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BEHAVIORAL SIGNIFICANCE OF VERTEBRATE TRACE FOSSILS FROM THE UNION CHAPEL SITE

ANTHONY J. MARTIN
Department of Environmental Studies, Emory University, Atlanta, Georgia 30322, USA

NICHOLAS D. PYENSON
Department of Integrative Biology, University of California at Berkeley, Berkeley, California 94720, USA

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ABSTRACT: The Union Chapel site is one of the world's most important for Early Pennsylvanian vertebrate trace fossils. Most of these vertebrate trace fossils consist of tracks made by temnospondyl amphibians and other tetrapods, but some are trails left by the fins of swimming fish. The exceptional quality and quantity of the traces provide for a unique opportunity to interpret behavioral nuances of vertebrates from this time interval. Tracks were likely made on emergent muddy, freshwater-dominated estuarine tidal flats during low tides, whereas fish swimming traces were probably formed in very shallow water during either falling or rising tides. Fish trace fossils, identified as the ichnogenus *Undichna*, are the result of caudal and anal fins that dragged along muddy surfaces. These trails, which have wave-like forms with low amplitudes and long wavelengths, indicate relatively small fish (10-15 cm long). Some *Undichna* provide evidence of changes in swimming speed, abrupt turns, and possible schooling. Vertebrate tracks, most assignable to the ichnogenus *Cincosaurus*, indicate animals that ranged from about 10 cm to 1.5 m long and most may have represented growth stages of a single species of tracemaker. The trackways are most significant for the array of behaviors they reveal: shifts in speed and direction, lateral movements, obstacle avoidances, and possible group movement, all of which are rarely reported from the fossil record from any time, let alone from the Early Pennsylvanian. In short, vertebrate trace fossils from the Union Chapel site give paleontologically noteworthy insights into Early Pennsylvanian vertebrate behavior unknown from body fossils or most other trace fossils from rocks of this age.

INTRODUCTION

Fossil vertebrate tracks from strata in the immediate area of the Union Chapel site were recognized more than 70 years ago, when Aldrich and Jones (1930) first described a number of these tracks and attempted to classify them. Little was done to study these tracks any more until 2000, when members of the Alabama Paleontological Society (then known as the Birmingham Paleontological Society) investigated them. The rediscovery of this motherlode of vertebrate tracks was the main motivating force behind subsequent and laudable cooperation between amateur paleontologists, state agencies, and universities in efforts to document and preserve the site and the tracks (Rindsberg et al., 2001; Buta and Minkin, 2005). Of course, vertebrate tracks are not the only fossils that occur in this deposit; in total, the invertebrate burrow *Treptichnus* is probably the most commonly encountered fossil (Rindsberg et al., 2004). However, the vertebrate tracks were the main draw for attention from the amateur collectors and garnered the lion's share of media focus (Bourne, 2003; Toner, 2003; Sever, 2003). Although a thorough examination of the reasons for this admitted bias is beyond the range of this report, we can suggest two explanations: (1) most people, whether they have training in paleontology or not, easily recognize fossil vertebrate tracks as representative by-products of animal behavior; and (2) the quantity and quality of the vertebrate tracks from this site iare exceptional and likely exceed those of any known deposit of the same age anywhere in the world.

While keeping in mind this foundation of interest in the tracks, we felt that other vertebrate trace fossils, represented by fish swimming trails, are also important to consider because no fish body fossils have been found from this deposit or others of the same age in the southeastern United States. Nonetheless, track-bearing slabs are far more abundant than slabs with fish trails: out of more than 1200 slabs cataloged in the first three "track meets" held by the Alabama Paleontological Society (Rindsberg et al., 2001; Buta and Minkin, 2005), most of which have tracks, only 36 are known to have such trails. (Admittedly, this may be an artifact of the aforementioned collecting bias that favors an overrepresentation of tracks, and more *Undichna* have been found since.) Because of the large numbers of tracks and extensive trackways, we were able to make some population estimates of the trackmakers (as indicated by size ranges of track parameters), a study that would have been much more limited with the fish trace fossils. Such a population analysis was first done by Pyenson and Martin (2001) and followed up with a more quantitative assessment that modeled specific parameters of the Union Chapel tracks and trackways (Pyenson, 2002; Pyenson and Martin, 2002).

In this article, we will mention some information about the quantitative aspects of the Union Chapel fish trails and vertebrate tracks, but will focus more on interpreting the behaviors of their tracemakers. The Union Chapel material quite likely represents the best preserved and most abundant record of vertebrate populations and behavior from this time, meaning that it can provide a window to better understanding vertebrate evolution that otherwise would not be available to paleontologists. Moreover, some of the behaviors we report here are seldom interpreted from the geologic record, highlighting the scientific importance of the Union Chapel site for vertebrate paleontology.

DESCRIPTION OF UNION CHAPEL MINE VERTEBRATE TRACE FOSSILS AND POSSIBLE TRACEMAKERS

Fish trails and vertebrate tracks are preserved in a 2-3 m thick interval of gray, laminated, silty shale of the Pottsville Formation (Early Pennsylvanian) that was probably formed in the upper reaches of an estuarine tidal flat (Pashin, 2005). Interestingly, fish trails rarely occur on the same surfaces as the tracks, which may mean that each type of trace fossil represents different environmental and preservational conditions. For example, the trails were certainly made by swimming fish (elaborated later), so the water depths must have been at least the heights of the fish making the trails. However, vertebrate trackways show no evidence of being made underwater and, rather, point toward formation on emergent mudflats. For example, some of the smallest trackways have drag marks of both the ventral abdominal surfaces and tails, which would have been unlikely in a submerged environment where the tracemakers would have been more buoyant. Depositional rates in this environment were relatively high (Pashin, 2005), which probably aided the preservation of the trails and tracks. This happenstance combination of quick burial and fine-grained material in a quiet-water environment caused ideal conditions for preserving the excellent detail seen in the Union Chapel specimens (Martin and Rindsberg, 2004). Although Haubold et al. (2005a) interpret the majority of Union Chapel tracks as undertracks and we agree with this assessment, tracks are three-dimensional entities (Brown, 1999) and thus the undertracks should not be treated as inferior simply because they do not represent original top surfaces.

Fish trails occur as wave-like traces on bedding planes, showing both negative-relief (grooves) and positive-relief (casts of grooves), with the grooves on bed tops and casts on bed bottoms, respectively. Trails are invariably quite narrow and shallow, only 2-3 mm wide and 2-4 mm deep in most instances. Trail lengths often vary according to the size of collected slabs, in that some originate and end off the slabs, but some are at least 40 cm long. Amplitudes are typically low, varying from 1 to 4 cm, and when viewed in conjunction with wavelengths suggest that relatively small fish (mostly 10-15 cm long) were responsible for the traces. Trails can be placed into four categories based on form: (1) regularly spaced but discontinuous parts of single or coupled waveforms; (2) single waveforms, with some showing different amplitudes and wavelengths; (3) slightly offset and overlapping coupled waveforms, with one waveform of slightly lower amplitude; (4) completely out-of-phase overlapping and coupled waveforms, again with one waveform of slightly lower amplitude than the other (Fig. 1). In some instances, fish trails are evenly spaced and parallel to one another, and in other cases multiple trails overlap along the same trend (Fig. 2).

