Temporal and palaeoenvironmental distribution of manus- and pes-dominated sauropod trackways

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Abstract: Fossil tracks are a source of information about extinct animals that can supplement the osteological record, yet they are often overlooked in macroevolutionary studies. The substrates in which tracks are preserved are indicative of palaeoenvironment and habitat, and track morphology can be linked to the motion and loading of the limb. Sauropod dinosaurs represent the largest terrestrial animals ever to have existed, and the evolution of their body plan had direct consequences for their locomotion and subsequent morphology of their tracks. Here we show that the relative proportions of manus- and pes-dominated sauropod trackways appears to remain constant in the Jurassic and Cretaceous despite an apparent evolutionary anterior shift of centre of mass seen in the body fossil record. However, in Cretaceous rocks, manus-dominated tracks are most commonly recorded in cohesive substrates (e.g. mudstones), whereas pes-dominated tracks tend to be restricted to non-cohesive substrates (e.g. sandstones). This bias is not present in the Jurassic, and therefore may be the result of niche partitioning among sauropods associated with the Cretaceous diversification of the anatomically and environmentally specialized titanosaurs. In this respect, the ichnological record appears to provide complementary evidence to the osteological record and suggests a causative link between locomotion, ecology, and macroevolution in sauropod dinosaurs.

Supplementary material: The complete dataset of occurrences of MDTs and PDTs is available at http://www.geolsoc.org.uk/SUP18530.

Sauropod dinosaurs include the largest terrestrial animals to have ever evolved (Wilson 2002; Upchurch *et al*. 2004), and mass properties are regarded as a central driving force in their functional, behavioural, and evolutionary dynamics (Henderson 2006; Sander *et al*. 2010). Titanosaurs originated in the Middle Jurassic (Day *et al*. 2002) and subsequently diversified to dominate Cretaceous sauropod faunas (Upchurch *et al*. 2004), showing numerous anatomical specializations compared with other sauropods (Wilson & Carrano 1999). However, understanding the wider functional and behavioural implications of these specializations is hampered by their poor osteological record (Mannion & Upchurch 2010*a,b*) and the difficulties of establishing form–function relationships in extinct taxa purely from osteological evidence (Bates *et al*. 2009; Gatesy *et al*. 2009; Hutchinson & Allen 2009). Fossilized tracks and trackways represent an additional source of information about extinct vertebrates to that preserved in the body fossil record, and have previously provided useful insight into sauropod evolution (Lockley *et al*. 1994*a*; Wilson & Carrano 1999; Day *et al*. 2002; Lockley 2007) and distribution (Lockley *et al*. 1994*c*). Tracks are produced by a living animal in motion, and can subsequently provide primary direct information concerning locomotion (Thulborn & Wade 1989), palaeoenvironment (Lockley 1986), soft tissue preservation (Gatesy 2001), and ecological interactions (Lockley *et al*. 1994*b*).

