First record of stegosaur dinosaur tracks in the Lower Cretaceous (Berriasian) of Europe (Oncala group, Soria, Spain)

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Pascual C., Canudo J. I., Hernández N., Barco J. L. & Castanera D. 2012. — First record of stegosaur dinosaur tracks in the Lower Cretaceous (Berriasian) of Europe (Oncala group, Soria, Spain). *Geodiversitas* 34 (2): 297-312. http://dx.doi.org/10.5252/g2012n2a4

ABSTRACT

This paper describes for the first time a stegosaur track from the Cretaceous of Europe. It focuses on a cast that preserves pes-manus tracks recovered in the Huérteles Alloformation of the Berriasian of Soria (northern Spain). This track has been assigned to *Deltapodus* isp. on the basis of the pes morphology. Nonetheless, in the manus lacks the claw-shaped imprint of the pollex that

KEY WORDS
Stegosauria,
Deltapodus,
Berriasian,
Cameros Basin,
Soria,
Spain.

characterizes *Deltapodus brodricki* Whyte & Romano, 1994, the type ichnospecies of the ichnogenus *Deltapodus* Whyte & Romano, 1994. The stegosaurs were abundant and diverse in the Late Jurassic of the Iberian Peninsula, as evidenced by their ichnological and osseous record. The presence of *Deltapodus* isp. provides further support for the view that the stegosaurs did not disappear in the Jurassic-Cretaceous boundary crisis and kept going on the Iberian Peninsula for at least for the initial part of the Early Cretaceous.

MOTS CLÉS
Stegosauria,
Deltapodus,
Berriasien,
bassin de Cameros,
Soria,
Espagne.

RÉSUMÉ

Premier signalement de traces de stégosaure du Crétacé inférieur (Berriasien) d'Europe (groupe Oncala, Soria, Espagne).

Ce travail décrit pour la première fois une empreinte de stégosaure du Crétacé d'Europe. Il s'agit d'un moulage naturel qui conserve les ichnites de pieds et de mains, provenant de l'alloformation de Huérteles du Berriasien de Soria (nord de l'Espagne). Cette empreinte a été identifiée comme appartenant à *Deltapodus* sp., sur la base de la morphologie du pied. Cependant, dans la main, manque l'empreinte des griffes du pouce qui caractérise *Deltapodus brodricki* Whyte & Romano, 1995, l'espèce type de l'ichnogenre *Deltapodus* Whyte & Romano, 1995. Les stégosaures ont été très nombreux et variés durant le Jurassique supérieur sur la Péninsule Ibérique, tel que l'indique leur registre iconologique et osseux. La présence de *Deltapodus* isp. montre que les stégosaures n'ont pas complètement disparu lors de la crise de la limite Jurassique-Crétacé et qu'ils ont survécu pendant une partie du Crétacé inférieur dans la Péninsule Ibérique.

INTRODUCTION

The stegosaurs were a group of ornithischian dinosaurs that were relatively frequent during the Middle and Late Jurassic on a worldwide scale (Galton & Upchurch 2004) and during the Late Jurassic on the Iberian Peninsula (Pereda-Suberbiola & Galton 2001). However, until just a few years ago the ichnological record attributed to this group was very notable by its absence. One of the possible reasons suggested for this scarcity is that the habitat where these dinosaurs lived was unsuitable for the formation and preservation of tracks on account of the lack of moisture in the sediment (Dodson *et al.* 1980; Lockley & Hunt 1995). Other possibilities proposed are that this rareness is a consequence of misidentifications or that tracks will appear in the future in outcrops yet to be explored (Lockley & Hunt 1998) or even in well-known formations, as has happened with the material studied in this publication. Whatever the case, this lack of an ichnite record is in part an artefact resulting from the poor preservation of the tracks, which in quite a few cases has meant that what were initially considered to be sauropod tracks only subsequently came to be correctly identified as produced by stegosaurs (Whyte & Romano 2001; García-Ramos *et al.* 2008).

The few tracks attributed to stegosaurs are located in concrete areas and ages of the worldwide record: in the Middle Jurassic of the Cleveland Basin, Yorkshire, England (Whyte & Romano 1994, 2001; Romano & Whyte 2003; Whyte *et al.* 2007); in the Morrison Formation of the Upper Jurassic of Utah (Lockley & Hunt 1998; Milàn & Chiappe 2009); in the Upper Jurassic of Poland (Gierlinski & Sabath 2002); in the Lower Cretaceous of Australia (Long 1998); and recently, in the Upper Jurassic of Morocco (Belvedere & Mietto 2010). In the Iberian Peninsula they have been found

