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First record of a pterosaur landing trackway

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The terrestrial progression of pterosaurs, the flying reptiles of the Mesozoic Era, has been debated for over two centuries. The recent discovery of quadrupedal pterodactyloid pterosaur tracks from Late Jurassic sediments near Crayssac, France, shows that the hindlimbs moved parasagittally, as in mammals, birds and other dinosaurs, and the hypertrophied forelimbs could make tracks both close to the body wall and far outside it. Their manus tracks are unique in form, position and kinematics, which would be expected because the forelimbs were used for flight. Here, we report the first record of a pterosaur landing track, which differs substantially from typical walking trackways. The individual landed on both hind feet in parallel fashion, dragged its toes slightly as it left the track, landed again almost immediately and placed the hindfeet parallel again, then placed its forelimbs on the ground, took another short step with both hindlimbs and adjusted its forelimbs, and then began to walk off normally. The trackway shows that pterosaurs stalled to land, a reflection of their highly developed capacity for flight control and manoeuverability.

Keywords: Pterosauria; ichnology; functional morphology; Late Jurassic; Mesozoic vertebrates

1. INTRODUCTION

Pterosaurs, the flying reptiles of the Mesozoic Era, are generally regarded to be closely related to dinosaurs and their kin (e.g. Gauthier 1986); however, because they are so derived, many aspects of their functional morphology remain unsettled (Padian 1983, 2003; Wellnhofer 1991; Bennett 1997; Unwin 1997; Mazin *et al.* 2003). The Late Jurassic site known as 'Pterosaur Beach' (Lower Tithonian, Crayssac, southwestern France) (Hantzpergue & Lafaurie 1994; Mazin *et al.* 1995, 1997, 2001, 2003; Billon-Bruyat 2003) is the first site that is universally agreed to preserve unquestionable and numerous pterosaur tracks (Mazin *et al.* 1995; Padian 2003; see Lockley *et al.* 2008 for a review of various trackways assigned to pterosaurs). The Crayssac site is distinguished by the presence of several trackways that show manus prints far lateral to the pes prints, a situation impossible for any other known vertebrate with the possible exception of bats. A single Crayssac trackway, reported here, provides a unique source of information about both the aerial and terrestrial capabilities of these strange animals, and provides insights into locomotion that show how unusual these pterodactyloid pterosaurs were on the ground.

The Crayssac site preserves hundreds of vertebrate and invertebrate trackways deposited in a fine-grained limestone mud. The conditions of deposition of the sediments and of the preservation of footprints are unusual and noteworthy. The surface of this mud dried quickly, but retained a very thin topmost layer of ultrafine sediment (Mazin *et al.* 1995, 1997). In this layer the tracks of small invertebrates (e.g. isopods) were preserved in fine detail (Gaillard *et al.* 2005). In contrast, vertebrates such as pterosaurs, turtles, crocodylians and theropod dinosaurs usually perforated the surface crust, leaving tracks less distinct in detail but informative about locomotion, behaviour, substrate condition and paleoecology (Mazin *et al.* 1995, 1997, 2003; Billon-Bruyat 2003). Occasionally some very fine detail is preserved (Mazin *et al.* 1995, 2003), particularly in very small animals; however, the mud usually contained so much water that sediment slumped into the tracks of larger animals after deposition, obscuring critical features such as phalangeal formulae.

The hundreds of trackways excavated and prepared over the past decade include more than thirty that were made by pterodactyloid pterosaurs that typically walked quadrupedally (Mazin *et al.* 1995, 1997, 2003). In normal quadrupedal progression, the manus prints are typically located posterior to the closest pes prints (which belong to the next step cycle) and could be placed up to three times the interpedal width lateral to the pes prints (Mazin *et al.* 1995, 2003; figure 1). The hindlimbs proceeded in parasagittal fashion (Padian 1983, 2003), meaning that the pedes were placed below the hip joint rather than lateral to it (much as in sauropod dinosaurs; Wilson & Carrano 1999), and therefore the swing action of the hindlimb was parallel to the body axis (as in birds and most mammals) and not lateral to it (as in most reptiles). The pedes were apparently not placed directly underneath the body and very close to the sagittal plane, as in many birds and non-avian dinosaurs during walking (Lockley & Hunt 1995). They also demonstrate that the footfall pattern was not as in typical reptiles (LH–RF–RH–LF), but that the manus must

