

## Systematic review of Late Jurassic sauropods from the Museu Geológico collections (Lisboa, Portugal)

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### Abstract

The Museu Geológico collections house some of the first sauropods found in the Upper Jurassic sediments of the Lusitanian Basin, including the *Lourinhasaurus alenquerensis* and *Lusotitan atalaiensis* lectotypes, previously considered as new species of the genera *Apatosaurus* and *Brachiosaurus*, respectively. Several fragmentary specimens have historically been referred to those taxa, but for the most part of these systematic attributions are not supported herein, excluding a caudal vertebra from Maceira (MG 8804) considered as cf. *Lusotitan atalaiensis*. The material housed in the Museu Geológico comprises remains of non-neosauropod eusauropods (including turiasaurs) and neosauropods (indeterminate neosauropods, diplodocids, camarasaurids and basal titanosauriforms). Middle caudal vertebrae with lateral fossae, with ventral hollow bordered by pronounced ventrolateral crests and, which are quadrangular in cross-section, indicate for the presence of diplodocine diplodocids in the northern part of the Lusitanian Basin Central Sector during the Late Jurassic. A humerus collected from Praia dos Frades (MG 4976) is attributed to cf. *Duriatitan humerocristatus* suggesting the presence of shared sauropod forms between the Portugal and United Kingdom during the Late Jurassic. *Duriatitan* is an indeterminate member of Eusauropoda and the discovery of new material in both territories is necessary to confirm its systematic position. The studied material is in accordance with the previously recorded sauropod fauna in the Portuguese Late Jurassic, which includes non-neosauropod eusauropods (including turiasaurs), diplodocids and macronarians (including camarasaurids and basal titanosauriforms).

**Keywords:** Diplodocidae, Lusitanian Basin, Sauropoda, Upper Jurassic, *Duriatitan*

### Resumen

Las colecciones del Museu Geológico contienen algunas de las primeras referencias de saurópodos del Jurásico Superior de la cuenca lusitánica, incluyendo los especímenes tipo de *Lourinhasaurus alenquerensis* y *Lusotitan atalaiensis*, previamente considerados como nuevas especies de *Apatosaurus* y *Brachiosaurus*, respectivamente. Varios ejemplares incompletos fueron tradicionalmente referidos a estos taxones, atribución sistemática que es aquí refutada, excluyendo una vértebra caudal de Maceira (MG 8804) atribuida a cf. *Lusotitan atalaiensis*. Entre el material de saurópodos depositado en el Museu Geológico se ha identificado la presencia de eusaurópodos basales y neosaurópodos (formas indeterminadas, diplodócidos, camarasáuridos y Titanosauriformes basales). La presencia de vértebras caudales con fosas laterales, concavidad ventral limitada por crestas ventrolaterales y una sección transversal cuadrangular sugiere la presencia de diplodocinos en la región norte del Sector Central de la cuenca lusitánica durante el Jurásico Superior. Un húmero encontrado en Praia dos Frades (MG 4976) atribuido a cf. *Duriatitan humerocristatus* apunta a la presencia de formas compartidas entre el Jurásico Superior de Portugal y de Reino Unido. *Duriatitan* es un miembro indeterminado de Eusauropoda, y el descubrimiento de nuevo material en ambos territorios podrá confirmar esta atribución sistemática. El estudio del material clásico es congruente con la paleobiodiversidad conocida de saurópodos en el Jurásico Superior de Portugal, la cual contiene eusaurópodos basales (incluyendo turiasauros), diplodócidos y macronárticos (incluyendo camarasáuridos y Titanosauriformes basales).

**Palabras clave:** Diplodocidae, cuenca lusitánica, Sauropoda, Jurásico Superior, *Duriatitan*

## 1. Introduction

In the Lusitanian Basin (Portugal), Sauropoda is a well-represented group recorded from the Upper Jurassic to the uppermost Cretaceous (Sauvage, 1897-98; Lapparent and Zbyszewski, 1957; Dantas, 1990; Antunes and Mateus, 2003). In particular, concerning the Upper Jurassic record, sauropods are the most abundant dinosaur group, with hundreds of fossil occurrences in a sedimentary sequence ranging from the Kimmeridgian to the late Tithonian (e.g., Lapparent and Zbyszewski, 1957; Dantas, 1990; Bonaparte and Mateus, 1999; Yagüe et al., 2006; Mateus, 2005; Mocho et al., 2012; 2013a; 2013b; 2014a; 2014b; 2015; 2016; Mannion et al., 2012; 2013; Mateus et al., 2014). They are represented by four taxa: the camarasauro Lourinhasaurus alenquerensis (Lapparent and Zbyszewski, 1957; Dantas et al., 1998; Mocho et al., 2013a; 2014a), the diplodocid Dinheirosaurus lourinhanensis (Dantas et al., 1992; Bonaparte and Mateus, 1999; Mannion et al., 2012; recently considered as a species of *Supersaurus* by Tschoop et al., 2015), the basal macronarian Lusotitan atalaiensis, a possible brachiosaurid (Lapparent and Zbyszewski, 1957; Antunes and Mateus, 2003; Mannion et al., 2013) and the turiasaur *Zby atlanticus* (Mateus et al., 2014).

The Museu Geológico (Lisboa, Portugal) represents one of the most important sauropod collections (see Supplementary 1) in the Iberian Peninsula, having been referred to since the end of the 19<sup>th</sup> century and the first half of the 20<sup>th</sup> century (Sauvage, 1897-98; Zbyszewski, 1946; Lapparent and Zbyszewski, 1957). It houses the *Lourinhasaurus alenquerensis* and *Lusotitan atalaiensis* lectotypes, as well as several other specimens that were traditionally referred to these taxa. Beyond the historical significance of this collection, which includes some of the first referred, described and figured sauropod specimens from the Mesozoic of Portugal (Sauvage, 1897-98; Lapparent and Zbyszewski, 1957); specimens in this collection were also important for the understand of the evolutionary history of the sauropod faunas during the Portuguese Late Jurassic (Lapparent and Zbyszewski, 1957; Dantas, 1990; McIntosh, 1990a; 1990b; Dantas et al., 1992; 1998; Wilson and Sereno, 1998; Bonaparte and Mateus, 1999; Rauhut, 2000; Antunes and Mateus, 2003; Upchurch et al., 2004; Mateus, 2005). More recently, Portuguese Late Jurassic sauropods have been revised and new phylogenetic positions proposed (Mannion et al., 2012; 2013; Mocho et al., 2013a; 2014a). Given that, new specimens are being discovery and described (Mateus, 2005; Yagüe et al., 2006; Mocho et al., 2012; 2013b; 2014b; 2015; 2016; Mateus et al., 2014), it has proven essential to revise the systematic positions of the already named taxa. Excluding the type specimens of *Lourinhasaurus alenquerensis* and *Lusotitan atalaiensis*, no detailed work have been published on the majority of the old specimens housed in the Museu Geológico. Herein, we conduct a systematic revision of several of those specimens.

The relationships between the Portuguese and North American Late Jurassic dinosaur faunas has been largely discussed

(e.g., Galton, 1980; Pérez-Moreno et al., 1999; Hendrickx and Mateus, 2014; Ortega et al., 2013). A combination of shared and exclusive taxa was used as an argument to justify both processes of dispersion and vicariance (Galton, 1980; Pérez-Moreno et al., 1999; Antunes and Mateus, 2003; Escaso et al., 2007; Ortega et al., 2013). The relationships of the Portuguese Late Jurassic sauropods with taxa from the Upper Jurassic Morrison Fm. is lesser than considered in other groups, such as theropods (Ortega et al., 2013). The study of one of the most representative collections in sauropods from the Upper Jurassic of the Lusitanian Basin can contribute to understand the paleobiogeographical relationships between the groups of continental tetrapods during Upper Jurassic in the Peri-atlantic realm.

The described material was mainly collected north of Lisboa in the Upper Jurassic sediments of the Turcifal, Arruda and Bombarral Sub-basins (Fig. 1). Bombarral Sub-basin was divided in Bombarral-Alcobaça and Consolação Sub-basins by Taylor et al. (2013). In these sub-basins there are extensive areas where an Upper Jurassic to Lower Cretaceous sedimentary sequence crops out. The Upper Jurassic beds are dated from the middle Oxfordian to the base of Cretaceous (Fig. 2) (Schneider et al., 2009), and represents a third rifting episode (Rasmussen et al., 1998; Kullberg et al., 2006). This episode of rifting is marked by an internal differentiation of the Lusitanian Basin, resulting in the formation of several sub-basins (Bombarral, Turcifal and Arruda Sub-basins) followed by an important siliciclastic input, which progressively filled these sub-basins (Hill, 1988; Pena dos Reis et al., 2000; Kullberg et al., 2006). Since the Kimmeridgian, the sedimentary sequence is marked by a strong siliciclastic nature, with a continental signature in the top of the sequence up the top of the Upper Jurassic (e.g., Hill, 1988; Manuppella et al., 1999; Kullberg et al., 2006). Several formations are renowned for their abundant vertebrate fossil remains such as the Alcobaça, Praia da Amoreira-Porto Novo (Fig. 1c), Sobral (Fig. 1d), Freixial and Bombarral Formations (Fig. 1b). In Figure 2, there is a stratigraphic correlation between the nomenclature proposed for the Bombarral, Turcifal and Arruda Sub-basins (based on Hill, 1988; Manuppella et al., 1999; 2000; Pereda-Suberbiola et al., 2005; Kullberg et al., 2006; Yagüe et al., 2006; Escaso et al., 2007; Schneider et al., 2009; Azeredo et al., 2010; Malafaia et al., 2010).

*Anatomical abbreviations:* acet, acetabulum; acpl, anterior centroparapophyseal lamina; ant. spdl, anterior spinodiaphyseal lamina, at, anterior trochanter; bi, bifurcation; cprf, centroprezygapophyseal fossa; cr, caudal rib; cprl, centroprezygapophyseal lamina; dpc, deltopectoral crest; lb, lateral bulge; lt, lateral trochanter; ltf, lateral trochanter fossa; pa, parapophyses; part, posterior articulation; pca, posterior chevron articulation; pfr, pneumatic foramen; pfs, pneumatic fossa; pdcl, posterior centrodiaphyseal lamina; podl, postzygodiaophyseal lamina; post. spdl, posterior spinodiaphyseal lamina; prdl, prezygodiaophyseal lamina; pre, prezygapophysis; prpl, prezygoparapophyseal lamina; spol,

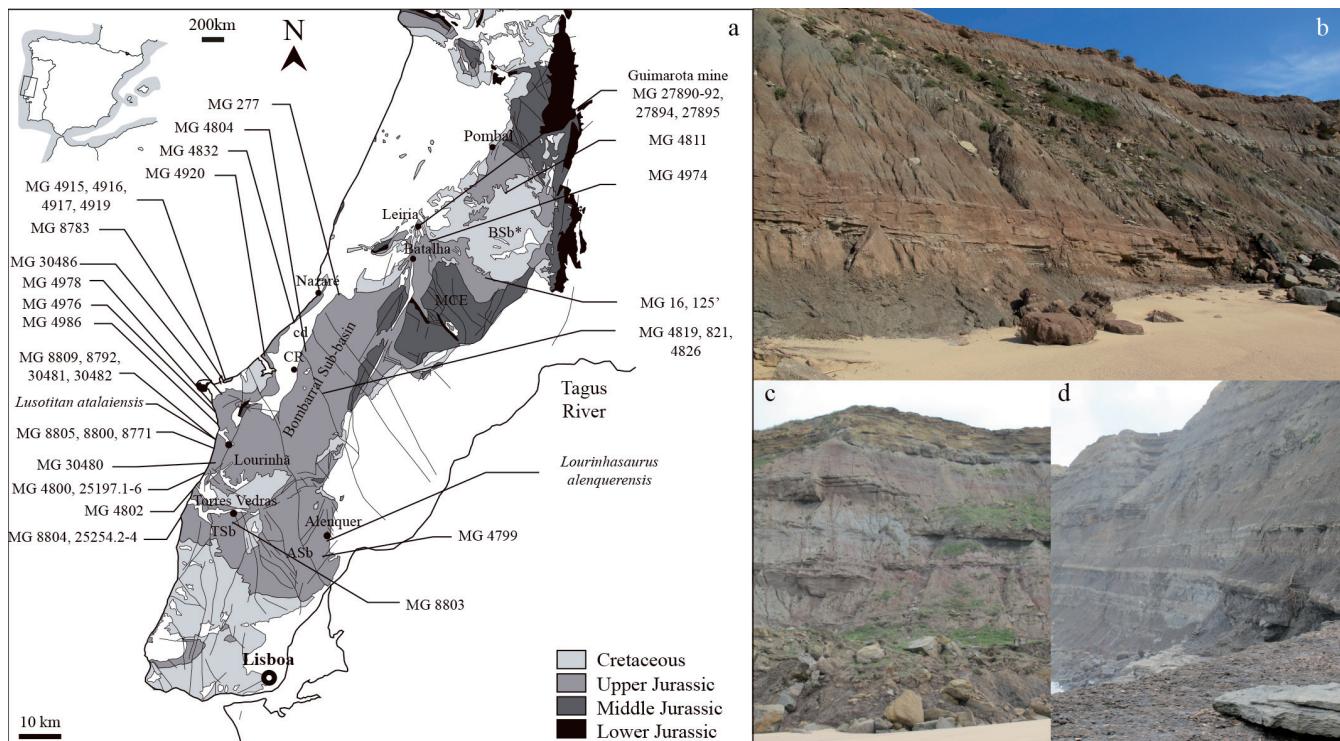


Fig. 1.- a. Geological map (adapted from Oliveira *et al.*, 1992) showing the Portuguese Mesozoic levels and the localities of the material of Museu Geológico referred to sauropods and collected Lusitanian Basin. b. Fluvial to lacustrine deposits of the Bombarral Fm. outcropping in Paimogo (Lourinhã); c. Fluvial meandriforme deposits of Praia da Corva (Torres Vedras); d. Delta plain deposits of the Sobral Fm. in Praia Azul (Torres Vedras). \*the locality is not precise; ASb- Arruda Sub-basin; BSb – Bombarral Sub-basin; cd – Caldas Diapir; CR – Caldas da Rainha town; TSb – Turcifal Sub-basin.

spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; sut, suture line; tia, tibial articulation; tap, triangular aliform process; vh, ventral hollow; vlc, ventrolateral crest. The terminology applied for vertebrae laminae and fossae follows Wilson (1999, 2012) and Wilson *et al.* (2011), respectively.

*Institutional abbreviations:* DFMMh, Dinosaurier-Freilichtmuseum Münchhausen/Verein zur Förderung der Niedersächsischen Paläontologie (e.V.), Germany; MG, Museu Geológico do Laboratório Nacional de Energia e Geologia, Lisboa, Portugal; NHMUK, Natural History Museum, London, UK; SHN, Sociedade de História Natural, Torres Vedras, Portugal (plus (JJS) for the José Joaquim dos Santos collection deposited in the Sociedade de História Natural).

## 2. Systematic Paleontology

- Dinosauria Owen, 1842
- Saurischia Seeley, 1887
- Sauropodomorpha Huene, 1932
- Sauropoda Marsh, 1878

### 2.1. Albergaria dos Doze

*Material:* Middle to posterior caudal vertebra (MG 4811).

*Locality and horizon:* The precise locality and formation from which the vertebra comes is unknown. Lapparent and

Zbyszewski (1957) referred that this vertebra comes from Albergaria dos Doze, 250m N45-W from the S. José Chapel (in the railway). In Albergaria dos Doze, the present railway intersect Cretaceous sediments, “Cenomaniano inferior, Albian, Aptiano, Neocomiano”, nevertheless the referred point is close to the river Arunca, which intersect the Upper Jurassic sediments of the “Complexo Vale de Lagares” (Teixeira *et al.*, 1968) that corresponds to the Alcobaça Formation, Kimmeridgian to basal Tithonian in age (Kullberg *et al.*, 2006). The stratigraphy of this area is uncertain, and the Upper Jurassic sediments outcropping in the Albergaria dos Doze might correspond to the Bombarral Fm. (e.g., Malafaia *et al.*, 2010). In this work, we consider the age for this vertebra as uncertain.

*Description:* Middle or posterior caudal vertebra lacking the neural arch (Fig. 3a.I-a.VI). The centrum is cylindrical, with a marked longitudinal crest on the lateral face. The centrum bears an amphicoelous condition, concave anterior and posterior articular facets. The posterior articulation is slightly compressed dorsoventrally. The ventral face is transversely convex-to-flat, having smooth ventrolateral crests associated to the articulations for the chevron. The posterior articulations for the chevron are more developed than the anterior ones, and both present a semi-elliptical outline. The neural arch is placed at midpoint of the centrum dorsal surface with a slight anterior displacement.

