PALÆO VERTEBRATA

Late Campanian theropod trackways from Porvenir de Jalpa, Coahuila, Mexico

Héctor RIVERA-SYLVA[a], Eberhard FREY[b], Anne S. SCHULP[c,d], Christian A. MEYER[e], Basil THÜRING[f], Wolfgang STINNESBECK[g] & Valentin VANHECKE[c,h]

a Museo del Desierto, Laboratorio de Paleontología, Saltillo, Mexico
b Staatliches Museum für Naturkunde Karlsruhe, Departement of Geosciences, Karlsruhe, Germany
c Naturalis Biodiversity Center, Leiden, the Netherlands
d Faculty of Earth and Life Sciences, Vrije Universiteit Amsterdam, the Netherlands
e Department of Environmental Sciences, Research unit Geology & Palaeontology,University of Basel, Switzerland
f Natural History Museum Basel, Department of Geosciences, Basel, Switzerland
g Heidelberg University, Institute of GeoSciences, Heidelberg, Germany
h 4Visualisation, Zoetermeer, the Netherlands
** Corresponding author: hrivera@museodeldesierto.org*

Abstract: Confident attribution of bipedal tridactyl dinosaur tracks to theropods or ornithopods can be challenging. Here we describe trackways produced by tetanuran dinosaurs, previously attributed to hadrosaurs, from Coahuila State, northeastern Mexico. Multiple trackways headed in the same direction suggest gregarious behaviour in these late Campanian theropods.

Keywords: Dinosaur tracks, Campanian, Theropoda, Tetanurae, Ornithopoda, Cerro del Pueblo Formation, Las Águilas, Mexico

Submitted 24 January 2017, Accepted 22 September 2017
Published Online 29 November 2017, doi: 10.18563/pv.41.2.e1

INTRODUCTION

The morphology of dinosaur trackways, if well preserved, is generally sufficiently characteristic to allow for accurate attribution of a trackway to a trackmaker. However, this is not always the case in trackways formed by bipedal tridactyl dinosaurs: theropod and ornithopod tracks are occasionally hard to distinguish (e.g., Romilio & Salisbury, 2011; Schulp & Al-Wosabi, 2012, and refs therein).

Although the Late Maastrichtian theropod *Tyrannosaurus rex* is arguably the best-known carnivorous dinosaur in the eye of the public, the evolution of tyrannosaurid dinosaurs during the preceeding approximately fifteen million years of the Cretaceous has only recently been charted in more detail, based on new discoveries made in the last decade (e.g., Brusatte & Carr, 2016 and refs therein). Perhaps surprisingly, the trackway record of tyrannosaurid dinosaurs from the latest Cretaceous is even more sparse than the body fossil record (e.g., McCrea *et al*., 2014; Smith *et al*., 2016, and refs therein).

We therefore feel a more detailed description of a series of trackways of tridactyl dinosaurs from the Campanian of Porvenir de Jalpa, Coahuila, Mexico, is warranted, as we consider these tracks, previously interpreted as ornithopod tracks, to be theropod in origin (Figs. 1, 2). The size of the tracks, the similar-sized theropod body fossil record from the region, and the presence of tyrannosaurid teeth from the same strata, make a tetanuran, probably a tyrannosaurid track maker a likely candidate. Because this tracksite preserves trackways made by multiple individuals all headed in a single direction, this interpretation may add new evidence on gregarious behaviour in tyrannosaurid dinosaurs (Fig. 2; e.g., Currie, 1998; Currie & Eberth, 2010).

