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First Record of Gregarious Behavior in Robust Medium-Sized Jurassic Ornithopods: Evidence from the Kimmeridgian Trackways of Asturias (N. Spain) and Some General Considerations on Other Medium-Large Ornithopod Tracks in the Mesozoic Record

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ABSTRACT
At least four parallel trackways of medium-sized and robust ornithopods are described from the Upper Jurassic Tereñes tracksite in Asturias (N. Spain). While the tracks and trackways of small and gracile ornithopods are common in the Jurassic record, large ornithopods are very rare in this period. Ornithopod gregarious behavior has been recorded from many Cretaceous ichnoassemblages, but there are few examples from the Jurassic, and these always relate to small individuals. The Asturian tracks are quite different from known ichnogenera, but they are not sufficiently well preserved to propose a new one. Medium-large Jurassic ornithopods with robust feet such as *Draconyx* or *Cumnoria* are the best candidates to be the trackmakers.

KEYWORDS
Ornithopod trackways; gregarious behaviour; Kimmeridgian; Tereñes Formation; Asturias; N. Spain

Introduction

The Jurassic successions in Asturias (N. Spain) are exposed along 60 km of coast between Gijón and Ribadesella. This region, named "The Dinosaur Coast" (Fig. 1), is well known for having produced many vertebrate tracks, and this is why it was designated a Natural Monument in 2001 by the Government of Asturias. Numerous dinosaur (sauropod, theropod, ornithopod, and stegosaur), pterosaur, crocodile, turtle, and lizard tracks have been described (García-Ramos et al., 2006; Lockley et al., 2008; Piñuela Suárez, 2015). Dinosaur footprints were first discovered in the Upper Jurassic (Kimmeridgian) of Asturias in 1969 by J.C. G.-R., La Griega Beach tracksite is particularly well known. Yet, it was not until 1975 (published in 1977) when the same researcher first described dinosaur tracks from Asturias (García-Ramos, 1977), mainly from the Lastres Formation (Fig. 2A), the youngest in the Jurassic succession of this region.

Ornithopod footprints are not common in the Jurassic outcrops of Asturias. Only two medium-sized prints were described by; Piñuela Suárez (2000, 2015) in the Lastres Formation from Villaviciosa (Asturias) with similar length and width and rounded "heel." The digit traces are broad and short, with the digit III imprints being a little longer than the other two; they have a relatively high divarication angle. There is no evidence of claws, and the ends of the digits are rounded or pointed. The tracks were attributed to ornithopods and assigned to the ichnogenus *Iguanodontipus* (see below the problems regarding this ichnogenus). The rest of the ornithopod footprints from Asturias are smaller than or quite different in shape from those described from Villaviciosa and the Tereñes examples; some of them were included in *Anomoepus* (Piñuela et al., 2008).

Our purpose is twofold; on the one hand, to describe the trackways belonging to medium-sized ornithopods from the Tereñes tracksite, Kimmeridgian in age, and to discuss the ichnotaxonomic affinities of the tracks; and on the other hand, to interpret the parallel orientation and the uniform direction of movement that these trackways show. The evidence of these kinds of trackways, abundant and well known from several sites from the Cretaceous (Brazil, Canada, China, Japan, South Korea, Spain, the United Kingdom, and USA) and very scarce in the Jurassic (USA and Portugal), have been described only for small ornithopods; for this reason the Tereñes trackways have interesting palaeobiological and palaeoecological implications.

Geographic and geological setting

The tracksite is located on the sea cliffs of Tereñes, a town in the Ribadesella municipality (Asturias, N. Spain)

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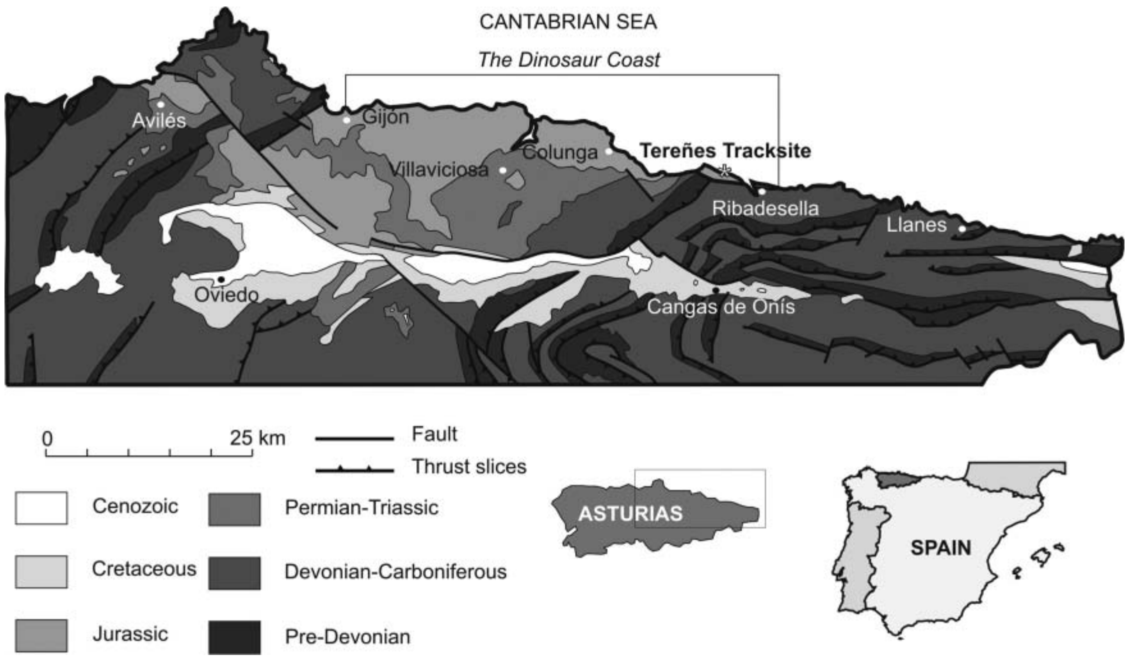

