# The dentition of megalosaurid theropods

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Theropod teeth are particularly abundant in the fossil record and frequently reported in the literature. Yet, the dentition of many theropods has not been described comprehensively, omitting details on the denticle shape, crown ornamentations and enamel texture. This paucity of information has been particularly striking in basal clades, thus making identification of isolated teeth difficult, and taxonomic assignments uncertain. We here provide a detailed description of the dentition of Megalosauridae, and a comparison to and distinction from superficially similar teeth of all major theropod clades. Megalosaurid dinosaurs are characterized by a mesial carina facing mesiolabially in mesial teeth, centrally positioned carinae on both mesial and lateral crowns, a mesial carina terminating above the cervix, and short to well-developed interdenticular sulci between distal denticles. A discriminant analysis performed on a dataset of numerical data collected on the teeth of 62 theropod taxa reveals that megalosaurid teeth are hardly distinguishable from other theropod clades with ziphodont dentition. This study highlights the importance of detailing anatomical descriptions and providing additional morphometric data on teeth with the purpose of helping to identify isolated theropod teeth in the future.

Key words: Theropoda, Tetanurae, Megalosauridae, dentition, teeth, morphometry.

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## Introduction

Although dental morphology of several theropods such as *Majungasaurus* (Fanti and Therrien 2007; Smith 2007), *Tyrannosaurus* (Smith 2005), *Troodon* (Currie 1987), and *Buitreraptor* (Gianechini et al. 2011) have been described in detail, the anatomy of the dentition of the vast majority of theropods is poorly documented and sometimes even lacks a description (e.g., Madsen 1976a; Currie and Zhao 1993; Madsen and Welles 2000; Allain 2002; Benson 2010a; Brusatte et al. 2010a). As noted by Smith (2005), Smith et al. (2005), Brusatte et al. (2007), Buckley et al. (2010), and Han et al. (2011), morphology and size of denticles, length of the carinae, and crown ornamentations (i.e., interdenticular sulci, longitudinal ridges, flutes, etc.), are pivotal features to identify isolated teeth and should be explored further in many theropod taxa. Likewise, discriminant analysis based on dental measurements appeared to be a promising technique (yet to be used with caution, see Buckley et al. 2010) that facilitates the taxonomic identification of isolated teeth. Therefore, additional morphometric data on teeth still needs to be collected for a large number of theropods (Smith et al. 2005; Han et al. 2011).

Megalosauridae are medium to large-sized carnivorous tetanurans from the Middle to Late Jurassic of Africa, Asia, Europe, and North America (Carrano et al. 2012). These basal tetanurans include the first dinosaur to be formally described, *Megalosaurus bucklandii*, by William Buckland in 1824 (Naish 2012), and one of the largest Jurassic terrestrial predators, *Torvosaurus*, known from embryos and adult material from the United States and Portugal (e.g., Britt 1991; Araújo et al. 2013; Hendrickx and Mateus 2014b). Megalosauridae is the sister-clade of Spinosauridae among megalosaurian Megalosauroidea, and includes two sub-families, Afrovenatorinae and Megalosaurinae (Carrano et al. 2012). Megalosaurid theropods have received considerable interest over the past years leading to a better understanding of their anatomy, and several taxa from the Middle Jurassic of England and the Late Jurassic of Portugal have been redescribed (i.e., *Eustreptospondylus*,

*Magnosaurus*, *Duriavenator*, *Megalosaurus*, *Torvosaurus*; Benson 2008, 2009, 2010a, b; Benson et al. 2008; Sadleir et al. 2008; Hendrickx and Mateus 2014b). Yet, the morphology and morphometry of megalosaurid teeth are particularly poorly known compared to other theropod clades (e.g., Spinosauridae, Abelisauridae, Tyrannosauridae, Troodontidae, Dromaeosauridae). Therefore, we comprehensively described the dentition of Megalosauridae, which was compared with and distinguished from other theropods based on qualitative features and quantitative data through morphological analyses.

*Institutional abbreviations*.—AMNH, American Museum of Natural History, New York, USA; BYU-VP, Brigham Young University Vertebrate Paleontology, Provo, USA; IGM, Institute of Geology, Ulaan Baatar, Mongolia; ML, Museu da Lourinhã, Lourinhã, Portugal; MNHN, Muséum national d'Histoire naturelle, Paris, France; MNN, Musée National du Niger, Niamey, Niger; NCSM, North Carolina Museum of Natural Sciences, Raleigh, USA; NHMUK, Natural History Museum, London, UK; OUMNH, Oxford University Museum, Oxford, UK; PVL, Fundación "Miguel Lillo", San Miguel de Tucumán, Argentina; QW, Giant Buddha Temple Museum, Leshan, China; UA, Université d'Antananarivo, Antananarivo, Madagascar.

*Other abbreviations*.—AL, apical length; CBL, crown base; CBR, crown base ratio; CBW, crown base width; CH, crown height; CHR, crown height ratio; CTU, crown transverse undulation density; DA, distoapical denticle density; DAVG, average distal denticle density; DB, distobasal denticle density; DC, distocentral denticle density; DDT, dentine thickness distally; DLAT, dentine thickness labially; DLIT, dentine thickness lingually; DMT, dentine thickness mesially; DSDI, denticle size density index; FABL, fore-aft basal length; MA, mesioapical denticle density; MAVG, average mesial denticle density; MB, mesio-basal denticle density; MC, mesiocentral denticle density; MCE, mesial carina extent; MCL, mid-crown length; MCR, mid-crown ratio; MCW, mid-crown width; MDE, mesiobasal denticles extent.

# Material and methods

*Material*.—We examined and collected morphometric data on the dentition of all representatives of each megalosaurid genus sensu Carrano et al. (2012) preserving teeth, i.e., *Eustreptospondylus oxoniensis* (Walker 1964), *Magnosaurus nethercombensis* (Huene 1923), *Afrovenator abakensis* (Sereno et al. 1994), *Dubreuillosaurus valesdunensis* (Allain 2002), *Duriavenator hesperis* (Waldman 1974), *Megalosaurus bucklandii* (Mantell 1827), *Torvosaurus tanneri* (Galton and Jensen 1979), and the newly named *Torvosaurus gurneyi* (Hendrickx and Mateus 2014b; see SOM 6 in Supplementary Online Material available at http://app.pan.pl/SOM/app60-Hendrickx_etal_SOM.pdf). Only the teeth (QW200701) of the possible megalosaurid *Leshansaurus qianweiensis* (Li et al. 2009; Carrano et al. 2012) from the Late Jurassic of China could not be examined. The teeth of each of these megalosaurids have been briefly described in the scientific literature and the detailed description of the dentition of Megalosauridae here given is based on our personal observations of each specimen.

*Nomenclatures and phylogenetic definitions*.—The anatomical, positional, directional, and morphometric nomenclatures follow the recommendations of Hendrickx et al. (in press b; Fig. 1; see also SOM 1). These authors mostly rely on the anatomical and topological definitions proposed by Smith and Dodson (2003) and the morphometric terms and abbreviations given by Smith et al. (2005). The theropod phylogeny adopted here follows the classification summarized by Hendrickx et al. (in press a) for nonavian theropods. We also follow the phylogenetic definitions compiled by Hendrickx et al. (in press a: table 1) for nonavian theropod clades.

*Morphometric analysis*.—We performed a morphometric analysis to understand whether megalosaurid teeth can be morphometrically identified and differentiated from other theropods based on quantitative data. We followed the methodology developed by Smith (2005) and Smith et al. (2005) and performed a discriminant analysis (or canonical variate analysis, CVA) using PAST3 (Hammer et al. 2001) on numerical data collected by Smith (2005) and Smith et al. (2005), and updated by Smith and Lamanna (2006), Smith and Dalla Vecchia (2006), and Smith (2007). Additional morphometric data were collected from Sereno and Brusatte (2008), Molnar et al. (2009), and Hocknull et al. (2009) for Allosauroidea, and Larson and Currie (2013) for Deinonychosauria (see supplemental information of Larson and Currie 2013 for source of data collected from other authors). Original measurements were also taken on the teeth of 46 theropod taxa deposited in 24 museums from Europe, North America and South America (see SOM 3).

A first discriminant analysis was performed on the whole dataset, and theropod teeth were first grouped by clades, then by genera. Each clade was selected at the family and superfamily levels (Coelophysoidea, Noasauridae, Abelisauridae, Megalosauridae, Spinosauridae, Allosauridae, Neovenatoridae, Carcharodontosauridae, Tyrannosauridae, Dromaeosauridae, Troodontidae) following the phylogenies obtained by Pol and Rauhut (2012) for Ceratosauria, Carrano et al. (2012) for Coelophysoidea and non-coelurosaur Tetanurae, Brusatte et al. (2010b) for Tyrannosauroidea, and Turner et al. (2012) for Deinonychosauria (see SOM 3). Only a few groupings are paraphyletic (i.e., non-neotheropod Theropoda, non-abelisauroid Ceratosauria, and non-tyrannosaurid Tyrannosauroidea), but members of each paraphyletic group share similar dentition (CH personal observations). In this analysis, the theropods *Erectopus*, *Nuthetes*, and *Richardoestesia*, with uncertain affinities, as well as *Dilophosaurus* and *Piatnitzkysaurus*, were analyzed at the genus level (see SOM 3).

