM THE LOWER JURASSIC MOENAVE FORMATION, ST. GEORGE, UTAH

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Abstract—A large and exceptionally well-preserved collection of dinosaur swim tracks, attributable to the ichnogenus *Characichnos*, is preserved as natural casts and reported in detail for the first time from the St. George Dinosaur Discovery Site at Johnson Farm (SGDS) in southwestern Utah. Approximately 3200 individual claw marks, typically in sets of three and rarely singular or paired, were made predominantly by small theropod dinosaurs in a size range consistent with the ichnogenus *Grallator*. About 95% of all dinosaur footprints on multiple track-bearing horizons at the SGDS are *Grallator* ichnites. Larger and less abundant *Eubrontes*-type swim tracks are associated with *Grallator*-type swim tracks at the SGDS. "Typical" *Eubrontes* and *Grallator* footprints occasionally occur among the swim tracks, providing further support for referring to swim tracks as "*Eubrontes*-type" and "*Grallator*-type." Abundant invertebrate grazing traces and burrows indicate organic-rich, well-oxygenated sediments within the upper 1-2 cm of mudstone directly below the infilling sandstone unit of the SGDS "Main Track Layer" in which the swim tracks are preserved. Well-preserved sedimentary structures associated with a marginal lacustrine shoreline paleoenvironment suggest multiple animals swimming and/or floundering, mostly in a southerly direction, against a north-flowing current that paralleled the paleo-shoreline. Simultaneous formation of swim tracks on a clay-rich substrate, together with rapid burial of the traces, has resulted in exceptional preservation of skin impressions, scale scratch lines, and possible fine details on the cuticle of claw tips.

INTRODUCTION

Tracks made by swimming dinosaurs and other vertebrates, such as crocodylomorphs and turtles, have become popularly known among paleontologists as "swim tracks." They provide a conjecture-inspiring but controversial topic for investigation. They are of interest because they provide insight into the behavior of ancient vertebrates in aquatic environments, but they are controversial because they display irregular morphologies that are very often difficult to interpret. Unlike a track made by an animal walking on firm ground that supports most or all of its weight, a swimming animal may touch the subaqueous substrate while fully or partially buoyant. As a result, swim tracks rarely show regular step and stride patterns. Instead, they are often incomplete, occurring in irregular and confusing configurations. This incompleteness often makes it difficult to identify the track maker or to distinguish between manus and pes prints if the track maker was quadrupedal.

In this paper, we present a preliminary description of one of the largest and best-preserved *true* swim track assemblages ever recorded. They are from the Lower Jurassic (earliest Hettangian) Moenave Formation at the St. George Dinosaur Discovery Site at Johnson Farm (SGDS) in southwestern Utah (Fig. 1). We also demonstrate that these ichnites were unequivocally made by theropod dinosaurs of the type that made typical terrestrial locomotory tracks nearby (i.e., *Grallator* and *Eubrontes*). In places, it is even possible to demonstrate that there are gradations between walking tracks and slide or swim tracks. We briefly compare these swim tracks with examples from other localities.

VERTEBRATE SWIM TRACKS: A HISTORICAL PERSPECTIVE

In western North America, swim tracks have been reported from a number of Mesozoic deposits. These include Triassic tracks attributed to amphibians and phytosaurs (Boyd and Loope, 1984; Lockley et al., 2005, Lockley and Milner, this volume), and Cretaceous tracks, first assigned to ornithischian dinosaurs (McAllister, 1989a, b) and pterosaurs (Gillette and Thomas, 1989), but later identified as crocodylomorph tracks (Bennett, 1992; Lockley and Hunt, 1995). Likewise, Late Jurassic tracks in France attributed to hopping dinosaurs (Bernier et al., 1982, 1984) were later reinterpreted as the swim tracks of turtles (Thulborn, 1989, 1990). These examples serve to indicate the potential for confusion in correctly attributing swim tracks to the actual track makers.

Focusing only on purported dinosaurian swim tracks, there has been lively debate about so-called "swim tracks" of sauropods, theropods, and ornithopods. In all cases, such debate has had significant ramifications for our views into the behavior of the dinosaurs in question. Bird (1944) claimed to have found the manus-dominated trackway of a swimming sauropod in the Early Cretaceous of Bandera County, Texas. Following his original example, others (Coombs, 1975; Bird, 1985; Ishigaki, 1989; Thulborn, 1990; Czerkas and Czerkas, 1990; Norman, 1985; Lee and Huh, 2002) then interpreted these and other manus-dominated sauropod trackways as indicative of swimming ability in sauropod dinosaurs. This generated a "sauropod swim tracks paradigm." Thus, incomplete manus-only or manus-dominated trackways were used to support the notion of aquatic/swimming sauropods. This paradigm contrasts with the idea that the trackways were, in fact, undertracks of walking sauropods (Lockley and Rice, 1990; Lockley 1991; Lockley et al., 1994; Lockley and Meyer, 2000) that were predominantly terrestrial, rather than aquatic, animals.

Purported ornithopod swim tracks from the upper Hettangian Przysucha Formation in the Holy Cross Mountains of Poland (Gierliñski and Potemska, 1987; Pieñkowski and Gierliñski, 1987) are, like those of the sauropods discussed above, probably undertracks (Lockley, 1991).

In contrast, theropods have traditionally been viewed as hydrophobic, and many older texts indicate that sauropods escaped from theropods simply by entering the water (e.g., Colbert, 1945, p. 73; Andrews, 1953, p. 58-59; Hotton, 1963, p. 95; Colbert, 1965, p. 95, 133; Paul, 1988, p. 44-47). This speculative scenario was called into question by Coombs (1980) while describing purported theropod swim tracks from the Lower Jurassic East Berlin Formation at Dinosaur State Park, Connecticut. According to Coombs (1980), the theropod track maker was probably the same kind of animal responsible for making abundant *Eubrontes* tracks at the same locality. This example is highly

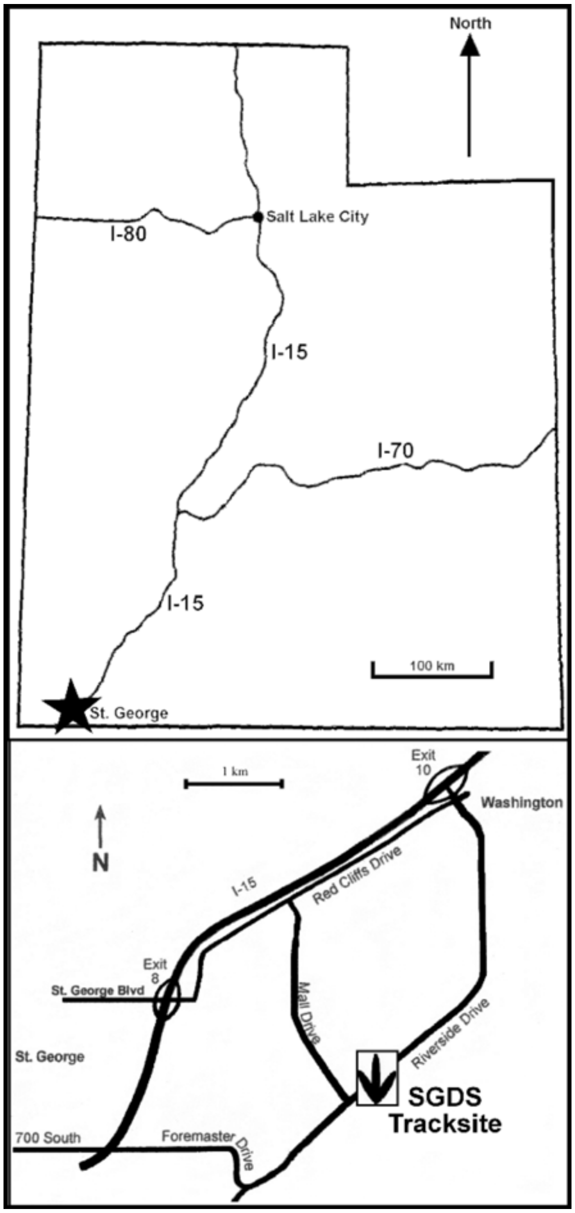

FIGURE 1. Index maps showing location of the St. George Dinosaur Discovery Site at Johnson Farm in southwestern Utah.

relevant to the SGDS site at which both walking *Eubrontes* tracks and somewhat similar swim tracks coincide in Lower Jurassic deposits of the Moenave Formation (Kirkland et al., 2002; Milner et al., 2004, 2005a, b, this volume; Milner and Lockley, 2006). This will be discussed in more detail below.

Contrasting with the tendency of ichnologists to name and classify "typical" fossil tracks, few supposed swim tracks had been named until recently. Exceptions include the purported hopping dinosaur tracks from France (named *Saltosauropus*, meaning "hopping saurian track" [Bernier, 1984]) that are now considered turtle swim tracks (Thulborn, 1989), and the recently named *Characichnos* (meaning "scratch mark") from the Middle Jurassic Saltwick Formation of England (Whyte and Romano, 2001). *Characichnos* has since been identified in the Lower Jurassic Zagaje Formation of Poland (Gierliński et al., 2004). Additional, albeit unnamed, theropod swim tracks are reported from the Lower Cretaceous of Spain (Ezquerra et al., 2004) and from the Whitmore Point Member of the Moenave Formation and the Kayenta Formation in Zion National Park, Utah (DeBlieux et al., 2003, 2005, this volume).

