Journal of South American Earth Sciences 20 (2005) 253–257

Journal of
South American
Earth Sciences

www.elsevier.com/locate/jsames

Occurrence of sauropod dinosaur tracks in the Upper Jurassic of Chile (redescription of *Iguanodonichnus frenki*)

Karen Moreno *, Michael J. Benton

Earth Sciences Department, University of Bristol, Bristol BS8 1RJ, UK

Received 7 July 2003; accepted 20 May 2005

Abstract

New observations from the only studied Upper Jurassic dinosaur unit in South America, the Baños del Flaco Formation, Chile, are presented herein. The original description of the ichnospecies *Iguanodonichnus frenki* contains several mistakes and information that needs updating. Therefore, we provide a redescription, including new data collected in the field, that supports *I. frenki* as a sauropod in origin on the basis of the following features: step angles average less than 110°; pes prints intersect the trackway midline; pes prints are longer than wide, with the long axis rotated outward; the claw impression of digit I is prominent and directed forward; and claws on digits II, III, and IV are strongly reduced. These morphological characteristics might give clues about the pes morphology of the South American Jurassic sauropods, whose foot bone remains are scarce. The presence of this sauropod ichnospecies in the Late Jurassic agrees with Early–Middle Jurassic faunal associations in South America.

Keywords: Chile; Dinosaur footprints; Parabrontopodus; Sauropod; Upper Jurassic

Resúmen

En el presente trabajo se realizan nuevas observaciones acerca de las huellas de dinosaurios de la Formación Baños del Flaco, las cuales representan el único registro conocido para Jurásico Superior en América del Sur. La descripción original de la icnoespecie *Iguanodonichnus frenki* posee diversos errores y contiene información que necesariamente debe renovarse. En el presente trabajo realizamos su redescripción, incluyendo nueva información colectada en terreno, la cual indica que *I. frenki* es saurópodo en origen en base a las siguientes características: promedio de ángulo de paso menor a 110°; huellas pedales intersectan el eje de la pista; huella pedal más larga que ancha, eje longitudinal dirigido hacia afuera; impresión de garra correspondiente al dígito I es prominente y se dirige hacia delante; garras reducidas en dígitos II, III y IV. Estas característica morfológicas proveen pistas acerca de la morfología pedal de los saurópodos Jurásicos de América del Sur, cuyos restos oseos de piés son escasos. La presencia de esta icnoespecie de saurópodo concuerda con otras asociaciones faunísticas halladas en el Jurasico Temprano-Medio de América del Sur.

Palabras clave: Parabrontopodus; Huellas de dinosaurios; Chile; Jurásico Superior; Saurópodo

1. Introduction

The Jurassic–Cretaceous boundary marks a major transition in dinosaurian evolution, with a switch from sauropods to ornithopods as the dominant herbivores (Bakker, 1971; Weishampel and Norman, 1989). The skeletal records show major changes from classic Late Jurassic dinosaurian faunas, such as those of the Morrison Formation that contain abundant remains of six to seven genera of sauropods, to the Early Cretaceous Wealden of Europe with its rare sauropods but abundant *Iguanodon*. The story of this transition in South America has been unclear, largely because of the rarity of Jurassic dinosaur finds. Middle Jurassic dinosaur remains from Chubut province, Argentina, include the cetiosaurids *Amygdalodon patagonicus*, *Patagosaurus fariasi*, *Volkheimeria chubutensis*, and *Tehuelchesaurus benitezii* and the allosaurid *Piatnitzkysaurus floresi* (Bonaparte, 1979; Rich et al., 1999). Two Early–Middle Jurassic trackbeds from the Botucatu Formation of Brazil and La Matilde Formation of Argentina (Leonardi, 1989) both contain a small theropod and ornithopod ichnofauna.

* Corresponding author.
E-mail address: dinohuella@yahoo.com (K. Moreno).