Figure 1. Location of Tereñes tracksite in Ribadesella (Asturias, N. Spain). Geological map of the central-eastern area of Asturias based on the cartography of the Geology Department, University of Oviedo (modified after Aramburu and Bastida, 1995).

(Fig. 1). The rocks at this site belong to the Ribadesella Group (Kimmeridgian), mainly to the middle unit, the Tereñes Formation (Fig. 2).

During the Kimmeridgian, the sea level rose in Asturias retreating the coastline towards the SW. This coastline was placed in the interior of the territory that Asturias occupies today giving it a northwest–southeast trend, quite different from the current profile (E-W). A restricted shallow sea (shelf lagoon), developed in front of this coastline, was separated from the open ocean by a threshold or barrier of tectonic origin (semi-graben) which impeded the entry of stenohaline marine faunas from the outside. The shelf lagoon was little affected by wave-reworking, except during occasional storms and tides (García-Ramos et al., 2010a, 2011).

The Tereñes Formation, about 160 m thick, has been divided into three informal members, separated by minor erosional discontinuities (Fig. 2A) (García-Ramos et al., 2010b; Fürsich et al., 2012).

At least fourteen track-bearing levels have been recognized in the Tereñes sea-cliffs, all of them preserved in the middle member, about 8–10 m thick. This member consists of dark grey silty marls with some intercalations of thin bedded limestones, sandstones, and calcareous intraformational conglomerates, the latter in the lower part (Fig. 2B). Small bivalve shell beds, with scattered gastropods and ostracods, are profusely distributed along the succession. Dinosaur footprints are found frequently associated with transgression surfaces in a muddy littoral environment (García-Ramos et al., 2010b; Fürsich et al., 2012). Desiccation cracks occur at several levels, indicating deposition in very shallow water settings with periodic emergence.

The parallel trackways are preserved on the top of a sandy marlstone bed (Figs. 2 and 3) containing small bivalves and gastropods as well as several fish remains (scales, teeth and bones). Mud cracks are not present on this surface, but they are very common in the rest of the middle member. Forty centimeters below the track-bearing bed, there is a limestone layer with a theropod trackway consisting of seven consecutive medium-sized footprints preserved as concave epireliefs.

Description of the trackways

The ornithopod tracksite we mapped, using a grid of 10 cm, reveals a total of 43 footprints, including the four parallel ornithopod trackways described in detail below, and other isolated ornithopod and theropod footprints (Fig. 4). The direction of movement indicated by the trackways is towards the south. Many of the footprints are not well preserved due to the present erosional processes on the sea cliffs, mainly wave action. Measurements for three trackways are given in the Table 1.

The morphology of the pes tracks, preserved as negative relief epichnia, is tridactyl and mesaxonic with three stout, relatively short, broad-spreading and blunt ending digits. The digit III is a little longer than the other two, and the divarication angle between II-III and III-IV is relatively similar (see