Proposed dinosaur swim tracks were also reported by Kvale et al. (2001a, b) from the Middle Jurassic Gypsum Springs Formation of Wyoming. They only referred to these ichnites as dinosaur swim tracks and made no determination as to whether they pertain to a theropod or ornithopod. Uncertainty by the authors (Kvale et al., 2001a) was also expressed as to whether these proposed swim tracks are dinosaurian or were made by a "crocodylian."

All of these examples of purported or definitive dinosaur swim tracks are based on relatively small sample sizes. The SGDS has, in contrast, yielded more than 3200 traces, most of which are very well preserved and easily correlated with the foot morphology of abundant *Grallator* and associated *Eubrontes* ichnites.

MATERIALS AND METHODS

Soon after the time of the original discovery (May 4, 2001 by ARCM), approximately 80 talus blocks containing about 250 swim tracks were salvaged from the spoil piles excavated from Bodega Bay Development Corporation (BBDC; called the Darcy Stewart [DS] sites in Milner et al., this volume) and Washington County School District (WCSD) properties. Subsequently, in January, 2003, during excavations on WCSD property for the construction of Fossil Ridge Intermediate School, an approximate 14 x 12 m (= 168 m^2) area was excavated and partially mapped. Designated as "Dinosaur Swim Track Quarry #1" (DSQ1), the area produced about 140 large sandstone blocks ranging in size from 0.2 x 0.1 x 0.1 m to 3 x 1.1 x 0.6 m (weighing from 0.02-11 metric tons). As a result, an estimated 2500 swim track claw marks were identified and collected. The following year, in February, 2004, during further excavations of BBDC property, "Dinosaur Swim Track Quarry #2" (DSQ2) was opened immediately adjacent to, and as a continuation of, DSQ1. DSQ2 resulted in the collection of an additional 23 *in situ* blocks (most of very large size) that were carefully mapped and extracted from an area measuring about 16 x 5 m (= 80 m^2). This led to the identification of approximately 450 additional swim tracks. During these excavations, data collection, although constrained by tight time scheduling, was facilitated by the cooperation of many partners, leading to the success of the day-to-day exploration, salvage, and transportation of excavated material during the active development of these properties (see Acknowledgments below).

Preparation of the swim track blocks is complicated, and has never before been attempted on such a large scale. In general, the swim tracks represent natural casts of narrow striations with high relief, some of which terminate in well-preserved claw and phalangeal pad impressions. When initially excavated (overturned), the undersurfaces were embedded in a finer grained material that was typically 1-2 cm thick. This material weathered rapidly on exposure, so volunteers were organized to clean surfaces carefully and restore and harden the delicate casts using cyanoacrylate and Acryloid B-72 in acetone solution. Subsequently, representative material was traced, photographed, and replicated. Preparation of these blocks is ongoing.

The most comprehensive documentation is being accomplished by photographing all the surfaces with an 8.0 megapixel Nikon Coolpix 8700 digital camera, and then piecing together a photo-mosaic of the reconstructed surface. This project also is ongoing, and will be published elsewhere. This method enabled the development of a coherent understanding of the orientation of the swim traces across a large area. However, not all swim track blocks could be restored to their original orientations because many had been moved by private excavation activities prior to the initiation of a systematic scientific method.

GENERALIZED STRATIGRAPHY, SEDIMENTOLOGY AND PALEOENVIRONMENTAL INTERPRETATION

At the SGDS, the Moenave Formation is about 74 m thick. It is divided into the lower Dinosaur Canyon Member (about 56.5 m thick) and the upper Whitmore Point Member (about 17.5 m thick) (Fig. 2; Kirkland and Milner, 2005, this volume). The Moenave unconformably

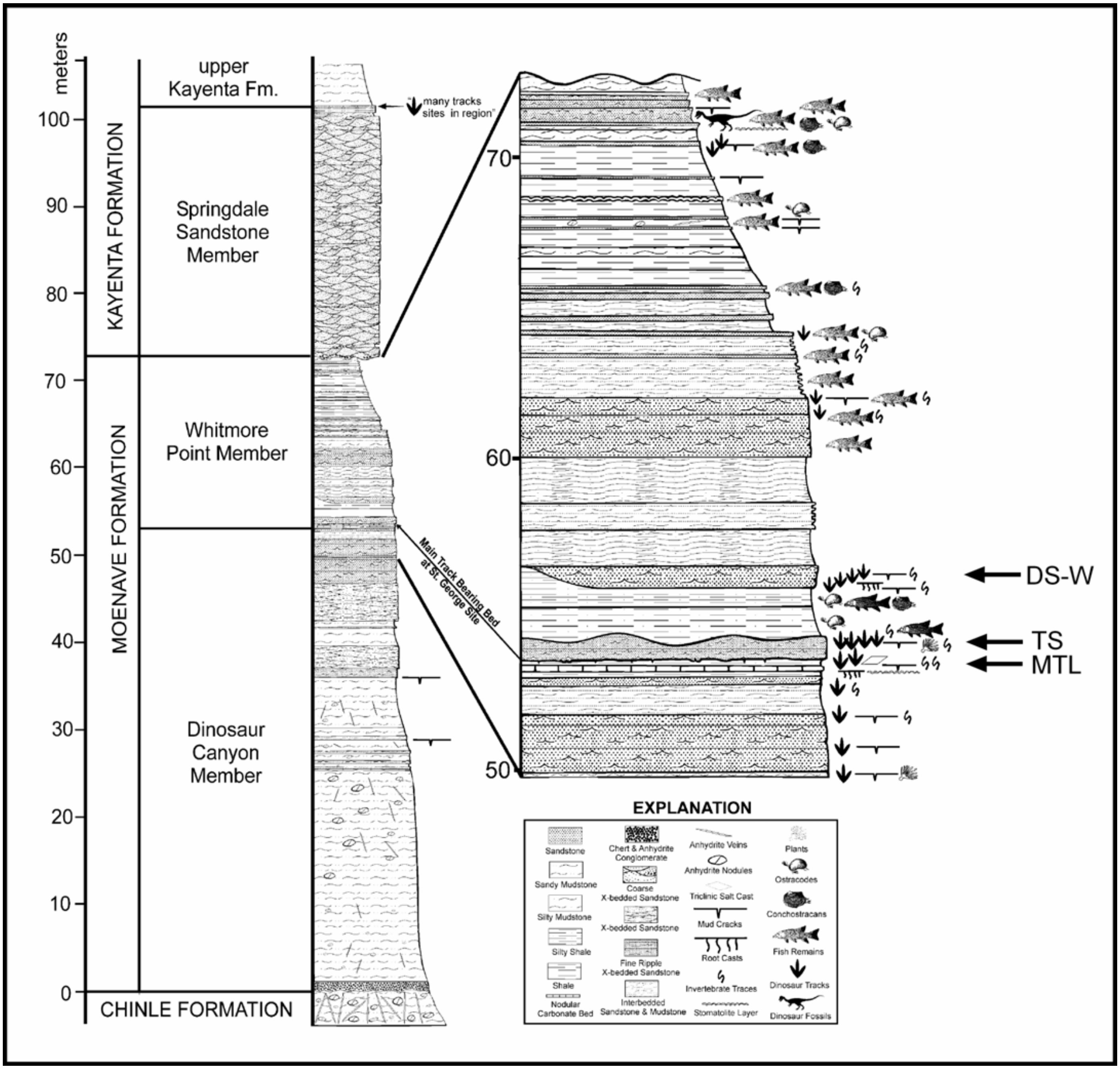

FIGURE 2. Stratigraphic section showing horizons mentioned in this paper. Abbreviations: MTL, "Main Track Layer" at base of main track-bearing sandstone; TS, "Top Surface" of main track-bearing sandstone; DS-W, "Stewart-Walker Tracksites."

overlies the Upper Triassic Owl Rock Member of the Chinle Formation (per local usage), and, in turn, is unconformably overlain by the Springdale Sandstone Member of the Lower Jurassic Kayenta Formation (Lucas and Tanner, this volume). Toward the west in Nevada, this unconformity is angular at a regional scale with the Whitmore Point Member eroded away such that the Springdale Sandstone Member directly overlies the Dinosaur Canyon Member (Marzolf, 1993, 1994). The Triassic-Jurassic boundary is located somewhere within the Dinosaur Canyon Member (Kirkland and Milner, this volume). Based on some of the track types (*Eubrontes*, *Batrachopus*, and *Anomoepus*) and body fossils, the age of the upper portion of the Moenave is interpreted as Early Jurassic (earliest Hettangian).

This study focuses on ichnites from the lower 5 m of the Whitmore Point Member, particularly from the base of the main track-bearing sandstone called the "Main Track Layer" (MTL; Figs. 2-3). Tracks have been identified at 25 stratigraphic levels in the immediate vicinity of the SGDS (Fig. 2), and several of these layers have been mapped *in situ* (Milner et al., this volume; Williams et al., this volume).

