J Iber Geol (2017) 43:257–291
DOI 10.1007/s41513-017-0021-7

RESEARCH ARTICLE

Analysis of diversity, stratigraphic and geographical distribution of isolated theropod teeth from the Upper Jurassic of the Lusitanian Basin, Portugal

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Received: 27 November 2016 / Accepted: 6 June 2017 / Published online: 14 July 2017

Abstract

Purpose Isolated theropod teeth are abundant in the Upper Jurassic of the Lusitanian Basin and are an important source to reconstruct the diversity of this group as well as its geographic and stratigraphic distribution. However, reliably identification of isolated teeth is complex, especially for those morphotypes related to poorly represented groups. Herein a set of isolated theropod teeth collected in different sites from the Upper Jurassic of the Lusitanian Basin ranging from the late Kimmeridgian to late Tithonian in age are described and discussed.

Methods These teeth were grouped in seventeen distinct morphotypes based first on morphology and comparative anatomy. Multivariate statistical analyses were performed in order to assign each morphotype to a certain taxon.

Results The current analysis shows the presence of several groups of theropods such as *Ceratosaurus, Torvosaurus,* and *Allosaurus* beside morphotypes identified as belonging to indeterminate Megalosauroidea and Allosauroidea and morphotypes tentatively assigned to Tyrannosauroidea, Dromaeosauridae, and *Richardoestesia*. This faunal composition, namely the presence of a non-megalosaurid megalosauroid possibly related to the piatnitzkysaurid *Marshosaurus*, indicates a higher diversity of theropods in the Late Jurassic of the Lusitanian Basin than previously known, based on more complete specimens. Results obtained from this analysis partially agree with previous studies of other collections with isolated theropod teeth from the Upper Jurassic of Portugal such as those of the Guimarota coal mine. However, the presence of velociraptorine dromaeosaurids, compsognathids, and troodontids reported from this site could not be confirmed in the sample herein analyzed. This analysis also indicates a great similarity of the theropod faunas from the Late Jurassic of the Lusitanian Basin and other European chronocorrelative localities such as those from Spain and Germany.

Electronic supplementary material The online version of this article (doi:10.1007/s41513-017-0021-7) contains supplementary material, which is available to authorized users.

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Keywords Multivariate analysis · Ceratosauria · Megalosauroidea · Allosauroidea · Coelurosauria

Resumen

Objetivo Los dientes aislados de dinosaurios terópodos son un registro abundante en el Jurásico Superior de la cuenca lusitánica pudiendo llegar ser una importante contribución para comprender la diversidad y la distribución geográfica y estratigráfica de estas faunas. Sin embargo, la identificación de dientes aislados y su asignación a un determinado taxón es compleja, especialmente en el caso de morfotipos relacionados con grupos poco conocidos en el mismo registro. En este estudio se presenta el resultado del análisis de un conjunto de dientes aislados de terópodos procedentes de diferentes localidades de la cuenca lusitánica datadas en el Jurásico Superior, concretamente entre el Kimmeridgiense superior y el Tithoniense superior.

Métodos Estos dientes se han agrupado en diecisiete morfotipos a partir del estudio morfológicco y de la comparación anatómica. Se realizaron análisis estadístico multivariante para comprobar la identificación de cada morfotipo.

Resultados El resultado de este análisis ha revelado una gran diversidad de grupos de terópodos que incluye *Ceratosaurus*, *Torvosaurus* y *Allosaurus* además de morfotipos identificados como pertenecientes a Megalosauroidea indet. y Allosauroidea indet. Además, se han reconocido también algunos morfotipos preliminarmente asignados a Tyrannosauroidea, Dromaeosauridae y *Richardoestesia*. Esta composición faunística, tal como la presencia de non-megalosauridos megalosauroides posiblemente relacionado al piatnitzkysaurido *Marshosaurus*, sugiere una mayor diversidad de terópodos de la que se conoce actualmente a partir de ejemplares más completos. Los resultados obtenidos soportan, en parte, algunos estudios previos de otras colecciones con dientes aislados del Jurásico Superior de Portugal, como por ejemplo los de la mina de Guimarota. No obstante, la presencia de terópodos velociraptorinos, compsognathidos y troodontidos, citados en Guimarota, no se ha podido confirmar en la muestra estudiada. Este análisis indica también una grande semejanza de las faunas de terópodos del Jurásico Superior de la cuenca lusitánica y de otras localidades sincrónicas europeas como por ejemplo de España y Alemania.

Palabras clave Análisis multivariante · Ceratosauria · Megalosauroidea · Allosauroidea · Coelurosauria

1 Introduction

The Portuguese record of theropod dinosaurs is abundant and diverse, including mainly medium- to large-sized forms belonging to primitive theropods, such as Ceratosauria or basal groups of Tetanurae (e.g. Mateus 1998; Pérez-Moreno et al. 1999; Rauhut and Fechner 2005; Mateus et al. 2006; Hendrickx and Mateus 2014a, b; Malafaia et al. 2015). Small-sized and more derived theropods are so far represented mainly by isolated teeth. These include the primitive tyrannosauroid *Aviatyrannis* from the Guimarota fossil site and several isolated elements, identified as belonging to compsognathids, dromaeosaurids, troodontids, and to taxa with uncertain relationship, such as *Paronychodon* and *Richardoestesia* (Zinke and Rauhut 1994; Zinke 1998; Rauhut 2003; Malafaia et al. 2010; Hendrickx and Mateus 2014b). *Archaeopteryx* is also reported in this record based on a single tooth (Weigert 1995).

Previous studies on Late Jurassic dinosaur faunas from the Lusitanian Basin have referred isolated theropod teeth to a particular genus and/or species (Zinke and Rauhut 1994; Zinke 1998; Hendrickx and Mateus 2014b). Yet some authors have suggested that most isolated theropod teeth are not diagnostic to specific or generic levels, especially when it is not possible to compare them with those associated with diagnostic cranial or postcranial elements collected from equivalent sedimentary levels (e.g. Williamson and Brusatte 2014). However, some recent works proposed that a combination of morphological and statistical analysis may allow assignment of isolated theropod teeth to a higher taxonomic level (Smith et al. 2005; Hendrickx and Mateus 2014b; Hendrickx et al. 2015; Gerke and Wings 2016). The specimens studied here are grouped into morphotypes, which are identified primarily based on morphological features. A multivariate statistical analysis of morphometric data is also used to help the identification of the specimens.

Institutional abbreviations: CPT, Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain; ML, Museu da Lourinhã, Lourinhã, Portugal; SHN, Sociedade de História Natural, Torres Vedras, Portugal.

Morphometric abbreviations: AL, apical length; CBL, crown base length; CBR, crown base ratio; CBW, crown base width; CDA, crown distal angle; CH, crown height; CHR, crown height ratio; CMA, crown mesial angle; DC, distocentral denticle density; MC, mesiocentral denticle density; DSDI, denticle size density index.

2 Materials and methods

A total of 118 isolated theropod teeth are described. These specimens were found in different localities where the Upper Jurassic formations of the Lusitanian Basin crop out (see below and Supplementary Data, Table 1S). The specimens were grouped into 17 morphotypes based first on morphology and comparative anatomy. Also a principal components analysis (PCA) using PAST3 software package (Hammer et al. 2001) was performed to test the individualization of the different morphotypes (Fig. 1). We also performed a cladistic analysis of the morphotypes herein described based on the datamatrix of Hendrickx and Mateus (2014b), but the result obtained when including our sample is a large politomy, which does not help the identification of the studied teeth.

All specimens are deposited in the publicly accessible collections of the Sociedade de História Natural (SHN) in Torres Vedras, Portugal. These specimens derive from surface collection surveys and from paleontological excavations performed by the SHN.

Measurements of the specimens were taken with standard digital calipers (see Supplementary Data, Table 2S). Pictures of the denticles and other morphological observations were taken with a Zeiss Stemi 2000-C binocular microscope. The measurement variables include CBL (crown base length), CBW (crown base width), CH (crown height), AL (apical length), and the number of mesial (MC) and distal (DC) denticles at the crown mid-height. The CBR (crown base ratio = CBW/CBL), CHR (crown height ratio = CH/CBL), CMA (crown mesial angle = ar cos $((CBL^2 + AL^2 - CH^2)/2 \times CBL \times AL))$ and CDA (crown distal angle = ar cos $((CBL^2 + CH^2 - AL^2)/2 \times CBL \times CH))$ were also calculated, but were not included in the multivariate analysis because they are non-independent variables that would weight those variables. Descriptive terminology follows Hendrickx et al. (2016).

Multivariate statistical analyses were performed in order to assign each morphotype to a certain taxon. A stepwise discriminant function analysis (DFA) using the software IBM SPSS Statistics 17.0 program (SPSS Inc., Chicago, IL, USA) was developed using squared Mahalanobis distances and the covariance matrix for separated groups. Multivariate analyses were performed using the datasets published by Hendrickx et al. (2015) and Gerke and Wings (2016). A first analysis was performed using the complete dataset of Gerke and Wings (2016) (see Supplementary Data, Table 3S). The percentage of correct classified sample obtained was low, with only 54.6–62.6% of cases correctly identified. A reduced analysis, excluding all taxa represented by less than three specimens and that were also incorrectly classified on the first analysis (*Berberosaurus* and *Megalosaurus*) increased the reclassification rate to 80.5%. Because there are some differences in the measurement methodology used for the specimens in the datasets of Gerke and Wings (2016) and Hendrickx et al. (2015) we performed separated analyses based on the two datasets in order to verify results congruence.

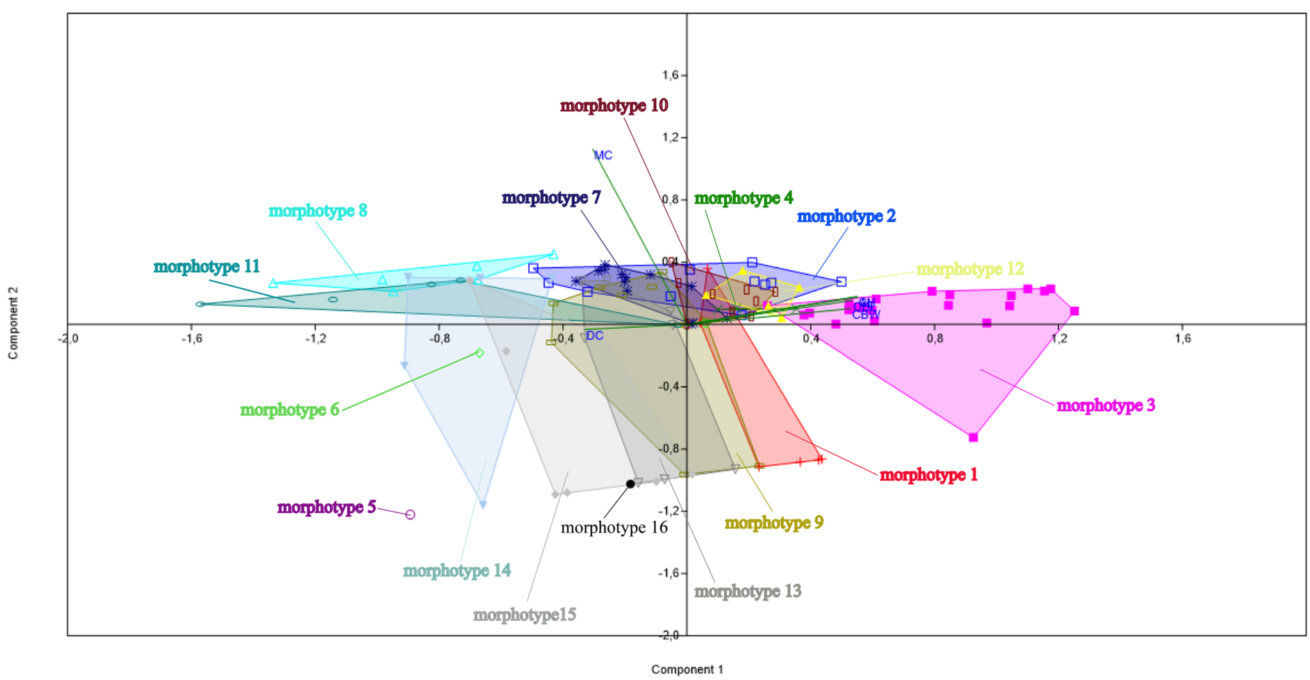


Fig. 1 Plot of loadings from the principal component analysis showing the morphospace occupied by the different morphotypes described here. The specimens are grouping along the first two canonical axes of the principal components (Eigenvalue of axis 1 = 0.294, which accounts for 58.111% of the total variation; Eigenvalue of axis 2 = 0.187, which accounts for 37.138% of the total variation). The variables log-transformed CBL, CBW, CH, AL, MC, and DC were used in the analysis

3 Geological setting

The teeth studied in this work were recovered from different outcrops in the Central Sector of the Lusitanian Basin, mainly in the coastal area of the southern end of the Bombarral Sub-basin (=Consolação Sub-basin sensu Taylor et al. 2014) and in the northern end of the Turcifal Sub-basin (Fig. 2). Most of these specimens were collected in the Praia da Amoreira-Porto Novo Formation (sensu Manuppella et al. 1999), which is interpreted as late Kimmeridgian in age and crops out along most of the littoral region between Torres Vedras and Peniche. This sedimentary sequence consists mainly of sandstone channel bodies intercalated with massive mudstone levels, representing deposits of distal fluvial meander systems (Hill 1989; Mateus et al. 2013; Taylor et al. 2014).

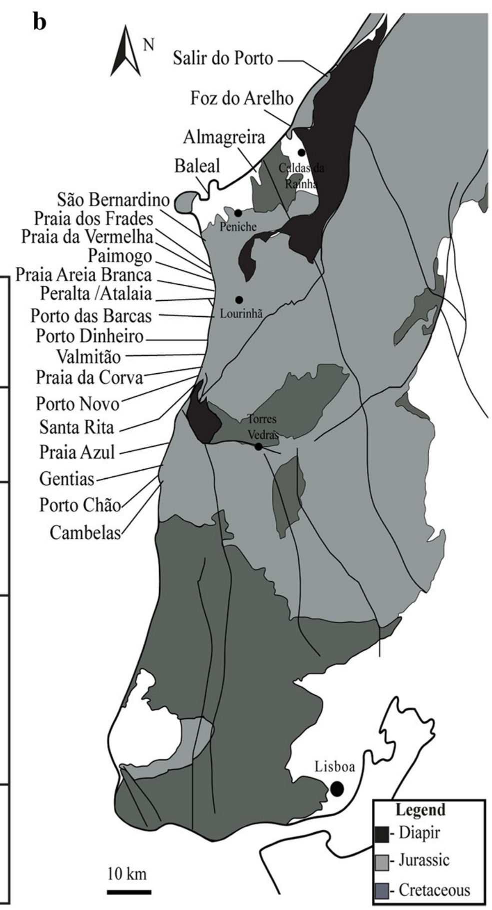
Other specimens come from the upper Kimmeridgian–lower Tithonian Sobral Formation (Praia Azul Member sensu Hill 1988). This unite is mainly composed of marls and mudstones with rare intercalations of sandstone channel bodies (Hill 1989) and is interpreted as representing transitional systems such as deltas, sandy bay shorelines and brackish lagoons (Fürsich 1981; Werner 1986; Mateus et al. 2013; Taylor et al. 2014).

Some teeth collected in the northern part of the Consolação Sub-basin come from sediments of the Bombarral Formation interpreted as Tithonian in age (Manuppella et al. 1999; Schneider et al. 2009). These sediments correspond mostly to micaceous sandstones deposited in meandering fluvial systems, punctuated by marine marls (Rocha et al. 1996; Kullberg et al. 2013).

Finally, in the Arruda Sub-basin, (southern part of the Lusitanian Basin), a few teeth were also collected in Tithonian levels of the Freixial Formation (chronologically equivalent to the Bombarral Formation). The Freixial Formation is composed of thick layers of red mudstones, with abundant levels of well-developed pedogenic carbonate concretions, intercalated with cross-bedded sandstones. These sediments are interpreted as deposits of coastal delta plains and distal fluvial environments (Hill 1988).

a

b



c

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<tr><th colspan="3" rowspan="2">Crono stratigraphy</th><th colspan="4">Litoral region from Santa Cruz to Salir do Porto (Consolação Sub-basin)</th><th rowspan="2">Turcifal Sub-basin</th></tr>
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<tr><td rowspan="4">Upper Jurassic</td><td rowspan="2">Tithonian</td><td>U</td><td colspan="2">Bombarral Fm.</td><td>Santa Rita Mb. / Assenta Mb.</td><td rowspan="3">Lourinhã Formation</td><td>Freixial Fm.</td></tr>
<tr><td>L</td><td colspan="2">Sobral Fm.</td><td>Porto Novo Mb. / Praia Azul Mb.</td><td>Sobral Fm.</td></tr>
<tr><td rowspan="2">Kimmeridgian</td><td>U</td><td>Praia da Amoreira - Porto Novo Fm.</td><td rowspan="2">Alcobaça Beds</td><td>Porto Novo Mb.
Praia da Amoreira Mb.</td><td>Amaral Fm.</td></tr>
<tr><td>L</td><td>Consolação Fm.</td><td colspan="2">Abadia Fm.</td><td>Abadia Fm.</td></tr>
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Fig. 2 Geologic and stratigraphic settings of the specimens described; **a** location of the Lusitanian Basin in the Iberian context; **b** simplified geological map of the Central Sector of the Lusitanian Basin (modified from Oliveira et al. 1992) showing the sites where the specimens were collected; **c** chronostratigraphic table for the Upper Jurassic of the Lusitanian Basin showing the correlation between the nomenclatures proposed by different authors (Hill 1988; Manuppella et al. 1999) for the Consolação Sub-basin and the chronostratigraphy for the Turcifal Sub-basin. *L* lower, *U* upper

4 Description, results and discussion of the morphotypes

4.1 Ceratosauria

4.1.1 Morphotype 1

Ceratosauridae
Ceratosaurus sp.

Material: SHN.205, 236, 254, 457, 461, 462 (Fig. 3).

Geographical provenance: Praia da Corva (Torres Vedras), Porto Dinheiro (Lourinhã), and Praia da Vermelha (Peniche).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian).

Description: This morphotype is represented by six fairly complete tooth crowns, which correspond to moderately large teeth with AL of 31.27–37.58 mm (average 34.79 mm) (see Supplementary Data, Table 2S). The crowns are moderately elongated (CHR: 2.41–3.56; average 2.97) and subcircular in cross-section (CBR: 0.92–1.43; average 1.26). The mesial margins are slightly convex and the distal margins are nearly straight; thus the crowns are subtriangular in lateral view and the apex is centrally positioned.

Transverse undulations are generally absent or slight. Most of these specimens do not have interdenticular sulci except SHN.461 (Fig. 3e), which has very short sulci, perpendicular to the carina, between the distal denticles. The enamel texture is made of a series of thin and irregular crenulations (braided enamel texture) and the crown lingual surface shows well-marked vertical ridges (flutes sensu Hendrickx et al. 2016). Most crowns have 5–6 flutes extending almost the whole crown height. The flutes are restricted to the mid-section of the lingual surface in SHN.205 (Fig. 3a) and only two well-marked flutes are visible in SHN.254 (Fig. 3b). Most of these teeth have rounded mesial margins devoid of a mesial carina except in SHN.205 and 254, which both have a serrated mesial carina extending from the apex down to the crown mid-height or restricted to the apex, respectively. When present, the mesial carina slightly curves toward the lingual surface basally. The distal carina is centrally positioned or slightly displaced labially. Slightly concave vertical surfaces are present on the lingual surface adjacent to the distal carina and a small concave surface is also visible on the labial surface of SHN.205.

Mesial denticles are much smaller than the distal ones, with 19 and 11.5 denticles per 5 mm at the central part of the mesial and distal carinae respectively (DSDI >1.2). The mesial denticles are rounded (Fig. 3a$_{\mathrm{VIII}}$) and the distal denticles are subquadrangular to slightly higher mesiodistally than apicobasally, with symmetrically rounded external margins (e.g. Fig. 3d$_{\mathrm{VI}}$, e$_{\mathrm{III}}$). The distal denticles are closely packed with narrow interdenticular space.