MATERIAL & METHODS

Locality and stratigraphy

The dinosaur tracks discussed here are preserved at the Las Águilas dinosaur locality, located northeast of the village of Porvenir de Jalpa, in the municipality of General Cepéda, Coahuila State, NE Mexico (25°31'7"N 101°40'38"W; Fig. 1). This Late Campanian site was discovered in February 2003 by amateur palaeontologist José Lopez-Espinoza, at the time preparator and assistant researcher at the Museo del Desierto (MUDE) at Saltillo, Coahuila. The strata are exceedingly rich in invertebrate and vertebrate remains, among them dozens of semi-articulated partial skeletons of dinosaurs (Eberth *et al*., 2004, Vogt *et al*., 2016), but also a variety of dinosaur ichnotaxa (Rodríguez de la Rosa *et al*., 2003, 2004; Meyer *et al*., 2008). The first descriptions of the trackways concerned was presented by Rodríguez de la Rosa *et al*. (2003, 2004) and Rodríguez de la Rosa (2007), who interpreted most of the trackways as having been produced by hadrosaurs.

Geological setting

The tracks are preserved in the Cerro del Pueblo Formation, which is part of the Difunta Group, consisting of shallow marine to coastal and deltaic deposits (Eberth *et al*., 2004, Meyer *et al*. 2005, Vogt *et al*., 2016). The sediments originated from a river system located in Chihuahua and western Coahuila, which opened into the Palaeogulf of Mexico. Progression of the delta front gradually moved the coastlines towards the east. The matrix at the Las Águilas trackway site consists of a pale yellow to buff coloured fine-grained sandstone, which was deposited in a shallow channel environment. Occasional ripple marks suggest coverage by shallow, slow moving water. The absence of desiccation cracks implies that the mud was still water-covered or at least moist, when the dinosaurs walked over the mud pan. Vogt *et al*. (2016) presented a detailed overview of the geological setting of the tracksite and the surrounding dinosaur-bearing strata, which therefore will not be repeated here. Recent Sr dating places the Las Águilas dinosaur-bearing strata into the latest Campanian (73 my ±1; Vogt *et al*., 2016).

Fauna

The Las Águilas area is remarkable for its tracksites but also for the abundance of dinosaur body fossils – mainly hadrosaurs and to a lesser extent theropods assigned to Ornithomimosauridae, Tyrannosauridae and Dromaeosauridae (Meyer *et al.* 2005, Frey *et al*., 2015). During an excavation campaign in September 2014 a new locality was discovered nearby the Las Águilas site that yielded remains of Ornithopoda (Hadrosaurinae, Lambeosaurinae and Thescelosauridae), Ornithomimosauridae, Dromaeosauridae, Tyrannosauridae, Ceratopsia, Ankylosauria but also bones of Pterosauria, four different types of turtles, eusuchian and dyrosaurid crocodilians, plesiosaurs and lepisosteid fishes (Frey *et al*., 2015).

Accessibility

In 2009, the tracksite and surrounding area was fenced off by the Instituto de Antropología y Historia (INAH) Coahuila, the entity responsible to safeguard sites of archaeological and palaeontological importance in Mexico. Drainage trenches were implemented to avoid flooding of the tracks (Fig. 2). Access to the site is now directed by fences and a raised wooden plank path. Keys must be obtained from the Porvenir de Jalpa ejido (cooperative), which is the owner of the area. The municipality of General Cepéda, and even more so, the people of Porvenir de Jalpa take care of the site and did an enormous effort to enhance the infrastructure of the site in creating an access road, parking areas and information panels. At that time, guided tours could be booked. Today, however, funds have run dry, and some of the facilities have fallen into disrepair. So far, there is no roof that would protect the tracksite from ongoing weathering. The tracksite has already significantly degraded over the past decade, and vegetation has now started to overgrow the tracks. The tracksite was never properly mapped, when it still was in a good condition. Now, mapping would be difficult because of the bad state of preservation of most of the tracks, but would still be worth the effort.