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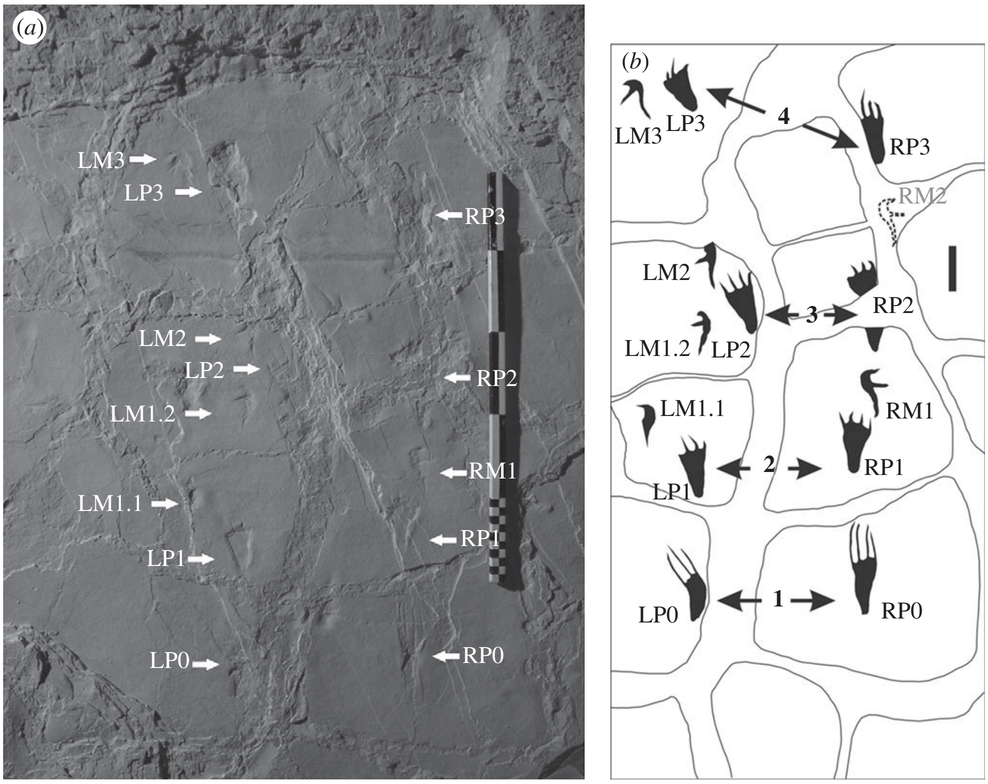

Figure 1. Unusual pterodactyloid trackway (CR01.02, Lower Tithonian, Crayssac, France), showing landing behaviour. (*a*) Photograph of the trackway, with manus and pes prints indicated by white arrows. The trackways are so shallow that even in strongly oblique light (note shadow of scale bar) their outlines and features are difficult to photograph. (*b*) Drawing of the trackway. Field scale, 50 cm. Scale bar, 5 cm. RP, right pes print; LP, left pes print; RM, right manus print; LM, left manus print. The numbers correspond to the discussion in the text. RM2 (white) is partly reconstructed because mudcracking has distorted its original features.

have been raised before the next forward step of the ipsilateral foot (LH–LF–RH–RF), suggesting that the quadrupedal pattern was secondary (Padian 2003, 2008). The metatarsus must have been held at a low angle (Clark *et al.* 1998), as in crocodiles (Brinkman 1980) and basal dinosaurs (Gatesy *et al.* 1999), because it is always impressed in the Crayssac pterodactyloid tracks. Although most trackways indicate relatively slow progress, skeletal reconstructions indicate that in some instances the animals moved fast enough to run (i.e. in suspended phase with all feet simultaneously off the ground; Mazin *et al.* 2001). Morphological descriptions and diagnoses of these typical pterodactyloid trackways are discussed by Mazin *et al.* (1995, 2003) and Padian (2003).

One set of pterodactyloid trackways from Crayssac, however, is so unusual that it cannot be explained by typical walking behaviours. Instead, it appears to represent landing, a behaviour that so far has been unreported.