Results and discussion: The DFA analysis assigned two specimens (SHN.236 and SHN.457) to *Torvosaurus* and one specimen (SHN.205) to *Raptorex* and *Erectopus* (see Supplementary Data, Table 4S). However, the general morphology of these specimens, subcircular in cross-section, presence of a large number of small denticles in the distal carinae, absence of mesial carina or restricted to the apical end, and the presence of well-marked vertical flutes in the lingual surface, is also compatible with mesial teeth of *Ceratosaurus* (Gilmore 1920; Madsen and Welles 2000). In particular, the presence of flutes is an unusual character for theropod teeth only known in some juvenile specimens of *Coelophysis* (Buckley 2009), some ceratosaurs (Madsen and Welles 2000; Carrano et al. 2002), *Sinosaurus* (Hendrickx, pers. commun.), spinosaurids (Charig and Milner 1997; Canudo et al. 2008; Serrano-Martínez et al.2015, 2016), *Paronychodon* (Larson 2008; Larson and Currie 2013), some compsognathids, including *Scipionyx* (Dal Sasso and Maganuco 2011), some dromaeosaurids such as *Austroraptor* (Novas et al. 2008a; Williamson and Brusatte 2014; Hendrickx et al. 2015), *Richardoestesia*, and *Zapsalis* (Larson and Currie 2013; Hendrickx, pers. commun.).

Some specimens assigned to *Paronychodon* have well-developed flutes in the lingual surface, but teeth identified to this taxon typically lack denticles, are much smaller and more labiolingually compressed (Larson and Currie 2013) than those of morphotype 1. *Paronychodon*-like teeth from the Cretaceous of Spain (Rauhut 2002) and from the Upper Jurassic and Upper Cretaceous of Portugal (Zinke and Rauhut 1994; Zinke 1998) have serrated distal carinae and in some of them both carinae are serrated, but in these specimens there are well-developed flutes in both lingual and labial surfaces. On the other hand, in some dromaeosaurids such as *Velociraptor*, the flutes are rather rounded ridges on the labial surface (Hendrickx and Mateus 2014b; Hendrickx et al. 2015). Finally, morphotype 1 can be distinguished from the teeth of coelophysoids and compsognathids based in the larger size of the crowns as these taxa possess small crowns (CH <15 mm) and in the much higher number of distal denticles (>30 denticles per 5 mm) (Hendrickx and Mateus 2014a; Hendrickx et al. 2015).

Vertical grooves and ridges on the lingual side of the crowns are present in premaxillary and mesial dentary teeth of *Ceratosaurus* (Madsen and Welles 2000) and in some other ceratosaurs such as *Masiakasaurus* (Carrano et al. 2002). This feature has been traditionally considered

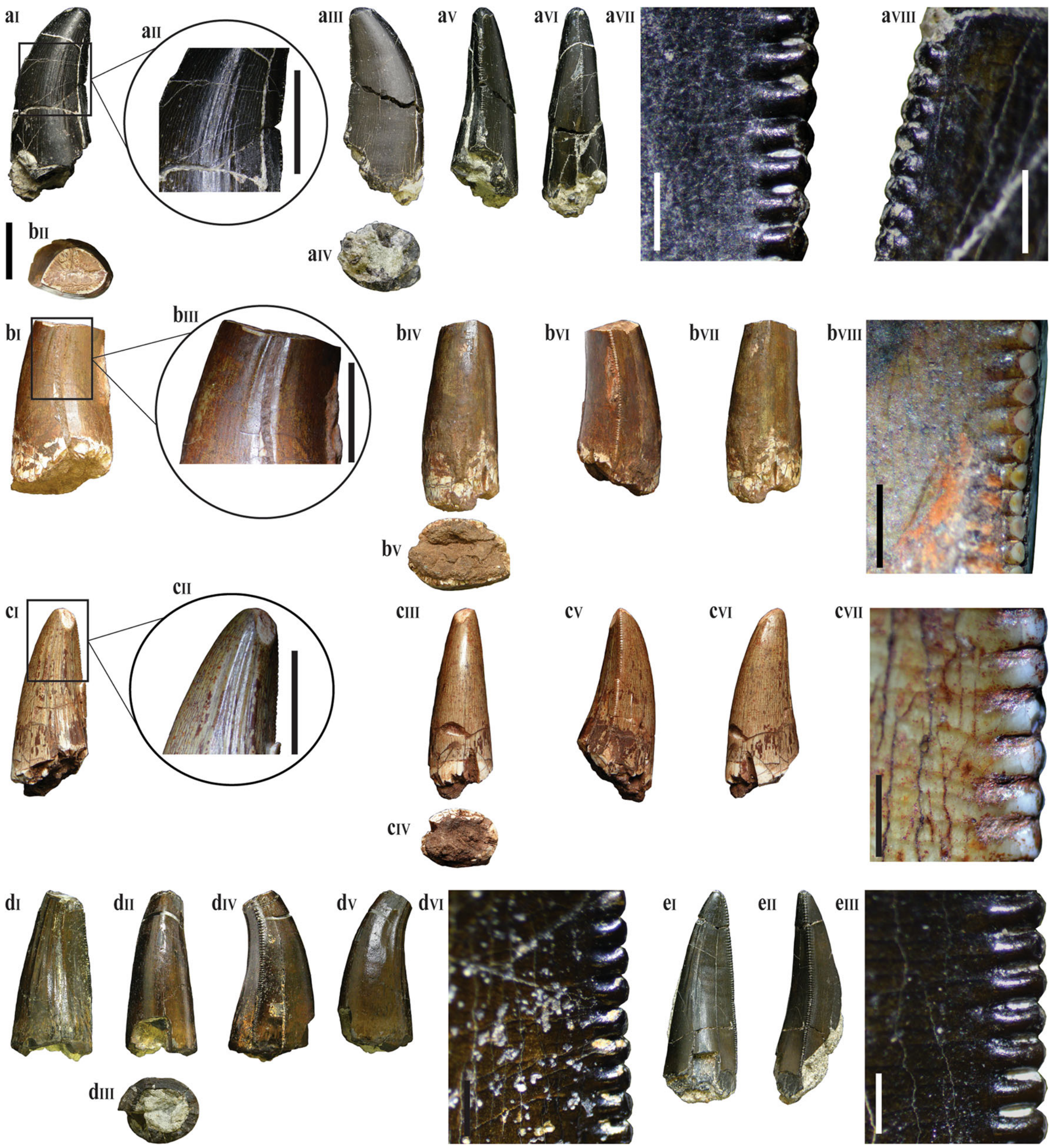

Fig. 3 Morphotype 1: **a** SHN.205; **b** SHN.254; **c** SHN.236; **d** SHN.457; **e** SHN.461 in lingual ($\mathbf{a_{I}}$, $\mathbf{b_{I}}$, $\mathbf{c_{I}}$, $\mathbf{d_{I}}$, $\mathbf{e_{I}}$), labial ($\mathbf{a_{III}}$, $\mathbf{b_{IV}}$, $\mathbf{c_{III}}$, $\mathbf{d_{II}}$), distal ($\mathbf{a_{IV}}$, $\mathbf{b_{VI}}$, $\mathbf{c_{V}}$, $\mathbf{d_{IV}}$, $\mathbf{e_{II}}$), and mesial ($\mathbf{a_{VI}}$, $\mathbf{b_{VII}}$, $\mathbf{c_{VI}}$, $\mathbf{d_{V}}$) views; detail of the flutes ($\mathbf{a_{II}}$, $\mathbf{b_{III}}$, $\mathbf{c_{II}}$); cross-section at the apical end ($\mathbf{b_{II}}$) and at the crown base ($\mathbf{a_{IV}}$, $\mathbf{b_{V}}$, $\mathbf{c_{IV}}$, $\mathbf{d_{III}}$); detail of the distal ($\mathbf{a_{VII}}$, $\mathbf{b_{VIII}}$, $\mathbf{c_{VII}}$, $\mathbf{d_{VI}}$, $\mathbf{e_{III}}$) and mesial ($\mathbf{a_{VIII}}$) denticles. *Scale bars* for the crowns: 10 mm; for the denticles: 1 mm

diagnostic for mesial teeth of *Ceratosaurus* and been used for the identification of isolated teeth of this taxon (Meyer and Thuring 2003). Some teeth from Upper Jurassic levels of the Tendaguru Formation, first assigned as *Labrosaurus* (?) *stechowi* by Janensch (1920), were interpreted afterwards as *Ceratosaurus* sp. based on the presence of flutes in the lingual surface (Madsen and Welles 2000; Rauhut 2011). Likewise, a tooth from the Upper Jurassic Virgula beds, near Moutier in Switzerland, first assigned as *Labrosaurus meriani* by Janensch (1920) and as *Megalosaurus meriani* by Huene (1926), was assigned to *Ceratosaurus* sp. by Madsen and Welles (2000) based on this character. This feature is also reported in other ceratosaurs such as *Masiakasaurus* or a specimen from the Late Jurassic–Early Cretaceous of Uruguay (Carrano et al. 2002; Soto and Perea 2008). However, the presence of vertical grooves on the lingual surface of the crown may be a diagnostic feature at least among Upper Jurassic theropods from the Morrison Formation and from the Lusitanian Basin (Hendrickx, pers. commun.).

Flutes are present also, with various degrees of development, in the baryonychines *Baryonyx* (Charig and Milner 1997; Fowler 2007; Buffetaut 2007, 2011; Canudo et al. 2008; Mateus et al. 2011), *Suchomimus* (Sereno et al. 1998), in other spinosaurids such as *Irritator* (Sues et al. 2002) and some specimens of *Spinosaurus* (Bouaziz et al. 1988). The fluted mesial teeth of *Ceratosaurus* show remarkable similarity with baryonychine teeth and based on this similarity it was recently proposed that some teeth originally identified as belonging to *Ceratosaurus* from the Late Jurassic of Tendaguru could not be assigned with confidence to this taxon (Fowler 2007). Later, Buffetaut (2011) reinterpreted two teeth from this African record as belonging to a new species of spinosaurid *Ostafrikasaurus crassiserratus*. However, these teeth show some differences with spinosaurid teeth, such as the number of denticles, suggesting that their identification remains uncertain (Rauhut 2011).

In general, teeth of baryonychines (e.g. *Baryonyx* and *Suchomimus*) differ from those of morphotype 1 in the greater number of denticles (25 denticles per 5 mm) on both mesial and distal carinae (Charig and Milner 1986; Sereno et al. 1998; Mateus et al. 2011). More derived spinosaurids, including *Spinosaurus* (Sereno et al. 1998; Dal Sasso et al. 2005) and *Irritator* (Sues et al. 2002), have teeth with non-serrated carinae. The teeth of spinosaurids have, in general, a larger number of flutes (between 2 to 20; Hendrickx, pers. commun.) and usually in both lingual and labial surfaces (Charig and Milner 1997; Sues et al. 2002; Canudo et al. 2008; Mateus et al. 2011).

Summarizing, morphotype 1 shares with *Ceratosaurus* several features, including: (1) larger size of the denticles (also shared with the putative spinosaurid *Ostafrikasaurus*), (2) lower number of flutes, which are only on the lingual surface, (3) irregular crenulated enamel, which is more similar to ceratosaurs ornamentation than to the veined surface structure (sensu Hendrickx et al. 2016) of most spinosaurids (Sues et al. 2002; Buffetaut 2007; Sereno et al. 1998; Mateus et al. 2011; Serrano-Martínez et al. 2016), and (4) restriction of the mesial carina to the apical part of the crown (also shared with some *Baryonyx* teeth from Spain), whereas in spinosaurids the mesial carina extends to the root (Canudo et al. 2008).

SHN.205 is somewhat distinct from the other specimens included here in morphotype 1 because it has a well-developed and serrated mesial carina, a more oval cross-section of the crown base, and the flutes are restricted to the mid-section of the lingual surface. This tooth has a morphology similar to some teeth from the Tendaguru Formation identified as possibly belonging to *Ceratosaurus* (Madsen and Welles 2000; Rauhut 2011) and may correspond to a more distal position in the tooth row.

Based on the shared morphological characters and on the presence of other *Ceratosaurus* specimens represented by non-dental material in the Upper Jurassic of the Lusitanian Basin (Mateus et al. 2006; Malafaia et al. 2015), morphotype 1 is here identified as mesial teeth of *Ceratosaurus*.

4.1.2 Morphotype 2

Ceratosauridae
cf. Ceratosaurus

Specimens: SHN.212, 218, 263, 269, 305a, 307, 321a–c, 359c, 459 (Fig. 4).

Geographical provenance: Cambelas, Santa Rita, Porto Novo and Praia da Corva (Torres Vedras), Peralta (Lourinhã), Praia da Vermelha and Baleal (Peniche).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian), ?Sobral Formation (upper Kimmeridgian-lower Tithonian), and Freixial Formation (upper Tithonian).

Description: Large ziphodont teeth with AL between 21.48 and 74.42 mm (average 43.93 mm), CBL between 6.9 and 29.02 mm (average 17.9 mm), and CBW between 5.05 and 13.46 mm (average 8.31 mm). The crowns are quite elongated (CHR between 1.54 and 2.86; average 2.34), blade-shaped and strongly labiolingually-compressed (CBR between 0.32 and 0.5; average 0.41).

These teeth have slight transverse undulations. The interdenticular sulci are absent in most specimens. The enamel is generally smooth, but in some specimens it may show a series of thin irregular crenulations. The crowns have well-developed and serrated mesial and distal carinae that extends to the cervix. They are usually parallel and centrally positioned. However, in some specimens the distal carina slightly twists labially at the base of the crown. The crowns are slightly recurved apically with the mesial margin convex and the distal margin almost straight to slightly concave in lateral view. The basal cross-section is lenticular and in some specimens there is a shallow depression on the lingual surface. The lingual and labial surfaces of most crowns are almost flat or slightly convex.

There is an average of 14 denticles per 5 mm in the central section of both carinae (see Supplementary Data, Table 2S). The mesial denticles are short mesiodistally with rounded to almost flat apices. The distal denticles are subquadrangular in the mid-section of the carina (Fig. 4a$_{IX}$, b$_{VII}$, c$_{VII}$), but become horizontally subrectangular toward the base of the crown (Fig. 4a$_{VIII}$).

Results and discussion: The DFA based on the reduced dataset of Gerke and Wings (2016) and on the dataset of Hendrickx et al. (2015) recovered three specimens (SHN.263, 269, 305a) as belonging to *Piatnitzkysaurus* and *Erectopus* respectively, one specimen (SHN. 459) as

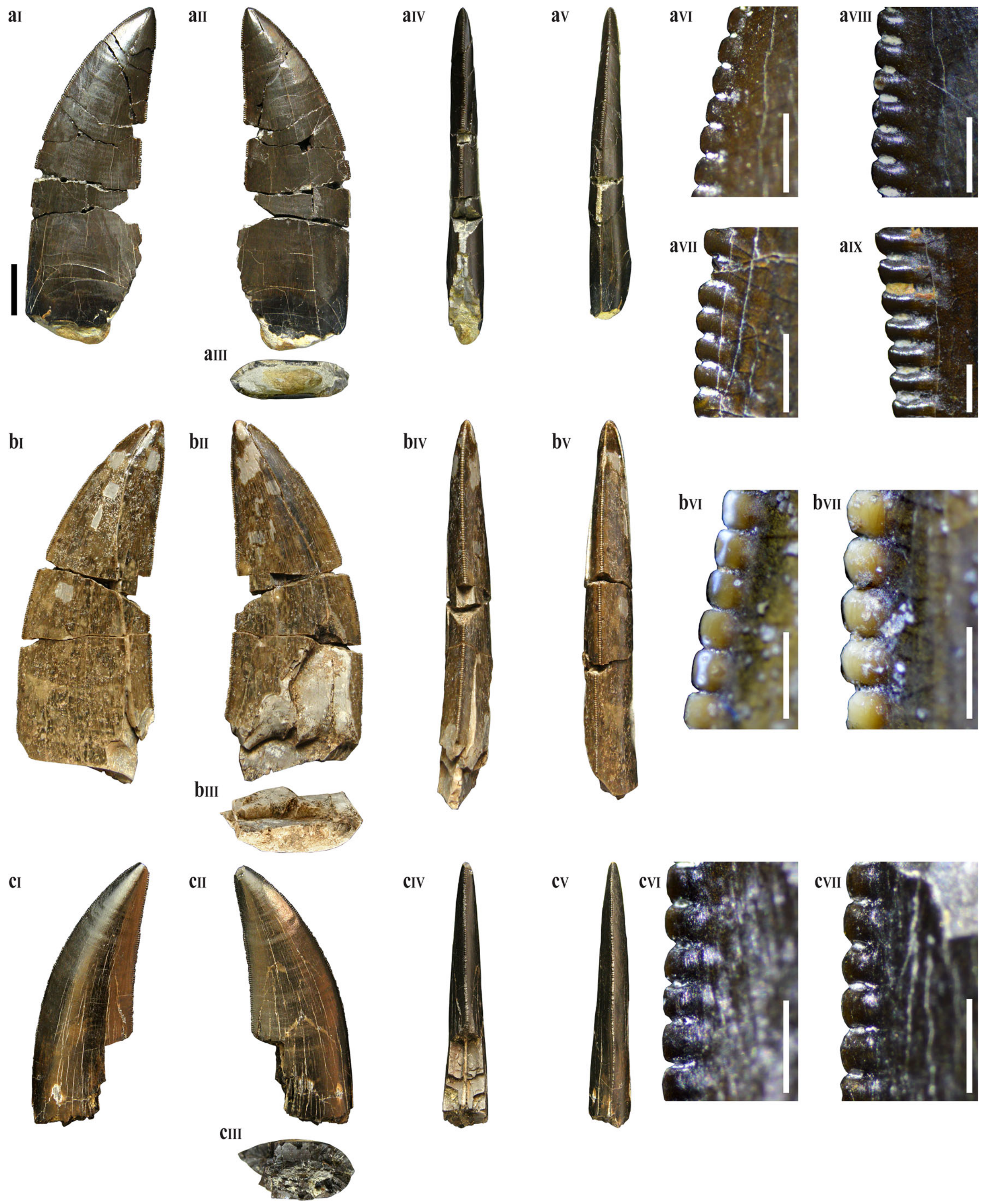

Fig. 4 Morphotype 2: **a** SHN.305a; **b** SHN.263; **c** SHN.269 in lingual ($\mathbf{a_I}$, $\mathbf{b_I}$, $\mathbf{c_I}$), labial ($\mathbf{a_{II}}$, $\mathbf{b_{II}}$, $\mathbf{c_{II}}$), distal ($\mathbf{a_{IV}}$, $\mathbf{b_{IV}}$, $\mathbf{c_{IV}}$), and mesial ($\mathbf{a_V}$, $\mathbf{b_V}$, $\mathbf{c_V}$) views; cross-section at the crown base ($\mathbf{a_{III}}$, $\mathbf{b_{III}}$, $\mathbf{c_{III}}$), detail of the mesial denticles at the apical end ($\mathbf{a_{VI}}$) and at the mid-section ($\mathbf{a_{VII}}$, $\mathbf{b_{VI}}$, $\mathbf{c_{VI}}$) of the crown; detail of the distal denticles at the apical end ($\mathbf{a_{VIII}}$) and at the mid-section ($\mathbf{a_{IX}}$, $\mathbf{b_{VII}}$, $\mathbf{c_{VII}}$) of the crown. *Scale bars* for the crowns: 10 mm; for the denticles: 1 mm

Alioramus and one specimen (SHN.321b) as *Raptorex* and *Neovenator* (see Supplementary Data, Table 4S).

This morphotype shows some unusual features, such as the strongly labiolingually-compressed crowns (in most specimens CBR <0.5), with almost flat lingual and labial surfaces and the presence of mesial carina extending to the cervix. The strongly compressed crowns are similar to those of *Ceratosaurus* (Madsen and Welles 2000; Hendrickx et al. 2015), *Genyodectes* (Rauhut 2004), *Erectopus* (Allain 2005), and some isolated teeth from the Upper

Jurassic of Germany (morphotypes C and D of Gerke and Wings 2016). However, morphotype 2 differs from the lateral teeth of most *Ceratosaurus* and *Genyodectes* in the absence of a concave or flat, vertical surface adjacent to the distal and/or mesial carinae, a character that has been interpreted as a ceratosaurian synapomorphy (Rauhut 2004; Hendrickx et al. 2015). The strongly compressed blade-shaped morphology of morphotype 2 is also shared with two different morphotypes of isolated theropod teeth from the Upper Jurassic of Germany identified as belonging to a possible megalosaurid and as Ceratosauria *incerta sedis* (morphotypes C and D of Gerke and Wings 2016) and with some teeth from the Upper Jurassic of the African Tendaguru Formation identified as possibly belonging to a carcharodontosaurid (Rauhut 2011). The specimens from Germany are interpreted as belonging to a possible ceratosaurian theropod based on the strongly compressed crowns and the mesial carina extending to the cervix (Gerke and Wings 2016). However, these specimens, similarly to morphotype 2, do not have the characteristic concave surface along the mesial and/or distal carinae that is generally present in ceratosaurian teeth (Rauhut 2004).

