

A new trackway possibly made by a trotting theropod at the Las Hoyas fossil site (Early Cretaceous, Cuenca Province, Spain): Identification, bio-dynamics, and palaeoenvironmental implications

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ABSTRACT

Dinosaur footprints have recently been identified at the Las Hoyas fossil site, renewing interest in its trace fossils as aids in the interpretation of the area's palaeoenvironment and palaeocommunity. The varied tetrapod print morphologies found seem to have been influenced by the contemporaneous presence of microbial mats. This paper updates the information on tetrapod traces at the site and describes a new dinosaur trackway containing four tridactyl footprints. Although the trackway is not particularly well-preserved, the morphology of the toe marks, the heel surface, and the general morphology of the prints strongly suggest they were produced by a theropod dinosaur of medium size. Further, the ratio between the stride length and the deduced hip height suggest the trackmaker was trotting. Interestingly, the footprints are very similar in size to the pes of *Concavenator*, a carcharodontosaurid dinosaur known from skeletal material at the same locality. This new ichnological evidence reveals tetrapod prints to be more abundant toward the top of the site's stratigraphic succession. This suggests that, over time, the ecosystem evolved toward more frequent dry periods - the dinosaurs present became able to walk in areas with shallow water and big dinosaurs walked across the ponding zone of Las Hoyas.

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Moratalla, J.J., Marugán-Lobón, J., Martín-Abad, H., Cuesta, E. and Buscalioni, A.D. 2017. A new trackway possibly made by a trotting theropod at the Las Hoyas fossil site (Early Cretaceous, Cuenca Province, Spain): Identification, bio-dynamics, and palaeoenvironmental implications. *Palaeontologia Electronica* 20.3.59A: 1-14. <https://doi.org/10.26879/770> palaeo-electronica.org/content/2017/2073-theropod-trackway-at-las-hoyas

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KEYWORDS: Barremian; Carcharodontosaurid; footprints; trotting dinosaur; microbial mats; taphonomy

Submission: 24 March 2017 Acceptance: 13 November 2017

INTRODUCTION

Although the deposits at the Las Hoyas site (Province of Cuenca, Spain) are known mainly for their abundant and well-preserved body fossils (Buscalioni and Poyato-Ariza, 2016), the site's trace fossils have proved essential in arriving at an understanding of the area's palaeoecological and palaeoenvironmental setting (Fregenal-Martínez and Meléndez, 2016). By complementing the body fossil record, trace fossils allow a much more complete picture of the fauna that inhabited the Las Hoyas palaeoecosystem to be discerned.

Invertebrate trace fossils at Las Hoyas were first documented by Fregenal-Martínez and Moratalla (1995) and Fregenal-Martínez et al. (1995). The ichnoassemblage was later updated by Buatois et al. (2000), who reported the presence of the ichnogenera *Cruziana*, *Helminthoidichnites*, *Lockeia*, *Palaeophycus*, and *Treptichnus*, and more recently by Gibert et al. (2016), who included the ichnogenus *Planolites*. The fish ichnotaxon *Undichna unisulca* is also frequent in the locality (Gibert et al., 1999). This ichnofacies is named *Mermia* and contains signs of characteristic benthic invertebrate activity - mainly that of crustaceans, worms, and insect larvae within continental environments (Buatois and Mángano, 2011). This *Mermia* interpretation is congruent with the body fossils present, which mainly represent obligate aquatic organisms such as benthic invertebrates and fish (Gibert et al., 1999; Buatois et al., 2000; Buscalioni and Fregenal-Martínez, 2010; Gibert et al., 2016). The Las Hoyas *Mermia* ichnoassemblage is rather peculiar, however, given the presence of archosaur trackways (Gibert et al., 2016).

The archosaur ichnofossils at Las Hoyas are less abundant than those of invertebrates, but have yielded significant information on the palaeoecology and palaeoenvironmental conditions of the ecosystem (Buscalioni and Fregenal-Martínez, 2010; Fregenal-Martínez and Meléndez, 2016). The tetrapod ichnofossils include some shallow footprints forming a crocodile trackway (Moratalla et al., 1995), a discovery that obliged the established palaeoenvironmental interpretation of a

deep lake to be revisited and replaced with that of a rather shallow aquatic environment (Moratalla et al., 1995; Fregenal-Martínez and Meléndez, 2016). Buscalioni and Fregenal-Martínez (2010) reported Las Hoyas to have few tetrapod traces, although crocodylian body fossils are abundant. Dinosaurs are represented only by three specimens and species: *Pelecanimimus polyodon* (Pérez-Moreno et al., 1994), *Concavenator corcovatus* (Ortega et al., 2010), and cf. *Mantellisaurus* (Llandres et al., 2013). In fact, dinosaurs appear to have been only incidental organisms in the Las Hoyas ponding area (Buscalioni et al., 2008; Buscalioni and Fregenal-Martínez, 2010).

Early field work also yielded an isolated tridactyl footprint. This isolated footprint was first attributed to *Pteraichnus* (Lockley et al., 1995), then tentatively identified as turtle (Moratalla et al., 1995), and thereafter was reinterpreted as a theropod dinosaur (Vullo et al., 2009). New tetrapod ichnofossils were found in subsequent campaigns, including a theropod trackway composed of seven footprints (figure 5 in Gibert et al., 2016). This paper updates the information regarding the abundance of tracks in the stratigraphic succession of the Las Hoyas site. A second dinosaur trackway (LH-Y-1-001) is described, its state of preservation assessed, and its palaeoenvironmental implications discussed.

