The distribution of dental features in non-avian theropod dinosaurs: Taxonomic potential, degree of homoplasy, and major evolutionary trends

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ABSTRACT

Isolated theropod teeth are some of the most common fossils in the dinosaur fossil record and are continually reported in the literature. Recently developed quantitative methods have improved our ability to test the affinities of isolated teeth in a repeatable framework. But in most studies, teeth are diagnosed on qualitative characters. This can be problematic because the distribution of theropod dental characters is still poorly documented, and often restricted to one lineage. To help in the identification of isolated theropod teeth, and to more rigorously evaluate their taxonomic and phylogenetic potential, we evaluated dental features in two ways. We first analyzed the distribution of 34 qualitative dental characters in a broad sample of taxa. Functional properties for each dental feature were included to assess how functional similarity generates homoplasy. We then compiled a quantitative data matrix of 145 dental characters for 97 sauropodischian taxa. The latter was used to assess the degree of homoplasy of qualitative dental characters, address longstanding questions on the taxonomic and biostratigraphic value of theropod teeth, and explore the major evolutionary trends in the theropod dentition.

In smaller phylogenetic datasets for Theropoda, dental characters exhibit higher levels of homoplasy than non-dental characters, yet they still provide useful grouping information and optimize as local synapomorphies of smaller clades. In broader phylogenetic datasets, the degree of homoplasy displayed by dental and non-dental characters is not significantly different. Dental features on crown ornamentations, enamel texture and tooth microstructure have significantly less homoplasy than other dental features and can be used to identify many theropod taxa to ‘family’ or ‘sub-family’ level, and some taxa to genus or species. These features should, therefore, be a priority for investigations seeking to classify isolated teeth.

Our observations improve the taxonomic utility of theropod teeth and in some cases can help make isolated teeth useful as biostratigraphic markers. This proposed list of dental features in theropods should, therefore, facilitate future studies on the systematic paleontology of isolated teeth.
INTRODUCTION

Theropods are a lineage of bipedal dinosaurs including birds and their most recent common ancestors (e.g., Padian and Chiappe, 1998; Chiappe and Witmer, 2002; Long and Schouten, 2008; Naish, 2012). Although non-avian theropods were mostly carnivores, there is abundant evidence for substantial trophic variation within the group, including herbivory (e.g., Kobayashi et al., 1999; Zanno et al., 2009; Sander et al., 2010; Zanno and Makovicky, 2011), omnivory (e.g., Holtz et al., 1998) and piscivory (e.g., Charig and Milner, 1997; Amiot et al., 2010; Xing et al., 2013b). This trophic diversity is reflected in a diverse array of tooth shape and dental morphologies within the group (Currie et al., 1990; Hendrickx and Mateus, 2014a; Hendrickx et al., 2015d).

Like fishes, crocodiles, squamates and other groups of dinosaurs, non-avian theropods are polyphyodont animals, i.e., they continuously replaced their teeth throughout their lifespan (Smith et al., 2005; Hendrickx et al., 2015d). Teeth, and particularly tooth enamel, are robust skeletal elements (Hillson, 2005), and most toothed theropods had 50 or more teeth that were replaced every one to two years (Fiorillo and Currie, 1994; Erickson, 1996). Consequently, theropod teeth are one of the most common fossils in terrestrial Mesozoic formations (e.g., Erickson, 1996; Smith et al., 2005; Blob and Badgley, 2007) and are constantly reported in the literature (e.g., Currie et al., 1990; Rauhut and Werner, 1995; Baszio, 1997; Zinke, 1998; Sankey et al., 2002; Sweetman, 2004; Maganuco et al., 2005; Vullo et al., 2007; Larson, 2008; Casal et al., 2009; Lubbe et al., 2009; Ősi et al., 2010; Han et al., 2011; Sues and Averianov, 2013; Larson and Currie, 2013; Richter et al., 2013; Torices et al., 2015; Kear et al., 2013; Madzia, 2014; Hendrickx and Mateus, 2014a; Cobos et al., 2014; Tavares et al., 2014; Fanti et al., 2014; Brusatte and Clark, 2015; Csiki-Sava et al., 2016; Gerke and Wings, 2016; Alonso et al., 2017; Malafaia et al., 2017a; Avrahami et al., 2018; Frederickson et al., 2018; Averianov et al., 2019; Wongko et al., 2019; Young et al., 2019).

Isolated theropod teeth provide taphonomic, paleoenvironmental and paleoecological data (e.g., Briggs and Crowther, 2001; Amiot et al., 2004, 2006, 2009, 2011; Rogers et al., 2007; Fanti et al., 2014; Gerke and Wings, 2016; Hassler et al., 2018; Frederickson et al., 2018). They may also provide evidence for paleodiversity, biostratigraphy (i.e., temporal/geographic ranges of theropod taxa), and anatomical information on clades when articulated skeletal fossils are missing or poorly represented (Brusatte et al., 2007; Larson et al., 2016). In addition, the size and morphology of theropod teeth and their denticles provide important functional, positional and trophic data that can be used to form hypotheses for body size, bite force and feeding behavior (e.g., D’Amore, 2009; D’Amore and Blumenhershine, 2009; Reichel, 2010; Brink et al., 2015; Monfroy, 2017; Torices et al., 2018). Despite the importance of theropod teeth, their detailed morphology is often poorly known, leading to imprecise taxonomic assignments (e.g., Ősi et al., 2010; Amiot et al., 2011; Carrano et al., 2012; Ruiz-Omeñaca et al., 2012; Torices et al., 2015; Madzia, 2014; Gerke and Wings, 2016). Such taxonomic imprecision obscures potentially useful information.
that teeth may provide for paleogeographic and stratigraphic distributions of theropod clades.

Morphometric multivariate analyses have shown promise for identifying isolated teeth (e.g., Smith et al., 2005; Larson and Currie, 2013) and recent studies have indicated that qualitative characters can also be useful for differentiating taxa, even for theropods with similar dentition (Hendrickx and Mateus, 2014a; Hendrickx et al., 2015c). Relatively few theropods have had their dentition studied in detail, with notable exceptions of Coelophysis (Buckley and Currie, 2014), Majungasaurus (Fanti and Therrien, 2007; Smith, 2007), megalosaurids (Hendrickx et al., 2015c), Albertosaurus (Buckley et al., 2010), Tyrannosaurus (Smith, 2005), Troodon (Currie, 1987) and Buitreraptor (Gianechini et al., 2011b). Recent research has shown that much variation in teeth remains to be described, particularly with respect to denticle shape, cross-sectional geometry, extension of the mesial carina and the presence of crown ornamentations.

The scarcity of information on theropod tooth morphology leads to taxonomic assignments on the basis of a priori assumptions of their phylogenetic affinities (Smith, 2005). The current literature contains many tooth-based taxonomic assessments based on scarce or poorly understood data (e.g., Soto and Perea, 2008; Buffetaut, 2011; Vullo et al., 2014; Mo and Xu, 2015; Serrano-Martínez et al., 2015, 2016). For example, the marginal undulations visible on the crown of some carcharodontosaurids is often considered as a key character of this clad, leading some authors (e.g., Chure et al., 1999) to assign isolated teeth to Carcharodontosaurus solely based on this feature when, in fact, it has a broader taxonomic distribution (Brusatte et al., 2007). Another example is the presence of mesial denticles significantly smaller than the distal denticles, a dental feature long thought to characterize dromaeosaurid teeth (e.g., Rauhut and Werner, 1995; Milner, 2002; Sweetman, 2004) but also seen on the crowns of other distantly related clades (Rauhut et al., 2010). A broader, more comprehensive understanding of the distribution of key dental morphologies in theropods will reduce errors in taxonomic assessments of isolated teeth.

This research investigates the distribution of 34 discrete dental characters in 200 sauropods, mostly non-avian theropods, and provides functional properties for each of them. We then use a data matrix of 145 dentition-based characters coded in 97 sauropod taxa and a variety of trees from the literature to map the distribution of these characters and to assist other systematists in developing dental character sets. Using our character distributions, we evaluate the taxonomic value of theropod teeth and propose dentition-based synapomorphies for several theropod lineages. We also evaluate homoplasy in different partitions within dental characters and compare our assessments to homoplasy levels in character sets derived from the rest of the skeleton. Finally, we explore the major transformations occurring in the dentition of non-avian theropods throughout their evolution. Our findings should be of broad use to improve the accuracy of taxonomic assessment of isolated theropod teeth, facilitate future study on the systematic paleontology of isolated theropod teeth and ultimately to improve their potential as biostratigraphic markers.

MATERIALS AND METHODS

Material

We investigated dental features on teeth preserved within the upper and lower jaws as well as isolated teeth belonging to a total of 198 taxa bracketed phylogenetically between the basal sauropods Herrerasaurus ischigualastensis (Reig, 1963; Sereno and Novas, 1994) and the basal avialan Archaeopteryx lithographica (Godefroit et al., 2013a; Foth et al., 2014; Lefèvre et al., 2017; Appendix 1.1). The basal saurischians Daemonosaurus (Sues et al., 2011), Eodromaeus (Martínez et al., 2011) and Eoraptor (Sereno et al., 1993, 2013), as well as the Scansoriopterygidae (Czerkas and Yuan, 2002) and the Anchioniidae (sensu Xu et al., 2016; Agnolin et al., 2019; ‘Anchiornithidae’ of Foth and Rauhut, 2017 and ‘Anchiorninae’ of Hu et al., 2018), recently recovered as non-avian theropods by some authors (Sues et al., 2011; Brusatte et al., 2014; Xu et al., 2015b, 2017; Baron et al., 2017; Cau et al., 2017; Müller et al., 2018; Hu et al., 2018), were also included in this study. Of these 200 taxa, we examined firsthand the dentition of 125 taxa deposited in 35 scientific collections from Argentina, France, Belgium, Germany, Italy, Spain, Portugal, Qatar, Switzerland, the United Kingdom, South Africa, China, Canada and the United States (Appendix 1.1). Anatomical observations were assisted with the use of an AM411T Dino-Lite Pro digital microscope. The dentition of a further 34 non-avian theropod taxa was examined from high-quality casts and high-resolution photographs provided by colleagues. Publications with well-illustrated and/or
well-described teeth were used to study an additional 41 taxa (Appendix 1.1).

**Nomenclature on the Theropod Dentition and Theropod Classification**

The anatomical, positional, directional and morphometric nomenclature used in this study (Figure 1) follows the terminology proposed by Hendrickx et al. (2015d). This terminology is partly based on the measurements provided by Smith et al. (2005) and the directional terminology defined by Smith and Dodson (2003). We also follow the dental notation proposed by Smith and Dodson (2003), which identifies 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 (e.g., Rmx3 for the third right maxillary tooth). When referred to cranial and mandibular bones, the non-standardized traditional Owenian/Romerian directional and anatomical terms (Harris, 2004; Wilson, 2006) were favored over the terminology of the *Nomina Anatomica Veterinaria* (ICVGAN, 2012) and the *Nomina Anatomica Avium* (Baumel, 1993), because they are the most commonly used in the

![Figure 1](image-url)
non-avian theropod literature (Eddy and Clarke, 2011; Hendrickx and Mateus, 2014b; Hendrickx et al., 2015a). Consequently, ‘anterior’ and ‘posterior’ are used as directional terms rather than the veterinarian alternatives ‘cranial’ and ‘caudal’, respectively.

The theropod phylogeny used to investigate the distribution of dental features in non-avian theropods mostly follows the classification recently summarized by Hendrickx et al. (2015b), with variation in the phylogenetic position of Eoraptor, Eodromaeus, Daemognosaurus, Dracovenator, Limusaurus and Megaraptor. The classification here—followed is based on the results obtained by: Müller et al. (2018, fifth phylogenetic analysis), based on the dataset of Langer et al. (2017), for non-neotheropod Saurischia; Ezcurra’s (2017) nomenclature for ‘basal clade among Troodontidae. We follow Cau et al. (2017) based on the dataset of Brusatte et al. (2014) for non-tyrannosauroid Coelurosauria as the sister clade of Proceratosauridae (Figure 2). We also follow the phylogenetic tree obtained by Cau et al. (2017) based on the dataset of Brusatte et al. (2014) for non-tyrannosauroid Coelurosauria, with Anchirodhinae being recovered as a basal clade among Troodontidae. We follow Ezcurra’s (2017) nomenclature for ‘Syntarsus’ kayentakatae and Meganosaurus rhodesiensis, also known as Coelophysis kayentakatae and Coelophysis rhodesiensis (e.g., Nesbitt and Ezcurra, 2015; Martinez and Apaldetti, 2017; Pichowski et al., 2019), based on the phylogenetic distribution of these two distantly related taxa among Coelophysoidea. The phylogenetic placement of Sciurumimus at the base of the megalosaurid clade follows the result of the cladistic analysis obtained by Rauhut et al. (2012). Aorun was recently suggested to be the basalmost Alvarezsauriformes by Xu et al. (2018), a paper which came out at the final stage of the correction of this manuscript. The dental evolution of theropods is, therefore, explored based on the phylogenetic placement of Aorun at the base of Coelurosauria. We, however, briefly discuss the evolution of the dentition in Maniraptoriformes based on the inclusion of this taxon within Alvarezsauriformes. We finally adopt the phylogenetic definitions compiled by Hendrickx et al. (2015b) and Hendrickx and Carrano (2016) for each of the non-avian theropod clades, with the exception of Abelisauridae (here being defined as the most inclusive clade containing Carnotaurus sastrei but not Ceratosaurus nasicornis and Noasaurus leali) and Caenagnathoidea (here defined as the least inclusive clade containing Avimimus portentosus, Oviraptor philoceratops and Caenagnathus collinsi).

In most cladistic analyses recently performed on Coelurosauria, Compsognathidae are more closely related to Maniraptoriformes than to Tyrannosauroidea (e.g., Senter, 2007, 2011; Smith et al., 2008; Dal Sasso and Maganuco, 2011; Carrano et al., 2012; Turner et al., 2012; Choiniere et al., 2014a; Brusatte et al., 2014), and the name Neocoeurosauria (Hendrickx, 2015; Paul, 2016) is here used to refer to the clade Compsognathidae + Maniraptoriformes. Likewise, the clade Troodontinae (Gilmore, 1924), defined by Martyniuk (2012, p. 178) as “<Troodon formosus & Sauornithoides mongoliensis", or the least inclusive clade containing Troodon formosus and Sauornithoides mongoliensis, here corresponds to the least inclusive clade containing Sinovenator changii and Troodon formosus, most members of which have teeth bearing denticles. Finally, as for the clade Caenagnathoidea (i.e., Avimimus + Caenagnathidae + Oviraptoridae; sensu Qiu et al., 2019) which gathers edentulous taxa, the clade Ornithomimimshere refers to toothless ornithomimosaurs, which includes the ‘family’-level clades Ornithomimidae and Deinonychidae (sensu Lee et al., 2014b). This node-based taxon can be defined as the least inclusive clade containing Ornithomimus velox and Deinocerurus mirificus (for another definition, see Sereno, 2017).

**Distribution and Degree of Homoplasy of Dental Features**

The distribution, degree of homoplasy and phylogenetic utility of qualitative dental characters were assessed by using a modified version of the dentition-based data matrix created by Hendrickx and Mateus (2014a; Appendices 2, 3.1 and 3.2). To this original dataset of 60 taxa, we removed the poorly known paravian Richardoestesia gilmorei (Currie et al., 1990) and added 38 new theropod taxa, especially focusing on those with peculiar dentition [e.g., Chilesaurus (Novas et al., 2015); Halszkaraptor (Cau et al., 2017); Limusaurus (Wang et al., 2017a)] and basally branching members of major theropod clades (e.g., Nqwebasaurus; De Klerk et al., 2000; Choiniere et al., 2012). Herrerasaurus ischigualastensis (Reig, 1963; Sereno and Novas, 1994) and Archaeopteryx lithographica (Meyer, 1861; Howgate, 1984; Rauhut,
FIGURE 2. Phylogeny and stratigraphic distribution of theropod dinosaurs. Figure modified from Hendrickx et al. (2015b; see references therein). The theropod silhouettes are from Conty (Eodromaeus), the Smithsonian Institution (Daemonosaurus; modified), Julio Garza (Dilophosauridae), Gregory S. Paul (Metriacanthosauridae), T. Michael Keesey (Deinocheiridae), Funkmonk (Alvarezsauroidea and Therizinosauria), Jaime Headden (Caenagnathidae), and Scott Hartman (all other silhouettes). All silhouettes other than those from the Smithsonian Institution and Gregory S. Paul were downloaded from phylopic.org and are under a Creative Commons Attribution-NonCommercial-ShareAlike 3.0 Unported License unless stated otherwise (see Appendix 1.2).
teeth that differ significantly in their morphology that the majority of theropod shed teeth belong to true (i.e., characters 38 to 121). Likewise, given that the majority of theropod shed teeth belong to the lateral dentition (i.e., maxillary and dentary teeth that differ significantly in their morphology from that of premaxillary and mesial dentary teeth; Hendrickx et al. 2015c), the distribution of characters on the lateral dentition (i.e., characters 67 to 121) was also examined.

**Degree of homoplasy of dental characters.** Several methods were performed to evaluate the role of dentition-based characters in phylogenetic reconstruction and to measure the degree of homoplasy of dental features.

- To assess the amount of homoplasy in dental characters and to quantify their utility in providing grouping information, we employed the ensemble consistency and retention indices (CI and RI, respectively; Kluge and Farris, 1969; Farris, 1989) and the individual character consistency and retention indices (ci and ri, respectively). CI is a measure of the amount of homoplasy of an entire dataset on a tree, whereas ci measures the amount of homoplasy in a given character on this tree (Kitting et al., 1998) CI and ci range from 1 (i.e., a CI of 1 denotes that there is no homoplasy and a ci of 1 that the character is non-homoplastic) to a value that asymptotically approaches 0 with increasing amounts of homoplasy, and, for CI, with increasing character sample size. Conversely, RI measures the amount of homoplasy retained as a local synapomorphy (i.e., meaning how many of the homoplastic characters still convey some grouping information) of an entire dataset for a tree, whereas ri measures the amount of homoplasy retained as a local synapomorphy for a given character on this tree. RI and ri range in value from 1 (i.e., all characters fit the tree perfectly; non-ambiguous synapomorphy) to 0 (i.e., no character is synapomorphic for a certain clade; non-synapomorphic character). We also used CI and RI for mean values of ci and ri that were calculated for a set of characters related to the same dentition sub-unit. To provide a baseline assessment of homoplasy, we calculated CI and RI in all eight trees of the non-avian theropod classification. The 145 dental characters and the stats.run script available in TNT (http://phylo.wikidot.com/tntwiki) were used to determine the most consistent tree topology in terms of dental features. We calculated CI and RI in data-sets restricted to non-averostran Saurischia (9 taxa), Ceratosauria (14 taxa), Megalosauroidea (14 taxa), Allosauroidae (13 taxa), Coelurosauria (47 taxa), Maniraptoriformes...
(35 taxa), Paravians (19 taxa) and Dromaeosauridae (11 taxa) to determine the theropod lineages with lowest homoplasy levels in terms of dental characters and to quantify the utility of dental characters for grouping information. Uninformative characters were deactivated using the command XINACT before calculating CI and RI values for each topological tree and each clade.

- To assess and compare the degree of homoplasy between dental and non-dental characters, we appended our dentition-based characters to eight of the most recent datasets on non-avian theropods [i.e., Lee et al. (2014a) based on Cau et al.’s (2014) data matrix, Choiniere et al. (2014a) and Wang et al. (2017a) for non-avian Theropoda; Tortosa et al. (2014) and Rauhut and Carrano (2016) for Ceratosauria; Carrano et al. (2012) for non-coelurosaur Tetanurae; and Cau et al. (2015) using Brusatte et al.’s (2014) dataset and Foth and Rauhut (2017) for Coelurosauria; see Appendix 3.6], by firstly removing the preexisting dental characters from each dataset. All eight resulting supermatrices were imported to Mesquite 3.2 (Maddison and Maddison, 2017) and the tree topology obtained by the authors of each of these data matrices was built with the same software. The CI and RI were calculated on these trees using TNT for each resulting supermatrix after all uninformative characters were deactivated and when the dental characters were: i) included in the dataset, ii) excluded from the supermatrix, and iii) considered separately (i.e., all non-dental characters were excluded from the dataset).

- We then calculated the consistency (ci) and retention (ri) indexes for all dental and non-dental characters in all five supermatrices using the TNT scrip CharStats.run (Ramírez, 2013) and performed a one-sample t-test and Mann-Whitney U-test to ascertain if there were statistically significant differences between the mean values of ci (here noted CI) and ri (here noted RI) of dental and non-dental characters. These statistics, which are parametric and non-parametric estimators of differences in mean between two sets of characters, were performed in all eight supermatrices using PAST3 (Hammer et al., 2001), and the corresponding p-values and Mann-Whitney-scores are found in Appendix 4.1 and 4.2.

- To know whether particular partitions of the dentition and tooth are more reliable than others, we calculated ci and ri for each of the 145 dental characters in all eight theropod tree topologies and measured the mean value of ci and ri (here noted CI and RI, respectively) for each dentition sub-unit, which we arbitrarily pre-defined (i.e., pre-maxillary, maxillary, dentary and palatal teeth, crowns, carinae, denticles and ornamentations for the mesial and lateral dentition, enamel texture and microstructure, and root). We then performed an ANOVA test to identify differences in variance between dentition sub-units using the ci and ri values of all 145 dental characters in the most consistent topological tree. To make post hoc identifications, of which sub-units varied significantly, we calculated Mann-Whitney pairwise comparisons using Bonferroni-corrected p-values on the ANOVA data using PAST3 (Appendix 4.1 and 4.2).

Institutional Abbreviations

- **AM**, Albany Museum, Grahamstown, South Africa
- **AMNH**, American Museum of Natural History, New York City, USA
- **ANSP**, Academy of Natural Sciences, Philadelphia, Pennsylvania, USA
- **AODF**, Australian Age of Dinosaurs Fossil, Australian Age of Dinosaur Museum of Natural History, Winton, Queensland, Australia
- **BMMS**, Bürgermeister Müller Museum, Solnhofen, Germany
- **BMNH**, Beijing Museum of Natural History, Beijing, China
- **BP**, Evolutionary Studies Institute (formerly “Bernard Price Institute for Palaeontological Research”), University of the Witwatersrand, Johannesburg, South Africa
- **BSPG**, Bayerische Staatsammlung für Paläontologie und Historische Geologie, München, Germany
- **BYU-VP**, Brigham Young University Museum of Vertebrate Paleontology, Provo, USA
- **CAGS**, Chinese Academy of Geological Sciences, Beijing, China
- **CCMGE**, Chernyshev’s Central Museum of Geological Exploration, Saint Petersburg, Russia
- **CEU**, College of Eastern Utah, Price, Utah, USA
- **CMNH**, Carnegie Museum of Natural History, Pittsburgh, USA
- **CV**, Chongqing Museum of Natural History, Chongqing, China
- **DINO**, Dinosaur National Monument, Vernal, Utah, USA
- **DLXH**, Dalian Xinghai Museum, Dalian, Liaoning Province, China
- **DMNH**, Perot Museum of Nature and Science, Dallas, Texas, USA
- **DMNS**, Denver Museum of
Nature and Science, Denver, Colorado, USA; DMR-TF, Department of the Mineral Resources, Palaeontological collection, Bangkok, Thailand; DNHM, Dalian Natural History Museum, Dalian, Liaoning Province, China; ELDM, Erenhot Dinosaur Museum, Erenhot, Inner Mongolia, China; FMNH, Field Museum of Natural History, Chicago, USA; FPDM, Fukui Prefectural Dinosaur Museum, Katsuyama, Fukui, Japan; FRDC-GS, Fossil Research and Development Center, Gansu Bureau of Geology and Mineral Resources Exploration, Lanzhou, China; GR, Ghost Ranch Ruth Hall Museum of Paleontology collections, Ghost Ranch Conference Center, New Mexico, USA; HG, Palaeontological Center, Bohai University, Jinzhou City, China; HGM, Henan Geological Museum, Zhengzhou, Henan Province, China; HMN, Museum für Naturkunde, Berlin, Germany; ISIR, Indian Statistical Institute, Kolkata, India; IVPP, Institute for Vertebrae Palaeontology and Paleoanthropology, Beijing, China; JFPM, Geological Museum of the Jilin University, Changchun, Jilin province, China; JME, Jura Museum Eichstätt, Eichstätt, Germany; JMP, Jinzhou Museum of Palaeontology, Jinzhou, Liaoning Province, China; JZMP, Jinzhou Museum of Palaeontology, Jinzhou, Liaoning Province, China; KMV, Kunming Municipal Museum, Guandu district, China; LDM-LCA, Lufeng Dinosaur Museum-Lufeng Chuanjie A'na, A'na, China; LFGT, Bureau of Land and Resources of Lufeng County, Lufeng, Yunnan, China; LH PV, Long Hao Institute of Geology and Paleontology, Hohhot, Nei Mongol, China; LHC, Las Hoyas Collection, Universidad Autónoma de Madrid, Madrid, Spain; LPMB, Liaoning Paleontological Museum, Liaoqing, China; MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; MB, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; MCCM, Museo de Ciencias de Castilla-La Mancha [now MUPA, Museo de Paleontología de Castilla-La Mancha], Cuenca, Spain; MCF-PVPH, Museo Municipal ‘Carmen Fuñes,’ Plaza Huincul, Argentina; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MG, Museu Geológico, Lisbon, Portugal; MHNA-PV, Muséum d’Histoire Naturelle d’Aix-en-Provence, France; MIWG, Dinosaur Isle, Isle of Wight Museum Services, Sandown, UK; ML, Museu da Lourinhã, Lourinhã, Portugal; MLP, Museo de La Plata, La Plata, Argentina; MMCN-PV, Museo Municipal ‘Ernesto Bachmann,’ Villa El Chocón, Neuquén, Argentina; MML, Museo Municipal de Lamarque, Río Negro, Argentina; MNA, Museum of Northern Arizona, Flagstaff, Arizona, USA; MNHN, Muséum national d’Histoire naturelle, Paris, France; MNN, Musée National du Niger, Niamey, Niger; MNUF, Mongolia National University, Ulaanbaatar, Mongolia; MOR, Museum of the Rockies, Bozeman, Montana, USA; MPCA, Museo Provincial Carlos Ameghino, Cipolletti, Río Negro, Argentina; MPCD, Institute of Palaeontology and Geology, Mongolian Academy of Sciences (formerly IGM), Ulaanbaatar, Mongolia; MPCO.V, Museo de Paleontología de Cruzeiro do Oeste, Cruzeiro do Oeste, Brazil; MPEF-PV, Museo Paleontológico ‘Egidio Feruglio,’ Trelew, Argentina; MPMP-V, Museo Padre Molina Paleontología de Vertebrados, Río Gallegos, Santa Cruz, Argentina; MSM, Mesa Southwest Museum, Mesa, Arizona, USA; SMNM, Museo di Storia Naturale di Milano, Milan, Italy; MSP, Arizona Museum of Natural History, Mesa, Arizona, USA; MUCPV, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; MWC, Museum of Western Colorado, Fruita, Colorado, USA; NCSM, North Carolina Museum of Natural Sciences, Raleigh, USA; NGMC, National Geological Museum of China, Beijing, China; NHFO, Natural History Fossil Collection, Qatar Museum Authority, Doha, Qatar; NHMUK PV, Natural History Museum, London, UK; NIGP, Nanjing Institute of Geology and Palaeontology, Nanjing, China; NMC, Canadian Museum of Nature, Ottawa, Ontario, Canada; NNMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; NMW, National Museum Wales, Cardiff, UK; OCP, Office Chérifien des Phosphates, Khouribga, Morocco; OUMNH, Oxford University Museum, Oxford, UK; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; PMoL, Paleontological Museum of LiaoNing, Shenyang, Liaoqing, China; PULR, Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Fundación ‘Miguel Lillo,’ San Miguel de Tucumán, Argentina; PVLS, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; QG, Zimbabwe Natural History Museum, Bulawayo, Zimbabwe; RMM, McWane Science Center, Birmingham, Alabama, USA; ROM, Museum of the Rockies, Bozeman, Montana, USA; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; SBA-SA, Soprintendenza per i Beni Archeologici di Salerno Avellino Benevento e Caserta, Salerno, Italia; SGM, Ministère de l’Énergie et des Mines, Rabat, Morocco; SMA, Sauriermuseum Aathal, Aathal, Switzerland; SMINS, Staatliches Museum für Naturkunde, Stuttgart,
RESULTS

Summary

- ‘Super’-family and ‘family’-level clades are better defined by dental characters than major theropod clades such as Ceratosauria, Maniraptora and Tetanurae.
- Spinosauridae (21 synapomorphies), followed by Allosauroidea (7), and Abelisauridae, Tyrannosauridae, and Therizinosauria (6), are the best-supported clades in terms of dental features.
- CI values of the dentition-based data matrix are particularly low (~0.2) in all eight trees of the theropod phylogeny, and RI values are close to 0.45.
- The tree topology hypothesizing Epidexipteryx as the basalmost oviraptorosaur is the most consistent in terms of dental features.
- Megalosauroidea is the theropod clade with the least amount of dental homoplasy, and whose dental characters provide the most useful grouping information.
- Excluding dental characters improves CI and RI in all eight supermatrices (i.e., character matrices that combine our dentition-based data matrix with different recently published matrices on the theropod skeleton).
- CI values are not significantly different when including or excluding dental characters in Choiniere et al.’s (2014a) and Lee et al.’s (2014a) matrices dealing with non-avian theropod classification.
- Highest CI values of dental characters are obtained for the datasets of Tortosa et al. (2014) and Rauhut and Carrano (2016) on ceratosaur relationships.
- Among all dental sub-units, the crown enamel texture and microstructure show the highest CI and RI values.