The numbers of mesial and distal denticles is slightly higher in the teeth of morphotype 2 than in *Ceratosaurus* and other ceratosaurs such as *Majungasaurus*, as well as in *Carcharodontosaurus* (Smith et al. 2005; Hendrickx et al. 2015). The morphology of these specimens from the Lusitanian Basin is similar to the possible metriacanthosaurid *Erectopus* from the Lower Cretaceous of France. They share compressed crowns, both mesial and distal carinae extending to the cervix and the number and shape of denticles (Allain 2005). The general morphology of morphotype 2 is similar to those of lateral teeth of *Ceratosaurus*, sharing with this taxon the following features: (1) strongly labiolingually compressed crowns, (2) mesial carina reaching the cervix, (3) sigmoid mesial carina and centrally positioned distal one, and (4) presence of numerous, closely-packed traverse undulations (Hendrickx et al. 2015). Based on this similarity and despite the absence of a concave surface along the mesial and/or distal carinae, morphotype 2 is here tentatively interpreted as lateral teeth of *Ceratosaurus*.

4.2 Megalosauroidea

4.2.1 Morphotype 3

Megalosauridae
Megalosaurinae
Torvosaurus gurneyi
Specimens: SHN.067, 202, 215, 221, 247, 257, 266, 268, 294, 303–304, 319–320, 362, 364, 374, 381, 401, 440–442, 470 (Fig. 5).

Geographical provenance: Gentias, Santa Rita, and Praia da Corva (Torres Vedras), Valmitão, Porto Dinheiro, and Peralta (Lourinhã), Praia dos Frades, Baleal, and Almagreira (Peniche), Salir do Porto (Caldas da Rainha).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian), ?Sobral Formation (upper Kimmeridgian-lower Tithonian), and Freixial Formation (upper Tithonian).

Description: Very large ziphodont teeth, with AL between 37.98 and 152.84 mm (average 87.17 mm), CBL between 21.54 and 48.38 mm (average 32.25 mm), and CBW between 12.02 and 23.49 mm (average 16.78 mm). The crowns are very elongated (CHR between 1.45 and 3.01; average 2.46), blade-shaped and moderately labiolingually compressed (CBR between 0.35 and 0.72; average 0.54). The crowns are slightly recurved distally with the distal margin somewhat concave. The mesial margin is convex and the apex is positioned near the level of the base of the distal carina.

Most crowns have well-marked transverse undulations extending across the entire mesiodistal length of both labial and lingual surface, and some of them show additional marginal undulations next to the distal carinae. Interdenticular sulci delimited by well-developed caudae extending obliquely to the carina are also present in most specimens, typically adjacent to the distal carinae (Fig. 5d_{I}). The enamel has a rough ornamentation due to the presence of thin, sinuous and apicobasally-oriented grooves and ridges (braided texture). The mesial and distal carinae are serrated and centrally positioned at their margins. However, in some specimens the mesial carina is slightly twisted lingually. The mesial carina extends along half or three-quarters of the crown height but in some teeth (SHN.257, 401, 440) it is restricted on the apical part of the crown. On the other hand, the distal carina extends always well below the cervix. Most crowns are lanceolate in cross section (Fig. 5a_{V}, b_{III}), but some specimens have a reniform section (Fig. 5c_{III}) due the presence of a well-marked concavity at the base of the lingual surface (lingual depression sensu Hendrickx et al. 2015). The lingual and labial surfaces are slightly convex.

There is an average of 7.5 denticles per 5 mm in the central section of the mesial and distal carinae. The mesial denticles are short, with rounded or almost flat apices (Fig. 5b_{VII}, c_{VIII}, d_{VII}) and the distal denticles are subquadrangular, with symmetrically rounded apices (Fig. 5b_{VI}, c_{VII}, d_{VI}) and positioned perpendicularly to the carinae. The denticles are separated by broad interdenticular spaces especially in the mid-section of the distal carina (Fig. 5a_{VIII}), but they are usually more closely packed toward the apex (Fig. 5a_{IX}) and near the base of the crown.

Fig. 5 Morphotype 3: **a** SHN.067; **b** SHN.401; **c** SHN.441; **d** SHN.266; in labial ($\mathbf{a_{IV}}$, $\mathbf{b_{I}}$, $\mathbf{c_{I}}$, $\mathbf{d_{II}}$), lingual ($\mathbf{a_{II}}$, $\mathbf{b_{II}}$, $\mathbf{c_{III}}$, $\mathbf{d_{III}}$), distal ($\mathbf{a_{VI}}$, $\mathbf{b_{IV}}$, $\mathbf{c_{IV}}$, $\mathbf{d_{IV}}$), and mesial ($\mathbf{a_{VII}}$, $\mathbf{b_{V}}$, $\mathbf{c_{V}}$, $\mathbf{d_{V}}$) views; cross-section at the crown base ($\mathbf{a_{V}}$, $\mathbf{b_{III}}$, $\mathbf{c_{III}}$), detail of the distal denticles at the mid-section ($\mathbf{a_{VIII}}$, $\mathbf{b_{V}}$, $\mathbf{c_{VII}}$, $\mathbf{d_{VI}}$) and at the apical part ($\mathbf{c_{VI}}$) of the crown; detail of the mesial denticles ($\mathbf{a_{IX}}$, $\mathbf{b_{VII}}$, $\mathbf{c_{VIII}}$, $\mathbf{d_{VII}}$); detail of the marginal undulations ($\mathbf{a_{I}}$) and of the enamel ornamentation ($\mathbf{a_{III}}$); detail of the interdenticular sulci and caudae ($\mathbf{d_{I}}$). *ce* cervix. *Scale bars* for the crowns: 50 mm; for the denticles: 1 mm; ($\mathbf{a_{I}}$, $\mathbf{a_{III}}$, and $\mathbf{d_{I}}$): 10 mm

Results and discussion: The DFA based on the dataset of Hendrickx et al. (2015) assigns fourteen specimens of morphotype 3 to *Torvosaurus*, one (SHN.362) to *Megalosaurus*, one (SHN.294) to *Ceratosaurus*, and one (SHN.470) to *Erectopus*. The results based on the reduced dataset of Gerke and Wings (2016) is more ambiguous, assigning five specimens to *Torvosaurus* and the other teeth to different taxa including *Carcharodontosaurus*, *Acrocanthosaurus*, and *Tyrannosaurus* (see Supplementary Data, Table 4S). This result probably reflects the similarity in the tooth to the general morphology among most large-sized theropod taxa based on morphometric features (Hendrickx and Mateus 2014b; Hendrickx et al. 2015).

The most distinctive feature of this morphotype is the large size of some crowns, which is comparable with *Torvosaurus* (Britt 1991; Hendrickx et al. 2015), *Tyrannosaurus* (Smith 2005; Brochu 2003) and some carcharodontosaurids such as *Acrocanthosaurus* (Harris 1998; Currie and Carpenter 2000). These teeth are comparable to other specimens previously described in the Upper Jurassic of the Lusitanian Basin and assigned to *Torvosaurus* (Hendrickx and Mateus 2014a, 2014b; Hendrickx et al. 2015). Similarities between the morphotype 3 and lateral teeth of *Torvosaurus* include: (1) moderately labiolingually compressed crowns, (2) centrally-positioned mesial carina that ends at approximately crown mid-height whereas the distal carina terminates well beneath the cervix, and (3) shallow concavity present on the basolingual central part of the crown (Hendrickx and Mateus 2014a, b; Hendrickx et al. 2015). The unusually low denticle density, the presence of well-marked interdenticular sulci and caudae, sometimes in both carinae, and the braided texture of the enamel are other features shared with some megalosaurids, including *Torvosaurus* and *Megalosaurus* (Hendrickx et al. 2015; Hendrickx and Mateus 2014a).

Morphotype 3 also shares some characteristics with some specimens described in the Upper Jurassic of Spain (Suñer et al. 2005; Canudo et al. 2006; Royo-Torres et al. 2009; Cobos et al. 2014; Gascó et al. 2012) and Germany (Gerke and Wings 2016). These similarities may indicate that they probably belong to the same taxon or a closely related form, as was previously suggested.

4.2.2 Morphotype 4

Megalosauridae
Megalosaurinae
cf. Torvosaurus gurneyi
Specimens: SHN.305b, 359a, 456 (Fig. 6).
Geographical provenance: Cambelas and Porto Novo (Torres Vedras), Porto Dinheiro (Lourinhã).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian) and Freixial Formation (upper Tithonian).

Description: Moderately large, mostly slender and relatively elongated crowns (CHR: 2.4 and CBL: 16.57 mm in average). The general morphology of these specimens is similar to morphotype 3, but the crowns are narrower mesiodistally and the mesial carina extends almost to the cervix and twists lingually at the base. Also the distal carina is displaced labially in morphotype 4 whereas in morphotype 3 this carina is somewhat parabolic in distal view, but is centrally positions on the distal margin.

SHN.359a (Fig. 6b) has several deep transverse and marginal undulations in both labial and lingual surfaces, but these structures are absent in the other specimens. The crowns have braided ornamented enamel (Fig. 6a$_{VI}$, c$_{VIII}$), which is more clearly visible in SHN.459a and SHN.456.

The denticles are large, with about 10 denticles per 5 mm in the central section of the mesial and distal carinae. The distal denticles have symmetrical hemicircular apices (Fig. 6b$_{VI}$, c$_{VI}$) and are subquadrangular in lateral view in the mid-section of the carina, but are slightly wider mesiodistally than apicobasally close to the base of the crown. The mesial denticles are rectangular, wider apicobasally than mesiodistally and the apices are almost flat (Fig. 6b$_{VII}$, c$_{VII}$). The denticles are smaller toward the apex and toward the base in both carinae. The mesial and distal denticles are perpendicular to the carinae along the entire height of the crowns and are separated by narrow interdenticular spaces. Interdenticular sulci and caudae are absent in all specimens.

Results and discussion: The DFA result assigns the specimens of morphotype 4 to *Carcharodontosaurus*, *Majungasaurus*, and *Allosaurus* (see Supplementary Data, Table 4S). However, these specimens are similar to morphotype 3 in several features, such as (1) distal carina that extends well below the cervix, (2) similar density of large denticles on the mesial and distal carinae, (3) well-developed transverse and marginal undulations, and (4) ornamentation of the enamel. Morphotype 4 differs from morphotype 3 in the lingually-displaced mesial carina extending to the cervix.

These specimens are also similar to some isolated teeth from the Upper Jurassic of Germany, interpreted as belonging to an indeterminate megalosaurid (morphotype A of Gerke and Wings 2016) and to some specimens from the Tendaguru Formation of Tanzania tentatively assigned to Carcharodontosauria (Rauhut 2011). Morphotype 4 shares with these German and Tanzanian specimens a mesial carina that reaches the cervix, similar denticles density, quadrangular mesial denticles and the well-developed marginal undulations (Rauhut 2011; Gerke and Wings 2016).

In *Torvosaurus*, it seems that the mesial carinae always ends well above the cervix (Hendrickx and Mateus 2014a; Hendrickx et al. 2015). However, in one isolated tooth from Portugal (ML857: Hendrickx and Mateus 2014b), as well as in some specimens of morphotype 3 described above, the mesial denticles extend for about one fifth of the crown height, suggesting that this feature is somewhat variable for this taxon. The general similarity between morphotype 3 and 4 may suggest that they belong to the same taxon and that these differences could be related with intraspecific variation or with different positions in the tooth row.

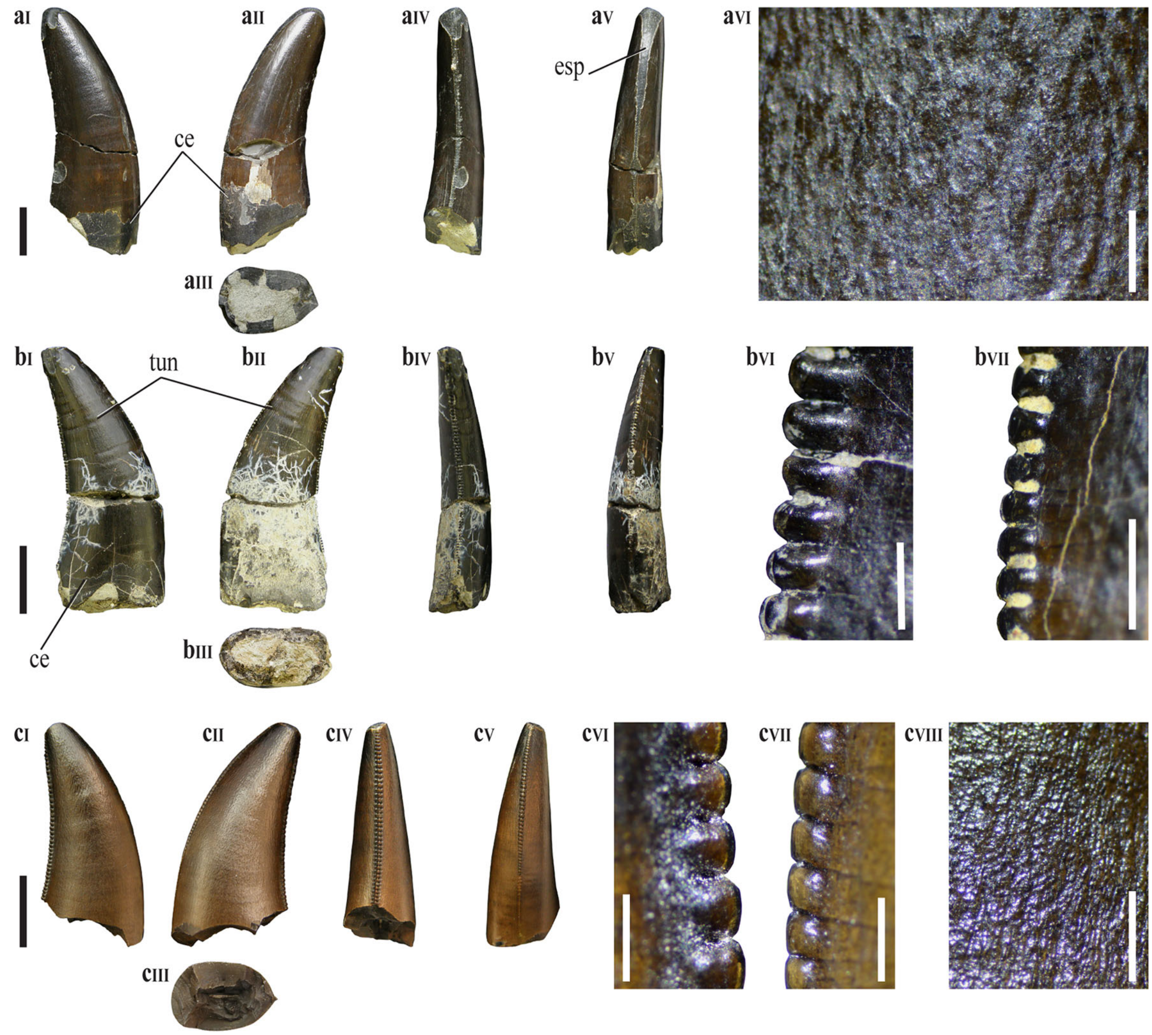

Fig. 6 Morphotype 4: **a** SHN.305b; **b** SHN.359a; **c** SHN.456 in labial ($\mathbf{a_I}$, $\mathbf{b_I}$, $\mathbf{c_I}$), lingual ($\mathbf{a_{II}}$, $\mathbf{b_{II}}$, $\mathbf{c_{II}}$), distal ($\mathbf{a_{IV}}$, $\mathbf{b_{IV}}$, $\mathbf{c_{IV}}$), and mesial ($\mathbf{a_V}$, $\mathbf{b_V}$, $\mathbf{c_V}$) views; cross-section at the crown base ($\mathbf{a_{III}}$, $\mathbf{b_{III}}$, $\mathbf{c_{III}}$); detail of the enamel ornamentation ($\mathbf{a_{VI}}$, $\mathbf{c_{VIII}}$); detail of the distal ($\mathbf{b_{VI}}$, $\mathbf{c_{VI}}$) and mesial ($\mathbf{b_{VII}}$, $\mathbf{c_{VII}}$) denticles. *ce* cervix, *esp* enamel spalling, *tun* transverse undulations. *Scale b*ars for the crowns: 10 mm; for the denticles: 1 mm; ($\mathbf{a_{VI}}$ and $\mathbf{c_{VIII}}$): 10 mm

4.2.3 Morphotype 5

Megalosauridae
Megalosaurinae
cf. Torvosaurus gurneyi
Specimens: SHN.264 (Fig. 7).

Geographical provenance: Valmitão (Torres Vedras).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian).

Description: This morphotype includes a single specimen corresponding to a complete and well-preserved crown. This specimen is very small, with AL of 7.62 mm, CBL of 4.35 mm, and CBW of 2.26 mm. The crown is very short (CHR: 1.56), slightly compressed labiolingually with an oval cross-section at the base (CBR: 0.52). The crown is strongly recurved apically with the mesial margin strongly convex apically, but almost straight in the basal three-quarters. The distal margin is almost straight. The crown shows a tenuous braided enamel texture and well-developed interdenticular sulci between the distal denticles. Both carinae are serrated with the distal carina extending to the cervix whereas the mesial carina is only restricted to the apical end. The crown is symmetrical, with the mesial and distal carina positioned in the mesial and distal margins, respectively.

There is an average of 5 and 5.5 denticles per mm in the central and centroapical section of the distal and mesial carinae, respectively (DSDI near 1), but denticles are absent in the central section of the mesial carina (see Supplementary Data, Table 2S). The distal denticles are rectangular, slightly higher mesiodistally than apicobasally and with symmetrically circular apices (Fig. 7f). The

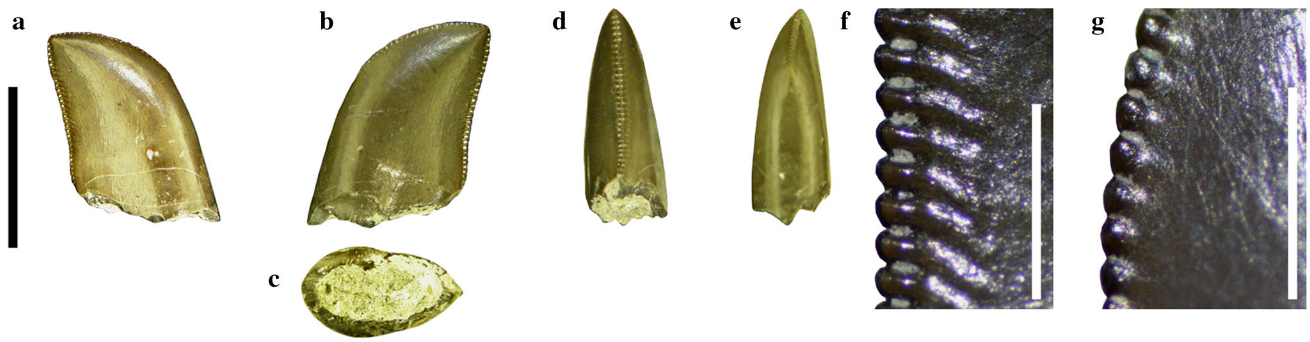

Fig. 7 Morphotype 5: SHN.264 in labial (**a**), lingual (**b**), distal (**d**), and mesial (**e**) views; cross-section at the crown base (**c**); detail of the distal (**f**) and mesial (**g**) denticles. *Scale bars* for the crown: 5 mm; for the denticles: 1 mm

mesial denticles are very low and subquadrangular (Fig. 7g). The distal denticles are smaller near the base and gradually increase in size to the apex. In the mid-section of the distal carina, the denticles are separated by broad interdenticular spaces, which are more than one third of the apicobasal width of the denticle (Fig. 7f).

