New sauropod trackways from the Middle Jurassic of Portugal

VANDA F. SANTOS, JOSÉ J. MORATALLA, and RAFAEL ROYO-TORRES

Santos, V.F., Moratalla, J.J., and Royo-Torres, R. 2009. New sauropod trackways from the Middle Jurassic of Portugal. *Acta Palaeontologica Polonica* 54 (3): 409–422. DOI: 10.4202/app.2008.0049.

The Galinha tracksite reveals a sequence of Bajocian–Bathonian limestones belonging to the Serra de Aire Formation (West-Central Portugal) and is one of the few sites in the world where Middle Jurassic sauropod dinosaur tracks can be found. This tracksite is characterised by the presence of long, wide gauge sauropod trackways, the Middle Jurassic age of which suggests these dinosaurs were more widely distributed over time than previously thought. Two trackways contain unique pes and manus prints with morphologies that allow a new sauropod ichnotaxon to be described: *Polyonyx gomesi* igen. et isp. nov. On the basis of different manus/pes prints and trackway features, the proposal is made to subdivide Sauropodomorpha ichno-morphotypes into five groups: *Tetrasauropus*-like, *Otozoum*-like, *Breviparopus*/*Parabrontopodus*-like; *Brontopodus*-like, and *Polyonyx*-like. *Polyonyx gomesi* igen. et isp. nov. is thought to represent a non-neosauropod eusauropod, with a well developed manus digit I. The posterior orientation of this digit print suggests they were made by a eusauropod dinosaur with a posteriorly rotated pollex. The manus print morphologies observed in two trackways suggest a stage of manus structure intermediate between the primitive non-tubular sauropod manus and the tubular metacarpal arrangement characteristic of more derived sauropods. The low heteropody (manus:pes area ratio 1:2) of the trackway renders it possible they could have been made by eusauropods such as *Turiasaurus riodevensis*, which has a similar manus:pes area ratio. The *Polyonyx* igen. nov. trackway was made by non-neosauropod eusauropod, and suggests that wide gauge sauropod trackways were not exclusively made by Titanosauriformes.

Key words: Dinosauria, Sauropoda, trackways, ichno-morphotypes, Middle Jurassic, Portugal.

Vanda Faria dos Santos [vsantos@museus.ul.pt], Museu Nacional de História Natural da Universidade de Lisboa, R. Escola Politécnica, 58, 1250-102 Lisbon, Portugal; CGUC – Centro de Geofísica da Universidade de Coimbra (FCT - MCTES), Av. Dr. Dias da Silva, 3000-134 Coimbra, Portugal;
J. Joaquín Moratalla [j.moratalla@igme.es], Instituto Geológico y Minero de España, C/ Rios Rosas, 23, 28003 Madrid, Spain;
Rafael Royo-Torres [royo@dinopolis.com], Fundación Conjunto Paleontológico de Teruel-Dinópolis, Av. Sagunto s/n, 44002 Teruel, Spain.

Received 16 July 2008, accepted 26 March 2009, available online 16 July 2009.

Introduction

The Middle Jurassic Galinha tracksite is located on the eastern side of Serra de Aire in the municipal area of Bairro, 10 km from Fátima, within the Serra de Aire and Candeeiros Natural Park (Fig. 1). It contains very well-preserved Middle Jurassic sauropod manus and pes prints, in two of the longest sauropod trackways on record (two continuous sequences measuring 142 and 147 m). This tracksite was briefly described by Santos et al. (1994). Since then, a second Middle Jurassic tracksite has been found at Vale de Meios (Santarém), 80 km north of Lisbon. At this new site dozens of theropod trackways made by different sized trackmakers were discovered (Santos et al. 2000; Santos 2003; Santos and Rodrigues 2003), although no sauropod tracks have been identified there until recently. Santos et al. (2008) reported the existence of at least two sauropod trackways.

The sauropod trackways at the Galinha tracksite are of the wide gauge type (Santos et al. 1994: figs. 2, 3). Before this discovery was made, wide gauge sauropod trackways were not considered so widely distributed over time (Lockley et al. 1994b; Santos et al. 1994). The trackways contain exceptionally large manus prints in relation to the pes prints and, although manus claw traces have only very rarely been recorded in the literature, at the Galinha tracksite there are manus and pes prints with large claw impressions. These manus and pes prints present morphological features that distinguish them from the currently known sauropod manus and pes prints. Lockley and Meyer (2000) suggested trackways from the Galinha tracksite are distinctive enough to be recognised as a new ichnospecies. Although wide gauge sauropod trackways have been assigned to *Brontopodus* isp., those of the Galinha tracksite cannot be included in this ichnogenus due to their different manus print morphology. This paper provides a description of these sauropod tracks and a new ichnogenus and ichnospecies are formally proposed. The morphologies of the sauropod manus prints of this taxon yield information about the arrangement of the metacarpals

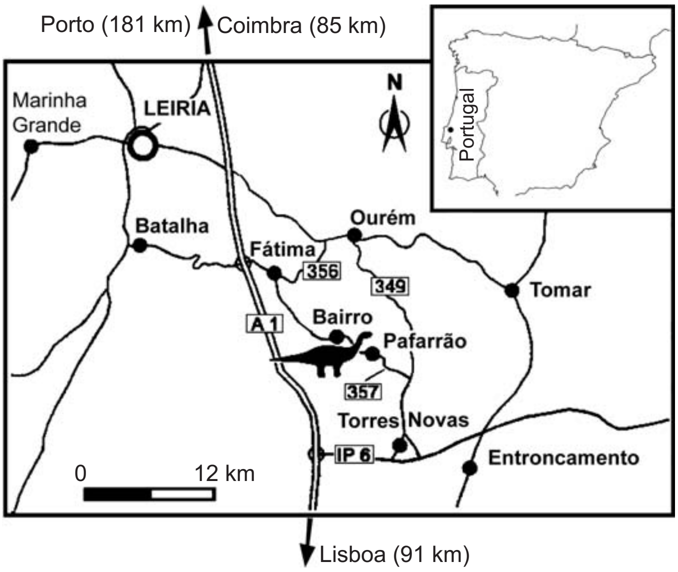

Fig. 1. Location map of the Galinha dinosaur tracksite (Bairro, Serra de Aire, West-Central Portugal). Modified from Santos et al. 1997.

and allow inferences about sauropod manus osteological structure. Further, the manus prints of the Galinha tracksite, with a long digit I appearing consistently throughout the length of two wide gauge sauropod trackways, suggest this trackway type is different from the wide gauge trackways attributed to titanosaurs; in the latter group the manus digit/claw I is absent (Salgado et al. 1997).

Institutional abbreviation.—MNDPDSA, Monumento Natural das Pegadas de Dinossáurio da Serra de Aire (Serra de Aire Dinosaur Tracks Natural Monument), Portugal.

Other abbreviations.—Dga, glenoacetabular distance; Dmp, manus-pes distance; h, hip high; λ, stride length; Pl, pes print length; Pw, pes print width; Wit and Wot, inner and outer trackway width.

Geological and stratigraphic setting

The main track level of the Galinha tracksite is a single bedding surface of about 40,000 m^2 forming the floor of an abandoned limestone quarry. A second faint trackway of probable dinosaur tracks occurs on a small, exposed surface 4 m above this level. Azerêdo et al. (1995) studied a 14 m-thick sequence of micritic limestone (Fig. 2) at the site, beginning 5.2 m below the main track level and ending at the top of the highest level observed. Based on microfacies and palaeoenvironmental studies, these authors suggested that this sequence was deposited in lacustrine, paralic and very shallow, restricted marine conditions. Some evidence from the main track level (e.g., nerineid gastropods, marine ostracods, and echinoderm fragments) suggests it was associated with shallow marine conditions (a confined, shallow, marginal marine palaeoenvironment). This palaeoenvironment developed in the innermost part of a prograding carbonate ramp, the general depositional system operating in the Lusitanian Basin at that time (Azerêdo 1993). The studied sequence of micritic limestone at the Galinha tracksite has no good stratigraphic bio-markers, however, the lithostratigraphic framework of

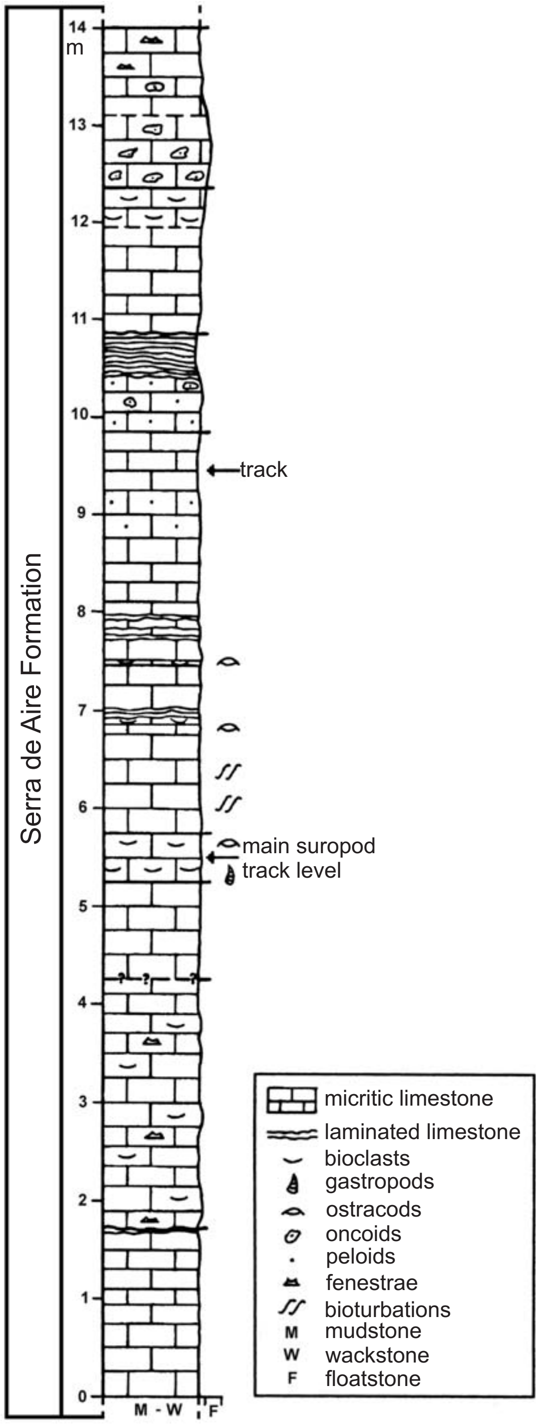

Fig. 2. Sequence of micritic limestone beginning 5 meters below the main sauropod track level of the Galinha tracksite from Serra de Aire Formation, Bajocian–Bathonian boundary (Bairro, Serra de Aire, West-Central Portugal). Modified from Azerêdo et al. (1995).

the region and its microfauna suggest that these levels belong to the Serra de Aire Formation, close to the Bajocian–Bathonian boundary (Azerêdo 1993; Azerêdo et al. 1995; Manuppella et al. 2000).

