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ARTICLE

A PROPOSED TERMINOLOGY OF THEROPOD TEETH (DINOSAURIA, SAURISCHIA)

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ABSTRACT—Theropod teeth are typically not described in detail, yet these abundant vertebrate fossils are not only frequently reported in the literature, but also preserve extensive anatomical information. Often in descriptions, important characters of the crown and ornamentations are omitted, and in many instances, authors do not include a description of theropod dentition at all. The paucity of information makes identification of isolated teeth difficult and taxonomic assignments uncertain. Therefore, we here propose a standardization of the anatomical and morphometric terms for tooth anatomical subunits, as well as a methodology to describe isolated teeth comprehensively. As a corollary, this study exposes the importance of detailed anatomical descriptions with the utilitarian purpose of clarifying taxonomy and identifying isolated theropod teeth.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/ujvp

INTRODUCTION

Theropod shed teeth are abundant in the terrestrial fossil record and are frequently described (e.g., Currie et al., 1990; Rauhut and Werner, 1995; Baszio, 1997; Zinke, 1998; Ősi et al., 2010; Han et al., 2011; Larson and Currie, 2013; Sues and Averianov, 2013), yet their morphology is surprisingly poorly known. Dentition has been thoroughly described for some theropod taxa, e.g., *Coelophysis, Majungasaurus, Tyrannosaurus, Troodon*, and *Buitreraptor*, and some Upper Cretaceous theropods of Northern America (e.g., Currie, 1987; Currie et al., 1990; Fiorillo and Currie, 1994; Baszio, 1997; Fiorillo and Gangloff, 2001; Sankey et al., 2002; Smith, 2005, 2007; Fanti and Therrien, 2007; Brinkman, 2008; Longrich, 2008; Sankey, 2008; Buckley, 2009; Larson et al., 2010; Gianechini et al., 2011b; Larson and Currie, 2013; Gates et al., 2015). Yet, several pivotal theropod taxa with well-preserved dentitions still lack a thorough dental description (e.g., *Allosaurus, Ceratosaurus, Sinraptor*, and *Yangchuanosaurus*), leading numerous authors to identify isolated theropod teeth to broad clades with uncertainty (e.g., Ősi et al., 2010; Amiot et al., 2011; Carrano et al., 2012; Ruiz-Omeñaca et al., 2012; Madzia, 2014). Nevertheless, due to the elevated apatite concentration, teeth are the hardest known skeletal structures (Martin, 1999). Thus, isolated teeth are key pieces of evidence to assess vertebrate paleoecological diversity and are often used for stable isotopic studies with various applications (e.g., Amiot et al., 2004, 2006, 2010b, 2011). A better understanding of theropod anatomy and morphological variation is therefore central to help resolving systematic relationships and to provide paleoecological clues. Tooth morphology is tied to diet, which has extensive evolutionary repercussions, such as morphological convergence, more than other parts of the skeleton. Yet, theropod teeth have been shown to possess many diagnostic features of taxonomic value (e.g., Currie et al., 1990; Smith, 2005, 2007; Smith et al., 2005; Hendrickx and Mateus, 2014a). Although theropod teeth seem simple at first sight, this is effectively a result of the absence of comprehensive studies on tooth anatomy and morphological variation among theropods, as well as the lack of a uniform anatomical nomenclature.

This contribution proposes a standardized list of anatomical, morphological, and morphometric terms and abbreviations for each tooth anatomical subunit and each measurement previously taken on theropod teeth. Additionally, we propose a methodology to describe isolated teeth thoroughly.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **DMNH**, Dallas Museum of Natural History, Dallas, Texas, U.S.A.; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **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; **MSNM**, Museo di Storia Naturale di Milano, Milan, Italy; **NCSM**, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A.; **NHMUK**, Natural History Museum, London, U.K.; **OUMNH**, Oxford University Museum, Oxford, U.K.; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **ROM**, Museum of the Rockies, Bozeman, Montana, U.S.A.; **SGM**, Ministère de l'Énergie et des Mines, Rabat, Morocco; **SMU**, Southern Methodist, University, Dallas, Texas, U.S.A.; **UA**, Université d'Antananarivo, Antananarivo, Madagascar; **UCRC**, University of Chicago Research Collection, Chicago, Illinois, U.S.A.; **UMNH**, Natural History Museum of Utah, University of Utah, Salt Lake City, Utah, U.S.A.

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POSITIONAL NOMENCLATURE

Although the taxonomic and systematic value of theropod dentitions is lower than that of mammalian dentitions, theropod teeth are usually identifiable to the family level, with some isolated teeth identifiable to the species level (e.g., Currie et al., 1990; Smith et al., 2005; Fanti and Therrien, 2007; Larson and Currie, 2013; Hendrickx and Mateus, 2014a). The crown, carinae, denticles, and enamel structures exhibit taxonomically informative morphological variability among theropods (Currie et al., 1990; Smith et al., 2005; Larson and Currie, 2013; Hendrickx and Mateus, 2014a). Unfortunately, the directional, orientation, and anatomical terminology used has been inconsistent. We hereby propose standardizing this terminology. Each term is illustrated (Figs. 1–6) and followed by a definition, and each anatomical and morphometric term is associated with a two- to four-letter abbreviation to be used in illustrations (Figs. 1–4, 7).

Positional nomenclature largely follows the dental orientation proposed by Smith and Dodson (2003). This positional nomenclature works by identifying the side of the jaw (i.e., left = L; right = R), followed by the abbreviation of the tooth-bearing bone (i.e., premaxilla = pm; maxilla = mx; dentary = dt) and then the position occupied along the tooth-bearing bone. The first tooth is the mesial-most one. As an example, Lpm2 refers to the second left premaxillary tooth, and Rdt7, seventh right dentary tooth.

Tooth Orientation

Apical—The direction from the cervix to the apex (Fig. 1C, E). This term is bidirectional and can refer to the direction towards the crown apex for the crown or towards the root apex for the root (Smith and Dodson, 2003).

Basal—The direction from the apex to the cervix (Fig. 1C, E). The term is also bidirectional and refers to the direction towards the cervix for both the crown and root (Smith and Dodson, 2003).

Mesial—The direction towards the jaw symphysis (Smith and Dodson, 2003; Fig. 1C). Mesial can refer also to the surface facing the jaw symphysis.

Distal—This term is used slightly differently for teeth versus denticles. For teeth, distal refers to the direction away from the jaw symphysis and towards the posterior end of the jaw (Smith and Dodson, 2003; Fig. 1C). For denticles, distal refers to the direction away from the crown, from the denticle base to the denticle apex (Fig. 1E).

Proximal—From the denticle apex to the base, proximal refers to the direction towards the crown (Smith and Dodson, 2003; Fig. 1E).

Labial—The surface or direction pointing from the skull outwards, thus towards the lips or cheeks (Smith and Dodson, 2003; Buckley, 2009; Fig. 1D).

Lingual—The surface and direction towards the skull midline, thus facing the tongue (Smith and Dodson, 2003; Buckley, 2009; Fig. 1D).

Tooth Situation and Position

Isolated Tooth—Tooth shed or non-articulated with the tooth-bearing bone (Buckley, 2009).

Shed Tooth—Tooth lost in vivo, either falling out due to the eruption of the replacement tooth or when processing food (e.g., biting, impaling, shearing, chewing), and therefore only preserving the crown and the basal-most part of the root (Fiorillo and Currie, 1994).

In Situ Tooth—Tooth within the alveolus of the tooth-bearing bone (Buckley, 2009).

Erupted Tooth—Tooth that grew outside the tooth-bearing bone, thus fully visible in the mouth.

Unerupted Tooth—Tooth within the alveolus and still inside the jaw, and therefore not visible or only partially visible in the mouth.

Mesial Dentition—Premaxillary teeth as well as mesial-most dentary and, in some cases, maxillary teeth that share a morphology similar or closer to that of premaxillary teeth than more distal dentary and maxillary teeth. The mesial dentition corresponds to the ‘mesialmost dentition’ of Hendrickx and Mateus (2014a).

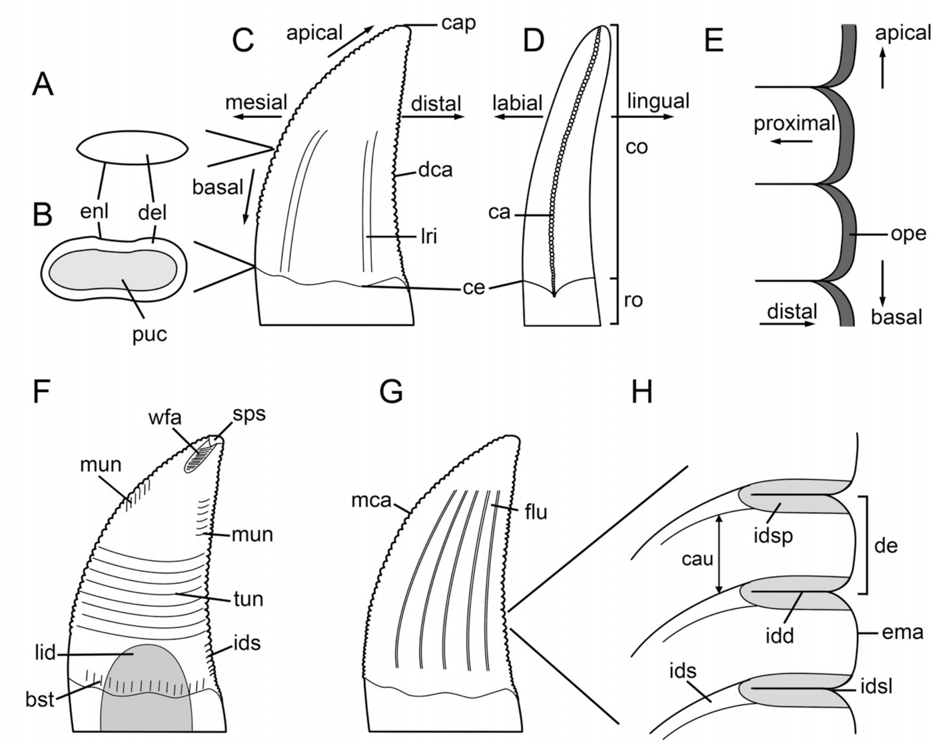

FIGURE 1. Anatomical terminology used in this study. **A**, mid-height cross-section of crown C, in apical view; **B**, basal cross-section of crown C, in basal view; **C**, idealized lateral theropod tooth in labial view; **D**, idealized lateral theropod tooth in distal view; **E**, idealized distal denticles of theropod crown; **F**, idealized lateral theropod tooth in lingual view showing crown ornamentations and attributes; **G**, idealized fluted theropod tooth, in labial view; **H**, idealized distal denticles showing denticle structures, in labial view. **Abbreviations**: **bst**, basal striation; **ca**, carina; **cap**, crown apex; **cau**, cauda; **ce**, cervix; **co**, crown; **dca**, distal carina; **de**, denticle; **del**, dentine layer; **enl**, enamel layer; **ema**, external margin; **flu**, flute; **idd**, interdenticular diaphysis; **ids**, interdenticular sulcus; **idsl**, interdenticular slit; **idsp**, interdenticular space; **lid**, lingual depression; **mun**, marginal undulation; **mca**, mesial carina; **ope**, operculum; **puc**, pulp cavity; **ro**, root; **sps**, spalled surface; **tun**, transverse undulation; **wfa**, wear facet.

