Lockley, M.G. & Lucas, S.G., eds., 2014, Fossil footprints of western North America: NMMNHS Bulletin 62

A BONANZA OF NEW TETRAPOD TRACKSITES FROM THE CRETACEOUS DAKOTA GROUP, WESTERN COLORADO: IMPLICATIONS FOR PALEOECOLOGY

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Abstract—Despite reports of ~80 dinosaur and other tetrapod tracksites in the “mid” Cretaceous (Albian-Cenomanian) Dakota Group of eastern Colorado, until recently almost nothing was known of the track record in the Dakota Group of western Colorado, the geographical region known as the “Western Slope.” This picture has changed dramatically in recent years with the discovery in 2011-2012 of about 30 new Dakota Group tracksites in and around the newly designated Dominguez-Escalante National Conservation Area (D-E NCA), administered by the Bureau of Land Management (BLM). Tracks are evidently so abundant in this region as to constitute a western slope “dinosaur freeway” comparable to the “Eastern Slope” dinosaur freeway previously named to denote the regional extensive track-bearing beds in the Dakota Group of the Colorado Front Range, and the High Plains region of southeastern Colorado and northeastern New Mexico, east of the continental divide. For convenience we refer to the two regions as the eastern and western slopes and preliminarily compare and contrast the track types and relative abundances that characterize the ichnofaunas in the two regions.

The Dakota Group in the D-E NCA area represents a carbonaceous facies, rich in the “walking” tracks of dinosaurs that progressed over emergent, but often highly saturated substrates, and “swimming” tracks of aquatic tetrapods (crocodylians, turtles and pterosaurs). Preliminary indications suggest that while most track types found in the east are also represented in the west, relative abundances are significantly different. For example, in the D-E NCA area ankylosaur and pterosaur tracks are much more common than in eastern Colorado. Much additional study is needed to ascertain whether the Dakota Group is consistently track-rich throughout the entire outcrop extending through multiple states on both sides of the Rocky Mountain continental divide. This preliminary study, which provides the first description of abundant tetrapod track samples from western slope facies, permits the first meaningful comparison between the western slope samples and those from the well-sampled facies belts of the eastern slope, dinosaur freeway outcrops.

INTRODUCTION

The Dominguez-Escalante National Conservation Area (D-E NCA) represents a large area (>300 square miles) of uninhabited upland on the northeastern flanks of the Uncompahgre Plateau in western Colorado (Fig. 1). Parts of the area are known paleontologically for abundant dinosaur remains. Skeletal remains are common in the bone-rich Upper Jurassic Morrison Formation, and tracks occur in various pre-Morrison, Jurassic and Late Triassic sites in this region, broadly defined as the Western Slope (of Colorado). Ironically, in 2009, when the D-E NCA was first created little or nothing was known of the vertebrate faunal potential of Cretaceous deposits in this region. However, in two short years (2011-2012), a sufficient number of Cretaceous tracksites (~30) have been discovered, as well as a few additional Jurassic sites, to warrant preliminary reports on the vertebrate tracks of the D-E NCA. Herein we present a preliminary illustrated report of new finds from the Dakota Group in this area, as a companion paper to a summary of all known (Jurassic and Cretaceous) stratigraphic units with tracks in the D-E NCA (Lockley et al, 2014a, this volume).

Despite the abundance of tetrapod tracksites reported from the Dakota Group of the high plains region of eastern Colorado and northeastern New Mexico (Eastern Slope), which in turn gave us the original concept of the Dinosaur Freeway (Lockley et al., 1992), until recently reports of tetrapod tracks from the Dakota Group of the western slope (i.e., on the Colorado Plateau, west of the continental divide) have been comparatively rare. Recent discoveries of many track-rich sites on the flanks of the Uncompahgre Plateau suggest that this lack of reports reflects a lack of study in this region. In the present study we have examined a number of sites in the so called “carbonaceous” coal-bearing, coastal plain deposits found along the northern flanks of the newly established D-E NCA, between Grand Junction and Delta (Fig. 1). As outlined here, there are many sites where tracks attributable to dinosaurs, crocodylians, and pterosaurs are abundant and diverse. These add significantly to the overall track record of the Dakota Group by demonstrating the presence of trackmaking groups that are unknown, rare, or poorly represented in this unit in other areas.

GEOLOGICAL SETTING

Young (1960) presented a landmark study of the Dakota Group of the Colorado Plateau. In his terminology the Dakota Group includes both the Cedar Mountain Formation (the lower unit) and the Naturita Formation, the upper unit. The two units are distinguished on the basis of carbonaceous content, with the Naturita Formation representing “carbonaceous mudstone, coal, persistent conglomeratic sandstones and beach sandstones deposited on or adjacent to the shore of the Mancos Sea” (Young, 1960, p. 156). The relationship between these two units is sum-

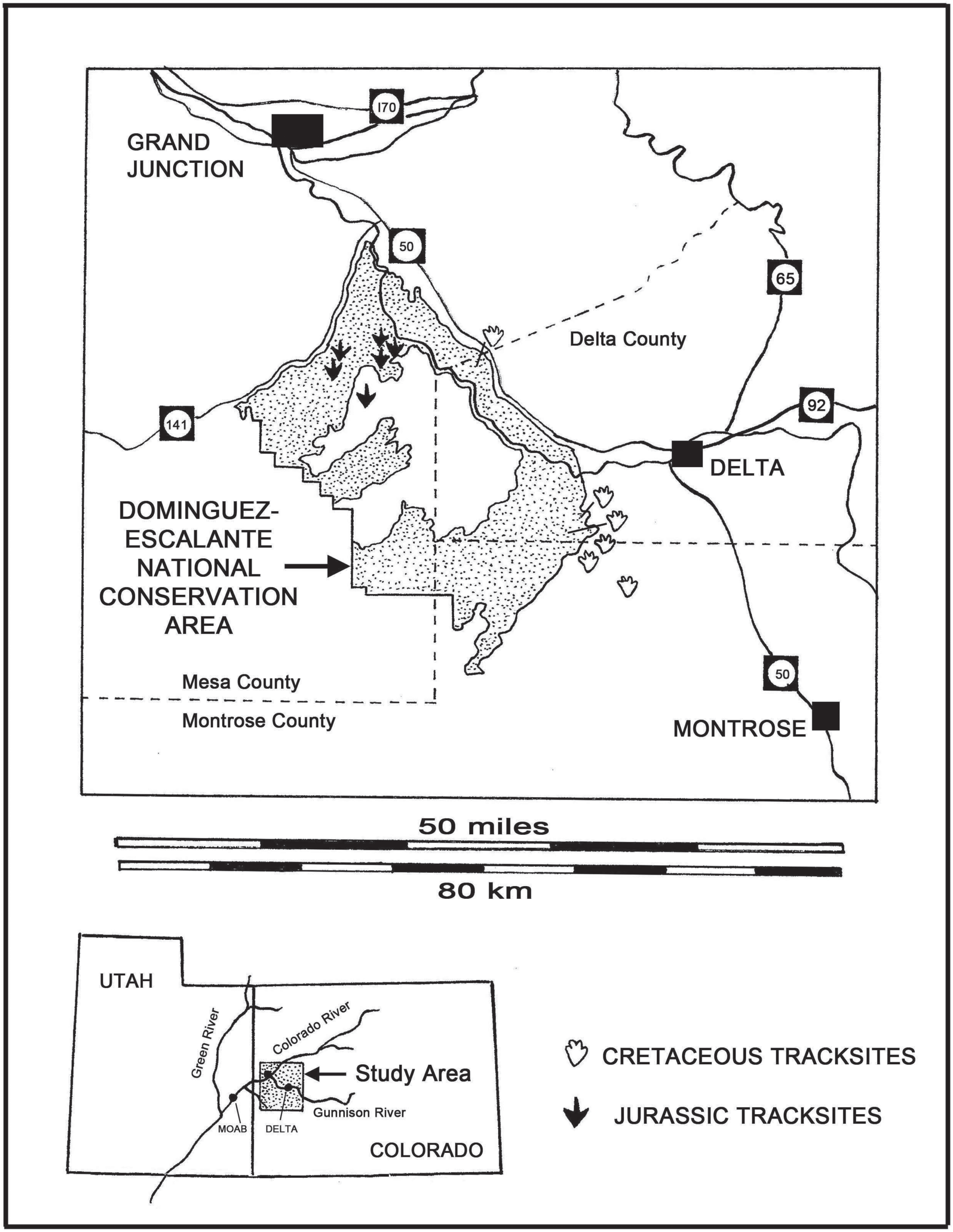


FIGURE 1. Map showing location of study area in western Colorado in and around the Dominguez-Escalante National Conservation Area (D-E NCA), covering parts of three counties (Mesa, Delta and Montrose). The stippled area is the non-wilderness part of the D-E NCA, which encloses a wilderness area (white). The concentration of Jurassic tracksites in the northern part of the area is described elsewhere in this volume (Lockley et al., 2014a). The concentration of Cretaceous tracks in the southern part of the area, and immediately outside the southern boundary, is described herein.

marized as follows "Cedar Mountain deposits are the products of inland floodplains which extended far inland from the lowland and coastal areas in which Naturita deposits were formed" (Young, 1960, p. 158). The Burro Canyon Formation is used as an alternate name for the Cedar Mountain Formation in this area.

In the study area between Grand Junction and Delta, where we have now discovered numerous tetrapod tracksites and associated invertebrate traces, Young (1960) described the Naturita Formation as being about "three-fourths" comprised of lagoonal facies rich in carbonaceous mudstone, with minor siltstone, sandstone, conglomerate and coal deposited in coastal swamps, estuaries and lagoons in a coastal belt that may have been up to 150 miles (~240 km) wide.

Given the preliminary nature of this study and the small area so far investigated it is premature to comment on the validity of the work done by Young (1960), which involved a much larger area. However, in the following section we present preliminary observations on a representative section to help place the many track finds in context

LOCALITIES, STRATIGRAPHIC SECTIONS AND MATERIAL (Fig. 2)

As this is a preliminary study primarily aimed at providing an overview of the abundance of vertebrate tracksites discovered in recent years, we present only a general stratigraphic framework based on representative sections measured in the south of the study area (Fig. 1). Generally speaking, the Dakota Group in the study area can be described as characteristic of typical coastal plain coal-bearing facies, already known to be rich in ornithopod and crocodylian tracksites in eastern Colorado. These sequences are mud- and clay-rich with intercalated coaly carbonaceous units and relatively thin ripple-cross-laminated fine-grained sandstones, and a few coarser channel sandstone units (Fig. 2). The strata dip gently to the northeast off the Uncompahgre Plateau, and, because the study area is quite small, the sections measured to date are quite close together.