GEOLOGICAL SETTING

The Las Hoyas fossil site consists of finely laminated limestones within the La Huérguina Formation, a unit that records late Hauterivian-Barremian continental sedimentation in the southwestern Iberian Basin (Serranía de Cuenca, Spain) (Figure 1). On the basis of charophytes, ostracods, and palynomorphs the site has been dated as Late Barremian (Diéguez et al., 1995; Martín-Closas and Diéguez, 1998). The deposit represents a lacustrine to palustrine wetland in a freshwater carbonatic lentic ecosystem with a seasonal subtropical climate. There is no evidence of any marine influence (Poyato-Ariza et al., 1998; Bailleul et al., 2011). The wetland was drained by

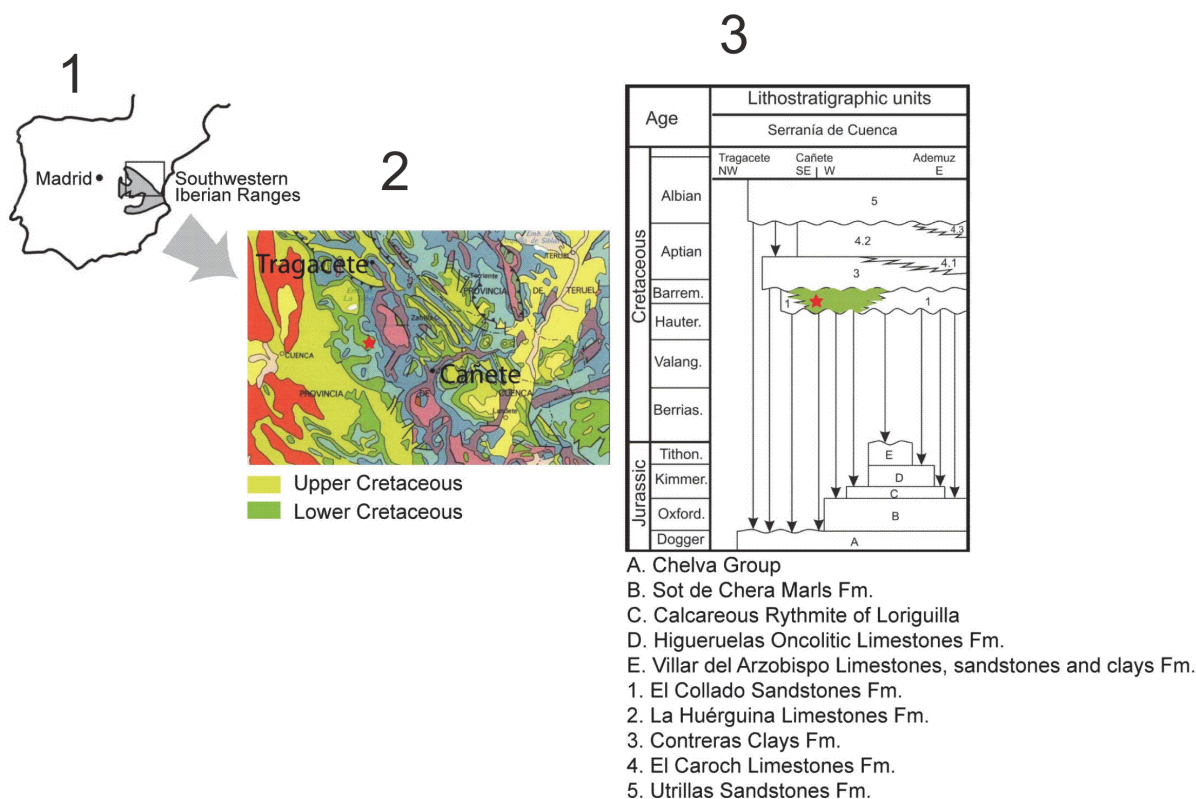


FIGURE 1. 1. Location of the Southwestern Iberian Ranges on the Iberian Peninsula. 2. Lithostratigraphic units of the Cretaceous of Iberian Basin. 3. Informal stratigraphy of La Huérguina Limestones Fm. in Las Hoyas and surrounding sub-basins (modified from Fregenal-Martínez and Meléndez, 2000).

carbonatic-rich water fed by groundwater and/or karstic aquifers (Fregenal-Martínez et al., 2014). The watered areas were shallow and covered by microbial mats (Briggs et al., 1997; Gupta et al., 2008). These ponding surfaces experienced seasonal oscillations in their water level (Fregenal-Martínez and Meléndez, 2000).

The laminated limestones of Las Hoyas reflect two petrographically differentiated facies associations (Fregenal-Martínez, 1998). One is the result of the sedimentation by traction and decantation of allochthonous elements (e.g., detrital carbonate particles, plant debris) and bio-induced calcium carbonate, deposited during seasonal flooding and longer-term wetter periods. The other is an autochthonously-produced facies composed of carbonate generated by the growth of thick mats of microbial communities during drier periods (Fregenal-Martínez, 1998). During drier periods, the depth of the water column was reduced to probably just a few centimeters. The drier facies are richer in fossils than the wetter facies and, in addition, dinosaur and crocodile footprints are commonly found

on the drier facies (Fregenal-Martínez and Buscalioni, 2009; Buscalioni and Fregenal-Martínez, 2010).

DISTRIBUTION AND TAPHONOMIC ASSESMENT OF TETRAPOD TRACES

The Las Hoyas site has been the subject of layer-by-layer excavation since 1991 (Buscalioni and Fregenal-Martínez, 2010; Buscalioni and Poyato-Ariza, 2016). Small square areas of about 30 m² are suitable for testing the homogeneity of the fossil associations throughout the layers. Each excavated area was named according to a color (Figure 2). The set of excavated squares follows a stratigraphic succession from Yellow (East) to Light Grey (West). Correlation of the squares was done by combining the analysis of microfacies and the fossil content at each layer (Buscalioni and Fregenal-Martínez, 2010), and by connecting some sampled areas in the locality (see Figure 2, corridors “Milky Line” and “Ma-Wh path”). Along the stratigraphic succession, some prints were found isolated on small areas, whereas on the extended

