Brief report

Acta Palaeontologica Polonica 56 (3): 651–658, 2011

New finds of stegosaur tracks from the Upper Jurassic Lourinhã Formation, Portugal

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Eleven new tracks from the Upper Jurassic of Portugal are described and attributed to the stegosaurian ichnogenus *Deltapodus*. One track exhibits exceptionally well-preserved impressions of skin on the plantar surface, showing the stegosaur foot to be covered by closely spaced skin tubercles of ca. 6 mm in size. The *Deltapodus* specimens from the Aalenian of England represent the oldest occurrence of stegosaurs and imply an earlier cladogenesis than is recognized in the body fossil record.

Introduction

The European stegosaur track record is scarce, compared to the number of tracks described for other dinosaur groups. The track *Deltapodus brodricki* Whyte and Romano, 1994, described from the Aalenian, Middle Jurassic, of Yorkshire, was the first track to be identified as a stegosaur track due to its distinct tridactyl configuration which is a close match to the stegosaurian pedal skeleton (Whyte and Romano 1994, 2001).

Deltapodus tracks are now known from the Middle Jurassic Ravenscar Group of Yorkshire (Whyte et al. 2007), the Upper Jurassic of Asturias (Garcia-Ramos et al. 2006, 2008; Lockley et al. 2008) and Teruel, Spain (Cobos et al. 2008, 2010), the Upper Jurassic Lourinhã Formation of Portugal (Mateus and Milàn 2008, 2010), the Brushy Basin Member of the Morrison Formation of Utah, USA (Milàn and Chiappe 2009), and the Upper Jurassic Iouaridène Formation of Morocco (Belvedere and Mietto 2010). Here we describe 11 new specimens (nine pes and two manus tracks) of *Deltapodus* recently collected from the Upper Jurassic Lourinhã Formation of Portugal, and discuss their palaeoenvironmental context compared with the other known records of of *Deltapodus*.

Although *Deltapodus* is here regarded as a valid ichnogenus, the senior author urges a discussion on the validity of binomial Linnean (ichno)species and (ichno)genus names to tracks and ichnofossils.

Abbreviations.—PN, Peralta North; PS, Peralta South; VF, Vale Frades; PBN, Porto Barcas North; PBS, Porto Barcas South; PD, Porto Dinheiro.

Geological setting

The Upper Jurassic Lourinhã Formation (sensu Hill 1989; Martinius and Gowland 2010; Kullberg et al. in press) is exposed in the central-western part of Portugal and especially in the vicinity of the small town of Lourinhã approximately 70 km north of Lisboa (Fig. 1). The sediments of the Lourinhã Formation were deposited in the Lusitanian Basin and comprise in excess of 400 m of terrestrial sediments, deposited during the latest Jurassic (Late Kimmeridgian–Early Tithonian), during the initial rifting stage of the Atlantic Ocean (Hill 1989).

The sediments predominantly consist of thick beds of red and green clay, interbedded with massive, fluvial sandstone bodies and heterolithic beds. The Lourinhã Formation has yielded an extensive vertebrate fauna (Lapparent and Zbyszewski 1957; Galton 1980; Antunes 1998; Antunes et al. 1998; Mateus et al. 1998, 2006; Antunes and Mateus 2003; Pereda-Superbiola et al. 2005; Mateus 2006; Escaso et al. 2007) and abundant carbonized fragments of plants and large fossilized logs (Pais 1998). The frequent sedimentologic shifts between flood-plain mudstones and fluvial sandstone bodies create the perfect environment for track preservation, and numerous well-preserved tracks and trackways have been described from the Lourinhã Formation (Antunes and Mateus 2003; Milàn et al. 2005; Mateus and Milàn 2008, 2010).

New *Deltapodus* tracks

Nine, well-preserved *Deltapodus* pes tracks and two manus tracks were discovered in coastal cliff sections west of Lourinhã (Fig. 1). In the following account, the specimens are named after the locality from where they were collected (Table 1). All specimens were found preserved as natural casts and are stored in the collection of the Museum da Lourinhã.

Vale Frades (VF).—The first *Deltapodus* pes track, discovered in 2003, was preserved as an eroded natural cast of sandstone on a pedestal of clay. The track was found together with a large ornithopod track (Mateus and Milàn 2008). Anatomical details are not preserved, except for the three short blunt toes and a relatively wide square heel (Table 1, Fig. 2A).

Peralta (PN and PS).—A pes track, found north of the beach of Peralta (PN), has faint skin striations in the heel area and on the sides of the digits. The heel in this specimen is rounded, tapering to a slightly pointed end (Fig. 2B). Another larger pes track (PS) was found in situ in the steep coastal cliffs south of the beach (Table 1, Fig. 2C).