All fish trails are assignable to the ichnogenus *Undichna* (Anderson, 1976), a trace fossil commonly reported from Early Pennsylvanian strata in other parts of the world (Archer and Maples, 1984; Turek, 1989, 1996; Buatois and Mángano, 1994; Buatois et al., 1997; Soler-Gijón and Moratalla, 2001). We currently have too little information to infer whether more than one species of fish caused the various forms of *Undichna* in this deposit, but because they are so limited in size, they represent either juveniles of different species, juveniles and small adults of different species, or adults of one small-sized species. We do know that the majority of these fish had both caudal and anal fins and were likely jawed fish because of their swimming movements, as explained later.

The vast majority of the thousands of Union Chapel vertebrate tracks documented thus far are relatively small (less than 2 cm wide), but a few large tracks are as much as 12 cm wide. Based on the range of track sizes, trackway widths, and glenoacetabular distances (the distance between successive front-foot tracks on the same side), trackmakers were probably about 10 cm to 1.5 m long (Pyenson, 2002). Front-foot (manus) tracks typically show four toes, whereas hind-foot (pes) tracks normally show five toes; pes tracks are also distinguishable because they are significantly larger (about 60%) than manus tracks (Fig. 3). Although track preservation certainly varied enough that not all toes were impressed in every track, the most consistently observed number of toes on the manus and pes were four and five, respectively (Pyenson, 2002). Relatively small tracks not only demonstrate this same arrangement, but also show greater morphological detail, such as an elongated fourth toe on the pes (Fig. 4). Toe lengths are otherwise nearly equal in the manus and pes tracks examined in this study. The first three toes of the manus and pes are the most parallel to the direction the trackmaker was traveling, whereas the fourth and fifth digits tend to diverge toward the outside of the trackways.

Most track forms are assignable to the ichnogenus *Cincosaurus*, which was named by Aldrich (in Aldrich and Jones 1930) based on material from the same deposit near the UCM site. The sum of these characteristics coupled with the known body fossil record for vertebrates strongly suggest that most of the trackmakers were temnospondyl amphibians, a group originally recognized by Zittel (1888) and updated by Steyer (2000). Temnospondyls are amphibians that were common during the Early Pennsylvanian (Carroll, 1988; Benton, 1997). The age estimated for the formation of the Union Chapel deposit is about 308 million years (Pashin, 2005), which is at the beginning of the known evolutionary history for egg-bearing vertebrates (amniotes), such as reptiles (Carroll, 1988; Benton, 1997). Although our study did not delve into the details of identifying all trackmakers, others have concluded that a lesser number of amniotes may have been present as well (Aldrich and Jones, 1930; Lucas et al., 2004; Haubold et al., 2005a).

The hypothesis that most tracks were made by temnospondyls is supported foremost by the common association of four-digit manus and five-digit pes in trackways, which are characteristic of that group of

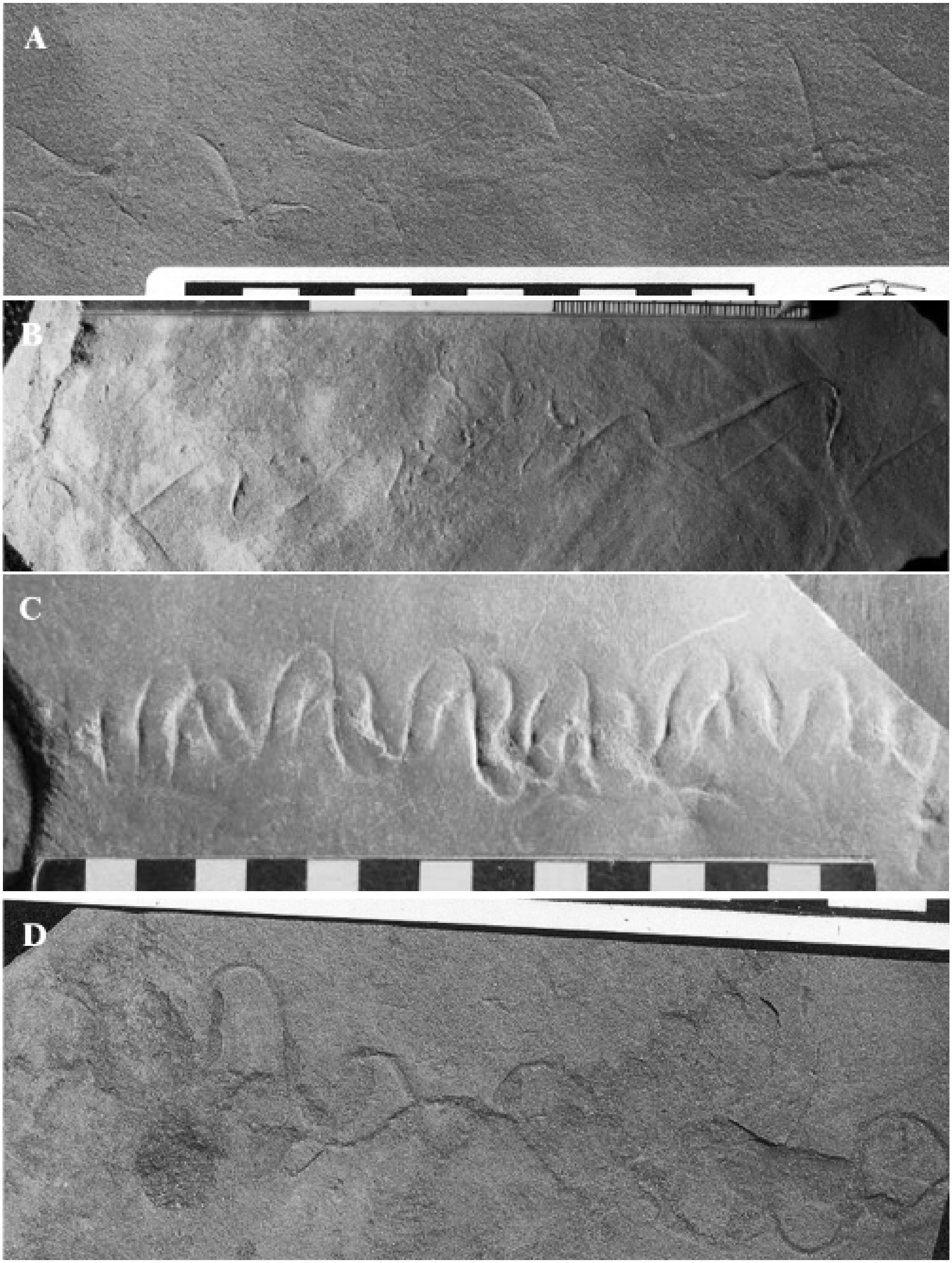

FIGURE 1. Categories of fish trails (*Undichna*) in the UCM deposit based on morphology. A - Discontinuous waveforms (UCM 455); B - singlewaveforms (UCM 1734); C - Slightly offset and overlapping waveforms (UCM number not identified); D - completely out of phase overlapping and coupled waveforms (UCM 728).