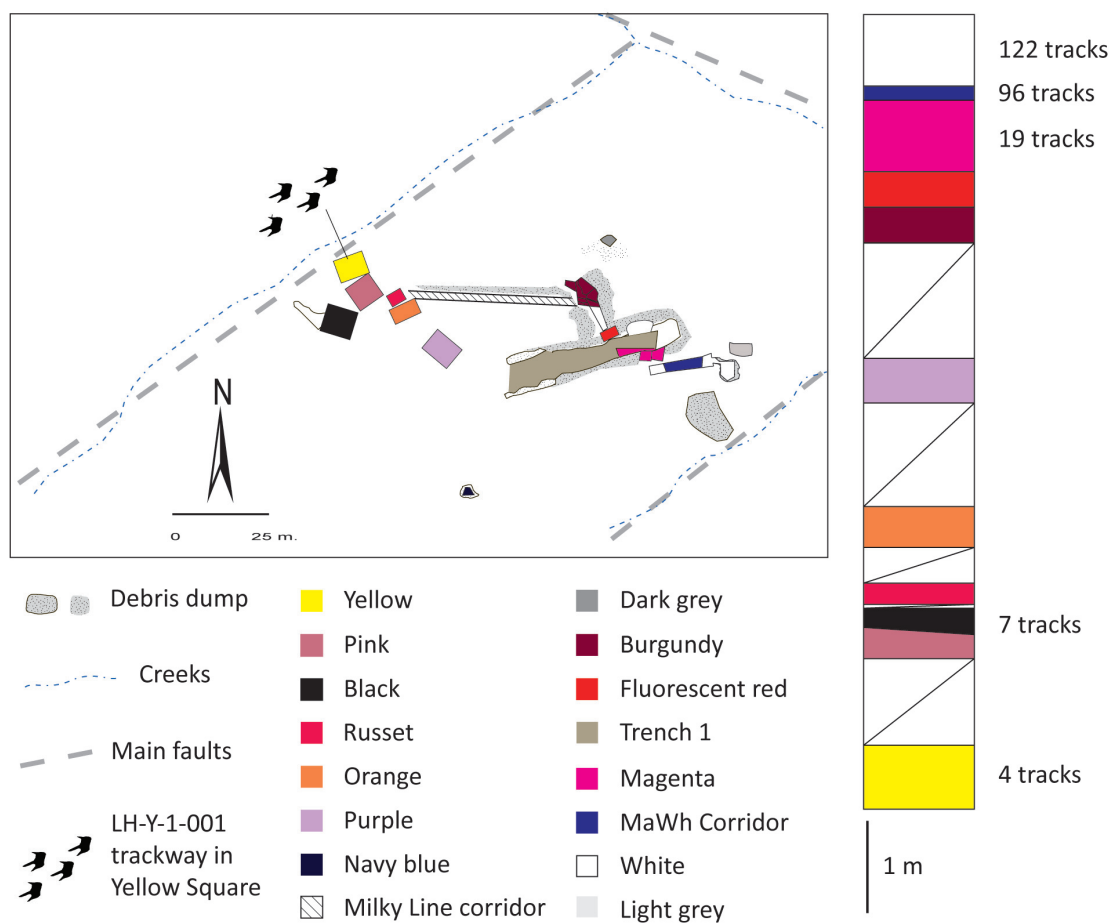


FIGURE 2. Map of the Las Hoyas quarry (upper Barremian, Cuenca, Spain) with the position of the E-W excavated Squares, in color (modified from Buscalioni and Fregenal-Martínez, 2010). As shown in the box, the stratigraphic succession of the squares, and the associated richness in the number of tetrapod tracks.

excavated squares, a set of traces or even trackways were discovered. The number of tetrapod traces increased from the bottom (Yellow) to the top (Light Grey) of the stratigraphic succession, with the top squares (Magenta, Ma-Wh Corridor, and White Squares) containing about 75% of all known tetrapod tracks (Figure 2). The newly discovered dinosaur trackway LH-Y-1-001 is on the Yellow Square and it is the most basal trackway in the stratigraphic succession (Figure 2).

Fishes were the main vertebrate trace producers. *Undichna* appeared as a rather common ichnotaxon in all layers, as reported by Gibert et al. (1999). Tetrapods, represented by crocodylian and dinosaur traces, were identified by isolated manus and pes prints. The mean length of dinosaur footprint (tip of III digit to heel) was 337 mm (range 80-600 mm). Tetrapod prints are frequently linked to tail drag marks, or the prints occur with *Undichna* and invertebrate traces; they may also occur as a profuse number ($n = 80-90$) of small, sub-rounded

undetermined prints of with a mean diameter of 40 mm (Figure 3.6).

In general, tetrapod autopodia appeared preserved as blurred prints, with the digits not sharply defined, diffuse pes/manus outlines, and prints commonly stretched. Both prints and undertracks appear rather shallow, and overtracks, when present, irregular; sediment that fills the tracks is laminated in some parts, but not in others. Thus, the makers of most of the tetrapod traces could only be unequivocally determined in exceptional cases (Gibert et al., 2016). Despite this unexceptional preservation, two types of footprints may be sorted in the locality: (1) shallow prints that reflect the gross outline of the feet (Figure 3.2 and 3.5); and (2) deep, traceable prints that show a more detailed impression of the toes (Figure 3.1, 3.3, and 3.4).

