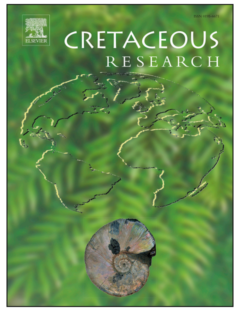
Accepted Manuscript



New theropod display arena sites in the Cretaceous of North America: Clues to distributions in space and time

Martin G. Lockley, Karen J. Houck, Neffra Matthews, Richard T. McCrea, Lida Xing, Kaori Tsukui, Jahandar Ramezani, Brent Breithaupt, Ken Cart, Jason Martin, Lisa G. Buckley, Glade Hadden

PII: S0195-6671(17)30286-0

DOI: 10.1016/j.cretres.2017.09.009

Reference: YCRES 3698

To appear in: *Cretaceous Research*

Received Date: 7 June 2017

Revised Date: 24 August 2017

Accepted Date: 12 September 2017

Please cite this article as: Lockley, M.G., Houck, K.J., Matthews, N., McCrea, R.T., Xing, L., Tsukui, K., Ramezani, J., Breithaupt, B., Cart, K., Martin, J., Buckley, L.G., Hadden, G., New theropod display arena sites in the Cretaceous of North America: Clues to distributions in space and time, *Cretaceous Research* (2017), doi: 10.1016/j.cretres.2017.09.009.

New theropod display arena sites in the Cretaceous of North America: clues to distributions in space and time.

Martin G. Lockley[1], Karen J. Houck[1], Neffra Matthews[2] Richard T. McCrea[3], Lida Xing [4], Kaori Tsukui[5], Jahandar Ramezani [5], Brent Breithaupt[6,] Ken Cart [7], Jason Martin [8], Lisa G. Buckley[3], Glade Hadden[9],

[1] University of Colorado Denver, Campus Box 172, Denver Colorado 80217-3364, USA, Martin.Lockley@UCDenver.edu *communicating author*

[2] National Operations Center, USDOI-Bureau of Land Management, Denver, Colorado 80225,

[3] Peace Region Palaeontological Research Center, Box 1540, Tumbler Ridge, British Columbia, V0C 2W0, Canada,

[4] School of the Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China

[5] Earth, Atmospheric & Planetary Sciences, Massachusetts Institute of Technology, 77 Massachusetts Ave, Cambridge, MA 02139

[6]Wyoming State Office, Bureau of Land Management, Cheyenne, Wyoming, 82003, USA.

[7] 3072 Bison Ave, Grand Junction, CO, 81504, USA,

[8] 3245 Downey Ct., #2, Clifton, CO, 81520, USA,

[9]Bureau of Land Management, Uncompahgre Field Office, 2465 S. Townsend Ave., 81401 Montrose, Colorado, 81401,USA.

Abstract

Previously-unknown large scale scrapes attributed to Cretaceous theropod dinosaurs from the Naturita Formation (formerly the Dakota Sandstone) of western Colorado were recently named as *Ostendichnus bilobatus* and interpreted as evidence of "nest scrape display," a type of courtship behavior previously known only in extant avians. However, comparatively little is known of the morphology, distribution and preservation potential of either modern or ancient nest scrapes. Further study of the initially described samples combined with new discoveries brings the total number of known in Colorado sites to five, one with two scrape-bearing levels. Combined, these site preserve a total of more than 100 recognizable scrapes from all these sites. We also identify the first *O. bilobatus*-like scrape from the Cretaceous of Canada. Although variable, a majority of the large sample of Colorado scrapes have the diagnostic characteristics of *O. bilobatus,* with two lateral troughs separated by a median ridge, and are sufficiently distinct to allow measurement of salient features such as scrape size, depth, and median ridge and average trough width. These provide data which indicate that theropod nest scrapes range from ~50 to ~200 cm in length and up to ~25 cm in depth, presumably indicate dinosaurs of different sizes, and variable time and energy spent in creation of individual scrapes. Scrape orientations are highly variable. Three of the sites occur at about the same stratigraphic level, although they are ~3.0-~6.0 km apart, suggesting that display arena sites may have been large, involving many dinosaurs and repeat activity in sequential breeding seasons. High-precision U-Pb zircon analyses by the CA-ID-TIMS method from a volcanic ash bed above the scrape bearing levels at Roubideau Creek (Colorado) yielded a weighted mean $^{206}Pb/^{238}U$ date of 97.689 ± 0.037 Ma (2σ internal error) and indicate a Cenomanian age for *O. bilobatus* scrapes in western Colorado.

Keywords: Colorado; Dakota Sandstone; Cenomanian; theropods; tracks; breeding behavior

1. Introduction

Multiple examples of the newly-named large trace fossil *Ostendichnus bilobatus* from the Cretaceous Dakota Group of Colorado (Fig. 1), were presented as evidence for "nest scrape display" behavior among large theropod dinosaurs (Lockley et al., 2016a). The trace fossil consists of paired, elongate grooves containing multiple scratch marks, made by theropod claws, on fluvio-lacustrine sandstone bedding planes. Four sites were initially reported, two of which revealed multiple, diagnostic, mostly well-preserved *O. bilobatus* traces suggestive of "display arenas" or "leks." In some cases the traces were directly associated with diagnostic theropod tracks. Associated traces in which the diagnostic bilobed ichnospecies morphology is less well-preserved are also attributed to cf. *Ostendichnus* or labelled as *O. bilobatus*–like and inferred to be due to variation in the intensity of the original activity of the theropod tracemakers and /or pre-burial and /or post exhumation weathering. The fact that a majority of these scrapes contain well-defined scratch marks indicates that the traces were preserved with little modification or deterioration of the details of surface relief soon after they were made, and thus may provide clues to the nature of the depositional environment at the time the scrapes were registered, and so help us understand the settings chosen by theropods for nest scrape display activity.

Although "nest scrape display" behavior is well known in certain extant ground nesting birds (avian theropods), including multiple species of the genus *Charadrius* (Bomford, 1986) and closely related genera (Cairns, 1982; Bergstrom, 1988; Whitfield and Brade, 1991), the distribution of scrapes has not been documented (mapped) except in the case of *Strigops habroptila,* the rare New Zealand parrot known as the Kakapo (Powesland et al., 1992), for which scrapes were referred to as "bowls." Harris (1984) described a single example of a trace resembling *O. bilobatus* attributed to a puffin, but did not comment on how widespread such traces might be. However, scraping behavior is common among extant birds, which may build, or begin building, multiple “play nests” (Goethe, 1937; Darling, 1938). Thus, nest scrape display rituals often result in construction of such “play” or pseudo nest building traces as are made by various extant birds engaged in such behavior. The preservation potential of such scrapes in different paleoenvironments with different substrates is unknown but evidently moderately good in the Dakota Sandstone (or Naturita Formation , *sensu* Carpenter, 2014) deposits described here. The preservation potential of small scrapes in the fossil record is discussed by Kim et al., (2016) in an intriguing report of a set of small scrapes from the Cretaceous of Korea, provisionally attributed to the theropod trackmaker of *Minisauripus* tracks (Lockley et al., 2008; Kim et al., 2012; Xing et al., 2016).

Other factors pertaining to nest scrape occurrences include the size of populations of nest-scraping birds and the preferred size of their territories and display arena sites. Extant birds nesting in larger colonies often stimulate breeding among other colony members more successfully and earlier than individuals in small colonies (Darling, 1938). Such questions point to the need for detailed studies of extant bird courtship and nest scrape display. Inferring preservation potential, after millions of years, especially in the case of small scrapes made by small birds, is inevitably conjectural. However, we can more rigorously evaluate the context of scrape sites in terms of paleoenvironments by considering local geological evidence of preferred paleosubstrates, or more generally assessing broadly defined habitats or physiographic regions. The records of scrapes made by large, Cretaceous non-avian theropods (Lockley et al., 2016a) help us understand the distribution of the traces and associated substrate types as they are preserved in the rock record. Although we cannot be sure that modern avians inherited nest scrape behavior from 100-million-year-old theropods, rather than evolving such behavior independently, the avian and non-avian theropod behavioral similarities, and the environments and paleoenvironments in which the behaviors were carried out, need to be explored using the spatial and temporal data on scrape distributions now becoming available.

Here we report on, newly-discovered display arena sites. One is a large site preserved in relatively close geographical proximity to the larger, western Colorado sites described by Lockley et al., (2016a). We also report on additional scrapes found at two of the previously known sites, including one which contains two scrape-bearing levels. The new site and additional scrapes provide the opportunity to better describe the inter-site distribution of the three largest sites in space and time and a detailed account of the intra-site variation in size, depth and distribution of scrapes.

Lastly we briefly describe a compelling example of an *O.bilobatus*-like scrape from the Lower Cretaceous (Albian) Gates Formation, at the W2 track site near Grande Cache, Alberta, which is one of the better known dinosaur tracksites in western Canada (McCrea et al., 2000, 2001). It is noteworthy that the scrape feature from this visually spectacular site is similar in general morphology, inferred depositional environment, and age to those from Colorado.

2 Material and Methods

2.1 Field mapping and data collection

The discovery of the new site herein named the “Club Gulch west” site (CGw) increases the number of known scrape sites in the Dakota Sandstone to five. Four of these sites occur in western Colorado and are named Duncan Road (DR), Roubideau Creek (RC), Club Gulch (CG) and the aforementioned CGw. The fifth site occurs at Dinosaur Ridge (DiRi) near Denver in eastern Colorado (Fig. 1). At the RC site scrapes occur at two stratigraphic levels (Fig. 2). Lockley et al. (2016a) presented photogrammetric maps of the two previously known, large, nest scrape display sites: the RC site with eight reported scrapes, and the CG site with ~60 scrapes. These findings are augmented by two other sites with isolated scrapes, one (DR) near the other large sites in Western Colorado and the other at Dinosaur Ridge (DiIRi), a well-known site in eastern Colorado.

The CGw site described here preserves at least 28 recognizable *Ostendichnus bilobatus* and cf. *Ostendichnus* scrapes in an ENE-WSW trending outcrop about 70 m long and 2 m wide (Fig. 3). Thus the three largest sites reveal multiple scrapes and occur within a triangular area with a maximum E-W extent of about 6 km. (Fig. 3) All of the scraped surfaces are found in elongate outcrops more or less aligned with the NE- ENE trends of drainages spilling off the northeast flank of the Uncompahgre uplift, shown with same orientation in Figure 3. With the additional scrapes reported here, the five known sites collectively provide a sample of at least 100 *Ostendichnus* scrapes (Table 1). This sample does not include the additional scrape here reported from the Albian of western Canada.

As outlined by Lockley et al. (2016a, supplemental information), the RC and CG sites were documented with both traditional compass and tape mapping and three–dimensional photogrammetic imaging. This method is reiterated here, although the methods used in our new photogrammetric surveys are briefly noted. The CGw site described here was also mapped using traditional compass and tape mapping. Complete photogrammetric imaging was not practical due to the presence of a number of relatively large trees that overshadowed some of the scrapes. Moreover, these trees and the location of the sandstone bed on the crest of a ridge resulted in slight southward (SSE) displacement of the blocks by root wedging and subsequent soil creep. However, the best preserved scrapes were photographed to obtain 3D photogrammetic images (Fig. 4), and a latex mold and replica were made to reposit at the Museum of Western Colorado (MWC) as MWC 8476 (see Lockley et al., 2016a, supplemental Information for methodology). In addition stratigraphic sections were measured, and re-checked, at all three sites (Fig. 2; see Lockley et al., 2016a, supplemental information, fig. S1 for further details of the RC and CG sites). The newly described *O. bilobatus*-like scrape from Canada was recorded using a scaled 3D photogrammetric model produced in Agisoft Photoscan (v.1.0.4) The photographs of the near vertical track surface were taken from ground level and the base of the surface. Measurements of the scrape trace were made using MeshLab v1.3.3 and through the use of the color depth map generated in CloudCompare v2.6.3.beta. The methods and software used are essentially identical to those outlined in the previous study of the Colorado sites (Lockley et al., 2016a).

Lockley et al. (2016a) reported a single set of *Ostendichnus bilobatus* scrapes from the Dakota Sandstone (= Naturita Formation, *sensu* Carpenter, 2014) at the DiRi site in eastern Colorado, the only *O. bilobatus* site currently known outside western Colorado. In that study one set of DiRi scrapes was illustrated using a 3D image (Lockley et al., 2016a, fig. 4b). During the course of the present study, a second well-preserved set of scrapes was identified at Dinosaur Ridge. Both were subjected to photogrammetric analysis and both were replicated by making a latex mold and fiberglass replica, given the University of Colorado Museum of Natural History (UCM) specimen numbers (UCM 200.66 and UCM 200.67, Fig. 5). Interest in the scrapes, visible and easily-accessible at Dinosaur Ridge, is leading to the design of new interpretative signs and revision of the explanatory guidebook (Lockley and Marshall, 2014, in prep). The DiRi scrapes were also featured in a Science Channel documentary *Secrets of the Underground* released in 2017. (http://www.sciencechannel.com/tv-shows/secrets-of-the-underground/videos/secrets-of-the-underground-promo). Furthermore, using 3D printing techniques it was possible to make a full sized replica of the *O.bilobatus* type specimen for an exhibit at the Naturalis Biodiversity Center in Leiden in the Netherlands (Breithaupt et al., 2017).