Porto Barcas (PBN and PBS 1–6).—On the north side of Porto Barcas, an asymmetric pes track (PBN) was collected. Striations

http://dx.doi.org/10.4202/app.2009.0055

Table 1. Dimensions (in cm) of the new *Deltapodus* specimens from the Lourinhã Formation, Portugal.

Location of specimen	Specimen number	Track	Length	Width	Depth
Vale Frades (VF)	ML1342	Pes	36	29	8
Peralta North (PN)	ML1343	Pes	35	29	19
Peralta South (PS)	ML1344	Pes	42	32	22
Porto Barcas North (PBN)	ML1345	Pes	41	33	18
Porto Barcas South 1 (PBS 1)	ML1346	Pes	56	44	17
Porto Barcas South 2 (PBS 2)	ML1347	Pes	50	41	16
Porto Barcas South 3 (PBS 3)	ML1348	Pes	43	34	15
Porto Barcas South 4 (PBS 4)	ML1349	Pes	43	36	12
Porto Barcas South 5 (PBS 5)	ML1351	Manus	28	45	13
Porto Barcas South 6 (PBS 6)	ML1352	Manus	22	34	28
Porto Dinheiro (PD)	ML1350	Pes	38	32	13

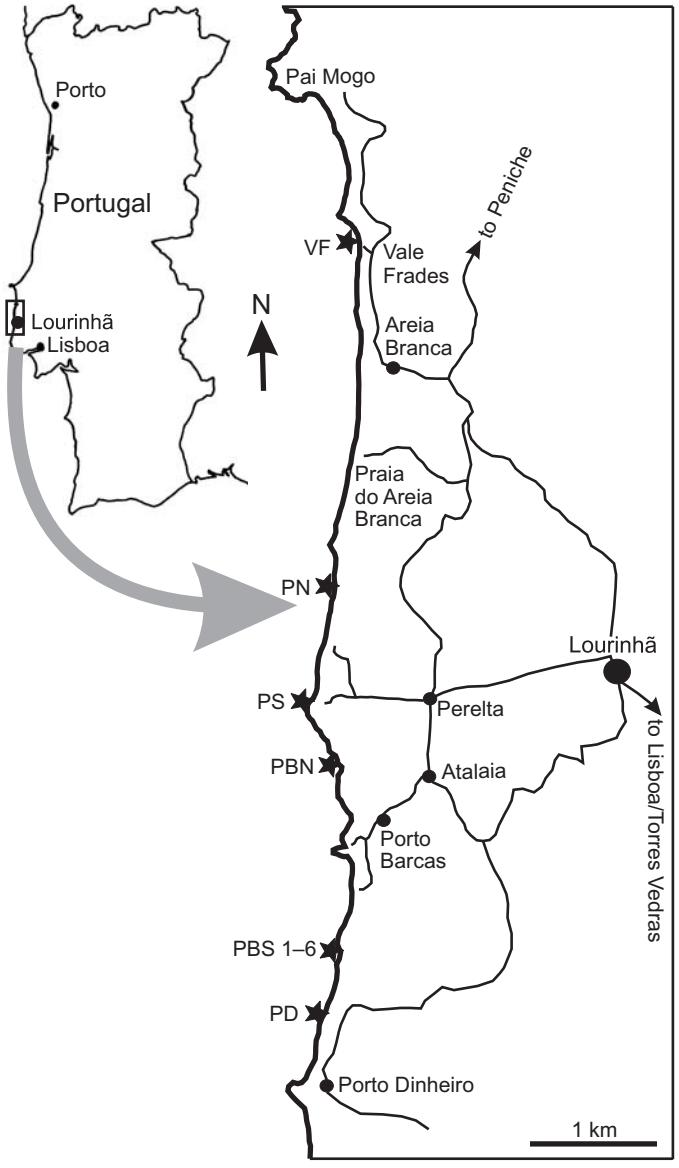

Fig. 1. Location map. The eleven new specimens of *Deltapodus* were found along the coast west of the town Lourinhã, in the central-west of Portugal. Each specimen has been given an abbreviation corresponding to the locality where it was found.

from the skin are preserved on parts of the track walls (Table 1, Fig. 2D).

Four pes and two manus tracks were found south of the beach of Porto Barcas. The largest pes track (PBS 1) has faint striations from the skin preserved on parts of the trackwalls. The track is slightly deformed sideways as if the animal's foot has been sliding anterolaterally through the sediment (Fig. 2E).