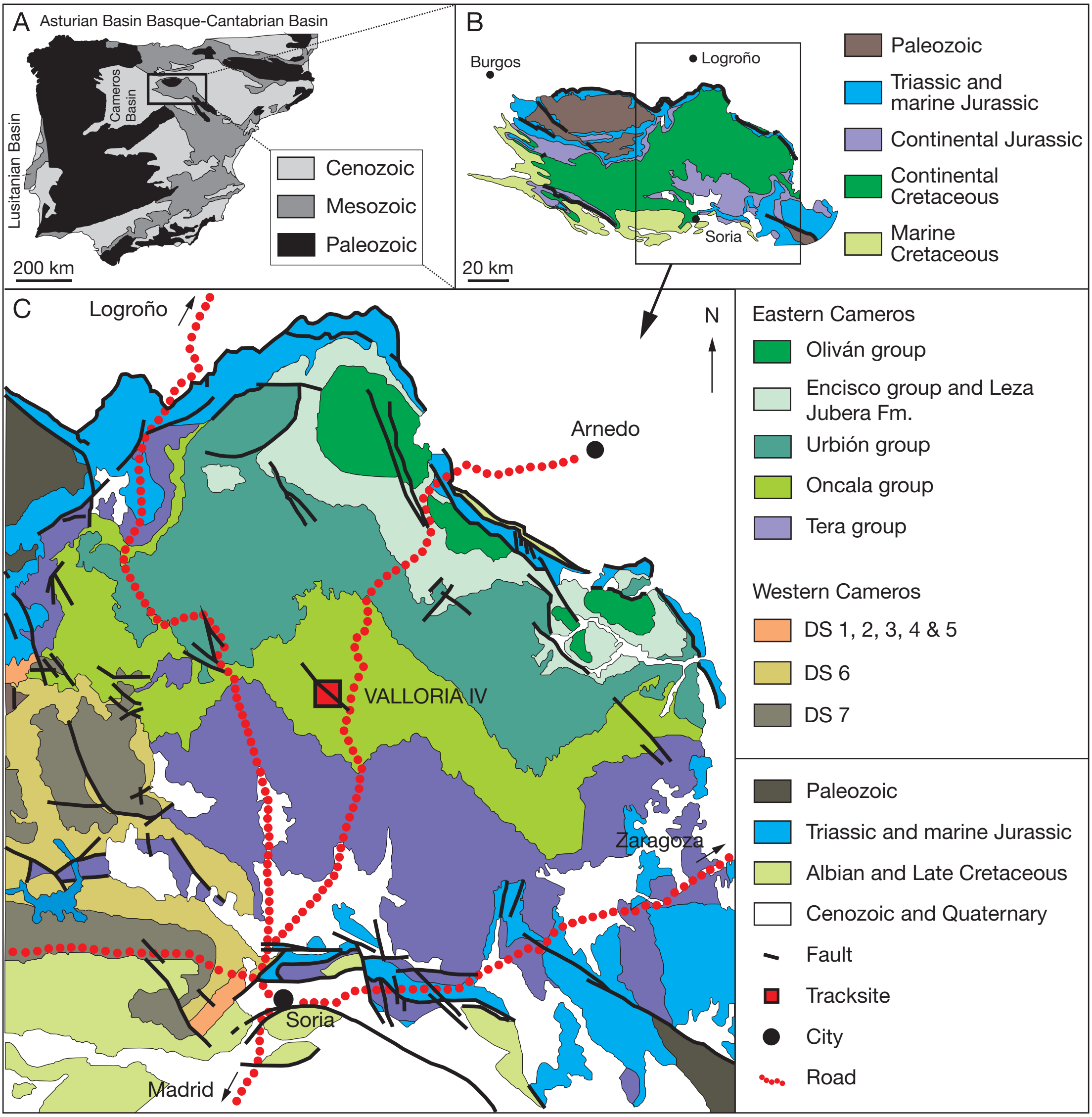

Fig. 1. — Geographical and geological situation of Valloria in Las Aldehuelas, Soria, Spain: **A**, geological sketch of Iberian Peninsula with the geographical position of the Cameros Basin; **B**, geological Map of the Cameros Basin; **C**, detail of the geology of Valloria locality. Based on Moratalla & Hernán (2005). Abbreviation: **DS**, depositional sequence.

in the Kimmeridgian of Asturias (García-Ramos *et al.* 2006; Lockley *et al.* 2008; Piñuela *et al.* 2009), in the Kimmeridgian-Tithonian of Portugal (Antunes & Mateus 2003; Mateus & Milàn 2008, 2010; Mateus *et al.* 2011), and in the Jurassic-Cretaceous boundary of Teruel (Cobos *et al.* 2010).

The Cameros Basin is a megatracksite that includes a great number of ichnological outcrops with varied and abundant tracks made by Mesozoic reptiles from the Lower Cretaceous, especially dinosaurs (Moratalla & Sanz 1997; Pérez-Lorente 2002; Hernández-Medrano *et al.* 2008). The beginning of the Cretaceous is especially rich in ichnites in the province of Soria (Fig. 1), where dinosaur tracks made by theropods, ornithopods, sauropods and birds/aviforms have been described, as well as tracks made by pterosaurs, crocodiles and turtles (Moratalla & Sanz 1997; Pérez-Lorente 2002; Barco *et al.* 2006; Hernández-Medrano *et al.* 2008). Up to now, however, no track attributed to Stegosauria had been described in the Cameros Basin, or indeed in any other region of the European Cretaceous.

The aim of this paper is to describe for the first time a pes-manus set attributed to a stegosaur, recovered from the Lower Cretaceous of the Cameros Basin. Moreover, the assignation of the possible trackmaker will be discussed, as well as the palaeobiogeographical implications that can be deduced.

GEOGRAPHICAL AND GEOLOGICAL LOCATION

The tracks studied in this paper were found isolated in the Valloria IV tracksite. Geographically, this is located in the eastern Cameros Basin, in the northern sector of the Iberian Range (Fig. 1). The tracksite is located on the right bank of the stream Fuente Mingo, just a few metres from the locality of Valloria in Las Aldehuelas, Soria, Spain (National Topographical Map of Spain 1:50 000, no. 280). Its UTM coordinates are: x = 551 269; y = 4 651 952; z = 1230 m. The Valloria IV tracksite forms part of a series of small outcroppings located close to one another and named Valloria I to X. A rich and diverse range of vertebrate tracks is preserved in them, including 450 tracks made by theropod dinosaurs, sauropods, ornithopods, birds/aviforms and pterosaurs (Hernández-Medrano *et al.* 2008). The tracks at Valloria form part of a project spotlighting palaeontological sites known as the “Ruta de las Icnitas de las Tierras Altas de Soria”, which seeks to protect the most significant and easily accessible tracksites so they can be visited by the public (Barco *et al.* 2009).

Lithologically, Valloria IV is composed of a set of levels of muddy sandstones and grey sandy siltstone, which is occasionally very dark with a high organic matter content. There are also intercalations of slightly calcareous muddy sandstones. The tracks under study come from a layer of greenish-grey muddy sandstone. The end of the Upper Jurassic and beginning of the Lower Cretaceous saw the deposition of geological units greatly influenced by tectonic activity, with formations that were very thick at their depocentre but that rapidly pinched out at the edges, giving rise to boundaries that are sometimes difficult to interpret. As a result, diverse nomenclatures have been proposed for these geological units, and the boundaries have varied with the authors in question. Nonetheless, identifying the Valloria outcroppings poses few problems. The materials belong to subunit IVb of the Huérteles Alloformation (Gómez Fernández & Meléndez 1994), included in the Oncala group (Tischer 1966), which forms part of the Tithonian-Berriasian deposit sequence (Alonso & Mas 2003).

The sedimentation of the Huérteles Alloformation was produced in a playa-lake system with a marked asymmetry in the distribution of its environments. The materials from the Valloria IV tracksite are of a terrigenous nature and were deposited in the proximal environments of this complex system (Gómez Fernández & Meléndez 1994). The estimated age of the Huérteles Alloformation is Berriasian, possibly Middle Berriasian (Martín-Closas & Alonso Millán 1998; Schudack & Schudack 2009). This datation has been proposed on the basis of the content of ostracods and charophytes and by stratigraphic correlation.

MATERIAL AND METHODS

ABBREVIATIONS

MNS	Museo Numantino de Soria, Spain.

Other abbreviations

h	acetabular height;
L_f	length of pes;
L_h	length of manus;
IH	heteropody index = $(Lf \times Wf)/(Lh \times Wh)$;
W_f	width of pes;
W_h	width of manus.

