

Were non-avian theropod dinosaurs able to swim?

Supportive evidence from an Early Cretaceous trackway, Cameros Basin (La Rioja, Spain)

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ABSTRACT

A fundamental question remaining unanswered in dinosaur behavior is whether they had the ability to swim. We report the discovery of an exceptional swimming dinosaur trackway, with 12 consecutive footprints, in lacustrine nearshore sediment from the Early Cretaceous Cameros Basin, La Rioja, Spain. The singular morphology of these footprints strongly suggests a floating animal clawing the sediment as it swam. Diagnostic traits of theropod dinosaur footprints are identifiable in these peculiar elongated S-shaped ichnites. Paleoenvironmental reconstruction indicates an upper shoreface setting with a maximum water depth of ~3 m, substantiating the swimming hypothesis. Ichnological analysis of the trackway shows that this theropod used a pelvic paddle motion, similar to that of modern bipeds, and swam with amplified asymmetrical walking movements to maintain direction into a leftward water current. After recent hints of swimming dinosaurs, this new evidence persuasively demonstrates that some non-avian theropod dinosaurs were swimmers.

Keywords: ichnology, non-avian theropod dinosaur, swimming trackway, Cretaceous, Spain.

INTRODUCTION

It is widely accepted that dinosaurs probably filled ecological niches now occupied by terrestrial mammals, possibly suggesting similar behaviors. A crucial, still-unanswered question, however, concerns the ability of dinosaurs to swim. Although many large mammals developed efficient swimming, either to cross natural barriers (e.g., Elephantidae) or as predators (e.g., Ursidae), no evidence has been documented so far to demonstrate that dinosaurs were able to swim. This question is of primary importance for investigations into the anatomy and ecology of dinosaurs that increasingly focus on their locomotory capabilities and dynamics (e.g., Gatesy et al., 1999; Day et al., 2002). Paleontological data and biomechanical investigations have not yet established the ability of dinosaurs to swim, so the ichnological record needs to be considered more closely to gather evidence of swimming. Numerous trackways are preserved in fluvial and lacustrine sediments in the vast global dinosaur ichnological record. This strongly suggests that some dinosaurs, in the manner of several large mammals, may well have colonized aquatic environments and occupied ecological niches requiring swimming capabilities. However, very few reports of dinosaur swimming traces exist in the literature (e.g., Coombs, 1980), and they often represent misleading evidence (e.g., Lockley, 1991).

During the Early Cretaceous, the extensional Cameros Basin formed a vast perennial lake recording one of the highest densities of dinosaur trackways in the world. Nearly 10,000 footprints of walking dinosaurs have been found preserved in mudflat limestones and deltaic sandstones exposed during fairly short-lived episodes of lake lowstands. The dinosaur

track record of the basin, which contains ornithopod and sauropod traces, is dominated by tracks of theropods, including doubtful webbed theropod tracks (Casanovas Cladellas et al., 1993). The La Virgen del Campo track site (LVC), upper Barremian to Aptian in age (Enciso Group), was preserved on a delta that prograded on the southern margin of Lake Cameros (Doublet, 2004). This site (zones 1–3) has already yielded numerous footprints of walking theropod dinosaurs and recent excavation (zone 4) exposed the new trackway described here. We report the discovery of this exceptional theropod trackway that sheds new light on the swimming ability of carnivorous dinosaurs, and provides persuasive evidence to support the hypothesis that some theropods were able to swim efficiently.

PALEOENVIRONMENTAL SETTING

The LVC site exhibits a continuously exposed surface at the top of a 2.5-m-thick sheet-like sandstone that persists laterally over at least 1.5 km before pinching out into bioturbated siltstone (Fig. 1). The upward-coarsening sequence illustrated contains open-lacustrine, lower shoreface, delta-front, and upper shoreface facies (see Doublet, 2004). The lower part of the section shows massive to parallel-laminated mudstone with freshwater bivalves and ostracodes, interpreted as open-lacustrine deposits. Upward in the section, the lower shoreface is represented by parallel-laminated siltstone and very fine grained sandstone interbedded with mudstone. The presence of thin sets of wave-ripple cross-lamination in sandstone demonstrates intermittent wave action. The lower shoreface facies is scoured by fine- to medium-grained sandstones with plane beds, current ripple forms, and cross-stratifications. These sandstones, stacked into a meter-thick unit, are interpreted as a delta-front facies. They are topped by upper shoreface and beach deposits. Symmetrical wave-ripple laminations and forms are stacked into an upward-fining sandstone unit, suggesting permanent fair-weather wave action under very shallow water conditions.