In order to protect sensitive sites we have referred to important localities in general terms. For example, sites are found near some of the main roads through the area, including Saw Mill Mesa Road (within the D-E NCA), 25 Mesa Road (along the D-E NCA boundary) and along Banner Road (outside the D-E NCA). Different constraints and guidelines apply to collecting by permit holders in these D-E NCA and non-D-E NCA areas, and some sites are more productive and sensitive than others. However, it is fair to say that tracks are common in many areas, and often found already eroded out of outcrops, mostly as natural sandstone casts. In some cases such "loose" specimens are in danger of disintegration and, with authorization from the BLM, we have collected or molded them. Specimens collected during the present study (2011 and 2012), from within D-E NCA and non-D-E NCA areas, have been reposited at the University of Colorado Denver (CU prefix), and have been transferred permanently to the University of Colorado Museum of Natural History (UCM prefix). Full details of specimens and localities collected are available to *bona fide* researchers through the Bureau of Land Management (BLM) and UCM: see acknowledgments. In the sections that follow, specimen numbers are cited to give an indication of the material available, but individual sites are not described in detail except where *in situ* surfaces have been mapped.

In and around the D-E NCA, the Dakota Group is about 25 to 30 meters thick. To date, sections have been measured at four different localities. A representative section is shown in Fig. 2. The measured section contains ornithopod, ankylosaur, and pterosaur tracks but, as noted below, other track types occur in other sections nearby.

Approximately 4 meters thick, the lowermost section is composed mostly of conglomeratic sandstone and conglomerate in channel-form deposits with basal scour and trough cross-bedding. These are interpreted as fluvial channel deposits. Dinosaur tracks are rare in these deposits. Possible ankylosaur scratch or "digging" marks, to be described elsewhere, were found in the top of a fluvial channel deposit, and some poorly preserved ornithopod tracks were found at the base of another.

The middle is approximately 15 to 18 meters thick. The unit contains a variety of lithologies, including sandstone, siltstone, shale, impure coal, and volcanic ash. The sandstones occur in bodies about 1 to 2.5 meters thick. Climbing ripples are abundant, as are planar laminae. Sets of planar cross-beds about 0.3 to 0.6 meters thick are common, as are mud chips and root traces. These sandstones are interpreted as levee and crevasse splay deposits. In the upper part of this heterolithic interval, some of the sand bodies have abundant mud drapes and trace fossils typical of the *Skolithos* ichnofacies (*Skolithos, Arenicolites, Diplocraterion*). This is interpreted as evidence of marine inundation and tidal influence.

Siltstone and shale beds in the heterolithic interval are nearly all laminated. They contain varying amounts of carbonaceous debris, and commonly grade laterally or vertically into impure coal. These are interpreted as overbank deposits that formed on a swampy floodplain with some marine influence. Most of the volcanic ash beds occur in these fine-grained overbank deposits. The ash beds are light gray to light tan, clay-rich, and vary from 2 to 15 cm in thickness. Most are structureless, though a few have planar laminae or ripple cross-laminae. The structureless beds are interpreted as ashfall deposits; the laminated and cross-laminated beds are interpreted as reworked ash deposits. Ash is also present to varying degrees in all other lithologies of the Dakota Group in the D-E NCA.

The heterolithic interval contains nearly all of the dinosaur tracks found in the four measured sections. Tracks were most commonly made in wet, silty or muddy floodplain deposits, that were then covered by sandy crevasse splay deposits. They are thus preserved as convex hyporeliefs on the undersides of sandstone beds.

The uppermost 3 to 6 meters of the Dakota Group are composed mostly of thinly bedded sandstone, siltstone, and shale. The sandstone beds have horizontal trails and vertical burrows typical of the *Skolithos* ichnofacies. Beds are commonly separated by mud drapes. In places, channel-form sandstone bodies can be seen. These are up to a few meters thick, and are commonly trough cross-bedded. These lithologies are interpreted as tidally-influenced shoreline deposits and tidal channel deposits. The pterosaur tracks in the D-E NCA came from tidally-influenced shoreline deposits or tidally-influenced crevasse splay deposits. They are commonly associated with horizontal trails. They formed when the animals scraped their hind feet against the substrate while swimming over silt or sand in very shallow water (depth approximately equal to the length of a pterosaur's hind leg). The tracks were later covered by a mud drape and another layer of sand. They are thus also preserved as convex hyporeliefs on the undersides of the upper sand layers.

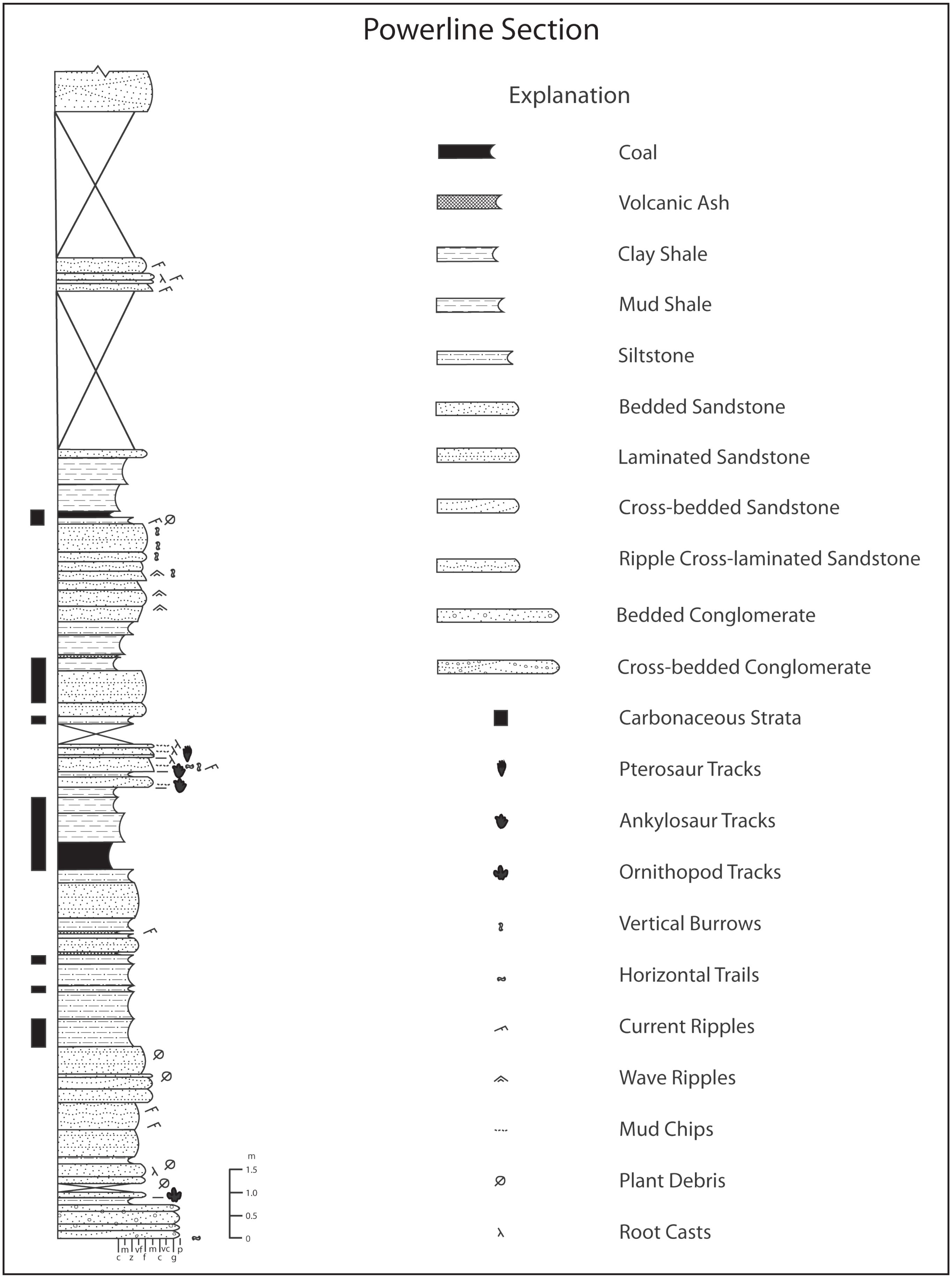


FIGURE 2. A representative section of the Dakota Group from 25 Mesa Road, very near the boundary between Delta and Montrose counties, about 7 miles SW of Delta, Colorado.