Distribution of Apomorphic Dental Characters

Our sample of eight trees shows that the majority of theropod clades and OTUs are diagnosed by dentition-based characters that show homoplasy across our taxonomic sample (Figures 3 and 4; Appendices 3.1 and 5). In non-avetheropod theropods, most major clades such as Neotheropoda, Averostra, Ceratosauria, Tetanurae, Orioniides and Megalosauroidea are defined by zero-to-two dentition-based synapomorphies, whereas three or more dental features support most ‘family’-level clades such as Ceratosauridae, Abelisauridae, Piatnitzkysauridae and Spinosauridae. In Avetheropoda, most major clades and ‘super-family’ and ‘family’-level subclades such as Avetheropoda, Allosauroidea, Neovenatoridae, Carcharodontosauridae, Coelurosauria, Tyrannosauroidea, Compsognathidae, Ornithomimosauria, Therizinosauria, Maniraptoriformes, Pennaraptora, Dromaeosauridae and Troodontidae are also supported by three or more dentition-based synapomorphies. The distribution of crown-based characters (i.e., characters related to the mesial and lateral crowns and excluding those on the size, disposition and outline of premaxillary, maxillary and dentary alveoli as well as the root and enamel microstructure) also shows that many ‘super-family’, ‘family’ or ‘sub-family’ level clades are defined by a combination of three or more crown-based characters (Appendices 3.1 and 5, Tree topology 9). Likewise, the majority of theropod genera are diagnosed by two or more crown-based autapomorphies, particularly so in non-maniraptori-
FIGURE 3. Dentition-based synapomorphies in non-coelurosaur Saurischia. Dentition-based synapomorphies on a tree following the topology obtained by Müller et al. (2018) for non-averostran Saurischia, Rauhut and Carrano (2016) and Wang et al. (2017a) for Ceratosauria, and Rauhut et al. (2016) for non-coelurosaurian Tetanurae, Brusatte and Carr (2016) for Tyrannosauroidea. The list of dental synapomorphies for each clade is provided in Table 1. Abbreviations: CBR, Crown Base Ratio; d, number of dentary teeth; de, number of denticles; DSDI, denticle size density index; m, number of maxillary teeth; pm, number of premaxillary teeth. For silhouette acknowledgements see Appendix 1.2.
FIGURE 4. Dentition-based synapomorphies in Coelurosauria. Dentition-based synapomorphies on a tree following the topology obtained by Cau et al. (2017) based on the dataset of Brusatte et al. (2014) for non-tyrannosauroid Coelurosauria. The list of dental synapomorphies for each clade is provided in Table 1. Abbreviations: CHR, Crown Height Ratio; d, number of dentary teeth; dc, distal carina; DSDI, denticle size density index; lad, labial depression; m, number of maxillary teeth; mc, mesial carina; pm, number of premaxillary teeth. For silhouette acknowledgements see Appendix 1.2.
form theropods and Dromaeosauridae. However, fewer than two lateral crown-based autapomorphies characterize most non-avian theropod genera, especially among non-ziphodont theropod clades with simple dentition (i.e., Ornithomimosauria, Alvarezsauroidae, Oviraptorosauria and Troodontidae; Appendices 3.1 and 5, Tree topology 10). Subtle differences in the distribution of dentition-based synapomorphies occur between each non-avian theropod tree represented here. However, most major theropod clades (i.e., Averostra, Avetheropoda, Maniraptoriformes, Neo-coelurosauria, Maniraptora and Pennaraptora) are diagnosed by the same number of apomorphic dental features in the large majority of trees (Appendices 3.1 and 5).

With 21 synapomorphies, Spinosauridae is by far the best-supported clade in terms of dentition-based features (Figure 3; Table 1). It is followed by the clades Spinosaurinae and Allosauroidae, with seven synapomorphies each. With six synapomorphies, the clades Abelisauroidae, Tyrannosauridae, Pantyrranosauria and Therizinosauridae are also well-supported by dental characters (Figures 3 and 4; Table 1). On the other hand, no dental synapomorphies support the clades Neotheropoda, Ceratosauria, Tetanurae, Ornithocheiridae, Alvarezsauroidae and Troodontidae + Avialae (see discussion).

The folidont and putative theropod Chilesaurus shows the most dentition-based, tooth-based and lateral crown-based autapomorphies of any individual theropod genus (23, 16 and 9, respectively; Appendices 3.1 and 5). It is followed by Epidexipteryx and Scirurumimus (12) as well as Dracovenator and Jianchangosaurus (11), whereas Saurornitholestes and Deinonychus are supported by 10 dentition-based characters. Jianchangosaurus (10), Eoraptor (9), Afrovenator (8), Scirurumimus (8), Acrocanthosaurus (8), Troodon (8) and Dracovenator (7) are also diagnosed by more than six crown-based autapomorphies, whereas Afrovenator (8), Piatnitzkysaurus (6), Eoraptor (6) and Skorpiovenator and Eodromaeus (5 each) display the unique combination of more than four lateral crown-based characters. Out of the 93 toothed taxa included in our data matrix, 74 and 62 are diagnosed by one or more crown-based and lateral crown-based apomorphic characters, respectively. Among the theropods showing apomorphic dental features, 31 are diagnosed by three or more crown-based characters, whereas 38 taxa are diagnosed by two or more lateral crown-based autapomorphies.

Degree of Homoplasy of Dental Features

Degree of homoplasy and grouping information of dental characters. With values ranging from 0.2075 (tree 4) to 0.209 (tree 5), CI is particularly low and relatively similar in all eight trees (Appendix 4.2, Table A1). Likewise, RI values vary slightly between trees and range from 0.448 (tree 4) to 0.4531 (tree 5). With 1210 steps and CI and RI of 0.2091 and 0.4531, respectively, the tree hypothesizing the scansoriopterygid Epidexipteryx as the basalmost oviraptorosaur (tree 5), is the most consistent in terms of dental features (Appendix 4.2, Table A1). On the other hand, the longest tree (tree 4), which provides the least consistent explanation of our dental observations, hypothesizes that megaraptors are tyrannosaurids (1219 steps; CI of 0.2075 and RI of 0.448).

With CI and RI values of 0.689 and 0.707, respectively, Megalosauroidea (n = 14) is the non-avian theropod clade with the least amount of dental homoplasy, and whose dental characters provide the most useful grouping information (Appendix 4.2, Table A2). Ceratosauria (n = 14; CI of 0.683 and RI of 0.653) and Allosauroidae (n = 13; CI of 0.547; RI of 0.448) show the second and third lowest amount of dental homoplasy, respectively. On the other hand, coelurosaurians (n = 47; CI of 0.341; RI of 0.498), followed by maniraptoriforms (n = 35; CI of 0.378; RI of 0.472) and paravians (n = 19; CI of 0.472; RI of 0.502), have the highest amount of dental homoplasy, whereas dental characters provide the least important grouping information among non-averostran theropods (n = 9; RI of 0.174; CI of 0.513) and Dromaeosauridae (n = 11; RI of 0.329; CI of 0.51).

Excluding dental characters generally improves CI and RI (Figure 5.1). The highest values of CI and RI were obtained when dentition-based characters are excluded from the dataset in all eight supermatrices, whereas the lowest values of CI and RI occurred when the dentition-based data matrix was considered separately (Figure 5.1; Appendix 4.2, Table A3). CI, although strongly correlated with the number of taxa, does not show a significant relationship to the number of characters (Sanderson and Donoghue, 1989). CI values show little variation when dental characters are either included or excluded for the supermatrices of Choiniere et al. (2014a) and Lee et al. (2014a) (Figure 5.1; Appendix 4.2, Table A3). Mann-Whitney U-test scores based on CI values confirm that the difference between dental and non-dental characters is not statistically significant for those two datasets (p-values > 0.05; Table 2; Appendix 4.2, Table A4).
**TABLE 1.** List of unambiguous dental synapomorphies in 40 theropod clades illustrated in Figures 3 and 4 and based on a data matrix of 145 dental characters coded in 97 saurischian taxa.

<table>
<thead>
<tr>
<th>Clade</th>
<th>Unambiguous dental synapomorphy</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Eoraptor + Theropoda</td>
<td>Character 4: partial overlap of the first and second premaxillary alveoli in palatal view</td>
</tr>
<tr>
<td>2. Dracovenator + Neotheropoda</td>
<td>Characters 15, 120: slightly constricted premaxillary tooth row in palatal view; braided oriented enamel surface texture not clearly visible with light</td>
</tr>
<tr>
<td>3. Liliensternus + Dilophosaurus + Averostra</td>
<td>Character 31: first dentary tooth/alveolus substantially smaller than second and third dentary teeth/alveoli</td>
</tr>
<tr>
<td>4. Dilophosaurus + Averostra</td>
<td>Characters 56: 14 to 19 mid-crown denticles per five millimeters on the distal carina (DC) of mesial teeth in subadults/adults</td>
</tr>
<tr>
<td>5. Averostra</td>
<td>Character 15: unconstricted premaxillary tooth row in palatal view</td>
</tr>
<tr>
<td>6. Abelisauridae</td>
<td>Characters 8, 9, 45, 46, 51: mesial and distal premaxillary teeth subequal in size than the first six mesial maxillary teeth (or alveoli); salinon-shaped outline of basal cross-section of the crown in the mesialmost tooth; concave surfaces adjacent to the mesial distal carina on the lingual side of the mesial teeth; mesial carina extends to the cervix or just above it in mesial teeth</td>
</tr>
<tr>
<td>7. Ceratosauridae</td>
<td>Characters 5, 69, 94: overlap of the second and third premaxillary alveoli in palatal view; largest crown in subadults/adults higher than six centimeters; subquadrangular mesial denticles at two-thirds of the crown in lateral teeth</td>
</tr>
<tr>
<td>8. Noasauridae</td>
<td>Characters 31, 40: first dentary tooth/alveolus subequal size in than second and third dentary alveolus; largest crown in subadults/adults shorter than one centimeter</td>
</tr>
<tr>
<td>9. Abelisauridae</td>
<td>Characters 3, 4, 13, 25, 91, 99: premaxillary alveoli all mesio-distally oriented; no overlap of the first and second premaxillary alveoli in palatal view; subrectangular premaxillary and maxillary alveoli; distal denticles hooked and apically inclined from distal margin in lateral teeth</td>
</tr>
<tr>
<td>10. Megalosauroidea</td>
<td>Character 82: mesial carina extending to base of crown or slightly above the cervix in lateral teeth</td>
</tr>
<tr>
<td>11. Piatnitzkysauridae</td>
<td>Characters 19, 104, 108, 112, 113: 18 to 19 maxillary teeth/ alveoli; distal denticles larger than mesial ones in lateral crowns (DSDI &gt; 1.2); short and poorly developed interdenticular sulci between mid-crown denticles on the distal carina in lateral teeth; tenuous and numerous transverse undulations on the crown surface of lateral teeth</td>
</tr>
<tr>
<td>12. Megalosauria</td>
<td>Character 53: mesial carina facing labially in mesialmost teeth</td>
</tr>
<tr>
<td>13. Megalosauridae</td>
<td>Character 28: fewer than 15 dentary teeth/alveoli</td>
</tr>
<tr>
<td>14. Megalosauridae more derived than Sciurumimus</td>
<td>Characters 5, 56, 108, 109: overlap of the second and third premaxillary alveoli in palatal view; nine to 13 denticles per five millimeters on the distal carina at mid-crown in mesial teeth; short and poorly developed interdenticular sulci between basal and mid-crown denticles on the distal carina in lateral teeth</td>
</tr>
<tr>
<td>15. Spinosauridae</td>
<td>Characters 2, 7, 8, 11, 12, 14, 15, 22, 23, 25, 30, 33, 45, 51, 63, 70, 76, 82, 110, 141, 142: more than six premaxillary teeth; distal premaxillary teeth smaller than mesial premaxillary teeth; mesial premaxillary and maxillary teeth subequal in size; second premaxillary tooth/alveolus significantly smaller than third and fourth tooth/alveolus; distalmost premaxillary tooth significantly smaller than more mesial teeth; premaxillary teeth anterior to external naris; strongly lateromedially constricted premaxillary tooth rows; first maxillary tooth/alveolus significantly smaller than second tooth/alveolus; procumbent mesial maxillary teeth; subcircular maxillary alveolus; mesialmost dentary teeth significantly larger than more distal ones; terminal rosette of the dentary bearing four teeth; outline of the basal cross-section of mesial teeth subcircular; mesial carina extending well-beneath the cervix in mesial teeth and to the base of crown or slightly above the cervix in lateral teeth; flutes present on the lingual surface of mesial teeth; distal margin of lateral teeth convex, with apex centrally positioned; CBR &gt; 0.75 in lateral teeth; subcircular cross-sectional outline of lateral teeth; flutes on both lingual and labial sides of lateral teeth; root strongly tapered apically and oval to subcircular in cross-section at mid-root</td>
</tr>
<tr>
<td>16. Avetheropoda</td>
<td>Characters 41, 50, 51: labiolingual compression of the crown weak (0.75 &lt; CBR &lt; 1.2, tooth subcircular) in mesial teeth; mesial carina of mesial teeth slightly twisted, curves onto the mesiolingual surface; mesial carina extends to the cervix or slightly above it in mesial teeth</td>
</tr>
<tr>
<td>Table 1 (continued)</td>
<td></td>
</tr>
<tr>
<td>---------------------</td>
<td></td>
</tr>
<tr>
<td><strong>Clade</strong></td>
<td><strong>Unambiguous dental synapomorphy</strong></td>
</tr>
<tr>
<td>17. Allosauroida</td>
<td>Characters 5, 46, 55, 56, 87, 94, 108, 112: overlap of the second and third premaxillary alveoli in palatal view; concave surface on the labial and lingual surfaces adjacent to the distal and mesial and distal carinae, respectively, in mesial teeth; nine to 13 mesial and distal denticles per five millimeters in mesial teeth, and nine to 15 in the mesial carina of lateral teeth; subquadrangular mesial denticles at two-thirds height of crown in lateral teeth; short and poorly developed interdenticular sulci between distal denticles at mid-crown in lateral teeth; tenuous or well-visible transverse undulations on the crown surface of lateral teeth</td>
</tr>
<tr>
<td>18. Metriacanthosauridae</td>
<td>Characters 74, 120: surface centrally positioned on the labial surface of the crown roughly flattened in lateral teeth; irregular and non-oriented enamel surface texture</td>
</tr>
<tr>
<td>19. Allosauria</td>
<td>Characters 9, 109: distal premaxillary teeth/alveoli subequal in size than the first six mesial maxillary teeth/alveoli; short and poorly developed interdenticular sulci in basal denticles of the distal carina</td>
</tr>
<tr>
<td>20. Neovenatoridae</td>
<td>Characters 22, 74, 75: first maxillary tooth significantly smaller than second maxillary tooth; surface centrally positioned on the labial surface of the crown roughly flattened in lateral teeth; concave surface adjacent to the distal carina on the labial and lingual surfaces, in lateral teeth</td>
</tr>
<tr>
<td>21. Carcharodontosauridae</td>
<td>Characters 45, 46, 97: subcircular, ovoid or elliptical outline of basal cross-section of the crown in the mesialmost tooth; concave surface adjacent to the carina absent in mesial teeth; biconvex mesial denticles</td>
</tr>
<tr>
<td>22. Coelurosauria</td>
<td>Characters 56, 87, 104: more than 20 distal denticles at mid-crown and more than 30 mesial denticles at two-thirds height of the crown in mesial and lateral teeth, respectively; distal denticles larger than mesial ones in lateral crowns (DSDI &gt; 1.2)</td>
</tr>
<tr>
<td>23. Tyrannosauroidea + Neocoelurosauria</td>
<td>Character 95: mid-crown denticles (DC) on distal carina as long mediocostally as apicobasally, subquadrangular, in lateral teeth</td>
</tr>
<tr>
<td>24. Tyrannosauroidea</td>
<td>Characters 5, 6, 30, 50, 52, 54: overlap of the second and third as well as third and fourth premaxillary alveoli in palatal view; mesialmost dentary teeth significantly smaller than mid- and distal dentary teeth; mesial carina of mesial teeth strongly twisted, curving onto the lingual surface; distal carina of mesial teeth strongly labially deflected and facing mostly lingually</td>
</tr>
<tr>
<td>25. Pantyrranosauria</td>
<td>Characters 3, 42, 45, 50, 56, 87: all premaxillary alveoli labio-lingually oriented; important baso-apical elongation of the crown (2.5 &lt; CHR ≤ 3) in mesial teeth; U-shaped outline of basal cross-section of the crown in the mesialmost tooth; mesial carina almost straight and strongly lingually deflected in mesial teeth; fewer than 20 distal denticles per five millimeters at mid-crown in the mesial dentition of subadults/adults, and fewer than 30 mesial denticles per five millimeters at two-thirds height in the lateral dentition</td>
</tr>
<tr>
<td>26. Tyrannosauridae</td>
<td>Character 4: overlap of the first and second premaxillary alveoli in palatal view almost complete</td>
</tr>
<tr>
<td>27. Neocoelurosauria</td>
<td>Characters 49, 84: unserrated distal carina in mesial teeth; distal carina extends well-above the cervix in lateral teeth</td>
</tr>
<tr>
<td>28. Compsognathidae + Maniraptoriformes</td>
<td>Characters 45, 120: subcircular outline of basal cross-section of the crown in the mesialmost tooth; smooth or irregular non-oriented enamel surface texture of the crown</td>
</tr>
<tr>
<td>29. Compsognathidae</td>
<td>Characters 22, 43, 140: First maxillary tooth significantly smaller than second maxillary tooth; strongly distally recurved mesial teeth; root with convex mesial and distal margins, root significantly larger than base crown</td>
</tr>
<tr>
<td>30. Maniraptoriformes</td>
<td>Characters 19, 44, 70, 72, 76: more than 19 maxillary teeth; distal margin of the mesial crowns straight in lateral view; weak (i.e., CBR &gt; 0.75) labiodistal compression of the lateral crowns; margin of crown convex, so that the crown apex of lateral teeth is centrally positioned; subcircular cross-sectional outline at the base crown in lateral teeth</td>
</tr>
<tr>
<td>31. Ornithomimosauria</td>
<td>Characters 18, 25, 26, 73: maxillary teeth absent in the anterior most and/or most of the posterior portion of the maxilla; maxillary alveoli merged to form an open groove; distalmost maxillary tooth aligned to the anteroventral rim of the antorbital fenestra; mesial margin of lateral teeth slightly convex, almost straight</td>
</tr>
<tr>
<td>32. Alvarezsauridea + Maniraptora</td>
<td>Character 32: mid-dentary teeth/alveoli subequal in size than mesial maxillary teeth/alveoli</td>
</tr>
<tr>
<td>33. Maniraptora</td>
<td>Character 140: root with convex margins, root significantly larger than crown base</td>
</tr>
</tbody>
</table>
CI values between dental and non-dental characters are significantly different (t-test and Mann-Whitney U-test with p-values <0.05) for all other supermatrices (Figure 5.1). There are also significant differences in RI for dental and non-dental characters for all eight supermatrices (Table 2). CI values are lower for dental characters in all eight supermatrices and range from 0.239 to 0.591 in all datasets. The highest CI values for dental characters are found in two datasets on ceratosaurs [i.e., Rauhut and Carrano (2016) and Tortosa et al. (2014); Appendix 4.2, Table A4]. Similarly, dental characters always show lower RI values, varying from 0.379 to 0.559, with the highest value obtained for the dataset of Tortosa et al. (2014; ceratosaurs; Appendix 4.2, Table A4).

Degree of homoplasy and grouping information of each dental sub-units/characters. With values of 0.62 and 0.565, the dentition sub-units showing the highest CI scores are the crown enamel texture and microstructure (n, the total number of characters on crown enamel texture and microstructure in the dataset = 20) as well as the mesial crown ornamentations (n = 4), respectively (Figure 5.2; Appendix 4.2, Table A4). The lowest CI scores are for the carina (0.183; n = 8) and crown (0.215; n = 9) morphology in the mesial dentition, but also for the carina (0.216; n = 10), denticle (0.222; n = 23) and crown (0.216; n = 10) morphology of the lateral dentition (Figure 5.2). Characters on the premaxillary (n = 17), maxillary (n = 9) and dentary teeth (n = 10) as well as on the root morphology (n = 6) also show particularly low CI values (average values from 0.229 to 0.286). The highest RI scores are for the enamel texture and microstructure (0.58), premaxillary teeth (0.472) and carina morphology of both mesial and lateral dentitions (~0.46; Figure 5.2). The lowest RI scores are for the lateral crown ornamentations (0.231; n = 10; Figure 5.2). Most of the 34 dental features that we highlight have CI scores below 0.3 and RI scores above 0.4. This is particularly the case for lateral dentition characters, half of which have RI values higher than 0.45 (Appendix 4.2, Table A6). ANOVAs show that there is no statistically significant difference of variance in RI values between each of the dentition sub-units (Appendix 4.2, Table A8). On the other hand, the difference of variance in CI between enamel characters and characters on the premaxillary and dentary teeth, mesial and lateral crown morphology, carina morphology, and lateral denticle morphology is statistically significant (Appendix 4.2, Table A7).

**DISCUSSION**

**Summary**

- The high levels of homoplasy exhibited by dental features result from a large amount of convergence in the dentition of distantly related theropod taxa with similar feeding strategies.
- Dental characters are the least homoplasmatic and provide the most important grouping.
information for Megalosauroidea and Cera-
tosauria. This results from the highly special-
ized dentition of Spinosauridae and the
diagnostic dentition of Ceratosauridae and
Abelisauridae.

• Dental features always convey less group-
ing information than characters derived from
the rest of the skeleton. Nevertheless, over
broad phylogenetic ranges such as non-
avian theropods, dentition-related charac-
ters might be just as homoplastic as non-
dental characters.