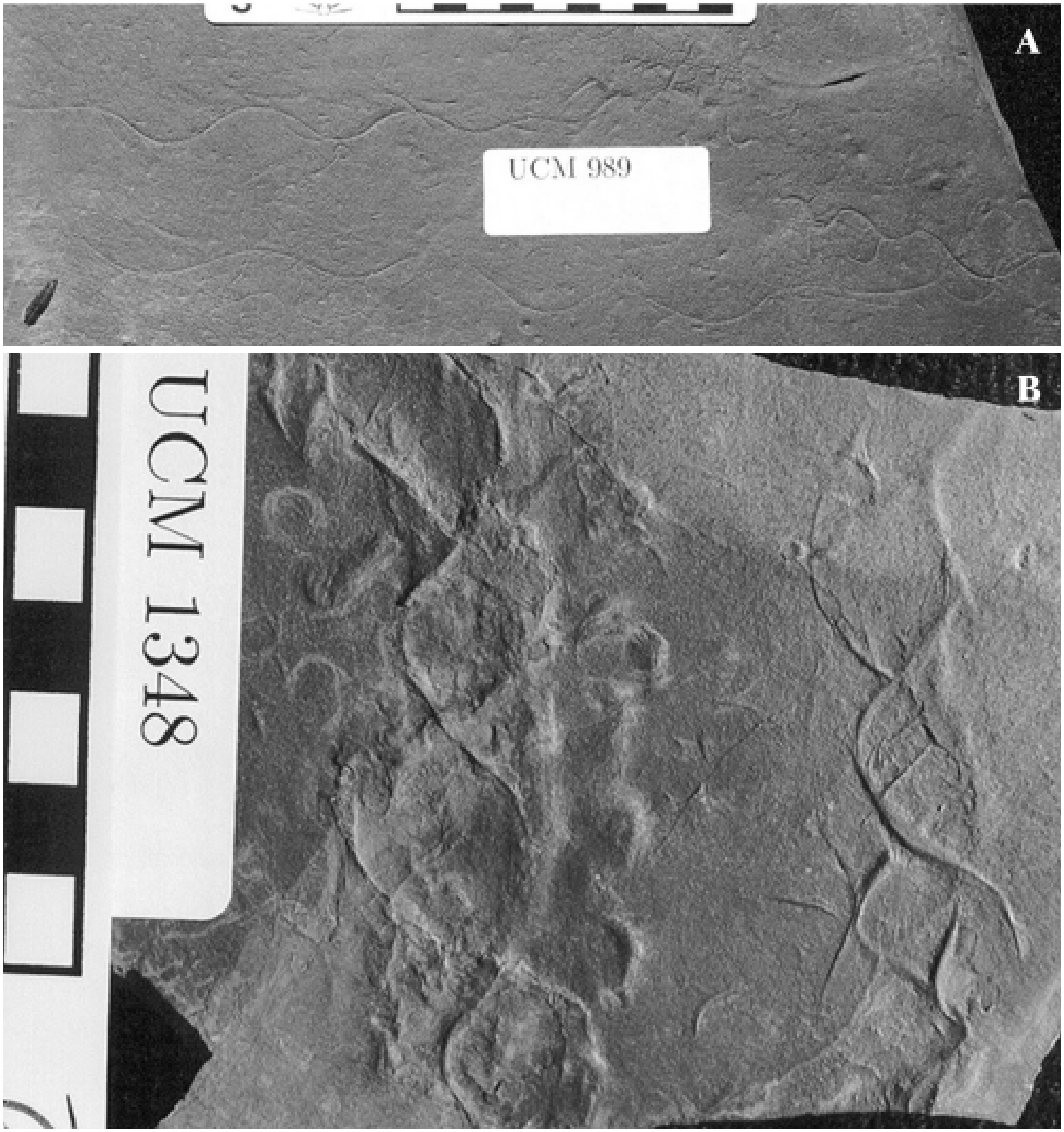

FIGURE 2. Multiple *Undichna* on same slabs. A - *Undichna* showing parallelism (UCM 989); B - *Undichna* showing both parallelism and overlapping (UCM 1348).

amphibians (M. Coates, personal commun. to Pyenson, 2002). Size-frequency distributions of track widths also approximate population curves of modern amphibians (Duellman and Trueb, 1994), which are skewed so that the majority of the tracks fall into smaller size ranges and comparatively fewer are in the larger size ranges (Pyenson, 2002; Pyenson and Martin, 2002). Furthermore, statistical methods applied to 94 Union Chapel trackways showed very high positive correlations ($r^2 > 0.85$) between all paired comparisons of manus width, pes width, trackway width, and glenoacetabular distance, an expected outcome for a population of the same or similar species (Pyenson, 2002; Pyenson and Martin, 2002). Tracks with different forms, like many other trace fossil forms, might be ascribed to various combinations of sediment quality and behavioral interactions with the sediment, and not necessarily different species of trackmakers (Bromley, 1996).

In terms of feeding habits, all modern adult amphibians are carnivores, although some juvenile amphibians eat plant material and invertebrates (Duellman and Trueb, 1994), but no evidence pertinent to feeding hab-

FIGURE 3. Left-side manus-pes pair of amphibian tracks (*Cincosaurus cobbi*), displaying significant size difference between smaller manus and larger pes (UCM number not identified).

its of the Union Chapel tetrapods is known. The deposit contains much allochthonous plant material (Dilcher et al., 2005) and trace fossil evidence for many invertebrates in and on the mud flats (Rindsberg and Martin, 2004; Rindsberg et al., 2004), which conceivably could have sustained a large population of juvenile amphibians or amniotes.

Fortunately, many of the tracks do not occur as isolated examples but are associated with definite trackways, which for our purposes are defined as any sequence of more than two steps by opposite sides of the trackmaker (i.e., left-right-left or right-left-right). These trackways show important parameters needed for interpreting populations and behavior: pace, stride, straddle, pace angulation, glenoacetabular distance, and any deviations that trackways might take from a straight line, all of which are measurable in well-preserved trackways (Figure 5). All trackways show clear evidence of vertebrates walking on four legs (quadrupedalism) and most consist of same-side manus-pes pairs that alternate in a diagonal pattern (Fig. 3). A few trackways have only pes impressions, which gives a false appearance of bipedalism; we are certain that such occurrences represent undertracks of more deeply impressed pes tracks, where the more shallowly impressed manus tracks were recorded in overlying layers. This conclusion is also supported by a few examples of shallow manus prints paired with deep pes prints in the same trackways. Moreover, the larger-sized pes also could have obliterated any preceding smaller-sized manus print if the trackmaker directly registered its pes onto the manus print, thus leaving only pes prints to see.

