Turiasauria-like teeth from the Upper Jurassic of the Lusitanian Basin, Portugal

Pedro Mocho\textsuperscript{a,b,c1,*}, Rafael Royo-Torres\textsuperscript{d2}, Elisabeta Malafaya\textsuperscript{e,b3}, Fernando Escaso\textsuperscript{c,b4}, Bruno Silva\textsuperscript{b5} and Francisco Ortega\textsuperscript{c,b6}

\textsuperscript{a}Unidad de Paleontología, Universidad Autónoma de Madrid, Darwin 2, 28049 Madrid, Spain; \textsuperscript{b}Laboratório de Paleontologia e Paleoecologia, Sociedade de História Natural, Polígono Industrial do Alto do Ameal, Pav.H02 e H06, 2565-641 Torres Vedras, Portugal; \textsuperscript{c}Grupo de Biología Evolutiva, Facultad de Ciencias, UNED, c/ Senda del Rey, 9, 28040 Madrid, Spain; \textsuperscript{d}Fundación Conjunto Paleontológico de Teruel-Dinópolis/Museo Aragonés de Paleontología, Av. Sagunto s/n, E-44002 Teruel, Spain; \textsuperscript{e}Faculdade de Ciências e Instituto Dom Luiz, Universidade de Lisboa, Edificio C6, Campo Grande, 1749-016 Lisboa, Portugal

(Received 1 December 2014; accepted 7 May 2015)

Turiasauria is a clade of eusauropods with a wide stratigraphic range that could extend from the Bathonian to the lower Aptian including Turiasaurus, Losillasaurus, Zby and putatively, Galveosaurus, Atlasaurus and isolated remains from Middle Jurassic-to-Lower Cretaceous. Some are characterised by the presence of heart-shaped teeth. Several tooth occurrences from the Portuguese Upper Jurassic with this type of morphology (SI: 1.1–1.8) are reported and discussed. If this morphology is regarded as synapomorphic of Turiasauria, the teeth will be tentatively related to this clade. From a sample of 43 teeth, three main morphotypes are described. Three hypotheses might explain the morphological variation: (1) the range of tooth morphologies indicates variation in the jaw, (2) the range of tooth morphologies indicates taxonomic variation or (3) a combination of both. The general wear pattern in morphotypes I and II starts with a distal facet, then the appearance of mesial/apical facet and finally a ‘V’-shaped facet. In morphotype III, the wear begins with a mesial facet. The variability observed for Portuguese Upper Jurassic specimens is congruent with the morphological variability along the tooth row shown by other sauropods with spatulate/spoon-shaped teeth and it is considered the most parsimonious hypothesis to explain it.

Keywords: Sauropoda; Eusauropoda; Turiasauria; Upper Jurassic; Lusitanian Basin; Teeth

Introduction

The sauropods are one of the vertebrate groups better represented in the last part of the Portuguese Upper Jurassic of the Lusitanian Basin (Kimmeridgian-Tithonian). Their study improves the understanding of vertebrate faunas and their paleobiogeography in this period. Recent works suggest that Iberian sauropods are represented by endemic genera (Dantas et al. 1998; Bonaparte and Mateus 1999; Casanovas et al. 2001; Antunes and Mateus 2003; Sánchez-Hernández 2005; Royo-Torres et al. 2006; Mateus et al. 2014) closely related to groups well represented in other continents during the Upper Jurassic like brachiosaurids (Antunes and Mateus 2003; Mannion et al. 2013), diplodocids (Bonaparte and Mateus 1999; Mannion et al. 2012; Mocho, Royo-Torres, Malafaya, et al. 2014) or camarasaurs (Mocho, Royo-Torres, et al. 2014). The supposed close relationship of the Portuguese sauropods with taxa from the North American Upper Jurassic of the Morrison Formation (e.g., Lapparent and Zbyszewski 1957) is less close than it is interpreted in other dinosaur groups. In fact, there are references to genera and even species of theropods, ornithopods and stegosaurs with an amphi-Atlantic distribution (Galton 1980; Mohr 1989; Pérez-Moreno et al. 1999; Martin 2000; Mateus and Antunes 2000a; Mateus and Antunes 2000b; Ortega et al. 2006; Mateus et al. 2006; Escaso et al. 2007; Malafaia et al. 2007, 2010, In press; Ortega et al. 2009; Escaso et al. 2010).

This study analyses a sample of 43 sauropod teeth collected in several Upper Jurassic localities of the Lusitanian Basin. They are tentatively assigned to Turiasauria, a basal eusauropod clade, based on its heart-shaped morphology. The meaning of three distinct morphotypes is also discussed. Several other heart-shaped teeth from Europe and Africa are also compared with the present sample. The information provided allows to propose a stratigraphic range for this tooth morphology in the Iberian Upper Jurassic wider than was previously thought.

Turiasauria clade

Currently, in the Iberia Peninsula, there are eight sauropod species ranging from Kimmeridgian to lower Berriasian: Aragosaurus ischiaticus Sanz et al. 1987; Lourinhasaurus alenquerensis (Lapparent and Zbyszewski 1957); Dinheirosaurus lourinhanensis Bonaparte and Mateus 1999; Lusotitan atalaiensis (Lapparent and Zbyszewski 1957); Galveosaurus herreroi Sánchez-Hernández 2005; Losilla-
aurus giganteus Casanovas et al. 2001; Turiasaurus riodevensis Royo-Torres et al. 2006; and Zby atlanticus Mateus et al. 2014.

Turiasauria is defined as a stem-based taxon including all eusauropods more closely related to T. riodevensis than to Saltasaurus loricatus Bonaparte and Powell 1980 (Royo-Torres et al. 2006). Therefore, it includes Turiasaurus, Losillasaurus, Zby, ‘Neosodon’, ‘Cardiodon’ and putatively Galveosaurus (Royo-Torres et al. 2006, 2009; Royo-Torres and Cobos 2009; Royo-Torres and Upchurch 2012; Mateus et al. 2014) and Atlasaurus (Royo-Torres, Cobos, et al. 2014; Xing et al. 2015). The inclusion in Turiasauria of three Spanish sauropods from the Villar del Arzobispo Formation: Turiasaurus, Losillasaurus (Tithonian-lower Berriasian) and Galveosaurus (Tithonian-lower Berriasian) is based on some phylogenetic hypotheses (Royo-Torres et al. 2006, 2009, 2012; Royo-Torres, Upchurch, et al. 2014; Royo-Torres and Upchurch 2012; Carballido and Sander 2014; Mocho, Royo-Torres, et al. 2014). Galveosaurus has been considered in different phylogenetic positions along its history. It was considered as a cetiosaurid (Sánchez-Hernández 2005), a basal eusauropod (Canudo et al. 2006), after it was proposed as a possible neosauropod (Barco et al. 2005), suggesting first its inclusion in Diplodocoidea (Barco 2005) and later in Macronaria? (Barco et al. 2006). Galveosaurus was also considered as a non-titanosauriform macronarian (Barco 2009; Barco et al. 2009; Carballido et al. 2011; Carballido and Sander 2014; Mannion et al. 2013). D’Emic (2012) noted the possibility that the holotype material of Galveosaurus might represent more than one individual. For this author, the presence of an elongate cervical vertebra and middle caudal vertebrae with anteriorly set neural arches might relate Galveosaurus to Titanosauriformes. The presence of a rounded proximolateral corner of the humeri suggested affinities to Brachiosauridae (D’Emic 2012), but this feature is also present in basal eusauropods, in particular, in turiasaurs (e.g. Casanovas et al. 2001; Royo-Torres et al. 2006, 2009; Royo-Torres and Upchurch 2012). The discovery of more material and an accurate systematic revision will be important to obtain a more precise phylogenetic approach for this taxon.

More recently, the presence of more turiasaurian occurrences in Spain, Portugal, France, the UK, Tanzania and Morocco has been suggested (Mateus 2009; Royo-Torres et al. 2009; Royo-Torres and Cobos 2009; Santos et al. 2009; Ortega et al. 2010; Cobos et al. 2011; Mocho et al. 2012; Royo-Torres and Upchurch 2012; Mateus et al. 2014; Royo-Torres, Cobos, et al. 2014; Suñer et al. 2014; Xing et al. 2015). From Spain, an unnamed specimen from Rio de la Vega (Teruel) with postcranial material (Royo-Torres et al. 2009) and an isolated caudal vertebra from Veguiillas de la Sierra (Teruel) were related to Turiasaura (Royo-Torres et al. 2008). Both specimens come from the Villar del Arzobispo Formation, considered as Tithonian-lower Berriasian in age (Mas et al. 1984, 2004). Also, Canudo et al. (2010) refer to cf. Turiasaurus riodevensis a fragment of a dentary with some teeth from the Kimmeridgian of Asturias (Spain).