• Crown ornamentations and microstructure
should be prioritized when attempting to
ascribe theropod teeth to a certain taxon as
they are the least homoplastic dental sub-

FIGURE 5. CI and RI scores obtained in eight supermatrices separated into skeleton-based, non-dental based and
dental-based data matrices, and CI and RI values for each dentition sub-unit. 1, CI and RI scores in eight supermatric-
escues combining our dentition-based data matrix to eight of the most recent datasets on non-avian theropods, cerato-
saurs, non-coelurosaur tetanurans and non-avian coelurosaur, when dental characters are included (whole
skeleton), excluded (non-dental), and considered separately (dental); 2, CI and RI values measured for each dentition
sub-unit in eight trees of the theropod classification (see Appendix 4.2, Table A5). Abbreviations: dent, dentition.
unit and convey the most important grouping information.  
• Among the 34 dental features we highlight, longitudinal ridges and flutes on the crown are the least homoplastic. Additionally, crown height and thickness, the presence and extension of the mesial carina, the cross-sectional outline and enamel surface texture convey the most important grouping information. Conversely, the absence of denticles on the mesial carina, a labially deflected distal carina, the shape of mesial/distal denticles, the difference in size between mesial and distal denticles, and the presence and development of transverse/marginal undulations and interdenticular sulci provide little grouping information.  
• Few theropod taxa bear diagnostic crowns that can be identified at the genus level due to morphological convergence and the variability of dental features (e.g., extension of the mesial carina, presence of mesial denticles, labial/lingual depressions, longitudinal ridges, marginal and transverse undulations) along the tooth row in a single individual.  
• Most isolated theropod shed teeth, which are typically from the lateral dentition, do not show taxonomic precision sufficient for fine-scale biostratigraphic analysis. Nevertheless, some theropod taxa such as Majungasaurus, Piatnitzkysaurus, Afrovenator, Acrocanthosaurus, Tyrannosaurus, Saurornitholestes, and Troodon have highly diagnostic teeth that may be useful biostratigraphic markers.  
• The most important evolutionary transition in the dentition of theropod dinosaurs occurred with the emergence of Spinosauridae, which are characterized by a highly specialized dentition showing a strong adaptation towards piscivory. Several authors have proposed a list of evolutionary steps leading to the derived dentition of Spinosauridae based on putative spinosaurid teeth from the Jurassic of Africa. These isolated teeth, however, likely belong to non-spinosaurid theropods so that the timing and novelty sequence of the apomorphic dental characters displayed by spinosaurids (e.g., flutes, minutes denticles, veined enamel texture) remain unknown.  
• Two important evolutionary steps in the dentition of theropods occurred during the radiation of Allosauroidea and Tyrannosauroidea. Both clades evolved independently transversely thick asymmetrical mesial teeth with J-shaped and/or salinon-shaped cross-sectional outline and a mesial carina that migrated mesiolingually. These evolutionary changes can be functionally explained by an anteroposterior shortening of the premaxilla possibly as the result of adaptation to a diet involving increased levels of bone-crunching and bone-biting, with a high degree of torsion applied on the mesial dentition.  
• The most important transition in the evolution of the coelurosaur dentition, marked by tooth simplification, occurred with the radiation of Maniraptoriformes and likely results from a trophic shift between carnivory and herbivory. The changes in tooth morphology can be summarized by three evolutionary steps: i) a loss of mesial denticles in both mesial and lateral teeth, and a loss of distal denticles in mesial teeth in basal neocoeurosaurians; ii) the development of conical mesial teeth and an irregular enamel surface texture in the clade Compsognathidae + Maniraptoriformes; and iii) an increase in the number of maxillary teeth, the loss of a distal curvature in both mesial and lateral teeth, and the development of lateral teeth with a subcircular outline in Maniraptoriformes.  

Taxonomic Potential of Theropod Teeth  
Homoplasy and grouping information in theropod dental features. Dentition-based characters exhibit high levels of homoplasy among non-avian theropods (CI values are ~0.21 for each of the theropod trees we examined). However, the homoplasy present in dental characters is apportioned in such a way that they still provide useful grouping information and are thus potentially of taxonomic value (RI values ~0.45). CI and RI increase when dental characters are not taken into consideration in all eight supermatrices (Figure 5.1), indicating that non-dental characters are typically less homoplastic and convey more grouping information than dentition-based features. Megalosauroids and ceratosaurians were revealed to be the theropod clades with the least amount of dental homoplasy. Dental characters also provide the most important grouping information in these two clades (Appendix 4.2, Table A2). High CI and RI values in Megalosauroidea and Ceratosauria likely result from the derived and highly peculiar dentition of Spinosauridae (see below) and the diagnostic dentition of Ceratosauridae and Abelisauridae. CI and RI val-
ues obtained in each non-avian theropod clade also reveal that the amount of dental homoplasy and the usefulness of dental characters in providing grouping information are neither greater nor lower in basal or derived theropod lineages.

The data matrices of Choiniere et al. (2014a) and Lee et al. (2014a), which returned relatively similar CI values regardless of dental character inclusion/exclusion from the supermatrices (Figure 5.1; Table 2; Appendix 4.2, Table A4), are two out of three of the larger, more comprehensive data- sets in non-avian theropods, and thus large differences in homoplasy levels between dental and non-dental characters in other smaller datasets might be an artifact of low character and taxon sample size in other theropod datasets. These results may also indicate that over broad phylogenetic ranges, or when huge numbers of characters are sampled, dental characters might be just as homoplasic as other characters. Nevertheless, significant differences of CI values between dental and non-dental characters in Wang et al.’s (2017a) dataset on non-avian theropods, which is the second largest used in this study, suggests that characters on the dentition tend to be more homoplastic than the rest of the skeleton even over broad phylogenetic ranges. The significant differences in RI among dental and non-dental characters in all eight supermatrices (Table 2), and when dental characters are included and excluded from each of these datasets, clearly indicate that dental features always convey less grouping information than the rest of the skeleton. The highest CI values for dental characters were obtained from the datasets of Tortosa et al. (2014) and Rauhut and Carrano (2016), which show 0.5 to 0.6 values, respectively. This suggests that dental features are less homoplastic for ceratosaurs. This may result from the low sample size of these datasets, which only contain 15 to 16 taxa. Analysis of clades within datasets with more characters shows that ceratosaurs, as well as megalosauroids, have less dental homoplasy than other theropod lineages. Meaningful differences, which cannot be attributed to known effects of sample size on CI and RI, indeed appear to be present between groups of relatively similar sample sizes that have independent lineage histories such as Ceratosauria, Megalosauroidea, Allosauroida, and Dromaeosauridae. RI values for dental characters range from 0.42 to 0.48 in the datasets dealing with ceratosaurs, non-coelurosaur tetanurans and non-avian coelurosaurs, providing relatively similar grouping information in each of these clades. Dental characters provide more useful grouping information in Megalosauroidea and Ceratosauria than in Allosauroida, Coelurosauria, Maniraptoriformes or Paravians.

The high degree of homoplasy among dental features can be explained by a large amount of convergence in the dentition of distantly related theropod taxa with similar feeding strategies. The lateral dentitions of ceratosaurs, piatnitzkysaurids, allosauroids, basal tyrannosauroids and dromaeosaurids have many dental features in common and only subtle differences such as the extension of the mesial carina on the crown, the difference in size between mesial and distal denticles and the presence and extension of labial and/or lingual depressions on the crown can differentiate them (C.H. personal obs.). This also explains the strong homoplasy displayed by characters on premaxillary, maxillary and dentary teeth, as well as the crown, carina and denticle morphology of both mesial and lateral dentitions. All these dental features appear to be dominated by functional constraints so that distantly related theropods with similar feeding strategies will rapidly and convergently acquire these characters throughout their evolu-

**TABLE 2.** p-values of the t-test and Mann-Whitney U-test (M-W) for CI and RI values between dental and non-dental characters in five datasets of the theropod skeleton. Significantly similar values between dental and non-dental sets of characters are bolded.

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Clade</th>
<th>t-test, ci</th>
<th>t-test, ri</th>
<th>M-W, ci</th>
<th>M-W, ri</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brusatte et al. (2014)</td>
<td>Non-avian Coelurosauria</td>
<td>2.14E-10</td>
<td>4.67E-14</td>
<td>6.77E-10</td>
<td>2.26E-15</td>
</tr>
<tr>
<td>Carrano et al. (2012)</td>
<td>Non-coelurosaur Tetanurae</td>
<td>2.29E-09</td>
<td>5.42E-13</td>
<td>4.61E-10</td>
<td>1.03E-12</td>
</tr>
<tr>
<td>Choiniere et al. (2014a)</td>
<td>Non-avian Theropoda</td>
<td>0.22025</td>
<td>7.31E-07</td>
<td>0.4483</td>
<td>2.01E-07</td>
</tr>
<tr>
<td>Foth and Rauhut (2017)</td>
<td>Non-avian Coelurosauria</td>
<td>0.001355</td>
<td>1.66E-07</td>
<td>0.006778</td>
<td>1.69E-07</td>
</tr>
<tr>
<td>Lee et al. (2014a)</td>
<td>Non-avian Theropoda</td>
<td>0.014723</td>
<td>2.43E-08</td>
<td>0.096904</td>
<td>2.71E-08</td>
</tr>
<tr>
<td>Rauhut and Carrano (2016)</td>
<td>Ceratosauria</td>
<td>5.47E-09</td>
<td>1.99E-10</td>
<td>4.15E-08</td>
<td>5.93E-10</td>
</tr>
<tr>
<td>Tortosa et al. (2014)</td>
<td>Ceratosauria</td>
<td>0.015288</td>
<td>0.0008158</td>
<td>0.018854</td>
<td>0.0077152</td>
</tr>
<tr>
<td>Wang et al. (2017a)</td>
<td>Non-avian Theropoda</td>
<td>0.0027452</td>
<td>9.99E-08</td>
<td>0.0005687</td>
<td>2.19E-08</td>
</tr>
</tbody>
</table>
tion. On the other hand, crown ornamentations (CI of 0.49) and microstructure (CI of 0.62), although bearing functional properties and linked to diet (e.g., Sander, 1999; Brink et al., 2015, 2016; Wang et al., 2015), are the least homoplastic possibly because they require more complex developmental/genetic mechanisms to evolve than other dental features under the same evolutionary pressure. Indeed, crown microstructure has been suggested to bear some phylogenetic potential in dinosaurs (Hwang, 2005, 2010; Wang et al., 2015).

The ANOVA test found statistically significant differences in CI values between characters of the enamel morphology and premaxillary teeth, mesial and distal crown, carina morphology, and lateral denticle morphology (Appendix 4.2). This is due to the particularly high values of CI in enamel-related characters, with seven out of 17 characters on the enamel microstructure having CI and RI scores of 1. Nevertheless, such high CI and RI values for characters on enamel microstructure should be considered cautiously as they obviously result from low sampling size. Information on crown histology was taken from Hwang (2007), who investigated the enamel microstructure in 24 distantly related theropod taxa, of which 15 are included in our data matrix. In addition, eight of the characters provided by Hwang (2007) are applicable only to 10 taxa, and five of the characters are restricted to six taxa. Interestingly, Hwang (2005, 2007) observed a large amount of homoplasy in enamel microstructure among theropods but the results of our study appear to show the reverse pattern. Our study suggests that, among all dental characters displayed by isolated shed teeth, features on enamel texture and microstructure convey the most important grouping information (RI is 0.58) of all dental subunits and should be investigated first in order to assign theropod teeth to taxa with more confidence. Our low sampling size might nonetheless negate the effects of Hwang’s (2007) larger dataset as increasing numbers of taxa drives these metrics down in a predictable pattern.

Homoplasy and grouping information in the 34 dental characters highlighted. Low CI scores in most of the 34 dental characters examined (CI values of 0.251) demonstrate that most of these features are strongly homoplastic (CI is less than 0.3, and typically around 0.2; Appendix 4.2, Table A6). Longitudinal ridges (CI is 0.75) and flutes (0.54) on the crown are the dental characters with the least amount of homoplasy and the only characters with CI values higher than 0.5. Nonetheless, significantly higher RI values (RI is 0.39) reveal that many dental characters provide some grouping information and can still be optimized as local synapomorphies of less inclusive theropod clades. This is particularly the case of dental features on the lateral dentition and characters related to: crown thickness (RI = 0.59), height (RI = 0.54), presence of the mesial carina (RI = 0.57), extension of the mesial carina (RI = 0.52), cross-sectional outline (RI = 0.6), and enamel surface texture (RI = 0.61).

With CI and RI equal to 1, when characters on enamel microstructure are excluded, subrectangular alveoli in the premaxilla (found in Abelisauridae only) and a mesial dentition bearing a longitudinal ridge centrally positioned on the lingual surface [seen in Tyrannosauridae and Raptorex, a possible juvenile of Tarbosaurus (Fowler et al., 2011b)] are the only non-homoplastic and uniquely synapomorphic dental characters of theropod subclades (Appendix 4.2, Table A5). With RI higher than 0.7, a premaxillary tooth row anterior to the external naris, the shape of the maxillary alveoli, the spacing of the dentary teeth, the presence of serrations on the distal carina and a twisted mesial carina in mesial teeth, the presence of flutes in lateral teeth, and the presence of minute or very large denticles along the distal carina in the mesial and lateral teeth, are dental characters that also convey important grouping information and have potential taxonomic value. Likewise, with RI higher than 0.6, the presence of an alveolar groove in the dentary, the crown thickness and cross-sectional outline, and the extension of the mesial carina, as well as the presence of a constriction between crown and root, the extension of the mesial and distal carinae and the shape of mesial denticles at two-third of the crown height in the lateral dentition, are dental features that provide useful grouping information.

Among the 34 dental features we highlight, additional features that convey relatively good grouping information are: basal constriction at the cervix in lateral teeth (RI of 0.625), absence of mesial and distal carinae (0.59 and 0.5), cross-sectional outline in lateral teeth (0.57), and straight or convex distal profile in the lateral crown (0.58). On the other hand, with an RI score equal or lower than 0.4, procumbent premaxillary, maxillary or dentary teeth (RI is 0.14 on average), absence of denticles on the mesial carina (0.29), a labially deflected distal carina (0.23), the shape of mesial and distal denticles (0.24), distal denticles significantly smaller/larger than mesial denticles (0.29), transverse and marginal undulations (0.31), and the presence and development of interdenticular...
sulci between mid-crown distal denticles (0.25) provide little grouping information. Finally, with RI equal to 0, procumbent premaxillary teeth, the presence of basal striations, denticles on the mesial carina and interdenticular sulci between distal denticles in mesial teeth, the shape of mesial denticles and the presence of longitudinal ridges in lateral teeth, as well as the presence of longitudinal grooves in mesial and lateral teeth are dental features that are optimizing as localized autapomorphies of phylogenetically distant taxa and, consequently, do not convey grouping information. The combination of these features may, nonetheless, narrow down the phylogenetic distribution of isolated teeth to a certain taxon.

**Distribution of dental characters in theropods and their biostratigraphic value.** The distribution of dentition-based and crown-based characters on theropod trees reveals that dental features tend to better-diagnose ‘super-family’ and ‘family’ level clades than major theropod clades such as Ceratosauria, Maniraptora, Orionides, Paraves and Tetanurae (Appendix 5). The distribution of crown-based features has also shown that most theropod OTUs are diagnosed by fewer than three crown-based autapomorphies and fewer than two lateral crown-based apomorphic characters (Appendix 5, Tree topology 9 and 10). This suggests that few theropod taxa bear diagnostic crowns that can be identified at the genus level, and that most isolated theropod shed teeth, which are typically from the lateral dentition, do not show taxonomic precision sufficient for fine-scale biostratigraphic analysis. Taxa diagnosed by four lateral crown-based autapomorphies or more include *Acrocanthosaurus, Afrovenator, Chilesaurus, Majungasaurus, Megaraptor, Pliatnitzkysaurus, Sauornitholestes, Sciuromimus, Skorpiovenator, Troodon* and *Tyrannosaurus*. Several authors such as Baszio (1997), Fiorillo and Gangloff (2001), Smith et al. (2005), and Fanti and Therrien (2007) have successfully identified isolated crowns to these taxa, and biostratigraphic correlations of the deposits containing these fossils can be inferred based on theropod shed teeth only (Larson and Currie, 2013).

Many theropod shed teeth are, however, not diagnostic to the genus level due to both morphological convergence and to the variability of dental features along the tooth row within a single individual. For example, the crowns of Megalosauridae, Carcharodontosauridae and Dromaeosauridae are typically characterized by the presence of a mesial carina not reaching the cervix (Hendrickx et al., 2015c), pronounced marginal undulations (Brusatte et al., 2007), and longitudinal ridges and/or deep, apicobasally extended labial/lingual depressions (Gianechini et al., 2011b; Evans et al., 2013), respectively. But each of these features is varyingly represented along the tooth row (Figure 6). The dentition of *Acrocanthosaurus atokensis* (NCSM 14345), for instance, displays strong marginal undulations in Rmx3 whereas Rmx1, Rmx2 and Rmx4 lack these undulations (Figure 6.1). The same appears for transverse undulations that are well-visible on the labial surface of Rmx1 to 6 but only seen on the lingual surface in Lmx2 and Lmx4 (personal obs.). In the left maxilla of *Alioramus altai* (MPC-D 100-1844), a lingual depression is visible in some teeth but absent in others, while the mesial carina reaches the cervix in Lmx4 and extends far above the root in Lmx3 (Figure 6.2). Important intra-individual variation also occurs along the tooth row in the troodontid *Byronosaurus jaffei* (MPC-D 100-983), in which some maxillary and dentary crowns are strongly foldidont and lack longitudinal ridges and labial depressions (Figure 6.3). Yet, more distal teeth tend to be devoid of constriction between root and crown and display a single, well-visible longitudinal ridge and a deep depression labially (Figure 6.3). Despite these dental variations along the tooth row, isolated theropod teeth can often be assigned to ‘family’ or ‘sub-family’ level clades with confidence, some of them up to the genus level, therefore providing important information on the biogeographic and stratigraphic ranges for these taxa and clades, and stratigraphic information for deposits preserving highly diagnostic theropod shed teeth.

**Evolutionary Transformations in the Non-Avian Theropod Dentition**

The distribution of 145 dental characters on the theropod general consensus tree allows us to identify several evolutionary transformations within the dentition across Theropoda. These evolutionary steps can be summarized as follow:

**Number of teeth.** (1) Increase in the number of premaxillary teeth to more than five in Spinosaursauridae. (2) Decrease in the number of maxillary teeth to fewer than ten in Avialae (i.e., Epidexipteryx + Archaeopteryx), to fewer than 15 in the clade Dilophosaurus + Averostra, carcharodontosaurines, and the clade Microraptorinae + Eudromaeosauria (ACCTRAN for the latter), and to fewer than 20 in pennaraptorans. (3) Increase in the number of maxillary teeth to 15 in allosauroids (ACCTRAN), to more than 14 in proceratosaurids, and to more
than 19 teeth in maniraptoriforms and derived troodontids (i.e., troodontids more derived than Sinusonasus; ACCTRAN for the latter). (4) Increase in the number of dentary teeth to more than 25 in baryonychines, maniraptoriforms, and troodontids (ACCTRAN for the two latter). (5) Decrease in the number of dentary teeth to fewer than 15 in ceratosaurs (ACCTRAN), megalosauroids, neocoelurosaurs and avialans (ACCTRAN for the two latter), and to fewer than 26 in pennarapto-rans (ACCTRAN).

**Tooth loss.** (1) Loss of distal premaxillary teeth in the clade Caudipteridae + Caenagnathoidea. (2) Loss of premaxillary teeth in Ornithomimosauria more derived than Pelecanimimus, Therizinosau-ria/Therizinosauroidea and Caenagnathoidea. (3) Loss of distal maxillary teeth in Ornithomimosauria, possibly in Scansoriopterygidae and a basal clade comprising Almas and Jinfeongopteryx among Troodontidae. (4) Loss of the mesialmost dentary teeth in Oviraptorosauria and derived Therizinosauroidia, and loss of distal dentary teeth in ornithomimosaur more derived than Pelecanimimus, possibly also in Scansoriopterygidae. (5) Loss of maxillary and dentary teeth in Ornithomimosauria more derived than Shenzhousaurus and in the clade Caudipteridae + Caenagnathoidea among Oviraptorosauria. (6) Loss of palatal teeth in theropods (ACCTRAN).

**Tooth row extension.** (1) Distal displacement of the tooth-row throughout the evolution of theropods, with the distalmost maxillary tooth: lying posterior to the anterior rim of orbit in non-dilophosaurid and non-averostran theropods (DELTRAN); being anterior or aligned to the anteriormost rim of orbit and posterior to the posteriormost rim of the antorbital fenestra in non-tetanuran averostrans, Liliensternus (unknown) and dilophosaurids (ACCTRAN); being anterior or aligned to the posteriormost rim of the antorbital fenestra in non-ornithomimosaur maniraptoriforms and non-troodontid and avialan paravians (ACCTRAN); being aligned to the anteriormost rim of the antorbital fenestra in troodontid and avialan paravians (ACCTRAN). (2) The tooth row even extends anterior to the anteroventral rim of the antorbital fenestra in ornithomimosaur and possibly alvarezsaurids.

**Dentition size.** (1) Decrease in crown size in coelurosaur and noasaurids (ACCTRAN), whose mesial and lateral dentitions include teeth of less than one centimeter in apicobasal height. (2) Increase in crown size in Tyrannosauroidea and Dromaeosauridae more derived than Graciliraptor,
whose dentition encompasses teeth of more than one centimeter, and Ceratosauridae, Allosauroida
(ACCTRAN) and derived Tyrannosauroidea, which all bear teeth of more than six centimeters. (3)
Decrease in size of distal premaxillary teeth in spinosaurids, oviraptorosaurs (ACCTRAN) and
microraptorine dromaeosaurids, whose mesial premaxillary teeth are significantly larger than the
distal ones. (4) Isodonty (teeth of equal width and close height) of premaxillary and mesial maxillary
teeth in Abelisauroida, mesial premaxillary and maxillary teeth in Spinosauridae, and distal pre-
maxillary and mesial maxillary teeth in Allosauroidea and Avialae (DELTRAN). (5) Isodonty of maxillary
teeth in Paraves (ACCTRAN) or Dromaeosauridae (DELTRAN), and morphometric heterodonty (n.b.,
here referred to as teeth of different width and height, not shape) in troodontids, whose mesial
maxillary teeth are significantly smaller than those from the posterior portion of the maxilla. (6)
Decrease in size of mesialmost maxillary teeth in ceratosaurids, tyrannosaurids, and paravians
(ACCTRAN), whose mid-maxillary teeth are significantly larger than the mesialmost maxillary teeth.
(7) Decrease in size of mesialmost dentary teeth in tyrannosaurids and abelisaurids, whose mid-den-
tary teeth are significantly larger than mesial dentary teeth. There is an increase in size of the
mesialmost dentary teeth in Spinosauridae, derived therizinosaurids (i.e., Eshanosaurus +
Ertlikosaurus), and possibly Scansoriopterygidae. (8) Decrease in size of the first dentary tooth, com-
pared to the second and third dentary teeth, in neotheropods more derived than Coelophysis, and
paravians (ACCTRAN). (9) Increase in size of the first dentary tooth, which is equal in size to more
distally positioned dentary teeth, in noasaurids, Neocoeoelurosauria (ACCTRAN), and the sister-
clace of the clade encompassing Almas among Troodontidae.
Alveoli. (1) Development of subrectangular alveoli in Abelisauroidea, subcircular maxillary alveoli in
Spinosauridae and Maniraptoriformes (ACCTRAN), and oval/lenticular maxillary alveoli in
Pennaraptora. (2) Merging of alveoli to form an open groove in ornithomimosaurs and possibly
alvaresaurids for the maxilla, and in troodontids and possibly alvaresaurids for the dentary.
Basal constriction. (1) Mesiodistal constriction at the level of the cervix in mesial teeth in neocoeluro-
saurs (ACCTRAN) and in carcharodontosaurines, alvaresaurids and maniraptoriforms (DELTRAN
for the two latter) in lateral teeth. (2) Loss of a con-
striction in the lateral dentition in dromaeosaurids,
and in the mesial dentition in non-halszkaraptorine
dromaeosaurids (ACCTRAN). (3) Development of
an important constriction in the lateral dentition of
therizinosaurids.
Basal crown cross-sectional outline. (1) Devel-
opment of a salinon-shaped cross-section of the
crown base in the mesialmost dentition of Abelis-
auroidea and Allosauroida, and a U-shaped
cross-section in pantyrranosaurians. (2) Develop-
ment of a D-shaped or J-shaped cross-section of
the base-crown in the mesialmost teeth in Dromae-
osauroidea and Coelurosauria more derived than
Bicentenaria. (3) Development of a subcircular
cross-section of the base-crown in the mesial den-
tition of carcharodontosaurids and neocoeoelu-
saurs more derived than Ornitholestes, in the
lateral dentition of maniraptoriforms, and in the
mesial and lateral dentitions of spinosaurids. (4)
Labiolingual constriction of the crown base at mid-
length of the tooth, creating a figure-8-shaped
cross-section of the crown, in the lateral dentition
of non-halszkaraptorine dromaeosaurids.
Crown curvature. (1) Loss of a concave distal pro-
file in the lateral dentition of Abelisauroidea
(ACCTRAN) or Abelisauroidea (DELTRAN), spino-
saurines (ACCTRAN) and paravians. (2) Develop-
ment of a convex distal profile of the lateral crowns
in Maniraptoriformes and a concave distal profile of
the lateral crowns in Dromaeosauridae.
Denticle/carina loss. (1) Loss of a mesial carina in
the mesial and lateral dentitions (ACCTRAN), and
loss of distal denticles in the mesial dentition of
Neocoeoelurosauria. (2) Loss of a distal carina in the
lateral dentition of Maniraptoriformes (ACCTRAN)
or Paraves (DELTRAN). (3) Loss of mesial and dis-
tal serrations in the mesial and lateral dentitions of
Spinosaurinae. (4) Development of a denticulated
distal carina in the mesial dentition of Therizino-
sauridea and Eudromaeosauria (ACCTRAN), and
in the lateral dentition of troodontids more derived than
Byronosaurus, and the clade gathering
Microraptorinae and Eudromaeosauria.
Denticle shape. Development of asymmetrically
convex or hooked denticles in the lateral dentition
of Abelisauroidea, Troodontidae more derived than
Byronosaurus, and Therizinosauroida
(ACCTRAN).
Distal denticles larger than mesial denticles
(DSDI > 1.2). (1) Reduction in size of mesial denti-
cles compared to distal ones in Noasauridae
(excluding Limusaurus), Piatnitzkysauridae and
Coelurosauria. (2) Increase in size of mesial denti-
cles compared to distal ones in Carcharodontosauridae
(ACCTRAN). (3) Increase in the size of
mesial denticles in adult Theropoda more derived than Eotyrannus, and Therizinosauria (ACCTRAN) becoming equally sized as the distal denticles.

**Interdenticular sulci.** Development, in the lateral dentition, of interdenticular sulci between apical denticles in the mesial carina of Allosauria (ACCTRAN) and Megalosaurinae more derived than Duriavenator, and in the lateral dentition of neotheropods more derived than Litiens sternus (DELTRAN). (2) Apico-basal shortening of the mesial carina, terminating well-above the cervix, in the lateral dentition of Megalosauria, Carcharodontosauria and Coelurosauria more derived than Bicentenaria (ACCTRAN for the two latter).