Results and discussion: The DFA based on the reduced dataset of Gerke and Wings (2016) classifies the specimen SHN.264 to *Torvosaurus* whereas the result based on the dataset of Hendrickx et al. (2015) assigned this tooth as *Neovenator* (see Supplementary Data, Table 4S). This specimen shares with some dromaeosaurids such as *Velociraptor* and *Bambiraptor* a subequal number of denticles in the mesial (apically) and distal (at mid-crown) carinae and the broad interdenticular space between mid-crown denticles on the distal carina (Godefroit et al. 2008; Hendrickx et al. 2014b). The general morphology of the crown is similar to some lateral teeth of *Compsognathus* in the relatively straightness of the base and the strongly backward curvature of the tip (Peyer 2006). Other isolated theropod teeth tentatively assigned to *Compsognathus* were described in the Upper Jurassic of the Lusitanian Basin (Zinke 1998). The specimen described here shares morphology with some of these isolated teeth from the Guimarota fossil site, especially with a morphotype interpreted as belonging to the anterior part of the tooth row, the strongly recurved apical end of the crown. However, these specimens from Guimarota differ from SHN.264 in several aspects, including the absence of denticles on the mesial carina or on both mesial and distal carinae in some teeth and the presence of a small constriction between the crown and the root (Zinke 1998). In some *Compsognathus* specimens, the teeth are confluent between the crown and the root and not constricted as occur in morphotype 5, but mesial denticles are not present in mesial or lateral teeth (Zinke 1998; Peyer 2006). However, compsognathid teeth like those of *Compsognathus* (Peyer 2006), *Scipionyx* (Dal Sasso and Maganuco 2011), *Juravenator* (Göhlich and Chiappe 2006), and *Sinosauropteryx* (Currie and Chen 2001) are typically very elongated, with few relatively large denticles. Beside, most compsognathid teeth, with the exception of *Juravenator*, have an unserrated mesial carina and interdenticular sulci are generally absent. The low crown of SHN.264 suggests that this tooth probably comes from the distalmost part of the jaw. The denticle size and shape, the presence of interdenticular sulci and the braided enamel texture are similar to those of *Torvosaurus*. Based on these shared features and the results of the DFA analysis, morphotype 5 is here tentatively identified as belonging to a juvenile *Torvosaurus*.

4.2.4 *Morphotype 6*

Megalosauroidea
Specimens: SHN.446, 450 (Fig. 8).
Geographical provenance: Santa Rita (TorresVedras) and Peralta (Lourinhã).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian), ?Sobral Formation (upper Kimmeridgian-lower Tithonian).

Description: This morphotype includes two specimens, but SHN.450 is incomplete lacking the apical part. SHN.446 is a complete, moderately large-sized crown with AL of 14.63 mm, CBL 6.2 mm, and CBW 3.57 mm (see Supplementary Data, Table 2S). This specimen has a slender, elongated (CHR: 2.26) crown in lateral view. The crown is slightly recurved distally with the distal margin concave, the mesial margin is convex, and the apex is positioned distally to the base of the distal carina. The crown cross-section is oval, slightly labiolingually compressed (CBR: 0.57), with the labial surface convex and the lingual surface flat. The mesial and distal carinae are serrated with the distal carina extending slightly below the cervix and the mesial carina ending approximately at mid-height. The mesial carina is placed in the mesial margin, but the distal carina is displaced labially and is strongly sigmoidal in distal view. The enamel is smooth without transverse

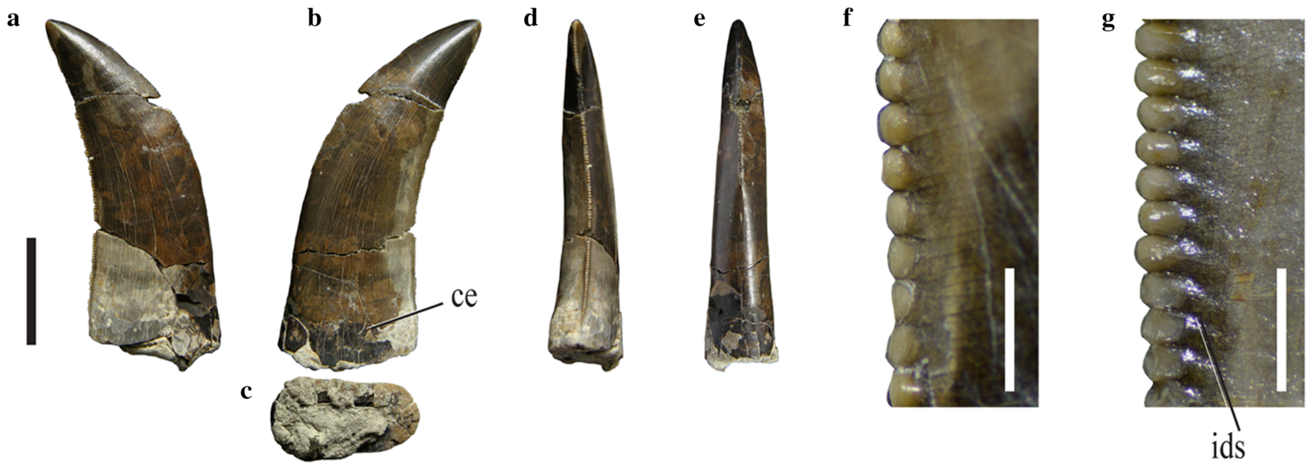

Fig. 8 Morphotype 6: SHN.446 in lingual (**a**), labial (**b**), distal (**d**), and mesial (**e**) views, cross-section at the crown base (**c**), detail of the mesial (**f**) and distal (**g**) denticles. *ce* cervix, *ids* interdenticular sulci. *Scale bars* for the crowns: 10 mm; for the denticles: 1 mm

undulations. However, short interdenticular sulci are present between the denticles, but only at mid-section of the distal carina (Fig. 8g). The distal carina has 20 denticles per 5 mm in the central section; the mesial denticles are poorly preserved so it is not possible quantify their density.

Results and discussion: The DFA excluding the variable MC, since the poor preservation of the mesial carina does not allow the determination of the number of denticles, assigns SHN.446 and SHN.450 as *Deinonychus*, *Majungasaurus*, and *Dromaeosaurus* (see Supplementary Data, Table 4S). This morphotype has a general morphology similar to morphotype 4, namely in the slender and elongated shape of the crown, in lateral view. However, SHN.446 differs from morphotype 4 in several aspects, including the higher number of denticles, the presence of interdenticular sulci, and absence of ornamentation of the enamel. This specimen has a general morphology similar to lateral teeth of *Megalosaurus* (Benson 2010) and some isolated teeth from the Upper Jurassic of Germany tentatively assigned to the piatnitzkysaurid *Marshosaurus* (morphotype J of Gerke and Wings 2016). These specimens share the slender, elongation of the crown and similar serration density in the distal carinae (Hendrickx et al. 2015; Gerke and Wings 2016). However, SHN.446 differs from the German morphotype in being slightly larger and less labiolingually compressed. A PCA performed upon the set of teeth belonging to *Megalosaurus*, *Torvosaurus*, some isolated teeth from the Upper Jurassic of Spain and Germany and the specimens of morphotypes 3, 4, 5, and 6 described here show that the specimens of morphotype 4 fall outside the morphospace occupied by morphotype 3, herein interpreted as belonging to *Torvosaurus* and within the morphospace occupied by *Megalosaurus* (Fig. 9). There is an almost complete overlap of the morphospaces of morphotype 3, *Torvosaurus*, the morphotype A from Germany and some isolated megalosauroid teeth from Spain. The specimen SHN.450 is placed within the morphospace of *Megalosaurus*, but SHN.446 falls outside the morphospace of all represented taxa. Based on these results and on the general similarity with *Megalosaurus* and especially with some isolated teeth from Germany, morphotype 6 is here assigned to an indeterminate megalosauroid.

4.2.5 Morphotype 7

Megalosauroidea
Specimens: SHN.226a–b, 239, 318, 321d, 330, 444–445, 448, 451–453, 464 (Fig. 10).

Geographical provenance: Praia da Corva and Porto Novo (Torres Vedras), Valmitão, Atalaia, Peralta, and Paimogo (Lourinhã), Almagreira (Peniche).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian), Sobral Formation (upper Kimmeridgian-lower Tithonian).

Description: Teeth of medium to small sizes (AL average: 31.35 mm; CBL average: 12.86 mm and CBW average: 6.55 mm). The crowns are relatively elongated (CHR average: 2.18) and strongly compressed labiolingually (CBR average: 0.51). These specimens have slightly recurved crowns in which the distal margin is slightly concave, the mesial margin is strongly convex and the apex is positioned slightly distal to the base of the distal carina.

Slight transverse undulations on the crown are present in several specimens. Well-marked, diagonal interdenticular sulci are present in most teeth (Fig. 10c_{VI}, d_{VI}). They are more developed between distal denticles, but in some specimens also present in the mesial carina. The enamel is mostly smooth or shows ornamentation consisting on a

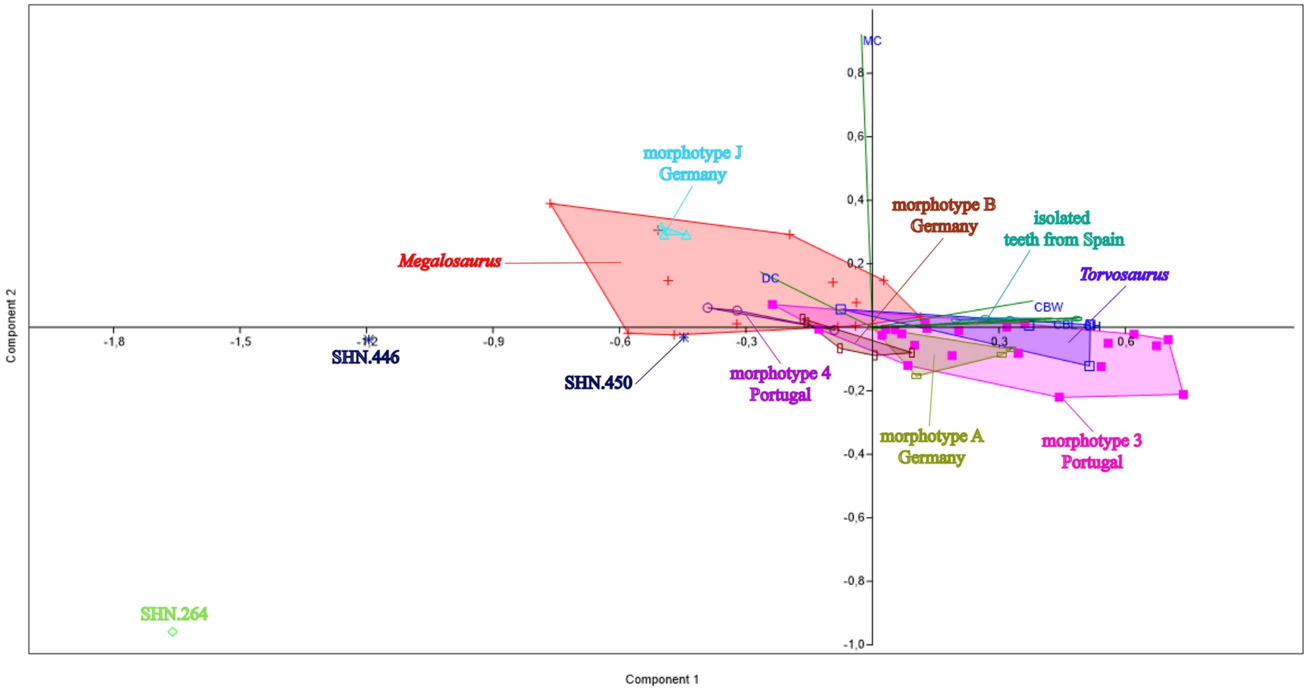

Fig. 9 Plot of loadings from the principal component analysis of a set of teeth belonging to *Megalosaurus*, *Torvosaurus*, the morphotypes 3, 4, 5, and 6 described here, and some isolated teeth from the Upper Jurassic of Spain and Germany (morphotype *A*, *B* and *J*). The specimens are grouping along the first two canonical axes of the principal components (Eigenvalue of axis 1 = 0.196, which accounts for 82.69% of the total variation; Eigenvalue of axis 2 = 0.030, which accounts for 12.858% of the total variation). The variables CBL, CBW, CH, AL, MC, and DC log-transformed were used in the analysis

series of very thin and irregular crenulations only visible with binocular microscope. The mesial and distal carinae are serrated, with the mesial carina usually extending approximately until the crown mid-height or being restricted to the apical end. The mesial carina is centrally positioned, but the distal carina shows a marked labial displacement. The lingual surface is usually flat or slightly convex and the labial surface is convex. In distal view, the distal margin slightly curves lingually forming a slight concavity at the base of the lingual surface. The cross-section of the crown base is elliptical or lenticular.

The number of denticles is much higher in the mesial than in the distal carina (DSDI equal or higher than 1.2). There is an average of 19.5 and 15.7 denticles per 5 mm in the mid-section of the mesial and distal carinae respectively. The interdenticular space is narrow in both carinae. The mesial denticles are usually vertical rectangular and with rounded or flat apices whereas the distal denticles are horizontal rectangular and have slightly asymmetrical rounded apices.

Results and discussion: The results of DFA for morphotype 7 is ambiguous with the specimens assigned to different theropod taxa including *Allosaurus*, *Raptorex*, *Piatnitzkysaurus*, *Megalosaurus*, *Erectopus*, and *Alioramus* (see Supplementary Data, Table 4S).

The specimens grouped here in morphotype 7 are similar to those of morphotype 6 except in the more slender and elongated crown in morphotype 6. The general morphology of morphotype 7 is similar to those of some anteriormost lateral teeth of *Allosaurus*, but differs from this taxon in the more labiolingually compressed crowns (CBR average = 0.51), the mesial carina restricted to the apical part of the crown, whereas in *Allosaurus* the mesial carinae usually extend close to the cervix, and a higher number of mesial than distal denticles (DSDI equal or higher than 1.2) (Hendrickx et al. 2015). The combination of features of morphotype 7 is compatible with megalosauroid lateral teeth. In particular, the mesial denticles that are slightly smaller than the distal ones and the slender, elongated crown are shared with *Marshosaurus* (Madsen 1976; Hendrickx et al. 2015; Gerke and Wings 2016). Based on this combination of features and the similarity with some isolated teeth from the Upper Jurassic of Germany (morphotype J of Gerke and Wings, 2016), morphotype 7 is here assigned as belonging to an indeterminate megalosauroid taxa tentatively related to *Marshosaurus*.

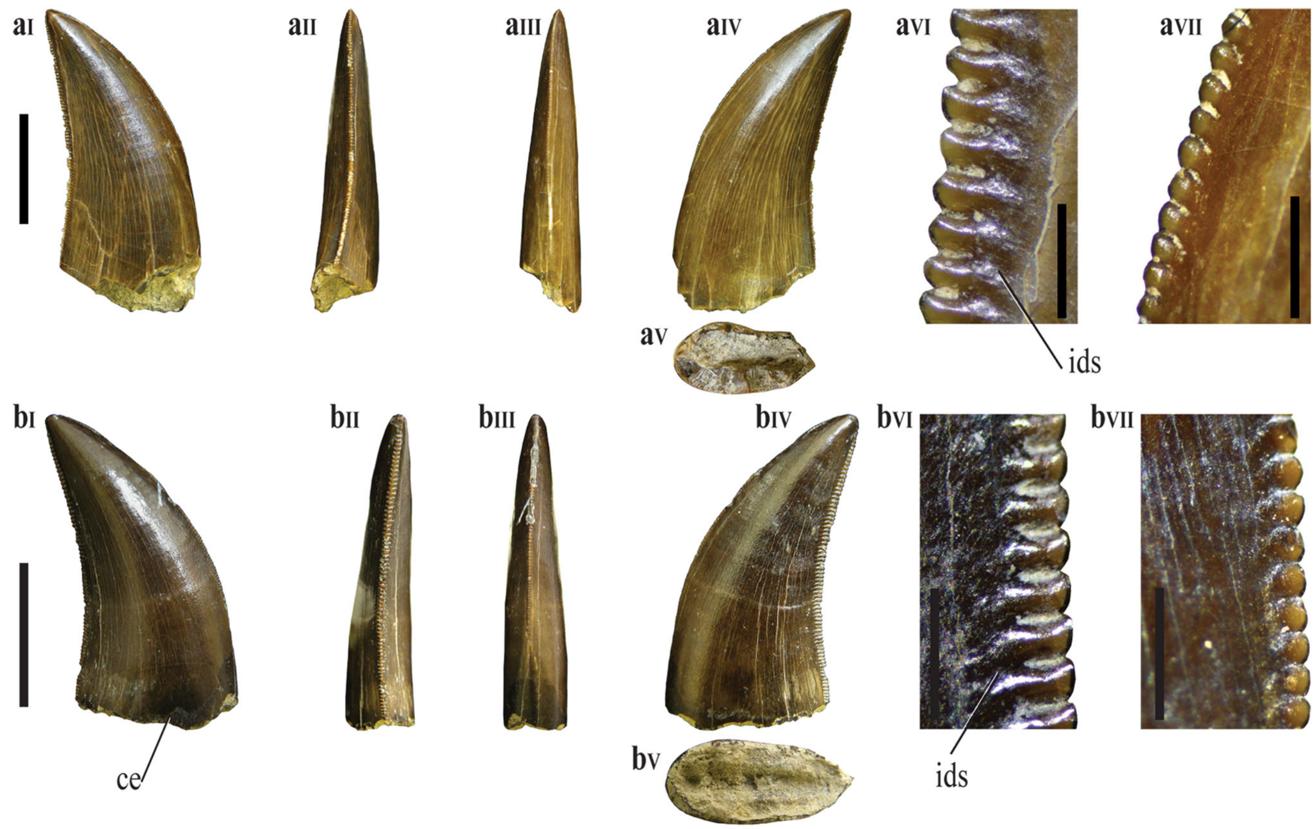

Fig. 10 Morphotype 7: **a** SHN.452; **b** SHN.444 in labial ($\mathbf{a_I}$, $\mathbf{b_I}$), distal ($\mathbf{a_{II}}$, $\mathbf{b_{II}}$), mesial ($\mathbf{a_{III}}$, $\mathbf{b_{III}}$), and lingual ($\mathbf{a_{IV}}$, $\mathbf{b_{IV}}$) views; cross-section at the crown base ($\mathbf{a_V}$, $\mathbf{b_V}$); detail of the distal ($\mathbf{a_{VI}}$, $\mathbf{b_{VI}}$) and mesial ($\mathbf{a_{VII}}$, $\mathbf{b_{VII}}$) denticles at the mid-crown. *ce* cervix, *ids* interdenticular sulci. *Scale bars* for the crowns: 10 mm; for the denticles: 1 mm

4.2.6 Morphotype 8

Megalosauroidea
Specimens: SHN.289, 290,323, 346, 359b, 455 (Fig. 11).
Geographical provenance: Praia da Corva and Porto Novo (Torres Vedras), Valmitão, Porto das Barcas, and Peralta (Lourinhã), ?Salir do Porto (Caldas da Rainha).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formaton (upper Kimmeridgian) and ?Sobral Formation (upper Kimmeridgian-lower Tithonian).

Description: Small crowns with AL between 8.85 and 19.37 mm (average 13.61 mm), CBL between 3.66 and 8.35 mm (average 6.29 mm), and CBW between 1.73 and 4.21 mm (average 3.29 mm). The crowns are relatively elongated (CHR between 1.72 and 2.38; average 2.08), triangular in lateral view and incrassate to slightly labiolingually compressed (CBR between 0.45 and 0.65; average 0.52).

These teeth show an irregular enamel texture and subtle transverse undulations. Both carinae are serrated with the distal reaching the cervix whereas the mesial carina is restricted to the apical part of the crown. The mesial carina is centrally positioned, but the distal carina twists strongly labially to the base of the crown. The crowns are slightly curved apically with the mesial margin convex and the distal margin slightly concave in lateral view. The crowns are lenticular (Fig. 11b_{III}, c_{III}) to subcircular (Fig. 11a_{III}) in cross-section. The lingual and labial surfaces are slightly convex.

An average of 5.8 and 4.6 denticles per mm is found in the central section of the mesial and distal carinae respectively and the DSDI is higher than 1.2 in most specimens (see Supplementary Data, Table 2S). The mesial denticles are mesiodistally short with rounded apices. The distal denticles are subquadrangular in outline with slightly asymmetrical rounded apices and they have a slight apical orientation in the apical end of the crown.

Results and discussion: The result of DFA for morphotype 8 assigns the specimens to different taxa, including *Masiakasaurus*, *Proceratosaurus*, and *Deinonychus* (see Supplementary Data, Table 4S).

