SEDIMENTOLOGY AND PALEOECOLOGY OF A DIVERSE EARLY JURASSIC TETRAPOD TRACKSITE IN LESOTHO, SOUTHERN AFRICA

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ABSTRACT

An Early Jurassic tetrapod tracksite in the upper Elliot Formation at Moyeni, southern Lesotho, displays a variety of trackways attributed to large- and medium-sized theropod (*Neotrisauropus*-type) and ornithischian (*Moyenisauropus*-type) dinosaurs, basal crurotarsal archosaurs (chirotheroid-type), and a short-legged basal tetrapod (*Episcopopus*-type). The tracks are on a low-angle pointbar and are buried with loessic floodplain fine-grained sediment. Calcic paleosols indicate a warm semiarid climate. Many of the footprints were imprinted through an algal mat in a water-margin setting. Convergence of several trackways toward a single point suggests repeated visits to drink or cross the river. One of the two large *Moyenisauropus*-type trackways has a narrow gauge that suggests an upright, parasagittal gait, whereas the other shows changes in gauge width, stance, and posture as it proceeded up the pointbar slope. At least three resting traces with manus, metatarsal, and tail impressions attributable to the *Moyenisauropus*-type ornithischian are also preserved. Discovery of two manus-pes pairs of chirotheroid-type footprints in the Moyeni section highlights a mismatch between the body-fossil and trace-fossil records. Chirotheroid tracks are generally thought to be restricted to the Triassic, and their discovery at the Moyeni tracksite compounds the problem of where to place the Triassic-Jurassic boundary in this succession. Three possible scenarios could explain the occurrence of chirotheroid-type tracks at Moyeni: (1) the tracksite is Late Triassic in age; (2) the chirotheroid tracks were made by archosaurs other than basal crurotarsans; (3) the tracks are correctly identified and the age of the Moyeni section is correctly assigned, but the inferred range of chirotheroid-type tracks is incorrect. We suggest that the latter two are the most likely explanations.

INTRODUCTION

Vertebrate fossils are relatively common in the Lower Jurassic upper Stormberg Group of Karoo-aged basins of southern Africa, but they are of relatively low diversity and are dominated by the prosauropod dinosaur *Massospondylus* (Kitching and Raath, 1984). In contrast, contemporaneous floodplain paleosurfaces, especially in the upper Elliot Formation, preserve diverse assemblages of tetrapod footprints that were, in their original description, ascribed to more than 56 ichnospecies (Ellenberger, 1970, 1974). These were later reduced by synonymy to 5 ichnogenera (Olsen and Galton, 1984). If it is accepted that all these tracktypes were made by different trackmakers, then they represent a much greater diversity of tetrapod taxa than is indicated by the body fossils and, thus, would be a useful source of additional information about the faunal communities at the time.

In this study, we combine sedimentological and ichnological analyses of one of these trackway sites, Moyeni (Quthing) in southern Lesotho, to test the validity of the numerous ichnospecies and learn more about the composition of Early Jurassic tetrapod faunas in southern Gondwana (Fig. 1). We demonstrate that the apparent diversity in tracktypes can be attributed to several causes other than biological diversity. Along some trackways, the footprint morphology changes with variations in media consistency and slope as well as adjustments in the locomotion of the animal.

Fossil footprints were first discovered in Lesotho in mid-1881 by French missionaries, Dr. Eugene Casalis and Rev. Robert Henry Dyke, while picnicking behind the Morija mission station (Ambrose, 2007). They found a set of large tridactyl prints preserved in epirelief on the base of a fallen block of Clarens sandstone. A few years later Frédéric Christol (1897, p. 298) described a sketch of these tracks with "petrified footprints of birds or of lizards." Recently Ellenberger et al. (2006) reported on Bushman paintings dated between 1810 and 1820 in Lesotho that depict a three-toed footprint along with painted outlines of a bipedal animal that resembles modern reconstructions of ornithopod dinosaurs. If these paintings are genuine, this would be the earliest report of dinosaur tracks in Africa.

Another French missionary, Dr. Paul Ellenberger, conducted the most extensive and thorough scientific investigation of the Lesotho dinosaur tracksites to date. From 1953 to 1970, he mapped and described 170 ichnospecies of fossil tracks from 58 sites throughout the country, mostly within the Elliot and Clarens formations, but including at least 2 from underlying Burgersdorp strata (Ellenberger, 1972, 1974). He focused on the Moyeni paleosurface in southern Lesotho, which he considered to be the most diverse Late Triassic footprint site with over 47 different track types (Fig. 1). Olsen and Galton (1984) subsequently synonymized all but one of Ellenberger's ichnotaxa with previously described tracks from Lower Jurassic strata of Europe and North America, thus reducing the number of Moyeni tracktypes to four. Following Olsen and Galton's (1984) Early Jurassic date for the Moyeni footprints, the Triassic-Jurassic boundary in the main Karoo Basin was positioned roughly midway through the Elliot Formation at a large spherical nodule horizon marking the last occurrence of such large prosauropods as *Euskelosaurus* and the first occurrence of the smaller prosauropod *Massospondylus* (Fig. 2; Kitching and Raath, 1984). In this study, we retain Ellenberger's ichnotaxa to facilitate identification of individual trackways at the Moyeni site and use the suffix -type to recognize that there are ichnotaxonomic issues that need to be clarified but cannot be addressed here.

GEOLOGICAL SETTING

The Upper Triassic to Lower Jurassic Elliot Formation is a fluvial redbed succession that accumulated in the center of the continental main Karoo Basin of southwestern Gondwana under progressively more arid climatic conditions (Eriksson, 1985). The Elliot Formation, whose provenance is mainly from the Gondwanide orogenic belt to the south, thins northward from a maximum of 480 m at the study site in southern Lesotho to <30 m in the northern Free State of South Africa
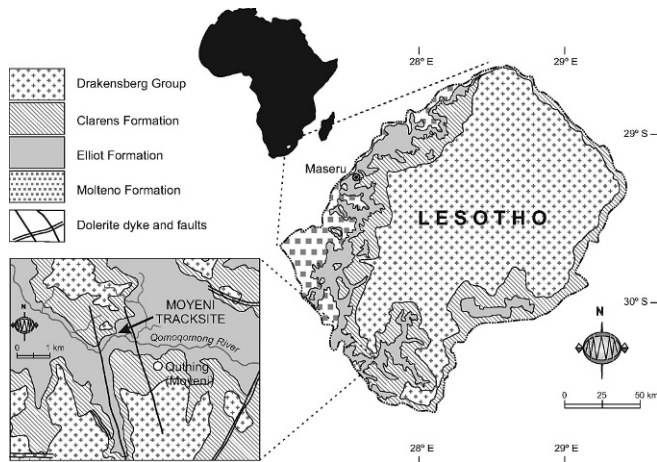
FIGURE 1—Regional geology of the Moyeni dinosaur tracksite in southern Lesotho.

(Fig. 1). Catuneanu et al. (1998) interpreted the tectonic setting of the Elliot basin as a reciprocal foresag crustal flexure landward of the east-west–trending foredeep in front of the Cape Fold Belt. They cite the rapid northward thinning of the Elliot Formation as it passes over the edge of the stable Kaapvaal Craton as evidence in support of this interpretation.

Paleontological evidence suggests that the age of the Elliot Formation ranges from Upper Triassic (Norian) for the lower Elliot strata to lower Lower Jurassic (Toarcian) for the upper Elliot strata

(Kitching and Raath, 1984). These estimates are in reasonable accordance with a single radiometric date of 183 Ma for lavas interbedded with the top of the overlying Clarens Formation (Fig. 2; Duncan et al., 1997), but the exact positioning of the Triassic-Jurassic boundary is still unresolved.

