The largest European theropod dinosaurs: Remains of a gigantic megalosaurid and giant theropod tracks from the Kimmeridgian of Asturias, Spain (#23659)

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The largest European theropod dinosaurs: Remains of a gigantic megalosaurid and giant theropod tracks from the Kimmeridgian of Asturias, Spain

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The Kimmeridgian Vega, Tereñes and Lastres formations of Asturias have yielded a rich vertebrate fauna, represented by both abundant tracks and osteological remains. However, skeletal remains of theropod dinosaurs are rare, and the diversity of theropod tracks has only partially been documented in the literature. Here we describe the only non-dental osteological theropod remain recovered so far, an isolated anterior caudal vertebra, as well as the largest theropod tracks found. The caudal vertebra can be shown to represent a megalosaurine megalosaurid and represents the largest theropod skeletal remain described from Europe so far. The tracks are also amongst the largest theropod footprints reported from any setting and can be assigned to two different morphotypes, one of which similar to *Megalosauripus sensu lato*, and the other being morphologically most similar to *Grallator*-like tracks, characterized by a strong mesaxony, and thus representing a more gracile trackmaker. We discuss the recently proposed distinction between robust and gracile large to giant theropod tracks and their possible trackmakers during the Late Jurassic-Berriasian. In the absence of complete pedal skeletons of most basal tetanurans, the identity of the maker of Jurassic giant theropod tracks is difficult to establish. However, the notable robustness of megalosaurine megalosaurids fits well with the described robust morphotypes, whereas more slender large theropod tracks might have been made by a variety of basal tetanurans, including allosaurids, metriocanthosaurids or afrovenatorine megalosaurids, or even exceptionally large ceratosaurs. Concerning osteological remains of large theropods from the Late Jurassic of Europe, megalosaurids seem to be more abundant than previously recognized and occur in basically all Jurassic deposits where theropod remains have been found, whereas allosauroids seem to be represented by allosaurids in Western Europe and

metriacanthosaurids in more eastern areas. Short-term fluctuations in sea level might have allowed exchange of large theropods between the islands that constituted Europe during the Late Jurassic.

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Abstract

The Kimmeridgian Vega, Tereñes and Lastres formations of Asturias have yielded a rich vertebrate fauna, represented by both abundant tracks and osteological remains. However, skeletal remains of theropod dinosaurs are rare, and the diversity of theropod tracks has only partially been documented in the literature. Here we describe the only non-dental osteological theropod remain recovered so far, an isolated anterior caudal vertebra, as well as the largest theropod tracks found. The caudal vertebra can be shown to represent a megalosaurine megalosaurid and represents the largest theropod skeletal remain described from Europe so far. The tracks are also amongst the largest theropod footprints reported from any setting and can be assigned to two different morphotypes, one of which similar to *Megalosauripus sensu lato*, and the other being morphologically most similar to *Grallator*-like tracks, characterized by a strong mesaxony, and thus representing a more gracile trackmaker. We discuss the recently proposed distinction between robust and gracile large to giant theropod tracks and their possible trackmakers during the Late Jurassic-Berriasian. In the absence of complete pedal skeletons of most basal tetanurans, the identity of the maker of Jurassic giant theropod tracks is difficult to establish. However, the notable robustness of megalosaurine megalosaurids fits well with the described robust morphotypes, whereas more slender large theropod tracks might have been made by a variety of basal tetanurans, including allosaurids, metriocanthosaurids or afrovenatorine megalosaurids, or even exceptionally large ceratosaurs. Concerning osteological remains of large theropods from the Late Jurassic of Europe, megalosaurids seem to be more abundant than previously recognized and occur in basically all Jurassic deposits where theropod remains have been found, whereas allosauroids seem to be represented by allosaurids in Western Europe and metriacanthosaurids in more eastern areas. Short-term fluctuations in sea level might have allowed exchange of large theropods between the islands that constituted Europe during the Late Jurassic.

INTRODUCTION

In the Late Jurassic, Europe was an assemblage of numerous smaller to large islands, separated by shallow epicontinental seas (Cosentino et al., 2010: fig. 7). Apart from the Fennoscandian shield, representing the largest continental mass in north-eastern Europe, larger landmasses included, from east to west, the Bohemian Massif (approximately where the Czech Republic lies today), the London-Brabant Massif and the Rhenian Isle (extending from the area around London to the lower Rhine embayment), the Massif Central (south-central France), the Armorican Massif (mainly the Bretagne today), the Irish Massif in the north-west, and the Iberian Massif (Portugal and parts of western Spain). During parts of the Late Jurassic, the London-Brabant-Rhenian Massif and the Bohemian Massif might have been connected in the north, and the Armorican Massif might have partially had a connection with the Massif Central (Thierry et al. 2000; Meyer, 2012). All of these landmasses certainly possessed a fauna of terrestrial vertebrates, but little is still known about many of these faunas.

Apart from the record of the Iberian Peninsula, in which abundant terrestrial vertebrates are mainly found in Late Jurassic terrestrial to transitional sediments of the Lusitanian (see Mocho et al., 2017, and references therein) Maestrazgo and South Iberian basins (Royo-Torres et al., 2009; Aurell et al., 2016; Campos-Soto et al., 2017), most records of Late Jurassic dinosaurs from Europe come from shallow marine sediments, such as the famous lithographic limestones of southern Germany (Rauhut & Tischlinger, 2015; Tischlinger et al., 2015), the Upper Oxford Clay and Kimmeridge Clay of England (see Benson, 2008a; Benson & Barrett, 2009; Barrett et al., 2010; Carrano et al., 2012), the marine carbonates at Oker, Germany (Sander et al., 2006), or the Calcaire de Cleval Formation in eastern France (Mannion et al., 2017). Interestingly, the sparse evidence from these more eastern occurrences seems to indicate some differences with the fauna from western Iberia. Whereas the latter fauna is closely comparable to the contemporaneous fauna of the Morrison Formation of western North America (Mateus, 2006), with even several shared genera being present (Pérez-Moreno et al., 1999; Antunes & Mateus, 2003; Escaso et al., 2007; Malafaia et al., 2007, 2015, 2017a; Hendrickx & Mateus, 2014), at least the theropod fauna from more eastern European localities seems to show some Asian influence, with the metricanthosaurid *Metriacanthosaurus* from the Oxfordian of England (Huene, 1926; Walker, 1964; Carrano et al., 2012), possible metriacanthosaurid teeth in the Kimmeridgian of northern Germany (Gerke & Wings, 2016), and compsognathid and paravian theropods from the Kimmeridgian-Tithonian of the Solnhofen Archipelago (Ostrom, 1978; Wellnhofer, 2008; Tischlinger et al, 2015; Foth & Rauhut, 2017).

Apart from the abundant record from the Lusitanian, South Iberian and Maestrazgo Basins, Late Jurassic dinosaur remains have also been reported from the Kimmeridgian Vega, Tereñes and Lastres Formations of Asturias, Spain (García-Ramos et al., 2006). In the Late Jurassic, Asturias lay between the Lusitanian Basin and the Armorican Massif, either as part of smaller islands (Cosentino et al. 2010), or as part of the Iberian Massif (Thierry et al., 2000), and its fauna is thus of great interest for understanding European Late Jurassic dinosaur biogeography. Dinosaurs from these units, principally from the Vega and Lastres formations, include mainly ornithischians, with stegosaurs (Ruiz-Omeñaca et al., 2009a, 2013) and ornithopods (Ortega et al., 2006; Ruiz-Omeñaca et al., 2007, 2009b, 2010, 2012) having been reported. Sauropods are rare and include remains of a turiasaur (Canudo et al., 2010) and a diplodocid (Ruiz-Omeñaca et al., 2008). Theropod remains are also rare and consist mainly of isolated teeth (Canudo & Ruiz-Omeñaca, 2003; Ruiz-Omeñaca et al., 2009c). The only skeletal remain of a theropod is a large anterior caudal vertebra, which was briefly described by Martínez et al. (2000) and referred to an unspecified ceratosaur (see also Canudo & Ruiz-Omeñaca, 2003). This specimen, which is remarkable for its extremely large size, is re-evaluated here. Furthermore, the Kimmeridgian of Asturias has yielded a rich dinosaur track record (García-Ramos et al., 2006; Milàn et al., 2006; Avanzini et al., 2008; 2012; Lockley et al., 2008; Piñuela Suárez, 2015; Castanera et al., 2016; Piñuela et al., 2016), including isolated tracks of giant theropods (Piñuela Suárez, 2015), which are also documented here.

Geological setting

The main and best-exposed Jurassic outcrops in the Asturias region extend along the sea cliffs between Gijón and Ribadesella localities (Fig. 1). The Jurassic rocks in the eastern part of Asturias overlie diverse Variscan and Permian-Triassic units and can be grouped into two main lithologically and environmentally characterized units. The lower one is predominantly made up of carbonate rocks of littoral-evaporitic (Gijón Formation) and open marine origin (Rodiles Formation). The upper unit mainly comprises siliciclastic rocks of fluvial (Vega Formation), restricted marine (shelf lagoon) and coastal (fluvial-dominated lagoonal deltas) origin, respectively represented by the Tereñes and Lastres formations (Fig. 2A).

The Vega Formation, with an estimated thickness of 150m, consists of alternating white, pale grey and reddish sandstones and red mudstones with several sporadic conglomeratic beds typically arranged in minor finnig-upward cycles within a major cycle of the same character (Fig. 2B). These rocks represent fluvial deposits formed by ephemeral and highly sinuous streams separated by extensive floodplains on which calcareous palaeosols (calcretes) developed (García-Ramos et al., 2010a; Arenas et al., 2015).

Based on datations with ostracods and pollen and spores, the age of the Vega Formation is probably Kimmeridgian (Schudack and Schudack, 2002; Barrón, 2010).

The climate during sediment deposition represents warm and semi-arid conditions with a strongly seasonal precipitation regime, as indicated by the local presence of gypsum crystals and veins, the palynological composition (Barrón, 2010) and the most frequent palaeosol varieties (Gutierrez and Sheldon, 2012).

Fossil prospecting in the Vega Formation ~~of the~~ type locality along the coast 6 km west of Ribadesella town (Fig.1) yielded the theropod caudal vertebra documented in this study. The fossil bone occurred in a 0.65m thick grey bed of polygenic calcareous microconglomerate (see asterisk in Fig. 2B), which includes mainly carbonate clasts from underlying marine Jurassic units (Gijón and Rodiles formations), together with intraformational limestone and lutitic fragments from the Vega Formation. The calcareous microconglomerate passes upwards to a cross-bedded sandstone. Both lithologies are arranged in at least two finning-upwards channelised levels, showing rapid lateral variations in both thickness and grain-sizes.

The vertebrate bone bed represents an amalgamation of small lenticular channels (scours) showing several episodes of lateral accretion. Their origin is related to channelised flows produced by extreme flooding events associated with heavy rainfall periods. These high discharge processes are probably supplied by the rapid recharge of water springs from an uppermost Triassic-Lower Jurassic rock aquifer emerging from a nearby fault-controlled calcareous relief located to the south (García-Ramos et al., 2010a; Arenas et al., 2015; Lozano et al., 2016).

A tip of a large theropod tooth (MUJA-1226) from the same level as the vertebra described here was reported by Martínez et al. (2000) and described in more detail by Ruiz-Omeñaca et al. (2009c). This crown tip is strongly labiolingually compressed, shows centrally placed, serrated carinae, mesiodistally long, rectangular denticles, antapically directed interdenticular sulci, and an anastomosing enamel texture (Fig. 3; see Ruiz-Omeñaca et al., 2009c). All of these characters are found in megalosaurid teeth, such as teeth of *Torvosaurus* (Hendrickx et al., 2015), so this specimen most probably represents a megalosaurid.

The same level also included some small oncoids, vegetal remains, turtle fragments, crocodile teeth (Ruiz-Omeñaca, 2010), and a sauropod caudal vertebrae (MUJA-0650), as well as poorly-preserved quadrupedal dinosaur footprints.

The Lastres Formation is about 400 m thick unit and consists of grey sandstones, lutites and marls with occasional conglomeratic levels (Fig. 2A). The depositional environment was characterised by a succession of fluvial-dominated lagoonal deltas. The main deposits include prodelta, crevasse-splay, levee, distributary channel, delta front, interdistributary bay and delta-abandonment facies (Avanzini et al., 2005; García-Ramos et al., 2006; 2010b). Within the Lastres Formation, several short-term transgressive events are recorded by muddy and calcareous laterally extensive shell beds with abundant brackish-water bivalves and gastropods. This formation has provided numerous ~~reptile~~ tracks, not only belonging to dinosaurs, but also to pterosaurs, crocodiles, turtles and lizards (García-Ramos et al., 2006; Piñuela Suárez, 2015). The footprints here studied were found as loose and isolated sandstone casts on the sea cliffs, thus no precise descriptions of the levels are provided, but most of the Lastres Formation theropod tracks are related to crevasse-splay facies.