Sauropod manus-dominated or manus-only trackways (herein referred to collectively as MDTs) are trackways in which the hind feet leave either faint or no impressions whereas the forefeet do produce clear and/or deep impressions. Pes-only and pes-dominated trackways (PDTs) represent the reverse case. Manus-dominated trackways are always the result of the pes failing to leave an impression, though PDTs may be formed either by the manus failing to deform the substrate or through overstepping, whereby the pes partially or wholly obliterates the preceding manus print. Manus-dominated trackways have previously been interpreted as having been produced by 'punting' or wading animals (Bird 1944; Ishigaki 1989; Wilson & Fisher 2003; Henderson 2004), implying an aquatic ability otherwise unsupported by osteological remains. However, other workers have since rejected this hypothesis in favour of a preservational mechanism in which manus-only trackways are the result of substrate conditions and undertrack phenomena, or exceptional preservation (Lockley & Rice 1990; Lockley *et al*. 1994*c*; Vila *et al*. 2005; Hwang *et al*. 2008; Song 2010). Recently Falkingham *et al*. (2011*a*) showed that manus-dominated trackways (MDTs) or pes-dominated trackways (PDTs) could be the result of specific substrate shear strength and underfoot pressures (as a function of the relative surface areas of the manus and pes and of the centre of mass (CM) position of the animal). Falkingham *et al*. (2011*a*) proposed that sauropods with a more anterior CM position would be more likely to produce MDTs at the sediment surface, even when walking on land, whereas those animals with a posterior CM would show a tendency to produce PDTs.
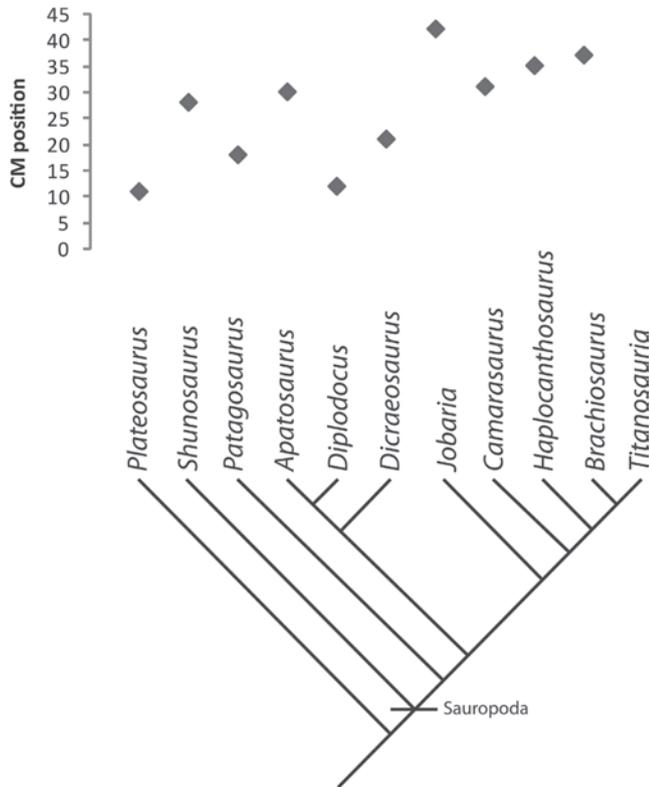
Fig. 1. Phylogenetic relationships and CM positions (% gleno-acetabular distance anterior to the acetabulum) for selected sauropod taxa predicted by Henderson (Henderson 2006). The poor osteological record for titanosaurs means that at this time no predictions of CM position have been made for this group. Modified from Henderson (2006).

This hypothesis has wider implications when viewed in the context of previous interpretations of sauropod body plan evolution and its links to locomotion and biodiversity. Henderson (2006) proposed a size-related shift in CM position within the Sauropoda, with smaller forms retaining a plesiomorphic, posteriorly positioned CM and larger forms possessing a more anteriorly located CM position (Fig. 1). Lockley (2007) also noted a link between the evolution of heteropody (variation in relative sizes of manus and pes) and CM position. Unfortunately, assessing the phylogenetic and temporal nature of this trend is difficult because the osteological remains of titanosaur sauropods, which dominated Cretaceous sauropod faunas, are in general poorly known (Mannion & Upchurch 2010*b*). In this paper we test the hypothesis that temporal, and therefore by inference phylogenetic, sauropod CM evolution can be observed in fossil trackways by comparing the number of MDTs and PDTs recorded in Jurassic and Cretaceous strata and whether this CM evolution is consistent with reconstructions based on osteological evidence. We also test whether there is any relationship between MDTs and PDTs and the lithology of the rocks they are found in, as cohesive and non-cohesive substrates respond in mechanically distinct ways, and this may distort or bias any overall signal.

Materials and methods

A comprehensive dataset of 34 occurrences of MDTs and PDTs was compiled from the literature (Table 1), based on revisions and updates to the dataset presented by Mannion & Upchurch (2010*a*).

For each report, information on locality, formation, geological age, and lithology were recorded. In instances where multiple trackways were reported from a single locality, the data were considered as a single entry unless it was specifically stated that the trackways occurred on distinct bedding surfaces, in which case one entry was created for each bedding surface. Where both MDTs and PDTs were reported from a single site, one entry was created for each trackway type. Lithology was grouped according to whether the original substrate was cohesive (i.e. mudstone, limestone, etc.) or non-cohesive (i.e. sandy substrates), as these categories behave in mechanically distinct ways (Falkingham *et al.* 2010).