*Discussion:* MG 4811 was initially assigned to *Megalaosaurus pombali* by Lapparent and Zbyszewski (1957). This

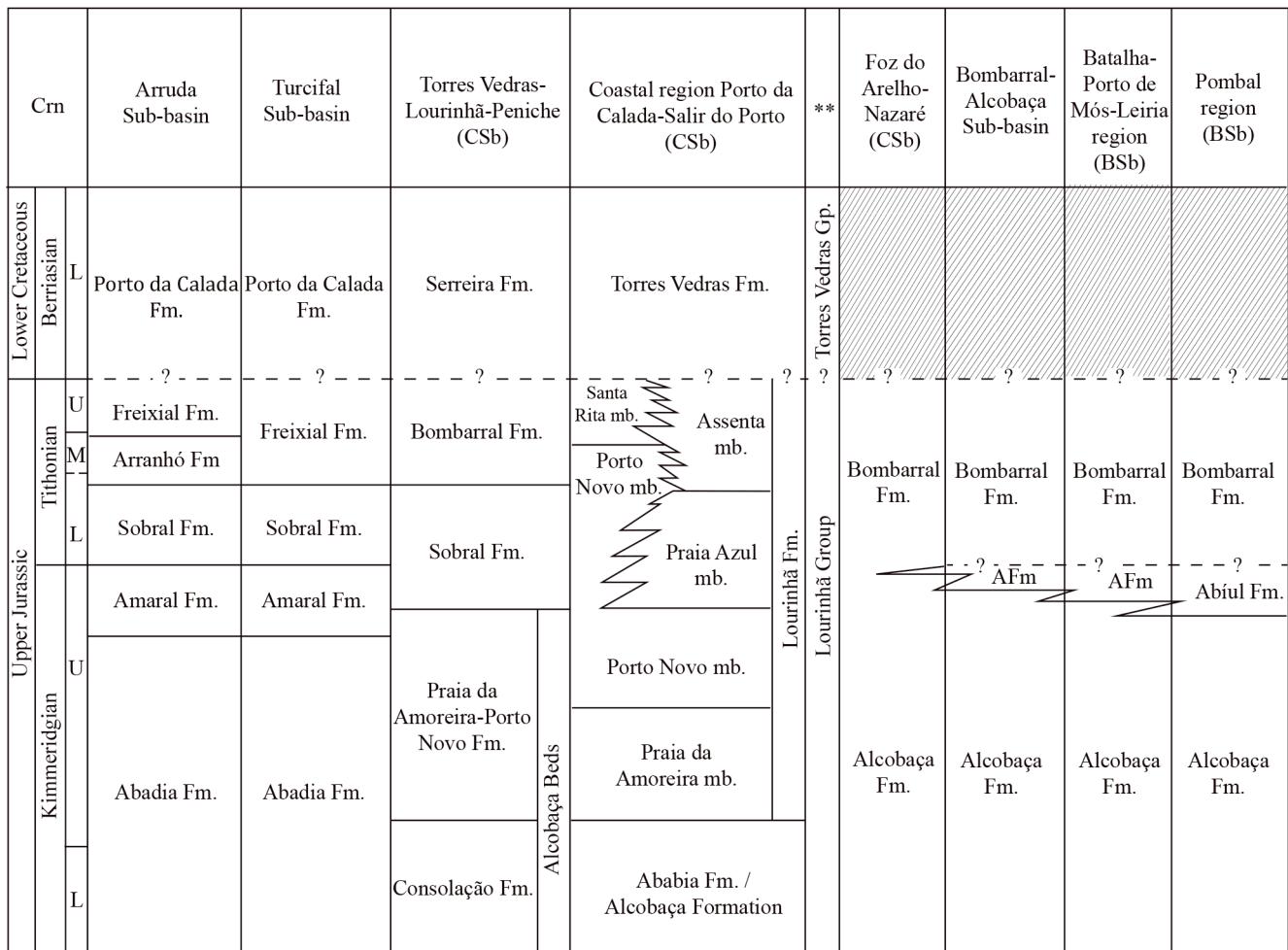


Fig. 2.- Stratigraphic correlation between the nomenclature proposed for the Upper Jurassic sub-basin of the Central Sector of the Lusitanian Basin [Bombarral Sub-basin in split in several areas: Consolação Sub-basin (Torres Vedras-Lourinhã-Peniche, Foz do Arelho-Nazaré coastal sector), Bombarral-Alcobaça Sub-basin, Batalha-Leiria region and Pombal region], from the left to the right: i) Turcifal Sub-basin (based on Pereda-Suberbiola *et al.*, 2005; Kullberg *et al.*, 2006; Schneider *et al.*, 2009); ii) Arruda Sub-basin (Kullberg *et al.*, 2006); iii) Consolação Sub-basin areas: Torres Vedras-Lourinhã-Peniche (based on Manuppella *et al.*, 1999), Foz do Arelho-Nazaré coastal sector (Kullberg *et al.*, 2006; Azerêdo *et al.*, 2010); iv) Bombarral-Alcobaça Sub-basin (based on Kullberg *et al.*, 2006; Azerêdo *et al.*, 2010); v) Batalha-Leiria region (based on Manuppella *et al.*, 2000; Kullberg *et al.*, 2006; Escaso *et al.*, 2007) and vi) Pombal region (Kullberg *et al.*, 2006; Malafaia *et al.*, 2010). The stratigraphy proposed by Hill (1988) for the coastal sector from Porto da Calada to Salir do Porto is also plotted. Crn – Chronostratigraphy; \*\**sensu* Yagüe *et al.*, 2006. BSb, Bombarral Sub-basin (following Kullberg *et al.*, 2006); CSb, Consolação Sub-Basin (following Taylor *et al.*, 2013).

taxon was considered *nomen dubium* by Antunes and Mateus (2003). Mateus (2005) referred this caudal vertebra to an indeterminate theropod. The presence of an anteroposteriorly short neural arch seems to exclude this caudal vertebra from Theropoda, and its general morphology more closely resembles that of sauropod middle and posterior caudal vertebrae. This middle or posterior caudal vertebra bears some

features that could help to discriminate it from some morphotypes present in the Iberian Late Jurassic. This vertebra can be differentiated from the middle and posterior caudal vertebrae of *Lusotitan* and *Galveosaurus* (Barco, 2009; Mannion *et al.*, 2013), by the presence of a well-developed amphicoelous centrum, a neural arch placed at midpoint of the centrum dorsal surface, and having a centrum, which is not

Fig. 3.- (next page) Sauropod caudal vertebra of the Museu Geológico. Sauropoda indet., middle or posterior caudal vertebra (MG 4811) in anterior (a.I), posterior (a.II), left (a.III), right (a.IV), dorsal (a.V) and ventral (a.VI) views. Sauropoda indet., anterior caudal vertebra (MG 4804) in anterior (b.I), posterior (b.II), left (b.III), right (b.IV), dorsal (b.V) and ventral (b.VI) views. Sauropoda indet., middle caudal vertebra (MG 8805) in anterior (c.I), posterior (c.II), left (c.III), right (c.IV), dorsal (c.V) and ventral (c.VI) views. Sauropoda indet., anterior caudal vertebra (MG 4800) in anterior (d.I), posterior (d.II), left (d.III), right (d.IV), dorsal (d.V) and ventral (d.VI) views. Sauropoda indet., middle caudal vertebra (MG 4802) in anterior (e.I), posterior (e.II), left (e.III), right (e.IV), dorsal (e.V) and ventral (e.VI) views. Eusauropoda indet., middle caudal vertebra (MG 8800) in anterior (f.I), posterior (f.II), left (f.III), right (f.IV), dorsal (f.V) and ventral (f.VI) views. Cf. *Lusotitan atalaiensis*, middle caudal vertebra (MG 8804) in anterior (g.I), posterior (g.II), left (g.III), right (g.IV), dorsal (g.V) and ventral (g.VI) views. Scale bar: 5cm. The traced line indicates lost bone.



markedly dorsoventrally compressed. In *Aragosaurus* (Sanz et al., 1987; Royo-Torres et al., 2014), the articulations are slightly flatter and the lateral faces do not bear longitudinal crests as in MG 4811. The position of the neural arch at midpoint of the centrum (with a slight anterior displacement) differs from that of Titanosauriformes in which the neural arch is anteriorly displaced (e.g., Salgado et al., 1997; D'Emic, 2012). The vertebra is also distinguished from Diplodocinae middle and posterior caudal vertebrae through the absence of several features such as a transversely concave ventral face, marked ventrolateral crests and a quadrangular cross-section (e.g., Wilson, 2002; Whitlock, 2011). *Lourinhasaurus*, *Turiasaurus*, *Losillasaurus* and *Zby* do not preserve middle caudal vertebra (Casanovas et al., 2001; Royo-Torres et al., 2006; Mateus et al., 2014; Mochó et al., 2014a). This vertebra is considered here as Sauropoda indet.

## 2.2. Atalaia

**Material:** Three dorsal vertebra fragments (MG 8809) including a transverse process and a partial neural arch preserving the prezygapophysis.

**Locality and horizon:** Atalaia (Lourinhã). Sobral Formation, late Kimmeridgian-basal Tithonian in age (Fürsich, 1981; Manuppella et al., 1999; Kullberg et al., 2006).

**Description:** Three previously unpublished fragments of neurapophyses from Atalaia are described (Fig. 4). One of those fragments corresponds to the left prezygapophysis and parapophysis of a middle or a posterior dorsal vertebra. The prezygapophysis is transversely compressed and bears a flat surface supported by a simple and dorsally unbifurcated centroprezygapophyseal lamina (cprl). The prezygapophysis is linked with a rough parapophysis by a prezygoparapophyseal lamina (prpl) interrupted at midlength. The parapophysis is supported by a simple anterior centroparapophyseal lamina (acpl). A poorly preserved transverse process is also preserved. This transverse process culminates in a subrectangular diapophysis, with a rough and concave surface. The diapophysis would face laterally or dorsolaterally. Three laminae depart from the diapophysis: i) the posterior centroparapophyseal lamina (pcpl), posteriorly directed; ii) a subhorizontal and posterior one, the postzygodiapophyseal lamina (podl); and iii) a subhorizontal and anterior one, the prezygodiapophyseal lamina (prdl). The dorsal surface of the transverse process is flat near the diapophysis but a deep fossa is situated medial to this flat area. The distal end of the transverse process is anteriorly deflected in dorsal view.

**Discussion:** These fragments come from the same locality as the *Lusotitan atalaiensis* lectotype, and the preservation is similar. Furthermore, they seem to represent individuals of comparable size. Nevertheless, there is no evidence that these fragments are associated with the *Lusotitan* specimen. The presence of an acpl is common in almost all middle and posterior dorsal vertebrae of sauropods (e.g., Wilson, 2002; Carballido and Sander, 2014), as well as the other set of ob-

served laminae: cprl, pcpl, podl and prdl (e.g., Wilson, 1999; Upchurch et al., 2004). At the moment, these fragments have to be assigned to Sauropoda indet.

## 2.3. Porto das Barcas

**Material:** Middle caudal vertebra (MG 8805).

**Locality and horizon:** Porto das Barcas (Lourinhã). Sobral Formation, late Kimmeridgian-basal Tithonian in age (Fürsich, 1981; Manuppella et al., 1999; Kullberg et al., 2006; field observ., PM).

**Description:** MG 8805 is a transversely deformed middle caudal vertebra (Fig. 3c.I-c.VI). The neural arch is placed at midpoint of the centrum (with a slight anterior displacement). The anterior and the posterior articulations are concave. A longitudinal crest could be recognized in the lateral face above the midheight of the centrum. The posterior ventrolateral crests are also present and associated to the chevron posterior articular facets. The posterior facets for the chevron are semicircular. The anterior ventral border of the centrum is not preserved, therefore it is impossible to verify the presence of anterior facets for the chevron. The ventral face is transversely convex.

**Discussion:** This vertebra was originally assigned to *Apatosaurus alenquerensis* (Lapparent and Zbyszewski, 1957, pg. 38). Antunes and Mateus (2003) and Mateus (2005, p.86; specimen number mistakenly stated as MG 8800) attributed this vertebra to *Lourinhasaurus alenquerensis*. Nevertheless, it is not possible to compare MG 8805 with *Lourinhasaurus alenquerensis* due to the absence of middle caudal vertebrae in the latter specimen (Lapparent and Zbyszewski, 1957; Mochó et al., 2014a). The position of the neural arch near the midpoint of the centrum excluded it from Titanosauriformes, which is characterized by anteriorly displaced neural arches (e.g., Salgado et al., 1997; D'Emic, 2012). No more relevant features are present in order to propose a more precise position within Sauropoda for this specimen, and it should be considered as Sauropoda indet.

## 2.4. Porto Novo

**Material:** Anterior caudal vertebra (MG 4800).

**Locality and horizon:** Porto Novo (Maceira, Torres Vedras). Praia da Amoreira-Porto Novo Formation, late Kimmeridgian-basal Tithonian in age (Manuppella et al., 1999).

**Description:** This vertebra probably corresponds to a subadult individual because the neural arch and the caudal ribs are not fully fused (Fig. 3d.I-d.VI). The facets for the chevron are rudimentary near the anterior articulation and absent near the posterior one. The caudal ribs are dorsoventrally deep. These two features (deep caudal ribs and the presence of rudimentary chevron articulations) suggest that this vertebra corresponds to one of the anteriormost vertebrae of the tail. The vertebra is anteroposteriorly short and subcircular in anterior view, with a slight dorsoventral compression. The

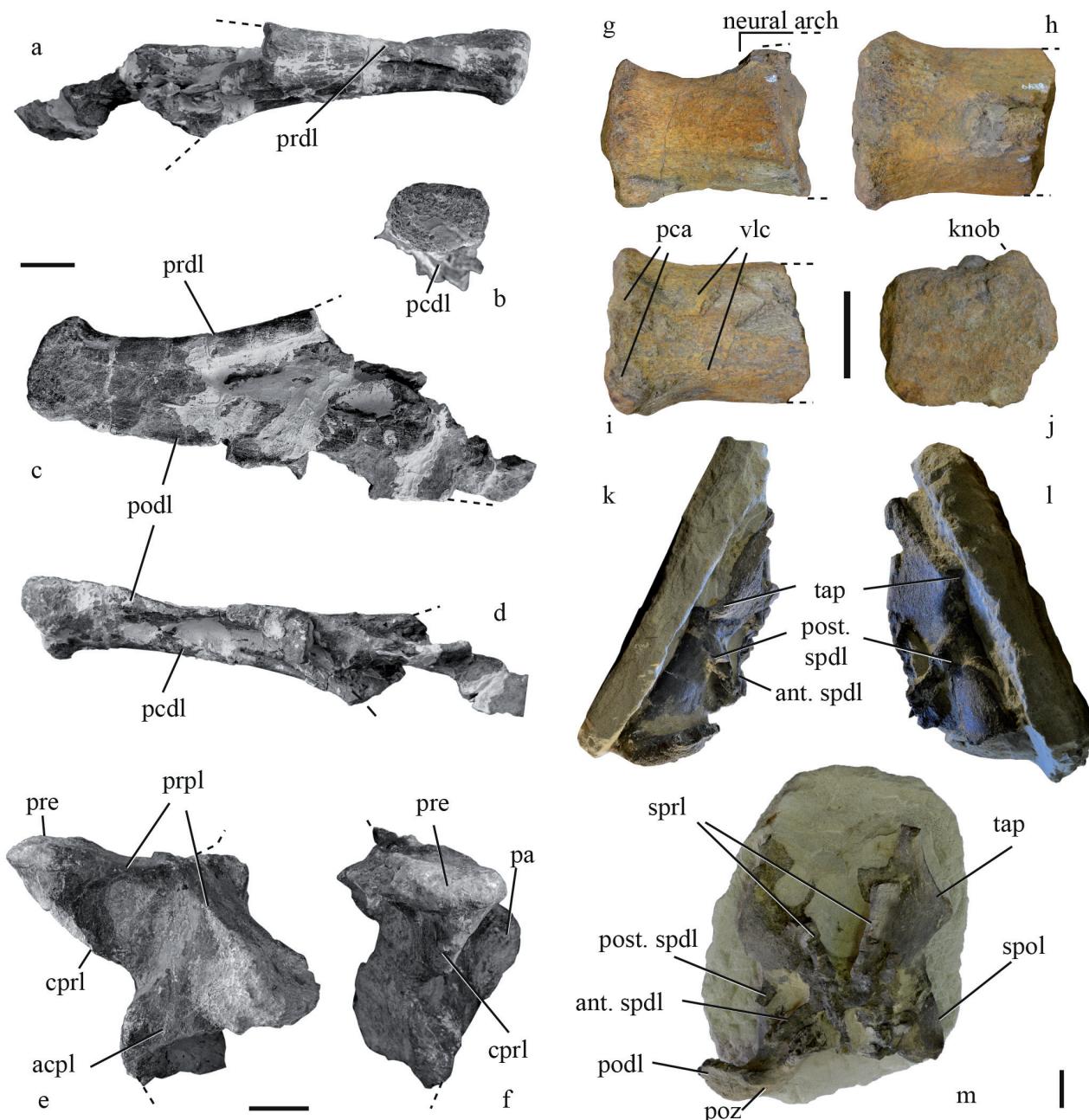


Fig. 4.- Sauropoda indet., middle or posterior dorsal neural arch fragments from Atalaia (MG 8809). Left transverse process in anterior (a), lateral (b), dorsal (c) and posterior (d) views. Partial neural arch in lateral (e) and anterior (f) views. Sauropoda indet., posterior caudal vertebra from Praia de Almoinhas? (MG 8799) in right (g), dorsal (h), ventral (i) and posterior (j) views. Eusauropoda indet., partial posterior cervical or anterior dorsal neural arch from Foz do Arelho (MG 4920) in right (k), left (l) and anterior (m) view. Scale bar: 5cm. The traced line indicates lost bone.

anterior and posterior articular faces are concave, the anterior more concave than the posterior one. The ventral face is transversely flat-to-convex and a slight longitudinal crest is present. The neural arch is anteriorly displaced. The lateral face is dorsoventrally convex and no pneumatic fossae or foramina are present, only a small foramina (as noted Mannion et al., 2013).