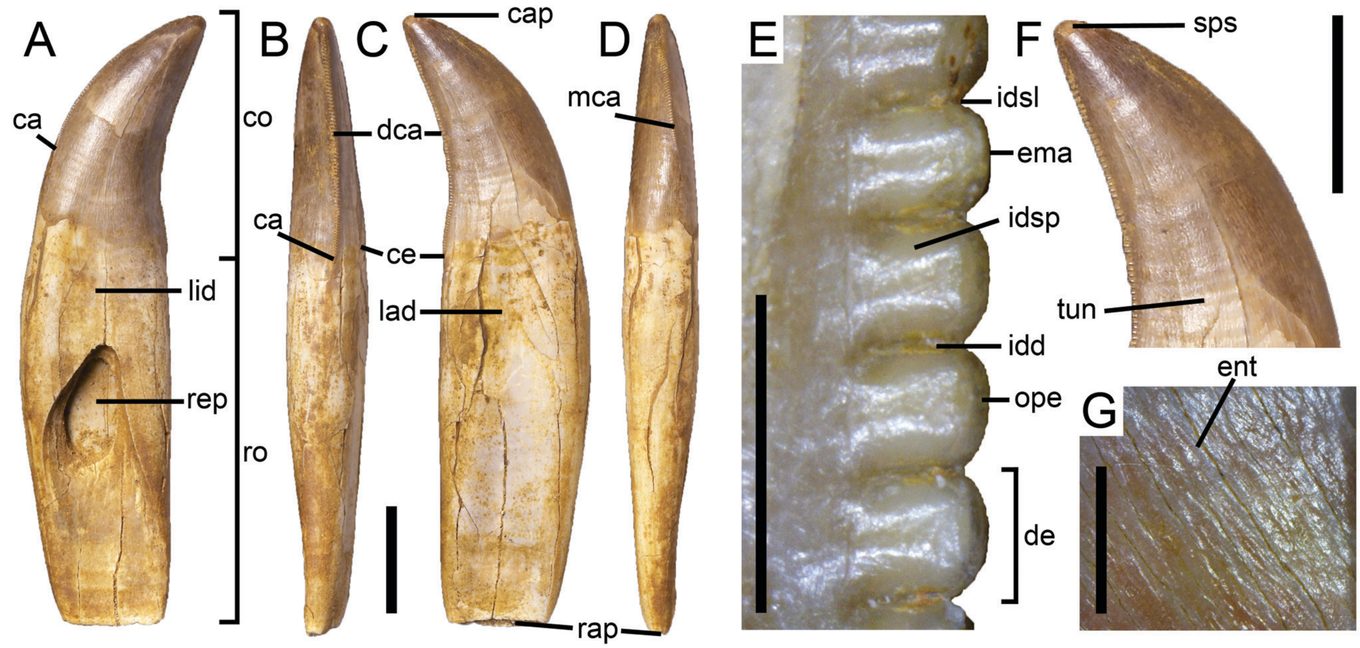

FIGURE 2. Crown, root, and denticle anatomy of an isolated tooth of *Alioramus altai*, IGM 100–1844. **A–D**, Tooth in **A**, lingual; **B**, distal; **C**, labial; **D**, mesial views, and close up of **E**, distocentral denticles; **F**, crown, and **G**, enamel surface, in labial views (courtesy of Mike Ellison © AMNH). **Abbreviations**: **ca**, carina; **cap**, crown apex; **ce**, cervix; **co**, crown; **dca**, distal carina; **de**, denticle; **ema**, external margin; **ent**, enamel texture; **idd**, interdenticular diaphysis; **ids**, interdenticular sulci; **idsl**, interdenticular slit; **idsp**, interdenticular space; **lid**, lingual depression; **mca**, mesial carina; **rep**, resorption pit; **ro**, root; **sps**, spalled surface; **tun**, transverse undulation. Scale bars equal 1 cm (**A–D**, **F**) and 1 mm (**E**, **G**).

Mesial Tooth—Tooth belonging to the mesial dentition.

Lateral Dentition—Maxillary and dentary teeth that share a morphology significantly differing from that of mesial teeth (Hendrickx and Mateus, 2014a). Because the morphology of teeth gradually changes mesio-distally along the dentition, there is no precise boundary but a transitional zone between mesial and lateral dentition. The boundary between these two dentition types is arbitrary. In some theropods such as spinosaurids, premaxillary and lateral maxillary/dentary teeth share a similar morphology so that the distinction between mesial and lateral dentition is not relevant in these taxa.

Lateral Tooth—Tooth belonging to the lateral dentition.

ANATOMICAL NOMENCLATURE

The anatomical terms of the theropod dentition were grouped in three main sections: tooth anatomy, denticle anatomy, and crown and enamel ornamentations. The terms for each tooth subunit were selected by their relevance in the theropod literature, and a reference to the first occurrence of each term was given, except for those referring to other parts of the skeleton or to non-vertebrate organisms (e.g., apex, cervix, carina, denticle), or whose origin is prior to the 19th century. The anatomical terminology follows the nomenclature proposed by Smith and Dodson (2003) and Smith et al. (2005) for general tooth anatomy, Abler (1992), Buscalioni et al. (1997), and Smith (2007) for denticle anatomy, and Schubert and Ungar (2005) and Hendrickx and Mateus (2014a) for crown ornamentations and enamel textures. The large majority of terms have already been used by these authors, and only interdenticular diaphysis and enamel undulation are here proposed for the first time.

Tooth Anatomy

Crown (co)—Portion of the tooth covered with enamel, typically situated above the gum and protruding into the mouth (Schwenk, 2000; McGraw-Hill, 2003; Figs. 1D, 2A). The crown ('couronne' of Fauchard, 1728, and Cuvier, 1805; 'corona dentis' of Illiger, 1811; Owen, 1840) is composed of a layer of hard, shiny enamel, and an inner core of resilient dentine, and is internally excavated by the pulp chamber (Hillson, 2005). In theropods with labiolingually narrow teeth, the crown includes two wide labial and lingual surfaces, and two narrow mesial and distal surfaces, which often have carinae.

Crown Base (cob)—Region of the crown immediately apical and adjacent to the basal limit of the enamel layer.

Root (ro)—Portion of the tooth beneath the gum and embedded in an alveolus or an open alveolar groove ('racine' of Fauchard, 1728, and Cuvier, 1805; 'radix dentis' of Illiger, 1811; Owen, 1840; Hillson, 2005; Figs. 1D, 2A). In dinosaurs, the root is composed of a layer of dentine delimiting the outer limit of the pulp cavity. Peyer (1968) considered the root as the part of the tooth embedded in the jawbone and covered with cementum. Because this definition only applies to mammals, Peyer (1968) suggested using the term root only for mammals and proposed the terms 'basal portion,' or 'base,' for non-mammal vertebrates. Smith et al. (2005) and Smith (2005) followed Peyer's (1968) suggestion for theropods and used the terms 'tooth base' to describe the portion of the tooth beneath the crown. Because this portion is roughly analogous to the mammal root (Smith et al., 2005) and corresponds to the part of the tooth anchored in an alveolus, the term root, which is the most commonly used by authors describing theropod teeth (C. H. pers. observ.), is favored instead of 'tooth base.'

Root Base (rob)—Region of the root immediately apical and adjacent to the basal limit of the enamel layer.

Apex (ap)—Tip of the crown (crown apex; Figs. 1C, 2C) or the root (root apex; Fig. 2C, D) of a tooth (Schwenk, 2000; McGraw-Hill, 2003; Smith and Dodson, 2003). The word apex gives the name 'apical' to the direction towards crown tips and 'root apical' to the direction towards root tips (Smith and Dodson, 2003).

The crown apex can be serrated, smooth, or worn, showing spalled surfaces or wear facets.

Cervix (ce)—Transition between the crown and the root and corresponding to the basal extension of the enamel layer ('colet' of Fauchard, 1728, and Cuvier, 1805; Smith and Dodson, 2003; Hillson, 2005; Nelson and Ash, 2009; Figs. 1C, D, 2B, C). The cervix is short for 'cervix dentis,' also known as the 'tooth neck' (Smith and Dodson, 2003).

Cingulum (ci)—Mesiodistal and labiolingual expansions of the crown base that form a shelf surrounding the crown (Illiger, 1811; Owen, 1840; Sander, 1997; Langer and Ferigolo, 2013). Although a cingulum was noticed in some isolated teeth of *Paronychodon* (Sankey et al., 2002), theropods do not usually possess a cingulum at the base of their crown. The therizinosauroid *Eshanosaurus* seems, however, to be an exception (Barrett, 2009).

Carina (ca)—A sharp, narrow, and well-delimited ridge or keel-shaped structure running apicobasally on the crown and, in some cases, on the root base, and typically corresponding to the cutting edge of the tooth (McGraw-Hill, 2003; Reichel, 2012; Brink and Reisz, 2014; Figs. 1D, 2A, B). The carina (used back to the 19th century, e.g., Eastman, 1899) differs from flutes and longitudinal ridges in being a much smaller and better-delimited ridge with acute corners. It can be serrated or not, straight or twisted. The carina can extend either to the crown apex or below it, and can reach the cervix or terminate above or below it. The carina can also be split, which is usually caused by trauma, aberrant tooth replacement or genetic factors (Erickson, 1995). The carina is denoted the 'keel' by some authors (e.g., Farlow et al., 1991; Abler, 1992; Holtz et al., 1998).

Mesial Carina (mca)—Ridge located on the mesial margin of the crown (Smith and Dodson, 2003; Figs. 1G, 2D). The mesial carina usually faces mesially, but this keel can also face labially, mesiolingually, or completely lingually in mesial teeth.

Distal Carina (dca)—Ridge located on the distal margin of the crown (Smith and Dodson, 2003; Figs. 1C, 2B, C). The distal carina usually faces distally but can also be displaced labiodistally, linguodistally, or completely lingually in mesial teeth. The distal carina usually reaches the cervix and sometimes extends onto the root base.

Split Carina (spc)—Abnormality of the crown consisting of a bifurcation of the carina into two serrated/unserrated segments (Erickson, 1995; Fig. 4P). Split carinae are frequent in tyrannosaurid teeth (Currie et al., 1990; Erickson, 1995) and have also been reported in other theropod taxa such as *Allosaurus* (Erickson, 1995) and a carcharodontosaurid (Sereno and Brusatte, 2008).

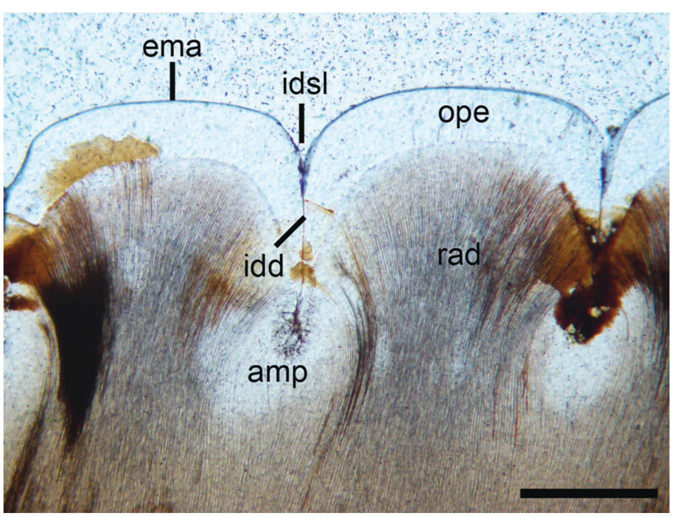

FIGURE 3. Internal anatomy of mesial denticles of an indeterminate tyrannosaurid, ROM 57981, from the Oldman Formation? of Alberta, Canada (courtesy of Kirstin Brink). **Abbreviations**: **amp**, ampulla; **ema**, external margin; **idd**, interdenticular diaphysis; **idsl**, interdenticular slit; **ope**, operculum; **rad**, radix. Scale bar equals 100 μm.

Enamel Layer (enl)—Outer hard mineralized surface covering the crown and mostly composed of hydroxyapatite ('émail' of Fauchard, 1728, and Cuvier, 1805; Owen, 1840; Reid, 1997; Sander, 1997, 1999; Stokosa, 2005; Fig. 1A, B). The enamel layer is acellular and almost entirely inorganic: it includes 96% of inorganic material approximating hydroxyapatite $Ca_{10}(PO_4)_6(OH)_2$. The enamel layer is composed of long crystallites, much longer than those of the dentine, that are packed together to make a dense, very finely crystalline mass, so that enamel is a particularly hard substance (Hillson, 2005). Enamel is formed by cells called ameloblasts that are located in the internal enamel epithelium, at the enamel-dentine junction (EDJ; Sander, 1999; Hillson, 2005).