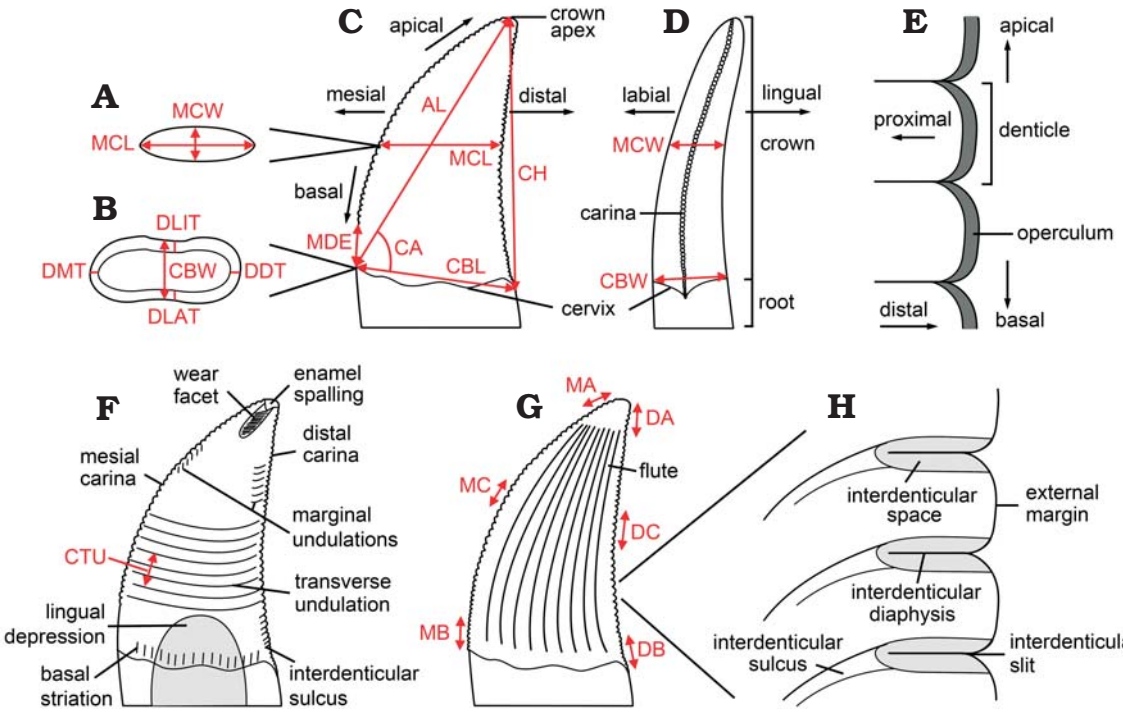


Fig. 1. Anatomical and morphometric terminology used in this study. **A**. Mid-height cross-section of crown C showing MCW (mid-crown width) and MCL (mid-crown length), in apical view. **B**. Basal cross-section of crown in C showing CBW (crown-base width), DDT (dentine thickness distally), DLAT (dentine thickness labially), DLIT (dentine thickness lingually), and DMT (dentine thickness mesially), in basal view. **C**. Idealized lateral theropod tooth showing general theropod anatomy and AL (apical length), CA (crown angle), CBL (crown-base length), CH (crown height), MCL, and MDE (mesial denticles extent), in labial view. **D**. Idealized lateral theropod tooth showing MCW and CBW. **E**. Idealized distal denticles showing basal, apical, proximal, and distal directions. **F**. Idealized lateral theropod tooth showing several crown ornamentations morphology and CTU (crown transverse undulation density), in labial view. **G**. Idealized fluted theropod tooth showing DA (disto-apical denticle density), DB (disto-basal denticle density), DC (disto-central denticle density), MA (mesio-apical denticle density), MB (mesio-basal denticle density), and MC (mesio-central denticle density), in labial view. **H**. Idealized distal denticles showing denticle anatomy, in labial view.

In order to better discriminate teeth that are morphologically similar to those of megalosaurids, a second morphometric analysis was performed on a reduced dataset encompassing theropods with large ziphodont teeth (i.e., non-abelisaurid Ceratosauria, Abelisauridae, Megalosauridae, Allosauridae, Neovenatoridae, Carcharodontosauridae, and Tyrannosauridae; see SOM 4). Theropods have a pseudoheterodont dentition (i.e., dentition in which the crown morphology gradually changes along the jaw so that mesial and lateral teeth differ significantly in their morphology; Hendrickx et al. in press b) and to visualize morphospace occupation of mesial and lateral dentitions, a third discriminant analysis was performed on a dataset including taxa with enough data on the dentition (i.e., *Ceratosaurus*, *Majungasaurus*, *Dubreuillosaurus*, *Allosaurus*, *Acrocanthosaurus*, *Gorgosaurus*, *Tyrannosaurus*; see SOM 5). In this analysis, we did not consider data collected on mesial teeth of *Tyrannosaurus* by Smith (2005), who mistook CBL (which should be measured between points A and B; Smith 2005: fig. 1C) for CBW (measured between points C and D; Smith 2005: fig. 1C), and only our own measurements were taken into consideration for the mesial dentition in this tyrannosaurid.

CBL, CBW, CH, AL, CBR, CHR, MCL, MCW, MCR, MC, and DC (Fig. 1) were used in the two analyses, as these variables best represent the amount of difference among theropod teeth and characterize crown size, width, elongation, thickness along the crown, and denticles size (Smith et al. 2005; CH personal observations). Smith et al. (2005) methodology, which was followed by other authors (e.g., Smith and Dalla Vecchia 2006; Smith and Lamanna 2006; Kear et al. 2013; Richter et al. 2013), uses ratio variables such as CA, CBR, CHR, and DSDI. These non-independent variables weigh the variables used in the ratios, therefore each morphometric analysis was first performed without ratio variables. The latter were then included in a second analysis in order to visualize the influence of ratios and how they overemphasized variables on the results.

All values were log-transformed to better reflect a normally distributed multivariate dataset (Smith et al. 2005; Kear et al. 2013; Larson and Currie 2013, see rationalization in Samman et al. 2005, and references therein). Contrary to Smith et al. (2005), crown angle values (CA) sensu Smith et al. (2005) were not used in the morphometric analyses as this angle can be affected by the extent of the enamel layer both mesially and distally (Buckley et al. 2010) and only weakly reflects apical displacement (CH personal observations). Additionally, CA values obtained by Smith (2005) and Smith et al. (2005) differ from those calculated in this study using the same formula (i.e., the law of cosines on CBL, CH, and AL), and Smith (2005) and Smith et al. (2005) likely used

another method to calculate CA. We also favoured MC and DC instead of MAVG and DAVG because they are affected by the absence of data for both basal and apical denticles, typically smaller than mid-crown denticles and often unpreserved (CH personal observations). Likewise, we did not generate any size-corrected variables on MC and DC as denticle size, like tooth size, remains an important factor in the study of theropod teeth and can vary independently from tooth dimension (Smith et al. 2005; CH personal observations). Teeth with a great deal of missing data can blur the morphometric signal, and as the initial dataset included a large number of teeth (more than 2000 specimens initially), only complete teeth with data on crown height (CH), length (CBL), width (CBW) and number of distal denticles per 5 mm (DC) were selected. Unserrated teeth were also included, and MC and DC were treated as missing data. The final dataset comprised 995 teeth belonging to 62 theropod taxa and 19 groups, and the reduced dataset with large ziphodont theropods includes 393 teeth belonging to 33 taxa and 11 groupings.

The morphospace occupied by each megalosaurid was visualized in a fourth discriminant analysis performed on a dataset including Megalosauridae only (see SOM 6). In this analysis, all morphometric variables (i.e., CBL, CBW, CH, AL, CBR, CHR, MCL, MCW, MCR, MDE, MEC, CTU, DMT, DDT, DLAT, DLIT, MA, MC, MB, DA, DC, DB, MAVG, DAVG, TDD, DSDI, CA) were employed, and ratios (MAVG, DAVG, CBR, CHR, MCR, MEC, DSDI, CA) were first excluded, then taken into consideration in a second analysis. We selected teeth with two variables or more, and the measurements were not log-transformed, as the absence of mesiobasal denticles and transverse undulations was taken into consideration. In this analysis, missing data (coded with a question mark) differ from those that are absent (like denticles and transverse undulations) and have zero as value.

# The dentition of Megalosauridae

**Tooth count**.—Like the majority of nonavian theropods, all megalosaurids that have the premaxilla preserved (*Eustreptospondylus*, *Duriavenator*, *Dubreuillosaurus*, and *Torvosaurus*) bear four premaxillary teeth (Allain 2002; Benson 2008; SOM 2: Table 1), even in *Torvosaurus*, which has often been considered to have only three premaxillary teeth (e.g., Galton and Jensen 1979; Holtz et al. 2004; see Britt 1991; Benson 2008). The maxilla of Megalosauridae shows ten to 14 maxillary alveoli (SOM 2: Table 1), and an exact tooth count is known in *Dubreuillosaurus* and *Megalosaurus* which both have 13 maxillary teeth (Allain 2002; Benson 2010a), and *Afrovenator* which bears 14 teeth (Sereno et al. 1994). In megalosaurid dentaries, the typical condition is 13 to 15 teeth (SOM 2: Table 1), and a complete dentary with 13 teeth is only known in *Dubreuillosaurus* (Allain 2002). Nevertheless, based on comparison of the preserved part of the left and right dentaries of *Eustreptospondylus* (OUMNH J.13558), we estimate a tooth count of 14 dentary teeth in this taxon.

On average, the premaxillary teeth of megalosaurids are smaller but more elongated than the lateral teeth. In all megalosaurids, the largest teeth erupt from the maxilla, at the level of the second to sixth maxillary alveoli. In fact, the maxillary alveoli are larger on average than the dentary alveoli in all megalosaurid specimens (i.e., *Eustreptospondylus*, *Dubreuillosaurus*, *Duriavenator*, and *Torvosaurus*). The maxillary teeth are also much longer than those of the dentary in *Dubreuillosaurus*, whereas the difference in size between maxillary and dentary teeth is more subtle in *Duriavenator* (SOM 6). As noticed in *Torvosaurus* (Britt 1991), megalosaurids display an overlap between the first and second, and second and third premaxillary alveoli, the second alveolus usually overlaps more than 75% of the first, and the third alveolus overlaps approximately 50% of the second one. The fourth premaxillary alveolus does not, however, overlap the third one in megalosaurids (*Eustreptospondylus*, *Dubreuillosaurus*, and *Torvosaurus*). There is an overlap of about 25% to 50% between the second and first dentary alveoli. There is no subnarial gap in megalosaurids and all alveoli are subequally separated with all teeth pointing ventrally or dorsally and slightly anterodorsally in the *Duriavenator* mesial dentary teeth (Benson 2008). In the mesial dentition, the long axis of the premaxillary alveoli is anteroposteriorly oriented, i.e., labiolingually oriented in the most mesial one and mesiodistally in the more distal ones. The first dentary alveolus is always much smaller than the more distal alveoli. The dentary alveoli are subcircular in the most mesial one, then lenticular in the more distal ones, differing from the subrectangular alveoli of some other theropods such as abelisaurids (e.g., Hendrickx and Mateus 2014b). Additionally, the tooth row ends at the level of the lacrimal contact of the maxilla, well anterior from the posterior tip of the jugal ramus. Therefore, megalosaurid taxa possess the synapomorphic character of Tetanurae of having an antorbital tooth row (Gauthier 1986).