**Discussion:** MG 4800 was originally assigned to *Brachiosaurus atalaiensis* (Lapparent and Zbyszewski, 1957, pl. XXVI, 94), to *Lusitanian atalaiensis* by Antunes and Mateus (2003) and to *Lourinhasaurus alenquerensis* by Mateus

(2005). Mannion et al. (2013) assigned MG 4800 to an indeterminate sauropod. The anteriormost preserved centrum of *Lourinhasaurus* occupies a position in the caudal series between third and eighth caudal (Mocho et al., 2014a). The presence of deeper caudal ribs suggests that MG 4800 is probably more anterior than the preserved caudal vertebrae of *Lourinhasaurus*. The Porto Novo vertebra is amphicoelous, differing from the condition observed in anterior caudals of *Lourinhasaurus* that have a flat posterior face with a central smooth concavity (Mocho et al., 2014a). One of the proposed autapomorphies for this taxon is the presence of a

circular spinoprezygapophyseal fossa (sprf) on the anterior caudal vertebra, also described in *Jobaria* (Sereno *et al.*, 1999). Nevertheless, the absence of the neural arch in MG 4800 prevents us from testing the presence of this feature in this specimen. *Lusotitan atalaiensis* is also distinguished from MG 4800 by the presence of a flat posterior articular face (Mannion *et al.*, 2013). The caudal vertebrae of *Aragosaurus ischiaticus* present a flat-to-concave posterior face (Royo-Torres *et al.*, 2014) resembling the condition present in MG 4800. At the moment, we consider that this vertebra does not present any significant feature in order to propose a more accurate systematic approach, and we prefer to attribute it to Sauropoda indet.

## 2.5. Praia de Santa Cruz

**Material:** Middle caudal vertebra (MG 4802).

**Locality and horizon:** Alto da Vela (Torres Vedras), south of Praia de Santa Cruz. Praia da Amoreira-Porto Novo Formation, late Kimmeridgian-basal Tithonian in age (Manupella *et al.*, 1999).

**Description:** Partial middle caudal vertebra lacking the neural arch (Fig. 3e.I-e.VI). The lateral face of this vertebra lacks any crest. The neural arch has a slight anterior displacement. The ventral face is transversely flat-to-convex. The anterior and posterior articulations are concave and dorsoventrally compressed but the outline is slightly eroded. In the ventral face, there are semicircular facets for the chevron articulation near the posterior and anterior articulations. The posterior ones are more developed than the anterior ones. No pneumatic fossae or foramina are present in the lateral and ventral faces of MG 4802.

**Discussion:** Lapparent and Zbyszewski (1957) assigned this vertebra to *Apatosaurus aenquerensis*. Antunes and Mateus (2003) and Mateus (2005, labelled as MG 4804) referred MG 4802 to *Lourinhasaurus aenquerensis*. However, is not possible to compare MG 4802 with *Lourinhasaurus aenquerensis* due to the absence of middle caudal vertebrae in the latter specimen (Lapparent and Zbyszewski, 1957; Mocho *et al.*, 2014a).

This middle caudal vertebra only bears a slight anterior displacement of the neural arch more pronounced than in MG 4811 or MG 8805. A marked anterior displacement of the neural arch in anterior and middle caudals is considered a synapomorphy of Titanosauriformes (Salgado *et al.*, 1997; Upchurch *et al.*, 2004; D'Emic, 2012). Several taxa outside Titanosauriformes can present a slight anterior displacement on the neural arch on middle caudal vertebrae (Osborn and Mook, 1921; Janensch, 1929; McIntosh *et al.*, 1996a, 1996b) different from the marked anterior displacement present in the basal eusauropod *Cetiosaurus* (Upchurch and Martin, 2003) and in titanosauriforms (e.g., Gomani, 2005; Rose, 2007; González Riga, 2009; D'Emic, 2013; Mannion *et al.*, 2013) or *Galveosaurus* (Barco, 2009).

This vertebra is not as dorsoventrally compressed as that of *Lusotitan* (Mannion *et al.*, 2013) and does not bear circular

and smooth excavations on the ventral face as occur in *Lusotitan* (pers. observ., PM). The middle caudal vertebrae of *Lusotitan* also bear two other features that allow distinguishing them from MG 4802: the presence of transverse pits on the articulations and a flat posterior articulation (Lapparent and Zbyszewski, 1957; Mannion *et al.*, 2013).

In conclusion, no remarkable features are present in order to obtain a more accurate taxonomic determination for MG 4802, and for the moment, should be considered as Sauropoda indet.

## 2.6. Praia das Almoinhas?

**Material:** Posterior caudal vertebra (MG 8799).

**Locality and horizon:** The label associated to this bone refers it, with doubt, to the Praia das Almoinhas locality. No references about this locality were found. Mateus (2005) suggested two possible localities for this vertebra: *i*) Casais do Almoinha close to Salir de Matos and where the Tithonian-aged Bombarral Formation crops out (Kullberg *et al.*, 2006; Azeredo *et al.*, 2010), and *ii*) the Vale Almoinha close to Cambelas (Torres Vedras) where the Tithonian-aged Freixial Fm. crops out (Pereda-Suberbiola *et al.*, 2005; Kullberg *et al.*, 2006).

**Description:** MG 8799 is the posterior part of a posterior caudal vertebra that preserves part of the neural arch (Fig. 4g-j). The posterior articular face is generally flat, bearing a central concavity. The dorsal margin of the posterior face has two semicircular projections. The lateral face bears a longitudinal crest at midheight. Near the posterior articulation, the ventral face bears two semi-circular-to-circular articulations for the chevron. From these facets project two smooth ridges that delimit a transverse concave region that disappears anteriorly by the smoothing of these ventral crests. Anterior to these crests, the ventral face becomes flat. The centrum has a diamond-shaped cross-section.

**Discussion:** This specimen was originally assigned to *Brachiosaurus atalaiensis* (Lapparent and Zbyszewski, 1957), and later to *Lusotitan atalaiensis* (Mateus, 2005). Mannion *et al.* (2013) considered it an indeterminate sauropod. It is not possible to determine the relative position of the neural arch and two scenarios, with different implications, can be posed. If the neural arch has a central position, the centrum should be appreciably longer, with at least four times the dorsoventral width of the posterior articulation, feature common in diplodocids (see Wilson, 2002; Upchurch *et al.*, 2004; Whitlock, 2011). If not, the neural arch should present an anterior position, a synapomorphy of Titanosauriformes (e.g., Upchurch *et al.*, 2004) and convergent with *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003). Nevertheless, the posterior vertebrae of *Cetiosaurus* have a concave posterior face. A slight transverse concavity is observed in the ventral surface of MG 8799, bordered by smooth ventrolateral ridges. Similar ridges are also observed in a posterior caudal vertebra referred to *Europasaurus* (DFMMh/FV 995, pers. observ., PM). Transverse concave ventral faces in mid-

dle caudal vertebrae are also present in diplodocids (Osborn, 1899; McIntosh, 2005; Remes, 2006) and in some titanosaurs such saltasaurids (Wilson, 2002; Upchurch *et al.*, 2004), nevertheless, this concavity is much more developed than in MG 8799, as occurs in MG 4819, 4821, 4826, also described in this study. At the moment, this vertebra is considered as Sauropoda indet.

Eusauropoda Upchurch, 1995  
Eusauropoda indet.

## 2.7. Salir de Matos

*Material:* Anterior caudal vertebra (MG 4804).

*Locality and horizon:* Salir de Matos (Caldas da Rainha). Bombarral Formation, Tithonian in age (Manuppella *et al.*, 1999; Azerêdo *et al.*, 2010).

*Description:* This vertebra is probably one of the last anterior caudal vertebrae based on the reduced caudal ribs (Fig. 3b.I-b.VI). Anterior and posterior articulations are concave and bear a subcircular outline, with a slight dorsoventral compression. The neural arch is located in the anterior part of the centrum. In the ventral face, there are semicircular chevron articulations near the anterior and posterior articulations of the centrum, being the posterior ones more developed. From the chevron articulations start smooth longitudinal crests that never reach the midpoint of the centrum. These crests are different from the marked lateroventral crests present in diplodocids (e.g., Osborn, 1899; McIntosh, 2005; Remes, 2006). Between these lateroventral crests, there is a sagittal smooth crest at the midpoint of centrum. Not taking into account this sagittal crest, the ventral face is convex at midpoint. The lateral face lacks pneumatic fossae or foramina and bears a longitudinal crest close to the transition between the ventral and the lateral face.

*Discussion:* This vertebra was originally assigned to *Apatosaurus alenquerensis* by Lapparent and Zbyszewski (1957). This referral was followed by Antunes and Mateus (2003) and it was subsequently assigned to cf. *Lourinhasaurus alenquerensis* by Mateus (2005). Nevertheless, this taxonomic attribution could not be supported because it is not possible to compare it with *Lourinhasaurus* due to the absence of posteriormost anterior caudal vertebrae attributed to this taxon (Mocho *et al.*, 2014a).

Salgado *et al.* (1997) and D'Emic (2012) considered the anterior position of the neural arch in the anterior and middle caudal vertebrae as a diagnostic feature of Titanosauriformes. Nevertheless, anteriorly displaced neural arches in the anterior caudals have a wider distribution within Sauropoda (Hatcher, 1901; Osborn and Mook, 1921; Ostrom and McIntosh, 1966; McIntosh *et al.*, 1996a; 1996b; Casanovas *et al.*, 2001; Ouyang and Ye, 2002; Upchurch and Martin, 2003; Allain and Aquesbi, 2008; Remes *et al.*, 2009; Royo-Torres and Upchurch, 2012). This condition is so far synapomorphic of Titanosauriformes only when restricted to the last ante-

rior and middle caudal vertebrae (see Mocho *et al.*, 2014a). As stated previously, the basal eusauropod *Cetiosaurus* has an anteriorly displaced neural arch in its anterior and middle caudal vertebrae (Upchurch and Martin, 2003). Consequently, MG 4804 should be considered to represent an indeterminate eusauropod. The presence of a smooth sagittal ventral crest is shared with the tail collected in São Bernardino (MG 4978) that will be described below in detail. The absence of pneumatic foramina, ventrolateral crests and a transversely concave ventral face differentiates this vertebra from those of the Diplodocidae (see Osborn, 1899; Hatcher, 1901; Lull, 1919; McIntosh, 2005; Remes, 2006).

## 2.8. Foz do Arelho

*Material:* Presacral neural spine, tentatively interpreted as an anterior dorsal vertebra (MG 4920).

*Locality and horizon:* Monte da Cruz do Facho, Foz do Arelho (Caldas da Rainha). Bombarral Formation, Tithonian in age (Manuppella *et al.*, 1999; Kullberg *et al.*, 2006; Azevêdo *et al.*, 2010).

*Description:* A partial presacral neural spine was collected from Foz do Arelho (MG 4920, Fig. 4k-m). This neural spine might represent a bifurcated neural spine or the posterior sector of dorsal neural spine. This neural spine preserves part of the postzygapophyses, and lacks the prezygapophyses and the anterior face of the neural spine. The posterior face of this neural spine is not prepared and it is covered by sediment. From the postzygapophysis parts two laminae. One of them is the spdl and the other one is interpreted as a single lateral spinopostzygapophyseal lamina (lat. spol, but it is not possible to confirm the presence of a medial spol), which diverge ventrally. The lat. spol reaches a dorsolaterally expansion of the spines, interpreted herein as the triangular aliform process. Two laminae are tentatively recognized as spinodiapophyseal laminae: a short posterior spinodiapophyseal laminae (post. spdl), which connects with the lat. spol just below the triangular aliform process; and an incomplete anterior spinodiapophyseal laminae (ant. spdl) longer than the post. spdl. Part of the spinoprezygapophyseal laminae is also preserved. The broken base of the neural arch reveals some internal camerae.

*Discussion:* The presence of ant. spdl and post. spdl is a common feature within sauropods (Wilson, 2012) and suggests that this neural spine is probably from an anterior dorsal vertebra (following Wilson, 1999). An incipient triangular aliform process is interpreted in MG 4920. This feature was considered a synapomorphy of *Jobaria* + Neosauropoda by Wilson (2002) and *Mamenchisaurus* + Neosauropoda (Carballido *et al.*, 2011). Some authors considered the presence of this feature in other basal eusauropods such as *Shunosaurus* and *Patagosaurus* (Carballido and Sander, 2014). The presence of a triangular process is apparently restricted to Eusauropoda, suggesting the placement of MG 4920 within this clade.

## 2.9. Porto das Barcas

**Material:** Middle caudal vertebra (MG 8800).

**Locality and horizon:** Porto das Barcas (Lourinhã). Sobral Formation, late Kimmeridgian-basal Tithonian in age (Fürsich, 1981; Manuppella et al., 1999; Kullberg et al., 2006; field observations, PM).

**Description:** MG 8800 is a partial middle caudal vertebra lacking its neural arch (Fig. 3f.I-f.VI). The anterior and posterior articular faces are concave and dorsoventrally compressed. The neural arch has a slight anterior displacement. The lateral face bears a longitudinal crest slightly ventrally displaced (this crest is very close to the transition between the lateral and the ventral faces). The ventral surface of the centrum is transversely flat-to-convex. The posterior articular facets for the chevron are semicircular, well developed and concave. In lateral view, they are ventrally projected. The anterior facets for the chevron are not present, probably due to the present erosion of the anterior articulation of the centrum.

**Discussion:** This vertebra was originally assigned to *Apatosaurus aenquerensis* (Lapparent and Zbyszewski, 1957, pg. 38, pl. XVIII, fig. 49). Antunes and Mateus (2003) and Mateus (2005) attributed it to *Lourinhasaurus aenquerensis*. However, the absence of middle caudal vertebrae in *Lourinhasaurus* lectotype precludes us from testing this attribution. MG 8800 is dorsoventrally compressed as in *Lusotitan atalaiensis* (Lapparent and Zbyszewski, 1957; Mannion et al., 2013) and *Galveosaurus* (Barco, 2009). Dorsoventrally compressed caudal centra are common in basal titanosauriforms (Janensch, 1950; Tidwell et al., 1999; 2001; Upchurch et al., 2004; Canudo et al., 2008; Royo-Torres, 2009), and also occur in some basal eusauropods (Upchurch and Martin, 2003). This vertebra also presents a slight anterior position for the neural arch, but it is not so marked as in titanosauriforms (e.g., Salgado et al., 1997; Wilson, 2002; Upchurch et al., 2004; D'Emic, 2012), or in the basal eusauropod *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003). This vertebra does not share a transversely concave ventral surface or lateral pneumaticity with Diplodocinae (Wilson, 2002; Whitlock, 2011). Dorsoventrally compressed anterior and middle caudal centra are absent in basal sauropods (e.g., Cooper, 1984; Yadagiri, 2001; Rauhut, 2003; Allain and Aquesbi, 2008; Bandyopadhyay et al., 2010; McPhee et al., 2014). The presence of dorsoventrally compressed centrum is a feature just present in basal titanosauriforms and some non-neosauropod eusauropods (e.g., Upchurch and Martin, 2003; Upchurch et al., 2004), suggesting that MG8800 might correspond to a member of Eusauropoda.

## 2.10. São Bernardino

**Material:** Partial tail composed by 15 anterior to middle caudal vertebrae (MG 4978).

**Locality and horizon:** São Bernardino (Peniche). Praia da Amoreira-Porto Novo Formation, late Kimmeridgian-basal Tithonian in age (Manuppella et al., 1999).

**Description:** This partial tail is composed by 15 centra from the anterior-to-middle sector (Fig. 5, 6). Here we describe the existing caudal vertebrae as CdA-to-CdO. Almost all of the centra lack the neural arch with the exception of CdG and CdO that preserve part of neural arch pedicels. The preserved centra present some oblique deformation. Regardless of the deformation, it is interpreted that the anterior centra have an original slight dorsoventral compression. In anterior/posterior view, they have a hexagonal outline. The anterior centra are amphicoelous. The posterior face becomes progressively flat toward the anterior part of the series. The ventral face is transversely narrow, becoming wider in more posterior centra. These vertebrae present a longitudinal and sagittal smooth crest that is present up to CdE (on the anterior half of the ventral face) and reappear in CdK-to-CdM.

The anterior caudal vertebrae bear dorsoventrally and transversely short caudal ribs that are posterolaterally oriented. In anterior view, the caudal ribs are laterally directed with a slight dorsal projection that can be related with deformation. Short and rudimentary caudal ribs suggest that these vertebrae are the posteriormost anterior caudal vertebrae. The caudal ribs are present up to CdF, considered here as the last anterior centra. Sauropods generally have 10 (in titanosaurs) to 20 (in most basal sauropods) caudal vertebrae with caudal ribs (e.g., Wilson and Sereno, 1998; Wilson, 2002). Non-titanosaurian eusauropods generally have 15 caudal vertebrae with caudal ribs. Assuming the presence of at least 15 caudal vertebrae with caudal ribs in the São Bernardino sauropod, the anteriormost nine caudal vertebrae are not preserved.

In CdB, just below the caudal rib, there is a longitudinal crest on the lateral face. This longitudinal crest moves to a more ventral position along the caudal series. In CdC, CdD and CdE, in the point where the crest touch the posterior and anterior articulation appears a lateral projection, which slightly extends to the lateral face. In middle caudal vertebrae, these crests become less pronounced. In CdF, there is another longitudinal crest on the lateral surface of the centrum near the caudal rib (the last caudal rib of the series). This crest keeps this position up to the last preserved caudal centrum. The articular facets for the chevron are semicircular, being the posterior ones more pronounced than the anterior ones. Between CdD and CdJ, the articular facets for the chevron bear a marked anteroventral projection. Short and smooth longitudinal crests appear from these articulations. The anterior preserved caudal vertebrae lack the neural arch, but they are clearly placed in the anterior half of the centrum, a common situation in the anteriormost caudal vertebrae of sauropods (Mocho et al., 2014a).