Some of the trackways are remarkable for their continuity and epitomize why the Union Chapel specimens are exceptional when compared to tetrapod trace fossils in similarly aged rocks. For example, one slab (UCM 76 and its counterpart UCM 84) has more than 200 tracks on it, with one trackway showing 76 measurable and continuous paces in an unbroken sequence (Fig. 6). The small sizes of most tracks were surely advantageous for collectors, who were able to carry away entire trackways (rather than just individual tracks), which in turn were amenable for professionals to conduct detailed studies on amphibian behavior.

INTERPRETATIONS OF VERTEBRATE BEHAVIOR

In terms of behavior, Union Chapel vertebrate trace fossils most fundamentally provide convincing evidence of fish swimming and quadrupedal walking by amphibians. Furthermore, swimming or walking at relatively low speeds is seemingly the norm represented by Union Chapel trace fossils, although both fish trails and trackways contain evidence of variations in speed.

Relative fish swimming speeds can be estimated by looking at their wavelengths versus amplitudes; for example, *Undichna* that have high amplitudes with short wavelengths (i.e., high frequencies) imply that the fish were moving their tails faster than normal in the given distance traveled (Gilbert et al., 1999). Fish swimming can be categorized on the basis of their primary mode of propulsion, such as whether it is provided by full-body, fin, or tail movement (Sfakiotakis et al., 1999). Tail-based propulsion, which is typical of jawed fishes, causes a wave-like movement of the caudal and anal fins on

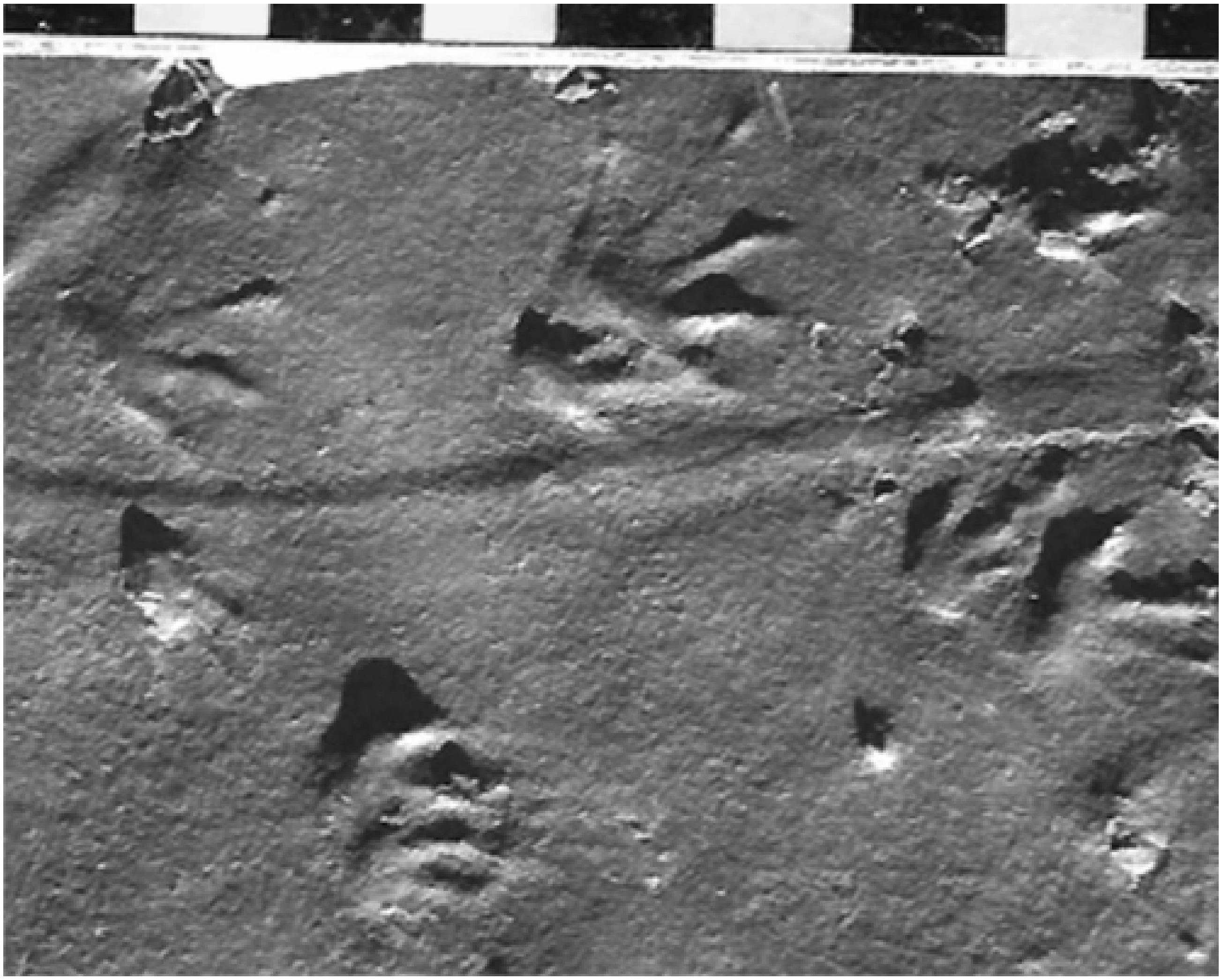

FIGURE 4. Foot morphology of manus and pes from specimen UCM 469, with larger pes overlapping manus; pes has elongated digit IV and bulbous tips to distal parts of toes. Note the sinuous tail drag mark in the middle of the trackway.

fish, so we conclude that in Union Chapel *Undichna* the lower ends of these two fins cut through the sediment, thus making the double undulating lines seen in most specimens. Moreover, because the caudal fin represents a greater range of movement in tail-based propulsion, its trace must be the higher amplitude waveform, whereas the lower amplitude one belongs to the anal fin. Using this principle and knowing that most fish swimming motion should be forward, the anal fin trace should be cross-cut by the caudal fin trace. Indeed, this supposition is borne out by the lower amplitude waveforms being cross-cut by the higher-amplitude ones in all UCM *Undichna* where double waveforms were seen.

Regardless of which fin made the traces, the larger-amplitude waveforms represent greater amounts of movement, so shorter wavelengths along a single trail should correlate generally to greater speed. Several specimens of Union Chapel *Undichna* (e.g., UCM 1304 and UCM 1729: Fig. 7) show just such variations along the length of their trails, where high-amplitude waveforms are succeeded by low-amplitude waveforms or vice versa. This behavior can be demonstrated by watching some aquarium fish beat their tails rapidly to increase their speed, followed by less rapid beats and smaller movements of the tail once the fish reach their desired speeds.