At the LVC site, dinosaur tracks occur in the upper shoreface facies. Zones 1–3 are characterized by wave ripples (ripple wavelength = 2.5 cm), overprinted by footprints of walking dinosaurs. Above this, zone 4 displays two sets of ripple marks: a first pervasive set of rounded ripples is overlain by a second 0.5-cm-thick set of vortex ripples (ripple wavelength = 4.1 cm) scattered over the bedding surface. In plan view, these ripple marks are sharp-crested, slightly asymmetric (Ripple Symmetry Index [RSI] = 1.8; Reineck and Wunderlich, 1968), and straight to slightly sinuous, showing tuning-fork bifurcations. The average ripple index (RI = 7.4; Reineck and Wunderlich, 1968) indicates combined flow ripples that were certainly produced by a drift current flowing from the NE. The scratch marks left by footprint 3 on the second set of ripples indicate that the animal was crossing the site when these ripples were formed.

TRACKWAY

The 15 m trackway consists of a series of 12 ichnites (6 asymmetric pairs) of 2 or 3 well-imprinted scratch marks (Fig. 2). Mean measurements for the 5 left and 5 right strides are 243.4 and 270.8 cm, respec-

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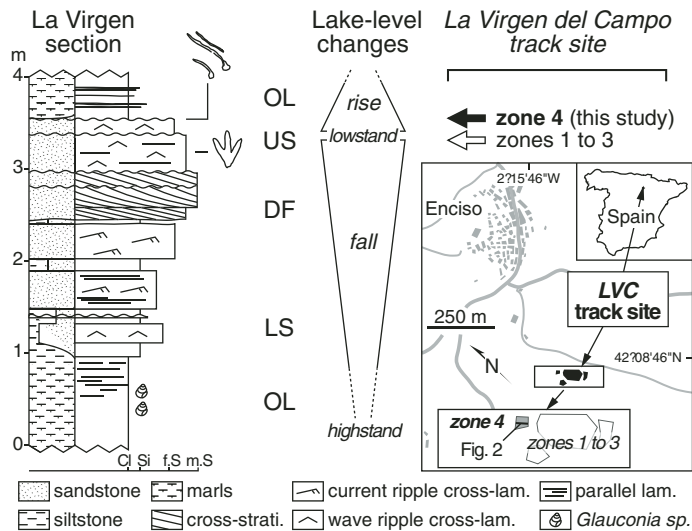


Figure 1. Map and paleoenvironmental interpretation of La Virgen del Campo (LVC) track site. Lake-level changes are reconstructed from vertical stacking of sedimentary facies, based on sequence stratigraphy analysis. DF—delta-front; LS—lower shoreface; OL—open lacustrine; US—upper shoreface; strati.—stratification; lam.—lamination.

tively (taken from rear ends of the longer groove of each set); average oblique pace length is 120.7 cm for right-to-left prints and 183.1 cm for left-to-right prints, and average external and internal trackway widths are 125 cm and 44 cm, respectively.

The footprints consist of two or three long slender grooves (a, b, and c from the interior of the trackway to the exterior), interpreted as scratch marks made on the sediment by the distal parts (claws or toe tips) of the trackmaker's hindfoot digits, as there are no pairs of manus-pes prints. Groove b, in the middle of each right set and on the left side of each left set, is always the longest and clearest imprint. Grooves a and b are ~15 cm apart. Almost all of these scratch marks exhibit a sharp anterior tip, sometimes with tiny elongated sand mounds at the posterior end. These features are only found in true footprints (Thulborn and Wade, 1989) and, together with the delicate nature of the scratches, rule out the ghost trace hypothesis (Gierlinski et al., 2004).

The left and right sides are morphologically distinct (Fig. 2). Left ichnites consist of two or three long parallel, sometimes slightly S-shaped, scratch marks (e.g., print 4), all the prints pointing parallel to the trackway axis. Only print 6 bears an imprint of digit c. Groove a is from 17 cm to 46 cm long and groove b is from 39.5 cm to 60 cm long. The scratch marks in print 4 have a slight S shape that starts in an outward direction from the trackway axis and ends in an inward direction. Right ichnites, except print 1, consist of three S-shaped parallel grooves. Unlike left prints, right prints are all directed at an inwardly rotated angle of ~40° to the trackway axis. Groove a is from 13.5 cm to 34.8 cm long and groove b is from 25 cm to 54.3 cm long. Claw scratch marks c are always preserved as shallower, shorter traces, and vary in length from 10 cm to 27 cm. The distance between scratch marks a and b is always greater than that between b and c.