The first evidence of turiasaurian remains in the Lusitanian Basin was based on an isolated tooth (Royo-Torres et al. 2006, 2009) from Alcóbaça Formation (Kimmeridgian). Subsequently, Mateus (2009) referred to Turiasaurus riodevensis, an incomplete specimen composed by an almost complete hindlimb associated with a scapula, a coracoid, a tooth and a middle chevron, collected in Vale de Pombas (ML 368). This specimen was firstly related to Camarasaurus (Mateus 2005), but a recently systematic revision established a new genus and species, Zby atlanticus, which was tentatively placed within Turiasauria as a closely related form to Turiasaurus riodevensis (Mateus et al. 2014). Ortega et al. (2010) assigned to Turiasaurus some teeth collected on the region of Torres Vedras (Portugal) from the upper Kimmeridgian-Tithonian sediments of the Freixial Fm. and Praia de Amoreira-Porto Novo Fm. Santos et al. (2009) described a new ichnospecies (Polyonyx gomesi Santos et al. 2009) in the Galinha tracksite from the Middle Jurassic of the Maciço Calçário Estremeno (Portugal) that they related to a basal eusauropod, probably a form within the Turiasauria clade. If these footprints belong to Turiasaura, they would be, for now, one of the most ancient occurrences for this clade, together with some teeth from the UK (see Royo-Torres and Upchurch 2012). This ichnospecies might also be present in the Villar del Arzobispo Fm. So far, no trackway has been described, but some isolated manus and pes has been related with Polyonyx (Cobos et al. 2008; Royo-Torres 2009; Santos et al. 2009) in two sites from the El Castellar locality in Teruel (Spain).

Several teeth collected in the Middle and Upper Jurassic of UK and in the Upper Jurassic of France were also related to Turiasauria due the similarities shared with the Iberian heart-shaped teeth (Royo-Torres et al. 2006, 2009, Royo-Torres, Cobos, et al. 2014; Royo-Torres and Upchurch 2012), particularly the teeth of ‘Neosodon’ (Moussaye de la 1885; Buffetaut and Martin 1993) and ‘Cardiodon rugulosus’ (1841 (Owen 1841, 1844, 1875), three Middle Jurassic teeth from Peterborough (the UK) assigned to ‘Cetiosaurus leedsi’ (NHMUK R3377, Hulke 1887) and five teeth from the Upper Jurassic of Aylesbury (the UK) previously assigned to ‘Hoplosaurus’ and ‘Pelorosaurus’ (one numbered NHMUK R2004–5 and three numbered NHMUK R2565; Lydekker 1893; Woodward 1895).

More recently, the reassessment of some Gondwanan sauropods from Tendaguru Formation (Tithonian) in Tanzania could provide evidence for the presence of Turiasauria in Gondwana during the Upper Jurassic, suggesting a wider paleobiogeographic range than previously thought. Royo-Torres and Cobos (2009) and
Royo-Torres, Cobos, et al. (2014) related to Turiasauria a complete right manus (HMN MB.R.2093.1-12), a partial caudal series described by Bonaparte et al. (2000, HMN MB.R.2091.1-30), an astragalus (HMN MB.R.2095.6) and a humerus (HMN MB.R.2910). Royo-Torres, Cobos, et al. (2014) and Xing et al. (2015) also suggested the placement of *Atlasaurus* from the Middle Jurassic (Bathonian-Callovian) of Morocco inside Turiasauria.

**Geological settings**

The described teeth were mainly collected northwestern of Lisbon, along the coastal cliffs between the localities of Cambelas and Praia da Gralha in Torres Vedras, Lourinhã, Caldas da Rainha, Alcobaca and Peniche municipalities (Figure 1). In this area, outcrops an Upper Jurassic to Lower Cretaceous sedimentary sequence, deposited in the Lusitanian Basin. The Upper Jurassic beds are dated from middle Oxfordian to the base of Cretaceous (Schneider et al. 2009), and represent a third rifting episode (Rasmussen et al. 1998, Kullberg et al. 2006) marked by an internal differentiation resulting in the formation of several sub-basins (Turcifal, Arruda and Bombarral 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 on

![Geological map](image)

**Figure 1.** Geological map (adapted from Oliveira et al. 1992) showing the Portuguese Mesozoic levels and the localities from where come the studied heart-shaped teeth. The number in parenthesis is the number of teeth found in each locality.
Different stratigraphic approaches have been proposed for the Upper Jurassic sequence of these sub-basins (e.g. Hill 1988; Leinfelder 1993; Manuppella et al. 1999; Kullberg et al. 2006; Schneider et al. 2009; Martinius and Gowland 2011; Taylor et al. 2014; see Figure 2). The teeth described were found in sediments from several Upper Jurassic formations of the Lusitanian Basin, including Montejunto (?), Alcobaca, Praia da Amoreira-Porto Novo, Sobral, Freixial and Bombarral Formations. All of them, except the Montejunto Fm., were included in the Lourinha Group proposed by Yaguë et al. (2006). One of the first references of this tooth morphology in the Portuguese Upper Jurassic was found near Ourém (MG 16, Sauvage 1897–98), probably from Montejunto Fm. or Alcobaca Fm, upper Oxfordian or Kimmeridgian-basal Tithonian in age, respectively (Mouterde et al. 1979; Manuppella et al. 1999, 2000)

Most of the teeth come from the ‘Lourinha Formation’ (unit proposed by Hill 1988), which includes the Praia da Amoreira-Porto Novo (included in the Alcobaca Beds sensu Manuppella et al. 1999), Sobral, Freixial and Bombarral Formations (Manuppella et al. 1999) (Figure 2). Figure 2 shows the correspondences among some stratigraphic approaches as well as the stratigraphic position of the teeth analysed here. “Lourinha Formation” sensu Hill (1988) is interpreted as upper Kimmeridgian-basal Berriasian in age (Leinfelder 1986; Hill 1988; Leinfelder and Wilson 1989; Mohr 1989; Manuppella et al. 1999). This unity was subdivided in five members by Hill (1988) that in part corresponds to the formations proposed by Manuppella et al. (1999) (see Figure 2). The Sobral Fm. (= Praia Azul member of Lourinha Fm. sensu Hill 1988) is a relatively well-dated unit, upper

| Cm | Turcifal sub-basin | Bombarral sub-basin | Coastal region Porto da Calada-Salir do Porto | * | Alcobaca Region | Morphotypes |
|----|--------------------|---------------------|---------------------------------------------|---|----------------|-------------|
| L  | Porto da Calada Fm.| Serreira Fm.        | Torres Vedras Fm.                            |   |                | CPT:121,3    |
| U  | Freixial Fm.       | Bombarral Fm,**     | Santa Rita mb.                               |   |                | SHN (JJS) 140|
| M  | Sobral Fm.         | Sobral Fm.          | Praia Azul mb.                               |   |                | SHN 503, 506|
| U  | Amural Fm.         | Praia da Amoreira-Porto Novo Fm. | Porto Novo mb. | | | SHN 144, 153 |
| L  | Abadia Fm.         | Consolação Fm.      | Praia da Amoreira mb.                         |   |                | SHN 138, 145,150, 506|

Figure 2. Stratigraphic correlation between the nomenclature proposed for Turcifal sub-basin (based on Pereda-Suberbiola et al. 2005; Kullberg et al. 2006; Schneider et al. 2009), Bombarral sub-basin (based on Manuppella et al. 1999), the coastal sector from Porto da Calada to Salir do Porto (based on Hill 1988) and Alcobaca region (based on Kullberg et al. 2006; Azeredo et al. 2010), and the respective stratigraphic position of the described teeth by morphotype. Cm, Chronostratigraphy; U, upper; M, middle; L, lower; *sensu Yaguë et al. 2006; **other formations are identified in Lourinha region by Manuppella et al. 1999 as lateral correlatives of Bombarral Fm.
Kimmeridgian to lower Tithonian in age (Fürsich 1981). It is also important to refer that the coastal sedimentary sequence south of Sizandro river mouth, which corresponds to the transition of Sobral Fm. and Freixial Fm. (Assenta member of Hill 1988), is progressively younger to the south, with a stratigraphic range from lower to upper (? ) Tithonian (Leinfelder 1988; Hill 1988; Schneider et al. 2009). Some teeth were found in the coastal cliffs of Salir do Porto and São Martinho do Porto and in Fervença locality where outcrops the Alcobaça Fm. (sensu Camarate França and Zbyszewski 1963; Azeredo et al. 2010). The Alcobaça Fm. in Salir do Porto was dated to the lower Kimmeridgian (Schneider et al. 2009). Considering the inclination of strata and the present cartographic data, it is reasonable to consider a younger age to Serra do Bouro outcrops, probably middle (? ) Kimmeridgian to Tithonian, where Alcobaça Fm. transits to the Bombarral Fm., near Boavista do Bouro locality (Camarate França and Zbyszewski 1963; Azeredo et al. 2010). The Tithonian Bombarral Fm. is on the top of the upper Kimmeridgian-to-lower Tithonian Sobral Fm. in Bombarral and Turcifal sub-basins (Manuppella et al. 1999). Summarising, all the analysing heart-shaped teeth from Portugal are recorded from the upper Oxfordian (?) to the lower-to-upper Tithonian on the Upper Jurassic of the Lusitanian Basin.