Although PDTs can be produced through overstepping, their occurrences were included in the dataset because we considered PDTs produced through overstepping to be a constant through time, and therefore any significant variation in PDT abundance might be explained through CM evolution; that is, if PDTs that are formed through preferential loading become more or less abundant over time or substrate, the total number of PDTs reported will show that signal. As it may be impossible to differentiate between a PDT produced through overstepping and one produced through differential foot loading, we included all PDTs to test for differences in PDT abundance between substrate and through time.

For similar reasons, we included isolated tracks in our dataset. That is, although an isolated track may be the result of abnormal preservation, any bias in MDT or PDT formation should equally affect the overall number of isolated manus or pes tracks. We also ensured, where possible, that the isolated tracks were preserved *in situ*.

Whether a track was reported as being a true track or undertrack was not taken into consideration when collating the dataset. There were two reasons for this: first, it can be very difficult to identify a track as a surface track or a (shallow) undertrack; second, the process of preferentially forming and preserving manus or pes tracks at the surface extends into the subsurface undertracks. Deeper manus tracks at the original tracking surface result in deeper undertracks than for the pes at any given substrate layer, and vice versa. As such, even if a reported MDT or PDT is an undertrack, it is highly likely that the original tracking surface showed similar bias between manus and pes track formation (Falkingham *et al.* 2011*a,b*).

Although the relative size of the manus and pes, in conjunction with CM position, does have a direct relationship with underfoot pressure, this study does not directly consider the effects of varying heteropody, and in this paper MDT or PDT refers only to the presence or absence or bias of manus or pes tracks. Indeed, the very nature of MDTs and PDTs makes a discussion of heteropody difficult, if not impossible, in this case.

Barnard's exact test (Barnard 1945; Cardillo 2009) was used to determine whether there is a statistically significant difference between the occurrence of MDTs and PDTs in the Jurassic and Cretaceous, and between cohesive and non-cohesive substrates.

Results

Throughout the Jurassic and Cretaceous, MDTs and PDTs occur in almost equal numbers (Fig. 2a), and there is no significant association between track type and geological age ($P = 0.872$).

Our second analysis tested for any association between MDTs and PDTs in cohesive or non-cohesive substrates. MDTs were more common than PDTs in cohesive substrates, whereas PDTs were most prevalent in non-cohesive substrates (Fig. 2b). However, Barnard's exact test found that this association was not, or was only weakly, statistically significant ($P = 0.079$).

The temporal distribution of MDTs and PDTs in cohesive and non-cohesive substrates is shown in Figure 2c. The distribution of

Table 1. *Occurrences of MDT or PDT used to investigate temporal and palaeoenvironmental (substrate type) distribution*