At all sites recognizable scrapes were numbered (Fig. 3), and all lengths, widths and depths of diagnostic, bilobed scrapes were recorded and tabulated, with anterior orientation when such measurements could be determined (Table 1). In the case of cf. *Ostendichnus* scrapes occurring as oval, sub-circular or near-circular bowls or hollows, the maximum and minimum diameters and depths were recorded, along with the orientation of the long axes, which usually coincide with direction of scrape marks (Fig. 6). Individual examples of scrape overlap were recorded. Although the width of median ridges that separate the two troughs (left and right scrapes) in bilobed scrape sets is variable, we recorded representative ridge width near the mid-point of the long axis. After subtracting, the width of the median ridge from the total width of the scrape, half the remaining scrape width represents the mean width of each trough (Fig. 6). Generally in well-developed scrapes the width of each trough is similar. Trough width in turn approximates foot width as confirmed in cases where individual tracks are associated with troughs (Lockley et al.,2016a, fig. 3a).

There is no previous methodological precedent for measuring the orientation of scrapes. The method used here involves obtaining the azimuth (between 1^o and 180^o) of the long axis of scrapes from photogrammetric images and maps of the three main sites (RC, CG, CGw: Fig. 3). This method applies equally well to bilobed and oval scrapes, especially those where scratch marks run parallel to the long axis of the whole scrape, which is typical in most cases. A few scrapes such as those from the upper level at RC (Fig. 7) are incomplete and out of context, i.e., not *in situ*, and so do not obviously fit either the bilobed or oval shape categories. Given that orientations on rose diagrams (Fig.7) are recorded in 15^o sectors, taking measurements from photogrammetic images of sites RC and CG, with a grid overlay on the computer screen, produces results at least as consistent and accurate as measurements taken individually with compass or from hand drawn maps: i.e., from sites CGw and DiRi. As discussed below, the CGw site contains blocks that are slightly displaced by root wedging and soil creep, though not rotated. The long axes of scrapes do not indicate the anterior orientation in most cases. This is partly because the claws of the foot in motion can leave distally tapered scratch marks on anterior entry and on posterior exit. To date only 10 scrape sets have provided unequivocal anterior orientations (shown in bold in Table 1). For this reason both the azimuthal directions between 1^o and 180^o and the reciprocal orientations between 181^o and 360^o are plotted on rose diagrams (Fig. 8) so as not to assume directionality in cases where it is not known. To prevent duplicating the total of measured orientations (N), where anterior is not known, each azimuth is plotted as ½ N (between 1^o and 180^o) as is the reciprocal ½ N + 180^o (in the 181-360^o sector). Separate plots are presented for each of the main sites as well as for the combined sample. In addition to the orientation data (Table 1), a few additional orientation data points were obtained from the maps for scrapes that did not yield other reliable measurements. Lastly it should be noted that we report *modal* not mean scrape orientations (Table 2). This is because the large number of "bimodal" measurements (e.g., 1^o or 181^o) would produce misleading averages (e.g., mean = 91^o) with no meaningful values related to actual (modal) orientations.

2.2 Methods of U-Pb geochronology

Zircons were isolated from a ca. 0.5 kg volcanic ash sample from Roubideau Creek using standard crushing, as well as magnetic and density separation techniques. Individual zircon grains were hand selected and analyzed following the procedures described in Ramezani et al. (2011). The selected grains were pre-treated by a chemical abrasion method modified after Mattinson (2005) involving thermal annealing at 900 °C for 60 hours and leaching in concentrated HF at 210 °C for 12 hours in order to mitigate the effects of radiation-induced Pb loss in zircon. The EARTHTIME ET535 mixed ^{205}Pb-^{233}U-^{235}U tracer (Condon et al., 2015 and McLean et al., 2015) was used in the analyses and isotopic measurements were made either on the VG Sector 54 or Isotopx X62 multi-collector mass spectrometers equipped with Daly photomultiplier ion-counting systems at the Massachusetts Institute of Technology (MIT). Reduction of mass spectrometric data, as well as calculation of dates and propagation of uncertainties were done using the Tripoli and U-Pb_Redux software and associated algorithms (Bowring et al., 2011; McLean et al., 2011).

Complete U-Pb data are given in Table 3 and the results and date distribution plot discussed below. All uncertainties are reported at 2σ level and correspond to the analytical (internal) errors only, except for the weighted mean date in Section 3.3 where the total uncertainty (incorporating those of tracer calibration as well as U decay constants of Jaffey et al., 1971) is reported in brackets. The age of the tuff sample is derived from the weighted mean ^{206}Pb/^{238}U date of the analyzed zircons and is considered to be the best approximation for the depositional age of the scrape-bearing beds which lie ~10 m and ~14 m below the ash bed.

3 Results

3.1 Scrape size, distribution and orientation

As shown in Tables 1 and 2 a total of 58 scrapes provided reliable measurements from a total sample of 98 scrapes from four sites including DiRi: Tables 1 and 2. The single set of triple scrape marks from the DR site have a maximum length of 140 cm, and combined width of all three scrapes 98cm (Lockley et al., 2016a, fig. 4a). However, these measurements were not included in the present analysis, due to the unusual triple configuration and the small sample size (N=1). Likewise the scrapes found on two blocks from a level above the main RC site are illustrated (Fig. 7) but not included in the analysis due to incompleteness and lack of adequate context by which their morphologies could be categorized. In fact the traces on the larger of the two surfaces (Fig. 7a) resemble only slightly elongated tridactyl tracks, and are not obviously a single or multiple scrape set. Nevertheless, adding the two (N=2) illustrated sets of traces (Fig. 7) to the DR scrape report results in a total of 101 scrapes. Of the 58 scrapes (57.4%) that were measured, 37 (63.4%) were bilobed, and the remainder more or less bowl shaped. A small number of scrapes from the CG site overlap, but none from the RC and CGw site do, although several are located close to one another. The scrape set from Grand Cache, Alberta adds an additional report of scrapes to the total recorded from the Colorado sites, but this isolated report is not included here in our tabulations.

Only two well-defined scrapes have been identified at DiRi on a locally undulating surface with many irregularities and small (5-10 cm wide) log impressions. The scrapes are similar in width, but one is much longer (180 cm) than the other (95 cm). Both scrapes have similar median ridge widths (20-21 cm) but the longer scrapes are deeper and appear to contain a tridactyl track in the middle of the right side trough (arrow in Figure 5A). The considerable difference in scrape length (L180/ L95 = 189%) compared with the differential width (W83/W80 = 103%), i.e., the aspect ratio, reflects the fact that scrapes were made by anterior-posterior motion of the foot, parallel to the long axis of the troughs (Fig. 6) without significant transverse side-to-side movement. A considerable number of bowl shaped depressions occur on this surface, but even though they resemble a few "bowl-shaped" features from the western Colorado sites, or even the Kakapo bowls described by Powesland et al. (1992) they lack scratch marks, and so cannot be interpreted as scrapes with certainty.

The 8 measured scrapes from the RC site are part of a sample of 11 scrapes, of which a few are poorly preserved. Scrapes from this site have the largest mean size among the three western Colorado samples with multiple scrapes (Table 2). They average ~120 cm long, ~86 cm wide and 10.6 cm deep (N=8) even though scrapes 1, 2, 7 and 10 are relatively short (mean L~91, W76 and D5 cm respectively), as compared with scrapes 4, 5, 6 and 9 (mean L~153, W~96, and D~18 cm). This suggests a bimodal distribution which is consistent with the identification of a large track about 30 cm wide in the holotype *Ostendichnus bilobatus* scrape (RC 5) and a smaller theropod track ~18 cm wide in scrape 7 (Lockley et al., 2016a). However, despite this length differential between the two groups (L153/L91 = 168%) the width differential is less pronounced (L96/W76 cm = 126%). Scrape 8 consists of an arcuate set of scrapes on the periphery of a large oval bowl, (compare Fig. 3 with Lockley et al., 2016a, fig 3a).

The CG site reveals at least 58 identifiable scrapes of which 33 yielded reliable measurements (Tables 1, 2). Some recognizable scrapes could not be measured accurately because they were overlapped by other scrapes rendering their outlines and shapes obscure. Some of the largest and deepest scrapes (e.g., CG8, CG9, CG22 and CG25) are non-bilobed bowls (cf. Powesland et al., 1992), with large clear scrape marks (Lockley et al., 2016a, fig. 2a). Conversely, the CG site also reveals some of the smallest and shallowest scrapes (e.g., CG5, CG6, CG20 and CG46) which are recognizably bilobed with individual troughs suggesting foot widths of about 20 cm. In some cases these small scrapes are as wide, or wider, than long. As noted by Lockley et al., (2016a) two scrapes, here designated as CG31 and CG46, have shallow sand aprons behind them indicating the orientation of the theropods when scraping and ejecting or spraying sand posteriorly,

The CGw site was not discovered or documented prior to the description of scrapes from the other sites (Lockley, et al., 2016a). This site reveals at least 28 identifiable scrapes of which 15 yielded reliable measurements (Tables 1 and 2). Some recognizable scrapes were not measured because they were overlapped by other scrapes rendering their outlines and shapes difficult to measure accurately. In general, the mean size of the scrapes is less than at the other sites (Table 2): i.e., 84% as long and 80% as wide as the mean value for all sites (Table 2). This might be due in part to the location of the site on a ridge that has been exposed to weathering for longer than the more-recently exhumed sites at CG, RC and DiRi. However, it is noticeable that the mean scrape width and mean width estimated for individual troughs is noticeably less than for the other sites. Mean trough width which is a general indication of foot width is only 20.3 cm compared with 31.0-34.3 for the other three sites. The best preserved set of scrapes, CGw2 shows a clearly defined tridactyl scrape with a width of 21 cm and the middle toe trace the longest. This scrape was molded and replicated as Museum of Western Colorado specimen (MWC 8476).

The long axis orientations of all clearly bilobed or elongately oval scrapes were measured. In most cases scratch marks also aligned with the long axes of scrapes. The combined results for all three of the large western Colorado sites (N=79) indicate a slight preference for a NE-SW trend (Fig. 8). The orientations of 11 scrapes from the RC site show a NNE-SSW trend, but this is the smallest sample. The orientations for the CG site, with the largest sample (N =45) show a ENE-WSW trend, and the CGw site (N= 23) shows a NNW-SSE trend. Only two scrape orientations were measured at DiRi as 0^{o} and 270^{o}. No preferred orientation can be inferred from such a small sample. Possible interpretations of the data from the Western Slope sites are discussed below.

Length width and depth data from the CGw sites (N=13) indicate its scrapes are markedly shorter than those (N=38) recorded from the other sites (Fig. 9). However the mean depth of the scrapes from the CGw site is about average for all sites and larger than the mean for the CG site. The implications of this data are discussed below.

In addition to scrapes found on the surfaces described here, there are a few recognizable tracks (Fig. 10) associated with each of three sites (RC, CG, and CGw). With the exception of a possible ankylosaur manus track from the CGw site, all the tracks are theropodan. RC5 and RC7 are unequivocally associated with scrapes 5 and 7 respectively, and represent theropods of significantly different sizes. The larger one has been labelled as *Irenesauripus* (Lockley et al., 2016a). Both indicate relatively robust theropods with low angles of divarication between digits II and IV. In contrast the theropod track recorded from the CG site (Fig. 10C) has slender, more widely divaricated digits and resembles a large *Magnoavipes*. Likewise the track from CGw, recorded near CGw7 also resembles *Magnoavipes*, but is much smaller. Neither is sufficiently well preserved to apply this ichnogenus name with absolute certainty. The tridactyl track CGw2 appears to be a single scrape that could be interpreted as a single track, with low divarication, that was elongated by scraping motion. As discussed below, the variance of sizes and shapes allows for varied interpretations of possible scrape makers.

A scrape trace remarkably similar to *Ostendichnus bilobatus* was occurs in the Lower Cretaceous (Albian) Gates Formation, at the W2 track site near Grande Cache, Alberta, Canada (Fig 11). This bilobed trace is visible in previously published images of this track site (McCrea 2000 – fig. 4a; McCrea et al., fig. 20.8). The size and shape of the traces is consistent with the dimensions of the larger Colorado scrapes. The overall morphology and the similarity of measured dimensions support the identification of the W2 scrape trace as *Ostendichnus bilobatus*. This is the first recognized example of this ichnotaxon outside of Dakota Sandstone (= Naturita Formation, sensu Carpenter, 2014) of Colorado, which is early Cenomanian in age as constrained by the U-Pb date of the ash bed reported herein. Thus, the Albian age of the Canadian scrapes is broadly contemporaneous with *Ostendichnus* sites from western Colorado. The diminutive Korean scrapes (Kim et al., 2016) were not labelled as *Ostendichnus*.

3.2 *Sedimentological context of the scrape sites*.