1. The shallow prints tend to preserve an incomplete contour (Figure 3.2), whereas

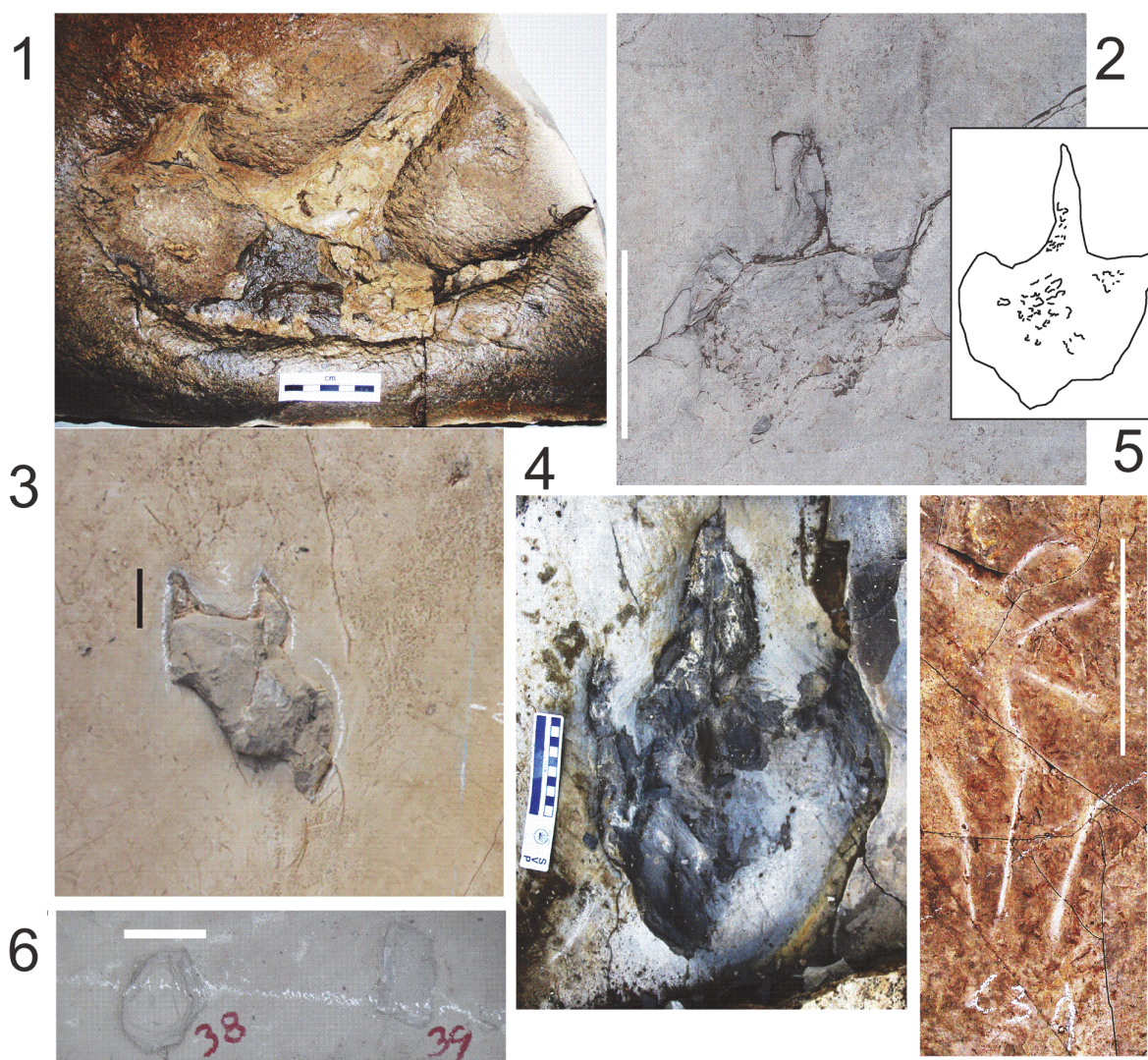


FIGURE 3. Preservation of tetrapod traces at Las Hoyas (Late Barremian, La Huérguina Formation). **1.** Stretched isolated footprint (MCCM-LH- 6500) that was formerly attributed to *Pteraichnus*. **2.** Dinosaur footprint of a trackway composed of two prints in White Square layer #8.2, showing a chipped surface inside; scale bar 15 cm. **3.** Theropod left footprint of the trackway recorded in Magenta Square. **4.** Theropod right footprint of the same trackway as Figure 3.3 recorded in Magenta Square. **5.** Hand and foot of a crocodylomorph recorded in White Square, layer #5, scale bar 13 cm. The image has been equalized to enhance the scratches of the foot toes. **6.** Traces attributed to undetermined tetrapod preserved as sub-elliptical prints closely placed from MaWh Corridor (LH-29959).

some of the prints are scratches in the sediment (see the hand-foot of a crocodylomorph in Figure 3.5). None of this shallow-print type shows a well-shaped overtrack with inner layers; conversely the track is rather smooth or preserves internally a chipped surface (Figure 3.2).

2. The group of deep prints preserves the foot contour, even though foot contours can be unequally conserved throughout the same trackway. Unequally preserved

footprints in the same trackway may combine sheared and well-shaped traces (Figure 3.3–4). The deep footprints display a stack of internal laminated overtracks, the outline is bounded by a displacement rim bulging around the track, and the rim is set of sharply visible radial fractures. A paradigmatic deep-type at Las Hoyas is the footprint once attributed to *Pteraichnus* (Figure 3.1, 4).



FIGURE 4. Drawing of the distorted footprint MCCM-LH 6500 (Las Hoyas, Late Barremian) showing the taphonomic features of a print likely produced on a moist to unsaturated microbial mat. **1-3:** layers of sediment fill that form a stack of internal overtracks; **dr:** displacement rim; **rf:** radial fissures or striation marks.

