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TRACKS OF DIMINUTIVE DINOSAURS AND HOPPING MAMMALS FROM THE JURASSIC OF NORTH AND SOUTH AMERICA

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ABSTRACT: Tridactyl tracks of diminutive dinosaurs, with feet no larger than those of modern starlings and sparrows have been reported from Lower and Middle Jurassic eolian deposits of North and South America respectively. The former, from the Navajo Sandstone of Arizona, have not been named, but the latter, from the La Matilde Formation, Argentina, have been assigned to the ichnospecies *Wildeichnus navesi* (Casamiquela, 1964). Very small footprints attributed to hopping mammals are also known from the Lower Jurassic Botucatu Formation of Brazil, and from the Middle Jurassic La Matilde Formation of Argentina. The latter tracks are pentadactyl and have been assigned to the ichnospecies *Ameghinichnus patagonicus* (Casamiquela 1964). Collectively these footprints indicate that small vertebrates (both mammals and dinosaurs) were characteristic of Jurassic eolian deposits. Moreover the trackway evidence indicates that some mammals developed hopping gaits by the Early Jurassic.

INTRODUCTION

Studies of track assemblages from eolian deposits often reveal that footprints of diminutive animals, both vertebrate and invertebrate, are frequently well-preserved. For example, Permian deposits such as the Coconino and DeChelly Sandstones of Arizona (Gilmore, 1926; Lockley *et al.*, 1995) are replete with the tracks of relatively small mammal-like reptiles and well-preserved trackways of arthropods. Similar track assemblages can also be found in Jurassic eolian deposits, such as the Navajo Sandstone of western North America (Lockley and Hunt, 1995; Rainforth and Lockley, 1996), and Jurassic deposits of South America (Casamiquela, 1964; Leonardi, 1994). Despite the importance of tracks as the main, or only, source of paleontological information in most of these eolian deposits, few workers, other than vertebrate ichnologists, have paid much attention to the available evidence. The purpose of this paper is therefore to describe examples of well-preserved tracks of small vertebrates, both mammalian and dinosaurian, that shed interesting light on the affinity and behavior of trackmakers in Jurassic eolian environments.

MATERIAL

Diminutive Dinosaur Tracks, Navajo Sandstone, Lower Jurassic

Trackways of diminutive dinosaurs associated with the eolian facies of the Lower Jurassic Navajo Sandstone have been reported from a locality known as Copper Mine in northern Arizona. The tracks are only 3.5 cm in length (Figure 1c). Such dimensions indicate an animal with a foot the size of a starling or sparrow (Figure 1a; Headstrom, 1971), and a hip height of about 14 – 17.5 cm (if hip height is 4 or 5 x foot length). The trackmaker covered 20 – 25 cm, or between six and seven foot lengths, per step (= 12 – 14 foot lengths per stride). Calculations of speed suggest that they were moving at six to nine kilometers per hour, a considerable speed for a diminutive animal.

Diminutive Dinosaur Tracks, La Matilde Formation, Middle Jurassic

Casamiquela (1964) also reported diminutive dinosaur tracks from the Middle Jurassic La Matilde Formation at Estancia Laguna Manantiales in the province of Santa Cruz in southern Argentina, and named the tracks *Wildeichnus navesi* (Figure 1b). Like the tracks from the Navajo Sandstone, these are also diminutive, starling-sized footprints measuring about 5 cm in length. Judging by its much shorter strides, however, this trackmaker was not moving quite so fast.