Scanning and analysis

Here we present a description and discussion of the tracks and trackways preserved at the Las Águilas site. Two field campaigns were executed in 2005 and 2006 in cooperation with the Museo del Desierto at Saltillo (MUDE). Official permits were given by the INAH and all collected vertebrate remains were deposited in the Museo del Desierto. The 3D-scanning project of the Las Águilas trackways was executed in March 2015 in order to record and preserve as much information as is still available after a decade of erosion and degradation of the track site. High resolution 3D scans were combined with photogrammetry, and a quantitative analysis and identification of the tridactyl tracks was performed. After manually cleaning the track-bearing surface using brooms and brushes, the best-preserved tracks were scanned using an Artec EVA structured light scanner. The images were processed in Artec Studio 9, in combination with regular photogrammetry. Photography for the latter was acquired with a Canon 550D camera with a 50mm f/1.4 prime lens, and processed with Agisoft Photoscan 1.1. Single point accuracy of the Artec EVA is within 0.1 mm, while overall accuracy is 1 mm, or less. Data are available from MUDE and SMNK. 3D files (in .ply format) of the tracks are available as supplementary online information.

Figure 1. Geographic location of the site (indicated by the green star).

DESCRIPTION & DISCUSSION

The Las Águilas track site discussed here measures about 25 m NW-SE x 8 m across. The site preserves about sixty footprints, a tally which includes an estimate from the trampling zone. At least eleven individual trackways are clearly distinguished. These comprise seven trackways (which we all interpret as made by tetanurans; see below), all orientated parallel to each other in a south-eastern direction (Figs. 2, 3 A, B), one hadrosaur trackway also heading SE, tracks made by a dromaeosaurid that walked S, and two large tetanuran trackways conjoined with a juvenile heading towards the NW. One single hadrosaur manus print was recognized with a NW orientation.

The depth of the largest tracks is about 80 mm, which suggests that the surface sediment was soft to a maximum of about 150 mm at least in the north-eastern half of the site. In the south-western half of the site the sediment was softer to a deeper level. This is indicated by the undulating margins of the tracks and sediment squeezed up between the toes. The depth of some footprints reaches to about 120 mm, which suggests the presence of a compressive mud layer of about 200 to 250 mm thickness. Many footprints are confluent and form a trampling horizon in the north-western third of the site, where single imprints are no longer visible (‘dinoturbation’; Fig. 2).

When the site was discovered and excavated over a decade ago, the trackways were excellently preserved, especially in the south-eastern half of the exposed area (e.g. Rodríguez de la Rosa *et al*., 2003, 2004; Rodríguez de la Rosa, 2007). The north-western part has been exposed to erosion for over a decade and experienced some weathering, but the nature of these tracks was clearly distinctive (Fig. 3). By now, the impact of erosion is significant (Figs. 2, 3A). Because the tracks are preserved on a dip-slope, run-off water further excavated existing fissures and created new flow channels, frequently following the margins of the tracks. Currently, only a sequence of three tracks of a large theropod (approximately 8 metres body length) is preserved well enough to be re-studied. The ornithomimosaur track reported and depicted by Rodríguez de la Rosa (2007, p.341, fig. 1B) is now completely eroded, but we identified hadrosaur footprints of a medium-sized animal with an estimated length of about 4.5 metres, the manus print of a very large hadrosaurid of at least 9 metres estimated body length, and the didactyl footprint of a medium-sized dromaeosaurid of approximately 3 metres length. In this contribution we focus on the well-preserved theropod trackways.

Hadrosaurid or theropod?

In some cases it is difficult to tell ornithopod trackways apart from theropod trackways. In the absence of tell-tale ornithopod manus imprints, confusion between ornithopod and relatively short and wide (length/width ratio c. 1.0) theropod tracks can easily arise, as pointed out by Thulborn (1990: 219) and Farlow

Figure 2. Las Águilas track site in the year 2009. The seven theropod trackways are still, but barely visible. The lines mark the individual trackways, the dotted line the dinoturbated area. In the foreground the drainage trench and the plank way are visible.