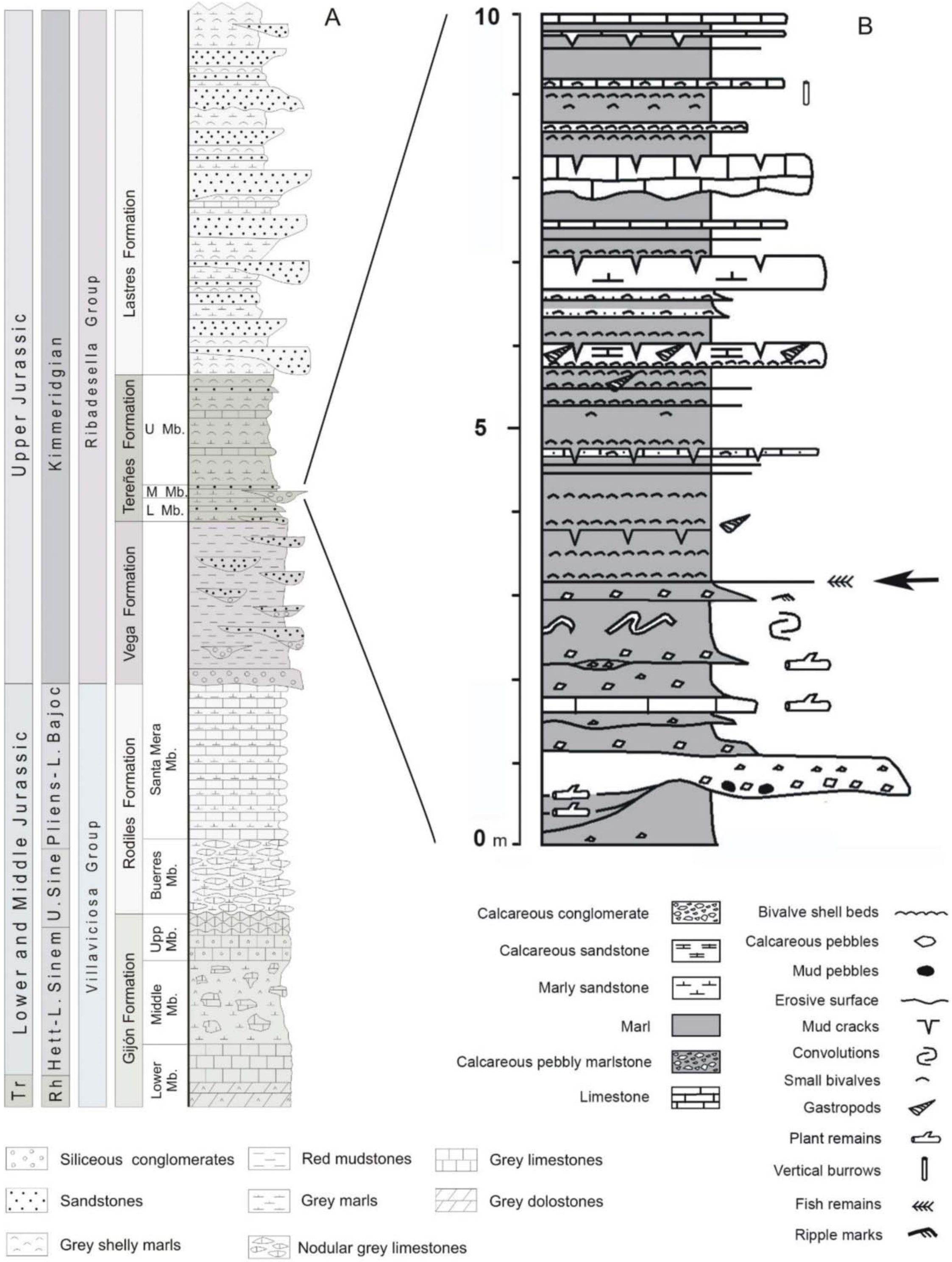

Figure 2. A. General log (not to scale) of the Asturian Jurassic (modified after García-Ramos et al., 2011). B. detailed log from the Middle Member of the Tereñes Formation (modified after García-Ramos et al., 2010a,b). The arrow in the log shows the location of the bed with the ornithopod trackways.

Table 1). The "heel" impression is rounded and symmetrical. The depth, varying between 2 and 4 cm, is similar in all footprints. In general, the footprints show a negative or inward rotation of approximately 5–13°. The trackways do not show manus prints.

Ornithopod trackway 1 (OT1)

Trackway 1 (3.4 m in length) reveals five consecutive footprints, but only four of them were measured (Fig. 4). The length and width averages are 28.0 and 36.2 cm, respectively,

Figure 3. A. Surfaces with the dinosaur trackways preserved; note the ornithopod trackways in the foreground and the theropod trackway in the background. B. The ornithopod track-bearing surface with interpretative drawings. See scale in Fig. 4.

so the tracks are wider than long (l/w ratio = 0.77). Mean pace (step) and stride are 79.5 and 159.3 cm, respectively, and the pace angulation average is 163°. The best preserved footprint is number three (Figs. 4, 5A, 6E). The orientation is about 185°.

Ornithopod trackway 2 (OT2)

This is the longest trackway (Fig. 4). It extends about 4.2 m and comprises seven recognizable footprints (only six were measured). The length and width averages are 30.3 and 35.3 cm, respectively, with a l/w ratio of 0.86. Mean pace (step) and stride are 68.6 and 130.8 cm, respectively, and the pace angulation average is 151°. The best preserved footprint is number three (Figs. 4, 5B, 6F). The orientation is about 180°.

Ornithopod trackway 3 (OT3)

This trackway preserves six consecutive footprints, and the total length is 4.0 m (Fig. 4). The length and width averages are 28.8 and 34.8 cm (l/w ratio = 0.83). Mean pace (step) and stride are 64.3 and 126.4 cm, respectively, and the pace angulation average is 151°. The best preserved footprint on the tracksite, number six, is from this trackway (Figs. 4, 5C, 6G). The orientation is about 187°.

Ornithopod trackway 4 (OT4)

Measurements were not taken on this trackway due to the poor preservation of the four tracks (Fig. 4), but the outline of the footprints appears to be similar to those reported in the other ornithopod trackways, and the orientation is also similar, about 197°.