Institutional abbreviations. BYU, Brigham Young University, Provo, USA; IVPP; Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MOR, Musem of the Rockies, Bozeman, USA; MUJA, Museo del Jurásico de Asturias, Colunga, Spain; NHMUK, Natural History Museum, London, UK; OUMNH, Oxford University Museum of Natural History, Oxford, UK

DESCRIPTION

Osteological remains

The vertebra MUJA-1913 is a large anterior caudal vertebra that has most of the centrum and the base of the neural arch preserved (Fig. 4); the zygapophyses, neural spine and most of the transverse processes are missing. The centrum is notably robust and amphi-platycoelous, with the articular surfaces being oval in outline and slightly higher than wide. The anterior articular surface has suffered from erosion, so that its exact size and morphology cannot be established, but the posterior articular surface is only slightly concave and only slightly higher (c. 150 mm) than wide (c. 140-145 mm as reconstructed; the right rim is eroded). In lateral view, the posterior articular surface is notably offset ventrally in respect to the anterior surface (Fig. 4A). The length of the centrum as preserved is c. 140 mm, but approximately 10 mm might be missing anteriorly, so that the centrum was approximately as high as long. In ventral view, the centrum is moderately constricted to a minimal width of c. 90 mm between the articular ends. Ventrally, a broad, but shallow ventral groove is present, which becomes more marked posteriorly between the poorly developed chevron facets (Fig. 4C). The lateral sides of the centrum are strongly convex dorsoventrally and offset from the ventral surface by the broadly rounded edges of the ventral groove. On the dorsal part of the lateral side of the centrum, below the base of the neural arch, a notable, large pleurocentral depression is present (Fig. 4A). This depression is deeper posteriorly than anteriorly, with the anteroventral part of the depression forming a small lateroposteroventrally facing platform that is offset from the deeper posterior part by a rounded, but notable oblique step.

The walls of the neural arch are massive, and the neural canal is large (c. 35 mm in diametre) and round to slightly oval in outline. The base of the massive transverse process is placed entirely on the neural arch and extends for approximately the anterior three-fourths of the centrum. Posteriorly, the transverse process is supported ventrally by a stout, posterolaterally facing posterior centrodiapophyseal lamina, the ventral end of which does not reach the posterodorsal end of the centrum (Fig. 4B). Whereas the left lamina forms a sharp, posterolaterally facing edge, the right lamina seems to be more rounded, although this might be due to erosion. An anterocentrodiapophyseal lamina is only indicated by a slight depression on the anterior side of the base of the transverse process. The transverse process was laterally and strongly posteriorly directed, but has almost no dorsal inclination. Posteriorly, a large postzygocentrodiapophyseal fossa is present between the posterior centrodiapophyseal lamina and the lamina extending ventrally between the medial ends of the postzygapophyses and the neural canal (Fig. 4B); as the postzygapophyses are missing and the median lamina is poorly preserved, it is unclear if a small hyposphene might have been present, but at least a marked ventral expansion of this lamina was certainly absent. A small, ridge-like lamina extending from the dorsal margin of the transverse process towards the dorsomedial rim of the neural canal subdivides the postzygocentrodiapophyeal fossa into a larger, conical ventral recess and a smaller, much shallower dorsomedial depression (Fig. 4B).

Anteriorly, a small depression is present on the roof of the neural canal, being offset from the massive dorsal surface of the transverse process by a small, transverse step (Fig. 4D). The base of the broken neural spine is transversely narrow and extends over the entire length of the neural arch, showing the eroded bases of the slightly anteriorly diverging spinoprezygapophyseal laminae anteriorly.

Asturian theropod tracks

Five tracks of very large or gigantic theropods (footprint length (FL) more than 60 cm), were reported from the Kimmeridgian Lastres Formation of Asturias by Piñuela Suárez (2015). Following the definition of Marty et al. (2017), according to which giant theropod tracks are those of a FL longer than 50 cm, two more Asturian tracks can be added in the present study (see table 1 for measurements). The footprints (all more than 53 cm long) are preserved as sandstone casts and can be classified into two groups by morphology (Piñuela Suárez, 2015).

Morphotype A is represented by four tracks (Argüero, Oles and Tazones specimens and MUJA-1889; Fig. 5), which, although slightly different in morphology, are robust and weakly mesaxonic. The FL/FW ratio is very low (0.88-1.16), one of them (Argüero; Fig. 5A) is even wider than long and another has similar length and width. The digit impressions are broad and generally show claw marks (Fig. 5). The divarication angle (II^IV) lies between 36º and 40º. In some of these tracks the digital pads are subtly visible. Based on the morphology, the Asturian footprints would form part of the *Megalosauripus-Kayentapus*-group proposed by Piñuela Suárez (2015), even though the tracks attributed to the latter ichnogenus never present such sizes. The specimens of morphotype A are thought to represent more graviportal theropods (Piñuela Suárez, 2015).

Morphotype B is represented by three footprints (MUJA-1263, MUJA-0213 and Argüero specimens; Fig. 6), which ~~seem to be~~ much longer than wide (digit IV is lacking in two of them) and with a strong mesaxony. Pad impressions are only preserved in MUJA-1263 (Fig. 6A), despite being the cast of a shallow undertrack. ~~Thus,~~ in this specimen the claw impressions are wide and robust, whereas in the other two they are very narrow in comparison with the digit width. The morphology of these footprints does not fit in large or very large known theropod ichnogenera, but rather in smaller ones characterized by a high mesaxony, such as *Grallator* (Piñuela Suárez, 2015). The problematic issue of vertebrate ichnogenera and their sizes was discussed by Bertling et al. (2006), who noted that they were “reluctant to use size at the ichnospecies rank and reject it altogether at higher ranks” (Bertling et al., 2006: 274). This set of tracks seems to represent more cursorial theropods (Piñuela Suárez, 2015) than morphotype A.

DISCUSSION

Systematic affinities of MUJA-1913

Despite the incomplete preservation of the caudal vertebra reported here, its systematic affinities can be narrowed down to at least a higher taxonomic category, although not to generic or species level. Large-bodied theropod dinosaurs reported from the Late Jurassic of Europe so far include members of the Ceratosauridae (Antunes & Mateus, 2003; Mateus et al., 2006; Malafaia et al., 2015), Megalosauridae (Antunes & Mateus, 2003; Mateus et al, 2006; Carrano et al., 2012; Hendrickx & Mateus, 2014; Malafaia et al., 2017a), Metriacanthosauridae (Huene, 1926; Walker, 1964; Carrano et al., 2012), and Allosauridae (Pérez-Moreno et al., 1999; Mateus et al., 2006; Malafaia et al., 2007, 2008a, 2010). Thus, comparisons of MUJA-1913 will mainly be with these clades.

Concerning the position of MUJA-1913 within the caudal vertebral column, this element can be quite confidently identified as a second or third caudal vertebra. Arguments in favour of this are the well-developed posterior centrodiapophyseal lamina, which is only present in the anteriormost caudal vertebrae, but is usually already less pronounced by caudal vertebra four (Madsen, 1976). On the other hand, the first caudal usually lacks chevron facets, but they are present on the posterior end of the centrum in MUJA-1913.

As no vertebral material of *Ceratosaurus* (the only ceratosaurian genus identified from the Jurassic of Europe so far) or any other ceratosaur has been described from the Jurassic of Europe, comparisons can only be made with *Ceratosaurus* from the Morrison Formation of the western US (Gilmore, 1920; Madsen & Welles, 2000). Anterior caudal vertebrae of this taxon differ from MUJA-1913 in the considerably higher than wide articular facets of the centrum (Madsen & Welles, 2000: pl. 7), the lack of a pronounced offset of the articular facets (Gilmore, 1920; Madsen & Welles, 2000), presence of a considerably narrower, deeper and better defined groove on the ventral side (Gilmore, 1920: pl. 22; Madsen, 1976: fig. 8B), the presence of a large, ventrally expanded hyposphene in the anterior caudals, and the relatively smaller and not subdivided postzygocentrodiapophyseal fossa (Madsen & Welles, 2000). The anterior caudal vertebrae of *Ceratosaurus* have marked pleurocentral depressions on the dorsolateral side of the centrum (see Gilmore, 1920: pl. 22), but these are larger and less well-defined than in MUJA-1913. Concerning other ceratosaurian lineages, anterior caudal vertebrae of abelisaurs differ markedly from MUJA-1913 in lacking noted pleurocentral depressions, having well-developed hyposphenes in anterior caudals (with the exception of *Majungasaurus*; O'Connor, 2007), and usually strongly dorso-latero-posteriorly directed transverse processes (see Méndez, 2014). A referral of MUJA-1913 to Ceratosauria (Martínez et al., 2000; Canudo & Ruiz-Omeñaca, 2003) thus seems untenable.

The anterior caudal vertebrae of the metriacanthosaurids *Metriacanthosaurus* (OUMNH J 12144) and *Sinraptor* (IVPP 10600; Currie & Zhao, 1993) and the allosaurid *Allosaurus* (e.g. MOR 693; Madsen, 1976) have centra that are notably higher than wide, have less notably offset anterior and posterior articular facets, narrow towards their ventral side and lack both a notable pleurocentral depression on the lateral side of the centrum as well as the subdivision of the postzygocentrodiapophyseal fossa. Furthermore, a well-developed, ventrally expanded hyposphene is present in the anterior caudal vertebrae of metriacanthosaurids, and the ventral groove, if present, is notably narrower in allosauroids. In contrast, the anterior caudal vertebrae of the megalosaurine megalosaurids *Megalosaurus* and *Torvosaurus* are very similar to MUJA-1913. Both of these taxa have very massive anterior caudal vertebral centra with a broad, posteriorly deepening ventral groove and a pronounced offset of the articular surfaces (NHMUK R 9672; BYU 13745; Britt, 1991; Benson, 2010), and the presence of marked pleurocentral depressions on the lateral sides of the caudal centra was found to be a megalosaurine synapomorphy by Rauhut et al. (2016). Furthermore, these taxa lack expanded hyposphenes in the caudal vertebrae and a subdivision of the postzygocentrodiapophyseal fossa into a larger ventrolateral and a smaller, very shallow dorsomedial portion is also present in at least one vertebra of *Megalosaurus* (NHMUK R 9672), and seems to be also present in *Torvosaurus* (BYU 13745, BYU 5086). A small depression on the dorsal roof of the anterior part of the base of the transverse process, very similar to that in MUJA-1913, is also present in the anteriormost preserved caudal vertebra of the megalosaurid *Wiehenvenator* (Rauhut et al., 2016). Given these similarities, including the possibly apomorphic characters of marked pleurocentral depressions and a subdivided postzygocentrodiapophyseal fossa, we refer MUJA-1913 to an indeterminate megalosaurine megalosaurid. Given that the genus *Torvosaurus* has been identified from the Late Jurassic of the Iberian Peninsula (Antunes & Mateus, 2003; Hendrickx & Mateus, 2014; Malafaia et al., 2017a), this vertebra might represent this taxon, but a positive generic or specific identification of this incomplete element is impossible.

Size of MUJA-1913

One striking feature of the vertebra from the Vega Formation is its enormous size. With a posterior centrum height of 150 mm, MUJA-1913 is larger than most anterior caudals for which measurements can be found in the literature. In particular, anterior caudals of *Torvosaurus tanneri* are about 25% smaller (Britt, 1991), an anterior caudal of *Spinosaurus aegyptiacus* is c. 10% smaller (Stromer, 1915), and one of the largest theropod caudals from the Jurassic, for which measurements were given, a possible carcharodontosaurid caudal from the Tendaguru Formation (Rauhut, 2011), is also c. 25% smaller than the specimen described here. Larger caudal vertebrae are present in the gigantic Cretaceous carcharodontosaurids (e.g. Canale et al., 2015) and *Tyrannosaurus* (Brochu, 2003), but might also be found in the largest allosauroid predators of the Late Jurassic Morrison Formation of the western USA (Chure, 1995, 2000; Williamson & Chure, 1996), though no measurements are available in the literature for these specimens. However this may be, Hendrickx & Mateus (2014) argued that the holotype of *Torvosaurus guerneyi* represented the largest theropod dinosaur yet recorded from Europe (see also specimens described by Malafaia et al., 2017a). This specimen includes a partial anterior caudal vertebra, the posterior articular surface of which is about 15% smaller than that of MUJA-1913.