Manus or pes dominated?	Country	Location	Epoch	Trackway or single tracks?	Cohesive or non-cohesive?	First reference
Manus	USA	Medina River tracksite	Early Cretaceous	Trackway	Cohesive	Bird 1944
Manus	Italy	Porto Corsini–Cava di Sarone tracksite	Early Cretaceous	Single tracks	Cohesive	Dalla Vecchia 1999
Manus	Morocco	Trackway A, B, C and E (Demnat North)	Late Jurassic	Trackway	Non-cohesive	Ishigaki 1989
Manus	Portugal	Lagosteiros Bay (Pedro la Mua)	Late Jurassic	Trackway	Cohesive	Lockley *et al.* 1994*b*
Manus	Portugal	Lagosteiros Bay (Pedro la Mua)	Late Jurassic	Trackway	Cohesive	Lockley *et al.* 1994*c*
Manus	USA	Gaudalupe River	Early Cretaceous	Trackway	Cohesive	Lockley *et al.* 1994*c*
Manus	Switzerland	Courtedoux tracksite	Late Jurassic	Trackway	Cohesive	Marty *et al.* 2003
Manus	Switzerland	Combe Ronde tracksite	Late Jurassic	Trackway	Cohesive	Marty *et al.* 2006
Manus	Portugal	Lagosteiros Bay (Pedro la Mua)	Late Jurassic	Trackway	Cohesive	Meyer *et al.* 1994
Manus	Portugal	West of Lourinha	Late Jurassic	Single tracks	Cohesive	Milàn *et al.* 2005
Manus	USA	South San Gabriel River upper tracksite	Early Cretaceous	Single tracks	Cohesive	Pittman & Lockley 1994
Manus	USA	Blanco River	Early Cretaceous	Trackway	Cohesive	Pittman 1992
Manus	USA	Shell, Bighorn Basin dinosaur tracks	Late Jurassic	Single tracks	Non-cohesive	Platt & Hasiotis 2006
Manus	USA	Shell, Bighorn Basin dinosaur tracks	Late Jurassic	Single tracks	Non-cohesive	Platt & Hasiotis 2006
Manus	Portugal	Galinha tracksite	Middle Jurassic	Trackway	Cohesive	Santos *et al.* 1994
Manus	Spain	Mina Esquirol tracksite	Late Cretaceous	Trackway	Cohesive	Vila *et al.* 2005
Pes	Argentina	Picun Leufu	Early Cretaceous	Trackway	Non-cohesive	Calvo 1991
Pes	Brazil	Rio Grande do Sul State locality	Late Jurassic	Trackway	Cohesive	Dentzien-Dias *et al.* 2008
Pes	USA	Two Mile Creek tracksite	Late Jurassic	Single tracks	Cohesive	Foster & Lockley 1997
Pes	USA	Black Ridge Trail I tracksite	Late Jurassic	Single tracks	Cohesive	Foster & Lockley 2006
Pes	USA	Boundary Butte tracksite	Late Jurassic	Single tracks	Non-cohesive	Foster & Lockley 2006
Pes	USA	Cleveland–Lloyd area tracksite (SW of quarry)	Late Jurassic	Single tracks	Cohesive	Foster & Lockley 2006
Pes	USA	San Rafael River tracksite	Late Jurassic	Single tracks	Non-cohesive	Foster & Lockley 2006
Pes	USA	Liberty Cap Trail (West Monument Mesa) tracksite	Late Jurassic	Single tracks	Cohesive	Foster & Lockley 2006
Pes	USA	Upper Ute Canyon tracksite	Late Jurassic	Single tracks	Non-cohesive	Foster & Lockley 2006
Pes	Mongolia	Yagaan Khovil	Late Cretaceous	Single tracks	Non-cohesive	Ishigaki & Matsumoto 2009
Pes	Brazil	São Domingos	Early Cretaceous	Trackway	Non-cohesive	Leonardi 1989
Pes	China	Gansu main tracksite 2	Early Cretaceous	Trackway	Non-cohesive	Li *et al.* 2006
Pes	Portugal	Lagosteiros Bay (Pedro la Mua)	Late Jurassic	Trackway	Cohesive	Lockley *et al.* 1994b
Pes	Portugal	Porto Dinheiro	Late Jurassic	Single tracks	Cohesive	Mateus & Milàn 2009
Pes	USA	Lost Spring tracksite	Late Jurassic	Trackway	Cohesive	Meyer *et al.* 1994
Pes	USA	Briar Plant Quarry, Nashville	Early Cretaceous	Trackway	Cohesive	Pittman & Gillette 1989
Pes	USA	Shell, Bighorn Basin dinosaur tracks	Late Jurassic	Single tracks	Non-cohesive	Platt & Hasiotis 2006
Pes	Australia	Broome	Early Cretaceous	Trackway	Non-cohesive	Thulborn *et al.* 1994

Jurassic tracks shows no apparent bias across the two substrates, with PDTs slightly more common than MDTs irrespective of substrate type (Fig. 2c). However, in Cretaceous rocks, MDTs are almost exclusively found in cohesive substrates, whereas PDTs are mostly restricted to non-cohesive substrates (Fig. 2c). Barnard's exact test, implemented separately for cohesive and non-cohesive substrates from the Jurassic and Cretaceous, produces P values of $P = 0.961$ and $P = 0.0063$ respectively, suggesting that there is no significant bias in MDT or PDT occurrence depending on substrate during the Jurassic, but that there is a significant correlation between substrate type and MDT or PDT preservation in Cretaceous rocks.