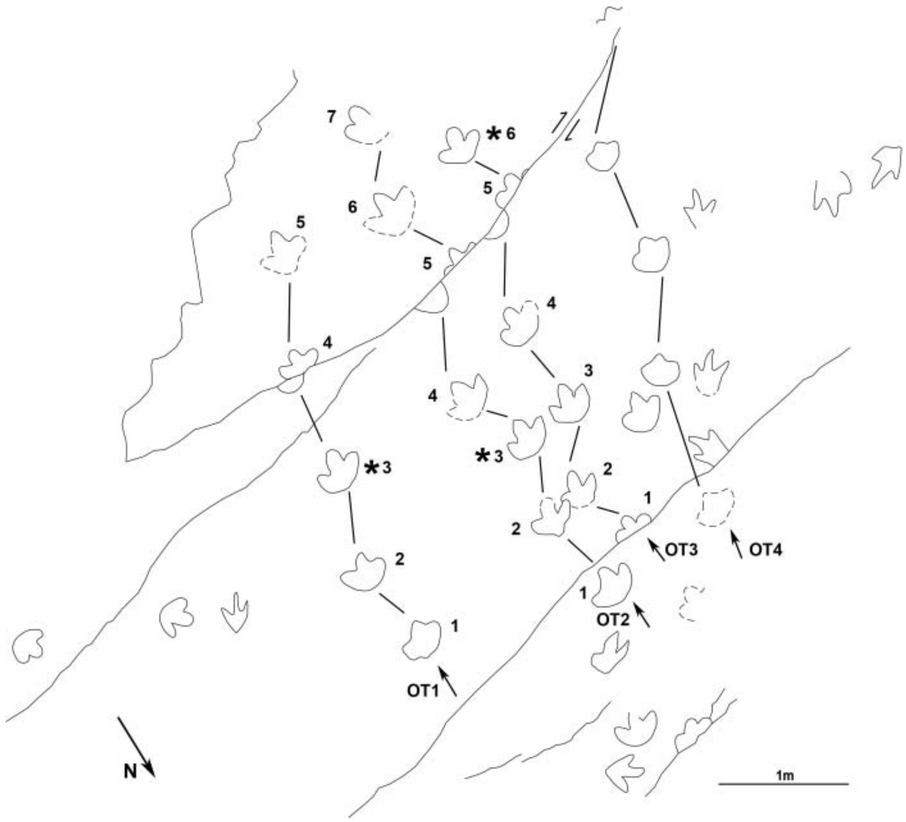

Figure 4. Map of the parallel ornithopod trackways on the Tereñes tracksite. The asterisk indicates the best preserved prints in each of the three trackways OT1–OT3.

Interpretation and discussion of the ornithopod tracks and trackways

Taking into account the characteristics of the tracks and trackways such as tridactyl pes wider than long, broad, and blunt digits, wide divarication angle, rounded and symmetrical heel, the short pace (less than two times footprint length), and the lack of manus traces, allows us to attribute them to bipedal ornithopods. The length of the tracks (L), between 28.0 and 30.3 cm indicate relatively large individuals (L > 25; Thulborn, 1990; Dalla Vecchia, 1998). Tentatively, we follow the classification proposed by Marty (2008) for bipedal dinosaurs in which the Asturian footprints are between medium (20cm < L < 30cm) and large (L > 30cm) sizes. The hip heights of these ornithopods, calculated using the morphometric parameter h = 5.9 L (Thulborn, 1990), was between 165.2 and 178.8 cm. The displacement speed varies between 2.3 and 3.4 km/h *sensu* Alexander (1976).

Table 1. Measurements (average, in centimeters and degrees) of the ornithopod trackways (OT) from the Tereñes (Asturias, Spain).

	OT1	OT2	OT3
Pes length (L)	28.0	30.3	28.8
Pes width (W)	36.2	35.3	34,8
L/W	0.77	0.86	0.83
Digit II length	9.8	8.6	9.8
Digit III length	11.7	12.2	11.8
Digit IV length	9.0	9.1	8.5
Interdigital angle II-III	58	55	38
Interdigital angle III-IV	52	57	43
Pace	79.5	68.6	64.3
Stride	159.3	130.8	126.4
Pace angulation	163	151	151
Hip height (L > 25; h = 5.9 L)	165.2	178.8	169.9
Velocity (km/h)	3.4	2.3	2.3

Isolated footprints and trackways belonging to large ornithopods are very common in the Cretaceous record; some relatively well-preserved examples are shown in Table 2.

In contrast, only three references to large Jurassic ornithopod tracks have been reported, and they are from Germany (Diedrich, 2011), Portugal (Mateus and Milan, 2008), and Yemen (Schulp and Al-Wosabi, 2012). This low number of clear medium-to-large-sized ornithopod tracks could be due to the very difficult problem of distinguishing between theropod and ornithopod tracks (Schulp and Al-Wosabi, 2012; Castanera et al., 2013a,b). The German footprint is longer than wide and the divarication angle is low. The impression of digit III is relatively longer than the others and is medially turned near the end. Based on the footprint outline and the poor preservation (probably undertracks), we consider a theropod rather than an ornithopod dinosaur to have been the trackmaker. The Portuguese track, which is as broad