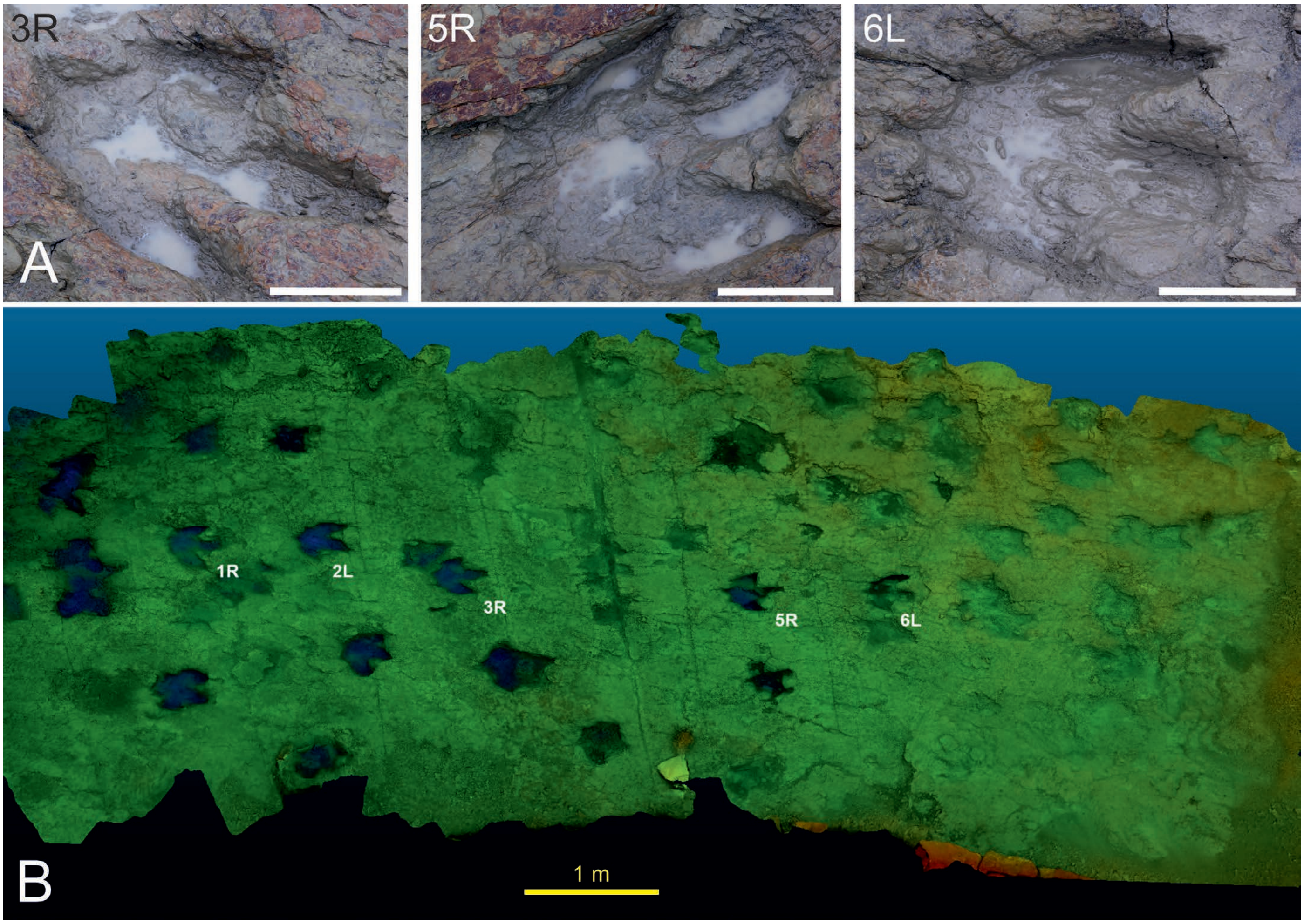


Figure 3. A-Three examples of well-preserved tetanuran tracks (see also Table 1; scale bars are 10 mm); **B**-3D-contour plot of three trackways of tyrannosaurids.