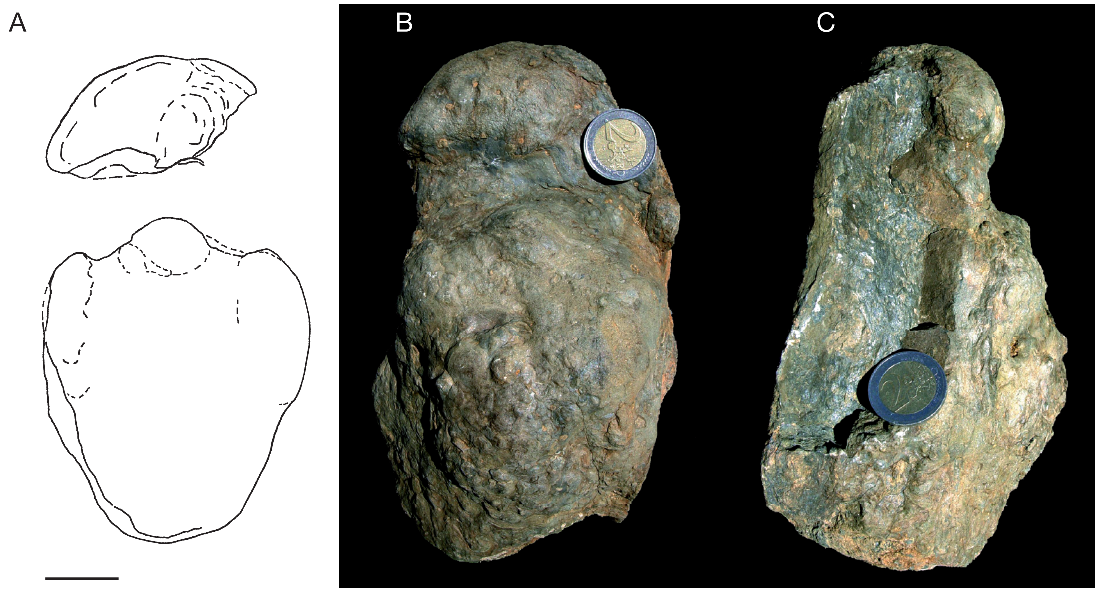

Fig. 2. — Holotype of *Deltapodus* isp. (MNS 2009/64) from the Early Cretaceous (Berriasian) of Soria (Spain): **A**, interpretative drawing, made from the bottom of the track, reflecting the true shape of the foot in plantar (**B**) and lateral (**C**) views. Scale bar: 2.5 cm.

Material

Deltapodus isp. (MNS 2009/64) is deposited in the Museo Numantino de Soria, Spain. The acronym used refers to the name of the museum, the year of inscription, and the registration number.

Methods

The width and length of the tracks were measured in accordance with the traditional norms (perpendicular and parallel to the anteroposterior axis of the track, respectively: Thulborn 1990; Romero-Molina *et al.* 2003). The heteropody was calculated in accordance with the criteria proposed by Dutuit & Ouazzou (1980), in a simplified form: IH = $(L_f \times W_f)/(L_h \times W_h)$. The acetabular height was determined on the basis of reconstructions of stegosaur skeletons. The Sorby Geology Group of the University of Sheffield also calculates that it is equivalent to 6 times the width of manus or to 5 times the length of pes. As regards the shoulder height, they consider that it can be calculated by multiplying the width of pes by 3.5. There is no model specifically for calculating the length of the trackmaker in stegosaurs, in consequence of which this was obtained as a function of the ratio between h, using data from a *Stegosaurus* skeleton, and the value of h obtained as indicated above.

SYSTEMATICS

Order ORNITHISCHIA Seeley, 1887
Suborder THYREOPHORA Nopcsa, 1915
Clade EURYPODA Sereno, 1986
Infraorder STEGOSAURIA Marsh, 1877
Genus *Deltapodus* Whyte & Romano, 1994

Deltapodus isp.
(Fig. 2)

Description

The specimen MNS 2009/64 refers to two tracks preserved in convex hyporelief that form a right pes-manus set attributed to a single individual. The size of the tracks is relatively small (Table 1). The pes track is subpentagonal in shape, elongated anteroposteriorly. It is mesaxonic, with imprints of three short, wide digits with blunt

TABLE 1. — Measurements (in cm) of ichnites attributed to stegosaurians. Hypothetical tracks from Thulborn (1990), *Stegopodus czerkasi* Lockley & Hunt, 1998 from Lockley & Hunt (1998), *Deltapodus brodricki* Whyte & Romano, 1994 from Whyte & Romano (2001), *Deltapodus brodricki* (MF) from Milàn & Chiappe (2009), *Deltapodus ibericus* Cobos, Royo-Torres, Luque, Alcalá & Mampel, 2010 from Cobos *et al.* (2010). Abbreviations: see Material and methods.

	Hypothetical tracks	***Stegopodus czerkasi***	***Deltapodus brodricki***	***Deltapodus brodricki* (MF)**	***Deltapodus ibericus***	***Deltapodus* isp. (Las Cuestas I)**
L_f	1.0 L_f	44 = 1.0 L_f	40 = 1.0 L_f	31 = 1.0 L_f	44 = 1.0 L_f	11.2 = 1.0 L_f
W_f	0.9 L_f	38 = 0.86 L_f	34 = 0.85 L_f	22 = 0.71 L_f	30 = 0.68 L_f	9 = 0.8 L_f
L_f/W_f	1.11	1.16	1.18	1.41	1.46	1.24
L_h	0.55 L_f	22 = 0.5 L_f	12.75 = 0.32 L_f	10 = 0.32 L_f	22 = 0.5 L_f	4.75 = 0.42 L_f
W_h	0.65 L_f	26 = 0.59 L_f	29.25 = 0.73 L_f	20 = 0.64 L_f	31 = 0.7 L_f	8 = 0.71 L_f
L_h/W_h	0.85	0.85	0.44	0.50	0.70	0.59
IH	2.5	2.9	3.65	3.41	1.93	2.65

endings at their anterior end. The width of the track is greatest in the anterior part (Figs 2; 3). Digit III is projected forwards, whereas II and IV are directed slightly medially and laterally, respectively. The imprint of the heel is large, wide and blunt. The depth of the pes track is variable, reaching a maximum (3 cm) towards the midpoint of its length. In its middle part an irregularity in the surface can be observed, possibly caused by the individual treading on what were probably plant remains.

The manus track is located in an anterior position in relation to pes and slightly medially in relation to its anteroposterior axis. The imprint of manus exhibits an ellipsoid shape with the longer axis running lateromedially and the shorter anteroposteriorly, and it is slightly entaxonic. Its mesodistal width is almost twice its anteroposterior length (Table 1). It is practically symmetrical and shows on its anterior edge the blunt, scarcely marked imprints of the distal end of digits I to IV. On its posterolateral side it displays a small depression, as a result of which the outline of the track at this point is concave.