0895-9811/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jsames.2005.05.012

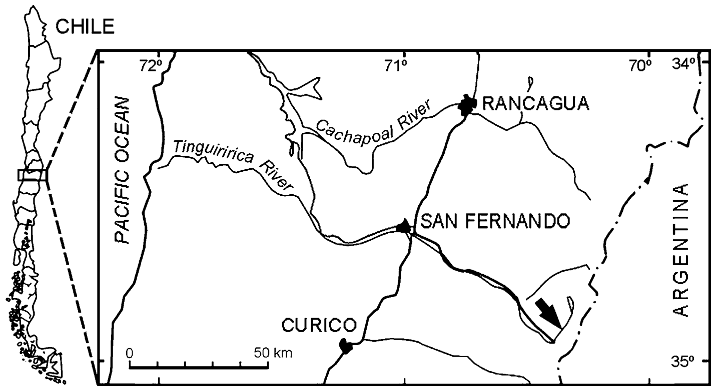

Fig. 1. Location map showing Chile and part of Region VI. The arrow shows the Termas del Flaco locality.

Dinosaur footprints are known from seven localities in Chile (Salinas et al., 1991). The best known is Termas del Flaco, approximately 100 km southeast of the city of San Fernando, VI Region (Fig. 1). This tracksite represents the only studied Upper Jurassic track-bearing unit in South America and has been subject to constant revision since Casamiquela and Fasola (1968) first described two ichnospecies of dinosaurs, *Iguanodonichnus frenki* and *Camptosaurichnus fasolae*, from this locality, identified as ornithopod tracks.

In subsequent works, several authors (Dos Santos et al., 1992; Farlow, 1992; Lockley et al., 1994a; Sarjeant et al., 1998) dismissed the ichnospecies *I. frenki* as a *nomen dubium* and suggested instead a sauropod affinity for this ichnite, on the basis of evidence that a step angle less than 110° is characteristic of Sauropoda, not of Ornithopoda (Dos Santos et al., 1992). They further argued that the apparent bipedalism resulted from an overlap of manus and pes prints (Lockley et al., 1986). These authors based their discussion entirely on the description by Casamiquela and Fasola (1968), not on the actual tracksite.

The second ichnospecies from this locality, *C. fasolae*, is characterized by three pedal digits and half-moon-shaped footprints of the forelimbs. Sarjeant et al. (1998) attributed this ichnospecies to a theropod, because Casamiquela and Fasola (1968) presented low-quality pictures, no captions, and error-filled descriptions. Moreno and Rubilar (1997) and Rubilar et al. (1998) presented a redescription (unknown to Sarjeant et al., 1998) of the original trackways and descriptions of the newly discovered trackways from the same outcrop. The new trackways belong to two different ornithopod footprint morphologies: (1) *C. fasolae,* which averages 21 cm long (range: 17–24 cm) and 15 cm wide (range: 13–17 cm), with pace angulations of 160° and the occasional presence of manus prints and (2) a form with more rounded pedal morphology, 40% wider than *C. fasolae*, that averages 21 cm long (range: 20–23 cm) and 18 cm wide (range: 16–20 cm), with pace angulations of 150° and no preserved manual prints. Furthermore, Moreno and Rubilar (1997) and Rubilar et al. (1998) also described two morphologies of theropod ichnites: (1) medium-sized footprints ranging 22.5–26.5 cm long and 25 cm wide and (2) small-sized footprints measuring 16–20 cm long and 16–18 cm wide, in which the middle digit (digit III) was much larger than the functional laterals (digits II and IV).

Actually, the Termas del Flaco tracksite reveals the presence of a theropod–ornithopod–sauropod ichnocoenosis in a carbonate platform environment (Moreno, 2000; Moreno and Pino, 2002). However, the identity of *I. frenki* and discussions about the validity of its name have not been clarified. Therefore, the main goal of this article is to provide a redescription of the footprints using new data collected in the field that support the sauropod affinity and correct some historical mistakes. We also draw attention to its characteristic morphology, which leads to a discussion about the little information we have about Jurassic sauropods in South America.

2. Systematic paleontology

Family: Sauropoda

Ichnogenus: *Iguanodonichnus* (Casamiquela and Fasola, 1968; Moreno and Benton, this paper).

Type ichnospecies: *Parabrontopodus macintoshi* (Lockley et al., 1994a), Late Jurassic, Morrison Formation.

Iguanodonichnus frenki (Casamiquela and Fasola, 1968; Moreno and Benton, this paper) (see Figs. 2–6).

