



## Some observations on trackway evidence for gregarious behavior among small bipedal dinosaurs

Martin G. Lockley<sup>a,\*</sup>, Masaki Matsukawa<sup>b</sup>

<sup>a</sup> *Geology Department, University of Colorado at Denver, P.O. Box 173364, Denver, CO 80217-3364, USA*

<sup>b</sup> *Department of Science Education, Tokyo Gakugei University, Koganei, Tokyo 184, Japan*

Received 17 July 1997; revised version received 18 December 1997; accepted 13 October 1998

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### Abstract

Although trackway evidence for social behavior (herding or gregariousness) has been demonstrated for large, mainly quadrupedal dinosaurs, until recently footprint evidence for herding among small bipedal dinosaurs has been sparse. Recent reports now increase the number of sites suggestive of social behavior to nine, found in strata of Early Jurassic through mid-Cretaceous age in Europe, North America and East Asia. Present evidence suggests that small gregarious dinosaurian bipeds included both theropod and ornithomimid species. © 1999 Elsevier Science B.V. All rights reserved.

*Keywords:* parallel trackways; gregariousness; social behavior; dinosaurs

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### 1. Introduction

“Some dinosaurs were herding by the Early Jurassic, leaving open the possibility for development of complex social systems over the next 140 million years” (Coombs, 1990, p. 36).

“The track record . . . tells us about the evolution of social behavior . . . and when such behavior first arose. We know . . . small theropods were probably gregarious at least by Early Jurassic times” (Lockley, 1991, p. 110).

It is now generally accepted that there is abundant trackway evidence for gregarious behavior among large herbivorous dinosaurs — most notably Late Jurassic and Early Cretaceous sauropods and large Cretaceous ornithomimids (iguanodontids and hadrosaurids). Trackway evidence for gregarious be-

havior among other dinosaurs, however, is more scattered and ambiguous, but as indicated in the above quotations, it appears that some bipedal dinosaurs (probably theropods) were engaged in gregarious behavior by the Early Jurassic (Coombs, 1990; Lockley, 1991). The purpose of this paper, therefore, is to review new trackway evidence with particular attention to the spoor of small tridactyl bipeds. This exercise allows us to broaden our perspective on the trackway evidence for gregarious dinosaurs in space and time.

Recent discoveries of tracksites indicating gregarious behavior among small Jurassic bipedal dinosaurs in North America, Europe, and Asia have implications for the origins and frequency of gregarious behavior among ornithomimids and theropods. There is a general perception that tridactyl footprints are hard to differentiate owing to conservative and convergent morphology. While there is some

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\* Corresponding author. E-mail: mlockley@carbon.cudenver.edu

truth to this, such perspectives are largely untested and, moreover, based on limited knowledge. Recent discoveries indicate that distinctive ichnotaxa can be differentiated from among the large number of tridactyl assemblages known in the Mesozoic (Matsukawa et al., 1997; Lockley et al., 1998a). Such progress improves our understanding of the spatial and temporal distribution of distinctive ichnotaxa and the extent to which evidence of gregarious behavior may be associated with particular track types.

## 2. Criteria for inferring gregarious behavior from trackways

Two important criteria must be satisfied in order to make a compelling case for gregarious behavior based on tracks. First, there must be evidence of multiple trackways of the same type on the same surface or within a very restricted stratigraphic interval. Second, it is important to find evidence of parallel trackways indicating preferred direction of travel. Ostrom (1972) suggested that parallel trackways either resulted from a biological explanation (i.e., gregarious behavior) or a 'physically controlled' pathway such as a shoreline corridor. Lockley (1991) elaborated these alternative explanations to suggest that parallel trackways might also reflect gregarious behavior influenced by physical constraints.

Lockley (1989) also introduced the concept of intertrackway spacing as a parameter for measuring regularity of spacing between trackways in parallel sets. Where spacing is reminiscent of birds flying in formation or soldiers marching, and where parallel trackways curve or swerve in unison, the suggestion of a group in motion is compelling. Similarly, at sites where groupings of small or large parallel trackways are identified, it is reasonable to infer that individuals belonging to particular age groups were traveling together (cf. Lockley and Hunt, 1995a,b). There is no magic or arbitrary number of adjacent parallel trackways that constitutes a minimum number for indicating gregarious behavior. Factors such as size and intertrackway spacing must also be taken into consideration. In short, while mapping of tracksites and description of trackways can be approached objectively, interpretations remain subjective to some degree. Coombs (1990) offers further insight on the

criteria that must be considered in the study of gregarious behavior among dinosaurs, though his review is not confined to trackway evidence.