The first track-bearing horizon discovered was the MTL at the SGDS, revealing tracks and associated mudcracks preserved as robust sandstone natural casts at the base of a thick (30-70 cm), well-sorted, fine-grained sandstone bed, about 53 m above the Owl Rock-Moenave contact (Figs. 2-3). Track casts and associated sedimentary structures at the SGDS museum locality (the original discovery site), and nearby several localities to the northwest, represent features that were made in subaerially exposed conditions (Fig. 4). The berms and swales of the "Top Surface" tracksite (Fig. 2), situated at the top of the main track-bearing sandstone bed at the original discovery site east of Riverside

Drive, are oriented perpendicular to the shoreline at the SGDS, and represent reworking of the sand sheet by shoreline erosion and redeposition (see Kirkland and Milner, this volume, for further discussion). This is supported by cross-cutting of pre-existing bedding planes and track horizons.

Important relationships between local paleogeography, trackway orientations, and sedimentary structures at the SGDS are evident, leading to important paleoenvironmental interpretations of the Moenave Formation in this region. It is possible to trace and partially map the MTL from the SGDS museum site ("onshore" location; Figs. 3-4) toward the northwest and over to DSQ1 and DSQ2, where abundant dinosaur swim tracks (*Characichnos*), subaqueous invertebrate traces (cf. *Palaeophycus*), and sedimentary structures represent an "offshore" location along the same MTL bedding surface (Figs. 3, 5). The dinosaur swim tracks are actually concentrated in a channel-like depression filled by the main track-bearing sandstone that paralleled the paleo-shoreline and situated approximately 80 m to the northwest (Fig. 3).

This same pattern can be seen in sedimentary structures preserved on the MTL across the entire area, evidence of being formed onshore and offshore. Sedimentary structures, such as mudcracks (Fig. 4A), sulfate salt crystal casts (Fig. 4B), and rain drop impressions (Fig. 4C) can typically be formed only when the sediment is subaerially exposed. Offshore, near-shore, and shoreline aqueous-subaqueous sedimentary structures include a variety of current and symmetrical ripples (Figs. 5A-B), tool marks (Fig. 5C), flute casts, and scratch circles (Fig. 5D; Metz, 1991, 1999; Droser et al., 2002, fig. 2A; Rygel et al., 2004, fig. 9). In the offshore, channel-like feature mentioned above, current flow was from the north and paralleled the shoreline, based primarily on scratch circles, tool marks, flute casts, and other sedimentary structures (Fig. 5).

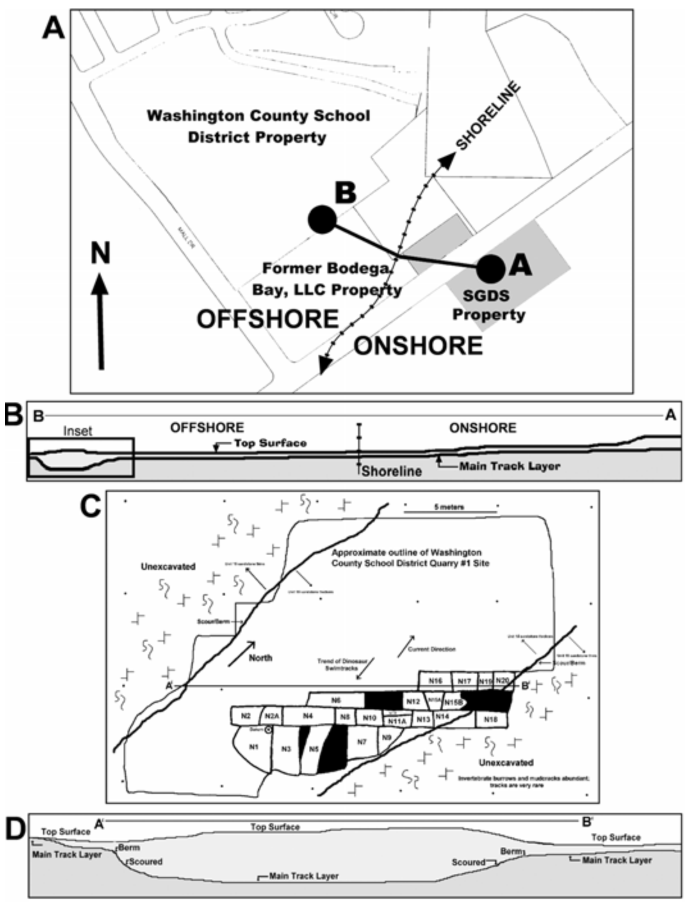

FIGURE 3. Map and paleoenvironmental interpretation of the SGDS MTL. **A**, Transect from museum site (A) on SGDS property (in gray) to swim track quarries (B) on WCSD and former BBDC properties. The estimated position of the paleo-shoreline is indicated (hatched line) for the MTL based on orientation and preservational types from tracks, invertebrate traces and sedimentary structures. **B**, Cross-section of transect A-B in **A** showing variation in bed thicknesses of the MTL and Top Surface. The estimated shoreline is for the MTL only. **C**, Map of the swim track quarries showing position of trough and transect A'-B' in **B**. **D**, Cross-section showing trough containing abundant swim tracks on the MTL surface, the variability in thickness of the MTL sandstone, and the Top Surface topography.

Dinosaur swim tracks at the SGDS are interpreted as being preserved along the western margin of freshwater Lake Dixie (Kirkland et al., 2002; Milner and Lockley, 2006). Natural casts of dinosaur footprints and swim tracks formed from infilling by fine-grained, well-sorted sand. The main track-bearing sandstone covers a 15 cm-thick horizon of purplish-gray, silty shale, and mudstone-claystone. Abundant invertebrate grazing traces and burrows indicate organic-rich, probably well-oxygenated sediments within the upper 1-2 cm of mudstone directly below the MTL.

The MTL in the area west of Riverside Drive (Figs. 1, 3) that preserves the natural casts of the swim traces was laid down predominantly by unidirectional currents (toward the north, as mentioned above). Thinner bedding planes near the base of the MTL at the SGDS are separated by clay-rich mudstone drapes that may represent fluctuations in sedimentation rate prior to a possible "main depositional event" influx of sediment that initially buried the track-bearing surface. Lateral variation in thickness (in some cases completely pinching out) of the main track-bearing sandstone reflects its subsequent erosion and that the sediment was deposited with local thickness variation due to underlying topography. Fluvial depositional environments are typically associated with asymmetrical ripples produced by unidirectional currents. However, sedimentary features of the main track-bearing sandstone – thin, laterally extensive bed geometry and climbing-ripple cross-bedding – do not support a fluvial channel origin, but instead indicates deposition in an offshore lacustrine setting, perhaps by longshore currents (Kirkland and Milner, this volume).

Areas located northwest of the paleo-shoreline have an MTL that is bioturbated with abundant invertebrate feeding-grazing trails and burrows (Lucas et al., 2005, this volume; Fig. 3). The main track-bearing sandstone in this area ranges in thickness from 10-20 cm from the paleoshoreline to where it thickens in the channel-like trough described above (Fig. 3). The MTL below this thinner main track-bearing sandstone bed has abundant scours, flute casts (with current orientations toward the north), and rare, scoured-out dinosaur tracks (Fig. 5F) and scoured mudcracks. This surface likely indicates a shallow, near-shore environment. Vertebrate tracks and traces crossing the mudflat and beach indicate that the track makers possibly ventured out into shallow waters of the lake, and that they could potentially leave footprints in a substrate showing varying states of cohesion and submergence. Mudcracks and some of the poorly preserved dinosaur tracks would have formed during a lake level regression and may represent an extension of the same surface (MTL) preserved to the east of Riverside Drive. Scouring of these mudcracks and tracks, and the formation of flute casts, probably occurred contemporaneously with the initial deposition of the basal portion of the MTL sandstone in this area. This contemporaneous deposition may have been responsible for the simultaneous and rapid burial of swim tracks, other ichnites, and sedimentary structures as the sand swept across the exposed, underlying fine sediments. Changes in substrate and environment would likely give rise to a wide range of preservational track types (Whyte and Romano, 2001).