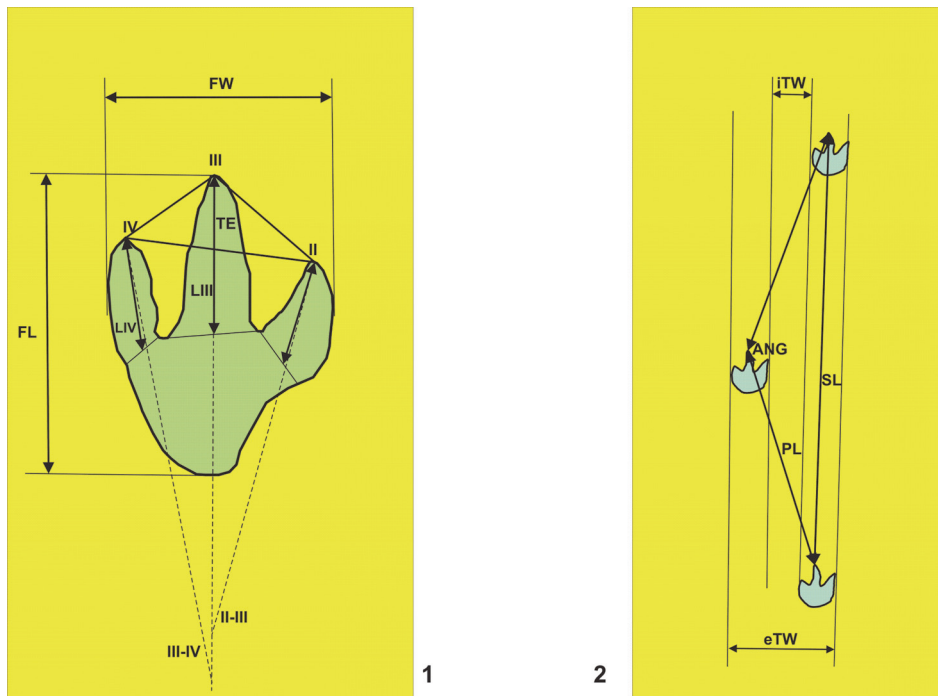


FIGURE 5. Measurements used in this study. **1.** Variables related to a footprint: **FL**, footprint length; **FW**, footprint width; **LII**, **LIII**, **LIV**, length of the digits; **II-III**, angle between the axis of digit II and digit III; **III-IV**, the same angle relative to digits III and IV; **TE**, toe extension, that is, the anterior projection of digit III. **2.** Variables related to a trackway: **ANG**, angle between three consecutive footprints; **eTW**, external trackway width; **iTW**, internal trackway width; **PL**, pace length; **SL**, stride length.

SYSTEMATIC ICHNOLOGY

Methods. The new trackway—LH-Y-1-001—was mapped, measured, and quantified using the variables described in Figure 5. The trackway was also mapped using a Breuckmann SmartScan 3D HE-color scanner, with 3D high resolution white light. Furthermore, a camera reflex Canon 5D mark II was used for photograph support. The hip height (H) of the trackmaker was estimated using the method of Thulborn (1990) for theropod tracks longer than 25 cm ($H = 4.9FL$) (FL: footprint length). This method avoids the generalization of Alexander (1976) ($H = 4FL$), and it is more conservative with respect to the estimated speed.

Referred Material. LH-Y-1-001 was composed of four consecutive tridactyl footprints named LH-Y-1-001/1, LH-Y-1-001/2, LH-Y-1-001/3 and LH-Y-1-001/4, following the direction of movement (Figures 6–7).

Horizon. The trackway LH-Y-1-001 was found on the top layer of the Yellow Square (Figure 2). The Yellow Square is at the base of the stratigraphic succession of the excavated area defined between the West and East main faults (Figure 2).

Preservation. The footprints of LH-Y-1-001 are shallow, with incomplete contours; footprints are rather flat and covered by a thin, non-laminated overtrack (Figure 6).

DESCRIPTION

Trackway LH-Y-1-001 is composed of four tridactyl footprints (right-left-right-left) of medium size (Table 1) made by an animal walking in bipedal fashion (Figures 5-6). It shows a direction of movement of 234° (Table 2). Both strides seem to be quite long (292 cm and 317 cm). In contrast, the pace angle is quite small (154° as mean value). The first pace (138 cm) is shorter than the second (165 cm).

Print 1 (LH-Y-1-001/1) is incompletely preserved; only the central and lateral digits are visible. The medial digit, the heel surface, and the medial rear outline have not been preserved. In fact, the rear part of the print suggests that the proximal end of the autopodium did not, at least in this print, make contact with the substrate. At 13 cm in length, this incomplete print is only half the length of the remaining prints in the trackway. It is, however, slightly deeper than the rest (Figure 6.2).

Print 2 (LH-Y-1-001/2), with short digits, is unambiguously tridactyl and longer (28 cm) than wide (24 cm). The digits are slightly acuminate and the hypoxes rather distally located. The heel sur-

face is wide with a relatively broad posterior outline. This print is very shallow (<1 cm in depth) (Figure 6.3).

Print 3 (LH-Y-1-001/3) is also clearly tridactyl, with long, slender digits. Digit III is V-shaped, distally acuminate, and clearly longer than digits II and IV. Digit II is somewhat shorter than digit IV and shows slight medially curving. This track is also very shallow (Figure 6.4).

Print 4 (LH-Y-1-001/4) is poorly preserved making observation of the track morphology difficult. In fact, such measurements as total length and the width have not been considered for calculation of the means (Tables 1–2). Despite these issues, the general size and shape seem to be analogous to the preceding footprints ($n^\circ 2$ and $n^\circ 3$), and, in particular, this fourth footprint confirms the trackway pattern.

The mean footprint length/width ratio (FL/FW) (based on tracks 2 and 3) is 1.14, confirming the tracks to be slightly longer than they are wide. At a mean of 10.1 cm, digit III is clearly the longest of all; the TE projection (*sensu* Weems, 1992) is about 8.12 cm (Figure 5). Digits II and IV are clearly shorter than the middle digit (digit III), and the mean length of digit II is about 17.7% less than that of the digit IV (Table 1). The divarication angle (II-IV) is variable; print 2 shows a value of 20° while that of print 3 is 39° . However, the latter print is the best preserved, thus 39° might be the most accurate measure. The hip height (H), calculated according to Thulborn (1990) for theropod footprints longer than 25 cm, was 134.75 cm, suggesting an animal some 4.0-4.5 m long, or a medium-sized theropod.