Dentin Layer (del)—Hard bone-like tissue comprising the bulk of a tooth beneath the enamel layer (Owen, 1840; Currie and Padian, 1997; McGraw-Hill, 2003; Fig. 1A, B). The dentine layer is composed of mineral and organic matter. It is composed of 20% organic material (including 85–95% of collagen), 10% water, and 70% inorganic material formed by crystallites shorter than those of enamel and mostly composed of hydroxyapatite (Avery, 2001). Dentine is a living tissue formed by odontoblasts, long and narrow cells that occupy closely spaced tunnels called dentine tubules and line the sides of the pulp cavity (Hillson, 2005).

Pulp Cavity (puc)—The space within the central part of a tooth containing the dermal pulp and made up of the pulp chamber and a root canal ('pulpe centrale' of Cuvier, 1805; Owen, 1840; McGraw-Hill, 2003; Fig. 1B).

Resorption Pit (rep)—Depression or shallow concavity centrally positioned on the lingual side of the root that receives a replacement tooth (Fig. 2A). The resorption pit (Hopson, 1964) is equivalent to the 'replacement pit' of Norell and Hwang (2004) and the 'unerupted tooth fossa' of Hendrickx and Mateus (2014a).

Denticle Anatomy

Serration (se)—A projection along the carina of a tooth, whether composed of enamel or by both enamel and dentine (Brink and Reisz, 2014). Sander (1997) defined the serrations as the line of denticles along the cutting edge of the crown, yet this definition applies to the carina instead.

Denticle (de)—An elaborate type of serration corresponding to a projection of dentine covered with enamel along the carina ('dentelure' of Cuvier, 1805; Owen, 1840; Currie and Padian, 1997; McGraw-Hill, 2003; Brink and Reisz, 2014; Figs. 1H, 2E, 8). The denticles are termed serrations by many authors (e.g., Farlow et al., 1991; Abler, 1992; Holtz et al., 1998). Yet, a serration is, in some cases (e.g., Holtz, 1998), considered a smaller version of a denticle, the serrations being the small and sharp projections on the carinae of theropod teeth and teeth of other carnivores, whereas the denticles are the larger and coarser projections on the constricted teeth of plant eaters. Brink and Reisz (2014) gave, however, a different definition of serration and denticle, the latter being an elaborate version of a serration characterized by a core of dentine and an enamel cap. Because the carinae of theropod crowns always seem to bear well-delimited serrations showing an external layer of enamel (C. H. pers. observ.), the term denticles is preferred for theropod teeth. The denticles are always located on the carinae, the smallest denticles being typically at the base and top of the carinae. The morphology of denticles varies significantly within the tooth and among theropods (Fig. 8). Yet, it usually corresponds to a rounded bump with a symmetrical or asymmetrical convex margin, in some cases strongly apically recurved. The denticles project either perpendicularly from the crown margin or are apically inclined with a main axis oriented diagonally from the carina.

Mesial Denticle (mde)—A projection of dentine covered with enamel along the mesial carina. The mesial denticles tend to be lower than the distal ones and are typically devoid of interdenticular sulci. The shape of mesial denticles is usually subrectangular, with an apicobasal elongation axis, to subquadrangular.

Distal Denticle (dde)—A projection of dentine covered with enamel along the distal carina (Fig. 2E). The shape of distal denticles is typically subquadrangular to subrectangular, with a proximodistal elongation axis.

External Margin (ema)—Distal-most border of a denticle (Figs. 1H, 2E, 3). The external margin (ema) typically corresponds to the outer edge of the operculum and is equivalent to the 'outer margin/end' of Buscalioni et al. (1997).

Interdenticular Diaphysis (idd)—Junction between two neighboring denticles ('diaphysis' of Abler, 1992 and Buscalioni et al., 1997; Figs. 1H, 2E, 3).

Interdenticular Space (idsp)—Narrow gap between two neighboring denticles, forming a chamber (Abler, 1992; Buscalioni et al., 1997; Figs. 1H, 2E). The interdenticular space (Zhang and Barnes, 2000) is also known as 'cella' (Abler, 1992; Buscalioni et al., 1997; Canudo et al., 2009; Fanti et al., 2014) and 'interdenticle space' (Sankey et al., 2002). It varies in length relative to denticle shape and is particularly large in apically recurved denticles.

Interdenticular Slit (idsl)—Narrow opening on the distal end of the interdenticular space, separating two neighboring denticles (Cillari, 2010; 'interdenticle slit' of Currie et al., 1990; Buscalioni et al., 1997; Sankey et al., 2002; Figs. 1H, 2E, 3). Also known as the 'interdental sulcus' (e.g., Brink et al., 2015).

Interdenticular Sulcus (ids)—Fine groove that continues a short distance onto the labial and lingual surfaces of the crown arising from between two neighboring denticles (Smith, 2007; Benson, 2009; Figs. 1H, 4B). The interdenticular sulci (sensu Smith, 2007), also known as 'blood grooves' (e.g., Currie et al., 1990; Zinke, 1998; Azuma and Currie, 2000; Fanti and Therrien, 2007; Fanti et al., 2014), can be short or well developed, perpendicular to the carina or curving basally.

Cauda (cau)—Raised, paddle-shaped tail delimited by two neighboring interdenticular sulci and running a short distance onto the labial and lingual surfaces of the crown from the base of a denticle (Abler, 1992; Figs. 1H, 4B). Caudae and interdenticular sulci form a complex on the crown surface called the caudae/interdenticular sulci complex by Smith and Lamanna (2006), Smith and Dalla Vecchia (2006), and Smith (2007).

Radix (rad)—Cylindrical core of enamel and dentine beneath the operculum and composing most of the internal structure of the denticle (Abler, 1992; Fig. 3). The radix (sensu Abler, 1992) is made of hexagonal enamel layers invaded by thin radiating structures of the tooth's dentine interior (Abler, 1992).

Operculum (ope)—Dome-shaped outer layer of the denticle composed of enamel (Abler, 1992; Figs. 2E, 3).

Ampulla (amp)—Flask-shaped space at the junction of each pair of opercula, beneath the interdenticular diaphysis (Abler, 1992; Fig. 3). The ampulla, which is roughly equivalent to the 'interdental fold' of Brink et al. (2015), is made of globular, and in some cases, sclerotic dentine (Brink et al., 2015).

Crown Ornamentations and Attributes

Wear Facet (wfa)—Surface, typically elliptical in outline, evinced of parallel striations, occurring on the lingual or labial surfaces of the crown, but not both, and formed by repeated tooth-to-tooth contact (Schubert and Ungar, 2005; Figs. 1F, 4K). Wear facets are uniformly flat surfaces that follow the long axis of the crown and never occur on the mesial and distal surfaces of the crown (Schubert and Ungar, 2005).

Spalled Surface (sps)—Irregular surface of enamel flaking, typically extending to the apex of the tooth (Fig. 1F, 2F, 4A). The spalled surfaces (sensu Schubert and Ungar, 2005) are usually short and squat, and irregularly shaped. They occur on all surfaces of the crown and result from forces produced during contact between crown and food (Schubert and Ungar, 2005).

Flute (flu)—Narrow apicobasally oriented groove separated by two subparallel and acute ridges (Figs. 1G, 4H, I). Flutes (from the term 'fluting' of Owen, 1840) are also referred to as 'striations' (Carrano et al., 2002), 'ribs' (Buffetaut, 2007; Buffetaut et al., 2008), 'longitudinal grooves' (Madsen and Welles, 2000), 'longitudinal ridges' (e.g., Currie et al., 1990; Sankey, 2008; Buckley, 2009) or 'ridges' (e.g., Charig and Milner, 1997; Buffetaut, 2011; Fanti et al., 2014).

Longitudinal Groove (lgr)—Long and shallow, apicobasally oriented channel along the crown delimited by two convexities (Fig. 4J). There is usually only a single longitudinal groove on the crown, typically restricted to the vicinity of the mesial carina. These grooves should not be confused with narrow flutes bounded by acute ridges and the wide labial/lingual depression centrally positioned on the crown (e.g., Fig. 4O).

Longitudinal Ridge (lri)—Apicobasally long and narrow convexity on the crown (Figs. 1A, 4G, L, M). Longitudinal ridges can be labiolingually wide/shallow or acute/prominent and forming a crest. Longitudinal ridges should not be confused with ridges delimiting flutes because they are widely spaced, strongly divergent, and in some cases bifurcated. Longitudinal ridges are usually unique and centrally positioned on the crown (Fig. 4M), double (Fig. 4L), or numerous and widespread (Fig. 4G). They can either follow the main axis of the tooth or extend diagonally on the crown.

Basal Striation (bst)—Short apicobasally oriented furrow restricted to the base of the crown (Gilmore, 1942; Figs. 1F, 4N).

Enamel Undulation (enu)—Mesiodistally oriented corrugated structure on the external surface of the tooth and typically on the labial and lingual margins, composed of parallel ridges and grooves of varying strength and length (Brusatte et al., 2007). Enamel undulation encompasses transverse and marginal undulations. The term 'enamel wrinkle' (Hellman, 1928) is commonly employed to describe transverse and marginal undulations (e.g., Brusatte and Sereno, 2007). However, we favor the use of 'undulations' rather than 'wrinkle' for these two types of enamel structures because the term 'wrinkle' can also refer to the millimeter scale wrinkling of the enamel texture (e.g., Buffetaut et al., 2008; Buffetaut, 2011; Mateus et al., 2011), so the term 'undulation' is less confusing and also better illustrates these enamel ornamentations.

Transverse Undulation (tun)—Band-like enamel wrinkle extending along most of the crown width, typically from one carina to the other (Figs. 1F, 2F, 4E, F). Transverse undulations (Cope, 1877), also known as 'bands' (Fanti et al., 2014), 'bands of growth' (Ősi et al., 2010), 'transverse wrinkles' (e.g., Benson et al., 2008), 'transverse bands' (e.g., Sereno et al., 1996), and 'transversal undulations' (Araújo et al., 2013; Hendrickx and Mateus, 2014a, 2014b), appear on the crown, and more rarely on the root (e.g., *Baryonyx, Neovenator*). Transverse undulations do not necessarily contact both mesial and distal carinae because they can also be restricted to the medial part of the tooth. Transverse undulations can be clearly visible or subtle, numerous and closely packed, or just a few and widely separated (Brusatte et al., 2007; Hendrickx and Mateus, 2014a). Their mesial and distal extremities can curve apically adjacent to the carinae (Brusatte et al., 2007).