DESCRIPTION OF SGDS SWIM TRACKS AND ASSOCIATED TRACES

Swim Track Morphotypes and Swimming Orientations

The SGDS reveals a variety of track types. These include typical

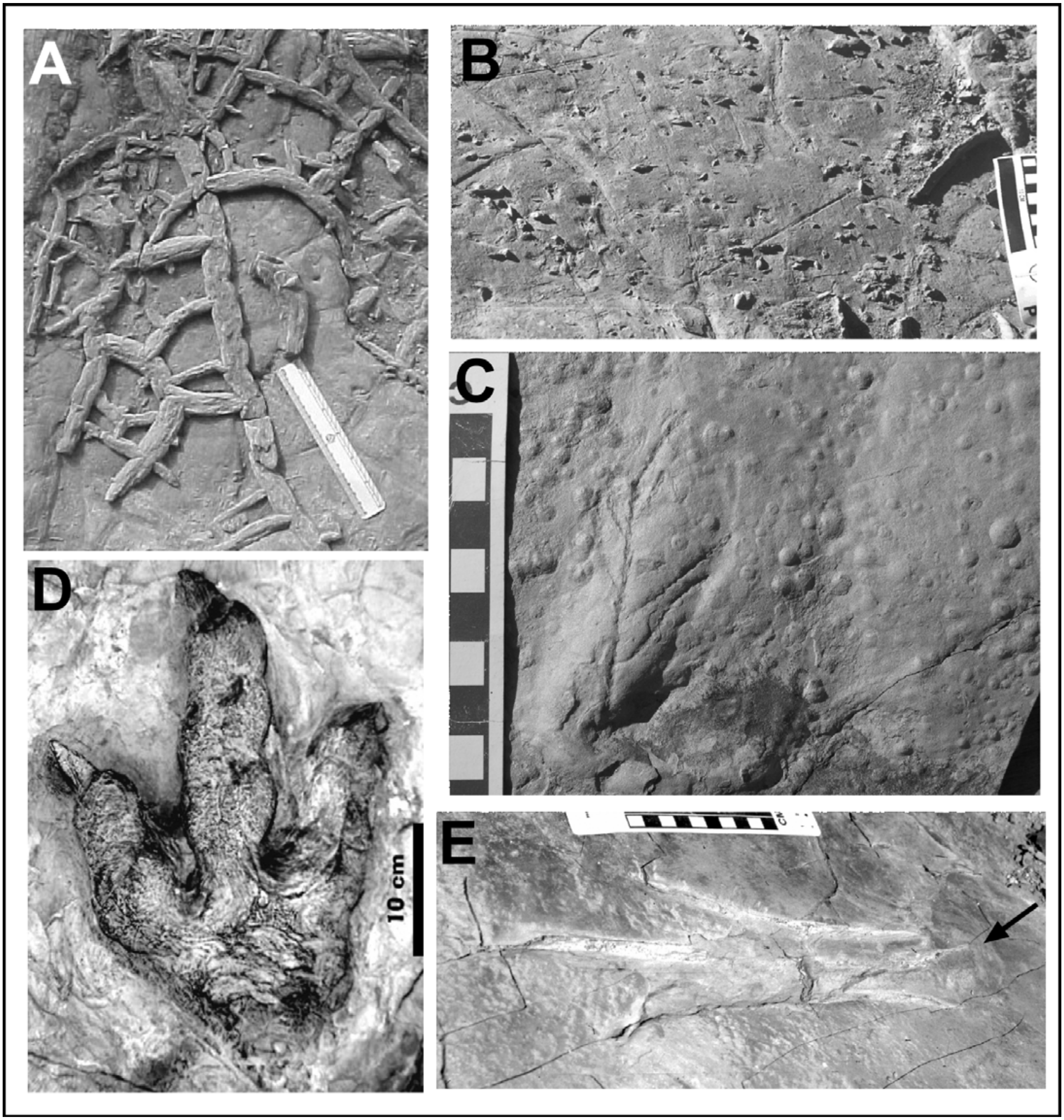

FIGURE 4. Sedimentary structures and ichnites that indicate an "onshore" paleoenvironment for the SGDS MTL. **A**, Mudcracks (SGDS.10). **B**, Salt crystal casts (SGDS.40). **C**, Rain drop impressions with *Pagiophyllum* branch (SGDS.491). **D**, A left *Eubrontes* track showing the asymmetry of digit III with the wider part of the digit situated laterally and the narrower part medially (SGDS.9). **E**, *Grallator* scrape or sliding track showing sediment mounded up caudally (black arrow) (SGDS.74).

walking to running theropod tracks of *Grallator* and less common *Eubrontes* (Fig. 4D), slightly elongate tracks resembling scratch marks (animals that may have purposely scratched at the substrate in search of food, etc., in the opinion of ARCM and JIK) or slide marks (in the opinion of MGL) (Fig. 4E), and highly elongate tracks that we refer to herein as swim tracks (Fig. 5E). It should be kept in mind that the vast majority (~95%) of tracks at the site are those of *Grallator*, formed subaerially while walking, with a few *Eubrontes* tracks in which the typical foot morphology is clearly seen (Milner et al., 2005a). This leads to the inference that the scratch/slide marks and swim tracks represent a different mode of preservation of traces made by the same track makers.

The scratch/slide marks (Fig. 4E) are characterized by three parallel traces that extend back from a more or less recognizable, tridactyl theropod track. Such traces are relatively uncommon and typically occur in isolation on surfaces where normal walking traces predominate. These scratch/slide marks have only been found on the SGDS "Top Surface"

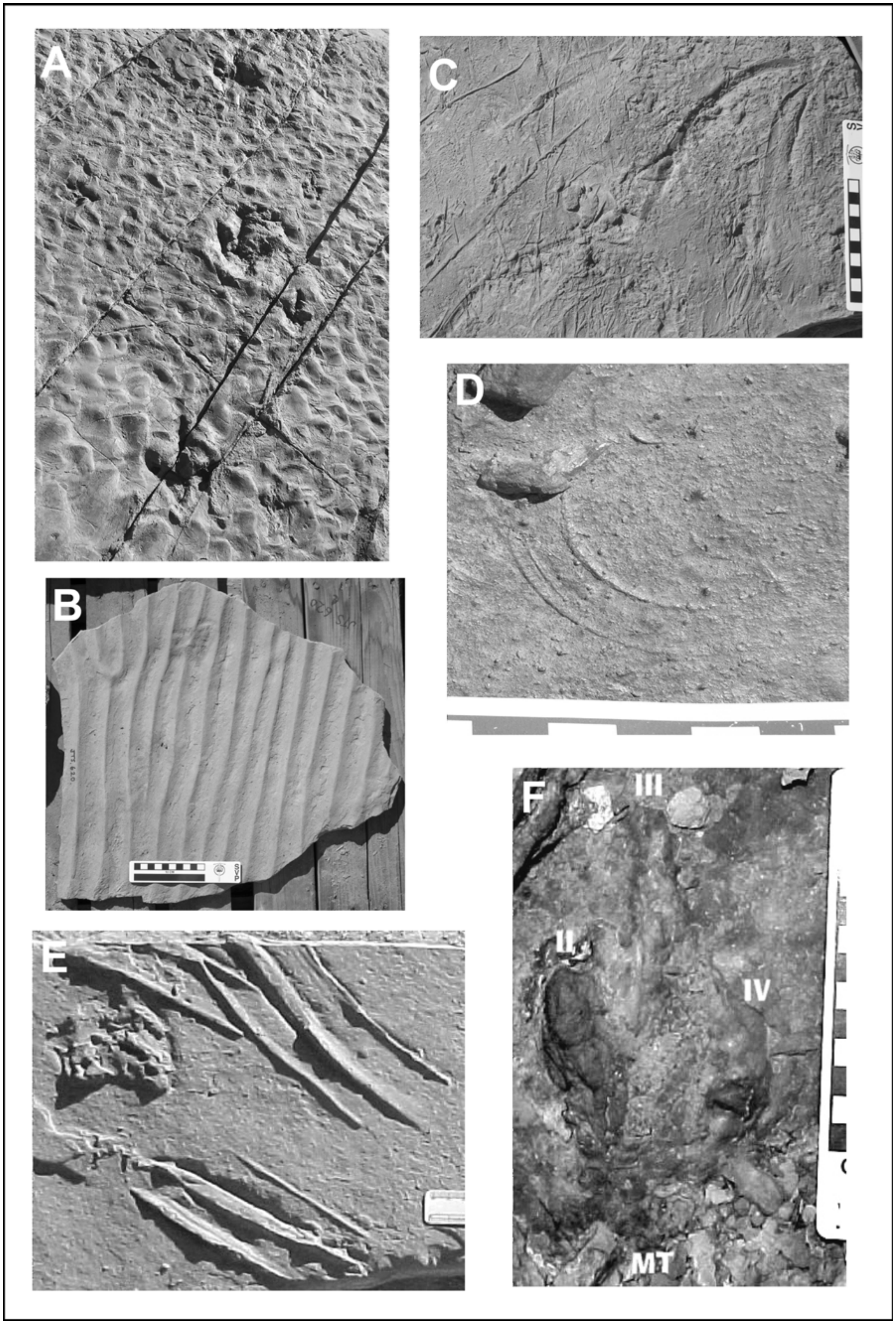

FIGURE 5. Ichnites and sedimentary structures that indicate paleoenvironments on the SGDS MTL and Top Surface. **A**, Current ripples formed prior to *Eubrontes* and *Grallator* trackways (SGDS.18). **B**, Symmetrical wave-form ripples indicate onshore or beach environments (SGDS.630). **C**, Tool marks (SGDS.621). **D**, Subaqueous scratch circles (specimen number pending). **E**, Original swim tracks (*Grallator*-type) discovered on May 4, 2001 by ARCM (SGDS.47). **F**, Scoured cf. *Grallator* track (Field # DS.128).

tracksite (Figs. 2-3). In contrast, swim tracks generally consist of more elongate, parallel to subparallel "scrape marks" (as the name *Characichnos* implies) that occur in high densities, almost invariably *without* associated walking traces.