DISCUSSION

Trackmaker Identification

The features of the prints of trackway LH-Y-1-001 (i.e., their generally elongated nature, acuminate digits, mesaxonic condition, the V-shape of digit III, the rather medially directed digit II, the relatively straight digit IV, the fact that digit II is slightly shorter than digit IV, and the digit II-III divarication angle smaller than that of III-IV [Figure 5]), strongly indicate that the trackmaker was a theropod dinosaur. The size of the footprints suggests the dinosaur was medium-sized; the estimated hip height was about 134 cm and the estimated body length 4.0-4.5 m. Identifying the trackmaker beyond that of it being a theropod is, however, not an easy matter. For example, bony foot elements for theropods are not abundant (especially in the European fossil

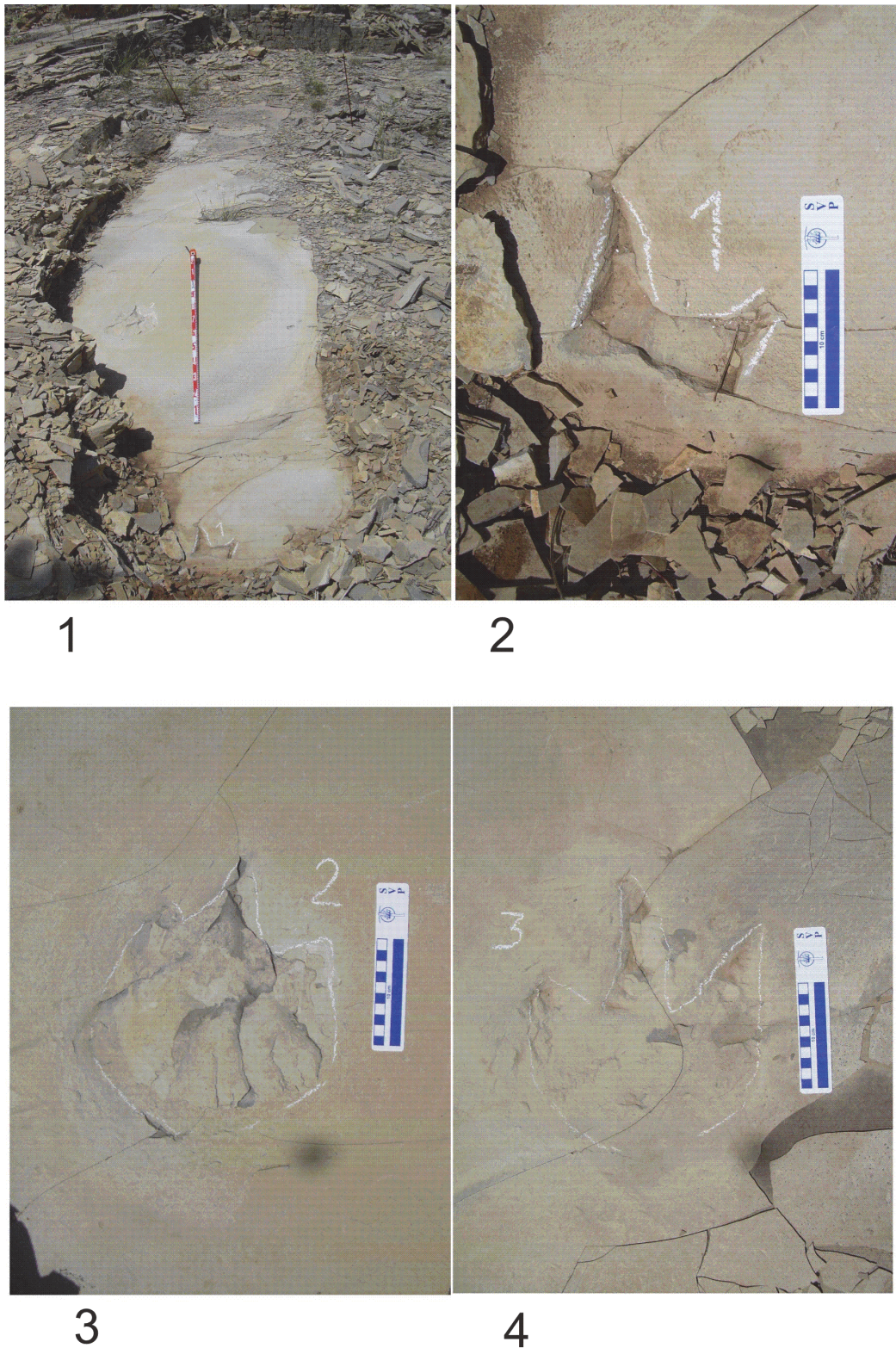


FIGURE 6. 1. Photograph of the trackway LH-Y-1-001 of the Late Barremian of Las Hoyas outcrop (La Huérguina Formation). 2. Footprint LH-Y-1-001/1. 3. Footprint LH-Y-1-001/2. 4. Footprint LH-Y-1-001/3.

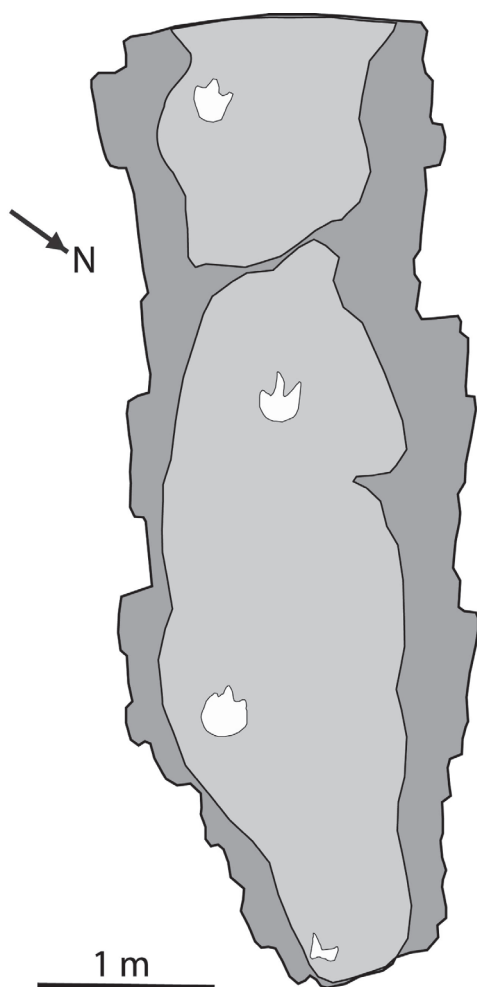


FIGURE 7. Map of the trackway LH-Y-1-001 from the Las Hoyas fossil site Late Barremian (La Huérguina Formation).