Etymology: In honor of Dr Samy Frenk (Casamiquela and Fasola, 1968).

Material: Trackways 3, 5, and 8 in situ.

Holotype: Trackway 3 (Figs. 2 and 4), cast of footprint 6, SGPV1151.

Repository: Museo Nacional de Historia Natural, Santiago, Chile.

Locality: 100 m northeast of Termas del Flaco, northern side of Tinguiririca River, Chile (Fig. 1).

Stratigraphic position: Late Jurassic, Tithonian (Biró-Bagóczky, 1984), Baños del Flaco Formation (Klohn, 1960).

Diagnosis of the ichnogenus: Sauropod trackway of medium size (footprint length approximately 50–70 cm), characterized by small space between trackway midline and inside margin of pes tracks. Step angle less than 110°. Pes footprint longer than wide, with long axis rotated outward. Pes claw impression corresponding to digit I is long and narrow and follows

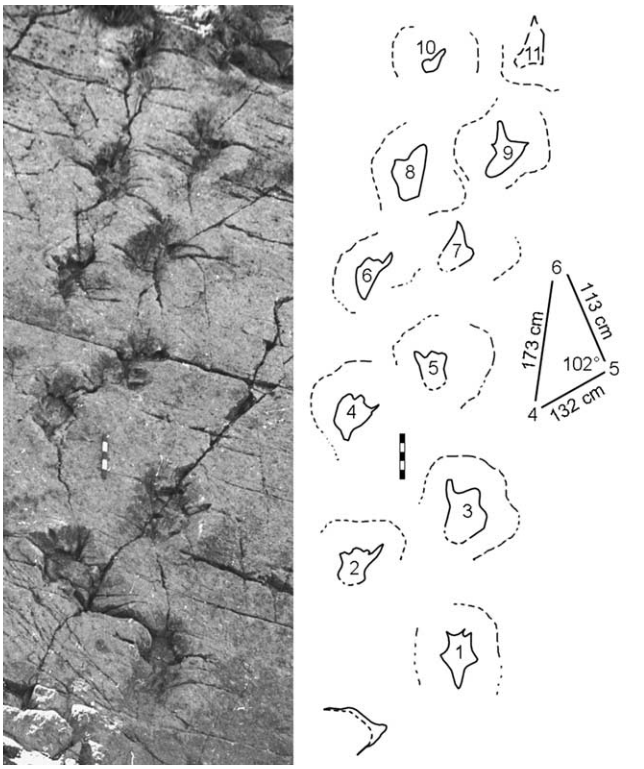

Fig. 2. Photograph and interpretive sketch of trackway number 3, *I. frenki*. Triangular diagram shows the mean distances between prints and the step angle. Scale = 50 cm.

a straight line parallel to the footprint axis. Claw impressions in digits II–IV are broad and much less developed than digit I.

Description: Only pedal impressions are preserved in trackways 3 and 8, averaging 62 cm in length (range: 55–72 cm) and 35 cm in width (range: 25–45 cm). The sagittal axis of the elongated pedal footprint is externally rotated. Step angles average 98°. Claw impressions belonging to digit I are approximately 11 cm long and 5 cm wide and tend to follow a straight line parallel to the footprint axis. Claws on digits II–IV are not prominent. Impressions of pedal claws corresponding to digit I are clearly visible in footprints 2, 3, 5–7, and 9 of trackway 3 (Figs. 2 and 4) and footprints 1, 3– 5, and 9 of trackway 8 (Fig. 3).

Trackway 5 is a convex hyporelief with no claw detail and poor preservation; it describes an open curve with minimal breadth between tracks (Fig. 5). The footprint shape is rather more rounded than in the other trackways. At the mid-trackway (highest point of the curve) point, the footprints are more eroded. It shows alternating large (average 55 cm long, 45 cm wide) and small (average 24 cm long and 35 cm wide) impressions, with a manus/pes heteropody ratio of approximately 0.5. Nevertheless, weathering does not allow a better morphological description and may promote an incorrect idea of the true dimensions, probably by altering the heteropody ratio. The only diagnostic feature is a step angle less than 110°, which allows only tentative assignment to sauropod tracks.