2. RESULTS

The trackway (original CR01.02 preserved in place in the museum-quarry at Crayssac, cast at the University of Lyon 1; figure 1) is that of a small pterodactyloid (pes length approx. 5 cm). It consists of four pairs of pes prints (which lack the fifth digit and are therefore pterodactyloid) and some associated manus prints. The prints are separated by mud-filled cracks that formed as the original sediment dried. In contrast to typical pterodactyloid walking trackways (figure 2*b*), the step lengths of the first three sets of pedal tracks are unusually short, and the tracks of the pedes are nearly parallel to each other transversely. The tracks of the pedes face forward and are placed virtually beneath the hip joints, so the stance was erect. Therefore, the prints of the feet are not in front of each other, as they would be in the trackways of many birds and bipedal dinosaurs during walking, but are about a body width apart, as in other pterodactyloid trackways at this site. As usual, the foot impression is deepest at the metatarso-phalangeal joint.

The first set of pedal prints of the series (figure 1: LP0–RP0), as noted above, are most unusual in being transversely parallel to each other. Furthermore, they have no typical corresponding manus prints lateral or posterior to them, and there are no manus or pes prints behind them. The impressions of the metatarsal region of the foot are of the same length, with a V-shaped form, at the same depth as in typical trackways and, as usual, the metatarso-phalangeal area is the most deeply impressed. The phalangeal portion of the impression is, however, elongated to more than three times its normal length. Impressions of the claws can be seen in their usual positions, particularly in the better preserved right track, but from this point forward the claw impressions become shallower, and the first and fourth claw traces begin to converge on the inner ones.

The second set of pedal prints (figure 1: LP1–RP1), quite unusually, is only a short distance in front of the first set (compare with figure 2*b*), and the tracks of the two pedes are again laterally parallel. Otherwise they