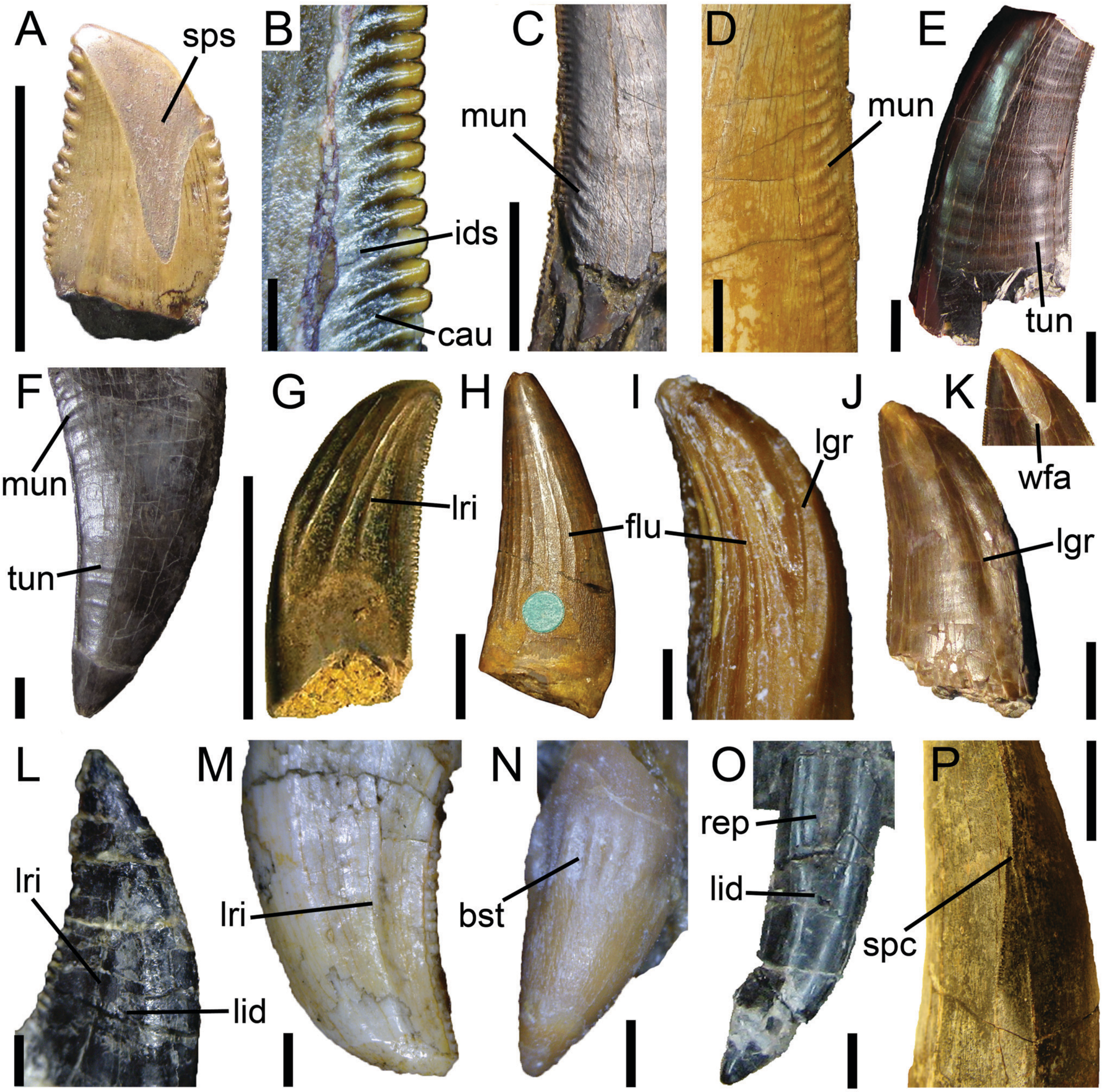

FIGURE 4. Crown ornamentation and attributes in non-avian theropods. **A**, shed crown of *Troodon formosus*, DMNH 22337, in lingual view; **B**, distal denticles of an indeterminate Abelisauridae, ML 327, in lingual view; **C**, distocentral part of an isolated crown of cf. *Megalosaurus bucklandii*, OUMNH J.23014, in labial view; **D**, distocentral part of an isolated crown of *Carcharodontosaurus saharicus*, UCRC PV6, in lingual view; **E**, isolated crown of *Megalosaurus bucklandii*, OUMNH J.29866, in lingual view; **F**, sixth right maxillary tooth of *Acrocanthosaurus atokensis*, NCSM 14345, in labial view; **G**, shed tooth of *Paronychodon* sp., NHMUK R.8405, in lingual view (Cillari, 2010); **H**, shed tooth of an indeterminate baryonychine (formerly *Suchosaurus cultridens* nomen dubium), NHMUK R.36536, in labial? view; **I**, third right dentary tooth of *Masiakasaurus knopfleri*, UA 8680, in linguodistal view; **J**, shed tooth of an indeterminate Abelisauridae, ML 327, in lingual view; **K**, close up of the apicolingual portion of the shed tooth of an indeterminate Abelisauridae, ML 327, in lingual view; **L**, fifth left maxillary crown of *Bambiraptor feinbergi*, AMNH 30556, in labial view; **M**, fourth left maxillary tooth of *Velociraptor mongoliensis*, AMNH 6515, in labial view; **N**, first right premaxillary tooth of *Proceratosaurus bradleyi*, NHMUK R.4860, in labial view; **O**, eighth left maxillary tooth of *Allosaurus fragilis*, UMNH VP 5393, in lingual view (courtesy of Stephen Brusatte); **P**, isolated tooth of *Eocarcharia*, MNN GAD15, in mesial view (courtesy of Juan Canale). **Abbreviations**: **bst**, basal striation; **cau**, cauda; **flu**, flute; **ids**, interdenticular sulci; **lid**, lingual depression; **lgr**, longitudinal groove; **lri**, longitudinal ridge; **mun**, marginal undulation; **rep**, resorption pit; **spc**, split carina; **sps**, spalled surface; **tun**, transverse undulation; **wfa**, wear facet. Scale bars equal 1 cm (**A**, **C**–**H**, **J**–**K**, **O**–**P**) and 1 mm (**B**, **I**, **L**–**N**).

Marginal Undulation (mun)—Mesiodistally elongated wrinkle restricted to the vicinity of the crown and adjacent to the mesial and/or distal carinae (Figs. 1F, 4C, D, F). Marginal undulations (Hendrickx and Mateus, 2014a, 2014b; Hendrickx et al., 2015) are also called 'enamel folds' (Buffetaut et al., 2005; Vullo and Néraudeau, 2010), 'marginal wrinkles' (e.g., Kocsis et al., 2002; Brusatte et al., 2007), 'crenulations' (Coria and Currie, 2006; Molnar et al., 2009), 'arcuate wrinkles' (Sereno et al., 1996), 'arcuate enamel wrinkles' (Canale et al., 2009), 'arcuate marginal enamel wrinkles' (Novas et al., 2005; Brusatte and Sereno, 2007), or 'enamel wrinkles' (Fanti et al., 2014). Marginal undulations can extend perpendicular to the crown margins or be strongly diagonally oriented, forming closely packed diagonal ridges.

Labial/Lingual Depression (lad/lid)—Wide concavity centrally positioned on the labial and/or the lingual side of the tooth, and typically extending along more than one-half of the width of the tooth surface (Figs. 1F, 2A, C, 4O). The labial and lingual depressions (Elzanowski and Wellnhofer, 1993), also referred to as 'furrows' (Novas et al., 2008), 'supradental groove' (Gong et al., 2010, 2011), and 'labial grooves' for the labial depression (e.g., Gianechini et al., 2011a; Gong et al., 2011), are typically weakly delimited, but they can be bounded by two well-marked longitudinal ridges, as in *Buitreraptor* and *Bambiraptor* (Gianechini et al., 2011b; Fig. 4L). On the crown, the apicobasal extension of the depression is variable, but this concavity is, in most cases, restricted to the basal part of the crown. On the root, the apicobasal extension of the lingual, and sometimes labial, depression is much more prominent, the concavity covering more than two-thirds of the root.

Enamel Texture (ent)—Pattern of sculpturing on the crown surface at submillimeter scale (Figs. 2G, 6). In theropods, the enamel texture (Kohn, 1942) can be irregular, braided, veined, or anastomosed (see below).

MORPHOLOGICAL NOMENCLATURE

Tooth and Dentition Type

Four types of tooth morphology in Theropoda are here defined based on the following dental features: the presence or absence of a constriction between crown and root, the labiolingual narrowness of the crown, the presence or absence of denticles, and the lingual curvature of the tooth. Although the first dental type, 'ziphodont,' was coined by Langston (1975) and is commonly used in the scientific literature, the others are new. These dental types define four types of dentition based on the morphology of the most common teeth composing the lateral dentition, and each of them is related to a particular feeding mechanism and diet.

Ziphodont—Strongly labiolingually narrow crown (i.e., crown in which labiolingual width is less than 60% of mesiodistal length) with a distal curvature, typically serrated carinae, and no constriction at the cervix (Fig. 5A). The term ziphodont comes from the Ancient Greek *ξίφοσ* (ksífos, 'sword') and *δοντι* (dónti, 'tooth') meaning 'blade-shaped teeth' and derives from the taxon *Crocodilus ziphodon* erected by Marsh (1871a). The species received this name because the crocodile "was remarkable in having smooth compressed teeth, with serrated edges, resembling the teeth of some of the carnivorous dinosaurs" (Marsh, 1871b:104). Langston (1975) was the first to propose the term ziphodont to gather crocodiles sharing this tooth morphology. This term is now sometimes very restrictive because it refers to serrated crowns only (e.g., D'Amore, 2009; Brink and Reisz, 2014; Brink et al, 2015). Yet, we do not consider the presence of denticles as a compulsory feature for the ziphodont type of crown, and unserrated blade-shaped teeth born by some compsognathids and unenlagiines are here described as ziphodont.

Folidont—Crown with a pronounced constriction (i.e., base of crown occupying 85% or less of largest crown width; Hendrickx and Mateus, 2014a) at the level of the cervix, thus displaying a lanceolate leaf-shaped outline in lateral view (Fig. 5B, C). The term folidont comes from the Latin 'folium' (leaf) and the Ancient Greek '*δοντι*' (dónti, or tooth) meaning 'leaf-shaped tooth.' Folidont crowns can be distally recurved as in Troodontidae, or straight as in Therizinosauria and Alvarezsauroidea (Xu et al., 2001; C. H. pers. observ.). Folidont teeth can also be unserrated, or bear minute to large apically recurved denticles as in Therizinosauria and Troodontidae. In *Carcharodontosaurus* (SGM Din-1), *Proceratosaurus* (Rauhut et al., 2010), *Compsognathus* (Zinke and Rauhut, 1994), *Microraptor* (Xu et al., 2000; Hwang et al., 2002), and *Richardoestesia* (Hendrickx and Mateus, 2014a), some teeth also have a constricted crown at the cervix, but the constriction is not significant enough to provide the crown with an overall lanceolate shape; these theropods therefore possess a ziphodont dentition.

Pachydont—Labiolingually expanded, non-constricted, and distally recurved crown in which labiolingual width is greater than 60% of mesiodistal length, from cervix to apex (modified from Holtz, 2001; Fig. 5D). The term pachydont comes from the Ancient Greek '*παχύσ*' (pakhus, or thick) and '*δόντι*' (dónti, or tooth) meaning 'thick tooth.' Pachydont crowns occur in the mesial dentition of many non-maniraptoriform and dromaeosaurid theropods, yet they characterized the whole dentition of Tyrannosauridae. Pachydont teeth are also present anteriorly in the lateral dentition of *Allosaurus* and *Acrocanthosaurus* (C. H. pers. observ.), and in some notosuchians such as *Notosuchus terrestris* (Lecuona and Pol, 2008).

Conidont—Conical crowns that have minute denticles or no denticles at all, and typically fluted surface (Fig. 5E). The term conidont comes from the Ancient Greek '*κώνοσ*' (konos, or cone, spinning top, pine cone) and '*δοντι*' (dónti, or tooth) meaning 'cone-shaped tooth.' Conidont teeth differ from pachydont teeth in their acutely pointed apices, weakly distally recurved crowns, and minute denticles or unserrated carinae. Conidont crowns forming the whole dentition are present in Spinosauridae, and possibly the dromaeosaurid *Austroraptor* (Novas et al., 2009). Because we do not consider the presence of flutes as a mandatory feature for the conidont condition, conidont crowns are also born by basal ornithomimosaurs and constitute the mesial dentition of therizinosaurs and basal oviraptorosaurs.

Ziphodonty—Lateral dentition mostly composed of ziphodont teeth. De Andrade et al. (2010) define ziphodont dentitions differently, as dentitions where all teeth possess denticulate carinae. However, if the large majority of ziphodont theropods show serrated teeth, some of them, such as *Buitreraptor* and *Compsognathus*, whose teeth do not always bear denticles, are still considered to have a ziphodont dentition. Ziphodonty is common in meat-eating dinosaurs and can be seen in non-neotheropod Theropoda, Coelophysoidea, Dilophosauridae, Ceratosauria, non-spinosaurid Megalosauroidea, Allosauroidea, non-tyrannosaurid Tyrannosauroidea, Compsognathidae, and Dromaeosauridae. A ziphodont dentition is also present in non-theropod amniotes such as sphenacodontids, basal archosaurs, crurotarsians, and living varanids such as the Komodo Dragon (e.g., Langston, 1975; Auffenberg, 1981; Farlow et al., 1991; Senter, 2003; D'Amore, 2009; De Andrade et al., 2010; Young et al., 2010).