A fish behavior related to changes in speed is abrupt turning, which is indicated by a few Union Chapel *Undichna* specimens. Abrupt turns are inferred from specimens with sharp bends (nearly 60°) to their trails accompanied by double lines that parallel one another and then converge (Fig. 8A). The double lines are probably from the caudal and anal fins, which at their widest separation represent their anatomical distance from one another on the tracemaking fish. These traces would have been made as the fish turned and then started to straighten out its path, which would have caused the caudal fin to align with the anal fin and thus make the two converge. In some cases these parallel lines then merge into a "normal" *Undichna* with a coupled waveform (Fig. 8B).

Some slabs containing multiple specimens of Union Chapel *Undichna* also suggest group behaviors, such as schooling and following. Schooling behavior, the tandem movement of fish of the same species in a group

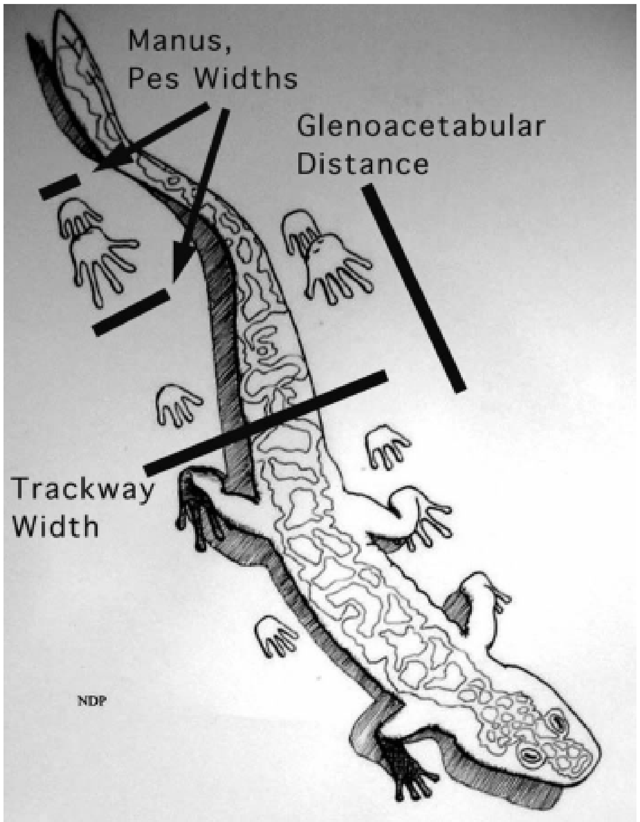

FIGURE 5. Schematic diagram of trackmaking temnospondyl and various measurements that can be made from a well-preserved trackway.

("school"), is interpretable from slabs that show more than one *Undichna* of similar size that parallel one another (Fig. 2A). Schooling fish often space themselves regularly to decrease the effects of turbulence (Sfakiotakis et al., 1999), thus trails left by schooling fish should show even spacing as well.

Following behavior, where one fish follows the path of another fish, should cause overlapping multiple trails: two such compound trails are observed in one Union Chapel specimen (UCM 1348: Fig. 2B). Following can happen in schooling but also could be caused by predation, when a predatory fish pursues a prey fish. However, if the waveforms of overlapping trails show very similar amplitudes and wavelengths, then a reasonable conclusion is that these are from similar-sized fish, which is atypical for a predator-prey situation. Furthermore, UCM 1348 also shows the same parallelism and spacing of trails postulated for schooling. Consequently, where fish followed and swam next to one another, these trails were made by a school of the same species of fish where following and swimming next to one another occurred. As far as we are aware, this is the oldest known evidence for group behavior in fish from the geologic record.

Amphibian trackway patterns are typical of diagonal walkers, where the manus print is either in front of or indirectly registered by the pes print and left-right and right-left alternations of these pairs form a diagonal pattern (Brown and Morgan, 1983; Rezendes, 2002). Pace angulation, which is the angle between left-right or right-left steps, is often less than 150° in Union Chapel trackways, which suggests a more sprawling posture; in contrast, upright postures tend to form trackway patterns with angulations closer to 180°, or like walking a "tightrope" (Schult and Farlow, 1992). Variations in speed are also demonstrated by trackways that show differences in pes paces, which show up as slight "understeps" or "oversteps" by the pes as it was placed slightly behind or in front of the manus, respectively (e.g., Fig. 3 for the latter). Based on our observations of Union Chapel trackways, "understeps" are represented by the majority of manus-pes placements and thus designate a normal walking gait, whereas "oversteps" indicate a faster than normal gait, and direct register is in between. However, Peabody (1959) noted that differences in torso lengths can affect the placement of a manus and pes; for example, a temnospondyl with a very long torso would have always had its pes register far behind the manus. Nevertheless, torso lengths of most trackmakers, as definable from glenoacetabular distances, were probably not abnormally long (Pyenson, 2002). As a result, we attribute most variations in manus-pes placement to behavior and not so much anatomical differences. Sprawling postures caused somewhat sinuous movements to the trackmakers, which is corroborated by wave-like traces of occasional tail drags evident midway between the tracks (Fig. 4). However, no trackways display any evidence of trotting, galloping, bounding, or other major variations of four-legged locomotion.

Perhaps most significantly for tracks of this age, more detailed information regarding behavior is indicated by the tracks. For example, changes in speed, sideways movements, abrupt turns, tail and belly drags, and obstacle avoidances are all inferrable from Union Chapel trackways. One bedding plane also shows as many as five similarly sized individuals moving in the same direction, which suggests group behavior.

Changes in speed can be easily detected by observing the manus-pes placement in a trackway, as mentioned previously. One of the outstanding attributes of the Union Chapel trackways is that so many of them show continuous sequences of manus-pes tracks, providing an opportunity to see step-by-step nuances in locomotion. For example, as mentioned before, two trackways on UCM 76 (and its counterpart UCM 84) made by similarly sized individuals have more than 200 manus and pes impressions preserved. As a result, careful measurements of the pes paces for one of the trackways revealed subtle variations in speed over the course of the trackway, but also showed an overall "moving average" for the trackmaker indicating that it gradually slowed down (Pyenson, 2002, Fig. 18). Sideways movement off the straightforward trend of a trackway is also a product of changes in speed, and several trackways accordingly display manus and pes impressions that register both to the inside and outside of a trackway (Fig. 4). Of course, abrupt turns in trackways also represent changes in speed because the trackmaker had to either stop or otherwise slow its movement to make turns that in some cases are almost 90°. As men-