Hopping Vertebrate Tracks, Botucatu Formation, Lower Jurassic

Leonardi (1994) reported diminutive tracks of a hopping vertebrate from the Lower Jurassic Botucatu Formation of Brazil, and suggested that the tracks might be of dinosaurian origin (Figure 2). Although the tracks

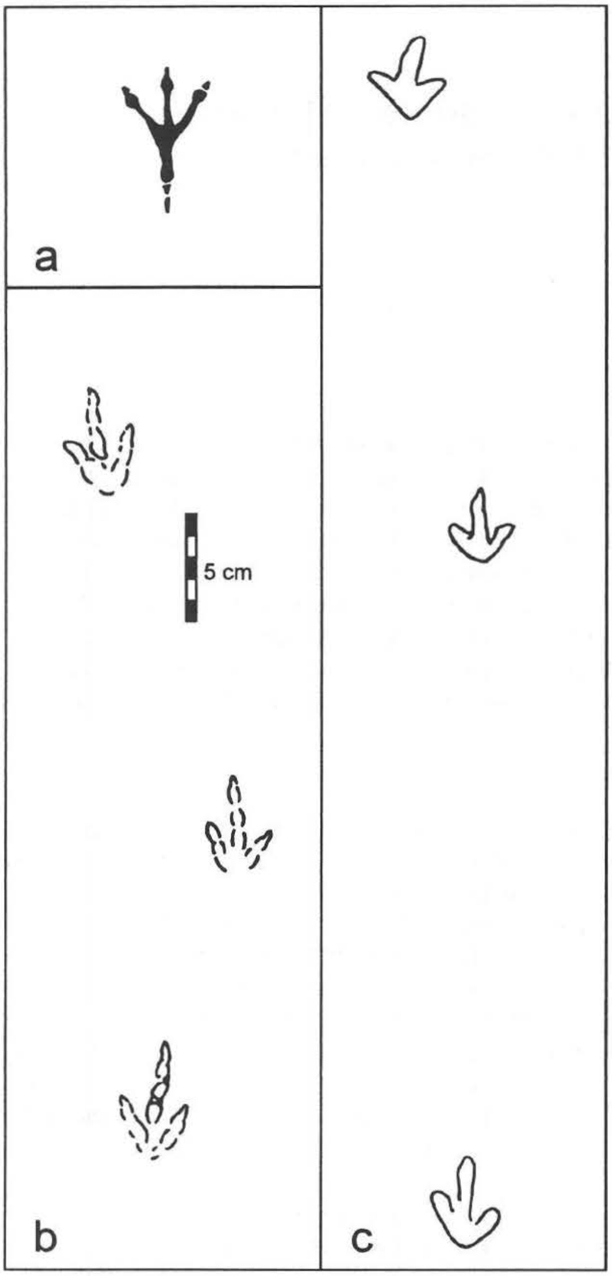

FIGURE 1. (a) Footprints of a modern starling. (b) Wildeichnus navesi from the Middle Jurassic of Argentina. (c) Unnamed diminutive dinosaur tracks from the Navajo Sandstone, Arizona. All to same scale.

are tridactyl, they have a pronounced transverse heel pad which makes them appear similar to tracks of mammals and mammal-like reptiles. In addition the middle toe impression is not much longer than the two lateral toe impressions, and so in this respect they are also different from typical tridactyl dinosaur footprints. We therefore infer that they are either tracks of mammals or of small mammal-like reptiles such as those responsible for making numerous *Brasilichnium* tracks in the Botucatu Formation.