Assuming a foot/hip height ratio in the range of 4–5.9 for sauropods (Alexander, 1976; Thulborn, 1989), the hip of the trackmaker would be approximately 3.1 ± 0.6 m high. This size would lead to a stride length/hip height ratio of 0.5–0.7, which indicates a walking gait (Thulborn and Wade, 1984) at a speed of 0.3–0.4 m/s, as estimated by the equation provided by Alexander (1976).

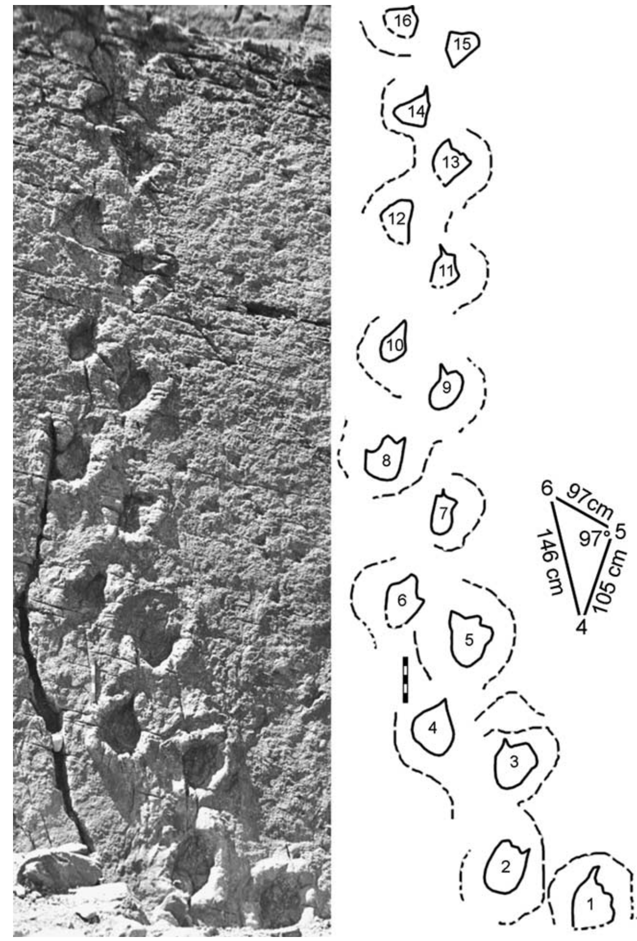

Fig. 3. Photograph and interpretive sketch of trackway number 8, *I. frenki*. Manus and pes print outlines and mean dimensions are shown at top left. Triangular diagram shows the mean distances between prints and the step angle. Scale = 50 cm.

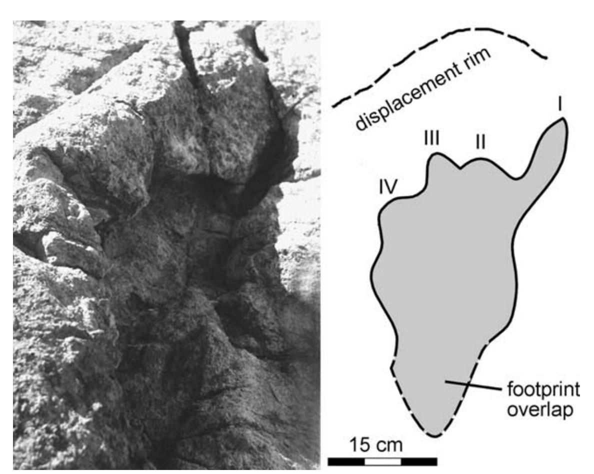

Fig. 4. Photograph and interpretive sketch of footprint number 6 of trackway number 3, *I. frenki*.