Generally, a mudstone compaction ratio is about 3:1, but it may be less in continental sediments depending on many factors (Nadon, 1997). The majority of claw marks and swim tracks were likely close to perpendicular to bedding when they were made. Most of the claw marks and thin swim tracks have been laterally distorted and vertically compressed in that they are now preserved at an average angle of about 45º or greater due to compaction.

At least three categories of swim tracks at the SGDS appear to be present, all preserved as natural casts in high density assemblages (Fig. 6A). These include:

(1) Inferred down-current traces that:
- have variable claw impression depths (typically 5-7 cm)
- always have the deepest and longest trace made by the mesaxonic digit (presumably digit III; Fig. 6B)
- are accompanied by *Grallator* tracks that resemble normal walking footprints (Fig. 6C);

(2) Traces oriented up-current that:
- consist of ubiquitous, parallel scrape marks (*Characichnos*)
- vary considerably in overall length (ranging in size from 5-40 cm long and 5-8 cm wide)
- are usually in sets of three, although occasionally possess only two or one claw marks (digit III is assumed to always be present)
- digit III marks are longer and deeper, while digits II and IV are shorter and shallower than digit III (Figs. 5E, 6A, D-E); and

(3) Cross-current swim tracks that:
- are usually oriented more in an up-current than down-current direction
- are usually situated at an angle of approximately 45° to current flow direction
- have similar lengths and widths as the down-current swim tracks (Fig. 6F).

It is important to note that down-, up- and cross-current traces are all found on the same surfaces in the channel-like trough at the base of the main track-bearing sandstone described above (Fig. 3). Down- and cross-current traces (*Grallator*) are uncommon relative to the up-current swimming traces.

All observations were made independently of those of Whyte and Romano (2001), who had made similar observations about Middle Jurassic, British swim tracks. Whyte and Romano (2001) concluded that the two styles of preservation they observed actually represented two different track-making episodes that related to changing water levels through time. This raises an important taxonomic consideration: are *Characichnos* traces, therefore, merely extramorphological variants of *Grallator* and other tridactyl theropod track types made during identical behaviors as produce "typical" *Grallator* tracks, or are they distinct "behavioral variants?" This matter is revisited below.

Detailed Preservation of Swim Tracks

Preserved claw tips on the SGDS swim tracks project backward, indicating that the track-making animals were swimming in the opposite direction to claw tip orientation (i.e., caudally-projected claw tips: Figs. 6C, E, G-H). Some claw tips at the SGDS are so well preserved that details of the *in vivo* claw tips can be recognized (Figs. 6G-H). Morphological details of the living animal can be identified, such as smooth areas cut by the claw cuticle and the boundary between cuticle and scaly skin, with the fleshy part of the toe prominently raised above the cuticle by as much as 0.8 cm. Further delicate details of the skin include very common scale scratch lines (Figs. 6G-H) and rare skin impressions. Scale scratch lines on the sides of swim tracks range in width from 1-1.5 mm.

Since claw tips of the well-preserved SGDS swim tracks project backward, it is also possible to determine whether a swim track was made by a left or right foot, both for *Grallator* and *Eubrontes*. The SGDS swim tracks are so well-preserved that, on many specimens, impressions made by the distal phalangeal pads can be clearly distinguished from the claw marks themselves, making this collection unique. The majority of SGDS swim tracks preserve marks made only by the claws and show no evidence of the distal phalangeal pads. Digit III is asymmetrical in each ichnotaxon when formed subaerially, with the more prominent and rounded portions of the phalangeal pads on the lateral side of the toe and a straighter medial side of the digit; in the swim tracks, the claw is also positioned more medially than laterally on each impression of digit III (Fig. 4D). Therefore, when looking at the SGDS theropod swim tracks, the medial sides of both the distal phalangeal pad and the claw are narrow, and the lateral sides are thicker.

Comparison of Swim Tracks with Known SGDS Track Ichnotaxa

Grallator-type Swim Tracks

Due to the large quantity of smaller dinosaur swim tracks at the SGDS localities, and because 95% of all dinosaur footprints at the SGDS are those of *Grallator*, we interpret that most of the smaller swim tracks are "*Grallator*-type." The widths between digits II-IV of "typical" *Grallator* tracks at the SGDS range from 8-14 cm, whereas in swim track sets, widths range from 5-8 cm (Figs. 4E, 5E, 6C). In theory, appression between digits II-IV while swimming is probably due to the animals purposely forming their appendage into more of an oar or paddle-like structure to better push against the water in order to create better forward propulsion.

The widths of the bases of the claws of *Grallator*-type swim tracks range from 0.5-1.0 cm, and the distal phalangeal pads of the toes are wider, with a range of 3.0-3.5 cm, giving a ratio of 1:3. Subaerially-formed *Grallator* tracks at the SGDS (Figs. 4E, 5F, 6C) have the same 1:3 ratio. All of these measurements were taken from *Grallator* tracks formed subaerially at the SGDS and from *Grallator*-type swim tracks from the MTL sites.

Scale scratch line (Figs. 6B, F-G) widths on *Grallator*-type swim tracks have a width range of 1.0-1.5 mm. Unfortunately, no skin impressions from the distal phalangeal pads are preserved on any of the SGDS subaerially-formed tracks recovered thus far, although scale scratch lines have been identified on SGDS *Grallator* footprints on this part of the toe. Additionally, scales with a variety of diameters occur on different parts of the foot both on *Grallator* and *Eubrontes* tracks, with *Eubrontes* scales only slightly larger when comparing similar portions of the foot. Likewise, scale scratch line widths on *Eubrontes* tracks and *Eubrontes*-type swim tracks are also in the same size range as those seen in *Grallator* tracks and *Grallator*-type swim tracks.

Eubrontes-type Swim Tracks

Subaerially-formed *Eubrontes* tracks (Fig. 4D) are much less common than *Grallator* (Milner et al., this volume). The pattern described for *Grallator*-type swim tracks is also seen with purported *Eubrontes*-type swim tracks from DSQ1 and DSQ2, including asymmetry of digit III, scale scratch lines, and occasional preservation of distal phalangeal pads. Aside from subaerially formed *Eubrontes* tracks, two other large forms of theropod track types must be considered at the SGDS site: *Gigandipus* and cf. *Kayentapus* (see Milner et al., this volume). The widths between digits II-IV of "typical" *Eubrontes* tracks at the SGDS range from 18-28 cm, but in the only measurable swim track set (Fig. 7A), the width is about 30 cm. A narrower width is expected. However, the swim track in question may have been produced by a larger individual, or the digits could have been splayed farther apart by the way they impacted the substrate. As mentioned above, like the aforementioned *Grallator* footprints and *Grallator*-type swim tracks, digit III is asymmetrical in *Eubrontes* tracks and swim tracks. This asymmetry is