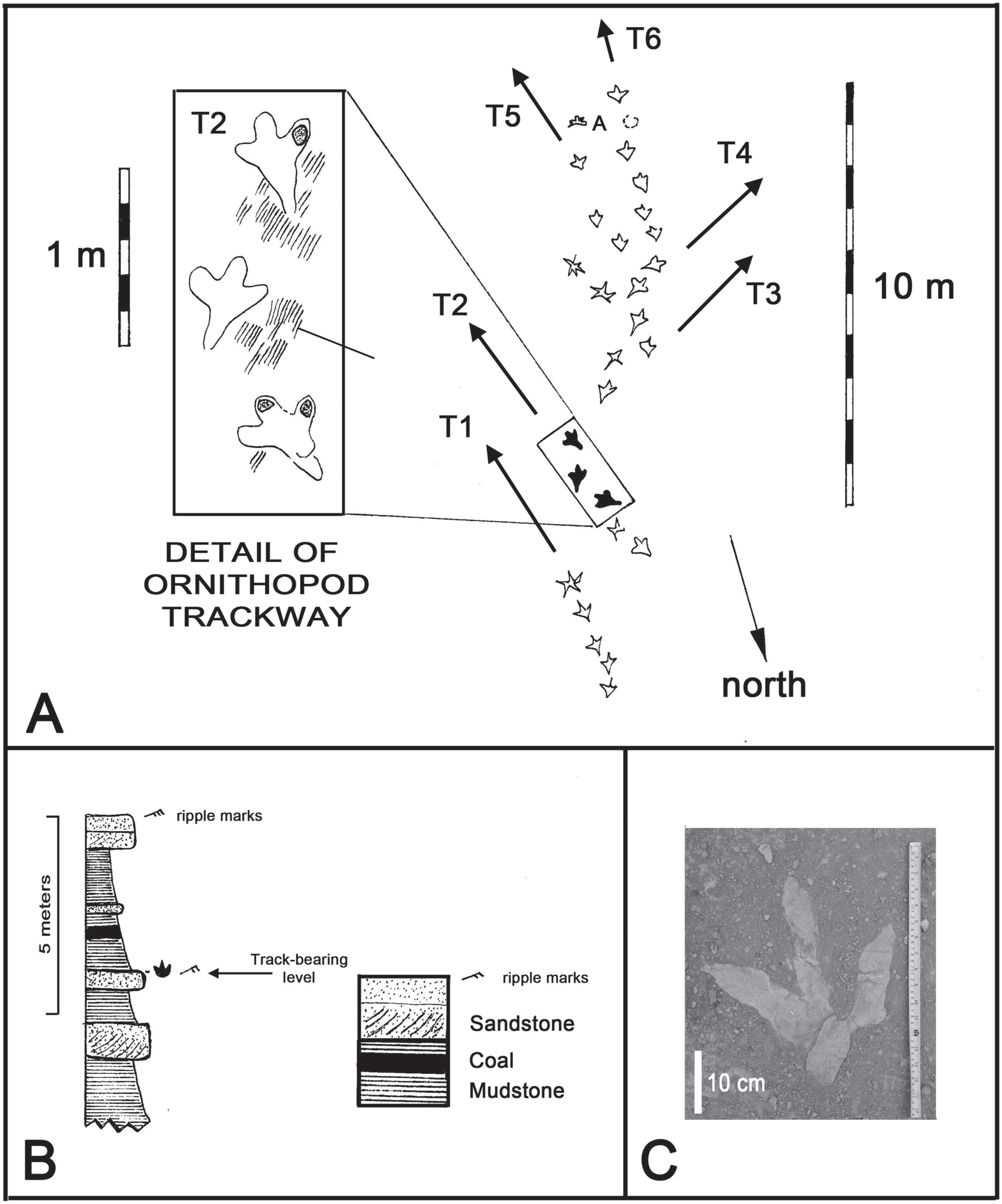


FIGURE 3. A, Map of tracksite from the Banner Road, shows at least six ornithopod trackways (T1-T6), and detail of best-preserved trackway segment (T2). B, Shows the stratigraphic section at the site. C: photo inset shows a theropod track from the same surface nearby.

When examined from bottom to top, the Dakota Group in the D-E NCA shows a record of the progressive marine inundation of a coastal area that was receiving a large amount of sediment. These conditions were very conducive to the formation and preservation of tracks. Tectonic uplift and volcanic activity to the west created an abundant supply of sediment, while tectonic subsidence and sea level rise in the area of the D-E NCA created space for many layers of sediment to accumulate without being removed by erosion. These sediment layers functioned as surfaces for track registration, and as covering materials to bury and preserve tracks.

In the case of the dinosaur tracks, tectonic subsidence and sea level rise probably also contributed to high water tables and wet conditions that were conducive to the formation of deep tracks. Rising sea level and volcanic ash falls probably contributed to crevassing as river channels experienced decreased gradients and became choked with sediment. These sandy crevasse splay deposits were important in filling and preserving tracks at all four localities, where sections have been measured to date. In the case of the pterosaur tracks, settling of mud during slackwater tidal conditions created mud drapes that enabled the track-bearing sandstone beds to split cleanly and reveal the tracks in the outcrop.

DESCRIPTION OF TRACK TYPES

Tracks in the area are dominated by those of archosaurs, with only a few tracks attributed to turtles. Archosaur traces fall into three major categories: dinosaur, pterosaur and crocodylian tracks. The dinosaur tracks are most diverse, representing theropods, ornithopods, and ankylosaurs: these almost exclusively represent tracks made by animals walking on emergent surfaces, or surfaces covered by shallow water. Many tracks are remarkably deep, indicating very wet substrates or high water tables. Consistent with this inference of wetland habitats we find a large number of "swim" tracks made by pterosaurs, crocodylians, and a smaller number attributable to turtles. Surface trails produced by limulids have also been identified and are briefly described below.

Dinosaur Tracks

A Representative Site

To date, we have recorded few sites where tracks are found *in situ* on large surface exposures. One such site, found in the Banner Road area (outside the D-E NCA), consists of a small (~30m^2) gully exposure on which about 30 ornithopod tracks, comprising at least six trackways have been identified (Fig. 3). The track-bearing surface consists of a thin ripple-marked sandstone, with ripple crest orientations from ENE-WSW. This surface is overlain by dark gray-black mudstone with well-developed coaly layers. As indicated in Figure 3, the best-preserved tracks, which are in trackway 2, are about 25 cm wide. Footprint length is difficult to measure accurately as tracks have long heel marks interpreted as the result of the foot sliding into the soft substrate as the deep tracks registered. However, the heel traces, as well as those of the central toe (digit III), clearly show the strong positive (inward) rotation (~15-25^o, for trackway 2) typical of ornithopod trackways. Many of the tracks in other trackways are poorly preserved, however, it is possible to determine that the dimensions of tracks in trackway 2 are typical of most of the other measurable ornithopod tracks. These are the only ornithopod trackways found *in situ* at this point in the present study.

A single ankylosaur manus track was identified on the mapped surface (Fig. 3), and nearby several other loose ornithopod and ankylosaur track casts (Figs. 4-5) were found. We also found an *in situ* theropod track a little distance away from the mapped area, but on the same surface (Fig. 3C). This is one of very few theropod tracks so far identified in the study area.

Ornithopod Tracks, Figs. 4-5

In addition to the aforementioned Banner Road site where ornithopod trackways are found *in situ*, a number of ornithopod tracks have been found as isolated natural casts (Fig. 4). Several of these were collected, although the exact horizon from which they originated is unknown. One well-preserved pes and manus set, from a slab originating from a known horizon, was molded and replicated (CU 207.53). A number of other casts and molds, also from known horizons, were traced but not molded or replicated. Pes tracks are generally about as wide (W) as long (L) (L/W ~1.0). The pes size range is about 25-50 cm. Manus tracks are small (L ~ 10 cm, W ~ 12 cm) and rarely preserved as casts. Due to their small size and lack of distinctive morphology they would likely be difficult to identify with confidence.

Ankylosaur Tracks, Figs. 5-6

Ankylosaur track preserved as natural casts are relatively abundant in the study area. Most are found as loose casts (Fig. 5) and in some cases may be seen *in situ* prior to eroding out (Fig. 5C). To date, only one *in situ* trackway segment, preserved as positive impressions on a sandstone surface, has been identified from the Banner Road area (Fig. 6A). Another trackway segment, preserved as a series of natural casts (Fig. 6B) on a fallen block, appears to show three consecutive pes tracks and two associated manus tracks representing only one side of a trackway. Another pair of molds on a fallen block (Fig. 6C) shows two apparently consecutive tracks preserved only as toe traces. Thus, many modes of preservation have been observed.

Overall, the presently-known sample of ankylosaur tracks is significantly larger than the ornithopod track sample. In addition to the aforementioned trackway segments, eight manus casts and 22 pes casts have been collected, molded and/or traced: a majority of these are shown in Figure 6D-E. Many of the deeper pes tracks show well-preserved vertical striations made by the scaly integument as the foot penetrated the soft muddy substrate. One of the most interesting specimens is a small pes track only ~8 cm long and wide. The remaining pes tracks range from 20 to 32 cm long and 24 to 37 cm wide. Manus tracks range from 15 to 20 cm long and 20 to 30 cm wide.