**Mesial teeth**.—As in most basal theropods, megalosaurids bear ziphodont teeth and have a pseudoheterodont dentition with mesial and lateral teeth. In Megalosauridae, the mesial dentition includes the premaxillary teeth, the first maxillary tooth, and the first two dentary teeth. The premaxillary teeth and first dentary teeth are weakly labiolingually compressed, and are smaller as well as more elongated in average than the lateral teeth. Unfortunately, only *Dubreuillosaurus* and *Duriavenator* have preserved complete erupted mesial teeth. The first and second teeth of the left premaxilla of *Dubreuillosaurus* are the only erupted and complete premaxillary teeth present in all Megalosauridae (Figs. 2A). The second tooth of the *Duriavenator* right dentary is the only complete and erupted mesial dentary tooth in this clade (Benson 2008). The bases of the second premaxillary tooth and the second dentary tooth have also been preserved in the left premaxilla of *Duriavenator* and the right dentary of *Magnosaurus*, respectively. The mesial unerupted teeth are partially visible in the second left and third right premaxillary

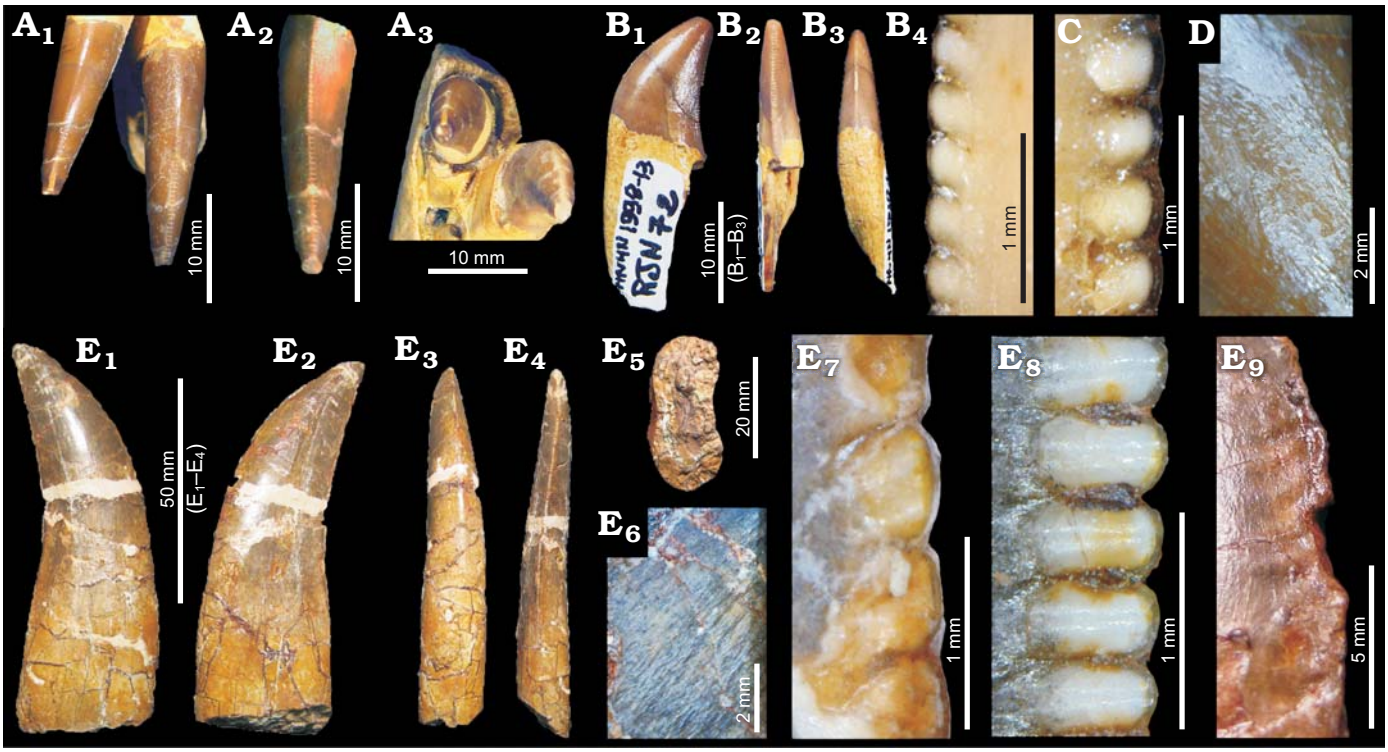


Fig. 2. Dentition of Afrovenatorinae from the Middle Jurassic of France and Niger. **A**–**D**. Teeth and denticles of *Dubreuillosaurus valesdunensis* Allain, 2002 (MNHN 1998-13). **A**. First and second left premaxillary teeth in anterior ($A_1$) and palatal ($A_3$) views, and second left premaxillary tooth in distal view ($A_2$). **B**. Isolated lateral tooth in lingual ($B_1$), distal ($B_2$), and mesial ($B_3$) views, with detail of mesial denticles in lateral view ($B_4$). **C**. Distal denticles of sixth right dentary tooth in lateral view. **D**. Enamel texture of sixth right maxillary tooth. **E**. Isolated tooth of *Afrovenator abakensis* Sereno, Dutheil, Larochene, Larsson, Lyon, Magwene, Sidor, Varricchio, and Wilson, 1996 (MNN UBA1) in lingual ($E_1$), labial ($E_2$), mesial ($E_3$), distal ($E_4$), and basal ($E_5$) views, with details of enamel texture ($E_6$), mesial ($E_7$) and distal ($E_8$) denticles, and marginal undulations adjacent to the mesial carina ($E_9$).

alveoli of *Eustreptospondylus* (Fig. $3A_1$), the second left premaxillary alveolus of *Duriavenator*, the first right dentary alveolus of *Magnosaurus*, and in the first left dentary alveolus of *Torvosaurus* (BYUVP 2003) and *Megalosaurus* (NHMUK R.8305). Isolated mesial teeth were found for *Torvosaurus* (ML 962; Hendrickx and Mateus 2014a, b) and *Megalosaurus* (NHMUK R2635; NHMUK R3221; NHMUK R44806; CH personal observations). Among taxa with teeth, *Afrovenator* and *Leshansaurus* are the only megalosaurids in which the morphology of mesial teeth is unknown.

The crown base ratio of mesial teeth varies from 0.63 to 0.75 (0.72 and 0.73 in *Dubreuillosaurus* Lpm1 and Lpm2; 0.71 in *Magnosaurus* Rdt1; 0.63 in *Duriavenator* Lpm2 and 0.67 for Ldt2; 0.65 in an isolated tooth of *Torvosaurus*; SOM 6) giving a subcircular outline to the base crown in cross section (Benson 2008). The crown height ratio fluctuates from 2 to 2.8 (2.1 in *Dubreuillosaurus* Lpm1 and Lpm2; 2 in *Duriavenator* Rdt2; 2.75 in an isolated tooth of *Torvosaurus*; SOM 6), which corresponds to a moderately to strongly elongated crown. The mesial teeth are usually poorly to moderately curved distally and their distal margin is always concave. There is no concave area on the lingual surface of the crown, adjacent to the carinae. In fact, mesial crowns of megalosaurids have strongly convex labial and lingual margins, with no concavity on the lingual surface, as in lateral teeth.

An important feature of mesial teeth of megalosaurids is the central position of the mesial carina, serrated but not twisted lingually, which faces anteriorly and develops only on the apical half of the crown, extending basally well above the cervix. The distal carina is also serrated and centrally positioned to weakly offset labially, and faces posteriorly (Britt 1991; Allain 2002; Benson 2008; CH personal observations). Therefore, both carinae are aligned on the same plane that passes through the apex of the tooth, and this plane is parallel to the true sagittal plane of the skull (i.e., parallel to the antero-posterior axis of the skull independent of the orientation of the tooth row) in all mesial teeth of Megalosauridae. The mesial serrations occupy between 55 to 65% of the crown height. The distal carina, on the other hand, extends basally below the cervix, so that the base crown has a lanceolate shape in cross section and is not U-shaped, D-shaped or J-shaped as in allosauroids and tyrannosauroids (Hendrickx and Mateus 2014a). The mesial carina of the first two premaxillary teeth and the first dentary tooth face labially, whereas the distal carina faces labiodistally. The distal carina is straight or slightly sigmoid in distal view and the carina bears denticles that are similar in size than those of mesial carina (DSDI close to 1; Smith et al. 2005).

Mesial and distal denticles decrease in size towards the base of the crown and similarly towards the crown apex. When the crown apex is preserved, the denticles are clearly

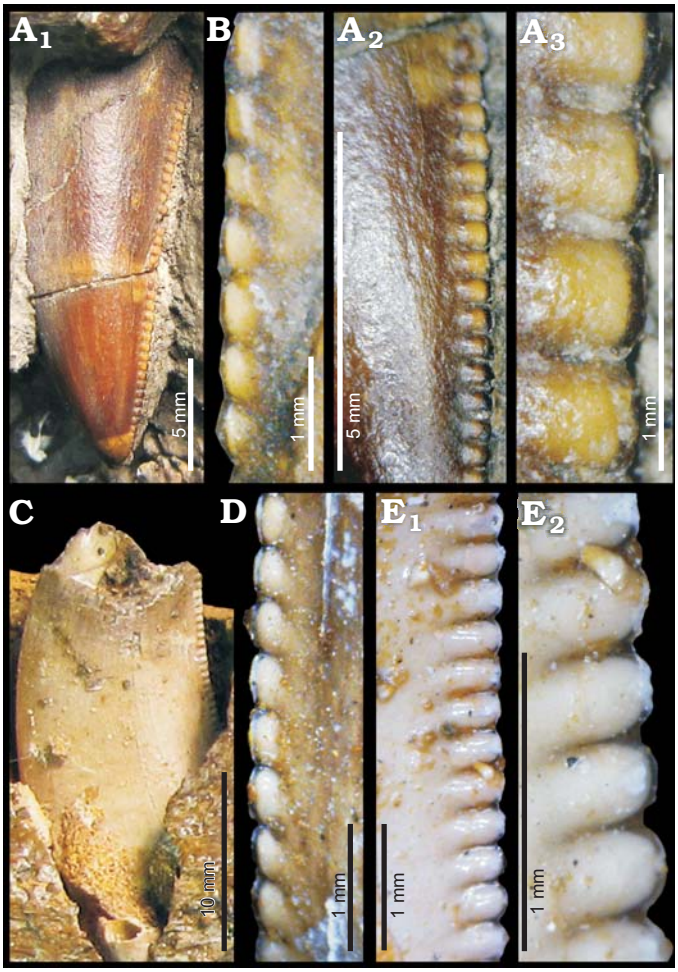


Fig. 3. Dentition of *Eustreptospondylus* and *Magnosaurus* from the Middle Jurassic of England. **A**, **B**. Crown and denticles of *Eustreptospondylus oxoniensis* Walker, 1964 (OUMNH J.13558). **A**. Third right premaxillary tooth in lingual views; details of crown ($A_1$), distal serrations and enamel texture ($A_2$), apicodistal denticles ($A_3$). **B**. Apicomesial denticles of the sixth left maxillary tooth in lingual view. **C**–**E**. Crown and denticles of *Magnosaurus nethercombensis* von Huene, 1923 (OUMNH J12143). **C**. Crown of fifth dentary tooth in lingual view. **D**. Mesial denticles of the third dentary tooth in lingual view. **E**. Distal denticles of the ninth right dentary tooth in lingual views.