The centrum of the middle caudal vertebra (from CdG) is almost subcircular in anterior/posterior view, and in some cases, the dorsoventral width could be higher than the transverse width (e.g., CdG or CdH). The last preserved centra have a slight dorsoventral compression. The centra are amphicoelous. The ventral face is generally flat-to-convex and presents a smooth sagittal crest up to CdM, as occurs in the

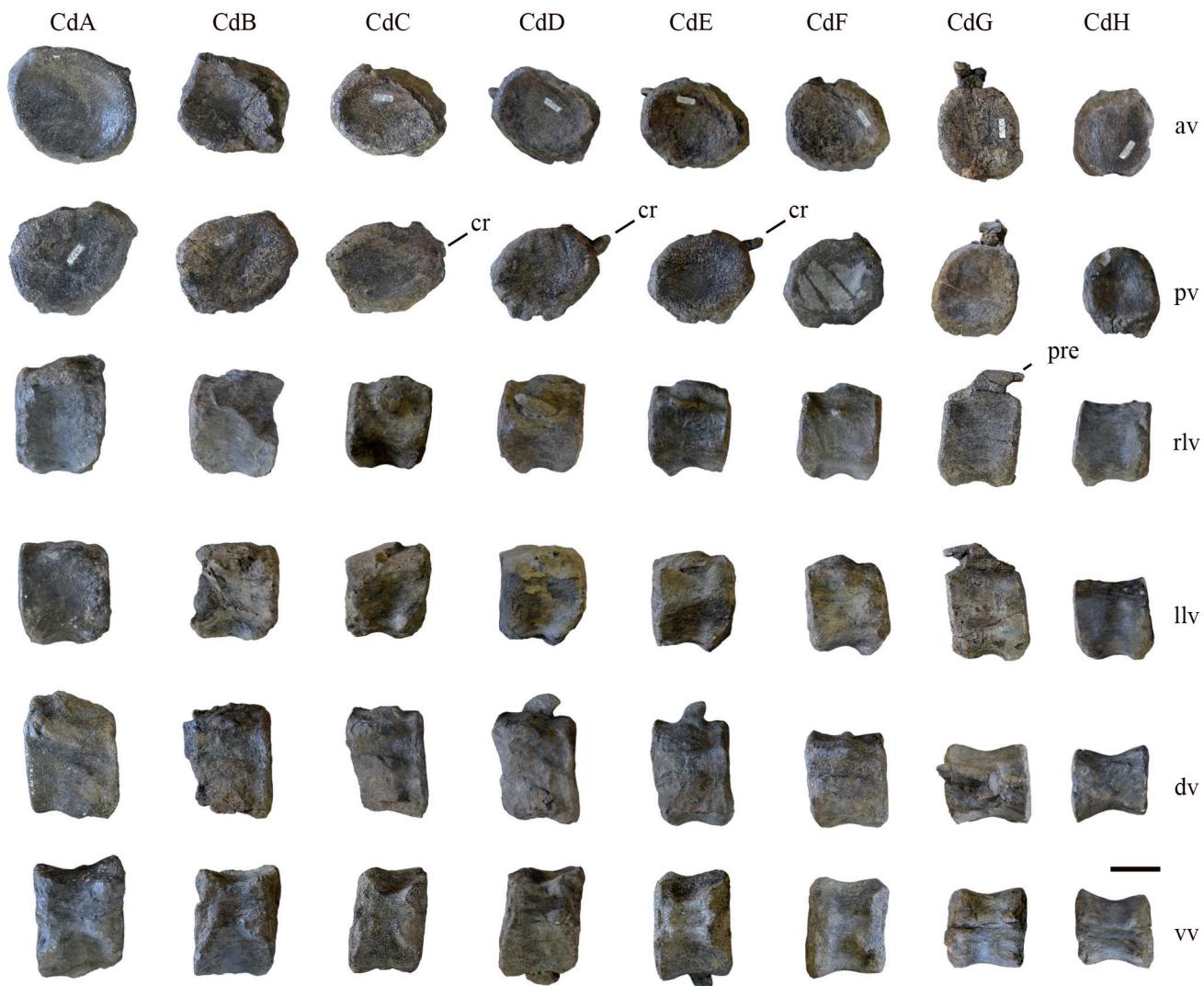


Fig. 5.- *Eusauropoda* indet., partia caudal series from São Bernardino. Caudal vertebrae from CdA to CdH in anterior (av), posterior (pv), right (rv), left (lv), dorsal (dv) and ventral (vv) views. Scale bar: 10cm.

anterior caudal vertebrae. From CdI up to the last preserved centrum, the posterior face becomes less concave, suggesting that the posterior face might acquire a flat articulation in the posterior caudal vertebrae as in *Lusotitan atalaiensis* (Mannion et al., 2013). The neural arch is slightly displaced to the anterior half of the centrum, but does not touch the anterior articulation.

**Discussion:** Several partial tails have been described in the Upper Jurassic of Portugal (Lapparent and Zbyszewski, 1957; Mateus, 2005; Yagüe et al., 2006; Mannion et al., 2013; Macho et al., 2014a; 2016), and the tail recovered in São Bernardino, which belong to an individual with an appreciable size, is probably one of the most complete ones. However, none of the vertebrae include a well-preserved neural arch. The São Bernardino tail was briefly described and assigned to *Apatosaurus ahenquerensis* by Lapparent and Zbyszewski (1957). More recently, Antunes and Mateus (2003) supported this taxonomic attribution, referring this tail to *Lourinhasaurus ahenquerensis*. Mateus (2005, p.75) proposed a more care-

ful attribution as cf. *Lourinhasaurus ahenquerensis*. This tail does not preserve centra that can be compared directly with *Lourinhasaurus ahenquerensis*, since the preserved centra of *Lourinhasaurus* are anterior than the preserved centra of MG 4978, so, this taxonomic attribution could not be supported. The anterior and middle preserved centra of São Bernardino sauropod are generally dorsoventrally compressed (excluding CdG and CdH) as occur in several basal titanosauriforms (Janensch, 1950; Tidwell et al., 1999; 2001; Upchurch et al., 2004; Canudo et al., 2008; Royo-Torres, 2009) or some non-neosauropod eusauropod forms (Upchurch and Martin, 2003).

The possession of middle caudal vertebrae (which we regard as the last anterior caudal vertebrae) with posteriorly projecting caudal ribs, usually reaching the posterior margin of the centrum, is considered synapomorphic for Titanosauriformes (D'Emic, 2012). The posterior orientation of the caudal ribs is a common feature within Titanosauriformes (Mannion et al., 2013) and in some cases, they reach and

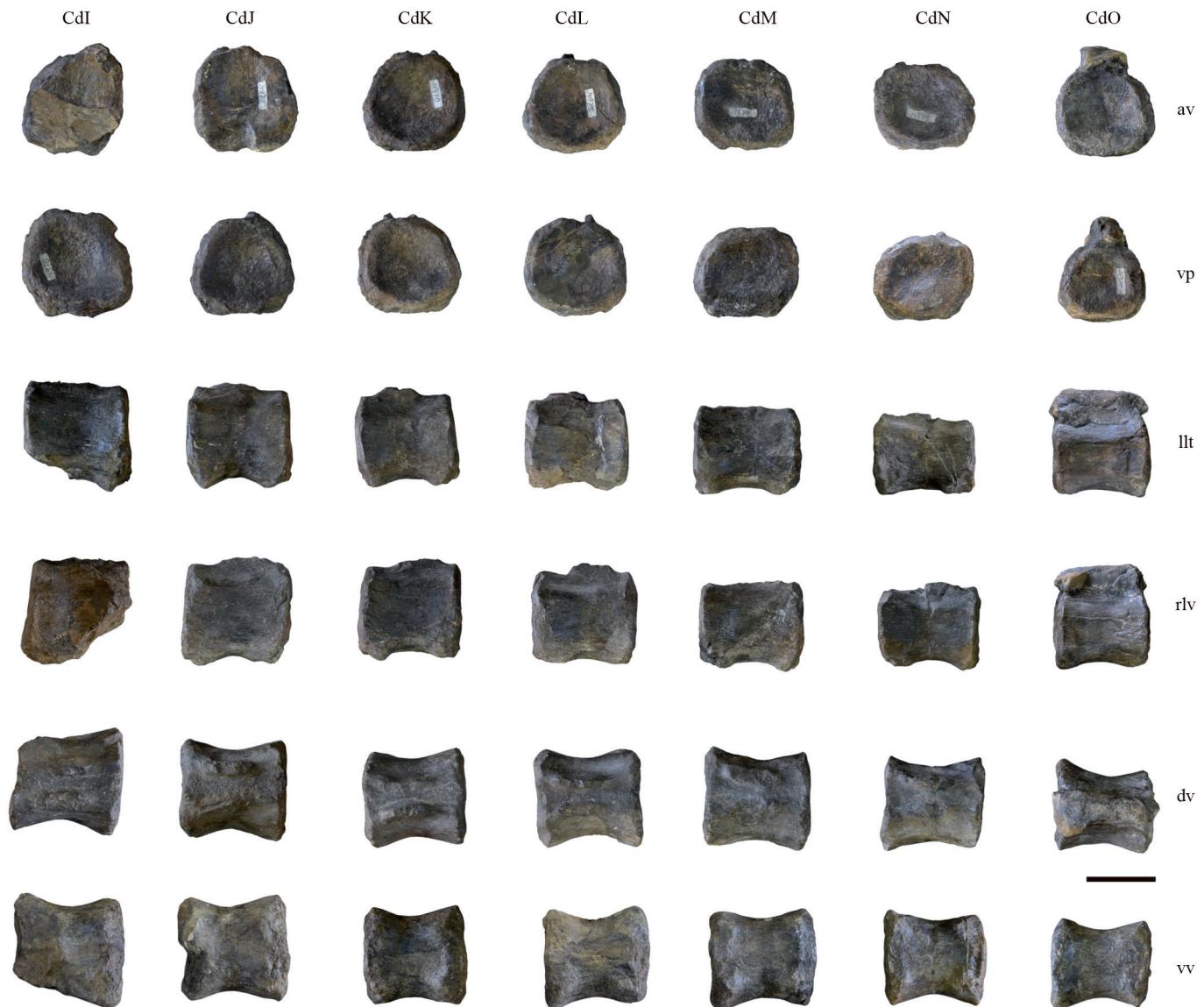


Fig. 6.- Eusauropoda indet., partia caudal series from São Bernardino. Caudal vertebrae from CdI to CdO in anterior (av), posterior (pv), right (rv), left (lv), dorsal (dv) and ventral (vv) views. Scale bar: 10cm.

surpass the posterior articulation, as in *Lusotitan* (Mannion *et al.*, 2013), *Sonorasaurus* (Ratkevich, 1998) and *Tastavinsaurus* (Royo-Torres *et al.*, 2009). Some taxa outside Titanosauriformes also possess posteriorly projecting caudal ribs in the last anterior caudal vertebrae, such as *Spinophorosaurus* (pers. observ., PM), *Omeisaurus* (Mannion *et al.*, 2013) and *Jobaria* (D'Emic, 2012), although this projection is not as well-developed as in titanosauriforms. In the case of MG 4978, the caudal ribs are short and far from the posterior articulation, which distinguish them from the apomorphic condition for titanosauriforms defined by D'Emic (2012). In sauropods, posteriorly oriented caudal ribs are not present outside Eusauropoda (e.g., Cooper, 1984; Allain and Aquesbi, 2008).

In this sauropod, the neural arches are slightly displaced anteriorly, but not to the same degree as in *Lusotitan atalai-*

*ensis* and other titanosauriforms (e.g., Tidwell *et al.*, 2001; Mannion *et al.*, 2013). In conclusion, the dorsoventrally compressed caudal centra, posteriorly oriented caudal ribs and slight anterior displacement of the neural arch are common features within Eusauropoda and not recorded in basal sauropods (e.g., Cooper, 1984; Allain and Aquesbi, 2008; Bandyopadhyay *et al.*, 2010), suggesting the attribution of the São Bernardino sauropod to Eusauropoda. One particular feature is the presence of a smooth sagittal crest on the ventral face that is just shared by MG 4804 from Salir de Matos (Caldas da Rainha). The validity of this character as a diagnostic feature, that in some cases seems to be affected by the presence of fractures, should be confirmed with new material as well as the relationship between São Bernardino and Salir dos Matos sauropods. The lateral projections of the posterior articulation on the transition between the anterior

and the middle caudals are also uncommon and might be a unique feature of this taxon.

### 2.11. Atouguia da Baleia?

*Material:* Proximal end of a right fibula (MG 30486).

*Locality and horizon:* MG 30486 is referred with doubt to Atouguia da Baleia (Peniche). Praia da Amoreira-Porto Novo Formation, late Kimmeridgian-basal Tithonian in age (Manuppella et al., 1999).

*Description:* A proximal end of a right fibula is preserved (Fig. 7a-e). This fibula bears a well-marked triangular tibial scar. On the ventral border of this scar, next to the posterior border of the fibula, there is a pronounced bulge. This scar faces medially and bears a slight proximal deflection. The anterior trochanter is broken, but it is interpreted that it had a crest-like morphology. Two crests and an anteroposterior wide concavity compose the lateral trochanter. Within this concavity, there is a posteriorly displaced rough tuberosity. The medial face of the fibular shaft is flat.

*Discussion:* Despite the incompleteness of this fibula, some features can be discussed. The anterior trochanter is not complete but had a crest-like morphology. This morphology is present in derived titanosauriforms such as *Tastavinsaurus*. D'Emic (2012) suggested that the presence of a crest-like anterior trochanter is a synapomorphy of *Sauroposeidon* + (*Tastavinsaurus* + (Euhelopodidae + (*Chubutisaurus* + Titanosauria))). Nevertheless, in MG 30486 this anterior crest is rudimentary as occur in some basal titanosauriforms such as *Lusotitan* (Lapparent and Zbyszewski, 1957; pers. observ., PM) or *Giraffatitan* (Janensch, 1961) and in the non-neosauropod eusauropod *Turiasaurus* (Royo-Torres et al., 2006).

Another important feature is the morphology of the lateral trochanter. The lateral trochanter shows a wide morphological variability within sauropods (see Royo-Torres, 2009) being difficult to codify in morphological data matrices. MG 30486 has a wide concave lateral trochanter bordered laterally and medially by short proximodistal crests. This morphology is also present in *Turiasaurus riodevensis* (Royo-Torres et al., 2006), a putative turiasaur found in San Lorenzo (Teruel, Cobos et al., 2011) and *Cetiosaurus oxoniensis* (pers. observ., PM). The presence of a lateral trochanter composed by a fossa and bordered by two proximodistal crests is also present in *Suuwassea* (Harris, 2007) and *Rapetosaurus* (Curry Rogers, 2009). Several authors noted the presence of lateral trochanters composed of two proximodistal crests (e.g., see scoring of Mannion et al., 2013) or the presence of an oval/circular tuberosity associated to a crest, as occurs in *Tastavinsaurus* (Royo-Torres, 2009).

The presence of a rudimentary crest-like anterior trochanter and a lateral trochanter composed by a wide fossa bordered by two proximodistal crests might be exclusive for Turiasauria and *Cetiosaurus*, which might relate this specimen to the Eusauropoda clade. *Suuwassea* also presents a wide fossa,

but lacks the presence of a rudimentary crest-like anterior trochanter.

cf. *Duriatitan* Barrett et al., 2010

cf. *Duriatitan humerocristatus* (Hulke, 1874)

### 2.12. Praia dos Frades

*Material:* Right humerus (MG 4976), incorrectly identified as a left humerus in the MG exhibition.

*Locality and horizon:* Praia dos Frades (Peniche). Praia da Amoreira-Porto Novo Formation, late Kimmeridgian- basal Tithonian in age (Manuppella et al., 1999).

*Description:* MG 4976 is a right humerus lacking the proximal and distal ends (Fig. 7f-j). The distal part of this specimen is reconstructed. The deltopectoral crest is rough and laterally directed, with a slight medial deflection. The anterior face of the proximal end lacks the fossa observed in *Lusotitan* or *Lourinhasaurus* (Mannion et al., 2013; Mocho et al., 2014a), but this could be due to the incompleteness of the proximal end. On the posterior face of the proximal end, there is a pronounced proximodistal crest posterior to the deltopectoral crest, conferring a triradiate outline to the cross-section of the proximal end. The diaphysis is elliptical in cross-section. The distal end is expanded and the anterior face of the most distal preserved part is convex. The humerus exhibits a significant torsion of the extremities. The posterior face of the distal end bears a slight concavity bordered by two proximal smooth crests that probably would connect with the missing radial and ulnar condyles.

*Discussion:* MG 4976 is an incomplete humerus with some particular morphological aspects. Lapparent and Zbyszewski (1957) alluded to a right humerus from Praia de Frades, which probably corresponds to MG 4976. This humerus was initially assigned to *Apatosaurus alenquerensis* (Lapparent and Zbyszewski, 1957) due to the presence of some shared features such as the narrowness of the shaft and the position of the deltopectoral crest. Antunes and Mateus (2003) attributed this humerus to *Lourinhasaurus alenquerensis* and Mateus (2005) considered it as ?*Lourinhasaurus alenquerensis*. MG 4976 bears some important differences when compared with the humeri of *Lourinhasaurus* and other Iberian Late Jurassic taxa such as *Lusotitan*, *Aragosaurus*, *Zby*, *Turiasaurus*, *Losillasaurus* and *Galveosaurus* (Sanz et al., 1987; Casanovas et al., 2011; Royo-Torres et al., 2006; 2014; Barco, 2009; Mannion et al., 2013; Mateus et al., 2014; Mocho et al., 2014a).

