A review of vertebrate track assemblages from the Late Jurassic of Asturias, Spain with comparative notes on coeval ichnofaunas from the western USA: implications for faunal diversity in siliciclastic facies assemblages.

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ABSTRACT - Upper Jurassic tetrapod tracks from Asturias (Spain) are similar to those from the famous Morrison Formation of the Rocky Mountain Region (western USA). Both regions provide evidence of diverse faunas comprising dinosaurs (theropods, sauropods and ornithischians), pterosaurs, crocodilians and turtles which indicate faunas consistent with known skeletal remains. Almost all these groups are represented by at least two, if not as many as four or more, distinctive track morphotypes, giving a cumulative ichno-diversity of at least 12- 15 ichnotaxa. At least half of these are diagnostic to the ichnogenus level. Thus, the ichnofaunas provide a useful, generalized census of the Upper Jurassic faunas in these regions. Although there are some ambiguities about the probable identities of the makers of some tridactyl tracks, both assemblages are remarkably similar in overall composition. Most differences between the ichnofaunas reflect subtle distinctions that reflect differences in size and diversity within the major track groups. Some differences can also be attributed to preservational factors. The Asturian assemblages is dominated by isolated specimens from cliff outcrops in a small area, whereas the Morrison ichnofaunas is based on in situ sites from a very large area of more than 500,000 km^2.

Key words: *Upper Jurassic, ichnology, Asturias, Morrison Formation, dinosaurs, pterosaurs*

INTRODUCTION

To this day the Morrison Formation of the western United States remains the most famous and productive source of dinosaurs and other vertebrates of Upper Jurassic age (Foster, 1998; 2000; 2003). In recent years the vertebrate ichnofauna of the Morrison Formation has also become fairly well-known (Lockley et al., 1998a; Foster and Lockley, 2006). However, until recently comparison between the Late Jurassic ichnofaunas of North America, Europe and other areas has been constrained by a number of factors. These include facies control of ichnofaunas, lack of precise age dating and lack of well-preserved or well-studied ichnofaunas. For example, despite the recent increase in the documentation of Late Jurassic ichnofaunas from Europe, most derive from carbonate platform facies in Switzerland (Meyer & Thüring, 2003: pp.109-114) and Portugal (Lockley et al., 1994a; Lockley and Meyer, 2000) and are characterized by low diversity sauropod-theropod dominated assemblages (the *Brontopodus* ichnofacies: Lockley et al., 1994b). Elsewhere in Europe the Late Jurassic track record is sparse in comparison with that of the Lower Cretaceous (Moratalla & Sanz, 1997; Moratalla et al., 1988; 1992; 1994).

The purpose of this paper, therefore, is to outline the well-preserved ichnofaunas from the Late Jurassic of Asturias, Spain, most of which have been discovered quite recently, and compare them with those from the Late Jurassic of the Morrison Formation in the western United States that originate from predominantly siliciclastic (non-carbonate) facies. Recent studies (Garcia-Ramos et al., 2002a; 2004; 2006) have summarized the Asturian ichnofauna (in Spanish) and in a series of brief notes, brochures and book reviews (Garcia-Ramos et al., 2000; 2001; 2002a, b, c; Lires et al., 2000; 2001; 2002 a, b; Pinuela et al., 2002 a, b, c; Lockley, 2003). Some of the non-dinosaurian tracks have also been described recently, in English, by Avanzini et al. (2005; 2007).

The Asturian vertebrate ichnofauna, like that of the Morrison Formation, has until recently remained poorly known. For this reason few formal names have been applied to the tracks. For example, until recently the only names applied to Asturian tracks were *Gigantosauropus asturiensis* and *Hispanosauropus hauboldi* (Mensink and Mertmann, 1984), and *Brontopodus* (Lires et al., 2001a). The former two names refer to tracks made by a large sauropod and theropod respectively, and, despite significant errors of interpretation

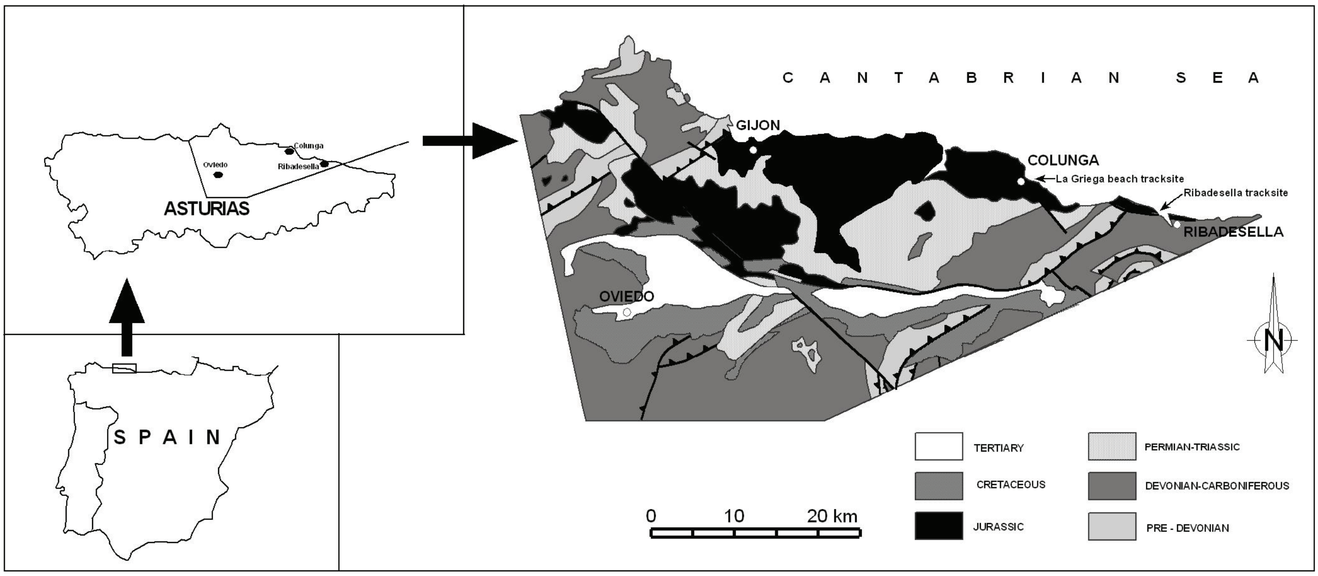


Figure 1 – Locality map showing Jurassic track-bearing outcrops between Gijon and Colunga in east central Asturias, with the famous ichnotype localities (La Griega and Ribadessella) marked (after Lockley et al. 2007).

on the part of Mensink and Mertmann (1984), the tracks have since been correctly re-interpreted (Lires et al., 2001a; Lockley et al., 2007). Tracks from two different outcrops were assigned to ichnogenus *Pteraichnus* (García-Ramos et al., 2000; Piñuela et al., 2002a; Piñuela et al., 2007a). Recently the ichnogenus name *Emydhipus* (Fuetnes Vidarte et al., 2003) has been applied to turtle tracks (Avanzini et al., 2005). The ichnogenus *Deltapodus* has been suggested for purported stegosaurian tracks (Piñuela et al., 2007b; Gierlinski and Sabath, this volume), but the affinity of these tracks remains controversial.

In the case of the Morrison Formation all formal track names have been introduced quite recently. These include: *Pteraichnus* (Stokes, 1957) *Parabrontopodus* (Lockley et al., 1994c), *Stegopodus* (Lockley and Hunt, 1998), *Dinehichnus* (Lockley et al., 1998b) and *Hatcherichnus* (Foster & Lockley., 1997). The former three, as their names imply, are interpreted as pterosaur, sauropod and stegosaur tracks. The latter two are interpreted as ornithopod and crocodilian tracks respectively.

GEOGRAPHICAL AND GEOLOGICAL SETTING OF THE ASTURIAN TRACKSITES

Tracksites known from the Upper Jurassic of Asturias are found at various localities along a series of coastal exposures between Ribadesella (in the east) and Gijon (in the west), a distance of about 60 km (fig. 1). Since the track-bearing outcrops of the coast are no more than 100 m wide, the total track-bearing out crop is no more than 6 km^2. The track bearing layers are associated with three different formations: in ascending order these are the Vega, Tereñes and Lastres Formations (fig. 2) all of which show significant lateral variation within the outcrop belt.

The Vega Formation unconformably overlies the fully marine Rodiles Formation, and consists of a series of fluvial red beds about 150 m in thickness. Deep vertical root traces, small gypsum veins and caliche palaeosols indicate that these rocks were deposited under semi arid conditions with ephemeral flow regimes.

The Tereñes Formation, is also about 150 m thick and reflects a subsequent rise in sea level that led to the deposition of extensive organic-rich marls in a shallow water restricted and tideless sea, protected in their outer margin by a tectonic threshold. Mudcracks, salt pseudomorphs and localized gypsum layers indicate periods of evaporation and repeated emergence.