DISCUSSION

Reports of Swimming Dinosaurs

Until now, evidence of swimming among theropods relied upon two morphotypes. The swimming nature of the first morphotype found in the Early Jurassic of Connecticut (Coombs, 1980) was recently reinterpreted as a trackway produced on firm dry ground (Farlow and Galton, 2003), because most of Coombs' diagnostic features duplicate Australian tracks preserved on a substrate showing evidence of gradual drying (Thulborn

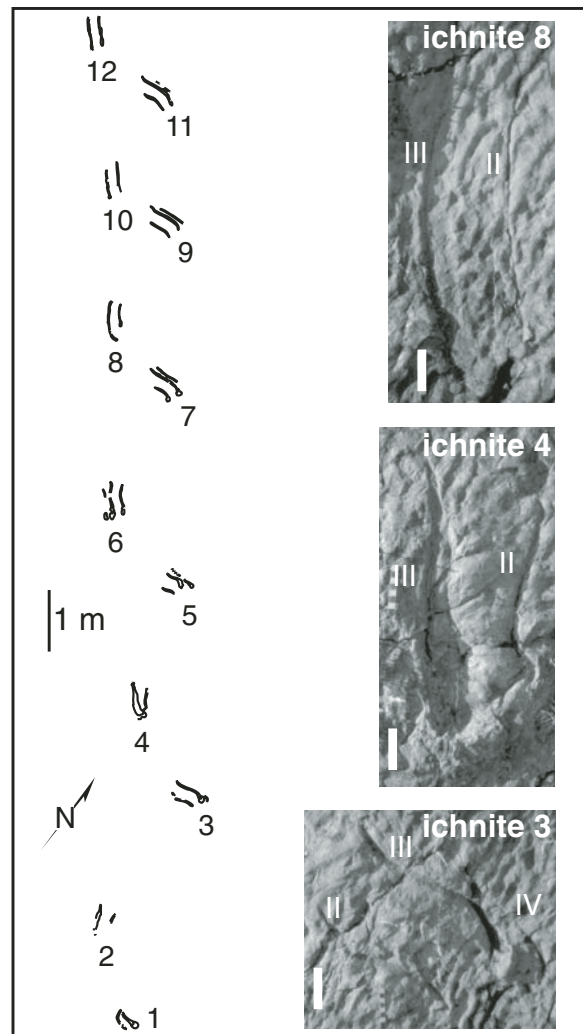


Figure 2. Swimming dinosaur trackway, La Virgen del Campo track site zone 4. Movement of animal is toward NW. Digits are numbered II, III, and IV. On ichnite 3, medium vortex ripples are cut by anterior tip of claws II and III. Scale bar = 10 cm.

and Wade, 1989). Footprints of a lesser rhea walking on nearly hardened plaster of paris also share most of the characteristics of this morphotype, ostensibly precluding a swimming origin (Farlow and Galton, 2003). There is a slight resemblance between the LVC footprints and the second morphotype (*Characichnos tridactylus*), ascribed to a swimming dinosaur (Whyte and Romano, 2001; Gierlinski et al., 2004). Unfortunately the poor preservational context of these footprints did not allow the authors to draw definite conclusions as to the dinosaur's swimming ability.

Sauropod dinosaur manus-only footprints have been reported (see Lockley, 1991, for review), suggesting that these dinosaurs could move in large bodies of water. Lockley (1991) revised the swimming sauropod trackways described by Bird (1944) and Ishigaki (1989) as undertracks, and showed that they were incompatible with swimming. Similar swimming ornithomimid dinosaur trackways were also reported in several studies (e.g., Gierlinski and Potemka, 1987; McAllister, 1989; Thulborn and Wade, 1989), but Lockley (1991) and Bennett (1993) reinterpreted them as undertracks or as crocodylian tracks mistakenly assigned to ornithomimids. Discoveries of a hadrosaur trackway (Currie, 1983) and natural casts of manus-only sauropod trackways (Lee and Huh, 2002; Lockley et al., 1994) were interpreted as a record of dinosaurs walking

along the bottom of a body of water, but these were later disputed by Thulborn (2004). These examples give evidence of walking locomotion rather than active swimming.