A slightly smaller specimen (PBS 2) (Table 1, Fig. 2F) has well-preserved skin impressions covering the plantar surface of the track, as well as striations preserved on the track walls (Fig. 3). The cast reveals a skin texture consisting of closely packed subrounded tubercles 4–8 mm in diameter and one millimetre high. There is no significant difference in size or shape of the "scales" within the plantar surface, although laterally the "scales" are slightly smaller (4–5 mm wide). The tubercles are evenly distributed over all the plantar surface and only the hoof-like distal parts of the digits are smooth (Fig. 3), though some of the detail is obscured by invertebrate burrows that cross the track just behind the digits. The heel of the track is square in outline. Specimen PBS 3 lacks part of the heel and one side, and has only faint striations preserved on the track walls. It appears to have been tapering towards the heel, as in PBN (Fig. 2G). Another incomplete specimen (PBS 4) lacks parts of two digits. The width of the track decreases posteriorly, giving the track a triangular appearance (Fig. 2H).

Two natural casts of deeply impressed manus tracks (PBS 5 and 6) were found associated with the pes tracks. The manus casts are semilunate in shape, without any indications of free digits. One specimen (PBS 5) is eroded and shows no striations from the skin (Table 1, Fig. 4A). The other specimen (PBS 6) is widest at the bottom, suggesting the soft sediment of the track walls partly converged after withdrawal of the foot (Table 1, Fig. 4B$_1$, B$_2$). The front of the manus is smooth, without indications of individual digits, and striations from the skin being dragged through the substrate can be traced from top to bottom of the cast (Fig. 4B$_3$).

Porto Dinheiro (PD).—A probable left pes (PD) was associated with theropod tracks of varying sizes and large sauropod tracks (Mateus and Milàn 2010). Faint striations from the skin are preserved on the sides of the cast, and the shape of the heel is square (Fig. 2I).