The diachronous transitional facies relationship of the Elliot Formation with underlying braidplain deposits formed in a humid climate of the Molteno Formation and the overlying ephemeral stream and barchanoid dune deposits of the Clarens Formation is highly suggestive of a continuum of laterally juxtaposed environments with an overriding climatic aridification (Fig. 2; Visser and Botha, 1980; Smith et al., 1993). The paleoenvironment represented by the Elliot Formation is interpreted as a distal arid alluvial plain dominated by rubified floodplain mudrock with thick lenticular medium and high-sinuosity channel sandstone bodies in the lower strata and more tabular crevasse-splay and multistory sheet sandstones of a flood fan–dune facies (Visser and Botha, 1980, p. 60) in the upper part. The pinkish red color is primarily due to pedogenic and early diagenetic oxidation of iron derived from ferruginous silicate and clay minerals in the alluvium (Eriksson, 1985). Toward the upper contact with the eolianites of the Clarens Formation through the so-called transition beds (Visser and Botha, 1980), the Elliot Formation is dominated by massively bedded loessic siltstone beds with columnar ped structures, vertically oriented carbonate rhizoliths and calcified fissures (Smith and Kitching, 1997). It is not uncommon to find intervals of dark grey conchostracan-bearing playa mudstones (Kitching and Raath, 1984; Bordy et al., 2004), which indicate the gradual change from the warm temperate to hot, arid conditions in this part of Pangea (Kent and Tauxe, 2005; Rowe et al., 2007).
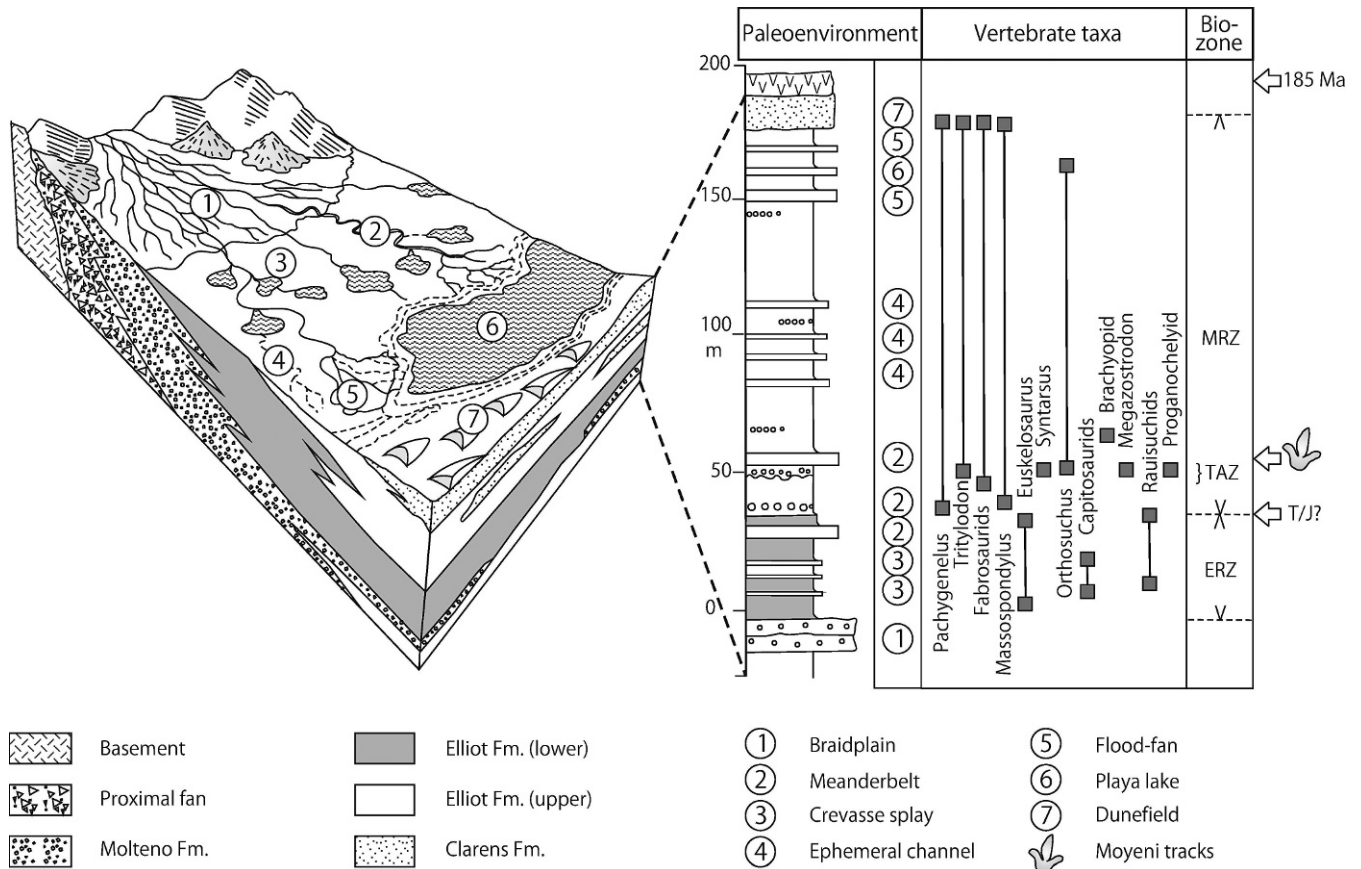

FIGURE 2—Paleogeographic setting, biostratigraphy, and lithostratigraphy of Stormberg Group in Moyeni district of southern Lesotho. Biostratigraphic ranges and zonation from Kitching and Raath (1984). ERZ = *Euskelosaurus* range zone; TAZ = *Tritylodon* acme zone; MRZ = *Massospondylus* range zone.

FIGURE 3—General view of part of Moyeni dinosaur tracksite showing ripple-marked flanks and smooth top of an elongate bar.

PALEOENVIRONMENT OF THE MOYENI TRACKSITE

Ellenberger (1974) interpreted the depositional environment of the Moyeni tracksite as an emergent elongated sandbank formed at the mouth of a river issuing into a large lake. Noting that many of the oscillation ripples were structures caused by wind shear on shallow water, he was convinced that the surface was for the most part an island surrounded by water. He was also aware of some of the overlying mudrocks having loessic characteristics and remarked on fossil desert rose structures in the playa facies. While accepting Ellenbergers's (1974) observations and interpretation as basically sound, here we interpret the sedimentary sequence below and above the paleosurface as having accumulated on the inside bank of a meander loop rather than in a lacustrine setting, with the main trackway surface preserved on one of several scroll bars making up a low-angle point bar.

The main trackway exposure at Moyeni (Fig. 3) is on the upper surface of one of several fine-grained sandstone beds that emanate from the top of a 4 m-thick sandstone body and interfinger with overlying mudrocks (Fig. 4). When followed down into the main sandstone body, the beds thicken to form one of six laterally overlapping accretion units separated by gently dipping scour surfaces. The units are from 0.5 m at the base of the sandstone to 0.15 m thick as they protrude from the top. The lower parts of each accretion unit are trough cross-bedded but pass upward into ripple cross-stratification. Where directly overlain by mudrock, the upper surface is commonly covered with small current ripple forms. In cliff-section exposures, the irregular scour surfaces at the base of each accretion unit can be traced laterally for distances of 50–60 m. From close to the base of the sandstone, these units climb upward at an angle of roughly 20° and terminate at the base of one of the sandstone tongues. These scours are interpreted as hiatal surfaces between lateral accretion events in a river with highly fluctuating flow regime; they represent one of the main indicators of deposition in meandering rather than straight or braided fluvial channels (Allen, 1963; Schumm, 1972; Shepherd, 1987).

Paleocurrent directions recorded mainly from rib and furrow structures on the tracksite surface and surrounding area (within ~150 m) show a distinct swing through nearly 160° from SSW–NE (Fig. 5). The same paleocurrent trend is indicated by the few trough cross-bedded scour fills exposed on this surface (Fig. 6A). Figure 6B shows meter-scale terrace structures on the Moyeni surface that are arcuate in plan view and elongate in the direction of paleoflow. The interference ripple structures covering their convex surface attest to bidirectional shallow water flows similar to those observed on the Usri river point bar in India (Purkait, 1983). Such a pattern of paleocurrent directions on the upper surface of a laterally accreted, fine-grained sandstone body is compelling evidence that the Moyeni tracksite is preserved on the lower slopes of a low-angle point bar, some 150 m wide, with a dip of ~20° toward the channel thalweg (Fig. 7).

Mudrocks immediately overlying the track-bearing sandstone are uncharacteristically olive-green rather than the common reddish brown that is considered to be the primary state for upper Elliot Formation mudrocks (Bordy et al., 2004). Here, the color change is almost certainly the result of contact metamorphism from a nearby dolerite sill (see base of section, Fig. 4) and does not have any paleoenvironmental significance. Evidence for semiarid paleosols in this facies includes calcified rectilinear shrinkage fissures, arcuate slickensided claystone-lined skew planes, horizons of oblate calcareous nodules sometimes reworked into shallow depressions (Smith and Kitching, 1997), rough-surfaced horizontal and vertical rhizocretions with distinctive rectilinear bends, and fossil bones commonly coated with, and rarely expanded by, hematite mineralization. This suite of paleopedogenic structures is interpreted as having formed in immature calcic vertisols (Blodgett, 1985; Gustavson, 1991), which suggests relatively fast aggradation rates on warm (mean annual temperatures of 24–27°C), seasonally wet (mean annual rainfall 500–700 mm) floodplains.