Folidonty—Lateral dentition mostly composed of folidont teeth. Folidonty should not be confused with phyllodonty (Ancient Greek '*φύλλο*,' fýllo or leaf, and '*δόντι*,' dónti or tooth), which also means 'leaf-shaped tooth' but refers to tooth plates with multiple superimposed sets of replacement teeth in fishes (Estes, 1969). A folidont dentition occurs in derived theropods such as Therizinosauria, Alvarezsauroidea, Oviraptorosauria, Troodontidae, and Avialae (Zanno and Makovicky, 2011). It is also present in ornithischians, some sauropodomorphs, and iguanas (e.g., Barrett, 2000; Araújo et al., 2011; Becerra et al., 2013).

Pachydonty—Lateral dentition mostly composed of pachydont teeth. In theropods, pachydonty exists in mature Tyrannosauridae such as *Gorgosaurus, Tarbosaurus*, and *Tyrannosaurus*, which possess typical incrassate/banana-like crowns all along the dentition (Holtz, 2003, 2008).

Conidonty—Lateral dentition mostly composed of conidont teeth. Conidont theropods include spinosaurids, basal ornithomimosaurs, and perhaps some dromaeosaurids. The conidont dentition of Spinosauridae includes large fluted teeth with minute or no denticles, whereas the conidont dentition of basal ornithomimosaurs shows reduced and unserrated crowns. Among non-theropod tetrapods, conidonty also exists in many crocodilians, pliosaurs, plesiosaurs, and mosasaurs (Owen, 1840–1845; Massare, 1987; Prasad and de Lapparent de Broin, 2002; Longrich, 2008).

Pseudoheterodonty—Dentition in which the crown morphology gradually changes along the jaw so that mesial and lateral teeth differ significantly in their morphology. A pseudoheterodont dentition differs from the heterodont dentition by the absence of a clear distinction of the crown morphologies along the jaw (e.g., incisors, canines, molars), and the teeth of a pseudoheterodont dentition can only be identified as belonging to the mesial or the lateral part of the jaw. Toothed theropods other than some derived tyrannosaurids (see Smith, 2005) are pseudoheterodont because the crown morphology gradually changes from a mesial to a lateral dentition. Pseudoheterodonty can also occur within the lateral dentition as in *Byronosaurus* and *Xixiasaurus*, which bear folidont teeth that gradually change into ziphodont teeth distally.

Cross-section Type

The cross-section outline of a crown is an important feature providing information on the crown position along the tooth row as well as important systematic data. There is a diversity of possible shapes of the crown cross-section (Fig. 5F–T) and it can be used not only to assign the tooth to the mesial or lateral dentition, but also to a certain theropod clade. This is particularly the case for mesial teeth, in which the large variety of cross-section types can be used as a diagnostic feature in theropods (C. H. pers. observ.). Because the cross-section outline varies along the crown height, the cross-section type here refers to the basal cross-section shape taken at the cervix. Different cross-section outlines are usually termed 'D-shaped' by many authors, and we decided to make a distinction between 'U'-shaped, 'D'-shaped, 'J'-shaped, and salinon-shaped outlines of the crown base in cross-section (Fig. 5N–T). Gradational changes across the premaxillary and dentary arcade between a 'D'-shaped/salinon-shaped and 'J'-shaped outline may occur in a single specimen, the 'D'-shaped/salinon-shaped cross-section being present in the mesial-most teeth, with the 'J'-shaped cross-section outline occurring in more distal teeth of the mesial dentition (e.g., Fanti and Therrien, 2007:fig. 7).

Subcircular Cross-section—Circle-shaped outline of the transverse section of a conical or subconical crown with subsymmetrical and convex mesial, distal, labial, and lingual margins (Fig. 5F).

Elliptical Cross-section—Ellipse-shaped outline of the transverse section of a laterally narrow crown with labiolingually convex and subsymmetrical mesial and distal margins, and wide labiolingually convex and subsymmetrical labial and distal surfaces (Fig. 5G).

Subrectangular Cross-section—Rectangle-shaped outline of the transverse section of a laterally narrow crown with subparallel lingual and labial sides, and mesial and distal margins, all separated by four rounded angles (Fig. 5H).

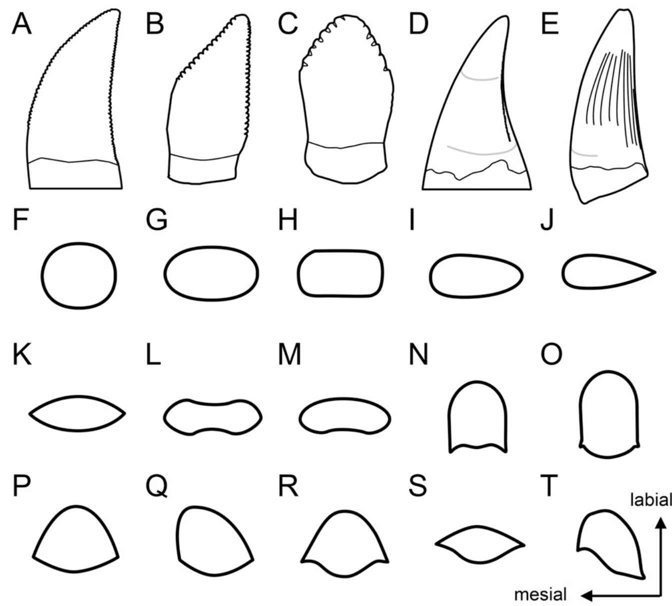

FIGURE 5. Crown types and cross-section outlines of the crown base at the cervix in non-avian theropods. **A**, ziphodont (blade-shaped) tooth; **B**, recurved folidont (lanceolate) crown; **C**, straight folidont (lanceolate) tooth; **D**, pachydont (incrassate) tooth; **E**, conidont (cone-shaped) crown; **F**, subcircular cross-section; **G**, elliptical cross-section; **H**, subrectangular cross-section; **I**, oval cross-section; **J**, lanceolate cross-section; **K**, lenticular cross-section; **L**, figure-8-shaped cross-section; **M**, reniform cross-section; **N**, 'U'-shaped cross-section with central ridge on the lingual margin; **O**, 'U'-shaped cross-section with convex lingual margin; **P**, symmetrical 'D'-shaped cross-section; **Q**, asymmetrical 'D'-shaped cross-section; **R**, salinon-shaped cross-section; **S**, parlinon-shaped cross-section; **T**, 'J'-shaped cross-section.

Oval Cross-section—Egg-shaped outline of the transverse section of a laterally narrow crown with a wide labiolingually convex mesial margin and a narrow labiolingually convex distal surface (Fig. 5I).

Lanceolate Cross-section—Lance-shaped outline of the transverse section of a laterally narrow crown with a labiolingually convex mesial margin and a sharp distal edge or carina (Fig. 5J).

Lenticular Cross-section—Lens-shaped outline of the transverse section of a laterally narrow crown with sharp and subsymmetrical mesial and distal edges or carinae (Fig. 5K).

Figure-8-shaped Cross-section—Hippopede-shaped outline of the transverse section of a laterally narrow crown with labiolingually convex mesial and distal margins, and mesiodistally convex labial and lingual surfaces (Fig. 5L).

Reniform Cross-section—Bean- or kidney-shaped outline of the transverse section of a laterally narrow crown with labiolingually convex mesial and distal margins, and one concave labial or lingual surface, the opposite surface being convex (Fig. 5M).

'U'-shaped Cross-section—Outline of the transverse section of a mesial crown with both carinae facing lingually, subsymmetrical mesial and distal margins, a convex labial surface, and a concave, convex (Fig. 5N), or biconcave lingual surface (Fig. 5O). The 'U'-shaped condition, also designated as 'D-shaped,' 'incisiform,' or 'subincisiform' (e.g., Currie et al., 1990; Carr and Williamson, 2004; Holtz, 2004), is shared by most tyrannosauroids, and perhaps some other basal coelurosaurs such as *Zuolong* (Choiniere et al., 2010).

'D'-shaped Cross-section—Outline of the transverse section of a mesial crown with both mesial and distal carinae facing linguomesially and linguodistally, respectively, and a wide mesiodistally convex labial and lingual surfaces (Fig. 5P). This outline is, in some cases, asymmetrical if the convexity of the labial surface is displaced mesially (Fig. 5Q). A 'D'-shaped cross-section is present in some allosauroids.

Salinon-shaped Cross-section—Outline of the transverse section of a mesial crown with both mesial and distal carinae facing linguomesially and linguodistally, respectively, subsymmetrical mesial and distal crown sides, a convex labial margin, and a biconcave lingual margin (Fig. 5R). A cross-section with a labiolingually narrow salinon-shaped outline (salinon sensu Khelif, 2010), here described as a parlinon-shaped cross-section (parlinon sensu Khelif, 2010), occurs in lateral teeth, with the biconcave surface facing either lingually or labially (Fig. 5S).

'J'-shaped Cross-section—Comma-shaped outline of the transverse section of a mesial crown with a mesial carina facing mesiolingually, a convex labial surface, and a sigmoid lingual surface due to a concavity adjacent to the mesial carina (Fig. 5T).

Enamel Texture Type

The morphology of the enamel texture is often omitted in the description of theropod dentitions and isolated theropod teeth, yet the enamel texture seems to have some phylogenetic potential in non-avian theropods (Buffetaut et al., 2008; Hendrickx and Mateus, 2014a; Hendrickx et al., 2015). The nomenclature of enamel texture type follows the terminology of Hendrickx and Mateus (2014a), and an additional type of texture, the anastomosed enamel texture, is here defined for the first time.

Smooth—Absence of enamel texture so that the enamel surface does not show any irregularity.

Irregular—Non-oriented enamel texture with no pattern (Fig. 6A).

Braided—Oriented enamel texture made of alternating and interweaving grooves and sinuous ridges (Fig. 6B). The ridges can be short, moderately elongated or very long, but always apicobasally oriented on the crown and never convergent.

Veined—Oriented enamel texture made of deep alternating grooves and long sinuous and/or dichotomized ridges obliquely oriented and converging mesiobasally or distobasally on the crown (Fig. 6C). The veined enamel texture has also been called 'granular texture' (Charig and Milner, 1997; Sues et al., 2002; Hasegawa et al., 2010), 'textured enamel' (Sereno et al., 1998), 'fine wrinkling' or 'wrinkles' (Buffetaut et al., 2008; Buffetaut, 2011), and 'sculptures' (Hasegawa et al., 2010; Mateus et al., 2011).

Anastomosed—Enamel texture consisting of multiple ridges dividing and reconnecting in an irregular way (Fig. 6D). These multiple ridges can connect at a submillimeter scale, giving an almost foraminate texture to the enamel (C. H. pers. observ.).

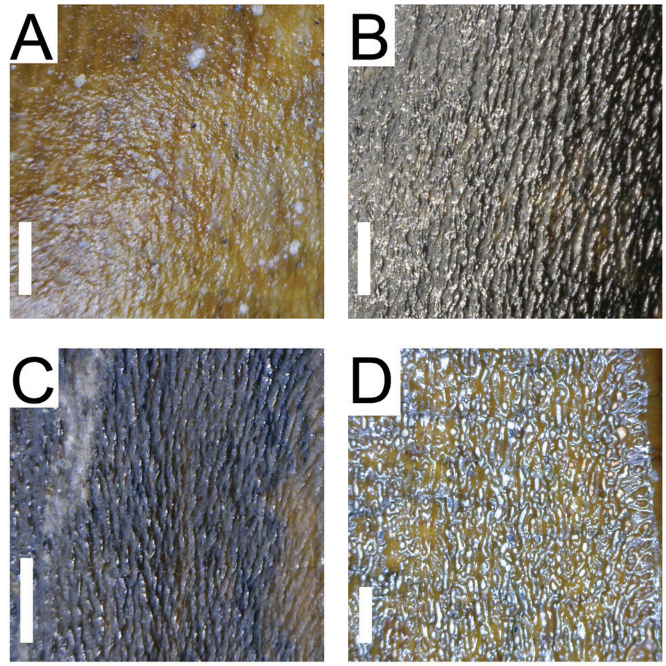

FIGURE 6. Diversity of enamel texture in non-avian theropods in lateral view. **A**, irregular enamel texture of the sixth right maxillary tooth of *Majungasaurus crenatissimus*, FMNH PR2278; **B**, braided enamel texture of an isolated tooth of *Acrocanthosaurus atokensis*, SMU 7646; **C**, veined enamel texture of an isolated tooth of *Baryonyx walkeri*, NHMUK R.9151–26; **D**, anastomosed enamel texture of an isolated tooth of *Spinosaurus* sp., MSNM V6422. Scale bars equal 1 mm.