The deltopectoral crest in this humerus is proximodistally short as occurs in Turiasauria (Royo-Torres et al., 2006; Mateus et al., 2014) and Brachiosauridae (Janensch, 1961; Tidwell et al., 1999; Mannion et al., 2013), but not in *Lourinhasaurus* (Mocho et al., 2014a). On the other hand, the distal end of the humerus presents an appreciable torsion respect to the proximal end, as occurs in other sauropods (e.g., Salgado



Fig. 7.- *Eusauropoda* indet., proximal end of a right fibula (MG 30486) from ?Atouguia da Baleia (Peniche) in lateral (a), medial (b), anterior (c), posterior (d) and proximal (e) views. Cf. *Duriatitan humerocristatus*, partial right humerus (MG 4976) from Praia dos Frades (Peniche) in anterior (f), posterior (g), lateral (h), medial (i) and proximal (j) views (the proximal end of MG 4976 is not complete). *Sauropoda* indet., distal end of humerus (MG 30484) from ?Alenquer in posterior (k) view. Scale bar: 10cm. The traced line indicates lost bone.

and Bonaparte, 1991; Harris, 2007); this feature is absent in *Lourinhasaurus*, *Galveosaurus*, *Zby*, *Turiasaurus*, *Losilasaurus* and *Aragosaurus* (Casanovas et al., 2001; Royo-Torres et al., 2006; 2014; Barco, 2009; Mateus et al., 2014; Mocho et al., 2014a). Proximodistally short deltopectoral crests seems to be restricted to some eusauropod groups (Turiasauria and Brachiosauridae), suggesting the relationships of MG 4976 with the Eusauropoda clade.

Another feature that seems to be exclusive to this humerus in the context of the Iberian Late Jurassic sauropods is the

presence of a proximodistal crest on the posterior face of the proximal end, posterior to the deltopectoral crest. This feature is also described as an autapomorphy of *Duriatitan humerocristatus* found in the British Upper Jurassic sediments of the Clay Formation, early Kimmeridgian in age (NHMUK 44635, Barrett et al., 2010). Based on its slenderness, some authors considered that the *Duriatitan* humerus might represent a brachiosaurid (e.g., McIntosh, 1990a; 1990b; Upchurch and Martin, 2003; Upchurch et al., 2004). Barrett et al. (2010) and Mannion et al. (2013) were more cautious

in considering it as a basal titanosauriform. Mannion *et al.* (2013) also noted the presence of slender humeri in the non-neosauropod *Lapparentosaurus* from the Middle Jurassic of Madagascar. Although poorly preserved, these authors considered that the deltopectoral crest might present a slight medial orientation that could relate this humerus to Titanosauriformes. Nevertheless, a slight medial displacement is also observed outside Titanosauriformes such as in *Cetiosaurus* (Upchurch and Martin, 2003). When compared with *Duriatitan*, MG 4976 also presents a similar deltopectoral crest orientation: anteriorly projected, but occupying a slight medial position relatively to the lateral margin of the humerus. If we accept the presence of an acute crest on the posterior face of the proximal end as an exclusive feature of the monospecific genus *Duriatitan humerocristatus*, MG 4976 should be related to this British Late Jurassic taxon. However, at the moment, and taking into account the incompleteness of MG 4976 and *Duriatitan* type specimen, we consider the humerus from Praia de Frades as cf. *Duriatitan humerocristatus*.

Neosauropoda Bonaparte, 1986  
Neosauropoda indet.

### 2.13. Castanheira

*Material:* Middle or posterior dorsal vertebra (MG 4799).  
*Locality and horizon:* Castanheira (Vila Franca de Xira). Abadia Formation, early-middle (?) Kimmeridgian in age (Leinfelder and Wilson, 1989; Kullberg *et al.*, 2006).

*Description:* Partial centrum of a middle or posterior dorsal vertebra, only the right side is preserved (Fig. 8a-f). The centrum is opisthocoelous. The ventral surface of the pneumatic foramen is preserved, and it slopes ventromedially, suggesting that the pneumatic foramen is deep.

*Discussion:* MG 4799 was initially referred to as a metatarsal V of *Apatosaurus athenaeensis* (Lapparent and Zbyszewski, 1957). Mannion *et al.* (2013) considered it to be a procoelous caudal vertebra. Nevertheless, this specimen is herein interpreted as a partial dorsal vertebra. Deep pneumatic foramina on dorsal vertebrae are common in neosauropods such as diplodocoids (excluding Dicraeosauridae, *sensu* Salgado *et al.*, 1997) and basal macronarians (Wedel, 2003; Upchurch *et al.*, 2004), and this feature was considered as a synapomorphy of *Omeisaurus* + Neosauropoda by Wilson and Sereno (1998). Ventrally deep pneumatic foramina could be distinguished from the medially deep pneumatic foramina (or fossae) of non-neosauropod eusauropods such as turiasaurs (e.g., *Turiasaurus* and *Losillasaurus*), *Jobaria* (Sereno *et al.*, 1999), *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003), *Cetiosauriscus* (pers. observ., PM), *Patagosaurus* (Bonaparte, 1986) and *Spinophorosaurus* (Remes *et al.*, 2009). Presuming the absence of mamenchisaurids outside East Asia during the Late Jurassic (Carballido and Sander, 2014), it is acceptable to consider that this dorsal vertebra represents an indeterminate neosauropod.

Diplodocoidea Marsh, 1884  
Flagellicaudata Harris and Dodson, 2004  
Diplodocidae Marsh, 1884 (*sensu* Upchurch, 1995)  
Diplodocinae Janensch, 1929  
Diplodocinae indet.

### 2.14. São Gregório da Fanadia

*Material:* Three incomplete middle-to-posterior caudal vertebrae (MG 4819, 4821, 4826).

*Locality and horizon:* Porto de Barros, 150m NW of São Gregório da Fanadia (Caldas da Rainha). Bombarral Formation, Tithonian in age (Manuppella *et al.*, 1999; 2000; Kullberg *et al.*, 2006; Azeredo *et al.*, 2010).

*Description:* In the collections of the Museu Geológico there are three incomplete caudal vertebrae (Fig. 8g-u). On the basis of their similar general morphology, they will be described together. There are two posterior articular faces (MG 4819 and MG 4826, Fig. 8g-k and Fig. 8q-u, respectively) and one anterior one (MG 4821, Fig. 8l-p). Lapparent and Zbyszewski (1957) referred the presence of one caudal vertebra broken into two pieces that probably are MG 4819 and MG 4821. If these two fragments are a unique vertebra, the ratio of centrum length to centrum height is higher than 2.0. The preserved anterior articular face is flat as well as one of the posterior ones. The articular face of MG 4826 is slightly concave and probably represents the posteriormost centrum of this set. The articular faces are wider next to the ventral border. They have a quadrangular cross-section with marked ventrolateral crests. These ventrolateral crests delimit a transversely concave ventral face. The lateral face bears a smooth pneumatic fossa. Despite the poor preservation, the anterior and posterior articular facets for the chevron are preserved. In lateral view, they present an appreciable ventral development. In MG 4821, the neural arch almost reaches the anterior articulation. On the other hand, in MG 4819 and MG 4826, the neural arch is not as close to the posterior articulation. In MG 4826, the neural arch is not fused to the centrum, suggesting that it does not belong to a mature individual.

*Discussion:* One vertebra in two pieces was identified by Lapparent and Zbyszewski (1957), but in the collections there are three fragments of at least two caudal vertebrae (the union between MG 4819 and MG 4821 is not confirmed). MG 4826 is figured by Lapparent and Zbyszewski (1957, pl. XXV, fig. 86). These vertebrae were considered as caudal vertebrae of *Megalosaurus pombali* (Lapparent and Zbyszewski, 1957), a taxon considered as a *nomen dubium* by Antunes and Mateus (2003). Mateus (2005) assigned them to an indeterminate theropod.

Attached to the label of MG 4821 was found the following note: “*Barosaurus* at *Diplodocus*” from McIntosh dated of 15/10/1973. Despite the incompleteness of these three middle/posterior caudal centra, they have an important combination of features. The presence of a well-developed concave

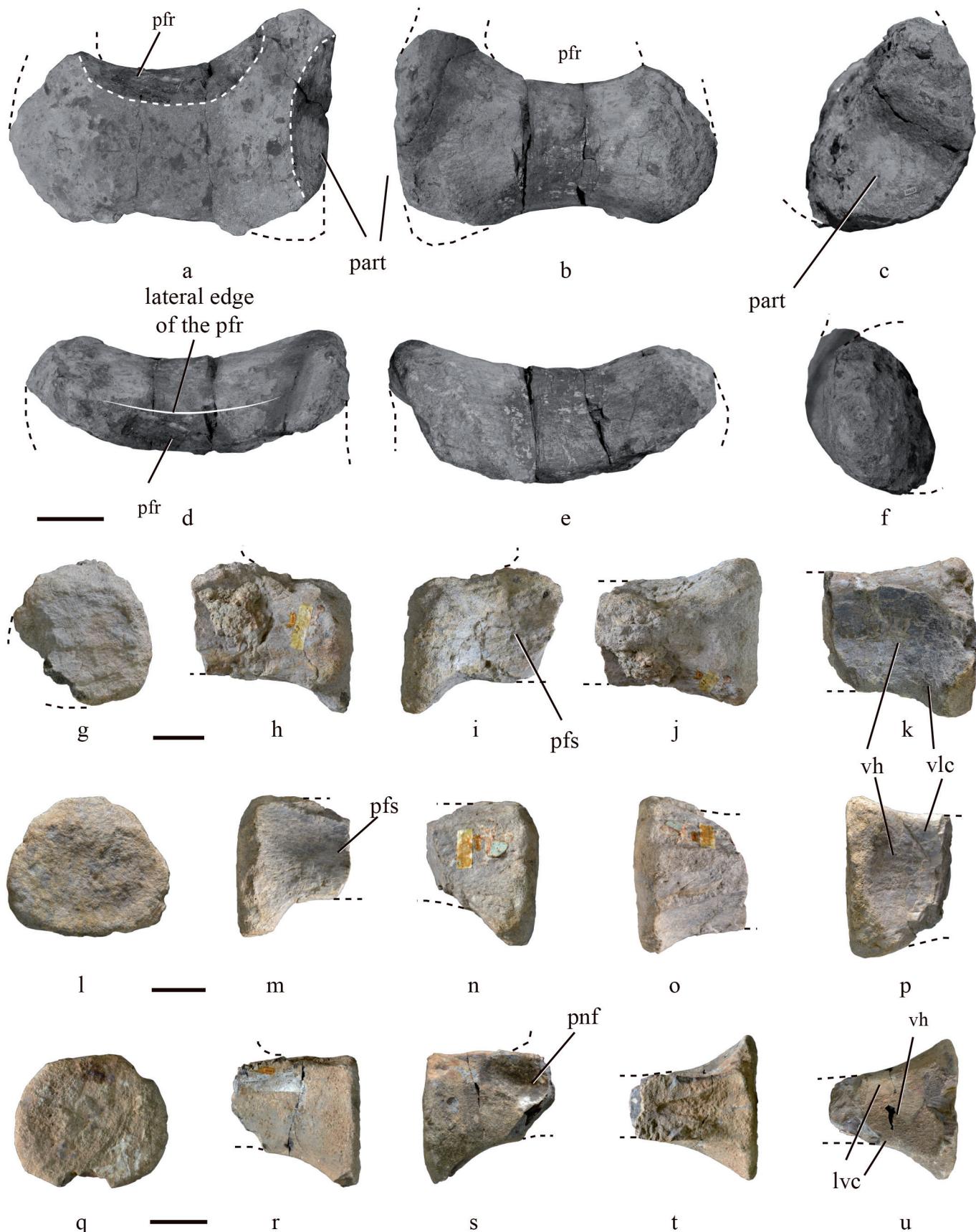


Fig. 8.- *Neosauropoda* indet., partial dorsal centrum (MG 4799) from Castanheira (Vila Franca de Xira) in left (a), right (b), posterior (c), dorsal (d), ventral (e) and anterior (f) views. *Diplodocinae* indet., middle and posterior caudal vertebrae (MG 4819, 4821, 4826) from São Gregório da Fanadia (Caldas da Rainha): MG 4819 in posterior (g), left (h), right (i), dorsal (j) and ventral (k) views; MG 4821 in anterior (l), left (m), right (n), dorsal (o) and ventral (p) views; MG 4826 in posterior (q), left (r), right (s), dorsal (t) and ventral (u) views. Scale bar: 5cm. The traced line indicates lost bone

ventral face on anterior, middle and posterior caudal vertebrae bordered by well-marked lateroventral crests were acquired at least two times along the evolutionary history of sauropods: in diplodocines (Osborn, 1904; McIntosh, 2005; Remes, 2006; Whitlock, 2011) and in some titanosaurs such as saltasaurids (e.g., Powell, 1992; Wilson, 2002; Upchurch *et al.*, 2004; Gomani, 2005). The presence of a longitudinal ventral hollow on anterior and middle caudal vertebrae was considered as synapomorphy of Diplodocinae (e.g., Wilson, 2002; Carballido *et al.*, 2011) as well as for Titanosauria (e.g., Wilson, 2002; D'Emic, 2012). Nevertheless, this feature presents an uncertain phylogenetic distribution within Titanosauria, or even within Titanosauriformes (depending the phylogenetic approach) being present in the some Chinese somphospondylians such as *Daxiatitan* (You *et al.*, 2008), *Huanghetitan liujiaxiensis* (You *et al.*, 2006) and *H. ruyangensis* (Lü *et al.*, 2007) (placed within Titanosauria by Mannion *et al.*, 2013).

The presence of a quadrangular cross-section of the centrum was also considered as a synapomorphy of Diplodocinae (Wilson, 2002; Carballido *et al.*, 2011; although Whitlock, 2011 restricted this feature to anterior caudal vertebrae: character #136) and shared by São Gregório da Fanadia specimens. This condition differs from the more cylindrical middle caudal vertebrae of titanosaurs (e.g., Powell, 1992; Gomani, 2005; D'Emic, 2012). The flat articulations also distinguish these caudal vertebrae from the procoelous middle caudal vertebrae of lithostrotian titanosaurs (e.g., Powell, 1992; Salgado *et al.*, 1997; Sanz *et al.*, 1999; Gomani, 2005). The general morphology of these vertebrae is indistinguishable from that of the middle and posterior caudal vertebrae of the diplodocines *Diplodocus*, *Barosaurus* and *Tornieria*. The presence of pneumatic fossae in the lateral face of middle caudal vertebra are only recorded in the Morrison and Tendaguru diplodocines (Osborn, 1899; McIntosh, 2005; Lucas *et al.*, 2006; Remes, 2006) and in some cases they are perforated by pneumatic foramina as occur in *Diplodocus* (e.g., Osborn, 1899). The presence of pneumatic fossae, transversely concave ventral surface bordered by well-developed lateroventral crests and a quadrangular cross-section are the criteria to relate these vertebrae to an indeterminate diplodocine.

## 2.15. Porto Novo II

**Material:** Six associated fragments including three incomplete middle/posterior caudal centra (MG 25197.4-6), two dorsal rib fragments (MG 25197.1 and MG 25197.3), and an indeterminate element (MG 25197.2).

**Locality and horizon:** Porto Novo, Maceira (Torres Vedras). Praia da Amoreira-Porto Novo Formation, late Kimmeridgian-basal Tithonian in age (Manuppella *et al.*, 1999).

**Description:** Three fragments of incomplete middle caudal vertebrae from which it is not possible to obtain much information (not figured). The preserved articular faces (anterior or posterior) are flat-to-concave. The articular facets for the

chevron are not preserved. The ventral face is transversely concave and bordered by well-developed ventrolateral crests. The centra bear a quadrangular cross-section.

**Discussion:** The presence of a transversely concave ventral surface bordered by well-developed lateroventral crests and a quadrangular cross-section are used to relate this remains with the Diplodocinae clade (see discussion for the São Gregório da Fanadia specimens, MG 4819, 4821 and 4826).

Macronaria Wilson and Sereno, 1998  
Titanosauriformes Salgado *et al.*, 1997  
Titanosauriformes indet.

## 2.16. Praia de Areia Branca

**Material:** Left incomplete femur (MG 4986).

**Locality and horizon:** Praia de Areia Branca (Lourinhã). Bombarral Formation, Tithonian in age (Manuppella *et al.*, 1999).

**Description:** MG 4986 is a left femur (Fig. 9a-e) of large size. It is one of the largest femora found in the Portuguese Upper Jurassic record, but only the proximal end is preserved. The femur has a straight shaft in lateral and anterior views. The femoral head is dorsomedially projected. The anterior face of the femoral head is eroded as well as the posterior face of the femoral proximal end. The linea intermuscularis cranialis on the femoral anterior face is absent. The proximal one-third of the femur is medially deflected, resulting in a marked lateral bulge on the lateral face of the femur. This lateral bulge is thicker anteroposteriorly in the point of the deflection. On the posterior face, an incipient trochanteric shelf is developed below the greater trochanter region. The shaft is compressed anteroposteriorly (ratio transverse/anteposterior width of the shaft is 2.76). The fourth trochanter is poorly preserved.