In the upper Elliot Formation, body fossils are most common in overbank red mudrocks. During this investigation, three semiarticulated *Massospondylus* skeletons and a scatter of fabrosaurid limb bones, ribs, and vertebrae were found in the Moyeni section (Fig. 4). These specimens, like most of the fossils from the upper Elliot, are preserved in 1–3-m-thick, massive loessic siltstone beds. Although lacking mature caliche horizons, these beds do display horizons of claystone-lined, columnar ped structures indicating immature vertisol development (Smith and Kitching, 1997). The articulated bones are uncrushed, nonweathered, and only lightly encrusted with a dark reddish brown hematite-rich precipitate. This taphonomic style is typical of the *Massospondylus* range zone (Kitching and Raath, 1984;
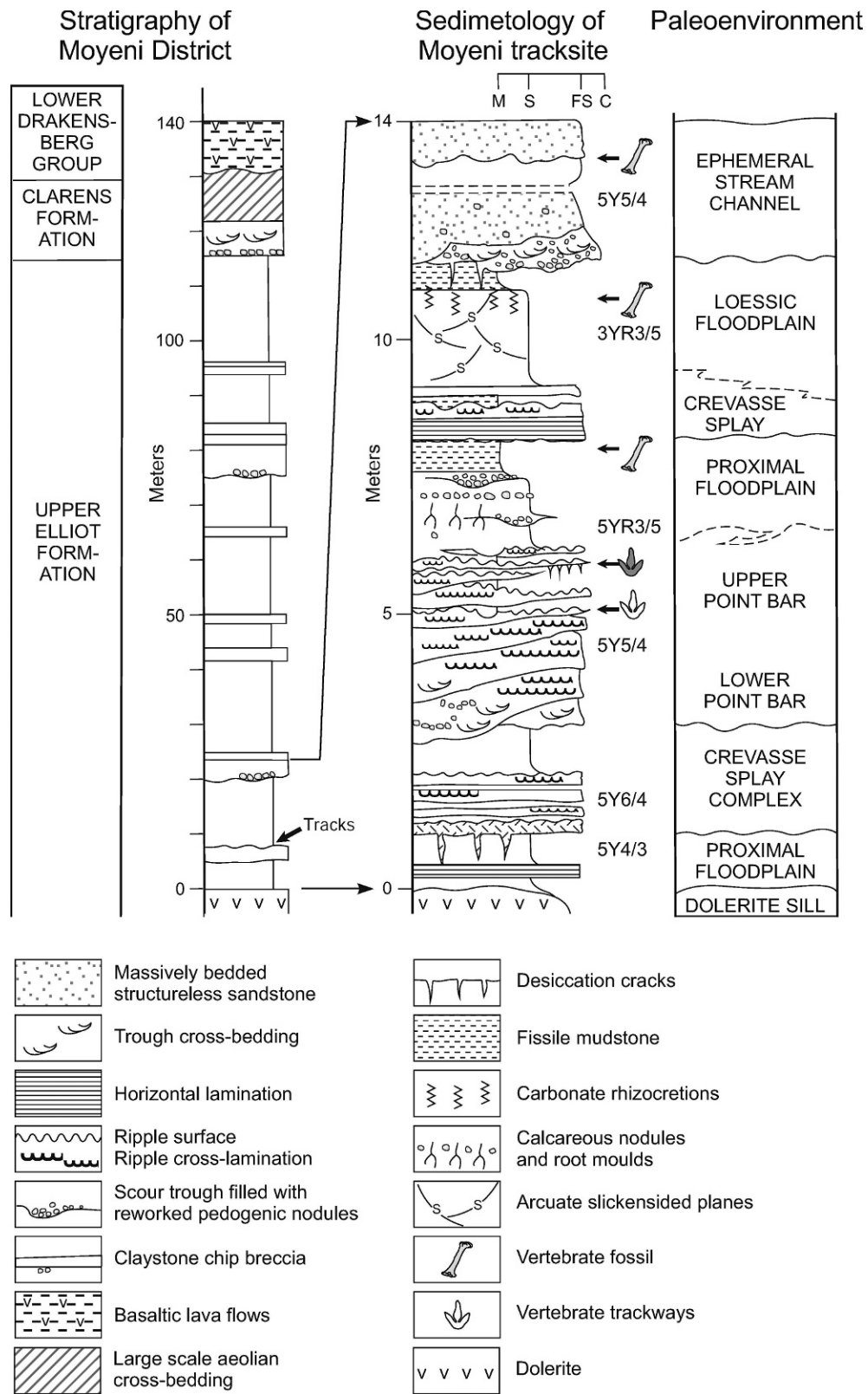
FIGURE 4—Sedimentology and interpreted depositional environment of Moyeni dinosaur tracksite.

Fig. 2) and confirms that the floodplain habitat of these relatively small herbivorous prosauropod and basal ornithischian dinosaurs was periodically covered with a thick layer of windblown dust. These dust storms rapidly buried skeletons exposed on the surface, and by increasing the floodplain accretion rate, they effectively prevented the soil profiles in this facies from reaching maturity.

SEDIMENTOLOGY AND ICHNOLOGY

The Depositional Event

The Moyeni paleosurface, like many others in the Elliot Formation, was deposited during a single flood event followed by a brief period of
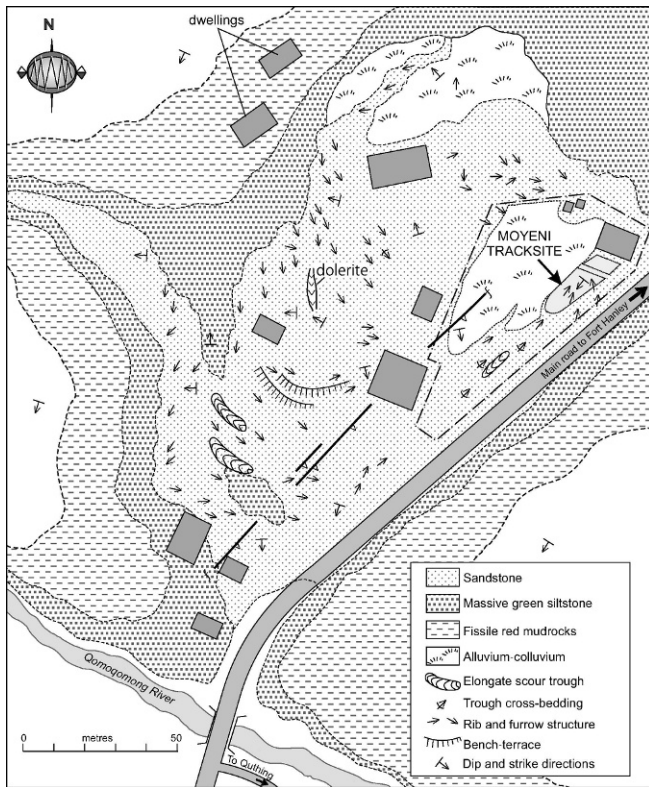
FIGURE 5—Sedimentation of Moyeni tracksite sandstone; paleocurrent directions measured from exposures of track-bearing sandstone surrounding Moyeni tracksite.
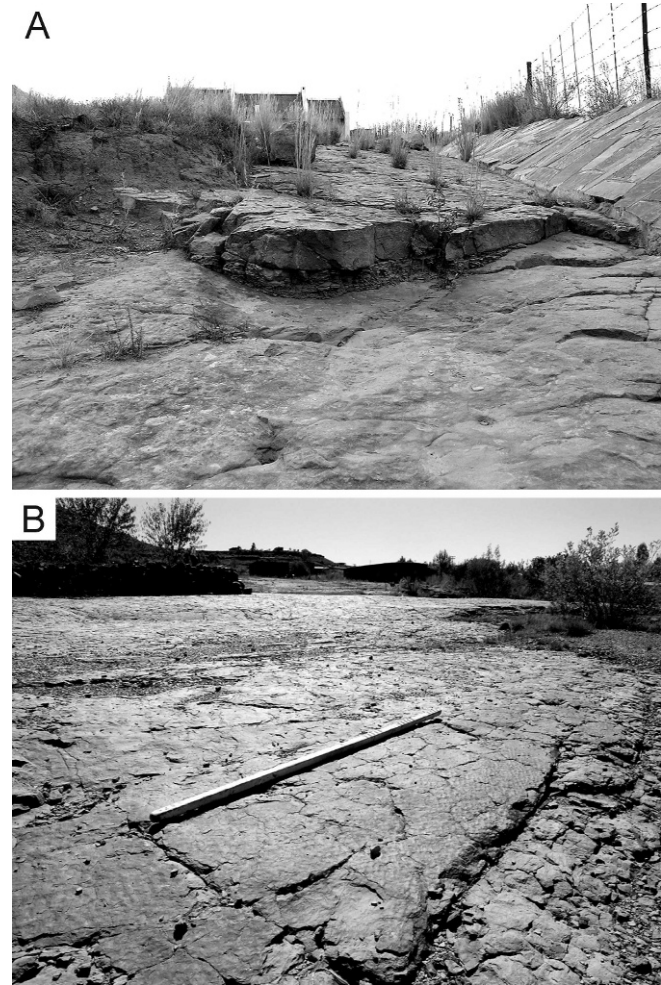

FIGURE 6—Sedimentation of Moyeni tracksite sandstone; A) Trough cross-bedded sandstone filling an elongate scour immediately beneath track-bearing surface ~25 m southwest of tracksite (see Fig. 5). Scour measures 10.5 m long by 1.6 m wide. B) Ripple-marked crescentic bar with falling water-level terraces located on top of same point bar as tracksite. See Figure 5 for exact location. Staff = 1 m long.

emergence when the sedimentary bedforms were overprinted with runoff, falling water level, and desiccation features, as well as a wide range of vertebrate and invertebrate tracks and trails before being buried in a similar flood event. Like a snapshot of the ancient floodplains, they contain valuable information of the fluvial hydrology, sedimentation, local climate, and biological activity.