Discussion

In this study we find no statistical support for any systematic distribution of MDTs and PDTs throughout the Jurassic and Cretaceous. In Jurassic rocks, PDTs slightly outnumber MDTs, whereas in Cretaceous outcrops even numbers of MDTs and PDTs are found. There is therefore no indication of an overall evolutionary trend towards dominance of sauropods with an anterior CM position. The Late Jurassic sauropod fauna (from which the majority of Jurassic tracks are known) was mixed, comprising taxa with posterior CM positions (e.g. the diplodocoid *Diplodocus*), and also those with more anterior CM positions (e.g. the titanosauriform *Brachiosaurus*) (Henderson 2006). The slightly higher number of PDTs than MDTs in the Jurassic may be a function of faunal composition: diplodocoids and non-titanosauriforms (e.g. *Camarasaurus*) were the most abundant and diverse taxa in many regions, with titanosauriforms often a rare component (e.g. in the Morrison Formation of North America) or entirely absent (e.g. Asia) in Jurassic ecosystems (Foster 2003; Upchurch *et al.* 2004). Alternatively, it may reflect the observation that PDTs can
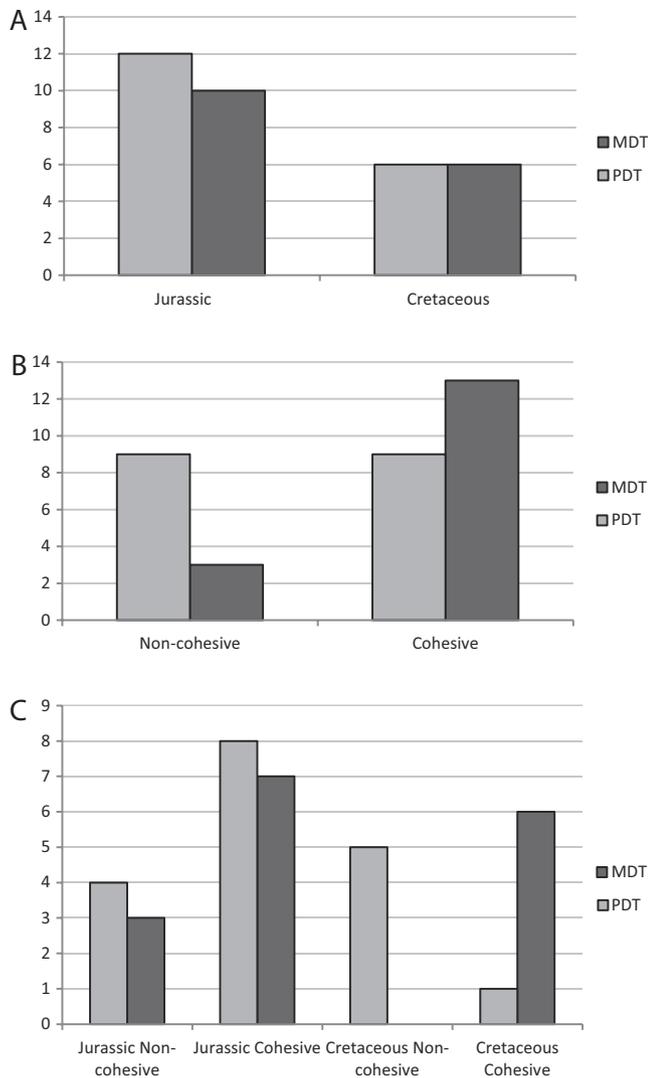
Fig. 2. (a) Graph showing the numbers of manus- and pes-dominated trackways found in Jurassic and Creataceous rocks. (b) Graph showing the presence of manus- and pes-dominated tracks in lithified cohesive and non-cohesive substrates. (c) Graph showing the temporal distribution of manus- and pes-dominated tracks across substrate type.

be produced by any quadruped whose gait includes overstepping, in which the pes obliterates the track left by the manus (Thulborn 1990). The body fossil record indicates that in the Cretaceous the sauropod fauna was composed almost entirely of derived titanosauriforms (predominantly titanosaurs), with a small contribution from aberrant diplodocoids (rebbachisaurids) that display some degree of convergence on the titanosaur body plan (Upchurch *et al.* 2004; Sereno *et al.* 2007; Mannion & Upchurch 2010*a*). However, this is not expressed by an increase in MDTs. This may be because the Cretaceous sauropod fauna was more diverse than currently suggested by osteological material, or it may be that as body form evolved, so too did locomotor mechanics and/or heteropody (Lockley 2007), resulting in underfoot pressures inconsistent with the simple static model of mass distribution to the feet used here and by Falkingham *et al.* (2011*a,b*).