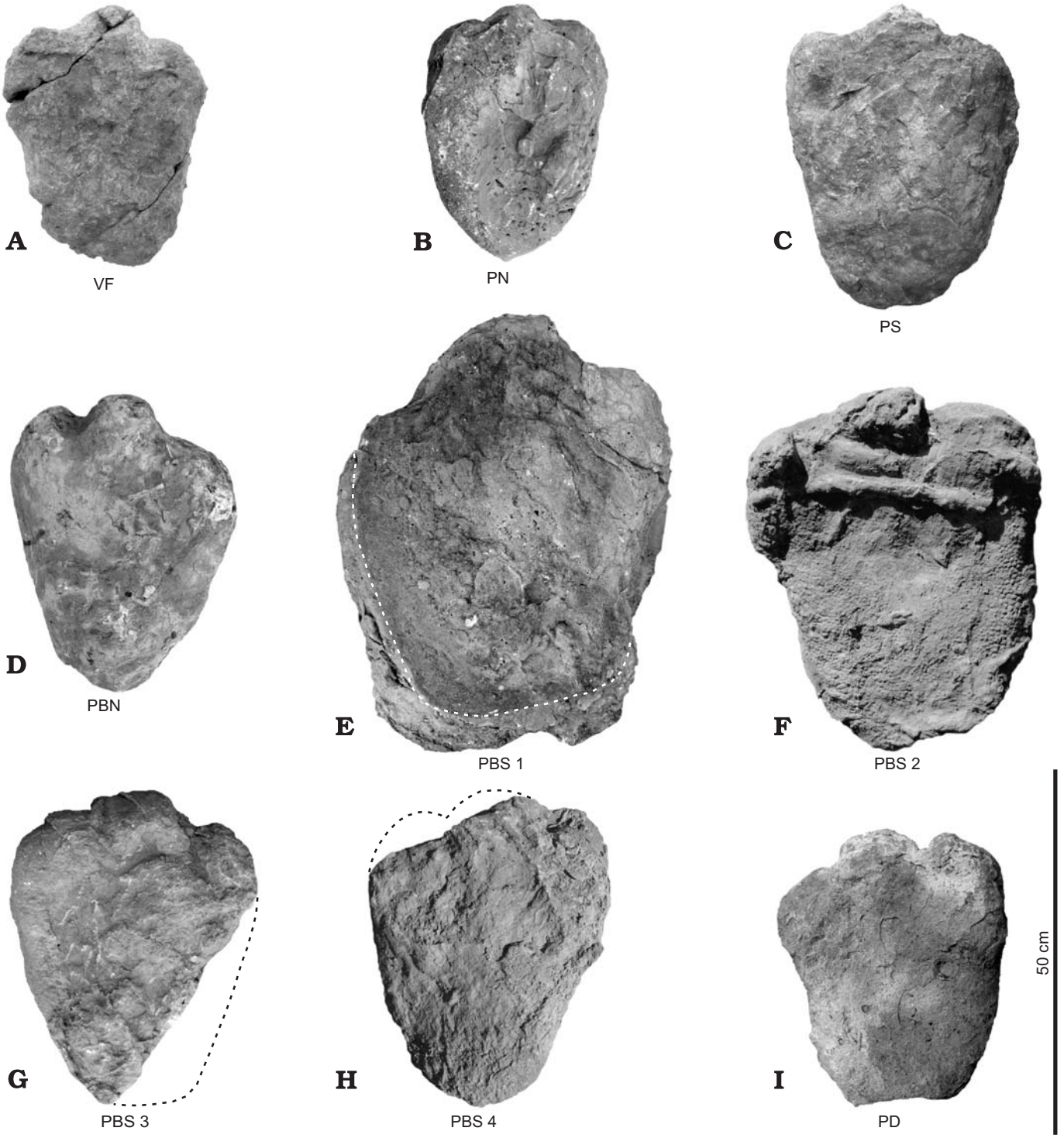

Fig. 2 . The nine studied specimens of *Deltapodus* pes tracks from the Lourinhã Formation (Upper Jurassic, Portugal). ML1342 (**A**), ML1343 (**B**), ML1344 (**C**), ML1345 (**D**), ML1346 (**E**), ML1347 (**F**), ML1348 (**G**), ML1349 (**H**), ML1350 (**I**). The abbreviations below each track refers to the location it was found (Fig. 1). All tracks are reproduced to same scale.

Discussion

The ichnogenus *Deltapodus* is characterized by having tridactyl, mesaxonic pes prints that are generally triangular in outline, widest across the lateral digit impressions and slightly longer than wide. The short digits are blunt and rounded. Manus prints are entaxonic, irregular, but broadly crescentic in outline and approximately twice as wide as long with occasional impressions of an inward directed pollex (Whyte and Romano 1994). All the Portuguese material may be confidently assigned to *Deltapodus* and the range in morphology present in the Portuguese pes specimens is no greater than that seen in the English Ravenscar Group speci-

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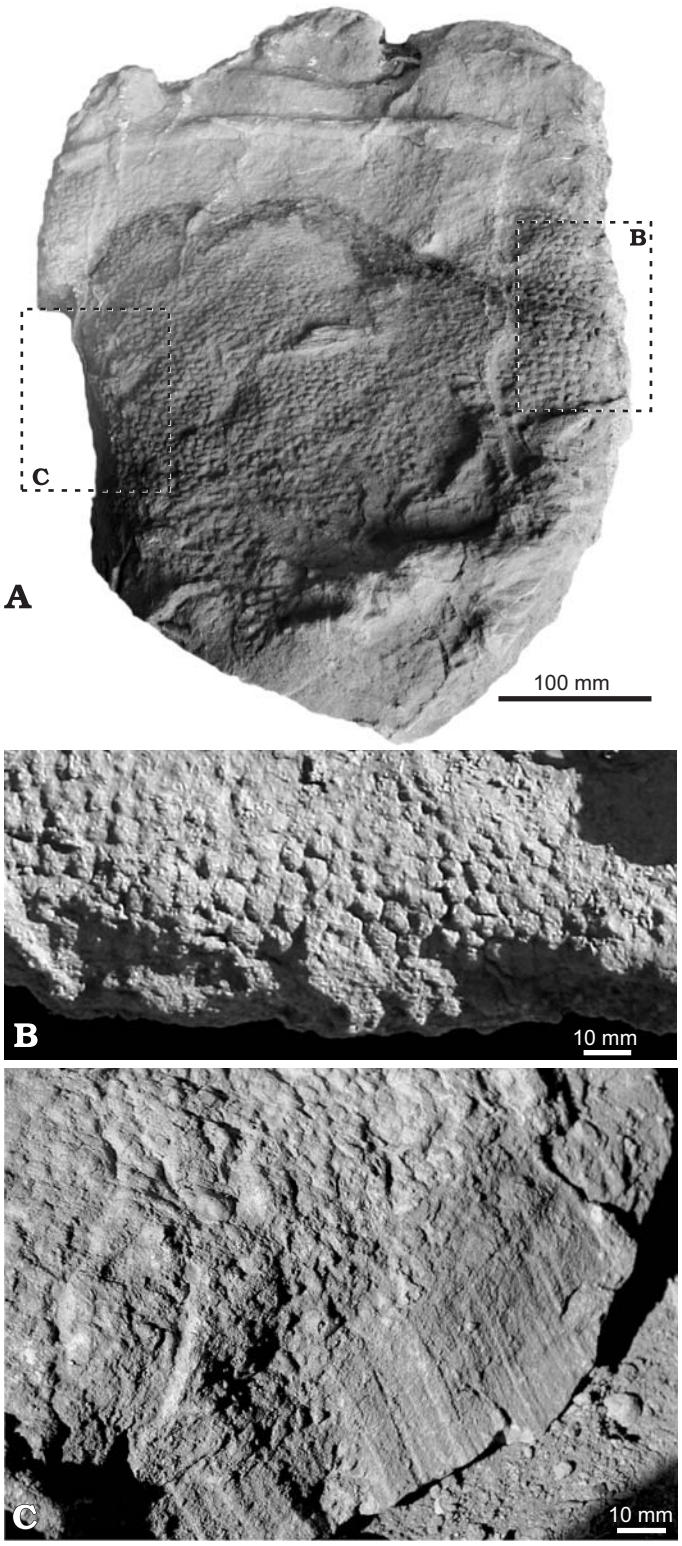