The Lastres Formation consists of about 400 meters of grey sandstones, conglomerates, mudstones and marls. Current ripples and sole marks are common indicators of unidirectional fluvial flow and in some places *in situ* tree trunks, shell accumulations and well- preserved plant fossils indicate rapid deposition. The general setting is considered a fluvial-dominated deltaic system (García-Ramos & Gutierrez Claverol, 1995; García-Ramos et al., 2002a; 2004; 2006).

GEOGRAPHICAL AND GEOLOGICAL SETTING OF THE MORRISON FORMATION TRACKSITES

In contrast to the relatively localized distribution of tracksites in the Upper Jurassic of Asturias, tracksites in the Morrison Formation of the Western United States are spread out over a much larger area, comprising parts of Colorado, Oklahoma, New Mexico, Arizona, Utah, Wyoming and South Dakota. This area represents on the order of at least 500,000 km^2 (fig. 3), and the stratigraphy is generally much

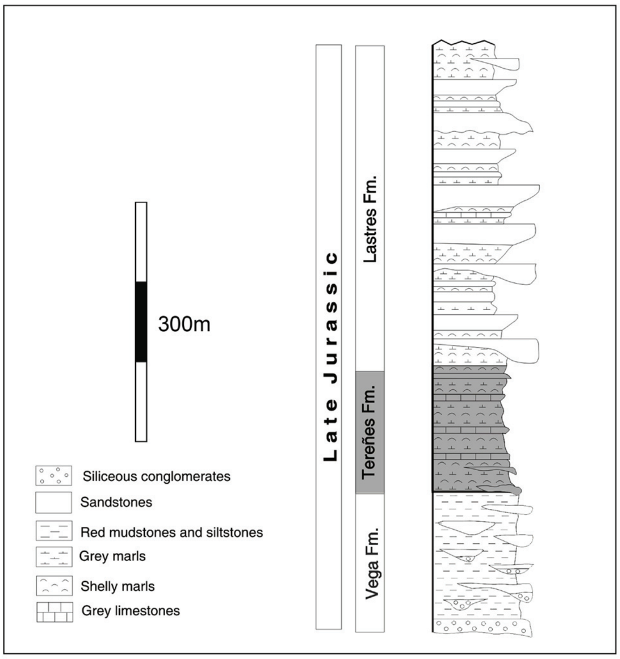


Figure 2 – Simplified stratigraphy of track bearing formations, Upper Jurassic of Asturias.

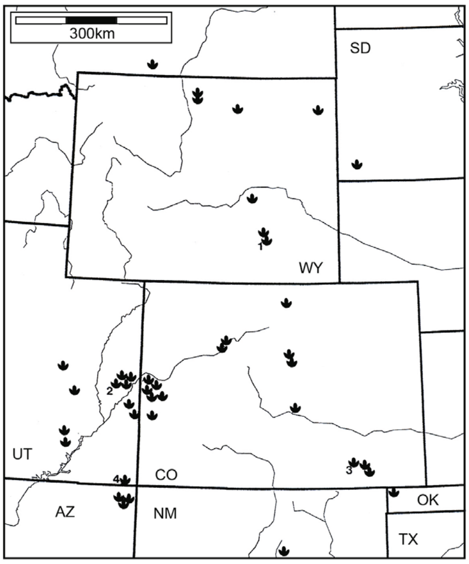


Figure 3 – Simplified locality map for approximately 40 tracksites in the Morrison Formation, western USA. Modified after Foster (1998). Sites 1-4 represent selected dinosaur track sites that have been mapped: 1: Como Bluff, 2: Hidden Canyon, 3: Purgatoire and 4: Boundary Butte. See text for details.

less locally-variable than the Asturian successions. In most areas east of the Rocky Mountains the Morrison is undivided, but to the west the formation is often divided into two members: the basal sand-dominated Saltwash and the overlying mud-dominated Brushy Basin. Other members have been named and the relationship of basal units of the Morrison to underlying units such as the marginal marine Sundance and Summerville Formations is somewhat controversial. However, the overall pattern of Middle and Upper Jurassic marine deposits giving way to predominantly terrestrial successions, is somewhat similar to that outlined for the Asturian successions.

In addition to similarities in the age of the Asturian and western USA successions, both were deposited at similar subtropical latitudes, and both exhibit various fluvio-lacustrine facies mosaics. Both facies complexes are dominated by siliciclastic deposition, though both also indicate evidence of carbonate-evaporite deposition at least locally.

DESCRIPTION OF ASTURIAN TRACKS

Theropod tracks

Theropod tracks clearly show the greatest variation in size and shape of any group of tracks in the Asturian assemblage. They range from about 5 to about 82 cm in length and include many examples with well defined digital pad impressions that resemble typical lower Jurassic *Grallator* tracks. (fig. 4). There is no well-defined methodology established for distinguishing among different theropod track types (Lockley, 2000), and indeed it is difficult to distinguish between theropod, ornithopod (or other ornithischian) and bird tracks in some cases. Thulborn (1990) suggested some general rules, noting that blunter and shorter digits with U rather than V shaped terminations were typical of ornithopod rather than theropod tracks. He also noted the lack of claw impressions in ornithopod tracks. Lockley (1999; 2001, 2007a) has suggested that theropod and ornithopod tracks can generally be distinguished on the basis of trackway pattern and length-width ratios, with theropod tracks being typically elongate, with long steps and correspondingly high pace angulation values (approaching 180^{o}). By contrast ornithopod tracks tend to be as wide or wider than long, with shorter steps, correspondingly lower pace angulation values and moderate to pronounced inward rotation of the foot axis. Some ornithopod trackways indicate quadrupeal progression. It also appears that theropod tracks have better-defined pad impressions in comparisons with ornithopod tracks for footprints of the same size. However, the clarity of pad impressions is size dependent, decreasing in larger footprints. In addition, the clarity of pad impressions is dependent on preservational factors including the type of substrate and the dynamics of foot emplacement.

Thulborn (1990) suggested an arbitrary differentiation between large and small theropod tracks on the basis of size (foot length 25 cm). This convention has also been followed by Olsen et al., (1998). Various authors also note that bird tracks can be distinguished from theropod tracks on the basis of size, digit divarication angles and slenderness of the digits (Currie, 1981; Lockley et al., 1992). However, de-

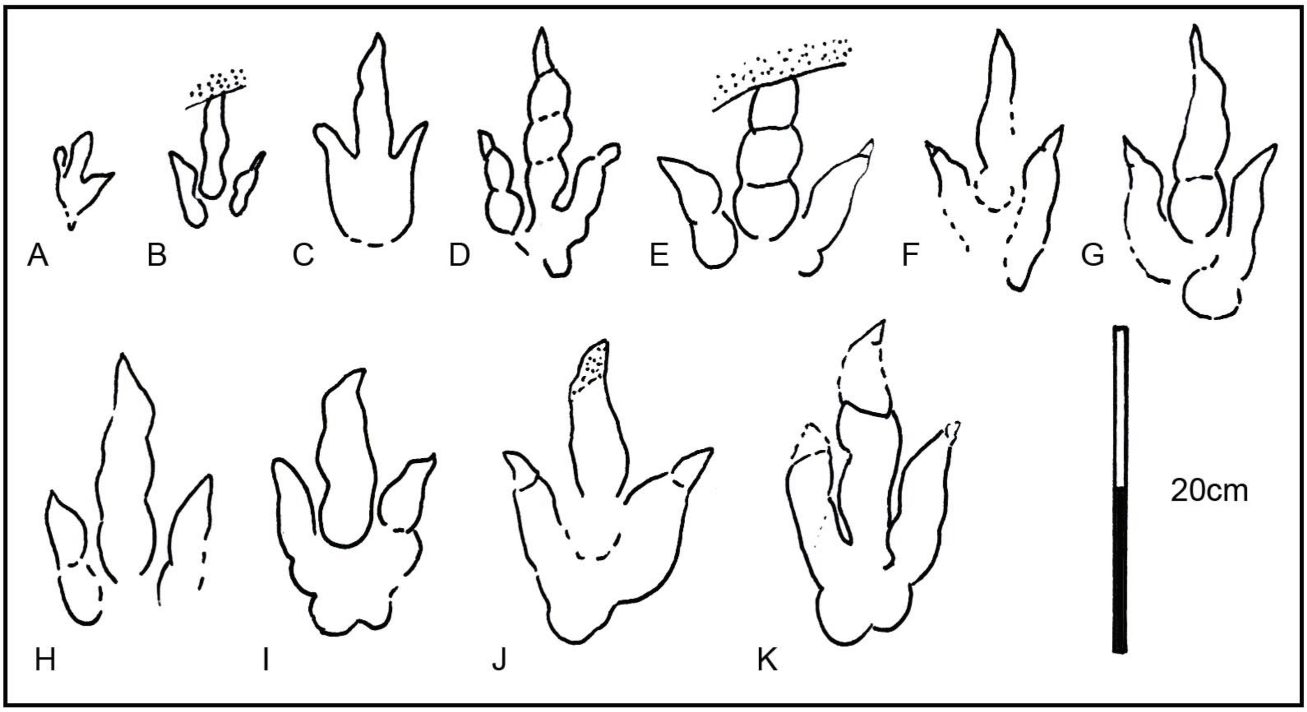


Figure 4 – Small 'grallatorid' theropod tracks from the Upper Jurassic of Asturias, foot lengths less than 25 cm, arranged in order of increasing size (A-K). Based on CU Denver tracings 799-800.

spite these guidelines there is great diversity among theropod tracks and among tridactyl tracks in general.