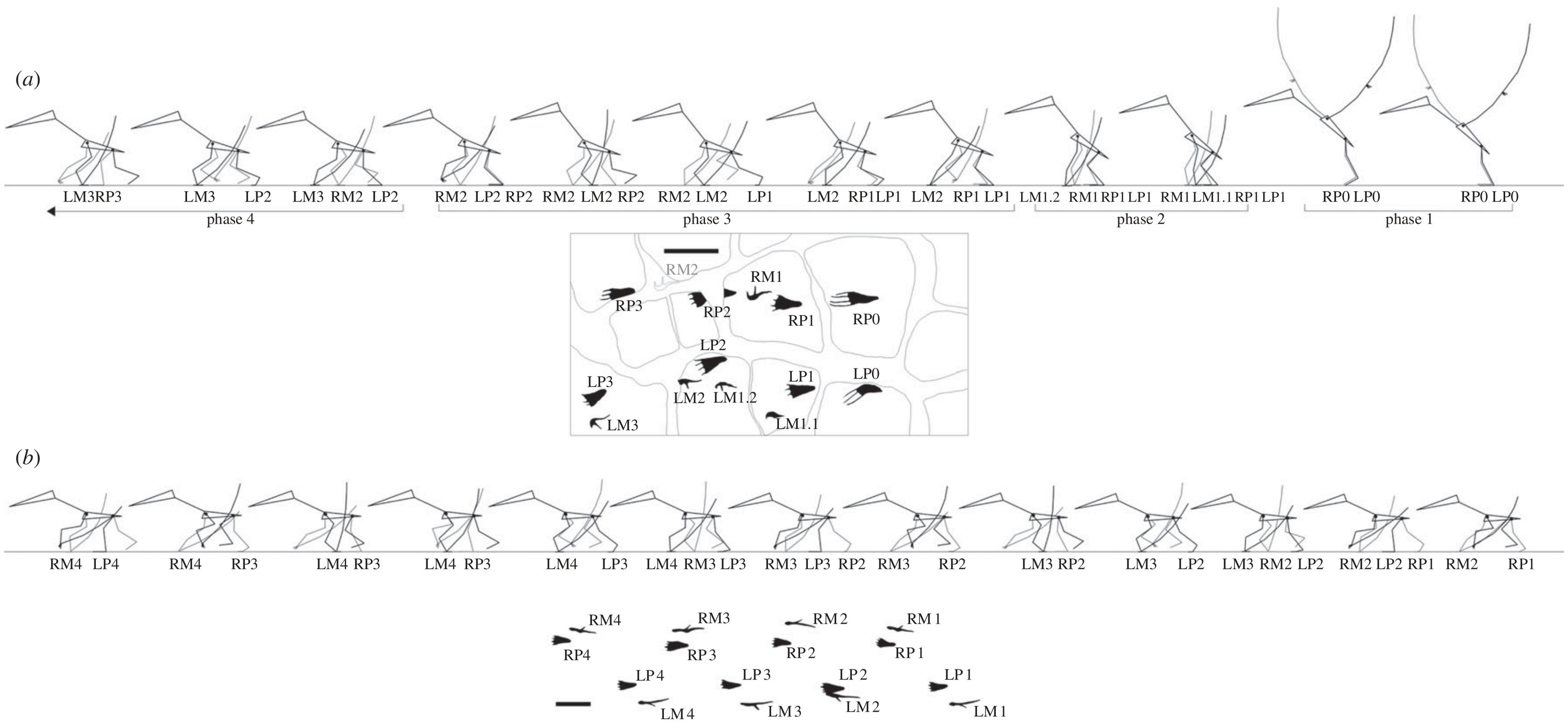

Figure 2. Comparison between the sequential animation of the landing sequence and a normal walking sequence. (*a*) The landing sequence, based on the landing track CR01.02, Lower Tithonian, Crayssac, France. Phase 1 corresponds to the first set of pedal tracks, which reflects bipedal terrestrial contact. Phase 2 corresponds to the pause of the animal after landing, with all four limbs on the ground, transversely parallel to each other. The distance between ipsilateral pes and manus is very short, and the body is erect. Phase 3 corresponds to the first walking sequence, as the animal arranges its limbs in preparation for normal terrestrial progression. The distance between manus and pedes increases and the body acquires a subhorizontal position. Phase 4 corresponds to the start of normal terrestrial progression. (*b*) The walking sequence, based on the typical terrestrial trackway CR96.22, Lower Tithonian, Crayssac, France. Note that the manus prints are posterior to the pes prints, the mediolateral distance between the pedes is shorter and the pace length is longer than in the landing track. Scale bars, 10 cm. RP, right pes print; LP, left pes print; RM, right manus print; LM, left manus print. The numbers correspond to the discussion in the text.

show the typical characteristics of pedal prints at this site. The phalangeal impressions have resumed their normal length. Manus prints are visible for the first time, immediately anterolateral to those of the pes. This configuration is unusual because in all the other pterodactyloid walking trackways at this site the pedal prints are plainly anterior to those of the manus, even when the manus is far lateral to the pes (figure 2*b*; see Mazin *et al.* 2003).

In the third set of prints (figure 1: LP2–RP2), the tracks of the pedes are again nearly parallel. The left footprint is accompanied by two closely set manus prints, as if the animal were righting itself, but mud has filled the post-desiccation crack in the sediment where the associated right manus print(s) would be expected, if there were any; only a faint indication remains.

The fourth set of pedal prints (figure 1: LP3–RP3) indicates the beginning of a turn to the left, starting with the right foot, and the pace distance is greater (and more normal) than in the first three sets of tracks. The left manus print is preserved slightly anterolateral to the left pedal print, and a faint indication of a right manus print is apparent. Beyond this point, a local microfault in the quarry has made it impossible to follow the trackway further.

It is clear that LP0 and RP0 are the first of the naturally impressed sequence for the following reasons. We closely surveyed and mapped the area to a distance of 3 m behind the trackway and 2 m in each direction to the side of a line posterior to the trackway, and confirmed that there were no tracks behind or to the side of this trackway that could possibly be interpreted as continuous with it. Two other normal walking pterodactyloid trackways cross this area nearly 2 m behind the preserved trackway that we discuss here; however, they are oblique and perpendicular to it, respectively, and cannot be continuous with it. Although a fault in the bedding plane makes it impossible to pursue the trackway beyond the fourth set of preserved pedes (noted above), no such faults are present in the area posterior to the landing trackway, so the area behind the first tracks in our sequence is at exactly the same level.