**Anatomical abbreviations**

Awf, apical wear facet; bwf, wear facet at the base of the crown; cwf, carina wear facet; lag, labial groove; lic, lingual crest; SI, slenderness index, “v” wf, “V”-shaped wear facet.

**Institutional abbreviations**

BHN, Muséum d’Histoire Naturelle de Boulogne-sur-Mer, Boulogne-sur-Mer, France; FCPT-D, Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain (plus CPT for the fossil material deposited in the museum [Museo Aragónés de Paleontología]); HMN, Humboldt Museum für Naturkunde, Berlin, Germany; MG, Museu Geológico do Laboratório Nacional de Energia e Geologia, Lisboa, Portugal; ML, Museu da Lourinhã, Lourinhã, Portugal; MNHN, Muséum National d’Histoire Naturelle, Paris, France; MUJA, Museo del Jurásico de Asturias, Asturias, Spain; NHMUK, Natural History Museum, London, UK; SHN, Sociedade de História Natural, Torres Vedras, Portugal (plus [JJS] for the José Joaquim collection deposited in the Sociedade de História Natural).

**Systematic Paleontology**

Dinosauria (Owen 1841); Saurischia (Seeley 1887); Sauropoda (Marsh 1878); Eusauropoda (Upchurch 1995); ?Turasauria (Royo-Torres et al. 2006)

**Material**

Forty-three complete and partial preserved teeth: SHN (JJS) 127–133, 135, 136, 139–142, 146–149, 151, 154, 504; SHN 134, 137, 138, 143–145, 150, 152, 153, 501–503, 505–512; MG 16, 277, 4832. (Table 1)

**Description of general morphology**

Each tooth crown has a heart-shaped spoon-like morphology, compressed labiolingually and presenting an enamel with wrinkled texture. In generally, the crown is slightly apicomesially projected and the teeth reach the maximum mesiodistally width near the base of the apex (the apex is considered herein as the apical portion of the tooth, apical to the sagittal deflection of mesial and distal edge). Excluding the most worn teeth, the slenderness index (SI: crown height/maximum crown breadth; sensu Upchurch 1998) ranges between 1.1 and 1.8.

On the labial face, the teeth display an apicobasal bulge bounded by shallow grooves with the same orientation. The lingual face has a low apicobasal ridge, which might extend along the entire apicobasal length. The mesial and distal edges are not parallel and diverge from the base of the tooth. The transition between the row and crown is marked in all the teeth. The teeth exhibit asymmetrical ‘D’ to lenticular-shaped cross section with a strongly convexity labial face and a flat-to-smooth concave lingual face. The maximum labiolingual width is located near the mesial edge, resulting in steeply angled mesial part on labial surface. The asymmetrical apex deflects distally and could bear mesial, distal and apical wear facets depending of the wear development. The mesial and distal edges of the apex are straight to slightly convex and concave, respectively, in labial/lingual view. Generally, the distal edge of the apex is longer than the mesial one (excluding the morphotype III, see below). Crown-to-crown occlusion produced “V”-shaped wear facets. Some teeth are heavily worn and, in some cases, it is possible to observe the dentine. The wear facets will be commented in detail after the definition and description of the three proposed morphotypes.

The wrinkling pattern of the enamel is similar to those present in several spatulate- or spoon-like teeth (e.g. Camarasaurus, Turiasaurus, “Neosodon”) marked by an alternation between apicobasal and waved grooves and ridges. Along its length, these ridges join together forming an anastomosed pattern. This pattern is smoother at the tip of the apex probably because of abrasion, like in other sauropod teeth (e.g. Amygdalodon, Carballido and Pol 2010).

**Definition of the morphotypes**

Despite a general morphology shared by every studied tooth, a division into three different morphotypes is
Table 1. Studied heart-shaped teeth from the Portuguese Upper Jurassic (see appendix 1 to measurements).

| Locality                  | Formation*                      | Age                  | Wear        | Morphotype | SI  |
|---------------------------|---------------------------------|----------------------|-------------|------------|-----|
| Valmitão Norte            | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Moderate   | III or II  | 1.21|
| Praia dos Frades          | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Absent/weak | III        | 1.12|
| Praia de Pedrogãos        | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Strong     | ?          | ?   |
| Praia de Pedrogãos        | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Strong     | II         | 1.12|
| Praia dos Frades          | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Moderate   | I          | 1.54|
| São Bernardino            | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Moderate   | I          | 1.41|
| Valmitão Norte            | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Absent/weak | I          | ?   |
| Valmitão Norte            | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Moderate   | II         | 1.32|
| Porto das Barcas          | Sobral Fm.                      | Upper Kimmeridgian-lower Tithonian | Moderate   | ?          | ?   |
| Praia da Corva            | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Moderate   | III        | 1.30|
| Cambelas                  | Freixial Fm.                    | Tithonian            | Absent/weak to moderate | I       | 1.81|
| Baleal                    | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Moderate   | II         | 1.39|
| Praia da Corva            | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Absent/weak | I          | 1.55|
| Salir do Porto            | Alcobaça Fm.                    | Lower Kimmeridgian   | Absent/weak | III        | ?   |
| Salir do Porto            | Alcobaça Fm.                    | Lower Kimmeridgian   | Absent/weak | II         | 1.43|
| ?                         | ?                               | ?                    | Moderate    | II         | 1.41|
| ?                         | ?                               | ?                    | Strong      | III        | 1.06|
| Salir do Porto            | Alcobaça Fm.                    | Lower Kimmeridgian   | Moderate    | ?          | ?   |
| Salir do Porto            | Alcobaça Fm.                    | Lower Kimmeridgian   | Absent/weak | ?          | ?   |
| Salir do Porto            | Alcobaça Fm.                    | Lower Kimmeridgian   | Absent/weak | ?          | ?   |
| Valmitão                  | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Absent/weak | ?          | ?   |
| São Bernardino            | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Absent/weak | III        | 1.23|
| Porto Novo                | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Absent/weak | II         | 1.42|
| Valmitão Norte            | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Moderate   | ?          | 1.41|
| Porto Dinheiro            | Sobral Fm.                      | Upper Kimmeridgian-lower Tithonian | Absent/weak | II        | 1.33|
| Praia da Corva            | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Moderate (?)| II        | ?   |
| Serra do Bouro            | Bombarral Fm.                   | Tithonian            | Moderate    | II         | ?   |
| Serra do Bouro            | Bombarral Fm.                   | Tithonian            | Moderate    | I or II    | 1.66|
| Porto Dinheiro            | Sobral Fm.                      | Upper Kimmeridgian-Tithonian | Absent/weak | II        | ?   |
| Praia da Gralha           | Alcobaça Fm.                    | Lower Kimmeridgian   | Moderate    | I          | ?   |
| Foz do Arelho             | Bombarral Fm.                   | Tithonian            | Absent/weak | I          | ?   |
| Foz do Arelho             | Bombarral Fm.                   | Tithonian            | Moderate    | II         | 1.30|
| Valmitão Sul              | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Absent/weak | III(?)     | ?   |
| Valmitão Norte            | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Moderate to strong | II | ? |
| Valmitão Sul              | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Moderate   | ?          | ?   |
| Serra do Bouro            | Bombarral Fm.                   | Tithonian            | Absent/weak | II         | 1.34|
| Valmitão Sul              | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Absent/weak | II         | 1.32|
| Praia da Corva            | Praia de Amoreira-Porto Novo Fm.| Upper Kimmeridgian-basal Tithonian | Strong     | ?          | ?   |
| ?                         | ?                               | ?                    | ?           | II         | ?   |

(Continued)
here proposed. Nevertheless, the absence of clear morphological limits between the described morphotypes indicates that these could represent a gradient of morphological variation of the same taxonomic unit (see discussion below). Morphometric analyses were discarded because the original tooth morphology is obliterated in most of the preserved teeth by a significant worn. SHN (JJS) 127, 129, 136, 151, 154 and 504, SHN 134, 143, 152, 507, 510 and MG 16 and 277 could not be assigned to any of the morphotypes due to their preservation state or by the presence of severe worn.

| Locality            | Formation* | Age              | Wear           | Morphotype | SI |
|---------------------|------------|------------------|----------------|-------------|----|
| Foz de Areiho       | Bombarral Fm. | Tithonian       | Absent/weak   | II          | 1.47 |
| São Martinho do     | Alcobaça Fm. | Lower Kimmeridgian | Moderate      | II          | 1.48 |
| Porto               |            |                  |                |             |     |
| Fervença            |            | Lower Kimmeridgian |               |             |     |
| Ourem               |            | Middle-to-upper Oxfordian or Kimmeridgian-basal Tithonian |             |     |

Notes: The stratigraphic information is based on Manuppella et al. (1999), Kullberg et al. (2006) and Azeredo et al. (2010).