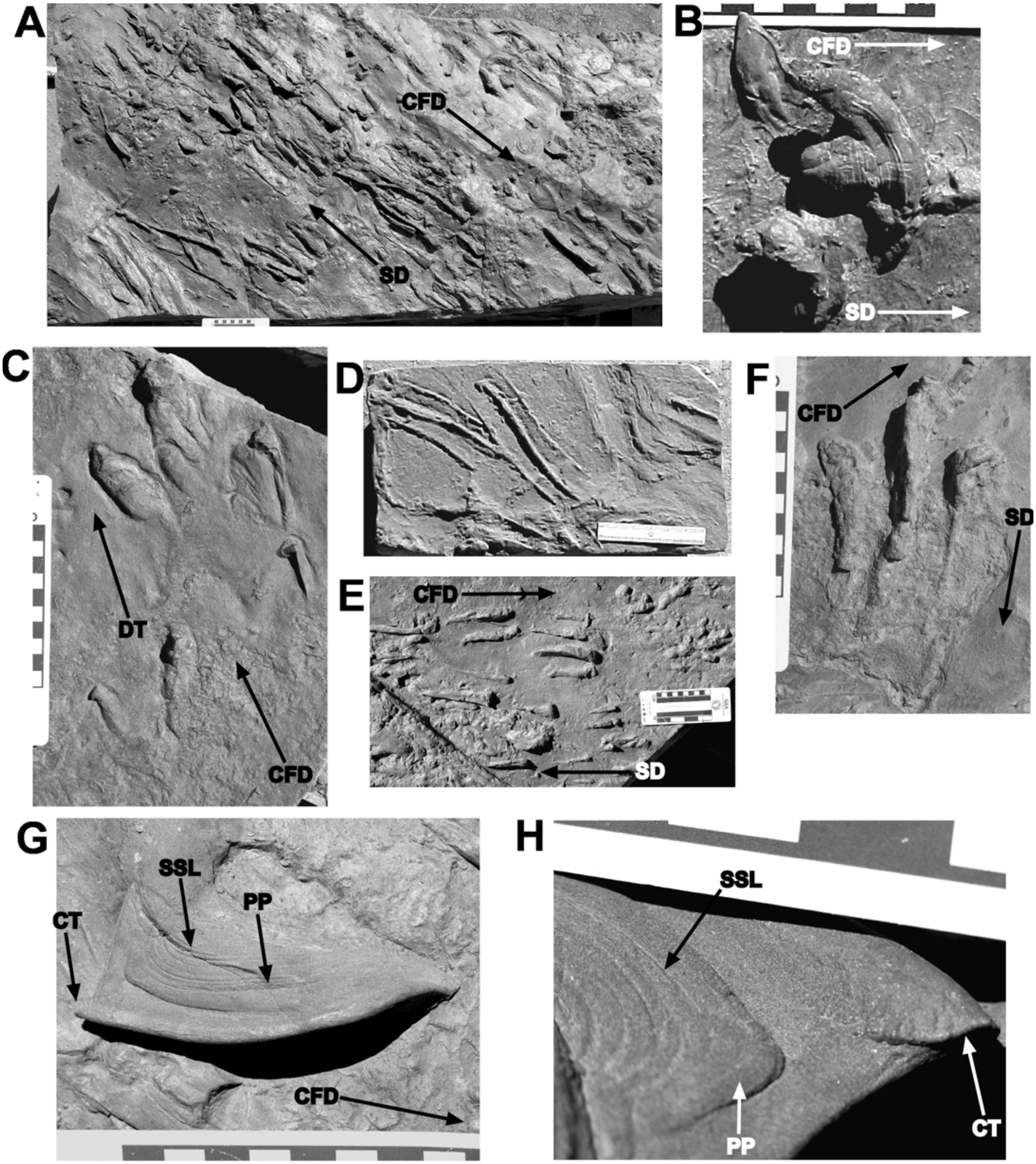

FIGURE 6. *Grallator*-type swim tracks from the SGDS MTL. **A**, Block showing high density of parallel swim tracks (Field # SW.29). **B**, Down-current swim track set (Field # SW.104). **C**, "Normal" *Grallator* track in a down-current orientation (Field # SW.90). **D**, Elongate, up-current swim tracks (SGDS.167-4). **E**, Shorter, up-current swim tracks (Field # SW.103). **F**, Swim track set cross-cutting current in a more up-current orientation (Field # SW.77). **G**, *Grallator*-type swim track details showing claw mark, claw tip and scale scratch lines (SGDS.361). **H**, Close-up of claw tip, from **G** showing possible cuticle details (SGDS.361). Abbreviations: CFD, current flow direction; CT, claw tip; DT, direction of travel; PP, distal phalangeal pad; SD, swim direction; SSL, scale scratch lines. Scales in cm.

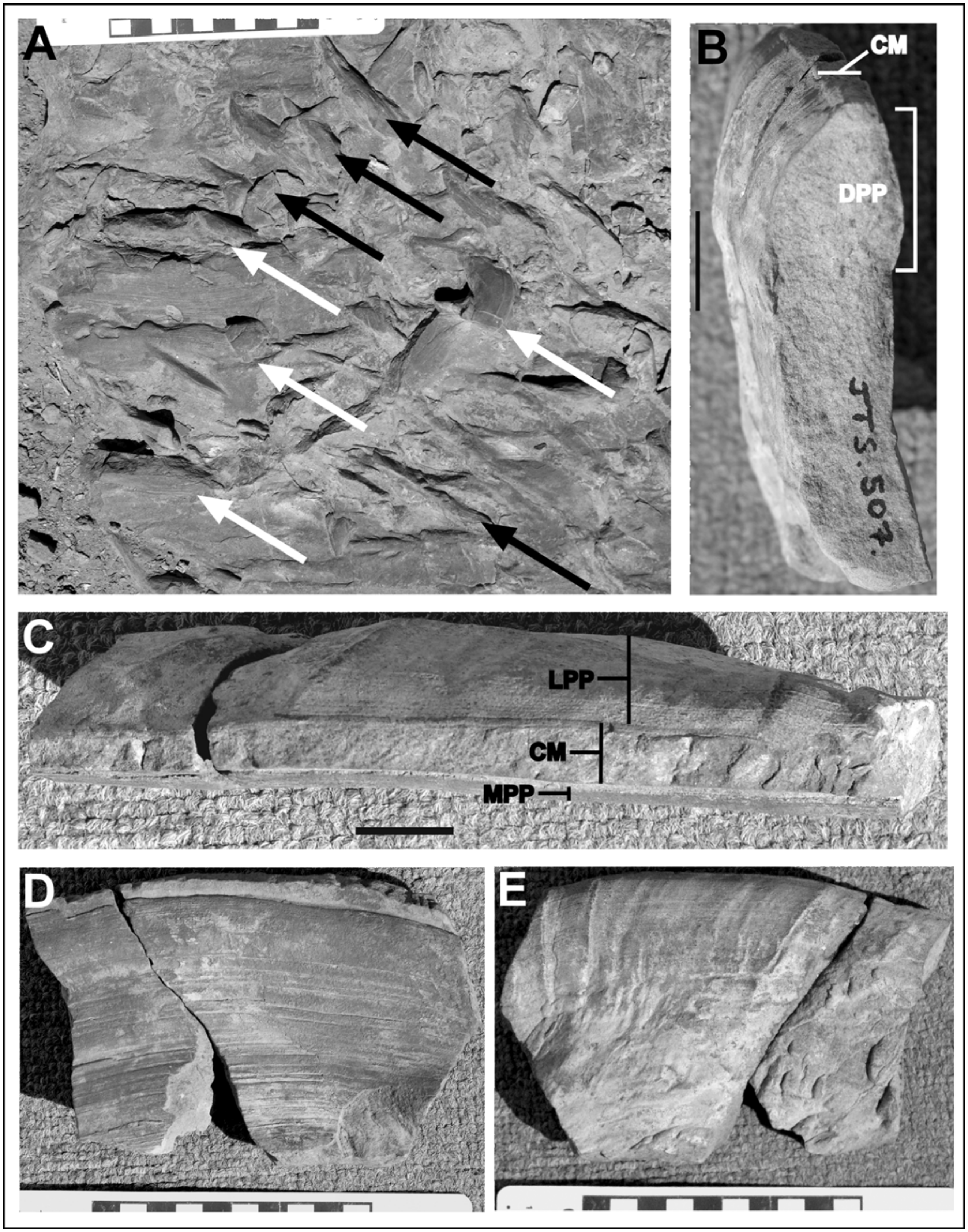

FIGURE 7. Possible *Eubrontes*-type swim tracks. **A**, Large, possible *Eubrontes*-type swim tracks (white arrows) associated with abundant *Grallator*-type swim tracks (black arrows) (SGDS.805). **B-E**, *Eubrontes*-type swim track toe and claw mark (SGDS.507). **B**, Distal view, showing claw and asymmetry of digit. Scale bar = 2 cm. **C**, Distal view of toe and claw showing asymmetrical shape of digit and claw. Scale bar = 2 cm. **D**, Medial view of digit showing claw mark and clear scale scratch lines. **E**, Lateral view of digit showing claw mark and scale scratch lines. Abbreviations: CM, claw mark; DPP, distal phalangeal pad; LPP, lateral side of distal phalangeal pad; MPP, medial side of distal phalangeal pad.

clearly shown on specimen SGDS.507 (Figs. 7B-C), which represents an isolated example of an undetermined and large theropod digit. Scale scratch lines are prominent on the sides of these specimens (Figs. 7D-E).

The claw base widths of *Eubrontes*-type swim tracks range from 0.7-1.3 cm, and the distal phalangeal pad of the toes range from 5.3-5.5 cm (Figs. 7B-C). Because of the rarity of interpreted *Eubrontes*-type swim tracks, it is more difficult to determine which of the digits (i.e. II, III, or IV) made the large swim tracks. Digits II and IV tend to be narrower than digit III, rendering the 1:3 claw/distal phalangeal pad ratio estimate inaccurate.

Several *Eubrontes* tracks (and possible scoured-out tracks) are preserved among the swim tracks at DSQ1 and DSQ2 (Fig. 8A). An impressive *Eubrontes* track with a metatarsal impression, associated scale scratch lines, and slide marks (Figs. 8B-C) indicates an interesting movement of the animal. This deep left track has an estimated foot length of about 30 cm (54 cm with metatarsal) and approximate width of 19 cm (Fig. 8B). This track likely represents a theropod dinosaur at rest, standing in the water with a north-flowing current toward its cranial left side, while the animal was facing northeast. The orientation of scratch circles and other sedimentary structures support this interpretation. Judging from the slide marks on the substrate (Fig. 8C), it appears as though the dinosaur attempted to advance forward and was pushed off balance to the left (i.e., in an oblique, down-current direction). The animal then advanced slightly forward – but the trace then grades into features too chaotic to allow clear interpretation. Abundant *Grallator*-type swim tracks are associated on the same block with several of them formed after the *Eubrontes* track maker moved away (Figs. 8B-C).