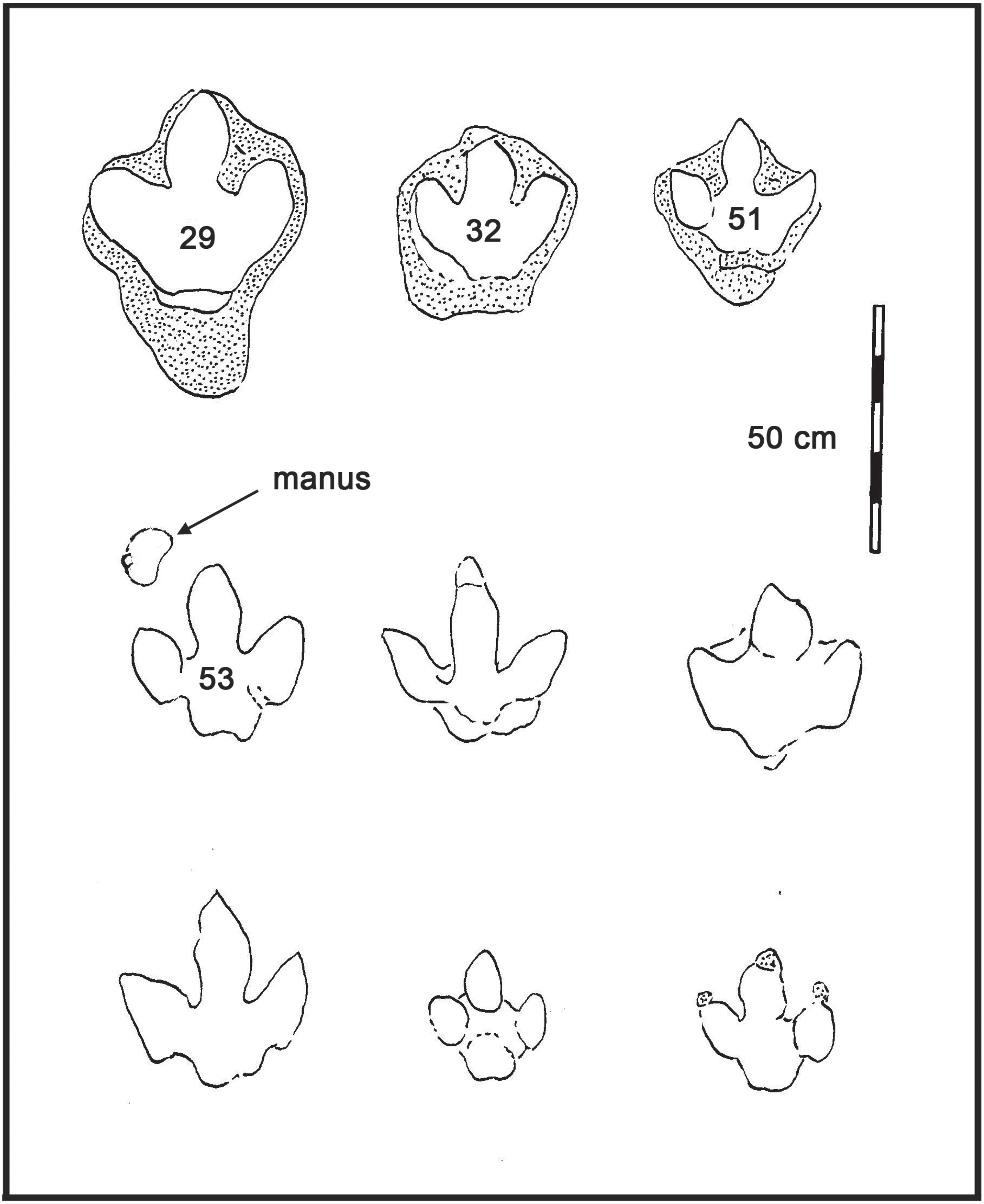


FIGURE 4. Ornithopod tracks from various sites. Numbers are specimen number suffixes in the CU 207 series. Unnumbered tracks were traced, but not collected

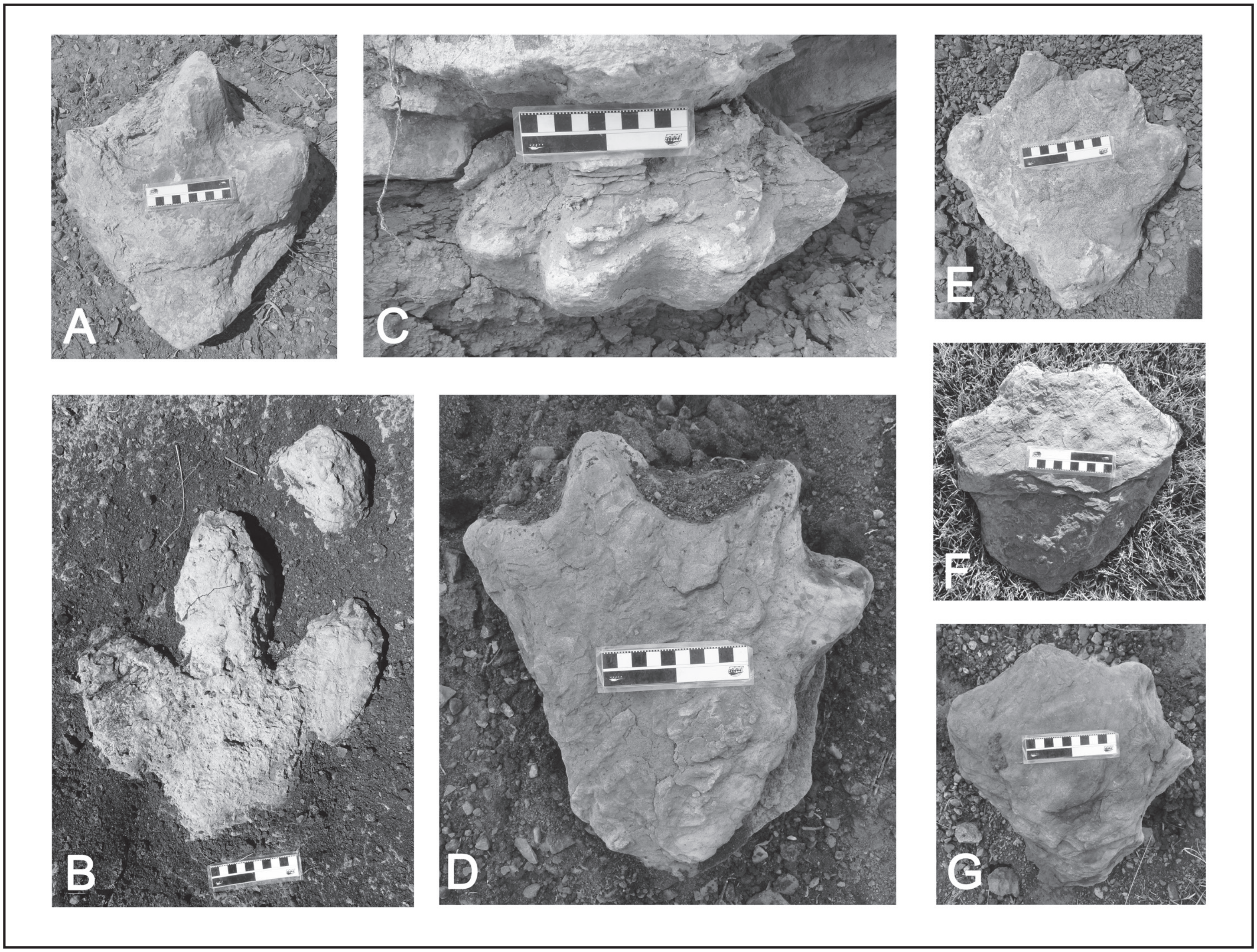


FIGURE 5. Ornithopod and ankylosaur track casts, as found in the field. A, A typical pes cast (CU 207.51), B, A manus-pes set (CU 207. 53). C, An *in situ* ankylosaur pes track cast was photographed then collected (CU 207. 64) from the underside of a sandstone bed, in a gully, from which it was about to erode out. D, A well preserved ankylosaur pes cast (CU 207.34). E-G, Additional examples of ankylosaur pes casts. Scale bars in cm, compare with Figures 4 and 6

Non Dinosaurian Tracks

Swim Tracks: Diagnostic and Non-Diagnostic Features

Before describing the diagnostic features of pterosaur, crocodylian and turtle swim tracks identified from the study area it is important to note that swim tracks attributable to many vertebrate groups are inherently variable. Variability and the implications for trackmaker identification can be understood in the following general categories:

1) Individual tracks may show traces of any number of the digits of the front and hind feet: i.e., from 1-5 depending on the trackmaker involved. If the trackmaker's foot, or the foot of several trackmakers, touched the substrate more than once in the same place, more than five digit traces may be registered (or more digit traces than the maximum number of digits on the foot of any given track maker).
2) Only the distal part of the toes (claws) may be registered in some cases. In other cases tracks may represent registration of the entire foot, including the heel.
3) Dragging of feet as they register may elongate the length of tracks and digit traces beyond dimensions that are diagnostic of foot length.
4) Swimming animals rarely produce regular trackways or trackway patterns over any distance, although bottom-walking turtles may produce regular patterns (see below).
5) Inter-digital web traces may or may not be present depending on the depth of tracks, the track maker taxon involved, and the substrate conditions.
6) Size may be a useful indicator of trackmaker taxon but there is considerable overlap between the sizes of the feet of various swim trackmakers, whether these represent different species or individuals of different sizes (e.g., juveniles and adults).
7) Inferences about the behavior of extant and extinct swim trackmakers may help discriminate the affinity of swim tracks that might otherwise be ambiguous.

For these reasons, we begin each of the following sections with brief comments on the diagnostic features of swim tracks of the various groups discussed.

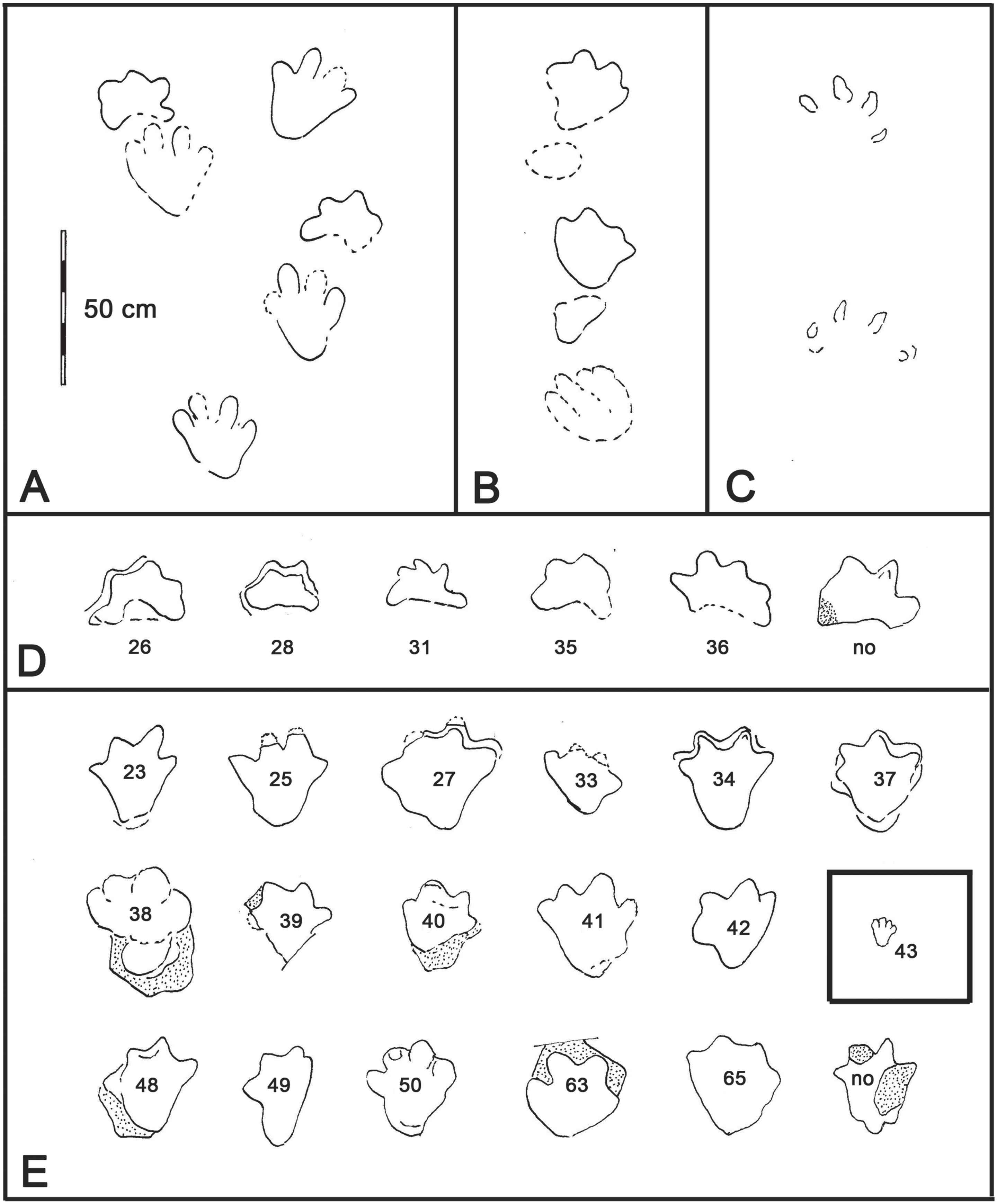


FIGURE 6. Ankylosaur trackway segments (A-C) and isolated tracks (D-E) . Numbers are specimen number suffixes in the CU 207 series. Note baby ankylosaur pes track (CU 207.43).