Figure 8 is a compilation of the sedimentary structures and invertebrate trace fossils visible on the surface of the Moyeni scroll bar. The exposure has an elongate, flat-topped convex bar form with a northeast-southwest trend and sloping surfaces dipping ~25°. Asymmetrical, small current ripples, parting lineation, and small-scale trough cross-bedding (Fig. 8) all indicate a northeasterly unidirectional flow for the main depositional event interpreted as the waning stages of a channel-confined flood surge. Straight to mildly sinuous-crested ripple forms are preserved all along the lower slopes of the bar. Above the rippled zone is a smooth surface where most of the finely imprinted invertebrate traces are visible. Over the flat bar top, the sandstone has a distinctively pustular surface texture (Fig. 8), and it is in this zone that most of the vertebrate footprints are preserved.

It is likely that during peak discharge, as the transverse barform migrated onto the point bar, it was entirely covered with ripples. Only during waning flood did the sand surface become modified into these 3 zones where shoaling caused washout of the bar-top ripples, followed by emergence and runoff. Dendritic rills and semicircular patches of wrinkle marks preserve evidence of the latter (Fig. 9A). It is possible that the dish-shaped wrinkle structures are undertracks but as they are not paired or regularly spaced, this seems unlikely. The absence of desiccation cracks and comparison with similar emergence features in modern arid zone rivers (e.g., Kuiseb River in Namibia, Ward, 1987; Smith, 1993) makes it likely that the Moyeni paleosurface was only exposed for 10 days or so. The pustular surface texture on the bar top is superficially similar to adhesion warts or runzel marks imparted by wind shear on exposed damp sand (Reineck and Singh, 1975). Closer

inspection, however, shows the texture to be smoother and more regular than that normally associated with wind action. An alternative explanation is that the surface was sculptured by drying and shrinking of a *Spirogyra*-like algal mat that was lowered onto bar top as the water level dropped and formed Kinneya-type wrinkle structures (Porada et al., 2008) on the underlying sand surface. The latter interpretation implies one or two periods of restricted flow or ponding of water in a swale setting, allowing time for the algae to propagate. Such slack-water conditions are evidenced by a very fine grained sand veneer that has settled out of suspension onto the bar surface and in which the runoff rills, wrinkle marks, and invertebrate trails were subsequently preserved. Sand volcanoes (Fig. 9B) that erupted on the flanks of the bar at this time were probably caused by methane gas escaping from anaerobic decomposition of buried organic matter.

Invertebrate colonization of the bar began while it was still partially submerged. Sinuous, threadlike grooves on the surface are interpreted as the feeding trails of nematodes and distinctive beaded trails (c.f. *Homosiroidea meandrica*; Fig. 9D) probably imply the foraging behavior of aquatic isopods (Netto et al., 2009) or possibly insect larvae (Chamberlain, 1975). These are common elements of the subaqueous freshwater *Mermia* ichnofacies (Buatois and Mángano, 1995); however, these types of traces have been observed in moist terrestrial sediments rather than in ephemeral pools of standing water (Hasiotis, 2008) and suggest terrestrial conditions in ancient deposits
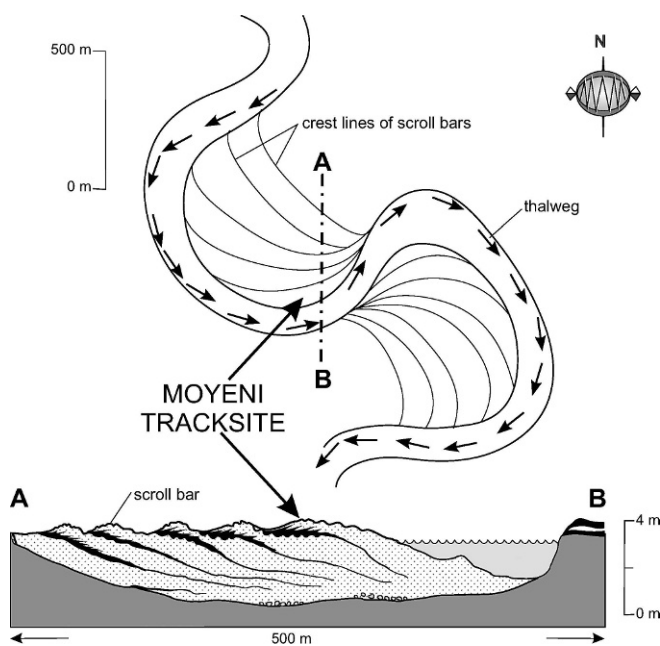
FIGURE 7—Reconstruction of interpreted position of Moyeni tracksite on ancient point bar.

(e.g., Hasiotis, 2004). As interstitial water drained from the exposed bar top, it was colonized by scratch burrowers, probably scarabaeid beetle larvae, that foraged for organic fines in the sediment and left behind numerous unlined, backfilled, meniscate burrows referable to the ichnogenus *Naktodemasis* (Figs. 8, 9C; Smith et al., 2008; Counts and Hasiotis, 2009).

Tetrapod Activity

More than 250 tetrapod footprints and trackways are preserved on the Moyeni exposure, all as natural molds, and have no preferred direction of movement. In this study, the entire exposed surface was mapped using a 1 m-square grid, and all preserved footprints were individually drawn to a scale of 1:10 (Fig. 10). Footprints are more abundant and particularly well preserved on the algal-mat-bound

surface of the bar top, although several trackways continue downslope into the ripple-marked area of the bar. Many of the tracks are superimposed, indicating the area was visited frequently over a short period of time. Analysis of the alignment of the main trackways indicates three separate points where a number of trackways both converge and radiate, suggesting repeated visits to these particular spots.

Neotrisauropus-Type Footprints.—Numerous large footprints form a single trackway tangential to the length of the scroll bar (Fig. 10). The footprints are tridactyl, elongate, and digit III projects farther anteriorly than digits II and IV (Fig. 11). The well-preserved pads of the digits imply a 3–4–5 phalangeal formula; there are no traces of digit V or the metatarsus. Impressions of digits II–IV bear distinctively pointed claw marks. The trackway consists of 25 consecutive tridactyl prints with an average pes print length of 28 cm. The long axes of the relatively narrow tracks parallel to the midline and the average divarication angle between digits II and III and III and IV is 25°. *Neotrisauropus*-type tracks were made by an obligatory-bipedal, functionally tridactyl animal in which the foot impressions almost lie on a straight line. Track dimensions give a calculated hip height of ~1.4 m (Thulborn, 1989; Henderson, 2003). The parasagittal gait, tridactyl footprints with a distinct divergence between digit IV and digits II and III and pointed claw marks support the hypothesis that the *Neotrisauropus*-type footprints were made by theropod dinosaurs (J. Wilson, personal communication, 2009).

The ichnotaxon *Neotrisauropus* was erected by Ellenberger (1970, 1974) to include a series of relatively large tridactyl bipedal footprints from several sites in Lesotho, including the Moyeni site. It was subsequently synonymized with *Grallator* by Olsen and Galton (1984).