Thus, given that the specimen from the Vega Formation probably belongs to a closely related taxon, this specimen probably represents the largest theropod dinosaur recorded so far in Europe, and represents an apex predator of more than 10 m in length.

It should be noted that Pharisat (1993) briefly reported large theropod caudal vertebrae from the Oxfordian of Plaimbois-du -Miroi, Doubs, France (see also Allain & Pereda-Suberbiola, 2003), which, according to the measurements given, are of closely comparable size to MUJA-1913. Although no detailed description of these elements has ever been published, the general shape of the centra and neural arches, the presence of a marked pleurocentral depression in the slightly more posterior vertebra, the almost circular outline of the posterior articular surface and the absence of a hyposphene in the probably first caudal, and the subdivision of the postzygocentrodiapophyseal fossa into a dorsomedial platform and a larger, conical ventrolateral depression indicate megalosaurid affinities for these elements (observations based on unpublished photographs provided by Daniel Marty and Christian Meyer).

Other large Late Jurassic theropods from Europe have been reported on the basis of isolated teeth (e.g. Lapparent, 1943; Buffetaut and Martin, 1993; Rauhut & Kriwet, 1994; Canudo et al., 2006; Ruiz-Omeñaca et al., 2009c; Cobos et al., 2014; Gerke & Wings, 2016; Malafaia et al., 2017b), and some of these specimens might represent animals that match MUJA-1913 in size (e.g. specimen described by Cobos et al. [2014]; largest specimens described by Malafaia et al. [2017b]). However, as relative tooth size varies widely in theropods, a direct size comparison is impossible.

Ichnological evidence of giant theropods from the Kimmeridgian of Asturias

Regarding the giant theropod track record, Cobos et al. (2014) recently proposed that the Late Jurassic-Early Cretaceous (Berriasian) theropod tracks can be divided in two main groups (Ichno-group 1: *Bueckeburgichnus-Hispanosauropus-Megalosauripus* vs Ichno-group 2: *Iberosauripus*), which can be distinguished by their narrowness / robustness, the proportion of the length of digit III (mesaxony) or footprint proportions (FL/FW ratio). The authors proposed that these two main groups might have been produced by members of Allosauridae and Megalosauridae, respectively.

We partially agree with the two ichno-groups related to the narrowness/robustness and strong/weak mesaxony proposed by Cobos et al. (2014) but less so with the ichnogenera included within them (due to unresolved problems in ichnotaxonomy), and the identification of some trackmakers (see below). The validity of the Cretaceous German ichnogenus *Bueckeburgichnus* Kuhn, 1958, based on a poorly preserved footprint, is questionable, because the irregular shape of the digits and the relatively high total divarication angles suggesting extramorphological characters. Besides, the ichnogenus was created on the basis of only one specimen. Thus, the outline of the track reflects only partially the pedal morphology of the theropod. The tracks included in this ichnogenus were considered to be *Megalosauripus* by Piñuela Suárez (2015; see also Hornung et al., 2012).

The same applies to *Hispanosauropus* (Mensink and Mertmann, 1984; Lockley et al., 2007) from the Kimmeridgian of Asturias, considered to be no valid ichnogenus by Piñuela Suárez (2015), who included these Asturian tracks also in *Megalosauripus*. The poor preservation, which again does not reflect faithfully the foot morphology of the trackmaker, the probability of destruction and thus loss of the topotype located on an unstable sea cliff and the lack of a cast in any museum are enough reasons to reject the validity of this ichnogenus (see also Lockley et al., 2007).

Another problem concerns the comparison between *Megalosauripus* (Lockley et al., 2000; Fanti et al., 2013) and *Iberosauripus* (Cobos et al. ,2014).

On one hand, both shallow and deep undertracks belonging to large theropods, very frequent in Asturias and usually preserved as casts, are normally wider than the casts of the true tracks (Piñuela Suárez, 2015). This gives rise to footprints with relatively broader digit impressions, similar to *Iberosauripus*.

On the other hand, tracks produced in carbonate sediments, as in the case of *Iberosauripus*, are often not well preserved. They sometimes tend, as in the undertracks, to be wider than the foot of the trackmaker and show also broader digit impressions. Moreover, according to Razzolini et al. (2017) the material of *Iberosauripus grandis* is rather poorly preserved. As stated correctly by Dalla Vecchia (2008: 99) "the footprint morphology is highly influenced by the properties of the substrate, mainly in carbonate sedimentary settings" (see also Dalla Vecchia and Tarlao, 2000; Belvedere et al., 2008; Fanti et al., 2013).

Thus, the substrate might have played a role when *Iberosauripus* was produced by giant theropods, giving similar footprints to the type specimen of *Megalosauripus* (Lockley et al., 2000; see also Lockley et al., 1996). Although some detailed comparisons have recently been offered by Marty et al. (2017) and Razzolini et al. (2017), a detailed revision of the ichnogenus *Megalosauripus* and an evaluation of the possible impact of locomotion and substrate in the production of similar tracks, such as *Iberosauripus*, but also *Jurabrontes* (Marty et al., 2017) are necessary to clarify the ichnotaxonomic status of these tracks.

Following from the previous considerations, we propose two morphogroups, one of them represented by the Asturian morphotype A and identified as *Megalosauripus*-like tracks and the other by the Asturian morphotype B. The notably divergent morphology of the tracks included in morphotypes A and B indicates that at least two taxa of giant theropod were present in the Kimmerdigian of Asturias. In general terms, the two morphotypes conform to the distinction proposed by Cobos et al. (2014) in that morphotype A represents a very robust animal, whereas morphotype B seems to stem from ~~much~~ more gracile theropods.

With up to 82 cm, the Asturian specimens show footprint lengths that fall within the range of the largest tracks in the world (Boutakiout et al., 2009; Piñuela Suárez, 2015; Marty et al. 2017). Some of these large predators from the Late Jurassic of Asturias apparently had cursorial adaptations, as deduced from the morphological study of their footprints (morphotype B), which show strong mesaxony (*sensu* Lockley, 2009); their claw impressions, when preserved, are long and very narrow. These dinosaurs were as large as, but more agile than trackmakers of *Megalosauripus*-like tracks*,* and the largest theropod trackmakers from the Jurassic of Asturias were thus similar in size to *Tyrannosaurus rex*, based on known footprints of that taxon (e.g. Lockley & Hunt, 1994; Manning et al., 2008; McCrea et al., 2014) and foot skeletons (e.g. Brochu, 2003).

Late Jurassic apex predators in Europe

Apart from the ichnotaxonomic questions discussed above, the question remains which theropod groups are represented by these giant tracks. As noted above, Cobos et al. (2014) suggested a division of theropod tracks into two larger categories of robust and gracile prints (regardless of the exact identification to ichnogenus or ichnospecies level), which they considered to represent megalosaurids and allosaurids, respectively. The main argument for this identification was the relative robustness or slenderness of the tracks: as the only well-known Late Jurassic megalosaurid, *Torvosaurus*, is a very robust animal (Britt, 1991; Hendrickx & Mateus, 2014; Malafaia et al., 2017a), whereas the best known allosaurid, *Allosaurus*, is ~~much~~ more gracile (e.g. Gilmore, 1920~~),~~ Cobos et al. ~~(~~2014: 37-38) argued that the more robust tracks were probably made by megalosaurids, whereas the more slender tracks correspond to allosaurids.

However, this suggestion is somewhat simplistic and problematic for several reasons. The first and obvious problem (also noted by Cobos et al., 2014) is that no complete pes is known in any Jurassic non-coelurosaurian tetanuran with the exception of *Allosaurus* (Madsen, 1976), nor for any large ceratosaurian. Even in the very complete holotype specimen of the metriacanthosaurid *Sinraptor dongi*, several pedal phalanges are missing (Currie & Zhao, 1993), and at the most isolated phalanges are known for megalosaurids (Sereno et al., 1994; Allain & Chure, 2002; Sadleir et al., 2008). Thus, a synapomorphy-based correlation (sensu Carrano and Wilson, 2001) between pedal morphology and trackways in large basal tetanurans is currently impossible. However, known complete pedes of *Allosaurus* (e.g. Gilmore, 1920; Evers, 2014) do not seem to show the extreme differences in digit III as opposed to digits II and IV that would lead to the mesaxony seen in one of the largest footprints ascribed to morphotype B described here (MUJA-0213). This extreme mesaxony is a strange situation in large theropod tracks as generally they tend to show lower mesaxony values than smaller theropod tracks (e.g.: *Grallator-Eubrontes* plexus; Lockley, 2009).

A second problem in the identification proposed by Cobos et al. (2014) is that it neither takes the systematic nor the morphological variation of known Jurassic averostrans that reach large to giant sizes into account. First, allosaurids are not the only large allosauroids known from Europe, with the English metriacanthosaurid *Metriacanthosaurus* representing an animal of similar or even greater size than known specimens of *Allosaurus* from Europe (Huene, 1926; Walker, 1964; Pérez-Moreno et al., 1999; Mateus et al., 2006; Malafaia et al., 2010). However, the better known metriacanthosaurids from China are similar in proportions and robustness to *Allosaurus* (e.g. Dong et al., 1983; Currie & Zhao, 1993; Gao, 1999), and the pes of *Sinraptor* does also not seem to be significantly different from that of *Allosaurus* (see Madsen, 1976; Currie & Zhao, 1993). Thus, the more slender tracks of Ichno-Group 1 of Cobos et al. (2014) might represent metriacanthosaurids as well as allosaurids. On the other hand, the largest allosaurid known from the Late Jurassic Morrison Formation of North America, *Saurophaganax*, is a more robustly built animal (Chure, 1995, 2000), whereas afrovenatorine megalosaurids, such as *Afrovenator* (Sereno et al., 1994) and *Eustreptospondylus* (Sadleir et al., 2008) are rather gracile animals. Although *Eustreptospondylus* from the Callovian-Oxfordian boundary of England represents the youngest afrovenatorine currently known from Europe (and, possibly globally, depending on the uncertain age of *Afrovenator*), the Late Jurassic European theropod fossil record is insufficient to completely rule out their survival into later stages, and at least caution is advisable in identifying tracks as allosauroid on the basis of their slenderness only.

Finally, the basal ceratosaur *Ceratosaurus*, known from the Late Jurassic of Portugal (Antunes & Mateus, 2003; Mateus et al., 2006; Malafaia et al., 2015) is a rather large animal as well (Gilmore, 1920; Madsen & Welles, 2000). Although the holotype of *Ceratosaurus nasicornis* has been estimated with a total length of slightly more than 5 m (Gilmore, 1920), the type of *C. dentisulcatus* is about 22% larger (Madsen & Welles, 2000), and other specimens (e.g. BYU 881) reach sizes comparable to that of large specimens of *Allosaurus*. As *Ceratosaurus* is also a rather gracile animal, exceptionally large individuals of this or a closely related taxon could also have made the more gracile tracks.

Concerning megalosaurine megalosaurids, no pedal elements other than metatarsals have been described for any of the included genera *Duriavenator*, *Megalosaurus*, *Wiehenvenator*, and *Torvosaurus* (Galton & Jensen, 1979; Britt, 1991; Benson, 2008b, 2010; Hanson & Makovicky, 2014; Hendrickx & Mateus, 2014; Rauhut et al., 2016; Malafaia et al., 2017a). However, at least *Megalosaurus*, *Wiehenvenator* and *Torvosaurus* are notable for their extreme robustness, and Williamson & Chure (1996: 78) cite a personal communication by James Madsen, according to which the pedal phalanges of *Torvosaurus* are notably short and wide. These observations are thus in agreement with the suggestion by Cobos et al. (2014) that the very robust tracks with a low mesaxony might represent (megalosaurine) megalosaurids. Nevertheless, we agree with Marty et al. (2017) that caution is advisable in assigning giant theropod tracks from the Jurassic to any clade unless better data on pedal morphology in basal tetanurans becomes available.

Regardless of the exact identification of the trackmaker, European sites have yielded some of the largest known Jurassic theropod tracks, such as the trackways described from the Middle Jurassic of Oxforshire, UK, (Day et al., 2004) and Vale de Meios, Portugal, (Razzolini et al., 2016), which were made by giant theropods, tentatively attributed to *Megalosaurus* and to the Megalosauridae, respectively. Recently, Marty et al., (2017) described new giant theropod tracks (*Jurabrontes curtedulensis*) from the Kimmeridgian of NW Switzerland. This new ichnotaxon is characterized by tracks that are slightly longer than wide and show weak mesaxony, and, as the authors suggested, can be included within the main features of the Ichno-Group 2 of Cobos et al., (2014). These authors emphasized that some of the *Jurabrontes* tracks are among the largest theropod tracks worldwide. However, the Kimmeridgian of Asturias is the only Jurassic European site that has yielded tracks of two giant theropods (gracile and robust) so far, indicating that two different clades of giant theropods were present here.