Fig. 3. *Deltapodus* track PBS 2 (ML 1347) from the Lourinhã Formation (Upper Jurassic, Portugal). **A**. Plantar view. **B**. Detail of scaly skin impressions. **C**. Vertical striations of the skin on the cast surface.

mens (Romano and Whyte 2003: fig. 21), and when plotted on a scatter diagram of pes length against pes width they fall well within the confines of the ichnospecies (Fig. 5). The only significant feature of the Portuguese material that distinguishes it from the larger sample from the Ravenscar Group is that pes tracks of the former are generally larger and indeed record the largest *Deltapodus* pes track yet known (Fig. 2).

The specimens from Asturias (Lockley et al. 2008), are similar to the Portuguese and English material (Whyte and Romano 1994, 2001), and the specimen from Utah (Milàn and Chiappe 2009) does not differ morphologically from the European material. The African specimens (Belvedere and Mietto 2010) are not well-preserved, but appear relatively narrower in the heel area than the European and American specimens, and are still included in *Deltapodus brodricki*. Recently, Cobos et al. (2010) erected the name *Deltapodus ibericus* for tracks with slightly different track and trackway parameters, although the general dimensions of individual *D. ibericus* tracks fall well within the confines of the scatterplot for *D. brodricki* (Fig. 5).

A relatively small *Deltapodus*-like print (22.5 cm long, 16.5 cm wide) has been recorded (Mohabey 1986) from the late Maastrichtian Infratrappean Limestone of Jetholi Talao, India, in association with a dinosaur egg clutch. The print was originally identified as a sauropod left manus track (Mohabey 1986) but, if indeed a true *Deltapodus*, it is by far the youngest occurrence of this ichnotaxon whose currently known range is otherwise Aalenian to Tithonian.

Though pes dimensions show a good coherent relationship (Fig. 5), it was clear in the original concept of *Deltapodus* that there was considerable variation in pes track outline, posterior margin configuration and digit impressions (Whyte and Romano 1994; see also Whyte and Romano 2001: fig. 3; Romano and Whyte 2003: fig. 21). However, no clear indication of more than one ichnospecies was apparent as most variation was considered to be due to preservation rather than reflecting a major morphological or behavioural difference. Among the nine new pes tracks from Portugal, there appear to be three different morphotypes, distinguished by their general shape and heel outline. Specimen PN (Fig. 2B) has relatively parallel sides and terminates in a drop-like shape. Specimens PBN (Fig. 2D), PBS 3 (Fig. 2G), and PBS 4 (Fig. 2H) have straight sides converging to a rounded heel, giving the track a triangular shape; and specimens VF (Fig. 2A), PBS 1 (Fig. 2E), PBS 2 (Fig. 2F), and PD (Fig. 2I) have sub-parallel sides and a more angular heel outline. Such outlines are also apparent in some of the Ravenscar Group specimens (Romano and Whyte 2003: fig. 21J A and C, respectively). While the three morphotypes may conceivably represent different ichnospecies, the inadequate data sample and lack of complete trackways prevents any firm conclusions being drawn at present.