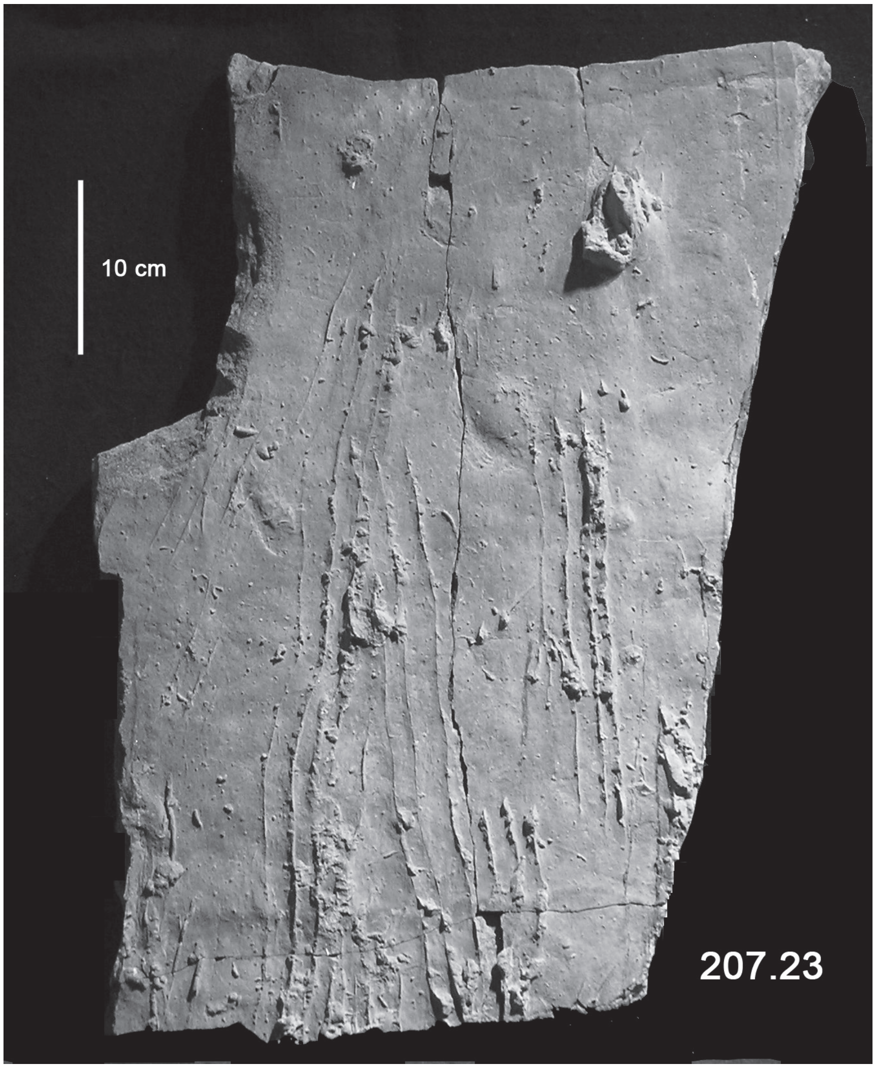


FIGURE 7. Set of pterosaur swim tracks showing characteristic claw traces that indicate diagnostic pes digit length ratios II=III > I=IV.

Diagnostic Features of Pterosaur Swim Tracks, Figs. 7-9

Pterosaur swim tracks are distinct from walking trackways, which show regular manus and pes sets configured in trackways with characteristic pace, stride and pace angulation patterns. The pes creates a narrow heel trace with a rounded postero-lateral pad representing the proximal part of digit V. The distal end of the pes traces indicates four slender digit traces, of which II and III are equal in length and slightly longer than the traces of digits I and IV. In contrast, swim tracks are typically attributable to the pes "scraping" the substrate, leaving only incomplete tracks (toe tip traces) that are sometime elongated into long parallel striations many times the length of normally registered pes tracks, which show narrow heel traces (Lockley and Wright, 2003). Individual pes footprints may be registered in swim track assemblages (e.g., Kukihara and Lockley, 2012). In such cases they may help identify swim tracks. Sometimes such fully registered pes tracks are associated with, or terminate at the ends of swim tracks that give clues to trackmaker locomotion and behavior. Pterosaur pes swim tracks, like those of walking pterosaurs are also characterized by having, at the touch down point, two longer digit traces (II and III) of equal length flanked by two short digit traces (I and IV) also of equal length (length formula II=III > I=IV). Web traces, if present, appear attached to the distal ends of the digit traces just behind the claw traces: i.e., the pterosaur pes was fully, not partially webbed.

Pterosaur Swim Tracks From the D-E NCA

A number of slabs interpreted as pterosaur swim tracks have been reported from various localities in and around the D-E NCA. These finds are surprising because, until recently, only one site among 80 recorded sites, from the eastern slope, had been reported to yield pterosaur tracks (Kukihara and Lockley, 2012). Two other eastern slope sites are reported elsewhere in this volume (Lockley et al., 2014b; Lockley and Schumacher, 2014).

One of the most striking D-E NCA swim track assemblages (Fig. 7) is characterized by sets of four, very fine, parallel striations that begin with the aforementioned diagnostic symmetric arrangement of sharp claw traces (II=III > I=IV). Another assemblage of five slabs (Fig. 8) indicates some large pterosaur pes tracks exhibiting a variety of preservations. Some consist only of a set of four distal toe traces with the length formula II=III > I=IV (Fig. 8B). Others include a characteristic narrow heel with the short laterally-located trace of the proximal digit V pad (Fig. 8A,C). Yet others show traces of well-developed webbing between the toes (Figs. 8E and 9).

Preliminary studies of the pterosaur tracks illustrated here indicate that they range in width from 4 to 12 cm. As noted above track length may be difficult to determine accurately if there is any evidence of scraping motion that would elongate the traces produced. However, in the case of several tracks with well- defined heel traces, footprint lengths range from 18 to 30 cm. The significance of such large traces is discussed below.

Diagnostic Features Of Crocodylian Swim Tracks

A number of recent studies have demonstrated that crocodylian swim tracks are common in the Dakota Group (Lockley et al., 2010; Kukihara et al., 2010; Kukihara and Lockley, 2012). These are almost exclusively assemblages of isolated manus and pes tracks with no discernible trackway patterns. Only two reports of trackways suggestive of walking (Mehl, 1931; Lockley, 2010; Houck et al., 2010) are known, but both deal with trackways that have poor preservation. Thus it is necessary to turn to modern trackway studies (Farlow and Elsey, 2010) in order to understand the configurations of typical trackways registered on land. These, usually produced by the high walk, show a tetradactyl pes track with a posteriorly-tapered heel. Pes digits I-III are robust with strong claws, but pes digit IV is more slender and less-well developed. Digit length ratio III>II=IV > I). The manus track is pentadactyl with the traces of digits II-IV much longer than the traces of digits I and V, and without a conspicuous posterior heel trace (digit length ratio III>II and IV > I and V). Neither the manus or the pes has well-developed webbing. Rather the webbing only extends across the proximal part of the hypices between digits.