The general morphology of morphotype 8 is similar to morphotype 9 described below, but they differ in some details, including (1) the mesial carina is restricted to the apical part of the crown, whereas it extends near the cervix in morphotype 9 and (2) DSDI >1.2 in morphotype 8 and

Fig. 11 Morphotype 8: **a** SHN.323; **b** SHN.289; **c** SHN.290 in labial ($\mathbf{a_I}$, $\mathbf{b_I}$, $\mathbf{c_I}$), lingual ($\mathbf{a_{II}}$, $\mathbf{b_{II}}$, $\mathbf{c_{II}}$), distal ($\mathbf{a_{IV}}$, $\mathbf{b_{IV}}$, $\mathbf{c_{IV}}$), mesial ($\mathbf{a_V}$, $\mathbf{b_V}$, $\mathbf{c_V}$) views; cross-section at the crown base ($\mathbf{a_{III}}$, $\mathbf{b_{III}}$, $\mathbf{c_{III}}$); detail of the distal denticles at mid-crown ($\mathbf{a_{VI}}$, $\mathbf{b_{VI}}$, $\mathbf{c_{VI}}$) and apically ($\mathbf{b_{VII}}$); detail of the mesial denticles ($\mathbf{a_{VII}}$). *Scale bars* for the crowns: 10 mm; for the denticles: 1 mm

near 1 in morphotype 9. This combination of features is more compatible with megalosauroid theropods and particularly the higher number of mesial than distal denticles is a feature shared with *Marshosaurus* (Hendrickx et al. 2015; Gerke and Wings 2016). Morphotype 8 is here identified as belonging to a juvenile megalosauroid tentatively related to the piatnitzkysaurid *Marshosaurus*.

4.3 Allosauroidea

4.3.1 Morphotype 9

Allosauridae
Allosaurus sp.
Specimens: SHN.255, 285, 316, 321e, 354, 363b, 373, 375, 384,449 (Fig. 12).

Geographical provenance: Porto Novo (Torres Vedras), Porto Dinheiro, Atalaia, Porto das Barcas, Peralta, and Praia da Areia Branca, (Lourinhã), Praia dos Frades and Almagreira (Peniche).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian), ?Sobral Formation (upper Kimmeridgian-lower Tithonian), and Freixial Formation (upper Tithonian).

Description: Teeth of medium to small sizes (AL average: 28.98 mm; CBL average: 11.9 mm and CBW average: 6.26 mm). The crowns are relatively elongated (CHR average: 2.23) and strongly compressed labiolingually (CBR average: 0.53). These specimens have slightly recurved crowns in which the distal margin is slightly concave, the mesial margin is strongly convex and the apex

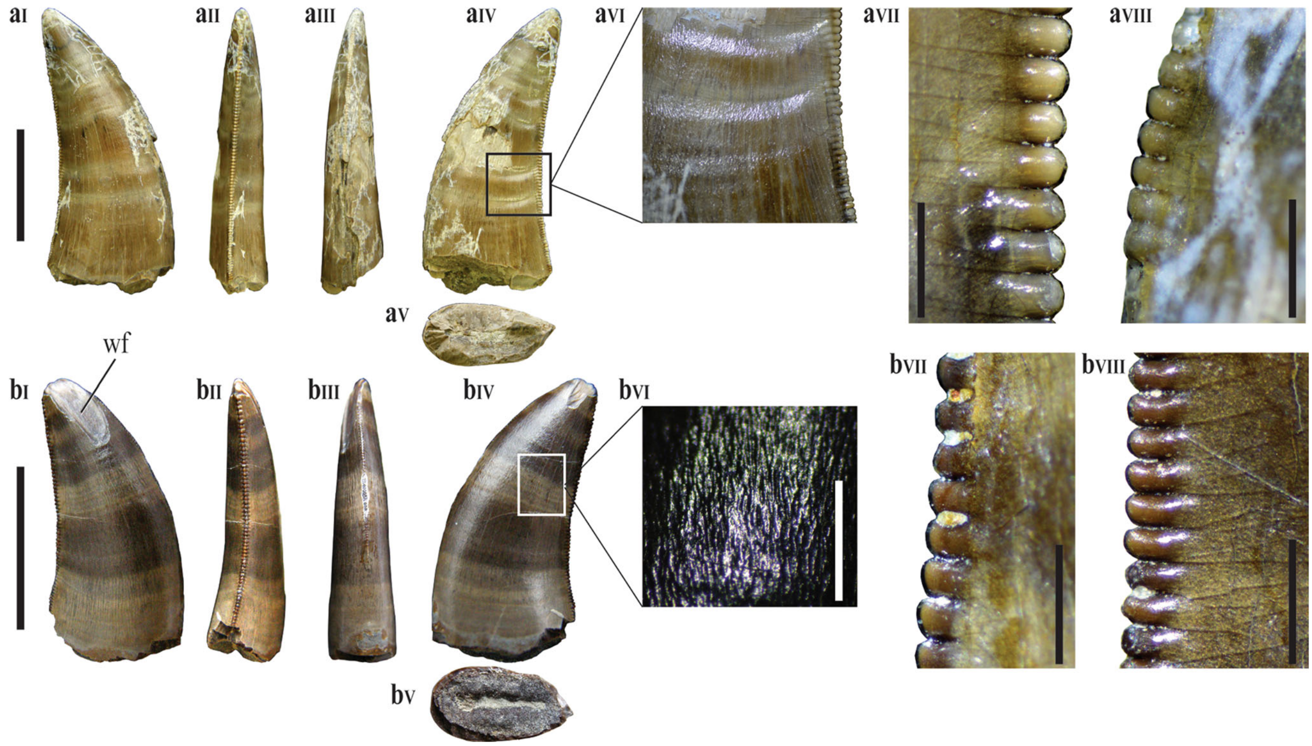

Fig. 12 Morphotype 9: **a** SHN.285; **b** SHN.375 in labial (**a$_{I}$**, **b$_{IV}$**), distal (**a$_{II}$**, **b$_{II}$**), mesial (**a$_{III}$**, **b$_{III}$**), and lingual (**a$_{IV}$**, **b$_{I}$**) views; cross-section at the crown base (**a$_{V}$**, **b$_{V}$**); detail of the transverse undulations (**a$_{VI}$**) and of the enamel ornamentation (**b$_{VI}$**); detail of the distal denticles at the mid-section (**a$_{VII}$**, **b$_{VIII}$**) and at the base (**b$_{VII}$**) of the crown; detail of the mesial denticles (**a$_{VIII}$**) denticles. *wf* wear facet. *Scale bars* for the crowns: 10 mm; for the denticles: 1 mm; (**b$_{VI}$**): 1 mm

is positioned at the level of the distalmost point of the crown base.

Transverse undulations on the crown are present in several specimens. In some crowns (SHN.285: Fig. 12a) they are very deeply-marked extending across the lingual and labial surfaces. The deep undulations in this specimen might be related with some kind of biological or taphonomic process. Well-marked, diagonal interdenticular sulci are present in most teeth. They are more developed between distal denticles, but in some specimens are also present in the mesial carina. The enamel usually shows an ornamentation consisting on a series of very thin and irregular crenulations only visible with binocular microscope (Fig. 12b$_{VI}$). The mesial and distal carinae are serrated with the mesial carina extending more than two thirds of the crown height. The mesial carina is centrally positioned, but the distal carina shows a marked labial displacement. The lingual surface is flat or slightly convex and the labial surface is convex. In distal view, the distal margin slightly curves lingually forming a slight concavity at the base of the lingual surface. The cross-section of the crown base is elliptical. Some specimens show a flat or slightly concave vertical surface adjacent to the distal carina on the lingual surface (Fig. 12b$_{I}$).

The number of denticles in the mesial carina is slightly lower than in the distal carina, with an average of 11.9 and 16.8 denticles per 5 mm in the mid-section of the respective carinae, but the DSDI is near 1 in all specimens. The interdenticular space is narrow in both carinae. The mesial denticles are vertical rectangular and bear rounded or flat apices, whereas the distal denticles are horizontal rectangular and have slightly asymmetrical, rounded apices.

Results and discussion: The results of DFA for morphotype 9 identify these teeth to distinct taxa, including *Allosaurus*, *Erectopus*, *Megalosaurus Raptorex*, and *Alioramus* (see Supplementary Data, Table 4S). Morphotype 9 shares with allosauroid lateral teeth the moderate labiolingually-compressed crowns, the distal denticles slightly inclined toward the tip of the crown, especially in the apical end of the crown, and the presence of a concave surface adjacent to the mesial carina on the lingual side (Han et al. 2011; Hendrickx et al. 2015; Gerke and Wings 2016).

The combination of morphological characters of the teeth grouped in the morphotype 9 herein described is compatible with lateral teeth of *Allosaurus*. Based on this combination of features and since the presence of *Allosaurus* in the Upper Jurassic of the Lusitanian Basin is well documented (Pérez-Moreno et al. 1999; Rauhut and

Fechner 2005; Mateus et al. 2006; Malafaia et al. 2010), morphotype 9 is tentatively assigned as lateral teeth of *Allosaurus*.

4.3.2 Morphotype 10

Allosauridae
Allosaurus sp.
Specimens: SHN.204, 232, 250, 274–275, 363a, 367, 454, 460 (Fig. 13).
Geographical provenance: Gentias, Amoeiras, Santa Rita, and Praia da Corva (Torres Vedras), Valmitão and Peralta (Lourinhã), Almagreira (Peniche).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian), ?Sobral Formation (upper Kimmeridgian-lower Tithonian), and Freixial Formation (upper Tithonian).

Description: Moderately large teeth, with AL between 31.47 and 41.27 mm (average 35 mm), CBL between 13.87 and 19.55 mm (average 16.39 mm), and CBW between 9.88 and 15.01 mm (average 13.28 mm). The crowns are moderately elongated (CHR between 1.74 and 2.33; average 2.07) and subcircular in cross-section with low labiolingually compression ratios (CBR between 0.51 and 1; average 0.78). The crowns are triangular in lateral view with the distal carina slightly concave and the mesial carina strongly convex. The apex is centrally positioned and does not surpass the level of the distal carina.

Most of these specimens show well-marked transverse undulations and interdenticular sulci between distal denticles. In SHN.454 (Fig. 13d), the crown shows unusual deep transverse undulations, especially in the mid-section of both lingual and labial surfaces. In the remaining part of the crown transverse undulations are much shallower and widely spaced. These deep undulations similar to those of SHN.285 (morphotype 9) may be related to some kind of abnormal biological or taphonomic process.

The enamel is usually smooth or shows thin and irregular crenulations (Fig. 13a$_{IV}$, b$_{IV}$). Serrated mesial and distal carinae are present and both extend to the cervix (except in SHN.204 in which the mesial ends slightly above the cervix). Both carinae are positioned in the lingual surface. In SHN.460 (Fig. 13e), the mesial carina is positioned mostly in the mesial margin, but strongly twists lingually to the base. This specimen is also more labiolingually compressed relative to the other elements of morphotype 10. These features suggest that SHN.460 corresponds to a more distal position in the tooth row and is compatible with lateral teeth of *Allosaurus* (Hendrickx et al. 2015).

In lateral view, the mesial margin is slightly convex and the distal margin is almost straight. Crown cross-sections are subcircular and in some specimens they are salinon-shaped (sensu Hendrickx et al. 2016) with the mesial and distal carinae facing linguomesially and linguodistally, respectively, and vertical concavities on the lingual surface adjacent to both carinae (Fig. 13a$_{III}$).

An average of 13 and 12 denticles per 5 mm is found in the mid-section of the mesial and distal carinae, respectively (see Supplementary Data, Table 2S). The mesial denticles are round and very short mesiodistally whereas the distal denticlea are subquadrangular with rounded apices. The denticles are separated by narrow interdenticular spaces and project perpendicularly to the carina.

Results and discussion: The results of the DFA based on the dataset of Hendrickx et al. (2015) assign three teeth (SHN.204, 232, and 275) to *Allosaurus* and the remaining elements to different taxa including *Genyodectes* (SHN.460), *Torvosaurus* (SHN.274), the tyrannosaurids *Gorgosaurus* and *Daspletosaurus* (SHN.454 and 363a), and *Suchomimus* (SHN.367) (see Supplementary Data, Table 4S). The classification of some specimens to spinosaurids and basal tyrannosauroids is not surprising due to the similar morphometric data, especially the CBR and CHR.

The teeth herein grouped in morphotype 10 share with mesial teeth of *Allosaurus* the incrassate crowns (CBR >0.6), a character also typical in teeth of some spinosaurids (e.g. *Baryonyx*, *Suchomimus*, *Spinosaurus*) and tyrannosauroids (Charig and Milner 1997; Dal Sasso et al. 2005; Smith 2005; Sereno et al. 1998; Hendrickx et al. 2015). These teeth also share with mesial teeth of *Allosaurus* the strongly twisted mesial carina that extends to the cervix and the presence of shallow concave surfaces adjacent to the distal and in some crowns additionally on the mesial carina in the lingual surface, giving them a salinon-shaped cross-section (Hendrickx et al. 2016). The general morphology of these crowns is similar to the mesial teeth of *Allosaurus* and other allosauroids such as *Sinraptor* (Currie and Zhao 1993; Hendrickx et al. 2015), but may be distinguished from those of more derived allosauroids including *Acrocanthosaurus* (Currie and Carpenter 2000) because in these taxa the mesial carina ends well above the cervix. Spinosaurid teeth usually have fluted teeth and with either non-serrated carinae or higher number of denticles (Charig and Milner 1986; Sues et al. 2002; Sereno et al. 1998; Mateus et al. 2011). Tyrannosauroids have incrassate crowns, but the lingual and labial surfaces are convex and the mesial carina ends well above the cervix (Smith 2005; Hendrickx et al. 2015; Gerke and Wings 2016).

Based on the combination of features discussed above the specimens of morphotype 10 are assigned with confidence to *Allosaurus*, most of them corresponding to mesial teeth, except SHN.460, which is a lateral tooth.

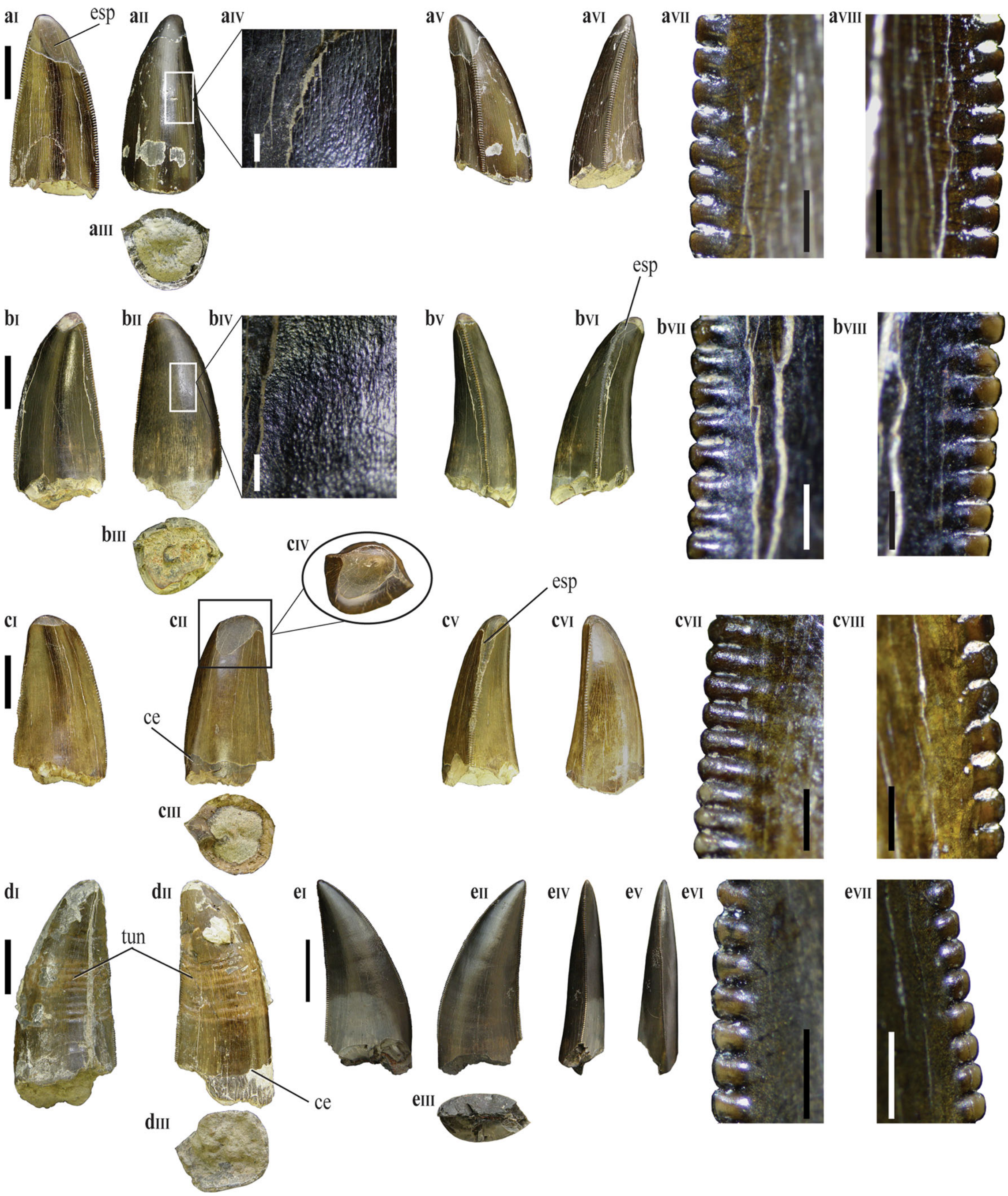

Fig. 13 Morphotype 10: **a** SHN.232; **b** SHN.275; **c** SHN.274; **d** SHN.454; **e** SHN.460 in lingual ($\mathbf{a_{I}}$, $\mathbf{b_{I}}$, $\mathbf{c_{I}}$, $\mathbf{d_{I}}$, $\mathbf{e_{II}}$), labial ($\mathbf{a_{II}}$, $\mathbf{b_{II}}$, $\mathbf{c_{II}}$, $\mathbf{d_{II}}$, $\mathbf{e_{I}}$), distal ($\mathbf{a_{VI}}$, $\mathbf{b_{V}}$, $\mathbf{c_{V}}$, $\mathbf{e_{IV}}$), and mesial ($\mathbf{a_{V}}$, $\mathbf{b_{VI}}$, $\mathbf{c_{VI}}$, $\mathbf{e_{V}}$) views; cross-section at the crown base ($\mathbf{a_{III}}$, $\mathbf{b_{III}}$, $\mathbf{c_{III}}$, $\mathbf{d_{III}}$, $\mathbf{e_{III}}$); detail of the enamel ornamentation ($\mathbf{a_{IV}}$, $\mathbf{b_{IV}}$); detail of the distal ($\mathbf{a_{VII}}$, $\mathbf{b_{VIII}}$, $\mathbf{c_{VII}}$, $\mathbf{e_{VI}}$) and mesial ($\mathbf{a_{VIII}}$, $\mathbf{b_{VII}}$, $\mathbf{c_{VIII}}$, $\mathbf{e_{VII}}$) denticles; detail of the wear facet ($\mathbf{c_{IV}}$). *ce* línea cervical, *eps* enamel spalling, *tun* transverse undulations. *Scale bars* for the crowns: 10 mm; for the denticles: 1 mm; ($\mathbf{a_{IV}}$ and $\mathbf{b_{IV}}$): 1 mm

4.3.3 Morphotype 11

Allosauridae
Allosaurus sp.
Specimens: SHN.227, 283,345, 368, 434 (Fig. 14).

Geographical provenance: ?Santa Rita (Torres Vedras), Valmitão and Porto Dinheiro (Lourinhã), Praia da Vermelha (Peniche), Salir do Porto (Caldas da Rainha).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian).