## 3. Gregariousness among large herbivorous dinosaurs

### 3.1. *Sauropods and large ornithopods*

For historical and ichnotaxonomic reasons, it is convenient to review the trackway evidence for gregarious behavior among sauropods and large Cretaceous ornithopods before turning our attention to smaller bipedal dinosaurs. Bird (1939, 1941, 1944) was the first to suggest that parallel brontosaurus tracks from the two sites in the Cretaceous of Texas indicate herd behavior (Fig. 1). Similar evidence was reported from the Late Jurassic of Colorado (Lockley et al., 1986), Portugal (Lockley et al., 1994), and Utah (Barnes and Lockley, 1994). Parallel sauropod trackways have been reported from additional sites in the Cretaceous of Texas (Pittman, 1992; Pittman and Lockley, 1994). Despite an abundance of sauropod trackways in South Korea, there is little compelling evidence of groups progressing as herds (Lim et al., 1989, 1994).

Parallel trackway evidence for gregarious ornithopods was reported by Currie (1983) for Lower Cretaceous ornithopods (iguanodontids) from Canada. Multiple stratigraphic levels with parallel ornithopod tracks are known from the Cretaceous of South Korea (Lim et al., 1989, 1994), and multiple sites with parallel ornithopod trackways are also known from the Cretaceous of Colorado and New Mexico (Lockley et al., 1992; Lockley and Hunt, 1995a,b; Lockley, 1995, 1997). There is also scattered evidence for gregarious behavior from tracksites in the Lower Cretaceous of England (Delair and Lander, 1973; Delair, 1981).

### 3.2. *Ceratopsids and other large quadrupedal dinosaurs*

Lockley and Hunt (1994, 1995a,b) reported abundant ceratopsid tracks from the Upper Cretaceous of Colorado, but only one site with several parallel trackways. Trackways of other large quadrupedal

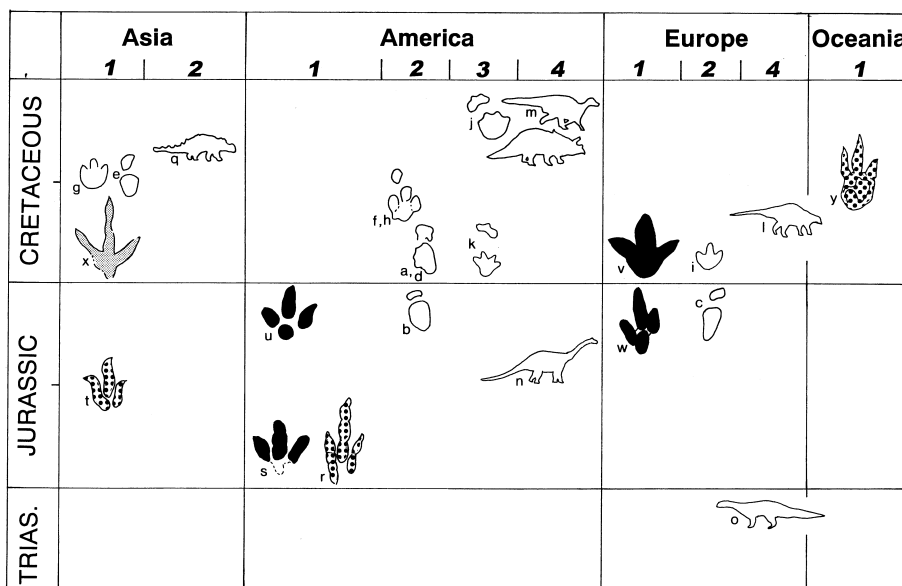


Fig. 1. Chronological and geographical distribution of gregarious dinosaurs. (1) Footprints of small bipeds. (2) Sauropods and large ornithomorphs. (3) Ceratopsids and other large quadrupedal dinosaurs. (4) Skeletal records. Solid, scattered dot and mesh tracks show ornithomorph, theropod and possible ornithomorph, respectively. Letters, a to y, with tracks show occurrence locality: a = Texas, b = Colorado, c = Portugal, d = Texas, e = South Korea, f = Alberta, g = South Korea, h = Colorado and New Mexico, i = England, j = Colorado, k = Alberta, l = Belgium, m = Montana, n = Argentina, o = Germany, p = Alberta, q = Inner Mongolia, r = Connecticut, s = Utah, t = Liaoning, u = Utah, v = Spain, w = Portugal, x = Japan, y = Australia.

dinosaurs such as stegosaurids and ankylosaurids (thyreophorans) are not well enough known to indicate behavioral patterns. Multiple ankylosaurid trackways are known only from one or two sites in the Lower Cretaceous of Canada (Psihoyos and Knoebber, 1995; Richard McCrea, written communication, 1997) but no discernable parallel orientations have been reported.