Lockley et al. (2016, Supplementary Information., SI fig. 1) described the lithology of the scrape at the main RC site as a 0.5 m unit of matrix-rich, granular, medium to coarse, sandstone comprising the upper part of a channel fill deposit approximately 1m thick and 6m wide, and overlain by 15 cm of coal. The CG scrape-bearing unit was described as a bedding plane surface at the top of a thinly bedded, very fine sandstone unit interpreted as a crevasse splay or similar overbank deposit, overlain by papery, organic rich mudstone. It was also noted that where the 5-10 cm thick upper layer of sandstone had been removed, small inliers with small scale symmetric ripple marks with a WSW-ENE ripple crest trend were exposed. The scrape-bearing sandstone at CG was thought to be stratigraphically higher than the scrape bearing sandstone at RC. This tentative conclusion is again implied in the correlation shown here (Fig. 2). The discovery of the new CGw site has allowed us to measure a third section (Fig. 2) and walk out an approximate correlation with the scrape-bearing beds at the Club Gulch (CG) site, which confirmed that the scrape bearing bed at CGw is in fact stratigraphically a little higher than at the other sites. However, based on the tentative correlations suggested here, two conclusions are pertinent: 1) there is considerable lateral variation in beds over short distances of less than 3 km, and 2) all four scrape bearing levels, including the upper level at RC are interpreted to lie within a ~4 meter stratigraphic interval, within a geographic region of about 6.0 km in lateral extent.

Placing these sections in a broader context, requires that we recognize the Dakota Sandstone as a transgressive deposit that records the initial incursion of the Western Interior Seaway into the area of western Colorado during the Cenomanian, as dating evidence (below) confirms. The Dakota Sandstone is about 20 m thick and consists of a conglomeratic lower interval, a heterolithic middle interval, and a sand-rich upper interval. These intervals are interpreted as braided river deposits, swampy coastal plain deposits, and marine shoreline deposits, respectively (Lockley et al., 1992, 2006, 2010, 2014; 2016a; Fig. 2).

Though one scrape site occurs at the contact between the conglomeratic interval and the heterolithic interval, the other three sites occur within the heterolithic interval. This could be interpreted to mean that the swampy coastal plain of the Western Interior Seaway was the preferred location for theropods to perform mating displays during the breeding season, and that the coastal plain was their breeding ground. However, it could also be interpreted to mean that the low-energy conditions along the coastal plain were more conducive to the preservation of scrape marks than the higher-energy conditions of the braidplain or the marine shoreline.

The lower site in the RC section occurs at the top of a lens-shaped conglomerate bed interpreted to be a braided stream channel deposit. The upper site at RC occurs on the top of 0.2 m of massive fine sandstone in a sequence of interbedded coal deposits and subaerial splay deposits. The massive sandstone gives few clues to its exact mode of deposition.

The site at CGw occurs on the top of a one-meter-thick normally graded bed of conglomeratic sandstone interpreted to be the result of a splay that was deposited in a shallow lake. East of the CGw site, similar deposits have symmetrical wave ripples and vertical root traces on their upper surfaces, implying that the lakes were ephemeral, and that the lake bed deposits became emergent at times.

The site at CG occurs on the top of 0.3 m of thinly bedded sandstone, interpreted as the result of a splay that was deposited in an ephemeral lake, as wave ripples a few cm below the scraped surface imply. Horizontal root traces on the scrape surface support this interpretation by indicating a high water table.

All of the scrape marks occur on the tops of sandstone beds that were either deposited subaerially or became emergent. It seems that soft, moist expanses of sand were preferred for theropod display arenas. Two of the four scrape surfaces (CG and lower RC) were covered by low-energy deposits like shale or coal. The CGw site is overlain by clayey soil that is likely weathered shale. The low-energy deposits probably aided in preserving the tracks during burial. The easily erodable nature of the shale and coal relative to the sandstone likely aided in the discovery of the scrape marks, by facilitating the exhumation of the more resistant sandstone surfaces as the softer material was eroded away.

The *Ostendichnus* trace from W2 site within the Gates Formation in Canada was registered on an iron and organic rich, relatively fine-grained sandstone that is dominated by ankylosaur (*Tetrapodosaurus borealis*) trackways, with only one large theropod trackway (possibly *Irenesauripus* isp.), and one small theropod trackway (cf. *Irenichnites gracilis*). The W2 scrape trace has no tracks leading up to or away from it and it is likely that this trace was made either by a track-maker that had traversed an overlying bedding plane and excavated down to this track level, or perhaps the scrape was registered on this surface at a time when the sand was too firm to leave deep recognizable tracks. The substrate and vertebrate ichnofauna are somewhat intermediate between those preserved within the fine-grained and high-organic content sediments, which are characteristic of the *Tetrapodosaurus* ichnofacies, as found in most of the other sites in this area, and those of the coarse-grained and low organic content substrates which are dominated by tracks made by bipeds. Since *Tetrapodosaurus* tracks from Colorado are often very deep and associated with fine grained substrates, as in Canada, it is possible to infer that they frequented subenvironments with wetter substrates than those preferred by theropods.

3.3. U-Pb age constraints on scrape sites

The sampled ash bed at RC is 20 cm-thick, visibly recessed in the outcrop and has a pale yellow weathering color that is distinct from the surrounding Dakota sandstones and siltstones. Sharp lithologic boundaries, lack of bedding and the massive nature of the deposit suggest that the bed was formed by an ash fall.. A total of 8 single zircon grains were analyzed from the RC ash bed by the U-Pb CA-ID-TIMS method following the procedures described in 2.2. Seven of the analyses define a statistically coherent cluster with a weighted mean $^{206}Pb/^{238}U$ date of 97.689 ± 0.037 [0.12] Ma and a mean square of weighted deviates (MSWD) of 1.5 (Table 3, Fig. 12). This age is mid-Cenomanian according to the latest compilation of the geologic time scale (GTS2016: Ogg et al., 2016) and the Cenomanian-Turonian age calibration of Eldrett et al. (2015).

The dated volcanic ash lies stratigraphically 14 m and 10 m above the lower and upper scrape-bearing horizons at RC, respectively. Although the new U-Pb date does not directly constrain the scrapes because of stratigraphic distance, it provides a good (minimum) approximation for the depositional ages of the scrape-bearing horizons. The new mid-Cenomanian age reported here for the Dakota Formation strata at RC is consistent with the recent U-Pb CA-ID-TIMS zircon geochronology from Dakota Formation in eastern Utah (Barclay et al., 2015) that preserves an important angiosperm plant fossil record.

4. Discussion

The results of the present study have several implications, pertaining to the size frequency and morphology of scrapes, their abundance and distribution in space and time, and their relationship to sedimentary facies. The occurrence of a diagnostic *O. bilobatus*-like scrape in the Albian of Canada (Fig. 11) in a similar coastal plain setting and in association with theropod tracks is particularly intriguing from a paleogeographical point of view because it significantly broadens the known distribution of these scrape traces in space and time. One of the questions raised by the original discovery was when such nest scrape display behavior originated. The Gates Formation of western Canada is considered (middle) Albian in age based on ammonoid fossils collected from its basal marine sandstones (Stott, 1968), although lateral changes in thickness and facies prevents robust age constraints on the terrestrial scrape bearing strata. A general Albian to Cenomanian age can be assigned to the known North American scrapes at this time. According to Kennedy et al. (2014) the Gates Formation is Albian in age, between 100 and 113 Ma, which potentially makes the Canadian scrapes up to 15 million years older than those from Colorado. Given that the Albian-Cenomanian boundary defines the Early and Late Cretaceous boundary, technically the age of the Canadian scrapes is Early Cretaceous and the Colorado scrapes are

Late Cretaceous. According to Kang and Paik (2013) the estimated age of the Haman Formation from which the small Korean scrapes were reported (Kim et al., 2016) is Albian or Cenomanian.

The age and definition of the Albian-Cenomanian stage boundary, which is the boundary between the Lower and Upper Cretaceous, have been much discussed Scott et al. (2009), and discussion and dating have been refined in the recent decades. At present, $^{40}Ar/^{39}Ar$ geochronology from the basal Cenomanian ammonite zones in Japan (Obradovich et al., 2002) combined with cyclostratigraphy and other biostratigraphic constraints from the GSSP section in southern France (Gale, 1995) are used to extrapolate an age of 100.5 ± 0.4 Ma for the Albian-Cenomanian boundary (Ogg and Hinnov, 2012). [Compare with previous estimates of 99.6 - 97.3 Ma (Scott et al., 2009)]. Barclay et al. (2015) reported three Cenomanian U-Pb CA-ID-TIMS dates from air-fall ash horizons from the Dakota Formation at Westwater, Utah a locality only 92 km northwest of the RC site, which may represent a similar stratigraphic level to the RC site. The Westwater site gave weighted mean $^{206}Pb/^{238}U$ dates that ranged from 97.949 ± 0.037 Ma to 97.601 ± 0.049 Ma, the youngest of which is fairly comparable to the date reported here from RC (97.689 ± 0.037Ma). This date, according to Ogg et al., (2016) is middle Cenomanian.

The scrapes at Dinosaur Ridge in eastern Colorado are considered largely similar in age to those from Western Colorado, i.e., probably Cenomanian, and also younger than those from Canada. They occur in what has been referred to as Sequence 3 of the Dakota Group in this area (Weimer, 1989; Lockley et al., 2016b) which yielded dates in the range of 100-97 Ma according to Holbrook et al. (2006). This sequence has an estimated age range of ca.100.9 Ma to 97.2 Ma based on biostratigraphic and sequence stratigraphic projections, as well as graphic correlations involving bentonite beds with $^{40}Ar/^{39}Ar$ dates (Scott et al., 2009). These Cenomanian dates associated with the onset of the T6 transgression contrast with the Albian U-Pb dates of 104.6 Ma and 103.7 Ma obtained by the MIT lab from the from the lower part of the Dakota Group at Dinosaur Ridge referred to as the Plainview Sandstone, and associated with Sequence 2 and the T5 transgression. Lockley and Marshall, (2014 and in prep). These underlying Sequence 2 units reveal different invertebrate and vertebrate ichnofaunas from those found in the track-rich, Sequence 3 deposits, well known as aggrading, early transgressive systems tract, discussed in many ichnological papers (Lockley et al., 1992, 2006; 2010, 2016a,b, and references therein). According the stratigraphy of Weimer and Land (1972) the dated volcanic ashes in Sequence 2 at Dinosaur Ridge lie 60-70 meters below track rich beds of Sequence 3.

The best-preserved bilobed scrapes from DiRi and all three of the larger Western Slope sites are similar in morphology and easily assigned to *Ostedichnus bilobatus*. The maximum lengths of scrapes from the RC, CG and DiRi sites (180-210 cm) are very similar, and the depths and dimensions of the median ridges and troughs are also comparable (Tables 1 and 2). The scrape length (~240 cm) and width (~107.0 cm) and depth (9-12 cm) of the Canadian scrape is consistent with the largest Colorado scrapes although the width of the median ridge (~38 cm) is greater.

The maximum length of scrapes (110 cm) and mean trough width (20.3 cm) recorded from the CGw site are significantly less than those from the other sites. This suggests that the scrape makers active at this site were smaller animals, and /or possibly less active. This conclusion is tentatively supported by the occurrence of a single shallow tridactyl *Magnoavipes*-like track from the CGw site with a length and width of 21 cm and 19 cm, respectively (Figs. 3 and 10). However, there is no evidence that this track maker was also the scrape maker. As noted above, although some of the scrape makers at the RC site were large (foot width ~30-35 cm measured in RC 5, and inferred from mean trough width: Table 2) smaller scrape makers were also active at the RC site, as proven by at least one unequivocal smaller track (width 18 cm) associated with scrape RC7 (Lockley et al., 2016a, fig. 3c).

These size frequency data have intriguing implications. Based on recognizable tracks we can infer that both large and small theropods were active at the RC site, and based on trough widths the same inference is possible for the CG site, from which a theropod track (width 39 cm) was also reported by Lockley et al., (2016a, fig 2a: Fig. 10C). Scrape CGw2 (Fig. 4A,B) is essentially an elongate theropod track 21 cm wide. Thus, the CGw site provides no unequivocal evidence of theropod scrape makers with feet wider than 21 cm. Possible interpretations of theropod track makers of different sizes are as follows: 1) they represented different species, 2) they represent different sized sexual dimorphic individuals of the same species or 3) they represent different sized individuals of the same sex: i.e., juvenile vs. adult age cohorts.

All of the larger sites indicate that bilobed scrapes (*O. bilobatus*) are more common than non-bilobed and mostly oval bowls. This indicates a certain degree of uniformity of activity among scrape makers: i.e., not much lateral or rotational movement once a nest scrape display activity was initiated by an individual. This could indicate a directional focus by the scrape maker, making it reluctant to change position in most cases. The reasons for this are conjectural, but most likely reflect certain repeated or stereotyped motions, or body orientations and visual focus during courtship rituals, perhaps in order to keep other ?conspecific individual dinosaurs (mate or rivals) in view. The less diagnostic bowl shapes traces appear to indicate more variability in foot motion leading to mixing or blending of scrapes made by both left and right feet. The possibility of overprinting of scrapes (over-scraping) cannot be ruled out but seems unlikely given that there are no reports of such behaviors from extant avian theropods. Where there is slight overlap of adjacent scrapes, as in case of very large oval scrapes, CG8-CG11which are up to 2.1 meters long and characterized by similarly good preservation, (Lockley et al., 2016a, fig. 2 a), it is possible they were all made by the same energetic individual moving short distances in a short period of time (rather than being made by different individuals in the same area during a short time period). As noted below, bowls and bilobed traces that lack scrape marks likely indicate longer periods of exposure prior to burial, but those with clear scrape marks and sand aprons indicate excellent preservation conditions.