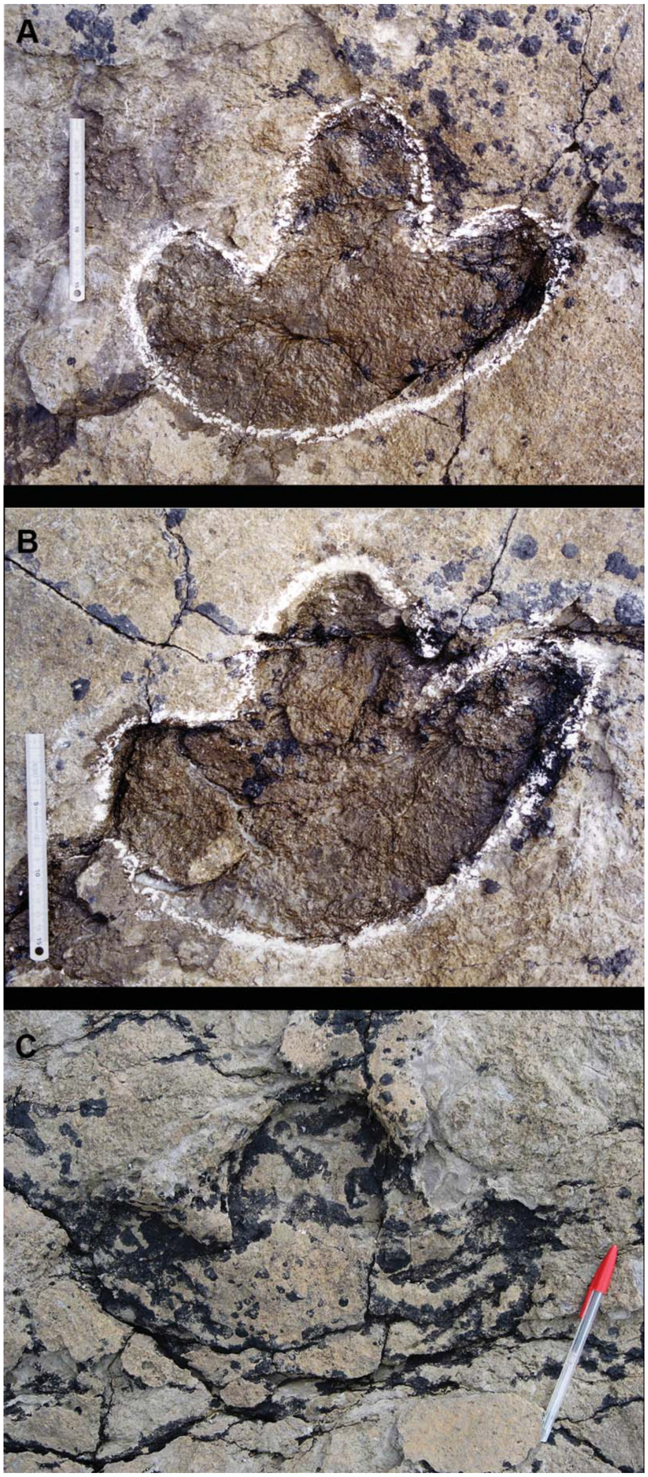

Figure 5. Best preserved footprints of the ornithopod tracksite. A. Track 3 in OT1. B. Track 3 in OT2. C. Track 6 in OT3. The scale is 15 cm.

as long, is typical of ornithopods, but it has well-developed, relatively long, and narrow digits, as do theropods. When tracks are isolated and not well-preserved (as in this case), in that they do not show diagnostic characters, it is difficult to distinguish whether the trackmaker was a theropod or an ornithopod (see Castanera et al., 2013b). Mateus and Milàn (2008) assigned the Portuguese footprint to an ornithopod, but we cannot rule out the possibility of a theropod affinity. Sometimes the footprints even show a different outline along the same trackway because the extramorphologic characters play an important role in the preservation of the tracks (Sarjeant, 1988; Thulborn, 1990; Razzoloni et al., 2014). This is the case of Yemeni tracksite; but beside that, some of the Yemeni tracks show asymmetry, with relatively long digit III impressions, medially rotated, and a low divarication angle. The pace or step is short, but the pace angulation is high. These characteristics are more related to theropod than to ornithopod trackways.

Thus the Tereñes footprints are the only ones that may reasonably be attributed to medium-sized Jurassic ornithopods.

Ichnotaxonomic attribution

Relatively large tridactyl and mesaxonic footprints, wider than long or as long as wide, were often attributed to medium-large ornithopods by numerous authors, including Thulborn (1990), Dalla Vecchia et al. (2002), Farlow et al. (2006), and Lockley et al. (2014). Moreover, they proposed other characteristics for these tracks, such as high divarication angle, symmetrical and posteriorly rounded or bilobed "heel," relatively short and stout digits with rounded or blunt distal part, weak mesaxony (Lockley, 2009) and sometimes quadripartite configuration. The trackways are wide with a low pace angulation and an inward footprint rotation. On the basis of these criteria, a number of ichnogenera were created belonging to large ornithopods; the most popular are *Amblydactylus* (Sternberg, 1932), *Caririchnium* (Leonardi, 1984), *Iguanodontipus* (Sarjeant et al., 1998), *Ornithopodichnus* (Kim et al., 2009), *Hadrosauropodus* (Lockley et al., 2003), and *Jiayinosauropus* (Dong et al., 2003); a review was recently published by Lockley et al. (2014) and Díaz-Martínez et al. (2015).

Tracks of the same trackway may be very different in shape due to extramorphological features (Sarjeant, 1988; Thulborn, 1990; Razzolini et al., 2014). For this reason, to create a new ichnotaxon it is necessary, in our opinion, that the footprints be part of a trackway with at least four consecutive tracks in bipedal dinosaurs and eight in quadrupedal dinosaurs, in order to compare two left or two right tracks or pairs, respectively; something similar was proposed by Peabody (1955) and Sarjeant (1989). In special occasions, when the preservation is very good, only two footprints or two pairs would be used, in bipedal and quadrupedal, respectively. On the other hand, undertracks are very common in the geological record, and in specific situations, theropods may produce