contiguous over the tip. Mesial and distal denticles differ significantly in their morphology, except in *Dubreuillosaurus*. Mesial denticles are subquadrangular to subrectangular in outline, with a basoapical axis of elongation, at two-thirds of the crown (Fig. 3B). The distal denticles are always subquadrangular at mid-crown (Fig. $3A_2$, $A_3$). The denticles project perpendicularly from the main axis of the carina and have symmetrically convex external margins, and apically hooked denticles have not been observed in any megalosaurids. The interdenticular space of all denticles is narrow and the interdenticular sulci are either totally absent (e.g., *Dubreuillosaurus*) or weakly developed in between the distal denticles at mid-length of the crown (e.g., *Magnosaurus*, *Eustreptospondylus*; Fig. $3A_2$) or more basally (*Torvosaurus*). Mesial and apicodistal denticles do not possess interdenticular sulci (Fig. 3B). Due to tooth size disparity, the density of denticles is variable among megalosaurids. There are seven to eight denticles per 5 mm on mesial and distal carinae at mid-crown (or at two third of the crown) in *Torvosaurus* (Hendrickx and Mateus 2014b), eight to nine in *Duriavenator*, 11–12 in *Dubreuillosaurus* and *Eustreptospondylus*, and 13–15 in *Magnosaurus* (SOM 6). Mesial teeth do not display grooves, flutes or apparent wide transverse or short marginal undulations on the crown surface; only subtle to tenuous transverse undulations may be visible (Hendrickx and Mateus 2014b).

**Lateral teeth**.—Megalosaurid lateral teeth are an ideal example of ziphodont morphology in non-avian theropods, i.e., the teeth are blade-shaped, strongly laterally compressed, recurved distally, and serrated on both carinae. Complete lateral teeth are preserved in all members of megalosaurids but *Eustreptospondylus* and *Magnosaurus*. *Eustreptospondylus* only includes the base of one erupted maxillary tooth and several partially visible unerupted teeth, whereas *Magnosaurus* shows several damaged and incomplete erupted and unerupted teeth. In *Afrovenator* there are three isolated teeth, and only one is complete and weakly damaged (Fig. $2E_1$–$E_4$).

The crown base ratio of megalosaurid lateral teeth ranges between 0.35 (*Torvosaurus*, ML 1100, Lmx2) to 0.63 (*Magnosaurus*, Ldt5), with average values ranging from 0.45–0.55 (0.42 in *Afrovenator*; 0.44 in *Dubreuillosaurus*; 0.45 in *Duriavenator*; 0.47 in *Torvosaurus*; 0.53 in *Megalosaurus*, and 0.61 in *Magnosaurus*) (see SOM 6), thus moderately labiolingually compressed crowns. The crown height ratio varies considerably with tooth position, from 1.4 for very short crowns (*Dubreuillosaurus*, isolated tooth) to 2.8 for strongly elongated teeth (*Torvosaurus*, isolated tooth ML 500). In Megalosauridae, *Dubreuillosaurus* possesses shorter dentition, with an average of 1.65 for the lateral teeth, whereas *Torvosaurus* (ML 1100) has the most elongated and longest crowns, with a crown elongation of 2.3 on average and a height of 128 mm for the largest crown (*Torvosaurus*, ML 1100, Lmx3; see SOM 6). Crown elongation cannot be properly measured in *Eustreptospondylus* and *Magnosaurus* as the teeth are unerupted, but the dentition of these two taxa display short crowns (CHR <2), as short as those of *Dubreuillosaurus*.

As in mesial teeth, the serrated mesial carina is not twisted and does not reach the cervix whereas the distal carina terminates well beneath the crown cervix. The basal extent of the mesial carina is variable; the most basal denticles appear only on the apical third of the crown (*Megalosaurus*, Lmx3) or at the basal one fifth of the crown (*Duriavenator*, Rmx6). The mesial carina extends along 40% to 80% of the crown height, from the apex to the basal half of the tooth (see SOM 6). As in mesial teeth, the mesial carina is straight or weakly diagonally oriented, but always centrally positioned on the lateral crowns, unlike the distal carina. The latter is usually weakly sigmoid or bowed lingually and centrally positioned to slightly offset labially on the crown in distal view, as in

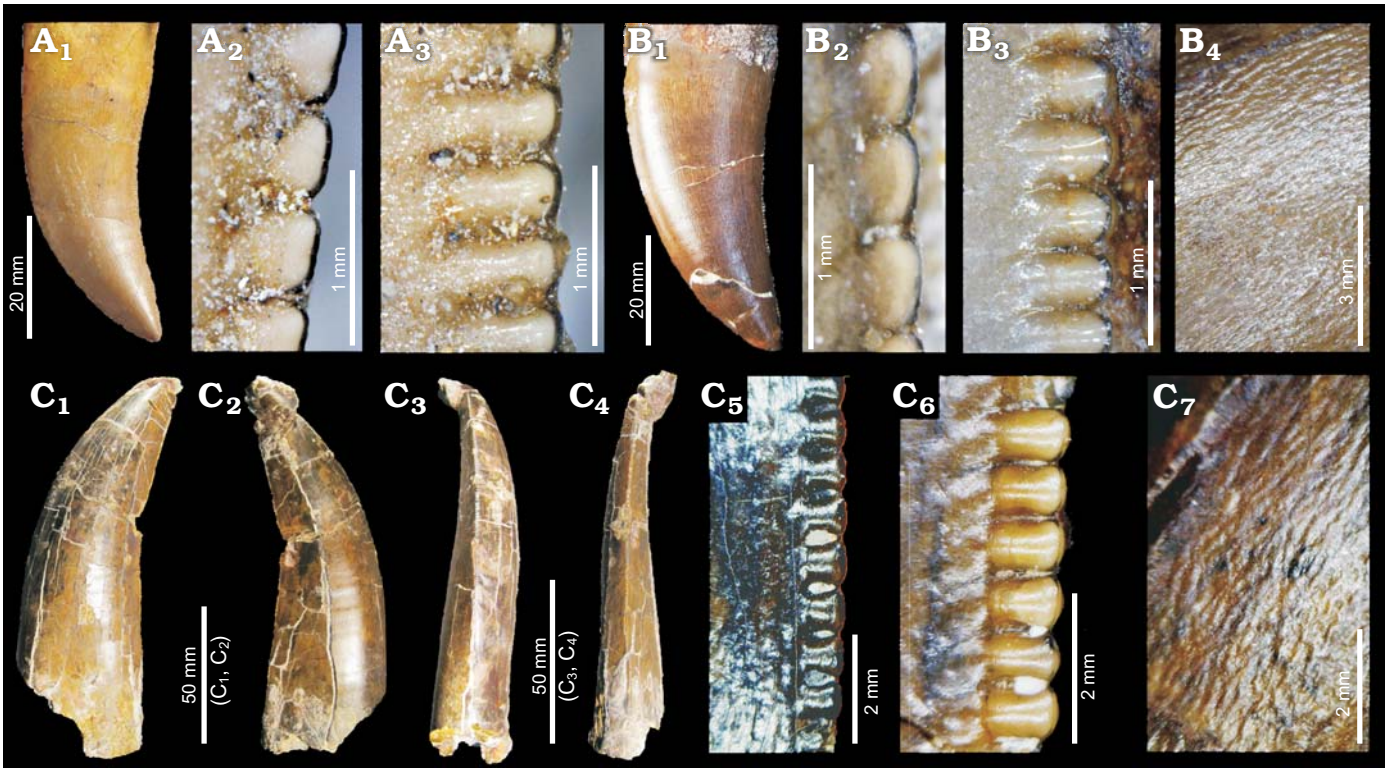


Fig. 4. Dentition of Megalosaurinae from the Middle and Late Jurassic of Europe. **A**. Sixth right maxillary tooth of *Duriavenator hesperis* Waldman, 1974 (NHMUK R.332), crown ($A_1$), mesial ($A_2$) and distal ($A_3$) denticles in lingual views. **B**. Sixth right dentary tooth of *Megalosaurus bucklandi* Mantell, 1827 (OUMNH J13505), crown ($B_1$), mesial ($B_2$) and distal ($B_3$) denticles in labial views, enamel texture ($B_4$). **C**. Isolated tooth of *Torvosaurus* cf. *gurneyi* Hendrickx and Mateus, 2014b (ML 500) in lingual ($C_1$), labial ($C_2$), mesial ($C_3$), and distal ($C_4$) views, with details of mesial ($C_5$) and distal ($C_6$) denticles, and enamel texture ($C_7$) in lateral views.

*Dubreuillosaurus* (Fig. $2B_2$) and *Afrovenator* (Fig. $2E_4$). The labial margin of the teeth is strongly convex and does not display any concave or flattened surface adjacent to the carinae. The lingual surface is weakly to strongly concave, but not flattened. There is, however, a large flattened surface or shallow concavity, centrally positioned on the basolingual part of the crown, representing the track of the erupting replacement crown. This concave area is clearly visible in *Torvosaurus*, *Megalosaurus*, *Duriavenator*, and *Afrovenator* lateral teeth, whereas the basolingual surface of the lateral crowns is flat in *Dubreuillosaurus* (Fig. $2B_1$) and *Magnosaurus*. In cross section, the crown base of megalosaurid lateral teeth is lenticular, with the lingual margin straight or slightly to strongly concave in its central part.