As shown in fig. 4 there are a large number of tracks that resemble the classic Liassic Lower Jurassic Grallator (Hitchcock, 1858) or what we herein call the 'grallatorid morphotype' (fig. 4). These are typically small (foot length less than 20-25 cm) with low digit divarication angles and well defined digital pads in all cases where preservation is moderately good.

A second category of theropod tracks is characterized by moderately large size (up to 30-35 cm in foot length or width), but large digit divarication angles (up to 90-100^{o}). We refer to these as a gracile morphotype (fig. 5). They resemble tracks such as *Kayentapus*, from the Lower Jurassic of the western USA (Welles, 1971) and *Magnoavipes* from the Mid Cretaceous of the western USA (Lee, 1997; Lockley et al., 2001). However, we note only general resemblances and do not imply that either of these ichnogenus labels is suitable for the Asturian tracks. Both these ichnogenera, but particularly *Magnoavipes*, have many avian characteristics such as slender digits and wide digit divarication angles, and are somewhat convergent with the avian morphotype described in the following section.

Avian morphotype

The most intriguing tridactyl tracks in the Asturian assemblages are those from the Villaviciosa locality described by Piñuela et al (2002b) as the tracks of avian dinosaurs (fig. 6). These tracks are characterized by highly divergent slender digit impressions and a short posteriorly-directed hallux. The tracks are significantly wider (11-14 cm) than long (9-11 cm) with digit divarication angles up to 145^{o}. No such slender tracks are known from any other Jurassic locality, although two tracks with similar wide divarication angles were reported by Lockley et al. (1998a) from the Morrison Formation of Colorado.

***Hispanosauropus* morphotype**

Hispanosauropus hauboldi is the only theropod track from the Asturian assemblages that has been named. The original type specimen chosen by Mensink and Mertmann (1984) was 51 cm long and 36 wide. Although the holotype, a field specimen cannot be found, and may be lost to erosion, other tracks with the same shape and dimensions have been located at the type locality (Lockley et al., 2007). Moreover, it appears that this morphotype is not uncommon in the Asturian assemblages and may be preserved both as natural casts and molds. In most examples some digit pad impressions are present (fig. 7), but they are not usually well defined. There seems little doubt that this morphotype represents robust theropod that was different from the species that made the somewhat smaller and more gracile grallatorid tracks described above. As noted elsewhere (Lockley et al., 2000) the relationship between *Hispanosauropus* and the concept of megalosaur tracks (*Megalosauripus*) is complex.

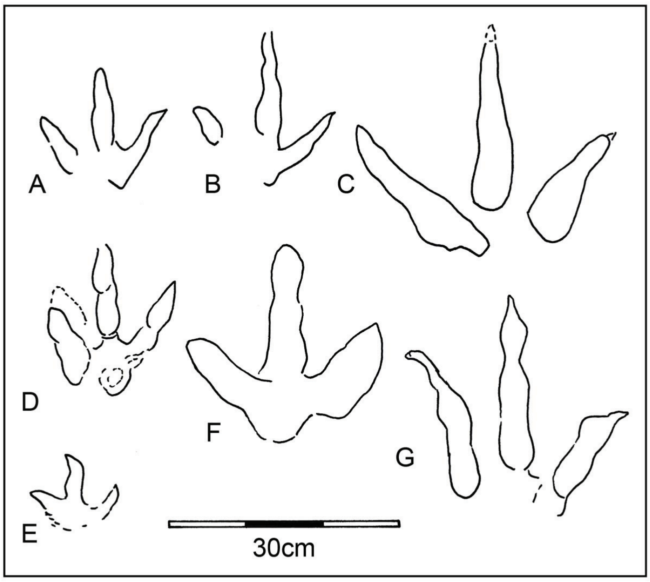


Figure 5 – Large slender toed gracile tridactyl tracks from the Upper Jurassic of Asturias. Tracks A-C are from the Faro de Tazones locality (based on CU Denver tracing 801). Although a theropod affinity is inferred, some tracks are convergent with gracile ornithopod tracks (cf. fig. 14).

Sauropod tracks

Global surveys of sauropod tracks (Lockley et al., 1994c, d) suggest that they fall into two broad categories: narrow-gauge and wide-gauge. The former typically have a small manus, the latter a large manus, thus defining more or less heteropody (posterior emphasis) respectively. Both types have been reported from the Jurassic, and both types appear to be represented in the Late Jurassic of Asturias.

Although many isolated sauropod tracks have been found on fallen blocks or in cross section, relatively few well-preserved manus-pes sets or trackway segments have been found in situ. The best example of associated manus and pes tracks is probably the specimen found on a fallen block at the Acantilados de Quintuelles (Villaviciosa). The pes track was illustrated by García-Ramos et al., 2002a, p. 118; 2004 p. 31). This specimen shows well-preserved pes digit impressions and an associated manus, from the same trackway also with digit traces (fig. 8). It is, however, common to find isolated manus casts (García-Ramos et al., 2002a, p. 118) that show no traces of individual digit morphology.

There are visually spectacular examples of presumed sauropod trackways observable on the inaccessible cliff surface near Ribadesella (García-Ramos et al., 2002a, p 185; 2004, p.112), and a distinctive wide-gauge trackway found on the wave cut platform at Tereñes has also been interpreted as a sauropod trackway (García-Ramos et al., 2002a, p. 178 ; 2004, p.105), but reinterpreted as stegosaurian trackway (García-Ramos et al., 2006) and atributtable

Figure 6 –Avian-like tracks from the Upper Jurassic of Asturias: after García-Ramos et al. (2002a, p 117). Note very wide digit divarication angle (~120º).

to *Deltapodus* (Piñuela et al., 2007 b). Gierlinski and Sabath (this volume) also suggest it may be a stegosaur trackway, attributable to the ichnogenus *Deltapodus*.

There is no doubt that both sauropod tracks (*Brontopodus*) and purported stegosaur/thyreophoran tracks (*Deltapodus*) occur in the Asturian ichnofaunas. However, the reinterpretations of Gierlinski and Sabath (this volume) suggest that the tracks are not always easily distinguished in all cases, especially where preservation is sub-optimal. One obstacle to differentiating these tracks is that until now very few *Deltapodus* trackways have been recognized. Indeed, as

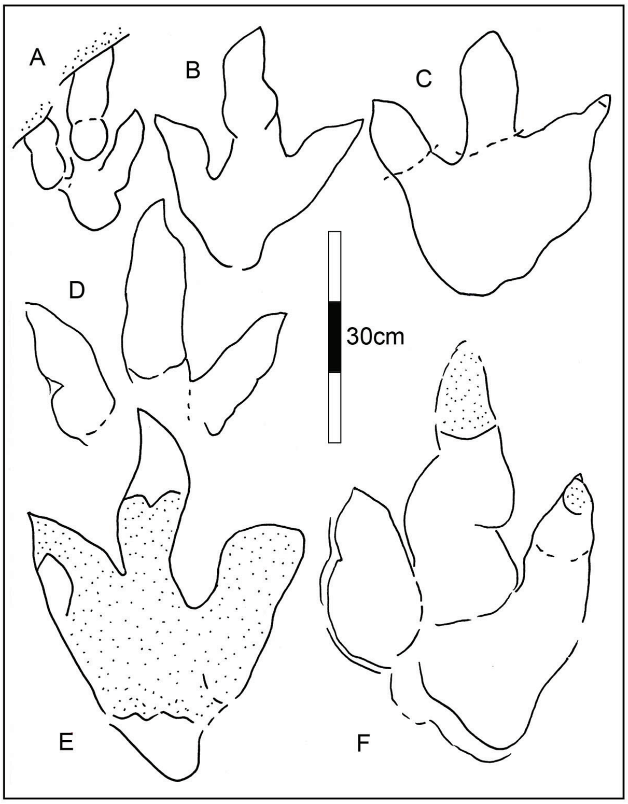


Figure 7 – Robust theropod tracks with foot lengths greater than 25 cm. A: resembles a large grallotorid track. B-E: *Hispanosauropus* morphotype (D: after Lockley et al., 2007).