One of the puzzles of all the Colorado sites is the lack of well-preserved tracks on the originally horizontal, non-scraped surfaces between the conspicuous scrapes. (The Canadian site, Fig. 11, proves the exception to this pattern). At all three of the larger western Colorado sites the few faintly recognizable tracks are all shallow and inconspicuous, while a few deeper ones are integrated within the scrapes: i.e., deliberate scrape or digging traces that were not overprinted (over-scraped) or obscured by repeated scrape activity. However, with one exception all recognizable tracks are attributable to theropods (Fig. 10). The sedimentological implications of this observation are that the sand was firm and not easily compacted. We infer that such substrates were favored, over others with different consistencies, for display scrape activity.

The inference that all three large western Colorado sites (RC, CG, CGw) occur at approximately the same stratigraphic level, also has intriguing implications. Given that the exposed surfaces at all three sites likely represent only a small part of the scrape surfaces that could potentially be exposed by excavation, it is natural to infer that the scraped surfaces were more extensive. However, the impracticality of such excavation renders the point moot. While it is possible that the individual sites preserve pieces of a single, extensive, isochronous display arena, comparable to a single surface megatracksite (Lockley and Hunt, 1995), the individual beds preserving the scrapes vary laterally in composition and texture, and pinch out over relatively short distances. This puts the single-surface interpretation in doubt and instead suggests multiple, more localized arenas with similar substrate conditions. Additionally, the occurrence of two scrape horizons at the RC site suggests that display arenas were established in the same area in sequential seasons. This would constitute display arena site fidelity analogous to nest site fidelity (Horner 1984), which is well known among avian and non-avian dinosaurs.

As reviewed by Lockley et al., (2016a) the evolutionary relationship between birds (avian theropods) and non-avian theropods is well established. Based on these phylogenetic relations there is also an extensive literature speculating on the likelihood that non avian theropods engaged in bird like courtship display behaviors using visual aids like crests, colorful feathers and energetic movements (Hone et al., 2011). However, until the discovery of the scrapes described from Colorado, there was absolutely no physical evidence for courtship display by non-avian theropods, and no claims that scrapes represented what ornithologists call "nest scrape display" and display arenas or leks (Lockley et al., 2016a). Seminal literature on avian courtship behavior, indicates that sociality is an impetus to successful breeding and fertility: i.e., larger colonies encourage breeding behavior among its individual members (Darling, 1938). This may account for, or at least correlate with, the flocking instinct and the development of lekking as a fruitful breeding strategy.

5. Conclusions.

1) Previous reports of the large nest scape display trace *Ostendichnus bilobatus* at four sites in the Cretaceous of Colorado, are here increased to six reports, five from the Dakota Group of Colorado and one from the Gates Formation of Canada. A seventh report of similar but very much smaller scrapes from the Haman Formation of Korea may represent nest scrape behavior but this small Korean trace has not been labelled as *Ostendichnus*.
2) All the reports are from the Albian and/or Cenomanian, and all the North American reports indicate large theropods inhabiting coastal plain deposits. The Korean scrapes are very small and associated with fluvio-lacustine deposits.
3) The new *O. bilobatus*-like traces increase the total sample from less than 70 to more than 100, providing a useful sample for characterizing the typical morphology and size range.
4) The three largest Dakota Group sites account for 95% of the sample and are all associated with a thin package of sandstone units deposited within an area with a lateral extent of about 6.0 km. Thus, the substrates or local paleogeography may have provided a preferred display arena setting for theropod dinosaurs.

5) Multiple scrape levels at the same site suggests display arena site fidelity.
6) A weighted mean $^{206}Pb/^{238}U$ date of 97.689 ± 0.037 from an ash bed 10 m above one of the Dakota scrape sites indicates a Cenomanian age, consistent with other dates of correlative deposits from the region.
7) While the Dakota Group, already famous for its abundance of vertebrate and invertebrate traces, remains the focal point for study of *O. bilobatus* and display arena sites, along with the beds in which this ichnotaxon appears abundant, the occurrences of similar traces in Canada and Korea suggest that nest scrape display traces were widely distributed and suggestive of a widespread theropodan mating or courtship behavior.

Acknowledgements

Research at all western Colorado sites, including permission to make MWC replica 8476, was conducted using permit COC76204 issued by the Bureau of Land Management, whom we thank for their cooperation. Research at Dinosaur Ridge including making of replicas UCM 200.66 and 200.67, was facilitated by History Colorado (Permit 2016-25), and Walther Thurner, C.F. Maier Associates , Golden Colorado. Manuscript coordination was facilitated by the offices of the University of Colorado Denver, Dinosaur Trackers Research Group, with in kind support from The Peace Region Palaeontological Research Center and the Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology. Christian Thurner also assisted with field work. We thank Gerard Gierlinski, Polish Geological Survey, Warsaw, and Jerry Harris, Dixie College, St. George, Utah for their helpful reviews of tis MS.

References

Barclay, R. S., Rioux, M., Meyer, L. B., Bowring, S. A., Johnson, K. R., and Miller, I. M. 2015. High precision U-Pb geochronology for Cenomanian Dakota floras in Utah. Cretaceous Research 52, 213-217.

Bergstrom, P. W. 1998. Breeding Displays and Vocalizations of Wilson's Plovers. Wilson Bulletin 100**,** 36-49.

Bomford, M. 1986. Breeding displays and calls of the banded dotterel (*Caradrius bicinctus*). Notornis 33**,** 219-232.

Bowring, J.F., McLean, N.M., Bowring, S.A., 2011. Engineering cyber infrastructure for U-Pb geochronology: Tripoli and U-Pb_Redux. Geochemistry Geophysics Geosystems 12.

Breithaupt, B., Schulp. A., Matthews, N. A., Lockley, M. G., McCrea, R. T., Buckley, L. G., Gierlinski, G., Xing, L., Vegterm K., Brouwer,)., Houck, K. J., Cart, K., Lim, J-D. Kim. K-S., Kong, D Y., Surmik, D. 2017. Nest scrape behavior in large theropods: from Colorado outcrop to Dutch showcase: visitors experience ancient dinosaur display behavior from fossil evidence. Geological Society of America, Abstracts with Program 49, (6) doi: 10.1130/abs/2017AM-306527

Cairns, W. E. 1982. Biology and behavior of breeding Piping Plovers. Wilson Bulletin 94**,** 531-545.

Carpenter, K. 2014. Where the sea meets the land: the unresolved Dakota Problem in Utah. *In* Maclean, J. S., Biek, R. F., & Huntoon, J. E. (eds) Geology of Utah's far south. Utah Geol. Assoc. Pub. 43, 257-372.

Condon, D.J., Schoene, B., McLean, N.M., Bowring, S.A., Parrish, R.R., 2015. Metrology and traceability of U-Pb isotope dilution geochronology (EARTHTIME Tracer Calibration Part I). Geochimica et Cosmochimica Acta 164, 464-480.

Darling, F. F. 1938. Bird flocks and the breeding Cycle. Cambridge University Press. 124 p.

Eldrett, J. S., Ma, C., Bergman, S. C., Lutz, B., Gregory, F. J., Dodsworth, P., Phipps, M., Hardas, P., Minisini, D., Ozkan, A., Ramezani, J., Bowring, S. A., Kamo, S. L., Ferguson, K., Macaulay, C., and Kelly, A. E., 2015, An astronomically calibrated stratigraphy of the Cenomanian, Turonian and earliest Coniacian from the Cretaceous Western Interior Seaway, USA: Implications for global chronostratigraphy: Cretaceous Research 56, -344.

Gale, A.S., 1995. Cyclostratigraphy and correlation of the Cenomanian Stage in Western Europe, in: House, M.R., Gale, A.S. (Eds.), Orbital Forcing Timescales and Cyclostratigraphy. Geological Society Special Publication 85, pp. 177-197.

Goethe, F. 1937. Beobachtungen ind Untersuchungen zue Biologie der Silbermowe (*Larsus a. argentatus* Pontopp.) auf der Vogelinsel Memmertsand. Journal fur Ornithologie 85, 1-119.

Harris, M. P.1984 *The Puffins,* T & A. D Poyser, Waterhouses, England, 224p.

Holbrook, J.M., Scott, R.W., and Oboh-Ikuenobe, F.E., 2006, Base-level buffers and buttresses: a model for upstream verses downstream control on preservation of fluvial geometry and architecture within sequences. Journal of Sedimentary Research 76, 162-174.

Hone, D. W. E., Naish, D. & Cuthill, I. C. Does Mutual sexual selection explain the evolution of head crests in pterosaurs and dinosaurs. Lethaia, doi: 10.1111/j.1502-3931.2011.00300.x.

Horner, J. 1984. The nesting behavior of dinosaurs. Scientific American 250, 130-137.

Jaffey, A.H., Flynn, K.F., Glendenin, L.E., Bentley, W.C., Essling, A.M., 1971. Precision Measurement of Half-Lives and Specific Activities of ^{235}U and ^{238}U. Physical Review C 4, 1889-1906.

Kang, H-C, and Paik, I.S. 2013 review on the geological ages of the formations in the Gyeongsang Basin, Korea. Journal of the Geological Society of Korea, 49, 17-29

Kennedy, W.J., Galeb, A.S., Huberc, B.T., Petrizzod, M.R., Bowne, P., Barchettad, A., Jenkyns, H.C. 2014. "Integrated stratigraphy across the Aptian/Albian boundary at Col de Pré-Guittard (southeast France): A candidate Global Boundary Stratotype Section". Cretaceous Research 51, 248–259. doi:10.1016/j.cretres.2014.06.005.

Kim, S-K., Lockley, M. G. Kim, J-Y, and Seo, S. J. 2012. The smallest dinosaur tracks in the world: occurrences and significance of *Minisauripus* from east Asia. Ichnos 19, 66-74

Kim, K.S., Lockley, M. G., Lim. J. D., Buckley, L. and Xing, L. 2016. Small scale scrapes suggest avian display behavior by diminutive Cretaceous theropods. Cretaceous Research 66, 1-5.

Lockley, M. G., Cart, K. Martin, J., Prunty, R., Houck, K., Hups, K., Lim, J-D., Kim, K-S. Houck, K., and Gierlinski, G. 2014. A bonanza of new tetrapod tracksites from the Cretaceous Dakota Group, western Colorado: implications for paleoecology. New Mexico Museum of Natural History and Science Bulletin 62, 393-409.

Lockley, M. G., Fanelli, D., Honda, K., Houck, K. and Matthews, 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, 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, p. 39-54, in Flores, R. (ed.), Mesozoic of the Western Interior, SEPM Midyear Meeting Fieldtrip Guidebook, 87 p.

Lockley, M. G., Holbrook, J. Kukihara, R., and Matsukawa, M. 2006. An ankylosaur-dominated dinosaur tracksite in the Cretaceous Dakota Group of Colorado and its paleoenvironmental and sequence stratigraphic context. New Mexico Museum of Natural History and Science, Bulletin 35: 95-104.

Lockley, M. G., and Hunt, A. P. 1995. Dinosaur Tracks and Other Fossil Footprints of the Western United States, Columbia University Press, 338p.

Lockley, M. G., Kim, S. H., Kim, J-Y Kim, K. S., Matsukawa, M. Li, R., Li. J and Yang, S-Y. 2008. *Minisauripus* - the track of a diminutive dinosaur from the Cretaceous of China and Korea: implications for stratigraphic correlation and theropod foot morphodynamics. Cretaceous Research 29, 115-130.

Lockley M. G., and Marshall, C. 2014. A field guide to the Dinosaur Ridge Area. (4th edition) A publication of the Friends of Dinosaur Ridge, Morrison, Colorado, p. 1-40.

Lockley M. G., and Marshall, C. *in prep*. A field guide to the Dinosaur Ridge Area. (5th edition) A publication of the Friends of Dinosaur Ridge, Morrison, Colorado,

Lockley, M. G., Xing, L. Matthews, N. A. and Breithaupt, B. 2016. Didactyl raptor tracks from the Cretaceous, Plainview Sandstone at Dinosaur Ridge, Colorado. Cretaceous Research 61, 161-168

Lockley, M. G., McCrea, R. T., Buckley, L., Lim, J. D., Matthews, N. A., Breithaupt, B. H., Houck, K., Gierlinski, G., Surmik, D., Kim K. S., Xing, L., Kong, D.Y., Cart, K., Martin, J. and Hadden, G. 2016. Theropod courtship: large scale physical evidence of display arenas and avian-like scrape ceremony behaviour by Cretaceous dinosaurs. Scientific Reports 6, 18952; doi: 10.1038/srep18952,

Mattinson, J.M., 2005. Zircon U/Pb chemical abrasion (CA-TIMS) method; combined annealing and multi-step partial dissolution analysis for improved precision and accuracy of zircon ages. Chemical Geology 220, 47-66.