The mesial denticles are subrectangular, with an apicobasally long axis in most megalosaurids such as *Eustreptospondylus*, *Magnosaurus* (Fig. 3D), *Dubreuillosaurus* (Fig. $2B_4$), *Afrovenator* (Fig. $2E_7$), *Duriavenator* (Fig. $4A_2$) and *Megalosaurus* (Fig. $4B_2$). In *Torvosaurus* and *Megalosaurus*, the mesial denticles are also subquadrangular (Fig. $4C_5$). The mesial denticles are usually perpendicular to the mesial margin of the crown. However, the mesial denticles tend to be apically inclined in some megalosaurids, such as *Afrovenator* (Fig. $2E_7$), *Dubreuillosaurus* (Fig. $2B_4$), and *Duriavenator* (Fig. $4A_2$), and resemble a parallelogram. The external margin of the denticles is symmetrically to asymmetrically convex and positioned apically when asymmetrical. The margin is usually parabolic, but it is also flat or even biconvex in some cases (Fig. $4A_2$), as clearly seen in some mesial denticles of *Duriavenator* (Rmx6) and *Megalosaurus* (NHMUK R234, Lmx5). At the crown mid-height, the distal denticles are subquadrangular in *Dubreuillosaurus* (Fig. 2C) and *Magnosaurus* (Fig. $3E_2$), and horizontally subrectangular in *Afrovenator* (Fig. $2E_8$), *Duriavenator* (Fig. $4A_3$), *Megalosaurus* (Fig. $4B_3$), and *Torvosaurus* (Fig. $4C_6$). The external margin is symmetrically convex and parabolic as in *Dubreuillosaurus* (Fig. 2C) and *Torvosaurus* (Fig. $4C_6$) to semi-circular in outline as in *Afrovenator* (Fig. $2E_8$) and some teeth of *Megalosaurus* (Fig. $4B_3$). Both mesial and distal denticles are not hooked apically in Megalosauridae, and there is about the same number of denticles on both carinae (DSDI close to 1). There are 13–17 denticles per 5 mm on both carinae at mid-height of crown (or at two-thirds) in *Dubreuillosaurus* (average of 16), 11–14 in *Magnosaurus* (average of 12.5), 8.5–13.5 in *Eustreptospondylus* (average of 11.5), 8–13 in *Duriavenator* and *Megalosaurus* (average of 11), 7.5–12 in *Afrovenator* (average of 9), and 6–9.5 in *Torvosaurus* (average 7.5) (SOM 6).

Interdenticular sulci are present in the lateral dentition of megalosaurid taxa, but not in all crowns. Interdenticular sulci are absent in some lateral crowns of *Dubreuillosaurus* and *Megalosaurus*. Likewise, there is some variation in the

length of the interdenticular sulci, as well as in their inclination along the tooth row, some being short and oriented perpendicular to the carinae, others being well-developed and strongly inclined basally (Benson 2009). Interdenticular sulci are rare in mesial denticles and occur in *Duriavenator*, *Megalosaurus* and *Torvosaurus*. In these taxa, the interdenticular sulci of the mesial denticles are always short and poorly developed. On the other hand, short to well developed interdenticular sulci are very often seen on the distal carina of megalosaurid teeth. Short to medium interdenticular sulci (0.3–0.5 mm) are present between the distal denticles of *Magnosaurus* (contra Benson 2010b), *Afrovenator*, *Dubreuillosaurus*, *Duriavenator* (Benson 2008) and *Megalosaurus* (Benson 2009), whereas there are strongly developed interdenticular sulci (~1 mm) in some crowns of *Megalosaurus* (Benson 2009) and most *Torvosaurus* teeth (Hendrickx and Mateus 2014b).

Megalosaurid teeth often display crown ornamentations such as large transverse undulations and short marginal undulations (Fig. $4C_2$), but flutes, ridges, or wide longitudinal concavities extending along the crown have not been noticed hitherto. Wide transverse undulations covering most of the tooth are common in megalosaurine teeth and visible in *Duriavenator* (Benson 2008), *Megalosaurus* (Benson 2009), and *Torvosaurus* (Hendrickx and Mateus 2014b). In *Duriavenator*, the transverse undulations are tenuous (Benson 2008), while in *Megalosaurus* and *Torvosaurus*, they are visible, numerous and closely-packed in some cases (Benson 2009; CH personal observations). These large transverse bands are absent in *Dubreuillosaurus*, *Magnosaurus*, and the only well-preserved crown of *Afrovenator*. Short undulations adjacent to the mesial and distal carinae are readily visible in *Afrovenator*, especially marginal to the mesial carina where they are visibly developed (Fig. $2E_9$). Some crowns of *Megalosaurus* and *Torvosaurus* also display these short undulations, either adjacent to both carinae (OUMNH J.29855, NHMUK R.234, ML 500) or in the vicinity of the distal carina only (NHMUK R47963). These marginal undulations are usually mesiodistally-oriented, but there is a diagonal orientation of these structures in some *Megalosaurus* teeth (OUMNH J.23014, NHMUK R.29855). The enamel of the crowns of megalosaurids has a braided texture with elongated intertwined ridges (Fig. 2D, $E_6$ and Fig. $4B_4$, $C_7$). This pattern differs from the deeply veined enamel texture visible in spinosaurids (e.g., *Baryonyx*, *Spinosaurus*, *Suchomimus*; e.g., Charig and Milner 1997; Hasegawa et al. 2010; Buffetaut 2012) and the irregular texture in Abelisauridae and most Maniraptoriformes (Hendrickx and Mateus 2014a).

# Comparison to the dentition of other theropods

**Morphological comparison**.—Teeth of Megalosauridae are easily distinguishable from those of Coelophysidae, Abelisauridae, Noasauridae, Spinosauridae, Tyrannosauroidea, Compsognathidae, Dromaeosauridae, Therizinosauria, and Troodontidae, all of which have highly specialized dentition. Therizinosauria and Troodontidae have leaf-shaped crowns with constricted cervix, and the teeth are unserrated or bear very few serrations, and either minute denticles or large pointed denticles sometimes changing dramatically in shape along the carinae (e.g., Currie 1987; Currie et al. 1990; Clark et al. 1994; Zhao and Xu 1998; Barrett 2000; Norell et al. 2009; Zanno 2010; Hendrickx and Mateus 2014b).

Coelophysids and compsognathids possess small crowns (CH <15 mm) lacking in most cases a serrated mesial carina in mesial teeth, and the distal carina bears minute denticles (>30 denticles per 5 mm; Buckley 2009; Hendrickx and Mateus 2014b).Teeth of abelisaurids are usually low and weakly recurved, and display a slightly concave, straight or convex distal profile, a mesial carina that always reaches the cervix, and an irregular and non-oriented enamel texture. They also possess hooked denticles in some taxa (e.g., *Rugops*, *Kryptops*, *Majungasaurus*), and the mesial teeth show a concave area adjacent to the mesial and, in some cases, the distal carina on the lingual surface of the crown (e.g., Fanti and Therrien 2007; Smith 2007; Hendrickx and Mateus 2014b). Teeth of noasaurids are small (CH <15 mm), the lateral teeth have a mesial carina reaching the cervix, the distal denticles are hooked apically in some taxa (e.g., *Masiakasaurus*), and are larger than mesial denticles. The mesial teeth are lanceolate and have a strongly twisted mesial carina and fluted lingual surface (Carrano et al. 2002; Hendrickx and Mateus 2014a). In spinosaurids, the mesial and distal serrations are minute or absent, the mesial carina always reaches the cervix, the enamel texture is deeply veined (except in *Irritator*) and the crowns are subcircular in cross-section and sometimes fluted on one or both lingual and labial surfaces (e.g., Charig and Milner 1997; Sereno et al. 1998; Sues et al. 2002; Hendrickx and Mateus 2014b).

Among Tyrannosauroidea, tyrannosaurids have incrassate crowns, and the mesial carina of the teeth making the transition between the mesial (premaxillary and first two dentary teeth; Smith 2005) and lateral dentition is strongly twisted. Likewise, mesial teeth are U-shaped (sensu Hendrickx and Mateus 2014a) in cross section, with both mesial and distal carinae facing lingually (Holtz 2004). The mesial teeth of some primitive tyrannosauroids have a mesial carina twisting lingually, and the lateral teeth have distal denticles larger than the mesial ones (Xu et al. 2006; Rauhut et al. 2010; Hendrickx and Mateus 2014a).

The lateral teeth of some Dromaeosauridae are devoid of serrated carinae, as in *Buitreraptor* (Gianechini et al. 2011) or lack a serrated mesial carina, as in *Tsaagan* (Norell et al. 2006) and some teeth of *Velociraptor* and *Bambiraptor* (CH personal observations). When present, the mesial carina of lateral teeth can be twisted, as in *Dromaeosaurus* (Currie et al. 1990; Currie 1995), or bear mesial denticles that are smaller than the distal ones, as in *Atrociraptor* (Currie and Varricchio 2004), *Deinonychus* (Ostrom 1969),

*Velociraptor* (Sues 1977; Barsbold and Osmólska 1999), *Bambiraptor* (Burnham 2004), *Saurornitholestes* (Currie et al. 1990), and *Acheroraptor* (Evans et al. 2013). The distal denticles can also be hooked apically, as in *Deinonychus* (Ostrom 1969), *Saurornitholestes* (Currie et al. 1990) and *Atrociraptor* (Currie and Varricchio 2004). Moreover, the lateral teeth tend to have a wide apicobasally elongated concavity on the basolabial surface of the crown (Gianechini et al. 2011; CH personal observations), a depression which is also usually well-developed on the lingual surface of the crown. These lingual and labial concavities are particularly clear in some dromaeosaurids such as *Sinornithosaurus* (Xu and Wu 2001) and were interpreted as a venom delivery duct (Gong et al. 2010, 2011). Finally, the mesial teeth of dromaeosaurids are different from those of Megalosauridae; they either lack a mesial carina, as in *Tsaagan* (IGM 100-1015) and *Velociraptor* (AMNH 6515), or the mesial carina curves strongly lingually, as in *Deinonychus* (Ostrom 1969), *Dromaeosaurus* (Currie et al. 1990; Currie 1995) and *Saurornitholestes* (Currie et al. 1990).