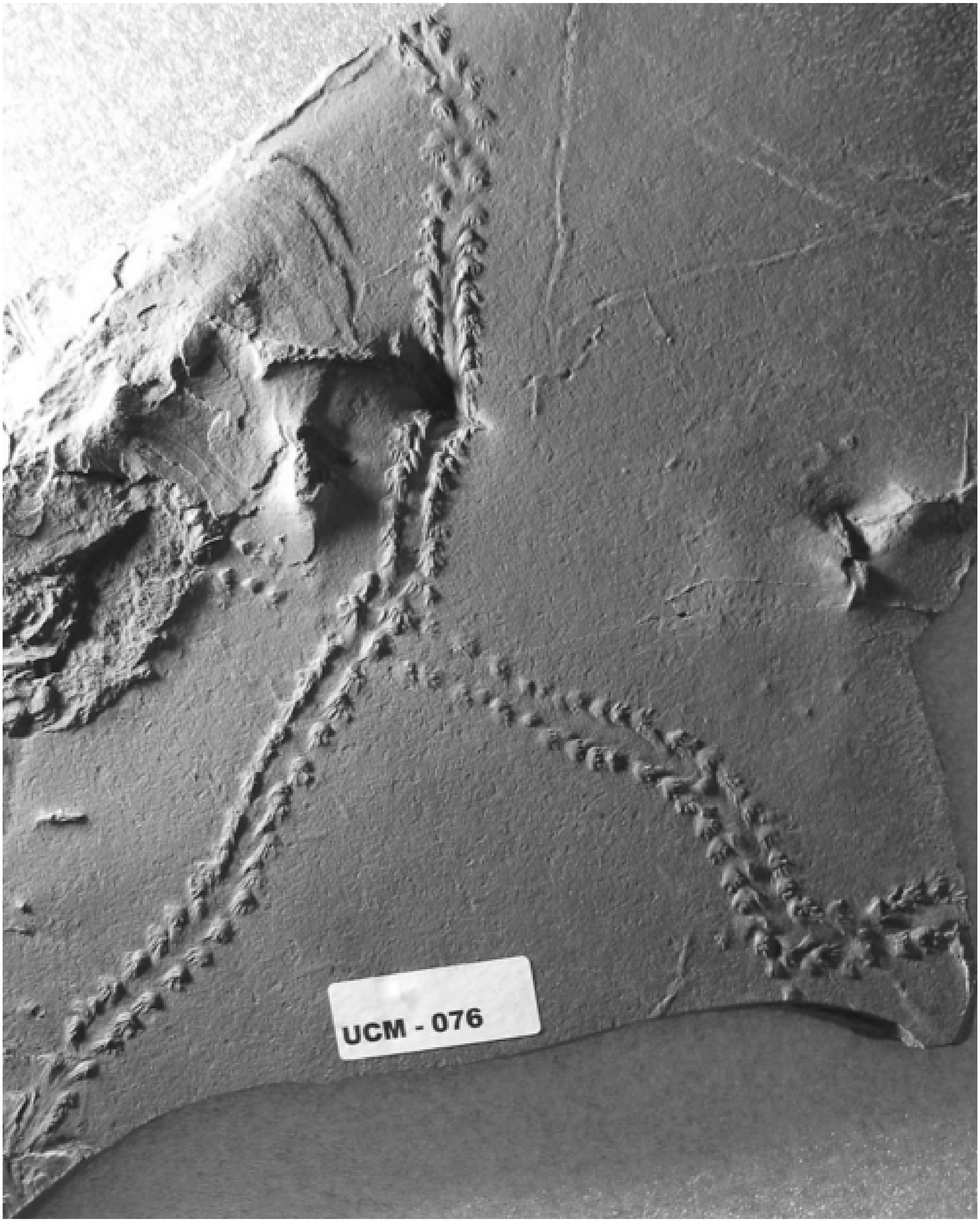

FIGURE 6. Two cross-cutting and lengthy temnospondyl trackways in UCM 76.

FIGURE 7. Variations in wavelength along a fish trail (*Undichna*), indicating changes in speed. A - UCM 1304; B - UCM 1729.

tioned previously, "belly"-drag marks also show up in a few trackways, which indirectly indicate a slowly moving animal on a sediment surface (Fig. 9). The reasons for these abrupt turns are unclear in a few examples, but two specimens have remarkable evidence for why the trackmakers turned: they were avoiding obstacles. In one example, a small trackmaker apparently bumped into and then walked around a buried xiphosuran ("horseshoe crab"), and in another example, a small trackmaker walked around a large buried plant fragment (Fig. 10). Such "stimulus-response" behaviors are rarely preserved in fossil vertebrate trackways from any geologic period, let alone in the Pennsylvanian Period (Lockley and Hunt, 1994).

Finally, one slab (UCM 1075) provides persuasive evidence for group behavior in tetrapods. On this slab are numerous shallowly impressed and overlapping medium-sized (pes about 4 cm wide, manus about 3 cm wide) tracks that were formed by at least four (perhaps five) similarly sized individuals (Fig. 11). The tracks all point in the same direction, which prompts several hypotheses: (1) multiple individuals, probably of the same species and age range, walked together or after one another on the same surface in this area at about the same time; (2) multiple individuals at different times walked through the area in a narrow landscape-induced pathway; (3) different individuals walked through the same area at different times and on different surfaces (where undertracks reached older surfaces); and (4) one individual trackmaker was repeating the same pathway in a loop. Of these, the first is the most probable because of the very similar morphology, size, direction, spacing, depth, and preservation of the tracks on what is apparently the same surface. With regard to the latter, the high sedimentation rate inferred for the Union Chapel deposit means that track formation had to have been in a relatively narrow time span (i.e., between low tide and high tide in a given cycle). If the first hypothesis is the best fit for now, it constitutes the oldest evidence for gregarious behavior in amphibians known from the geologic record. In fact, vertebrate trackways in general rarely provide convincing support of group behavior (such as herding and pack hunting), although it has been interpreted from some Permian reptile and Mesozoic dinosaur trackways (Lockley and Hunt, 1994; MacDonald, 1994).

SUMMARY

The Union Chapel site is quantitatively and qualitatively the most important in the world for vertebrate trace fossils from the Early Pennsylvanian Period. These trace fossils, which consist of numerous well-preserved fish trails (*Undichna*) and amphibian tracks (*Cincosaurus*), provide evidence for detailed interpretations of vertebrate behavior from 308 million years ago. Both fish trails and tracks were formed on mud flats of a freshwater-dominated estuary with high enough sedimentation rates that both types of trace fossils were buried quickly and preserved with considerable detail. Fish trails were likely made by relatively small, jawed fishes in shallow water (either during rising or falling tides), whereas tracks were probably made by temnospondyl amphibians during low tides, when mud flats were emergent.