Systematic ichnology

The Galinha trackways are different from all other known sauropod trackways, and a new ichnogenus and ichnospecies are proposed based on their distinctive characteristics.

Ichnogenus *Polyonyx* nov.

Etymology: *Polyonyx* means "evidence of many claw marks" from "poly" (Greek for several) and "onyx" (Greek for claw).

Type ichnospecies: *Polyonyx gomesi* isp. nov.

Diagnosis.—As for the type, and only known ichnospecies.

Polyonyx gomesi isp. nov.

Figs. 3–5.

Etymology: In memory of Jacinto Pedro Gomes (1844–1916), curator of the Museu Mineralógico e Geológico da Escola Politécnica (Lisbon, Portugal), the first naturalist to study (in 1884) dinosaur tracks in Portugal (Gomes 1916).

Holotype: A trackway in situ (142 m long with 94 consecutive manus-pes print sets; reference G5) at the Galinha tracksite classified as a Natural Monument—Monumento Natural das Pegadas de Dinossáurio da Serra de Aire (Serra de Aire Dinosaur Tracks Natural Monument), Portugal. In MNDPDSA centre there is a cast with a sequence of a left manus print, two pairs of manus-pes prints and a right pes print (reference MNDPDSA-G5).

Type horizon: Serra de Aire Formation, close to the Bajocian–Bathonian boundary, Middle Jurassic (Azerêdo 1993; Azerêdo et al. 1995).

Type locality: Galinha tracksite, Municipal area of Bairro, Serra de Aire, West-Central Portugal.

Diagnosis.—Wide gauge sauropod trackway revealing low heteropody (manus-pes area ratio 1:2) and two autapomorphies: (1) asymmetric manus prints with large digit I marks oriented in a medial direction with a large, posteriorly oriented, triangular claw mark, and impressions of digits II, III, IV and V; (2) pes prints with four claw marks: claws I–II with an anterior orientation, and III–IV laterally oriented. Manus digits II–V show a slightly bent arrangement.

Description.—This trackway is a wide gauge sauropod trackway with an inner trackway width 1.2 times the footprint width (Wit/Pw; see Tables 1 and 2, Fig. 5). The manus prints are wider than long with a rounded lateral edge (digit mark V), a large digit I mark oriented in a medial direction and with a large, posteriorly oriented, triangular claw mark I, and impressions of digits II–IV (Fig. 4A). Other manus prints of trackway G5 show digit II–IV marks at the anterior margin. The pes prints are longer than wide, oval shaped, and have four claw marks (claws I–II with an anterior orientation, and III–IV laterally oriented). The ichnospecies shows low heteropody (the pes area is about twice the manus print area). Occasionally, the manus print centres are closer to the trackway midline than the pes print centres. Both the manus and pes prints are rotated outward relative to the trackway midline. Considering the direction of the manus and pes print width in relation to trackway midline, the rotation values for the manus prints are vary from 25° to 50° and the pes print values from 25° to 42°. With respect to the pes print length, the outer trackway width is 2.7 times wider (Wot/Pl, Table 2), the manus-pes distance is 0.3–0.6 times longer (Dmp/Pl, Table 2), and the stride length is 3.4 times longer (λ/Pl, Table 2). The glenoacetabular distance is three times the pes print length (Dga/Pl, Table 2) and 1.1 times the outer trackway width (Dga/Wot, Table 2). The pace angulation value is about 95°.

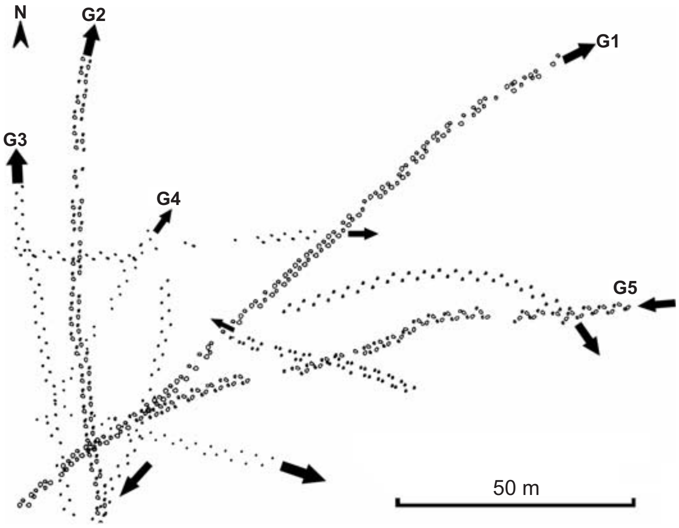

Fig. 3. Long sauropod trackways at the Galinha dinosaur tracksite (Bairro, Serra de Aire, West-Central Portugal). Trackway G1 is 147 m long and trackway G5 is 142 m long. Modified from Santos (2003).

Stratigraphic and geographic range.—Bajocian-Bathonian of West-Central Portugal.

Polyonyx isp.

Figs. 6, 7.

Material.—One trackway (147 m long) with 97 consecutive manus-pes print sets (reference G1).

Stratigraphic and geographic range.—As for the type ichnospecies.

Description of the Galinha trackways

At least 20 sauropod trackways, including several that show excellent preservation of both the manus and pes prints, and others that are manus-only sequences, are present at level 1 of the Galinha tracksite. The ten best-preserved trackways were studied and illustrated (Fig. 3) and individual tracks traced using transparent acetate overlays (Santos 2003). The space between the pes print medial margins shows them all to be wide gauge trackways.

DOI: 10.4202/app.2008.0049

Table 1. Characteristic values of sauropod tracks and trackways of Galinha tracksite (Bairro, Serra de Aire, West-Central Portugal). L, length; W, width; h, hip high; λ, stride length; Dga, glenoacetabular distance; Wot, Wit, outer and inner trackway width; Dmp, manus-pes distance. All values in centimetres. (*), obtained through manus prints; (**), estimated value.

Trackway	L × W		h	λ	λ/h	Dga	Wot	Wit	Dmp	Trackmaker speed (km/h)
	PES	MANUS								
G-1	95 × 70	40 × 75	380	315	0.8	300	215	60	56	4.0
G-2	80 × 65	42 × 60	320	320	1.0	270	180	40	40	5.1
G-3	–	27 × 45	–	300*	–	–	180	90**	–	–
G-4	–	20 × 34	–	380*	–	–	150	70**	–	–
G-5	90 × 60	38 × 58	360	310	0.9	270	240	70	25–50	4.1

Table 2. Characteristic values of sauropod tracks and trackways at Galinha tracksite (Bairro, Serra de Aire, West-Central Portugal) and *Brontopodus birdi* (modified from Farlow et al. 1989). Wot and Wit, outer and inner trackway width; Pl and Pw, pes print length; pes print width; Dmp, manus-pes distance; λ, stride length; Dga, glenoacetabular distance.

Trackway	Wot/Pl	Wit/Pw	Dmp/Pl	λ/Pl	Dga/Pl	Dga/Wot
Brontopodus birdi	1–1.5	0.8	0.5–1.2	2–5	3–4	1.3
G-1	2.3	0.9	0.6	3.3	3.2	1.4
G-2	2.2	0.6	0.5	4.0	3.3	1.5
G-5	2.7	1.2	0.3–0.6	3.4	3.0	1.1

Trackway G1: *Polyonyx* isp.—Trackway G1 is a 147 m long wide gauge sauropod trackway (Fig. 6) with 97 consecutive manus-pes sets with an inner trackway width of about 60 cm (Fig. 6A, Table 1). G1 contains oval pes prints and crescent shaped manus prints, sometimes overlapping but in general with a manus-pes distance of 56 cm (Table 1). The ratio of manus-pes distance/pes print length is 0.6 (Table 2). Both the manus and pes prints are rotated strongly outward relative to the trackway midline. The outward rotation values for the manus prints vary from 50° to 58°; the values for the pes prints vary between 23° and 35°. Bonnan (2003: 607) refers to a "supination" angle of about 55° for these manus prints and considered them to be "the most supinated tracks yet reported". Sometimes, the manus print centres are closer to the trackway midline than the pes print (Fig. 6A). The manus prints are wider than long (40 cm long by 75 cm wide, Table 1) and have a slightly bent metacarpal arch. They have rounded lateral and medial margins and a long and narrow impression (20 cm long by 6 cm wide) projecting from the centre of the track's rear margin and oriented in a posteromedial direction (Fig. 6B). The well-preserved oval-shaped pes prints which have no claw marks (Figs. 6A, 7) are longer than wide—95 cm long by 70 cm wide (Table 1). In general, both the manus and pes prints are 2 cm deep, surrounded by a rim (Fig. 7). The best-preserved pes impressions show two depressed areas separated by a rim perpendicular to the long axis of the pes (Figs. 6A, 7). This rim represents an anterior area where the foot pressed the ground at the last moment of the step cycle. The pes area is about twice the manus print area, and the pace angulation is about 113°.

Tables 1 and 2 provide the stride length and other characteristic values of the trackways and trackmakers. With respect to the pes print length (Pl), the stride length is 3.3 times longer and the glenoacetabular length is 3.2 times longer (λ/Pl and Dga/Pl, Table 2). The glenoacetabular distance is 1.4 times the outer trackway width (Dga/Wot, Table 2). The outer trackway width is 2.3 times the pes print length, and the inner trackway width is 0.9 times the pes print width (Wot/Pl and Wit/Pw, Table 2).

Trackway G2: no ichnotaxonomic assignment.—Trackway G2 is a 110 m-long wide gauge sauropod trackway with an inner trackway width of about 40 cm (Table 1), showing oval pes prints and crescent-shaped manus prints rotated outwards relative to the trackway midline (Fig. 3). The mean manus-pes distance is about 40 cm (Table 1) but sometimes the pes prints overlap the manus prints. The manus-pes distance/pes print length ratio is 0.5 (Dmp/Pl, Table 2). The manus prints are crescent shaped and wider than long (42 cm long by 60 cm wide, Table 1) with a slightly bent metacarpal arch. The oval shaped pes prints, none of which have claw marks, are longer than broad (80 cm long by 65 cm wide, Table 1). The manus:pes area ratio is 1:2 (low heteropody) and the pace angulation is about 112°.

With respect to the pes print length (Pl), the stride length is four times longer and the glenoacetabular length 3.3 times longer (λ/Pl and Dga/Pl, Table 2). The glenoacetabular distance is 1.5 times the outer trackway width (Dga/Wot, Table 2). The outer trackway width is 2.2 times the pes print length, and the inner trackway width is 0.6 times the pes print width (Wot/Pl and Wit/Pw, Table 2).

Trackways G3, G4: no ichnotaxonomic assignment.—Several wide gauge trackways are formed either by crescent-shaped manus impressions alone (Fig. 3) or dominated by manus prints (e.g., trackways G3 and G4, Table 1) with faint traces of pes toe impressions (Santos et al. 1994).