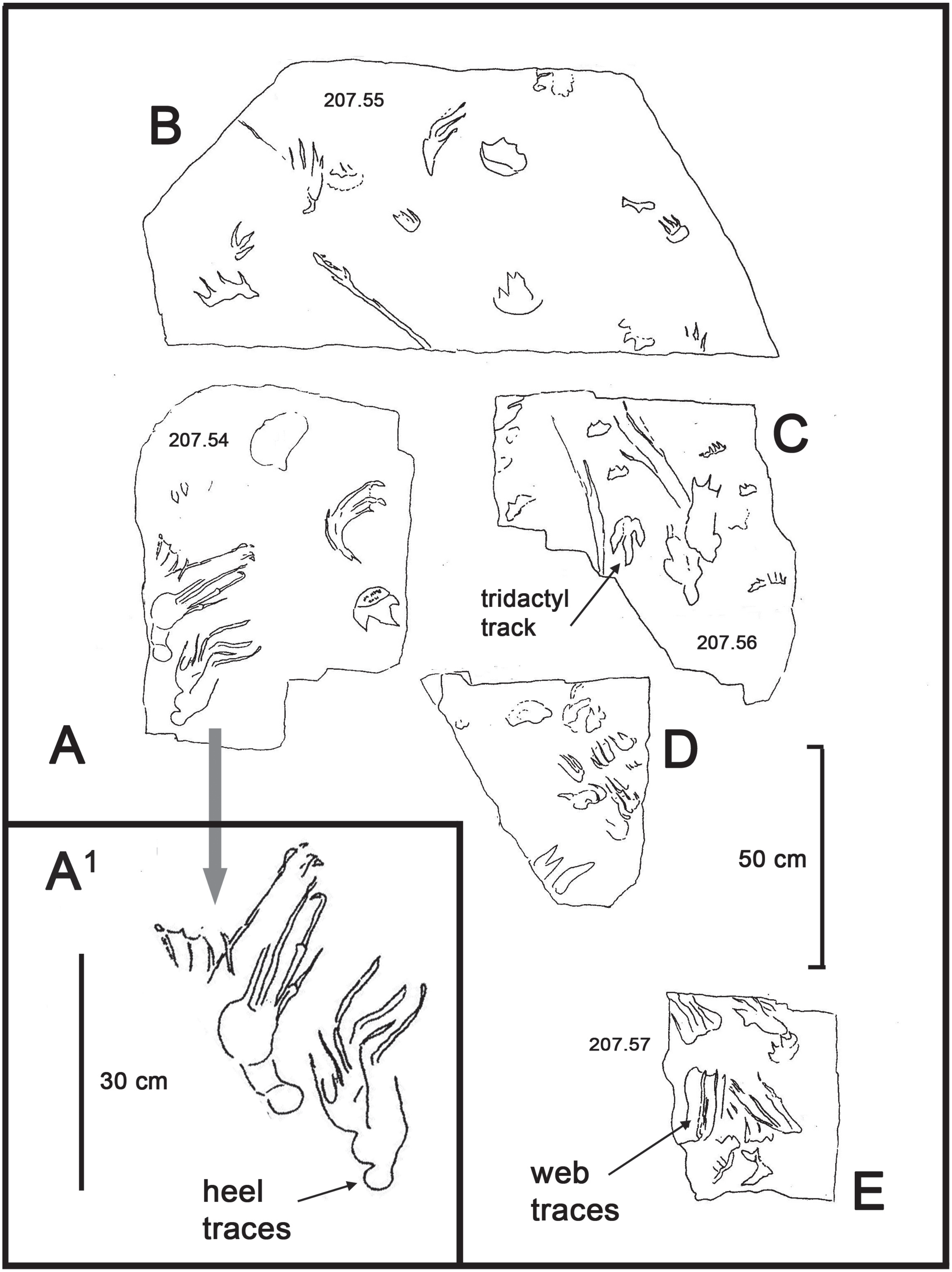


FIGURE 8. Five assemblages of pterosaur swim tracks CU 207.54-57. Compare 8E with Fig. 9.

FIGURE 9. An assemblage of pterosaur pes swim tracks (CU 207.57) showing well-developed inter-digital web traces. See Fig 8E for reversed line drawing. Scale bar in cm.

FIGURE 10. A typical crocodile swim track consisting of three digit traces. Scale bar in cm.

Crocodylian Swim Tracks From ahe D-E NCA, Figs. 10 and 11

Inferred crocodylian swim tracks are abundant at some localities in the study area. In general, they consist of tridactyl and tetradactyl, parallel, scrape marks that indicate track makers with robust digits up to ~2 cm wide (Fig 10). In many cases these scrape or scratch marks are very abundant and elongated for distances of up to a meter or more. In the case of the large mapped and replicated surface illustrated in Figure 11, all the traces are parallel, as recorded in other large crocodylian swim track assemblages from the Dakota Group of the Eastern Slope (Lockley et al., 2010).

In contrast, crocodylian swim tracks are more variable and incomplete. They often consist of only three toes traces. In the case of inferred tridactyl manus traces these digit traces likely represent digits II-IV because, if the trackmaker is reaching down from a buoyant position, rather than walking, digits I and V are too short to touch the substrate until the other digits are quite deeply implanted in the substrate. In the case of tridactyl pes traces, they likely represent digits II-IV especially if one trace (of digit 1) is shorter. However, in some cases the pes trace is tetradactyl and representative of typical pes morphology.

Diagnostic Features of Turtle Swim Tracks

Unlike pterosaurs and crocodylians, which have different manus and pes morphologies, likely to produce different footprint morphologies, turtles produce rather similar manus and pes swim tracks. For example, the turtle manus and pes is typically short and pentadactyl with well-developed webbing. In comparison with crocodylian swim tracks, which are usually tridactyl and tetradactyl and much larger, turtle tracks are typically short, wide and often pentadactyl. Likewise, the distinction between turtle and pterosaur tracks is also easily made in most places. Firstly pterosaur manus tracks are highly distinctive in shape and rarely occur in swim track assemblages, while pterosaur pes tracks are elongate and often show elongate scratch marks produced by a different swimming action (see below).

Turtles are known for the habit of bottom walking, which allows them to produce more or less regular trackway patterns similar to those they might theoretically produce on emergent surfaces. Thus, as discussed below, differences in behavior also produce rather different track way configurations both within track making groups and between different groups

Turtle Swim Tracks From the D-E NCA, Fig. 12

To date, only one unequivocal turtle trackway has been recorded from the study area (Fig 12). This trackway is remarkably well-preserved, consisting of several more or less complete manus-pes sets forming part of a wide trackway (internal trackway width ~20 cm), with short steps ~22 cm and low pace angulation (45^o). Individual manus and pes tracks are about 5 cm wide and 5 cm long with the middle digit traces (II-IV) well-delineated in most places and separated by traces of interdigital webbing. As is the case with many swim tracks they are characterized by posterior mounds of sediment cause by the pushing back of the foot during registration.

Limulid Tracks, Fig. 13

In the vicinity of 25 Mesa Road, just outside the D-E NCA boundary, a single surface associated with the lowermost unit of the Dakota Group, has yielded abundant small tracks attributed to limulids (horseshoe crabs). Most of these tracks are isolated, although they occur in abundance. In some cases the diagnostic "pusher" traces are seen in a trackway sequence (Fig. 13), that would indicate an animal about 7-8 cm wide. These are the first limulid tracks reported from the Dakota Group, and can be referred to the ichnogenus *Kouphichnium* , made famous in the classic study by Caster (1938). The limulid track-bearing bed also yields life position traces of bivalves: ichnogenus *Lockeia*, a senior synonym of *Pelecypodichnus* (Häntszchel, 1975)

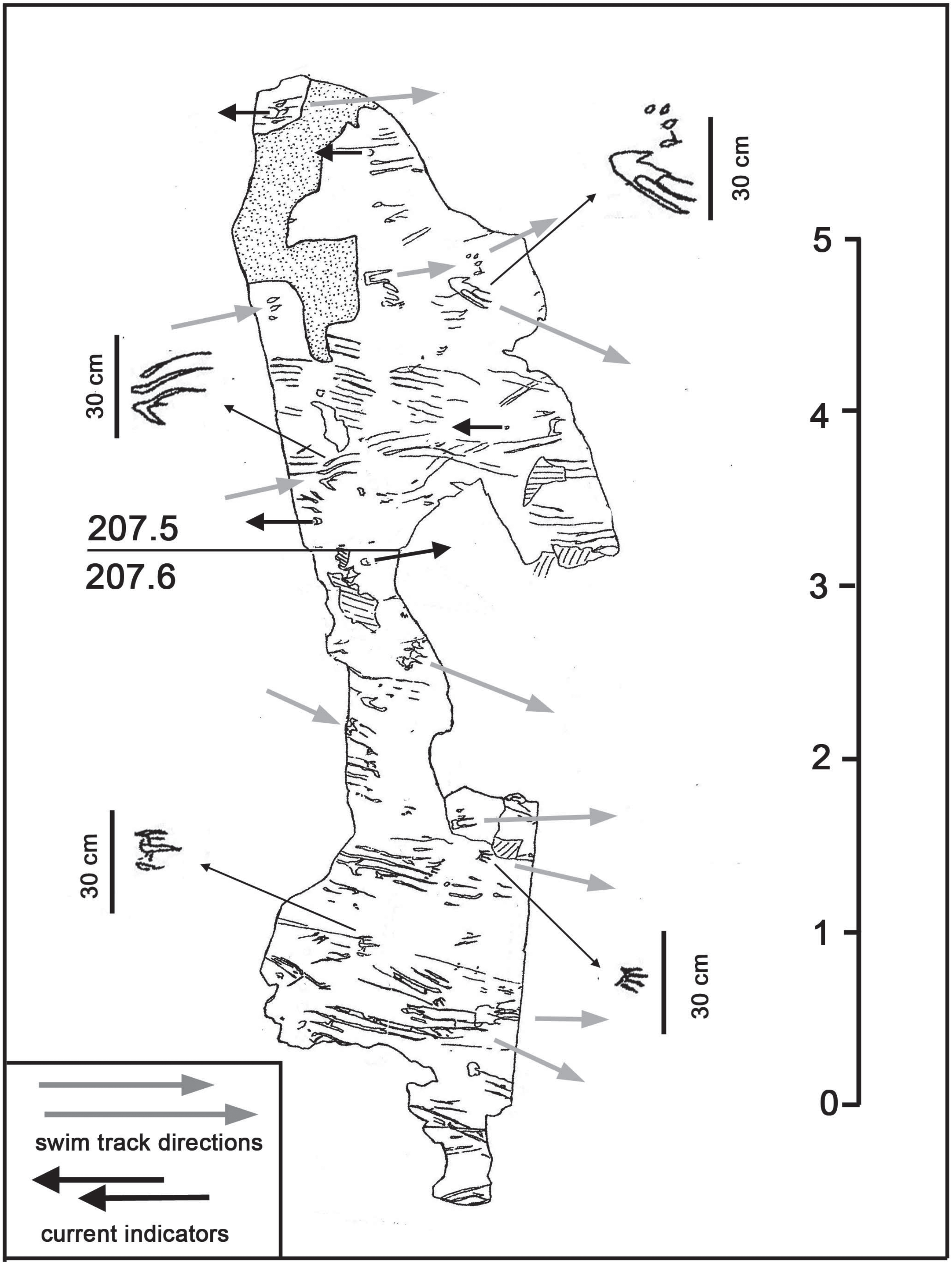


FIGURE 11. Large assemblage of elongate crocodylian tracks that are preserved in two parts as mold and replica (CU 207.5 and 207.6). Surface is ~ 6 m long and 1-2 m wide. Details of individual tracks are shown at twice map scale, with gray arrows indicating direction of travel. Black arrows indicate flow directions, mostly opposite to the track orientations.