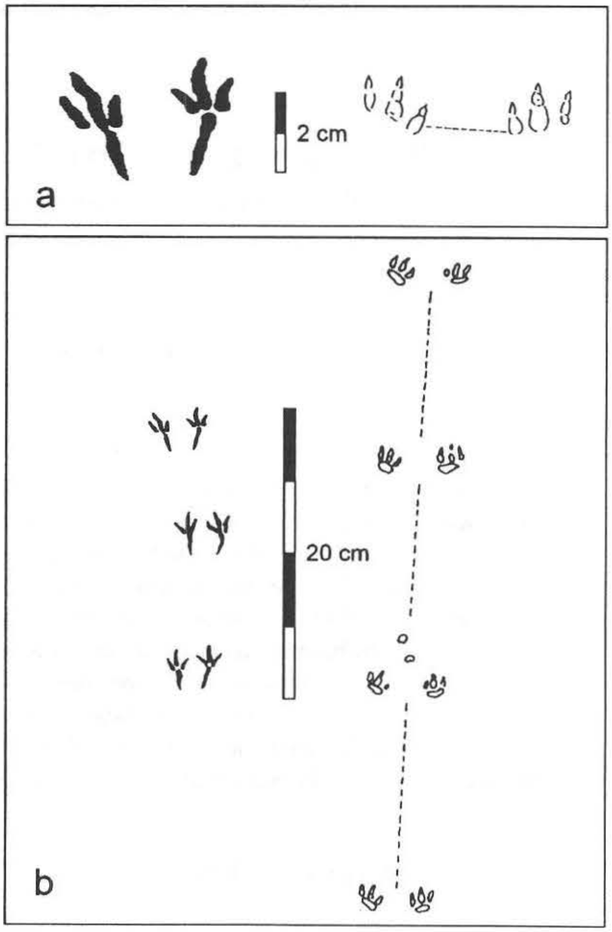

FIGURE 2. Tracks of a small hopping vertebrate from the Lower Jurassic Botucatu Formation (right) were attributed to a hopping dinosaur by Leonardi (1994), but may be of mammalian affinity (see text). They are no larger than the tracks of a modern sparrow (left). (a) Detail of a pair of tracks in (b).

The trackway indicates a hopping animal with feet only 2 cm in length, yet capable of bounding 15-20 cm. Such a creature had feet only half the size of the diminutive dinosaurs just described. As discussed below, if the track is mammalian then it is the oldest yet described. If it is of therapsid or dinosaurian affinity, it would be the first convincing example of a hopping gait attributed to representatives of either one of these groups.

Hopping Mammal Tracks, La Matilde Formation, Middle Jurassic

Tracks described by Casamiquela (1964) from the Middle Jurassic La Matilde Formation of Argentina, and named *Ameghinichnus patagonicus*, are among the most remarkable of all tracks known from the Mesozoic. They are even smaller than those from the Botucatu Formation, measuring less than 1 cm in either length or width. They indicate an animal capable of hopping a long way (9 cm) relative to footprint length, and also provide evidence of both hopping and alternating gaits (Figure 3). The tracks are well-preserved and clearly indicate five digits on both hind and front feet. They represent one of the most convincing examples of mammal tracks known from the Mesozoic. The tracks are clearly different from *Brasilichnium* (Leonardi, 1994), which is