Trackway G5: *Polyonyx gomesi* holotype.—Trackway G5 is a sauropod trackway with 94 consecutive manus-pes sets extending over a distance of 142 m (Figs. 3, 5). It shows oval

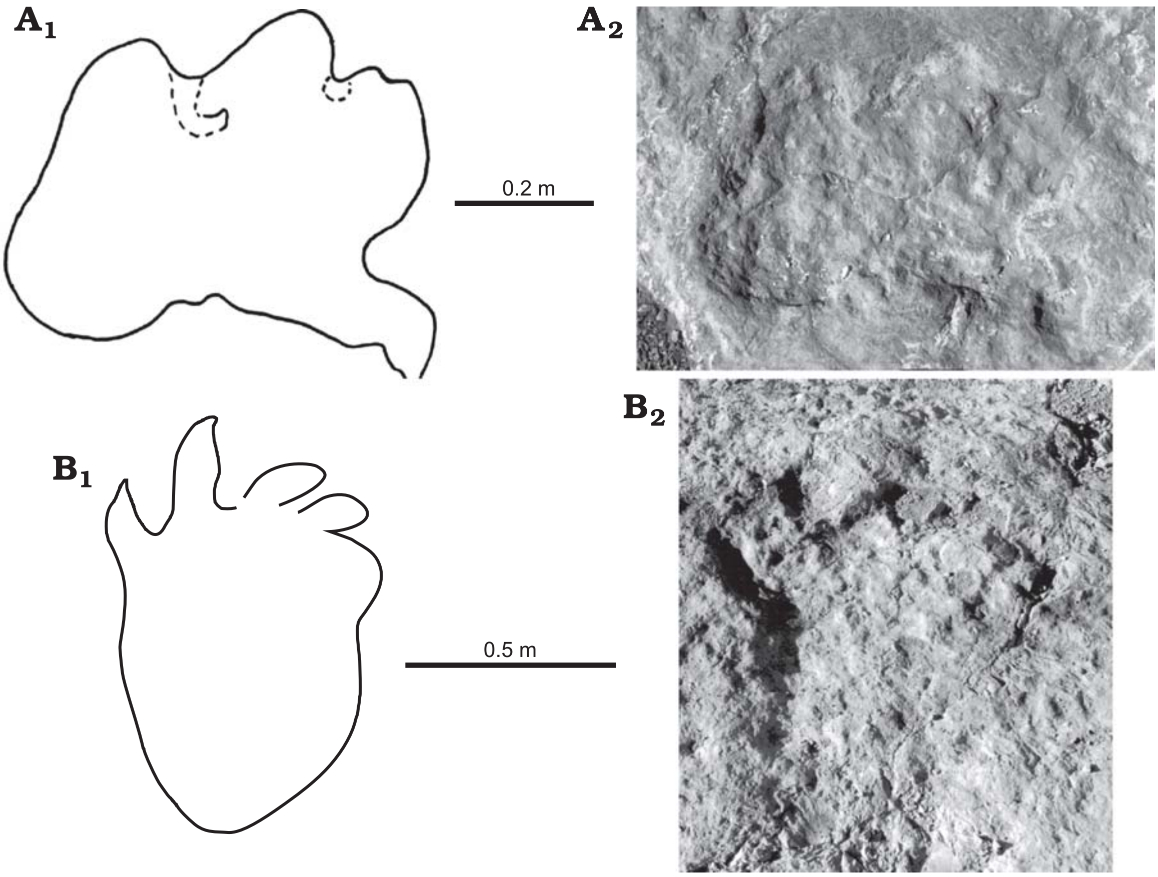

Fig. 4. *Polyonyx gomesi* igen. et isp. nov., sauropod manus and pes prints from trackway G5 at the Galinha dinosaur tracksite (Bairro, Serra de Aire, West-Central Portugal). **A**. Outline (A_1) and photograph (A_2) of a left manus print. **B**. Outline (B_1) and photograph (B_2) of a right pes print. Modified from Santos (2003).

pes prints and crescent shaped manus prints. The inner trackway width (Wit) is about 70 cm (Table 1). Sometimes the pes prints overlap the manus prints, but in general the manus-pes distance ranges from 25 to 50 cm (Table 1). The manus-pes distance/pes print length ratio is 0.3–0.6 (Dmp/Pl; Table 2). Both the manus and pes prints are outwardly rotated relative to the trackway midline. The outward rotation values for the manus prints vary from 25° to 50°; values for the pes prints are 25–42°. Sometimes the manus print centres are closer to the trackway midline than the pes print centres (Fig. 5). The manus prints are wider than long (38 cm long by 58 cm wide, Table 1) and are asymmetrical with a large digit I impression oriented in a medial direction, a large, posteriorly oriented, triangular claw I mark, and impressions of digits II–V with a slightly bent arrangement (Fig. 4A). Therefore, the manus impressions reveal a large claw I mark as well as impressions of digits II–V arranged in a slightly bent metacarpal arch. The well-preserved pes prints are longer than broad and oval shaped (90 cm long by 60 cm wide, Table 1), and show four claw marks: claws I and II show an anterior orientation and claws III and IV are laterally oriented (Fig. 4B). The best-preserved manus and pes prints are 2 cm deep and show a mud rim. Low heteropody (the manus:pes area ratio is 1:2) is another distinctive feature. The pace angulation is about 95°. Tables 1 and 2 show the stride lengths and other values of the G5 tracks and trackway. In relation to the pes print length, the stride length is 3.4 times longer and the glenoacetabular distance is 3 times longer (λ/Pl and Dga/Pl, Table 2). The estimated glenoacetabular distance is 1.1 times the outer trackway width (Dga/Wot, Table 2). The outer trackway width is 2.7 times the pes print length, and the inner trackway width is 1.2 times the pes print width (Wot/Pl and Wit/Pw, Table 2).

Comparison of the Galinha trackways with the general sauropod track record

Sauropod trackways from Galinha tracksite were compared with tracks from different places and ages. Few Lower Jurassic sauropod trackways are known. Narrow-gauge trackways similar to *Parabrontopodus* isp. with relatively small pes prints were reported by Gierliński (1997) from central Poland and by Leonardi and Mietto (2000) from Lavini di Marco (Italy). However, these trackways are clearly distinct from the much larger Portuguese Middle Jurassic wide gauge sauropod trackways, showing a smaller inner trackway width, high

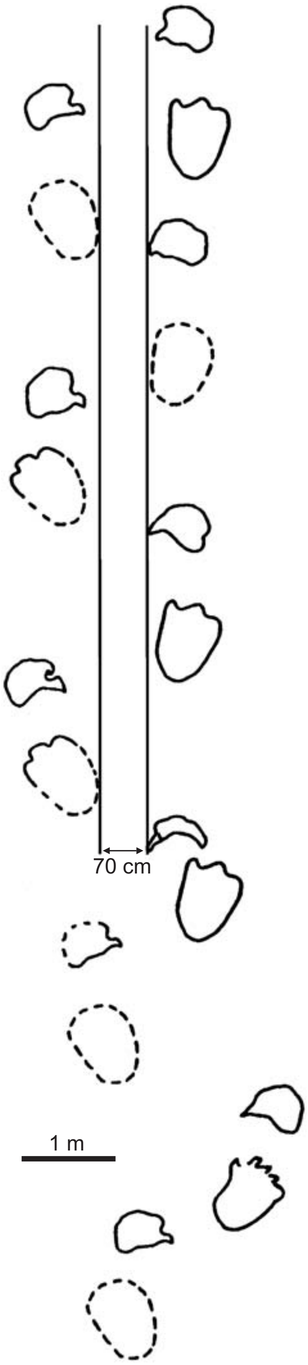

Fig. 5. Segment of G5 sauropod trackway at the Galinha dinosaur tracksite (Bairro, Serra de Aire, West-Central Portugal): *Polyonyx gomesi* igen. et isp. nov. Modified from Santos (2003).

heteropody, and crescent-shaped manus prints without digit/claw marks.

The Middle Jurassic sauropod track record is also poorly known. Narrow- and wide gauge sauropod trackways have been reported from the Middle Jurassic of Morocco (Dutuit and Ouazzou 1980; Ishigaki 1988, 1989); these authors report unnamed wide gauge trackways showing footprints with four digit impressions and manus prints with no digit marks. They also report narrow-gauge trackways such as *Parabrontopodus* isp. These Moroccan manus and pes print morphologies (Fig. 8H, J), and the size of the manus related to the pes prints, are different from the Portuguese Middle Jurassic sauropod track record (Fig. 8A, B, K). *Breviparopus taghbaloutensis* Dutuit and Ouazzou, 1980 from the Middle Jurassic of Morocco is represented by narrow-gauge sauropod trackway with anteriorly oriented pes claw marks (Fig. 8J), crescent-shaped manus prints without digit marks, and high heteropody (Ishigaki 1989). The inner trackway width, pes claw mark orientation and manus print shape of *B. taghbaloutensis* are similar to those of *Parabrontopodus* isp.

Romano et al. (1999) reported sauropod prints from the Middle Jurassic of Yorkshire, England. Some of the oval pes prints described show digit prints rotated outwards relative to the trackway midline that resemble those of *Brontopodus*. The manus prints are crescent-shaped with no digit impressions. These British prints differ from the Portuguese prints in manus and pes morphology and heteropody (Romano and Whyte 2003: 201). These have been reinterpreted as stegosaur tracks by Whyte and Romano (2001).

Day et al. (2002) reported long sauropod trackways from the Middle Jurassic of Oxford, England. Some of these trackways are wide gauge (Day et al. 2002, VFS, personal observation 2003) and are similar to the Portuguese trackways, but they do not show such low heteropody. Further, the manus prints show no digit/claw marks. Narrow-gauge trackways, very similar to *Parabrontopodus* isp., were also reported from the Oxford tracksite. However, these are quite different from the wide gauge sauropod trackways at the Galinha site.

Upper Jurassic sauropod trackways have been found at seven tracksites in Portugal but only two trackways reveal claw traces. At Lagosteiros Bay (Cabo Espichel) there are wide gauge trackways that show pes prints with four laterally rotated claw marks (Fig. 8M) and small crescent shaped manus prints without digit impressions (Meyer et al. 1994). These tracks were attributed to *Brontopodus* isp. (Meyer et al. 1994) based on their inner trackway width, their manus and pes print morphologies, and heteropody. However, they differ from trackways G1 and G5 at the Galinha tracksite with respect to their heteropody and manus/pes print morphologies (Fig. 8). A quadrupedal trackway with one very slight pes impression and seven crescent shaped manus prints with five prominent claw marks has been described for the Upper Jurassic of the Sesimbra region (Santos et al. 1995; Santos 2003). In this trackway, the manus claw I mark shows a medial orientation (Fig. 8C). The manus print morphology is quite different to all other known sauropod manus print morphologies (Fig. 8).