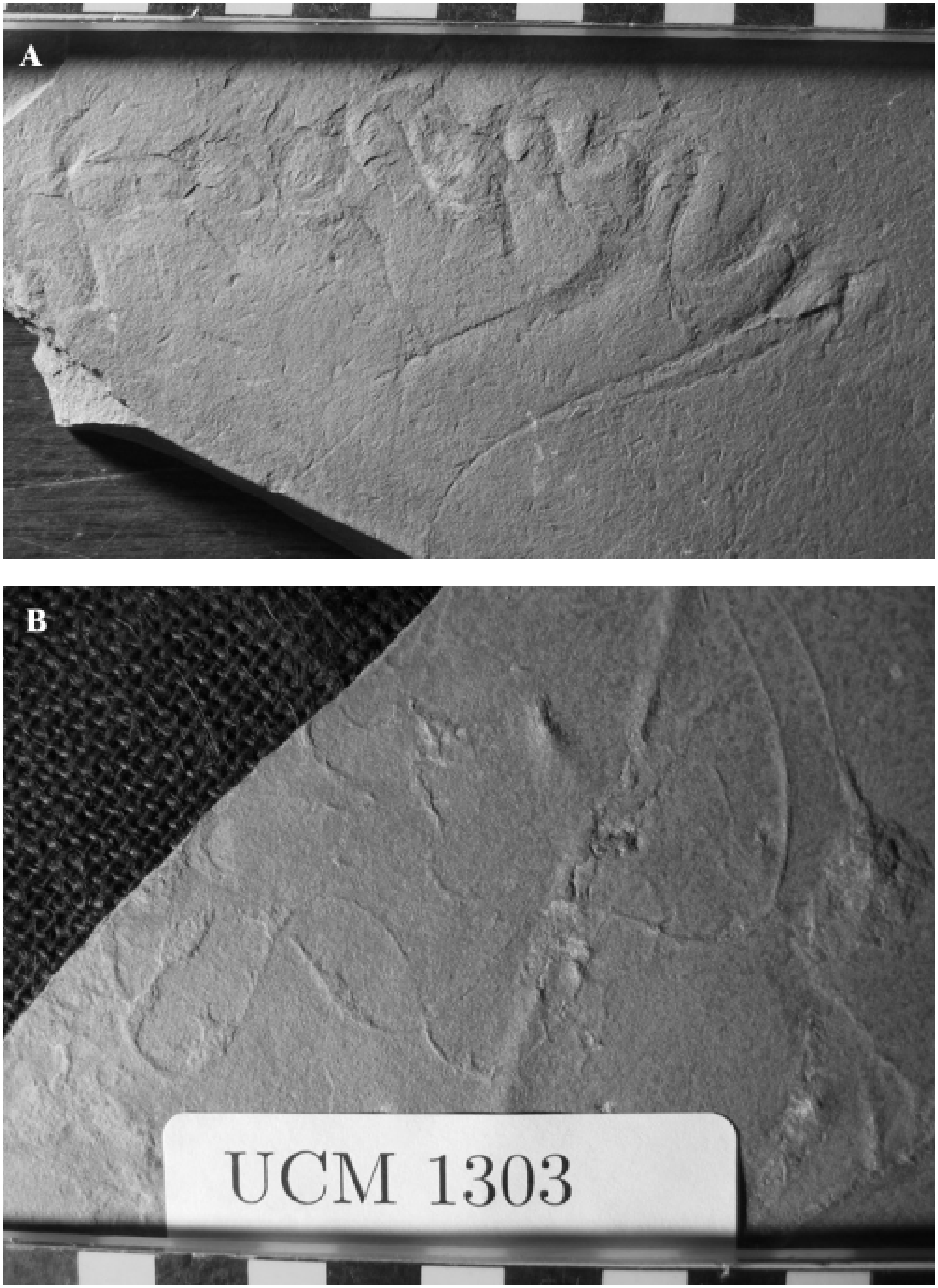

FIGURE 8. Evidence for abrupt turns of swimming fish indicated by UCM *Undichna* specimens. A - UCM; B - UCM 1303

Figure 9. Evidence for abrupt turns by trackmaker in UCM 76. Note "belly"-drag caused by trackmaking animal.

Although the number of fish species responsible for the *Undichna* specimens is unknown, we postulate that only a few species of tetrapods in various stages of its growth (juvenile to adult) made the wide size range of tracks observed in the Union Chapel deposit.

Undichna in the Union Chapel deposit are the result of caudal and anal fins that dragged along the top surfaces of mud flats, which is indicated by commonly coupled waveforms that have low amplitudes and long wavelengths. Changes in these wavelengths and sharp angles along individual trails indicate corresponding changes in swimming speed and abrupt turns, respectively. Group behavior ("schooling") is strongly suggested by parallel and overlapping fish trails on the same surfaces. These latter interpretations constitute the oldest known such behavior for fish in the fossil record.

Cincosaurus and other tracks in the Union Chapel deposit are the result of quadrupedal locomotion and show diagonal walking patterns made by a relatively sprawling gait. Trackways oftentimes have well-preserved manus and pes impressions that show varied placement in the course of any given trackway; tail-drag and "belly"-drag marks were also occasionally preserved. These traces collectively give nuanced clues about movement of the trackmakers, which include changes in speed and direction, lateral movements, obstacle avoidances, and possible group movement. Just as in the case of *Undichna* specimens, the evidence for group behavior is perhaps the oldest interpreted from the geologic record, highlighting the significance of the Union Chapel deposit for better understanding vertebrate behavior and evolution. We also hope that this study is