Table 1 – continued

Figure 3. Heart-shaped teeth assigned to the morphotype I. SHN (JJS) 140 in apical (a.I), lingual (a.II), labial (a.III), distal (a.IV) and mesial (a.V) views; SHN (JJS) 142 in apical (b.I), lingual (b.II), labial (b.III), mesial (b.IV) and distal (b.V) views; SHN (JJS) 132 in apical (c.I), lingual (c.II), labial (c.III), mesial (c.IV) and distal (c.V) views; SHN (JJS) 133 in labial (d.I) and lingual (d.II) views; and SHN 501 in labial (e.I) and lingual (e.II) views. Scale bar = 1 cm; grey circle = absent/weak worn; delimited grey circle = moderate worn; black circle = strongly worn.

Morphotype I (SHN (JJS) 131, 132, 133, 140, 142; SHN 501, 502, see Figure 3): The heart-shaped crowns are more apicobasally elongated and labiobasally compressed than the morphotypes II and III. They also bear the higher SI values, ranging between 1.8 and 1.6 (teeth with moderate wear have lower SI values, around 1.5–1.4). The labial face is markedly convex mesiodistally and weakly convex apicobasally. The lingual face is concave apicobasally and mesiodistally and the lingual crest can occupy all the apicobasal extension. In this morphotype, mesial and distal edges in the base of crown are closely parallel and straighter than in the
other two morphotypes. The apex is particularly longer in these teeth. It occupies one half or more than the total crown height (apex/crown height ratio $> 0.5$). In this morphotype, the apex presents a slight distal deflection, which is not so pronounced as in the morphotype II. The distal edge of the apex is concave and the mesial one is convex-to-straight. Both are criteria for the orientation of these teeth.

**Morphotype II** (SHN (JJS) 130, 135, 141, 147, 148; SHN 138, 144, 145, 150, 153, 503, 506, 508, 509, 511, 512, see Figure 4): It is more abundant in the sample, with a well-defined heart-shaped outline, crown projected apicomesially and a more pronounced curvature of the apex than in the morphotype I. This morphotype bears intermediate SI values, ranging between 1.5 and 1.3 (teeth with moderate or strong wear could reach a SI next to 1.2). The lingual surface is not so concave as the morphotype I. The lingual crest does not reach the base of the crown that develops a flat-to-convex mesiodistal platform. This platform is not so well individualised from the remaining lingual surface by a marked cingulum as that occurs in *Camarasaurus, Mamenchisaurus* or *Euhelopus* tooth (e.g. Suteethorn et al. 2013). Unlike morphotype I, the mesial and the distal edges of the crown are basally convex, resulting from a mesiodistal basal expansion of the crown. The apex is shorter than in morphotype I (apex/crown height ratio ranging between $= 0.5$ and 0.38).

**Morphotype III** (SHN (JJS) 128, 139, 146, 149; SHN 137, and SHN 505 with doubt, see Figure 5): This corresponds to heart- to subsquared-shaped teeth more compressed labiolingually and shorter than the other two morphotypes (SI $< 1.3$). The labial face is not so convex as in morphotypes I and II. The lingual face is concave apicobasally and flat-to-concave mesiodistally with a similar platform at the base of the crown as that occurs in the morphotype II, but less pronounced. The lingual apicobasal crest in this morphotype is incipient-to-absent. On the distal edge, in the transition between the apex and the base of the crown, there is a round shoulder lingually projected resulting from the concavity of the distal edge of the apex. Unlike morphotypes I and II, the distal edge is shorter than the mesial edge. The apex is shorter than in morphotypes I and II (apex/crown height ratio $< 0.3$). SHN (JJS) 139 (Figure 5(a)) presents a morphology between morphotypes II (SI higher than morphotype III) and III (apex shorter than morphotype II), but it is considered here as morphotype III because of the presence of a short apex.

**Wear pattern**

The sample presents variable wear patterns. We consider here three main states of wear: (i) absent or weak, without wear facets (e.g. Figure 4(a),(c),(e)), probably non-functional teeth, or teeth with marked mesial wear facets, but sometimes with a slight worn on the distal edge of the apex (e.g. Figures 3(b), 4(d) or 5(c)); (ii) moderate, wear facets in both edges of the apex and an incipient (Figures 3(d) and 4(b)) or well-marked (e.g. Figures 3(c), 4(h), 6(b), 10(d)–(e)) apical wear facet; (iii) strong, the three wear facets are fused in a unique ‘V’-shaped wear facet (Figure 6(d),(e),(f)). The wear facet on the distal edge is generally longer and more developed than the mesial one, except in the teeth of morphotype III. As far as can be checked, the wearing in morphotypes I and II begin in the distal edge (Figure 3(b) and 4(d)). In less worn teeth, the distal wear is always present and when the mesial one is also present, the distal one is more developed than the mesial one. In a more advanced wear state (moderate), the distal facet becomes more pronounced and the mesial one becomes well defined. An incipient-to-marked apical wear facet is generally associated with moderately worn teeth (e.g. SHN (JJS) 140 or SHN 508; Figures 3(a) and 4(b)). In more advanced stages of wear (strong wear), the mesial, distal and apical facets produce a unique ‘V’-shaped facet (SHN (JJS) 129 or SHN (JJS) 130, Figure 6). The morphotype III teeth show a different condition from the previous morphotypes: the wearing starts in the mesial edge, as in SHN 137 (Figure 5(c)).

Generally, teeth with incipient wear present wear facets with high lingual or labial inclination (almost vertical). More developed wear facets become progressively more subhorizontal (e.g. SHN (JJS) 141). In almost all studied teeth, the wear facets slope lingually, which might suggest a maxillary/premaxillary position (see Nowinski 1971, Calvo 1994, Barrett and Upchurch 1994, Upchurch and Barrett 2000, Carballido and Pol 2010). In SHN (JJS) 140, 141 and 148, the mesial and distal wear facets slope lingually. Nevertheless, on these teeth, the apical wear facet faces labially, what could suggest a mandibular position. In conclusion, the wear pattern in morphotypes I and II begins with the appearance of a distal facet (e.g. SHN (JJS) 142, SHN 138), and then the mesial and apical facets appear (e.g. SHN (JJS) 140, SHN 508) and finally a ‘V’-shaped facet develops. In morphotype III, the wear begins with a mesial facet (SHN 137), and then appear a distal and apical facets (SHN (JJS) 139) a finally a ‘V’-shaped facet (SHN (JJS) 149). Additionally, in some teeth, it is possible to observe a wear facet on the medial/distal side of the base (e.g. SHN (JJS) 148, Figure 6(d)).

**Discussion**

Enamel-wrinkled texture, crown overlapping, spoon-shaped crowns and “V”-shaped wear facets were traditionally considered as synapomorphic traits of eusauropod teeth (Wilson and Sereno 1998). Nevertheless,
Figure 4. Heart-shaped teeth assigned to the morphotype II. SHN (JJS) 147 in apical (a.I), lingual (a.II), labial (a.III), distal (a.IV) and mesial (a.V) views; SHN 508 in apical (b.I), lingual (b.II), labial (b.III), distal (b.IV) and mesial (b.V) views; SHN 144 lingual (c.I), labial (c.II), distal (c.III) and mesial (c.IV) views; SHN 138 in apical (d.I), lingual (d.II), labial (d.III), distal (d.IV) and mesial (d.V) views; SHN 512 in apical (e.I), lingual (e.II), labial (e.III), mesial (e.IV) and distal (e.V) views; SHN 145 in apical (f.I), lingual (f.II), labial (f.III), distal (f.IV) and mesial (f.V) views; SHN 503 in apical (g.I), lingual (g.II), labial (g.III), distal (g.IV) and mesial (g.V) views; SHN (JJS) 141 in apical (h.I), lingual (h.II), labial (h.III), distal (h.IV) and mesial (h.V) views. Scale bar = 1 cm; grey circle = absent/weak worn; delimited grey circle = moderate worn; black circle = strongly worn.
recent works show that these features appear earlier than expected in sauropod evolution (e.g. Upchurch, Barrett, et al. 2007; Upchurch, Barrett, Xijin, et al. 2007; Yates 2007; Allain and Aquesbi 2008; Carballido and Pol 2010). Regardless of the morphological variability of the discussed teeth, we might tentatively relate these teeth to the Turiasauria clade based on the presence of the following diagnostic features proposed by Royo-Torres et al. (2006): (i) heart-shaped crowns; (ii) a pointed and asymmetrical apex that is strongly compressed labiolingually and (iii) crowns with convex labial surfaces with a bulge extending apicobasally. A pointed and asymmetrical apex that is strongly compressed labiolingually is well developed in Turiasaurus and the rest of the Iberian heart-shaped teeth. Giraffatitan also present a similar morphology for the apex (Janensch 1936). Crowns with convex labial surfaces with a bulge extending apicobasally are also shared with Amygdalodon (Carballido and Pol 2010), Patagosaurus (Bonaparte 1986) and Tazoudasaurus (Allain and Aquesbi 2008). Finally, besides the presence of several isolated heart-shaped teeth along the Middle Jurassic to Early Cretaceous, at the moment, the heart-shaped tooth morphology is exclusively related with the turiasaurs Turiasaurus (Royo-Torres et al. 2006; Royo-Torres and Upchurch 2012), Zby (Mateus et al. 2014) and a turiasaurian specimen with cranial and postcranial material from Villar del Arzobispo (Cobos et al. 2011).