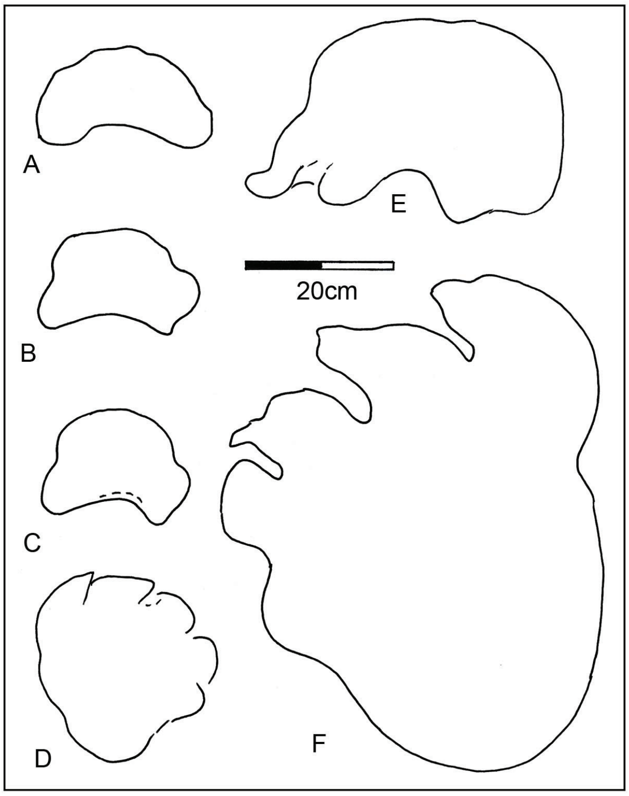


Figure 8 – Sauropod tracks from the Upper Jurassic of Asturias. A-C: manus tracks redrawn after García-Ramos et al. (2002a, p 118-119). D small pes track. E-F: right manus and left pes track from same trackway: note digit impressions.

noted below, the Asturian sample is the largest, but consists mainly of isolated pes tracks.

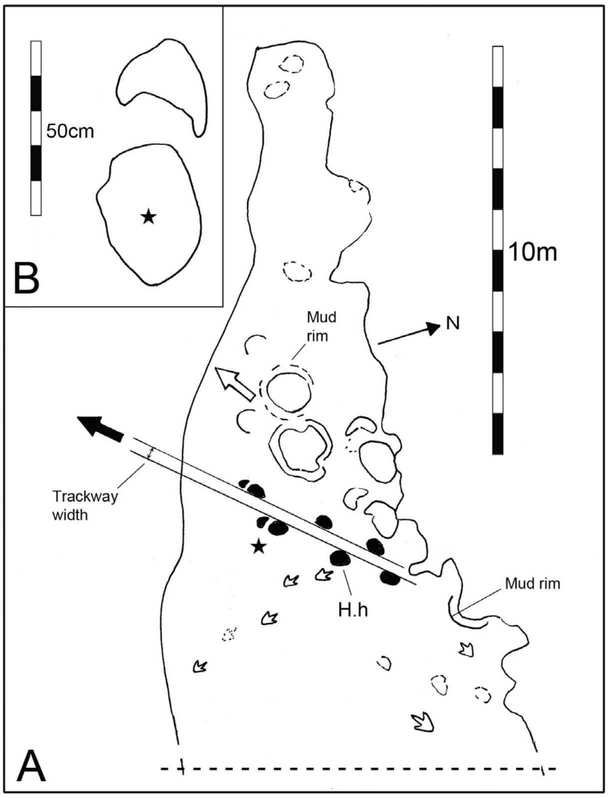
Gigantosauropus is another problematic track first attributed to a giant theropod by Mensink and Mertmann (1984). Recent restudies of the *Gigantosauropus* type locality (Lires et al. 2001a; Lockley et al.,2007) reveal that it is a sauropod trackway. In fact, in situ trackways reveal the presence of both large and small sauropod tracks (*Gigantosauropus* and *Brontopodus*). The former appear to be relatively narrow-gauge for such large ichnites, but the latter are wide-gauge (fig. 9). As noted by Lockley et al. (2007) the original study of *Gigantosauropus* by Mensink and Mertmann (1984) was seriously flawed and the ichnogenus is based on material that is not very well preserved.

Sauropod skin impressions

The problem of sauropod track identification, especially in cases of incomplete, distorted or poorly preserved tracks, such as may be seen in cross section in the Asturian cliff outcrops, can to some extent be mitigated if skin impressions are preserved. Recent reports of skin impressions associated with sauropod tracks from Asturias (Lires et al., 2001b; García-Ramos et al., 2002a: p. 110; 2004: p. 34; 2006: pp. 126-127), Korea, (Yang, 2003; Lockley et al., 2006) and Wyoming (Platt and Hasiotis, 2006) reveal very distinctive polygonal patterns (fig. 10). These polygons vary in diameter from about 0.5 to 4.5 cm, and, especially in the case of the larger polygons, are very similar to sauropod skin impressions from other parts of the body (Czerkas, 1994). However, not enough is known of the inter- and intraspecific variation in the size and shape of skin polygons in quadrupedal dinosaurs to consider any given pattern as unequivocally diagnostic. Thus, although large polygons of the type shown in figure. 10b are known to be associated with diagnostic sauropod tracks, the smaller variety (fig. 10a) may, as noted in the following section, belong to other quadrupedal dinosaurs such as stegosaurs.

'Stegosaurian' tracks

At least forty blunt-toed, elongate, tridactyl track casts have been found that appear to fall into a distinctive category, which we provisionally refer to as "stegosaurian." (fig. 11). In comparison with either theropod or ornithopod tracks of similar size they are all extremely short toed, with very elongate heel impressions that seem to suggest a very fleshy heel that tapers very little towards the posterior mar-



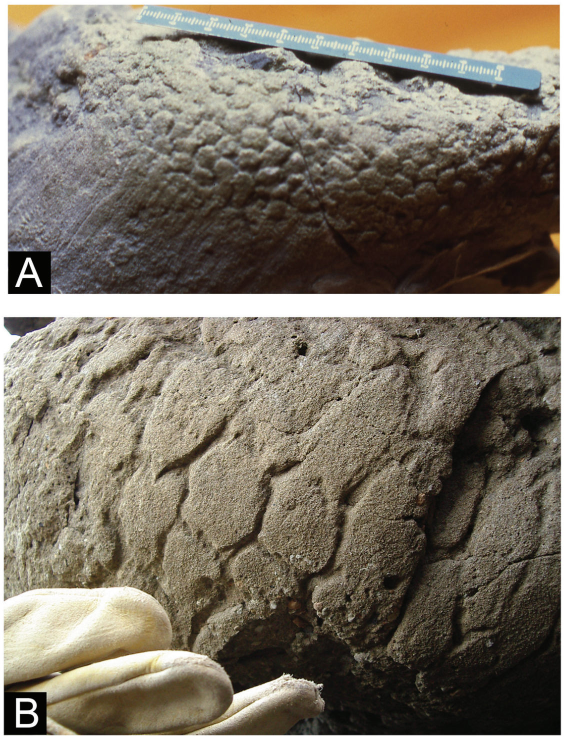


Figure 9 - A: Map of the *Gigandosauropus* type locality after Lockley et al., (2007). White arrow shows *Gigandosauropus,* representing a large sauropod, and black arrow shows *Brontopodus*, representing a small sauropod. The track marked H. h was incorrectly interpreted as a tridactyl theropod track (*Hispanosauropus hauboldi*) by Mensink and Mertmann (1984). B: shows detail manus pes set of *Brontopodus* from location in trackway marked with a star.

Figure 10 - Track casts with skin impressions. A. cresentic manus cast with small polygonal skin impressions and slide marks (left) after García-Ramos et al. (2002a, p 110). This cast could be attributable to a stegosaurian. B. coarser scale skin impressions (polygon diameter about 2 cm) attributable to a sauropod.

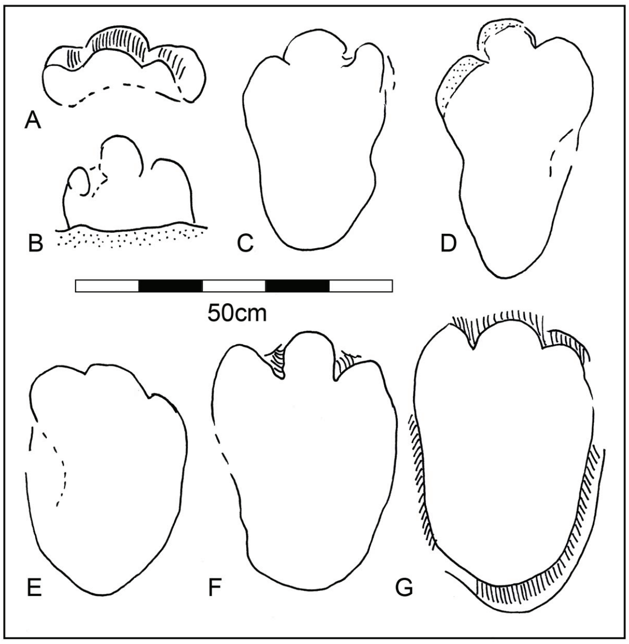


Figure 11 - A-G. *Deltapodus*-like tracks of possible stegosaur origin. All tracks are natural casts and are inferred to represent the pes. Tracks A and B are incomplete.