and Chapman (1997). Recently, a theropod tracksite in Australia was re-interpreted as an ornithopod track site by Romilio & Salisbury (2011). Similarly, the initial description of the Las Águilas site described here (see above) does not mention all the theropod tracks we recognize here. Only additional cleaning and detailed measurements allowed us to attribute some of the trackways preserved at Las Águilas to theropods (see discussion in Meyer *et al*., 2008). Most notably the high pace angulation is characteristic of theropod trackways. As an additional test, we here followed the analysis as outlined in Moratalla *et al*. (1988) and Schulp & Wosabi (2012). Measurements (Tab. 1) were acquired from the 3D model. Eight out of the nine quantitative criteria considered by Moratalla *et al.* (1988) end up on the 'more theropod-like' side of the proposed threshold value (Figs. 3, 4). The remaining criterion, the ratio between the length of digit 2 and the width at the base of this digit, ends up right on the threshold value, mainly because of the values obtained from the degraded track 5R and 6L (Fig. 3A). Taking all available data into account we can confidently conclude that the majority of tridactyl tracks still preserved in Las Águilas were produced by tetanurans.

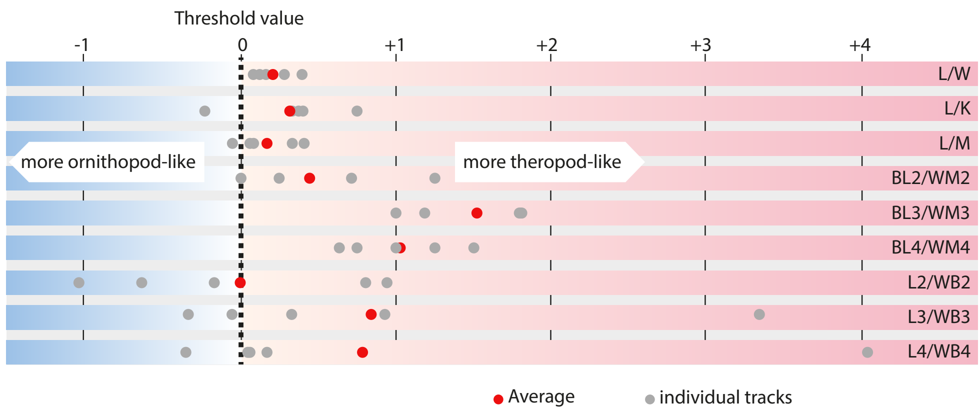
Implications on theropod behavior

There are seven theropod trackways, by elimination most likely made by tetanuran theropods. The tracks all emerge from the dinoturbated area, are headed in southeastern direction (Fig. 2). They were produced by animals about 8 m in length (Meyer *et al.* 2008). It would certainly be possible that the trampled area was produced by a pack of seven individuals, although the preservation of the tracks is clearly insufficient to prove this beyond doubt: the tracks heading out of the dinoturbated area parallel each other with fairly constant intertrackway spacing (Fig. 2). Such a configuration strongly hints at gregarious behaviour of the trackmakers. Interestingly, numerous hadrosaur tracks north of the site, on exactly the same level as the tetanuran tracks, were oriented in exactly the same direction as the tetanuran tracks (but have now been fully destroyed by illegal excavation attempts). Also, one hadrosaur track produced by an animal with an estimated length of about 6 m on the Las Águilas track site heads the same direction as the tyrannosaurid tracks. Although similarities in depth and preservation may suggest that the trackways were made during similar substrate conditions and possibly at approximately the same time, this in itself is not considered here as sufficient evidence for a direct interaction between the theropods and the hadrosaurs.