Concerning osteological remains, the identification of MUJA-1913 as a megalosaurid adds to the already diverse European fossil record of the clade. As discussed by Benson (2010), Carrano et al. (2012) and Rauhut et al. (2016), megalosaurids were taxonomically diverse and widespread in the Middle Jurassic of Europe. However, whereas megalosaurids are rare in the Kimmeridgian-Tithonian Morrison Formation of the western US (Foster, 2003; Rauhut et al., 2016), and unknown from the Late Jurassic of Asia, they seem to be abundant and wide-spread in the Late Jurassic of Europe. From the Lusitanian Basin, the large megalosaurid *Torvosaurus guerneyi* and several other megalosaurid postcranial specimens, numerous teeth, as well as eggs and embryos were described (Antunes & Mateus, 2003; Mateus et al., 2006; Malafaia et al., 2008b, 2017a, b; Araújo et al., 2013; Hendrickx &

Mateus, 2014). From the Late Jurassic Villar del Arzobispo Formation of the Iberian Range, Gascó et al. (2012) and Cobos et al. (2014) referred isolated teeth to the Megalosauridae, including the largest tooth specimen found in these rocks (Cobos et al., 2014). Likewise, Gerke & Wings (2016) identified the largest theropod teeth in their sample from the Kimmeridgian of northern Germany as probable megalosaurids. Furthermore, the early juvenile megalosaurid *Sciurumimus* was found in the Kimmeridgian Torleite Formation of Bavaria (Rauhut et al., 2012; the layers were referred to the Rögling Formation in that paper, but recent lithostratigraphic revisions place the Kimmeridgian beds at Painten in the Torleite Formation; Niebuhr & Pürner, 2014). Apart from the fragmentary skeleton of the large-bodied metriacanthosaurid *Metriacanthosaurus* from the Oxfordian Oxford Clay (Huene, 1926; Walker, 1964), all identifiable large theropod remains from the Late Jurassic of England seem to represent megalosaurids as well, including remains of a large maxilla and a very robust tibia from the Kimmeridge Clay (Benson & Barrett, 2009; Carrano et al., 2012). As noted above, the largest Jurassic theropod remains found in France (Pharisat, 1993) also seem to represent a megalosaurid. The specimen described here from the Kimmeridgian of Asturias fits well in this general panorama.

Thus, megalosaurid theropods seem to have represented the largest predators on all of the Late Jurassic European landmasses that we have fossil evidence for, together with allosaurids in the western parts of Europe and metriacanthosaurids in the eastern areas. As these parts of Europe were an assemblage of medium-sized islands and most of the sediments that have yielded theropod remains are either nearshore terrestrial or even marine beds, this seems to support the suggestion of Rauhut et al. (2016) that megalosaurids might have preferred nearshore environments, and that the apparent faunal change from megalosaurid-dominated to allosauroid-dominated faunas from the Middle to the Late Jurassic might rather reflect regional and environmental biases in the fossil record of Jurassic theropods.

Given the abundance and wide distribution of megalosaurids in the Late Jurassic of Europe, the question arises if different lineages of megalosaurids populated the different landmasses, possibly evolving in isolation from their Middle Jurassic predecessors, or if an interchange of megalosaurid taxa between the different islands might have been possible. The presence of abundant theropod tracks, the largest of which are often related to megalosaurids, in shallow marine or carbonate platform environments (e.g. Marty et al. 2017) might indicate that short time sea level changes may have allowed some faunal interchange between otherwise separate landmasses during the Late Jurassic (Meyer, 2012). Indeed, Marty et al., (2017) suggested that the Jura carbonate platform could have represented a “faunal exchange corridor” of the dinosaur faunas between the southern and the northern landmasses.

CONCLUSIONS

The presence of very large theropods in the Asturian Basin (Northern Spain) during the Upper Jurassic (Kimmeridgian) is confirmed by both the footprints and skeletal remains. Whereas the only skeletal remain of a giant theropod from the Vega Formation represents a megalosaurine megalosaurid, the track record indicates at least two taxa of giant theropods in the slightly younger Lastres Formation. Both osteological and ichnological evidence indicates that very large to giant theropod dinosaurs were widespread in Europe in the Late Jurassic, and the largest representatives seem to have been close to the maximum body size recorded for theropods. Given that Europe represented an assemblage of larger and smaller islands at that time, this is surprising, as maximum body size is usually correlated with available land mass in vertebrates (Marquet & Taper, 1998; Burness et al., 2001), and island dwarfing has been reported in dinosaurs (e.g. Sander et al., 2006; Stein et al., 2010). A possible solution to this apparent contradiction might be that short time sea level changes allowed faunal interchange between the different islands that constituted Europe repeatedly during the Late Jurassic. Dinosaur tracks preserved in shallow marine carbonate platform environments might be direct evidence for this (Marty et al., 2017). The preference of nearshore environments in megalosaurids, possibly in search for suitable food (Razzolini et al., 2016) might furthermore explain the wide distribution of this group in the European archipelago.

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REFERENCES

Allain R, and Chure DJ. 2002. *Poekilopleuron bucklandii*, the theropod dinosaur from the Middle Jurassic (Bathonian) of Normandy. *Palaeontology* 45:1107-1121.

Allain R, and Pereda Suberbiola X. 2003. Dinosaurs of France. *Comptes Rendus Palevol* 2:27-44.

Antunes MT, and Mateus O. 2003. Dinosaurs of Portugal. *Comptes Rendus Palevol* 2:77-95.

Araújo R, Castanhinha R, Martins R, Mateus O, Hendrickx C, Beckmann F, Schell N, and Alves L. 2013. Filling the gaps of dinosaur eggshell phylogeny: Late Jurassic Theropod clutch with embryos from Portugal. *Scientific Reports* 3:1924.

Arenas C, Piñuela L, and García-Ramos JC. 2015. Climatic and tectonic controls on carbonate deposition in syn-rift siliciclastic fluvial systems: A case of microbialites and associated facies in the Late Jurassic. *Sedimentology* 62:1149-1183.

Aurell M, Badenas B, Gasca J, Canudo J, Liesa C, Soria A, Moreno-Azanza M, and Najes L. 2016. Stratigraphy and evolution of the Galve sub-basin (Spain) in the middle Tithonian-early Barremian: Implications for the setting and age of some dinosaur fossil sites. *Cretaceous Research* 65:138-162.

Avanzini M, García-Ramos JC, Lires J, Menegon M, Piñuela L, and Fernández LA. 2005. Turtle tracks from the Late Jurassic of Asturias, Spain. *Acta Paleontologica Polonica* 50:743-755.

Avanzini M, Piñuela L, and García-Ramos JC. 2008. Paleopathologies deduced from a theropod trackway. Upper Jurassic of Asturias (N Spain). *Oryctos* 8:71-75.

Avanzini M, Pinuela L, and García-Ramos J. 2012. Late Jurassic footprints reveal walking kinematics of theropod dinosaurs. *Lethaia* 45:238-252.

Barrett P, Benson R, and Upchurch P. 2010. Dinosaurs of Dorset: Part II, the sauropod dinosaurs (Saurischia, Sauropoda), with additional comments on the theropods. *Proceedings of the Dorset Natural History and Archaeological Society* 131:113-126.

Barrón E. 2010. Las series fluviales del Jurásico Superior (Formación Vega). Palinología. In: García-Ramos JC, ed. *Guía de la excursión A del V Congreso del Jurásico de España*. Colunga: Museo del Jurásico de Asturias, 64–68.

Belvedere M, Avanzini M, Mietto P, and Rigo M. 2008. Norian dinosaur footprints from the “Strada delle Gallerie” (Monte Pasubio, NE Italy). *Studi Trentini di Scienze Naturali, Acta Geologica* 83:267-275.

Benson R, and Barrett P. 2009. Dinosaurs of Dorset: Part I, the carnivorous dinosaurs (Saurischia, Theropoda). *Proceedings of the Dorset Natural History and Archaeological Society* 130:133-147.

Benson RBJ. 2008a. New information on *Stokesosaurus*, a tyrannosauroid (Dinosauria: Theropoda) from North America and the United Kingdom. *Journal of Vertebrate Paleontology* 28:732-750.

Benson RBJ. 2008b. A redescription of '*Megalosaurus*' *hesperis* (Dinosauria, Theropoda) from the Inferior Oolite (Bajocian, Middle Jurassic) of Dorset, United Kingdom. *Zootaxa* 1931:57-67.

Benson RBJ. 2010. A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society* 158:882-935.

Bertling M, Braddy SJ, Bromley RG, Demathieu GR, Genise J, Mikuláš R, Nielsen JK, Nielsen KSS, Rindsberg AK, Schlirf M, and Uchman A. 2006. Names for trace fossils: a uniform approach. *Lethaia* 39:265-286.

Boutakiout M, Hadri M, Nouri J, Díaz-Martínez I, and Pérez-Lorente F. 2009. Rastrilladas de icnitas terópodas gigantes del Jurásico Superior (Sinclinal de Iouaridène, Marruecos). *Revista Española de Paleontología* 24:31-46.

Britt BB. 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. *BYU Geology Studies* 37:1-72.

Brochu CA. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Society of Vertebrate Paleontology, Memoir* 7:1-138.

Buffetaut E, and Martin M. 1993. Late Jurassic dinosaurs from the Boulonnais (northern France): a review. *Revue de Palebiologie, Volume spécial* 7:17-28.

Burness GP, Diamond J, and Flannery T. 2001. Dinosaurs, dragons, and dwarfs: the evolution of maximal body size. *Proceedings of the National Academy of Sciences* 98:14518-14523.

Campos-Soto S, Cobos A, Caus E, Benito MI, Fernández-Labrador L, Suarez-Gonzalez P, Quijada IE, Mas R, Royo-Torres R, and Alcalá L. 2017. Jurassic Coastal Park: A great diversity of palaeoenvironments for the dinosaurs of the Villar del Arzobispo Formation (Teruel, eastern Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 485: 154-177.

Canale J, Novas F, and Pol D. 2015. Osteology and phylogenetic relationships of *Tyrannotitan chubutensis* Novas, de Valais, Vickers-Rich and Rich, 2005 (Theropoda: Carcharodontosauridae) from the Lower Cretaceous of Patagonia, Argentina. *Historical Biology* 27:1-32.

Canudo J, Ruiz-Omenaca J, Aurell M, Barco J, and Cuenca-Bescos G. 2006. A megatheropod tooth from the late Tithonian - middle Berriasian (Jurassic-Cretaceous transition) of Galve (Aragon, NE Spain). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 239:77-99.

Canudo JI, and Ruiz-Omeñaca JI. 2003. Los restos directos de dinosaurios terópodos (excluyendo Aves) en España. In: Pérez-Lorente F, ed. *Dinosaurios y otros Reptiles Mesozoicos en España*. Logroño: Instituto de Estudios Riojanos, 347-374.

Canudo JI, Ruiz-Omeñaca JI, Piñuela L, and García-Ramos JC. 2010. Descripción de un dentario de cf. *Turiasaurus* (Sauropoda) del Kimmeridgiense de Asturias (España). In: Ruiz-Omeñaca JI, Piñuela L, and García-Ramos JC, eds. *Comunicaciones del V Congreso del Jurásico de España Museo del Jurásico de Asturias (MUJA), Colunga, 8-11 de septiembre de 2010*. Colunga: Museo del Jurásico de Asturias, 164-169.

Carrano MT, Benson RBJ, and Sampson SD. 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 10:211-300.

Carrano MT, and Wilson JA. 2001. Taxon distributions and the tetrapod track record. *Paleobiology* 27:564-582.

Castanera D, Piñuela L, and García-Ramos JC. 2016. *Grallator* theropod tracks from the Late Jurassic of Asturias (Spain): ichnotaxonomic implications. *Spanish Journal of Palaeontology* 31:283-296.

Chure DJ. 1995. A reassessment of the gigantic theropod *Saurophagus maximus* from the Morrison Formation (Upper Jurassic) of Oklahoma, USA. In: Sun A, and Wang Y, eds. *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*. Beijing: China Ocean Press, 103-106.

Chure DJ. 2000. A new species of *Allosaurus* from the Morrison Formation of Dinosaur National Monument (UT-CO) and a revision of the theropod family Allosauridae. Unpublished PhD thesis. New York: Columbia University.