**Discussion:** The proximal portion of a large femur from Praia de Areia Branca was reported by Lapparent and Zbyszewski (1957) and was assigned to *Brachiosaurus atalaiensis*. Antunes and Mateus (2003) assigned this femur to *Lusotitan atalaiensis*. This femur presents a lateral bulge that has been identified as a synapomorphy of Titanosauriformes (e.g., Salgado *et al.*, 1997; Wilson, 2002; Upchurch *et al.*, 2004; D'Emic, 2012) or of a more inclusive group within Macrognathia (Carballido *et al.*, 2011; Carballido and Sander, 2014). Some derived diplodocids also acquired a lateral bulge (e.g., Hatcher, 1901; Lull, 1919; McIntosh, 2005). The diaphysis has a marked anteroposterior compression as noted by Mannion *et al.* (2013), greater than that of any other Iberian Late Jurassic sauropod such as *Lourinhasaurus alenquerensis* (Mocho *et al.*, 2014a), *Turiasaurus riodevensis* (Royo-Torres *et al.*, 2006), the San Lorenzo turiasaur (Cobos *et al.*, 2011) and *Aragosaurus ischiaticus* (Sanz *et al.*, 1987; Royo-Torres *et al.*, 2014). The value presented by this femur for the ratio transverse/anteposterior width fits in the range that seems to be synapomorphic of the Titanosauriformes (Wilson, 2002;

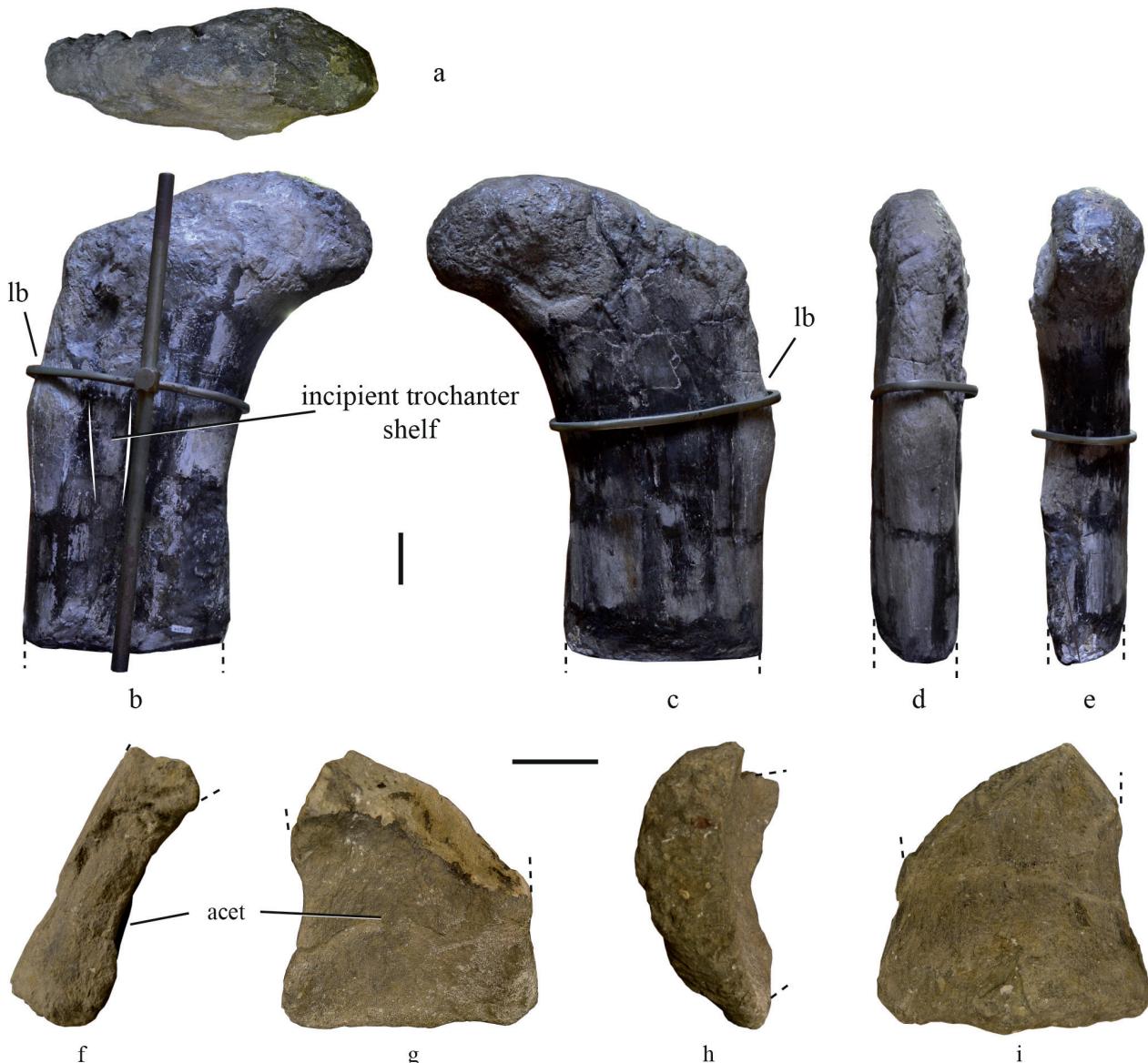


Fig. 9.- Titanosauriformes indet., (a-e) a proximal end of left femur (MG 4986) from Praia da Areia Branca (Lourinhã) in proximal (a), posterior (b), anterior (c), lateral (d) and medial (e) views; (f-i) iliac peduncle (MG 30485) from ?Alenquer in lateral or medial (f), posterior (g), ventral (h) and anterior (i) views. Scale bar: 10cm. The traced line indicates lost bone.

Upchurch *et al.*, 2004; see values presented by Mannion *et al.*, 2013).

Another feature generally present in Titanosauriformes is the trochanteric shelf on the posterior surface of the proximal end. This structure was suggested as a synapomorphy of Saltasaurinae (Otero, 2010), but D'Emic (2012) suggested that it is diagnostic for a more inclusive group including saltasaurines and *Alamosaurus*. Nevertheless, this trochanteric shelf seems to be more widely distributed in titanosauriforms, being present in other titanosaurs such as *Jainosaurus* (Wilson *et al.*, 2011), *Lirainosaurus* (Díez Díaz *et al.*, 2013), *Rapetosaurus* (Curry Rogers, 2009), *Ampelosaurus* (Le Louuff, 2005) or in basal titanosauriforms such as *Tastavinsaurus* (Royo-Torres, 2009) or *Giraffatitan* (Janensch, 1961). In the case of MG 4986, the trochanteric shelf is not so well-developed as in *Giraffatitan* or *Tastavinsaurus* (pers. observ.,

PM). The presence of a pronounced bulge, an incipient trochanteric shelf and an anteroposteriorly compressed femoral shaft allow us to conclude that this femur could be attributed to an indeterminate titanosauriform.

#### 2.17. Alenquer?

*Material:* Pubic peduncle from an ilium (MG 30485).

*Locality and horizon:* This bone is on a box with the scratched reference of Moinho Carmo (Alenquer), locality of *Lourinhasaurus alenquerensis* lectotype. In MG collections, some elements with a different state of preservation were clearly mixed with the lectotype of *Lourinhasaurus alenquerensis* (some of this material was moved to a different facility). Furthermore, only one individual was recognized in Moinho Carmo site (Lapparent and Zbyszewski, 1957; Mo-

cho *et al.*, 2014a), and the morphology of this pubic peduncle is distinct from *Lourinhasaurus* (see below).

**Description:** The pubic peduncle of an ilium is preserved in the MG collections (Fig. 9f-i). This peduncle is transversely elongated and it bears an arched profile with the convexity facing anteriorly in distal view. The distal surface is rough. The anterior and posterior face of the peduncle is transversely convex and concave, respectively.

**Discussion:** Transversely elongated pubic peduncle on the ilium (iliac pubic peduncle more than 1.5 times wider than long anteroposteriorly) is considered as a synapomorphy of Titanosauriformes (D'Emic, 2012) and present in MG 30485. MG 30485 differs from the morphology presented by *Lourinhasaurus* with a subtriangular outline, common in other non-titanosauriform sauropods such as *Camarasaurus* (Osborn and Mook, 1921; Ostrom and McIntosh, 1966), *Haplocanthosaurus* (Hatcher, 1903) or *Diplodocus* (Hatcher, 1901). For no other Iberian Late Jurassic sauropod have been described a transversely elongated iliac pubic peduncle (Casanovas *et al.*, 2011; Royo-Torres *et al.*, 2006; 2014; Barco, 2009; Mannion *et al.*, 2012; 2013; Mateus *et al.*, 2014)

cf. *Lusotitan* Antunes and Mateus, 2003

cf. *Lusotitan atalaiensis* (Lapparent and Zbyszewski, 1957)

## 2.18. Maceira

**Material:** Middle caudal vertebra (MG 8804).

**Locality and horizon:** The label accompanying this vertebra states that it was found in “Corte da Foz Velha de Maceira para Cambelas”, possibly from the sediments of the Freixial Formation, Tithonian in age (Pereda-Suberbiola *et al.*, 2005; Kullberg *et al.*, 2006).

**Description:** A middle caudal vertebra lacking the neural arch (Fig. 3g.I-g.VI). The dorsal surface of the centrum is eroded but the neural arch seems to be anteriorly displaced. The centrum is dorsoventrally compressed and both articulations are concave. The anterior articulation becomes wider ventrally. The lateral face of the centrum is convex and lacks evidence of longitudinal crests. The ventral face is convex-to-flat and bears undeveloped and semi-elliptical articulations for the chevron in the anterior border. Posterior to the anterior articulations for the chevron, there are two small excavations as occur in the middle caudal vertebrae of *Lusotitan* lectotype (pers. observ., PM).

**Discussion:** MG 8804 was originally assigned to *Brachiosaurus atalaiensis* (Lapparent and Zbyszewski, 1957, pl XXVI, fig. 95) and, later, to *Lusotitan atalaiensis* (Antunes and Mateus, 2003). This centrum is dorsoventrally compressed as in *Lusotitan atalaiensis*, several other basal titanosauriforms (Janensch, 1950; Tidwell *et al.*, 1999; 2001; Upchurch *et al.*, 2004; Canudo *et al.*, 2008; Royo-Torres, 2009), *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003) and *Galveosaurus* (Barco, 2009). This centrum bears a marked anterior displacement of the neural arch as in Titanosauri-

formes (Salgado *et al.*, 1997; D'Emic, 2012; Mannion *et al.*, 2013) and as in the non-neosauropod eusauropod *Cetiosaurus oxoniensis* (Upchurch and Martin, 2003). Another feature observed in MG 8804 is the presence of two circular depressions behind the anterior articulations for the chevron. These depressions are also observed in *Lusotitan atalaiensis* lectotype, and might represent an autapomorphy of this taxon. According to this feature, this centrum is tentatively referred to *Lusotitan atalaiensis*. Were it not for this feature, which is diagnostic of *Lusotitan*, MG 8804 should be considered as an indeterminate eusauropod on the basis of the following combination of characters: an anteriorly displaced neural arch on middle caudal vertebra and a dorsoventrally compressed centrum.

## 2.19. Other material

In the Museu Geológico several other specimens are also found such as the lectotype of *Lourinhasaurus alenquerensis* and *Lusotitan atalaiensis* described in detail by Mocho *et al.* (2014a) and Mannion *et al.* (2013), respectively. Nevertheless, other fragmentary specimens related to Sauropoda clade were also identified in the collections.

Three fragments (MG 25254.2-4) are associated and were found in a locality between Foz Velha da Maceira and Cambelas (Torres Vedras), one middle/posterior caudal vertebra (MG 25254.2) and three indeterminate fragments. MG 25254.2 is a middle or posterior caudal vertebra with a cylindrical form. The preserved articulation is concave. The ventral face is convex lacking ventrolateral or sagittal crests. There are rudimentary articulations for the chevron. Between these articulations the ventral surface is slightly concave. The vertebra is regarded as to an indeterminate sauropod. The indeterminate fragments should not be related to this clade.

Three heart-shaped teeth from Fervença (MG 277), São Martinho do Porto (MG 4832) and Ourém (MG 16) are also found in the collections. MG 277 and MG 16 were initially assigned to *Pelorosaurus humerocristatus* (Sauvage, 1897-98; Lapparent and Zbyszewski, 1957) and MG 4832 to *Turiasaura* (Royo-Torres *et al.*, 2009). Those teeth were recently referred with doubt to *Turiasaura* clade (Mocho *et al.*, 2015). Another tooth with a compressed cone-chisel morphology is also present in the collections (MG 8779, Sauvage, 1897-98; Lapparent and Zbyszewski, 1957) and was originally referred to *Morosaurus marchei* (Sauvage, 1897-98) and, later, to *Apatosaurus alenquerensis* (Lapparent and Zbyszewski, 1957). This morphology is common in titanosauriform teeth (see Calvo, 1994) but also present in *Europasaurus* (Carballido and Sander, 2014). A detailed description and discussion of this tooth and other unpublished compressed cone-chisel teeth of the Portuguese Upper Jurassic record is in progress. Finally, two teeth fragments were found in association with material attributed to “*Omosaurus lennieri*” (MG 8771) from Porto das Barcas (Lourinhã), where sediments of the upper Kimmeridgian-lower Tithonian Sobral Fm. crops out. These

teeth present a wrinkled texture that allow us to relate them to an indeterminate sauropod (e.g., Carballido and Pol, 2010).

MG 8803 is a fragment from a tibial distal end, specifically, part of the articular surface for the ascending process. This specimen was collected in Serra da Vila (Torres Vedras, locality referred on the figure 1 of Lapparent and Zbyszewski, 1957) and probably from the sediments of the Sobral Formation, late Kimmeridgian-basal Tithonian in age. MG 8792 are two dorsal rib fragments with an appreciable size, probably related to an indeterminate sauropod and they were found in Atalaia (Lourinhã) from the sediments of Sobral Fm., late Kimmeridgian-basal Tithonian in age. Some sauropod dorsal rib fragments (MG 30480), including a proximal end, were found in Ribamar (Lourinhã) where outcrops the Praia da Amoreira-Porto Novo Fm. (Manuppella *et al.*, 1999). A partial caudal neural spine (MG 30481) and a partial dorsal centrum (MG 30482) are associated in the collections of the Museu Geológico and are referred with doubt to the Atalaia locality (Lourinhã, Sobral Fm.). The association of these two bones on the field is not confirmed. The dorsal centrum bears deep pneumatic foramina, suggesting that it might represent a neosauropod form (see discussion for MG 4799). The anterior caudal neural spine does not bear important features and is considered to pertain to an indeterminate sauropod. An isolated middle caudal vertebra (MG 8802), found in the collections with unknown locality, is related to an indeterminate sauropod. Finally, a humeral partial distal end (MG 30484, Fig. 7k) with a transversely flat distal articulation of an indeterminate sauropod is referred with doubt to Alenquer locality.

### 3. Implications and conclusions

Museu Geológico collections include some of the first evidence of sauropods from the Upper Jurassic of the Lusitanian Basin, including the lectotypes of *Lourinhasaurus alenquerensis* and *Lusotitan atalaiensis* and several incomplete specimens previously referred to those taxa.

The revision of the material traditionally assigned to *Lourinhasaurus alenquerensis* (MG 4799, 4800, 4802, 4804, 4976, 4978, 8800, 8805) refutes the previous systematic approaches corresponding to indeterminate sauropod and eusauropod forms. On the other hand, MG 4800, 4986 and 8804 that were previously related to *Lusotitan atalaiensis*, corresponding to indeterminate sauropods and eusauropods. Only MG 8804 bears a putative autapomorphy of *Lusotitan atalaiensis*: the presence of two small circular depressions behind the anterior articulation for the chevron. According to the available information about Late Jurassic sauropod faunas (e.g., Wilson, 2002; Upchurch *et al.*, 2004; D'Emic, 2012; Mannion *et al.*, 2013), most of this material probably belongs to members of Eusauropoda, taking into account the absence of non-eusauropod sauropods during the Late Jurassic (e.g., Upchurch *et al.*, 2004; Remes *et al.*, 2009).

MG 4976 is a right humerus that shares the presence of a posterior and acute proximodistal crest on its proximal end with *Duriatitan humerocristatus*, a British Late Jurassic sauropod. The presence of a proximodistally constricted deltopectoral crest allowed us to assign this taxon to the Eusauropoda clade. MG 4976 is considered herein as cf. *Duriatitan humerocristatus*. If this interpretation is correct, *Duriatitan humerocristatus* would be the first Late Jurassic sauropod shared between Iberian Peninsula and United Kingdom. Although, the Portuguese Late Jurassic sauropods have classical been considered to have close affinities with the Morrison Formation sauropods (e.g., Lapparent and Zbyszewski, 1957; McIntosh, 1990a; 1990b; Mateus, 2006; Ortega *et al.*, 2006; 2009; 2013), the presence of forms typical of the European Upper Jurassic record are also present, such as the turiasaurian sauropods (Royo-Torres *et al.*, 2006; 2009; 2014; Mateus, 2009; Ortega *et al.*, 2009; 2010; 2013; Mocho *et al.*, 2012; 2015; Royo-Torres and Upchurch, 2012; Mateus *et al.*, 2014).

Some specimens collected in São Gregório da Fanadia (MG 4819, 4821, 4826) and Porto Novo (MG 25197.4-6) are tentatively assigned to the diplodocid clade, Diplodocinae. The presence of diplodocids in the Upper Jurassic of the Lusitanian Basin is demonstrated by the presence of *Dinheirosaurus* (Dantas *et al.*, 1992; Bonaparte and Mateus, 1999; Mannion *et al.*, 2012); the Moita dos Ferreiros diplodocine (Mateus, 2005; Mannion *et al.*, 2012; Tschopp *et al.*, 2015), and three new diplodocid specimens (SHN (JJS) 177, 178, 179; Mocho *et al.*, 2014b).