**Enamel undulations.** (1) Development of transverse undulations in some lateral crowns in Averostra (ACCTRAN), Megalosaurinae, and Dromaeosauridae more derived than Graciliraptora. (2) Development of pronounced and well-visible transverse undulations in some lateral crowns in Ceratosauria and Allosauria (both ACCTRAN). (3) Development of marginal undulations in some lateral crowns in Megalosaurinae more derived than Duriavenator, Tyrannosauridae more derived than Alioramus, and Orioni dides (ACCTRAN). (4) Development of mesiodistally elongated marginal undulations in some lateral crowns in Allosauria.

**Labial depression.** Development of a centrally positioned labial depression extending on the basal half or more than half of the crown in Megaraptora and non-halszkaraptorine Dromaeosauridae.

**Flutes.** Development of flutes on both labial and lingual surfaces in some lateral teeth in Spinosauridae and Microraptorinae (ACCTRAN).

**Enamel surface texture.** (1) Development of a braided oriented enamel texture in Microraptorinae + Eudromaeosauria, and a veined enamel texture in Spinosauridae (ACCTRAN). (2) Loss of an oriented enamel texture (to become an irregular and non-oriented texture) in Abelisauridae (ACCTRAN), Metriacanthosauridae, and Neocoe lurosauria more derived than Ornitholestes.

**Root.** Mesiodistal inflation of the root at mid-height in Compsognathidae and Maniraptora, and apical tapering of the root in Spinosauridae and Therizinosauria (ACCTRAN).

### Major Evolutionary Transitions in the Non-Avian Theropod Dentition

The distribution of dental characters based on our dentition-based data matrix allows us to highlight several major evolutionary trends in theropods.

**Spinosauridae.** The most important dental evolutionary transition occurred with the radiation of spinosaurid theropods (Figure 3; Table 1). With 21 dental synapomorphies, the spinosaurid dentition is highly specialized, from the conical fluted crowns bearing minute or no denticles at all to the terminal rosette of the upper and lower jaw with subcircular alveoli (e.g., Charig and Milner, 1997; Sereno et al., 1998; Sues et al., 2002; Dal Sasso et al., 2005; Hendrickx and Mateus, 2014a; Sales and Schultz, 2017). Several studies have shown that these theropods were semi-aquatic animals feeding, at least partially, on fish (e.g., Charig and Milner, 1997; Rayfield et al., 2007; Amiot et al., 2010; Ibrahim et al., 2014; Hendrickx et al., 2016; Hassler et al., 2018), suggesting that their peculiar dentition is linked to the specialized piscivorous diet.

Buffetaut (2011) and Serrano-Martínez et al. (2016) investigated the early evolution of the spinosaurid dentition based on isolated teeth from the Jurassic of Tanzania and Niger. According to these authors, dental adaptations towards piscivory were gradually acquired throughout the evolution of Spinosauridae. The teeth of the possible spinosaurid Ostafrikasaurus crassiserratus from the Tendaguru Formation (Late Jurassic) of Tanzania are characterized by large denticles (10 denticles per 5 mm), ‘wrinkled’ enamel texture, and weakly compressed fluted crowns (Buffetaut, 2011; Rauhut, 2011). This suggests that a reduction in denticle size or the disappearance of denticles entirely and a decrease of labiolingual compression (CBR) probably occurred after the Jurassic (Buffetaut, 2011). Likewise, the presence of a single non-fluted spinosaurid tooth (MUPE HB-87) with a veined enamel texture from the Irhazer Group (Middle Jurassic) of Niger suggests that veined texture of the enamel evolved early in spinosaurid evolution, unlike flutes that appeared later (Serrano-Martínez et al., 2016).

The taxonomy of these teeth is, however, questionable. The teeth referred to Ostafrikasaurus have many features present in the mesial teeth of Ceratosaurus such as flutes, large denticles and a moderate labiolingual compression (Rauhut, 2011; C.H. personal obs.). In addition, the fine ‘wrinkling’
described by Buffetaut (2011) is as pronounced as that observed in Ceratosaurus premaxillary teeth (UMNH VP 5278), and the crown even shows a smooth enamel texture on the labial side (Rauhut, 2011). This enamel surface texture differs significantly from the deeply veined or anastomosed enamel texture of spinosaurid crowns (C.H. personal obs.). Given that ceratosaurids were possibly present in the Kimmeridgian-Tithonian of Africa (Janensch, 1925; Rauhut, 2011), and although some teeth of Osafricasaurus do show flutes on both labial and lingual surfaces and present a mesial carina reaching the cervix, two features that were not observed in any mesial Ceratosaurus teeth, their similarity with ceratosaurid mesial teeth casts doubt on their spinosaurid affinity. We think that the tooth ascribed to Spinosauridae by Serrano-Martínez et al. (2016) unlikely belongs to this clade. Given the relatively low dentine density (17.5 denticles per 5 mm for MC and DC), a mesial carina terminating far above the cervix, and the braided texture of the enamel (i.e., the texture is not deeply veined, does not curve basally close to carina and strongly resembles the braided texture of megalosaurid teeth; see Hendrickx et al., 2015c; C.H. personal obs.), it is likely that MUPE HB-87 represents a tooth from the mesial dentition of a megalosaurid, most probably Afrovenator abakensis, rather than a spinosaurid.

The evolutionary steps proposed by Buffetaut (2011) and Serrano-Martínez et al. (2016) for the spinosaurid dentition based on putative spinosaurid shed teeth must, therefore, be considered as tentative. Likewise, given the amount of homoplasy in dental features, it is unlikely that the taxonomic attributions in those works are accurate. Although a reduction of dentine size, a decrease in labiolingual crown compression and the development of flutes and veined/anastomosed enamel texture had to occur through Spinosauridae evolution prior to the appearance of definitive spinosaurid taxa, the timing and sequence of these features remain unknown.

Avetheropoda. Two major evolutionary steps in the dentition of theropods occurred during the radiation of Allosauroidae and Tyrannosauroidea (Figures 3 and 4; Table 1). These dental changes affect the mesial and lateral dentitions of allosaurs but are restricted to the mesial dentition in tyrannosaurs. The outgroup condition for allosaurs and coelurosaurs is transversely narrow (i.e., CBR < 0.75) mesial teeth, in which the cross-sectional outline at the crown base is lanceolate. The dental evolution of basal avetheropods is marked by a transverse thickening of mesial teeth (CBR between 0.75 and 1.2), yet the lanceolate cross-sectional outline was retained by basalmost coelurosaurs such as Bicentenaria. Consequently, both allosaurs and coelurosaurs more derived than Bicentenaria independently evolved mesial teeth in which the mesial carina migrated mesiolingually, and concavities appeared adjacent to the mesial and/or distal carinae on the lingual surface of the crown, resulting in a J-shaped and/or salinon-shaped cross-sectional outline at the crown base in mesialmost teeth. Basal tyrannosaurids developed mesial teeth in which the mesial carina twists onto the mesiolingual surface whereas the distal carina moved labially and faces lingually (Figure 4; Table 1). These evolutionary changes in both Allosauroidae and Tyrannosauroidea likely result from an anteroposterior shortening of the premaxilla as well as an adaptation towards a diet involving bone-crunching and bone-biting, with a high degree of torsion applied on the mesial dentition. The mesial teeth of some tyrannosaurids share a high CBR and a relatively small angle between the mesial and distal carinae with basal allosaurs, indicating the ability to endure high mechanical stresses (Reichel, 2010, 2012). The mesial dentition of these groups was specialized for gripping and pulling on the prey, and the lingually deflected carinae of the mesial teeth, which have a U- or D-shaped cross-sectional outline, made them effective tools for defleshing carcasses (Reichel, 2012). The anteroposterior shortening of the premaxilla leads to the overlap of the second and third premaxillary alveoli, a dental feature seen in both Allosauroidae and Tyrannosauroidea. This shortening was accentuated in basal tyrannosaurs, in which the third and fourth premaxillary alveoli also overlap. Similarly, abelisaurid theropods had an anteroposterior shortening of their premaxillae and developed labiolingually thick mesial teeth showing a salinon, J-shaped or D-shaped cross-sectional outline. In Abellisauridae, the premaxillary alveoli remain mesiodistally oriented and do not overlap. In Tyrannosauroidea, these dental changes were accompanied by a decrease in size of the mesialmost dentary teeth. Conversely, allosaurs retained relatively large premaxillary and mesial dentary teeth, as well as a mesial dentition with distally-positioned distal carina and crowns with a strongly convex lingual margin. In Allosauroidae, the mesial and distal denticles remained equal in size, whereas basal tyrannosaurs are characterized by mesial denticles significantly smaller than distal denticles, a
dental feature present in basal coelurosaurs such as *Bicentenaria* (Novas et al., 2012) and *Zuolong* (Choiniere et al., 2010a). The development of interdenticular sulci between distal denticles and transverse undulations in lateral teeth also occurred in allosauroids, whereas the lateral teeth of basal tyrannosauroids resemble those of more basal coelurosaurs.

**Neocoelurosauria and the shift in feeding ecology in Maniraptoriformes.** The high number of dental synapomorphies diagnosing Maniraptoriformes (five; Figure 4; Table 1) marks an important transition in the evolution of the coelurosaur dentition characterized by tooth simplification. This transition has been suggested to be functionally linked to a switch in dietary preferences (Zanno and Makovicky, 2011; see below). Such dental transformation occurred gradually throughout the evolution of neocoelurosauria, and changes in tooth morphology seem to have occurred in three evolutionary steps.

1. Loss of mesial denticles in both mesial and lateral teeth, and loss of distal denticles in mesial teeth in basal neocoelurosauria. While basalmost coelurosaurs such as *Bicentenaria*, *Zuolong* and basal tyrannosauroids have denticulated mesial and distal carinae along the whole dentition, a mesial carina is absent in the mesial and distal dentitions of most compsognathids, and the distal carina is unserrated in the mesial teeth of these taxa. A mesial carina is, nevertheless, present in some mesial and lateral teeth of the basalmost neocoelurosaur *Ornitholestes* and *Fukuivenator*, but mesial denticles are absent and the carina is restricted to the apical portion of the crowns (Azuma et al., 2016; C.H. personal obs.). *Sinocalliopteryx*, which is a large and likely adult individual, appears to be the only member of Compsoognathidae that retained denticles on the distal and mesial carinae in mesial and lateral teeth, respectively (Ji et al., 2007). Conversely, *Ornitholestes* and all compsognathids with the exception of *Sinocalliopteryx* have unserrated mesial teeth and distally denticulated lateral teeth (Stromer, 1934; Ostrom, 1978; Currie and Chen, 2001; Hwang et al., 2004; Chiappe and Göhlich, 2010; Dal Sasso and Maganuco, 2011; C.H. personal obs.). The basal neocoelurosaur *Fukuivenator* is characterized by a dentition in which all teeth appear to be fully unserrated (Azuma et al., 2016), an apomorphic condition among neocoelurosauria given the presence of serrations in compsoognathids, *Ornitholestes*, basal alvarezsauroids, therizinosauroids and oviraptorosaurs (see below). The systematic position of *Fukuivenator* is still unresolved in Neocoelurosauria and this taxon might be a basal paravian closely related to basal dromaeosaurids such as *Halszkaraptor* due to the presence of D-shaped mesial teeth and unserrated crowns. Unlike *Fukuivenator,* some lateral teeth show denticles restricted to a certain portion of the distal carina in *Ornitholestes* (AMNH 619), *Compsoognathus* (MNHN CNJ 79; Dal Sasso and Maganuco, 2011), *Scipionyx* (Dal Sasso and Maganuco, 2011) and *Juravenator* (JME Sch 200). In these taxa the denticulated distal carina does not reach the cervix and/or the apex, marking a further step towards tooth simplification in coelurosaurus. Furthermore, the lateral dentition of *Compsoognathus* (MNHN CNJ 79; Stromer, 1934; Peyer, 2006) and *Ornitholestes* (AMNH 619) comprises both finely denticulated (i.e., more than 10 denticles per 1 mm) and completely unserrated carinae. Unserrated teeth are present in the mesial maxillary teeth of *Scipionyx* (Dal Sasso and Maganuco, 2011). The absence of denticles in the mesial and/or distal carinae of *Ornitholestes* and most compsognathids could be ontogenetic given that these specimens might represent young individuals (e.g., Ostrom, 1978; Currie and Chen, 2001; Hwang et al., 2004; Chiappe and Göhlich, 2010; Dal Sasso and Maganuco, 2011). Yet, given the absence of fully-grown specimens among many basal neocoelurosauria, and because the subadult specimen of *Fukuivenator* may represent a basal neocoelurosaur with unserrated mesial and lateral teeth, the absence of carina and denticles in neocoelurosauria is here considered as a derived dental character.

2. Conical mesial teeth and irregular enamel surface texture in the clade Compsoognathidae + Maniraptoriformes. The subcircular crown cross-section present in the mesial teeth of Compsoognathidae, Ornithomimosauria, Alvarezsauroidea and Oviraptorosauria contrasts with the J-shaped, D-shaped and/or U-shaped mesial teeth of the basal coelurosaurs *Zuolong* (Choiniere et al., 2010a), tyrannosauroids (e.g., Holtz, 2004; Rauhut et al., 2010) and the basal neocoelurosaur *Ornitholestes* (AMNH 619) and *Fukuivenator* (Azuma et al., 2016). Nevertheless, the basal ornithomimosaur *Pelecanimimus* (Pérez-Moreno et al., 1994) and the basalmost therizinosaur *Falcarius* (UMNH 15097) also show a D-shaped cross-sectional outline at the crown base in some mesial teeth, a dental feature here tentatively considered as autapomorphic to these taxa. It is, however, possible that unserrated mesialmost teeth with a D-shaped cross-section is synapomorphic for a clade excluding Compsoognathidae and gathering *Ornitholestes*, *Fukuivenator*, and maniraptoriforms, with D-shaped and unserrated mesial teeth being the plesiomorphic condition to basal ornithomimosauria and therizinosauria, a hypothesis developed below. The mesial dentition of compsoognathids retains the strong distal curvature of basal coelurosauria but the enamel surface texture of the crown is no lon-
ger braided and oriented. A braided surface texture of the enamel is clearly present in *Bicentenaria, Dilong, Guanlong, Ornitholestes,* and *Proceratosaurus* whereas it is irregular at least in *Compsognathus, Haplocheirus, Juravenator,* and *Nqwebasaurus.* A braided enamel surface texture is, however, present in is, however, present in some crowns of the basalmost alvarezsaurid *Aorun* (IVPP V15709), a possible autapomorphic feature of this taxon.

(3): Increase in the number of maxillary teeth, loss of mesial, and lateral teeth, and lateral teeth with a subcircular outline in Maniraptoriformes. Unlike non-maniraptoriform coelurosaurs, the distal profile of mesial and lateral teeth of basal maniraptoriforms is no longer concave but straight and convex, respectively, and all teeth have a subcircular cross-sectional outline. The combination of these dental features and the presence of a constriction define the conidont/folidont combination of these dental features and the presence of constricted teeth with a sub-circular cross-section outline. The dentition of this taxon shows D-shaped mesialmost teeth and distally recurved crowns, two plesiomorphic features present in basalmost coelurosaurs and *Ornitholestes.* Yet, *Fukuivenator* also bears unserrated teeth, as in ornithomimosaurians, and folidont lateral teeth, as in *Pelecanimimus,* therizinosaurs and basal oviraptorosaurs. A relatively similar dentition is that of the ornithomimosaurian *Pelecanimimus,* which shares with *Fukuivenator* the presence of D-shaped mesial teeth, unserrated teeth and folidont crowns. Nevertheless, *Pelecanimimus* bears a large number of premaxillary, maxillary and dentary teeth, which all seem to be constricted. It is, therefore, possible that basal maniraptoriforms like *Pelecanimimus* and *Falcarius* retained D-shaped/spatulate unserrated mesial teeth and distally recurved crowns present in basalmost coelurosaurs and *Ornitholestes,* and evolved a lateral dentition made of constricted teeth with a sub-circular cross-sectional outline at the crown base. In this scenario, denticles, lost in basalmost maniraptoriforms (i.e., *Fukuivenator* + maniraptoriforms), would be re-acquired in the clade *Alvarezsauroidea + Maniraptora* (e.g., *Aorun, Haplocheirus, Incisivosaurus,* and therizinosaurs), and independently lost in alvarezsaurids, caudipterids and paravians.

Choiniere et al. (2014b) note that the mesial dentition of *Haplocheirus* resembles that of derived alvarezsaurs in lacking serrations and having a ziphodont dentition whose teeth independently evolved into conidont or folidont teeth.

The sequence of these steps in the evolution of the neocoelurosaur dentition may change with the potential discovery of basal ornithomimosaurians, therizinosaurs and oviraptorosaurs in Jurassic deposits. If revealed to be a basal neocoelurosaur, *Fukuivenator* from the Early Cretaceous of Japan (Azuma et al., 2016), in fact, disrupts the succession of these steps. The dentition of this taxon shows D-shaped mesialmost teeth and distally recurved crowns, two plesiomorphic features present in basalmost coelurosaurs and *Ornitholestes,* and appears to be synapomorphic for maniraptoriforms. We, consequently, consider the mesial and lateral dentitions of *Haplocheirus* and *Aorun* to have a plesiomorphic morphology. Choiniere et al. (2014b) also hypothesized either different rates of dental evolution or different evolutionary intervals in the premaxilla and the maxilla to explain such heterodonty in *Haplocheirus.* Based on the
sequence of dental evolution observed in neocoeulurosaurs, we favor the second hypothesis and suggest that the mesial tooth crown morphology of neocoeulurosaurs changed first and appeared before an increase in tooth number, unlike what was inferred for troodontids (Choiniere et al., 2014b).

A large amount of evidence supports the hypothesis that the dental transition seen in the evolution of neocoeulurosaurs results from a trophic shift between carnivory and herbivory (Barrett and Rayfield, 2006; Zanno et al., 2009; Zanno and Makovicky, 2011). Direct evidence shows that compsognathids were carnivorous, feeding on an array of small, medium and possibly large-sized prey items such as fish, lizards, birds, theropods, ornithischians and mammals (e.g., Ostrom, 1978; Currie and Chen, 2001; Hwang et al., 2004; Peyer, 2006; Dal Sasso and Maganuco, 2011; Xing et al., 2012). Gastroliths in compsognathids were also found in Sinosauropteryx and Chen, 2000; Xing et al., 2012), which would suggest a partially herbivorous diet in this clade. The presence of small gastroliths combined with the absence of stones in the stomach content of other compsognathids suggest that these stomach stones, known as geo-gastroliths (sensu Wings, 2007), were ingested accidentally (Xing et al., 2012). On the other hand, the presence of a gastric mill in the basal ornithomimosaur Ngwebasaurus (De Klerk et al., 2000; Choiniere et al., 2012), Shenzhousaurus (Ji et al., 2003), and in the basal oviraptorosaur Caudipteryx (Ji et al., 1998; Zhou and Wang, 2000), implied by the size, distribution and estimated mass of the gastroliths compared to the mass of the animal (Wings and Sander, 2007; Choiniere et al., 2012), allows confident inference of herbivory in these taxa (Barrett, 2005; Zanno and Makovicky, 2011). An herbivorous lifestyle was also inferred in therizinosaurs and alvarezsaurids on the basis of the development of a large number of morphological features supporting herbivory such as: an edentulous premaxilla; the presence of a beak-like keratinous rhamphotheca; U-shaped and dorsally convex dentary; neck elongation; the reduction in bite force in therizinosaurs (Kirkland et al., 2005; Zanno et al., 2009; Zanno, 2010a; Lautenschlager, 2013, 2014; Lautenschlager et al., 2013); the presence of a dorsally convex dentary; a densely packed dentition; and conical/foliotent teeth in both therizinosaurs and alvarezsaurids (Zanno and Makovicky, 2011). Zanno and Makovicky (2011) have shown that a change in dentition morphology in maniraptoriforms was accompanied by the development of a large number of cranial and postcranal adaptations towards herbivory such as an elongation of the neck, the presence of an opisthophubic pelvis (this feature may be correlated with the ventilation system rather than herbivory; Macaluso and Tschopp, 2018) and the elongation of manual unguals (Paul, 1984; Zanno and Makovicky, 2011; Lautenschlager et al., 2013; Lautenschlager, 2014).

**DISTRIBUTION OF DENTAL FEATURES IN THEROPODA**

The study of the dental morphology in 160 taxa allows us to propose a list of 34 dental features, which when combined can help identify isolated theropod teeth with additional confidence. The distribution of several of these dental features is illustrated in three phylogenetic trees (Figures 3, 4, 7 and 8), a summary figure (Figure 9) and three tables (Tables 1, 3 and 4). A list of dental synapomorphies in 40 theropod clades illustrated in Figures 3 and 4 is provided in Table 1 based on our data matrix of 145 dental characters coded in 97 saurischian taxa. Table 3 provides the distribution of each dental feature in non-avian theropods whereas Table 4 lists the most important dental features seen in 31 theropod clades. A phylogenetic tree showing the distribution of each of these features for the mesial and lateral dentitions is also provided in Appendix 6. We finally provide functional properties for each dental feature in Table 3.

Although the theropod dentition varies morphologically through ontogeny (e.g., Carr, 1999; Carr and Williamson, 2004; Rauhut et al., 2012; Araújo et al., 2013), the teeth of post-hatchling individuals were also taken into consideration. The identification of teeth belonging to immature individuals can be difficult as their morphology may resemble that of distantly related taxa due to comparable diet or heterochronic processes (e.g., Rauhut et al., 2012). Nonetheless, little difference in tooth morphology and denticle shape and density have been shown to exist between juvenile and adult individuals of theropods like Coelophysis, Albertosaurus, and Gorgosaurus (Buckley et al., 2010; Buckley and Currie, 2014), and some theropod taxa also bear highly diagnostic teeth that can be referred to young individuals based on tooth size only (C.H. personal obs.).

Dentition-based characters are common in cladistic analyses and are often incorporated to help in assessing the relationships of non-avian theropods. The previous use of these dental characters and a discussion of their scorings are pro-
vided in Appendix 7. The datasets, results of the different analyses, and the list of taxa included in this study are provided as .xlsx files in Appendix 8.

Dentition type

Ziphodonty, a lateral dentition mostly composed of strongly labiolingually narrow crowns with a distal curvature, typically denticulated carinae, and absence of constriction at the cervix (Hendrickx et al., 2015d), is the plesiomorphic condition of theropods, sauropodomorphs or even dinosaurs in general (Sander, 1997; Langer and Benton, 2006; Cabreira et al., 2016; for a different hypothesis see Baron et al., 2017). A ziphodont dentition is present in Ornitholestes, non-alvarezsaurid Alvarazsauridae, Dromeosauridae and all non-maniraptoriform theropods other than Spinosauridae, Allosaurus and Tyrannosauridae. The anchiornithine Caihong may also be the only troodontid with a ziphodont dentition. Folidonty, a lateral dentition mostly composed of teeth with an important constriction at the level of the cervix, thus displaying a lanceolate leaf-shaped outline in lateral view (Hendrickx et al., 2015d), is present in Pelecanimimus, therizinosaurids, oviraptorosaurs other than Caudipteryx, Troodontidae (with the possible exception of the anchiornithine Caihong), and some Microraptor specimens. Only Allosaurus and mature Tyrannosauridae display a pachyodont dentition (see section on Crown base ratio greater than 0.75), a lateral dentition mostly composed of labiolingually expanded and distally recurved crown, in which the labiolingual width is greater than 60% of the mesiodistal length, from cervix to apex (Hendrickx et al., 2015c; C.H. personal obs.). Finally, conodonty, a lateral dentition mostly composed of conical crowns bearing minute denticles or no denticles at all (Hendrickx et al., 2015d), is present in all Spinosauridae, all toothed ornithomimosaurs with the exception of Pelecanimimus, the basal oviraptorosaur Caudipteryx (IVPP V12430, NGMC 97-4-A), and the unenlagiine Austroaraptor (Novas et al., 2009; Currie and Carabajal, 2012). A conidont mesial dentition, however, characterizes the basal members of the clades Oviraptorosauria (i.e., Incisivosaurus, Caudipteridae) and Scansoriopterygidae, while an unserrated subconidont/incisiform mesial dentition with a D-shaped cross-section characterizes some basal maniraptoriforms such as Falcarius, Fukuivenator and Ornitholestes (see section on D-shaped cross-section).

Remarks and synapomorphy. Most theropods are pseudoheterodont, characterized by a dentition where crown morphology gradually changes along the jaw so that mesial and lateral teeth differ significantly in their morphology (Hendrickx et al., 2015d). The basal saurischian Eoraptor (Sereno et al., 2013), the noasaurid Masasikasaurus (based on UA 8680 and the referred isolated lateral teeth), the basal maniraptoriform Fukuivenator (Azuma et al., 2016), the microraptorines Microraptor (Xu et al., 2000; Pei et al., 2014) and IVPP V13476 (Xu and Li, 2016), and the troodontids Byronosaurus (Makovicky et al., 2003), Daliansaurus (Shen et al., 2017a), IVPP V20378, Jinfengopteryx (Ji et al., 2005), Gobivenator (Tsuihiji et al., 2014), Sinovenator (IVPP V12615), Sinusonasus (IVPP V11527) and Xixiasaurus (Lü et al., 2010) possess a hetero-

FIGURE 7 (previous page). Distribution of dental features in non-neocoeleurosaur Theropoda. Phylogenetic tree based on the results obtained by Langer et al. (2017), for non-neotheropod Saurischia, Ezcurra (2017) and Wang et al. (2017a) for non-averostran Neotheropoda, Rauhut and Carrano (2016) and Wang et al. (2017a) for Ceratosauria, Carrano et al. (2012) and Rauhut et al. (2016) for non-coeleurosaurian Telanurae, Brusatte and Carr (2016) for Tyrannosauroidea, and Novas et al. (2012), Rauhut et al. (2012) and Choineire et al. (2014a) for the phylogenetic distribution of Bicentenaria, Sciurumimus and Zuolong, respectively. The branch colors represent the dentition types and the presence or absence of constricted crowns: ziphodont taxa with unconstricted crowns are in red, ziphodont taxa with a few constricted crowns are in green, conidont taxa are in turquoise, and pachyodont taxa are in yellow. The colors of taxa represent the presence or absence of serrations on the mesial and distal carinae for both mesial (left column) and lateral dentition (right column): toothless taxa are in grey, taxa with unserrated crowns are in green, taxa with a denticulated distal carina and a denticulated mesial carina not reaching the cervix are in red, taxa with a denticulated distal carina and a denticulated mesial carina reaching the cervix are in blue, and taxa with a denticulated distal carina and an unserrated mesial carina are in yellow. Taxa whose dentition is not known are on a white background. Taxa with distal denticles larger than mesial ones are boxed in green. Some compsognathid taxa possess a double condition in their mesial and lateral dentition: Juravenator bears mesial crowns with denticulated and unserrated distal carina, Compsognathus shows lateral crowns with unserrated and denticulated distal carina, and Sinocalliopteryx possesses denticulated and unserrated mesial carinae in the lateral teeth. Abbreviations: 8, figure-8-shaped cross-section of lateral teeth; D, D-shaped cross-section of mesial teeth; J, J-shaped cross-section of mesial teeth; O, subcircular/lanceolate cross-section of mesial teeth; S, Salinon-shaped cross-section of mesial teeth; U, U-shaped cross-section of mesial teeth.
dont lateral dentition that encompasses both ziphodont and foliodont teeth. Such heterodont dentition is here considered synapomorphic for Troodontinae (Figure 8). Most lateral teeth of these troodontids appear to be slightly to strongly constricted, thus having a foliodent dentition. If a ziphodont dentition, directly associated with faunivory, is the ancestral condition of theropods (e.g., Langer and Benton, 2006; Cabreira et al., 2016), a conodont dentition is synapomorphic for Spinosauridae and Ornithomimosauria. A pachydont dentition is synapomorphic for Tyrannosauroidea (see section on Crown base ratio greater than 0.75), whereas a foliodent dentition is a synapomorphy of Alvarezsauridae/Parvicursorinae and the clade Therizinosauria + Pennerapartora.