Moyenisauropus-Type Footprints.—The Moyeni assemblage includes at least two long trackways representing facultative bipedal progression (Fig. 12A). These trackways were made by trackmakers similar in size to *Neotrisauropus*, with an average footprint length of 22 cm. Pes prints are functionally tridactyl, but impressions of digit I and the metatarsus are present in some tracks. The footprints are rotated inward (~20°) with respect to the trackway midline. Internal digits (II, III, IV) of the pes are relatively broad, spread apart, and bear blunt unguals. In contrast with the *Neotrisauropus*-type footprints, pedal digit II is commonly divergent from digits III to IV. *Moyenisauropus* manus prints are much smaller than the pes, pentadactyl, rotated outward, and generally imprinted in front of and slightly external to the pes prints
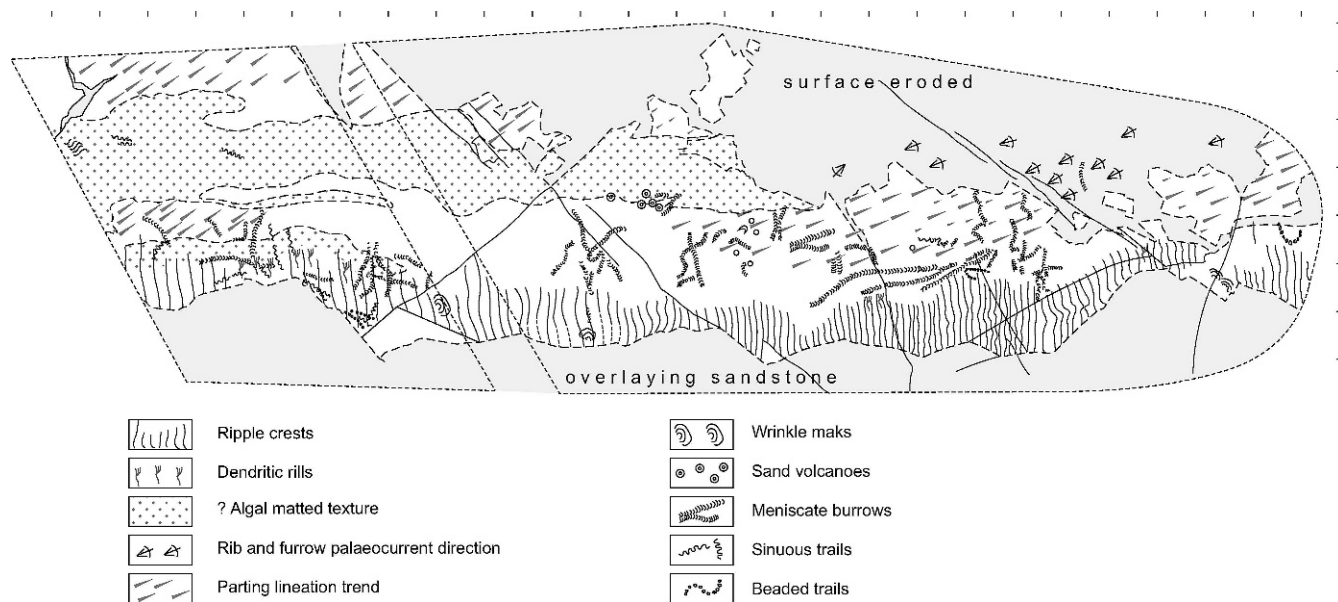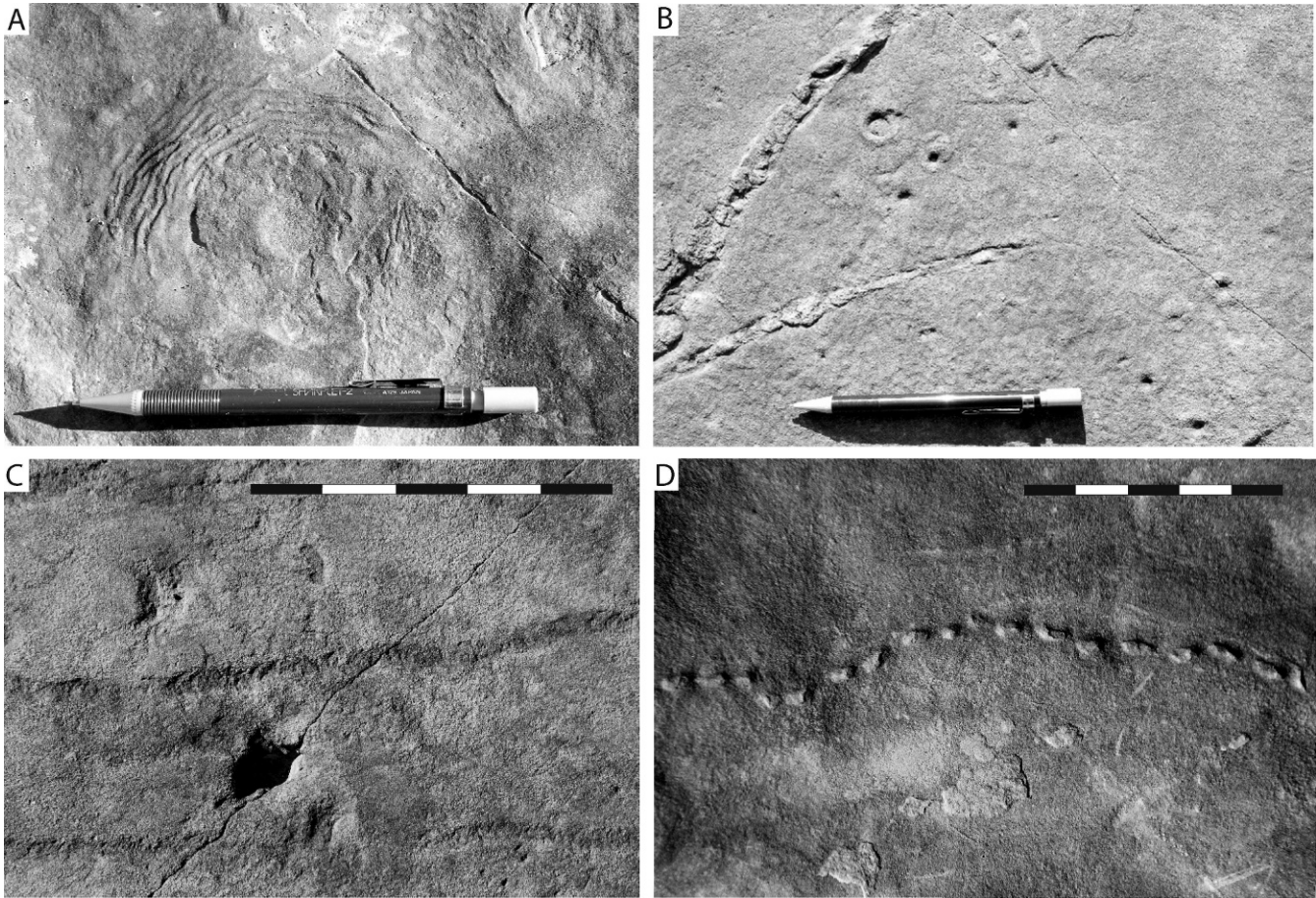

FIGURE 8—Distribution of sedimentary structures, emergence features, and invertebrate trace fossils on Moyeni paleosurface. Tick marks in meters.

FIGURE 9—Emergence features and invertebrate trace fossils on Moyeni trackway surface. A) Wrinkle marks in very fine sandstone veneer covering rippled portion of bar surface are evidence of a short period of subaerial exposure. B) Sand volcanoes probably caused by methane escaping from decomposing organic debris while scroll bar sand was still saturated. Pencil = 15 cm. C) Colonization of sediment after emergence by such scratch digging arthropods as beetles is evidenced by widespread occurrence of backfilled meniscate burrows (c.f. *Naktodemasis*) on many of the upper Elliot Formation paleosurfaces. Scale = 1 cm intervals. D) Beaded trails (c.f. *Hormosoroidea*) are interpreted as surface foraging traces (fodinichnia) of such organisms as isopods or insect larvae. Scale = 5 mm intervals.

(Fig. 12A). Manual digits are subequal in length and have blunt ends. Digital pads are not clear in the tracks, so it is not possible to infer manual or pedal phalangeal formulae. One of the two large *Moyenisauropus*-type trackways shows a relatively high pace angulation (average 160°), which suggests a narrow-gauge, upright, parasagittal gait. In contrast, the other shows a change in gauge-width, stance, and posture over the course of 17 steps. Early in the progression, the trackmaker walks with a quadrupedal, wide-gauge gait, but it changes to a narrow gauge (parasagittal) quadrupedal gait and eventually to a narrow-gauge, fully bipedal gait (J. Wilson, personal communication, 2009). In both of these *Moyenisauropus*-type trackways, estimated hip height of the trackmaker (Thulborn, 1989; Henderson, 2003) is ~1.2 m.

The Moyeni surface also includes numerous smaller tridactyl footprints, arranged in bipedal trackways that resemble the *Moyenisauropus*-type pes tracks in the absence of pointed unguals, the presence of three weight-bearing digits that are relatively broad and widely spread, digit II divergent from the two other digits, and pedes slightly rotated inward relative to the midline of travel. The footprints vary in length from 10–20 cm (Fig. 12B).

On the algal-mat-bound bar top in the northeastern portion of the trackway surface (Fig. 10), at least three resting traces attributable to the *Moyenisauropus*-type trackmaker are preserved (Fig. 13). In each case, the long axis of the manus and pes are parallel to one another and there is an associated, clearly defined tail impression. The pes prints are
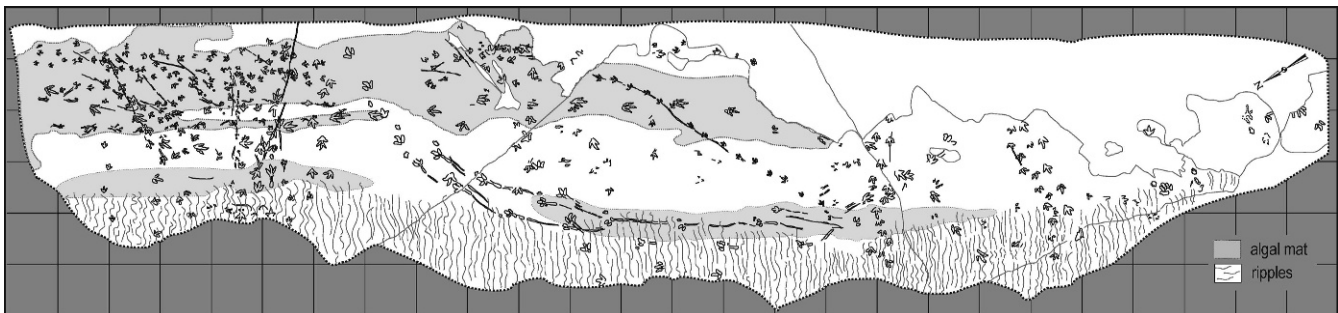
FIGURE 10—Map of tetrapod tracks on Moyeni paleosurface; note that densest cluster of small tridactyl prints is preserved on bar top in algal-mat–bound area. Grid lines = 1 m.