Heart-shaped morphology with pointed and asymmetrical apex that is strongly compressed labiolingually results in a so far exclusive combination of Turiasauria. The Turiasaurus riodevensis teeth (Royo-Torres et al. 2006; Royo-Torres and Upchurch 2012) are particularly similar to those of the morphotype II identified in the Portuguese Upper Jurassic, and some of them are virtually indistinguishable. The phylogenetic revision of the Iberian turiasaurs is in progress, which will include some new specimens, and will provide new information about the phylogenetic distribution of these characters along the eusauropod evolutionary history.

The SI values of our sample range between 1.1 and 1.8 and are probably related with the tooth morphology: lower, intermediate and higher SI values correspond to morphotypes III, II and I, respectively. This index was defined by Upchurch (1998) and it has been used to compare taxa and to understand evolutionary trends in teeth morphology and feeding mechanisms (e.g. Salgado and Calvo 1997; Barrett et al. 2002; Barrett and Wang 2007; Wilson and Upchurch 2009; Chure et al. 2010; Mannion 2010; Saegusa and Tomida 2011). Several eusauropods and basal macronarians with spoon-
spatulate-shaped teeth bear SI ranges with the same magnitude (see Supplementary material of Chure et al. 2010).

Modified from Chure et al. (2010), in Figure 7 we plotted the logged SI values found in the Portuguese Upper Jurassic heart-shaped teeth (excluding teeth with strong wear) together with other sauropodomorphs. The average for SI in *Turiasaurus* teeth (1.25) and in the Portuguese specimens (1.40) is slightly different, probably due to the size of the sample (three teeth) for *Turiasaurus*, which is composed by teeth with a morphology close to those of the morphotype II. Nevertheless, the SI average of *Turiasaurus* fits in the range of the Portuguese Upper Jurassic heart-shaped teeth. The SI range of our sample does not show any particular trend and they set within the morphospace occupied by non-neosauropod sauropods (Figure 7) as well as, *Turiasaurus* teeth. The presence of SI values close to 1 fits the morphotype III outside the morphospace occupied by the non-neosauropod sauropods.

We also plotted the Log_{10} SI for Sauropodomorpha, non-neosauropod eusauropods and five sauropod clades: Diplodocoidea, Brachiosauridae, Euhelopodidae and Lithostrotia (using Chure et al. 2010; D’Emic et al. 2013 data; see Appendix 2) versus the number of genera that have teeth included in our data (Figure 8). *Turiasaurus riodevensis* and the Portuguese Upper Jurassic heart-shaped are plotted together and they show a narrow range.

Figure 6. Heart-shaped teeth with marked worn. SHN (JJS) 131 in apical (a.I), lingual (a.II), labial (a.III), mesial (a.IV) and distal (a.V) views; SHN 152 in apical (b.I), lingual (b.II), labial (b.III), distal (b.IV) and mesial (b.V) views; SHN (JJS) 127 in apical (c.I), lingual (c.II), labial (c.III), distal (c.IV) and mesial (c.V) views; SHN (JJS) 148 in apical (d.I), lingual (d.II), labial (d.III), mesial (d.IV) and distal (d.V) views; SHN (JJS) 130 in apical (e.I), lingual (e.II), labial (e.III), mesial (e.IV) and distal (e.V) views; SHN (JJS) 129 in apical (f.I), lingual (f.II), labial (f.III), mesial (f.IV) and distal (f.V) views. Scale bar = 1 cm; grey circle = absent/weak worn; delimited grey circle = moderate worn; black circle = strongly worn.
than diplocoids, brachiosaurids or mamenchisaurids (a narrow range of the former two groups was previously noted by D’Emic et al. 2013).

Ortega et al. (2010) have already related SHN (JSS) 139 (Figure 4(a)) and 140 (Figure 3(a)) to *Turiasaurus*. Royo-Torres et al. (2006, 2009) included in Turiasauria a tooth housed in the Museu Geológico (MG 4832, Figure 9(a)) from the Alcobaca Formation in São Martinho do Porto (lower Kimmeridgian), as well as a tooth (MUJA-0635) found in the Upper Jurassic of Asturias (Spain) (Martínez et al. 2000). Mateus (2009) assigned as *Turiasaurus riodevensis* a tooth and postcranial material (ML 368) found in Vale das Pombas (Lourinhã), previously related with *Camarasaurus* (Mateus 2005), and now part of the *Zby atlanticus* holotype (Mateus et al. 2014). Two other sauropod teeth referred by Sauvage (1897–98) as ‘*Pelorosaurus humerocristatus*’ (Hulke 1874) found in Fervença (MG 277, Figure 9(a)) (lower
Kimmeridgian, Alcobac Fm.) and Ourém (middle-to-upper Oxfordian, Montejunto Fm. or Kimmeridgian-basal Tithonian, Alcobac Fm.) (MG 16, Figure 9(b)), also bear a heart-shaped morphology.

Royo-Torres et al. (2006, 2009) also included in Turiasauria the heart-shaped teeth related to 'Neosodon' (invalid taxon according to Upchurch et al. 2004) from the Tithonian of France (figured in Buffetaut and Martín 1993). Royo-Torres et al. (2009) distinguished them from Turiasaurus because they exhibit a more concave lingual face and a greater apicobasal development in the terminal part of apex, a feature shared with the herein proposed morphotype I. In fact, it is possible to identify, at least, two of the three morphotypes defined in this study, morphotypes I (BHN2R 113 and BHN2R 1102) and II (BHN2R 1101) (see figured teeth in Buffetaut and Martín 1993). Buffetaut and Martín (1993) also assigned to 'Neosodon' the teeth found in Fervença and Ourém, referred earlier. The morphological features present in the heart-shaped teeth of the French Upper Jurassic are not diagnostic and they share their overall morphology with heart-shaped teeth of Iberian Upper Jurassic (e.g. Royo-Torres et al. 2006; Mateus et al. 2014; this work) or the Middle/Upper Jurassic of the UK (Figure 10(a)–(c),(e); Royo-Torres and Upchurch 2012) and the Lower Cretaceous of France (Néraudeau et al. 2012) and the UK (e.g. Figure 10(d), Lydekker 1888, 1889; Upchurch et al. 2011). 'Neosodon' must be considered an invalid taxon because of the absence of diagnostic features. The teeth should not be used as infrageneric determinations as noted, for example, Canudo et al. (2002) or García and Cerda (2010). The SI for 'Neosodon' teeth (= 1.26–1.64) was obtained using the figured specimens on Buffetaut and Martín (1993), and fits in the SI range of Portuguese heart-shaped teeth.