Lires (2000) reported narrow and wide gauge sauropod trackways from the Upper Jurassic of Asturias (northern Spain) and recognised three different pes print morphotypes. One of these is similar to *Brontopodus* isp. pes prints (Fig. 8N) and therefore, different to the pes prints of trackways G1 and G5 at the Galinha tracksite. *Gigantosauropous asturiensis* from the Late Jurassic of Spain (Mensink and Mertmann 1984; Lockley et al. 1994a, 2007) is represented by a narrow-gauge trackway. However, there are no morphological

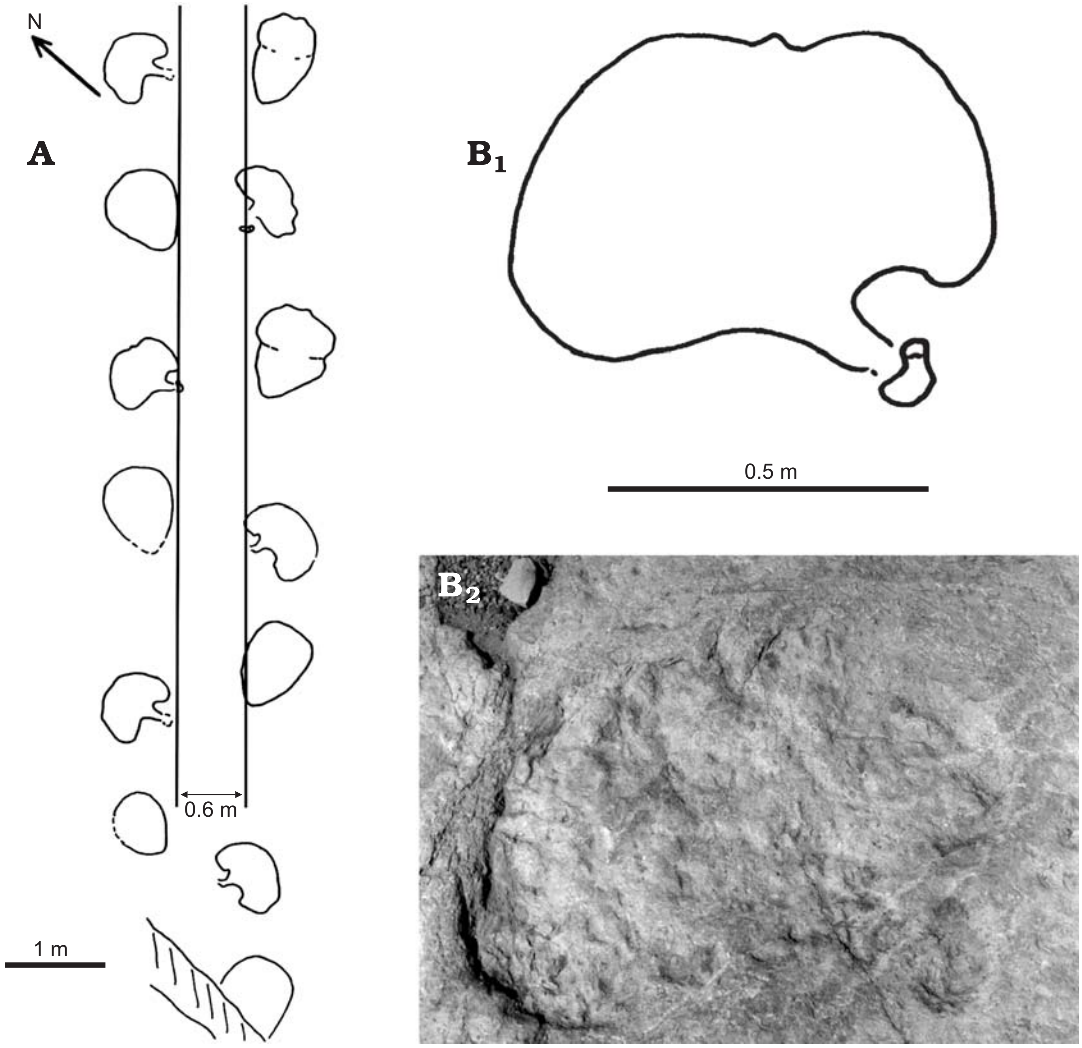

Fig. 6. *Polyonyx* isp., sauropod trackway G1 at the Galinha dinosaur tracksite (Bairro, Serra de Aire, West-Central Portugal). **A**. Trackway segment. **B**. Outline (B_1) and photograph (B_2) of left manus print with a slender and long impression in the centre of the track's rear margin oriented in a postero-medial direction. Modified from Santos (2003).

features that could allow a comparison with the sauropod trackways at the Galinha tracksite.

Lower Cretaceous sauropod trackways are also quite different from the Portuguese Middle Jurassic sauropod trackways at the Galinha tracksite in terms of their manus and pes print morphologies. Dalla Vecchia (1999) reported a manus print from the Upper Hauterivian–Lower Barremian of north-eastern Italy, showing a relatively well developed claw on digit I (Fig. 8D). This manus print reminds one of *Brontopodus birdi* Farlow, Pittman, and Hawthorne, 1989 manus print morphology. *Titanosaurimanus nana* Dalla Vecchia and Tarlao, 2000 from the Lower Cretaceous of Croatia shows small size U-shape manus prints with distinctive digit impressions (Fig. 8E), quite different from the manus print morphologies observed at the Galinha tracksite (Fig. 8A, B).

The Middle Jurassic sauropod trackways at the Galinha tracksite are clearly wide gauge with inner trackway width values even greater than those of *B. birdi* from the Lower Cretaceous of the USA (Table 2). Trackway G2 from the Galinha tracksite is not comparable to *B. birdi* in terms of manus and pes print morphologies. On the contrary, the general G2 manus print morphology is more similar to that of the G1 manus tracks than that of *Brontopodus*. Trackways G3 and G4 are manus-dominated, showing crescent shaped morphology (Fig. 3; Santos et al. 1994: fig. 5; Lockley and Meyer 2000: fig. 6.6.). Their arrangement suggests they are part of a wide gauge trackway. Despite the absence of digit marks, the morphology of the G3 and G4 manus prints seems to be more similar to the G1 manus prints than those of *Brontopodus*. Trackways G1 and G5 are distinct from *B. birdi* in terms of their heteropody and manus and pes print morphologies (Fig. 8). Shape analysis (using geometric morphometric techniques) performed on 30 sauropodomorph pes prints from the ichnological world record (Rodrigues and Santos 2004) corroborates the inference that the G5 trackway pes print morphology is clearly different from that of *Brontopodus* pes prints. Indeed, *B. birdi* pes prints show all their digit marks laterally oriented, with a small digit IV claw

DOI: 10.4202/app.2008.0049

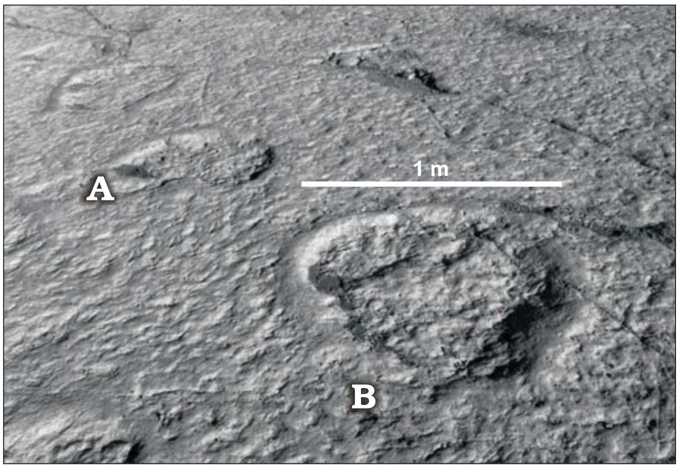

Fig. 7. *Polyonyx* isp., sauropod trackway G1 at the Galinha dinosaur tracksite (Bairro, Serra de Aire, West-Central Portugal). **A**. Sauropod right manus. **B**. Sauropod right pes prints. Photograph by Carlos Marques da Silva.

mark and a small digit V mark callosity, while along the G5 trackway at least ten pes prints reveal claw marks I and II to have an anterior orientation, and claw marks III and IV to be laterally oriented. Moreover, *Brontopodus birdi* pes prints have digit print IV situated in a more posterior position than in the G5 trackway pes prints. The Portuguese Middle Jurassic sauropod manus prints, with their slightly bent metacarpal arch, also show different morphology to *B. birdi* manus prints. In *B. birdi* these prints are U-shaped, reflecting an osteological tubular structure, and show clear evidence of rounded marks made by digits I and V in a more posterior position (Fig. 8F). Digits II–IV seem to be arranged together and their impressions are crescent-shaped. *Rotundichnus* is represented by a not particularly well-preserved wide gauge sauropod trackway from the Lower Cretaceous of Germany (Hendricks 1981). This is considered a *Brontopodus*-like trackway (Lockley et al. 2004). A Lower Cretaceous sauropod trackway with circular tracks from Argentina—*Sauropodichnus giganteus*—(Calvo 1991) is so poorly preserved that they cannot be used in any comparison with the Galinha trackways.

Sauropod tracks known from the Early Cretaceous of Korea were assigned to cf. *Brontopodus* (e.g., Lim et al. 1994; Huh et al. 2003; Lockley et al. 2008). Therefore, Korean sauropod tracks are clearly distinct, as the Portuguese Middle Jurassic sauropod tracks differ from those assigned to *Brontopodus*.

The Upper Cretaceous sauropod track record also yields U-shaped manus prints. Lockley et al. (2002) described several sauropod trackways from the Upper Cretaceous of Bolivia at the Humaca site. In these trackways the manus prints are semicircular with five rounded callosities or blunt claw impressions (Fig. 8G). The pes prints are sub-triangular and sometimes show three blunt, equidimensional claw impressions belonging to digits I–III (Lockley et al. 2002: 392). The morphology of these manus prints is different from those of the Portuguese Middle Jurassic sauropod manus prints (Fig. 8A, B). It is interesting to note that one trackway at the Toro Toro site (Leonardi 1994: 193) is wide gauge and its heteropody even lower than that of the Portuguese Middle Jurassic sauropod trackways. The Humaca site shows sauropod trackways with relatively high heteropody (Lockley et al. 2002: fig. 7) and others with low heteropody (Lockley et al. 2002: fig. 9). The trackways are narrow-gauge with inner trackway widths of about 0–15 cm, quite different from the Portuguese Middle Jurassic wide gauge trackways.