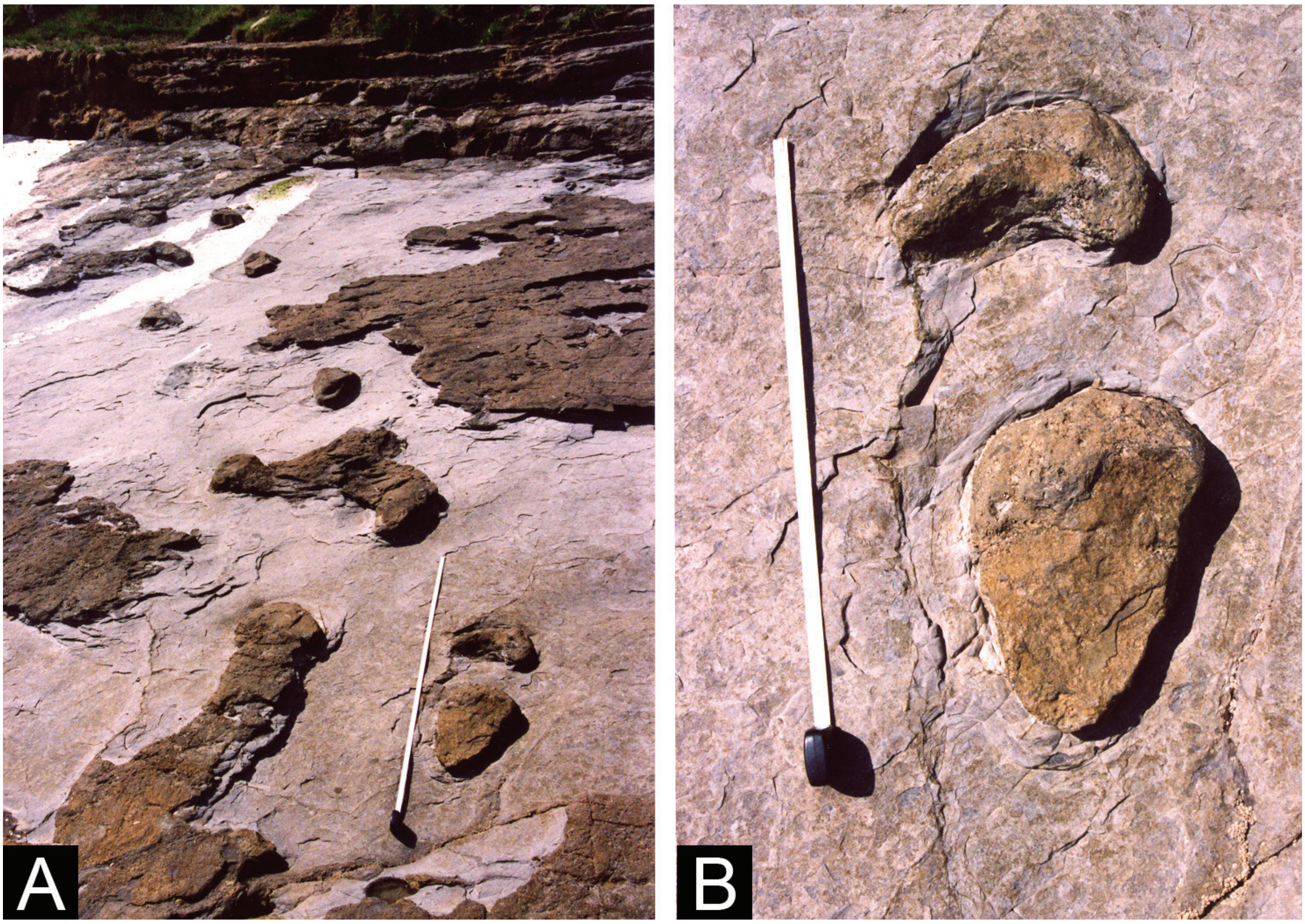


Figure 12 – **A**: trackway and B: detail of manus-pes set of *Deltapodus*-like tracks originally attributed to a sauropod but reinterpreted by Gierlinski and Sabath (this volume) as stegosaurian (ichnogenus *Deltapodus*).

gin. The toe impressions however, show one quite consistent feature: they are asymmetric about the central axis (digit III). Thus, although all are more or less sub-equal in length, one (probably medial digit II) is significantly wider than the other (lateral digit IV): see Gierlinski and Sabath (this volume). This track type, although superficially sauropod –like (Whyte and Romano, 1994) has many of the characteristics of the ichnogenus *Deltapodus* (Whyte & Romano, 2001) which has been attributed to a stegosaurian. Piñuela et al., 2007b, Gierlinski and Sabath, (this volume) argue that a visually spectacular trackway preserved on the foreshore at the Tereñes locality (Garcia-Ramos et al., 2002, p. 178) is an example of *Deltapodus* (fig. 12A). However, there is uncertainty about the affinity of these tracks. Although Garcia-Ramos et al. (2002, 2006) suggest a stegosaurian track maker, Gierlinski et al., (2005) and Gierlinski and Sabath (this volume) suggest that an ankylosaurian might also be considered.

Unfortunately, although the Tereñes trackway shows the wide-gauge trackway pattern quite clearly, and also reveals the crescentic shape of the manus (fig. 12) the natural impressions are filled by sediment from the overlying bed and so details of the digit impressions are not easily determined. By contrast all the isolated specimens (Fig 11) are all natural casts that lack associated manus tracks except in rare cases. Several of these casts show skin impressions and marginal striations that indicate that they are true footprint casts. The sample is in need of further study in order to more clearly define the diagnostic morphological features, and to determine whether the inference of stegosaurian affinity is justified. The track, with skin traces, illustrated by Lockley and Hunt (1995, fig 4.44) is likely not a sauropod pes track but a 'stegosaurian' pes track in the sense used here: i.e., similar to the Asturian *Deltapodus* morphothype.

Ornithopod-like tracks

A number of isolated tridactyl tracks from various localities have been attributed to ornithopods (García-Ramos et al., 2002a, 2004). Many of these are problematic for various reasons, including their similarity to tracks in various states of preservation that can be attributed to theropods or even to stegosaurs (*sensu* Gierlinski and Sabath). We discuss some of these problems, but can not hope to resolve