Cobos A, Lockley M, Gascó F, Royo-Torres R, and Alcala L. 2014. Megatheropods as apex predators in the typically Jurassic ecosystems of the Villar del Arzobispo Formation (Iberian Range, Spain). *Palaeogeography Palaeoclimatology Palaeoecology* 399:31-41.

Cosentino D, Cipollari P, Marsili P, and Scrocca D. 2010. Geology of the central Apennines: a regional review. *Journal of the Virtual Explorer* 36:11.

Currie PJ, and Zhao X-J. 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences* 30:2037-2081.

Dalla Vecchia FM. 2008. The impact of dinosaur palaeoichnology in palaeoenvironmental and palaeogeographic reconstructions: the case of Periadriatic carbonate platforms. *Oryctos* 8:89-106.

Dalla Vecchia FM, and Tarlao A. 2000. New dinosaur tracks sites in the Albian (Early Cretaceous) of the Istrian Peninsula (Croatia). Parte II, Paleontology. *Memorie di Scienze Geologische* 52:227-292.

Day JJ, Norman DB, Gale AS, Upchurch P, and Powell HP. 2004. A Middle Jurassic dinosaur trackway site from Oxfordshire, UK. *Palaeontology* 47:319-348.

Dong Z, Zhou S, and Zhang Y. 1983. [The dinosaurian remains from Sichuan Basin, China]. *Palaeontologia Sinica* 162:1-145. (in Chinese)

Escaso F, Ortega F, Dantas P, Malafaia E, Pimentel N, Pereda-Suberbiola X, Sanz J, Kullberg J, Kullberg M, and Barriga F. 2007. New evidence of shared dinosaur across Upper Jurassic Proto-North Atlantic: *Stegosaurus* from Portugal. *Naturwissenschaften* 94:367-374.

Evers SW. 2014. The postcranial osteology of a large specimen of *Allosaurus* "*jimmadsoni*" (Dinosauria: Theropoda) from the Late Jurassic of Wyoming, U.S.A. Unpublished M.Sc.-thesis. Munich: Ludwig-Maximilians-University.

Fanti F, Contessi M, Nigarov A, and Esenov P. 2013. New data on two large dinosaur tracksites from the Upper Jurassic of Eastern Turkmenistan (Central Asia). *Ichnos* 20:54-71.

Foster JR. 2003. Paleoecological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain Region, USA. *Bulletin of the New Mexico Museum of Natural History & Science* 23:1-95.

Foth C, and Rauhut O. 2017. Re-evaluation of the Haarlem *Archaeopteryx* and the radiation of maniraptoran theropod dinosaurs. *BMC Evolutionary Biology* 17:236.

Galton PM, and Jensen JA. 1979. A new large theropod dinosaur from the Upper Jurassic of Colorado. *BYU Geology studies* 26:1-12.

Gao Y. 1999. *A complete carnosaur skeleton from Zigong, Sichuan* - Yangchuanosaurus hepingensis. Chengdu: Sichuan Science and Technology Press.

García-Ramos JC, Aramburu C. and Piñuela L. 2010c. Las series fluviales del Jurásico Superior de Asturias (Formación Vega). In: García-Ramos JC ed. *V Congreso del Jurásico de España*. *Guía de campo (excursión A)*. *Las sucesiones margo-calcáreas marinas del Jurásico Inferior y las series fluviales del Jurásico Superior*. *Acantilados de playa de Vega (Ribadesella)*. Colunga: Museo del Jurásico de Asturias, 53-63.

García-Ramos JC, Piñuela L, and Aramburu C. 2010b. La Formación Tereñes en su localidad tipo. In: García-Ramos JC, and Aramburu C. eds. *V Congreso del Jurásico de España. Guía de campo (excursión B). Las Sucesiones Litorales y Marinas Restringidas del Jurásico Superior. Acantilados de Tereñes (Ribadesella) y de la Playa de La Griega (Colunga).* Colunga: Museo del Jurásico de Asturias, 15–40.

García-Ramos JC, Piñuela L, and Lires J. 2006. *Atlas del Jurásico de Asturias*. Oviedo: Ediciones Nobel.

García-Ramos JC, Piñuela L, and Rodríguez-Tovar FJ. 2011. *Post-workshop field trip guide of the XI International Ichnofabric Workshop*. Colunga: Museo del Jurásico de Asturias.

García-Ramos JC, Piñuela L, Uzqueda H, Poblet J, Bulnes M, Alonso JL, and Suárez-Vega LC. 2010a. Travertinos ricos en oncoides asociados a paleomanantiales y lagos efímeros próximos a fallas sinsedimentarias en el Jurásico Superior de Asturias. In: Ruiz-Omeñaca JI, Piñuela L, and García-Ramos JC, eds. *Comunicaciones del V Congreso del Jurásico de España*. Colunga: Museo del Jurásico de Asturias, 83-91.

Gascó F, Cobos A, Royo-Torres R, Mampel L, and Alcalá L. 2012. Theropod teeth diversity from the Villar del Arzobispo Formation (Tithonian–Berriasian) at Riodeva (Teruel, Spain). *Palaeobiology and Palaeoenvironments* 92:273-285.

Gerke O, and Wings O. 2016. Multivariate and cladistic analyses of isolated teeth reveal sympatry of theropod dinosaurs in the Late Jurassic of Northern Germany. *Plos One* 11(7):e0158334.

Gilmore CW. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bulletin of the United States National Museum* 110:1-154.

Gutierrez K, and Sheldon ND. 2012. Paleoenvironmental reconstruction of Jurassic dinosaur habitats of the Vega Formation, Asturias, Spain. *GSA Bulletin* 124:596-610.

Hanson M, and Makovicky P. 2014. A new specimen of *Torvosaurus tanneri* originally collected by Elmer Riggs. *Historical Biology* 26:775-784.

Hendrickx C, and Mateus O. 2014. *Torvosaurus gurneyi* n. sp., the largest terrestrial predator from Europe, and a proposed terminology of the maxilla anatomy in nonavian theropods. *Plos One* 9(3): e88905.

Hendrickx C, Mateus O, and Araújo R. 2015. The dentition of megalosaurid theropods. *Acta Palaeontologica Polonica* 60:627-642.

Hornung J, Böhme A, van der Lubbe T, Reich M, and Richter A. 2012. Vertebrate tracksites in the Obernkirchen Sandstone (late Berriasian, Early Cretaceous) of northwest Germany- their stratigraphical, palaeogeographical, palaeoecological, and historical context. *Palaeontologische Zeitschrift* 86:231-267.

Huene Fv. 1926. The carnivorous Saurischia in the Jura and Cretaceous Formations, principally in Europe. *Revista del Museo de La Plata* 29:35-167.

Kuhn O. 1958. *Die Fährten der vorzeitlichen Amphibien und Reptilien*. Bamberg: Verlagshaus Meisenbach.

Lapparent AFde. 1943. Les dinosauriens jurassique de Damparis (Jura). *Memoires de la Société géologique de la France, Nouvelle Série* 47:5-20.

Lockley MG. 2009. New perspectives on morphological variation in tridactyl footprints: clues to widespread convergence in developmental dynamics. *Geological Quarterly* 53:415–432.

Lockley MG, and Hunt AP. 1994. A track of the giant theropod dinosaur *Tyrannosaurus* from close to the Cretaceous/Tertiary Boundary, northern New Mexico. *Ichnos* 3:213–218.

Lockley M, García-Ramos JC, Piñuela L, and Avanzini M. 2008. A comparative review of vertebrate track assemblages from the Late Jurassic of Asturias, Spain and the western USA: implications for faunal diversity in association with siliciclastic facies assemblages. *Oryctos* 8:53-70.

Lockley M, Lires J, García-Ramos JC, Piñuela L, and Avanzini M. 2007. Shrinking the world´s largest dinosaur tracks: Observations on the ichnotaxonomy of *Gigantosauropus asturiensis* and *Hispanosauropus hauboldi* from the Upper Jurassic of Asturias, Spain. *Ichnos* 14:247-255.

Lockley MG, Meyer CA, and Santos VF. 2000. *Megalosauripus* and the problematic concept of megalosaur footprints. *Gaia* 15:313-337.

Lockley MG, Meyer C, Schulz-Pittman R, and Forney G. 1996. Late Jurassic dinosaur tracksites from Central Asia: A preliminary report on the world´s longest trackways. In: Morales M, ed. *Continental Jurassic Symposium Volume*. *Museum Northern Arizona, Bulletin* 60:137-140.

Lozano R, Delvene GM, Piñuela L, and García-Ramos JC. 2016. Late Jurassic biogeochemical microenvironments associated with microbialite-coated unionoids (Bivalvia), Asturias (Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 443:80-97.

Madsen JH. 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geological and Mineralogical Survey Bulletin* 109:3-163.

Madsen JH, and Welles SP. 2000. *Ceratosaurus* (Dinosauria, Theropoda). A revised osteology. *Miscellaneous Publication, Utah Geological Survey* 00-2:1-80.

Malafaia E, Dantas P, Ortega F, and Escaso F. 2007. Nuevos restos de *Allosaurus fragilis* (Theropoda: Carnosauria) del yacimiento de Andrés (Jurásico Superior; Centro-Oeste de Portugal). In: Cambra-Moo O, Martínez-Pérez C, Chamero B, Escaso F, de Esteban Trivigno S, and Marugán-Lobón J, eds. *Cantera Paleontológica*. Cuenca: Diputación Provincial de Cuenca, 255-271.

Malafaia E, Escaso F, Mocho P, Serrano-Martinez A, Torices A, Cachao M, and Ortega F. 2017b. Analysis of diversity, stratigraphic and geographical distribution of isolated theropod teeth from the Upper Jurassic of the Lusitanian Basin, Portugal. *Journal of Iberian Geology* 43:257-291.

Malafaia E, Mocho P, Escaso F, and Ortega F. 2017a. New data on the anatomy of *Torvosaurus* and other remains of megalosauroid (Dinosauria, Theropoda) from the Upper Jurassic of Portugal. *Journal of Iberian Geology* 43:33-59.

Malafaia E, Ortega F, Escaso F, Dantas P, Pimentel N, Gasulla J, Ribeiro B, Barriga F, and Sanz J. 2010. Vertebrate fauna at the *Allosaurus* fossil-site of Andres (Upper Jurassic), Pombal, Portugal. *Journal of Iberian Geology* 36:193-204.

Malafaia E, Ortega F, Escaso F, and Silva B. 2015. New evidence of *Ceratosaurus* (Dinosauria: Theropoda) from the Late Jurassic of the Lusitanian Basin, Portugal. *Historical Biology* 27:938-946.

Malafaia E, Ortega F, Escaso F, Silva B, Ramalheiro G, Dantas P, Moniz C, and Barriga F. 2008a. Análisis preliminar de un nuevo ejemplar de *Allosaurus* del Grupo Lourinhã (Jurásico Superior de Torres Vedras, Portugal). In: Huerta P, and Torcida Fernández-Baldor F, eds. *Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*. Salas de los Infantes, Burgos: Colectivo Arqueológico y Paleontológico de Salas, 243-251.

Malafaia E, Ortega F, Silva B, and Escaso F. 2008b. Fragmento de un maxilar de terópodo de Praia da Corva (Jurásico Superior. Torres Vedras, Portugal). *Palaeontologica Nova* 8:273-279.

Manning P, Ott C, and Falkingham P. 2008. A probable tyrannosaurid track from the Hell Creek Formation (Upper Cretaceous), Montana, United States. *Palaios* 23:645-647.

Mannion P, Allain R, and Moine O. 2017. The earliest known titanosauriform sauropod dinosaur and the evolution of Brachiosauridae. *Peerj* 5:e3217.

Marquet P, and Taper M. 1998. On size and area: Patterns of mammalian body size extremes across landmasses. *Evolutionary Ecology* 12:127-139.

Martínez R, García-Ramos J, Piñuela L, Lires J, Luna M, and Veigas D. 2000. Vértebras caudales de Sauropoda y Theropoda (Dinosauria: Saurischia) del Jurásico Superior de Asturias, España. In: Diez J, and Balbino A, eds. *I Congresso Ibérico de Paleontologia/XVI Jornadas de la Sociedad Española de Paleontología*. Évora: Sociedad Española de Paleontología, 113-114.

Marty D, Belvedere M, Razzolini NL, Lockley MG, Paratte G, Cattin M, Lovis C, and Meyer CA. 2017. The tracks of giant theropods (*Jurabrontes curtedulensis* ichnogen. & ichnosp. nov.) from the Late Jurassic of NW Switzerland: palaeoecological & palaeogeographical implications. *Historical Biology*:doi.org/10.1080/08912963.08912017.01324438.