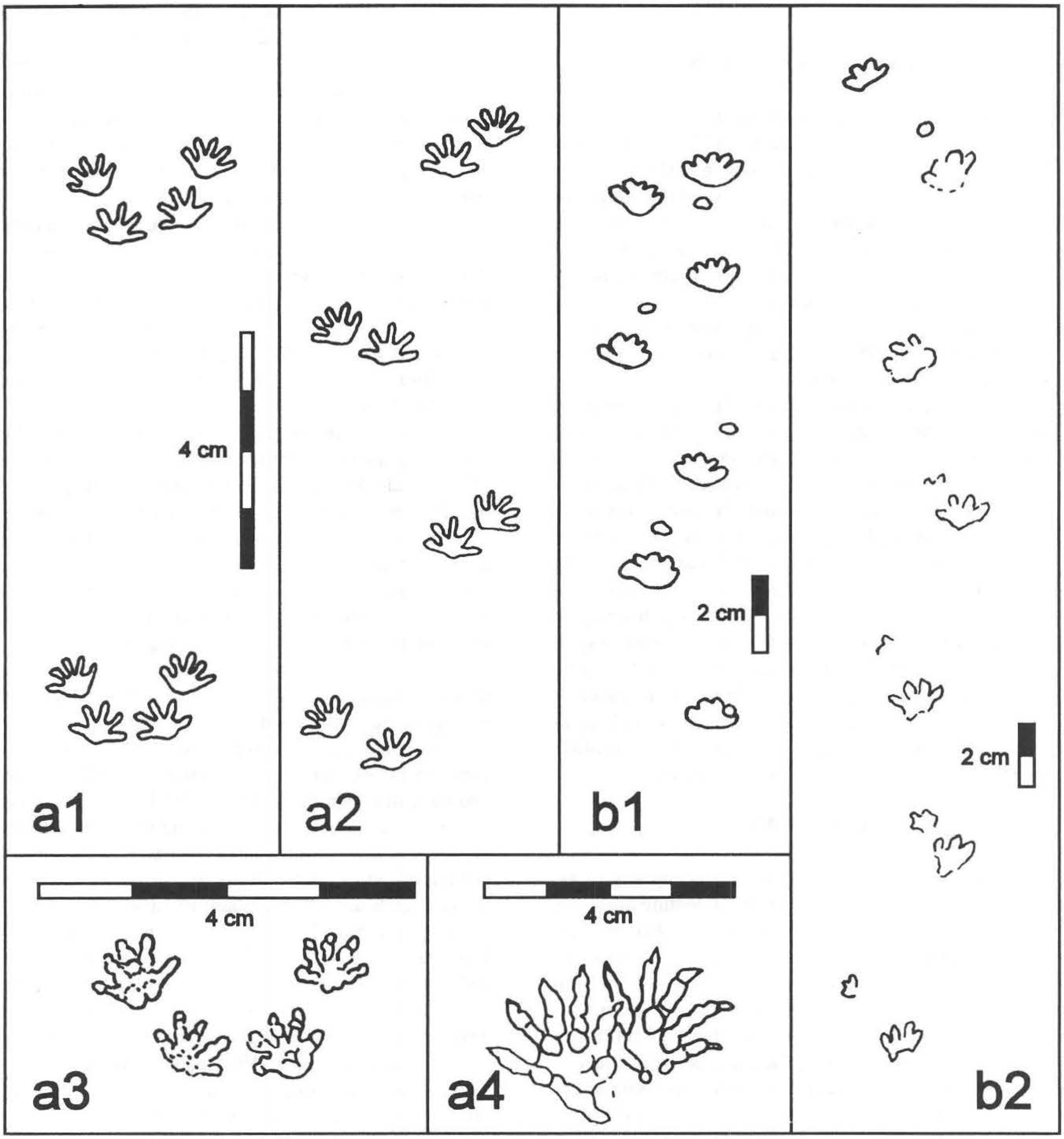

FIGURE 3. *Ameghinichnus patagonicus* (a1-4) from the Middle Jurassic of Argentina is one of the most distinctive of all Mesozoic mammal tracks, and provides evidence of hopping locomotion. (a1) and (a2) show hopping and alternate gaits with (a3) showing detail of (a1). (a4) *"Ameghinichnus"* after Olsen (1980) from Lower Jurassic of Eastern USA. (b1) and (b2), *Brasilichnium* trackways from Lower Jurassic of South America and North America respectively (cf. Lockley and Hunt, 1995).

characterized by a diminutive manus (therefore displaying obvious heteropody) rather than having manus and pes tracks of the same size (Figure 3).

Olsen (1980: Figure 20E) indicated that tracks attributable to *Ameghinichnus* occur in the Newark Supergroup. We note however that these tracks are much larger than the South American ichnites; they are also considerably older.

HOPPING DINOSAURS?

Leonardi (1994) was not the first to suggest the idea of hopping dinosaurs. Raath (1972) reported finding two similar dinosaur tracks side by side, in Lower Jurassic deposits of Rhodesia. He inferred that the tracks were those of the carnivorous theropod *Syntarsus*, and suggested that it might have "had a kangaroo-like saltatory gait, using both hind legs together". Unfortunately he did not illustrate a trackway of consecutive pairs of left and right feet, so the possibility exists that the tracks are those of two different animals that just happen to have been impressed side by side.