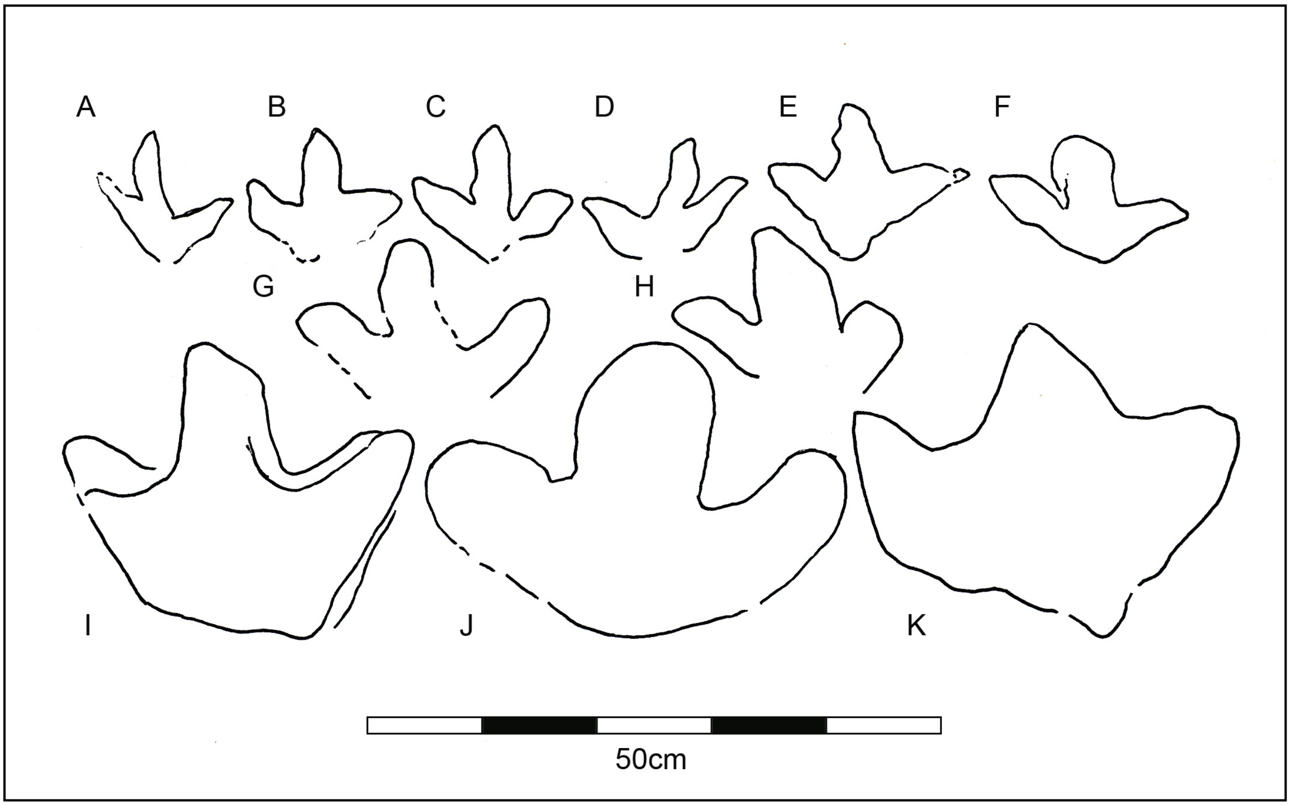


Figure 13 – Medium-sized ornithischian tracks: A-H are from the same surface and generally resemble *Moyenosauripus*. J-K are large tracks that resemble Cretaceous ornithopod (iguanodontid) footprints.

the identity of the trackmakers of all tridactyl tracks at this preliminary stage of study.

Medium-sized tridactyl tracks (width 12-22 cm) have been reported from the Tereñes locality. A least 18 medium-sized tridactyl ichnites found on a single block (García-Ramos et al., 2002a, p. 180) are blunt toed with wide digit divarication and no discrete pad impressions (fig. 13A-H). Although such characteristics are often ascribed to ornithopods, these tracks are enigmatic because they are unlike any previously described from the Upper Jurassic. It could be argued that they are somewhat similar to large *Anomoepus* tracks (Hitchcock, 1858) or to *Moyenosauripus* (*sensu* Gierlinski, 1991; Lockley and Meyer, 2000; Lockley and Gierlinski, 2006), but this label is tentative at best.

Tracks that more closely resemble classic *Anomoepus* (*sensu* Hitchcock 1858; Olsen and Rainforth 2003) are recorded from other localities near Faros de Tazones (Garcia Ramos et al., 2006, p. 151). These tracks range in size (foot length) from about 10-18 cm. Assignment of such tracks to *Anomoepus* is facilitated by the presence of small manus traces, which although incomplete in most cases, in one example (fig. 14) clearly reveal the diagnostic pentadactyl morphology associated with this ichnogenus.

Currently very little is known of the morphology and spatial and temporal distribution of *Anomoepus*-like tracks with both manus and pes sets from post Early Jurassic deposits. These are the first well-preserved tracks from the Late Jurassic attributable to this ichnogenus, and will be described elsewhere in more detail. However, similar tracks have recently been reported from the basal Cretaceous and assigned to the ichnogenus *Neoanomoepus* (Lockley et al., in press)

Larger blunt-toed tridactyl tracks, also from Tereñes, bear a close resemblance to tracks of large Cretaceous ornithopods such as iguanodontids (fig. 13J-K). The largest of these is in the size range of 40-45 cm (Piñuela et al., 2002c). However, such occurrences are anomalous because no large iguanodontid-like ornithopods are known from the Upper Jurassic of the world. As pointed out by Piñuela et al., 2002c and Gierlinksi and Sabath (this volume), the only large ornithopod known from this epoch is *Camptosaurus*, which has a relatively gracile foot which they consider likely to have left a gracile footprint such as *Dinehichnus* (Lockley et al., 1998b; Gierlinksi and Sabath, this volume). However, this

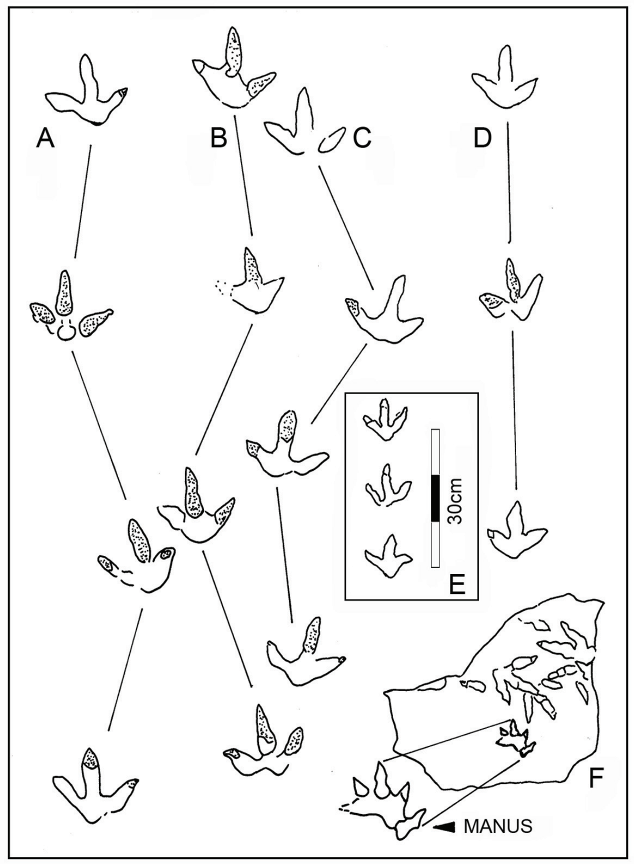


Figure 14 (left) – *Anomoepus*-like tracks and trackways. A-D trackways traced in the field. E: isolated individual tracks. F: a slab with an isolated pentadactyl manus track.

Figure 15 (below) – Small pterosaur manus and pes tracks after García-Ramos et al. (2002a, p 125) and Pinuela 2002a.

material is generally quite small (size range 10-28 cm). Small tracks of this type have been noted in the Upper Jurassic of Portugal, (Lockley et al., 1998b), and may also be present in the Asturias assemblage.

In this regard it is worth noting that large ornithopod tracks of the iguanodontid type (e.g., *Iguanodontipus*: Sarjeant et al., 1998) are undocumented in the Late Jurassic, and almost invariably appear only above the Jurassic-Cretaceous boundary (Lockley & Wright, 2001). Only one reference a giant Jurassic ornithopod track (70 cm long and 69 cm wide) is reported from Portugal (Mateus &Milan, 2005). However, we are not persuaded that these tracks are made by other ornithischians such as stegosaurs as suggested by Gierliński & Sabath (this volume).

Another possible indicator of ornithopod affinity among tracks from the Tereñes locality is the presence of parallel trackways (García-Ramos et al., 2002a: p. 176 ; 2004: p. 103; 2006: pp. 146-147; Piñuela et al., 2002c; Piñuela et al., 2007b), which are indicative of gregarious behaviour as commonly reported in large Cretaceous ornithopod track assemblages (Lockley et al., 2006). However, Gierlinski and Sabath infer that these may also be stegosaur tracks. Their inference is intriguing but it requires the interpretation that stegosaurs switched between quadrupedal, plantigrade and bipedal, digitigrade progression, respectively, to make *Deltapodus* tracks, with long pes heel traces (fig. 11), and ornithopod-like trackways without heel like traces (fig. 12). Purported Lower Jurassic thyreophoran tracks from France (LeLeouff et al., 1999) show both long and short pes heel traces in the same trackway, but have quite distinctive, elongate and segmented impressions of digits II-IV, that are quite distinct from any morphologies recognized in tridactyl traces from Asturias.

Pterosaur tracks

Pterosaur tracks from the Asturias assemblages are a particularly important part of the ichnofauna. They range in size from between 3.5 cm (fig. 15) and 18 cm (fig. 16 in pes length and in some cases show impressions of interdigital webbing and skin impressions. The largest (García-Ramos et al., 2000; 2002a: p. 124; 2006: p. 156) tracks are larger than any known from the Jurassic, and compare in size with tracks from the basal Cretaceous of England (Wright et al., 1997). For these reasons the tracks merit detailed study in their own right. As noted by Pinuela et al. (2002a) and García-Ramos et al., (2002a: pp. 124-125; 2006: pp. 156,158) there are a number of pterosaur track-bearing slabs that show high densities of footprints (fig. 15) typical of pterosaur track assemblages (Lockley et al., 1995; Mickelson et al., 2004). There are also a number of examples of tracks with web impressions and scratch marks indicative of swimming behavior (García-Ramos et al., 2000; Lockley and Wright, 2003).