Other trackways

While the focus of this contribution is on the theropod trackways, we briefly summarize the other trackways reported from the area:

Ornithomimosauridae — During the first years after discovery, two nicely preserved tracks of an ornithomimosaur



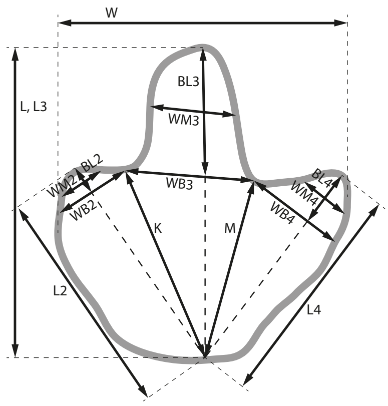


Figure 4. Graph of the hadrosaur and theropod characteristics of the five tridactyl tracks.

	(L/W)-1.25	(L/K)-2	(L/M)-2	(BL2/WM2)-2	(BL3/WM3)-2.2	(BL4/WM4)-2	(L2/WB2)-3.75	(L3/WB3)-4	(L4/WB4)-3.75
1R	0.17	0.23-	0.05-	0.25	1.80	0.64	0.94	0.33	0.35-
2L	0.28	0.38	0.09	1.25	1.80	1.50	0.81	0.93	0.06
3R	0.40	0.75	0.06	0.71	1.80	1.00	0.17-	3.33	0.18
5R	0.13	0.41	0.33	-	1.18	0.75	1.04-	0.33-	0.05
6L	0.09	0.34	0.42	-	1.01	1.25	0.63-	0.05-	4.03
Av.	0.21	0.33	0.17	0.44	1.52	1.03	0.02-	0.84	0.79

Table 1. Measurements on five best-preserved tetanuran tracks in [dimension]; abbreviations: L/W = length-width ratio, L/K = length talon-medial interdigit, BL = digit length, WM = digit width, L = length, WB = basal digit width, R = right, L = left, Av. = average.

were preserved in about the middle of the site. They had a length of about 250 mm and the animal headed to the north. These footprints are now destroyed; even though the recent discovery of the partial skeleton of an ornithomimosaur by a private collector and ornithomimosaurian bone fragments from a site nearby (see above) provide evidence that these animals populated the area.

Dromaeosauridae — There are two imprints of a didactyl track maker in the south-eastern corner of the track site heading south. These tracks have never been reported before and probably were only spotted because of the early morning light after heavy rainfall when we scanned the trackway layer. The trackmaker was a dromaeosaurid with a length of about 3 m.

Hadrosauria — The bulk of hadrosaur tracks was discovered north of the Las Águilas tracksite, but most of them are preserved as badly preserved infills. The best specimens showed the cloverleaf-shaped outline of the toes, but these were removed or destroyed (see above). They all headed in southwestern direction. However, one single hadrosaur footprint is preserved on the Las Águilas tracksite, facing the same direction. Again, the cloverleaf-shaped outline of the digits makes it easy to discern this print from the tetanuran ones. One single bean-shaped manus print facing to the northwest is also preserved. The dimension of about 400 x 150 mm indicates a track maker of at least 9 m in total body length.

CONCLUSIONS

The Campanian Las Águilas track site reveals an unusual and diverse assemblage of dinosaur tracks and trackways. The main site consists of a trampled part in the north-western quadrant with seven tetanuran trackways heading southeast. These seven tracks were produced by animals of the same size of about 8 m body length. The tracks are not only parallel to each other, but also at an almost constant intertrackway spacing – and in the same direction as the hadrosaur track preserved on the same surface. The other tracks that all appear to have been produced during a relatively narrow time span, indicate a surprisingly high diversity of theropods comprising tyrannosaurids, ornithomimosaurids and dromaeosaurids, but also the presence of a large hadrosaurid measuring 9 m in length or more.