Functional morphology. A ziphodont dentition is an adaptation for carnivory, being suited to slashing, cutting through flesh and defleshing (Abler, 1992; Schwenk, 2000; D’Amore, 2009; D’Amore and Blumenschine, 2009; Brink et al., 2015). Foliodonty is related to herbivory (Zanno and Makovicky, 2011; Pu et al., 2013) and omnivory (Holtz et al., 1998; Barrett, 2000; Longrich, 2008) as leaf-shaped teeth are suitable for puncturing, tearing apart and shredding fibrous plant fodder and/or small prey (Reisz and Sues, 2000; Sues, 2000). A strictly carnivorous diet has been proposed for derived troodontids with foliodent teeth (Zanno and Makovicky, 2011; Torices et al., 2018), yet a foliodent dentition appears to be characteristic of herbivorous and/or omnivorous extant animals. Among lepidosaurs, small constricted crowns with a low number of relatively large mesial and distal denticles, as seen in therizinosaurids and derived troodontids, is clearly present in herbivores such as Sauromalus and Iguana (Melstrom, 2017). Insectivorous and omnivorous lizards like Corytophanes and Ctenosaura also show small teeth with a constriction between crown and root, yet they all appear to be multicuspied (i.e., a crown with a low number (<5) of large and prominent convexities of different size, the apicalmost one being the largest), such tooth morphology is absent in theropods. Several lines of evidence, including bite marks on a ceratopsian bone (Jacobsen, 1997), shed teeth associated with ornithopod remains (Ryan et al., 1998), crown microstructure (Brink et al., 2015) and microwear pattern combined with Finite Element Analysis (FEA) (Torices et al., 2018), support the fact that at least the troodontid Troodon was a carnivore and a predator feeding on smaller or softer prey items such as invertebrates (Torices et al., 2018). Consequently, other closely related troodontids may have also had a strictly carnivorous diet (see sections on hooked denticles and small number of denticles on the carina). This is the case of foliodont troodontids with large apically pointed denticles like Zanabazar or with a lateral dentition combining foliodont and ziphodont teeth such as Byronsaurus, Sinusonasus, Gobivenator and Xixiasaurus [see Lü et al. (2010) for a different opinion]. The crowns of both pachydont and conodont dentitions are particularly labiolingually thick, with pachydont dentitions being present in apex predators adapted to bone-crunching and bone-biting involving a high degree of torsion (e.g., Holtz, 2003; Snively et al., 2006; Holtz, 2008; Reichel, 2010). Conversely, conodont dentitions are adapted to impaling and holding prey items (e.g., Charig and Milner, 1997; Holtz, 1998a; Sereno et al., 1998; Sues et al., 2002; Holtz et al., 2004; Xing et al., 2013b). Besides strengthening the tooth to

FIGURE 8 (previous page). Distribution of dental features in Neocoelurosauria. Phylogenetic tree of Cau et al. (2017) based on the dataset of Brusatte et al. (2014) for Neocoelurosauria, with changes brought by Lamanna et al. (2014) for Caenagnathoidea, and Xu et al. (2018) and Pu et al. (2013) for the phylogenetic position of Aorun and Jianchangosaurus, respectively. The branch colors represent the dentition types: ziphodont taxa with unconstricted crowns are in red, ziphodont taxa with a few constricted crowns are in green, taxa with both foliodont and ziphodont lateral dentition are in orange, foliodont taxa with unconstricted mesial crowns are in pink, foliodont taxa with constricted crowns only are in blue, and conodont taxa are in turquoise. Colors of taxa represent the presence or absence of serrations on the mesial and distal carinae for both mesial (left) and lateral dentition (right): toothless taxa are in grey, taxa with unserrated crowns are in green, taxa with a denticulated distal carina and an unserrated mesial carina are in yellow, taxa with denticulated mesial and distal carinae are in red, and taxa with both denticulated mesial and distal carinae not reaching the cervix are in blue. Taxa (Sinocalliopteryx, Compsognathus and Juravenator) showing both conditions (e.g., mesial dentition with unserrated teeth and lateral dentition with denticulated teeth) are bicolored. Taxa whose dentition is not known are on a white background. Some paravians such as Troodon, Velociraptor and Sauroitholestes possess a lateral dentition with denticulated and unserrated carinae. Taxa with denticulated denticles larger than mesial ones are boxed in green, and taxa with large typically hooked denticles are boxed in purple. Abbreviations: 8, figure-8-shaped cross-section of lateral teeth; D, D-shaped cross-section of mesial teeth; J, J-shaped cross-section of mesial teeth; O, subcircular/lanceolate cross-section of mesial (black ‘O’) and lateral (blue ‘O’) teeth; U, U-shaped cross-section of mesial teeth.
resist lateral bending during feeding, Reichel (2012) also suggested that pachydont teeth provided the ability of individual crowns to make wide cuts through meat. Conidont teeth are often used to infer a piscivorous diet (Baszio, 1997; Sankey, 2001; Brinkman, 2008). The presence of gastroliths in basal ornithomimosaurans and the oviraptorosaur Caudipteryx with minute conical teeth suggests that such dentition was also suited for herbivory (Makovicky et al., 2004; Zanno and Makovicky, 2011; Choiniere et al., 2012). It has also been suggested that the presence of small conical teeth in the mesial dentition of therizinosaurs and Incisivosaurus and the whole dentition of ornithomimosaurans and Caudipteryx is likely a functional precursor of a rhamphotheca, which is present in more derived forms of ornithomimosaurans, therizinosaurs and oviraptorosaurs (Zanno and Makovicky, 2011). The heterodont dentition displayed by some coelurosaurans has been interpreted as an indicator of a dietary shift from faunivory to herbivory or omnivory (Zanno and Makovicky, 2011). A heterodont dentition with simple conical teeth in the mesial portion of the jaws, in fact, characterizes non-carnivorous lepidosaurs such as iguanids (Barrett, 2000; Melstrom, 2017).

**Basal constriction of the crown**

**Whole dentition.** A mesiodistal constriction at the cervix is present in both mesial and lateral teeth in the ornithomimosaur Pelecanimimus (LHC 7777), many therizinosaurs such as Alxasaurus (Russell and Dong, 1993), Esthanosaurus (Xu et al., 2001; Figure 10.3), and Jianchangosaurus (Pu et al., 2013), the alvarezsaurid Shuvuuia (MPC-D 100-977), basal avialans such as some Archaeopteryx specimens (e.g., Rauhut et al., 2018; Kundrát et al., 2019) and troodontids (e.g., Currie et al., 1990; Baszio, 1997; Norell et al., 2000; Currie and Dong, 2001b; Sankey et al., 2002; Averianov and Sues, 2011). Given that the basal members of these clades either have no serrations at all (e.g., Anchiornis) or minute denticles (e.g., Falcarius, Sinovenator). As for Oviraptorosauria, this applies to the lateral dentition of Incisivosaurus given that caudipteryid have unappende teeth; *, the dentition of basal tyrannosaurids have a DSDI > 1.2 whereas some tyrannosaurid teeth have a DSDI < 0.9. Images of unserrated tooth (udca) and unserrated mesial carina (umca) by Jaime Headden, dente size (des) and hooked denticles (hd) from Currie et al. (1990, modified), and mesial denticle smaller than distal ones (md≠dd) from Ostrom (1969; modified).

**FIGURE 9** (previous page). Distribution of dental features in non-avian Theropoda. Phylogenetic tree based on Hendrickx et al. (2015b) and Cau et al. (2017), with the exclusion of megaraptorans here placed among Neovenatoridae (Benson et al., 2010; Carrano et al., 2012). Letters between brackets represent polymorphic features. Clade numbers: 1, Neotheropoda; 2, Averostra; 3, Ceratosauria; 4, Tetanurae; 5, Megalosauroidea; 6, Spinosauridae; 7, Avetheropoda; 8, Allosauroida; 9, Coelurosauria; 10, Tyrannosauridae; 11, Neocoeilourosauria; 12, Maniraptormorphaes; 13, Maniraptorana; 14, Paraves; 15, Dromaeosauridae; 16, Troodontidae; 17, Avialae. Abbreviations: 0, absent; 1, present at least in some teeth or some taxa; 2, present in all mesial teeth and, for the edentulism, edentulous premaxilla and anterior portion of the dentary; 3, present in the whole dentition and, for the edentulism, fully edentulous jaws; 4, present in some mesial and lateral teeth; 5, present in some mesial teeth (e.g., m<, distal denticles significantly larger than mesial ones in some mesial teeth; m-igr, longitudinal groove present in some mesial teeth); 6, present in mesial teeth and, for the edentulism, edentulous premaxilla and anterior portion of the dentary; 7, present in some lateral teeth (e.g., la>), mesial denticles significantly larger than distal ones in some lateral teeth; 8, figure-8-shaped cross-section at the cervix; 9, unknown; 10, inapplicable; 11, medium-sized denticles (i.e., between 15 and 250 denticles on the carina); 12, difference between mesial and distal denticles; 13, mesiodistal constriction of the cervix present in some lateral teeth; 14, presence of keratinized crown bases; 15, longitudinal groove present in some lateral teeth; 16, presence of lateral teeth in the mesial portion of the jaws, in fact, characterized non-carnivorous lepidosaurs such as iguanids (Barrett, 2000; Melstrom, 2017).
TABLE 3. Distribution of dental features in non-avian theropods and their hypothetical functionality, adaptation or causes.

<table>
<thead>
<tr>
<th>Dental feature</th>
<th>Distribution</th>
<th>Possible functionality, adaptation or causes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ziphodonty</td>
<td>Ornitholestes, non-alvarezsaurid Alvarezsauroidia, Dromaeosauridae, and non-maniraptoriform theropods other than Allosaurus, Austroraptor, Spinosauridae and Tyrannosauridae</td>
<td>Slashing, cutting flesh and defleshing (carnivory)</td>
</tr>
<tr>
<td>Folidonty</td>
<td>Pelecanimimus and all other Maniraptoriformes other than Ornitholestes, Aorun, Haplocheirus, Ornithomimosauria and Dromaeosauridae</td>
<td>Puncturing, tearing apart and shredding fibrous plant fodder and/or small prey (herbivory/omnivory or carnivory)</td>
</tr>
<tr>
<td>Pachydonty</td>
<td>Allosaurus and mature Tyrannosauridae</td>
<td>Bone-crunching (hypercarnivory)</td>
</tr>
<tr>
<td>Conidonty</td>
<td>Spinosauridae, Ornithomimosauria (Pelecanimimus excluded), Caudipteridae and Austroraptor</td>
<td>Piercing and impaling slippery prey (piscivory), or raking vegetation (herbivory); precursor of a rhamphotheca</td>
</tr>
<tr>
<td>Basal constriction</td>
<td>Chilesaurus, Pelecanimimus and non-dromaeosaurid Maniraptora, with the exclusion of non-alvarezsaurid Alvarezsauroidia, Oviraptorosauria and some Therizinosauria such as Falciarius and Eriksaurus for the whole dentition; Masiakasaurus, Majungasaurus, Chenanisaurus, Proceratosaurus, Ornitholestes and Halszkaraptor for mesial teeth; Carcharodontosauinae, Microraptor, Fukuivenator, Falciarius, Eriksaurus, Incisivosaurus, Protarchaeopteryx and possibly Scansoriopterygidae for lateral teeth</td>
<td>Crown strength?</td>
</tr>
<tr>
<td>CBR &gt; 0.75</td>
<td>Spinosauridae, Allosauridae, Tyrannosauridae, Ornithomimosauria, Alvarezsauroidia, Austroraptor, and Troodontidae for both mesial and lateral teeth</td>
<td>Crown strength (resisting higher stresses in different directions)</td>
</tr>
<tr>
<td>CHR &gt; 60mm</td>
<td>Non-neocoeleurosaur Averostra with the exclusion of Abelisauroidia, Piatnitzkysauridae and possibly Baryonychinae, Neovenatoridae and Proceratosaurida</td>
<td>Allometric feature</td>
</tr>
<tr>
<td>Unserrated crown</td>
<td>Limusaurus, Spinosaurinae and Maniraptormorformes other than non-alvarezsaurid Alvarezsauroidia, Therizinosauria, Incisivosaurus, derived Troodontidae, Microraptorinae, Eudromaeosauria and possibly Epidexipteryx for the whole dentition; Sciurumimus, some Coelophysoida, basal Tyrannosaurida and Microraptorinae, and most Compsognathidae for mesial teeth; Aorun, Ornitholestes and some Compsognathidae and Dromaeosauridae for lateral teeth</td>
<td>Crown simplification</td>
</tr>
<tr>
<td>Unserrated mesial carina, serrated distal carina</td>
<td>Many theropods from most clades for mesial teeth; Sciurumimus, some megaraptorans, Ornitholestes, Compsognathidae, basal Alvarezsauroidia, a few Dromaeosauridae and many derived Troodontidae for lateral teeth</td>
<td>Crown simplification</td>
</tr>
<tr>
<td>Concave surface adjacent to carinae</td>
<td>Abelisauroida, Allosaurus, Tyrannosauridae and many Paraves for mesial teeth; some non-neotheropod Sauruschia, Ceratosauridae, non-spinosaurid Megalosauroidea, Metriacanthosauroidae, Neovenatoridae and Therizinosauria for lateral teeth</td>
<td>Increase in enamel surface, better penetration and withdrawal</td>
</tr>
<tr>
<td>J-shaped cross-section</td>
<td>Abelisauroida, basal Tyrannosauridae, most non-carcharodontosaur Allosauroida, and some Eudromaeosauria for mesial teeth; Masiakasaurus and some Troodontidae for lateral teeth</td>
<td>Crown strength with linguodistal cutting edges</td>
</tr>
<tr>
<td>Salinon-shaped cross-section</td>
<td>Abelisauroida, Allosauridae and some Troodontidae for mesial teeth; some Troodontidae for lateral teeth</td>
<td>Crown strength with mesiodistal cutting edges</td>
</tr>
<tr>
<td>D-shaped cross-section</td>
<td>Metriacanthosauroidae, Allosauridae, some Noasauridae, Abelisauroida and Megasauratorm, Ornitholestes, Pelecanimimus, Halszkaraptor and some Troodontidae for mesial teeth</td>
<td>Crown strength with mesiodistal cutting edges</td>
</tr>
<tr>
<td>U-shaped cross-section</td>
<td>Zuolong, Ornitholestes and most Pantyrannosauria for mesial teeth</td>
<td>Crown strength with lingual cutting edges</td>
</tr>
<tr>
<td>Figure-8-shaped cross-section</td>
<td>Berberosaurus, Metriacanthosauroidae, some Megasauratorm, Tyrannosauridae and Troodontidae, and most Dromaeosauridae</td>
<td>Crown strength, better penetration and withdrawal?</td>
</tr>
</tbody>
</table>
### TABLE 3 (continued).

<table>
<thead>
<tr>
<th>Dental feature</th>
<th>Distribution</th>
<th>Possible functionality, adaptation or causes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mesial carina reaching the cervix</td>
<td>In some, if not all, mesial and/or lateral teeth of non-averostran Saurischia, Ceratosauria, Piatnitzkysaurus, Torvosaurus, Spinosauridae, Allosauroidea (excluding most Neovenatoridae), Pantyrranosauria, Eudromaeosauria and Troodon</td>
<td>Crown cutting along the whole crown height leading to deeper wounds</td>
</tr>
<tr>
<td>Twisted mesial carina</td>
<td>Dilophosaurus, Masiakasaurus, Allosauroidea, basal Tyrannosauroidea, and some Abelisauridae and Dromaeosauridae for mesial teeth only; Piatnitzkysaurus, Allosauridae, and some Tyrannosauroidea, Therizinosauria and Dromaeosauridae for lateral teeth</td>
<td>Slicing flesh on the crown width causing wide cuts and open wounds (predatory lifestyle?)</td>
</tr>
<tr>
<td>Split carina</td>
<td>Allosauroidea, Tyrannosauroidea, Segnosaurus, and Dromaeosauridae</td>
<td>Trauma, aberrant tooth replacement or genetic factors</td>
</tr>
<tr>
<td>Distal carina strongly deflected labially</td>
<td>Ceratosauridae, Masiakasaurus, Allosaurus, Sinraptor, Tyrannosauroidea and Dromaeosaurus for the mesial and some lateral teeth; Monolophosaurus, Deinonychus, Richardoestesia and several basal Saurischia, Carcharodontosaurus and Dromaeosauridae for mesial teeth, Saltiosaurus, Berberosaurus, Arocanodon, Piatnitzkysauridae and Neovenatoridae for some lateral teeth</td>
<td>Causing wide cuts and open wounds, possibly gripping function (predatory lifestyle?)</td>
</tr>
<tr>
<td>Hooked denticles</td>
<td>Eoraptor, Gojirasaurus, Abelisauroidea, Therizinosaurus, Euodromaeosauria, Troodontidae (including Anchiornithinae)</td>
<td>Slicing flesh, gripping function, possibly removing feather/fur</td>
</tr>
<tr>
<td>Small number of large denticles on the carina</td>
<td>Therizinosaurus, Troodontidae, Incisivosaurus, Microcarnot and Paronychodon</td>
<td>Slicing through resistant structures such as fibrous material (herbivory/omnivory)</td>
</tr>
<tr>
<td>Large number of minute denticles on the carina</td>
<td>Baryonychinae</td>
<td>Tooth simplification, precursor of unserrated crown</td>
</tr>
<tr>
<td>Sporadic variation of denticle size</td>
<td>Baryonychinae, Nuthetes, Segnosaurus and Richardoestesia</td>
<td>Dentine reduction due to tooth simplification</td>
</tr>
<tr>
<td>Bilobate denticles</td>
<td>Abelisauridae, Megalosauroidea, Erectopus, Carcharodontosaurusidae, Tyrannosauroidea</td>
<td>Trauma or genetic factor?</td>
</tr>
<tr>
<td>Distal denticles larger than mesial denticles</td>
<td>Non-averostran theropods, Ceratosaurus, Noasauridae, Abelisauridae, Piatnitzkysauridae, Baryonychinae, Allosaurus, Acrocanthosaurus, basal Coelurosauria, non-tyrannosaurid Tyrannosauroidea, juvenile Tyrannosauroidea, non-unenlagiine Dromaeosauridae, and Troodontidae</td>
<td>Piercing or slicing function?</td>
</tr>
<tr>
<td>Convex distal profile of the crown</td>
<td>Abelisauridae, Ceratosaurus, Spinosauridae, Ornithomimosaurus, Alvarezsauroidea, Therizinosaurus, and Oviraptorosaurus</td>
<td>Crown strength</td>
</tr>
<tr>
<td>Fluted crowns</td>
<td>Tawa, Coelophysis (juveniles), Masiakasaurus, Spinosauridae, an undescribed metriacanthosaurid and Austroraptor for most of all the dentition; Ceratosaurus, Scipionyx and Velociraptor for the mesial dentition; Saltiosaurus, Dilong and most Microraptoriae for the lateral dentition</td>
<td>Piercing, gripping and keeping slippery prey</td>
</tr>
<tr>
<td>Transverse undulations</td>
<td>Eodromaeus, Dracovenator, non-neocoealousaur Averostra, Falcarius, many eodromaeosaurusians and a few derived troodontids; non-neocoealousaur Averostra when numerous and covering most of the crown</td>
<td>Suction minimization, crown strength, or byproduct of growth</td>
</tr>
<tr>
<td>Marginal undulations</td>
<td>Ceratosaurus, Abelisauridae, non-neocoealousaur Tetanurae</td>
<td>Suction minimization, crown strength, or byproduct of growth</td>
</tr>
<tr>
<td>Interdenticular sulci</td>
<td>Tawa, non-neocoealousaur Averostra, Falcarius, many eodromaeosaurusians and a few derived troodontids</td>
<td>Distributing stresses and/or preventing suction, possibly hosting septic bacteria or helping entrance of venom</td>
</tr>
<tr>
<td>Longitudinal ridges</td>
<td>Allosaurus, Tyrannosauroidea, Microraptoriae for mesial teeth; Orkoraptor, Alvarezsauroida, Therizinosauria and Paraves for lateral teeth</td>
<td>Crown strength, venom delivery system?</td>
</tr>
<tr>
<td>Dental feature</td>
<td>Distribution</td>
<td>Possible functionality, adaptation or causes</td>
</tr>
<tr>
<td>---------------------------------</td>
<td>-----------------------------------------------------------------------------</td>
<td>------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Longitudinal groove</td>
<td>Abelisauridae, Paraves</td>
<td>Crown strength, venom delivery system?</td>
</tr>
<tr>
<td>Basal striations</td>
<td>Herrerasauridae, <em>Proceratosaurus</em></td>
<td>Crown strength, byproduct of growth?</td>
</tr>
<tr>
<td>Braided enamel texture</td>
<td>Non-abelisaurid Ceratosauria, non-spinosaurid Megalosauroidea, Carcharodontosaurus, <em>Aorun</em>, <em>Segnosaurus</em> and most non-averostran Theropoda, non-neocoeelurosaur Coelurosauria and Eudromaeosauria</td>
<td>Crown strength</td>
</tr>
<tr>
<td>Veined and anastomosed enamel texture</td>
<td><em>Incisivosaurus</em> for the premaxillary dentition; <em>Spinosauridae</em> for the whole dentition</td>
<td>Crown strength for particularly high stresses</td>
</tr>
<tr>
<td>Procumbent premaxillary teeth</td>
<td>* Daemonosaurus*, <em>Masiakasaurus</em>, <em>Chilesaurus</em>, <em>Similicaudipteryx</em>, <em>Ornitholestes</em>, <em>Epixiptheryx</em>, <em>Archaeopteryx</em></td>
<td>Procumbency: prehension of small to medium-sized prey and/or vegetation (possibly branch raking/stripping)</td>
</tr>
<tr>
<td>Procumbent maxillary teeth</td>
<td><em>Dracovenator</em>, <em>Coelophysoidea</em>, <em>Dilophosaurus</em>, <em>Masiakasaurus</em>, <em>Spinosauridae</em>, and <em>Scipsionyx</em> for mesial maxillary teeth; <em>Similicaudipteryx</em>, <em>Epixiptheryx</em>, <em>Archaeopteryx</em> and possibly <em>Chilesaurus</em> and <em>Nqwebasaurus</em> for the whole maxillary dentition</td>
<td></td>
</tr>
<tr>
<td>Procumbent dentary teeth</td>
<td><em>Herrerasaurus</em>, <em>Daemonosaurus</em>, <em>Dallansaurus</em>, <em>Megapnosaurus</em>, <em>Masiakasaurus</em>, <em>Duriavenator</em>, <em>Spinosauras</em>, <em>Ornitholestes</em>, <em>Haplocheirus</em>, <em>Inciavosaurus</em>, and some Tyrannosauroidea and Dromeosauridae for mesial dentary teeth; <em>Chilesaurus</em>, <em>Shenzhouasaurus</em>, <em>Similicaudipteryx</em> and <em>Epixiptheryx</em> for the whole dentary dentition</td>
<td></td>
</tr>
<tr>
<td>Laterocumbent and retrocumbent teeth</td>
<td><em>Spinosaurinae</em> (laterocumbent teeth); <em>Eoraptor</em>, some <em>Coelophysoidea</em> and basalmost Neotheropoda, and juvenile <em>Limusaurus</em> (retrocumbent premaxillary teeth); <em>Panguraptor</em>, <em>Sciurumimus</em> and several Dromeosauridae (retrocumbent maxillary teeth)</td>
<td>Hold and keep struggling and/or slippery prey, or keep an immobile bite</td>
</tr>
<tr>
<td>Partial/complete premaxillary edentulism</td>
<td>Partial: <em>Limusaurus</em> (juvenile), <em>Caudipteryx</em>; Complete: Therrisinosauridae, Caenagnathoidea, and Ornithomimosauria more derived than <em>Pelecanimimus</em></td>
<td>Edentulism: paralleled with the development of a rhamphotheca and gastric mill, weight saving demands, abandon of carnivory (herbivory or omnivory)</td>
</tr>
<tr>
<td>Partial/complete maxillary edentulism</td>
<td>Partial/anteriormost portion of the maxilla: <em>Limusaurus</em> (juvenile) and <em>Erikiksaurus</em>; Partial/posterior portion of the maxilla: <em>Limusaurus</em> (juvenile), basalmost ornithomimosaur (i.e., <em>Nqwebasaurus</em>, <em>Pelecanimimus</em>), <em>Shuvuuia</em>, <em>Erikiksaurus</em>, <em>Similicaudipteryx</em>, many troodontids, and <em>Epixiptheryx</em>; Complete: <em>Caudipteryx</em> + Caenagnathoidea, and Ornithomimosauria more derived than <em>Pelecanimimus</em></td>
<td></td>
</tr>
<tr>
<td>Partial/complete dentary edentulism</td>
<td>Partial/anteriormost portion of the dentary: <em>Limusaurus</em> (juvenile), Therrisinosauridae, and non-caenagnathoid Oviraptorosauria; Partial/posterior portion of the dentary: <em>Limusaurus</em> (juvenile), non-ornithomimid ornithomimosaur more derived than <em>Pelecanimimus</em>, <em>Similicaudipteryx</em>, and possibly <em>Protarchaeopteryx</em> and all Scansoriopterygidae; Complete: <em>Caudipteryx</em> + Caenagnathoidea, Ornithomimoidea</td>
<td></td>
</tr>
<tr>
<td>Complete edentulism</td>
<td>All theropods more derived than <em>Eodromaeus</em> for the pterygoid; <em>Limusaurus</em>, Ornithomimoidea and Caenagnathoidea for the whole skull</td>
<td></td>
</tr>
</tbody>
</table>
TABLE 4. Most conspicuous dental features in 31 theropod clades. Dental features for important subclades and taxa are also provided in brackets. *small crowns in comparison to the upper and lower jaws’ height.