FIGURE 11—*Neotrisauropus*-type footprints. Field photograph of a theropod left pes impression. Note how pustular surface texture has been destroyed by footprint, suggesting that this surface was covered by a thin algal mat at time animal walked along scroll bar. Scale bar = 25 cm.

symmetrical and preserve impressions of the three main digits (II–IV), a small digit I, and a prominent metatarsus. The pes digit impressions have pointed unguals, whereas their associated manus prints are smaller, pentadactyl, rotated outward, and do not bear ungual traces. There is no trace of pelvic structures preserved between the hind feet. Tail impressions have a U-shaped cross section, the proximal ends are rounded, and the distal ends taper and shallow gradually to a point. Two of the resting traces may have been made by the same animal, shifting its position slightly between impressions. The third was made by a different individual that faced the opposite direction. The individuals that made these resting traces are smaller than the two *Moyenisauropus*-type trackways described above, with an average pes length of 14 cm.

The *Moyenisauropus*-type footprints are attributed to basal ornithischian trackmakers on the basis of a symmetrical, functionally tridactyl foot with blunt unguals and a pentadactyl manus having subequal digits with gently rounded tips, thus lacking enlarged or sharp unguals (J. Wilson, personal communication, 2009). The ichnotaxon was erected by Ellenberger (1970), who recognized several different ichnospecies that were later synonymized by Olsen and Galton (1984) with *Anomoepus*, a position also followed by Olsen and Rainforth (2003) in their more recent review of *Anomoepus*. Ellenberger (1974) acknowledged that the ichnogenus *Moyenisauropus* includes a good deal of variation and requires further research, which is now in progress by us.

Chirotheroid-Type Footprints.—The Moyeni surface preserves two different track types that exhibit obligate quadrupedal locomotion. One is represented by the relatively wide, sprawling *Episcopopus*-type trackway with a central body impression. The second is a chirotheroid-type in which the pes prints are significantly larger than the manus,

pentadactyl, asymmetrical, and also bear a prominent posterolaterally everted digit V.

There are only two sets of manus-pes impressions of this type on the southwestern end of the surface, which is an area that was not mapped by Ellenberger (1974). The two manus-pes sets are not part of the same trackway. The best-preserved set is a left manus-pes pair that is deeply impressed into the sediment, suggesting both the hind and forelimbs bore weight during the step cycle (Fig. 14). The manus is strongly rotated outward in relation to the pes and relatively smaller; it is positioned just in front of and slightly external to the pes impression. The manus is tetradactyl, with subequal digits and blunt claw marks; digit pads are not discernible. The pes is pentadactyl and asymmetrical; digits I–IV are anteriorly directed, and digit V is strongly everted. Digits III and IV are similar in length, diminishing in size toward digit I, which is the shortest of the series. Digit V is also short, everted, and has blunt claw marks. Pedal digit pads are clearer than in the manus and suggest a pedal phalangeal formula of 2–3–4–4–2 (see Parrish, 1989).

The chirotheroid-type tracks at Moyeni represent a medium-sized, quadrupedal animal with an asymmetrical pes and manus. The stout digit V and phalangeal formula suggests they were probably made by a basal crurotarsan archosaur (Marsicano et al., 2005), as has long been suggested for other chirotheroid-type tracks (e.g., Haubold, 1986; Parrish, 1989; Lockley and Meyer, 2000).

Episcopopus-Type Footprints.—This trackway runs diagonally across the northeastern half of the surface and exhibits a consistent manual and pedal stride length (~60 cm), suggesting that the trackmaker maintained a constant speed (Fig. 15A). The trackway is relatively wide (~34 cm) with shallow footprints; in places, a conspicuous smooth body impression with slightly sinuous borders is evident. The pes and manus prints are apparently pentadactyl, equivalent in size (~13 cm width), and only the tips of the digits are printed on the surface. Claw marks are absent in both manus and pes (Fig. 15B). The most distinctive feature of this trackway is the presence of drag marks left by both the manus and pes prints during progression. The manus drags make a pronounced S-shaped impression, whereas the pes digits form an outward curving arc that partially overprint the manus drags (Fig. 15).

The identity of the *Episcopopus*-type trackmaker remains unresolved. The available information derived from the trackway indicates that the animal moved with a sprawling gait and probably had short limbs that allowed its body to touch ground during the step cycle. Ellenberger (1974) originally described *Episcopopus*, and it is the only one of his so-called upper Stormberg ichnogenera that Olsen and Galton (1984) regarded as valid. Ellenberger (1974) attributed *Episcopopus* to a chelonian trackmaker, an identification that was followed by Olsen and Galton (1984). The absence of definite claw marks in the footprints, however, excludes chelonians as candidates for the trackmaker. We have collected high-resolution, three-dimensional laser scans of the *Episcopopus*-type trackway and are currently working to identify the trackmaker and describe its locomotion.