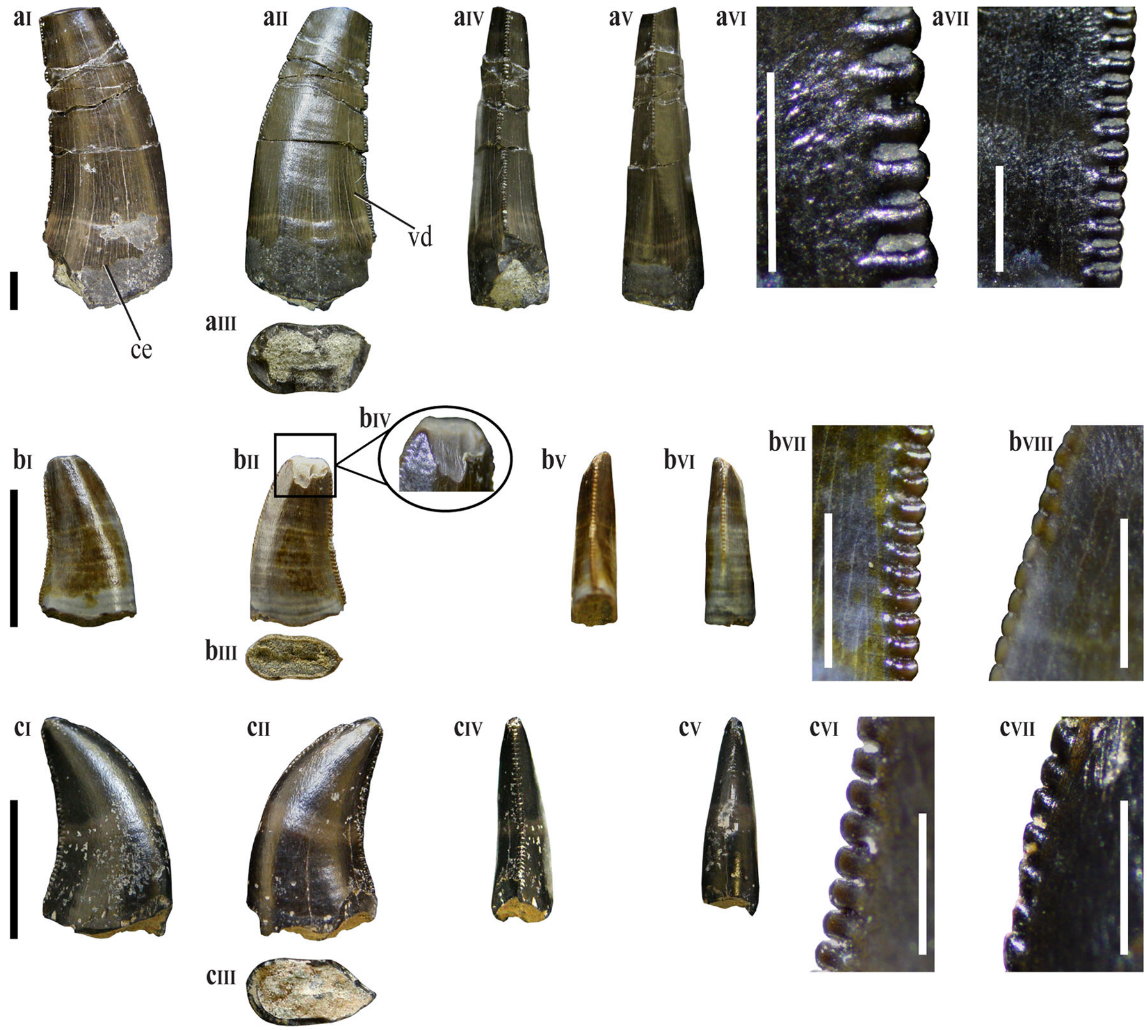

Fig. 14 Morphotype 11: **a** SHN.345; **b** SHN.283; **c** SHN.434 in labial ($\mathbf{a_I}$, $\mathbf{b_I}$, $\mathbf{c_I}$), lingual ($\mathbf{a_{II}}$, $\mathbf{b_{II}}$, $\mathbf{c_{II}}$); distal ($\mathbf{a_{IV}}$, $\mathbf{b_V}$, $\mathbf{c_{IV}}$); and mesial ($\mathbf{a_V}$, $\mathbf{b_{VI}}$, $\mathbf{c_V}$) views; cross-section at the crown base ($\mathbf{a_{III}}$, $\mathbf{b_{III}}$, $\mathbf{c_{III}}$); detail of the distal denticles at the mid-section ($\mathbf{a_{VI}}$, $\mathbf{b_{VIII}}$, $\mathbf{c_{VI}}$) and at the base ($\mathbf{a_{VII}}$) of the crown; detail of the mesial denticles ($\mathbf{b_{VIII}}$, $\mathbf{c_{VII}}$); detail of the wear facet ($\mathbf{b_{IV}}$). *Scale bars* for the crowns: 5 mm; for the denticles: 1 mm

Description: Small crowns with AL between 6.09 and 17.14 mm (average 12.16 mm), CBL between 3.08 and 6.56 mm (average 5.01 mm), and CBW between 1.23 and 3.35 mm (average 2.50 mm). The crowns are relatively elongated (CHR between 1.76 and 2.83; average 2.30), blade-shaped and slightly labiolingually compressed (CBR between 0.40 and 0.52; average 0.49).

These teeth show an irregular enamel texture and subtle transverse undulations. Both carinae are serrated with the distal reaching the cervix whereas the mesial carina extends for approximately two-thirds of the crown height. The mesial carina is always centrally positioned and not twisted, whereas the distal carina in some specimens is strongly displaced labially and somewhat sigmoidal in distal view. The crowns are slightly curved apically, with the mesial margin convex and the distal margin slightly concave in lateral view. The crowns are lenticular (Fig. 14b_{III}, c_{III}) in cross-section and some specimens have shallow basal concavities more marked in the lingual surface (Fig. 14a_{III}). Some specimens have a flat vertical surface adjacent to the distal carina in the lingual surface (Fig. 14a_{II}). The lingual surface of most crowns is flat and the labial surface is convex.

An average of 5.25 and 5 denticles per mm is present in the central section of the mesial and distal carinae respectively (see Supplementary Data, Table 2S). The mesial denticles are mesiodistally short with rounded apices. The distal denticles are subquadrangular in outline with slightly asymmetrical rounded apices and they have a slight apical orientation in the apical end of the crown.

Results and discussion: Except for the small size of the specimens, the general morphology of morphotype 11 is similar to morphotype 9. Morphotype 11 shares with morphotype 9 the distal carina strongly displaced labially and DSDI close to one. The denticles are slightly inclined apically. These features are also present in most lateral teeth of *Allosaurus* as was discussed above (Han et al. 2011; Hendrickx et al. 2014a; Gerke and Wings 2016). Some of these small specimens (e.g. SHN.345: Fig. 14a) share with some isolated teeth, assigned to a possible juvenile allosaurid collected in the Guimarota coal mine (Zinke 1998), the presence of well-developed median ridges on the lingual surface, which gives the appearance of two longitudinal grooves between the carinae and the median ridge (Fig. $14a_{II}$).

The result of DFA for morphotype 11 based on the reduced dataset of Gerke and Wings (2016) assigns three specimens (SHN.345, 368, and 434) to *Masiakasaurus* and one tooth (SHN.283) to *Velociraptor*. Based on the dataset of Hendrickx et al. (2015) most of the specimens (SHN.283, 345, 368) are identified to *Eoraptor* and one tooth (SHN.434) to *Masiakasaurus* (see Supplementary Data, Table 4S). This result may be explained because the specimens in the database for *Allosaurus* and other non-coelurosaurian tetanurans are large and possible adult or sub-adult individuals. However, based on the similarity with morphotype 9, including the shared presence of a slightly concave surface adjacent to the distal carina, the mesial carina ending slightly above the cervix, and DSDI close to 1, morphotype 11 is interpreted as belonging to a juvenile *Allosaurus*.

4.3.4 Morphotype 12

Allosauroidea
Specimens: SHN.213, 248, 344, 365, 430 (Fig. 15).
Geographical provenance: Gentias and Porto Chão (Torres Vedras), Praia dos Frades (Peniche).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian) and Freixial Formation (upper Tithonian).

Description: Moderately large crowns, relatively short (AL average: 42.12 mm; CHR average: 1.83), but robust (CBL average: 20.55 mm; CBW average: 11.56 mm). The crowns are slightly labiolingually compressed (CBR average: 0.56) and oval in cross-sections.

Transverse undulations and interdenticular sulci are usually absent or very slight. However, in SHN.365, short caudae are present especially between distal denticles (Fig. $15b_{VI}$). The enamel usually shows a series of thin irregular non-oriented texture. These teeth have well-developed and serrated mesial and distal carinae. The mesial carina ends approximately at mid-length, except in SHN.213 in which the mesial carina reaches the cervix, and the distal carina extends to the cervix. The mesial carina strongly twists lingually at the base of the crown whereas the distal carina is centrally positioned or slightly displaced labially. There are about 12 denticles per 5 mm in the mid-section of the mesial and distal carinae (see Supplementary Data, Table 2S). The crowns are slightly recurved apically with a convex mesial and an almost flat distal margin, in lateral view. The lingual surface is nearly flat to slightly convex whereas the labial surface is more convex.

Results and discussion: The outcome of the DFA is very indistinct with the specimens assigned to different taxa, including *Acrocanthosaurus*, *Carcharodontosaurus*, *Mapusaurus*, *Neovenator*, *Allosaurus*, *Megalosaurus*, *Duriavenator*, and *Genyodectes* (see Supplementary Data, Table 4S).

Morphotype 12 shows a great similarity with some teeth (ML327 and ML966) described by Hendrickx and Mateus (2014b) from the Upper Jurassic of Portugal and interpreted as Abelisauridae. The specimens herein described lack the longitudinal ridge and the apically hooked denticles described in ML327, but these features are not present in ML966. Morphotype 12 is also similar to some isolated teeth described in the Upper Jurassic of Germany (morphotype K of Gerke and Wings 2016). These Portuguese specimens may be distinguished from the German elements based on the presence of mesial denticles that are smaller apically than at the mid-section of the crown, while in the German specimens, they become progressively coarser toward the apex (Gerke and Wings 2016). Despite of the similarity of the German specimens with abelisaurid teeth, Gerke and Wings (2016) opted for consider these teeth as *Allosaurus* sp. because the presence of Abelisauridae in the Upper Jurassic of Laurasia needs to be confirmed based on more complete material (Rauhut 2012; Gerke and Wings 2016). Based on the combination of features described above, morphotype 12 is here interpreted as possible belonging to an indeterminate Allosauroidea.

4.4 Coelurosauria

4.4.1 Morphotype 13

Tyrannosauroidea
Specimens: SHN.222, 230, 249, 253, 337, 355, 429, 435 (Fig. 16).

Geographical provenance: Santa Rita and Praia da Corva (Torres Vedras), Valmitão, Porto Dinheiro, and Peralta (Lourinhã).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian) and ?Sobral Formation (upper Kimmeridgian-lower Tithonian).

Fig. 15 Morphotype 12: **a** SHN.213; **b** SHN.365; **c** SHN.248 in lingual ($\mathbf{a_I}$, $\mathbf{b_{II}}$, $\mathbf{c_I}$), labial ($\mathbf{a_{II}}$, $\mathbf{b_I}$, $\mathbf{c_{II}}$), distal ($\mathbf{a_{IV}}$, $\mathbf{b_{IV}}$, $\mathbf{c_{IV}}$), and mesial ($\mathbf{a_V}$, $\mathbf{b_V}$, $\mathbf{c_V}$) views; cross-section at the crown base ($\mathbf{a_{III}}$, $\mathbf{b_{III}}$, $\mathbf{c_{III}}$); detail of the distal denticles at the mid-section ($\mathbf{a_{VI}}$, $\mathbf{b_{VI}}$, $\mathbf{c_{VI}}$) at the base ($\mathbf{c_{VII}}$) of the crown; detail of the mesial denticles ($\mathbf{a_{VII}}$, $\mathbf{b_{VII}}$, $\mathbf{c_{VIII}}$). *Scale bars* for the crowns: 10 mm; for the denticles: 1 mm

Description: The specimens of morphotype 13 are similar to those of morphotype 9. The crowns are slightly smaller (AL average: 25.96 mm; CBL average: 11.28 mm; CBW average: 6.20 mm; and CHR average: 2.12), but the compression rate is similar (CBR average: 0.55) as well as the number of denticles in both carinae. The most distinctive character of morphotype 13 relative to morphotype 9 is the presence of a slight concavity centrally positioned at the base of the lingual surface (Fig. 16c_{IV}). In some crowns, well-marked concavity is present on the labial and lingual sides (Fig. 16a_I), giving them a reniform or eight-shaped cross-sections. Most specimens have some slight vertical ridges inside the basal concavity (Fig. 16a_I, c_{IV}). Another difference between morphotype 13 and morphotype 9 is the strongly twisted mesial carina in the specimens of morphotype 13 while in morphotype 9 the mesial carina is straight and centrally positioned.

Results and discussion: The result of the DFA for morphotype 13 is ambiguous. The specimens are assigned to different taxa, including *Raptorex*, *Torvosaurus*, *Ceratosaurus*, *Majungasaurus*, *Masiakasaurus*, and dromaeosaurids (see Supplementary Data, Table 4S).

The presence of a concave surface centrally positioned in the lingual surface at the crown base is reported in some allosauroid teeth (Hendrickx et al. 2015). Morphotype 13 is also similar to *Allosaurus* teeth in having asymmetrical crowns with the distal carina placed in the labial surface (Hendrickx et al. 2015). However, several features in some specimens (SHN.222), including: (1) mesial carina restricted to the apical part of the crown and curving lingually, (2) eight-shaped cross-section of the crown base, (3) relative incrassate crowns (CBR near 0.60 in most specimens), (4) presence of slight transversal undulations, (5) DSDI >1.2 are more compatible with coelurosaur

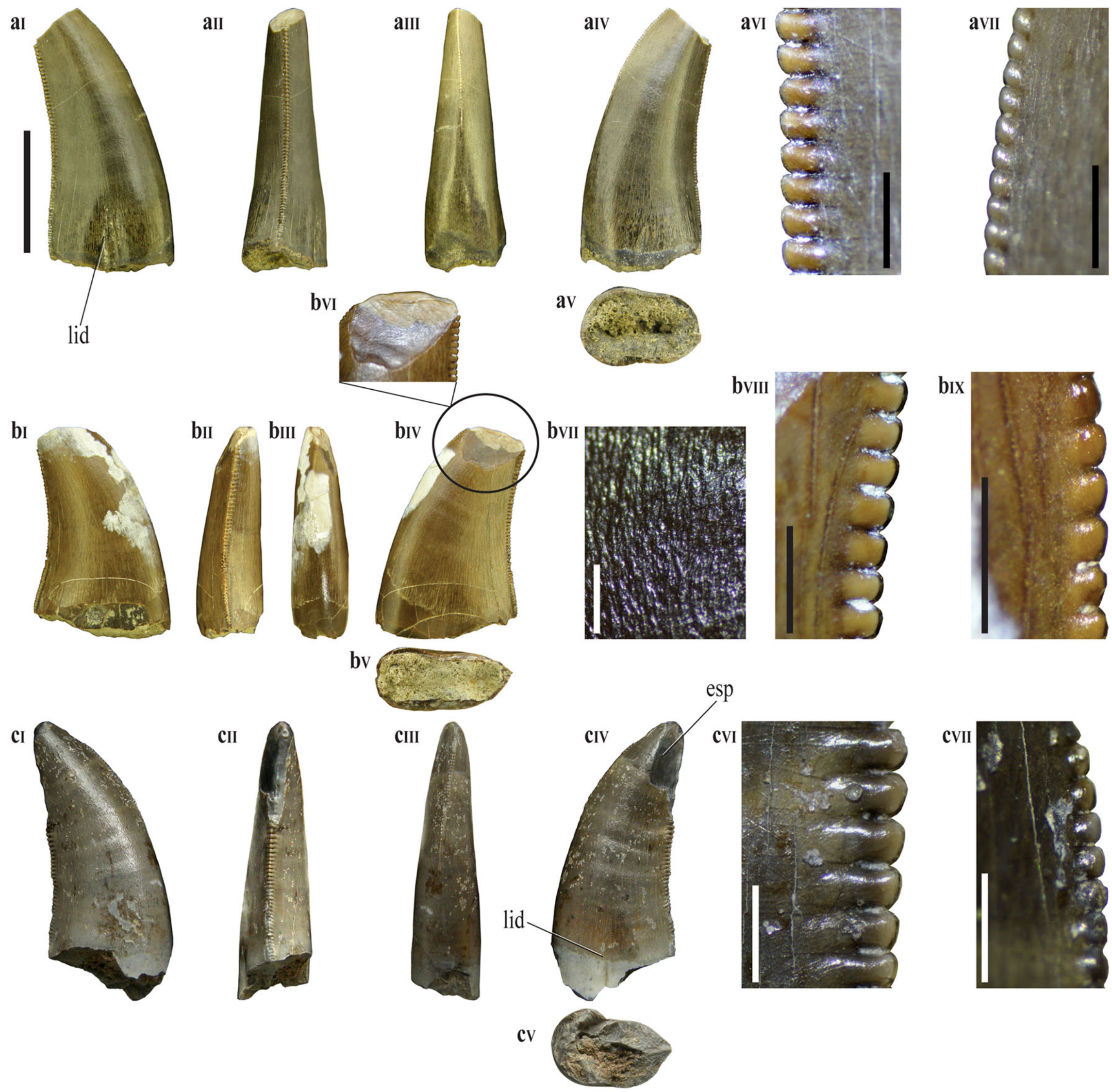

Fig. 16 Morphotype 13: **a** SHN.222; **b** SHN.429; **c** SHN.355 in lingual ($\mathbf{a_I}$, $\mathbf{b_I}$, $\mathbf{c_{IV}}$), distal ($\mathbf{a_{II}}$, $\mathbf{b_{II}}$, $\mathbf{c_{II}}$), mesial ($\mathbf{a_{III}}$, $\mathbf{b_{III}}$, $\mathbf{c_{III}}$), and labial ($\mathbf{a_{IV}}$, $\mathbf{b_{IV}}$, $\mathbf{c_I}$) views; cross-section at the crown base ($\mathbf{a_V}$, $\mathbf{b_V}$, $\mathbf{c_V}$); detail of the distal ($\mathbf{a_{VI}}$, $\mathbf{b_{VIII}}$, $\mathbf{c_{VI}}$) and mesial ($\mathbf{a_{VII}}$, $\mathbf{b_{IX}}$, $\mathbf{c_{VII}}$) denticles; detail of the wear facet ($\mathbf{b_{VI}}$) and of the enamel ornamentation ($\mathbf{b_{VII}}$). *eps* enamel spalling, *id* lingual depression. *Scale bars* for the crowns: 10 mm; for the denticles: 1 mm

tetanurans (Hendrickx et al. 2015). Based on this combination of features morphotype 13 is here tentatively assigned to a basal tyrannosauroid possibly related with *Aviatyrannis*, which is the only tyrannosauroid taxon currently known in the Portuguese record.

4.4.2 Morphotype 14

Tyrannosauroidea
Specimens: SHN.209, 219, 260, 265, 431 (Fig. 17).

Geographical provenance: Valmitão (Lourinhã), Foz do Arelho (Caldas da Rainha).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian), Bombarral Formation (Tithonian).