Buffetaut and Martín (1993) also warn for the similarities among 'Neosodon' teeth and the Cardiodon tooth from the British Bathonian. The specimen of Cardiodon figured in Owen (1844, 1875) shows a similar morphology to that found in Turiasaurus and 'Neosodon', which allowed Royo-Torres et al. (2006, 2009) to consider it as a Turiasauria member. Cardiodon is included in Eusauropoda because it has teeth with a broad spatulate outline, wrinkled enamel and a groove on the labial surface near the distal margin (Upchurch et al. 2004). The name Cardiodon has been retained because some authors consider that there are is distinct character to all other known spoon-like sauropod teeth: mildly convex lingual face (Upchurch and Martin 2003; Upchurch et al. 2004; Mannion 2010). However, there are other sauropods with
spoon-shaped teeth that also bear a convex lingual face, such as *Amygdalodon* (Carballido and Pol 2010). Furthermore, the heart-shaped teeth discussed here have a transversely convex lingual face at the base of the crown, which becomes transversely flat to slightly concave apically. This condition is also observed in a tooth referred to ‘*Cardiodon rugolosus*’ (Steel 1970; Upchurch and Martin 2003; NHMUK R1527) which has a transversely convex lingual face at the base of the crown and transversely flat to slightly concave lingual face apically. Taking into account the absence of a detailed description and figuration of this tooth, which allows testing the exclusivity of *Cardiodon* tooth morphology, and the loss of this specimen, we regard *Cardiodon* as *nomina dubia*, till the discovery of the type specimen or related information. Three teeth from the Lower Oxford Clay (middle Callovian) of Cambridgeshire (Martill 1988; Barrett 2006) previously assigned to ‘*Cetiosauriscus leedsi*’ (NHMUK R3377, Figure 10(b),(c)) also preserve a heart-shaped morphology previously related to Turiasauria (Royo-Torres and Upchurch 2012). Several specimens referred to ‘*Hoplosaurus*’ and ‘*Pelorosaurus*’ from the Upper Jurassic of the UK (NHMUK R2822, NHMUK R2565, NHMUK R2004-5, Figure 10(a),(e)) also fit in the general morphology here described.

Buffetaut and Martin (1993) pointed the similarities between ‘*Neosodon*’ and *Camarasaurus* teeth. Furthermore, Mateus (2005) related preliminary the Zby holotype with a heart-shaped tooth to *Camarasaurus* genus. However, it is possible to identify some differences in
Camarasaurus teeth (e.g., Osborn and Mook 1921; Ostrom and McIntosh 1966; McIntosh et al. 1996): (i) generally higher than heart-shaped teeth (SI: 1.53–2.447 sensu Chure et al. 2010); (ii) distal and mesial edges are straight and almost parallel in the base of the crown, while just the morphotype I of the heart-shaped teeth shows some degree of straightness and parallelism; (iii) the former shows shorter apices; (iv) Camarasaurus bears lingual facets and a marked and complex cingulum on the lingual face; (v) a lingual crest that appears only in the apex sector; (vi) lack of heart-shaped morphology that probably characterises the Turiasauria clade (the heart-shaped morphology fits in the spoon-shaped morphology and Camarasaurus was characterised by a spatulate-shape morphology); (vii) lingual projection of apex more pronounced than heart-shaped teeth; (viii) the labial face of the apex is more inflated and globose in Camarasaurus teeth. The most distal teeth of Camarasaurus could share some of these features with heart-shaped teeth.

In Europe, the heart-shaped morphology is not exclusive from the Middle and Upper Jurassic, being identified a few occurrences in the Lower Cretaceous. From Hauterivian-Barremian sediments of Anargac, in France, were found heart-shaped teeth (Néraudeau et al. 2012). Néraudeau et al. (2012) noted the similarities between the morphology of these teeth with Turiasaurus riodevensis and other Jurassic and Cretaceous occurrences. In the UK and Spain, there are also some heart-shaped teeth occurrences: (i) the Lower Cretaceous tooth figured in Lydekker (1889, NHMUK R1610, Figure 10(d)) from Wealden Group dated to Barremian-lower Aptian (Naish and Martill 2001), (ii) the holotype of Oplosaurus armatus Gervais 1852 from the Lower Cretaceous of the Isle of Wight (Figure 10(h); NHMUK R964, Wessex Formation, Lydekker 1888; Upchurch et al. 2011), and (iii) two teeth (CPT-678 and PBA-2) from the Hauterivian-Barremian (El Castellar Formation) of El Castellar and Galve localities (Teruel) referred to Oplosaurus armatus (Royo-Torres and Cobos 2007). Nevertheless, Oplosaurus, El Castellar and Galve teeth show some morphological features not yet identified in Upper Jurassic heart-shaped teeth such as the presence of vertically and mesiodistally oriented apical wear facets and the presence of lingual facets and a complex cingulum morphology that is also found in Camarasaurus or Euhelopus (e.g., Ostrom and McIntosh 1966; Wilson and Upchurch 2009).

Three teeth from Africa are related to the heart-shaped morphology. From the Middle Jurassic sediments of Madagascar, more precisely in Ankinganivalaka site (Läg 2008), was found a tooth (MNHN,F MAJ 423, Figure 10(f)) with an almost complete crown. This crown bears the typical heart-shaped morphology present in the morphotype II defined here. Another tooth (MNHN,F 1961-28, Figure 10(g)) from In Gall (Niger) (Lapparent 1960) also bears a heart-shaped morphology shared by the morphotype II. This tooth came from Irhazer Group sediments, probably not younger than upper Middle Jurassic (Raubitschek and López-Arbarello 2009). Finally, another tooth (UT-TEN15) from Tendamirah Quarry, Cabao Formation (Hauterivian-Barremian) in Libya (Le Loeuff et al. 2010) has a basal constriction and a crown similar to the morphotype I, and lacks the complex cingulum with associated lingual facets present in Camarasaurus or Euhelopus (Ostrom and McIntosh 1966; Wilson and Upchurch 2009).

Until the end of the twentieth century, neosauropod postcranial references dominate in Portuguese Upper Jurassic. This is incongruent with the relative abundance of these type teeth morphology assigned to Eusauropoda. However, the specimen of Vale das Pombas, Zby atlanticus (Mateus 2009; Mateus et al. 2014), and some new material in study, show that the occurrence of eusauropod postcranial material is not so rare. Therefore, the hypothesis that these teeth belong to a neosauropod form by convergence, or that this morphology corresponds to a more inclusive group than Turiasauria is not ruled out. New discoveries are necessary to confirm the link between these teeth and the occurrences related to Turiasauria.

Royo-Torres et al. (2006, 2009) and Royo-Torres and Upchurch (2012) considered that the heart-shaped morphology could be referred to the Turiasauria. At the moment, Turiasaurus and Zby are the only turiasaur with cranial and postcranial materials. In the light of some recent phylogenetic approaches (Royo-Torres et al. 2006, 2009, 2012; Royo-Torres, Upchurch, et al. 2014; Royo-Torres, Cobos, et al. 2014; Royo-Torres and Upchurch 2012; Mocho, Royo-Torres, et al. 2014; Mocho, Royo-Torres, Malafaia, et al. 2014), the non-neosauropod eusauropods have spoon-shaped teeth. If Turiasaurus, Losillassauras, Galveosaurus and Zby correspond to a monophyletic clade, their heart-shaped teeth could be considered as a synapomorphy of Turiasauria (the condition is unknown in Galveosaurus and Losillassauras). However, the presence of this type of tooth morphology in the Middle Jurassic to the Lower Cretaceous of Africa and Europe put in evidence that this particular morphology has a wider stratigraphic and paleogeographic distribution, that could reflect a wider phylogenetic distribution.

Other possibility is to consider that this morphology was acquired by convergence in several sauropod groups. This hypothesis could explain the presence of this tooth morphology in the Middle Jurassic of the UK and in the Lower Cretaceous of France and the UK, where it was not yet found or documented other turiasaurian cranial (non-teeth material) and postcranial remains. The presence of convergences in sauropod tooth morphology has already been identified between diplodocids and titanosaurs (e.g., Salgado and Calvo 1997) or mamenchisaurids and some macronarians (e.g., Suteethorn et al. 2013). Convergence in tooth
morphotypes has also been suggested for brachiosaurids and titanosaurs (Chure et al. 2010) and both with euheropodids (D’Emic et al. 2013).

The differences shown by the three proposed morphotypes can be explained by two different ways (or a combination of both): (i) the three morphotypes represent three distinct taxa (in generic or specific level) inside or outside the Turiasauria clade (this morphology could not be exclusive of the clade); or (ii) the three morphotypes belong to the same taxon and the variability is associated to a distinct position along the tooth row, as occurs in other sauropods such as Giraffatitan (Janensch 1936), Camarasaurus (Gilmore 1925), Abydosaurus (Chure et al. 2010) or Euhelopus (Wiman 1929; Wilson and Upchurch 2009; Poropat and Kear 2013). A slight heterodony was also suggested for the skull of Turiasaurus riodevensis (Royo-Torres and Upchurch 2012). The distinct wear pattern observed along the morphotypes also could be explained in the same way, or might represent a distinct taxon or function of the tooth row position.