Differentiating teeth of megalosaurids from those of Ceratosauridae, basal Megalosauroidea, and Allosauroidea is more difficult. These taxa have similar crown size (CH), thickness (CBR), and elongation (CHR), and a similar number of denticles along the carinae (DC and MC). Ceratosauridae have strongly labiolingually compressed lateral teeth (CBR <0.5) with a flattened lingual margin and a concave surface adjacent to the distal carina on the labial and lingual sides of the crown, and a wide concave area centrally positioned on the labial side of the crown (CH personal observations). Mesial teeth of *Ceratosaurus* are fluted lingually and the mesial carina of premaxillary crowns is absent (Currie and Carpenter 2000), whereas lateral teeth tend to have a mesial carina extending to the cervix. *Genyodectes* does not possess fluted teeth, but the premaxillary teeth are strongly elongated (CHR >2.5) and the distal carina is offset labially (Rauhut 2004).

Teeth of Megalosauridae are difficult to distinguish from those of Piatnitzkysauridae, but some differences exist. The mesial denticles of *Marshosaurus* and *Piatnitzkysaurus* are slightly smaller than the distal serrations (Madsen 1976b; CH personal observations), which is never the case in megalosaurids. Likewise, *Piatnitzkysaurus* posterior maxillary teeth have a distal margin that is straight to slightly convex, a mesial carina reaching the cervix, and they are thick labiolingually (CBR ca. 0.71 for Lmx13; PVL 4073). This is also the case in *Condorraptor* in which lateral teeth are thick labiolingually (CBR ca. 0.6). The preserved crowns of this taxon are strongly elongated (CHR almost 2.5), and do not display any interdenticular sulci between mesial and distal denticles (Rauhut 2005). There are 14 denticles per 5 mm on the distal carina, at mid-crown, in *Condorraptor*, and 11 to 15 in *Piatnitzkysaurus* (CH personal observations).

Teeth of allosauroids are very similar to those of Megalosauridae. Allosaurid crowns are typically thicker to those of megalosaurids. The first eight maxillary teeth have a crown base ratio above 0.6–0.7 on average, and only the most posterior lateral teeth have a CBR within the same range (0.3–0.6) as megalosaurid crowns (CH personal observations). This is also the case with mesial teeth in which the CBR varies 0.7–1.2. The mesial carinae of the mesial teeth of *Allosaurus* reach or extend close to the cervix, and always twist lingually, giving a D-shaped cross-section (sensu Hendrickx and Mateus 2014a) at the base of the crown. This is also the case for teeth situated in the transition of mesial and lateral teeth (first, second maxillary teeth) in which the mesial carina also twists towards the lingual side of the crown. A concave surface adjacent to the mesial carina can also be observed on the lingual side of mesial teeth, and the distal margin is convex. A similar condition is present in metriacanthosaurid mesial teeth such as *Sinraptor*, in which the mesial carina curves lingually (Currie and Zhao 1993) and the distal margin is convex. Allosaurid lateral teeth have a strongly displaced distal carina labially. The lateral dentition of metriacanthosaurids is weakly recurved distally and the distal profile of lateral crowns is either slightly concave or straight (CH personal observations). Furthermore, the lateral teeth of Metriacanthosauridae also have a mesiodistally-expanded concave or flattened surface centrally positioned on the labial margin of the crowns. Although not clearly observable in the lateral teeth of *Sinraptor dongi*, it seems that the mesial carina of lateral teeth extends to, or near to, the cervix. This feature is visible in *Sinraptor hepingensis* isolated teeth (ZDM 0024). Teeth of neovenatorids can be differentiated from those of megalosaurids by their relatively narrow lateral crowns typically displaying two concave surfaces adjacent to both mesial and distal carinae and separated by a mesiodistally narrow planar surface. The mesial carina extends to the cervix in the lateral teeth of some neovenatorids (e.g., *Fukuiraptor*) and, in mesial teeth, the mesial carina is placed lingually whereas the distal carina is deflected labially.

The mesial teeth of carcharodontosaurids are similar to those of megalosaurids. The mesial carina faces mesially or mesiolabially and, in some cases, can terminate well above the cervix as in the premaxillary teeth of *Acrocanthosaurus* (NCSM 14345). Importantly, the distal carina is strongly displaced labially in mesial teeth of Carcharodontosauridae, which is not the case in Megalosauridae. Lateral teeth of *Acrocanthosaurus* are large (average of 70 mm for the whole dentition), but the denticles are relatively small, with an average of 14 per 5 mm on the distal carina at mid-height (Smith et al. 2005), giving a large number of denticles (>200) along the crown of the longest teeth. *Acrocanthosaurus* teeth also display crown ornamentations such as marginal and transverse undulations as well as pronounced braided texture of the enamel. The lateral dentition of Carcharodontosaurinae possesses a mesial carina reaching the cervix or extending just above it, and typically displays pronounced arcuate marginal undulations on one side of the crown, on both lingual and labial surfaces. The distal profile of the lateral crown is usually straight or weakly concave in lateral view. Often the

distal profile of the lateral crowns of Carcharodontosaurinae display a diagnostic sigmoid outline, with the concavity covering the basal two-thirds and a convexity on the resting apical third of the crown. A similar distal profile is also present in at least one isolated tooth of the non-carcharodontosaurine, *Eocarcharia* (MNN GAD14).

**Morphometric comparison**.—Smith et al. (2005) were the first to perform a multivariate analysis on teeth belonging to theropods from basal to derived taxa. Their analysis included 325 teeth from 20 taxa, but non-neotheropod Theropoda, Megalosauridae, Neovenatoridae, and non-tyrannosauroid Tyrannosauroidea were not represented. We use 995 teeth pertaining to 62 theropod taxa and 19 major groups of theropods. Our dataset includes three times more teeth and taxa, and the morphometric analysis shows the morphospace occupation of teeth belonging to all major theropod clades for the first time. The results of the discriminant analysis at the generic and familial levels (Fig. 5) are relatively similar to those obtained by Smith et al. (2005: fig. 14) as the morphospace occupation of each taxon is driven by the size of the teeth (CH, CBL, CBW) and the number of denticles on the carinae (MC, DC), so that Troodontidae, Noasauridae, Spinosauridae, and Tyrannosauridae are distributed in different zones of morphospace.

In our analysis, theropod teeth occupy four morphospace areas (Fig. 5; see SOM 7), one including taxa with small teeth and large denticles (Troodontidae), a second for taxa bearing relatively small teeth and small denticles (non-neotheropod Theropoda, Coelophysoidea, Noasauridae, and Dromaeosauridae), a third with taxa possessing large teeth and minute denticles (Spinosauridae), and a fourth with ziphodont taxa having relatively large teeth and large denticles (non-noasaurid Ceratosauria, Megalosauridae, Allosauroidea, and Tyrannosauridae). Overlap exists between each of these areas, and clades bearing small teeth/denticles and large teeth/denticles show considerable overlap. This explains why only 66.5% and 71% of specimens were correctly classified to their genera and "clades", respectively. Such results contrast with the 97% of correctly classified specimens obtained by Smith et al. (2005), a percentage that can be explained by the small sample size, and the restricted number of taxa with similar dentition in their dataset. In this morphometric analysis, Troodontidae, non-theropod Theropoda, and Spinosauridae are the best classified theropods (>85% correctly classified; Table 1). The analysis had most difficulty classifying non-abelisaurid Ceratosauria (15%) and Megalosauridae (21%; Table 1) and, among the latter, 12% of megalosaurid teeth were classified as *Piatnitzkysaurus*, Allosauridae, Carcharodontosauridae, and basal Tyrannosauroidea, 9% as Ceratosauridae, and 6% as Abelisauridae, Neovenatoridae, and the enigmatic tetanuran *Erectopus*. In the same discriminant analysis performed at a generic level, megalosaurid taxa also show a low score, with 50% being successfully identified as those of *Torvosaurus*, 40% as *Duriavenator*, 30% as *Dubreuillosaurus*, and only 15% as *Megalosaurus* (see SOM 3).

The morphometric analyses performed on the reduced dataset, which includes large ziphodont teeth, reveals that megalosaurid teeth occupy the same morphospace as those of other ziphodont theropods (Fig. 6; see SOM 10). Megalosauridae, Ceratosauridae, Abelisauridae, Allosauridae, and Neovenatoridae still show considerable overlap (Fig. 6), and significant overlap with Tyrannosauridae and Carcharodontosauridae, so that separating teeth of megalosaurids from the teeth of other similarly sized theropods is particularly difficult. Indeed, while 68% of all specimens were correctly classified to their clades, only 42% of megalosaurid specimens were successfully assigned to Megalosauridae (see SOM 2: Table 1; SOM 4), and 40% to their respective a priori genera (60% to *Duriavenator*, 50% to *Torvosaurus* and *Dubreuillosaurus*, and 15% to *Megalosaurus*). In the discriminant analysis performed at the generic level, taxa with the best data (*Tyrannosaurus*, *Allosaurus*, *Acrocanthosaurus*, *Ceratosaurus*, *Megalosaurus*) show the largest morphospace occupation. This is because quantitative data were collected in teeth from across the jaws, where there is important morphometric variation between mesial and lateral dentition. Indeed, morphometric analysis performed on taxa whose mesial and lateral dentition could be considered separately clearly shows that mesial and lateral teeth from individual taxa occupy different portions of morphospace (Fig. 7). This is particularly the case

Table 1. Table of misclassification for the whole dataset grouped by clades (ratios excluded).