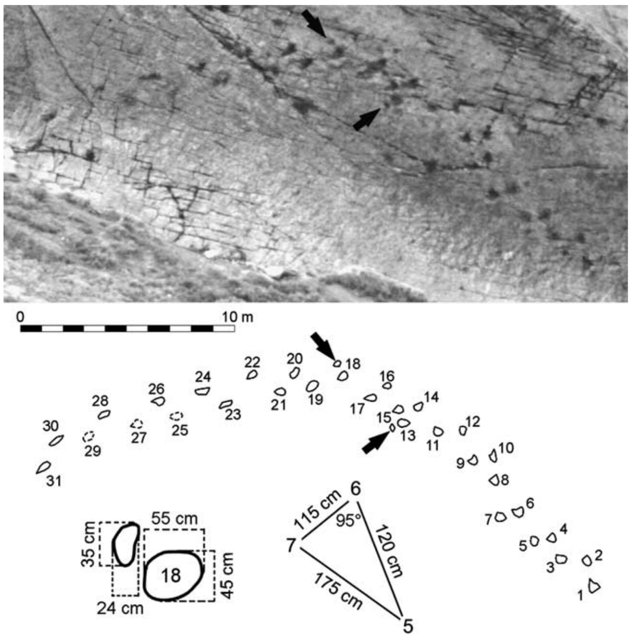

Fig. 5. Photograph and interpretive sketch of trackway number 5, *I. frenki*. Arrows show manus prints (see detailed sketch of trackset 18). Triangular diagram shows the mean distances between prints and the step angle.

3. Discussion

Casamiquela and Fasola (1968) based their diagnosis of *I. frenki* on the following: (1) its large size; (2) its apparently bipedal posture; (3) the then-current belief that ornithopods displayed an external rotation of the sagittal axis of the feet; (4) a step angle of less than 110°, which was identified as characteristic of Ornithopoda; (5) the dating available at the time, which indicated an Early Cretaceous age (Klohn, 1960), during which time large ornithopods such as Iguanodon were present; and (6) a tridactyl shape. These claims are incorrect in several points.

First, footprint size cannot be considered diagnostic because it varies with animal growth.

Second, bipedal posture apparently is observed in sauropod trackways in which sections of both quadrupedal and apparently bipedal walking can be found in a single trackway (e.g. Lockley et al., 1986). This apparent bipedalism in quadrupedal sauropods is caused by an overlap of the small forelimb footprints by the considerably larger hindlimb footprints; accordingly, some footprints of *I. frenki* show an elongated shape that reflects this footprint overlap (Fig. 4), which in turn produces the wide range of 'foot lengths' registered for these trackways.

Third, the external rotation of the footprint axis was identified with the ornithopod *Iguanodon* only as a consequence of erroneous early skeletal mounts that featured tail dragging and artificially outward-spread legs.

Fourth, also as a result of these errors, the step angle was miscalculated. Actually, a step angle of less than 110° is characteristic of Sauropoda (Dos Santos et al., 1992).

Fifth, the alleged Early Cretaceous age was reinterpreted by Biró-Bagóczky (1984) as Tithonian (Late Jurassic), a time during which evidence (footprints or bones) of large ornithopods such as *Iguanodon* is rare worldwide, whereas records of sauropods are more likely to be found in the Jurassic (Lockley et al., 1994b).

Sixth, we believe that the footprints were reported as having a tridactyl shape because of the authors' predisposition to find an iguanodon footprint, not because of an objective description. Being in the field, we were able to verify that not one of the footprints, including newly exposed material, had a tridactyl morphology.

To conclude, the diagnosis of these trackways as belonging to an iguanodontid is hereby discarded, and the genus *Iguanodonichnus* is attributed to basal sauropods, diplodocoids, or basal macronarians, which are all narrow-hipped sauropods (Day et al., 2002).

The main features of *I. frenki* are similar to the ichnogenus *Parabrontopodus*, with the exception of the tendency of the digit I impression to follow a straight line parallel to the footprint axis rather than an outward rotation. The absence of prominent claw impressions in digits II–IV is a morphological difference from *P. macintoshi* (Lockley et al., 1994a), *Brontopodus* from eastern Utah, and *Brontopodus* from Portugal (Meyer et al., 1994) (Fig. 6).