3. INTERPRETATION

We reconstructed the behaviour that produced this trackway as follows. The first pedal prints mark the inception of terrestrial progression, and show that an unusual kinematic process produced them. The elongated claw impressions, taken together with the transversely parallel pes prints and the absence of tracks behind this preserved series, indicate quite strongly that the animal was landing. The absence of associated manus prints shows that it did so bipedally. The heelprint in this landing trackway is not deeper or longer than usual, and there is no buildup of sediment around the heel, so the animal did not land heel first nor draw its claws posteriorly through the mud. Nor did its feet remain long in this first set of footprints. On the contrary, after being impressed, the claws were apparently dragged forward, and were at least slightly flexed because the metatarsus made no impression as it left the track. Furthermore, the anterior convergence of the claw marks matches the kinematics of terrestrial locomotion in birds and non-avian theropods (Gatesy *et al.* 1999), in that the toes are spread before impression and gathered together when lifted as the animal progresses forward. From these facts it is straightforward to infer that the feet were moving forward, not backward, in this first set of tracks.

The short distance between the first and second sets of pes prints recalls a short and immediate ‘stutter step’, perhaps a simultaneous hop with both feet. However, we note that parallel left and right prints are not known in typical walking trackways at Crayssac, so if the animal ‘hopped’ in this case (which cannot be established), it was unusual behaviour. At this point the animal stopped and rested its forelimbs on the ground for the first time (slightly anterior to the pedes). By the third set of pes prints, again placed transversely parallel to each other and with a short pace length, the pterosaur was apparently arranging its limbs in preparation for terrestrial progression. It then began to walk slowly, in this case advancing with the right foot first. In pterodactyloid pterosaurs the characteristic footfall pattern was LH–LF–RH–RF, which is a departure from the typical reptilian LH–RF–RH–LF (Bennett 1997; Padian 2003). The closeness of the first three sets of pedal prints, coupled with the unusual position of the associated manus prints, suggest that the animal’s trunk was initially oriented more vertically than the usual subhorizontal position reconstructed for typical pterodactyloid trackways (e.g. Mazin *et al.* 1995, 2003). As the trackway ends, the animal was beginning to turn towards the left, and to walk in a typical fashion (figure 1). At this point the position of the vertebral column probably became more horizontal, because the pace length has increased.

4. DISCUSSION

It might be argued that the first preserved set of manus tracks (LM1.1 and RM1) is incorrectly associated with the second pedal set (LP1 and RP1), and instead should be associated with the first (LP0 and RP0); and, correspondingly, that LM1.2 probably belongs with the second pedal set, of which the impression of the right manus is missing. As explained above, it is unlikely that the pedes were moving backward in the first pedal set, but rather forward. In either case, they reflect momentum. In contrast, the first manus prints show no evidence of momentum and are not more deeply impressed than any others, so they do not reflect an unusual force or locomotory motion. They cannot have been made after the third pedal set, because they are behind them; therefore, they are most probably associated with the second pedal set, slightly outside and in front of them, reflecting a temporarily more vertical posture of the vertebral column (consistent with landing after stalling; see below). They may have been impressed either slightly before or slightly after the second set of pedal prints was made.

It could be hypothesized that this trackway represents a landing from swimming on the surface of the water, rather than from flying. There are several reasons why this is unlikely. First, sediment under water, although near the water’s edge, would have been less competent than sediment exposed to the air; however, there is no difference in depth or distinctness in preservation among progressive footfalls in the landing trackway. Second,