The wide gauge sauropod trackways of the Fumanya tracksite (SE Pyrenees) were described by Schulp and Brokx (1999) and later by Vila et al. (2005). These lower Maastrichtian tracks (Oms et al. 2007) show subrounded manus prints with a U-shaped morphology. They are quite similar to

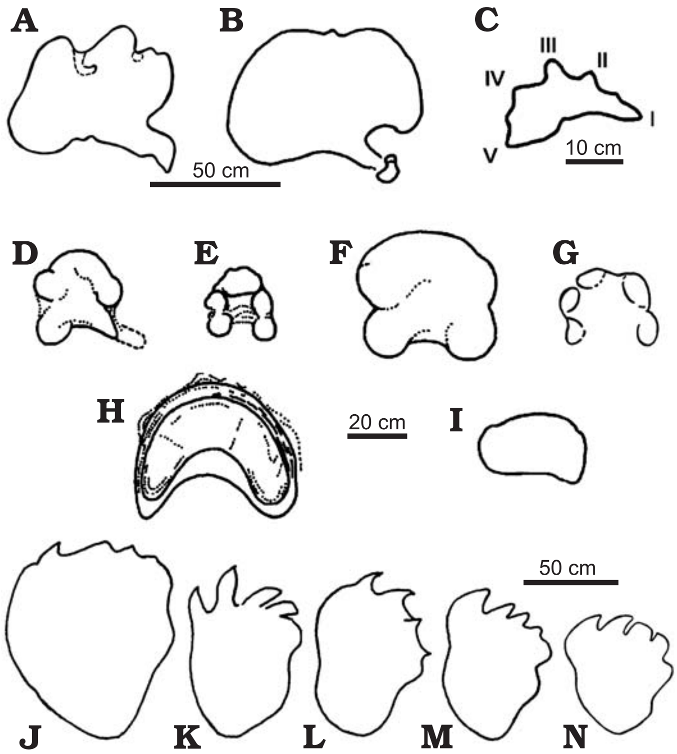

Fig. 8. Sauropod ichnites with well preserved morphologies from the general track record. **A**–**I**. sauropod manus prints (redrawn from Dalla Vecchia and Tarlao 2000). **A**. *Polyonyx gomesi* igen. et isp. nov. from the Middle Jurassic of Portugal. **B**. *Polyonyx* isp. from the Middle Jurassic of Portugal. **C**. left manus print of a quadrupedal dinosaur from the Upper Jurassic of Portugal. **D**. Unnamed print from the Lower Cretaceous of Italy. **E**. *Titanosaurimanus nana* from the Early Cretaceous of Croatia. **F**. *Brontopodus birdi* from the Lower Cretaceous of USA. **G**. Unnamed print from the Upper Cretaceous of Bolivia. **H**. *Breviparopus taghbaloutensis* from the Middle Jurassic of Morocco. **I**. *Parabrontopodus mcintoshi* from the Upper Jurassic of USA. **J**–**N**. Sauropod pes prints. **J**. *Breviparopus taghbaloutensis* from the Middle Jurassic of Morocco. **K**. *Polyonyx gomesi* igen. et isp. nov. from the Middle Jurassic of Portugal. **L**. *Brontopodus birdi* from the Lower Cretaceous of USA. **M**. *Brontopodus* aff. *B. birdi* from the Upper Jurassic of Portugal. **N**. Unnamed print from the Upper Jurassic of Asturias, Spain. A, B, K, after Santos et al. (1994); C, after Santos et al. (1995), Santos (2003); D, after Dalla Vecchia 1999; E, after Dalla Vecchia and Tarlao 2000; F, L, after Farlow at al. (1989); G, after Lockley et al. (2002); H, J, after Dutuit and Ouazzou (1980), Ishigaki (1989); I, after Lockley et al. 1994a; M, after Meyer et al. 1994, Santos 2003; N, after Lires 2000.

the characteristic *Brontopodus* isp. manus prints and therefore clearly distinct from the Portuguese Middle Jurassic sauropod tracks characterised by low heteropody and different manus print morphologies.

Dalla Vecchia (1999) and Dalla Vecchia and Tarlao (2000) analysed the world sauropod track record and suggested three sauropod manus morphotypes based on the configuration of digit I: Morphotype A, which comprises manus prints with a well-developed impression of the digit I claw (these authors considered trackway G5 from Galinha tracksite to belong to this morphotype); Morphotype B, characterised by manus prints with the intermediate development of a digit I claw (these authors considered trackway G1 from Galinha tracksite to belong to this morphotype); and morphotype C with manus prints without a claw I mark, and with rounded marks made by digits I and V (*Brontopodus* isp).

Discussion

There has been a long debate about why the claw I print is not normally preserved in sauropod manus prints (e.g., Ginsburg et al. 1966; Farlow et al. 1989), and in at least one paper it has been suggested that sauropods walked on their knuckles with their digits rotated backwards (Beaumont and Demathieu 1980). However, osteological studies revealed that the sauropod metacarpus was held fully erect with the metacarpals forming a semicircle in dorsal view; this is confirmed by the crescent shape of sauropod manus prints (see e.g., Farlow et al. 1989; McIntosh 1990; Meyer et al. 1994; Moratalla et al. 1994; Santos et al. 1994; Christiansen 1997).

Consequently, the osteological record and the ichnological evidence suggest that sauropods did not walk on their knuckles (Christiansen 1997). The Galinha tracksite shows the best preserved impressions of any sauropod manus digit I known to date.

Farlow (1992) was the first to recognise and define narrow and wide gauge sauropod trackways. Lockley et al. (1994a) proposed *Brontopodus birdi* (Farlow et al. 1989) to represent a wide gauge sauropod trackway and *Parabrontopodus* isp. (Lockley et al. 1986) as an example of narrow-gauge sauropod trackway (those with no space between the inner footprint margins). The inner trackway width of trackway G1 from the Galinha tracksite clearly renders it a wide gauge trackway, just like trackway G5 and *Brontopodus birdi* (Wit, Table 1; Wit/Pw, Table 2). This fact undoubtedly establishes the presence of wide gauge sauropod trackway makers in the Middle Jurassic of Portugal (Santos et al. 1994). Galinha trackways have manus and pes prints with morphological features totally different from *Brontopodus* isp. manus and pes prints and do not obviously suggest their inclusion in this ichnotaxon. The most interesting and distinctive feature of trackway G1 is the long and narrow impression at the centre of the manus track's rear margin, oriented in a posterior-medial direction. This mark can be observed with the same morphology and occupying the same position in both left and right manus prints along the trackway (Fig. 6). This consistency over the same trackway rules out the possibility of this impression being an extramorphological artefact. If taphonomic or preservational alterations were solely responsible for the peculiar morphology of this impression, it would not be reasonable to expect such a regular record of this impression along the trackway. It is also too long and slender to be a metacarpus impression. Moreover, the anatomical position of the sauropod metacarpus suggests that it did not touch the ground. The most posterior region of this slender impression seems to be the distal trace of a claw.

Trackway G5 shows manus prints with a large mark oriented in a medial direction, with the same morphology and occupying the same position in both left and right manus prints along the trackway (Figs. 4, 5). These regular and repeated manus print morphologies observed in the G1 and G5 trackways reflect the biological structure of the trackmaker's forefeet. Therefore, the following are here interpreted as a manus digit I mark: (i) the impression at the centre of the manus print's rear margin, oriented in a posterior-medial direction, in trackway G1; and (ii) the large impression oriented in a medial direction with a sharp, posteriorly oriented mark, in trackway G5. The posterior position of manus digit I impressions suggests that metacarpus I also occupies a posterior position, and consequently that the whole metacarpus was built as a semitubular structure. The morphology of the trackway G5 manus prints shows similarities and differences to the trackway G1 manus prints. The similarities are the slightly bent metacarpal arch and the low heteropody (manus:pes area ratio 1:2). However, the trackway G5 manus prints show five digit impressions, while the trackway G1 manus prints show only the digit I print. Also, the shape and the orientation of digit I in the manus prints are different: both originate at the centre of the track's concave posterior margin, but in trackway G5 digit I is slightly more medially positioned with an acuminated, posteriorly oriented distal end (Fig. 4). Finally, the trackway G5 pes prints show four conspicuous digit marks not seen in trackway G1 pes prints (Figs. 4, 6). Some of these morphological differences could be a result of preservation but others probably reflect anatomical structures. Despite these morphological differences between G1 and G5 trackways it is still uncertain which features are diagnostic at the ichnospecies level. For this reason the G1 trackway is attributed to *Polyonyx* isp.

According to Wilson and Sereno (1998), the pes ungual phalanges of sauropods are oriented in an external direction (as seen in the footprints illustrated in Fig. 8K–N), but this is not evident in *Polyonyx gomesi* igen. et isp. nov. The pes print digits I and II show an anterior orientation while digits III and IV have a lateral orientation (Fig. 8K). It is interesting to note that *Breviparopus taghbaloutensis* (Fig. 8J) pes prints also show anteriorly (or slightly laterally) directed digit claw marks.

Brontopodus birdi manus prints are also quite different from the sauropod manus prints at the Galinha tracksite. The former manus prints are U-shaped (suggesting all the metacarpals are arranged regularly) and show rounded marks of digits I and V almost side by side at the posterior margin.

DOI: 10.4202/app.2008.0049

Table 3. Sauropodomorpha ichno-morphotypes based on trackway features and pes and manus prints morphotypes (after Dalla Vecchia 1999; Dalla Vecchia and Tarlao 2000; Avanzini et al. 2003; D'Orazi Porchetti and Nicósia 2007).

Sauropodomorpha ichno-morphotypes	Main prints and trackways characteristics
Tetrasauropus-like	1. Narrow gauge trackways. 2. Elongated and tetradactyl pes prints with four inward arched and clawed digits, a well developed digit IV along the lateral margin of the foot and a very short digit I in medial margin. 3. Small manus prints with four inward arched claw marks. 4. High heteropody.
Otozoum-like	1. Trackmaker generally bipede and quadrupede. 2. Narrow-gauge trackway. 3. Elongated pes prints with four inward digit marks, a well-developed mark of digit IV along the lateral margin of the footprint. 4. High heteropody.
Breviparopus-like/ *Parabrontopodus*-like	1. Narrow-gauge trackway. 2. Wide pes prints with anteriorly (or slightly outwardly) directed claw or digit marks. 3. Crescent shaped manus prints. 4. High heteropody.
Brontopodus-like	1. Wide-gauge trackway. 2. Pes prints longer than broad, with large, outwardly directed claw marks at digits I–III, a small claw at digit IV and small callosity or pad mark at digit V. 3. U-shaped manus prints with rounded marks of digits I and V. 4. High heteropody.
Polyonyx-like	1. Wide-gauge trackway. 2. Pes prints with four claw marks (claws I–II oriented in an anterior direction; claws III–IV oriented laterally). 3. Asymmetric manus prints with large digit I mark oriented in a medial direction and a large triangular claw mark I posteriorly oriented, and impressions of digits II–V. Slightly bent disposition of manus digits II–III–IV and V. 4. Low heteropody.

This metacarpal arrangement suggests a tubular structure for *B. birdi* trackmaker manus. On the contrary, the sauropod manus prints at the Galinha tracksite suggest an incompletely tubular metacarpal arrangement; they are not arranged in such a regular pattern. Metacarpals II–V are slightly bent while metacarpal I is positioned in a more posterior position. It is therefore suggested that the sauropod manus morphologies preserved at the Galinha tracksite are the consequence of a semi-tubular metacarpal structure not yet reported. This arrangement would represent a functional tubular structure but with a more primitive metacarpal (semi-tubular) arrangement.