The worldwide fossil record of sauropods shows that the three pedal digits bore claws of decreasing size, and consequently, the absence of those claws has been attributed to the loss of material. As we present here for *I. frenki*, the notorious difference in claw morphology from a well-developed and nearly symmetric first pedal ungual impression through the rudimentary II and III impressions to the absence of a digit IV may explain some apparently incomplete fossil pes remains, such as *P. fariasi*, for which only one ungual has

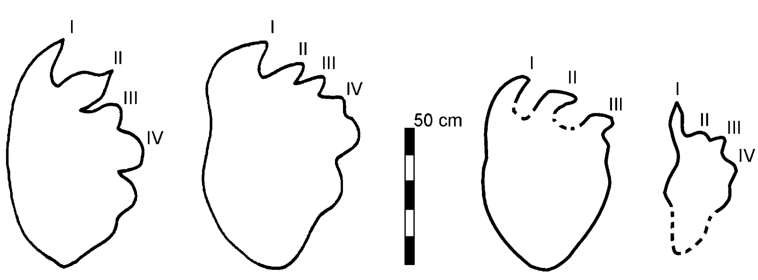

Fig. 6. Differences among *Brontopodus* from eastern Utah, *Brontopodus* from Portugal, *P. macintoshi*, and *I. frenki*; modified from Lockley et al. (1994a).

been recognized in the two specimens with preserved foot bones (Bonaparte, 1986). Our data suggest that the lack of the digit II–IV unguals may reflect foot morphology, not a particular preservation condition.

The ichnocoenosis of the Baños del Flaco Formation agrees with the Early–Middle Jurassic fauna described in Argentina and Brazil, which is composed of a reduced variety of sauropods (only cetiosaurids), small theropods, and small ornithopods. This description contrasts with the abundance and diversity of large sauropods and theropods found in Laurasia and suggests that such diversity may have appeared later on the South American continent, possibly after the late Early Cretaceous, from which the first diplodocids and titanosaurids are recorded (Calvo and Salgado, 1995; Salgado and Azpilicueta, 2000). According to these data, the faunal interactions appear to have occurred in a different way in South America. Moreover, no switch from sauropod to ornithopod as a dominant herbivore happened in the Jurassic–Cretaceous transition but rather likely occurred later in the Cretaceous.

Acknowledgements

The authors thank the Jurassic Foundation for funding and the following people for support during fieldwork: members of the Sociedad Paleontologica de Chile (SPACH), with special considerations to Alexander Vargas and David Rubilar; Dr Mario Pino and Robert Brümmer from the Instituto de Geociencias of the Universidad Austral de Chile; Dr Martin Lockley and Dr Gierard Gierlinski for reviewing and improving the manuscript; Dr Matthew Carrano for his helpful suggestions; and all those who collaborated disinterestedly with this work, including the villagers from Termas del Flaco.

References

Alexander, R., 1976. Estimates speed of dinosaurs. Nature 261, 129–130.

Bakker, R.T., 1971. The ecology of the brontosaurs. Nature 229, 172–174.

Biró-Bagóczky, L., 1984. New contributions to the paleontology and stratigraphy of some Tithonian-Neocomian outcrops on the Chilean part of the Andean Range between 33°45′ and 35° Lat. S. In: Westermann, G.E.G. (Ed.), Circum-Pacific Jurassic Report, Special Paper 3. International Correlation Program, Report No 2, Project 171, pp. 1–171.

Bonaparte, J.F., 1979. Dinosaurs: a jurassic assemblage from Patagonia. Science 205, 1377–1379.

Bonaparte, J.F., 1986. Les dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du jurassique moyen de Cerro Cóndor (Chubut, Argentina). Annales de Paléontologie 72, 247–289.

Calvo, J.O., Salgado, L., 1995. *Rebbachisaurus tessonei* sp. nov. a new sauropod from the Albian-Cenomanian; new evidence on the origin of the Diplodocidae. Gaia 11, 13–33.

Casamiquela, R.M., Fasola, A., 1968. Sobre pisadas de dinosaurios del Cretácico Inferior de Colchagua (Chile), vol. 30. Departamento de Geología, Universidad de Chile, pp. 1–24.

Day, J.J., Upchurch, P., Norman, D.B., Gale, A.S., Powell, H.P., 2002. Sauropod trackways, evolution and behavior. Nature 296, 1659.

Dos Santos, V.F., Lockley, G.M., Moratalla, J., Galopim de Carvalho, A.M., 1992. The longest dinosaur trackway in the world? Interpretations of Cretaceous footprints from Carenque, near Lisbon, Portugal. Gaia 5, 18–27.