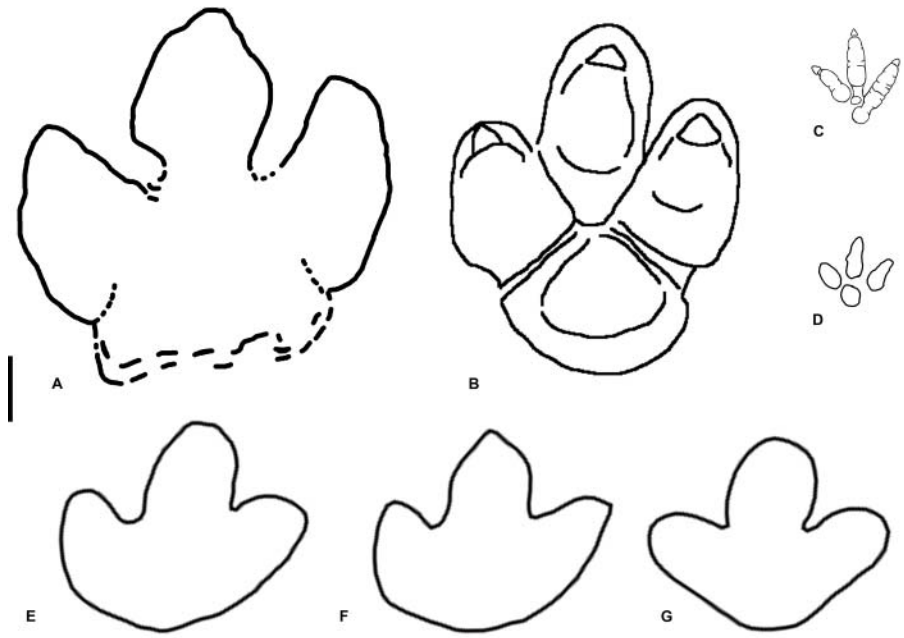

Figure 6. Comparison between some ichnogenera belonging to large and small ornithopods and the best preserved footprints of the Tereñes tracksite. A. *Hadrosauropodus* (after Lockley et al., 2003). B. *Caririchnium* (after Leonardi, 1984). C. *Anomoepus* (after Olsen and Rainforth, 2003). D. *Dinehichnus* (after Lockley et al., 1998a). E.-G. The Tereñes footprints (n° 3 in OT1, n° 3 in OT2, and n° 6 in OT4). Scale bar 10 cm.

undertracks with ornithopod outlines, as has happened in extensive samples from the Jurassic of Asturias (García-Ramos et al., 2009; Piñuela, 2012; Piñuela Suárez, 2015). Regarding the above criteria, we question the ichnogenera *Amblydactylus* and *Jiayinosauropus* because they were each described from only one poorly-preserved track. Similarly, we question *Iguanodontipus* and *Ornithopodichnus* because they were likely undertracks, produced by theropods in the case of *Iguanodontipus*. These problems will be discussed soon in a forthcoming paper. Dalla Vecchia et al. (2002, p. 30) also noted several problems with *Iguanodontipus* and concluded that "either *Iguanodontipus* includes theropod tracks, or trackway parameters and some footprint features are of little use in distinguishing between large theropod and

Table 2. Occurrences of Cretaceous medium-large ornithopod footprints around the world.

Country	Authors
Australia	Romilio and Salisbury (2011)
Bolivia	Leonardi (1984)
Brasil	Leonardi (1979)
Canada	Sternberg (1932); Currie (1983, 1989, 1995); Currie and Sarjeant (1979); Currie et al. (1991); Weems and Bachman (1997); Gangloff et al. (2004); Fanti et al. (2013)
China	You and Azuma (1995); Zhang et al. (2006); Xing et al. (2007, 2009, 2010)
Germany	Fischer (1998); Diedrich (2004); Hornung et al. (2012)
Japan	Matsukawa et al. (1997); the authors attributed these trackways to ornithopods, but the theropod affinity cannot be ruled out
Mexico	Rodríguez de la Rosa et al. (2004)
Mongolia	Currie et al. (2003); Ishigaki et al. (2009)
Norway	Lapparent (1962)
Poland	Gierliński et al. (2008)
Portugal	Santos et al. (2013)
Peru	Jaillard et al. (1993)
South Korea	Lim et al. (1989, 1995); Lee et al. (2000); Huh et al. (2001); Paik et al. (2006); Lockley et al. (2006, 2012a); Kim et al. (2009)
Spain	Moratalla et al. (1988, 1992,1994); Sanz et al. (1999); Barco et al. (2001); Llompart (2006); Pascual-Arribas et al. (2009); Cobos and Gascó (2012); Vila et al. (2013); García-Ortiz and Pérez-Lorente (2014)
Switzerland	Meyer and Thuring (2003)
UK	Dollo (1906); Delair and Lander (1973); Norman (1980); Delair (1989); Woodhams and Hines (1989); Sarjeant et al. (1998); Wright (1999); Lockwood et al. (2014)
USA	Ostrom (1972); Lockley et al. (1983, 1992, 2000, 2003); Lockley (1987, 1995, 1997); Parker and Rowley (1989); Carpenter (1992); Lockley and Hunt (1995); Cotton et al. (1998); Hamblin and Foster (2000); Matsukawa et al. (2001); Hunt and Lucas (2003); Fiorillo and Parrish (2004); Lucas et al. (2011); Fiorillo et al. (2014)

Table 3. Occurrences of Cretaceous parallel ornithopod trackways representing gregariousness, in the fossil record.