The two manus tracks from Lourinhã do not show the well marked digit I impression found in the holotype of *Deltapodus brodricki* but lie within the range of variation exhibited by manus prints from the type locality (Whyte and Romano 1994), and those observed in the *Deltapodus* trackways from Asturias (Lockley et al 2008). The manus casts were found loose below the cliff-face together with the pes casts, and can thus not be positively correlated with any of the pes casts. No other tracks were found at the locality, so we provisionally associate the

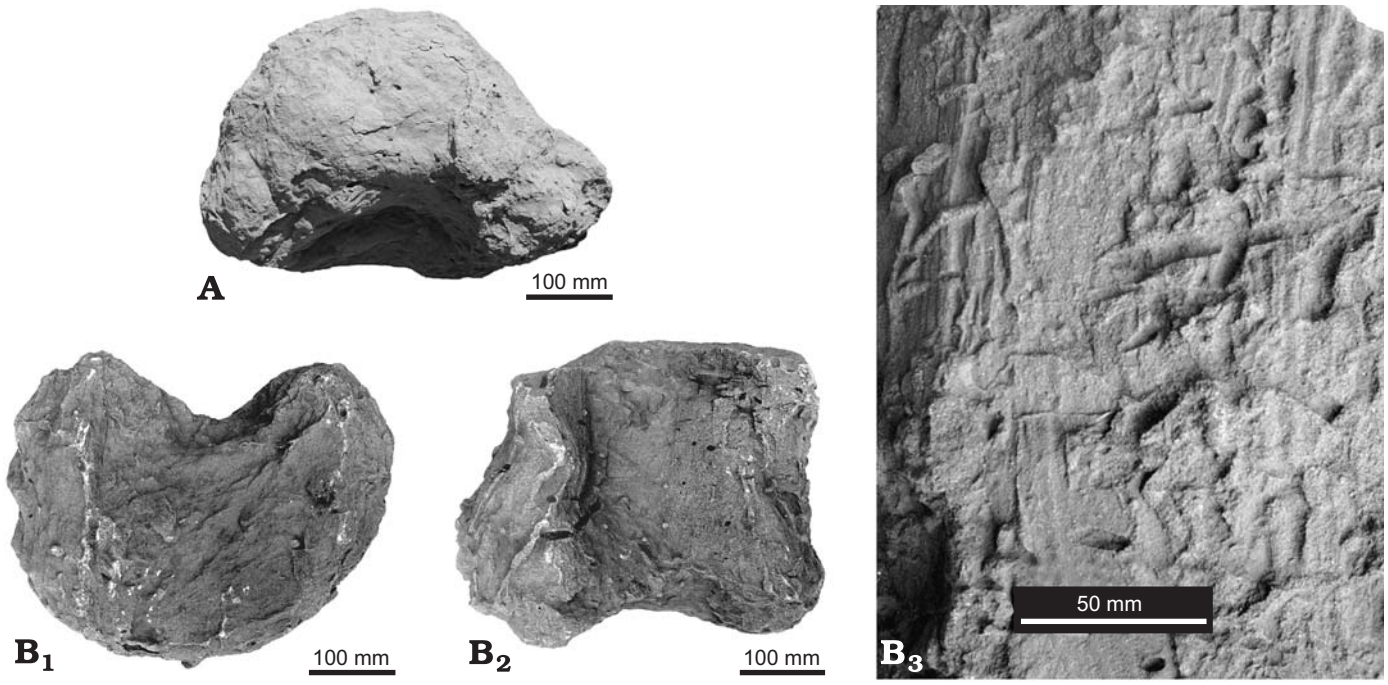

Fig. 4. The two associated natural casts of *Deltapodus* manus tracks found at Porto Barcas, Lourinhã Formation (Upper Jurassic, Portugal). Both tracks show a pronounced semilunate shape. **A**. Manus track PBS 5 (ML 1351) seen from below. **B**. Manus track PBS6 (ML 1352) seen from below (B_1), caudal view (B_2), and enlarged section of the front (B_3), showing the vertical striations covering the front and sides of the cast.

manus tracks to the pes tracks. Striations similar to those exhibited on some of the Portuguese tracks have also been recorded on pes prints from the Ravenscar Group (Romano and Whyte 2003: fig. 4). However the preservation of tuberculate skin imprints on the plantar surface of one of the Portuguese pes tracks is the first time such structures have been recorded in *Deltapodus* and thus add important information about the soft tissue anatomy of the trackmakers. Similar skin impressions are reported from the forelimb and shoulder area in a partly mummified stegosaur *Gigantspinosaurus sichuanensis* from the Upper Jurassic Shangshaximiao Formation, China (Xing et al. 2008). The skin pattern covering the body on this fossil is that of polygonal scales of 5.7 to 9.2 mm size, with occasional larger scales (Xing et al. 2008).