All inferred trackmakers are also known by body fossils from the area, although this record is mostly fragmentary. To date only one partial skeleton of a juvenile hadrosaur and that of an ornithomimosaur have been recovered, the latter being in private hands and thus not accessible according to international rules. More than 40 clusters of incomplete hadrosaur remains have been mapped in the area, which document the wealth in body fossils (Vogt *et al.*, 2014).

The Las Águilas site provides a window into the life of the late Campanian on the southernmost area of the North American continental block. The potential of the site is enormous, given that the two most important track-bearing sites have not yet been fully excavated. Recent surveys increased the knowledge on the biodiversity in the area not only on dinosaurs, but also on non-dinosaurian terrestrial tetrapods, invertebrates and plants. Most information on the fossil assemblages of the area comes from a new site that yields the remains of hadrosaurines, lambeosaurines, ankylosaurs, ceratopsians, tyrannosaurids, dromaeosaurids, pterosaurs, eusuchian and dyrosaurid crocodilians, a variety of turtles, plesiosaurs, and lepisoteid fishes aligned with numerous coprolites of turtles, crocodilians and likely small theropods (Frey *et al.*, 2015). To access this wealth for the future an effort must be made to support the people from Porvenir de Jalpa and make this site known better and accessible to the public.

ACKNOWLEDGEMENTS

First and foremost, we would like to thank the people of

Porvenir de Jalpa, who invested countless hours in helping make the site accessible to the public. Many thanks to José Lopez, who discovered the site. The Museo del Desierto supported the fieldwork by HR, DF, WS and CM. The Deutsche Forschungsgemeinschaft covered travel and fieldwork expenses for EF (FR1314/19) and WS (STI128/24 and STI128/30). Travel & Fieldwork for CM and BT was covered by the Kugler-Werdenberg Stiftung of the Natural History Museum Basel. Travel and fieldwork expenses for AS and VV were covered by Naturalis Biodiversity Center, Leiden.

-The authors declare no competing (financial) interests.

-Author contributions: All authors participated in the excavation and cleaning of the trackways. VV performed the scans and processed the 3D material. AS and VV acquired photogrammetry. CM & TB performed measurements on the tracksites. AS performed measurements on the scans and analysed the data.

BIBLIOGRAPHY

Brusatte, S. L., Carr, T. D., 2016. The phylogeny and evolutionary history of tyrannosaurid dinosaurs. Scientific Reports 6, 20252. https://doi.org/10.1038/srep20252

Currie, P.J., 1998. Possible evidence of gregarious behaviour in tyrannosaurids. Gaia 15, 271-277.

Currie, P.J., Eberth, D.A. 2010. On gregarious behavior in *Albertosaurus.* Canadian Journal of Earth Sciences 47(9): 1277-1289.

Eberth, D. A., Delgado-de Jesús, C. R., Lerbekmo, J. F., Brinkman, D. B., Rodríguez de la Rosa, R. A., Sampson, S. D., 2004. Cerro del Pueblo Fm (Difunta Group, Upper Cretaceous), Parras Basin, southern Coahuila, Mexico: reference sections, age, and correlation. Revista Mexicana de Ciencias Geológicas 21, 335-352.

Farlow, J. O., Chapman, R. E., 1997. The scientific study of dinosaur footprints, p. 519-553 *In:* Farlow, J. O., Brett-Surman, M. K. (eds.), The Complete Dinosaur, Indiana University Press, Bloomington and Indianapolis, Indiana.

Frey, E., Rivera-Sylva, H., Stinnesbeck, W., Padilla Guiterrez, J. M., González-González, A. H., Amezcua Torres, N., Schulp, A., Vanhecke, V., 2015. News on the Late Cretaceous Las Águilas dinosaur graveyard, Coahuila, Mexico. 13th Annual Meeting of the European Association of Vertebrate Palaeontologists Opole, Poland, 8-12 July 2015 – Abstracts: 71

McCrea, R. T., Buckley, L. G., Farlow, J. O., Lockley, M. G., Currie, P. J., Matthews, N. A., Pemberton, S. G., 2014. A "Terror of Tyrannosaurs": the first trackways of tyrannosaurids and evidence of gregariousness and pathology in Tyrannosauridae. Plos One 9, e103613-13. https://doi.org/10.1371/journal.pone.0103613

Meyer, C. A., Frey, E. D., Thüring, B., Etter, W., Stinnesbeck, W. 2005. Dinosaur tracks from the Late Cretaceous Sabinas Basin (Mexico). Kaupia 14, 41-45.