Several authors believe the sauropod manus probably functioned as a single, rigid, block-like structure with no intermetacarpal movements (McIntosh 1990; Upchurch 1994; Bonnan 2003). Movement of the phalanges of digits II–IV appear to have been restricted (e.g., Christiansen 1997) while a pollex claw, present in many sauropods, may have possessed a limited range of flexion and extension (see e.g., Thulborn 1990; Upchurch 1994). Thus, the sauropod manus appears to have functioned as a rigid structure to support the body weight, and had a claw I with some degree of movement. The semi-tubular arrangement of the metacarpus of the G1 and G5 trackmakers, plus the posterior-medial pollex orientation, suggest that this digit may have been capable of some independent movement. However, the orientation, length and general appearance of the digit I print is very constant over the trackway, suggesting that, at least during locomotion, its orientation was relatively fixed. It should be mentioned that the posterior-medial orientation of the manus digit I prints in the trackways suggests the presence of an unknown eusauropod with the pollex posteriorly rotated. The relatively large size of the manus and the semi-tubular arrangement of the metacarpus may have improved the support capability of the trackmaker manus during locomotion.

On the basis of different manus/pes prints and trackway features known in the track record Avanzini et al. (2003) suggested that Sauropodomorpha ichno-morphotypes could be subdivided into four main groups based on their pes print morphology: *Tetrasauropus*-like (sensu *Tetrasauropus* Ellenberger 1972), *Otozoum*-like, *Breviparopus*-like, and *Brontopodus*-like. Recently *Tetrasauropus* was amended and defined by D'Orazi Porchetti and Nicósia (2007) but it is still considered an ichnotaxon related to sauropodomorphs. Lockley et al. (2006) distinguish tracks from North America previously referred to *Tetrasauropus* from *Evazoum* (Nicosia and Loi 2003). *Tetrasauropus* is an ichnotaxa reserved to large-sized quadrupedal tracks with a tetradactyl pes showing a strong ectaxony, with the foot axis almost parallel to the midline of the trackway, strong claws which in the pes bend inward and the manus smaller than the pes (about 2/3) with four digits (D'Orazi Porchetti and Nicósia 2007). In addition to the proposal suggested by Avanzini et al. (2003) to subdivide Sauropodomorpha ichno-morphotypes into four groups we suggest that a fifth subdivision exists due to the manus/pes prints and trackway features of the ichnotaxon herein proposed: *Tetrasauropus*-like (sensu Ellenberger 1972; emended by D'Orazi Porchetti and Nicósia 2007), *Otozoum*-like, *Breviparopus*/*Parabrontopodus*-like; *Brontopodus*-like, and *Polyonyx*-like (Table 3).

Middle Jurassic sauropod trackmakers

Lockley et al. (1994a) suggested brachiosaurids as trackmakers of classic wide gauge sauropod trackways and later they have been assigned to Titanosauriformes according to the phylogenetic proposal of Wilson and Carrano (1999). However, the features of the wide gauge sauropod trackways at the Galinha tracksite, with a large manus claw I mark and manus prints with a slightly bent metacarpal arch, do not support such an assignation. Titanosauriformes have a reduced manus ungual phalanx I (Salgado et al. 1997; Wilson and Sereno 1998), therefore it is possible that the trackmakers of G1 and G5 were basal neosauropods or eusauropods rather than derived neosauropods. Henderson (2006) proposed through his models and analyses, that wide gauge pattern in sauropods may be the consequence of the position of their centre of mass and body weight distribution. This author came to the conclusion that wide gauge trackways were produced by large sauropods weighing more than 12 tons and with more anteriorly-positioned centres of mass (which gave them stability). This situation could have occurred more than once in sauropod evolution (see Henderson 2006: fig. 13). This relationship between wide gauge sauropod trackways and anteriorisation of overall morphology has been also proposed by other authors (e.g., Lockley et al. 2002).

The trackways at the Galinha tracksite show sauropod features, namely a quadrupedal gait and huge manus and pes prints (Carrano and Wilson 2001; Wilson 2002, 2005). Moreover, both the manus and pes prints show features of the Eusauropoda (Carrano and Wilson 2001; Wilson 2002, 2005): a manus digit I with two phalanges including a large ungual phalanx; pes prints with a digit I mark larger and more deeply impressed than the other digit marks; pes prints showing a semi-digitigrade pes with metatarsal spreading; and deep impressions of the pedal ungual phalanges in the pes prints. The evidence of pedal ungual prints offset laterally is a feature described for *Barapasaurus* and more derived taxa (Wilson 2002, 2005). In the Galinha trackways, the pedal ungual prints III and IV face anterolaterally. All pedal ungual phalanges with anterolateral orientation, or claws II and III turned either directly laterally or almost posterolaterally, are seen in neosauropod forms (Bonnan 2005) and are probably traits of the Neosauropoda. In contrast the sauropod trackways at the Galinha tracksite have features that, according to Carrano and Wilson (2001) and Wilson (2002, 2005), suggest that the trackmakers were not neosauropods. The very large manus prints with evidence of digit marks, including a large digit I ungual phalanx, evidently exclude their having been made by Titanosauriformes and/or brachiosaurids (Farlow 1992 and Lockley et al. 1994a). Furthermore, Diplodocoidea, the sister group of Macronaria, includes clades such as Diplodocidae with small manus:pes size ratios (Lockley et al. 2002; Apesteguia 2005; Wright 2005). This also excludes these animals as the potential makers of these tracks. Moreover, the manus prints from the Galinha tracksite suggest a semi-tubular metacarpal arrangement that excludes Neosauropoda. The non-vertical arrangement of the metacarpals is consistent with large manus prints characterised by separate phalanges and a digit claw I mark oriented in a posterior-medial direction. This, however, excludes diplodocoids, camarasaurs, brachiosaurs and titanosaurs (Upchurch 1994, 1998; Wilson and Sereno 1998; Wilson and Carrano 1999; Apesteguía 2005; Carrano 2005) as the trackmakers. Although the wide gauge sauropod trackway pattern has previously been attributed to brachiosaurids (e.g., Lockley et al. 1994a) and to Titanosauriformes (e.g., Wilson and Carrano 1999) or Titanosaurs (Day et al. 2002) the presence of clear, wide gauge trackways in the Middle Jurassic strongly suggests this type of trackway pattern was not exclusive to titanosauriformes sauropods; the Galinha trackmakers and this last sauropod group clearly had a common locomotion pattern (wide gauge).

A wide gauge titanosaur trackway is represented by *Brontopodus birdi* from the Lower Cretaceous at Paluxy River, Dinosaur Valley State Park (USA) (described by Farlow et al. 1989). This trackway is distinctive in that the manus print length and width are about the same, the manus is clawless, somewhat U-shaped and with the impressions of digits I and V slightly separated from the impression of the conjoined digits II–IV; the pes prints are longer than broad, with large, laterally directed claw marks for digits I–III (digit marks IV and V only seen in well-preserved prints). The heteropody shown is high, with the pes area about 3 to 6 times larger that of the manus print area. The manus prints are rotated outward with respect to the direction of travel, and the manus print centres are somewhat closer to the trackway midline than the pes track centres.

Titanosauriformes and titanosaurs were responsible for *Brontopodus*-like wide gauge trackways due to their hind limb structure (Wilson and Carrano 1999). These animals existed from the Middle Jurassic (with trackways clearly attributed to these sauropods at Ardley Quarry, Oxfordshire, reported by Day et al. 2002) to the Upper Cretaceous (Wilson and Carrano 1999). Titanosauriformes such as *Lapparentosaurus madagascariensis* (Bonaparte 1986a; Upchurch et al. 2004) from the Bathonian of Madagascar, and the titanosaur *Janenschia robusta* (Bonaparte et al. 2000; Upchurch et al. 2004) from the Upper Jurassic of Tendaguru (Tanzania), were also wide gauge (*Brontopodus*-like) trackmakers.

Probably both the G1 and G5 trackways (Middle Jurassic of Portugal) represent wide gauge basal eusauropod trackways (*Polyonyx*-like). These both show asymmetric manus prints that are wider than long and that have a rounded lateral edge (digit mark V), a large digit I mark oriented in a posterior-medial direction, impressions of digits II–V, and a slightly bent metacarpal arch; the pes prints are longer than broad, oval shaped, toe-less impressions or with four claw marks (claws I–II with an anterior orientation; claws III–IV are laterally oriented). Their heteropody is low (the pes area is about twice the manus print area). Occasionally the manus print centres are closer to the trackway midline than the pes print centres. Both

DOI: 10.4202/app.2008.0049

the manus and pes prints are rotated outward relative to the trackway midline. The characters of the wide gauge sauropod trackways at the Galinha site suggest that at least one basal eusauropod was able to produce wide gauge trackways. The osteological remains of basal eusauropods such as *Patagosaurus*, *Volkheimeria*, *Cetiosaurus*, *Cetiosauriscus*, and *Turiasaurus* (Upchurch et al. 2004; Royo-Torres et al. 2006) suggest they could have produced wide gauge trackways. They have some of the wide gauge trackmaker features described by Wilson and Carrano (1999), e.g., wider sacra, limb morphologies suggesting an angled posture, and increased eccentricity of the femoral midshaft. *Volkheimeria* (Bonaparte 1986b) and *Patagosaurus* (Bonaparte 1986b) show femora with the proximal part inclined medially, although they also show a lateral comb as in Titanosauriformes (Salgado et al. 1997). *Cetiosauriscus stewarti* Charig, 1980 (Woodward 1905: fig. 49), sometimes attributed to Diplodocoidea *incertae sedis* (Upchurch et al. 2004) but sometimes even exiled from Neosauropoda (Heathcote and Upchurch 2003), has a high eccentricity of the femoral midshaft similar to that seen in *Brachiosaurus* and *Saltasaurus* (Fig. 9).

The turiasaurs represent another group of basal eusauropods from the Middle Jurassic to Upper Jurassic–Lower Cretaceous boundary in Europe. The most complete taxon is *Turiasurus*, represented by manus and pes remains belonging to the same specimen (Royo-Torres et al. 2006). This seems to share features with the *Polyonyx* morphotype: a manus-pes area ratio of 1:2, a large manus digit I ungual phalanx (possibly articulated in a posterior position), and metatarsal V with a strongly expanded distal end that allows the impression of digit V to be made. Further, *Turiasaurus* has characteristics that could allow it to produce wide gauge trackways. For example, the proximal end of the humerus has a noticeable medial slant, similar to the femur of Titanosauriformes, and the femoral midshaft shows high eccentricity.