The occurrence of *Deltapodus* in flood plain deposits of the Lourinhã Formation is comparable to that in the type area of the ichnogenus in the Yorkshire (Cleveland) Basin (Romano and Whyte 2003; Whyte et al. 2007). A similar facies association is also recorded for the Upper Jurassic of Asturias (Garcia-Ramos et al. 2006, 2008; Lockley et al. 2008) and Teruel, in Spain (Cobos et al. 2008, 2010), the Iouaridène Formation of Morocco (Upper Jurassic) (Belvedere and Mietto 2010) and the Brushy Basin Member of the Morrison Formation (Upper Jurassic) of Utah, United States (Milàn and Chiappe 2009). This suggests a preferred flood plain habitat for the *Deltaopodus* trackmakers, though the contrasting sedimentologic characteristics of these sequences (siliciclastic, carbonate rich and red beds) point to a spectrum of palaeoclimates.

Deltapodus brodricki was at first considered to have been made by a sauropod (Whyte and Romano 1993, 1994), though it was recognised that some features were not typical of sauropod tracks. Critical reconsideration of the evidence together with new information led to a re-evaluation, and *Deltapodus* was assigned to a stegosaurian maker (Whyte and Romano 2001; Romano and Whyte 2003; Whyte et al. 2007). Tracks with other morphologies have previously been interpreted as being stegosaurian in origin (e.g., Lockley and Hunt 1998; Gierliński and Sabath 2008; see also Whyte and Romano 2001), but *Deltapodus* is still "arguably the most fully described ichnite attributed to stegosaurs" (Whyte and Romano 2001: 52). The articulated feet of *Kentrosaurus* and *Stegosaurus* (Galton and Upchurch 2004) indicate that stegosaurians had a pedal phalangeal formula of 0-2-2-2-0, with short, broad proximal phalanges, and broad and depressed unguals. This matches the digit characteristics of the pes of *Deltapodus*. Skeletal remains of stegosaurs are abundant in the Upper Jurassic of Europe, with several species present (Maidment et al. 2008; Mateus et al. 2009), which is consistent with the widespread occurrence of *Deltapodus*. Ankylosaurs, which have been considered as possible makers of *Deltapodus* (McCrea et al. 2001), are also known from the Middle and Upper Jurassic of Europe in the form of *Sarcolestes leedsi* from the Callovian of England and *Dracopelta* from the Kimmeridgian of Portugal (Vickaryous et al. 2004). However neither of these have preserved skeletal material of the feet; but, while the pes of other ankylosaurs can be penta-, tetra-, or tridactyl, the tridactyl *Euoplocephalus* (Coombs 1986) is only known from the Upper Cretaceous. Three different genera of stegosaurs are known from the Upper Jurassic of Portugal alone, namely *Stegosaurus*, *Dacentrurus*, and *Miragaia* (Mateus et al. 2008, 2009 and references therein). These may relate to the three slightly different morphotypes recognised within the *Deltapodus* tracks from the Lourinhã Formation, but future