### 3.3. Consistency of track and skeletal records

The evidence for gregarious behavior as inferred from the track record appears to be consistent with the skeletal record. For example, the famous Bernisart *Iguanodon* assemblage yielded 36 individuals from a single assemblage in the Lower Cretaceous of Belgium. Similarly, the occurrence of a *Maiasaura* bone bed in the Upper Cretaceous of Montana has frequently been cited as an example of an accumulation in which large numbers of individuals of the same species perished together (Horner and Gorman, 1988). Monospecific assemblages of sauropods have been reported from the Cretaceous of

South America (Coria, 1994), and the famous Trossigen sauropodomorph assemblage from the Late Triassic of Germany is often cited as evidence of gregarious behavior in the prosauropod *Plateosaurus* (Weishampel, 1984). Monospecific bone beds of ceratopsids have been reported from the Cretaceous of Canada (Currie and Dodson, 1984) and a family group of juvenile ankylosaurids has been reported from the Cretaceous of Inner Mongolia (Obata and Tomida, 1994).

## 4. Gregariousness among small bipedal dinosaurs

### 4.1. Defining the footprints of small bipeds

The definition of a small, rather than large, bipedal dinosaur is somewhat arbitrary. We have chosen a maximum foot length of 25 cm as a dimension that probably separated most gracile cursorial forms from larger subcursorial or mediportal taxa (Coombs, 1978). This foot length was also used by Thulborn (1990) to separate large from small bipeds.

If the maximum foot length in a given sample is no more than 25 cm, the mean size is considerably less. It is of course possible that assemblages of small tracks exist that represent juvenile representatives of a known ichnotaxon with a much larger maximum track size, but no such examples have been documented explicitly. Most large track assemblages give a reliable indication of the size range of tracks.

Another problem faced in attempting to interpret the tracks of small bipedal dinosaurs involves determining whether they are of theropodan or ornithopodan affinity. Thulborn (1990) has discussed this problem, as have other authors (Farlow and Lockley, 1993). Although there is no consistently reliable set of criteria the following morphological characteristics are useful in drawing the theropod–ornithopod distinction. Theropod tracks are generally longer than wide and form narrow trackways with relatively long steps and little positive or negative (inward or outward) rotation of the foot axis (midline of digit III). Theropod footprints are often asymmetrical with the posterior margin of digit IV located well behind the posterior margin of digit II. By contrast, small ornithopod tracks, classically modeled on *Anomoepus* and *Anomoepus*-like tracks such as *Moyenosauripus*, sometimes have associated manus tracks. Hallux impression may be associated with either ornithopod or theropod tracks, but their morphology and position is dependent on track depth as well as the anatomy of the trackmaker's foot.

#### 4.2. Assemblages with parallel trackways

In his classic paper on gregarious dinosaurs, Ostrom (1972) cited the Mount Tom site in Connecticut as a probable example of gregarious behavior among Lower Jurassic theropod dinosaurs whose footprints are assigned to the well-known ichnogenus *Grallator* (Hitchcock, 1858). The average length of these tracks is about 7.5 cm. This remains one of the few examples of Lower Jurassic evidence for gregarious dinosaurs and one of the few examples of trackway evidence for herding among theropods.

A second possible example of gregarious behavior was recently discovered at a tracksite in the Lower Jurassic Kayenta–Navajo beds of eastern Utah (Lockley et al., 1998b). Here three *Anomoepus* or *Moyenosauripus*-like trackways were recorded

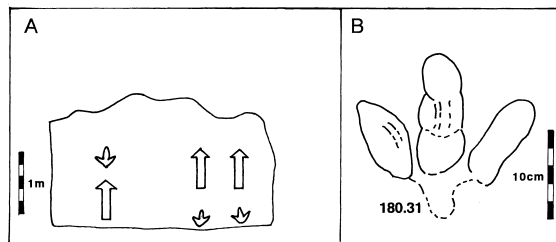


Fig. 2. (A) Three parallel trackways of an *Anomoepus*-like trackmaker, of probable ornithopod affinity, from the Lower Jurassic of eastern Utah. (B) Detail of individual track. Modified after Lockley et al. (1998b).

with parallel trends (Fig. 2). Footprint length and width are 19 cm and 20 cm, respectively, suggesting ornithopod affinity as generally inferred for *Anomoepus* and *Moyenosauripus* (Ellenberger, 1974; Thulborn, 1990; Gierlinski, 1991).