Description: Very small crowns with AL between 8.53 and 23.49 mm (average 14.53 mm), CBL between 4.35 and 7.68 mm (average 5.63 mm), and CBW between 3.26 and 5.36 mm (average 4.03 mm). The crowns are elongated (CHR between 2.01 and 2.88; average 2.44), and have a rounded cross-section at the base (CBR between 0.63 and 0.81; average 0.73). The crowns are slightly recurved with the mesial margin slightly convex and the distal margin almost flat to slightly concave. In some specimens, well-marked transverse undulations are present and the enamel

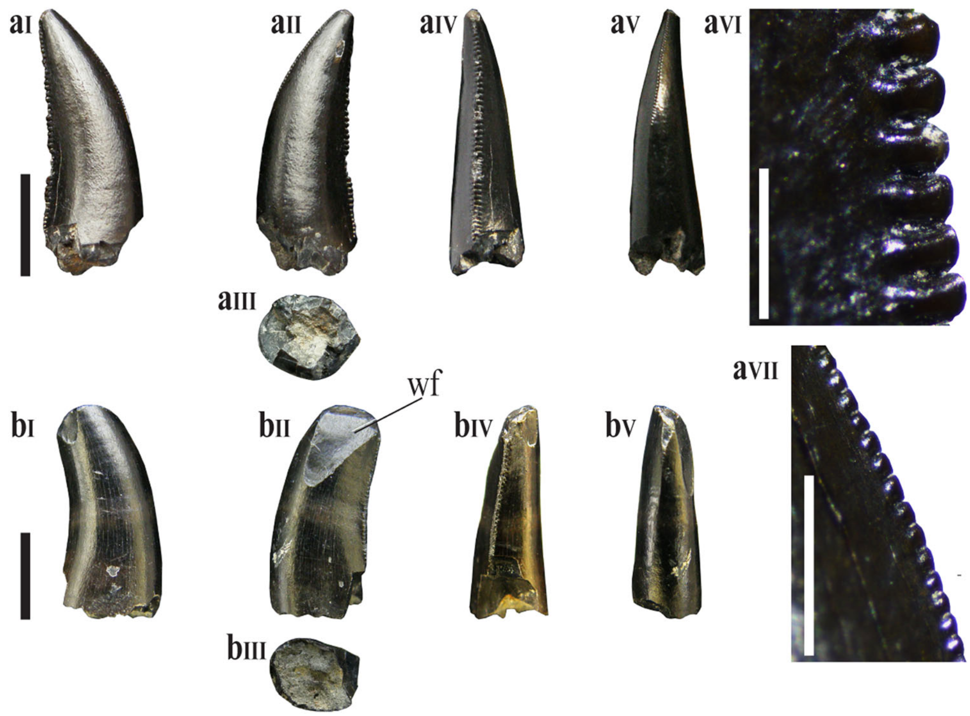

Fig. 17 Morphotype 14: **a** SHN.209; **b** SHN.431 in labial ($\mathbf{a_I}$, $\mathbf{b_I}$), lingual ($\mathbf{a_{II}}$, $\mathbf{b_{II}}$), distal ($\mathbf{a_{IV}}$, $\mathbf{b_{IV}}$), and mesial ($\mathbf{a_V}$, $\mathbf{b_V}$) views; cross-section at the crown base ($\mathbf{a_{III}}$, $\mathbf{b_{III}}$); detail of the distal ($\mathbf{a_{VI}}$) and mesial ($\mathbf{a_{VII}}$) denticles. *wf* wear facet. *Scale bars* for the crowns: 5 mm; for the denticles: 1 mm

shows irregular texture crenulations. Both carinae are serrated, with the distal carina extending to the cervix whereas the mesial carina ends approximately at mid-height of the crown. The distal carina is strongly displaced labially and the mesial carina is mostly centrally positioned or slightly twisted toward the base (Fig. 17b_{IV}). Both lingual and labial surfaces are strongly convex.

An average of 5 and 3.35 denticles per mm is found in the central section of the mesial and distal carinae respectively and the DSDI is greater than 1.2. The mesial denticles are very short mesiodistally with almost flat apices and the distal denticles are subquadrangular in outline with symmetrical rounded apices and positioned perpendicularly to the carinae.

Results and discussion: The DFA result based in the dataset of Hendrickx et al. (2015) identifies the specimens of morphotype 14 as belonging to *Masiakasaurus* (SHN.209), *Nuthetes* (SHN.260), *Megalosaurus* (SHN.265), and *Torvosaurus* (SHN.431) (see Supplementary Data, Table 4S). These teeth have a relatively high DSDI (>1.2), which is a feature shared by some basal tyrannosauroids such as *Proceratosaurus* and *Alioramus* and most dromaeosaurids including *Deinonychus*, *Dromaeosaurus*, and *Velociraptor* (Rauhut and Werner 1995; Rauhut et al. 2010; Gerke and Wings 2016). Morphotype 14 shares with some isolated teeth interpreted as possibly belonging to basal tyrannosauroids from the Upper Jurassic of Portugal (Zinke 1998) and Germany (Gerke and Wings 2016) the presence of a rounded cross-section of the crown base, the distal carina placed in the lingual surface and the presence of a concave vertical surface adjacent to the distal carinae. In addition, some specimens (SHN.209) show a braided enamel texture similar to that of basal tyrannosauroids. Based on this features the specimens of morphotype 14 are here interpret as belonging to a basal tyrannosauroid.

4.4.3 Morphotype 15

cf. Richardoestesia
Specimens: SHN.240, 272, 278, 308–309, 433, 436 (Fig. 18).

Geographical provenance: Praia Azul and Praia da Corva (Torres Vedras), Valmitão, Porto Dinheiro, and Porto das Barcas (Lourinhã).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian) and Sobral Formation (upper Kimmeridgian-lower Tithonian).

Description: Small crowns with AL between 13.06 and 19.21 mm (average 15.43 mm), CBL between 8.89 and 9.82 mm (average 7.60 mm), and CBW between 3.73 and 5.54 mm (average 4.38 mm). The crowns are low (CHR between 1.77 and 2.01; average 1.87), and slightly compressed labiolingually (CBR between 0.54 and 0.67; average 0.58). The crowns have a triangular shape in lateral view and are strongly curved distally. The distal carina is nearly straight or slightly concave and the mesial one is convex apically, but nearly straight in the basal half of the crown. The apex does not surpass the level of the distal carina.

These teeth have smooth enamel, without any undulations or interdenticular sulci. Both carinae are serrated with

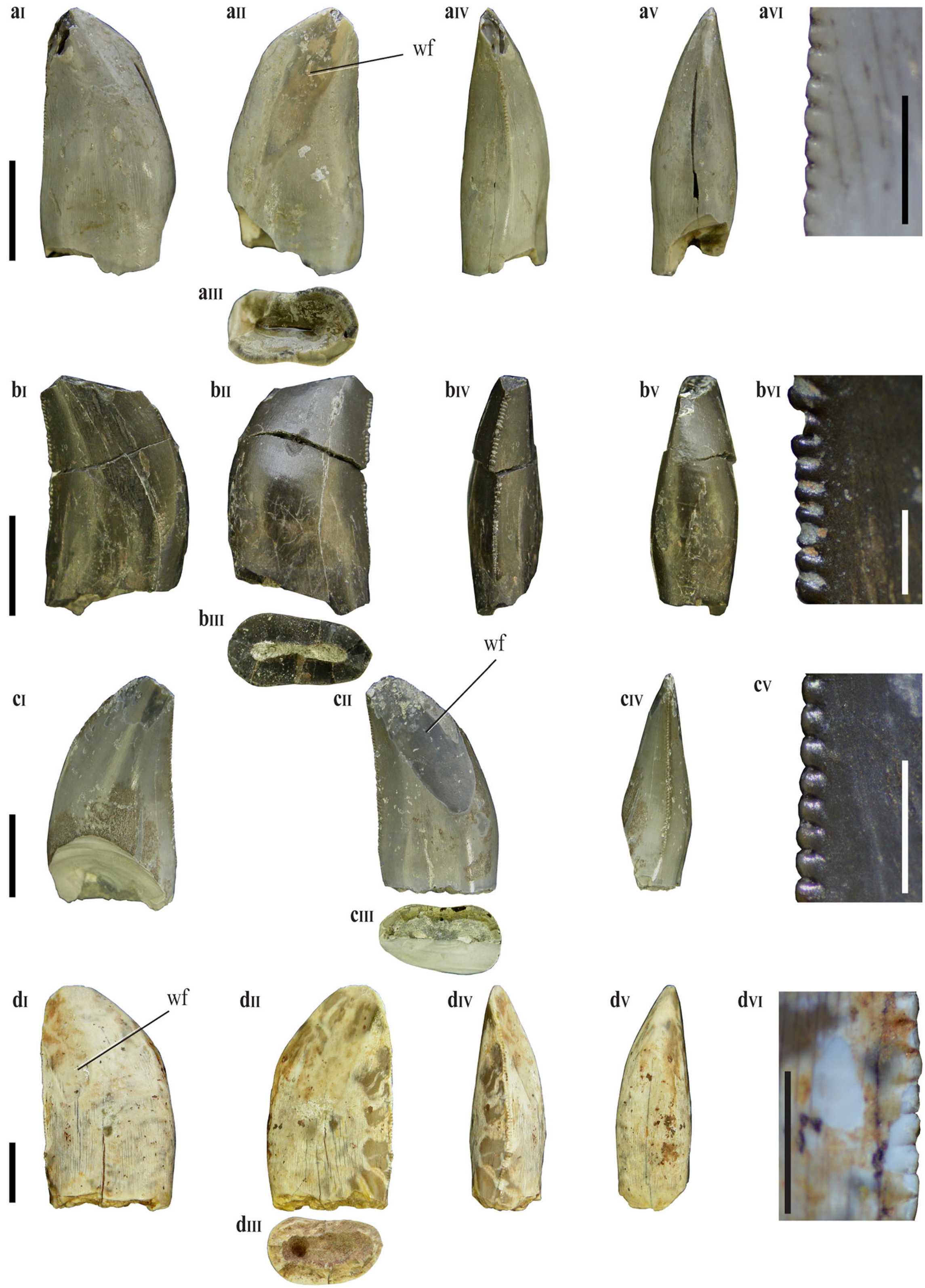

Fig. 18 Morphotype 15: **a** SHN.278; **b** SHN.436; **c** SHN.272; **d** SHN.433 in labial ($\mathbf{a_I}$, $\mathbf{b_{II}}$, $\mathbf{c_{II}}$, $\mathbf{d_I}$), lingual ($\mathbf{a_{II}}$, $\mathbf{b_I}$, $\mathbf{c_I}$, $\mathbf{d_{II}}$), distal ($\mathbf{a_{IV}}$, $\mathbf{b_{IV}}$, $\mathbf{c_{IV}}$, $\mathbf{d_{IV}}$), and mesial ($\mathbf{a_V}$, $\mathbf{b_V}$, $\mathbf{d_V}$) views; cross-section at the crown base ($\mathbf{a_{III}}$, $\mathbf{b_{III}}$, $\mathbf{c_{III}}$, $\mathbf{d_{III}}$); detail of the distal denticles ($\mathbf{a_{VI}}$, $\mathbf{b_{VI}}$, $\mathbf{c_V}$, $\mathbf{d_{VI}}$). *wf* wear facet. *Scale bars* for the crowns: 10 mm; for the denticles: 1 mm

the distal carina extending to the cervix and the mesial carina is restricted to the apical part of the crown. In most teeth, the mesial carina is strongly displaced lingually and curves lingually to the crown base and the distal carina is straight or slightly twists lingually to the base of the crown and placed mainly in the lingual surface. There are well-developed transverse concavities in the lingual and labial surfaces at the base of the crown (except in SHN.433: Fig. 18d) and therefore these specimens are eight-shaped in cross-section (Fig. 18a$_{III}$). A well-marked labiolingual and slight mesiodistal constrictions at the crown base are also present in all specimens, but is less marked in SHN.433. The lingual surface is almost flat to slightly concave and the labial surface is strongly convex.

An average of 5 and 4 denticles per mm can be found in the central section of the mesial and distal carinae, respectively (see Supplementary Data, Table 2S). The mesial denticles are short mesiodistally with rounded apices. The distal denticles are subquadrangular with rounded apices and positioned perpendicularly to the carinae.

Results and discussion: The result of DFA is not consistent. Based on the dataset of Hendrickx et al. (2015) these specimens are assigned to *Nuthetes* (SHN.272), *Megalosaurus* (SHN.308), and *Torvosaurus* (SHN.436) (see Supplementary Data, Table 4S).

These teeth have morphology distinct from all other morphotypes here described. Also, this morphology is not so common in theropod teeth from the Upper Jurassic. They show a well-marked labiolingual constriction between the crown and root. The crowns are strongly labiolingually inflated near the base and slightly recurved apically, with almost straight to slightly concave distal margin in lateral view. The mesial carina strongly twists lingually and is restricted to the apical part of the crown, and the cross-section of the crown base is eight-shaped due to the presence of well-marked concavities in both lingual and labial surfaces. The presence of a basal mesiodistal constriction between the crown and root is a character shared by many coelurosaurs, including some isolated teeth assigned to *Compsognathus* from the Guimarota fossil site (Zinke 1998), troodontids (Norell et al. 2000; Currie and Zhiming 2001), the dromaeosaurid *Microraptor* (Xu et al. 2000; Hendrickx et al. 2015), some carcharodontosaurins such as *Carcharodontosaurus* and *Giganotosaurus* (Hendrickx, pers. commun.), the ornithomimosaur *Pelecanimimus* (Pérez-Moreno et al. 1994; Hendrickx and Mateus 2014b), the alvarezsaurids *Shuvuuia* and *Mononykus* (Perle et al. 1993; Hendrickx and Mateus 2014b), basal oviraptorosaurs (Osmólska et al. 2004; Hendrickx and Mateus 2014b), therizinosaurs (Kirkland et al. 2005; Hendrickx and Mateus 2014b), and *Archaeopteryx* (Louchart and Pouech, 2017). A slight constriction is also present in at least some premaxillary teeth of *Proceratosaurus*, but not in the lateral teeth (Rauhut et al. 2010; Hendrickx et al. 2015).

An eight-shape cross-section of the crown base is a feature shared by some deinonychosaur coelurosaurians, including *Saurornitholestes* (Sullivan 2006; Hendrickx et al. 2015), *Pyroraptor* (Allain and Taquet 2000), and *Buitreraptor* (Gianechini et al. 2011), the enigmatic theropod *Richardoestesia gilmorei* (Currie et al. 1990; Larson 2008; Hendrickx et al. 2015), the tyrannosaurids *Proceratosaurus* (Rauhut et al. 2010) and *Alioramus* (Brusatte et al. 2009) and the neovenatorid *Orkoraptor* (Novas et al. 2008b).

This combination of features: (1) presence of mesiodistal and labiolingual constrictions, (2) eight-shaped cross-section at the crown base, (3) slight distal curvature, and (4) mesial carina restricted to the apical part of the crowns and twisting lingually is compatible with the morphotype generally assigned to *Richardoestesia* (Hendrickx and Mateus 2014b). Morphotype 15 also has morphology similar to some isolated teeth from the Guimarota coal mine identified as cf. *Compsognathus* (Zinke, 1998). However, Guimarota specimens lack basal concavities and they have a higher number of denticles (Zinke 1998). Recently, Hendrickx and Mateus (2014b) described an isolated tooth (ML 939) from the Upper Jurassic of the Lusitanian Basin with morphology similar to morphotype 15 and interpreted them as *Richardoestesia* aff. *R. gilmorei*. ML 939 differs from the morphotype 15 by the presence of: (1) slightly more labiolingually-compressed crowns (the crowns of morphotype 15 have an inflated appearance labiolingually at the crown base), and (2) a much higher number of denticles in the distal carina (Hendrickx and Mateus 2014b). Morphotype 15 and ML 939 differ from *Richardoestesia gilmorei* in a mesial restricted to the apical part of the crown (Hendrickx and Mateus 2014b).

Richardoestesia gilmorei was described by Currie et al. (1990) on the basis of a pair of lower jaws with a replacement tooth collected in the Upper Cretaceous of the Dinosaur Park Formation in Canada (Larson 2008; Torices et al. 2015). *Richardoestesia*-like teeth have been recovered from several sites and different ages including the Upper Jurassic of Portugal (Zinke 1998; Hendrickx and Mateus 2014b), the Lower and Upper Cretaceous of Spain (Rauhut 2002; Torices et al. 2015), and the Upper Cretaceous of Romania (Codrea et al. 2002; Weishampel et al. 2010). However, as proposed by some authors, isolated teeth from different stratigraphic intervals do most likely not belong to the same species although they may be similar in form to those of the type specimen from the Dinosaur Park Formation (Larson 2008). Based on this argumentation morphotype 15 is here assigned as cf. *Richardoestesia*.

4.4.4 Morphotype 16

Dromaeosauridae
Specimens: SHN.359d (Fig. 19).

Geographical provenance: Porto Novo (Torres Vedras).

Stratigraphical distribution: Praia da Amoreira-Porto Novo Formation (upper Kimmeridgian).

Description: This morphotype consists of a single specimen represented by a complete and well-preserved crown. This specimen is relatively small-sized with AL of 19.06 mm, CBL of 8.88 mm, and CBW of 4.76 mm (see Supplementary Data, Table 2S). The crown is relatively elongated (CHR: 1.97), slightly compressed labiolingually with oval cross-section at the base (CBR: 0.54). The crown is strongly recurved with a convex mesial margin and strongly concave distal margin. The apex is positioned quite distally to the level of the base of the distal carina. The enamel is smooth and neither transverse undulations nor interdenticular sulci are visible. Both carinae are serrated, with the distal carina extending to the cervix whereas the mesial carina is restricted to the apical end. The distal carina is strongly displaced lingually and the mesial carina is also twisted toward the base, but is mostly positioned on the mesial surface. The lingual and labial surfaces are convex and shallow concavities are visible at the base of the crown in both lingual and labial surfaces. The lingual concavity is associated with two small vertical ridges (Fig. 19d).

There is an average of 3.5 denticles per mm on the central section of the distal carina. The mesial denticles are poorly preserved and it is not possible verify their density on this carina. The distal denticles are rectangular, higher mesiodistally than apicobasally and are separated by narrow interdenticular sulci. In the basal part of the distal carina, the denticles are parabolic with symmetrically circular apices (Fig. 19g), but in the apical part of the distal carina, the denticles are slightly apically hooked (Fig. 18h).

Results and discussion: The DFA based on the dataset of Gerke and Wings (2016) classifies SHN.359d as *Majungasaurus*, whereas the result based on the dataset of Hendrickx et al. (2015) assigns this specimen to *Australovenator* (see Supplementary Data, Table 4S). This specimen shares with the lateral teeth of most dromaeosaurids the presence of a wide concavity on the basal end of both labial and lingual surfaces of the crown, the presence of two longitudinal ridges restricted to the crown base, the slightly apically hooked distal denticles, a DSDI >1.2, a lingually twisted mesial carina at the base of the crown, and the moderately labiolingual compression of the crown (Hendrickx and Mateus 2014b; Hendrickx et al. 2015). Based on these features, SHN.359d is here tentatively assigned to an indeterminate eudromaeosaurid. This clade has been tentatively identified in the Upper Jurassic of the Lusitanian Basin based on isolated specimens (Zinke 1998; Malafaia et al. 2014). However, this identification is only tentative, pending the discovery of more complete specimens.

4.5 Tetanurae indet

4.5.1 Morphotype 17

Specimens: SHN.277 (Fig. 20).
Geographical provenance: Peralta (Lourinhã).

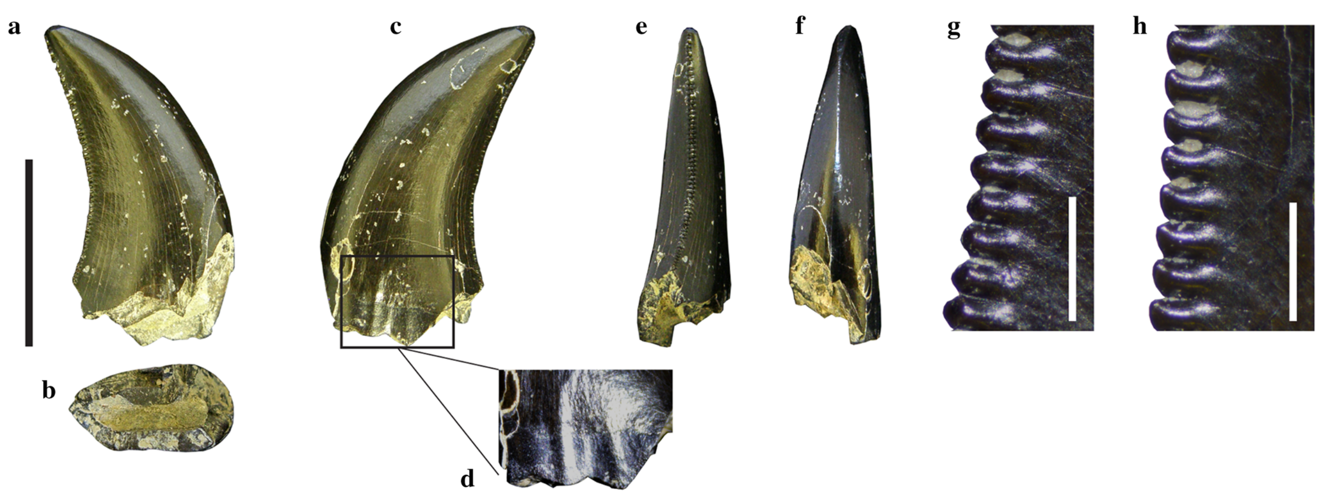

Fig. 19 Morphotype 16: SHN.359d in labial (**a**), lingual (**c**), distal (**e**), and mesial (**f**) views; cross-section at the crown base (**b**); detail of the crests at the base of the lingual surface (**d**); detail of the distal denticles at the base (**g**) and at the mid-section (**h**) of the crown. *Scale bars* for the crown: 10 mm; for the denticles: 1 mm

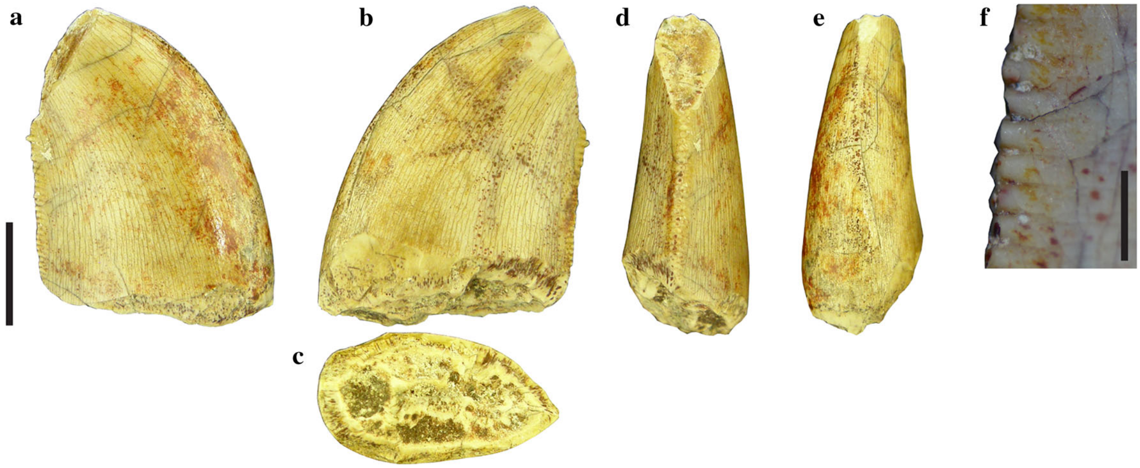

Fig. 20 Morphotype 17: SHN.277 in labial (**a**), lingual (**b**), distal (**d**), and mesial (**e**) views; cross-section at the crown base (**c**); detail of the distal denticles (**f**). *Scale bars* for the crown: 10 mm; for the denticles: 1 mm

Stratigraphical distribution: ?Sobral Formation (upper Kimmeridgian-lower Tithonian).