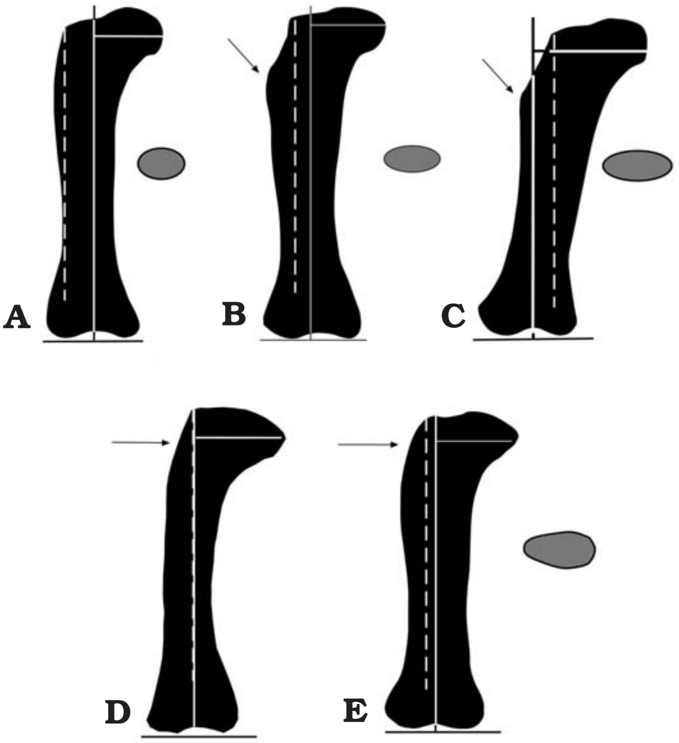

Fig. 9. **A**. Right femur of *Diplodocus* in anterior view. **B**. Right femur of *Brachiosaurus* in anterior view. **C**. Right femur of *Saltasaurus* in anterior view. **D**. Right femur of *Patagosaurus* in anterior view. **E**. Left femur of *Cetiosauriscus* in posterior view. A–C, after Wilson and Carrano (1999); D, after Bonaparte (1986b); E, after Woodward (1905).

Conclusions

At the Galinha tracksite there is an unequivocal evidence of wide gauge sauropod trackways produced by non-titanosauriformes. Their presence in the Middle Jurassic suggests that their sauropod makers were more widely distributed over time than previously thought. The proposed new ichnospecies *Polyonyx gomesi* igen. et isp. nov. is represented by a wide gauge sauropod trackway characterised by manus prints that are wider than long, and a large digit I mark oriented in a medial direction with a large, posteriorly oriented triangular claw mark. Digits II–V show a slightly bent arrangement. The pes prints show four claw marks, I–II with an anterior orientation, and III–IV laterally oriented. *Polyonyx* igen. nov. manus print morphology yields information about the display of the metacarpals and suggests an intermediate stage of manus structure between the non-tubular primitive sauropod manus and a tubular metacarpal distribution characteristic of more derived sauropods.

The Galinha tracksite is home to wide gauge trackways probably registered by a basal eusauropod and possibly a member of Turiasauria. We add a new ichno-morphotype, *Polyonyx*-like, to previous Sauropodomorpha subdivition now into five groups: *Tetrasauropus*-like, *Otozoum*-like, *Breviparopus/Parabrontopodus*-like, *Brontopodus*-like, and *Polyonyx*-like.

Acknowledgments

Special acknowledgment is due to António M. Galopim de Carvalho (Former Director of National Natural History Museum of Lisbon University, Portugal), José Luis Sanz (Universidad Autonoma de Madrid, Spain), and Martin Lockley (University of Colorado, Denver, USA) for their essential role in the start of this research. Particular tribute is also due to Rui Galinha, the owner of the Galinha Quarry until 1996. We are also indebted to José Alho and to all the staff at the Serra de Aire Dinosaur Tracks Natural Monument (António For, Aurélia Dias, Cláudia Catarino, Elisabete Oliveira, Fernando Pereira, Gabriel Simões, José Oliveira, Luísa Santos, Nuno Forner, Paulo Lucas, Rui Louro, Rui Marques, and Sónia Freitas). We would like also to thank Carlos Antunes (Lisbon University, Portugal), António Calixto, Carlos Madeira Abrantes, Armanda Teixeira, Gonçalo Bernardo, João Carvalho and Pedro Souto for fieldwork assistance. Special thanks go to Bernat Vila (Institut Català de Paleontologia, Barcelona, Spain), Carlos Marques da Silva (Lisbon University, Lisbon, Portugal), Jeffrey Wilson (University of Michigan, Ann Arbor, USA), José Carlos García-Ramos and José Lires (both Oviedo University, Oviedo, Spain), Luis Azevedo

Rodrigues (National Natural History Museum of Lisbon University, Lisbon, Portugal), Marco Avanzini (Museo Tridentino di Scienze Naturali, Trento, Italy), Mário Cachão (Lisbon University, Lisbon, Portugal), Per Christiansen (Natural History Museum of Denmark, Copenhagen, Denmark), and Sebastián Apesteguia (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina), for their useful comments that improved the manuscript. We thank Martin Lockley (University of Colorado, Denver, USA) and an anonymous reviewer for their comments. Special thanks are also due to Arnaldo Silva, Elizabeth Duarte, Gonçalo Pereira, Guadalupe Jácome, Luís Quinta, Maria Antónia Vieira, Mário Robalo, Nuno Pessoa e Costa Rodrigues, and Pedro Mauro Vieira for technical help and other type of assistance. Fundação para a Ciência e Tecnologia—FCT, partially supported this research with the Projects POCI/ CTE-GEX/ 58415/2004 and PPCDT/ CTE-GEX/58415/2004—"Survey and Study of Middle Jurassic through Late Cretaceous Terrestrial Vertebrates from Portugal—implications in paleobiology, paleoecology, evolution and stratigraphy". The authors want to acknowledge also the project CGL2006-10380 funding by the Ministerio de Ciencia e Innovación from Spain and the project CGL2006-13903 funding by the Ministério de Ciencia e Innovación from Spain, Gobierno de Aragón (FOCONTUR, Grupo de Investigación E-62) and Dinópolis. The present work is dedicated to the memory of Giuseppe Manuppella (1933–2004) an Italian-Portuguese geologist.

References

Apesteguia, S. 2005. Evolution of the titanosaur metacarpus. *In*: V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards, The Sauropodomorph Dinosaurs*, 321–345. Indiana University Press, Bloominton.

Azerêdo, A.C. 1993. *Jurássico médio do Maciço Calcário Estremenho (Bacia Lusitânica): análise de fácies, micropaleontologia, paleogeografia*. 403 pp. Unpublished Ph.D. thesis, Universidade de Lisboa, Lisboa.

Azerêdo, A.C., Ramalho, M.M., Santos, V.F., and Galopim de Carvalho, A.M. 1995. Calcários com pegadas de dinossáurios da Serra de Aire: microfácies e paleoambientes. *Gaia* 11: 1–6.

Avanzini, M., Leonardi, G., and Mietto, P. 2003. *Lavinipes cheminii* ichnogen., ichnosp. nov., a possible sauropodomorph track from the Lower Jurassic of the Italian Alps. *Ichnos* 10: 179–193.

Beaumont, G. and Demathieu, G. 1980. Remarques sur les extremites anterieures des Sauropodes (Reptiles, Saurischiens). *Comptes Rendus de l'Académie des Sciences* 15: 191–198.

Bonaparte, J.F. 1986a. The early radiation and phylogenetic relationships of the Jurassic sauropod dinosaurs, based on vertebral anatomy. *In*: K. Padian (ed.), *The Beginning of the Age of Dinosaurs*, 247–258. Cambridge University Press, Cambridge.

Bonaparte, J.F. 1986b. Los dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique moyen de Cerro Cóndor (Chubut, Argentina). *Annales de Paléontologie* 72 (4): 247–289.

Bonaparte, J.F., Heinrich, W.D., and. Wild. R. 2000. Review of *Janenschia* Wild with the description of a new sauropod from the Tendaguru beds of Tanzania and a discussion on the systematic value of procoelous caudal vertebrae in the Sauropoda. *Palaeontographica* 256: 25–76.

Bonnan, M.F. 2003. The evolution of manus shape in sauropod dinosaurs: implications for functional morphology, forelimb orientation and phylogeny. *Journal of Vertebrate Paleontology* 23: 595–613.

Bonnan, M.F. 2005. Pes anatomy in sauropod dinosaurs: implications for functional morphology, evolution, and phylogeny. *In*: V. Tidwell and K. Carpenter (eds.), *Thunder-Lizards, The Sauropodomorph Dinosaurs*, 346–380. Indiana University Press, Bloominton.

Calvo, J. 1991. Huellas de dinosaurios en la Formación Río Limay (Albiano–Cenomaniano?), Picun Leufu, Provincia de Neuquén, Republica Argentina. *Ameghiniana* 28: 241–258.

Carrano, M.T. 2005. The Evolution of Sauropod Locomotion: morphological diversity of a secondary quadrupedal radiation. *In*: K.A. Curry Rogers and J.A. Wilson (eds.), *The Sauropods: Evolution and Paleobiology*, 229–251. University of California Press, Berkeley.

Carrano, M.T. and Wilson, J.A. 2001. Taxon distributions and the tetrapod track record. *Paleobiology* 27 (3): 564–582.

Christiansen, P. 1997. Locomotion in sauropod dinosaurs. *Gaia* 14: 45–75.

Dalla Vecchia, F.M. 1999. A sauropod footprint in a limestone block from the Lower Cretaceous of northeastern Italy. *Ichnos* 6: 269–275.

Dalla Vecchia, F.M. and Tarlao, A. 2000. New Dinosaur track sites in the Albian (Early Cretaceous) of the Istrian peninsula (Croatia). Parte II—Paleontology. *Memorie di Scienze Geologiche* 52: 227–292.

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

D'Orazi Porchetti, S. and Nicósia, U. 2007. Re-examination of some large Early Mesozoic tetrapod footprints from the African collection of Paul Ellenberger. *Ichnos* 14: 219–245.

Dutuit, J.M. and Ouazzou, A. 1980. Découverte d'une piste de dinosaure sauropode sur le site d'empreintes de Demnat (Haut-Atlas Marocain). *Mémoire de la Société Géologique de France, New Series* 139: 95–102.

Ellenberger, P. 1972. Contribution à la classification des Pistes de Vertébrés du Trias: Les types du Stormberg d'Afrique du sud. (I partie). *Paleovertebrata, Mémoire extraordinaire, Montpellier* 104: 1–117.

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

Farlow, J.O., Pittman, J.G., and Hawthorne, J.M. 1989. *Brontopodus birdi*, Lower Cretaceous sauropod footprints from the U. S. Gulf coastal plain. *In*: D.D. Gillette and M.G. Lockley (eds.), *Dinosaur Tracks and Traces*, 371–394. Cambridge University Press, Cambridge.

Gierliński, G. 1997. Sauropod tracks in the Early Jurassic of Poland. *Acta Palaeontologica Polonica* 42: 532–537.

Ginsburg, L., Lapparent, A.F. de, Loiret, B., and Taquet, P. 1966. Empreintes de pas de Vertébrés tetrapodes dans les Séries continentales a l'Ouest d'Agades (Republique du Niger). *Comptes Rendus de l'Academie des Sciences* 263: 28–31.