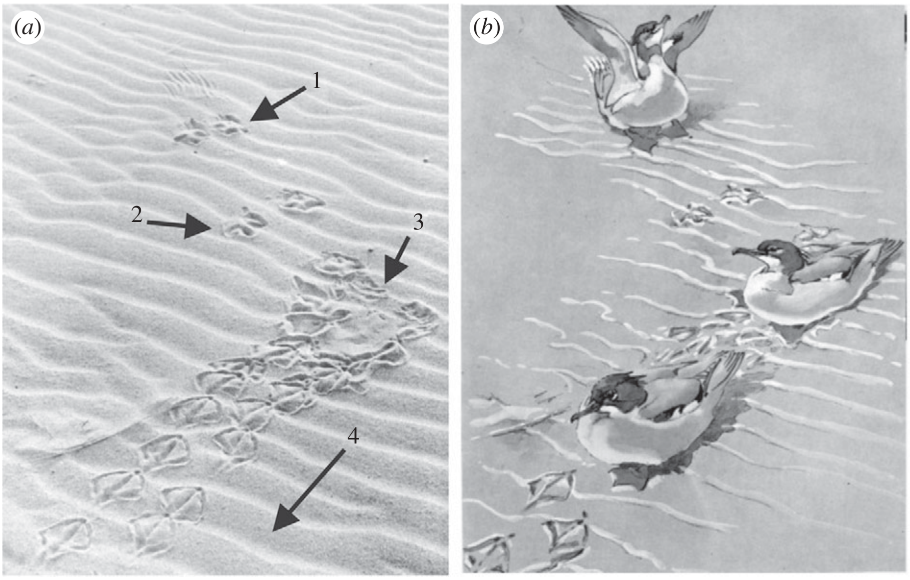

Figure 3. The landing behaviour of a living merganser. (*a*) The trackway of a merganser; footfalls correspond approximately to those of the landing pterosaur. (*b*) Restoration of the merganser trackway in (*a*). Both images from Ennion & Tinbergen (1967). The numbers correspond to the discussion in the text.

there is no evidence of hydrodynamic disturbance of the sediment that forms the trackway by the locomotion of sub-aquatic landing, as might be expected. Third, the slope of the plane of sedimentation on this beach was shallow enough to have been almost imperceptible (Hantzpergue & Lafaurie 1994; Billon-Bruyat 2003), so any paddling tracks before the first preserved set would also have been registered. Moreover, the energy of the tidal system at Crayssac was too low to erase footprints, as sedimentological analysis has shown (Gaillard *et al.* 2005). As far as can be determined, all Crayssac tracks were made sub-aerially and preceded desiccation and preservation of the sediments (Billon-Bruyat 2003).

5. CONCLUSIONS

The preserved evidence allows some inferences about the behaviour of pterodactyloid pterosaurs during landing. The trackway is not consistent with a running landing, such as some ducks, seabirds and shorebirds do today. Any 'braking' reflected in the first set of pedal prints is unlikely to have accounted for the extent of deceleration required in landing, because the distance between the first and second sets of pedal prints is about half the typical walking distance, and the first set of pedal prints is no more deeply impressed than any other in the series. The anterior prolongation of the claw marks suggests that after first touching the ground, the pterosaur still carried substantial forward momentum and was still partly in an aerial phase. It terminated this phase when it finally landed gently in the second set of pedal tracks.

Chatterjee & Templin (2004) and Unwin (2006) predicted, although on different grounds, that pterodactyloids would land bipedally, then proceed to walk quadrupedally, as Padian *et al.* (2004) and Billon-Bruyat *et al.* (2004) previously suggested. The Crayssac landing track generally confirms their predictions, although it differs in some details. In any case, this specimen provides the first clear empirical evidence of how small pterodactyloids landed, or could have landed (figure 2*a*), without eliminating other possibilities.

Based on the aforementioned, we infer that, like most birds, these pterosaurs used their wings to stall before landing. We cannot distinguish between a gliding stall, which relied solely on increasing the angle of attack of the wings, and one that assisted braking by flapping. However, either possibility requires sophisticated flight apparatus and neural control, which is supported by the advanced configuration of the pterodactyloid brain and ear region (Witmer *et al.* 2003). The second possibility also requires a very strong flapping ability, which is evident from the many details of the pterosaur skeleton and wing structure (Padian 1983; Padian & Rayner 1993), which in turn supports inferences of high basal metabolic rates for pterosaurs based on other lines of evidence (Cuvier 1809; Ricqlès *et al.* 2000). The anterior drag tracks of the claws in the first set of pedal prints indicate that even if the animal flapped to stall, it did not bring its forward speed to zero. Most living birds land on the ground by stalling and supinating the wings to a degree that greatly increases the lift generated, so that the body rotates forward and presents the feet first to the substrate. This model appears to account best for the landing behaviour that can be inferred from this trackway, and it reinforces other lines of evidence that indicate that pterosaurs were strong, manoeuverable flyers (Padian 1983; Padian & Rayner 1993; Witmer *et al.* 2003). The new trackway shows that these pterodactyloids landed bipedally like birds (Ennion & Tinbergen 1967; figure 3), and probably at a high angle (Genise *et al.* 2009), although they walked quadrupedally. Unfortunately, none of the several dozen extended trackways excavated and studied to date at Crayssac, so far provides any indication how these animals took off.

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