McCrea. R.T. 2000. Dinosaur footprints in the Lower Cretaceous (Albian) Gates Formation of Alberta, Canada: their use in palaeobiology and palaeoenvironmental interpretation. Journal of the Paleontological Society of Korea 4, 169-178.

McCrea, R.T., Lockley, M.G., and Meyer, C.A. 2001. Global distribution of purported anylosaur track occurrences, p. 413-454. In, Carpenter, K. (ed.), The armored dinosaurs. Bloomington and Indianapolis, University of Indiana Press.

McLean, N.M., Bowring, J.F., Bowring, S.A., 2011. An algorithm for U-Pb isotope dilution data reduction and uncertainty propagation. Geochemistry Geophysics Geosystems 12.

McLean, N.M., Condon, D.J., Schoene, B., Bowring, S.A., 2015. Evaluating uncertainties in the calibration of isotopic reference materials and multi-element isotopic tracers (EARTHTIME Tracer Calibration Part II). Geochimica Et Cosmochimica Acta 164, 481-501.

Obradovich, J.D., Matsumoto, T., Nishida, T., Inoue, Y., 2002. Integrated biostratigraphic and radiometric study on the Lower Cenomanian (Cretaceous) of Hokkaido, Japan. P Jpn Acad B-Phys 78, 149-153.

Ogg, J. G., Ogg, G. M., and Gradstein, F. M., 2016, A Concise Geologic Time Scale, Amsterdam, Elsevier.

Ogg, J.G., Hinnov, L.A., 2012. Cretaceous, in: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), The Geological Time Scale 2012. Elsevier, Amsterdam, pp. 793-853.

Powesland, R. G., Lloyd, B. D., Best, H. A. & Merton, D. V. 1992. Breeding biology of the Kakapo *Strigops habroptilus* on Stewart Island, New Zealand. Ibis 134, 361-373.

Ramezani, J., Hoke, G.D., Fastovsky, D.E., Bowring, S.A., Therrien, F., Dworkin, S.I., Atchley, S.C., Nordt, L.C., 2011. High-precision U-Pb zircon geochronology of the Late Triassic Chinle Formation, Petrified Forest National Park (Arizona, USA): Temporal constraints on the early evolution of dinosaurs. Geological Society of America Bulletin 123, 2142-2159.

Scott, R.W., Oboh-Ikuenobe, F.E., Benson, D.G., Jr. and Holbrook, J.M. 2009. Numerical Age Calibration of the Albian/Cenomanian Boundary: Stratigraphy 6, 17-32.

Stott, D.F., 1968. Lower Cretaceous Bullhead and Fort St. John Groups, between Smoky and Peace Rivers, Rocky Mountain foothills, Alberta and British Columbia, Geological Survey of Canada Bulletin 152. Department of Energy, Mines and Resources Canada, p. 279.

Weimer, R.J., 1989. Sequence stratigraphy, Lower Cretaceous, Denver Basin, Colorado U.S.A. In: Ginsburg, R.D., Beaudoin, B. (Eds.), Cretaceous resources, events and rhythms: NATO ASI Series. Kluwer Academic Publishers, Dordrecht, p. 1-8.

Weimer, R. J. and Land, C. B., Jr., 1972, Field guide to Dakota Group (Cretaceous) stratigraphy Golden-Morrison Area, Colorado; *in* Duff, K. S., ed., Environments of sandstone, carbonate, and evaporate deposition. The Mountain Geologist 9, 241-267

Whitfield, D. P., and Brade, J. J. 1991. The breeding behavior of the Knot *Calidris canutus*. Ibis 133, 246-255.

Xing, L., Lockley M. G., Yang, G. Benton, M., Xu, X., Zhang, J., Klein H., Persons, S. W., Cao, J., Kim, J.Y., Ran, H., Peng, G., Ye, Y., 2016. A new *Minisauripus* site from the Lower Cretaceous of China: implications for tracking small theropod species. Palaeogeography, Palaeoclimatology, Palaeoecology 452, 28-39.

List of Figures

Fig. 8. Scrape orientations from the RC, CG and CGw sites, with combined orientations for all three sites (lower right). *Key* shows that where anterior orientation of scrape is known, a full bar length is plotted in red. Where only long axis is known a half bar length is plotted in each direction.

Fig. 9. Scatter diagrams for scrape length-width (left) and length-depth (right). DiRi = Dinosaur Ridge, RC = Roubideau Creek, CGw = Club Gulch west, CG = Club Gulch. C refers to Canadian scrape. See text for details

Fig. 10. Theropod tracks from three western Colorado sites (RC, CG and CGw). A: cf. *Irenesauripus* found in scrape RC5, B: unnamed theropod track in scrape RC7, C: large slender-toed *Magnoavipes* like track found near CG 1, D. tridactyl "track-like scrape CGw2, E: smaller slender-toed *Magnoavipes* like track found near CGw7. See text for details

Fig. 11. A and B. *Ostenichnus bilobatus*-like traces from the Albian age Gates Formation at the W2 site, Grand Cache, Alberta. Note the location of the trace in relation to the larger surface (C) which also shows recognizable dinosaur trackways described by McCrea et al., 2000, 2001). The trace also seems to be associated with a topographically elevated portion of the surface.

Fig. 12. Date distribution plot of U-Pb zircon analyses from an ash bed at the Roubideau Creek (RC) site in Colorado. Each bar represents a single zircon analysis and bar height is proportional to the $^{206}Pb/^{238}U$ date uncertainty (2σ internal). Analysis not included in weighted mean age calculation is shown in grey. Horizontal line and its grey envelope signify the calculated weighted mean age and its 2σ internal uncertainty, respectively.

Table 1. Length (L), width (W), depth (D) and morphologic characteristics of bilobed (B) or non-bilobed (nb) scrapes, with median ridge width (mr), estimated mean trough width (tw) and orientation (or). All measurements in cms. DiRi: Dinosaur Ridge, RC: Roubideau Creek, CG: Club Gulch, CCwW: Club Gulch West. Orientation azimuths shown in bold indicate inferred anterior orientation of scrapes.

Table 2. Mean values (**bold**) for size, depth and other parameters pertaining to scrape data given in Table 1. Total numbers of measured and un-measured scrapes (not bold) for each site are given in text, and can be compared with the number of scrapes yielding one or more measurements. Not all scrapes yielded all measurable parameters: see Table 1 for details. B/nb indicates the totals of bilobed (B) versus non-bilobed (nb) scrapes recorded from each site, with bilobed traces dominating in all cases. Individual scrape orientations for measured scrapes are given in Table 1, with modal sector values summarized here. All measurements (**in bold**) in cm.

TABLE 3. U-Pb data for analyzed zircons from the Roubideau Creek ash bed, Colorado.

Table 1. Length (L), width (W), depth (D) and morphologic characteristics of bilobed (B) or non-bilobed (nb) scrapes, with median ridge width (mr), estimated mean trough width (tw) and orientation (or). All measurements in cms. DiRi: Dinosaur Ridge, RC: Roubideau Creek, CG: Club Gulch, CCwW: Club Gulch West. Orientation azimuths shown in bold indicate inferred anterior orientation of scrapes.

Scrape no.	L	W	D	B/nb	mr	tw	or		Scrape no.	L	W	D	B/nb	mr	tw	or
DiRi 1	180	83	21	B	21	31	**270**		CG29	100	70	14	nb	-	-	103
DiRi 2	95	80	10	B	20	30	0		CG 30	85	85	7	nb	-	-	81
RC 1	105	105	6	nb	-	-	45		CG 31	70	70	7	B	15	27.5	**212**
RC 3	90	44	8	nb	-	-	**80**		CG32	140	100	-	nb	-	-	164
RC 4	150	95	20	B	12	41.5	55		CG33	100	80	6	nb	-	-	127
RC 5	150	105	15	B	20	42.5	**195**		CG34	55	55	7	B	-	-	150
RC 6	190	110	19	B	17	46.5	**240**		CG40	40	55	5	B	10	22.5	97
RC 7	77	63	4	B	chec		**18**		CG41	110	72	7	nb	-	-	**210**
RC 9	120	90	-	B	chec		37		CG43	110	70	8	B	15	27.5	98
RC 10	75	75	2	B	-	-	20		CG 46	50	60	5	B	25	17.5	**52**
CG 1	-	60	7	nb	-	-	130		CG48	80	65	4	B	20	22.5	23
CG2	125	90	9	nb	-	-	130		CG49	120	65	6	B	-	-	55
CG 3	170	110	10	nb	-	-	120		CG50	50	40	2	B	-	-	64
CG4	70	80	7	B	20	30	110		CGw 2	62	56	6	B	10	23	**215**
CG 5	50	60	3	B	15	22.5	105		CGw 3	76	72	8	B	-	-	**190**
CG6	50	60	3	B	15	22.5	157		CGw 4	88	-	-	nb	-	-	**130**
CG8	170	125	21	nb	-	-	70		CGw 5	90	65	17	B	-	-	152
CG9	210	90	13	nb	-	-	83		CGw 13	105	40	10	nb	-	-	168
CG10	110	60	-	nb	-	-	120		CGw 15	60	-	10	nb	-	-	165
CG11	140	90	12	nb	-	-	112		CGw 16	80	45	13	nb	-	-	2
CG13	90	75	12	B	18	28.5	90		CGw 19	115	55	9	nb	-	-	0
CG15	110	65	10	B	12	26.5	45		CGw 21	45	45	10	B	-	-	110
CG16	100	70	5	B	15	27.5	37		CGw 22	70	70	9	B	20	25	50
CG17	120	85	9	nb	-	-	1		CGw 23	110	50	14	B	-	-	55
CG19	80	60	12	B	-	-	53		CGw 25	105	35	6	B	-	-	168
CG20	50	50	7	B	12	19	148		CGw 26	90	70	-	B	-	-	90
CG21	80	50	7	B	7	21.5	73		CGw 27	88	40	10	B	25	7.5	167
CG 22	170	85	25	nb	-	-	48		CGw28	105	70	15	B	-	-	153
CG25	175	100	20	nb	-	-	65									
CG 28	80	50	7	B	12	19	44									

Table 2. Mean values (**bold**) for size, depth and other parameters pertaining to scrape data given in Table 1. Total numbers of measured and un-measured scrapes (not bold) for each site are given in text, and can be compared with the number of scrapes yielding one or more measurements. Not all scrapes yielded all measurable parameters: see Table 1 for details. B/nb indicates the totals of bilobed (B) versus non-bilobed (nb) scrapes recorded from each site, with bilobed traces dominating in all cases. Individual scrape orientations for measured scrapes are given in Table 1, with modal sector values summarized here. All measurements (**in bold**) in cm.

Site	mean length	mean width	mean depth	B/nb	mean ridge width	mean trough width	Modal orient.	Total no. scrapes measured	Total scrapes per sample
DiRi	**137.5**	**81.5**	**15.5**	2/0	**20.5**	**31.0**	-	2	2
RC	**119.6**	**85.9**	**10.6**	6/2	**16.3**	**34.3**	16-30^o & 196-210^o	8	10
CG	**101.9**	**75.8**	**8.9**	18/14	**15.2**	**30.3**	61-75^o & 241-255^o	33	58
CGw	**85.3**	**58.8**	**10.5**	10/5	**18.3**	**20.3**	151-165^o & 330-346^o	15	28
Grand means	**101.3**	**73**	**10.7**	36/21	**16.3**	**27.8**	46-60^o & 226-240^o	58 (total)	98

TABLE 3. U-Pb data for analyzed zircons from the Roubideau Creek ash bed, Colorado.

	Composition				Ratios							Dates (Ma)				
Sample Fractions[†]	Pb_c[‡] (pg)	Pb*[‡] / Pb_c	Th / U	^{206}Pb[§] / ^{204}Pb	^{208}Pb[#] / ^{206}Pb	^{206}Pb[††] / ^{238}U	err (2σ%	^{207}Pb[††] / ^{235}U	err (2σ%	^{207}Pb[††] / ^{206}Pb	err (2σ%	^{206}Pb / ^{238}U	err (2σ)	^{207}Pb / ^{235}U	^{207}Pb / ^{206}Pb	corr. coef.
Weighted mean date: 97.689 ± 0.037/0.059/0.12 Ma (MSWD = 1.5)																
z1	0.2	63.3	0.6	3660.3	0.201	0.01526	(.06)	0.1012	(.37)	0.0481	(.35)	**97.665**	**0.054**	97.93	104.5	0.38
z3	0.3	13.0	0.4	792.8	0.158	0.01526	(.14)	0.1017	(1.62	0.0483	(1.58	**97.66**	**0.14**	98.4	116	0.32
z4	0.5	16.6	0.6	962.1	0.216	0.01527	(.12)	0.1015	(1.41	0.0482	(1.37	**97.72**	**0.11**	98.2	111	0.37
z5	0.5	25.8	0.5	1538.7	0.172	0.01528	(.08)	0.1014	(.84)	0.0481	(.81)	**97.754**	**0.080**	98.11	107	0.34
z6	0.2	8.0	0.6	481.3	0.193	0.01530	(.24)	0.1005	(2.99	0.0476	(2.89	**97.90**	**0.24**	97.3	83	0.43
z7	0.3	17.9	0.7	1020.1	0.239	0.01525	(.12)	0.1005	(1.36	0.0478	(1.32	**97.61**	**0.12**	97.3	89	0.41
z8	0.7	7.7	0.6	462.9	0.204	0.01525	(.28)	0.1016	(3.35	0.0483	(3.24	**97.61**	**0.27**	98.3	115	0.44
z9	0.3	11.2	0.4	688.6	0.155	0.01550	(.16)	0.1019	(1.99	0.0477	(1.94	99.15	0.16	98.5	83	0.37

Notes:

[†] All analyses are single zircon grains and pre-treated by the thermal annealing and acid leaching (CA-TIMS) technique. Data used in age calculations are in bold.