Trackway and Trackmaker

The S-shaped scratch marks are interpreted as having been formed while most of the animal's weight was supported by water, because of their sinuous form and great variation in length. Scratch marks strongly suggest that the claws scraped the sediment surface, and sand mounds deposited at the posterior end of several grooves indicate that sand was extracted from the front and moved by the claw to the rear part of each groove. These morphological traits are common features of reptilian swimming tracks (Swanson and Carlson, 2002), and resemble the two isolated scratch marks ascribed to a swimming dinosaur by Gierlinski et al. (2004). The swimming nature of the trackway is also supported by paleodepth estimates for zone 4 medium ripple marks, following the Airy wave theory method (Aspler et al., 1994). Unlike small ripple marks (zones 1–3) produced by wind waves in shallow water, a few centimeters deep, medium ripple marks were produced at deeper water depth. The analytical method yields a depth not greater than 3.2 m, consistent with the hypothesis of a large tetrapod that was not totally submerged but swimming above and just touching the sediment surface.

The trackway width and the distance between scratch marks for claws a and b both indicate that the trackmaker was a large animal. In the Early Cretaceous the only large terrestrial vertebrates were crocodylians, turtles, and dinosaurs. Crocodylian swimming traces are already known in the ichnological record. They are often represented by sets of three parallel scratch marks, sometimes associated with a fourth, and often preserved as sets of pes and manus prints (Foster and Lockley, 1997), unlike here. Foster and Lockley (1997) also showed that crocodylian swim tracks are typically more bulky and less elongate. In addition, print size and distance between claw scratch marks are often much smaller than our tracks (Bennett, 1993), most likely precluding a crocodylian origin. Turtle swimming tracks may show scratch marks, but significantly differ from the tracks described here. Flippers of marine turtles are unlikely to leave only two or three scrape marks, and they are expected to show a larger range of variation in number of lines preserved on the bottom, as well as leaving web marks when touching the sediment, such as observed by McAllister (1989) and Wright and Lockley (2001): these authors also showed that the grooves in sets of swimming turtle tracks are much closer to one another than observed here (e.g., a few millimeters). Swimming turtles have synchronous limb movements and would thus produce symmetrical trackways (Gaillard et al., 2003). In addition, present-day terrestrial Galapagos turtles have been reported to produce scratch marks while running on dry sand, but manus and pes traces were systematically imprinted and grooves of the same set were always very close to one another, often even touching one another (Fiorillo, 2005), a very different situation from that seen here. Turtle tracks are therefore unambiguously different from the LVC one. The LVC footprints share some morphological features with those documented for theropod dinosaur footprints formed on firm ground. Claw b scratch marks for left print 6 and for all right prints are the longest and deepest, while the distance between scratch marks for claws a and b is greater than that between claws b and c, forming an acute V shape. These characteristics duplicate those found in prints of walking theropod dinosaurs (e.g., Huh et al., 2006) and indicate that the trackmaker was most likely a theropod dinosaur. Grooves a, b, and c would therefore have been produced by hindfeet claws or toe tips II, III, and IV.

Swimming Style

This 15-m-long trackway offers the first opportunity to investigate the type of swimming of a bipedal dinosaur. The alternating sets of pes prints show that the animal used a discontinuous mode of propulsion resulting

from alternating movements of the two hind limbs. Terrestrial tetrapods exhibit two kinds of paddle swimming (discontinuous propulsion using the limbs): the pelvic paddle movement of bipeds and the pectoral-pelvic paddle movement of quadrupeds (Renous, 1994). The parallel left pes grooves described here and the absence of manus prints strongly suggest that the theropod used a pelvic paddle swimming motion. With this aquatic bird-like swimming style, the vertical movement of both legs articulates in a parasagittal plane, with a propulsion phase (extension) and a recovery stroke (flexion). The pelvic paddling technique requires an advanced mesotarsal ankle joint (Benton, 1997), present among dinosaurs, and it is consistent with our hypothesis. The S-shaped scratch marks show that the feet delineated curved movements on the sediment floor during the propulsion phase of each hind limb. This suggests that the movements of the hind limbs when walking (Gillette and Lockley, 1989) and swimming are very similar, even if the pes-sediment contact is very different. Studies of modern bipeds demonstrate that pelvic paddling imitates the walking motion of the hind limbs with accentuated flexion and extension phases, again supporting our interpretation (Renous, 1994).