Mateus O. 2006. Late Jurassic dinosaurs from the Morrison Formation (USA), the Lourinha and Alcobaça Formations (Portugal), and the Tendaguru Beds (Tanzania): A comparison. *New Mexico Museum of Natural History and Science Bulletin* 36:1-9.

Mateus O, Walen A, and Antunes MT. 2006. The large theropod fauna of the Lourinha Formatuion (Portugal) and its similarity to that of the Morrison Formation, with a description of new species of *Allosaurus*. *New Mexico Museum of Natural History and Science Bulletin* 36:123-129.

McCrea R, Buckley L, Farlow J, Lockley M, Currie P, Matthews N, and Pemberton S. 2014. A 'terror of tyrannosaurs': The first trackways of tyrannosaurids and evidence of gregariousness and pathology in Tyrannosauridae. *Plos One* 9(7): e103613.

Méndez AH. 2014. The caudal vertebral series in abelisaurid dinosaurs. *Acta Palaeontologica Polonica* 59:99-107.

Mensink H, and Mertmann D. 1984. Dinosaurier-Fährten (*Gigantosauropus asturiensis n.g. n.sp.; Hispanosauropus hauboldi n. g. n. sp.*) im Jura Asturiens bei La Griega und Ribadesella (Spanien). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1984(7):405-415.

Merino Tomé O, Suárez Rodríguez A, and Alonso JL. 2013. Mapa Geológico Digital continuo E. 1:50.000, Zona Cantábrica (Zona-1000). In: GEODE. *Mapa Geológico Digital continuo de España*.

Meyer CA. 2012. Dinosaur tracks in an ancient lower deltaic plain-interdistributary bay. In: Richter A, and Reich M, eds. *Dinosaur tracks 2011. An International Symposium, Obernkirchen, April 14-17, 2011. Abstract Volume and Field Guide to Excursions*. Göttingen: Universitätsverlag, 43.

Milàn J, Avanzini M, Clemmensen LB, García-Ramos JC, and Piñuela L. 2006. Theropod foot movement recorded from Late Triassic, Early Jurassic and Late Jurassic fossil footprints. In: Harris JD, Lucas SG, Spielmann J, Lockley MG, Milner ARC, and Kirkland JL, eds. *The Triassic-Jurassic Terrestrial Transition*. *New Mexico Museum of Natural History and Science Bulletin* 37:352–364.

Mocho P, Royo-Torres R, Escaso F, Malafaia E, Chaves C, Narvaez I, Perez-Garcia A, Pimentel N, Silva B, and Ortega F. 2017. Upper Jurassic sauropod record in the Lusitanian Basin (Portugal): Geographical and lithostratigraphical distribution. *Palaeontologia Electronica* 20.2.27A: 1-50.

Niebuhr B, and Pürner T. 2014. Lithostratigraphie der Weißjura-Gruppe der Frankenalb (außeralpiner Oberjura) und der mittel- bis oberjurassischen Reliktvorkommen zwischen Straubing und Passau (Bayern). *Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften* 83:5-72.

O'Connor PM. 2007. The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Society of Vertebrate Paleontology, Memoir* 8:127-162.

Ortega F, Escaso F, Gasulla J, Dantas P, and Sanz J. 2006. Dinosaurios de la Península Ibérica. *Estudios Geológicos* 62:219-240.

Ostrom JH. 1978. The osteology of *Compsognathus longipes* Wagner. *Zitteliana* 4:73-118.

Pérez-Moreno BP, Chure DJ, Pires C, Marques da Silva C, Dos Santos V, Dantas P, Póvoas L, Cachão M, Sanz JL, and Galopim de Carvalho AM. 1999. On the presence of *Allosaurus fragilis* (Theropoda: Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. *Journal of the Geological Society* 156:449-452.

Pharisat A. 1993. Vertebres de dinosaure (Theropode) dans l'Oxfordien de Plaimbois-du-Miroir (Doubs). *Societé d'Histoire Naturelle du Pays de Montbéliard* 1993:191-192.

Piñuela L, García-Ramos J, Romano M, and Ruiz-Omenaca J. 2016. First record of gregarious behavior in robust medium-sized Jurassic ornithopods: Evidence from the Kimmeridgian trackways of Asturias (N. Spain) and some general considerations on other medium-large ornithopod tracks in the Mesozoic record. *Ichnos* 23:298-311.

Piñuela Suárez L. 2015. Huellas de dinosaurios y de otros reptiles del Jurásico Superior de Asturias Unpublished Ph.D.-thesis, University of Oviedo.

Rauhut OWM. 2011. Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). *Special Papers in Palaeontology* 86:195-239.

Rauhut OWM, Foth C, Tischlinger H, and Norell MA. 2012. Exceptionally preserved juvenile megalosauroid theropod dinosaur with filamentous integument from the Late Jurassic of Germany. *Proceedings of the National Academy of Sciences* 109:11746-11751.

Rauhut OWM, Hübner TR, and Lanser K-P. 2016. A new megalosaurid theropod dinosaur from the late Middle Jurassic (Callovian) of north-western Germany: implications for theropod evolution and faunal turnover in the Jurassic. *Palaeontologia electronica* 19:1-65.

Rauhut OWM, and Kriwet J. 1994. Teeth of a big theropod dinosaur from Porto das Barcas (Portugal). *Berliner geowissenschaftliche Abhandlungen (E)* 13:179-185.

Rauhut OWM, and Tischlinger H. 2015. *Archaeopteryx*. In: Arratia G, Schultze H-P, Tischlinger H, and Viohl G, eds. *Solnhofen Ein Fenster in die Jurazeit*. Munich: Verlag Dr. Friedrich Pfeil, 491-507.

Razzolini NL, Belvedere M, Marty D, Paratte G, Lovis C, Cattin M, and Meyer CA. 2017. *Megalosauripus transjuranicus* ichnosp. nov. A new Late Jurassic theropod ichnotaxon from NW Switzerland and implications for tridactyl dinosaur ichnology and ichnotaxomy. PLoS One 12(7):e0180289.

Razzolini NL, Oms O, Castanera D, Vila B, dos Santos V, and Galobart A. 2016. Ichnological evidence of megalosaurid dinosaurs crossing Middle Jurassic tidal flats. *Scientific Reports* 6:31494.

Royo-Torres R, Cobos A, Luque L, Aberasturi A, Espilez E, Fierro I, Gonzalez A, Mampel L, and Alcala L. 2009. High European sauropod diversity during Jurassic-Cretaceous transition in Riodeva (Teruel, Spain). *Palaeontology* 52:1009-1027.

Ruiz-Omeñaca JI. 2010. Vertebrados fósiles (restos directos) de la Formación Vega. In: García-Ramos JC, ed. *V Congreso del Jurásico de España. Guía de campo (excursión A). Las sucesiones margo-calcáreas marinas del Jurásico Inferior y las series fluviales del Jurásico Superior. Acantilados de la playa de Vega (Ribadesella)*. Colunga: Museo del Jurásico de Asturias, 64–68.

Ruiz-Omeñaca JI, Pereda Suberbiola X, Piñuela L, and García-Ramos JC. 2013. First evidence of stegosaurs (Dinosauria: Thyreophora) in the Vega Formation, Kimmeridgian, Asturias, N Spain. *Geogaceta* 53:37-40.

Ruiz-Omeñaca JI, Piñuela L, and García-Ramos J. 2007. Una vértebra de un pequeño ornitópodo (Dinosauria: Ornithischia) del Kimmeridgiense (Formación Lastres) de Tazones (Villaviciosa, Asturias). *Geogaceta* 45:83-86.

Ruiz-Omeñaca JI, Piñuela L, and García-Ramos JC. 2008. Primera evidencia de dinosaurios diplodocinos (Sauropoda: Diplodocidae) en el Jurásico Superior de Asturias (Noreña). In: Ruiz-Omeñaca JI, Piñuela L, and García-Ramos JC, eds. *Libro de resúmenes XXIV Jornadas de la Sociedad Española de Paleontología Museo del Jurásico de Asturias (MUJA), Colunga, 15-18 de octubre de 2008*.

Ruiz-Omeñaca JI, Piñuela L, and García-Ramos J. 2009b. Nuevos restos de ornitópodo (Ornithischia: Ankylopollexia) del Jurásico Superior de Tazones, Asturias (Formación Tereñes). *Geogaceta* 45:59-62.

Ruiz-Omeñaca JI, Piñuela L, and García-Ramos J. 2010. El primer diente de ornitópodo del Jurásico Superior de España (Asturias). *Geogaceta* 48:83-86.

Ruiz-Omeñaca JI, Piñuela L, and García-Ramos J. 2012. New ornithopod remains from the Upper Jurassic of Asturias (North Spain). In: Royo-Torres R, Gascó F, and Alcalá L, eds. *10th Annual*

Meeting of the European Association of Vertebrate Palaeontologists. Teruel: Fundación Conjunto Paleontológico de Teruel – Dinópolis, 219-222.

Ruiz-Omeñaca JI, Piñuela L, García-Ramos JC, and Canudo JI. 2009c. Dientes de dinosaurios carnívoros (Saurischia: Theropoda) del Jurásico Superior de Asturias. In: Hurtado PH, and Torcida F, eds. *Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*. Salas de los Infantes: Colectivo Arqueológico y Paleontológico de Salas, 273-291.

Ruiz-Omeñaca JI, Piñuela L, García-Ramos J, and Pereda Suberbiola X. 2009a. A Dacentrurinae stegosaur from the Late Jurassic of Asturias (Northern Spain). *Journal of Vertebrate Paleontology, Program and Abstracts* 29:174A.

Sadleir R, Barrett PM, and Powell HP. 2008. The anatomy and systematics of *Eustreptospondylus oxoniensis*, a theropod dinosaur from the Middle Jurassic of Oxfordshire, England. *Monograph of the Palaeontographical Society* 160:1-82.

Sander PM, Mateus O, Laven T, and Knötschke N. 2006. Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur. *Nature* 441:739-741.

Schudack U, and Schudack M. 2002. New biostratigraphical data for the Upper Jurassic of Asturias (northern Spain) based on Ostracoda. *Revista Española de Micropaleontología* 31:1-18.

Sereno PC, Wilson JA, Larsson HCE, Dutheil DB, and Sues H-D. 1994. Early Cretaceous dinosaurs from the Sahara. *Science* 266:267-271.

Stein K, Csiki Z, Curry Rogers K, Weishampel DB, Redelstorff R, Carballido JL, and Sander PM. 2010. Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). *Proceedings of the National Academy of Sciences* 107:9258-9263.

Stromer E. 1915. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. spec. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-physikalische Klasse* 28:1-32.

Thierry J, Barrier E, Abbate E, Alekseev A, Ait-Ouali R, Ait-Salem H, Bouaziz S, Canerot J, Georgiev G, Guiraud R, Hirsch F, Ivanik M, Le Metour J, Le Nindre YM, Medina F, Mouty M, B N, Nikishin A, Page K, Panov D, A P, Poisson A, Sandulescu M, Sapunov I, Seghedi A, Soussi M, Tchoumatchenko P, Vaslet D, Vishnevskaya V, Volozh Y, Voznezenski A, Walley C, Wong T, Ziegler M, Ait-Brahim L, Bergerat F, Bracene R, Brunet M, Cadet J, Guezou J, Jabaloy A, Lepvrier C, and Rimmele G. 2000. Early Tithonian. In: Dercourt J, Gaetani M, Vrielynck B, Barrier E, Biju-Duval B, Brunet M, Cadet J, Crasquin S, and Sandlescu M, eds. *Atlas Peri-Tethys, Palaeogeographical maps*. Paris: CCGM/CGMW, Map 11.

Tischlinger H, Göhlich UB, and Rauhut OWM. 2015. Raubdinosaurier (Theropoda). In: Arratia G, Schultze H-P, Tischlinger H, and Viohl G, eds. *Solnhofen Ein Fenster in die Jurazeit*. Munich: Verlag Dr. Friedrich Pfeil, 481-490.

Walker AD. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. *Philosophical Transactions of the Royal Society of London, Series B* 248:53-134.

Wellnhofer P. 2008. *Archaeopteryx. Der Urvogel von Solnhofen*. Munich: Verlag Dr. Friedrich Pfeil.

Williamson TE, and Chure DJ. 1996. A large allosaurid from the Upper Jurassic Morrison Formation (Brushy Basin Member), west-central New Mexico. *Museum of Northern Arizona Bulletin* 60:73-79.

Figure 1

Geological map of the eastern Asturian sector, including the location of Vega beach (Ribadesella).

Modified after Merino-Tomé et al. (2013).