The pes-manus set is characterized by the great inequality between the depths of the two tracks, the pes track (3 cm) being greater (pf_p/pf_m = 1.5) than the manus track (2 cm). The imprints of pes and manus do not touch one another, although they are very close (1.5 cm). The distance between the distal zones of the two tracks is 6.25 cm, and their anteroposterior axes form an angle of 14°.

DISCUSSION

The identification of thyreophoran tracks is based on the bone anatomy of pes and manus. There is little record of tracks attributed to stegosaur manus. According to the fossil remains that are known (Fig. 4A), they had functionally tetradactyl manus with the digits arranged in a semicircle (Gilmore 1914; Thulborn 1990; Senter 2010). Their phalanges and unguals were extremely short and, as they were digitigrade, it is thought that they must have been covered in tissue, as in elephants, in such a way that they hardly protruded (Galton 1990), rather similar to what must have occurred in sauropod manus (Farlow 1992). In the case of elephants, which are also digitigrade, the digits are surrounded by a large pad of fibrous connective tissue that constitutes most of the support surface, cushioning impacts and contributing to a better distribution of weight during movement. Noteworthy is that whereas digit I had an elongated and flat ungual phalange, the other unguals resembled small blunt protuberances, which were very similar to one another in some cases as *Stegosaurus* (Thulborn 1990), or decreased in size towards the outside as *Kentrosaurus* Hennig, 1915 (Thulborn 1990). The fossil remains of pes are more numerous and better known; they are functionally tridactyl, ending distally in the form of a hoof (Galton & Upchurch 2004). The central digit (III) is the largest, whereas II and IV are similar in length to one another. Although they resemble those of iguanodontids, the angle between

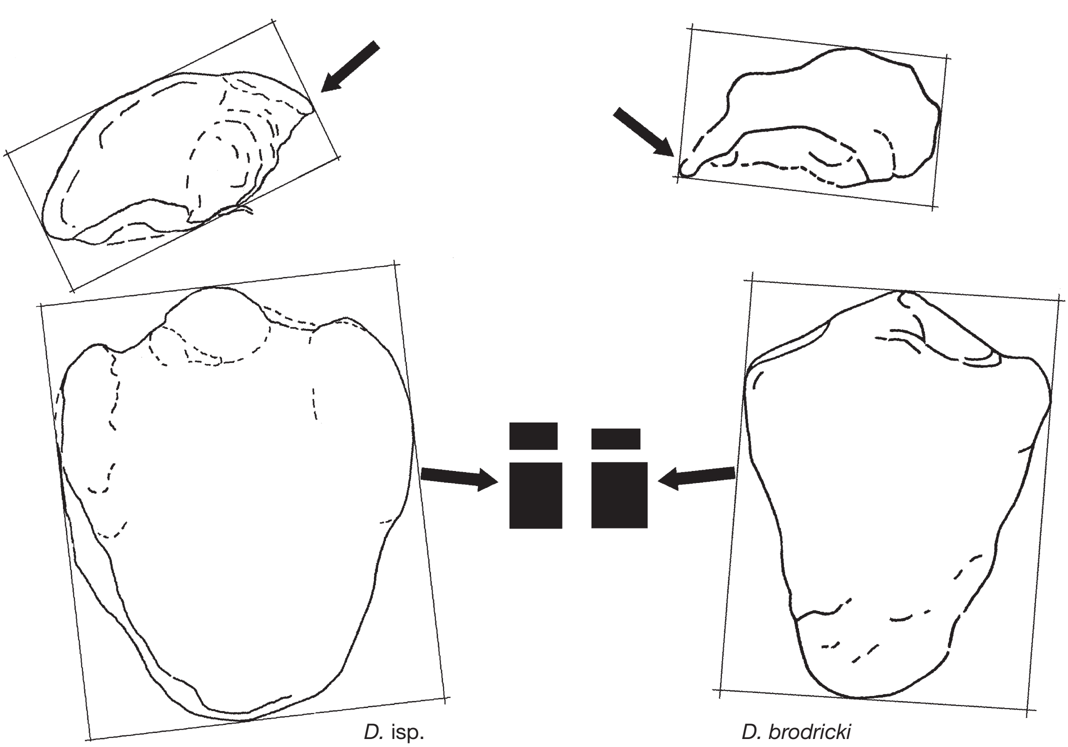

FIG. 3. — Comparison of *Deltapodus* isp. (specimen MNS 2009/64) and *Deltapodus brodricki* Whyte & Romano, 1994 (after Whyte & Romano 1994). The arrows shows the position of digit I. The squared ones are a representation of the surfaces of feet and hands. Not to scale.

them is slightly less, and there is a small proximal contact (Galton & Upchurch 2004).

On the basis of these bone characteristics, Thulborn (1990) established a hypothetical model for stegosaur pes and manus tracks (Fig. 4A). The manus tracks would be tetradactyl and slightly smaller in size than those of pes, which would be tridactyl and similar in appearance to the tracks of medium-size ornithopods. However, the possible existence of tissue surrounding the bones of pes and manus indicates a different morphology (Whyte & Romano 2001). Le Loeuff *et al.* (1999) describe some tracks that tally with Thulborn's model in the Lower Jurassic of France, but as Gierlinski & Sabath (2002) point out, no tracks with this morphology have been found in sediments from later than the Lower Jurassic. At present it is assumed that the pes tracks would be tridactyl, elongated, subtriangular or slightly subpentagonal, with marks made by short, blunt digits in the distal part, and an elongated and blunt heel in the proximal part (Whyte & Romano 1994, 2001) (Fig. 4B). Their overall appearance would be similar to that of sauropod pes. In both cases there would be a digital cushion in the posterior part, that would serve to support the metatarsals, which would be positioned slightly at an angle with respect to the ground (Lockley *et al.* 2008). The difference between the pes tracks of a stegosaur and those of a sauropod would inhere in the number of digits and in their forward-facing arrangement. It is possible that although digits II and IV were similar in length, the medial digit (II) was somewhat wider than the lateral (IV) (Gierlinski & Sabath 2002). For their part, the manus tracks have the shape of a narrow crescent, with few systematic characters (Whyte & Romano 1994, 2001; Milàn & Chiappe 2009).

As for the other major group of thyreophorans, the ankylosaurs, manus would be pentadactyl (Vickaryous *et al.* 2004), and pes would commonly be tetradactyl (the existence of pentadactyl and tridactyl pes has also been noted) (Fig. 4I). The tracks assigned to ankylosaurs show manus with an imprint of five digits arranged radially in the pattern of a star, whereas the pes tracks show the imprints of four digits and a wide and elongated heel (Carpenter 1984; Thulborn 1990). This would imply that their unguals, unlike those of stegosaurs, are not covered by a pad of tissue.