Coombs (1990) also cites Shikama (1942) as another example of a report of ‘multiple near-parallel trackways . . . indicating herding behavior’. The age of these tracks is Early Jurassic and the size averages around 7–12 cm. Shikama (1942) illustrates hundreds of tracks with parallel orientations.

To the best of our knowledge there is no Middle Jurassic evidence for gregarious dinosaurs. In the Upper Jurassic, however, there are several examples of parallel trackways suggestive of social behavior. The first example, from the Morrison Formation of Utah, pertains to 16 trackways of small ?ornithopods assigned to the ichnogenus *Dinehichnus socialis* (Lockley et al., 1998a). The average length of these tracks is about 15.4 cm (range 10 to 28 cm). Three parallel trackways of the same type (cf. *Dinehichnus*) have been reported from rocks of the same age in the Upper Jurassic of Portugal (Lockley et al., 1998a), and eight parallel trackways of comparable type are known from the Lower Cretaceous of Spain (Aquirrezabala et al., 1985). Mean footprint length for the Spanish sample is about 11 cm. Thus all trackways of this type occur in parallel sets (Lockley et al., 1998a).

Matsukawa et al. (1997) recently reported a large assemblage of small tridactyl trackways from the lowermost Cretaceous of Japan. Thirty-three trackways all assigned to the same ichnogenus — *Toymasauripus* — were recorded on the same bedding plane. These tracks range in length from 3.3 to 9.4

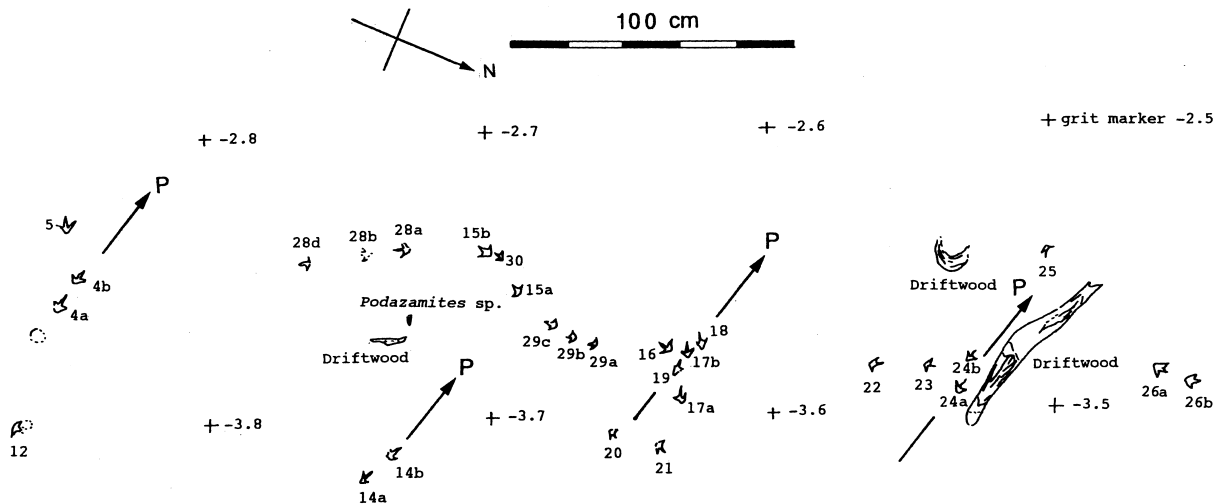


Fig. 3. Several trackways of *Toyamasauripus*, from the Lower Cretaceous of Japan, revealing parallel trackways, possibly indicating gregarious behavior. Modified after Matsukawa et al. (1997).

cm. They show signs of having been made by a gregarious trackmaker, where a set of four trackways show parallel orientation to the west and fairly regular intertrackway spacing (Fig. 3). It is possible that the trackmaker was an ornithopod, but the possibility of theropod affinity cannot be ruled out (Matsukawa et al., 1997).