record), making it difficult to identify an animal with a foot that precisely matches the anatomy revealed by the present tracks (see Demathieu, 1981; Henderson, 2003; Wilson, 2005).

Interestingly, however, these tracks are about the same size as the feet of the well-preserved carcharodontosaurid dinosaur, *Concavenator corcovatus* (Ortega et al., 2010; Cuesta and Fregenal-Martínez, 2012), found in the same locality. A detailed study of the feet of *Concavenator* revealed the presence of foot pads, the general morphology of their soft parts (Cuesta et al., 2015), and showed the foot phalanges of digit III to be approximately 25.8 cm long, very similar to the 27.5 cm recorded for prints 2 and 3 of LH-Y-1-001. Indeed, when the distal part of the metatarsal is taken into account, the overall length of the feet match even better. Consequently, the length of the

foot of *Concavenator* and the present footprints appear to be equivalent. In addition, the calculated value for the hip height of the trackmaker using Thulborn's equation results in a hindlimb length of 134.75 cm while the *Concavenator* skeleton has a hindlimb length of 137.9 cm. The agreement between these values cannot, however, unequivocally identify the trackmaker even as a carcharodontosaurid. In fact, the foot bones of the members of Carcharodontosauridae are poorly represented in the fossil record. Despite that, some carcharodontosaurid foot fossils are available for comparison. However, while specimen NCSM 14345 of the North American *Acrocanthosaurus atokensis* (Stovall and Langston, 1950; Currie and Carpenter, 2000) presents an almost complete foot, it lacks the more distal phalanges. Further, *Tyrannotitan chubutensis* (Novas et al., 2005) and *Mapusaurus roseae* (Coria and Currie, 2006) are only represented by few or incomplete metatarsals and few phalanges, and the bones of the latter may, in fact, belong to different individuals (Coria and Currie, 2006).

Trackmaker Movement

One of the most significant contributions of paleoichnology to dinosaurology is the possibility of estimating progression speeds, and even more important, indirect estimations of the momentum of the trackmaker. The first estimate of a trackmaker's speed, inferred from its own trackway, was made by Alexander (1976), who reported the following relationship:

$$V = 0.25 \times g^{0.5} \times SL^{1.67} \times H^{-1.17}$$

Equation 1

where V is the trackmaker's speed, g the acceleration of gravity, SL the stride length, and H the hip height.

The use of this equation with the trackway LH-Y-1-001 suggests the animal, although probably accelerating, had developed a mean velocity of 3.3 m/s (12.7 km/h). Interestingly, the biodynamic index (SL/H) of 2.26 for the studied trackway is within the range of trotting but not running (*sensu* Thulborn, 1982). Thus, the putative trackmaker, a theropod dinosaur, may have been exhibiting a trotting behavior. By way of comparison, human professional marathon runners have a mean race speed (over the 42 km course) of about 5.5 m/s (20 km/h). Thus, while the trackmaker may have been trotting, its mean velocity was lower than that of a human running a marathon. These findings should, of course, be taken cautiously since only two full strides are available for measurement. Further, the

TABLE 1. Track measurements for the trackway LH-Y-1-001 from the Las Hoyas fossil locality. **Rot**, angle between the track and the trackway midline (negative value implies inward rotation). **H**, hip height sensu Thulborn (1990). The rest of variables as in the Figure 5.1.

Track	FL	FW	LII	LIII	LIV	TE	II-III	III-IV	II-IV	FL-FW/FW	Rot	H
1	13	15		11	5			41°		(-) 0.13	-11°	
2	28	24	4.5	7.5	2.5	6.25	11°	9°	20°	0.16	0°	137.2
3	27	24	6.2	12.7	10.5	10	18°	24°	39°	0.12	-4°	132.3
4	26	22	8	12.5	8	5.5	24°	26°	46°	0.18	-12°	127.4
Mean	27.5	24	5.35	10.1	6.5	8.12	14.5°	16.5°	29.5°	0.14	-6.7°	134.75

TABLE 2. Trackway measurements from the trackway LH-Y-1-001 from the Las Hoyas fossil locality. **H**, hip height sensu Thulborn (1990); **V**, speed of progression (km/h); **DIR**, trackway direction. The rest of the measurements as in Figure 5.2 and Table 1.

Tracks	SL	PL	ANG	SL/H	SL/FL	eTW	iTW	iTW/FW	V	DIR
1-3	292		151°		10.61					
2-4	317		157°		11.52					
1-2		138								
2-3		165								
3-4		156								
Mean	304.5	153	154°	2.26	11.06	53.7	16.2	0.67	12.7	234°

second pace in the trackway is 19.5% longer than the first (165 vs. 138 cm). Despite the fact that the third pace is shorter (156 cm), the two preserved strides (292 and 317 cm, respectively) could suggest that the trackmaker may have been accelerating. However, similar physical evidence of acceleration in the fossil record is very scant (Kim and Huh, 2010).