The MNS 2009/64 tracks show characteristics similar to those identified as produced by stegosaur manus and pes, respectively. The projection forward of digit III of pes is minimal with respect to the other two, a character that is not observed in any other type of tridactyl pes, either theropod or ornithopod. Likewise, the manus track, similar in appearance to that of the sauropods reveals faintly the imprints of digits arranged in a fan-shape. Furthermore, in accordance with the centre of gravity of these reptiles, the posterior extremities must have exerted greater pressure on the substratum than the anterior ones, which would have resulted in pes prints that were deeper than the manus prints. It has been possible to corroborate this at Valloria IV (Table 1), where the depth of the pedal imprint is 1.5 times that of the manual imprint. For all these reasons we consider that *Deltapodus* isp. was produced by a stegosaur. Given the size of the tracks, the height of the hip can be estimated at 54-56 cm and that of the shoulders at 28 cm. From these measurements it can be deduced that the trackmaker would have only been about 170 cm in length. As such, either it is a species of small stature, or it is a juvenile form of a different, larger species.

To date, only two ichnotaxa attributed to stegosaurians have been described: *Deltapodus brodricki* Whyte & Romano, 1994 and *Stegopodus czerkasi* Lockley & Hunt, 1998, although others have been described without a concrete ichnotaxon yet having been assigned. *Deltapodus brodricki* presents manus prints that are entaxonic, wider than long (L_h/W_h = *c.* 0.5), crescent-shaped, and with the mark of the pollex claw directed towards the axis of the track (Whyte & Romano 1994). The pes tracks are longer than wide ($L_f/W_f = 1.18$), mesaxonic, tridactyl, with short digits with blunt ends (Whyte & Romano 1994). The heel imprint is elongated, the tracks being twice as long as wide (Whyte & Romano 1994). Recently, Gierlinski & Sabath (2008) have suggested that *Deltapodus* was produced by thyreophorans distinct from stegosaurs, but taking into account the tridactyl configuration of the stegosaur pes, which coincides with that of *Deltapodus*, we agree with Milàn & Chiappe (2009) that the trackmaker responsible for this ichnogenus is a stegosaur. The ichnospecies *Stegopodus czerkasi* is described on the basis of a natural cast from the Morrison Formation in Utah (USA). *Stegopodus* is characterized by having a tetradactyl manus that is slightly wider than long, with well-defined but short, blunt digits. The associated pes is tridactyl, with long digits that have blunt distal endings (Lockley & Hunt 1998).

Stegopodus differs from *Deltapodus* in that the manus print presents four separated digits, with a subcircular outline and without an imprint of the pollex claw, even when the track is entaxonic with a pronounced digit I (Fig. 4). The imprint of the associated pes is asymmetrical, with relatively long digits, and is only slightly longer than wide. It should be pointed out that the pedal imprint is not included in the ichnospecies because there are doubts as to whether it belongs to the same specimen (Lockley & Hunt 1998). Recently, Gierlinski & Sabath (2008) have produced an amended diagnosis of *Stegopodus*, including tracks produced by bipedal dinosaurs assigned by other authors to ornithopods, for example from the Kimmeridgian of Tereñes in Spain (Lockley *et al.* 2008). Their main argument is that at the end of the Jurassic there is no record of ornithopods with pes robust enough to produce such tracks, as does occur in the Cretaceous. For these authors, the tracks could have been produced by hypothetical bipedal stegosaurians. In this context, however, it should be noted that all reconstructions of stegosaurians from the Late Jurassic and Early Cretaceous are of forms that are clearly quadrupedal (Galton & Upchurch 2004), and as such the current record for this period of time does not support