doi:10.4202/app.2009.0055

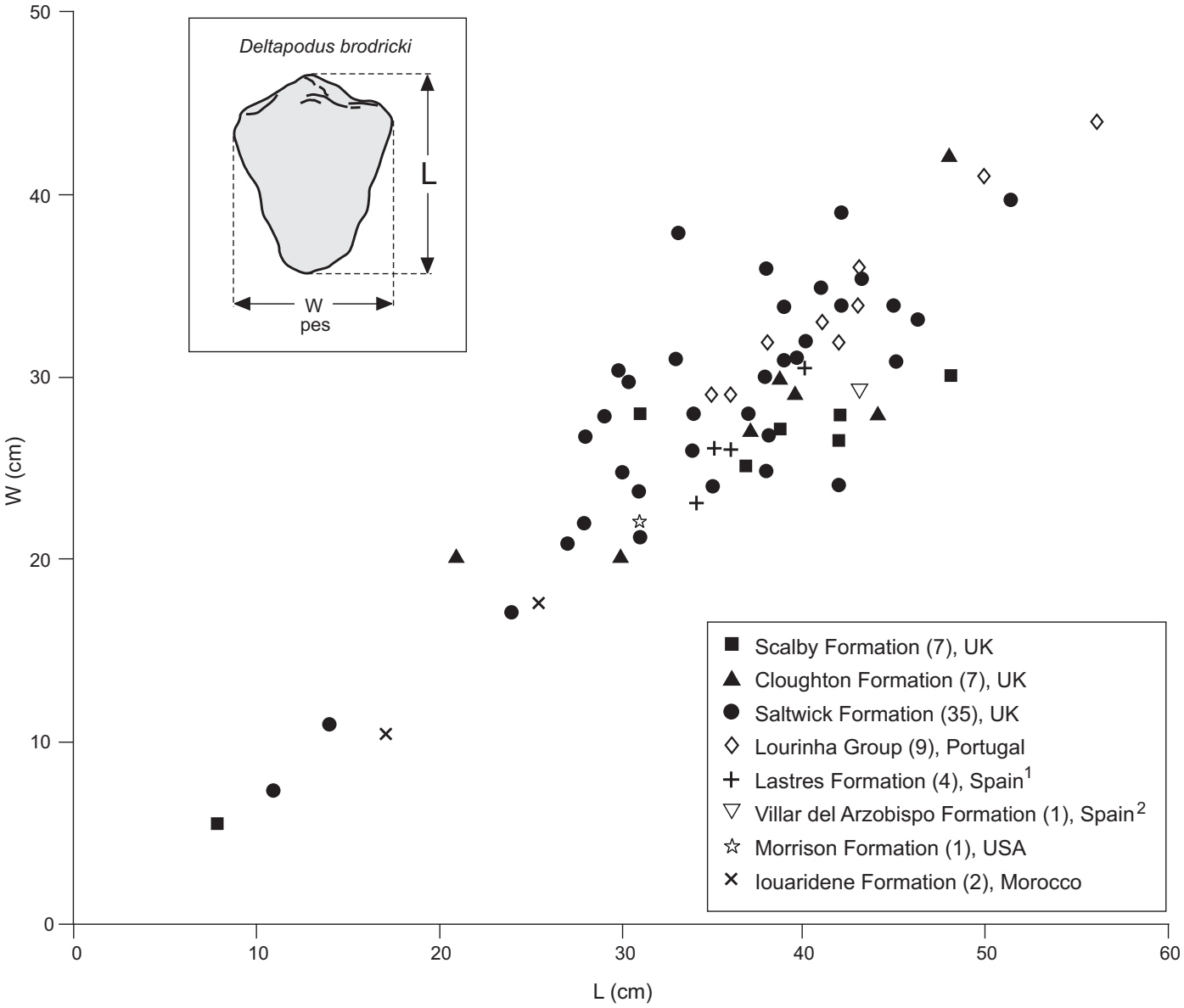

Fig. 5. Scatter diagram showing the relationship between pes footprint length (L) and footprint width (W) for specimens of *Deltapodus* from England, Portugal, Spain ([1] Asturias, [2] Teruel), USA and Morocco. The example from Teruel is a mean value (Cobos et al. 2010).

finds of additional stegosaur tracks and preferably complete trackways will shed more light on this.

The occurrence of *Deltapodus* in the Aalenian of England and its confirmation as a stegosaur track implies an earlier cladogenesis for the Stegosauria, than the Bajocian or Bathonian age implied by the skeletal record (Maidment et al. 2008). The known stratigraphic range of *Deltapodus* is at present restricted to the Middle to Late Jurassic (Aalenian to Tithonian) although the skeletal record of stegosaurs extends into the Lower Cretaceous (Maidment et al. 2008). Considerable doubt (Chatterjee and Rudra 1996; see also Maidment et al. 2008) has been cast on records of stegosaurs in the Late Cretaceous of India (Yadagiri and Ayasami 1979; Galton and Upchurch 2004) but they would be in accord with the record of a *Deltapodus*-like track in the Late Cretaceous (Mohabey 1986). The larger maximum size of pes prints (Fig. 5) from the Upper Jurassic of Portugal and Spain as compared to that of Middle Jurassic *Deltapodus* prints from Yorkshire may reflect an evolutionary trend for increased body size within the stegosaurs.

Conclusion

The discovery of 11 new *Deltapodus* tracks from the Lourinhã Formation of Portugal expands the known biogeographic distribution of this ichnogenus. One track exhibits exceptionally well-preserved impressions of skin on the plantar surface, providing unique information of the soft-tissue anatomy of the stegosaur pes, by showing the pes to have been covered by closely spaced skin tubercles of ca. 6 mm in size. The *Deltapodus* specimens from the Aalenian of England represent the oldest occurrence of undisputed stegosaur tracks. This implies an earlier cladogenesis of the group than suggested by the skeletal record.

Acknowledgements.—We are grateful for the critical and constructive reviews from Marco Avanzini (Museo Tridentino di Scienze Naturali, Trento, Italy), José-Carlos García-Ramos (Museo del Jurásico de Asturias, Asturias, Spain), and Susannah Maidment (The Natural History Museum, London, UK). The research of JM was supported by the Danish Natural Science Research Council. OM was supported by fellowship (BPD/25291/2005) of the Portuguese Fundação para Ciência de Tecnologia.

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Received 8 April 2009, accepted 23 December 2010, available online 29 December 2010.