<table>
<thead>
<tr>
<th>Clade</th>
<th>Dental features</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Non-neotheropod Theropoda</strong></td>
<td>Small to medium-sized ziphodont dentition; subcircular cross-section of mesial crowns; mesial carina of mesialmost crowns, when present, facing labially and not reaching the cervix; dentary teeth weakly to strongly procumbent; mesial carina, when present, straight and reaching the cervix in some lateral teeth; mesialmost basal striations on the crown (Herrerasaurus); procumbent premaxillary teeth ( Daemonosaurus); fluted mesial and lateral teeth (Tawa)</td>
</tr>
<tr>
<td>Coelophysoidea</td>
<td>Mesialmost teeth unserrated or with unserrated mesial carina; mesial dentition and mesial maxillary dentition with slender, elongated and strongly recurved (i.e., strongly concave distal profile) teeth; diastema between premaxillary and maxillary teeth; constricted tooth-row between premaxilla and maxilla; retrocumbent premaxillary teeth; procumbent mesial maxillary teeth; procumbent mesial dentary teeth ( Megapnosaurus and some Coelophys specimens); fluted mesial and lateral teeth (juvenile Coelophys)</td>
</tr>
<tr>
<td>Non-averostan Neotheropoda (Liliensternus, Zupaysaurus, Sinosaurus, Dracovenator, and Dilophosaurus)</td>
<td>Mesial dentary teeth significantly larger than mid- and posterior dentary teeth; terminal rosette of dentary with four to five teeth; mesial carina of mesial teeth denticulated, facing labially and extending basally well-above the cervix; mesial carina of mesial teeth centrally positioned or slightly labially deflected from the mesial margin of the crown; retrocumbent premaxillary teeth; procumbent mesial maxillary teeth; mesial carina of mesial teeth reaching the cervix in some lateral teeth; DSDI&gt;1.2 ( Dracovenator and Dilophosaurus)</td>
</tr>
<tr>
<td>Non-abelisauroid Ceratosauria (Berberosaurus, Saltrovenator, and Ceratosauridae)</td>
<td>Mesial carina of mesial teeth restricted to the apical portion of the crown and facing labially in mesialmost teeth; lateral dentition with a few strongly labiobuccally compressed crown (CVR&lt;0.4); mid-maxillary teeth taller than the dentary height; mesial and lateral crowns with a strongly labially deflected distal carina; labial surface of the crown weakly convex, almost flat, in some lateral teeth; mesial carina of lateral teeth extends to the cervix or slightly above it; concave surface(s) on the lingual and/or labial sides and adjacent to the mesial and/or distal carinae in some crowns; mesial teeth with fluted lingual surfaces ( Ceratosaurus)</td>
</tr>
<tr>
<td>Abelisauridae</td>
<td>Mesial carina reaching the cervix in mesial and lateral teeth; distal profile of crown weakly concave, straight or convex; lateral teeth with mesial and distal carinae on the mid-line of the mesial and distal profile, respectively; irregular enamel surface texture; subrectangular premaxillary and maxillary alveoli; Salinon to J-shaped cross-sectional outline of mesial teeth in most taxa; apically hooked distal denticles in some taxa</td>
</tr>
<tr>
<td>Noasauridae</td>
<td>Crown height lower than 2 cm; irregular enamel surface texture; mesial carina of lateral teeth reaching the cervix, DSDI&gt;1.2 (Noasaurinae); procumbent mesial dentition, mesial denticate teeth basally constricted, fluted and with a salinon-shaped cross-sectional outline ( Masiakasaurus, possibly in Noasaurinae); flutes, hooked distal denticles and constriction between crown and root in some lateral teeth ( Masiakasaurus); unserrated teeth and partial edentulism in juveniles, complete edentulism in adults ( Limusaurus, possibly in Elaphrosaurinae)</td>
</tr>
<tr>
<td>Piatnitzkysauridae</td>
<td>Mesial teeth mesiodistally short and elongated, with a lenticular cross-sectional outline at the cervix; mesialmost teeth with a mesial carina facing labially; DSDI&gt;1.2; mesial carina extending above the cervix in mesial and most lateral teeth; distal carina strongly deflected labially, enamel undulations and short to well-developed interdenticular sulci between distal denticles in some teeth; braided enamel texture; hooked distal denticles and mesial carina spiraling mesiolingually and reaching the root in some lateral crowns ( Piatnitzkysaurus)</td>
</tr>
<tr>
<td>Megalosauridae</td>
<td>Mesial teeth mesiodistally short and elongated, with a lenticular cross-sectional outline at the cervix; mesialmost teeth with a mesial carina facing labially; mesial carina extending well-above the cervix in mesial and lateral teeth; short to well-developed interdenticular sulci in between distal denticles in some teeth; braided enamel texture; transverse/marginal undulations in some teeth in most taxa; bilobate mesial denticles and well-visible transverse undulations in some lateral crowns (Megalosaurinae)</td>
</tr>
<tr>
<td>Spinosauridae</td>
<td>Conidont dentition; strong allometric heterodonty along the premaxillary, maxillary and dentary denticles, with the largest crowns bore mesially; more than 5 premaxillary teeth; procumbent mesial maxillary teeth; terminal rosette of dentary with four to five teeth; mesial carina reaching the cervix, and extending on part of the root, in most/all teeth; fluted mesial and lateral teeth; veined/anastomosed enamel surface texture; enamel curving basally adjacent to the carinae; large number of minute denticles changing sporadically in size along the carinae (Baryonychinae); unserrated and beaded carinae, laterocumbent teeth, and distal profile of crowns weakly concave, straight or convex (Spinosaurinae)</td>
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<tr>
<td>Clade</td>
<td>Dental features</td>
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<tr>
<td>Metriacanthosauridae</td>
<td>Mesial and distal crowns with denticulated mesial and distal carinae extending to the root; D- to salinon-shaped cross-sectional outline at the crown-base in mesialmost teeth; mesial crowns with mesial carinae spiraling mesiolingually and lingually positioned longitudinal groove adjacent to the mesial carina; lateral teeth with flat to concave labial depressions at the crown-base (8-shaped cross-sectional outline of some lateral teeth); short to well-developed interdenticular sulci between distal denticles; irregular enamel surface texture</td>
</tr>
<tr>
<td>Allosauridae</td>
<td>Pachydont dentition; mesial and distal crowns with denticulated mesial and distal carinae extending to the root, and well-beneath the cervix in some teeth; mesial crowns with lingually positioned longitudinal groove adjacent to the mesial carina; D- to J- and salinon-shaped cross-sectional outline at the crown-base in mesialmost teeth; mesial teeth and mesial maxillary crowns with mesial carinae spiraling mesiolingually; mesial and most lateral teeth with strongly labially deflected distal carina; marginal and transverse undulations well-visible on some crowns; short to well-developed interdenticular sulci in lateral teeth; dentition with a combination of irregular and braided enamel surface texture</td>
</tr>
<tr>
<td>Neovenatoridae (with Megaraptora)</td>
<td>J-shaped cross-section of mesial teeth with concave surface adjacent to mesial carina on the lingual surface of the crown; concave surfaces on the labial/lingual surfaces and adjacent to the distal carina in some lateral crowns; braided enamel surface texture; mesial carina absent and figure-8-shaped cross-section of lateral crowns (Megaraptor and Orkoraptor)</td>
</tr>
<tr>
<td>Carcharodontosauridae</td>
<td>Subcircular cross-section in mesialmost teeth; mesial carina of mesial teeth facing labially and not reaching the cervix; mesialmost teeth with strongly labially displaced distal carina; lateral crowns higher than 6 cm; DSDI&lt;0.9 in lateral teeth; mesial carina reaching the cervix in some/most lateral crowns; well-visible marginal and/or transverse undulations in some lateral teeth; short to well-developed interdenticular sulci in lateral teeth; braided enamel surface texture; bilobate mesial denticles in many taxa; weakly sigmoid distal profile with basal half concave and apical half convex (Carcharodontosauridae more derived than Acrocanthosaurus); weak constriction between crown and root in some lateral teeth (Carcharodontosaurinae); pronounced marginal undulations adjacent to mesial and distal carinae in lateral teeth (Carcharodontosaurus saharicus)</td>
</tr>
<tr>
<td>Non-tyrannosaurid</td>
<td>Mesial teeth significantly smaller than lateral teeth; J- to U-shaped cross-sectional outline of mesial teeth; concave surface adjacent to mesial carina in mesial teeth; DSDI&gt;1.2 in most taxa; some lateral crowns with a strongly labially deflected distal carina and a mesial carina extending above the cervix; interdenticular sulci between distal denticles in some lateral crowns; braided enamel surface texture; basal striations in mesial teeth (Proceratosaurus)</td>
</tr>
<tr>
<td>Tyrannosauroidea</td>
<td>Pachydont dentition; mesial teeth with U-shaped cross-sectional outline and longitudinal ridge centrally positioned on lingual surface; CBR&gt;1.2 in mesial teeth; transitional dentition with spiraling mesial carina and strongly labially deflected distal carina; short to well-developed interdenticular sulci in some teeth; irregular enamel texture and teeth with split mesial carinae in some taxa</td>
</tr>
<tr>
<td>Compsognathidae</td>
<td>Ziphodont dentition; teeth lower than 1 cm; conodont mesial/mesialmost teeth; distal denticulated carina not reaching the cervix and/or the apex in some lateral teeth; unserrated mesial dentition and lateral dentition with unserrated mesial carina in most taxa; retrocurvibent premaxillary teeth (Juravenator); mesial denticulated carina (Sinocalliopteryx)</td>
</tr>
<tr>
<td>Ornithomimosauria</td>
<td>Unserrated crowns; small crowns*, with crown height lower than 1 cm; conodont dentition made of subsymmetrical isodont crowns (all ornithomimosaurids but Pelecanimimus); posterior portions of maxilla and dentary edentulous (non-ornithomimid ornithomimosaurids); premaxilla and maxilla fully edentulous (ornithomimosaurids more derived than Pelecanimimus); complete edentulism (Ornithomimidea); D-shaped mesialmost teeth, constricted mesial and lateral teeth (Pelecanimimus)</td>
</tr>
<tr>
<td>Alvarezsauroidea (Aorun, Haplocheirus, and Alvarezsauridae)</td>
<td>Crown height lower than 1 cm; small crowns*: unserrated mesial teeth; closely packed mesial and lateral dentition with subsymmetrical (i.e., mesial and distal profiles convex), unserrated and weakly constricted isodont crowns (Alvarezsauridae/Parvicursorinae); faint longitudinal grooves on the apex (Mononykus)</td>
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<tr>
<td>Clade</td>
<td>Dental features</td>
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<tr>
<td>Therizinosauria</td>
<td>Foliodont dentition made of subsymmetrical isodont crowns with convex mesial and distal profiles; crown height lower than 1 cm; small crowns*; mesial and distal serrated carinae never reaching the cervix; partially edentulous dentary; edentulous premaxilla, mesial and distal serrated carinae extending above the cervix, small number of large typically apically oriented mesial and distal denticles (Therizinosauroida); Incisiform mesial teeth with a D-shaped cross section, minute denticles, twisted mesial carina, transverse undulations, and longitudinal ridges in some/all lateral teeth (Falcarius); split distal carina, sporadic variation of denticles size, conidont distalmost dentary dentition (Segnosaurus)</td>
</tr>
<tr>
<td>Oviraptorosauria</td>
<td>Conidont dentition; strong allometric heterodonty, with mesial teeth significantly larger than distal teeth; unserrated mesial crowns; lateral dentition with crown height lower than 1 cm; foliodent lateral dentition (Incisivosaurus and Similicaudipteryx); anastomosed enamel surface texture in mesial teeth (Incisivosaurus); partial premaxillary edentulism and complete maxillary and dentary edentulism (Caudipteryx); procumbent maxillary and dentary teeth (Similicaudipteryx); complete edentulism (Caenagnathoidea)</td>
</tr>
<tr>
<td>Halszkaraptorinae and Unenlagiinae</td>
<td>Large number of small crowns*; unserrated and strongly distally recurved crowns; irregular and non-oriented enamel surface texture; ridged/fluted lateral teeth (Unenlagiinae); ziphodont lateral crowns (Halszkaraptorinae and Unenlagiinae other than Austroraptor); weakly labiolingually compressed lateral teeth (Halszkaraptorinae and Unenlagiinae other than Buitreraptor); more than five closely packed premaxillary teeth and D-shaped mesial teeth (Halszkaraptor;possibly Halszkaraptorinae); conidont dentition, mesial dentary teeth significantly larger than distal ones (Austroraptor); strongly labiolingually compressed lateral teeth with 8-shaped cross-sectional outline at the crown-base (Buitreraptor)</td>
</tr>
<tr>
<td>Microraptorinae</td>
<td>Ziphodont dentition whose mesial and lateral dentitions include some unserrated crowns; some mesial teeth with a concave surface on the lingual surface and adjacent to the mesial carina; mesial carina not reaching the cervix; some lateral crowns with unserrated mesial carina and flattened/labial surface; labial depression on the crown-base in some lateral teeth; DSDI&gt;1.2 in lateral teeth (all microraptorines other than Microraptor); some constricted crowns in the mesial and lateral dentitions, unserrated mesial carina, and small number of distal denticles in some lateral crowns (Microraptor)</td>
</tr>
<tr>
<td>Dromaeosaurinae</td>
<td>Ziphodont teeth with serrated mesial and distal carinae in all lateral teeth; J-shaped mesial teeth; mesial dentition with serrated mesial carina spiraling mesiolingually and extending close to the cervix; transverse undulations in some teeth; DSDI&gt;1.2 in lateral teeth (all dromaeosaurines other than Dromaeosaurus); DSDI = 0 or &lt; 0.9, twisted mesial carina in lateral teeth (Dromaeosaurus); retrocumbent maxillary teeth, hooked denticles (Atrociraptor); procumbent dentary teeth (Utahraptor)</td>
</tr>
<tr>
<td>Velociraptorinae</td>
<td>Ziphodont dentition with serrated mesial and distal carinae in at least some lateral teeth, DSDI &gt; 1.2, mesial carina not reaching the cervix in most lateral teeth (all velociraptorines other than Tsagag); some lateral teeth with a figure-of-eight-shaped cross-sectional outline of the crown-base (all velociraptorines other than Deinonychus); many taxa with ridged lateral crowns (e.g., Bambiraptor, Velociraptor, Linheraptor, Acheroraptor); some taxa with retrocumbent maxillary teeth (e.g., Bambiraptor, Deinonychus); mesial carina absent/unserrated in all teeth (Tsagag); hooked distal denticles (Sauromitholestes); mesialmost teeth with fluted labial surface (Velociraptor)</td>
</tr>
<tr>
<td>Anchioniornithinae</td>
<td>Foliodent dentition with weakly to strongly distally recurved crowns; crown height lower than 1 cm; mesial dentition unserrated; mesial dentary teeth closely packed; teeth from middle and distal portion of the lateral dentition sparsely spaced; small crowns* (anchioniornithines other than Caihong); unserrated lateral teeth (anchioniornithines other than Caihong and Liaoningvenator); mesial denticles and apically hooked denticles in some lateral teeth (Caihong)</td>
</tr>
<tr>
<td>Jinfengopteryginae</td>
<td>Foliodent dentition with fully unserrated teeth; mesial teeth closely packed; small crowns*; dentary teeth resting in an open alveolar groove; posterior portion of maxilla edentulous; dentition with some unconstricted teeth (Jinfengopteryx)</td>
</tr>
</tbody>
</table>
TABLE 4 (continued).

<table>
<thead>
<tr>
<th>Clade</th>
<th>Dental features</th>
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<tbody>
<tr>
<td>Troodontinae</td>
<td>Folidont dentition with distally recurved crowns in the central and distal portions of the lateral dentition; D- to salinon-shaped mesial dentition; mesial teeth closely packed; dentary teeth resting in an open alveolar groove; fully unserrated dentition in many taxa (e.g., Mei, Xixiasaurus, Urbacodon, Gobivenator, Byronosaurus); heterodont lateral dentition made of folidont and ziphodont crowns in many basal forms (e.g., Xixiasaurus, Sinovenator, Jianianhuatlong, Byronosaurus); some lateral teeth with a small number of large distal denticles in derived forms (e.g., Sinornithoides, Troodon, Zanabazar, Saurornithoides); mesial denticulated carina (Troodon, Pectinodon); interdenticular sulci and transverse undulations in some teeth (Troodon)</td>
</tr>
<tr>
<td>Scansoriopterygidae</td>
<td>Conidont dentition; unserrated teeth; strong allometric heterodonty, with mesial teeth significantly larger than distal ones; procumbent premaxillary and dentary teeth; maxilla and dentary partially edentulous</td>
</tr>
</tbody>
</table>

2007; Shen et al., 2017a, 2017b; Xu et al., 2017; Pei et al., 2017b; Figure 10.2). If constricted teeth appear to be present in the majority, if not all troodontids, many of them (e.g., Byronosaurus, Dalianosaurus, Sinovenator, Sinusornasus, Xixiasaurus) have a lateral dentition that also includes non-constricted ziphodont teeth. Constricted teeth are typically present in the anterior portion of the maxilla and dentary, where they are closely packed. In non-maniraptoriform theropods, constricted teeth in the whole dentition are only present in the noasaurid Masiakasaurus (UA 8680, 9091; FMNH P 2476) and the basal tetanuran Chilesaurus (Novas et al., 2015; see Baron and Barrett (2017) for a different opinion on the classification of Chilesaurus). Yet not all teeth are constricted in Masiakasaurus, and the lateral teeth only show a weak constriction between crown and root (Figure 10.1).

Mesial dentition. A weakly constricted crown at the level of the cervix can be seen in the premaxillary teeth of some abelisaurids such as Chenanisaurus (Longrich et al., 2017) and Majungasaurus (Rpm1 of FMNH PR 2008). A basal constriction between crown and root is also present in some premaxillary teeth of the basal tyranosauroid Proceratosaurus (Rauhut et al., 2010; Figure 10.4), and the basal coelurosaur Ornitholestes (AMNH 619). Zinke and Rauhut (1994) mentioned the presence of a constriction in some mesial dentary teeth in the compsognathid Compsognathus. Although a weak constriction might be present in some premaxillary and lateral teeth, this feature is not clearly observable in the two Compsognathus specimens (MNHN CNJ 79; BSP AS I563). In dromaeosaurids, a week constriction is present in some premaxillary teeth of the basal dromaeosaurid Halszkaraptor (MPC-D 102-119). Zhou et al. (2000) noted a constricted premaxillary crown in the basal oviraptorosaur Caudipteryx but a close examination of the teeth of specimen IVPP V12430 failed to confirm this observation. As other toothed oviraptorosaurs, the premaxillary dentition of Caudipteryx is conidont.

Lateral dentition. In the oviraptorosaurs Incisivosaurus (IVPP V13326; Osmólska et al., 2004), Protarchaeopteryx (Ji et al., 1998), and Similicaudipteryx (Li et al., 2018, figure S3f), as well as the therizinosaur Elikosaurus (Zanno et al., 2016) and Falciarius (Zanno, 2010a), only the lateral dentition is constricted between crown and root, the mesial dentition of these taxa being conidont or subconical/incisiform (Zanno, 2010a; Zanno and Makovicky, 2011). Likewise, the juvenile megalosaurus Scirurimus (BMMS BK 11, Rdt4, Rdt6) and the carcharodontosaurs Carcharodontosaurus (SGM Din 1) and Giganotosaurus (MUCPV-CH-1) clearly show a ziphodont dentition but a few lateral teeth are weakly constricted at the cervix. Some lateral teeth of the microraptorine IVPP V13476 (Xu and Li, 2016) and most Microraptor specimens (e.g., IVPP V12330, V13320, V13475; BMNH PC881; Xu et al., 2000; Turner et al., 2012; Pei et al., 2014) are also constricted. A constriction between crown and root is also visible in at least one lateral tooth of the putative dromaeosaurid Richardoestesia gilmorei (Rdt13, Currie et al., 1990, figure 8.4G). Only the distal teeth of the lateral dentition are constricted in the basal maniraptoriform Fukuivenator (Azuma et al., 2016), a dental synapomorphy of this taxon.

Remarks and synapomorphy. Constricted teeth are present in the mesial and/or lateral dentition of abelisaurids, carcharodontosaurines, proceratosaurids and the majority of non-avian maniraptoriforms. With some exceptions (Scirurimus,
carcharodontosaurines, *Chilesaurus*, *Halszkaraptor*, *Masiakasaurus*, *Microraptor*, *Ornitholestes*, *Pelecanimimus*, *Proceratosaurus* and some abelisaurids), constricted teeth appear to be absent in all dromaeosaurids and all non-maniraptoriform theropods. It is unknown whether some lateral teeth of scansoriopterygids are weakly constricted as this condition cannot be positively confirmed in *Epidexipteryx* (IVPP V11579) and *Yi* (STM 31-2). Folidonty is synapomorphic for the clade Therizinosauria + Pennaraptora (Figure 8; Appendix 6.1 for lateral teeth). Constricted teeth were lost in the large majority of dromaeosaurids but appear to be retained, or re-acquired, in the mesial dentition in the basalmost member of Dromaeosauridae *Halszkaraptor* and in the lateral dentition of *Microraptor*. A folidont dentition appeared several times throughout the evolution of theropod dinosaurs, occurring in: *Pelecanimimus* (Pérez-Moreno et al., 1994); Alvarezsauridae/Parvicursorinae; and Therizinosauria + Pennaraptora.

**Functional morphology.** A marked constriction at the cervix, giving a lanceolate outline of the crown, is typically correlated with a diet involving a mixture of food, and primarily plant material (e.g., Galton, 1984, 1985; Barrett, 2000). Whilst the labiolingual compression of the tooth allows keeping a sharp edge that cuts food items, it is possible that a mesiodistal expansion of the crown relative to the root increases the surface area of the enamel as well as strengthening the crown by dissipating the forces applied apically along the tooth width. This hypothesis, however, requires to be tested with physical models or through FEA.

**Crown base ratio greater than 0.75**

A labiologically broad crown is the typical condition of mesial teeth in non-avian theropods. A crown base ratio (CBR) greater than 0.75 is present in the mesial dentition of the majority of ziphodont theropods. However, a weak labioliingual compression of the whole crown (and not only the base) is also present in the dentition of Spinosauridae, which bear subconical teeth (e.g., Charig and...
Milner, 1997; Sereno et al., 1998; Sues et al., 2002), and large/mature Tyrannosauridae, which possess pachydont teeth (e.g., Holtz, 2003, 2008; C.H. personal obs.). These taxa have a crown-base ratio higher than this arbitrary value in many or most teeth of the mesial and lateral dentitions. The allosauroid *Allosaurus* and the basal maniraptoriform *Omniotholites* have thick incrasastate lateral teeth (CBR >0.75) along part of the dentary row. Teeth from the maxilla and the distalmost portion of the dentary (typically from the eighth dentary crown in both *Allosaurus* and *Omniotholites*) are moderately (CBR around 0.5 to 0.7) to strongly (CBR of less than 0.5) labioblandly narrowed in these two taxa (C.H. personal obs.). In maniraptoriforms, the dentition of all ornithomimosaurs, therizinosaurids, alvarezsaurids and most likely *Caudipteryx* have a CBR higher than 0.75. The mesial and lateral den- titions of many troodontids, however (e.g., MPC-D 100-1128, *Byronosaurus*, *Zanabazar*), also have a subcircular cross-sectional outline at the crown base (C.H. personal obs.).

**Remarks and synapomorphy.** The subcircular outline of the crown is a synapomorphy of Spino- sauridae (Sereno et al., 1998) and Maniraptoriformes (Appendix 6.2 for lateral teeth), being present in at least some crowns in the basal forms of: spinosaurids (*Baryonyx*, Charig and Milner, 1997; *Ostafrikasaurus* if a Spinosauridae; Buffe- taut, 2011); ornithomimosaurs (*Nqwebasaurus*; Choiniere et al., 2012); alvarezsauroids (*Aorun*, *Haplocheirus*; Choiniere et al., 2014b); and theri- zinosaurids (*Falcaurus*; personal obs.). Pachydont lateral teeth (CBR >0.6) are absent in the non- tyrannosaurid tyrannosaurids *Xiongguanlong* (Li et al., 2010), *Guanlong* (IVPP V14531), the possibly immature *Dryptosaurus* (Brusatte et al., 2011; R. Molnar, personal commun., 2017) and *Raptorex* (Sereno et al., 2009), a probable juvenile of *Tarbosaurus* (Fowler et al., 2011b). This feature is present in the basal tyrannosaurids *Albertosaurus* (Buckley et al., 2010; Reichel, 2010) and *Gorgosaurus* (AMNH 5458; USMN 12814), and the alior- amine *Qianzhousaurus* (Lü et al., 2014) so that pachydont teeth (and pachydonty) are a synapomorphy of Tyrannosauroidea. It should be noted that some non-tyrannosaurid tyrannosaurids such as *Dilong* (IVPP 14242) and *Proceratosaurus* (Gerke and Wings, 2016) also bear pachyodont lateral teeth while most teeth of the lateral dentition of the alior- amine *Alioramus* are not pachyodont (Brusatte et al., 2012).