The material housed in the Museu Geológico suggests the presence of non-neosauropod eusauropods (turiasaurs) and neosauropods (indeterminate neosauropods, diplodocines, camarasaurids and titanosauriforms) on the Portuguese Upper Jurassic record, which is in accordance with the present known paleobiodiversity of this group for the Lusitanian Basin during the Late Jurassic. This collection also suggests the presence of a rich and diverse sauropod fossil record in the Upper Jurassic sediments, especially in the Alcobaça, Praia da Amoreira-Porto Novo, Sobral, Freixial and Bombarral Formations, that is also reflected by other vertebrate groups (e.g., Sauvage 1897-98; Lapparent and Zbyszewski; 1957; Galton, 1980; Pérez-Moreno *et al.*, 1999; Rauhut, 2000; Antunes and Mateus, 2003; Escaso *et al.*, 2007; 2010; 2014; Malafaia *et al.*, 2010, 2015; Pérez-García and Ortega, 2011; Hendrickx and Mateus, 2014). This collection further highlights that the West Portuguese region (Mafra, Torres Vedras, Lourinhã, Peniche, Alenquer, Caldas da Rainha, Leiria and Pombal) is one of the most productive with respect to Late Jurassic vertebrates of Europe.

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## References

- Allain, R., Aquesbi, N. (2008): Anatomy and phylogenetic relationships of *Tazoudasaurus naimi* (Dinosauria, Sauropoda) from the late Early Jurassic of Morocco. *Geodiversitas* 30, 345–424.
- Antunes, M.T., Mateus, O. (2003): Dinosaurs of Portugal. *Paleovol* 2, 77–95. doi:10.1016/S1631-0683(03)00003-4
- Azerêdo, A.C., Cabral, M.C., Martins, M.J., Loureiro, I.M., Inês, N. (2010): Estudo estratigráfico dum novo afloramento da Formação de Cabaços (Oxfordiano) na região da Serra do Bouro (Caldas da Rainha). *Comunicações Geológicas* 97, 5–22.
- Bandyopadhyay, S., Gillette, D.D., Ray, S., Sengupta, D.P. (2010): Osteology of *Barapasaurus tagorei* (Dinosauria: Sauropoda) from the Early Jurassic of India. *Palaeontology* 53, 533–569. doi:10.1111/j.1475-4983.2010.00933.x
- Barco, J.L. (2009): *Sistématica e implicaciones filogenéticas y paleobiogeográficas del saurópodo Galvesaurus herrerói* (Formación Villar del Arzobispo, Galve, España). Unpublished PhD Thesis, Universidad de Zaragoza, Zaragoza, Spain, 389 p.
- Barrett, P.M., Benson, R.B.J., 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.
- Bonaparte, J.F. (1986): Les dinosaures (Carnosaures, Allosaurides, Sauropodes, Cetiosaurides) du Jurassique Moyen de Cerro Cóndor (Chubut, Argentine). *Annales de Paléontologie* 72, 247–386.
- Bonaparte, J.F., Mateus, O. (1999): A new diplodocid, *Dinheirosaurus lourinhensis* gen et sp. nov., from the Late Jurassic beds of Portugal. *Revista del Museo Argentino de Ciencias Naturales* 5(2), 13–29.
- Calvo, J.A. (1994): Jaw mechanics in sauropod dinosaurs. *Gaia* 10, 183–193.
- Canudo, J.I., Royo-Torres, R., Cuenca-Bescós, G. (2008): A new sauro-
- pod: *Tastavinsaurus sanzi* gen. et sp. nov. from the Early Cretaceous (Aptian) of Spain. *Journal of Vertebrate Paleontology* 28, 712–731. doi:10.1671/0272-4634(2008)28[712:ANSTSG]2.0.CO;2
- Carballido, J.L., Pol, D. (2010): The dentition of *Amygdalodon patagonicus* (Dinosauria: Sauropoda) and the dental evolution in basal sauropods. *Comptes Rendus Palevol* 9, 83–93. doi:10.1016/j.crpv.2010.01.003
- Carballido, J.L., Sander, P.M. (2014): Postcranial axial skeleton of *Eurillasaurus holgeri* (Dinosauria, Sauropoda) from Upper Jurassic of Germany: implications for sauropod ontogeny and phylogenetic relationships of basal Macronaria. *Journal of Systematic Paleontology* 12 (3), 335–387. doi:10.1080/14772019.2013.764935
- Carballido, J.L., Rauhut, O.W.M., Pol, D., Salgado, L. (2011): Osteology and phylogeny relationships of *Tehuelchesaurus benitezii* (Dinosauria, Sauropoda) from the Upper Jurassic of Patagonia. *Zoological Journal of the Linnean Society* 163, 605–662. doi:10.1111/j.1096-3642.2011.00723.x
- Casanovas, M.L., Santafé, J.V., Sanz, J.L. (2001): *Losillasaurus giganteus*, un nuevo saurópodo del tránsito Jurásico-Cretácico de la cuenca de «Los Serranos» (Valencia, España). *Paleontología i Evolución* 32-33, 99–122.
- Cobos, A., Royo-Torres, R., Gascó, F., Alcalá, L. (2011): A new giant turiasaurian specimen from Riodeva (Teruel, Spain). In: A. van der Geer, A. Athanassiou (eds.), *Programs and Abstracts of 9th Annual Meeting of the European Association of Vertebrate Palaeontologists*, Creta, Greece, p. 18.
- Cooper, M.R. (1984): A reassessment of *Vulcanodon karibaensis* Raath (Dinosauria: Saurischia) and the origin of the Sauropoda. *Palaeontologia Africana* 25, 203–231.
- Curry Rogers, K. (2009): The postcranial osteology of *Rapetosaurus krausei* (Sauropterygia: Titanosauria) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 29(4), 1046–1086. doi:10.1671/039.029.0432
- D'Emic, M.D. (2012): The early evolution of titanosauriform sauropod dinosaurs. *Zoological Journal of the Linnean Society* 166 (3), 624–671. doi:10.1111/j.1096-3642.2012.00853.x
- D'Emic, M.D. (2013): Revision of the sauropod dinosaurs of the Lower Cretaceous Trinity Group, southern USA, with the description of a new genus. *Journal of Systematic Palaeontology* 11(6), 707–726. doi:10.1080/14772019.2012.667446
- Dantas, P. (1990): Dinossáurios de Portugal. *Gaia* 2, 17–26.
- Dantas, P., Sanz, J.L., Galopim de Carvalho, A.M. (1992): Dinossáurio da Praia de Porto Dinheiro (dados preliminares). *Gaia* 5, 31–35.
- Dantas, P., Sanz, J.L., Silva, C.M., Ortega, F., Santos, V.F., Cachão, M. (1998): *Lourinhasaurus* n. gen. novo dinossáurio saurópode do Jurásico superior (Kimmeridgiano superior-Titoniano inferior) de Portugal. *Actas do V Congresso de Geologia* 84, A-91–A-94.
- Díez Díaz, V., Pereda Suberbiola, X., Sanz, J.L. (2013): Appendicular skeleton and dermal armour of the Late Cretaceous titanosaur *Lirainosaurus astibiae* (Dinosauria: Sauropoda) from Spain. *Palaeontologia Electronica*, 16.2.19A: 18 pp. doi:palaeo-electronica.org/content/2013/502-titanosaur-skeleto
- Escaso, F., Ortega, F., Dantas, P., Malafaia, E., Pimentel, N.L., Pereda Suberbiola, X., Sanz, J.L., Kullberg, J.C., Kullberg, M.C., Barriga, F. (2007): New evidence of shared Dinosaur across Upper Jurassic Proto-North Atlantic: *Stegosaurus* from Portugal. *Die Naturwissenschaften* 94, 367–374. doi:10.1007/s00114-006-0209-8
- Escaso, F., Silva, B., Ortega, F., Malafaia, E., Sanz, J.L. (2010): A Portuguese specimen of *Camptosaurus aphanoecetes* (Ornithopoda: Camptosauridae) increases the dinosaurian similarity among the Upper Jurassic Alcobaça and Morrison Formations. *70th Meeting of the Society of Vertebrate Paleontology. Program and Abstracts*, Pittsburgh, p. 86A.
- Escaso, F., Ortega, F., Dantas, P., Malafaia, E., Silva, B., Gasulla, J.M.,

- Mocho, P., Narváez, I., Sanz, J.L. (2014): A new dryosaurid ornithopod (Dinosauria, Ornithischia) from the Late Jurassic of Portugal. *Journal of Vertebrate Paleontology* 34 (5), 1102–1112. doi:10.1080/02724634.2014.849715
- Fürsich, F.T. (1981): Salinity-controlled benthic associations from the Upper Jurassic of Portugal. *Lethaia* 14, 203–223. doi:10.1111/j.1502-3931.1981.tb01690.
- Galton, P.M. (1980): European Jurassic ornithopod dinosaurs of the families Hypsilophodontidae and Camptosauridae. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 160(1), 73–95.
- Gomani, E.M. (2005): Sauropod dinosaurs from the Early Cretaceous of Malawi. *Palaeontologia Electronica* 8 1–37. doi:palaeo-electronica.org/paleo/2005\_1/gomani27/issue1\_05.htm
- González Riga, B.J., Previtera, E., Pirrone, C. (2009): *Malarguesaurus floreniae* gen. et sp. nov., a new titanosauriform (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. *Cretaceous Research* 30, 135–148. doi:10.1016/j.cretres.2008.06.006
- Harris, J.D. (2007): The appendicular skeleton of *Suuwassea emilieae* (Sauropoda: Flagellicaudata) from the Upper Jurassic Morrison Formation of Montana (USA). *Geobios* 40, 501–522. doi:10.1016/j.geobios.2006.02.002
- Harris, J.D., Dodson, P. (2004): A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA. *Acta Palaeontologica Polonica* 49, 197–210. doi:app.pan.pl/acta49/app49-197.pdf
- Hatcher, J.B. (1901): *Diplodocus* (Marsh): its osteology, taxonomy and probable habits, with a restoration of the skeleton. *Memoirs of the Carnegie Museum* 1, 1–63.
- Hatcher, J.B. (1903): Osteology of *Haplocanthosaurus* with description of a new species, and remarks on the probable habits of the Sauropoda and the age and origin of the *Atlantosaurus* beds. *Memoirs of the Carnegie Museum* 2, 1–72.
- Hendrickx, C., Mateus, O.V. (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. doi:10.1371/journal.pone.0088905
- Hill, G. (1988): The sedimentology and lithostratigraphy of the Upper Jurassic Lourinhã Formation, Lusitanian Basin, Portugal. Unpublished Phd Thesis. Open University, 292 p.
- Huene, F. von. (1932): Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monograph Geologie und Palaeontologie* 4, 1–361.
- Hulke, J.W. (1874): Note on a large saurian humerus from the Kimmeridge Clay of the Dorset Coast. *Quarterly Journal of the Geological Society of London* 25, 386–389.
- Janensch, W. (1929): Die Wirbelsäule der Gattung *Dicraeosaurus*. *Palaeontographica Suppl.* 7 (2): 38–133.
- Janensch, W. (1950): Die Wirbelsäule von *Brachiosaurus brancai*. *Palaeontographica Suppl.* 7 (3), 27–93.
- Janensch, W. (1961): Die Gliedmaszen und Gliedmaszengürtel der Sauropoden der Tendaguru-Schichten. *Palaeontographica Suppl.* 7 (3), 177–235.
- Kullberg, J.C., Rocha, R.B., Soares, A.F., Rey, J., Terrinha, P., Callapez, P., Martins, L. (2006): A Bacia Lusitana: Estratigrafia, Paleogeografia e Tectônica. In: R. Dias, A. Araújo, P. Terrinha, J.C. Kullberg (eds.), *Geologia de Portugal no contexto da Ibérica*. Universidade de Évora, Évora, pp. 317–368.
- Lapparent, A.F., Zbyszewski, G. (1957): Les dinosaures du Portugal. *Memórias dos Serviços Geológicos de Portugal* 2, 1–63.
- Le Loeuff, J. (2005): Osteology of *Ampelosaurus atacis* (Titanosauria) from Southern France,. In: V. Tidwell, K. Carpenter (eds.), *Thunder-Lizards. The Sauropodomorph Dinosaurs*, Indiana University Press, pp. 115–137
- Leinfelder, R.R., Wilson, R.C.L. (1989): Seismic and sedimentologic features of Oxfordian-Kimmeridgian syn-rift sediments on the eastern margin of the Lusitanian Basin. *International Journal of Earth Sciences, Geologische Rundschau* 78, 81–104.
- Lü, J., Xu, L., Zhang, X., Hu, W., Wu, Y., Jia, S., Ji, Q. (2007): A new gigantic sauropod dinosaur with the deepest known body cavity from the Cretaceous of Asia. *Acta Geologica Sinica* 81, 167–176.
- Lucas, S.G., Spielmann, J.A., Rinehart, L.F., Heckert, A.B., Herne, M.C., Hunt, A.P., Foster, J.R., Sullivan, R.M. (2006): Taxonomic status of *Seismosaurus hallorum*, a Late Jurassic sauropod dinosaur from New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 36, 149–162.
- Lull, R.S. (1919): The sauropod dinosaur *Barosaurus* Marsh: redescription of the type specimens in the Peabody Museum, Yale University. *Memoirs of the Connecticut Academy of Arts and Sciences* 6, 1–42.
- Malafaia, E., Ortega, F., Escaso, F., Dantas, P., Pimentel, N.L., Gasulla, J.M., Ribeiro, B., Barriga, F., Sanz, J.L. (2010): Vertebrate fauna at the *Allosaurus* fossil-site of Andrés (Upper Jurassic), Pombal, Portugal. *Journal of Iberian Geology* 36, 193–204. doi:10.5209/rev\_JIGE.2010.v36.n2.7
- Malafaia, E., Ortega, F., Escaso, F., Silva, B. (2015): New evidence of *Ceratosaurus* (Dinosauria: Theropoda) from the Late Jurassic of the Lusitanian Basin, Portugal. *Historical Biology: An International Journal of Paleobiology* 27(7), 938–946. doi:10.1080/08912963.2014.915820
- Mannion, P., Upchurch, P., Mateus, O., Barnes, R.N., Jones, M.E.H. (2012): New information on the anatomy and systematic position of *Dinheirosaurus lourinhensis* (Sauropoda: Diplodocoidea) from the Late Jurassic of Portugal, with a review of European diplodocoids. *Journal of Systematic Palaeontology* 10(3), 521–551. doi:10.1080/14772019.2011.595432
- Mannion, P., Upchurch, P., Barnes, R.N., Mateus, O. (2013): Osteology of the Late Jurassic Portuguese sauropod dinosaur *Lusotitan atlaiensis* (Macronaria) and the evolutionary history of basal Titanosauriformes. *Zoological Journal of the Linnean Society* 168(1), 98–206. doi:10.1111/zoj.12029
- Manuppella, G., Antunes, M.T., Pais, J., Ramalho, M.M., Rey, J. (1999): *Notícia explicativa da Folha 30-A (Lourinhã)*. Departamento de Geologia do Instituto Geológico e Minerio, Lisboa, 155 p.
- Manuppella, G., Antunes, M.T., Costa Almeida, C.A., Azeredo, A.C., Barbosa, B., Cardoso, J.L., Crispim, J.A., Duarte, L.V., Henriques, M.H., Martins, L.T., Ramalho, M.M., Santos, V.F., Terrinha, P. (2000): *Notícia Explicativa da Carta Geológica de Portugal, folha 27-A (Vila Nova de Ourém)*. Departamento de Geologia do Instituto Geológico e Minerio, Lisboa, 83 p.
- Marsh, O.C. (1878): Principal characters of American Jurassic dinosaurs. Part I. *American Journal of Science* 16, 411–416.
- Marsh, O.C. (1884): Principal characters of American Jurassic dinosaurs. Part VII. On the Diplodocidae, a new family of the Sauropoda. *American Journal of Science* 27, 160–168.
- Mateus, O. (2005): Dinossauros do Jurássico Superior de Portugal, com destaque para os sauríquios. Unpublished PhD Thesis, Universidade Nova de Lisboa, 377 p.
- Mateus, O. (2006): Late Jurassic dinosaurs from the Morrison Formation, the Lourinhã and Alcobaça Formations (Portugal), and the Tendaguru Beds (Tanzania): a comparison. *New Mexico Museum of Natural History and Science* 36, 223–231.
- Mateus, O. (2009): The sauropod *Turiasaurus riodevensis* in the Late Jurassic of Portugal. *Journal of Vertebrate Paleontology* 29, 144A
- Mateus, O., Mannion, P.D., Upchurch, P. (2014): *Zby atlanticus*, a new turiasaurian sauropod Dinosauria, Eusauropoda) from the Late Jurassic of Portugal. *Journal of Vertebrate Paleontology* 34 (3), 618–634. doi:10.1080/02724634.2013.822875