Dinosaur skeletal organization is variable among clades, but their biomechanics suggest that many of them could run. Indeed, some appear to have been fast runners, especially small-to-medium size theropods and certain bipedal ornithomorphs (Russell and Béland, 1976; Thulborn and Wade, 1979, 1984; Farlow et al., 2000; Persons IV and Currie, 2016). However, trackways produced by running dinosaurs are quite rare, and most estimates from bipedal trackways suggest speeds of <10 km/h (Thulborn, 1990; Pérez-Lorente, 1996; Farlow et al., 2000). Some cases of “quick” dinosaur trackways have, however, been reported (Russell and Béland, 1976; Thulborn and Wade, 1979; Thulborn, 1981; Thulborn and Wade, 1984), with some suggesting speeds of up to 40 km/h (Farlow, 1981; Viera and Torres, 1995; Irby, 1996.). The theropod trackway reported here would, therefore, be on the average of that “quick” dinosaur pattern.

Palaeoenvironmental Implications of Trackway LH-Y-1-001

The palaeoenvironmental implications of LH-Y-1-001 trackway allow us to interpret the different types of track preservation and to review the pattern of relative abundance of tetrapod traces at Las Hoyas. The fact that most of the fossil record of Las Hoyas was influenced by the contemporaneous production of microbial mats (Gupta et al., 2008; Iniesto et al., 2016; Iniesto et al., 2017) suggests that these might have also affected the preservation of the tetrapod tracks. The production of carbonate by growing microbial communities characterizes the facies in which the dinosaur and crocodile tracks are found (Buscalioni and Fregenal-Martínez, 2010). These facies were deposited during periods in which the water column was reduced to probably several centimeters in depth (Fregenal-Martínez, 1998), i.e., the drier periods that affected this seasonal, subtropical wetland ecosystem.

Microbial mats favor the preservation of tetrapod tracks because a microbially-stabilized substrate behaves more plastically, the microbially-bound sediment preserves the imprint, and microbial mats often induce early cementation (Marty et al., 2009; Carmona et al., 2011; Dai et al., 2015). Further, a high spectrum of variation in footprint

shape has been experimentally demonstrated in present-day tidal flat environments with growing microbial mats and human trackmakers (Marty et al., 2009). These authors found that due to differences in water content and thickness of microbial mats related to the underlying sediment, the same trackmaker may produce a wide range of preservation types. Therefore, the two different morphologies (i.e., shallow or deep prints, see Figure 3) found at Las Hoyas were likely influenced by microbial mats.

The shallow footprints at Las Hoyas show analogies with those described by Marty et al. (2009) in dry to damp mats. In accordance with their results, the theropod footprint with a chipped surface inside (Figure 3.2) would suggest that the dinosaur cracked the mat after pressing its foot into the sediment. The absence of a well-shaped over-track, in this case, indicates a simple filling up. On the other hand, the deep footprints preserve better details of the toe outlines (Figure 3.1, 3.3 and 3.4). In these deep prints found at Las Hoyas (Figure 3.1 and 3.4), the underlying sediment was not penetrated. Instead, the superficial layer with the microbial mat was compressed and pushed into the underlying sediment (Figure 4). The impact of the foot formed a displacement rim all around the track, whereas the superficial microbial mat led to cracking around the foot (Figure 4) forming striation marks (Dai et al., 2015). These features are analogous to those of human prints produced in water unsaturated mats (see figure 5E in Marty et al., 2009); these taphonomic details have also been recognized in ornithopod tracks of the Early Cretaceous Jiaguan Formation (Dai et al., 2015). Furthermore, the distortion of some dinosaur footprints at Las Hoyas (Figure 3.1 and 3.3) prompts us to think that they could have been produced in a more watery setting of a slippery surface able to shear the tracks.

The preservation of the trackway LH-Y-1-001 matches with those produced on dry to damp mats following Marty et al. (2009). The presence of an irregular internal overtrack (Figure 6.3 and 6.4) might indicate that the mat kept growing covering the shallow true track. Moreover, running and jumping dinosaurs tend to produce ill-defined prints (Marty et al., 2009), and the optimal substrate consistency (soft and watered mud) for print formation may be mechanically unsuitable for running in

heavy animals. Hence, the type of preservation of LH-Y-1-001 concurs with a dry substrate required for a running locomotion pattern.

CONCLUSIONS

The footprints of trackway LH-Y-1-001 are noteworthy since they may record a fast moving dinosaur. The preservation of the footprints was influenced by microbial mats and the features observed in the three complete footprints are in agreement with their production on a dry to damp mat substrate. The poor preservation of the prints is probably also a consequence of the trotting of the trackmaker. The identity of the trackmaker cannot be known for certain, however, the trackway dimensions suggest that the trackmaker was an agile, medium-sized theropod with a long stride, features shared by *Concavenator corcovatus* known from this locality.

Reassessment on the number of tetrapod tracks at Las Hoyas suggests that they became more abundant towards the top of the stratigraphic succession (i.e., Magenta to White Square). In particular, the abundance of crocodile and dinosaur trackways in the White Square (Figure 2) indicates the recurrent presence of medium-to-large sized individuals. Still, we need to prove whether the increase in the number of archosaur tracks implies a change in the conditions of the palaeoecosystem. The big dinosaurs may have been more abundant only at that moment, and they were walking or crossing a shallow ponding zone as incidental organisms, insomuch as only their locomotion traces have been recorded.

ACKNOWLEDGMENTS

This paper was produced as part of project CGL2013-42643P for the study of the Las Hoyas site and SIFA161418 for the scanning of the trackway. Fundings are from the *Spanish Ministerio de Economía y Competitividad* (MINECO) and *Viceconsejería de Educación Cultura y Deportes of Junta de Castilla-La Mancha*. Article revised by A. Burton native corrector of English for scientific articles. PaleoyMas Company carried out the project of scanning and scaled photogrammetry. Thanks also to two anonymous referees for proposing very interesting suggestions improving remarkably the quality of the manuscript.

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