**Functional morphology.** The expansion of the crown labioblandly adds resistance and the ability to withstand bending loads applied from all directions (e.g., Therrien et al., 2005; Snively et al., 2006; Holtz, 2008; Reichel, 2010). Thick teeth in carnivorous theropods are adapted to resist contact with hard items such as bones and scales during prey capture and feeding. The mesial denti- tion was most likely subject to higher stress and loads than the lateral dentition during bites. In theropods, lateral crowns are as labioblandly wide as those of the mesial dentition in pachyodont and conidont theropod teeth, used for bone-crushing or to impale and hold prey, respectively (e.g., Therrien et al., 2005; Holtz, 2008). Interestingly, teeth with a CBR greater than 0.75 are also present in many maniraptoriforms such as ornithomimosaurs, ther- izinosaurids and alvarezsauroids, in which the cross- section of the crown base is sub-circular (e.g., Clark et al., 1994; Xu et al., 2001; Ji et al., 2003; Barrett, 2009; Choiniere et al., 2012; C.H. personal obs.). Increase in resistance of higher stresses in different directions in the dentition of these omnivo- rous/herbivorous theropods likely results from the consumption of hard plant material whereas labioblandly compressed blade-shaped ziphodont teeth of carnivores are suitable to slice through softer flesh.

**Crown height higher than 60 mm**

Absolute tooth size is a homoplastic feature that also varies allometrically and must be treated with caution for classification purposes. Nonetheless, this feature has proven to be useful to dis- criminate the teeth of different theropod taxa (Smith, 2005; Smith et al., 2005; Han et al., 2011). Theropods bearing crowns larger than 6 cm are only known in non-neocoelurosaur averostrans: Allosauroididea (e.g., *Acrocanthosaurus*, *Allosaurus*, *Carcharodontosaurus*, *Giganotosaurus*, *Mapusaurus*, *Sinraptor*), Ceratosaurus, Megalosauridae (e.g., *Afrovenator*, *Megalosaurus*, *Spinosaur*, *Torvosaurus*, *Wiehenvenator*), and some derived Tyrannosauroidea (e.g., *Albertosaurus*, *Bistahievenser*, *Tarbosaurus*, *Tyrannosaurus*). Abelisauroi- rids, baryonychines, neovenatorids, ptiatnitzkysaurids, proceratosaurids, and non-neo- coelurosaur averostrans, including dromaeosau- rids have shorter teeth (Young et al., 2019; C.H. personal obs.) with even the crowns of the largest dromaeosaurids such as *Utahraptor* being less than 5 cm in height (C.H. personal obs.). However, given the possible immaturity of *Baryonyx* and *Suchomimus* (Charig and Milner, 1997; Hendrickx et al., 2016) and because the longest crown mea- sured in *Suchomimus* is 54 mm, it is likely that
some baryonychines had crowns higher than 6 cm. Likewise, the largest crowns of the proceratosaurid *Yutyrannus* are slightly shorter than 60 mm (C.H. personal obs.), and some proceratosaurids or basal tyrannosauroids could have borne lateral crowns exceeding 60 mm.

**Remarks and synapomorphy.** In the discussion on the taxonomic affinities of a large-sized theropod tooth (IVPP V15310; CH = 92mm; AL = 102 mm) from the Late Jurassic Shishugou Formation of China, Xu and Clark (2008) cite *Carcharodontosaurus*, *Tyrannosaurus* and probably *Giganotosaurus* as the theropods with a crown height subequal or higher than 90 mm. We confirm that some *Giganotosaurus* lateral teeth have a CH higher than 9 cm (e.g., MUCPV-CH-1 L1) and add to this list *Torvosaurus* (e.g., BYU-VP 725 12817, ML 1100), *Acrocanthosaurus* (NCSM 14345, Lmx4) and most likely *Spinosaurus* based on the size of the partially complete Lmx4 in MSNM V4047.

With a CH of 145.5 mm, the largest known theropod crowns belong to the megalosaurid *Torvosaurus gurneyi* (SHN.401 and SHN.450; CBL of 48 mm) from the Upper Jurassic of Portugal (Mallafia et al., 2017a, 2017b). Other taxa may have possessed larger crowns: the spinosaurid *Spinosaurus* (CBL of 51 mm in Lmx4 of MSNM V4047 preserving the crown base only); the tyrannosaurid *Tyrannosaurus* (CH of 139 mm in Rdt3 of FMNH PR2081, the highest crown measured for this taxon; C.H. personal obs.); large-bodied tetanurae from the Kimmeridgian-Tithonian Tendaguru beds of Tanzania (CH slightly more than 135 mm; CBL of 54 mm in NHMUK PV R.6758) and the Berriasian-Valanginian Kirkwood Formation of South Africa (CBL >53 mm in MB R.2352; Galton and Molnar, 2012). A lateral dentition including crowns higher than 60 mm is here considered a synapomorphy of Ceratosauridae, Megalosaurinae more derived than *Duriavenator*, Allosauroidea, and a clade encompassing Tyrannosauroida + Bishtieversor or *Appalachiosaurus* (Appendix 6.3 for lateral teeth).

**Unserrated teeth**

**Mesial dentition.** In embryonic/juvenile individuals, unserrated teeth restricted to the mesial dentition have been recorded in *Aorun* (Choiniere et al., 2014a), *Archaeornithoides* (Elzanowski and Wellnhofer, 1993), *Coelophysis* (Colbert, 1989; Figure 11.1), *Dapselosaurus* (Currie, 2003), *Juravenator* (Chiappe and Göhlich, 2010), *Scipionyx* (Dal Sasso and Maganuco, 2011), *Scoliurimus* (Rauhut et al., 2012; Figure 11.2), *Timurlengia* (Averianov and Sues, 2012), *Torvosaurus* (Araújo et al., 2013) and *Troodon* (Varricchio et al., 2002). Unserrated teeth are also present in the premaxillary teeth of the “Jordan Theropod” LACM 28471 (Molnar, 1978), considered to be a specimen of *Nanotyrannus* (Larson, 2013) or a juvenile individual of *Tyrannosaurus* (Carr and Williamson, 2004). In mature individuals, unserrated teeth are restricted to the mesial dentition of some coelophysoids such as *Megapnosaurus rhodesiensis* (Raath, 1977) and ‘Syntarsus’ kayentakatae (Rowe, 1989), and the basal pantyrannosaurian *Xiongguanlong* (Li et al., 2010; Figure 11.4) and an indeterminate tyrannosaurid from the Cenomanian of Utah (Zanno et al., 2019). Most compsognathids such as *Compsognathus*, *Juravenator* and *Sinosauropteryx* also show unserrated mesial crowns, but these taxa may not have been fully grown individuals (i.e., juveniles to subadults; Currie and Chen, 2001; Peyer, 2006; Chiappe and Göhlich, 2010). Non-denticulate mesial teeth have also been identified in: anchiornithines (e.g., *Liangyingvenator*, *Caihong*; Shen et al., 2017b; Hu et al., 2018); *Falcarius* (UMNH 15097, 15223); *Haplocheirus* (Choiniere et al., 2014b); microraptorines (e.g., *Microraptor*, *Sinornithosaurus*, Shanag; Xu et al., 2000; Xu and Wu, 2001; Turner et al., 2007), non-anchiornithine troodontids (e.g., *Daliensaurus*, *Sinovenator*, *Sinusonasus*, *Sinornithoides*; Currie and Dong, 2001b; Xu et al., 2002b; Xu and Wang, 2004; Shen et al., 2017a); and *Ornitholestes* (AMNH 619).

**Whole dentition.** Unserrated teeth are present in the whole dentition of: the noasaurid *Limusaurus* [Wang et al.’s (2017a) data matrix]; spinosaurines such as *Irritator* (Sues et al., 2002; Figure 11.3), *Angaturama* (Kellner and Campos, 1996), and *Spinosaurs* (Stromer, 1915); the neocoelurosaur *Fukuivenator* (Azuma et al., 2016); basal ornithomimosaurids such as *Nqwebasaurus* (Choiniere et al., 2012; Figure 11.6), *Pelecanimimus* (Pérez-Moreno et al., 1994), and *Shenzhousaurus* (Ji et al., 2003), and all alvarezsaurids such as *Shuuvuia* (Chiappe et al., 1998; Figure 11.7) and *Mononykus* (Perle et al., 1993). Unserrated crowns are also present in the whole dentition of the basal oviraptorosaur *Caudipteryx* (IVPP 12430; NGMC 97 4 A; Figure 11.8), and all halszkaraptorine and unenlagiine dromaeosaurs such as *Halszkaraptor* (Cau et al., 2017), *Mahakala* (Turner et al., 2011), *Buittreptor* (Gianechini et al., 2011b; Figure 11.9) and *Austrotaptor* (Novas et al., 2009). Many non-anchiornithine troodontid like *Mei* (Xu and Norell, 2004), *Byronosaurus* (Makovicky et al., 2003), *Gobivena-
tor (Tsuihiji et al., 2014), Urbacodon (Averianov and Sues, 2007), Xixiasaurus (Lü et al., 2010), IVPP V20378 and the jinfengopterygines Jinfengopteryx (Ji et al., 2005), Almas (Pei et al., 2017b; Figure 11.10) and MPC-D 100-1128, also have non-denticulate crowns all along their jaws. Unerrated teeth are also present in the whole dentition of the anchiornithines Anchiornis (IVPP V16055; Hu et al., 2009; Pei et al., 2017a), Eosinopteryx (YFGP-T5197; Godefroit et al., 2013b), Aurornis (YFGP-T5198; Godefroit et al., 2013a) and the basal avialan Archaeopteryx (e.g., Martin et al., 1980; Eizanowski and Wellnhofer, 1996; Mayr et al., 2007).

Remarks and synapomorphy. Protarchaeopteryx, interpreted as a basal oviraptorosaur and a senior synonym of Incisivosaurus (Senter et al., 2004), was described as possessing denticulated teeth (Ji et al., 1998). However, Senter et al. (2004) noted that no serrations could be observed in the holotype specimen of Protarchaeopteryx NGMC 2125. Nevertheless, minute denticles (60 denticles per 5 mm) can be seen on the distal carina of Lmx6? in Incisivosaurus (IVPP V12430; contra Xu et al., 2002a) and a non-erupted dentary crown appears to have poorly delimited serrations on both mesial and distal carinae (C.H. personal obs.). Consequently, we follow Ji et al.'s (1998) description of Protarchaeopteryx and consider that serrations are likely to be present in NGMC 2125. The troodontid Zanabazar was described as having unserrated premaxillary teeth by Norell et al. (2009), yet the presence of denticles is clearly reported in the premaxillary teeth by Barsbold (1974) and at least distal serrations appear to be present in the mesial teeth of this taxon (Norell et
al., 2009, figure 22). In the same way, although scored as having unserrated premaxillary teeth by Zhang et al. (2008, character 346), Epimorphipteryx (IVPP V15471) appears to have an apicobasally short carina on the first right premaxillary tooth (r2 of Zhang et al., 2008, figure 1b) bearing minuscule serrations (C.H. personal obs.). All other teeth are unserrated and the presence of a denticulated carina on this tooth requires confirmation.

Besides Incisivosaurus and Epimorphipteryx, a combination of distally denticulated crowns and teeth is present in the lateral dentition of: the compsognathids Compsognathus (MNHN CNJ 79; Stromer, 1934; Peyer, 2006) and Scipionyx (Dal Sasso and Maganuco, 2011); Ornitholestes (AMNH 619); the basal alvarezsauroids Aorun (IVPP V15709) and Haplocheirus (Choiniere et al., 2014b); the dromaeosaurid Shanang (Turner et al., 2007), Microraptor (IVPP V13330, V13475; Wang et al., 2002), and IVPP V13476 (Xu and Li, 2016); and some anchiornithines and more derived troodontids such as Caichong (Hu et al., 2018), Liaoningvenator (Shen et al., 2017b), Jianianhualong (Xu et al., 2017), Sinovenator (IVPP V12615; Xu et al., 2002b) and Sinusonasus (IVPP V11527; Xu and Wang, 2004). Interestingly, these taxa typically have particularly small denticles (i.e., more than ten denticles per mm), suggesting that taxa with unserrated teeth derive from forms bearing crowns with minute denticles. This is exemplified by three clades with unserrated teeth namely, Spinosaurinae, Alvarezsauridae, and Caudipteridae, which evolve from baryonychines, Haplocheirus and Incisivosaurus-like theropods, respectively, whose teeth are finely denticulated.

Unserrated lateral dentition is absent in mature individuals of Allosauroidea, Ceratosauria, Coelophysoidea, non-neotheropod Theropoda, non-spinosaurine Megalosauroidea, non-unenlagiine Dromaeosauridae, Therizinosauria, Tyranosauroidea and most derived Troodontidae. The loss of denticles in lateral teeth is a trend that happened several times in the evolution of theropods. The teeth of Alvarezsauroidae, Ornithomimosauria, Oviraptorosauria and Spinosaurinae all lost denticles independently. With the presence of denticulated teeth in the basal members of Alvarezsauroidae (Haplocheirus), Therizinosauria (Falcarius) and Oviraptorosauria (Incisivosaurus), and the absence of denticles in basal taxa belonging to Avialae, Dromaeosauridae (Butterraptor, Halszkaraptor), Troodontidae (e.g., Almas, Anchionisornis, MPC-D 100-1128), and possibly Scansoriopterygidae, unserrated teeth is the apomorphic condition of the clade Paraves. Likewise, the presence of unserrated teeth is synapomorphic to Alvarezsauridae/Parvicosaurinae (Appendix 6.5), Aves (sensu Choiniere et al., 2010b), Ornithomimosauria (Appendix 6.5), Caudipteridae + Caenagnathoidea, and Spinosaurinae (Appendix 6.7 for lateral teeth). On the other hand, denticles were independently reacquired by Anchiornithinae (e.g., Caichong, Liaoningvenator), derived Troodontinae (i.e., Sinovenator + more derived forms; Appendix 6.5, and 6.7 for mesial teeth) and the clade Microraptorinae + Eudromaeosauria (sensu Turner et al., 2012; Appendix 6.5 and 6.7 for mesial teeth). The total absence of serrations was thought to be a synapomorphy of the Unenlagiinae by Novas et al. (2009) and Gianechini et al. (2011b), yet their closest ancestors seem to share this feature as well, and unserrated teeth in Unenlagiinae is therefore considered to be a plesiomorphic condition (Appendix 6.5 and 6.7 for mesial teeth).

**Functional morphology.** The absence of serrations indicates less efficiency of slicing food (Xing et al., 2013b). Unserrated teeth are therefore used to either spear into flesh (Xing et al., 2013b) and deeply injure prey items, or for cropping and browsing vegetation. The absence of denticles seems also to result in the simplification of the crown in the theropod clades whose derived forms have lost their dentition (Gianechini et al., 2011b).

**Unserrated mesial carina, denticulated distal carina**

**Mesial dentition.** Mesial teeth with unserrated/absent mesial carinaceae and denticulated distal carinae are present in most theropod clades. This feature is observed in: basal saurischians such as Eoraptor (PVSJ 512), Herrerasaurus (PVSJ 407) and Ischisaurus (PVSJ 605); the coelophysoid Coelophysis (CMNH 81765, 82931); the noasaurid Masiakasaurus (FMNH PR.2696); the megaraptoran Megaraptor (Porfiri et al., 2014); the basal pantyrannosauromorph Dilong (IVPP V14242) and Aviatyrannis (MG 27801 D172); some compsognathids such as Juravenator (Chiappe and Göhlich, 2010) and Sinocalliopteryx (Ji et al., 2007); the therizinosaur Ertikosaurus (MPC-D 100-111); n.b. although the anteriormost portion of the dentary is edentulous, we consider the distally denticulated first and second dentary teeth to be from the mesial dentition; the dromaeosaurid Tsagaan (Norell et al., 2006); and the troodontid Linhevenator (Xu et al., 2011a; the mesial carina is the unserrated one in Linhevenator; contra Xu et al., 2011a) and possibly Saurornithoides (AMNH
Large distal denticles can indeed be seen in the latter, but the mesial teeth are too badly preserved to rule out the presence of mesial serrations. The ceratosaurid *Ceratosaurus* has a denticulated mesial carina in the premaxillary and dentary teeth (UMNH VP 5278; contra Currie and Carpenter, 2000; Bakker and Bir, 2004).

**Lateral dentition.** In lateral teeth, this condition is present in: the noasaurid *Masiakasaurus* (FMNH PR 2476), the juvenile megalosaurid *Sciuromimus* (Rauhut et al., 2012); some megaraptorans such as *Orkoraptor* (Novas et al., 2008) and *Megalaptor* (Porfiri et al., 2014); and all compsaognaths, with *Sinocalliopteryx* and possibly *Juravenator* (a single tooth, Rmx8, shows what could be mesial denticles on the crown apex) having also a few lateral teeth with denticles on both carinae (e.g., JME Sch 200; Currie and Chen, 2001; Hwang et al., 2004; Peyer, 2006; Ji et al., 2007; Dal Sasso and Maganuco, 2011). A mesial carina is also absent in the lateral dentition of: the basal neocoelurosaur *Ornitohelastes* (AMNH 619); the basal *Alvarezsauridae* *Aorun* (Choiniere et al., 2014a) and *Haplocheirus* (Choiniere et al., 2014b); and the basal Oviraptorosauria *Incisivosaurus*. In paravians, a few dromaeosaurs such as *Linheraptor* (IVPP V16923), *Microaptor* (Xu et al., 2000; Hwang et al., 2002), *Saurornitholestes* (Currie et al., 1990), *Shanag* (Turner et al., 2007), *Tsaagan* (Norell et al., 2006; Xu et al., 2010) and *Velociraptor* (Godefroit et al., 2008) also show this condition. In Velociraptorinae, most teeth of *Linheraptor* and *Velociraptor* and all the dentition of *Tsaagan* lack a mesial carina. This dental feature is also seen in some anchiornithines like *Caihong* (Hu et al., 2018) and *Liaoningvenator* (Shen et al., 2017b), where distally denticulated teeth appear in the central and/or distal portion of the maxilla and dentary, and many non-anchiornithine troodontids including *Daliansaurus* (Shen et al., 2017a), *Pectinodon* (Carpenter, 1982; Larson and Currie, 2013), *Saurornithoides* (Norell et al., 2009), *Sinornithoides* (Norell et al., 2009), *Sinovenator* (IVPP V9612; Currie and Dong, 2001b), *Sinovenator* (IVPP V12615), *Sinu-sonasus* (IVPP V11527), *Troodon* (Currie, 1987) and *Zanabazar* (Norell et al., 2009). Minute mesial denticles restricted to the apical part of the crown have been observed in at least one maxillary tooth of the basal *Alvarezsauria* *Haplocheirus* (IVPP V14888; contra Choiniere et al., 2014b).

**Remarks and synapomorphy.** Similar to the loss of serrations for the whole dentition, the loss of mesial denticles happened several times convergently in the evolution of theropods. The presence of lateral crowns with unserrated mesial carina and denticulated distal carina seems to be the derived condition in Megaraptorida (sensu Benson et al., 2010) among Neovenatoridae, and neocoe-lurosaurids among Coelurosauria (Appendix 6.4 for lateral teeth). The reacquisition of denticles in the mesial carina also occurred independently in some anchiornithines like *Caihong* (Hu et al., 2018), derived troodontids like *Troodon* and *Pectinodon*, and in members of the clade Microraptoria + Eudromaeosauria.

**Concave surfaces adjacent to carinae on lateral teeth.**

A slightly concave or planar surface adjacent to the distal and mesial carinae in lateral teeth was considered to be a ceratosaurian (neoceratosaurian sensu Rauhut, 2004) synapomorphy by Rauhut (2004), however, this feature is widespread among non-coelurosaurs theropods. Among non-averostran theropods, a concave surface adjacent to the distal carina is visible on the labial (and in some cases lingual) side of some lateral crowns in the basal saurischian *Eodromaeus* (PVSJ 560, 561), the non-averostran neotheropod *Dilophosaurus* (UCMP 37303; Figure 12.1) and *Coelophysis* (CMNH 81765). As noted by Rauhut (2004), this concave surface is present in some Ceratosauria such as *Ceratosaurus* (USNM 4735; UMNH VP 5278) and *Genyodectes* (MLP 26-39; Rauhut, 2004), but we could not identify this dental feature in the lateral teeth of any Abelisauridae or Noasauridae. A planar surface, however, is observable on the labial surface and adjacent to the distal carina in one lateral tooth of *Skorpiovenator* (MMCN-PV 48).

A concave area adjacent to the distal carina, on the labiobasal part of the crown, is present in the megalosaurid *Piatnitzkysaurus* (MACN CH 895) and *Afrovenator* (MMN TIG1; Figure 12.2). This concave surface is also present on one or both labial and lingual sides all over the crown in the metriacanthosaurid *Sinraptor* (IVPP 10600; Figure 12.4), the neovenatorid *Neovenator* (MIWG 6348; Figure 12.3), and some megaraptorans such as *Fukuiraptor* (Azuma and Currie, 2000, figure 4; Molnar et al., 2009, figure 3E) and *Australovenator* (Hocknull et al., 2009, figures 20K, 21E). This dental character would, therefore, support the clade Neovenatoridae recovered by Benson et al. (2010) and Carrano et al. (2012), as tyrannosaurs do not seem to display this feature (C.H. personal obs.). The lateral teeth of some troodontids such as *Sinornithoides* (IVPP V9612), *Byronosaurus* (MPC-D 100-983) and *Urbacodon* (Averianov and
Sues, 2007) also show a concave surface adjacent to the distal carina on the lingual surface of the crown. Some mesial and/or lateral teeth of the basal therizinosaurs *Falcarius* (UMNH VP 14545) and *Jianchangosaurus* (Pu et al., 2013, figure 4B) show a deep concave surface adjacent to the distal carina on the lingual surface.

**Remarks and synapomorphy.** *Eoraptor* lateral teeth (PVSJ 512) are unique in having a strongly mesiodistally convex surface labiomesially situated (the ‘rounded eminence’ of Sereno et al., 2013) and adjacent to a mesiodistally concave surface marginal to the distal carina. A similar concave surface is also present in the vicinity of the mesial carina in some lateral teeth of this taxon. A concave or planar surface adjacent to carinae in some lateral teeth is considered to be synapomorphic for Neovenatoridae (Figure 3.20; Appendix 6.8 for lateral teeth) and possibly for Ceratosauridae and Metriacanthosauridae.

**Functional morphology.** The presence of concave surfaces marginal to carinae or mesially-situated on the tooth had several functional implications in theropods, namely to either enhance the structural strength and stability of the crown by increasing the surface area of the enamel (Folinsbee et al., 2007), or to allow rapid penetration and easier withdrawal during the bite (Freedman, 1957).

### J-shaped and salinon-shaped cross-section

**Salinon-shaped cross-section.** A concave surface marginal to both carinae and separated by a wide convexity on the lingual surface of the crown, therefore creating a salinon-shaped outline (sensu Hendrickx et al., 2015c; Figure 1.11) of the crown base in cross-section, is seen in the first mesial teeth (pm1-2, dt1) of abelisaurids such as *Abelisaurus* (MPCA 1, 5), *Indosuchus* (AMNH 1753) and *Majungasaurus* (Fanti and Therrien, 2007, figure 6C3; FMNH PR.2100; Figure 13.1). A concave surface adjacent to both carinae has also been observed in some mesial teeth of the noasaurids *Masiakasaurus* (e.g., UA 9128, FMNH PR.2182), the allosauroids *Allosaurus* (AMNH 600, 851; CMNH 21703; UMNH VP 2151, 6145, 7438) and *Sinraptor* (IVPP V10600), as well as the troodontids *Troodon* (Currie, 1987; Currie et al., 1990), *Urbacodon* (Averianov and Sues, 2007), and an indeterminate taxon from Uzbekistan (Averianov and Sues, 2007). A mesiodistally biconcave profile of the lingual surface of the crown is also present in the lateral teeth of the troodontid *Xixiasaurus* (the “distinct grooves adjacent to the carinae” of Lü et al., 2010, p. 384, figure 3A1).

**J-shaped cross-section.** A concave surface adjacent to the mesial carina only occurs on the lingual surface of more distal mesial teeth (pm3-4, mx1-2, dt2-3) of abelisaurids, which, therefore, have a J-shaped cross-sectional outline (Figure 1.12, 13) of the crown base. A J-shaped cross-sectional outline here refers to labioluminally wide (Figure 1.12) or narrow crowns (Figure 1.13) characterized by a spiraling mesial carina facing mesiolingually or lingually, a distally oriented distal carina and the pres-
ence of a concave surface adjacent to mesial carina on the lingual surface and, in some cases, to the distal carina on the labial surface of the crown. Such morphology of the crown is present in mesial teeth of: the noasaurid Masiakasaurus; the non-carcharodontosaurid allosaurs such as Allosaurus (e.g., AMNH 851, CMNH 21703); the megaraptorans Australovenator (White et al., 2015, figure 7A4, B3), Fukuiraptor (Currie and Azuma, 2006, figure 1D), Megaraptor (MUCPv 595), and Murusraptor (Coria and Currie, 2016); the tyrannosauroids Aviatyrannis (MG 27801 D90), Guanlong (IVPP V14531) and Proceratosaurus (NHMUK PV R.4860); and some paravians such as Atrociraptor (Currie and Varricchio, 2004; Figure 13.4), Deinonychus (Ostrom, 1969, figure 24D2), Dromaeosaurus (AMNH 5356; Currie et al., 1990), Linhevenator (Xu et al., 2011a), Sauromitholestes (Currie et al., 1990, figure 8.6i) and Sinornithosaurus (Xu and Wu, 2001). A concavity adjacent to the mesial carina on the lingual surface of the crown is also present in the lateral dentition of Masiakasaurus (FMNH PR 2471 dt4, UA 8680 dt6), some troodontids such as Xixiasaurus (Lü et al., 2010, figure 3A1), Zanabazar (Norell et al., 2009, figure 30, which illustrates the right mid-dental teeth in lingual view) and an indeterminate troodontid from Uzbekistan (Averianov and Sues, 2007, figure 7L).

**Remarks and synapomorphy.** One or two concave surfaces marginal to the carinae appeared convergently in the mesial teeth of Abelisauroidea, non-carcharodontosaurid allosaurs, basal coelurosaurs (e.g., Ornitholestes, Guanlong, Proceratosaurus), Dromaeosauridae and Troodontinae. A salinon-shaped outline in the mesial teeth is a possible synapomorphy of Abelisauroidea and Allosauroidea (Appendix 6.9 for mesial teeth).