Lockley et al. (in press) reviewed the global distri-

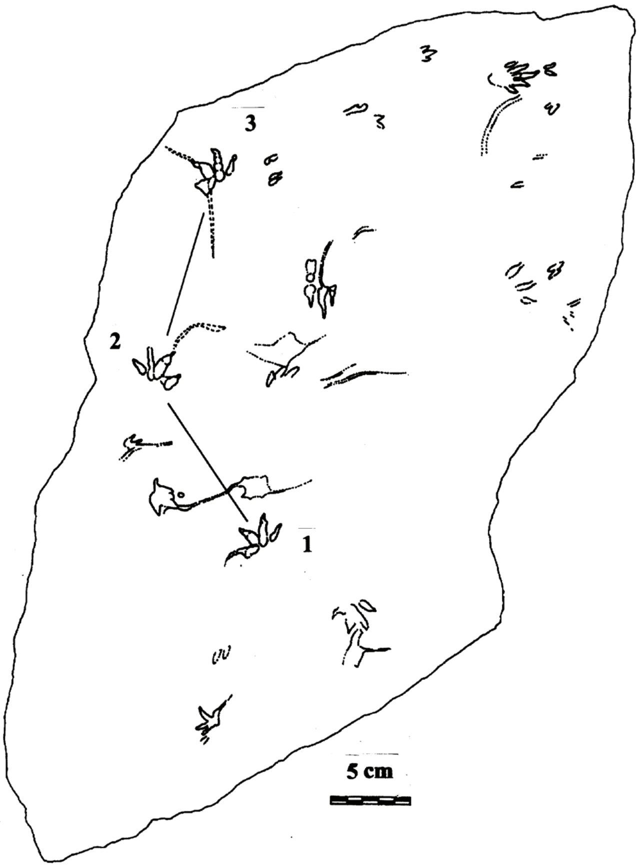


Figure 16 (top) – Large pterosaur track with skin impressions after García-Ramos et al. (2002a, p. 124) and Pinuela 2002a. Track is 18 cm long.

Figure 17 (right) – Crocodilian tracks from Upper Jurassic of Asturias. Map of MUJA specimen 0101 shows a sequence of right, left and right tracks (1-3) described by Avanzini et al. (2007, fig. 2).

bution of pterosaur tracks noting that at least 50 localities are known including 4 in the Upper Jurassic of Asturias (Pinuela et al., 2007a). At present all named pterosaur tracks from the Jurassic have been assigned to the ichnogenus *Pteraichnus* (Stokes, 1957), which was based on relatively small tracks (~8 cm). However, this is somewhat of a "catch all" ichnogenus, and it is possible that detailed studies of the variation in Asturian tracks, and especially the difference between the large tracks with skin impressions and web traces and the smaller ones that lack these features, will lead to ichnotaxonomic refinements.

Crocodilian tracks

Probable crocodilian tracks have been reported from a few localities in the Upper Jurassic of Asturias (Avanzini et al., 2007). These show significant variation in morphology (fig. 17) and have been assigned to four morphotypes (A-D) which include forms attributable to *Crocodylopodus* (Fuentes Vidarte & Meijide Calvo, 2001) and *Hatcherichnus* (Foster and Lockley 1997).

Turtle tracks

As summarized in a recent paper by Avanzini et al. (2005) turtle tracks resembling *Chelonipus* (Ruhle von Lilienstern, 1939) and the recently named *Emydhipus* (Fuentes Vidarte et al., 2003) have recently be recognized from the Asturian ichnofaunas (fig. 18). These tracks are very similar to turtle tracks reported from the Upper Jurassic Morrison Formation in Utah (Foster et al., 1999) and Colorado (Lockley and Foster 2006).

COMPARISON OF ASTURIAN AND MORRISON ICHNOFAUNAS

Although many Upper Jurassic ichnofaunas have been described from Europe, until recently the most distinctive are mostly in carbonate facies, such a those from Portugal (Lockley et al., 1994a). These are dominated by sauropod and theropod tracks and have been described as an example of the *Brontopodus* ichnofacies (Lockley et al., 1994d; Lockley & Meyer, 2000; Hunt & Lucas, 2007; Lockley, 2007b), which are characterized by low diversity. Thus, the Asturian ichnofaunas provide a valuable example of track assemblages in siliciclastic ichnofacies, and it is evident that they represent a much more diverse assemblage.

Probably the best known Upper Jurassic vertebrate ichnofaunas with which we can compare the Asturian track assemblages are those described from the Upper Jurassic Morrison Formation from the western USA (Lockley and Hunt, 1995; Lockley et al., 1998a; Foster & Lockley, 2006). These also originate from siliciclastic ichnofacies.

As shown in fig. 3, tracksites from the Morrison For-

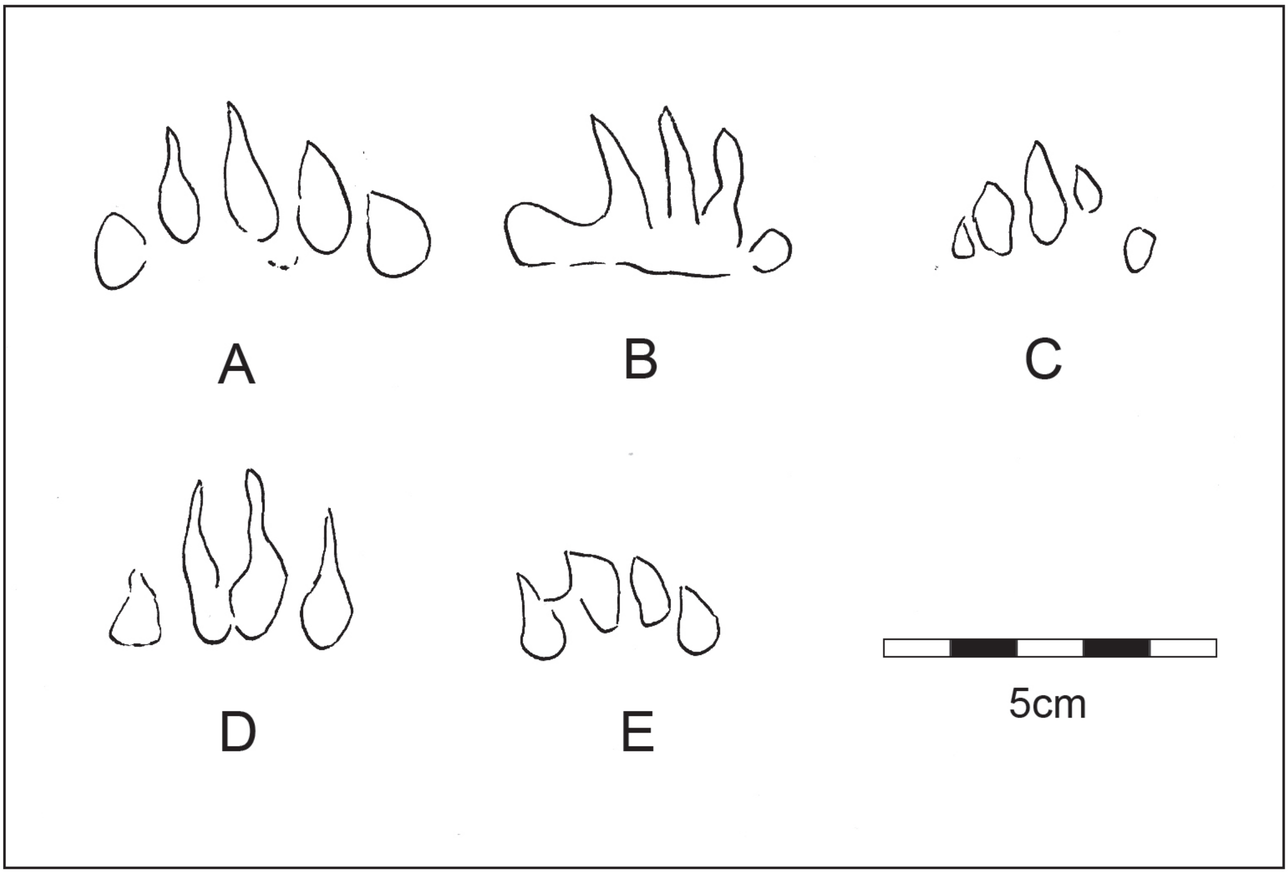


Figure 18 – Typical turtle tracks from the Upper Jurassic Morrison Formation (after Lockley & Foster, 2006, fig 6). Compare with tracks illustrated by Avanzini et al., (2005, fig 3).