DISCUSSION

The upper Elliot Formation body fossil fauna has several archosaur taxa, including the small, gracile noncrocodylian crocodylomorphs (sphenosuchians) and crocodyliforms (protosuchids), and dinosaurs. Such small- to medium-sized forms as the basal theropod *Syntarsus* (=*Coelophysis* Bristowe and Raath, 2004), the ornithischians *Lesothosaurus* and *Heterodontosaurus*, and the sauropodomorph *Massospondylus*, which is the most common fossil tetrapod in this interval, characterize the dinosaur fauna (e.g., Kitching and Raath, 1984; Lucas and Hancox, 2001; Rubidge, 2005). The only relatively large dinosaur from the upper Elliot Formation is the recently described theropod *Dracovenator* (Yates, 2005), which is the potential *Neotrisauropus*-type trackmaker. Associated fauna include primitive chelonians (*Australo-*
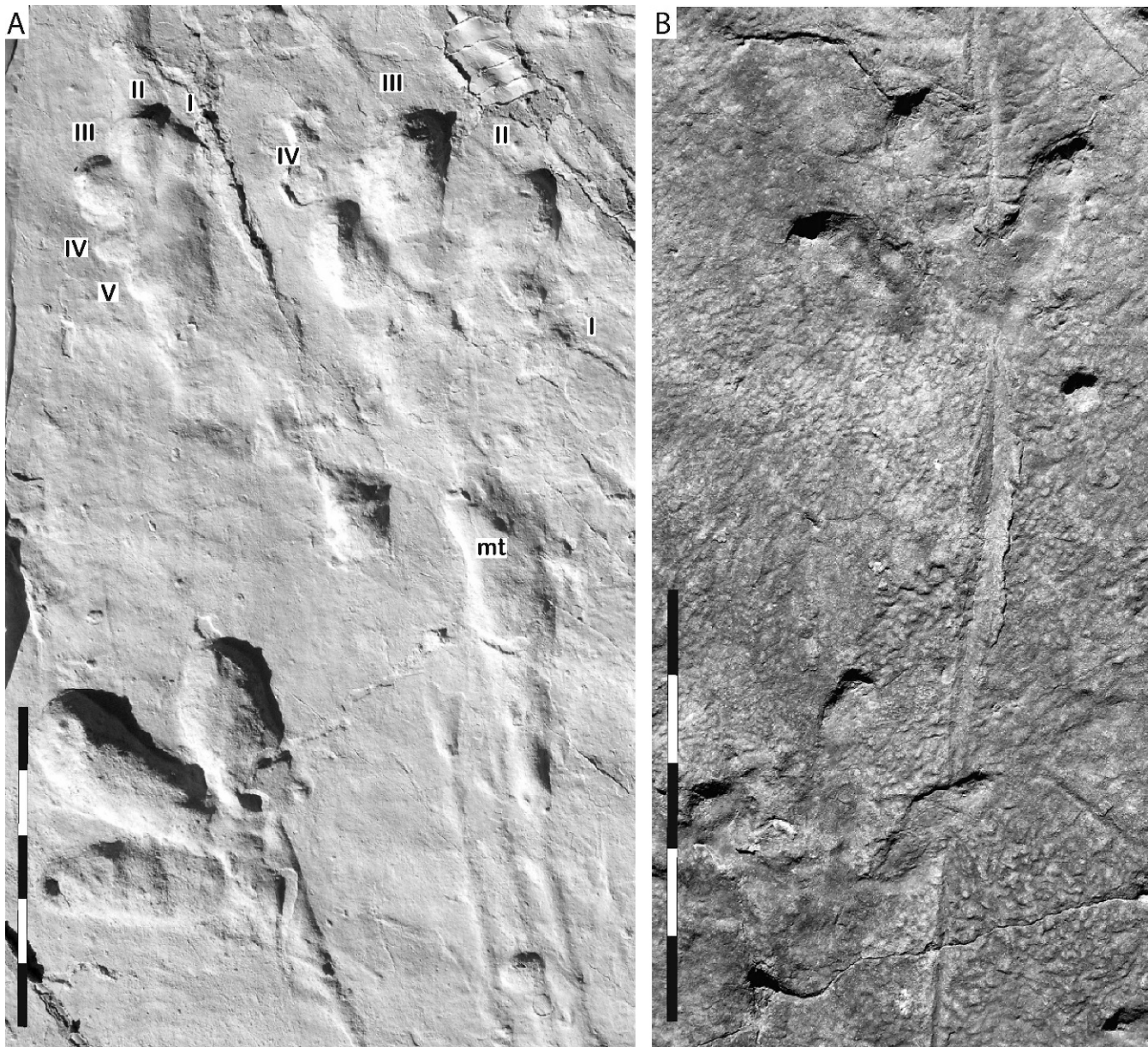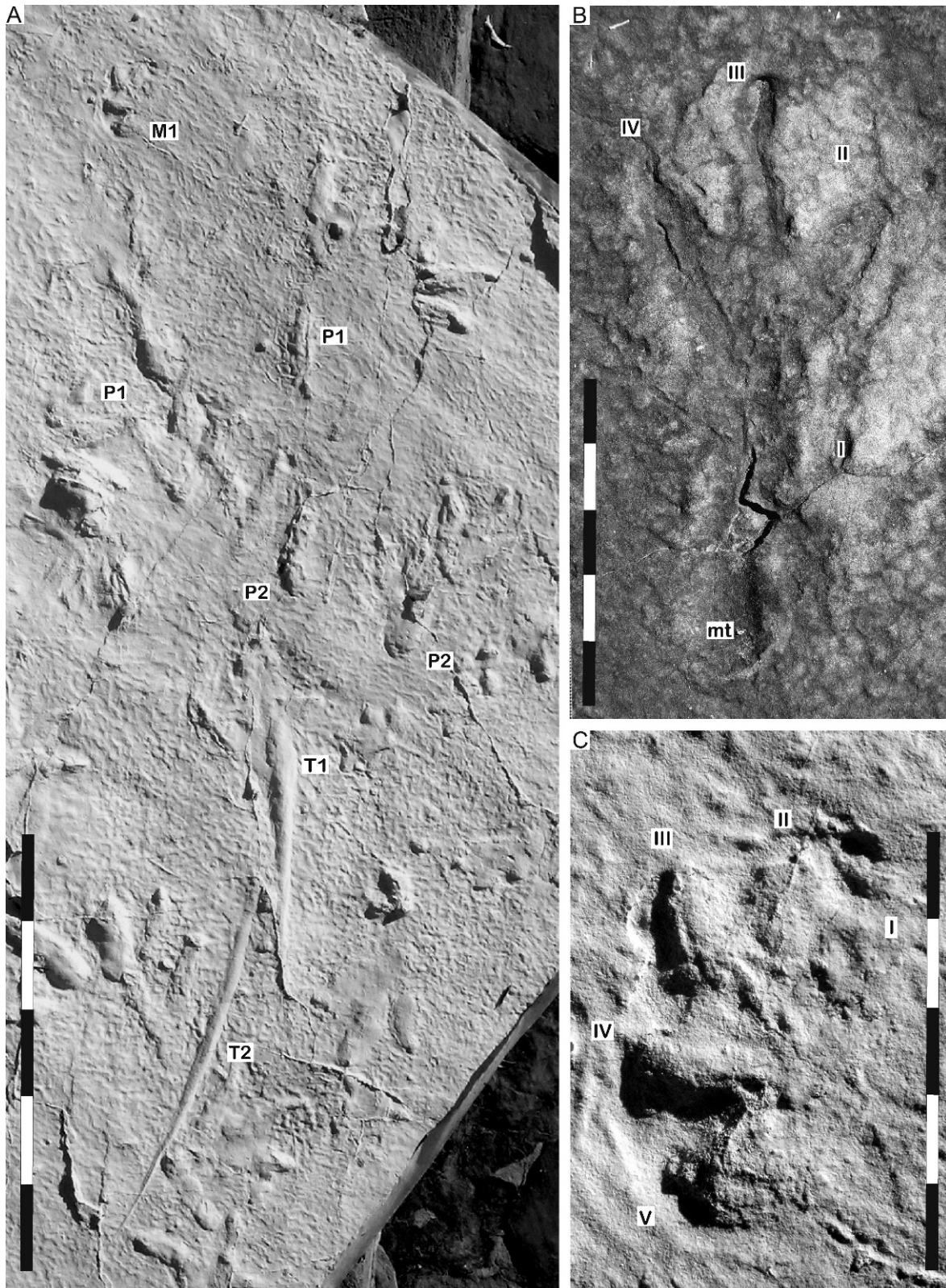
FIGURE 12—*Moyenisauropus*-type footprints. A) Plaster of Paris cast (positive) of a left manus-pes set illuminated from bottom left; tridactyl print lower left is part of a bipedal trackway with the same pes impression. Digits are identified with Roman numerals; mt = metatarsal impression. Scale bar = 10 cm. B) Field photograph of two consecutive *Moyenisauropus*-type pes prints on the algal-matted portion of the bar. Note that the feet are rotated inward and have overprinted an impression interpreted as a tail drag mark. Scale bar = 25 cm.

chelys), temnospondyls (Chigutisauridae), and numerous therapsids, including trithelodontids, tritylodontids, and basal mammals (e.g., Kitching and Raath, 1984; Lucas and Hancox, 2001; Rubidge, 2005). The Moyeni surface contains tridactyl footprints and trackways of bipeds, facultative bipeds, and quadrupeds. For the most part, the Moyeni trackways reflect the known fauna. There are some distinctive trackmakers, however, that are apparently not represented in the body fossil record. These include relatively large ornithischian dinosaurs (the large *Moyenisauropus*-type trackmaker) and relatively stout basal crurotarsal archosaurs (the chirotheroid-type trackmaker). In addition, the abundant fossils of the sauropodomorph *Massospondylus* are not mirrored in the trackway record. In fact, none of the footprints on the Moyeni surface could be confidently attributed to sauropodomorphs.

If the relative abundance of different track types is used as a rough indication of the original population dynamics, then *Neotrisauropus*-type and *Episcopopus*-type trackmakers are the least common, followed by

chirotheroid-type trackmakers, with the *Moyenisauropus*-type basal ornithischian being by far the most abundant. The *Episcopopus*-type trackway is superimposed by both the *Moyenisauropus*-type and *Neotrisauropus*-type prints, the last being the most recently imprinted tracks on the surface. It is also noticeable that the definition of the digit impressions generally improves through the overprinting sequence, which implies progressive drying and firming of the fine-grained sand after emergence. It is, thus, possible that the absence of claw impressions in the many *Moyenisauropus*-type tracks is due to them having been made in wet, fine-grained sand that deformed thixotropically under pressure of the planted foot rather than by a clawless animal.

Regarding what the animals where doing in this area, it is clear that most of them were walking rather than running, and there is no single preferred direction to the Moyeni trackways. Analysis of the alignment of the main trackways, however, indicates three separate points where a number of trackways both converge and radiate. Two foci lie on the

FIGURE 13—*Moyenisauropus*-type resting traces. A) Plaster of Paris cast (positive) of two *Moyenisauropus*-type resting traces, which include manus prints (M), pes prints (P), and tail drags (T); lighting from top right. Scale bar = 50 cm. B) Field photograph of natural mold (negative) of right P2 on A; mt = metatarsal impression. Scale bar = 25 cm. C) Detail of natural mold of M1. Scale bar = 10 cm.

inferred channel side of the bar form, ~18 m apart, and the third lies on the inner bank side of the bar. This suggests that the trackways are not strictly randomly oriented and may indicate repeated visits to access drinking or river crossing points.