Gomes, J.P. 1916. Descoberta de rastos de sáurios gigantescos no Jurássico do Cabo Mondego. *Comunicações Comissão Serviços Geológicos de Portugal* 11: 132–134.

Heathcote, J.F. and Upchurch, P. 2003. The relationships of *Cetiosauriscus stewarti* (Dinosauria; Sauropoda): implications for sauropod phylogeny. *Journal of Vertebrate Paleontology* 23 (3): 60A.

Henderson, D.M. 2006. Burly gaits: centers of mass, stability and the trackways of sauropod dinosaurs. *Journal of Vertebrate Paleontology* 26: 907–921.

Hendricks, A. 1981. Die Saurierfährten von Münchenhagen bei Rehburg-Loccum (NW-Deutschland). *Abhandlungen aus dem Landesmuseum für Naturkunde zu Münster in Westfalen* 43 (2): 1–22.

Huh, M., Hwang, K.G., Paik, I.S., Chung, C.H., and Kim, B.S. 2003. Dinosaur tracks from the Cretaceous of South Korea: Distribution, occurrences and paleobiological significance. *The Island Arc* 12: 132–144.

Ishigaki, S. 1988. Les empreintes de Dinosaures du Jurassique inférieur du Haut Atlas central marocain. *Notes et Mémoires Services Géologiques du Maroc* 334: 79–86.

Ishigaki, S. 1989. Footprints of swimming sauropods from Morocco. *In*: D.D. Gillette and M.G. Lockley (eds.), *Dinosaur Tracks and Traces*, 83–86. Cambridge University Press, Cambridge.

Leonardi, G. (ed.) 1994. *Annotated Atlas of South América tetrapod footprints (Devonian to Holocene)*. 248 pp. Companhia de Pesquisa de Recursos Naturais, Serviço Geológico do Brasil, Brasília.

Leonardi, G. and Mietto, P. (eds.) 2000. *Dinosauri in Italia*. 495 pp. Accademia Editoriale, Pisa-Roma.

Lim, S.-K., Lockley, M.G., Yang, S.-Y., Fleming, R.F., and Houck, K. 1994. *Brontopodus* and *Parabrontopodus* ichnogen nov. and the significance of wide-and narrow-gauge sauropod trackways. *Gaia* 10: 109–117.

Lires, J. 2000. *Icnitas de dinosaurios cuadrúpedos del Jurásico de Asturias. Morfometría, morfología e interpretación*. 62 pp. Memoria de Investigación, Universidade de Oviedo, Oviedo.

Lockley, M.G. and Meyer, C.A. 2000. *Dinosaur Tracks and other fossil footprints of Europe*. 323 pp. Columbia University Press, New York.

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

Lockley, M.G., Farlow, J.O., and 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., and Lucas, S.G. 1994b. The distribution of sauropod tracks and trackmakers. *Gaia* 10: 233–248.

Lockley, M.G., Schulp, A.S., Meyer, C.A., Leonardi, G., and Mamani, D.K. 2002. Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, Wide-gauge locomotion and gregarious behaviour. *Cretaceous Research* 23: 383–400.

Lockley, M.G., Wright, J.L., and Thies, D. 2004. Some observations on the dinosaur tracks at Munchehagen (Lower Cretaceous), Germany. *Ichnos* 11: 261–274.

Lockley, M.G., Lucas, S.G., and Hunt, A.P. 2006. *Evazoum* and the renaming of northern hemisphere "*Pseudotetrasauropus*": implications for tetrapod ichnotaxonomy at the Triassic–Jurassic boundary. *New Mexico Museum of Natural History and Science Bulletin* 37: 199–206.

Lockley, M.G., Lires, J., García-Ramos, J.C., Pinuela, L., and Avanzini, M. 2007. Shrinking the World's Largest Dinosaur Tracks: Observations on the Ichnotaxonomy of *Gigantosauropus asturiensis* and *Hispanosauropus hauboldi* from the Upper Jurassic of Asturias, Spain. *Ichnos* 14: 247–255.

Lockley, M.G., Kim, J.Y, Kim, K.S., Kim, S.H., Matsukawa, M., Rihui, L., Jianjun, L., and Yang, S.-Y. 2008. *Minisauripus*—the track of a diminutive dinosaur from theCretaceous of China and South Korea: implications for stratigraphic correlation and theropod foot morphodynamics. *Cretaceous Research* 29: 115–130.

Manuppella, G., Antunes, M.T., Almeida, C., Azerêdo, A.C., Barbosa, B., Cardoso, J.L., Crispim, J.A., Duarte, L.V., Henriques, M.H., Martins, L.T., Ramalho, M.M., Santos, V.F., and Terrinha, P. 2000. *Carta Geológica de Portugal (1/50 000), Notícia Explicativa da Folha 27-A (Vila Nova de Ourém)*. 156 pp. Instituto Geológico e Mineiro, Lisboa.

McIntosh, J.S. 1990. Sauropoda. *In*: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 345–401. University of California Press, Berkeley.

Mensink, H. and Mertmann, D. 1984. Dinosaurierfährten (*Gigantosauropus asturiensis* n. g. n. sp.; *Hispanosaurus hauboldi* n.g. n.sp.) im Jura Asturiens bei La Griega und Ribadasella (Spanien). *Neues Jahrbuch für Geologie und Paläontologie* 7: 405–415.

Meyer, C.A., Lockley, M.G., Robinson, J.W., and 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.

Moratalla, J.J., Mondejar, G.J., Santos, V.F., Lockley, M.G., Sanz, J.L., and Jiménez, S.J. 1994. Sauropod trackways from the Lower Cretaceous of Spain. *Gaia* 10: 75–83.

Nicosia, U. and Loi, M. 2003. Triassic Footprints from Lerici (La Spezia, Northern Italy). *Ichnos* 10: 127–140.

Rodrigues, L.A. and Santos, V.F. 2004. A Geometric Morphometrics Study on Sauropod Tracks. *In*: A.M.T. Elewa (ed.), *Morphometrics—Applications in Biology and Paleontology*, 129–143. Springer-Verlag, Heidelberg.

Romano, M. and Whyte, M.A. 2003. Jurassic dinosaur tracks and trackways of the Cleveland Basin, Yorkshire: preservation, diversity and distribution. *Proceedings of the Yorkshire Geological Society* 54: 185–215.

Romano, M., Whyte, M.A., and Manning, P.L. 1999. New sauropod dinosaur prints from the Saltwick Formation (Middle Jurassic) of the Cleveland Basin, Yorkshire. *Proceedings of the Yorkshire Geological Society* 52: 361–369.

Royo-Torres, R. Cobos, A., and Alcalá, L. 2006. A giant European dinosaur and a new sauropod clade. *Science* 314: 1925–1927.

Salgado, L., Coria, R.A., and Calvo, J.O. 1997. Evolution of titanosaurid sauropods. I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana* 34: 3–32.

Santos, V.F. 2003. *Pistas de dinossáurio no Jurássico–Cretácico de Portugal. Considerações paleobiológicas e paleoecológicas*. 365 pp. Unpublished Ph.D. thesis, Universidade Autónoma de Madrid, Madrid.

Santos, V.F. and Rodrigues, L.A. 2003. New data on Middle Jurassic Theropods from Portugal. 39 p. *51th Symposium of Vertebrate Palaeontology and Comparative Anatomy*. University Museum of Natural History, Oxford.

Santos, V.F., Lockley, M.G., Meyer, C.A., Carvalho, J., Galopim de Carvalho, A.M., and Moratalla, J.J. 1994. A new sauropod tracksite from the Middle Jurassic of Portugal. *Gaia* 10: 5–13.

Santos, V.F., Galopim de Carvalho, A.M., and Silva, C.M. da 1995. A jazida da Pedreira da Ribeira do Cavalo (Sesimbra) ou a história das pegadas de dinossáurio que nunca mais poderemos visitar. *Almadam, II Série* 4: 175–177.

Santos, V.F., Galopim de Carvalho, A.M., and Silva, C.M. da 1997. Pistas de Dinossáurios da Serra d'Aire-Jazida da Pedreira do Galinha. *Monumento Natural das Pegadas de Dinossáurio da Serra de Aire*, Bairro, 2pp.

Santos, V.F., Dantas, P., Moratalla, J.J., Araújo, M.G., and Galopim de Carvalho, A.M. 2000. Pegadas de terópodes em Alcanede, Portugal. *In*: J.B. Diez and A.C. Balbino (eds.), *I Congresso Ibérico de Paleontologia / XVI Jornadas de la Sociedad Española de Paleontología, Évora, Livro de Resumos*, 17. Universidade de Évora, Évora.

Santos, V.F., Rodrigues, L.A., and Alho, J.M. 2008. Middle Jurassic dinosaur tracksites from Portugal: where science meets natural heritage. *In*: A. Uchman (ed.), *The Second International Congress on Ichnology, Cracow, Poland, August 29-September 8, Abstract Book*, 113–114. Polish Geological Institute, Warsaw.

Schulp, A.S. and Brokx, W.A. 1999. Maastrichtian Sauropod Footprints from the Fumanya Site, Berguedŕ, Spain. *Ichnos* 6: 239–250.

Thulborn, R.A. 1990. *Dinosaur Tracks*. 410 pp. Chapman and Hall, London.

Upchurch, P. 1994. Manus claw function in sauropod dinosaurs. *Gaia* 10: 161–172.

Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society* 124: 43–103.

Upchurch, P., Barrett, P.M., and Dodson, P. 2004. Sauropoda. *In*: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria (2nd edition)*, 259–322. University of California Press, Berkeley.

Vila, B., Oms, O., and Galobart, A. 2005. Manus-only titanosaurid trackway from Fumanya (Maastrichtian, Pyrenees): further evidence for an underprint origin. *Lethaia* 38: 211–218.

Whyte, M.A. and Romano, M. 2001. Probable stegosaurian dinosaur tracks from the Saltwick Formation (Middle Jurassic) of Yorkshire, England. *Proceedings of the Geologists' Association* 112: 45–54.

Wilson, J.A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society* 136: 215–275.

Wilson, J.A. 2005. Overview of Sauropod Phylogeny and Evolution. *In*: K.A. Curry Rogers and J.A. Wilson (eds.), *The Sauropods: Evolution and Paleobiology*, 15–49. University of California Press, Berkeley.

Wilson, J.A. and Carrano, M.T. 1999. Titanosaurs and the origin of "wide-gauge" trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* 25: 252–267.

Wilson, J.A. and Sereno, P. 1998. Early evolution and higher level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology* 18 (2): 1–68.

Woodward, A.S. 1905. On parts of the skeleton of *Cetiosaurus leedsi*, a sauropodous dinosaur from the Oxford Clay of Peterborough. *Proceedings of the Zoological Society of London* 1: 232–243.

Wright, J.L. 2005. Steps in Understanding Sauropod Biology: the importance of sauropod tracks. *In*: K.A. Curry Rogers and J.A. Wilson (eds.), *The Sauropods: Evolution and Paleobiology*, 252–284. University of California Press, Berkeley.