MORPHOMETRIC NOMENCLATURE

Measurement variables and associated terms and abbreviations (Fig. 1) follow Smith et al. (2005), and additional measurements (with their respective terms and abbreviations) are proposed.

Crown Morphometry

Crown Base Length (CBL)—Maximum mesiodistal extent of the crown base at the level of the cervix (Smith et al., 2005; Fig. 7C). The crown base length, taken along the long axis of the crown base, between the basal-most point of the enamel layer on both mesial and distal surfaces of the crown, is equivalent to the fore-aft basal length (FABL) of some authors (e.g., Currie et al., 1990; Farlow et al., 1991; Sankey et al., 2002; Samman et al., 2005; Reichel, 2012; Larson and Currie, 2013).

Crown Base Width (CBW)—Labiolingual extent of the crown base at mid-length, perpendicular to the CBL, and at the level of the cervix (Smith et al., 2005; Fig. 7B, D). The crown base width (Sweetman, 2004), taken from the basal-most point of the enamel layer on both labial and lingual surfaces of the crown, is roughly similar to the cross-sectional thickness (CST) of Sankey et al. (2002) and Sankey (2008), the cross-sectional thickness (XSTHICK) of Samman et al. (2005), and the tooth basal width (BW) of Farlow et al. (1991), Fanti and Therrien (2007), Larson and Currie (2013), and many other authors (Supplementary Data, Table S1).

Crown Height (CH)—Maximum apicobasal extent of the distal margin of the crown. The crown height is taken from the distal-most point of the cervix to the apical-most point of the crown (Smith et al., 2005; Fig. 7C). The crown height is equivalent to the tooth crown height (THEIGHT) of Samman et al. (2005). It is also roughly equivalent, but slightly different from, the tooth height (Ht) of Sankey et al. (2002) and Sankey (2008) and the tooth crown height (TCH) of Farlow et al. (1991), Fanti and Therrien (2007), and many other authors (Supplementary Data, Table S1), which are taken from the cervix to the crown apex, perpendicular to CBW, without taking into account the crown curvature.

Apical Length (AL)—Maximum apicobasal extent of the mesial margin of the crown (Fig. 7C). The apical length, equivalent to the apical distance (AD) of Canudo et al. (2006), is taken from the mesial-most point at the cervix to the apical-most point of the crown (Smith et al., 2005).

Crown Angle (CA)—Angle created by the apical length AL and the crown base length (CBL; Smith et al., 2005; Fig. 7C). The crown angle, which can be calculated using the law of cosines, corresponds to $CA = \cos^{-1}(((CBL)^2 + (AL)^2 - (CH)^2)/2 \times CBL \times AL)$. Because the cervix is not always parallel to the

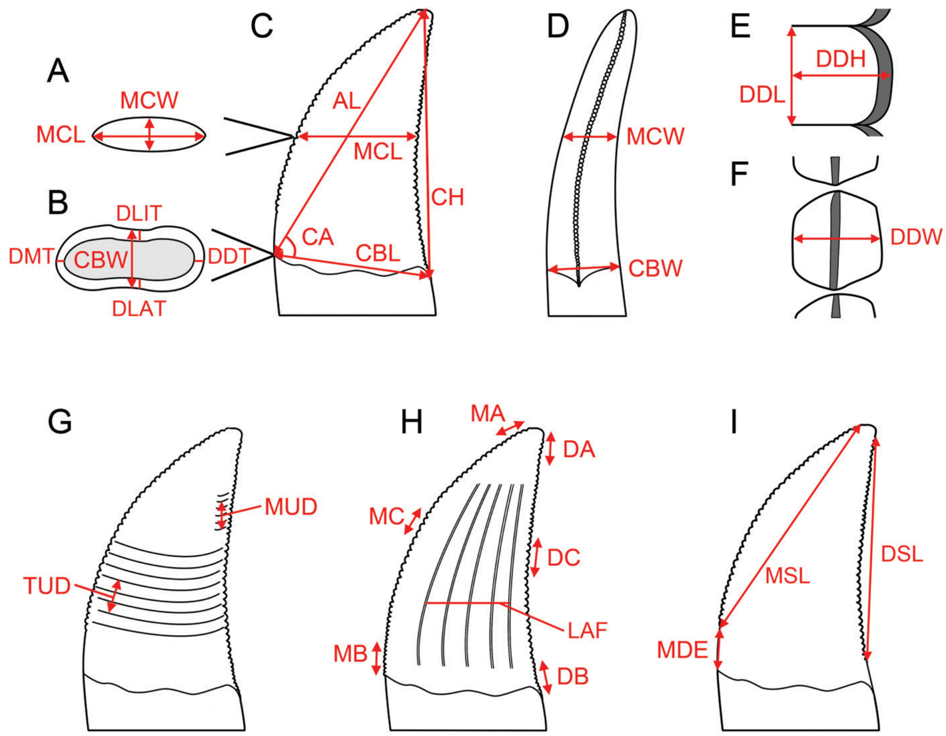

FIGURE 7. Anatomical and morphometric terminology used in this study. **A**, mid-height cross-section of crown C showing MCW (mid-crown width) and MCL (mid-crown length), in apical view; **B**, basal cross-section of crown in C showing CBL (crown base length), DMT (dentine thickness mesially), DDT (dentine thickness distally), DLAT (dentine thickness labially), and DLIT (dentine thickness lingually), in basal view; **C**, idealized lateral theropod tooth showing AL (apical length), CA (crown angle), CBL (crown base length), CH (crown height), and MCL (mid-crown length), in labial view; **D**, idealized lateral theropod tooth showing MCW (mid-crown width) and CBW (crown base width), in distal view; **E**, idealized distal denticles showing DDH (distal denticle height) and DDL (distal denticle length), in labial view; **F**, idealized distal denticles showing DDW (distal denticle width), in distal view; **G**, idealized lateral theropod tooth showing CMU (crown marginal undulation density) and CTU (crown transverse undulation density), in labial view; **H**, idealized fluted theropod tooth showing DA (distoapical denticle density), DB (distobasal denticle density), DC (distocentral denticle density), LAF (number of labial flutes), MA (mesioapical denticle density), MB (mesiobasal denticle density), and MC (mesiocentral denticle density), in labial view; **I**, idealized lateral theropod tooth showing MDE (mesial denticle extension), MSL (mesial serrated carina length), and DSL (distal serrated carina length), in labial view.

jaw margin, Buckley et al. (2010) proposed to measure a different crown angle (CA2) on images of teeth in lateral view. This angle is created by a mesiodistal line on the tooth, parallel to the jaw margin and passing by the distal-most point of the cervix, and a second line passing by the intersection of the previous one with the mesial margin of the tooth and the crown apex (i.e., apical-most point of the crown).

Crown Base Ratio (CBR)—Ratio expressing the labiolingual narrowness of the base crown and corresponding to the quotient of CBW by CBL (CBR = CBW ÷ CBL; Smith et al., 2005). The crown base ratio (CBR) is equivalent to the basal cross-sectional ratio (BCR) of Larson (2008), the lateral compression index (LCI) of Amiot et al. (2010a), and the reciprocal of the basal compression ratio (BCR) of Maganuco et al. (2005, 2007). A strongly labiolingually narrow crown has a quotient of less than 0.4, a moderately narrow tooth is around 0.5–0.6, a weakly narrow crown, with an ovoid cross-section, has a ratio fluctuating between 0.6–0.7, which usually corresponds to the CBR of a mesial tooth, and a subcircular crown has a ratio between 0.9 and 1.1 (Smith et al., 2005).

Crown Height Ratio (CHR)—Ratio expressing crown elongation and corresponding to the quotient of CH by CBL (CHR = CH ÷ CBL; Smith et al., 2005). The crown height ratio (CHR) is equivalent to the slenderness index (SI) of Vullo et al. (2007) and the reciprocal of the elongation ratio (ER) of Maganuco et al. (2005, 2007). A short tooth has a CHR value <1.5, a moderately elongated crown has a CHR varying from 1.5–2.5, and a strongly elongated crown has a ratio >2.5.

Mid-crown Length (MCL)—Maximum mesiodistal extent of the tooth at mid-height of the crown (Hendrickx et al., 2015; Fig. 7A, C). The mid-crown length (MCL) is roughly similar to the ML of Hocknull et al. (2009:table S16).

Mid-crown Width (MCW)—Maximum labiolingual extent of the tooth, perpendicular to the MCL, at mid-height of the crown (Hendrickx et al., 2015; Fig. 7A, D).

Mid-crown Ratio (MCR)—Thickness of the mid-crown corresponding to the quotient of MCW by MCL (MCR = MCW ÷ MCL; Hendrickx et al., 2015). The mid-crown ratio is equivalent or close to the crown base ratio (CBR) in most theropods, but differs from CBR in many folidont theropods in which the labiolingual narrowness of the crown is less important at mid-crown than at the base (C. H. pers. observ.).

Mesiobasal Denticle Extension (MDE)—Distance separating the basal-most mesial denticle from the cervix (Hendrickx et al., 2015; Fig. 7I). This measure is taken from the basal-most mesial denticle to a point situated on the same plane as the basal-most denticles, at the level of the cervix. The mesiobasal denticle extension is zero when the mesial denticulate carina reaches the cervix.

Mesiobasal Carina Extension (MCE)—Distance separating the basal-most part of the mesial carina from the cervix. This measure is taken from the basal-most point of the mesial carina to a point situated on the same plane of that point, at the level of the cervix. The mesiobasal carina extension (MCE) is equivalent to the distance between the base of the mesial carina and the base of the tooth crown (DMCTOB) of Samman et al. (2005).

Mesial Serrated Carina Length (MSL)—Maximum apicobasal extent of the mesial serrated carina (Buckley, 2009; Buckley et al., 2010; Fig. 7I). The mesial serrated carina length (MSL), taken between the basal-most and the apical-most denticles along the mesial carina, is equivalent to the anterior denticulate carina length (ADCL) of Buckley (2009) and Buckley et al. (2010), and roughly equivalent to the length of the mesial serration (MSH) of Cillari (2010), which is measured perpendicular to CBL. It corresponds to the difference between the mesiobasal denticle extension (MDE) and the apical length (AL) in the large majority of theropods, but differs from the result of this calculation in a few theropods whose mesial serrated carina does not reach the apex (e.g., *Troodon*).

Distal Serrated Carina Length (DSL)—Maximum apicobasal extent of the distal serrated carina (Buckley, 2009; Buckley et al., 2010; Fig. 7I). The distal serrated carina length (DSL), taken between the basal-most and the apical-most denticles along the distal carina, is equivalent to the posterior carina denticulate length (PCDL) of Buckley (2009) and Buckley et al. (2010). It is also similar to the crown height in most theropods, but shorter than CH in some coelurosaurs, such as compsognathids, therizinosaurs, and troodontids (C. H. pers. observ.).

Mesial Carina Length (MCAL)—Maximum apicobasal extent of the mesial carina along the crown (Buckley, 2009; Buckley et al., 2010). The mesial carina length, taken from the basal-most point to the apical-most point of the mesial carina, is equivalent to the anterior carina length (ACL) of Buckley (2009) and Buckley et al. (2010), and the anterior carina height (ACH) of Reichel (2012). The mesial carina length is similar to the mesial denticulate carina length in the serrated crown of most theropods, yet some of them have a denticulate carina that becomes unserrated basally and/or apically like in tyrannosaurids (Buckley et al., 2010).