mation are spread over and area that measures just over 900 km from north to south and a little more than 600 km from east to west: i.e., more than 500, 000 km^2. Foster (1998) reported about 40 sites from this area, and the number has since increased to more than 50 (Foster & Lockley, 2006). Thus, track site density is quite low: one site per 10,000 km^2. Many of these sites are small yielding only a few tracks: in this regard they resemble sites from Asturias. However, other sites are larger and surfaces of various sizes have been mapped in some detail: for example the Como Bluff Site (Southwell et al., 1996), the Hidden Canyon Site (Barnes & Lockley, 1994), the Purgatoire site (Lockley et al., 1986; 1997) and the Boundary Butte site (Lockley et al., 1998b). These allow us to make censuses of track-frequency at various individual sites, and compile ichnofaunal statistics for the whole region. The same potential exists in Asturias, although in this region many more of the tracks occur as isolated specimens associated with cliff erosion. As noted above the whole Asturian outcrop is estimated at 6 km^2, which is about 0.0012% of the Morrison area. This serves to demonstrate the high density of tracks recovered from the Asturian outcrops, as the result of exposure and accumulation by coastal erosion. There are a few large track-bearing surfaces in the Asturian assemblages, but although some of these have been mapped (García-Ramos et al., 2006: pp. 119, 124, 142, 147; Lires, et al. 2000, 2001a; Lockley et al., 2007; Piñuela et al., 2002c), many of the maps so far compiled, have yet to be published. Nevertheless, the Asturian literature is characterized by a number of well illustrated guidebooks (García-Ramos et al., 2002a; 2004; 2006) which give a useful indication of the general ichnological assemblage at many important sites. In addition the Asturian ichnofauna is represented by a large number of generally well-preserved specimens that have been brought together in one large collection at the Museum of the Jurassic of Asturias (MUJA). This is in contrast to the more scattered collections from the Morrison Formation of the western United States.

As suggested above, there are some problems with track identification which may cast doubt on inferences about track-maker affinity and so may compromise paleoecological census interpretations. For example, Lockley et al. (1986) inferred that most tridactyl tracks at the large Purgatoire site in Colorado were made by ornithopods. However this interpretation was subsequently changed (Lockley & Prince, 1988; Prince and Lockley 1989; Lockley et al., 1997), when it was realized that the tracks were those of theropods. Similarly, the work of Gierlinski and Sabath (this volume) casts doubt on the interpretation of a specific site with large orni-

TRACK TYPE	ASTURIAS	Western USA
Theropod type 1	Large grallatorid	-
Theropod type 2	Large gracile form	-
Theropod type 3	*Hispanosauropus*	Large robust form
Theropod type 4	large bird-like tracks	-
Sauropod narrow gauge	*Gigantosauropus*	*Parabrontopodus*
Sauropod wide gauge	*Brontopodus*	-
Stegosaurian	*Cf. Deltapodus*	*Stegopodus* and *Deltapodus**
Ornithopod type 1	*Anomoepus*	cf. *Anomoepus*
Ornithopod type 2	-	*Dinehichnus*
Ornithopod type 3	Wide divarication form	-
Ornithopod type 4	*Cf. Iguanodontipus?*	-
Pterosaur type 1	*Pteraichnus sp* (small)	*Pteraichnus*
Pterosaur type 2	*?Pteraichnus sp* (large)	-
Crocodile	*Crocodylopodus sp* and *Hatcherichnus*	*Hatcherichnus*
Lizard	Lacertoid form present	-
Turtle	*Emydhipus*	*Chelonipus*

Table 1 – Comparison between Upper Jurassic ichnofaunas from Asturias, Spain (Vega, Tereñes and Lastres Formations) and the Western United States (Morrison Formation). *Data from Milàn and Chiappe (in press).

thopod tracks in the Asturian assemblage by suggesting that they may be stegosaurian. Even the identification of some purported sauropod tracks is in doubt (as noted above). Such problems are to be expected when dealing with a sample that contains many isolated track casts.

However, while these problems may make a reliable census of Upper Jurassic tracks from Asturian somewhat difficult, the sample is large and the known ichnofaunas has been sufficiently well-described in preliminary publications to permit useful general comparisons (Table 1). Moreover, as the first large Upper Jurassic sample from a clastic facies in Europe, the assemblage is very useful for shedding new light on track types and details of morphology not previously known from comparable samples. The novel elements of the assemblage include the rare, but very distinctive, and large bird-like tracks with high digit divarication angles (fig. 6), the *Deltapodus*-like tracks of probable stegosaurian or related ornithischian affinity (figs 11-12) which show skin impression that evidently help distinguish them from sauropod tracks (fig. 10), and the large pterosaur tracks (fig. 16), which, globally, are the largest known in the Jurassic and the first ever found with skin impressions.

As shown in Table 1 the Upper Jurassic ichnofaunas of Asturias and the Western USA are generally quite similar in overall composition, though different in detail. For example, both ichnofaunas contain presumed, theropod, sauropod, stegosaur and ornithopod, dinosaur tracks as well as footprints of pterosaurs, crocodilians and turtles. However, in many cases, there are noteworthy differences in the track types when examined in detail. Many of these differences may be more apparent than real: i.e., they may be due to non-biological biases that pertain to preservation and the size of the sampled area, whereas other differences may reflect genuine biological differences in the composition of the faunas:

The following summary suggests the most noteworthy similarities and differences between the two ichnofaunas.

Theropod track types are diverse in both regions, and there are no obvious differences expressed in formal or well-defined ichnotaxonomic terms. Small grallatorid-like forms and larger gracile forms with wide digit divarication are known from both areas. The *Hispanosaurus* morphotype has not been formally identified in the Morrison Formation, though quite similar forms are known. The Asturian type herein referred to as bird like has not been identified in the Morrison Formation.

Both large and small sauropod track types have been identified in both assemblages, and even the skin impressions are similar in some cases: i.e. in the case of patterns that reveal larger diameter polygons.

The purported stegosaurian track *Stegopodus*, based primarily on a distinctive manus, has not been identified in the Asturian assemblage. Conversely the *Deltapodus* morphotype is quite common in the Asturian assemblage, but rare in the Morrison Formation. In the Asturian sample some casts show skin impressions.

Purported ornithopod tracks are evidently the most problematic general category in both areas. Tracks from the Morrison Formation have been assigned to the ichnogenera *Anomoepus* and *Dineichnus*, although in both cases the designation is based on pes morphology as no manus traces are reported. However, no purported ornithopod tracks from Asturias have been given formal ichnotaxonomic names, though we herein suggest that some tracks from the Faros de Tazones locality resemble *Anomoepus* in both manus and pes morphology. Tracks from the Terenes locality fall into two distinct categories: smaller varieties with relatively gracile widely divergent digits that we very tentatively compare with *Moyenosauripus* and much larger tracks that have a close resemblance to footprints of large Cretaceous ornithopods such as iguanodontids (fig. 13)

Pterosaur tracks are rare in the Morrison (Lockley et al., 2001) though they are common in the underlying Summerville Formation (Lockley et al., 1995, 2001; Mickelson et al., 2004; Lockley et al., in press). All know tracks from this Upper Jurassic top Summerville-lower Morrison interval in the western USA are relatively small (2- 10 cm approx). However, the Asturian tracks are significantly larger in maximum size (up to 18 cm) and include the aforementioned examples with skin impressions.

Crocodilian tracks are known from both the Morrison Formation and the Asturian assemblages. Morrison tracks (ichnogenus *Hatcherichnus*) are relatively large. By comparison the Asturian tracks are more diverse and include a number of small morphotypes, including *Crocodylopodus*, in addition to *Hatcherichnus*.

Turtle tracks are known from both the Morrison and the Asturian assemblages and are both quite similar. They have been assigned to *Chelonipus* and *Emydhipus* respectively. We regard these forms as very similar.

CONCLUSIONS

The Upper Jurassic ichnofaunas of Asturias in northern Spain are quite similar to those from the Morrison Formation of western North America. The main differences are that the Asturian ichnofauna is comprised of many isolated specimens which originate from a relatively small geographic area, whereas the American ichnofaunas is found spread out over a much larger region.

While the two ichnofaunas contain many tridactyl tracks of problematic affinity, most other tracks are easily attributed to various well-known groups. In the final analysis the to ichnofaunas both contain a diverse representation of dinosaur tracks (theropods, sauropods, stegosaurs, ornithopods, and possibly other ornithischians) together with footprints of pterosaurs, crocodilians and turtles. Almost all groups are represented by at least two if not as many as four or more distinctive morphotypes. Thus each ichnofaunas has a cumulative diversity of at least 12- 15 ichnotaxa, of which about half are diagnostic to the ichnogenus level.

Studies of the Upper Jurassic ichnofaunas of Asturias and the western USA are still in their infancy, and to date have produced tracks that have yet to be identified ichnotaxonomically with certainty. Nevertheless in both regions tracks are plentiful and evidently representative of the skeletal faunas in these areas. Thus, tetrapod tracks provide a useful complementary database which helps provide a general paleoecological picture of the vertebrate faunas of the Late Jurassic in these regions.

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