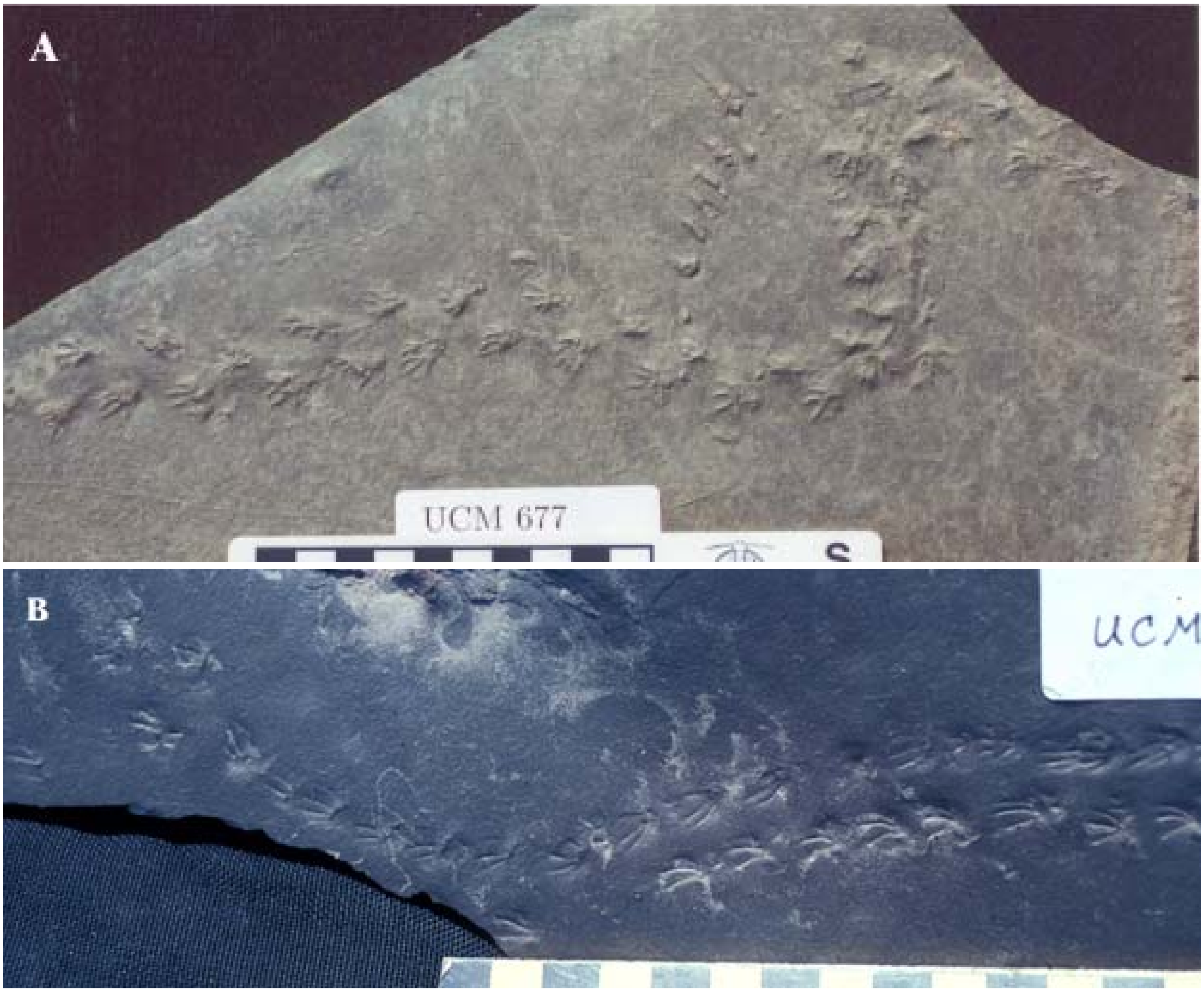

FIGURE 10. Evidence for abrupt turns by trackmakers as a result of obstacle avoidance. A - Avoiding a buried xiphosuran (UCM 677); B - Avoiding a plant fragment (UCM 484).

simply a beginning for further work that attempts to better understand vertebrate behavior as represented by Union Chapel trace fossils.

Editors' note: For additional photographs of vertebrate traces (both tetrapod trackways and Undichna*) from the Union Chapel Mine, see Haubold et al. (2005b).*

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Finally, we dedicate this paper to the paleontological legacy of Steve Minkin, who through his relentless

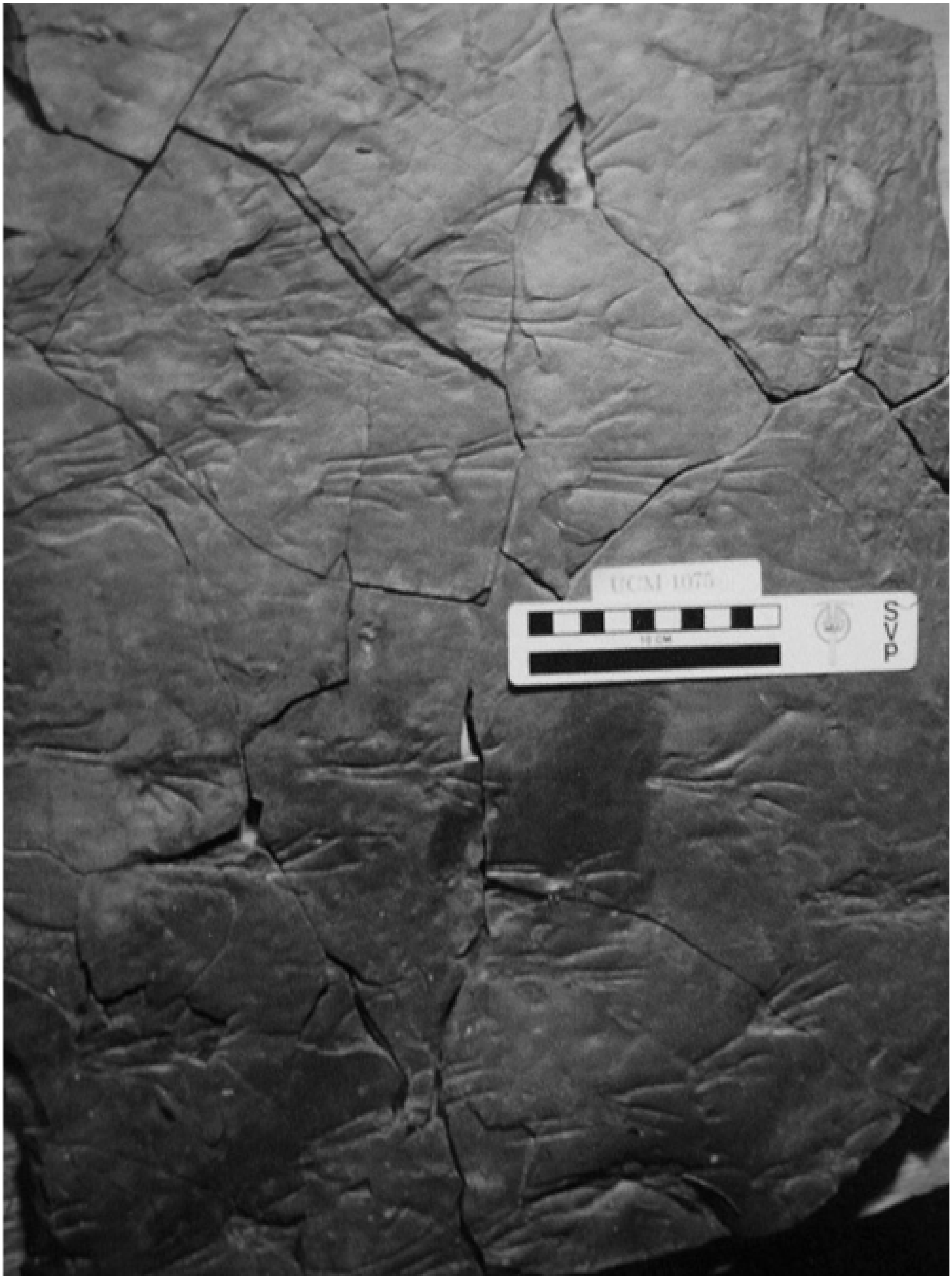

FIGURE 11. Evidence for group behavior in temnospondyls, showing multiple trackways with similarly sized tracks pointing in the same direction (UCM 1075).

scouting, collecting, cataloging, and networking provided the sparks responsible for much of the excellent science that emerged from the UCM site. We will miss him dearly but his tracks will live on.

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AUTHORS' E-MAIL ADDRESSES

Anthony J. Martin: geoam@learnlink.emory.edu
Nicholas D. Pyenson: pyenson@berkeley.edu