Distal Carina Length (DCAL)—Maximum apicobasal extent of the distal carina (Buckley, 2009; Buckley et al., 2010). The distal carina length, taken from the basal-most point to the apical-most point of the distal carina, is equivalent to the posterior carina length (PCL) of Buckley (2009) and Buckley et al. (2010). The distal carina length is also similar to the distal serrated carina length (DSL) in the large majority of theropods, and only a few of them, such as tyrannosaurids, seem to have different DSL and DCAL (Buckley et al., 2010).

Denticle Morphometry

Distal Denticle Height (DDH)—Maximum proximodistal extent of a denticle on the distal carina at mid-crown (Samman et al., 2005; Fig. 7E). The distal denticle height corresponds to the distal denticle height of middle denticles (DDHM) of Samman et al. (2005), the greatest denticle height (Dent. Ht) of Sankey et al. (2002) and Sankey (2008), the denticle length (CD) of Casal et al. (2009), the largest posterior denticle height (LPD-H) of Buckley (2009), and the height of denticle (DH) of Madzia (2014).

Distal Denticle Length (DDL)—Maximum apicobasal extent of a denticle on the distal carina at mid-crown, taken perpendicular to the DDH at the base of the denticle (Fig. 7E). The distal denticle length corresponds to the distal denticle width of middle denticles (DDWM) of Samman et al. (2005), the greatest denticle width (Dent. W) of Sankey et al. (2002) and Sankey (2008), the denticle height (AD) of Casal et al. (2009), and the largest posterior denticle length (LPD-L) of Buckley (2009).

Distal Denticle Width (DDW)—Maximum labiolingual extent of a denticle on the distal carina at mid-crown, taken perpendicular to the DDL at the base of the denticle (Fig. 7F). The distal denticle width corresponds to the largest posterior denticle width (LPD-W) of Buckley (2009).

Mesial Denticle Height (MDH)—Maximum proximodistal extent of a denticle on the mesial carina at two-thirds of the crown height (Samman et al., 2005). The mesial denticle height corresponds to the mesial denticle height of middle denticles (MDHM) of Samman et al. (2005), and the largest anterior denticle height (LAD-H) of Buckley (2009).

Mesial Denticle Length (MDL)—Maximum apicobasal extent of a denticle on the mesial carina at two-thirds of the crown height, taken perpendicular to the MDH at the base of denticle. The mesial denticle length corresponds to the mesial denticle width of middle denticles (MDWM) of Samman et al. (2005), and the largest anterior denticle length (LAD-L) of Buckley (2009).

Mesial Denticle Width (MDW)—Maximum labiolingual extent of a denticle on the mesial carina at mid-crown, taken perpendicular to the MDL at the base of the denticle. The mesial denticle width corresponds to the largest anterior denticle width (LAD-W) of Buckley (2009).

Distal Denticle Height Ratio (DHR)—Ratio expressing the distal denticle elongation and corresponding to the quotient of DDH by DDL (DHR = DDH ÷ DDL).

Distal Denticle Base Ratio (DBR)—Ratio expressing the distal denticle thickness at the base of the denticle and corresponding to the quotient of DDW by DDL (DBR = DDW ÷ DDL).

Mesial Denticle Height Ratio (MHR)—Ratio expressing the mesial denticle elongation and corresponding to the quotient of MDH by MDL (MHR = MDH ÷ MDL).

Mesial Denticle Base Ratio (MBR)—Ratio expressing the mesial denticle thickness at the base of the denticle and corresponding to the quotient of MDW by MDL (MBR = MDW ÷ MDL).

Distoapical Denticle Density (DA)—Number of denticles per 5 mm in the apical-most part of the distal carina (Smith et al., 2005; Fig. 7H). Given the fact that the serrated distal carina does not always reach the apex of the crown (e.g. *Sciurumimus, Compsognathus, Scipionyx*), the measurement is inapplicable if the apical-most part of the distal surface of the crown is unserrated. The distoapical denticle density corresponds to five times the posterior apical carina denticles per millimeter (PAD/mm) of Buckley et al. (2010).

Distocentral Denticle Density (DC)—Number of denticles per 5 mm on the distal carina at mid-crown, regardless the position of the carina on the crown (Smith et al., 2005; Fig. 7H). The distocentral denticle density corresponds to five times the posterior medial carina denticles per millimeter (PMD/mm) of Buckley et al. (2010).

Distobasal Denticle Density (DB)—Number of denticles per 5 mm in the basal-most part of the distal carina, regardless of the position of the carina on the crown or the root (Smith et al., 2005; Fig. 7H). The distobasal denticle density corresponds to five times the posterior basal carina denticles per millimeter (PBD/mm) of Buckley et al. (2010).

Mesioapical Denticle Density (MA)—Number of denticles per 5 mm in the apical-most part of the mesial carina (Smith et al., 2005; Fig. 7H). Similarly to the distal carina, the serrated mesial carina does not always reach the apex of the crown so that the measurement is inapplicable when the apical-most part of the mesial margin of the crown is unserrated. The mesioapical denticle density corresponds to five times the anterior apical carina denticles per millimeter (AAD/mm) of Buckley et al. (2010).

Mesiocentral Denticle Density (MC)—Number of denticles per 5 mm on the mesial carina at mid-crown, regardless of the position of the carina on the crown (Smith et al., 2005; Fig. 7H). The mesiocentral denticle density corresponds to five times the anterior medial carina denticles per millimeter (AMD/mm) of Buckley et al. (2010).

Mesiobasal Denticle Density (MB)—Number of denticles per 5 mm in the basal-most part of the mesial carina, regardless of the position of the carina on the crown or the root (Smith et al., 2005; Fig. 7H). The mesiobasal denticle density corresponds to five times the anterior basal carina denticle per millimeter (ABD/mm) of Buckley et al. (2010). In many cases, the mesial carina does not reach the cervix, and the measurement is therefore inapplicable if the basal-most part of the mesial margin of the crown is unserrated.

Average Mesial Denticle Density (MAVG)—Average number of denticles per 5 mm along the mesial carina (Smith et al., 2005). $\mathrm{MAVG} = ((\mathrm{MA} + \mathrm{MC} + \mathrm{MB}) \div 3)$.

Average Distal Denticle Density (DAVG)—Average number of denticles per 5 mm along the distal carina (Smith et al., 2005). $\mathrm{DAVG} = ((\mathrm{DA} + \mathrm{DC} + \mathrm{DB}) \div 3)$.

Denticle Size Density Index (DSDI)—Ratio expressing the size difference between mesial and distal denticles (Rauhut and Werner, 1995) and corresponding to the quotient of MC by DC ($\mathrm{DSDI} = \mathrm{MC} \div \mathrm{DC}$). This measurement is similar to that of Rauhut and Werner (1995) and differs slightly from that of Smith et al. (2005), because it does not take into consideration the average number of denticles along both carinae but only the mid-crown denticles on each carina. This reduces sampling error when basal and/or apical denticles, typically smaller than denticles at the mid-crown, are not entirely preserved due to wear.

Enamel Morphometry

Transverse Undulation Density (TUD)—Number of transverse undulations per 5 mm on the crown (Fig. 7G). The transverse undulation density (TUD) is equivalent to the crown transverse undulation density (CTU) of Hendrickx et al. (2015).

Marginal Undulation Density (MUD)—Number of marginal undulations per 5 mm on the crown (Fig. 7G).

Labial Flutes (LAF)—Number of flutes on the labial surface of the crown.

Lingual Flutes (LIF)—Number of flutes on the lingual surface of the crown (Fig. 7H).

Dentine Morphometry

Dentine Thickness Mesially (DMT)—Mesiodistal extent of the dentine layer in the most mesial part of the tooth, at the level of the cervix or in the basal part of the root (Hendrickx et al., 2015; Fig. 7B).

Dentine Thickness Distally (DDT)—Mesiodistal extent of the dentine layer in the most distal part of the tooth, at the level of the cervix or in the basal part of the root (Hendrickx et al., 2015; Fig. 7B).

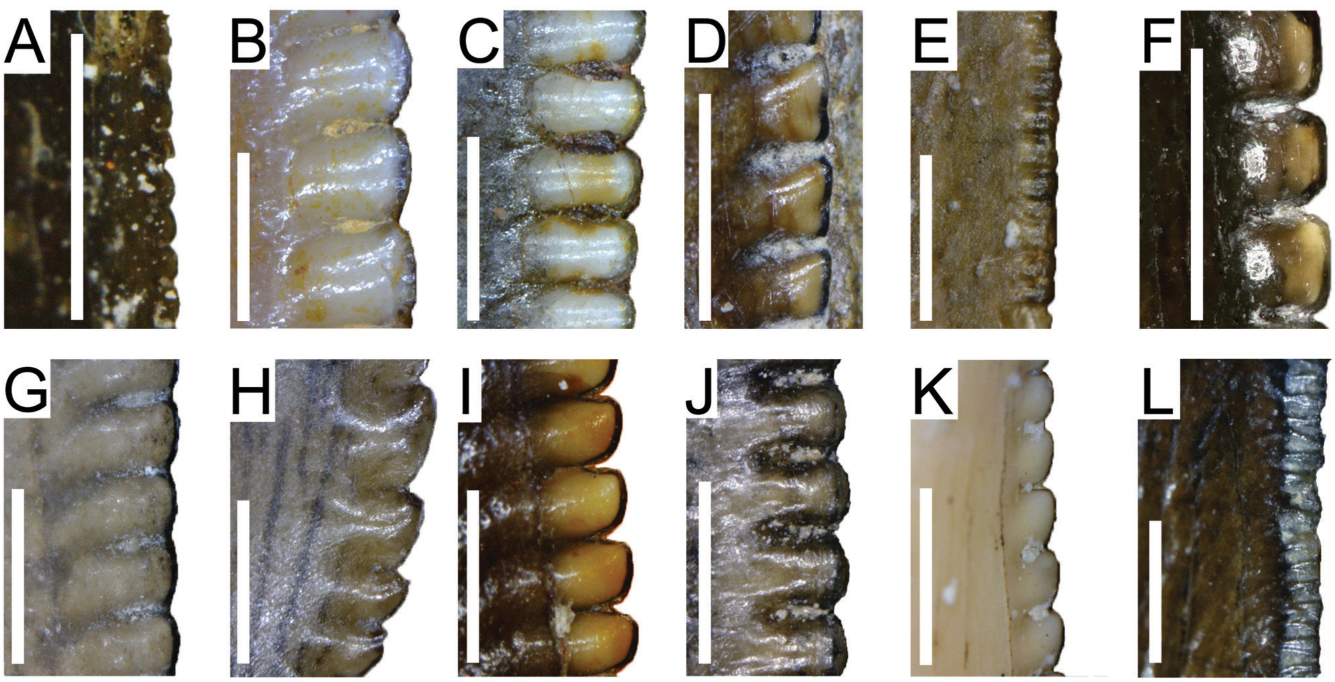

FIGURE 8. Morphological diversity of denticles in non-avian theropods in lateral view. **A**, apicobasally subrectangular distocentral denticles in the fourth left maxillary tooth (Lmx4) of *Eodromaeus murphi*, PVSJ 561; **B**, subquadrangular distocentral denticles in an isolated maxillary tooth of *Carcharodontosaurus saharicus*, SGM Din-1; **C**, proximodistally subrectangular distocentral denticles in an isolated tooth of *Afrovenator abakensis*, MNN TIG1; **D**, apically inclined and bilobate mesioapical denticles in an isolated tooth of *Megalosaurus bucklandi*, NHMUK R.234; **E**, minute subquadrangular distocentral denticles with regular morphological variation in an isolated tooth of *Suchomimus tenerensis*, MNN G73-3; **F**, subquadrangular mesioapical denticles with planar external margins in an isolated tooth of *Acrocanthosaurus atokensis*, SMU 74646; **G**, distocentral denticles with short interdenticular sulci and shallow interdenticular slits in the first left maxillary tooth (Lmx1) of *Erectopus superbus*, MNHN 2001–4; **H**, large and apically hooked distocentral denticles with dramatic size variation in an isolated tooth of *Troodon formosus*, DMNH 22837; **I**, weakly apically hooked distocentral denticles in an isolated tooth of an indeterminate Abelisauridae, ML 327; **J**, subquadrangular distocentral denticles with wide interdenticular chambers in an isolated tooth of an indeterminate Tyrannosauridae, DMNH 2130; **K**, apicobasally subrectangular and apically hooked distocentral denticles in an isolated tooth of *Masiakasaurus knopfleri*, FMNH PR2221; **L**, minute subrectangular distocentral denticles with an irregular morphological variation in an isolated tooth of *Baryonyx walkeri*, NHMUK R.9951-278. Scale bars equal 1 mm.