The 'gauge' of sauropod trackways has also been used to support macroevolutionary body plan changes. Although the distribution of wide- and narrow-gauge trackways was initially described

as narrow gauge dominated throughout the Jurassic, and wide gauge dominated during the Cretaceous (Lockley *et al.* 1994*a*), the data were later shown to display a more complex pattern, with a mixed distribution (almost evenly split) of wide- and narrow-gauge trackways in the Jurassic, and an almost complete absence of narrow-gauge trackways in the Cretaceous (Wilson & Carrano 1999; Wright 2005; Santos *et al.* 2009; Mannion & Upchurch 2010*a*). The massively constructed pectoral girdles of many derived titanosaurs (e.g. *Saltasaurus, Opisthocoelicaudia)* suggest that titanosaur forelimbs carried a substantial fraction of the body weight, an inference that is consistent with the hypothesis that titanosaurs and other large-bodied forms had a more anteriorly positioned CM (Henderson 2006), although the relatively poor record of titanosaurs makes this hypothesis difficult to test directly at this time. Analyses of trackway distribution currently represent the only direct evidence for this macroevolutionary trend, given the relatively poor Cretaceous sauropod body fossil record (Mannion & Upchurch 2010*b*). That the formation of MDTs requires a highly specific substrate strength (Falkingham *et al.* 2011*a*), whereas wide-gauge tracks can be formed in any track-bearing substrate may explain the discrepancy between patterns observed in these two types of track preservation.

Despite the small sample size of the present data, there appears to be a strong link between substrate and track type within Cretaceous rocks, with MDTs exclusively associated with cohesive substrates, and PDTs primarily associated with non-cohesive substrates. Given that substrate type appears to have little effect on the distribution of MDTs and PDTs in the Jurassic, we propose that this Cretaceous association is not the result of preservational or formational processes resulting from the mechanical response of the substrate, nor is it linked to behavioural or locomotory changes associated with traversing specific substrates; if this were the case the association with substrate type would be present in the Jurassic. Instead, if the formation of MDTs or PDTs is related to the sauropod *bauplan*, and consequently the morphology of different taxa (Falkingham *et al.* 2011*a*), then the Cretaceous distribution of manus- and pes-dominated trackways may signal niche partitioning or marginalization, with sauropods that possess contrasting body plans living in different environments, and thus producing tracks in different substrates. Although a far larger sample size is required to improve resolution of palaeoenvironmental trends in track-bearing horizons, the inference made here is consistent with recent work, by Mannion & Upchurch (2010*a*), that recovered contrasting environmental preferences for titanosaurs and non-titanosaurs. Those researchers proposed that the anatomical and locomotory specializations of titanosaurs may have allowed them to exploit different terrains from other sauropods, perhaps allowing their diversification in the middle Cretaceous, when other sauropods went extinct. Our findings are also consistent with prior work that indicated evidence of resource partitioning through microwear and skull structure (Fiorillo 1998; Christiansen 2000) or feeding behaviour (Whitlock 2011). It is possible that the floral turnover in the Cretaceous (i.e. the rise of angiosperms) may have resulted in habitat segregation between diplodocoids and titanosaurs.

Conclusions

A Jurassic to Cretaceous shift in CM position within the Sauropoda cannot be observed in the temporal distribution of manus- and pes-dominated tracks. Relative numbers of PDTs and MDTs are approximately equal throughout geological time, despite the body fossil record suggesting a general anterior shift in CM position.

In the Jurassic, substrate displays no correlation with formation or preservation of PDTs and MDTs. However, in the

Cretaceous, manus-dominated tracks are predominantly restricted to cohesive substrates (muds, etc.), whereas pes-dominated tracks are most commonly found in non-cohesive sandy substrates. This may be indicative of niche partitioning, with the anatomically specialized titanosaurs able to exploit new environments, which may have contributed to their success in the Cretaceous as other sauropods died out.

However, we add a cautionary note that this dataset currently remains small, and we believe that there is still a huge unexplored research potential in vertebrate ichnology, not just for more traditional behavioural, ecological, or biomechanical matters, but also for studying larger macroevolutionary trends.

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