Observing the variation in teeth morphology along the tooth row for Camarasaurus (Gilmore 1925) or Giraffatitan (Janensch 1936), some remarkable trends to the distal part of the tooth row can be enumerated: (i) decreasing of SI value (SI value varies at least a unit in both taxa: Camarasaurus = 2.7–1.7; and Giraffatitan = 3.5–2.5); (ii) decreasing of apex height; (iii) prominence in distal curvature of the apex; and (iv) progressive medial tooth imbrication. Assuming that the teeth described belong to a single taxon, the defined morphotypes (I, II and III) could represent different positions in tooth row fitting well in the variability observed for Camarasaurus (Gilmore 1925) or Giraffatitan (Janensch 1936). In this case, morphotype I should correspond to an anterior position, morphotype III to a more posterior position, and morphotype II located between morphotypes I and III. It is necessary to have a well-represented in situ tooth sequence of a turiasaurian individual to confirm if the three morphotypes fit in the range of a unique species or otherwise some of the morphotypes represent distinct taxa (inside or outside Turiasaurus). Anyway, taking into account the variability present in other taxa, the variation in teeth morphology along the tooth row of a unique taxa seems to be the most parsimonious hypotheses to explain the morphological variability in the Iberian sample.

Conclusions

Forty-three heart-shaped teeth from the Portuguese Upper Jurassic were described and tentatively referred to Turiasauria based on the presence of a heart-shaped crown and a pointed and distally projected apex. Till today, this tooth morphology was the only one found associated with skeletal remains in Turiasaurus and Zby, both considered as members of Turiasauria, suggesting that the heart-shaped morphology could be referred as a possible synapomorphy of this clade. This sample shows a great variability among which can be recognised three different morphotypes: morphotype I, high SI (1.8–1.6) values and high apex (an half of tooth total height), morphotype II, moderate apex and SI values (1.5–1.3), with well defined heart-shaped and more strong distal deflection; morphotype III, low SI values (< 1.3) and extremely low apex, with heart-shaped to subsquared-shaped form. Morphotypes I and II set within the morphospace occupied by other non-neosauropod sauropods, with the exception of the morphotype III, with lower SI values.

To explain the present morphological variability, two hypotheses (or combination of both) were mainly discussed: (i) these teeth belong to distinct taxa outside or inside Turiasauria or (ii) these teeth correspond to different positions on the tooth row of unique taxa. The morphological disparity shown by few sauropods (e.g. Turiasauria or Camarasaurus) along tooth row suggests that this variability could be explained by a slightly heterodony with morphotypes I, II and III located in mesial, middle and distal position, respectively. The presence of several teeth in different states of wear allows proposing a hypothetical general wear pattern for morphotypes I, II and III. In the former two morphotypes, the wear begins with the appearance of a distal facet, then the appearance of mesial and apical facets and finally a ‘V’-shaped facet. In morphotype III, the wear seems to begin with the appearance of a mesial facet.

Acknowledgements

We thank the following people for allowing to accessing specimens: M. Ramalho and R. Silva (MG, LNEG, Portugal), L. Chiappe and M. Walsh (NHMLAC, USA), R. Allain (MNHN, France), S. Chapman (NHMUK, UK), D. Schwarz-Wings (HM, Germany), E. Howlett (OUMNH, UK), R. Castaninha and C. Tomás (ML, Portugal), J. M. Herrero (MPG, Spain), L. Povoas and P. Dantas (MNHC, Portugal), M. Cachão and C. M. da Silva (GeoFCUL, Portugal), M. F. C. Pereira (MDT, IST, Portugal) and L. Alcalá (FCPT-Dinópolis, Spain). We also appreciate the critical comments of Michael D’Emic and José Luis Carballido for suggesting improvements to the manuscript. João Barrinha by the support in the early phase of photography process. We are also grateful to G. Ramalheiro, A. Mano and J. J. dos Santos (SHN, Torres Vedras, Portugal); I. Narváez, F. Marcos, and A. Pérez-García (UNED, Spain); S. Pereira and N. Pimentel (GeoFCul, Portugal), J. L. Sanz (UAM, Spain), F. Gascó and A. Cobos (FCPT-Dinópolis, Spain) for the support and comments. We thank D. Chure, B.B. Britt, J. Wilson, J.A. Whitlock and M. D’Emic for comments and permission to use their data in Figures 7 and 8.

Disclosure statement

No potential conflict of interest was reported by the authors.
Funding
This work was supported by “Fundação para a Ciência e Tecnologia” (Portugal) under PhD scholarship (grant number SFRH/BD/68450/2010), and Departamento de Educación, Universidad, Cultura y Deporte del Gobierno de Aragón, the Departamento de Industria e Innovación and the Fondo Social Europeo (FOCONTUR. Ref. E62), the Instituto Aragonés de Fomento, the Spanish Ministerio de Economía y Competitividad (CGL2013-41295-P Project DINITUR).

Supplemental data
Supplemental data for this article can be accessed here.

Notes
1. Email: p.mochopaleo@gmail.com
2. Email: royo@dinopolis.com
3. Email: emalafaia@gmail.com
4. Email: fescaso@ccia.uned.es
5. Email: laboratorio@alt-shn.org
6. Email: forttega@ccia.uned.es