The debate about hopping dinosaurs deepened when purported tracks of a hopping dinosaur were reported from Late Jurassic lithographic limestones at Cerin, near Lyons in France, and named *Saltasauropus* (Bernier *et al.*, 1984) At around the same time these authors also described the trackway of a giant turtle (Bernier *et al*, 1982). Thulborn (1989) suggested that the tracks had been made by a large sea turtle swimming near the bottom, an interpretation with which we agree (Lockley 1991). Thus we are left with little in the way of convincing evidence that dinosaurs developed hopping gaits. This does not deny the possibility of the trackway of a miniature hopping dinosaur in the Botucatu Formation of South America, but it does suggest that an alternate trackmaker should be seriously considered.

DISCUSSION

Mesozoic trackway evidence for hopping vertebrates (other than dinosaurs) raises fascinating questions about the locomotion of reptiles, mammal-like reptiles, mammals, and even birds. As usual however, the trackway evidence has not received much serious attention, or in some cases has been subject to controversial interpretations. Early and Middle Jurassic mammals are sufficiently rare that one would expect Casamiquela's discovery of the tracks of what are evidently Middle Jurassic mammals to create a flurry of interest among mammal paleontologists. But perhaps because his original publications were in Spanish (Casamiquela, 1964), his discovery was almost completely ignored. Similarly Leonardi's recent report (1994) of the trackway of what may have been a diminutive hopping dinosaur (or mammal) is equally fascinating, not least because of its Early Jurassic age.

As suggested above, the Botucatu trackway might be that of a mammal, because one can argue that hopping gaits are unknown among dinosaurs, but one might equally well postulate that the trackway is reminiscent of bird behavior. The arguments against this are that true (feathered) birds are unknown prior to the Upper Jurassic, and that the observed track morphology is not obviously bird-like. Thus the weight of evidence suggests that the mammal interpretation is most probable. If this is the case then we can go one step further, and infer that the hopping gait typical of such creatures as jerboas and kangaroo rats evolved among desert-dwelling mammals as early as the Lower Jurassic. Given the almost complete lack of Mesozoic mammal trackways, and the lack of skeletal remains that suggest hopping anatomy, and the diminutive size of the creatures involved, it is remarkable that this particular evidence of gait is preserved at all. Such eolian deposits provide ample track evidence for fruitful studies of the behavior and paleoecology of small vertebrates (Ahlbrandt *et al.*, 1978; Albers, 1975; Lockley and Hunt, 1995; Lockley *et al*,. 1995; Rainforth and Lockley, 1996; Stokes, 1978).

It is also interesting to consider these probable mammal gaits in the context of debates about the gaits of mammal-like reptiles, which were evidently among the first vertebrates to inhabit desert environments (Lockley *et al.*, 1995). They may have developed such gaits in response to the need to negotiate sloping sand dune surfaces. What is apparent is that at some point in time different mammal groups developed both hopping gaits and the more common alternating gait.

Finally it is interesting to consider possible relationships between gait, animal size and ecology. Hopping gaits are common among small vertebrates such as birds and mammals, as noted above. These gaits are not common in large modern vertebrates, except kangaroos, and have not been demonstrated for large fossil vertebrates, as outlined in the preceeding discussion. Small vertebrates are characteristic of desert environments (Ahlbrandt *et al.* 1978), however, so the evidence for hopping gaits among inhabitants of ancient desert is not surprising. It has also been noted that so called dwarf faunas are r-selected (small body size, early maturation, and high fecundity in unstable environments) rather than k-selected (large body size, delayed reproduction and development, and longer life spans in stable environments), see McNamara (1990). Such evidence would suggest that individuals of small vertebrate species, comprising dwarf faunas, were relatively abundant. Again the abundant trackway evidence from eolian deposits is consistent with this conclusion. Such predictable high abundance helps offset the bias against preservation of small vertebrate tracks in the fossil record (Lockley, 1991).

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