Perez-Lorente et al. (1997) also recently reported three parallel trackways of a small tridactyl trackmaker (pes length 21–25 cm), from the Lower Cretaceous (Berriasian) of Spain. Although the trackways were evidently all made by bipeds, and are interpreted as theropodan in origin, they are associated with the trackway of a single quadruped that appears to be of ornithopodan affinity.

When considered collectively the Late Jurassic and Early Cretaceous tracks from Utah, Portugal, the two Spanish sites and Japan probably all represent the activity of small gregarious ornithopods, though some may be theropods. Pending detailed studies of the foot morphology of potential trackmakers (cf. Farlow and Lockley, 1993) it is probably best to keep an open mind regarding possible candidates. So far, only the ichnogenus *Hypsilophodon* has been mentioned in connection with one of the Spanish sites (Aquirrezabala et al., 1985), and the possibility of a dryosaurid origin considered for the Utah ichnogenus *Dienhichnus*. A recent article by Fuentes Vidarte (1996) reported dozens of trackways of a

small slender-toed biped (mean foot length 12 cm), named *Archaeornithopus* and interpreted as avian in origin, from near the Jurassic–Cretaceous boundary in Spain. We agree with the avian interpretation, based on track morphology, but the possibility of a dinosaurian origin was discussed by the author. Because of the avian affinity of these tracks, this report of gregarious behavior is not included in Fig. 1, which refers only to dinosaurs.

Finally, we must consider the famous Lark Quarry site in the middle Cretaceous of Queensland where hundreds of parallel trackways of small bipedal dinosaurs have been interpreted as evidence of a stampede induced by the presence of a large carnivore (Thulborn and Wade, 1979, 1984). Although there can be little doubt that the trackmakers were gregarious, the interpretation of this site is controversial. Thulborn and Wade (1984) differentiated two ichnogenera *Skartopus* and *Wintonopus* from within the same assemblage, inferring that the former was theropodan in origin and the latter of ornithopod affinity. While this interpretation may be correct, with the 'narrow, tapering and sharply pointed digits' of *Skartopus* indicating theropod affinity and distinguishing it from *Wintonopus* (Thulborn, 1989, p. 55), the interpretation of carnivores and ornithopods mingling in large numbers has been questioned by some authors (Paul, 1988; Lockley, 1991). Given that Thulborn and Wade (1984) acknowledge con-

siderable variation in trackway morphology owing to preservation, a number of multiple working hypotheses should be considered. The tracks could also represent two different groups of ornithopods, two groups of theropods, or possibly a single taxon of either group. For our purposes we accept the interpretation of Thulborn and Wade (1984) and leave open the question whether their interpretation of trackmaker affinity is correct.

## 5. Discussion and conclusions

In addition to the now well-established trackway evidence for gregarious behavior among large, mainly quadrupedal, late Mesozoic dinosaurs (Late Jurassic and Cretaceous sauropods, ornithopods and ceratopsids), footprint evidence also suggests gregarious behavior among small bipedal dinosaurs (foot lengths less than 25 cm). Such evidence of gregarious behavior is reported from at least three Lower Jurassic sites, two Upper Jurassic sites, and four Lower to mid-Cretaceous sites, in Europe, North America and East Asia.

We conclude therefore that gregarious behavior was common among small bipedal dinosaurs from Early Jurassic times onwards, and that the behavior probably was characteristic of both theropods and ornithopods. Based on the distribution of track-sites which suggest gregarious behavior, the evidence suggests that such social behavior was widespread. When coupled with the evidence from large dinosaurs, it appears that most of the major groups of dinosaurs well represented by their tracks show evidence of gregarious behavior, at least among certain populations.

## Acknowledgements

This work was supported in part by a grant from the National Science Foundation to M. Lockley and from the Grant-in-Aid for Scientific Research (Grant No. 06640603 for Matsukawa, 1994–1996), the Japanese Ministry of Education, Science, Sports and Culture. Access to sites on the Navajo Nation were approved by written permission from The Navajo Nation Minerals Department, Window Rock,

Arizona. We thank our colleagues Vanda Faria dos Santos, National Museum Lisbon, Portugal, Christian Meyer, Solothurn Nature Museum, Switzerland, and Adrian Hunt, Mesa Museum Tucumcari, New Mexico, for their assistance and advice in helping document some of the sites discussed herein. Adrian Hunt also reviewed an earlier version of the manuscript and provided helpful suggestions.

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