Farlow, J.O., 1992. Sauropod tracks and trackmakers: integrating the ichnological and skeletal records. Zubia 10, 89–138.

Klohn, C., 1960. Geología de la Cordillera de los Andes de Chile Central, Provincia de Santiago, O'Higgins, Colchagua y Curicó. Instituto de Investigaciones Geológicas, Boletín 8, 1–95.

Leonardi, G., 1989. Inventory and statistics of South American dinosaurian ichnofauna and its paleobiological interpretation. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Track and Traces. Cambridge University Press, Cambridge, pp. 165–178.

Lockley, M.G., Houck, K.J., Prince, N.K., 1986. North America's largest dinosaur trackway site: implications for Morrison Formation paleoecology. Bulletin of the Geological Society of America 97, 1163–1176.

Lockley, M.G., Farlow, J.O., Meyer, C.A., 1994a. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. Gaia 10, 135–145.

Lockley, M.G., Meyer, C.A., Hunt, A.P., Lucas, S.G., 1994b. The distribution of tracks and trackmakers. Gaia 10, 233–248.

Meyer, C.A., Lockley, M.G., Robinson, J.W., Santos, V.F., 1994. A comparison of well-preserved sauropod tracks from the late jurassic of Portugal and the western United States: evidence and implications. Gaia 10, 57–64.

Moreno, K., 2000. Huellas de dinosaurios (Theropoda–Ornitopoda–Sauropoda) de la Formación Baños del Flaco, VI Región, Chile: paleoambiente y paleoetología. HD dissertation, Universidad Austral de Chile, Instituto de Geociencias, Valdivia, 50 pp.

Moreno, K., Pino, M., 2002. Huellas de dinosaurios (Theropoda–Ornitopoda–Sauropoda) de la Formación Baños del Flaco, VI Región, Chile: paleoambiente y paleoetología. Revista Geológica de Chile 29, 191–206.

Moreno, K., Rubilar, D., 1997. Presencia de nuevas pistas de dinosaurio (Theropoda-Ornithopoda) en la Formación Baños del Flaco, Provincia de Colchagua, VI Región Chile; Actas VIII Congreso Iberoamericano de Biodiversidad y Zoología de Vertebrados, Concepción.

Rich, T.H., Vickers-Rich, P., Gimenez, O., Cuneo, R., Puerta, P., Vacca, P., 1999. A new sauropod dinosaur from Chubut Province, Argentina. In: Tomida, Y., Rich, T.H., Vickers-Rich, P. (Eds.), Proceedings of the Second Symposium, Tokio National Science Museum Monographs Number 15, pp. 61–84.

Rubilar, D., Moreno, K., Vargas, A., 1998. A revision of dinosaur trackways (Theropoda–Sauropoda–Ornithopoda) at baños del Flaco Formation, VI Región, Chile. Ameghiniana 36 (1), 80.

Salgado, L., Azpilicueta, C., 2000. Un nuevo saltasaurino (Sauropoda, Titanosauridae) de la Provincia de Río Negro (Formación Allen, Cretácico Superior), Patagonia, Argentina. Ameghiniana 37 (3), 259–264.

Salinas, P., Marshall, L., Sepúlveda, P., 1991. Vertebrados continentales del Paleozoico y Mesozoico de Chile. VI Congreso Geológico Chileno, Antofagasta, vol. 1, pp. 310–313.

Sarjeant, W.A.S., Delair, J.B., Lockley, M.G., 1998. The footprints of *Iguanodon*: a history and taxonomic study. Ichnos 6 (3), 183–202.

Thulborn, R.A., 1989. The gaits of dinosaurs. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp. 39–50.

Thulborn, R.A., Wade, M., 1984. Dinosaur trackways in the Winton Formation (Mid-Cretaceous) of Queensland. Memoirs of the Queensland Museum 21 (2), 413–517.

Weishampel, D.B., Norman, D.B., 1989. Vertebrate herbivory in the Mesozoic; jaws, plants, and evolutionary metrics. Geological Society of America Special Paper 238, 87–100.