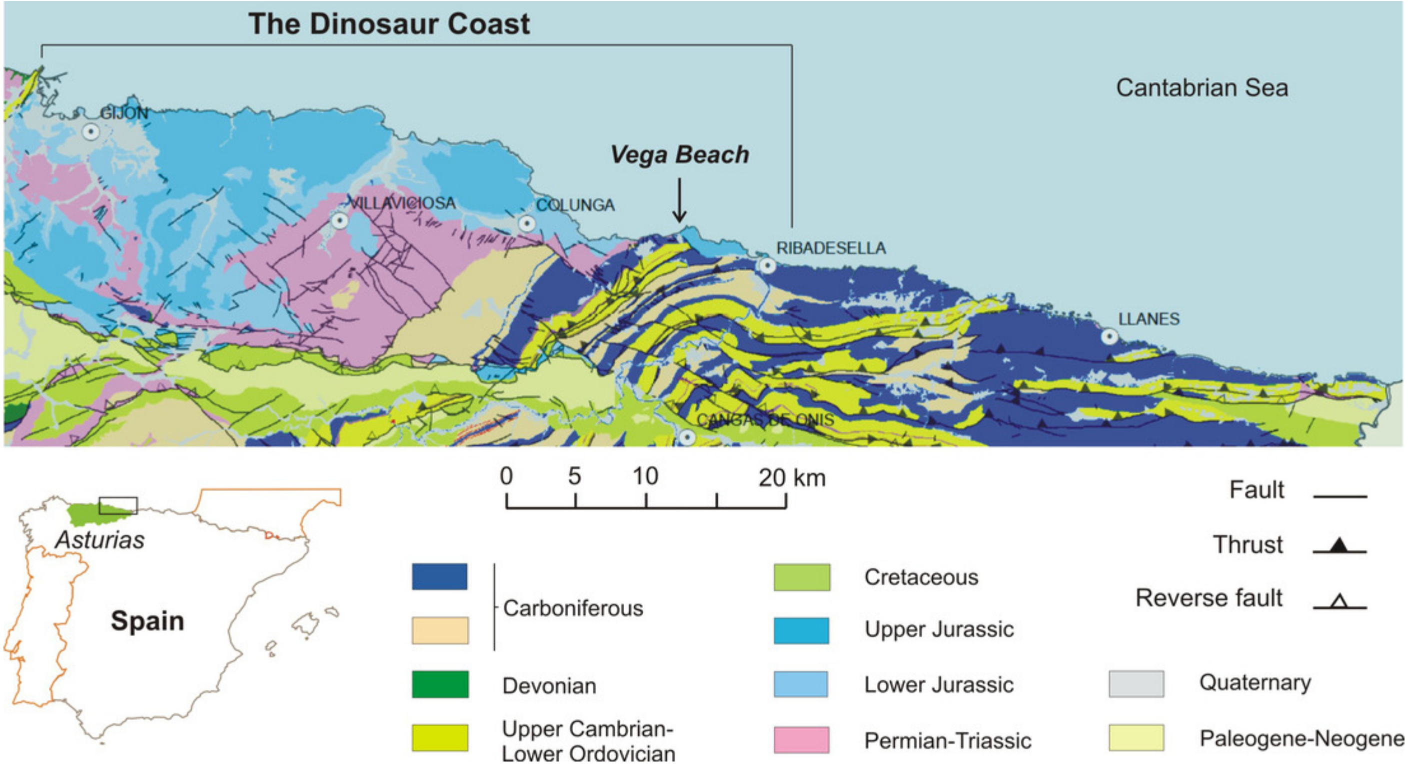

Figure 2

Geology of the Asturian Jurassic.

A, General stratigraphic log of the Asturian Jurassic along the Tazones-Ribadesella sector. Not to scale. Modified after García-Ramos et al. (2011). B, Detailed log of the lower part of the Vega Formation (after García-Ramos et al., 2010c). The level where the vertebra was found is indicated by an asterisk.

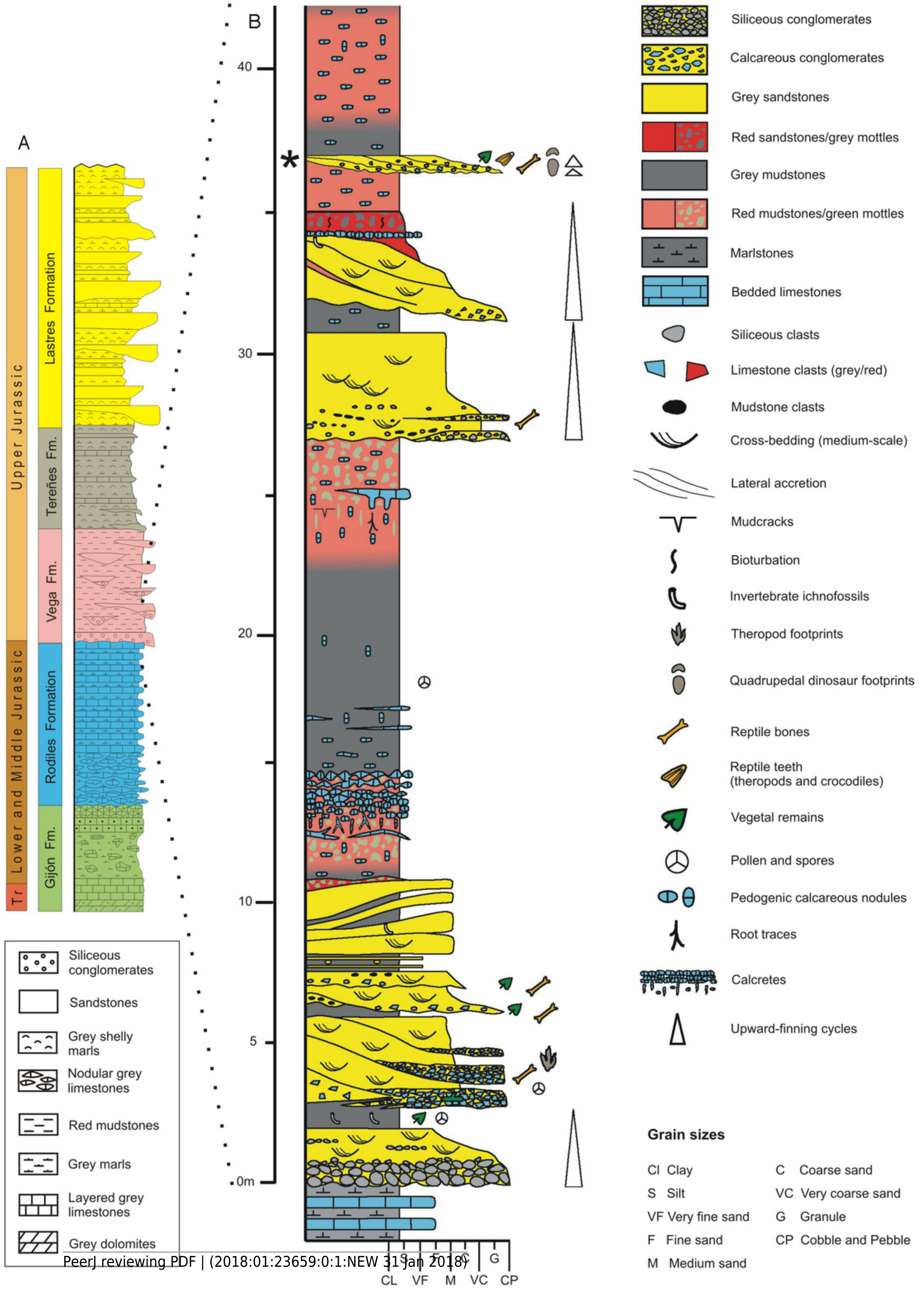
A
Tr
Lower and Middle Jurassic
Upper Jurassic
Gijón Fm.
Rodiles Formation
Vega Fm.
Tereñes Fm.
Lastres Formation
Siliceous conglomerates
Sandstones
Grey shelly marls
Nodular grey limestones
Red mudstones
Grey marls
Layered grey limestones
Grey dolomites
B
0m
5
10
20
30
40
*
CL
S
VF
F
M
C
VC
G
CP
Siliceous conglomerates
Calcareous conglomerates
Grey sandstones
Red sandstones/grey mottles
Grey mudstones
Red mudstones/green mottles
Marlstones
Bedded limestones
Siliceous clasts
Limestone clasts (grey/red)
Mudstone clasts
Cross-bedding (medium-scale)
Lateral accretion
Mudcracks
Bioturbation
Invertebrate ichnofossils
Theropod footprints
Quadrupedal dinosaur footprints
Reptile bones
Reptile teeth (theropods and crocodiles)
Vegetal remains
Pollen and spores
Pedogenic calcareous nodules
Root traces
Calcretes
Upward-finning cycles
Grain sizes
Cl Clay
S Silt
VF Very fine sand
F Fine sand
M Medium sand
C Coarse sand
VC Very coarse sand
G Granule
CP Cobble and Pebble

Figure 3

Tip of a large megalosaurid tooth from the Vega Formation.

A, general view in lingual or labial view. B, detail of distal serrations and anastomosing enamel ornamentation. Scale bars are 10 mm.

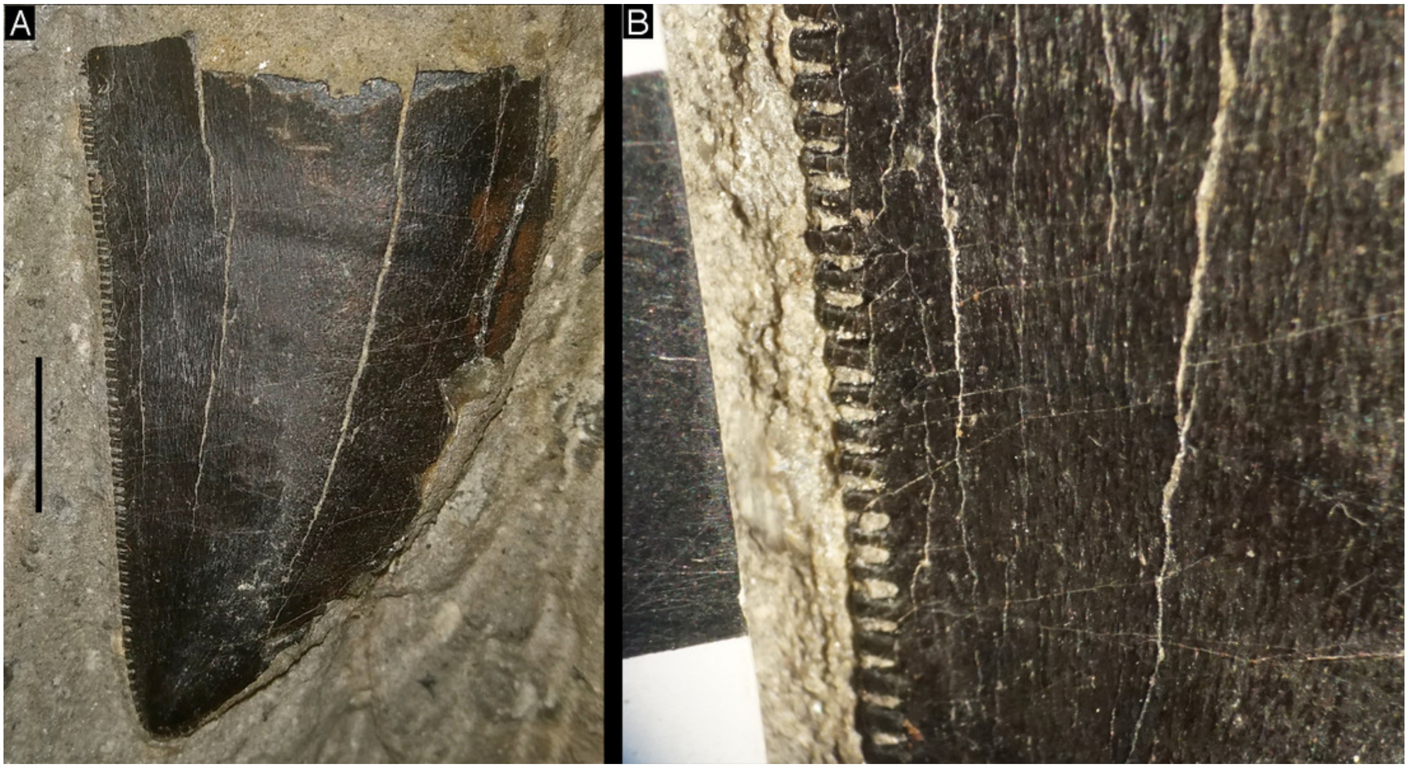

Figure 4

Anterior caudal vertebra of a giant megalosaurid from the Vega Formation, MUJA-1913.