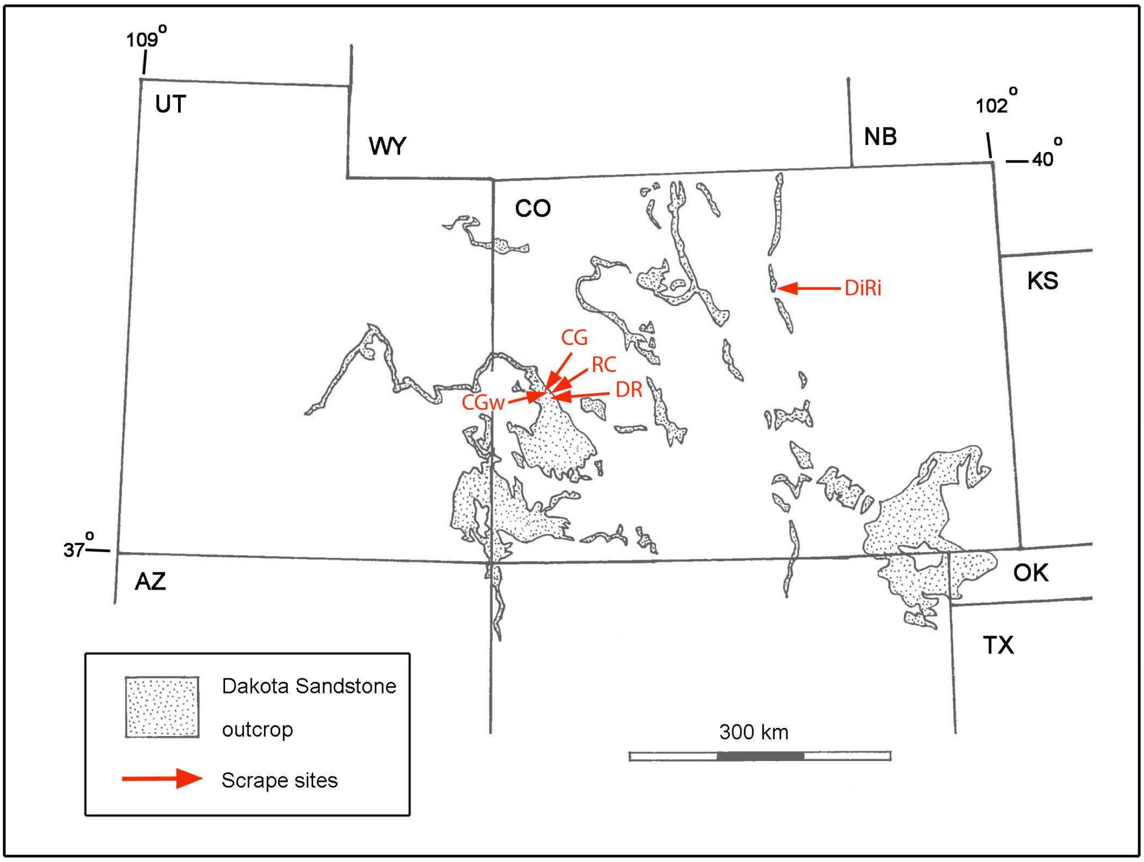
[‡] Pb_c is total common Pb in analysis. Pb* is radiogenic Pb concentration.

[§] Measured ratio corrected for spike and fractionation only.

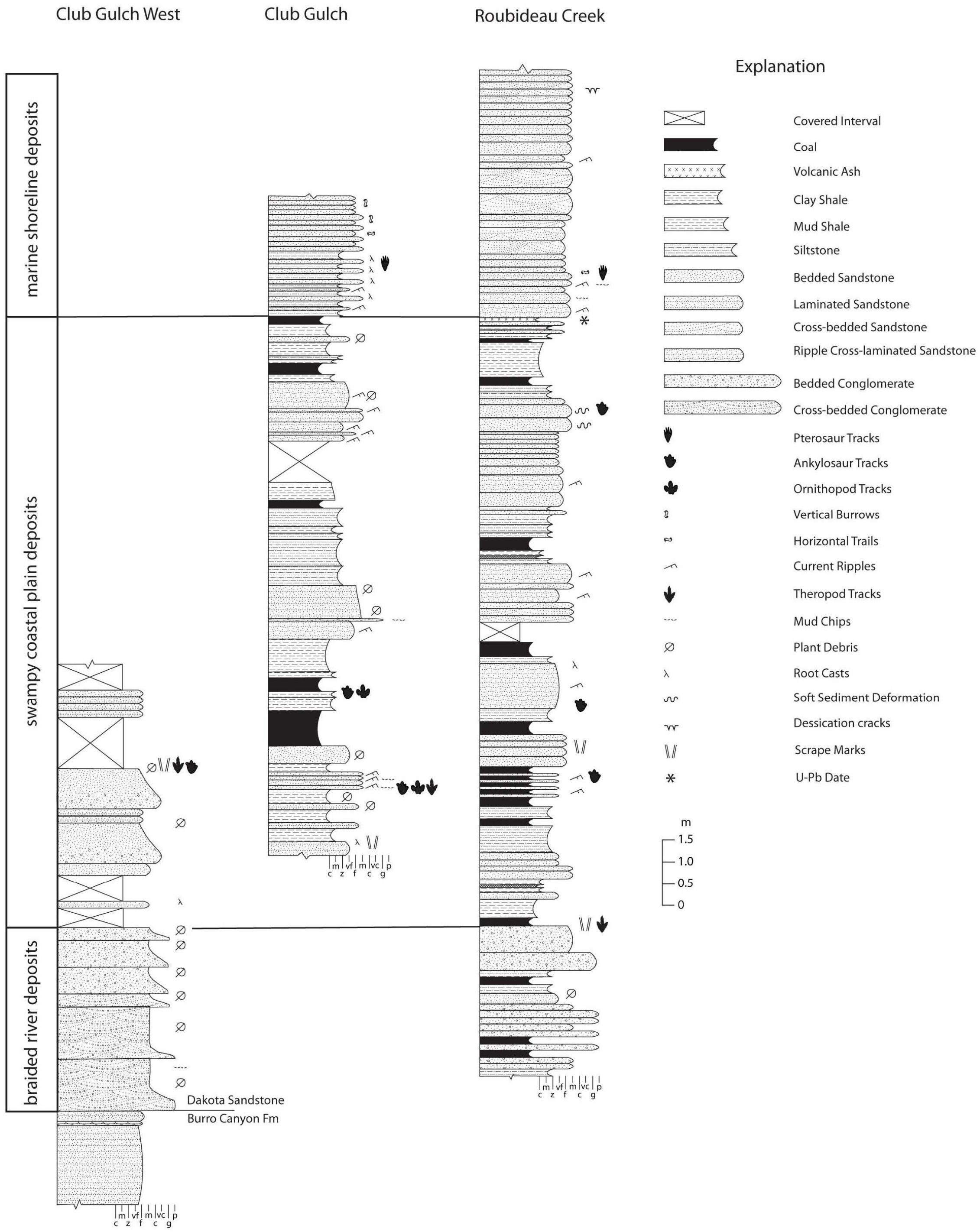
[#] Radiogenic Pb ratio.

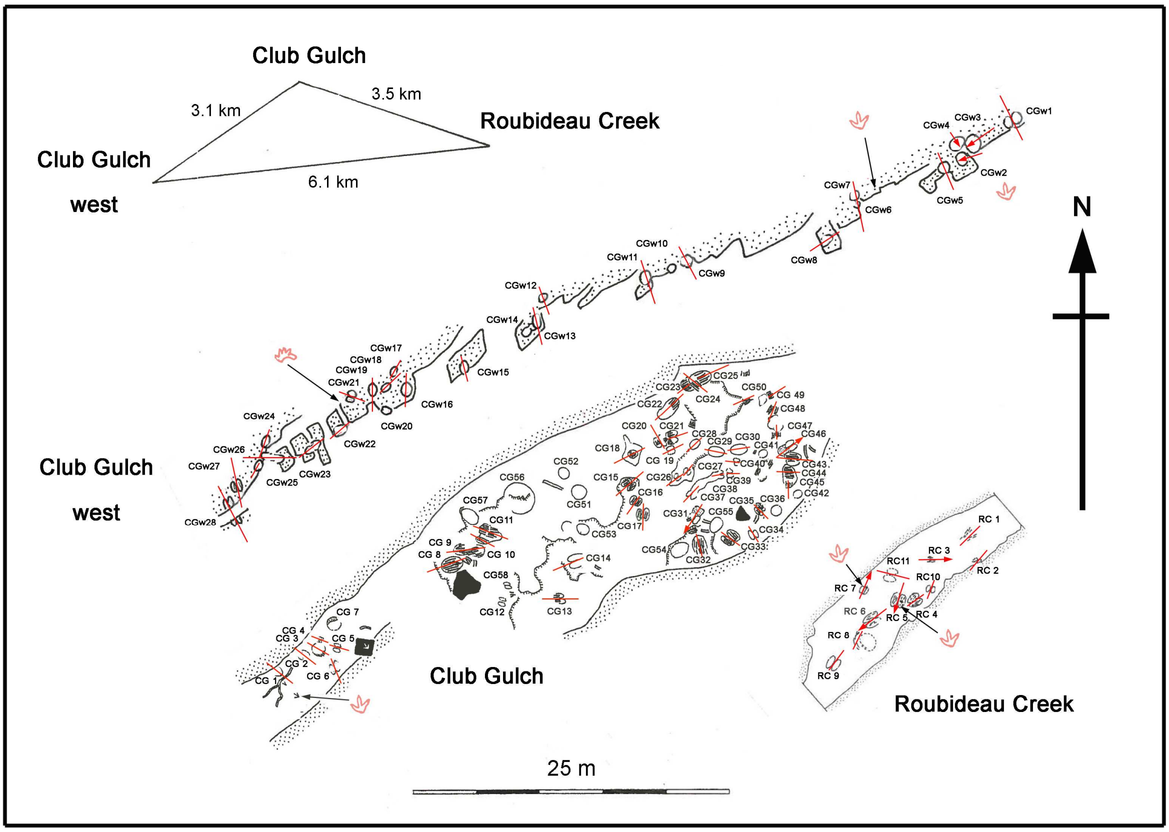
[††] Corrected for fractionation, spike, blank, and initial Th/U disequilibrium in magma. Mass fractionation corrections of 0.18%/amu ± 0.02%/amu (atomic mass unit) and 0.25%/amu ± 0.02%/amu were applied to single-collector Daly analyses on X62 and Sector 54 instruments, respectively. All common Pb is assumed to be blank. Total procedural blank was less than 0.1pg for U. Blank isotopic composition: $^{206}Pb/^{204}Pb = 18.15 \pm 0.48$, $^{207}Pb/^{204}Pb = 15.30 \pm 0.30$, $^{208}Pb/^{204}Pb = 37.11 \pm 0.88$.

Corr. coef. = correlation coefficient. Age calculations are based on the decay constants of Jaffey et al. (1971).