Country	Authors
Canada	Currie (1983, 1995)
China	Zhang et al. (2006)
Japan	Matsukawa et al. (1997); the authors attributed these trackways to ornithopods, but the theropod affinity cannot be ruled out
South Korea	Lim et al. (1989, 1995); Lee et al. (2000); Huh et al. (2001); Paik et al. (2006); Lockley et al. (2006, 2012a,b); Kim et al. (2009)
Spain	Agirrezabala et al. (1985); Casanovas Cladellas et al. (1993); Pérez-Lorente et al. (1997); Castanera et al. (2013a,b); García-Ortiz and Pérez-Lorente (2014)
UK	Delair and Lander (1973); Delair (1989) this one is uncertain
USA	Ostrom (1972); Lockley et al. (1983, 1992); Lockley (1987, 1995, 1997); Carpenter (1992); Lockley and Hunt (1995); Cotton et al. (1998); Matsukawa et al. (2001); Fiorillo et al. (2014)

ornithopod tracks." A similar case was observed by Castanera et al. (2013b), who provisionally classified *Therangospodus oncalensis*, thought to be a theropod, as *Iguanodontipus oncalensis*.

Hadrosauropodus (Lockley et al., 2003) was described on the base of a trackway with large tridactyl tracks (55 cm long) rotated inwardly and short pace (about twice the foot length). The footprints, wider than long, have an oval pad impression for each digit. The axis of the digits is parallel to the track axis. The heel is rounded, and the proximal margin is bilobed. Small manus prints can be associated. The divarication angle, the bilobed heel, and the presence of four oval impressions (three for the digits and one for the heel) are very different from the Tereñes tracks (Fig. 6A). For this reason, we cannot include the Asturian footprints in this ichnogenus.

The ichnotype of *Caririchnium* (Leonardi, 1984) is based on a quadrupedal dinosaur trackway from Sousa (Paraiba, Brazil) in which the pes prints were large and tridactyl, with short digits, ending in a small and rounded hoof. They show four pads (three belonging to each digit and one corresponding to the sole), which are separated from each other by short ridges (Fig. 6B). Due to these features, together with the presence of manus prints, not preserved in the Asturian tracks, we disregarded this ichnogenus for the Tereñes footprints.

Despite meticulous work by Lockley et al. (2014), the ichnogenera belonging to large ornithopods need more detailed and deeper revisions. The *Caririchnium* and *Hadrosauropodus* track outlines are very different from those of the Tereñes prints, so the Asturian tracks are not assigned to either ichnogenus. However, the preservation of the present material is not sufficient to create a new ichnotaxon.

Identification of possible trackmaker

Gierliński and Sabath (2008) interpreted these footprints from Tereñes as belonging to stegosaurs (*Stegopodus*), with bipedal and digitigrade progression. *Stegopodus* (Lockley and Hunt, 1998) was created on the basis of only one manus print and is not well preserved, so the validity of this ichnogenus could be called into question. Gierliński and Sabath (2008) included the pes track found with the holotype manus of *Stegopodus* in their revised description of this ichnogenus. However, this proposal does not remove the ambiguity about the morphology of this putative stegosaurian pes track. Some of the other prints proposed as *Stegopodus* by Gierliński and Sabath (2008) show the typical characteristics of deep undertracks (García-Ramos et al., 2009; Piñuela, 2012; Piñuela Suárez, 2015), and some of them may even have been made by theropods.

Stegosaur tracks and trackways attributed to another stegosaur ichnogenus, *Deltapodus* (Whyte and Romano, 1994; 2001), are common in the Upper Jurassic tracksites of Asturias (García-Ramos et al., 2008; Piñuela et al., 2007, 2014; Piñuela Suárez, 2015). The pes tracks are tridactyl and very elongated with blade-shaped or subtriangular outlines and blunt and extremely short digits, a morphology quite different from that which is recognized in the Tereñes trackways.

Moreover, stegosaur dinosaurs are considered as obligated quadrupeds by most researchers (Galton and Upchurch, 2004; Maidment and Barret, 2014; Maidment et al., 2014), so we reject the possibility of a stegosaur for the Tereñes trackmaker.

Based on the morphology and size of the Asturian prints, we assign them to medium-sized ornithopods, which are represented by Iguanodontia, excluding Dryosauridae (Norman, 2004). Concerning the age (Kimmeridgian) of the Tereñes tracksite, *Tenontosaurus, Rhabdodon, Zalmoxes*, and the *Hadrosaurifomes* are excluded from the list. Only the non-hadrosaurifom ankylopollexians would be candidates for the Tereñes trackmaker. The basal members of the Ankylopollexia, together with the dryosaurids, are the most abundant ornithopods in the Late Jurassic of the Iberian Peninsula (Ruiz-Omeñaca et al., 2012).

The largest ornithopod from the Jurassic of Portugal is *Draconyx loureiroi* (Mateus and Antunes, 2001). If the femur of the holotype were complete (about 80 cm), the estimated hip height would be about two meters (Mateus and Milàn, 2008); this size would correspond with the

Tereñes ornithopod trackmakers, with a hip height between 165 and 178 cm (*sensu* Thulborn, 1990).

Up to now, two dorsal vertebral centra are the only ornithopod bones known from the Tereñes Formation. They were identified as a juvenile indeterminate ankylopollexian (Ruiz-Omeñaca et al., 2008). Three anterior caudal vertebrae and the distal half of a right ischium from the Lastres Formation (Kimmeridgian) were assigned to Ankylopollexia indet (Ruiz-Omeñaca et al., 2012). A fragment of ossified tendon and a fragment of a right pubis were tentatively regarded to Ankylopollexia indet and Dryosauridae indet, respectively (Ruiz-Omeñaca et al., 2012). One isolated ornithopod tooth from the Lastres Formation is similar to that of C*amptosaurus dispar* from the Kimmeridgian-Tithonian of the USA, *Camptosaurus prestwichii* from the Kimmeridgian of the United Kingdom, and *Draconyx loureiroi* from Portugal, but also to that of the Late Jurassic *Dysalotosaurus lettowvorbecki* from Tanzania. Consequently, the tooth was assigned to Dryomorpha indet (Ruiz-Omeñaca et al., 2010). On the basis of current knowledge, *Camptosaurus prestwichii* was assigned to the genera *Cumnoria* and C*amptosaurus*, which includes a single species *C. dispar*, and is restricted to the Kimmeridgian–Tithonian of western North America (McDonald, 2011).