Description: This morphotype includes a single, partially preserved crown that preserves a small part of the cervical line delimiting the crown from the root adjacent to the distal margin. This specimen is relatively small, with AL of 19.64 mm, CBL of 12.26 mm, and CBW of 6.62 mm. The crown is short (CHR: 1.39), slightly compressed-labiolingually with oval cross-section at the base (CBR: 0.54). The crown is strongly recurved apically with the mesial margin strongly convex, but the distal margin is almost straight. The enamel is smooth and interdenticular sulci are absent. Both carinae are serrated with the distal carina extending to the cervix whereas the mesial carina ends above it and strongly twists lingually toward the base.

There is an average of 3 denticles per mm in the central section of the distal carina (see Supplementary Data, Table 2S). The mesial denticles are much eroded and it is not possible verifying the denticle density in this carina. The distal denticles are subquadrangular, separated by narrow interdenticular spaces (Fig. 20f).

Results and discussion: The DFA results excluding the MC variable classifies the specimen SHN.277 to *Neovenator* (see Supplementary Data, Table 4S). The general morphology of this specimen is similar to some isolated teeth from the Guimarota fossil site interpreted as putative premaxillary teeth of *Dromaeosaurus* (Zinke 1998). However, based on the CBR value, SHN.277 is here interpreted as a lateral crown and it shares with the specimens from Guimarota the strongly twisted mesial carina extending near to the cervix and the similar number of denticles in the central section of the distal carina. Nevertheless, the presence of strongly twisted mesial carina is also shared with several other tetanuran theropods, including *Allosaurus* (which also have similar number of denticles in the distal carina). The poor preservation of morphotype 17 does not allow an accurate identification and is here assigned as belonging to an indeterminate tetanuran.

4.6 Incomplete and poorly preserved teeth not assigned to a morphotype

Specimens: SHN.223, 313, 432 (Fig. 21).

SHN.223 is an incomplete, distorted, and very small tooth crown (AL ~10.35 mm) collected in the upper Kimmeridgian of Santa Rita (Torres Vedras). The crown is strongly compressed labiolingually and recurved distally. Thin but well-marked transverse undulations are visible in both lingual and labial surfaces. There is an average of 6 denticles per millimeter in the mesial carina, but the distal carina is not preserved. The mesial carina is incomplete to the base, so it is not possible verify the extension of the denticles. Nevertheless, they are present at least in ¾ of the crown height. The denticles are subquadrangular in outline with almost flat to slightly rounded apices.

SHN.313 (Fig. 21a) was collected in the upper Kimmeridgian of Valmitão (Torres Vedras) and corresponds to an almost complete crown, but it is somewhat worn, especially the distal carina. The crown is very slender, relatively tall, but narrow mesiodistally (AL: 12.7 mm; CBL: 4.6 mm). The cross-section of the base is oval in outline (CBR: 0.64) and both lingual and labial surfaces are slightly convex. The crown is recurved distally with the mesial margin convex and the distal margin concave. The distal carina is broken and the mesial carina is also poorly preserved with the denticles almost entirely abraded, but the mesial carina is mostly centrally positioned and slightly twisted toward the base.

SHN.432 (Fig. 21b) is an incomplete and poorly-preserved crown collected in Porto das Barcas (Lourinhã). The

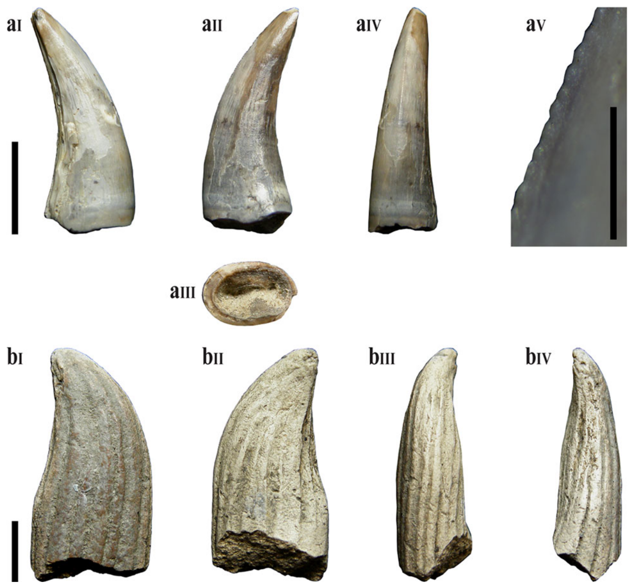

Fig. 21 Poorly preserved teeth not assigned to any morphotype: **a** SHN.313; **b** SHN.432 in labial (**a**$_{\mathbf{I}}$, **b**$_{\mathbf{I}}$), lingual (**a**$_{\mathbf{II}}$, **b**$_{\mathbf{II}}$), mesial (**a**$_{\mathbf{IV}}$, **b**$_{\mathbf{III}}$), and distal (**b**$_{\mathbf{IV}}$) views; cross-section at the crown base (**a**$_{\mathbf{III}}$); detail of the mesial denticles (**a**$_{\mathbf{V}}$). *Scale bars* for the crowns: 10 mm; for the denticles: 1 mm

most striking feature of this specimen is the presence of a series of vertical ridges and grooves that extend along the entire labial and lingual surfaces. Carinae seems to be absent in both mesial and distal surfaces, but this may be due to wear of the crown surface. The crown is wide and columnar in the basal part with almost straight mesial and distal margins, but strongly tapers to the apical end, becoming strongly convex mesially and concave distally.

The DFA based on the dataset of Gerke and Wings (2016) excluding the MC and DC variables classifies SHN.223 and SHN.313 as *Masiakasaurus* and SHN.432 as *Majungasaurus*. Based on the dataset of Hendrickx et al. (2015), SHN.223 is assigned to *Liliensternus*, SHN.313 to *Nuthetes*, and SHN.432 as *Dubreuillosaurus* (see Supplementary Data, Table 4S). SHN.223 has a general shape similar to those of lateral teeth of *Allosaurus* and shares with this taxon the mesial carina extending to near the cervix and the presence of numerous thin transverse undulations in the lingual and labial surfaces. SHN.313 has a conical shape of the crown, similar to those of baryonychines. The mesial carina does not reach the cervix contrary to most barionychines, with the exception of some isolated teeth from Spain (Canudo et al. 2008). However, the enamel texture seems to be smooth not veined as is the case in baryonychines. The vertical ridges in SHN.432 are similar to some isolated teeth described in the Upper Jurassic of Guimarota and in the Lower Cretaceous of Galve in Spain interpreted as a form closely related to *Paronychodon* (Zinke and Rauhut 1994). However, SHN.432 differs from the teeth of *Paronychodon* in the higher number of longitudinal ridges thatextend along the entire crown and are strongly twisted. This specimen could correspond to a mesial tooth of this taxon or a closely related taxon. Because the incompleteness and poor preservation of these specimens, they are here assigned as Theropoda indet.

5 General discussion of the diversity and stratigraphic distribution of the sample of isolated teeth herein described

The multivariate analysis of the sample of isolated teeth described here provide relatively robust results for the large morphotypes, but the classification of the smaller teeth based on this methodology proved to be more difficult. Similar results have been obtained by different authors (e.g. Gerke and Wings 2016). This may be caused in part because the small teeth could represent either smaller taxa or juvenile forms. Since ontogenetic changes in theropod teeth are rather poorly understood, the results of the multivariate analyses should be carefully considered (Gerke and Wings 2016).

Most of the isolated teeth herein analyzed may be related with well-known taxa in the Portuguese Upper Jurassic such as *Ceratosaurus*, *Torvosaurus*, and *Allosaurus* (Table 1). However, there are also some morphotypes that are not clearly related to a particular recognized taxon, including a morphotype assigned to a-non megalosaurid megalosauroid tentatively related to the piatnitzkysaurid *Marshosaurus* and an indeterminate allosauroid distinct from *Allosaurus*. This last morphotype could correspond either to a taxon whose teeth are still unknown (*Lourinhanosaurus*) or may represent a form not yet identified in the Portuguese record.

The most abundant specimens are those assigned to *Torvosaurus*, with a frequency of 22%, followed by those specimens assigned to *Allosaurus* with 20% (Fig. 22a). Small theropod teeth, despite being scarcer than those of large morphotypes, are also relatively abundant and diverse in the Upper Jurassic of the Lusitanian Basin. These teeth show morphologies traditionally related to derived coelurosaurian theropods more typical of Cretaceous strata (e.g. Larson 2008). The taxonomic identification of these morphotypes is complex; however the sample is particularly valuable for documenting these poorly represented clades in the Portuguese fossil record. Two morphotypes compatible with Tyrannosauroidea, a morphotype assigned to Dromaeosauridae, and a morphotype with morphology traditionally assigned to *Richardoestesia* were identified (Table 1).

Stratigraphically, most of the isolated teeth herein analyzed (70%) were collected in the Praia da Amoreira-Porto

Table 1 Taxonomic identification of the different tooth morphotypes described in this work

Morphotypes	Taxonomic identification
Morphotype 1	*Ceratosaurus* sp.
Morphotype 2	cf. *Cetatosaurus*
Morphotype 3	*Torvosaurus gurneyi*
Morphotype 4	cf. *Torvosaurus gurneyi*
Morphotype 5	cf. *Torvosaurus gurneyi*
Morphotype 6	Megalosauroidea
Morphotype 7	Megalosauroidea
Morphotype 8	Megalosauroidea
Morphotype 9	*Allosaurus* sp.
Morphotype 10	*Allosaurus* sp.
Morphotype 11	*Allosaurus* sp.
Morphotype 12	Allosauroidea
Morphotype 13	Tyrannosauroidea
Morphotype 14	Tyrannosauroidea
Morphotype 15	cf. *Richardoestesia*
Morphotype 16	Dromaeosauridae
Morphotype 17	Tetanurae indet.

Novo Formation, which is the most extensive sedimentary unit in the coastal region of the Central Sector of the Lusitanian Basin (Fig. 22b). The greatest diversity of theropod groups is also verified in the Praia da Amoreira-Porto Novo Formation with all morphotypes represented in this unit (Fig. 23). This distribution is coincidental with the abundance of theropods and other dinosaurs known in the Portuguese record based on non-dental remains. However, this higher incidence of finds along the coastline and in particular in the Praia da Amoreira-Porto Novo Formation may in part be an artifact due to more prospection in these areas.

6 Conclusion

The sample of isolated theropod teeth studied here represents a relatively diverse theropod fauna that includes *Ceratosaurus*, *Torvosaurus*, Megalosauroidea indet., *Allosaurus*, Allosauroidea indet., Tyrannosauroidea, cf. *Richardoestesia*, and Dromaeosauridae. This faunal composition indicates a higher diversity of theropods than currently known based on most complete specimens, especially among the small and more derived forms. The results of this analysis partially agree with previous studies of other collections with isolated theropod teeth from the Upper Jurassic of Portugal such as the analysis of the Guimarota coal mine collection. However, the presence of velociraptorine dromaeosaurids, compsognathids, and troodontids, which was reported in Guimarota is not confirmed in the sample analyzed here.

The composition of the theropod fauna resulting from the present study on isolated teeth supports previous hypotheses of a close relationship with the theropod faunas recorded from the North American Morrison Formation. Some similarity with isolated theropod teeth groups described in other Upper Jurassic sites of Europe, especially in Spain and Germany, is also recognized. Some morphotypes identified in this work show some similarity with isolated theropod teeth described in the Tendaguru Formation in Tanzania, which may have some paleobiogeographic implications. However, most of these African specimens are still poorly known and a more

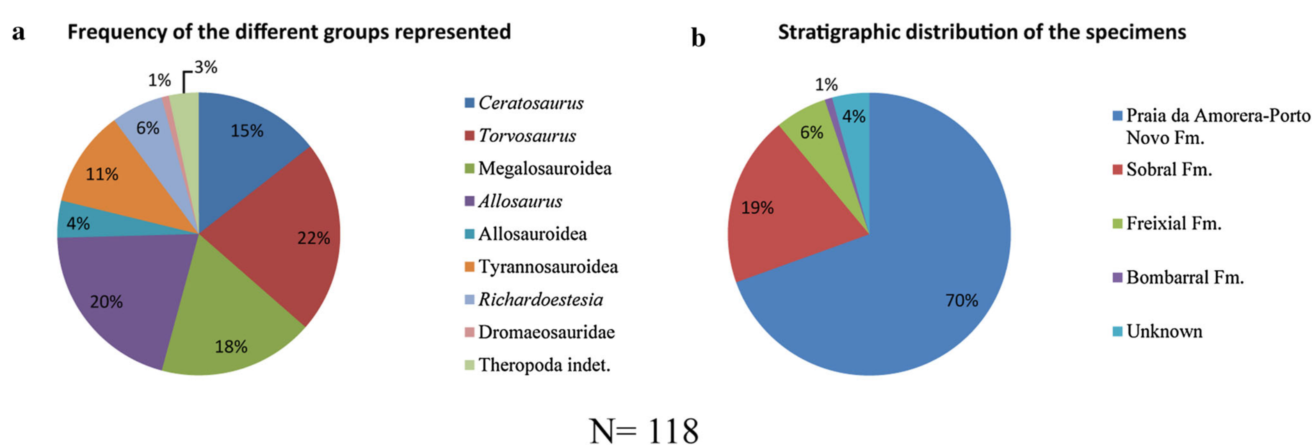

Fig. 22 Diversity and stratigraphic distribution of the isolated theropod teeth in the sample. **a** Frequency of the morphotypes; **b** distribution of the relative abundance of the specimens in the different stratigraphic units cropping out in the Central Sector of the Lusitanian Basin

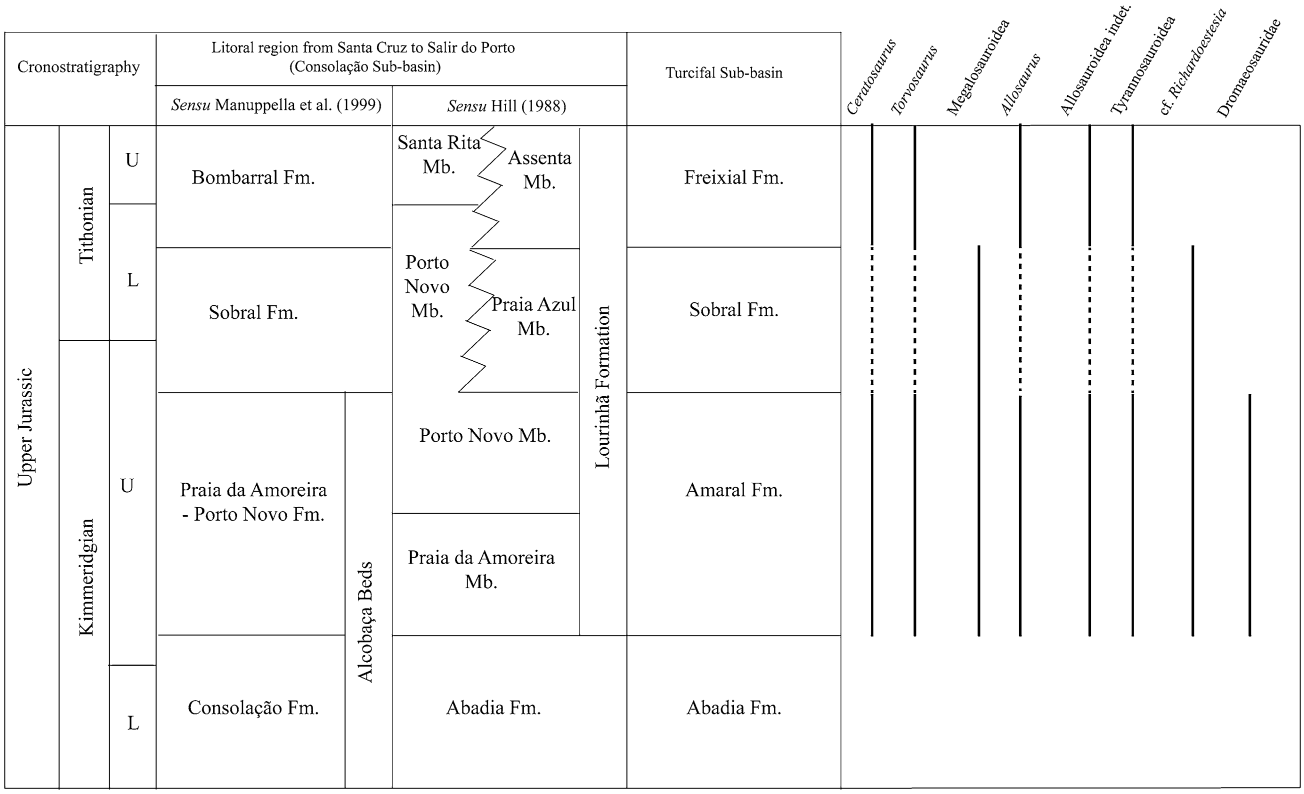

Fig. 23 Stratigraphic distribution of the different morphotypes of teeth identified in the sample

comprehensive comparison of these records is not possible at the moment.

Acknowledgements This work was supported by SFRH/BD/84746/2012 PhD scholarship, financed by the "Fundação para a Ciência e Tecnologia" (Portugal). Individual Grants to E.M. visits for review collections were financed by the Jurassic Foundation, Fundação Luso-Americana para o Desenvolvimento [Grant Number L07-V-22/2010] and Synthesys [Grant Number GB-TAF-2160 and FR-TAF-4911]. The study was also supported by a protocol between CMTV and SHN. We thank to the reviewers D. Weishampel, C. Hendrickx and O. Gerke for the comments and suggestions to the paper. We also thank S. Pereira for photographs of some elements, J. J. Santos and N. Pimentel for field assistance, and for allow accessing specimens to B. C. Silva (SHN, Portugal), R. Castanhinha and C. Tomás (ML, Portugal), V. Santos (MUHNAC, Portugal), E. Espilez and R. Royo-Torres (Fundación Conjunto Paleontológico de Teruel-Dinópolis, Spain), E. D. Berenguer and J. I. Canudo (Museo Paleontológico de Zaragoza, Spain), R. Allain (MNHN, France), L. Chiappe (NHMLAC, USA), L. Ivy and K. Carpenter (DMNH, USA), R. Scheetz and B. Britt (BYU, USA), M. Getty, M. Loewen, and R. Irmis (NHMU, USA), D. Chure (DINO, USA), S. Chapman (NHMUK, UK), P. Jeffery (OUMNH, UK), and T. Schossleitner and D. Schwarz (MfN).

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