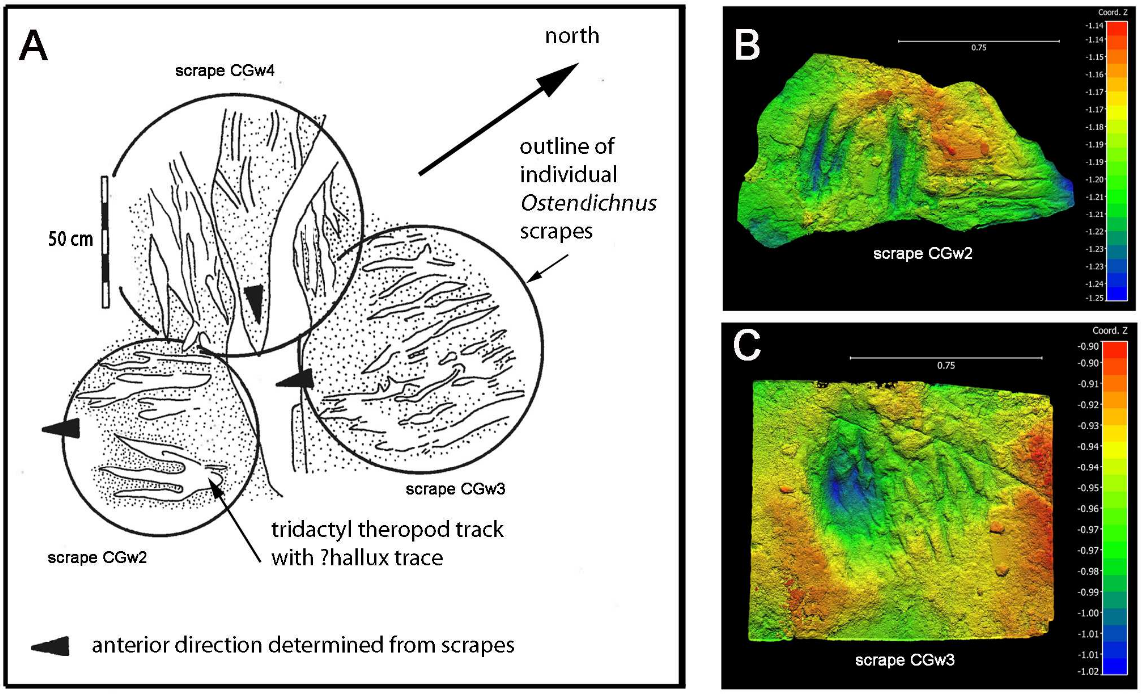


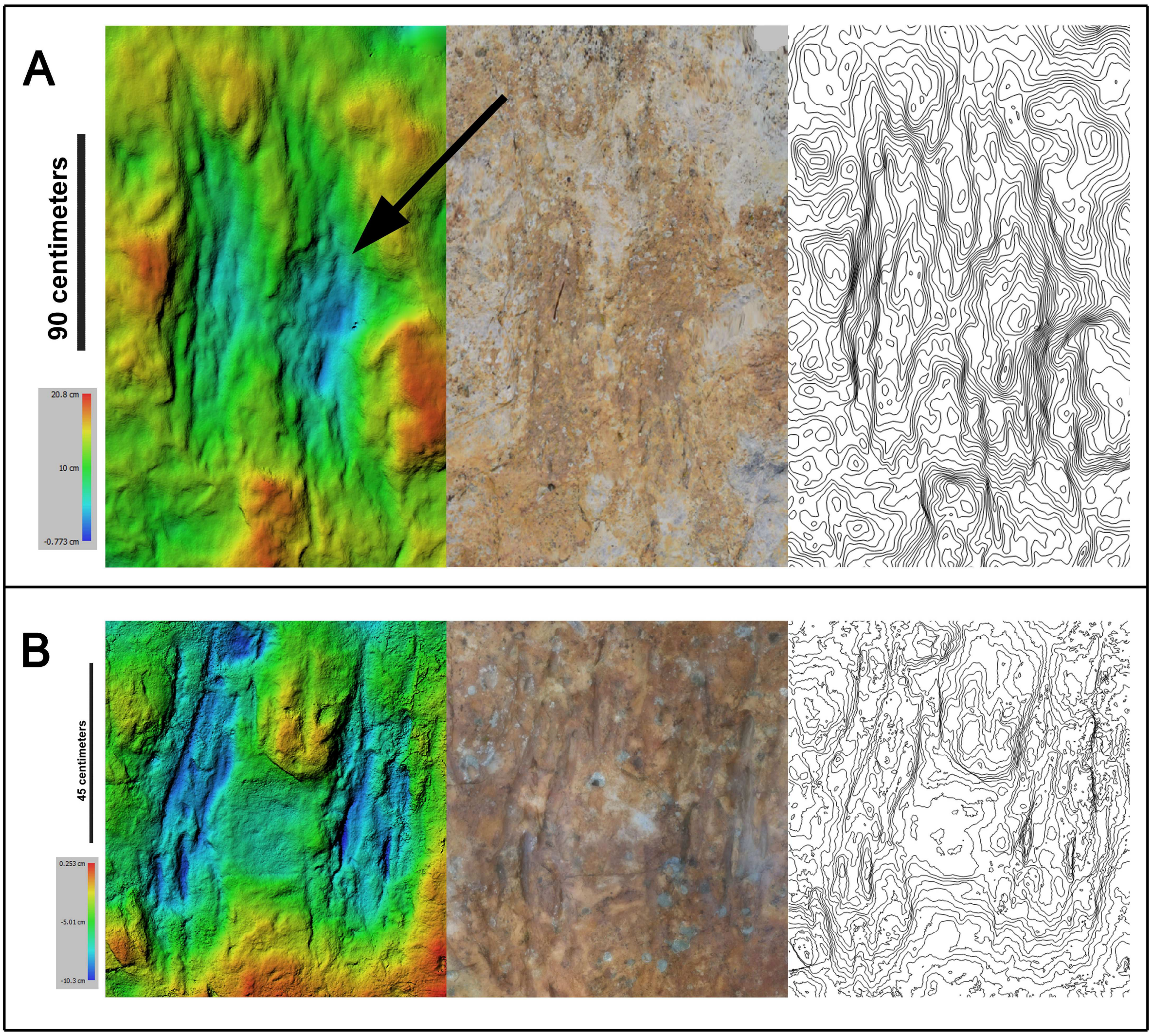
109°
102°
40°
37°
UT
WY
NB
CO
KS
AZ
OK
TX
DiRi
CG
RC
DR
CGw
Dakota Sandstone
outcrop
Scrape sites
300 km

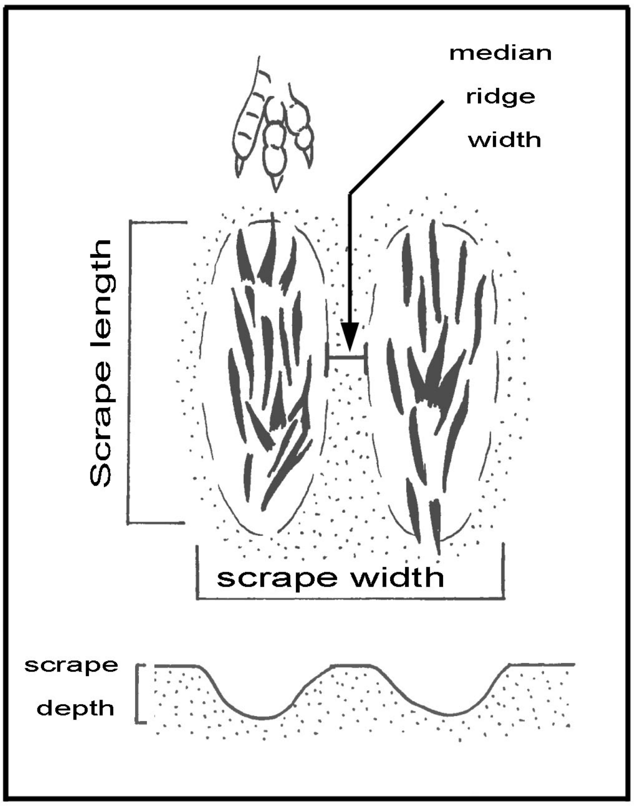

Club Gulch West
Club Gulch
Roubideau Creek
marine shoreline deposits
swampy coastal plain deposits
braided river deposits
Dakota Sandstone
Burro Canyon Fm
m vf m vc p
c z f c g
Explanation
Covered Interval
Coal
Volcanic Ash
Clay Shale
Mud Shale
Siltstone
Bedded Sandstone
Laminated Sandstone
Cross-bedded Sandstone
Ripple Cross-laminated Sandstone
Bedded Conglomerate
Cross-bedded Conglomerate
Pterosaur Tracks
Ankylosaur Tracks
Ornithopod Tracks
Vertical Burrows
Horizontal Trails
Current Ripples
Theropod Tracks
Mud Chips
Plant Debris
Root Casts
Soft Sediment Deformation
Dessication cracks
Scrape Marks
U-Pb Date
m
1.5
1.0
0.5
0

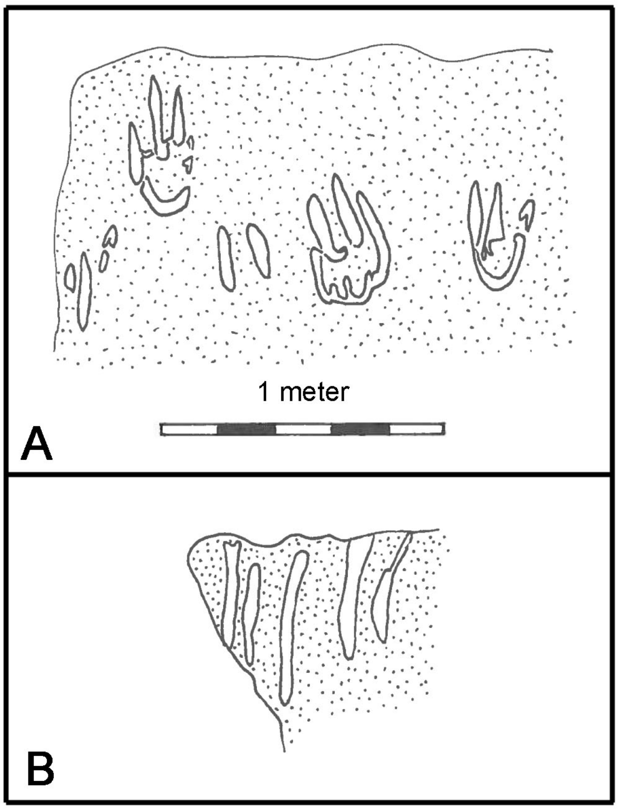


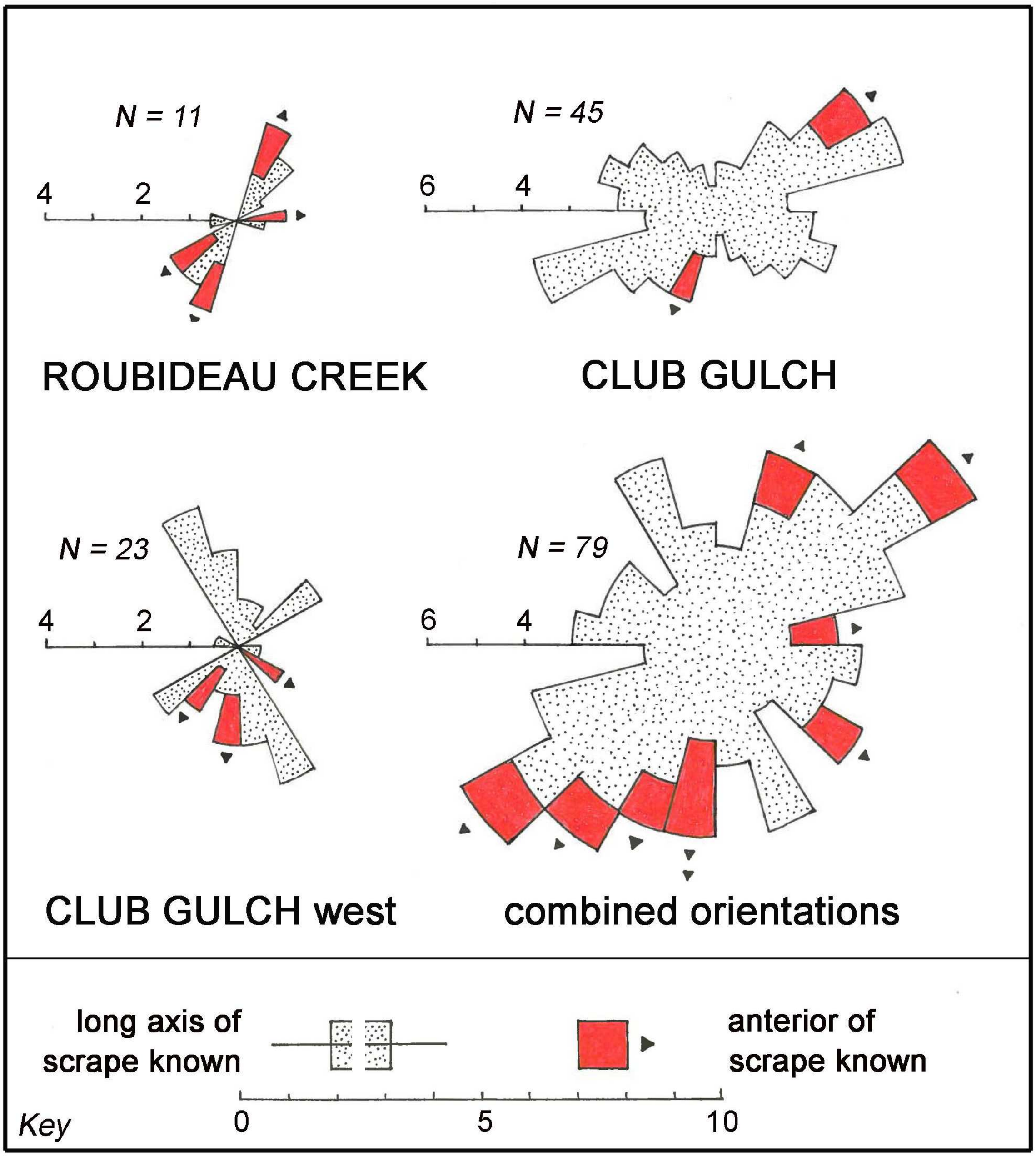
Club Gulch
3.1 km
3.5 km
Roubideau Creek
Club Gulch west
6.1 km
N
Club Gulch west
Club Gulch
Roubideau Creek
25 m