Other Types of Swim Tracks or Possible Swim Tracks at the SGDS

An unusual, elongate tail-drag-like trace, oriented at an angle of approximately 45° to the down-current flow direction (Fig. 9A) exists in DSQ1. The thinnest end of the trace (down-current direction) is approximately 1.5 cm wide. The thickest end is in the up-current direction and about 5 cm wide, with about 2 cm of relief. Along the thinner end is a sharp, prominent ridge extending about 20 cm (Fig. 9A) that grades to a smooth, rounded surface with decreasing width. The entire trace has long scale scratch lines on both sides, and has a total length of 114 cm (spanning two blocks; field # SW.103 and SW.15; specimen SW.103 has the majority of the trace and measures about 74 cm in length). The exact affinities of this trace are unclear; however, it is certain that this was made by a reptile, and likely a theropod dinosaur based on associated swim tracks and *Eubrontes* and *Grallator* footprints. It might be a tail-drag or swipe mark, or may have been caused by an animal placing an appendage on the substrate and dragging it down-current.

Another trace of interest found in DSQ1 is an isolated, *Batrachopus*-like footprint that measures 3 cm long and 2.5 cm wide (Fig. 9B). This natural cast specimen has 0.8 cm of relief, shows four digits, and represents a right pes track. What makes this footprint of interest is how it came to be preserved with subaqueous traces and sedimentary structures. It may have been made prior to swim track formation and burial of the track surface during a regressive lake phase, but given that this surface was buried quite rapidly, this suggestion seems unlikely. *Batrachopus* tracks are usually attributed to crocodylomorphs, and Early Jurassic crocodylomorphs, such as sphenosuchians, have limbs that suggest an erect, digitigrade stance, and are therefore more adapted for cursorial habits than modern crocodylians (Parrish, 1987; Wu and Chatterjee, 1993, p. 78). Protosuchians were probably more terrestrial than modern crocodylians, but not as specialized as sphenosuchians in the Triassic and Early Jurassic (Parrish, 1987; Carroll, 1988, p. 281). However, it is possible that a member of either of these crocodylomorph clades could have produced a track while partially or completely submerged to create the *Batrachopus*-like track in Figure 9B.

Several important cf. *Batrachopus* trackways are found at the

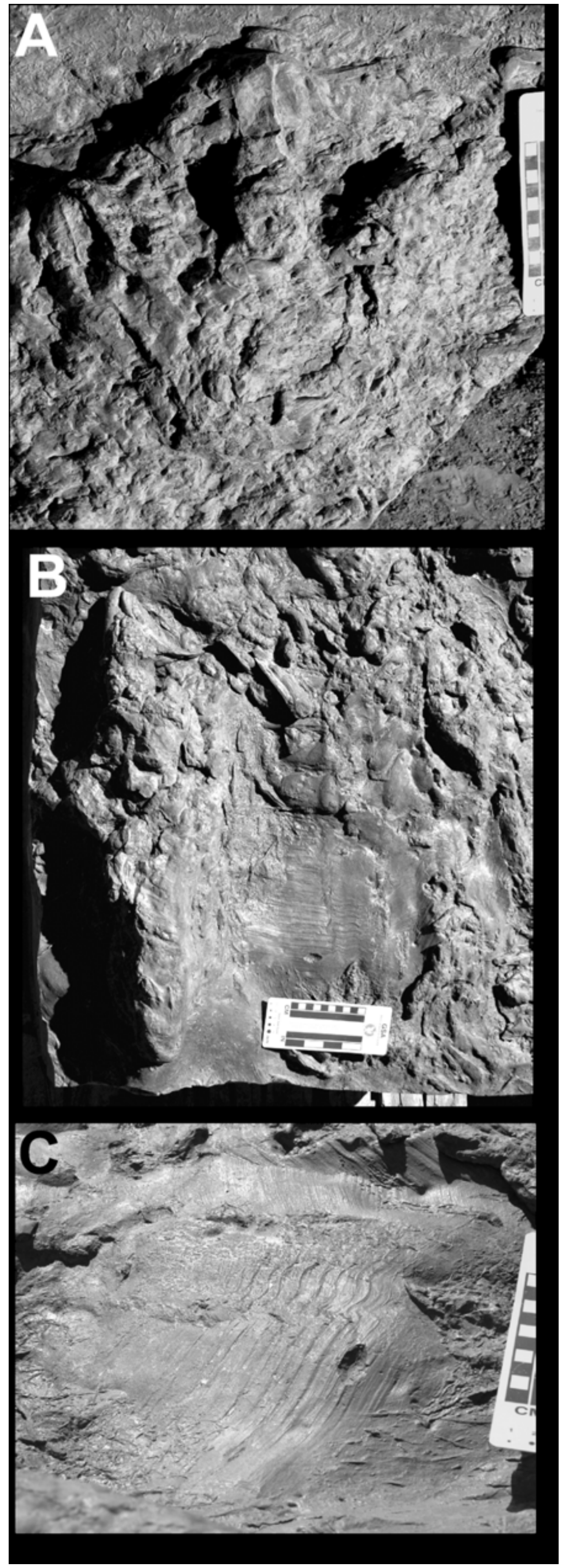

FIGURE 8. *Eubrontes* tracks. **A**, Right *Eubrontes* footprints associated with dinosaur swim tracks (Field # SW.103). **B-C**, *Eubrontes* track and deep metatarsal impression and scale scratch marks, with associated *Grallator*-type swim tracks (Field # SW.69). **B**, Cranial is toward the top of the photo. **C**, Close-up of scale scratch lines in **B**. Lines begin at original position of foot (bottom left of photo) and extend toward the track maker's left (toward top of photo). CFD, current flow direction.

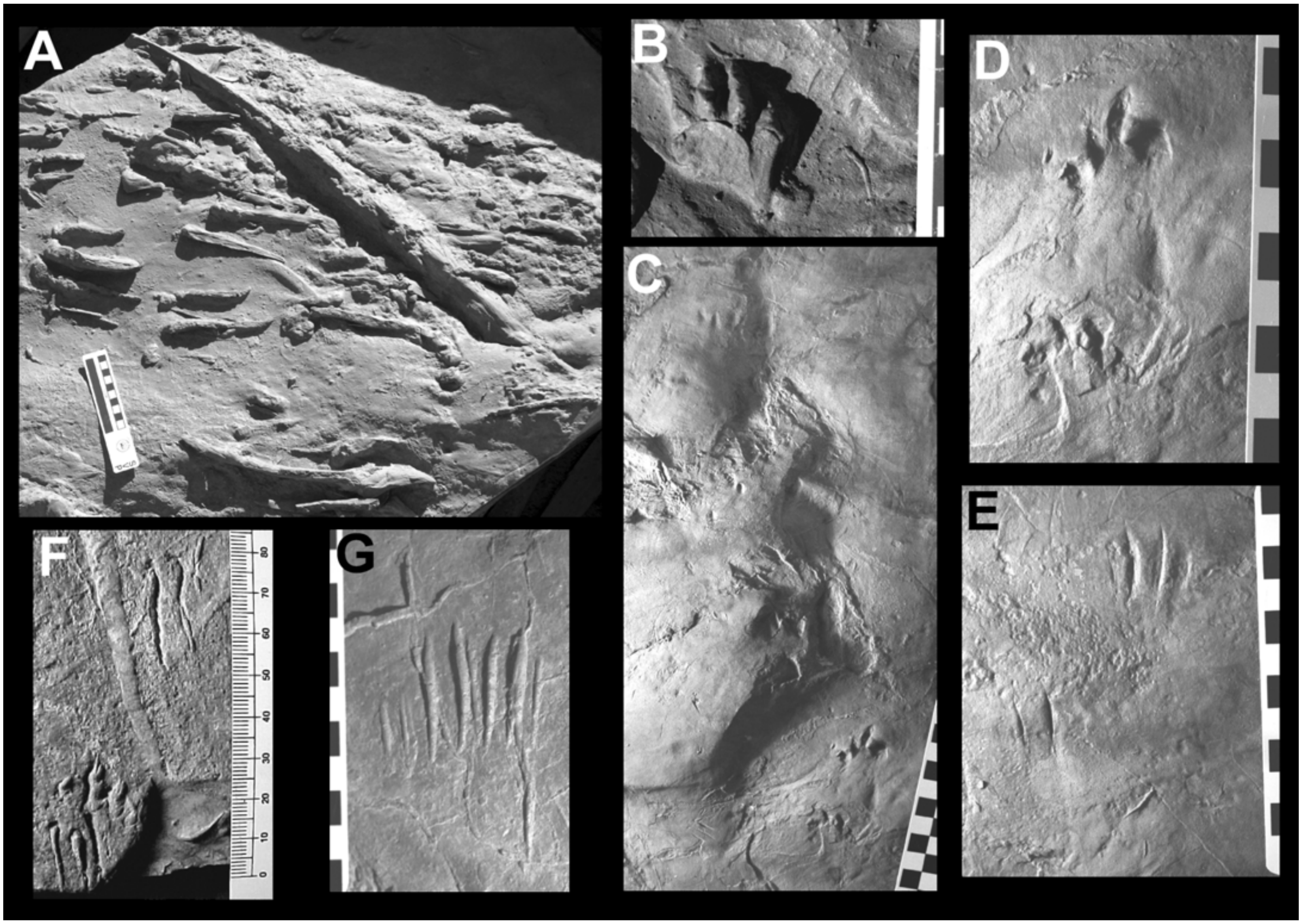

FIGURE 9. Other types of swim tracks and associated, enigmatic tetrapod-produced structures. **A**, "Tail swipe mark" with associated swim tracks (Field # SW.103). **B**, cf. *Batrachopus* track found associated with dinosaur swim tracks (Field # SW.29). **C-E**, "Top Surface" *Batrachopus* trackway transitioning from walk to swim (SGDS.18.T5). Notice the orientation of current ripples and the change in direction of the swim tracks. **F**, *Batrachopus* specimen transitioning from walk to swim (SGDS.176). **G**, Swim track of unknown affinity (SGDS.421).