Meyer, C. A., Frey, E., Thüring, B., 2008. The pitfalls of interpreting incomplete dinosaur trackways – an example of a dromaeosaurid trackway from the Late Cretaceous of the Sierra Madre Oriental (Cerro del Pueblo Formation, Late Campanian; Parras Basin, Coahuila, NE Mexico). 6th Meeting of the European Association of Vertebrate Paleontologist, Spišská Nová Ves, Slovak Republic, Volume of Abstracts, pp. 69-73.

Moratalla, J. J., Sanz, J. L., Jimenez, S., 1988. Multivariate analysis on lower Cretaceous dinosaur footprints: discrimination between ornithopods and theropods. Geobios 21, 395-408. https://doi.org/10.1016/S0016-6995(88)80042-1

Rodríguez de la Rosa, R. A., Eberth, D. A., Brinkman, D. B., Sampson, S. D., López-Espinoza, J., 2003. Dinosaur tracks from the Late Campanian Las Aguilas locality Southeastern Coahuila, Mexico. Journal of Vertebrate Paleontology, SVP Annual Meeting Abstracts, pp. 90A.

Rodríguez de la Rosa, R. A., Aguillón-Martínez, M. C., López-Espinoza, J., Eberth, D. A. 2004. The fossil record of vertebrate tracks in Mexico. Ichnos 11, 27-37. https://doi.org/10.1080/10420940490428841

Rodríguez de la Rosa, R. A., 2007. Hadrosaurian footprints from the Late Cretaceous Cerro del Pueblo Formation of Coahuila, Mexico. In: Díaz-Martinez, E., Rábano, I. (Eds.), 4th European Meeting of the Paleontology and Stratigraphy of Latin America / Cuadernos del Museo Geominero 8, Instituto Geológico y Minero de España, Madrid, pp. 339-343.

Romilio A., Salisbury S. W. 2011. A reassessment of large theropod dinosaur tracks from the mid-Cretaceous (late Albian-Cenomanian) Winton Formation of Lark Quarry, central-western Queensland, Australia: a case for mistaken identity. Cretaceous Research 32, 135-142. https://doi.org/10.1016/j.cretres.2010.11.003

Schulp, A. S., Al-Wosabi, M. 2012. Telling apart ornithopod and theropod trackways: a closer look at a large, Late Jurassic tridactyl dinosaur trackway at Serwah, Republic of Yemen. Ichnos 19, 194-198. https://doi.org/10.1080/10420940.2012.710672

Smith, S. D., Persons, W. S., IV, Xing, L., 2016. A tyrannosaur trackway at Glenrock, Lance Formation (Maastrichtian), Wyoming. Cretaceous Research 61, 1-4. https://doi.org/10.1016/j.cretres.2015.12.020

Thulborn, T., 1990. Dinosaur Tracks. London: Chapman and Hall., 410 pp. https://doi.org/10.1007/978-94-009-0409-5

Vogt, M., Stinnesbeck, W., Zell, P., Kober, B., Kontny, J., Herzer, N., Frey, E., Rivera-Sylva, H. E., Gutierrez, J. M. P., Amezcua, N. Huerta, D. F., 2016. Age and depositional environment of the "dinosaur graveyard" at Las Águilas, southern Coahuila, NE Mexico. Palaeogeography, Palaeoclimatology, Palaeoecology 441, 758-769. https://doi.org/10.1016/j.palaeo.2015.10.020