References
Allain R, Aquesbi N. 2008. Anatomy and phylogenetic relationships of Tacouda saurus naimit (Dinosauria, Sauropoda) from the Late Early Jurassic of Morocco. Geodiversitas. 30:345–424.
Antunes MT, Mateus O. 2003. Dinosaurs of Portugal. C R Palevol. 2(1):77–95. doi:10.1016/S1631-0683(03)00003-4.
Azevedo AC, Cabral MC, Martins MJ, Loureiro IM, Inês N. 2010. Estudio estratigrafico dum novo afloramento da Formacao de Caboias (Oxfordiano) na regiao da Serra do Bouro (Caldas da Rainha). Commun Geol. 97:05–22.
Barco JL. 2005. Estudio y comparacion del esqueletos axial de un sauroroipo (Dinosauria, Sauropodomorpha) procedente de la Formacion Villar del Arzobisp0 (Titonico-Berriasiense) de Galve, Teruel. Treb Mus Geol Barc. 13:15–59.
Barco JL. 2009. Sistematica e implicaciones filogeneticas y paleobiogeograficas del sauroroipo Galve saurus herrei (Formacion Villar del Arzobisp0, Galve, Espana) [Ph.D. dissertation]. Universidad de Zaragoza.
Barco JL, Canudo JJ, Cuenca-Bescós G. 2009. New data on the phylogenetic position of the sauroroipo Galve saurus (Titanoh-Berriasian, Spain). J Vert Paleontol. 29(Suppl.3):58A.
Barco JL, Canudo JJ, Cuenca-Bescós G, Ruiz-Omeñaca JJ. 2005. Un nuevo dinosaurio sauroipo, Galve saurus herrei, gen. nov., sp. nov., del tranśicion Jurassico-Cretacio en Galve (Teruel. NE de Espana). Rev Nat Aragon. 15:4–17.
Barco JL, Canudo JJ, Cuenca-Bescós G, Ruiz-Omeñaca JJ. 2006. Descripcion de las vertebras cervicales de Galve saurus herrei Barco, Canudo, Cuenca-Bescós & Ruiz-Omeñaca (2005, Dinosauria, Sauropoda) del tranśicion Jurassico-Cretacio en Galve (Teruel, Aragon, Espana). Rev Esp Paleontol. 21(2):189–204.
Barrett PM. 2006. A sauroroipo dinosaur tooth from the Middle Jurassic of Sky, Scotland. Trans R Soc Edinb Earth Sci. 97(1):25–29. doi:10.1017/S026353930001383.
Barrett PM, Hasegawa Y, Manabe M, Isaji S, Matsuoka H. 2002. Sauroroipo dinosauros from the Lower Cretaceous of eastern Asia: taxonomic and biogeographical implications. Palaeontology. 45(6):1197–1217. doi:10.1111/1475-4983.00282.
Barrett PM, Upchurch P. 1994. Feeding mechanisms of Diplodocus. Gaia. 10:195–203.
Barrett PM, Wang X-L. 2007. Basal titanosauriform (Dinosauria, Sauropoda) teeth from the Lower Cretaceous Yixian Formation of Liaoning Province, China. Palaeoworld. 16(4):265–271. doi:10.1016/j.palwor.2007.07.001.
Bonaparte JF. 1986. The early radiation and phylogenetic relationships of the Jurassic sauroipo dinosaurs, based on vertebral anatomy. In: Padian K, editor. The beginning of the Age of Dinosaurs. Cambridge: Cambridge University Press; p. 247–258.
Bonaparte JF, Heinrich W-D, Wild, R. 2000. Review of Juraschicia WILD, with the description of a new sauroipo from the Tendaguru beds of Tanzania and a discussion on the systematic value of prococolous caudal vertebrae in the sauroipo. Palaeontographica. 256:25–76.
Bonaparte JF, Mateus O. 1999. A new diplodocid, Dinheirosaurus loirisnhanesis gen et sp. nov., from the Late Jurassic beds of Portugal. Rev Mus Argent Cienc Nat. 5(2):13–29.
Bonaparte JF, Powell JE. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauroroipo-Coelurosauria-Carnosauria-Aves). Mém Soc Géol Fr. 139:19–28.
Buffetaut E, Martin M. 1993. Late Jurassic dinosaurs from the Boulonnais (Northern France): a review. Rev Paleobiol. 7:17–28.
Calvo JA. 1994. Jaw mechanics in sauroipo dinosaurs. Gaia. 10:183–193.
Camarate França J, Zbyszewski G. 1963. Noticia explicativa da folha 26-B, Alcoaça. Lisboa: Serviços Geológicos de Portugal.
Canudo JJ, Barco JL, García-Ramos JL, Piñuela L, Ruiz-Omeñaca JJ. 2006. The discovery of a singular fauna: the sauroipo from the Late Jurassic and Earliest Cretaceous of Spain. J Vert Paleontol. 26:47A.
Canudo JJ, Ruiz-Omeñaca JJ, Barco JL, Royo-Torres R. 2002. ? Sauroroipos asiaticos en el Barrenmien inferior (Cretacio Inferior) de Espana? Ameghiniana. 39:433–452.
Canudo JJ, Ruiz-Omeñaca JJ, Piñuela L, García-Ramos JC. 2010. Descripcion de un denticario de cf. Turiasaurus (Sauroroipo) del Kimmeridgiense de Asturias (España). In: Ruiz-Omeñaca JL, Piñuela L, García-Ramos JC, editors. Comunicaciones del V Congreso del Jurassico de Espana. Colunga: Museo del Jurassico de Asturias (MUJA); p. 164–169.
Carballido JL, Pol D. 2010. The dentition of Amygdalodon patagonicus (Dinosauria: Sauropoda) and the dental evolution in basal sauroipo. C R Palevol. 9(3):83–93. doi:10.1016/j.crpv.2010.01.003.
Carballido JL, Rauhl OWM, Pol D, Salgado L. 2011. Osteology and phylogenetic relationships of Tehuelchesaurus benzieii (Dinosauria, Sauropoda) from the Upper Jurassic of Patagonia, Zool J Linn Soc. 163(2):605–662. doi:10.1111/j.1096-3642.2011.00723.x.
Carballido JL, Sander PM. 2014. doi:10.1007/14772019.2013.764935. Postcranial axial skeleton of Europasaurus holgeri (Dinosauria, Sauropoda) from Upper Jurassic of Germany: implications for sauropod ontogeny and phylogenetic relationships of basal Macronaria. J Syst Paleontol. 12(3):335–387.
Casanovas ML, Santafe JV, Sanz JL. 2001. Llouisasauros giganteus, un nuevo sauroipo del tranśicion Jurassico-Cretacio de la cuenca de «Los Serranos» (Valencia, Espana). Paleontol Evol. 32:33–99–122.
Chure D, Britt BB, Whitlock JA, Wilson JA. 2010. First complete sauroroipo dinosaur skull from the Cretaceous of the Americas and the evolution of sauroipo dentition. Naturwissenschaften. 97(4):579–391. doi:10.1007/s00114-00-0560-6.
Cobos A, Royo-Torres R, Alcalá L, Luque L, Aberasturi A. 2008. Nuevos datos de las incisitas de dinosauros en la Formacion Villar del Arzobisp0 (Teruel). In: Ruiz-Omeñaca JL, Piñuela L, García-Ramos JC, editors. Libro de resumenes, XXIV Jornadas de la Sociedad Espanola de Paleontologia. Colunga: Museo del Jurassico de Asturias (MUJA); p. 25–26.
Cobos A, Royo-Torres R, Gascó F, Alcalá L. 2011. A new giant turiasaurian specimen from Rioveia (Teruel, Spain). In: van der Geer A, Athanasiou A, editors. Programs and Abstracts of 9th Annual Meeting of the European Association of Vertebrate Palaeontologists, Greece: Creta; p. 18.
Dantas P, Sanz JL, Silva CM, Ortega F, Santos VF, Cachão M. 1998. Lourinhhasaurus n gen. novo dinossaurio sauroroipo do Jurassico superior (Kimmeridgiano superior-Titoniano inferior) de Portugal. Acta Congr Geol. 84(1):A91–A94.
D’Emic MC. 2012. The early evolution of titanosauriform sauroroipo dinosaurs. Zool J Linn Soc. 166(3):624–671. doi:10.1111/j.1096-3642.2012.00853.x.
Owen R. 1841. A description of a portion of the skeleton of the *Cetiosaurus*, a gigantic extinct saurian Reptile occurring in the Oolitic formations of different portions of England. Proc Geol Soc. 3: 457–462.

Owen R. 1844. Odontography. Pt. III. London: Hippolyte Bailliére.

Owen R. 1875. Monograph of the Mesozoic formations. Part II. Monograph of the genus *Omosaurus*. Palaeontogr Soc (Monogr). 29: 45–93.

Pena dos Reis RPB, Proença Cunha CP, Dinis JL. 2000. Geologic evolution of the Lusitanian Basin (Portugal) during the late Jurassic. GeorResearch Forum. 6: 345–356.

Pérez-Moreno BP, Chure DJ, Pires CS, Silva CM, Santos VF, Dantas P, Póvoas L, Cachão M, Sanz JL, Galopim de Carvalho AM. 1999. On the presence of *Allosaurus fragilis* (Theropoda, Camarasauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. J Geol Soc. 156:449–452.

Perea-Suberbiola X, Dantas P, Galton LM, Sanz JL. 2005. Autopodium of the holotype of *Dacropyx zbyszewskii* (Dinosauria, Ankylopoidea) in the Late Jurassic of Portugal. Paper presented at: Abstract 271(3-4):259–267. doi:10.11016/pe.2008.10.019.

Rauhut OWM, López-Arbarello A. 2009. Considerations on the age of the tournier formation (Fullemmedden Basin, Niger, Africa): implications for gondwanan mesozoic terrestrial vertebrate faunas. Palaeocool. 271(3-4):259–267. doi:10.11016/pe.2008.10.019.

Royo-Torres R. 2009. Los dinosaurios sauropodos en la Peninsula Ibérica. In: Arqueológico-Paleontológico de Salas Colectivo, editor. Actas de las IV Jornadas Internacionales sobre Paleontología de dinosaurios en su entorno. p. 139–166.

Royo-Torres R, Alcalá C. 2012. A new specimen of the sauropod clade *Tastavinsaurus sanzi* from El Castellar (Teruel, Spain), and a phylogenetic analysis of the Laurusiformes. Cretac Res. 34:61–83.

Royo-Torres R, Cobos A. 2007. Teeth of *Oplosaurus armatus* (Sauropoda) from El Castellar (Teruel, Spain). Paper presented at: 5th Meeting of the European Association of Vertebrate Palaeontologists: Carcassonne-Espéraza. p. 52–55.

Royo-Torres R, Cobos A. 2009. Turiasaur sauropods in the Tendaguru Beds of Tanzania. J Vert Paleontol. 29(Suppl. 3):173A.

Royo-Torres R, Cobos A, Alcalá L. 2006. A giant european dinosaur and a new sauropod clade. Science. 314(5807):1925–1927. doi:10.1126/science.1132885.

Royo-Torres R, Cobos A, Alcalá L. 2008. Primeros restos directos de dinosaurios de la Sierra de Albarracín (Teruel). In: Ruiz-Omeña JJ, Pituella L, García-Ramos JC, editors. Libro de resúmenes. XXIV Jornadas de la Sociedad Española de Paleontología. Colunga: Museo del Jurásico de Asturias (MUA); p. 189–190.

Royo-Torres R, Cobos A, Gascó F, Mochó P, Ortega F, Alcalá L. 2014. Geographical and Stratigraphical distribution of the sauropod *Tataria* and Turiasauria clade. Paper presented at: Mid-Mesozoic: The Age of Dinosaurs in Transition. Utah.

Royo-Torres R, Cobos A, Luque L, Aberasturi A, Espí F, Fierro I, González A, Mampel I, Alcalá L. 2009. High European sauropod dinosaur diversity during Jurassic-Cretaceous transition in Roideva (Teruel, Spain). Palaeontology. 52(5):1009–1027. doi:10.1111/j.1475-4983.2009.00898.x.

Royo-Torres R, Upchurch P. 2012. The cranial anatomy of the sauropod *Turiasaurus riodevensis* and implications for its phylogenetic relationships. J Syst Palaeontol. 10(3):553–583. doi:10.1080/14772019.2011.598577.

Royo-Torres R, Upchurch P, Mannion PD, Mas R, Cobos A, Gascó F, Alcalá L, Sanz JL. 2014. The anatomy, phylogenetic relationships, and stratigraphic position of the Tithonian-berriasian Spanish sauropod dinosaur *Aragosaurus ictheicus*. Zool J Linn Soc. 171(3):623–655. doi:10.1111/zss.12144.