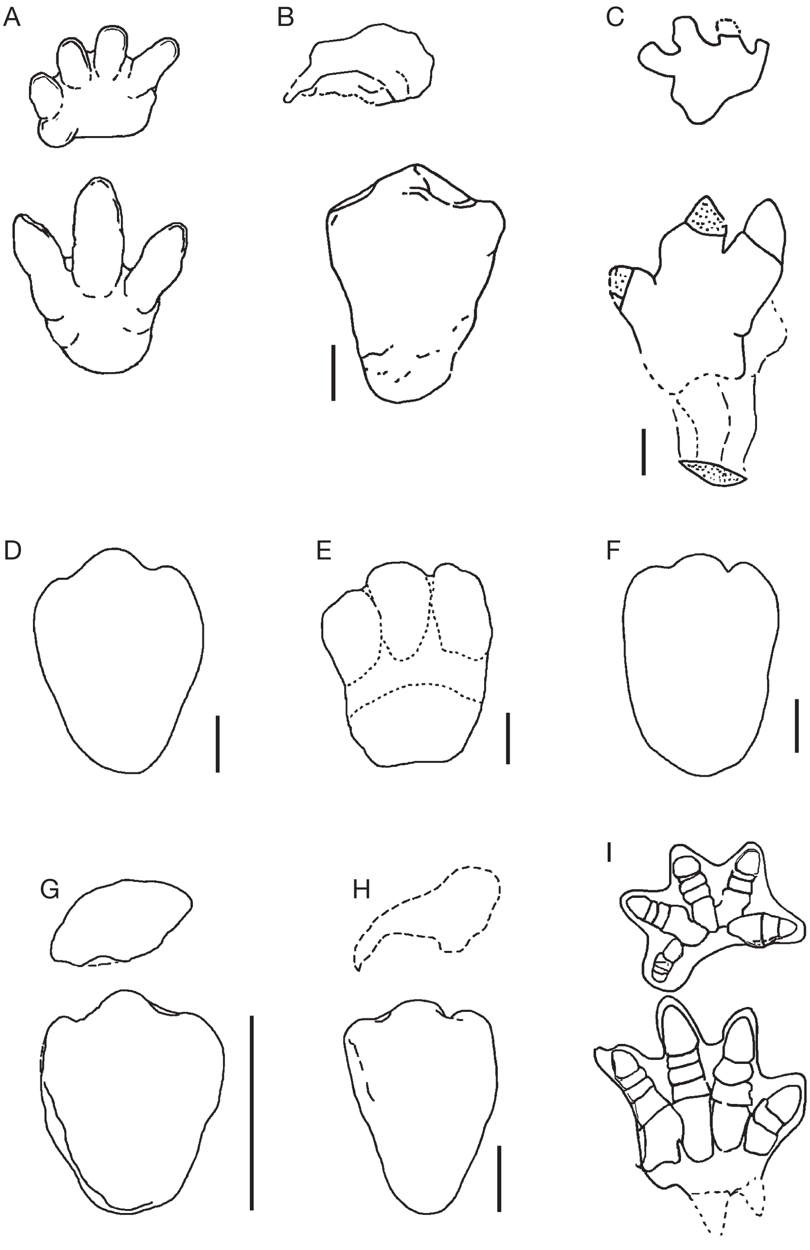

Fig. 4. — Comparison between *Deltapodus* isp. and other purported stegosaur and related tracks: **A**, hypothetical tracks of Stegosauridae from Thulborn (1990); **B**, *Deltapodus brodricki* Whyte & Romano, 1994 from the Middle Jurassic of England (Whyte & Romano 1994); **C**, *Stegopodus czerkasi* Lockley & Hunt, 1998 from the Salt Wash Member (Late Jurassic) of the Morrison Formation (Lockley & Hunt 1998); **D**, Stegosaur track from the Late Jurassic of Asturias, Spain (García-Ramos *et al.* 2006); **E**, Stegosaur pes print from the Lourinhã Formation (Late Jurassic) of Portugal (Mateus & Milàn 2010; Mateus *et al.* 2011); **F**, Stegosaur track from the Late Jurassic of Asturias, Spain (García-Ramos *et al.* 2006); **G**, *Deltapodus* isp., MNS 2009/64 from the Huérteles Alloformation (Berriasian, Early Cretaceous) of Spain; **H**, *Deltapodus brodricki* from Brushy Basin Member (Late Jurassic) of the Morrison Formation (Milàn & Chiappe 2009); **I**, hypothetical tracks of Ankylosauria based on *Sauropelta* (modified from Carpenter *et al.* 1984). Scale bars: 10 cm.

the hypothesis of bipedal stegosaurians. Moreover, Gierlinski & Sabath (2008) consider that the tracks similar to *Deltapodus* belong to ankylosaurs. Their principal argument is their resemblance of the tracks to *Tetrapodosaurus* Sternberg, 1932. It is an ichnogenus traditionally assigned to an ankylosaur. Nonetheless, the morphology both of pes and manus of the two ichnogenera is very different, and it thus seems inappropriate for them to belong to the same ichnotaxon. By the same token, it should be added that fossil remains of stegosaurians are abundant in the Late Jurassic of the Iberian Peninsula, even in the same formations as *Deltapodus* (Casanovas-Cladellas *et al.* 1995; García-Ramos *et al.* 2006; Escaso *et al.* 2007; Mateus *et al.* 2009; Piñuela *et al.* 2009; Cobos *et al.* 2010). By contrast, for this period of time the remains of ankylosaurs are virtually non-existent. For these reasons we follow those authors who relate *Deltapodus* to the stegosaurians.

MNS 2009/64 is clearly related to *Deltapodus*, sharing the general shape of pes and manus and the same L_f/W_f ratio (Table 1). Like *Deltapodus*, moreover, manus only presents the distal imprint of the digits, and pes is symmetrical and only shows the marks of the digit endings (Whyte & Romano 1994). By contrast, the manus associated with *Stegopodus* have the digits separated (Lockley & Hunt 1998).

Deltapodus only includes one ichnospecies, *Deltapodus brodricki,* from the Middle Jurassic of England (Whyte & Romano 1994), which has also been cited in the Upper Jurassic of North America (Milàn & Chiappe 2009). The morphological differences with respect to the tracks from Valloria IV are great enough to distinguish it from this ichnospecies. *Deltapodus* isp. lacks the claw-shaped imprint of the pollex that characterizes *D. brodricki* (Whyte *et al.* 2007; Milàn & Chiappe 2009); it has a relatively large manus; and the L_h/W_h ratio is greater. It is in general smaller in size than *D. brodricki*, although it would be included within the variation of the smallest specimens (Figs 3; 5).

The presence in the Iberian Peninsula of tracks assigned to *Deltapodus* is not new. They have been cited in the Kimmeridgian of Asturias (Piñuela *et al.* 2007, 2009; Gierlinski & Sabath 2008; García-Ramos *et al.* 2008) and the Kimmeridgian-Tithonian of Portugal (Mateus & Milàn 2010). In neither case have they been assigned to *Deltapodus brodricki* (Fig.4). Recently Cobos *et al.* (2010) described *Deltapodus ibericus* at the Jurassic-Cretaceous transition of Teruel. This ichnotaxon shares its general morphology with *Deltapodus* isp., including the absence of the claw-shaped imprint of the pollex. Taking into account the differences in measurements (Table 1), however, it seems more appropiate to use the open nomenclature for MNS 2009/64.

Long (1998) describes tracks that he assigns to stegosaurs in the Lower Cretaceous of Australia (Broome Sandstone). These tracks have manus with five digits in a crescent shape and wide pedal imprints. The Australian tracks differ from *Deltapodus* in that they have manus with five well-defined digits, they lack an imprint of the pollex claw, and the pes prints are wider and subsquare in section. Further, the manual imprints are proportionally bigger than those of *Deltapodus* and other proposed stegosaur tracks. The shape of the broome sandstone tracks tallies better with the morphology of the ankylosaurs. If this were to be confirmed, *Deltapodus* isp. would undoubtedly be the first record of a stegosaur track in the Lower Cretaceous.

THE IBERIAN STEGOSAURIANS AND THE TRACKMAKER OF *DELTAPODUS* ISP.

The fossil remains of stegosaurs are relatively frequent in the Upper Jurassic sequence of the Iberian Peninsula, having been cited in the Kimmeridgian-Tithonian and possibly reaching as far as the Lower Berriasian. Most of the remains have been assigned to the species *Dacentrurus armatus* (Owen, 1875) or *Dacentrurus* sp. Lucas, 1902. They have been cited in the Upper Kimmeridgian of the "Costa de los Dinosaurios" in Asturias (García-Ramos *et al.* 2006; Ortega *et al.* 2006) and in Portugal (Galton 1991; Antunes & Mateus 2003). They are also represented in the Jurassic-Cretaceous transition (Tithonian-Lower Berriasian) of the Iberian Range (Casanovas-Cladellas *et al.* 1995; Cobos *et al.* 2010). *Dacentrurus* is an exclusively European taxon that has traditionally been considered a primitive representative of the stegosaurs (Galton 1991; Casanovas-