| Clades | Number of teeth correctly assigned | Total | % correctly identified |
|---|---|---|---|
| Basal Theropoda | 25 | 29 | 86.2 |
| Coelophysoidea | 20 | 31 | 64.5 |
| Ceratosauridae | 4 | 26 | 15.4 |
| Noasauridae | 5 | 24 | 20.8 |
| Abelisauridae | 39 | 55 | 70.9 |
| *Erectopus* | 3 | 3 | 100 |
| *Piatnitzkysaurus* | 2 | 2 | 100 |
| Megalosauridae | 7 | 33 | 21.2 |
| Spinosauridae | 43 | 49 | 87.8 |
| Allosauridae | 18 | 31 | 58.1 |
| Neovenatoridae | 8 | 11 | 72.7 |
| Carcharodontosauridae | 47 | 64 | 73.4 |
| Basal Tyrannosauroidea | 23 | 39 | 59 |
| Tyrannosauridae | 129 | 164 | 78.7 |
| *Nuthetes* | 8 | 9 | 88.9 |
| Dromaeosauridae | 205 | 297 | 69 |
| Troodontidae | 77 | 82 | 93.9 |
| *Richardoestesia* | 42 | 45 | 93.3 |
| Total | 705 | 994 | 70.9 |

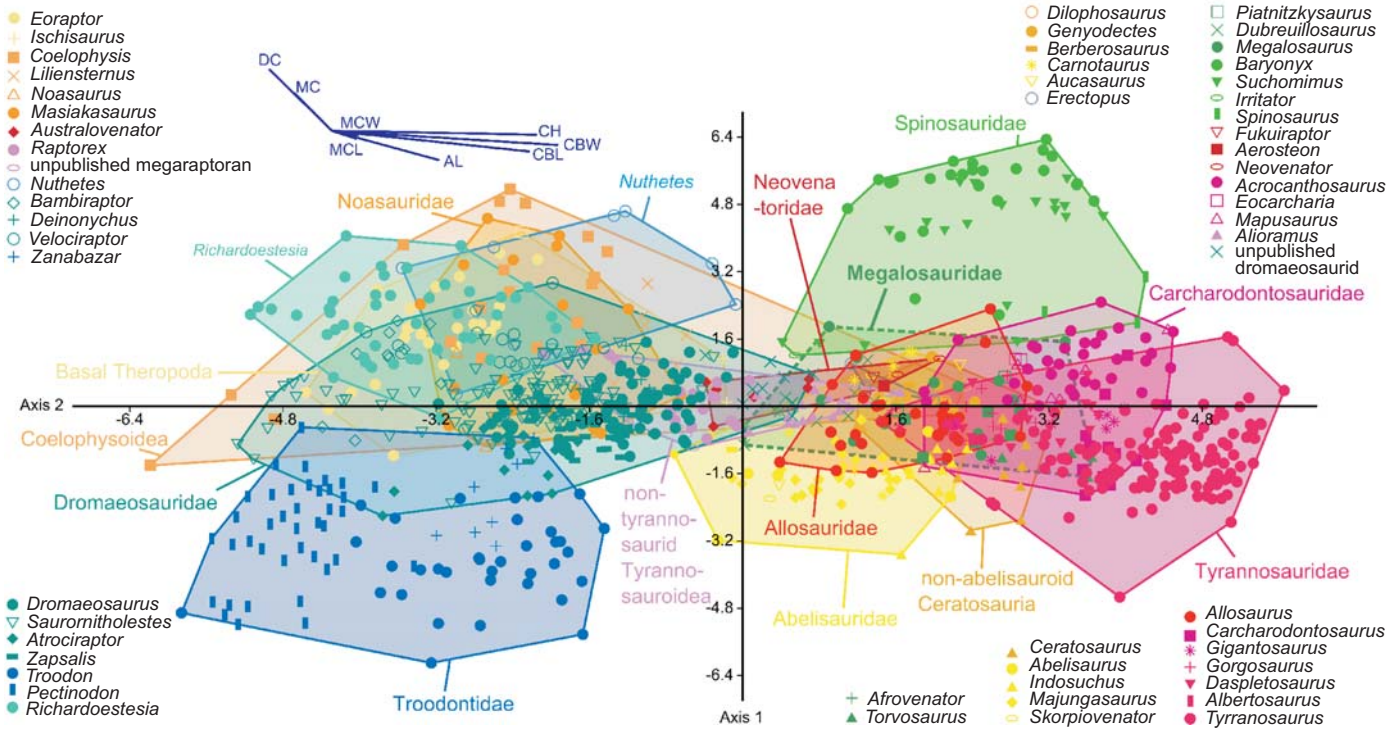


Fig. 5. Graphical results of the discriminant analysis of 995 teeth belonging to 62 theropod taxa and 19 groupings along the first two canonical axes of maximum discrimination in the dataset (Eigenvalue of Axis 1 = 7.561, which accounted for 61.52% of the variation; Eigenvalue of Axis 2 = 2.62, which accounted for 21.38% of the variation). Log-transformed CBL (crown base), CBW (crown base width), CH (crown height), AL (apical length), MCL (mid-crown length), MCW (mid-crown width), MC (mesiocentral denticle density), and DC (distocentral denticle density) were used in the analysis, and 70.97% of the specimens of nonavian theropods were correctly classified to their respective clades (see SOM 3). Morphospace occupation of megalosaurid teeth is delimited by a dashed line.

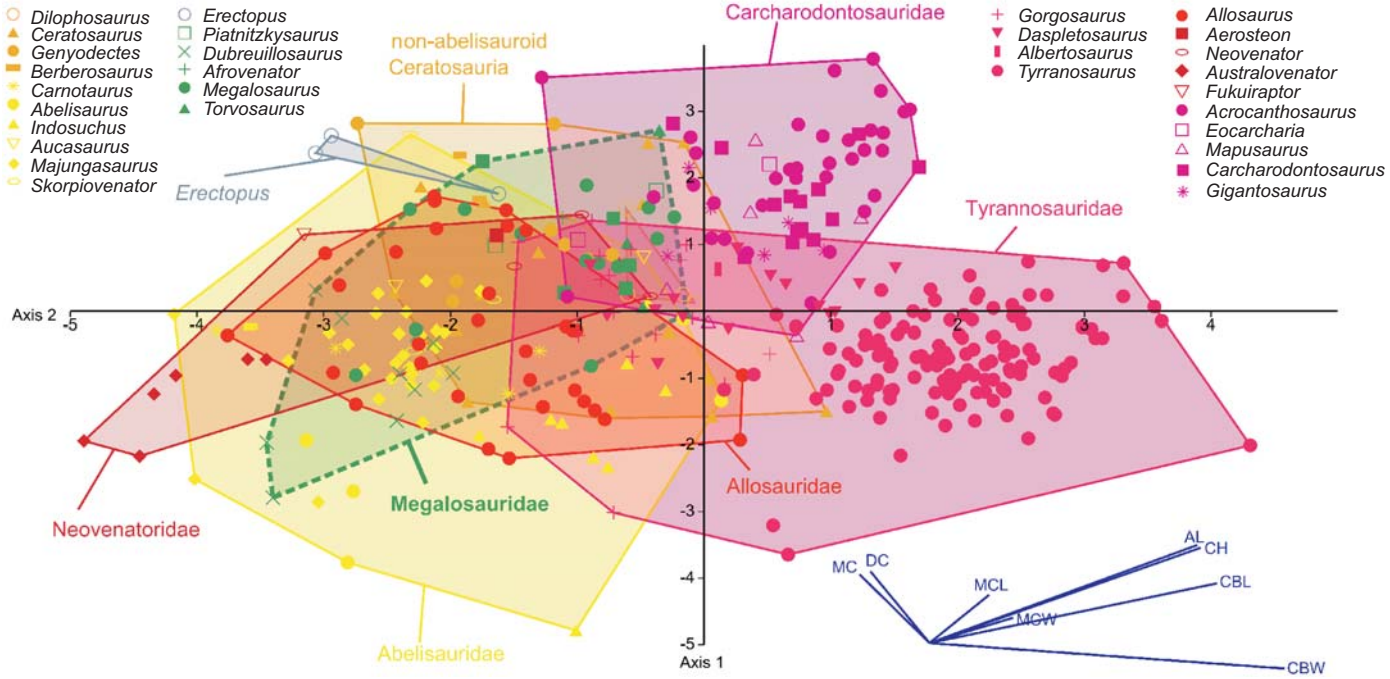


Fig. 6. Graphical results of the discriminant analysis of 393 teeth belonging to 33 taxa and 11 groupings of large ziphodont theropods along the first two canonical axes of maximum discrimination in the dataset (Eigenvalue of Axis 1 = 2.52, which accounted for 65.75% of the variation; Eigenvalue of Axis 2 = 0.89, which accounted for 23.24% of the variation). Log-transformed CBL (crown base), CBW (crown base width), CH (crown height), AL (apical length), MCL (mid-crown length), MCW (mid-crown width), MC (mesiocentral denticle density), and DC (distocentral denticle density) were used in the analysis, and 68.19% of the specimens were correctly classified to their respective clades (see SOM 4). Morphospace occupation of megalosaurid teeth is delimited by a dashed line.