- McPhee, B.W., Yates, A.M., Choiniere, J.N., Abdala, F. (2014): The complete anatomy and phylogenetic relationships of *Antetonitrus ingenipes* (Sauropodomorphes, Dinosauria): implications for the origins of Sauropoda. *Zoological Journal of the Linnean Society* 171, 151–205. doi: 10.1111/zoj.12127
- McIntosh, J.S. (1990a): Sauropoda. In: D.B. Weishampel, P. Dodson, H. Osmólska (eds.), *The Dinosauria*. University of California Press, Berkeley, CA, pp. 345–401
- McIntosh, J.S. (1990b): Species determination in sauropod dinosaurs with tentative suggestions for their classification. In: K. Carpenter, P.J. Currie (eds.), *Dinosaur systematics: approaches and perspectives*. Cambridge University Press, Cambridge, pp. 53–69.
- McIntosh, J.S. (2005): The genus *Barosaurus* Marsh (Sauropoda, Diplodocidae). In: V. Tidwell, K. Carpenter (eds.), *Thunder-Lizards: the sauropodomorph dinosaurs*. Indiana University Press, Bloomington, p. 38–77.
- McIntosh, J.S., Miles, C.A., Cloward, K.C., Parker, J.R. (1996a): A new nearly complete skeleton of *Camarasaurus*. *Bulletin Gunma Museum of Natural History* 1, 1–87.
- McIntosh, J.S., Miller, W.E., Stadtman, K.L., Gillette, D.D. (1996b): The osteology of *Camarasaurus lewisi* (Jensen, 1988). *Brigham Young University Geology Studies* 41, 73–115.
- Mocho, P., Ortega, F., Royo-Torres, R. (2012): Morphological variation of Turiasauria-like teeth and their stratigraphic distribution in Portuguese Upper Jurassic. *Fundamental!* 20, 161–163.
- Mocho, P., Royo-Torres, R., Ortega, F. (2013a): New approach to *Lourinhasaurus alenquerensis* (Macronaria, Camarasauromorpha) from the Portuguese Upper Jurassic. In: F. Torcida Fernández-Baldor, P. Huerta (eds.), *Abstract book of the VI International Symposium about Dinosaurs Palaeontology and their Environment*, pp. 91–92.
- Mocho, P., Royo-Torres, R., Ortega, F., Silva, B. (2013b): Macronarian record from the Upper Jurassic of Portugal. In: E. Maxwell, J. Miller-Camp, R. Anemone (eds.), *73st SVP Symposium of Vertebrate Paleontology (SVP), Los Angeles, USA 30th Octobre-2nd November. Program and Abstract*, p. 178.
- Mocho, P., Royo-Torres, R., Ortega, F. (2014a): Phylogenetic reassessment of *Lourinhasaurus alenquerensis*, a basal Macronaria (Sauropoda) from the Upper Jurassic of Portugal. *Zoological Journal of the Linnean Society* 170, 875–916. doi:10.1111/zoj.12113
- Mocho, P., Royo-Torres, R., Malafaia, E., Escaso, F., Ortega, F. (2014b): A preliminary evaluation of Diplodocidae record from the Upper Jurassic of Lusitanian Basin (W, Portugal). In: I. Pereira, F. Amaral, A. Vinhas (eds.), *IV CJIG, LEG 2014, Livro de Actas*. Pólo de Estremoz de UÉvora, Évora, p. 85–88.
- Mocho, P., Royo-Torres, R., Malafaia, E., Escaso, F., Silva, B., Ortega F. (2015): Turiasauria-like teeth from the Upper Jurassic of the Lusitanian Basin, Portugal. *Historical Biology: An International Journal of Paleobiology*. doi:10.1080/08912963.2015.1049948
- Mocho, P., Royo-Torres, R., Malafaia, E., Escaso, F., Narváez, I., Ortega, F. (2016): New data on Late Jurassic sauropods of central and northern sectors of the Bombarral Sub-basin (Lusitanian Basin, Portugal). *Historical Biology: An International Journal of Paleobiology*. doi:10.1080/08912963.2015.1137912
- Oliveira, J.T., Pereira, H., Ramalho, M., Antunes, M.T. (1992): Carta Geológica de Portugal, a escala 1:500000. Serviços Geológicos de Portugal.
- Ortega, F., Escaso, F., Gasulla, J.M., Dantas, P., Sanz, J.L. (2006): Dinosaurios de la Península Ibérica. *Estudios Geológicos* 62, 1–6.
- Ortega, F., Malafaia, E., Escaso, F., Pérez-García, A., Dantas, P. (2009): Faunas de répteis do Jurássico superior de Portugal. *Paleolusitana* 1, 43–56.
- Ortega, F., Royo-Torres, R., Gascó, F., Escaso, F., Sanz, J.L. (2010): New evidences of the sauropod *Turiasaurus* from the Portuguese Upper Jurassic. *Abstract Volume 8th Annual Meeting of the European Association of Vertebrate Palaeontologists*, p. 62.
- Ortega, F., Escaso, F., Malafaia, E., Mocho, P., Pérez-García, A. (2013): Paleobiogeografia dos répteis peri-Atlânticos do Jurássico Superior português: resposta a padrões de vicariância ou dispersão. In: N. Moreira, I. Pereira, F. Couto, H. Silva (eds.), *Livro de Actas III Congresso Jovens Investigadores em Geociências LEG 2013 & 6th Meeting of Post-Graduation in Physics and Earth Sciences of University of Évora*. Universidade de Évora, Évora, p. 17–20.dantas
- Osborn, H.F. (1899): A skeleton of *Diplodocus*. *Memoirs of the American Museum of Natural History* 1, 191–214.
- Osborn, H.F., Mook, C.C. (1921): *Camarasaurus*, *Amphicoelias* and other sauropods of Cope. *Memoirs of the American Museum of Natural History* new series, 3, 247–387.
- Ostrom, J.H., McIntosh, J.S. (1966): *Marsh's Dinosaurs. The collection from Como Bluff*. New Haven. Yale University Press, USA, 416 p.
- Otero, A. (2010): The appendicular skeleton of *Neuquensaurus*, a Late Cretaceous saltasaurine sauropod from Patagonia, Argentina. *Acta Palaeontologica Polonica* 55(3), 399–426. doi:10.4202/app.2009.0099
- Ouyang, H., Ye, Y. (2002): *The First Mamenchisaurian Skeleton with Complete Skull*. Sichuan Publishing House of Science and Technology, Chengdu, 111 p. [in Chinese].
- Owen, R. (1841–42): Report on British fossil reptiles. *Reports of the British Association for the Advancement of Science* 11, 60–204.
- Pena dos Reis, R.P.B., Proença Cunha, C.P., Dinis, J.L., Trincão, P.R. (2000): Geologic evolution of the Lusitanian Basin (Portugal) during the late Jurassic. *GeoResearch Forum* 6, 345–356.
- Pereda Suberbiola, X., Dantas, P., Galton, P. M., Sanz, J. L. (2005): Autopodium of the holotype of *Dracopelta zbyszewskii* (Dinosauria, Ankylosauria) and its type horizon and locality (Upper Jurassic: Tithonian, western Portugal). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 235 (2), 175–196.
- Pérez-García, A., Ortega, F. (2011): *Selenemys lusitanica*, gen. et sp. nov., a new pleurosternid turtle (Testudines: Paracryptodira) from the Upper Jurassic of Portugal. *Journal of Vertebrate Paleontology* 31(1), 60–69. doi:10.1080/02724634.2011.540054
- Pérez-Moreno, B.P., Chure, D.J., Pires, C., Silva, C.M., Santos, V.F., Dantas, P., Póvoas, L., Cachão, M., Sanz, J.L., Galopim de Carvalho, A.M. (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. doi:10.1144/gsjgs.156.3.0449
- Powell, J.E. (1992): Osteología de *Saltasaurus loricatus* (Sauropoda Titanosauridae). In: J.L. Sanz, A.D. Buscalioni (eds.), *Los dinosaurios y su entorno biótico*. Instituto ‘Juan de Valdes’, Serie ‘Actas Académicas’ /4, Cuenca, p. 166–230
- Rasmussen, E.S., Lomholt, S., Andersen, C., Vejbaek, O.V. (1998): Aspects of the structural evolution of the Lusitanian Basin in Portugal and the shelf and slope area offshore Portugal. *Tectonophysics* 300, 199–225. doi:10.1016/S0040-1951(98)00241-8
- Ratkevich, R. (1998): New Cretaceous brachiosaurid dinosaur, *Sonorasaurus thompsoni* gen. et sp. nov., from Arizona. *Journal of the Arizona-Nevada Academy of Science* 31, 71–82.
- Rauhut, O.W.M. (2000): The dinosaur fauna of the Guimarota mine.. In: T. Martin, B. Krebs (eds.), *Guimarota - A Jurassic Ecosystem*. Verlag Dr. Friedrich Pfeil, München, pp. 75–82
- Rauhut, O.W.M. (2003): The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology* 69, 1–214.
- Remes, K. (2006): Revision of the Tendaguru sauropod dinosaur *Tornieria africana* (Fraas) and its relevance for sauropod paleobiogeography. *Journal of Vertebrate Paleontology* 26, 651–669. doi:10.1671/0272-4634(2006)26[651:ROTTSD]2.0.CO;2
- Remes, K., Ortega, F., Fierro, I., Joger, U., Kosma, R., Ferrer, J.M.M., for the Project PALDES, for the Niger Project SNHM, Ide O.A., Maga, A. (2009): A New Basal Sauropod Dinosaur from the Middle

- Jurassic of Niger and the Early Evolution of Sauropoda. *PLoS ONE* 4(9), e6924. doi:10.1371/journal.pone.0006924
- Rose, P.J. (2007): A new titanosauriform sauropod (Dinosauria: Sauischia) from the Early Cretaceous of central Texas and its phylogenetic relationships. *Palaeontologica Electronica* 10.2.8A. doi:palaeo-electronica.org/paleo/2007\_2/00063/index.html
- Royo-Torres, R. (2009): El saurópodo de Peñarroya de Tastavins. *Monografías Turonenses* 6, 1–548.
- Royo-Torres, R., Upchurch, P. (2012): The cranial anatomy of the sauropod *Turiasaurus riodevensis* and implications for its phylogenetic relationships. *Journal of Systematic Palaeontology* 10(3), 553–583. doi:10.1080/14772019.2011.598577
- Royo-Torres, R., Cobos, A., Alcalá, L. (2006): A giant european dinosaur and a new sauropod clade. *Science* 314, 1925–1927. doi:10.1126/science.1132885
- Royo-Torres, R., Cobos, A., Luque, L., Aberasturi, A., Espílez, E., Fierro, I., González, A., Mampel, L., Alcalá, L. (2009): High European sauropod dinosaur diversity during Jurassic-Cretaceous transition in Riudeva (Teruel, Spain). *Palaeontology* 52(5), 1009–1027. doi:10.1111/j.1475-4983.2009.00898.x
- Royo-Torres, R., Upchurch, P., Mannion, P.D., Mas, R., Cobos, A., Gasco, F., Alcalá, L., Sanz, J.L. (2014): The anatomy, phylogenetic relationships and stratigraphic position of the Tithonian-Berriasian Spanish sauropod dinosaur *Aragosaurus ischiaticus*. *Zoological Journal of Linnean Society* 71(3), 623–655. doi:10.1111/zoj.12144
- Salgado, L., Bonaparte, J.F. (1991): Un nuevo saurópodo Dicraeosauridae, *Amargasaurus cazaui* gen. et sp. nov. de la Formación La Amarga, Neocomiano de la Provincia del Neuquén, Argentina. *Ameghiniana* 28, 222–236.
- Salgado, L., Coria, R.A., Calvo, J.O. (1997): Evolution of titanosaurid sauropods. I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana* 34, 332.
- Sanz, J.L., Buscalioni, A.D., Casanovas, M.L., Santafé, J.V. (1987): Dinosaurios del Cretácico Inferior de Galve (Teruel, España). *Estudios geológicos* vol. extr. Galve-Trempl, 45–64.
- Sanz, J.L., Powell, J.E., Le Loeuff, J., Martínez, R., Pereda-Suberbiola, X. (1999): Sauropod remains from the Upper Cretaceous of Laño (northcentral Spain). Titanosaur phylogenetic relationships. *Estudios del Museo de Ciencias Naturales de Álava* 14, 235–255.
- Sauvage, H. E. (1897–98): *Vértebrés fossiles du Portugal. Contribution à l'étude des poissons et des reptiles du Jurassique et du Crétacé*. Mémoires de la Direction des Travaux Géologiques du Portugal, 46 p.
- Schneider, S., Fürsich, F.T., Werner, W. (2009): Sr-isotope of the Upper Jurassic of central Portugal (Lusitanian Basin) based on oyster shells. *International Journal of Earth Sciences, Geologische Rundschau* 98, 1949–1970. doi:10.1007/s00531-008-0359-3
- Seeley, H.G. (1887): On the classification of the fossil animals commonly called Dinosauria. *Proceedings of the Royal Society of London* 43, 165–171.
- Sereno, P.C., Beck, A.L., Dutheil, D.B., Larsson, H.C.E., Lyon, G.H., Moussa, B., Sadleir, R.W., Sidor, C.A., Varricchio, D.J., Wilson, G.P., Wilson, J.A. (1999): Cretaceous sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. *Science* 282, 1342–1347. doi:10.1126/science.286.5443.1342
- Taylor, A.M., Gowland, S., Leary, S., Keogh, K.J., Martinus, A.W. (2013): Stratigraphical correlation of the Lourinhã Formation in the Consolação Sub-basin (Lusitanian Basin), Portugal. *Geological Journal* 49 (2), 143–162. doi:10.1002/gj.2505
- Teixeira, C., Zbyszewski, G., Torres de Assunção, C., Manuppella, G. (1968): *Notícia Explicativa da Carta Geológica de Portugal, folha 23-C (Leiria)*. Serviços Geológicos de Portugal, Lisboa, 99 p
- Tidwell, V., Carpenter, K., Brooks, B. (1999): New sauropod from the Lower Cretaceous of Utah. *Oryctos* 2, 21–37.
- Tidwell, V., Carpenter, K., Meyer, S. (2001): New titanosauriform (Sauropoda) from the Poison Strip Member of Cedar Mountain Formation (Lower Cretaceous), Utah. In D. Tanke, K. Carpenter (eds.), *Mesozoic Vertebrate Life*. Indiana University Press, Bloomington, pp. 139–165
- Tschopp, E., Mateus, O., Benson, R. (2015): A specimen-level phylogenetic analysis and taxonomic revision of Diplodocidae (Dinosauria, Sauropoda). *PeerJ* 3, e857. doi:10.7717/peerj.857
- Upchurch, P. (1995): Evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London Series B* 349, 365–390. doi:10.1098/rstb.1995.0125
- Upchurch, P., Martin, J. (2003): The anatomy and taxonomy of *Cetiosaurus* (Saurischia, Sauropoda) from the Middle Jurassic of England. *Journal of Vertebrate Paleontology* 23, 208–231. doi:10.1671/0272-4634(2003)23[208:TAATOC]2.0.CO;2
- Upchurch, P., Barrett, P.M., Dodson, P. (2004): Sauropoda. In: D.B. Weishampel, P. Dodson, H. Osmólska (eds.), *The Dinosauria II*. University of California Press, Berkeley, pp. 259–322.
- Wedel, M.J. (2003): Vertebral pneumaticity, air sacs, and the physiology of sauropod dinosaurs. *Paleobiology* 29(2), 243–255. doi:10.1666/0094-8373(2003)029<0243:VPASAT>2.0.CO;2
- Whitlock, J.A. (2011): A phylogenetic analysis of Diplodocoidea (Saurischia: Sauropoda). *Zoological Journal of the Linnean Society* 161, 872–915. doi:10.1111/j.1096-3642.2010.00665.x
- Wilson, J.A. (1999): A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology* 19 (4), 639–653. doi:10.1080/02724634.1999.10011178
- Wilson, J.A. (2002): Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society* 136, 217–276. doi:10.1046/j.1096-3642.2002.00029.x
- Wilson, J.A. (2012): New vertebral laminae and patterns of serial variation in vertebral laminae of sauropod dinosaurs. *Contributions from the Museum of Paleontology, University of Michigan* 32, 91–110.
- Wilson, J.A., Sereno, P.C. (1998): Early evolution and higher-level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology* 18 (suppl. 2), 1–68. doi:10.2307/3889325
- Wilson, J.A., Barrett, P.M., Carrano, M.T. (2011): An associated partial skeleton of *Jainosaurus cf. septentrionalis* (Dinosauria: Sauropoda) from the late Cretaceous of Chhota Simla, Central India. *Palaeontology* 54, 981–998. doi:10.1111/j.1475-4983.2011.01087.x
- Wilson, J.A., D'Emic, M.D., Ikejiri, T., Moacdieh, E.M., Whitlock, J.A. (2011): A nomenclature for vertebral fossae in sauropods and other saurischian dinosaurs. *PLoS ONE* 6(2), e17114. doi:10.1371/journal.pone.0017114
- Yadagiri, P. (2001): The osteology of *Kotasaurus yamanpalliensis*, a sauropod dinosaur from the Early Jurassic Kota Formation of India. *Journal of Vertebrate Paleontology* 21, 242–252. doi:10.1671/0272-4634(2001)021[0242:TOOKYA]2.0.CO;2
- Yagüe, P., Dantas, P., Ortega, F., Cachão, M., Santos, F.A.M., Gonçalves, R., Lopes, S. (2006): New sauropod material from the Upper Jurassic of Areia Branca (Lourinha, Portugal). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 240 (3), 313–342.
- You, H.-L., Li, D.-Q., Zhou, L.-Q., Ji, Q. (2006): *Huanghetitan liujiaxiensis*, a new sauropod dinosaur from the Lower Cretaceous Hekou Group of Lanzhou Basin, Gansu Province, China. *Geological Review* 52, 668–674.
- You, H.-L., Li, D.-Q., Zhou, L.-Q., Ji, Q. (2008): *Daxiatitan binglingi*: a giant sauropod dinosaur from the Early Cretaceous of China. *Gansu Geology* 17, 1–10.
- Zbyszewski, G. (1946): Les ossements d' découverts près de Baleal (Peniche). *Comunicações dos Serviços Geológicos de Portugal* 28, 135–144.