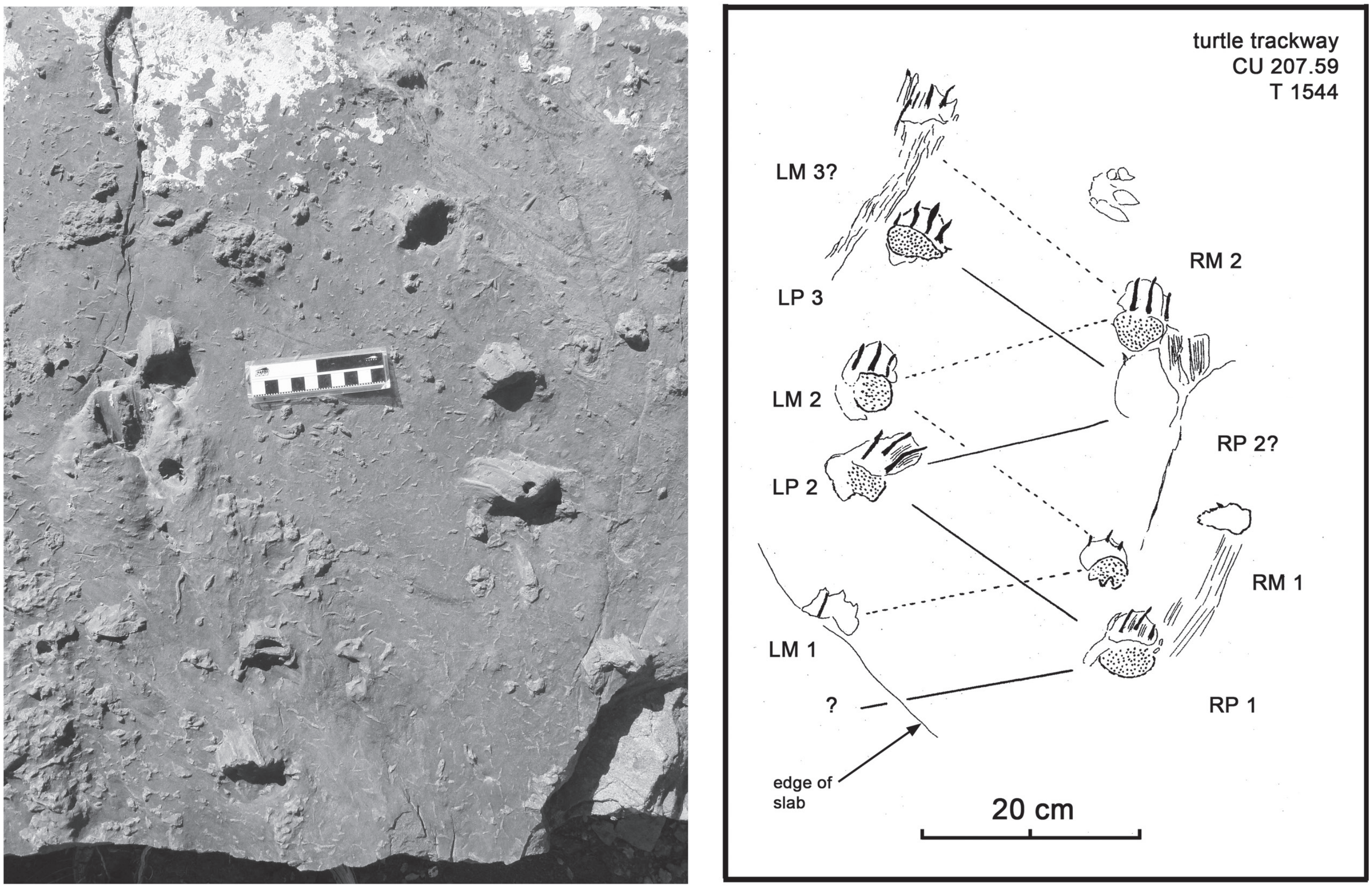


FIGURE 12. Turtle trackway (CU 207.59) preserved as natural cast (left) with reversed drawing of detail (right). Scale bar in cm.

DISCUSSION

As implied in the previous sections, it is convenient to divide our discussion into two parts: the first dealing with the tracks of walking dinosaurs on emergent surfaces or in very shallow water, the second dealing with the swim tracks produced by pterosaurs, crocodylians and turtles.

Previous studies of the dinosaur ichnology of the Dakota Group on the eastern slope have demonstrated that moderately large ornithopods (foot length 15-55 cm) were the dominant track making group, occurring in 72.8% (51/70) of localities: see Lockley et al. (2006, 2010) for quantitative censuses for more than 70 sites. Slender-toed theropods (ichnogenus *Magnoavipes*) attributed to ornithomimisaurs are the second most common group, occurring at 37.1 % (26/70) of sampled localities, with ankylosaur tracks being comparatively rare, occurring at only 4.3% (3/70) of localities. Pterosaur tracks are equally rare, also occurring at only 4.3% (3/70) of localities (Lockley et al., 2010, table 6). Because the *Magnoavipes* trackmakers were gracile emu-sized animals, and quite possibly toothless, they could not have preyed on large ornithopods. This has led to the suggestion that crocodylians, occurring at 27.0% (19/70) of localities and growing to at least 4-5 meters in length, were most likely the major predators (Lockley et al., 2010; Lockley and Lucas, 2011).

While it is premature to assess the relative abundance of different dinosaur groups represented by tracks in the western slope study area, it is clear that ankylosaur tracks are far more abundant than in the eastern slope area. To date, they have been found at more than 50% of the about 30 known tracks localities. A simple count of loose natural casts, and well preserved *in situ* casts and molds, as well as those collected, molded, traced and or/and illustrated herein shows the theropod/ornithopod/ankylosaur ratio to be 2/15/27 (or 4.5/34.0/ 61.5%) including the six trackways recorded from the Banner Road site: i.e., ankylosaur tracks make up almost 2/3 of the present census.

Regarding the swim tracks record outlined above for pterosaurs, crocodylians and turtles, we can again note that all three groups are known from the eastern slope. As stated, crocodylian tracks are far more abundant among eastern slope swim tracks, occurring at ~27.0% of localities, compared with 4.3 % for pterosaurs and only 1.4% for turtles. Given that only one obvious turtle trackway site is so far known on the Western Slope, it is possible that the sample in this region will reveal a correspondingly high proportion of crocodylian tracksites and low proportion of turtle tracksites. However, it is clear that pterosaur track sites are considerably more abundant on the Western Slope than appears to be the case based on the eastern slope census.

The pterosaur tracks are of particular interest because of the large size of some of the more diagnostic specimens, i.e., those with diagnostic heel traces. These are up to 30 cm long and ~12 cm wide, making them the largest pterosaur tracks known from North America. This allows estimates of wing spans on the order of 7-8m. Moreover, because it is inferred that pterosaurs were floating in shallow water, while touching the subaqueous substrates, we can estimate that water depth was no more than the length of the pterosaur hind leg, probably on the order of only 40-50 cm even in

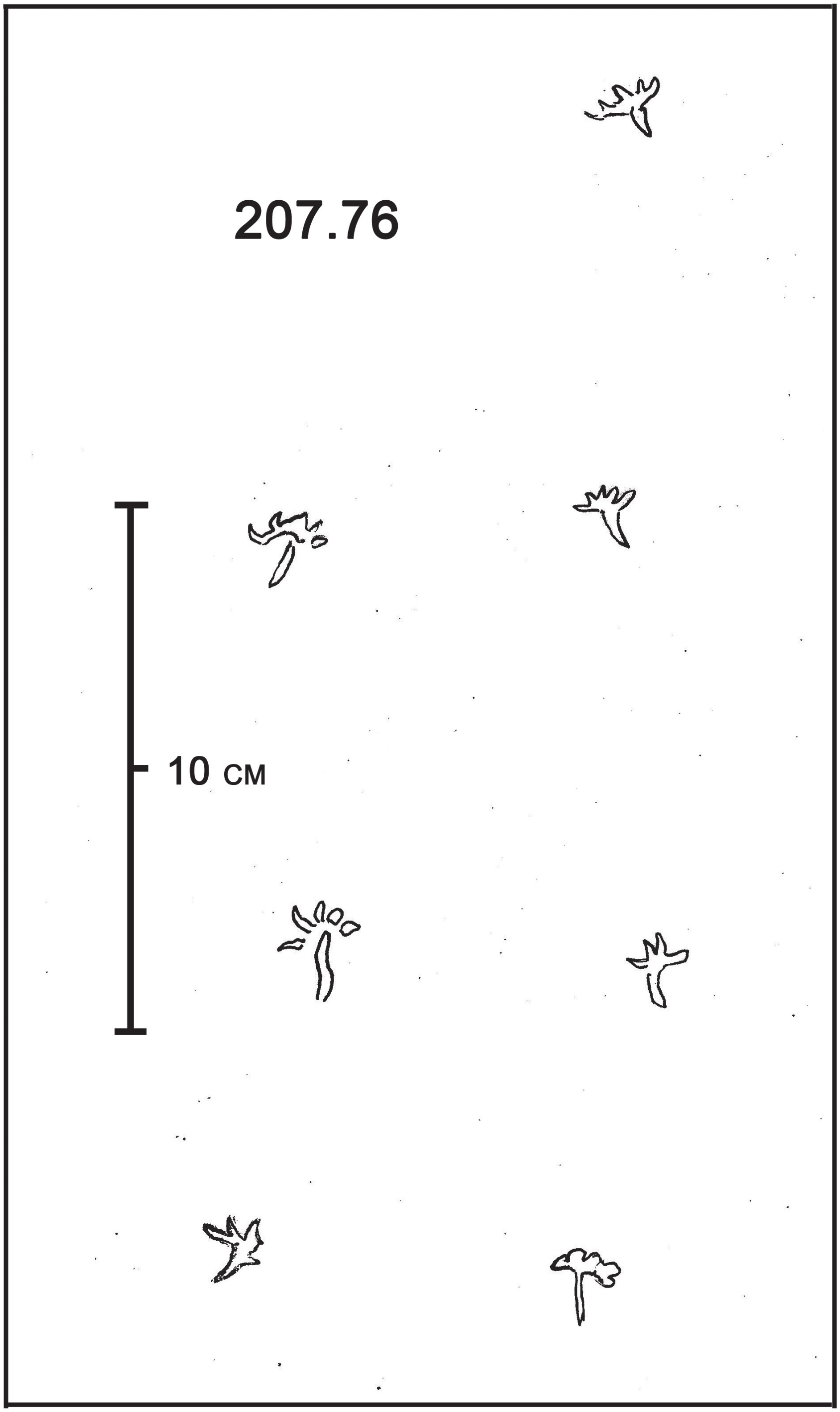


FIGURE 13. Limulid trackway (CU 207.76).

large pterosaurs. The relatively high abundance of tracks of different sizes, suggests that pterosaurs were abundant and represented by individuals of different sizes. If pterosaurs grew rapidly, like birds, it is probable that different-sized tracks represented different-sized species, rather than growth stages of a single of small number of species.