Taking into account the scarce Asturian ornithopod bone record and ruling out dryosaurids because they are smaller and more gracile than the Asturian trackmaker, a dinosaur related to *Draconyx* or *Cumnoria*, with a large, stout foot becomes a reasonable candidate for the Tereñes trackmakers.

Palaeoecological inferences: Gregarious behavior

Two main criteria must be satisfied for inferring gregarious behavior based on tracks: firstly, there have to be several trackways with similar footprints on the same surface; and secondly, the trackways must be parallel with the same direction of travel (Lockley and Matsukawa, 1999). Other suggested criteria to determine gregarious behavior are similarities in the intertrackway spacing (Lockley, 1989); footprint depth; and speed values and gait. Castanera et al. (2014) also analyzed the pace rhythm and transect length. However, the presence of a geographical barrier (e.g., a river channel, the sea or lake coastline) would force the dinosaurs to walk along it at different times, leaving tracks and trackways with similar orientations, and so not necessarily gregarious.

When individuals are travelling together in the same group and at the same time, they may push against each other, and their trackways may intersect occasionally (seen among modern herd animals). This behavior is visible in the two central trackways of Tereñes site, where there is a partial overlap of the footprint 2 in OT2 and the footprint 2 in OT3. The trackways separate in the two next steps, as a result of the impact force between the adjacent trackmakers, and then they move away and continue parallel (Fig. 4).

Stratigraphical and sedimentological information indicate that the medium-sized Asturian ornithopods were moving N-S on the extensive and flat muddy coast adjacent to a shelf lagoon. Statistical measurements of sedimentary structures, including wave ripples, indicate that the orientation of the coastline was NW-SE (Valenzuela, 1988). No evidence concerning a physically controlled pathway was found along this coastal plain.

Taking into account the parallel trackways indicating the same movement direction, as well as the similarity in the shape, size, and depth of the footprints and the lack of a recognizable geographic barrier, we suggest at least four medium-sized ornithopods travelling as a small group.

Parallel ornithopod trackways representing gregarious groups are relatively frequent in the Cretaceous record. Convincing examples are reported on Table 3.

However, only three references about ornithopod gregariousness are known for the Jurassic. One is from the Lower Jurassic of Utah where Lockley et al. (1998b) recorded three parallel trackways (*Anomoepus* or *Moyenisauropus*-like). The others are from the USA and Portugal (*Dinehichnus*), where Lockley et al. (1998a) reported the first convincing evidence of Late Jurassic ornithopod trackways.

Anomoepus (Hitchcock, 1848) is known from the Lower Jurassic of North America, Europe, and southern Africa. Olsen and Rainforth (2003) described these tracks as small- to medium-sized, asymmetrical and tridactyl, and almost as wide as long. Digits are relatively long and slender. The digital pad impressions are present, and the metatarsal-phalangeal pad of digit IV is located almost directly in line with the axis of digit III.

Dinehichnus (Lockley et al., 1998a), described from the Late Jurassic of Utah (USA) and Portugal, is a small to medium size tridactyl track and almost as broad as long, but in this case symmetric. There is a single elongate impression for each digit, sometimes with tapered claws, and they are relatively long and slender.

The trackmakers of *Anomoepus* and *Dinehichnus* were small to medium individuals with a much more gracile hind-foot than the Tereñes ornithopods, producing very different tracks (Fig. 6C, D). Thus, parallel trackways belonging to medium-sized ornithopods are not known in the Jurassic record, except those described here, showing that these large and robust dinosaurs adopted gregarious habits as early as the Late Jurassic and, at least, by the Kimmeridgian. In addition, as we suggested in the previous section, the best candidates to be the trackmakers are basal Ankyllopollexia. Thus, this would be the oldest evidence of gregarious behavior in this group of ornithopods and one of the few (see Castanera et al., 2013a) in this "basal" ornithopods.

Conclusions

The tridactyl Asturian prints, wider than long, with broad and blunt digits, high divarication angle and rounded and symmetrical "heel," are attributed to medium-sized bipedal ornithopods. They are not assigned to any of the large known Cretaceous ichnogenera because some of the latter need revising, and furthermore, *Caririchnium* and *Hadrosauropodus* show very different outlines. The preservation of the Tereñes footprints is not of sufficient quality to create a new ichnogenus.

These footprints are the first well-authenticated record of medium-sized ornithopods from the Jurassic. On the basis of present knowledge, it can be determined that Asturian trackmakers were ankylopollexian dinosaurs, probably related to *Draconyx* or *Cumnoria*, because *Camptosaurus* is restricted, at least for now, to USA.

Gregariousness among medium-sized ornithopods is indicated for the first time in the Jurassic record, on the basis of footprints, showing that these robust dinosaurs adopted gregarious habits as early as the Kimmeridgian.

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