The presence of chirotheroid-type footprints at Moyeni is potentially of biostratigraphic significance because of their widespread use as Triassic index fossils (e.g., Lockley and Meyer, 2000; Olsen et al., 2002; Klein and Haubold, 2007; Lucas and Tanner, 2007). Three possible
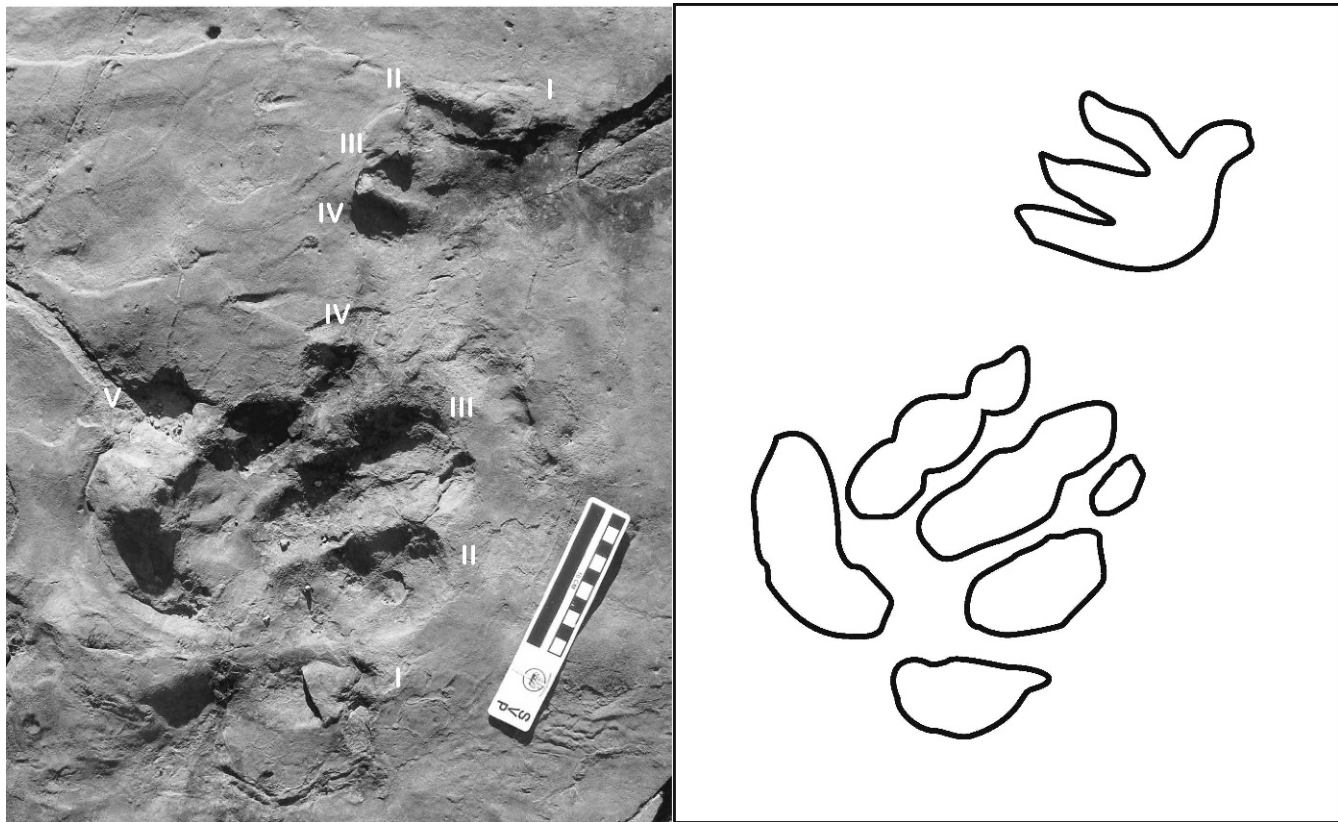
FIGURE 14—Chirotheroid-type footprints. Field photograph and interpretive outline of a left manus-pes set. Roman numerals indicate digit numbers. Scale bar = 10 cm.

scenarios could explain their presence in this assemblage. First, the upper part of the Elliot Formation could be wrongly dated as Lower Jurassic and should be reassigned an Upper Triassic age. If this is proven correct, then this would bring all the associated fauna, including the chelonians and basal mammals, into the Late Triassic. Second, the tracks could be misidentified, and could actually belong to an ichnotaxon that is known from the Jurassic. Although we have only two manus–pes pairs, we are confident that their morphology is consistent with that of chirotheroid-type tracks described elsewhere. The third explanation is that the tracks are correctly identified and the age is correctly assigned, but the inferred range of chirotheroid-type tracks is incorrect. Deciding which scenario is correct has important implications for understanding the patterns of diversification of the Gondwanan tetrapod faunas during the early Mesozoic and the magnitude of the putative tetrapod faunal extinction at the Triassic-Jurassic boundary (e.g., Benton, 1994; Lucas and Tanner, 2007) in this part of Gondwana.

CONCLUSIONS

Our reappraisal of the Early Jurassic dinosaur tracksite at Moyeni in Southern Lesotho highlights the advantages of combining sedimentological, ichnological, and biomechanical approaches to the field investigation of vertebrate trackways. The main findings of this study are as follows.

1. The Moyeni trackway surface, previously thought to be a lake shore, is reinterpreted as a gently dipping pointbar surface with ridge and swale topography on the inner bank of a river meander. Moist conditions associated with early emergence are implied by a very fine-grained veneer with terrestrial invertebrate traces. Many of the smaller tracks are imprinted into Kinneya-type wrinkled textures on top of the elongate bar form and were probably preserved as undertracks beneath a thin layer of filamentous algae.
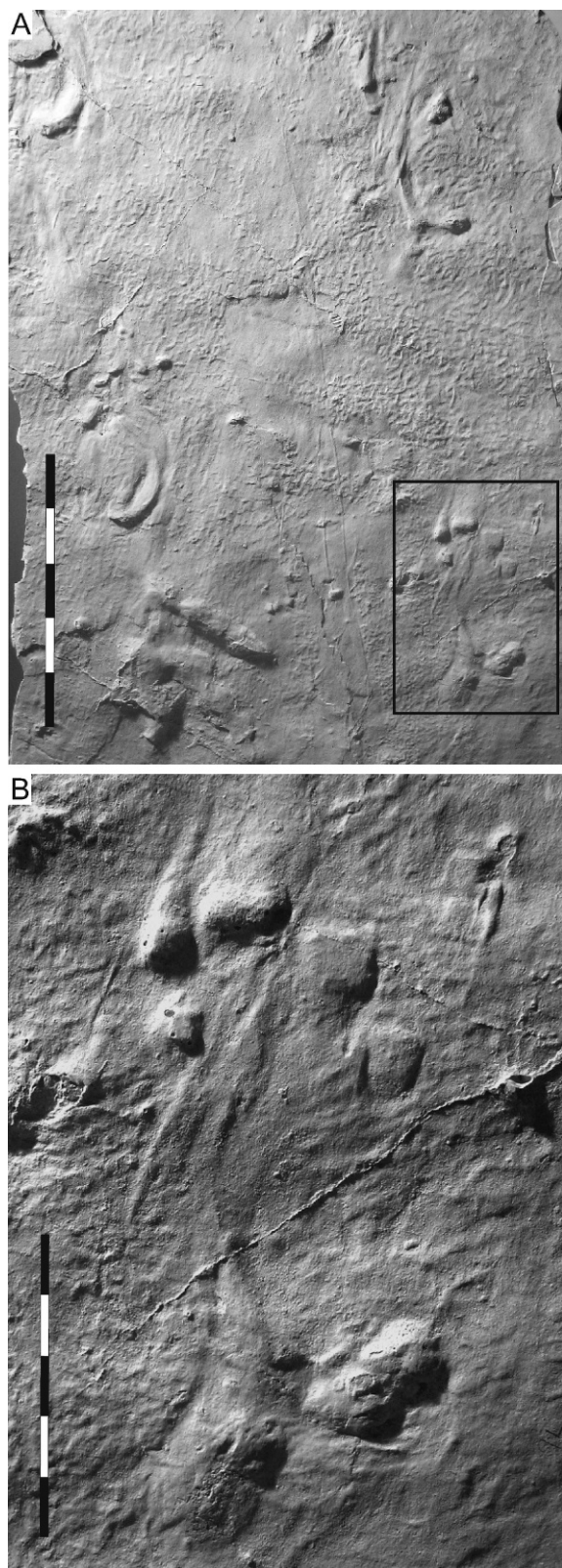
2. Biomechanical analyses of the both the *Moyenisauropus*-type (basal ornithischian) and *Neotrisauropus*-type (theropod) trackways show adjustments in locomotor behavior with changes in slope and cohesiveness of the bar surface. Convergence of these trackways toward certain points indicates repeated visits perhaps for drinking or crossing the river. Three resting traces with manus, metatarsal, and tail impressions attributable to the *Moyenisauropus*-type have also been identified.

3. This study has highlighted a mismatch between the body fossil and trace fossil record in the Moyeni section. Footprints of the prosauropod *Massospondylus*, the most common body fossil, were not identified in trackways, and body fossils of the common *Moyenisauropus*-type basal ornithischian trackmaker have not yet been found.

4. The presence of chirotheroid-type footprints on the Moyeni surface leads us to conclude that either their global stratigraphic range should be extended into the Jurassic, or the currently accepted position of the Triassic-Jurassic boundary in the Karoo Basin should be moved higher in the succession.

FIGURE 15—*Episcopopus*-type footprints. A) Plaster of Paris cast (positive) of trackway showing arcuate toe drags. Illuminated from top left, scale bar = 50 cm. B) Detail of manus-pes impressions outlined in A. Scale bar = 20 cm.

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