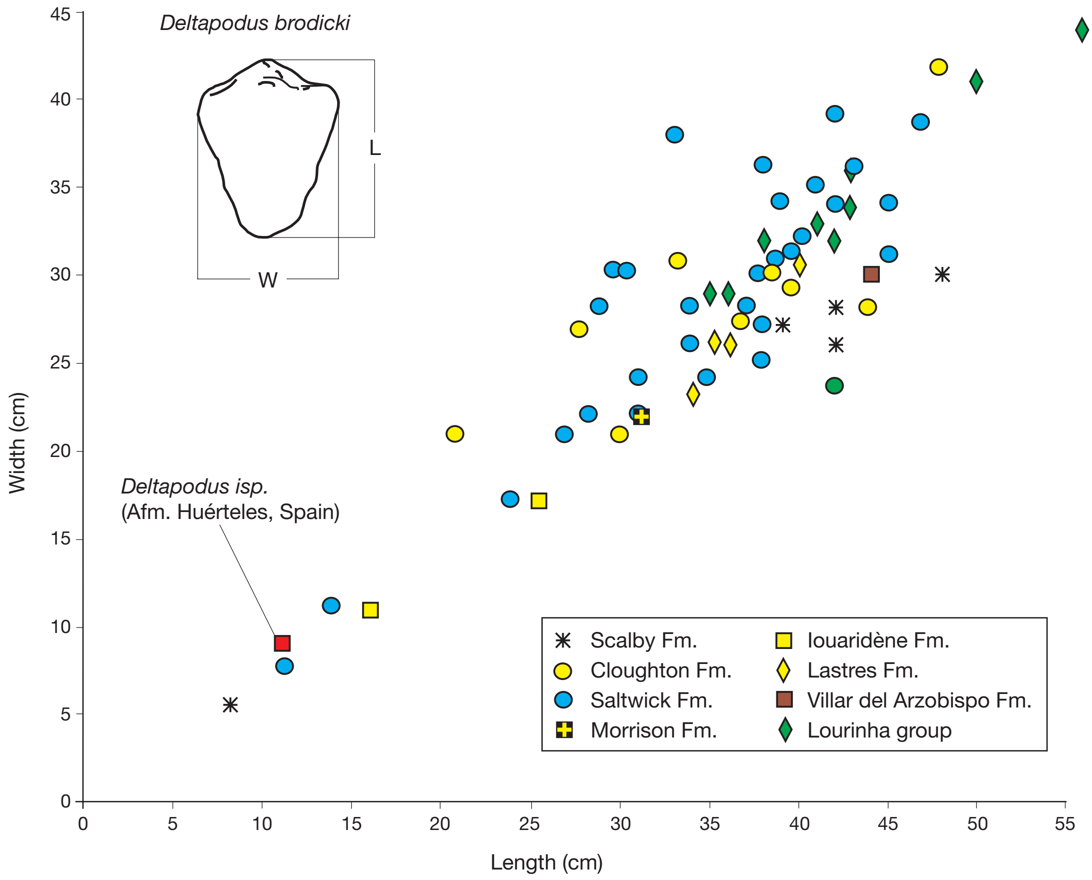

FIG. 5. — Scatter diagram showing plots of the footprint length against footprint width of *Deltapodus brodricki* Whyte & Romano, 1994 of the Middle Jurassic of England (Whyte *et al.* 2007). The square marks the position of the holotype of *Deltapodus* isp. (MNS 2009/64).

Cladellas *et al.* 1995; Pereda-Suberbiola & Galton 2001; Escaso *et al.* 2007; Maidment *et al.* 2008). Recently Mateus *et al.* (2009) have described the stegosaur *Miragaia* Mateus, Maidment & Christiansen, 2009 in the Upper Kimmeridgian-Lower Tithonian of Lourinhã (Portugal). In their phylogenetic proposal they include *Miragaia* in Dacentrurinae Mateus, Maidment & Christiansen, 2009, which underlines its close relationship with *Dacentrurus.* This further implies that there is a greater diversity among the taxa included within Dacentrurinae and that in many cases extensive revision is necessary (Maidment *et al.* 2008). Another important aspect of the paper by Mateus *et al.* (2009) is that their phylogenetic proposal includes *Miragaia* and *Dacentrurus* in the same clade, which is the sister group of *Stegosaurus*. This suggests that the dacenturines were not primitive forms, as has generally been accepted.

Recently, evidence of a second clade of stegosaurs has come to light in the Iberian Peninsula with the discovery of remains assigned to *Stegosaurus* in the Upper Kimmeridgian-Lower Tithonian of Casal Novo, Portugal (Escaso *et al.* 2007). This is the first citation of this genus from the Morrison Formation outside North America, it constitutes evidence of a connection between the Iberian Peninsula and North America via Newfoundland at the end of the Jurassic (Escaso *et al.* 2007). This does not exclude that a paleobiogeographic connection between Iberian Peninsula and North America via France or England existed.

The abundance of stegosaur remains in the Upper Jurassic of the Iberian Peninsula is consistent with what takes place elsewhere in the world. It was in the Late Jurassic that the diversity of taxa was greatest (Galton & Upchurch 2004), and this is the period when most of the tracks attributed to these ornithischians are found. The stegosaurs underwent a major crisis in the Jurassic-Cretaceous transition, becoming very scarce in the Lower Cretaceous. In the Iberian Peninsula there is fragmentary evidence of them from the Upper Hauterivian-Lower Aptian of Burgos and Teruel (Ruiz-Omeñaca 2000; Pereda-Suberbiola *et al.* 2003, 2005). Up to now, none has been cited in the Middle Berriasian-Lower Hauterivian of Iberian Peninsula, but this might simply be a taphonomic gap due to the scarcity of sites from this period of time. In this sense, the stegosaur tooth recently described in the Berriasian of France (Billon-Bruyat *et al.* 2010) suggests the presence the stegosaurians at the beginning of the Cretaceous in other parts of Europe.

Bearing in mind the diversity of representatives of the two clades of stegosaurs coexisting at the end of the Jurassic on the Iberian Peninsula, it would be rash to assign *Deltapodus* isp. to a particular taxon. Moreover, we do not know which of them managed to survive the Jurassic-Cretaceous crisis. Nonetheless, it is possible at least to narrow down the field. The genus *Stegosaurus* is known fairly well on the basis of the sites of the Morrison Formation. Its representatives present only digit I of manus with an elongated claw (Gilmore 1914; Thulborn 1990). For this reason the track it would produce would have a characteristic mark on digit I. Focusing on this character in particular, Milán & Chiappe (2009) relate the tracks they identify as *Deltapodus brodricki* from the Morrison Formation with *Stegosaurus*.

MNS 2009/64 lacks the claw marks on digit I, so *Stegosaurus* or related taxa cannot be the trackmaker because these display a well-developed pollex. The skeletal remains of *Dacentrurus* and related taxa are abundant in the Upper Jurassic of the Iberian Peninsula; this is thus the more probable trackmaker for *Deltapodus* isp. from Soria.