Two ichnological peculiarities of the trackway led us to investigate the way the dinosaur swam. The S-shaped right pes grooves are consistently more accentuated than the left prints. In the pelvic paddle swimming motion, the hydrostatic pressure exerted by the limbs is related to the amplitude of the movement they generate. Consequently, we propose that the difference in scratch mark shape stems from a difference in hydrostatic pressure on each autopod with the force exerted by the right pes being greater than that by the left pes. This also explains why left and right strides and paces are different. The orientation of the right footprints at 40° from the trackway axis is difficult to explain in terms of anatomy if we postulate that the sagittal plane (body axis) of the theropod was parallel to the trackway. This can be resolved by hypothesizing that the body axis was symmetrical to both feet. In this situation the theropod is shown to swim with an inward rotation of its feet (at about -20°). Thus we conclude that the theropod was swimming crosswise, with its sagittal plane at ~20°NE to the trackway axis (Fig. 3). It was therefore swimming obliquely toward the left and exerted a stronger hydrostatic force on its right side. With the combined effects of the hydrostatic gradient and the leftward orientation of its body, we might expect the animal to take a left turn under still water conditions. However, the trackway shows that the path of the theropod was nearly rectilinear. To explain this paradox we hypothesize that it was swimming into a leftward water current. The crest orientation of the medium ripples indicates a slow water current flowing from the left side of the animal at ~30° to the trackway axis (Fig. 3). The amplified movement of its right hind limb and the crosswise orientation of the body are tentatively interpreted as a response to the NE drift current in order to maintain balance and/or direction.

CONCLUSIONS

A well-preserved trackway of 12 footprints from La Virgen del Campo provides the first long and continuous record of the swimming locomotion of a non-avian theropod dinosaur. Following the first reports of swimming dinosaurs, our discovery brings new and compelling evidence to the debate on the ability of dinosaurs to swim. Hind-limb movements interpreted on the basis of the trackway analysis reveal that this dinosaur shared a similar swimming style with living bipeds, including aquatic birds. This is consistent with the fact that birds and non-avian theropod dinosaurs are closely related and that their front limbs are not suitable for any contact with the substrate when swimming. It is also shown that hind-limb movements when swimming are basically amplified walking movements. The excellent preservation of these tracks provides an invaluable opportunity for biomechanical modeling in order to improve our understanding of dinosaur swimming ability and physiology. We show that some non-avian theropod dinosaurs must have frequented palustrine

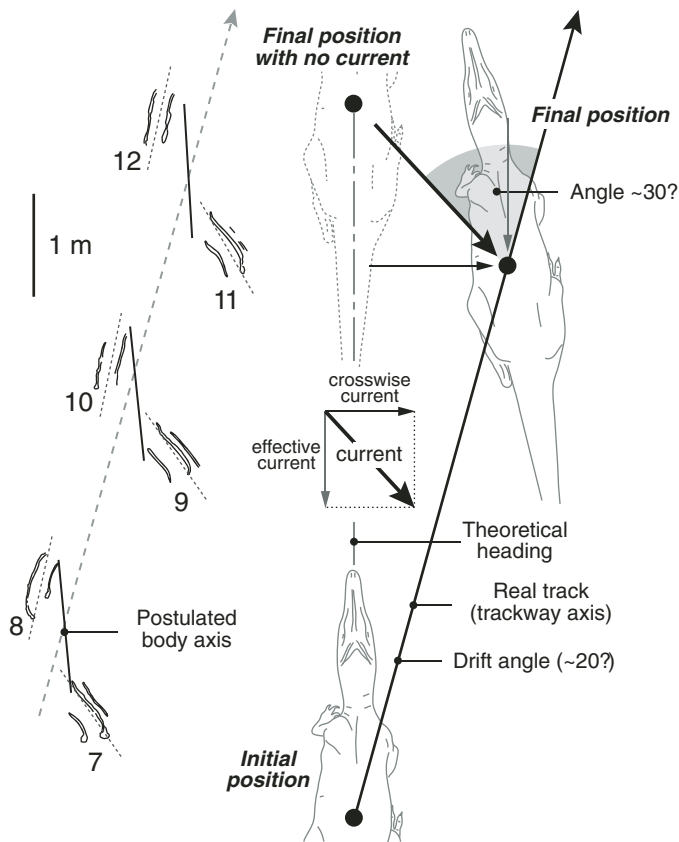


Figure 3. Reconstruction of theropod swimming against crosswise current flowing from left.

environments. They may well have occupied hitherto unsuspected ecological niches, so ecological traits such as diet and locomotion must now be explored in this new context.

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