A, left lateral view. B, posterior view. C, ventral view. D, dorsal view. ch, chevron facet; d, depression on anterior end of dorsal surface of transverse process; l, lamina dividing the conical postzygocentrodiapophyseal fossa from a shallow dorsal depression; pcd, pleurocentral depression; pcdf, postzygocentrodiapophyseal fossa; pcdl, posterior centrodiapophyseal lamina; vg, ventral groove. Scale bar is 50 mm.

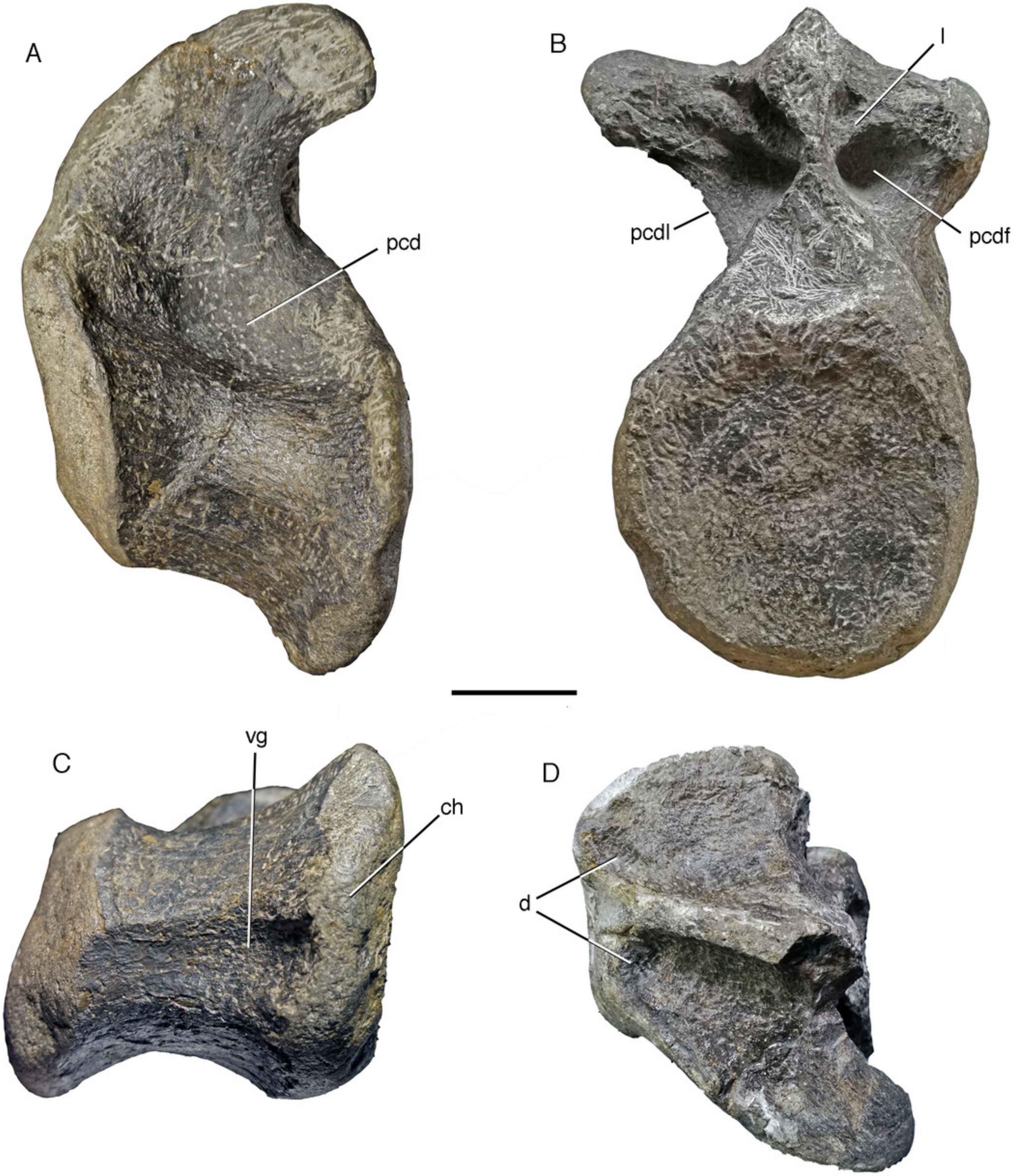
A
pcd
B
l
pcdl
pcdf
C
vg
ch
D
d

Figure 5

Asturian Jurassic footprints with a weak mesaxony and probably related to very large or giant megalosaurid theropod trackmakers (Morphotype A).

A, B and C specimens still on Argüero, Oles and Tazones sea cliffs, respectively. Noted track C does not preserved the end of the digit IV. D, MUJA-1889.

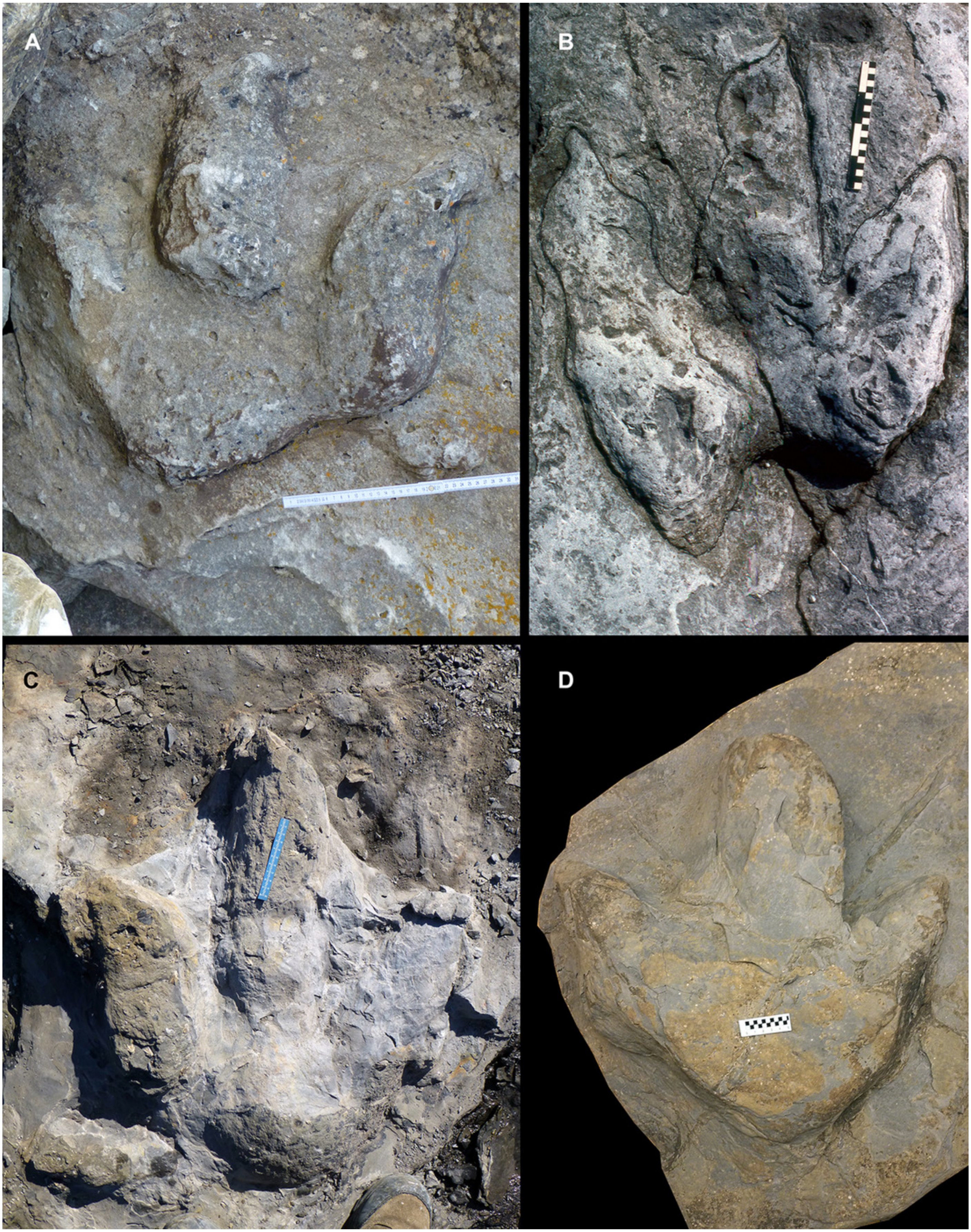
A
B
C
D

Figure 6

Giant Asturian Jurassic footprints, strongly mesaxonic (Morphotype B).

A, MUJA-1263. B, MUJA-0213, scale bar: 1 m. C, specimen still on Argüero sea cliffs.

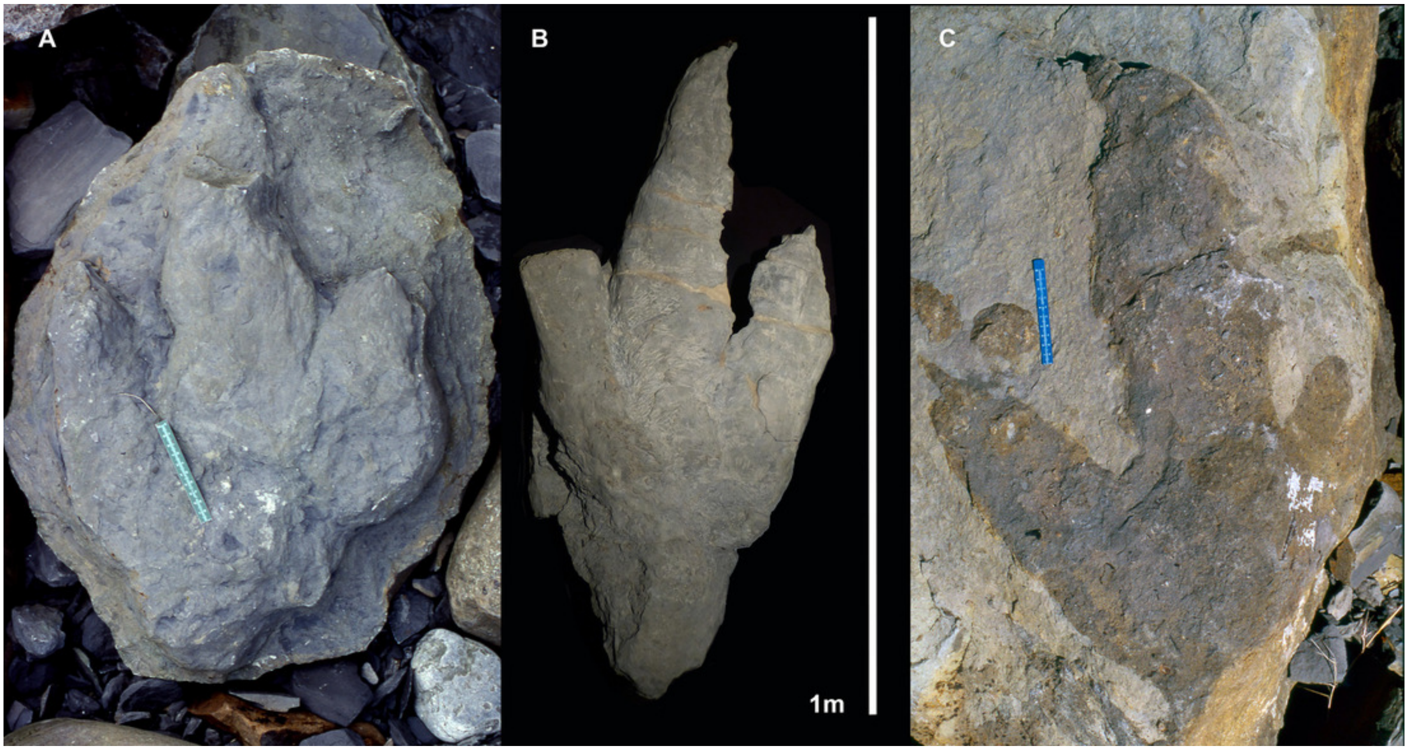

Table 1(on next page)

Measurements of the Asturian tracks.

R (Right foot) L (Left foot) FL (Footprint length), WL (Footprint width), II^IV total divarication angle. For the specimens see Figs. 5 and 6.

Table 1

Morphotype A	**Foot**	**FL**	**WL**	**FL/WL**	**II^IV**
Argüero	R	62	70	0.88	36
Oles	L	82	66	1.24	38
Tazones	L	57	>47	>1.16	38
MUJA-1889	L	53	53	1	40
Morphotype B					
MUJA-1263	R	62	38	1.63	15
MUJA-0213	R	78			
Argüero	R	67			