PALAEOBIOGEOGRAPHICAL IMPLICATIONS

The faunal turnover that took place between the Jurassic and the Cretaceous of Laurasia implies the extinction of some clades of primitive Sauropoda such as Turiasauria (Royo-Torres *et al.* 2006). Moreover, it is possible to recognize the replacement of the stegosaurs by the ankylosaurs, the camptosaurids by the iguanodontids, and the diplodocids and camarasaurids by Titanosauriformes (Bakker 1998; Canudo 2009). This renewal did not entail the complete extinction of the typical Jurassic forms, since the diplodocimorphs (i.e. rebbachisaurids) and the stegosaurs, for example, continued to be present in the Early Cretaceous of Laurasia (Pereda-Suberbiola *et al.* 2003, 2005; Billon-Bruyat *et al.* 2010; Torcida Fernández-Baldor *et al.* 2011). This suggests that the extinction was not sudden, but came about over a reasonably long period of time, the "Jurassic clades" remaining as residual forms that gradually disappeared in the course of the earliest Cretaceous. Relatively little is known about the time and manner in which this occurred, due to the worldwide scarcity in the dinosaur record at the beginning of the Cretaceous. One of the most exceptional areas for investigating this faunal turnover in the Jurassic-Cretaceous transition is the Iberian Peninsula, endowed as it is with both an osteological and an ichnological record of dinosaurs.

The palaeoichnological association of the Berriasian of the Cameros Basin has been known to be singular ever since work first began on the taxonomic description of the record. The association seems to be more characteristic of the Upper Jurassic than of the Lower Cretaceous. Lockley *et al.* (1998) have suggested that the Huérteles Alloformation may be Upper Jurassic in age, given the presence of dinosaur ichnotaxa typical of this age, such as *Therangospodus* Moratalla García, 1993 (emend. Lockley, Meyer & Moratalla 1998) and *Megalosauripus* Lesserisseur, 1955 (emend. Lockley, Meyer & Santos 2006) (Barco *et al.* 2004). Moreover, pterosaur tracks assigned to the genus *Pteraichnus* have been described (Pascual Arribas & Sanz Pérez 2000), a genus broadly distributed in the Oxfordian-Kimmeridgian of North America (Lockley & Hunt 1995; Bennet 1997). Furthermore, there are few tracks attributed to large ornithopods ("iguanodontids"), which is the fauna typical of the Lower Cretaceous in the nearby Enciso and Urbión groups (Moratalla & Sanz 1997). The presence of *Deltapodus* isp. at the Huérteles Alloformation seems to provide further evidence in support of this argument, since *Deltapodus* has been cited in levels of the Middle-Upper Jurassic (Whyte & Romano 1994, 2001; Piñuela *et al.* 2007, 2009; Gierlinski & Sabath 2008; García-Ramos *et al.* 2008; Mateus & Milàn 2008, 2010). However, geological and palaeontological studies indicate that the Huérteles Alloformation is Berriasian in age (Martín, Closas & Alonso-Millán 1998; Schudack & Schudack 2009). If so, the presence of the *Megalosauripus-Therangospodus* ichnological association in the Cameros Basin and possibly the rest of the Iberian Peninsula persists during the Berriasian and is not restricted solely to the Jurassic, as noted by Lockley *et al.* (1998). The presence of a Jurassic ichnoassociation at the base of the Iberian Cretaceous can be explained either in terms of the persistence of "Jurassic faunas" on the Iberian Archipelago at this time (Barco *et al.* 2004) or the scarcity in the ichnological dinosaur record in the Berriasian elsewhere in the world, especially in North America.

Without ruling out the scarcity of the record as an explanation for the presence of "Jurassic" faunas at the beginning of the Cretaceous on the Iberian Peninsula and in other parts of Europe, the endemism hypothesis is a possibility. The break-up of Pangaea at the end of the Upper Jurassic resulted in the separation of the faunas of Laurasia and Gondwana and the possible biogeographical isolation of parts of Europe. This isolation can be envisioned in the formation of the European Archipelago, a suitable location for the survival of "Jurassic faunas" in the earliest Cretaceous. Subsequent to the Berriasian, the dinosaur connection between Gondwana and Laurasia via the Apulian land bridge is well documented on one or several occasions during the course of the Lower Cretaceous (Dalla Vecchia 2005; Gheerbrant & Rage 2006; Canudo *et al.* 2009), accounting for the presence of dinosaurs faunas with African affinities on the Iberian Peninsula and in other parts of Europe (Canudo *et al.* 2008; Torcida Fernández-Baldor *et al.* 2011).

CONCLUSION

This paper describes *Deltapodus* isp., recovered in the Huérteles Alloformation, from the Berriasian of the Cameros Basin (Soria, Spain). This is the first record of stegosaur tracks from the Cretaceous of Europe and possibly the first worldwide. It is a pes-manus set, small in size, bearing a great resemblance to *Deltapodus brodricki* from the Jurassic, but with enough differences in the manual imprint to distinguish it from the other ichnospecies.

The presence of *Deltapodus* isp. in the Berriasian of Soria provides the first ichnological evidence of the persistence of the ichnogenus *Deltapodus* in the Lower Cretaceous. This could be a consequence of the worldwide scarcity in the ichnological record in Berriasian levels. However, there is another possible scenario, which would involve the persistence of "Jurassic faunas" only at the beginning of the Cretaceous in Europe, as seems to be indicated by the presence of the *Megalosauripus-Therangospodus* ichnoassociation in the Cameros Basin in Soria and the recent discoveries of stegosaurian teeth in the Berriasian of France. In other words, the presence of stegosaurs with Jurassic affinities in the Berriasian of Europe means that the replacement of Jurassic by Cretaceous faunas did not occur at the Jurassic-Cretaceous boundary, but this turnover took place over the course of the earliest part of the Lower Cretaceous. The moment when the Neocomian faunas replaced these Jurassic ones will be revealed by future palaeontological research.

Acknowledgements

We are grateful to the Ruta de las Icnitas and to the Community of Tierras Altas for providing the facilities to develop this research; to the MNS and to the Dirección General de Patrimonio Cultural de la Junta de Castilla y León for granting us permission to study and photograph the specimen. Rupert Glasgow translated the text into English. The comments of referees Kevin Padian, Ronan Allain and Annemarie Ohler have improved the quality of the paper. This paper forms part of projects CGL2007-62469 and CGL2010-16447, subsidized by the Spanish Ministry of Science and

Innovation, the European Regional Development Fund, and the project Grupos Consolidados del Gobierno de Aragon. Paleoymás has financed part of the research of JLB. DC acknowledges the support from the Ministry of Education (AP2008-01340).

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Submitted on 24 November 2009;
accepted on 17 January 2011.