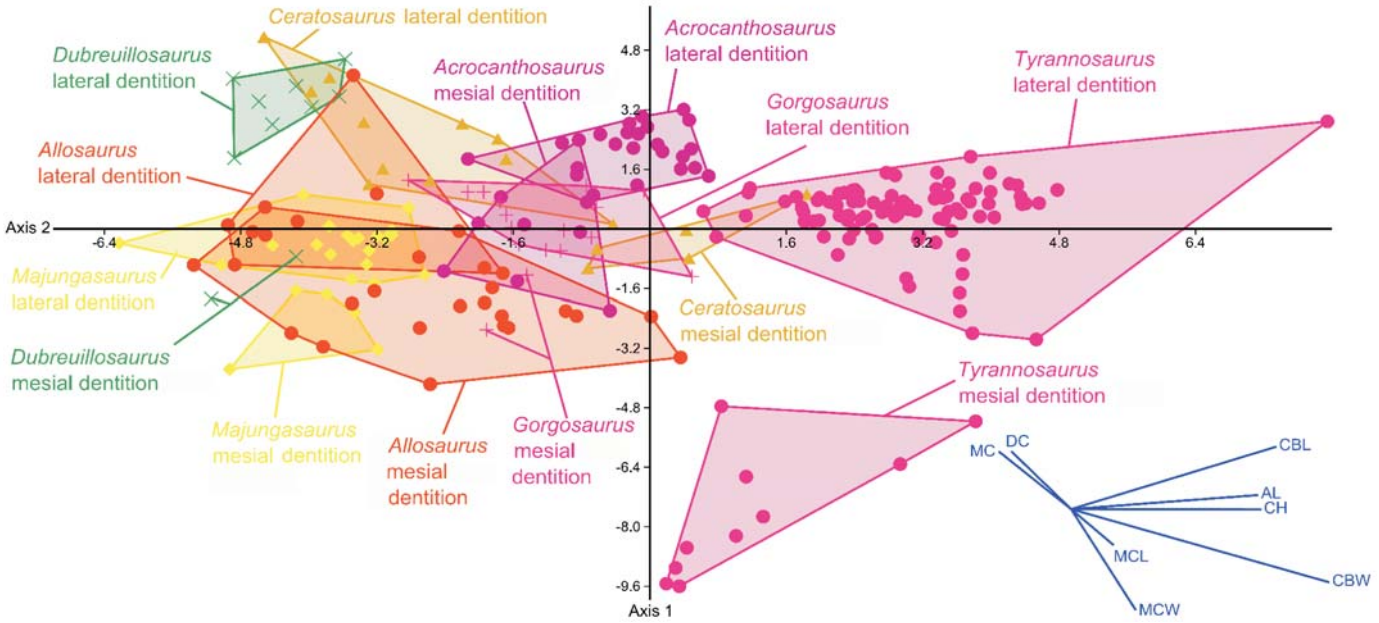


Fig. 7. Graphical results of the discriminant analysis of 232 teeth belonging to 7 taxa whose dentition was separated into mesial and lateral teeth, along the first two canonical axes of maximum discrimination in the dataset (Eigenvalue of Axis 1 = 7.99, which accounted for 50.73% of the variation; Eigenvalue of Axis 2 = 4.52, which accounted for 28.73% of the variation). Log-transformed CBL (crown base), CBW (crown base width), CH (crown height), AL (apical length), MCL (mid-crown length), MCW (mid-crown width), MC (mesiocentral denticle density), and DC (distocentral denticle density) were used in the analysis, and 84.48% of the specimens were correctly classified to their respective taxa and dentition type (see SOM 5).

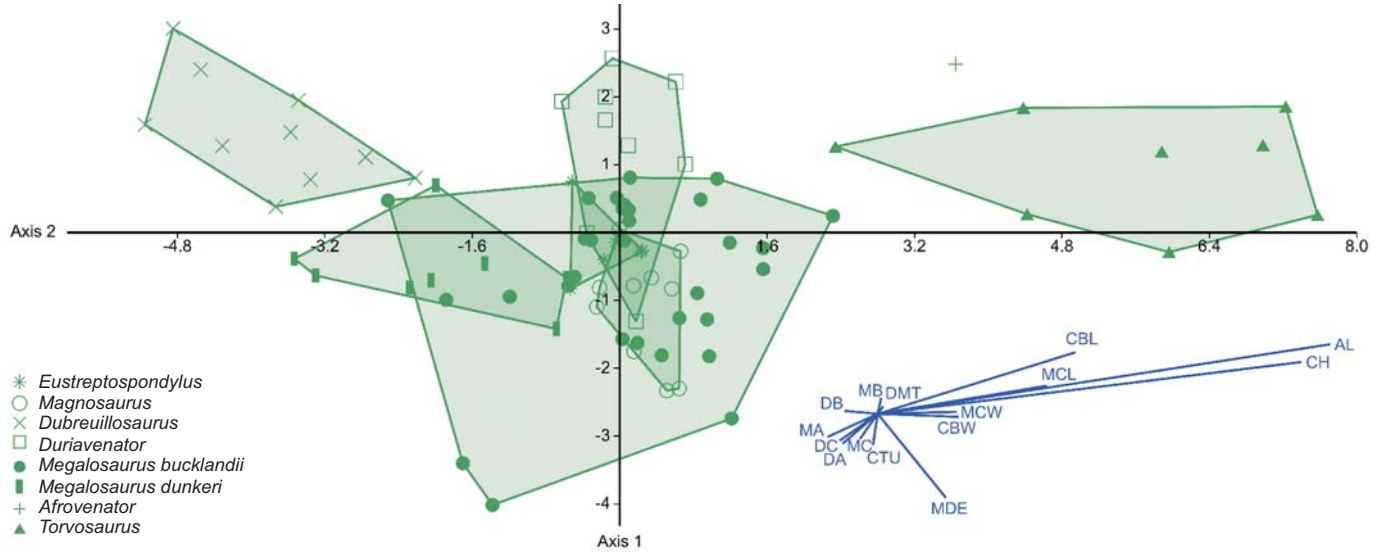


Fig. 8. Graphical results of the discriminant analysis of 81 teeth belonging to 7 taxa of Megalosauridae, and one indeterminate tetanuran ("*Megalosaurus dunkeri*"), along the first two canonical axes of maximum discrimination in the dataset (Eigenvalue of Axis 1 = 5.8, which accounted for 71% of the variation; Eigenvalue of Axis 2 = 1, which accounted for 12.36% of the variation). Raw data of CBL (crown base), CBW (crown base width), CH (crown height), AL (apical length), MCL (mid-crown length), MCW (mid-crown width), MDE (mesiobasal denticles extent), CTU (crown transverse undulation density), DMT (dentine thickness mesially), DDT (dentine thickness distally), DLAT (dentine thickness labially), DLIT (dentine thickness lingually), MA (mesioapical denticle density), MB (mesio-basal denticle density), MC,(mesiocentral denticle density), DA (distoapical denticle density), DB (distobasal denticle density), DC (distocentral denticle density) were used in the analysis, and 65.48% of the specimens were correctly classified to their a priori genera (see SOM 6).

in Megalosauridae (*Dubreuillosaurus*) and Tyrannosauridae (*Tyrannosaurus*) in which mesial and lateral teeth strongly differ in their thickness and elongation. Interestingly, overlap exists only in the two included allosauroids, *Allosaurus*, and *Acrocanthosaurus*, confirming that the distinction between mesial and lateral teeth is not that clear in this clade.

In the morphometric analysis of megalosaurid teeth only, 65.48% of specimens were correctly assigned to their genera (SOM 2: Table 3). In this analysis, the teeth of *Dubreuillosaurus*, *Torvosaurus* and *Afrovenator* occupy different areas of morphospace and do not overlap with other taxa. However, *Megalosaurus bucklandi* shows lim-

ited overlap with the teeth of "*Megalosaurus dunkeri*" and the closely related taxon *Duriavenator*, and 100% overlap with those of *Magnosaurus* and *Eustreptospondylus* (Fig. 8; see SOM 12). This can be explained by the very similar dentition of *Duriavenator* and *Megalosaurus* (CH personal observations), and the limited data and sample size for *Eustreptospondylus* and *Magnosaurus*, which did not preserve a single complete erupted tooth. As for "*Megalosaurus dunkeri*" from the Lower Cretaceous of England, the teeth might pertain to one or several non-megalosaurid taxa from the Lower Cretaceous, such as *Neovenator*. The identification of isolated teeth referred to "*Megalosaurus dunkeri*" will however be discussed elsewhere.

The results of the discriminant analysis show that teeth of most clades of large ziphodont theropods, including Megalosauridae, are hardly distinguishable in terms of crown dimensions and number of denticles. Discriminant analysis should be used cautiously to identify large ziphodont teeth. Quantitative identification is only robust for the teeth of a few theropod clades such as Troodontidae, Spinosauridae, and Tyrannosauridae, which have typical morphometric features. Megalosauridae, along with Abelisauridae, Ceratosauridae, Allosauridae, and Neovenatoridae, possess teeth and denticles of similar dimensions, and only morphological qualitative characters, such as those proposed in the previous section, can really help differentiate them. In order to improve a quantitative analysis for differentiating the large ziphodont teeth, geometric morphometrics may be promising. For example, sections of the teeth may be digitized using quasi-homologous landmarks and superimposed using Procrustes analysis or a similar technique.

Although the large sample size of theropod teeth in this study provides opportunities for investigations of cladistic and taxonomic variability in nonavian theropods, the large number of taxa and teeth represented blurs the results of discriminant analysis. Nevertheless, the latter can be strengthened by improving the sample size for each taxon but also by including additional morphometric variables, such as the elongation of mesial and distal denticles, the number of transverse undulations on the tooth, the extent of the mesial carina, the thickness of the dentine layer, and the curvature of the crown. Likewise, mesial and lateral dentitions, which have proven to be quantitatively distinct in theropods, should be considered separately for each taxon.

This study finally demonstrates that ratio variables have only weak influence on the results in most analyses. Discriminant analyses with and without ratio variables show nearly the same graphical results (see SOM 7, 8, 10–12), and significant variations could only be noted in the analysis of megalosaurid teeth (see SOM 12), and of theropod teeth separated into mesial and lateral dentitions (SOM 11). Likewise, the percentage of teeth correctly identified is rather similar in most analyses performed with and without ratio variables (see SOM 3–6). Nevertheless, important differences were noted in the discriminant analysis of the reduced dataset including large ziphodont theropod teeth at the generic level. In this analysis, 69.47% of specimens were correctly classified when excluding the ratios, whereas 34.61% were successfully identified when taking into account ratio variables. Given these results, it is recommended to avoid the use of ratio variables in discriminant analysis as they overemphasize some variables and do not help identify teeth.

# Conclusions

The dentition of Megalosauridae, often considered to be similar to the dentition of other ziphodont theropods, can be distinguished by qualitative characters rather than quantitative data. Anatomically, megalosaurid teeth are characterized by a combination of features only visible in this clade, namely: mesial teeth with a mesial carina facing mesiolabially, centrally-positioned carinae on both mesial and lateral crowns, a mesial carina terminating above the cervix, subquadrangular to subrectangular distal denticles with short to well-developed interdenticular sulci between them, symmetrically to asymmetrically convex external margin of the denticles, and braided and oriented texture of the enamel. It is therefore clear that spinosaurid, abelisaurid, troodontid, dromaeosaurid, or tyrannosaurid teeth are not the only theropods with diagnostic features, and a detailed study of the dentition of other important theropods such as *Dilophosaurus*, *Ceratosaurus*, *Allosaurus*, *Monolophosaurus*, *Sinraptor*, *Yangchuanosaurus*, *Dilong*, and *Guanlong*, with additional quantitative data collected for each of them, is critically required in order to help clarify the numerous variations existing between theropod clades (e.g., Ceratosauridae, Allosauridae, Metricanthosauridae, Neovenatoridae, and Proceratosauridae) with superficially similar dentitions.

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