SGDS museum site in the *in situ* "Top Surface" track layer (Figs. 2-3). All specimens consist of walking trackways transitioning into swim tracks; the best-preserved example of this is SGDS.18.T5 (Figs. 9C-E), which is associated with four other trackways that moved in the same direction (SSW), paralleling the paleo-shoreline. All begin with clear *Batrachopus* trackways that show manus/pes sets (Figs. 9C-D). As the topography of the tracked surface drops in elevation, these walking tracks transition into sets of parallel claw marks arranged in sets of two to four (Figs. 9C, E). There are six sets of alternating left and right swim tracks, with the sixth set turned westward. Associated current ripples are oriented in a NW direction (Fig. 9C), so perhaps the crocodylomorphs responsible for these trackways were being turned down-current as they entered the water and began to swim. The longest trackway (SGDS.18.T5) is approximately 95 cm long but may prove longer with future excavation.

Another *Batrachopus* specimen, preserved in convex epirelief, displays a partial trackway, possibly transitioning from a walk to a swim. It shows three claw-scrape marks leading up to three clear and well-preserved digit impressions (Fig. 9F). A fourth digit is present but without a claw-scrape mark leading up to it. This entire track is 4.6 cm long, and the claw-scrape marks are 1.8-2.2 cm long and 1 mm wide. The claws on the clear toe impressions are also 1 mm wide, and very small skin impressions are visible around the larger of the digits. The second set of tracks in this short trackway is located 1.7 cm away and consists of "swim" tracks showing three claw marks. The set is 1.5 cm wide, and the claw marks are 1 mm wide and range from 1.7-2.8 cm in length. *Batrachopus* swim tracks will be described elsewhere in the future.

Finally, an unusual swim-track specimen (SGDS.421; Fig. 9G) was found in 2003 by Dr. Paul Bybee (Utah Valley State College, Provo, Utah) in previously excavated rock piles northwest of the SGDS museum location, probably from the Stewart-Walker Tracksite level (Fig. 2; see Milner et al., this volume for further discussion of this tracksite). It is a set of about eight parallel claw marks, measuring 4.9 cm wide between the outer marks. These claw marks range in length from 1.6-6.2 cm and are 0.15-0.4 cm wide. The differing depths and thicknesses of the various claw marks make it look like coincidentally overlapping swim tracks made either by different limbs of the same animal or, more likely, different animals at different times. This trace could possibly be part of a turtle swim track, but until better specimens are discovered, it will remain of uncertain affinity.

DISCUSSION

As mentioned above, the ichnogenus *Characichnos* (Whyte and Romano, 2001) could be considered merely an extramorphological variant of "walking" track types found associated with or near the swim tracks. Because well-preserved swim tracks are found in close association with *Grallator* and *Eubrontes* tracks at the SGDS sites, we can attribute these swim tracks to the same track makers and refer to them as

Grallator-type and *Eubrontes*-type swim tracks. We do the same for *Batrachopus* and *Batrachopus*-like swim tracks, since tracks of this ichnotaxon also occur on the SGDS Top Surface tracksite transitioning from walking to swimming traces.

We accept the ichnogenus name *Characichnos* as a valid description of a behavioral character of the track producers. Where swim tracks are all that exist, they cannot be attributed to any particular subaerially produced, "walking" track ichnotaxon. Cases such as the SGDS swim track sites, at which swim tracks occur in close proximity to, and sometimes in direct association with, subaerially produced tracks, are relatively rare. Given that morphology is the main ichnotaxonomic criterion, *Characichnos* could be redefined as swim tracks of all bipedal dinosaurs, whether ornithischian or saurischian, that show three parallel scrape marks (see Lockley and Milner, this volume for further discussion of non-dinosaurian swim tracks with similar morphologies). Now that *Characichnos* has also been used as a label for a recently defined ichnofacies (Hunt and Lucas, in press), it is likely that the name will continue to be used by ichnologists. In short, the discovery of so many well-preserved swim tracks at the SGDS enhances the need to subject the *Characichnos* ichnogenus concept to further scrutiny.

We also infer that the "*Eubrontes*-swim tracks" described by Coombs (1980) from Dinosaur State Park may not be swim tracks, but are undertracks of *Eubrontes*. The interpretation of Coombs (1980) that swimming theropods could make unique and recognizable tracks may be valid, but the trace fossils may not be swim tracks (Galton and Farlow, 2003). Coombs also illustrated a "megalosaur" (Coombs, 1980, fig. 3; Galton and Farlow, 2003, fig. 21) producing the proposed swim tracks rather than a more likely producer of *Eubrontes* tracks, such as *Dilophosaurus* (Paul, 1988**,** fig. 2-10) or a similar, large ceratosaur. The overall morphological characteristics of the "swim tracks" described by Coombs (1980) do not correspond well with most SGDS swim tracks, which occur in sets of three with digit III displaying a longer and deeper claw mark, extending caudally and cranially beyond the lateral digit traces (II and IV) in most cases, unless moving in a down-current direction. The Dinosaur State Park "swim tracks" may have been produced on a very firm substrate as demonstrated by Farlow and Galton (2003), who obtained nearly identical tracks produced by a rhea walking on plaster of Paris that was nearly hardened (Galton and Farlow, 2003).

During the MTL depositional event, the majority of small theropods were evidently floundering against a current in a depression within the lake that paralleled the paleo-shoreline to the northwest of the SGDS museum site. The sheer number of subparallel swim tracks made by similarly-sized theropods implies that the track makers were moving in an organized group. Gregariousness has been previously suggested for Late Triassic and Early Jurassic theropods. The Whitaker *Coelophysis* Quarry at Ghost Ranch, New Mexico, in the Upper Triassic Rock Point Formation (Paul, 1988; Colbert, 1989, 1990), produced an assemblage that includes a probable pack or packs of *Coelophysis*. Similar coelophysoid assemblages involve multiple individuals of *Megapnosaurus rhodesiensis* from southern Africa (Raath, 1977, 1990; Paul, 1988), and a group of *Megapnosaurus kayentakatae* from the Early Jurassic (Sinemurian) Kayenta Formation of northeastern Arizona (Rowe, 1989). *Megapnosaurus* is presently the only theropod described by body fossils in the Moenave Formation (Lucas and Heckert, 2001), so it is quite possible that this animal, or one very similar, is responsible for the *Grallator* tracks at the SGDS. The large concentration of SGDS swim tracks support the hypothesis that these coelophysoid theropods exhibited gregarious behavior, apparently a common phenomenon among Triassic and Jurassic theropods (Ostrom, 1972; Raath, 1977, p. 19-21; Colbert, 1989, p. 16-17, 148; Currie, 1997; Lockley and Matsukawa, 1999; Lockley et al., this volume).

CONCLUSIONS

The *Megapnosaurus* or *Megapnosaurus*-like dinosaurs that occupied the Lake Dixie shores during the Early Jurassic Epoch (approximately 198 million years ago) ventured out into the lake waters. The excellent state of preservation of most of these traces suggests that sand swept along by this current filled the traces simultaneous with their formation. The high concentration of swim tracks indicates large groups of small, probably ceratosaurian dinosaurs, fighting or floundering against currents. The direction of natatory locomotion was parallel to the shoreline in a more or less southerly direction, opposite the caudally-directed claw marks preserved in the swim tracks. Occasionally, swim tracks are oriented cross-current or in the direction of current flow twoard the north.

Non-natatory *Eubrontes* trackways co-occur with the *Grallator*-type swim tracks. This indicates that larger, probably *Dilophosaurus*-like theropods were able to wade through areas where smaller theropods presumably had to swim. A water depth of 1-1.25 m can therefore be inferred from such *Grallator* swim track evidence. However, based on a single large, *Eubrontes*-like swim track, water depth varied to as much as 1.75 m. A simpler explanation, considering that in outcrop Lake Dixie was more than 100 km across, would be that the animal slipped on the smooth mud in the strong current. Smaller swim track claw marks were either made by smaller individuals (*Grallator* track maker juveniles and/or subadults) or by the manual unguals striking the muddy bottom. *Batrachopus* swim tracks also give insight into the behavior of small crocodylomorphs as they transitioned from emergent areas to shallow water along the shoreline and across areas of variable topography.

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