Dentine Thickness Lingually (DLIT)—Labiolingual extent of the dentine layer in the medial part of the labial side of the tooth, at the level of the cervix or in the basal part of the root (Hendrickx et al., 2015; Fig. 7B).

Dentine Thickness Labially (DLAT)—Labiolingual extent of the dentine layer in the medial part of the labial side of the tooth, at the level of the cervix or in the basal part of the root (Hendrickx et al., 2015; Fig. 7B).

METHODOLOGY TO DESCRIBE ISOLATED THEROPOD TEETH

Future authors may use the methodology below to facilitate the description of theropod teeth. This procedure is divided in five sections: tooth condition, crown, denticles, ornamentations, and root.

Condition

The state of preservation of the tooth is a first assessment of the quality of the data to be extracted. Therefore, details on fractures, eroded surfaces, taphonomic deformation (e.g., compression, tension, shear, torsion, and bending) must be determined because these may affect the original tooth morphology. Antemortem tooth deformation, such as wear facets and spalled surfaces, should not be included in this section, but under tooth ornamentations.

Crown

Each tooth needs to be correctly labeled and oriented with respect to the tooth row. In the case of isolated teeth, it is usually impossible to determine the actual position of the crown within the original tooth row using curvature, carina orientation, and labial and lingual depression. Yet, these features can help determine the relative orientation of the tooth (i.e., mesial, distal, labial, and distal sides of the tooth), and whether the isolated tooth belongs to the mesial or lateral dentition and, in some rare cases of theropods with significantly different dentition on the upper and lower jaws (e.g., *Byronosaurus*), to the left/right side of the cranium or mandible.

Most theropods have a distally curved crown; the mesial profile is thus more convex than the distal one. Tooth crowns such as those of Spinosaurinae and some indeterminate coelurosaurs such as *Richardoestesia isosceles* (Baszio, 1997; Sankey, 2001; Sankey et al., 2002) may, however, lack curvature, so it is difficult, if not impossible, to know their exact mesiodistal orientation when found isolated. Orienting the labial and lingual surfaces of the crown can also be problematic. Most theropod teeth have a depression on the basal part of the crown. This depression represents the track of the erupting, lingually positioned replacement crown. Therefore, the side displaying this basal depression corresponds to the lingual margin, and the concavity is then the lingual depression. This subunit of the tooth is sometimes planar, and the basal part of the crown that displays a stronger convexity is typically the basolabial surface of the crown. Some avetheropods have a biconcave cross-section at the crown base, giving a figure-8 shape (e.g., Gianechini et al., 2011b; Hendrickx and Mateus, 2014a; Fig. 5L), but the more concave surface is usually on the lingual side of the crown (C. H. pers. observ.). The orientation of the carinae also helps in determining the labiolingual orientation of an isolated crown. The distal carina is deflected labially in theropods when offset. Likewise, the mesial carina is displaced lingually, or curves towards the lingual side basally if not centrally positioned on the tooth (C. H. pers. observ.).

The heterodonty reported by many authors for the theropod dentition (e.g., Carrano et al., 2002; Smith et al., 2005; Rauhut et al., 2010; Reichel, 2010) derives mostly from the morphological difference between mesial and lateral teeth. The position of an isolated tooth along the tooth row is therefore often determinable, if they are the mesial teeth, or if they are located more distally within the lateral dentition. Despite intertaxic variation in mesial tooth morphology, there are several features that can be used to differentiate mesial from lateral teeth: the crown base ratio (CBR; sensu Smith et al., 2005), the asymmetrical profile of the crown in cross-section, and the presence of crown ornamentations. In ziphodont theropods, mesial teeth are typically broader than lateral teeth (i.e., CBR is greater than 0.64). This is, however, not the case in folidont, pachydont, and conidont theropods in which the crown base ratio of lateral teeth is often as high as those of the mesial dentition (C. H. pers. observ.). In some ziphodont and folidont theropods bearing serrated teeth (e.g., non-neotheropod Theropoda, Compsognathidae, Therizinosauroidea, some Deinonychosauria), mesial teeth are not denticulate, nor display a mesial margin with a carina. The mesial carina of many ziphodont and pachydont theropods typically spirals lingually or faces lingually when present, in mesial teeth. In these theropods, the distal carina remains either centrally positioned on its distal margin or is deflected labially (and very rarely lingually; C. H. pers. observ.). There are few cases of ziphodont theropods (e.g., Megalosauridae) in which both carinae remain centrally positioned, so that the mesial crowns are subsymmetrical, but the significant elongation (crown height ratio, or CHR, sensu Smith et al. [2005], greater than 2.5) and subcircular/elliptical cross-section of the crown base differentiate them from lateral crowns (Hendrickx et al. 2015). Likewise, mesial teeth of some ziphodont and pachydont theropods present a concave surface adjacent to one or both carinae (e.g., Abelisauridae, Allosauridae), fluted surface (e.g., Coelophysidae, Ceratosauridae, Noasauridae, Compsognathidae, Dromaeosauridae), longitudinal ridges or grooves (e.g., Tyrannosauroidea), or a small mesiodistal constriction at the level of the cervix (e.g., Tyrannosauroidea, Compsognathidae), several features that are typically absent in the lateral dentition.

Teeth can also vary in their crown shape (e.g., ziphodont, folidont, conidont, pachydont; Fig. 5), thickness (e.g., strongly, moderately, or weakly narrow; arbitrary divisions based on the CBR value), elongation (e.g., short, moderately elongated, or strongly elongated; arbitrary divisions based on the CHR value), curvature (e.g., labiodistal, distal, or labiolingual orientation of the crown apex), and mesial and distal profiles in lateral (e.g., strongly convex, weakly convex, straight, concave) and distal (e.g., straight, recurved labially/lingually, sigmoid) views. Details on the curvature of the labial and distal surfaces should be added (e.g., strongly or slightly convex, planar), as well as the extension of the crown enamel on each side of the crown (e.g., enamel extending more basally in the mesial/distal and labial/lingual part of the crown, symmetrical extension of the enamel on the crown). Additionally, we recommend adding details on the mesial and distal carinae, their morphology (e.g., serrated/unserrated, split, low/markedly developed), position (e.g., centrally positioned on the mesial/distal margin, deflected labially/lingually, facing labially/lingually, symmetrically positioned or not), extension (e.g., reaching the cervix, crossing the apex, terminating well below the apex, extending on the root), and orientation (e.g., straight, diagonally oriented, twisted). The presence of concave surfaces adjacent to the carinae, as well as any labial and/or lingual depressions, should also be reported, with further details on the position and extension on the crown surface, both labially and lingually. Finally, it is important to describe the cross-section outline of the crown base (e.g., subcircular, elliptical, lenticular, lanceolate, reniform, 'U'-shaped, 'D'-shaped, 'J'-shaped; see above) at the level of the cervix (Fig. 5F–T) and at mid-height of the crown.

Denticles

Important features when describing denticles include denticle morphology, and the number of denticles per unit distance (typically, 1 or 5 mm) on both carinae as well as at different locations on the crown, i.e., basally, at mid-crown and apically. A description of the denticle size density index should also be reported (e.g., mesial and distal denticles of similar size, distal denticles larger/smaller than mesial ones; based on denticle size density index value, or DSDI, sensu Rauhut and Werner, 1995) as well as information on denticle size variation (e.g., regular/irregular, changing smoothly/dramatically along the carinae). Denticle morphology is relatively diverse in non-avian theropods (Fig. 8), and the mesial and distal denticle morphology should be described in terms of its shape (e.g., chisel-shaped, lanceolate), elongation (e.g., subquadrangular, apicobasally subrectangular, proximodistally subrectangular), inclination (e.g., perpendicular to carina, apically inclined), outline of the external margin (e.g., symmetrically convex, asymmetrically convex, parabolic, subrectangular with planar surface, semicircular, bilobate, apically hooked), interdenticular space (e.g., shallow/deep, narrow/large), diaphysis (e.g., present/absent, shallow/deep), and slit (e.g., shallow/deep, concave/subtriangular, with or without a lamina joining two neighboring denticles). Finally, details on the interdenticular sulci should be reported for both sides and carinae, such as their curvature (e.g., straight or curving basally), inclination (e.g., horizontal or inclined basally), and extension (e.g., short, medium, or long and well developed). Because caudae are the result of interdenticular sulci, and the latter are more distinct and better visible than caudae (Smith, 2007; C. H. pers. observ.), we suggest favoring the description of interdenticular sulci instead of caudae.

Ornamentations and Other Attributes

A thorough description of the crown ornaments/attributes should include details on spalled surfaces, wear facets, flutes, transverse and marginal undulations, labial and lingual depressions, longitudinal grooves and ridges, and basal striations. These details should be given for both labial and lingual surfaces. It is important to specify details on the number of flutes, striations, and longitudinal grooves and ridges on the crown. Concerning transverse and marginal undulations, it is central to describe details of their density (e.g., numerous, just a few), orientation (e.g., horizontal, diagonal), extension (e.g., transverse undulations covering the crown, restricted to the crown center/vicinity), and discernibility (e.g., only visible at a certain angle, well visible in all crown orientations). To complete the description, details on the enamel texture should be provided, with information on the texture pattern (smooth, irregular, braided, veined, or anastomosed; Fig. 8) and orientation in the middle of the crown and marginal to the carinae.

Root

Isolated theropod teeth are typically shed teeth, thus only preserving portions of the basal part of the root. However, isolated teeth may also include the whole root, bearing witness to postmortem disarticulation of the teeth from the jaws and distancing from the tooth-bearing bones before burial. A description of the preserved root should include details on its height (e.g., shorter/longer than crown height), width (e.g., wider/narrower than crown width), morphology (e.g., labiolingually narrow, subcylindrical, tapered at the apex, with parallel/convex mesial and distal margins), ornamentations (e.g., transverse undulations, labial/lingual depressions), and cross-section at mid-height of the root (e.g., subcircular, oval, ‘8’-shaped, reniform). Morphology and depth of the resorption pit should also be provided. In shed teeth preserving the basal portion of the root, it is important to describe the thickness of the dentine layer mesially, distally, labially, and lingually in basal view, because the transverse extension of the dentine layer varies along the tooth jaw and between taxa (C. H. pers. observ.).

CONCLUSIONS

This study reveals the taxonomic value of theropod teeth and contributes to better understanding of the phylogenetic potential of isolated theropod teeth. Many features, including the extent and position of carinae, cross-section outline, size and morphology of denticles, and crown ornamentation and texture, are diagnostic, and help to identify the position of isolated teeth along the tooth row as well as the taxa to which they belong. A detailed description of the dentition of many pivotal theropods such as *Dilophosaurus, Ceratosaurus, Allosaurus, Monolophosaurus, Sinraptor, Yangchuanosaurus, Dilong*, and *Guanlong* is therefore critically required in order to help clarify the distribution of the numerous morphologies that exist in theropod clades with superficially similar dentitions (e.g., Ceratosauridae, Allosauridae, Metriacanthosauridae, Neovenatoridae, and Proceratosauridae). Likewise, the comprehensive description of isolated theropod teeth, typically abundant at dinosaur fossil sites, is crucial to help resolve their systematic position. The adoption of a methodology, and a standard positional, morphological, anatomical, and morphometric nomenclature, such as the one proposed here for the theropod dentition, will certainly help with description, measurement, and ultimately identification of isolated theropod teeth that can be helpful for paleobiogeographic and stratigraphic purposes.

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