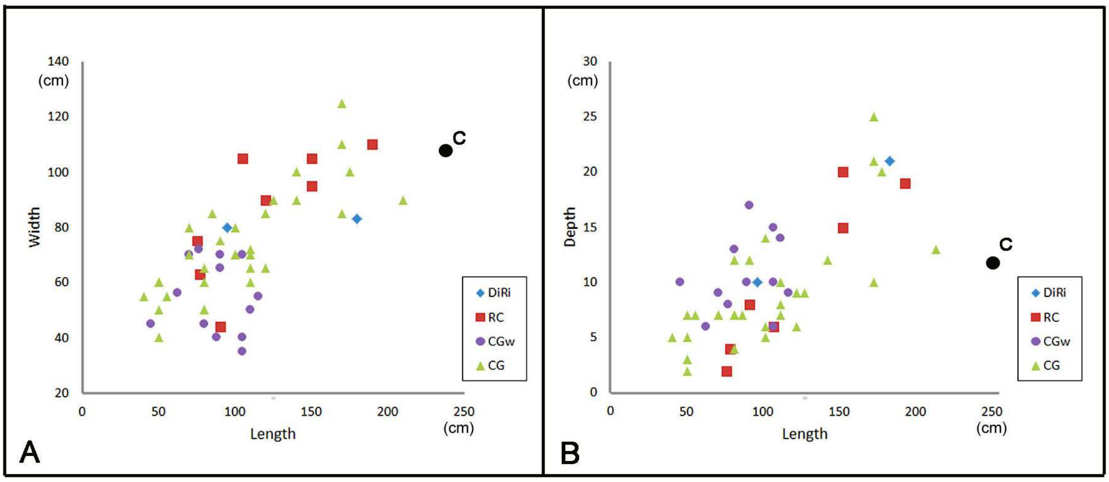

A
north
scrape CGw4
50 cm
outline of
individual
Ostendichnus
scrapes
scrape CGw3
scrape CGw2
tridactyl theropod track
with ?hallux trace
anterior direction determined from scrapes
B
0.75
Coord. Z
scrape CGw2
C
0.75
Coord. Z
scrape CGw3


A
90 centimeters
20.8 cm
10 cm
-0.773 cm
B
45 centimeters
0.253 cm
-5.01 cm
-10.3 cm

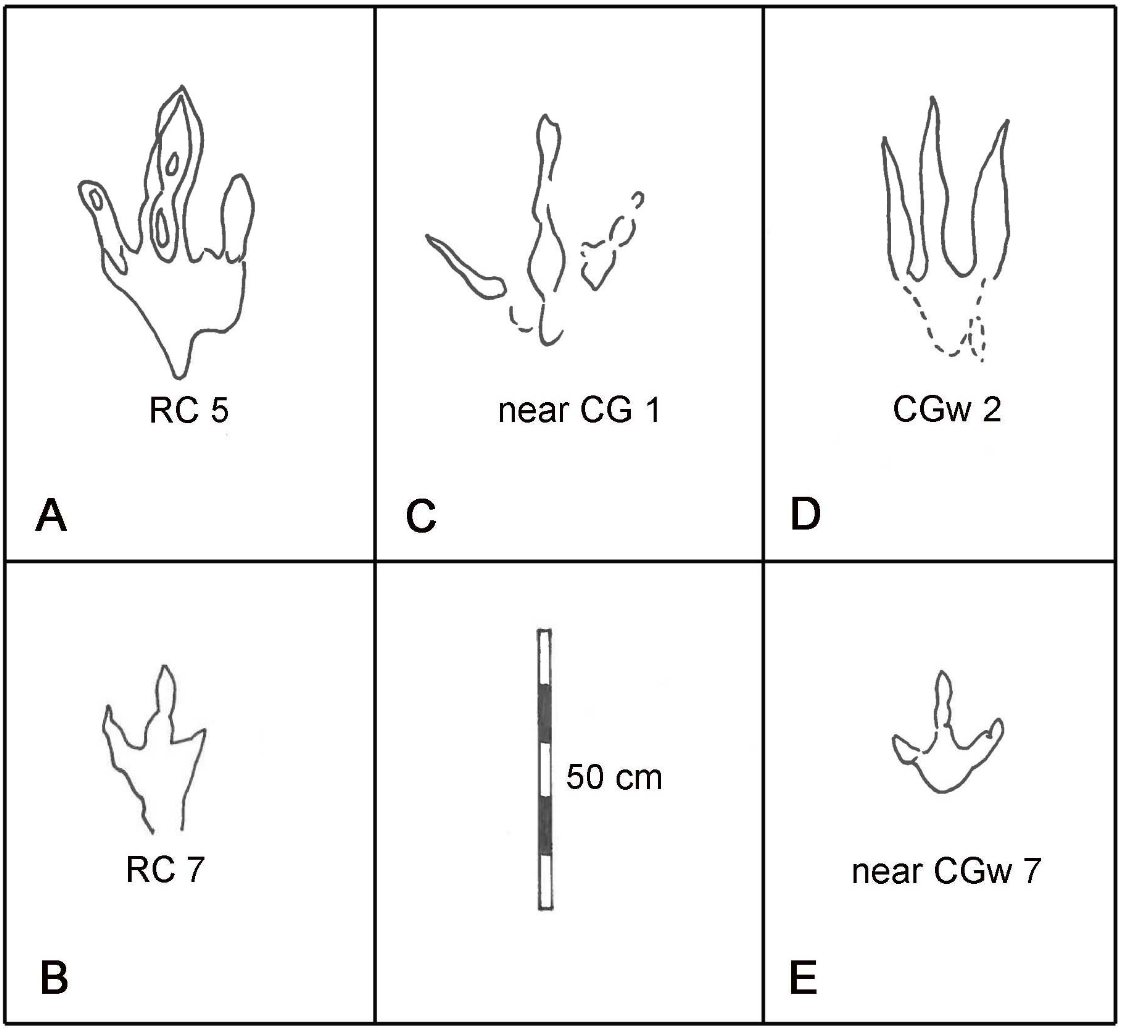

median
ridge
width
Scrape length
scrape width
scrape
depth

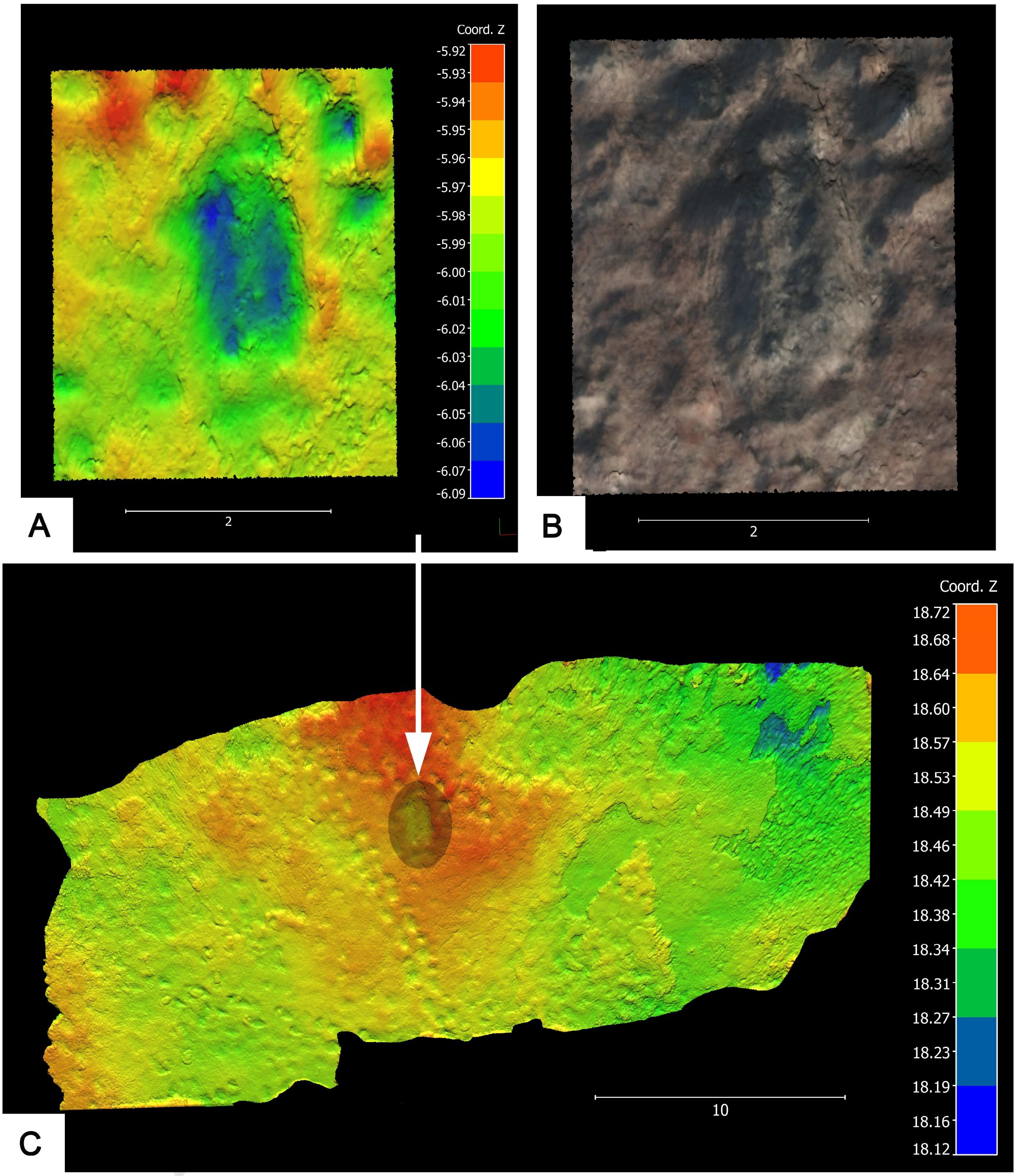

1 meter
A
B

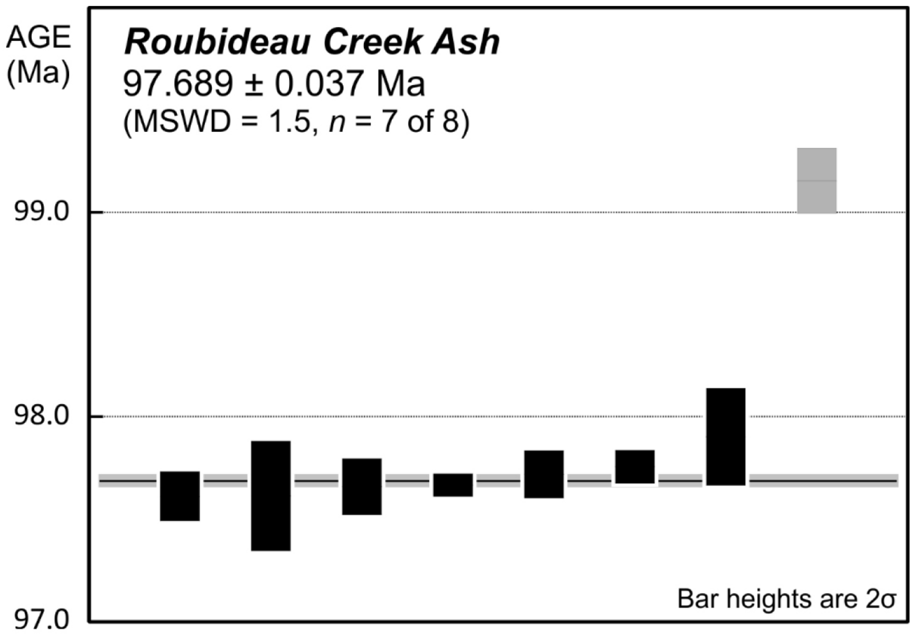

N = 11
4
2
ROUBIDEAU CREEK
N = 45
6
4
CLUB GULCH
N = 23
4
2
CLUB GULCH west
N = 79
6
4
combined orientations
long axis of
scrape known
anterior of
scrape known
Key
0
5
10



140
(cm)
120
100
80
60
40
20
Width
0
50
100
150
200
250
(cm)
Length
C
DiRi
RC
CGw
CG
A
30
(cm)
25
20
15
10
5
0
Depth
0
50
100
150
200
250
(cm)
Length
C
DiRi
RC
CGw
CG
B


RC 5
A
near CG 1
C
CGw 2
D
RC 7
B
50 cm
near CGw 7
E


Coord. Z
-5.92
-5.93
-5.94
-5.95
-5.96
-5.97
-5.98
-5.99
-6.00
-6.01
-6.02
-6.03
-6.04
-6.05
-6.06
-6.07
-6.09
2
A
2
B
Coord. Z
18.72
18.68
18.64
18.60
18.57
18.53
18.49
18.46
18.42
18.38
18.34
18.31
18.27
18.23
18.19
18.16
18.12
10
C


AGE
(Ma)
Roubideau Creek Ash
97.689 ± 0.037 Ma
(MSWD = 1.5, n = 7 of 8)
99.0
98.0
97.0
Bar heights are 2σ