Viewed as a whole, the Dakota Group is extraordinarily track-rich and correspondingly poor in its production of vertebrate skeletal remains. Indeed, with almost 80 tracksites known in the eastern slope region (Lockley et al., 2010 census, plus additions in this volume), and more than 30 sites now known in the study area, the Dakota Group has become one of the best sampled stratigraphic units in the world from the view point of vertebrate ichnology. Given that other researchers have reported additional sites (see acknowledgements) in and around the western slope study area, some noted elsewhere in this volume, we predict that the present census, including the very preliminary data presented herein, is destined to grow substantially.

ACKNOWLEDGMENTS

We thank the BLM for authorizing work done by MGL under NCA permit COC743338. Supplemental work was conducted by Kent Hups under permit CO75347. This study is part of a project supported by the Korea National Research Institute of Cultural Heritage (NRICH 1305-A21F). We particularly thank Glade Hadden, of the Montrose district BLM, for accompanying us in the field on several occasions to collect and/or mold selected specimens in danger of erosion or loss. David Noe and Jon White of the Colorado Geological Survey also made helpful observations during field visits, and both made constructive reviews of the manuscript. Specimens assigned the CU prefix, representing the University of Colorado Denver, Dinosaur Tracks Museum, have now been assigned the UCM prefix (without changing specimen numbers) to indicate their transfer to the University of Colorado Museum of Natural History. We also thank Andrew Milner, St. George Dinosaur Discovery Site at Johnson Farms, St. George, Utah, for looking over photographs of many specimens and giving his professional opinion of the likely trackmakers.

REFERENCES

Caster, K., 1938, A restudy of the tracks of *Paramphibius*: Journal of Paleontology, v. 12, p. 3-60.

Farlow J.O. and Elsey, R.M., 2010, Footprints and trackways of the American Alligator, Rockefeller Wildlife Refuge, Louisiana: New Mexico Museum of Natural History and Science, Bulletin 51, p. 31-40.

Häntszchel, W. 1975. Trace Fossils and Problematica. Treatise on Invertebrate Paleontology. Part W, Miscellanea, Supplement 1, 269 p.

Houck, K., Lockley, M.G. Caldwell, M. and Clark, B., 2010, A crocodile trackway from the Dakota Group (Cretaceous) of the Golden Area, Colorado: New Mexico Museum of Natural History and Science, Bulletin 51, p. 115-120.

Kukihara, R., Lockley, M.G. and Houck, K., 2010, Crocodile footprints from the Dakota Group (Cretaceous) John Martin Reservoir, Bent County, Colorado: New Mexico Museum of Natural History and Science, Bulletin 51, p. 121-136.

Kukihara, R and Lockley, M.G., 2012, Fossil footprints from the Dakota Group (Cretaceous) John Martin Reservoir, Bent County, Colorado: new insights into the paleoecology of the dinosaur freeway: Cretaceous Research, v. 33, p. 165-182.

Lockley, M.G., 2010, A solution to the *Mehliella* mystery: Tracking, naming, identifying and measuring the first crocodylian trackway reported from the Cretaceous (Dakota Group, Colorado): New Mexico Museum of Natural History and Science, Bulletin 51, p. 157-164.

Lockley, M.G., Fanelli, D., Honda, K., Houck, K. and Mathews N. A., 2010, Crocodile waterways and dinosaur freeways: implications of multiple swim track assemblages from the Cretaceous Dakota Group, Golden area, Colorado: New Mexico Museum of Natural History and Science, Bulletin 51, p. 137-156.

Lockley, M.G., Holbrook, J., Hunt, A.P., Matsukawa, M., and Meyer, C., 1992, The Dinosaur Freeway: A preliminary report on the Cretaceous megatracksite, Dakota Group, Rocky Mountain Front Range and Highplains; Colorado, Oklahoma and New Mexico; *in* Flores, R., ed., Mesozoic of the Western Interior, SEPM Midyear Meeting Fieldtrip Guidebook, p. 3954.

Lockley, M.G., Hups, K., Trujillo, K. and Gerwe, D.S., 2014a, Mesozoic vertebrate tracksites from the Dominguez-Escalante National Conservation Area of western Colorado: implications for paleoecology and management: New Mexico Museum of Natural History and Science, Bulletin 62, this volume.

Lockley, M.G., and Lucas, S.G., 2011, Crocs not theropods were likely top predators on the Cretaceous dinosaur freeway: Implications of a large track census: Journal of Vertebrate Paleontology, v. 31, p. 146.

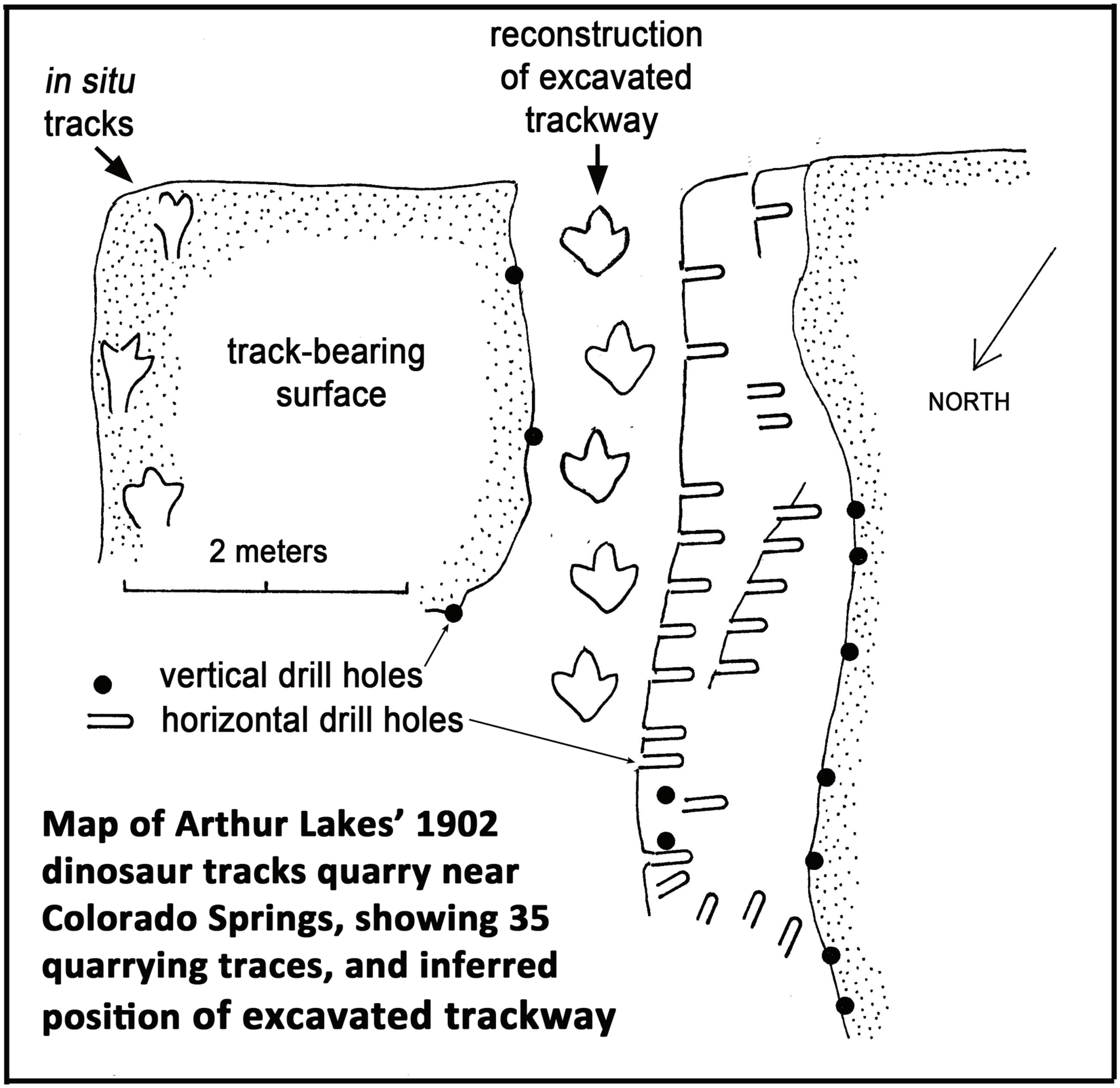
Lockley. M.G. and Schumacher, B., 2014, A new dinosaur and pterosaur track site in the Dakota Group (Cretaceous) of the La Junta area, Colorado: New Mexico Museum of Natural History and Science, Bulletin 62, this volume.

Lockley. M.G., Simmons, B. and Daggett, G., 2014b, A new dinosaur track site in the Dakota Group (Cretaceous) of the Golden area, Colorado: New Mexico Museum of Natural History and Science, Bulletin 62, this volume.

Lockley, M.G. and Wright, J., 2003, Pterosaur swim tracks and other ichnological evidence of behavior and ecology; *in* Buffetaut, E., ed., Evolution and Paleobiology of Pterosaurs. Geological Society of London, Special Publication, v. 217, p. 297-313.

Mehl, M.G., 1931, Additions to the vertebrate record of the Dakota Sandstone: American Journal of Science, v. 21, p. 441-452.

Young, R.G., 1960, Dakota Group of Colorado Plateau: Bulletin of the American Association of Petroleum Geologists, v. 44, p. 156-194.



Map of Arthur Lakes' 1902 dinosaur tracks quarry near Colorado Springs, showing 35 quarrying traces, and inferred position of excavated trackway