**D-shaped cross-section**

A symmetrically to asymmetrically D-shaped cross-section (Figure 1.10) can be observed in mesial teeth of some allosaurs such as Sinraptor (IVPP V10600) and Allosaurus (CMNH 1254, 21703; SMA 005/02; Figure 13.3). This morphology seems to have been lost in mesial teeth of Carcharodontosauridae, as the mesial crowns of Acrocanthosaurus (NCSM 14345), Giganotosaurus (MUCPv-CH-1, dt1), and Mapusaurus (MCPF-PVPH-108.166) display a mesial carina facing mesiolabially (C.H. personal obs.), forming a wide lenticular/lanceolate outline of the crown in cross-section. Although deformed, Ornitholestes mesial teeth are D-shaped in cross-section for the two distalmost premaxillary and the first two maxillary crowns (C.H. personal obs.). The neocoelurosaur Fukuivenator appears to share a relatively similar dentition, with unserrated and spatulate mesial teeth. In this taxon it is the mesialmost premaxillary (or teeth) which is D-shaped in cross-section, the more distal ones being sub-oval (Azuma et al., 2016). A similar morphology was observed in the mesial crown of Falcaurus (UMNH 15097), which is also unserrated and D-shaped in cross-section. A D-shaped cross-section was also noted in: a mesial isolated tooth of the noasaurid Vespersaurus (Langer et al., 2019); the premaxillary teeth of the abelisaurids Rahiolisaurus (pm1 of ISIR 550; C.H. personal obs.) and possibly an indeterminate taxon (pm1 of MPCN-PV 69; Gianechini et al., 2015, figure 2G); the megaraptoran Megaraptor (Porfiri et al., 2014); the basal ornithomimosaur Pelecanimimus (Pérez-Moreno et al., 1994); and the troodontid Byronosaurus (Averianov and

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**FIGURE 13.** Cross-section of mesial teeth in non-avian Theropoda. 1, Salinon-shaped cross-section in the first right premaxillary tooth of the abelisaurid Majungasaurus crenatissimus (FMNH PR.2008) in apical view; 2, U-shaped cross-section in an isolated premaxillary tooth of the basal pantyrranosaurian Eotyrannus lengi (MIWG 1997.550; reversed) in apical view; 3, D-shaped cross-section in the first left premaxillary tooth of the allosaurid Allosaurus fragilis (UMNH VP 9258; reversed) in apical view; 4, J-shaped cross-section in the second right premaxillary tooth of the dromaeosaurid Atrociraptor marshalli (TMP 1995.166.01) in apical view. Scale bars equal 5 mm.
mesial crowns with a D-shaped cross-section out-
serrated and somewhat spatulate/incisiform
crown (C.H. personal obs.). It is possible that
face adjacent to it on the lingual surface of the
spiraling mesial carina and a concave sur-
Megaraptor
(2016), and
Sues, 2016; the cross-section is, however, subcir-
cular according to Makovicky et al., 2003),
Dalianosaurus (Shen et al., 2017a), Sinusonasus
(UVPP V11527), Urbacodon, Xixiasaurus (Averi-
anov and Sues, 2016), and Zanabazar (Norell et al.,
2009). The cross-section at the crown-base in
Megaraptor is more J-shaped due to the presence of
the spiraling mesial carina and a concave sur-
face adjacent to it on the lingual surface of the
crown (C.H. personal obs.). It is possible that
unserrated and somewhat spatulate/incisiform
mesial crowns with a D-shaped cross-section out-
line is synapomorphic to a clade gathering
Fukuivenator, Ornitolestes, and maniraptoriforms, such
mesial crown morphology being plesiomorphic to
the basalmost members of the Therizinosauria
(i.e., Falcarius) and Ornithomimosauria (i.e., Pele-
caninimus and possibly Nqwebasaurus). It is
unknown whether the cross-sectional outline of the
mesial dentition of some troodontids such as
Byronosaurus, Dalianosaurus, Sinusonasus, Xixia-
saurus, and Zanabazar is D-, J- or salinon-shaped
but that of one premaxillary tooth of Urbacodon
(CCMGE 71/12455) genuinely appears D-shaped
based on the lingual profile of the crown (Averianov
and Sues, 2016, figure 4B). The cross-section of the
incisiform (sensu Cau et al., 2017) premaxillary
Teeth of the basal dromaeosaurid Halszkaraptor
also appear to be D-shaped at the crown-base.
Remarks and synapomorphy. As seen with the
mesial dentition of Abelisauridae and Allosauridae
there is a continuum of morphological variation
from a D-shaped/salinon-shaped cross-sectional
outline of the first mesial crowns to a more J-
shaped outline of the more distal crowns (Fanti and
Therrien, 2007). The differences in cross-section
morphologies are then positional and can, there-
fore, be subtle in theropods, so that D-shaped, sali-
non-shaped and J-shaped cross-sections are not
discrete conditions. A J-shaped/D-shaped cross-
section outline is synapomorphic to Dromaeosauri-
daes (Appendix 6.9 for mesial teeth).

U-shaped cross-section
A U-shaped cross-section of the crown at the
cervix (Figure 1.8-9) is typically referred to as
D-shaped outline by several authors (e.g., Hutt et al.,
2001; Sereno et al., 2009; Choiniere et al., 2010a).
However, D-shaped and U-shaped cross-sections
cannot be confused because the carinae of the lat-
ter are positioned on the same side of the tooth
and typically facing lingually, which is not the case
in a crown with a D-shaped cross-section, in which
the distal carina does not face lingually (C.H. per-
sonal obs.). A U-shaped cross-section of the crown
base is visible in the mesial teeth of the pantyran-
osauroids: Albertosaurus (Currie, 2003; Buckley
et al., 2010), Appalachiosaurus (RMM 6670), Das-
pelotosaurus (TMP 1994.153.01; Lehman and Car-
penter, 1990), Dilong (IVPP V14243; Xu et al.,
2004), Eotyrannus (Hutt et al., 2001; Figure 13.2),
Gorgosaurus (1991.36.500), Nanotyrannus (Mol-
nar, 1978; Carr and Williamson, 2004), Raptorex
(LH PV18; Sereno et al., 2009), Tarbosaurus
(Hurum and Sabath, 2003), Timurlengia (Averianov
and Sues, 2012), Tyrannosaurus (Smith, 2005),
Xiongguanlong (Li et al., 2010) and an indetermi-
nate tyrannosaurid from the Cenomanian of Utah
(if the mid-crown cross-section is indeed salinon-
shaped, the base crown is here considered U-
shaped; Zanno et al., 2019). A similar morphology
is seen in the premaxillary teeth of the non-tyran-
osauroid coelurosaur Zuulong (Choiniere et al.,
2010a) and in the first two premaxillary teeth of
Ornitholestes (AMNH 619).
Remarks and synapomorphy. In the basal tyran-
osauroids Aviatyrannis, Guanlong, and Procera-
tosaurus, the mesial carina of mesial teeth twists
lingually but does not face entirely lingually so that
the cross-section of mesial teeth is not U-shaped
but rather J-shaped. In many tyrannosauroids, the
lingual surface of mesial teeth is concave, bicon-
cave or planar, but in Ornitholestes and some
tyrannosauroids like Tarbosaurus and Tyran-
osaurus, the mesial margin is strongly convex, giving an
oval-shaped to the crown base’s cross-section
(Smith, 2005, figure 8A). Due to the obvious lingual
position of the carinae, the cross-sectional outline
of these crowns is still referred to as U-shaped. As
Dilong is currently placed as the basalmost mem-
ber of the Pantyranosauromorpha (Brusatte et al.,
2010b; Brusatte and Carr, 2016), mesial teeth with
an U-shaped cross-section of the crown base is a
possible synapomorphy of Pantyranosauromorpha (Fig-
ure 4) or a broader clade encompassing Ornitolo-
estes, Tyrannosauridae and Zuulong (Figure 7;
Appendix 6.9 for mesial teeth).

Figure-of-eight-shaped cross-section
The presence of a figure-of-eight-shaped outline
of the crown-base in cross-section, due to the
presence of labial and lingual depressions on the
crown base, is a common feature of dromaeosaur-
ids such as Bambiraptor (AMNH 30556), Buitre-
raptor (Gianechini et al., 2011b), Dromaeosaurus
(AMNH 5356), Pyroraptor (Allain and Taquet, 2000;
Gianechini et al., 2011b; C.H. personal obs.), Sau-
romitholestes (Currie et al., 1990; Sankey et al.,
50
2002), Tsaggaan (Norell et al., 2006) and the possible dromaeosaur Richardoestesia gilmorei (Currie et al., 1990; Hendrickx and Mateus, 2014a). This outcome, inferred from the presence of a deep labial depression on the crown and a basal depression commonly present lingually, is likely present in other dromaeosaurids such as Atrociraptor (TMP 1995.166.01), Graciliraptor (IVPP V13474), Microraptor (IVPP V16903; QM V1002; Xing et al., 2013b, figure S1) and Sinornithosaurus (IVPP V12811; Gianechini et al., 2011a). An eight-shaped cross-sectional outline is also likely present or was also observed in: the basal ceratosaur Berberosaurus (MNHN To 369); the allosaurid Allosaurus (Ldt13 of YPM-PU 14554 VII 3), the megaraptorans Megaraptor (Porfiri et al., 2014) and Orkoraptor (Novas et al., 2008); the troodontids Byronosaurus (Lmx14; Figure 6.3) and Xixiasaurus (Lü et al., 2010, figure 3A2); the tyrannosaurids Dilong (IVPP V14243), Proceratosaurus (Rauhut et al., 2010), and the two species of Alioramus, A. remotus (PIN 3141/1) and A. altai (Brusatte et al., 2012; Figure 6.2). Although large and fully mature tyrannosaurids do not appear to share this cross-sectional outline (C.H. personal obs.), this dental feature does not seem to be due to immaturity as Alioramus altai, Proceratosaurus, and the Dilong specimen IVPP V14243 were subadult individuals (Xu et al., 2004; Brusatte et al., 2009b, 2012; Rauhut et al., 2010). Deep and well-visible labial and lingual depressions are also present at the base of the crown in several mid-maxillary teeth of Sinraptor (IVPP 10600), giving a figure-8-shaped outline of the crown base in cross-section.

Remarks and synapomorphy. Based on our observations, the crown base of coelophysoids, abelisaurids, megalosauroids, allosaurs, carcharodontosaurs, compsognathids, alvarezsaurids, therizinosaurids and oviraptorosaurs does not have a figure-8-shaped cross-section (C.H. personal obs.). Such an outline was also reported in the non-averostran theropod Liliensternus (Gianechini et al., 2011b, figure 2c), yet it is likely that the figure-8-shaped outline corresponds to a cross-section in the root base and not at the base of the crown. A figure-8-shaped cross-section of the lateral crown base is considered to be a synapomorphy of Dromaeosauridae more derived than Halszkaraptorinae (Figure 8; Appendix 6.9 for lateral teeth).

Functional morphology. The presence of a deep labial depression on the crown of the microraptorbire Sinornithosaurus was interpreted as a venom delivery duct of a venomous animal by Gong et al. (2010, 2011). This hypothesis was, however, rejected by Gianechini et al. (2011b), who did not give an alternative morphological or functional interpretation, and Turner et al. (2012). The latter consider that the labial depressions are restricted to the root, which is exposed beneath the maxilla, as the teeth are partially released from their respective alveoli as a preservational artifact. Yet, labial and lingual depressions extending on most of the crown is a common feature in dromaeosaurids (C.H. personal obs.). Both labial and lingual depressions, in fact, result from the track of the erupting replacement tooth that grows lingually from the tooth root (e.g., Acrocanthosaurus, Elikosaurus, Falcarius, Genyoedectes, Megalosaurus, Richardoestesia, Torvosaurus), linguobasally within the root, beneath the crown of the erupted tooth (e.g., Albertosaurus, Alioramus, Allosaurus, Sinraptor), or labially from the tooth root (e.g., Halszkaraptor, Megaraptor, Sinornithosaurus). The labial and lingual depressions on the root and extending apically on the crown are then the tracks of the preceding tooth abutting against the labial lingual surface, and the succeeding tooth in contact on the lingual/labial surface of the root. Similar to the concave surface adjacent to carinae, the presence of a lingual and/or labial depression may also have some functional implications such as strengthening the crown or allowing rapid penetration and withdrawal of the tooth from the prey.

Mesial carina reaching the cervix

The mesial carina extends to the cervix or below in many theropods. This includes: the basal sauirischians Eodromaeus (PVSJ 560, 561) and Tawa (GR 241); the non-averostran theropods Coelophys (Buckley and Currie, 2014), Dilophosaurus (UCMP 37303), Dracovenator (the mesial denticles almost extend to the cervix in the single preserved maxillary tooth; C.H. personal obs.), and Liliensternus (Cillari, 2010), and almost all abelisaurid and spinosaurid teeth. The mesial carina of a single lateral tooth of the abelisaurid Arcovenator (MHNA.PV.2011.12.187) does not seem to reach the cervix, and a few isolated baryonychine crowns bear a mesial carina extending only on half or on two-thirds of the crown height (Canudo et al., 2008). In non-abelisaurid ceratosaurs, the mesial carina reaches the root in the lateral dentition of Ceratosaurus, Masiakasaurus, and Noasaurus but the mesial teeth of Ceratosaurus and Masiakasaurus bear a mesial carina terminating above the cervix. A mesial carina reaching the root can also be seen in some lateral teeth of the piatnitzkysaurid
Piatnitzkysaurus (PVL 4073). The mesial carina of the megalosaurid Monolophosaurus and the piatnitzkysaurid Marshosaurus extends above the cervix in the whole dentition.

The mesial carina extends on the entire crown height in allosauroids such as Allosaurus (e.g., USNM 8335; SMA 0005/02), Erectopus (MNHN 2001-4), Fukuiraptor (Currie and Azuma, 2006), and Sinraptor (IVPP 10600; ZDM T0024). This dental feature is also present in the large majority of carcharodontosaurid teeth, although the mesial carina of some Giganotosaurus lateral teeth extends slightly above the cervix (C.H. personal obs.). Only a few maxillary teeth show a mesial carina reaching the cervix in the basal carcharodontosaurine teeth, although the mesial carina of some Giganotosaurus lateral teeth extends slightly above the cervix (C.H. personal obs.), A mesial carina reaching the cervix in the basal carcharodontosaurine Acrocanthosaurus. A mesial carina reaching the cervix is present in some mesial and lateral teeth of: the tyrannosaurids Alotars (MPC-D 100-1844), Daspletosaurus (Carr and Williamson, 2004), Gorgosaurus (USNM 12814), Raptores (LH PV18), Shanshanosaurus (Currie and Dong, 2001a) and Tyrannosaurus (in which some mesial and lateral teeth have a mesial carina reaching the crown base (contra Smith, 2005; Rdt1 of CMNH 9380; Ldt1 and Rdt12 of FMNH PR.2081); the dromaeosaurids Atrociator (Currie and Varricchio, 2004), Dromaeosaurus (AMNH 5356) and Sauornitholestes (Currie et al., 1990; Baszio, 1997); and in the mesial and some lateral teeth of Troodon (Currie, 1987; Currie et al., 1990).

Remarks and synapomorphy. A mesial carina reaching the cervix is widespread among non-maniraptoriform theropods and is probably the ancestral condition in theropods. We only consider this dental feature to be synapomorphic for the clade Spinosauridae (Appendix 6.10 for lateral teeth). The denticulated mesial carina does not reach the cervix in: Eoraptor (PVSJ 512); the basal megalosauroids Marshosaurus and Monolophosaurus; the neovenatorids Australovenator (Hocknull et al., 2009), Murusraptor (Coria and Currie, 2016), and Neovenator (MIWG 6348); basal pantyranosaurians (e.g., Dilong, Eotyrannus); Haplocheirus; Therizinosaurs; Microraptorinae and the eudromaeosaurians Bambiraptor, Graciliaptor, and Velociraptor. The two preserved lateral teeth of the basal coelurosaur Zuoalong also have mesial denticles restricted to the apical half of the crown (IVPP V15912; Choiniere et al., 2010a). Hendrickx et al. (2015c) noted that the mesial carina of all megalosaurids terminates significantly above the cervix, yet two isolated teeth referred to Torvosaurus tanneri (BYU-VP 725 12817) and T. gurneyi (ML 857) bear a mesial carina reaching the root or extending close to it. A mesial carina terminating above the root in the lateral dentition is here considered a synapomorphy of Megalosauroidea and Maniraptora (Appendix 6.10 for lateral teeth).

Functional morphology. It has been demonstrated that the extension of the denticulate mesial carina correlates with the distal curving of the crown in ziphodont theropods, the tooth curvature decreasing mesially (D’Amore, 2009). The crown area that may not contact the flesh, called the ‘dead-space’, tends to be unserrated, and the dead-space that is produced during the puncturing by the denticulate margins of the crown is what allows for the removal for flesh (D’Amore, 2009).

The extension of the denticulate mesial carina in different clades of ziphodont and pachyodont theropods conforms to this model. For instance, the mesial carina of the poorly curved lateral crowns of Abellisauridae, Baryonychinae, Carcharodontosaurinae, and Ceratosauridae almost always reaches the cervix. However, this model only applies to meat-eating dinosaurs with ziphodont, pachydont and conidont teeth. Indeed, the denticles of herbivorous theropods with folidont dentition such as therizinosaurs were probably adapted to cut through hard fibrous material, and were consequently subject to different selection pressures (D’Amore, 2009).

Twisted mesial carina

Mesial dentition. A mesial carina spiraling on the crown from the mesial side apically to the mesiolingual or lingual side basally occurs in the mesial teeth of various theropods: the non-averostran neotheropod Dilophosaurus (UCMP 37302); the noasaurid Masiakasaurus (e.g., UA 8680; FMNH PR.2182, 2471); the large majority of allosauroids such as Allosaurus (e.g., AMNH 851; NHFO 455), Australovenator (Hocknull et al., 2009, figure 20B), Fukuiraptor (Currie and Azuma, 2006, figure 1D), Mapusaurus (MCF-PVPH-108.166), Sinraptor (Currie and Zhao, 1993) and Tyrannottitan (MPEF-PV 1156). A twisted carina is also present in the basal tyrannosaurids Aviatyrannus (MG 27801 D90, D172) and Proceratosaurus (NHMUK R.4860), with more derived tyrannosaurids having a straight mesial carina facing lingually. In the abelisaurids Indosuchus (AMNH 1753) and Majungasaurus (FMNH PR 2100) the mesial carina of the fourth premaxillary crown also weakly curves mesiolingually. The dromaeosaurids Deinonychus (Ostrom, 1969), Dromaeosaurus (Currie et al., 1990), Sinomithosaurus (Xu and Wu, 2001) and
Sauornitholestes (Currie et al., 1990) also have a spiraling mesial carina.

**Lateral dentition.** This condition appears in the mesialmost teeth of the lateral dentition in: Allosaurus (USNM 8335; UMNH VP 9168); tyrannosaurids such as Albertosaurus (DMNH 22019), Alioramus (MPC-D 100-1844; Brusatte et al., 2012), Appalachiosaurus (Carr et al., 2005), Daspletosaurus (TMP 1994.143.01), Proceratosaurus (NHMUK PV R.4860), Raptorex (LVH PV18), Tyrannosaurus (FMNH PR.2081; Smith, 2005) and Zhuangtiansaurus (Hone et al., 2011); and the dromaeosaurids Dromaeosaurus (AMNH 5356; Currie et al., 1990) and Sauornitholestes (TMP 94.12.844, TMP 88.121.39; Currie et al., 1990, figure 8.2V). In the holotype specimens of the piatnitzkyaurid Piatnitzkysaurus (PVL 4073) and the dromaeosaurine Dromaeosaurus, the mesial carina spirals onto the mesiolingual side of the crown even in more distal teeth of the lateral dentition (Currie et al., 1990; C.H. personal obs.), a dental autapomorphy in these two taxa. In Dromaeosaurus, a twisted mesial carina is, in fact, present in all teeth (Currie et al., 1990). A twisted mesial carina does not occur in the lateral dentition of Carcharodontosaurus, non-avetheropod theropods and Metriacanthosauridae. In non-eudromaeosaurian neocoeelurosaurids, this condition has only been observed in a few lateral teeth of the basal and derived therizinosaurids Falcarius (UMNH VP 14528; Button et al., 2017, supplemental figure S2) and Segnosaurus (the 'folded carina' sensu Zanno et al., 2016), respectively.

**Remarks and synapomorphy.** In Falcarius, the spiraling mesial carina, present in mesial maxillary and several dentary teeth (UMNH VP 14545; Button et al., 2017, supplemental figure S2), is unerrated in the basal half portion of the crown (n.b., the single fully erupted dentary tooth in specimen UMNH VP 14528 has most likely rotated in its alveoli so that the spiraling carina is the mesial carina; C.H. personal obs.). Unlike Falcarius, the spiraling mesial carina of Segnosaurus is denticulated along most of the carina and, in some cases, bears apicobasally tall and vertically oriented denticles creating the ‘lingual folding of the mesial carina’ noted by Zanno et al. (2016). Some dentary teeth of Segnosaurus also show the peculiarity of having a sporadic variation of denticle size along the mesial carina, a split distal carina, extracarinal mesial denticles, and a third denticulated carina centrally positioned on the lingual surface of the crown (Zanno et al., 2016). The combination of these autapomorphic dental features in Segnosaurus was interpreted by Zanno et al. (2016) as indicative of increased shredding capabilities and a higher degree of oral processing than in other therizinosaurids. A bifurcated distal carina, triple carinae, and extracarinal denticles have not been observed in the dentition of other therizinosaurids or theropods, and a sporadic variation of denticle size only occurs in the conodont teeth with minute denticles of baryonychine theropods. We conclude that these dental features, with the exclusion of the spiraling mesial carina, which is also present in Falcius, were likely caused by trauma and do not result from a highly specialized feeding strategy. A mesial carina twisting onto the crown in the lateral dentition is here considered to be synapomorphic for Tyrannosauroidea (Appendix 6.11 for lateral teeth).

**Functional morphology.** According to Bakker (1998), a mesial carina passing inward from the crown tip, associated with a distal carina passing outward, would keep shallow wounds open during an attack. The combination of a lingually twisted mesial carina and a strongly labially displaced distal carina would indeed enable to slice the flesh on a crown width when penetrating the prey item. This would ultimately result in wider wounds compared to bites made by labiolingually narrowed teeth with carinae positioned on the same sagittal plane. The presence of many crowns with twisted mesial carina in the lateral dentition of Allosaurus, Dromaeosaur and tyrannosaurids seems to support the hypothesis of a predatory lifestyle rather than obligate scavenging in these theropods although further work is required to test this hypothesis.

**Split mesial carina**

Split mesial carinae have been reported in several Tyrannosauroidea including Albertosaurus, Alectrosaurus, Daspletosaurus and Tyrannosaurus (TMP 1994.143.1; Currie et al., 1990; Erickson, 1995; Abler, 1997; Tanke and Currie, 1998; Smith, 2005; Cillari, 2010). This crown abnormality is not rare in the dentition of Tyrannosauroidea, and among 993 tyrannosaurid teeth examined by Erickson (1995), 11% displayed such a feature. Outside the clade of Tyrannosauroidea, a split carina has been reported from isolated theropod teeth with uncertain or broad affinities: a possible coelophysiod from the Middle Jurassic Toulunhe Formation of Liuhonggou, China (Maisch and Matzke, 2003); a possible dromaeosaurid from the Middle-Upper Jurassic Shishugou Formation of Wucaiwan, China (Morphotype 5; Han et al., 2011); a
tyrannosauroid from the Lower Cretaceous of the Rhenish Massif of Germany (Lanser and Heimhofer, 2015); and indeterminate theropods from the Upper Cretaceous Minhe Formation of China (Bohnin, 1953), Fruitland Formation of the San Juan Basin in New Mexico, USA, and the Bauru group of Brazil (Keliner, 1996). The theropod tooth from the upper portion of the Bauru group shows a morphology reminiscent to that of abelisaurid teeth (C.H. personal obs.), and a split carina is likely to be present in this clade. A split carina has also been identified in three allosaurid theropods, Allosaurus (Erickson, 1995) and two indeterminate carcharodontosaurids from Niger (Brusatte and Sereno, 2008) and Brazil (Candeiro and Tanke, 2008). In maniraptoriforms, the dromaeosaurid Dromaeosaurus albertensis from the Upper Cretaceous Prince Creek Formation of Alaska ( Fiorillo and Gangloff, 2001) and an indeterminate dromaeosaurid from the Barremian of Uña in Spain (Gangloff, 2001) and an indeterminate dromaeosaurids also show a bifurcated mesial carina. The therizinosaur Segnosaurus galbinensis from the Upper Cretaceous Bayan Shiree Formation of Mongolia (Zanno et al., 2016) has a split distal carina occurring at the crown base delimiting a flattened triangular facet. This is present from the second to the twelfth dentary tooth on both left and right dentaries (Zanno et al., 2016) and appears to be unique to this taxon. Although uniformly expressed across the dentary tooth row on both sides of the mandible, this condition is here interpreted as an abnormality possibly due to trauma.

Remarks and functional morphology. Besides the isolated tooth MNN GAD15 illustrated and ascribed to a carcharodontosaurid by Brusatte and Sereno (2008), we did not observe split carina in the dentition of any non-tyrannosauroid taxa examined first hand, suggesting that this condition is not common outside Tyrannosauridae. Erickson (1995) equates the presence of split carinae as caused by trauma, aberrant tooth replacement, or genetic factors. The presence of this abnormality in many specimens of tyrannosauroids and at least three allosaurid taxa indicates that this feature may have some taxonomic potential and should be considered in phylogenetic analyses.

Distal carina strongly deflected labially.

Whole dentition. The distal carina of mesial and some lateral teeth is strongly displaced labially (i.e., the distal carina is at the level of the labial margin of the crown in distal view) in the crowns of: the ceratosaurids Ceratosaurus (USNM 4735) and Genyodectes (MLP 26-39); the noasaurid Masiakasaurus (UA 8680; FMNH PR.2201, 2221, 2476), and the dromaeosaurid Dromaeosaurus (AMNH 5356). In the allosaurids Allosaurus (USNM 8335; SMA 005/02) and Sinraptor (IVPP V10600), a strongly labially displaced distal carina occurs in the crowns from the distal portion of the mesial dentition and the mesial portion of the lateral dentition. In the tyrannosauroids Alioramus (MPC-D 100-1844), Gorgosaurus (USNM 12814; AMNH 5458), Proceratosaurus (NHMUK PV R.4860), Raptorex (LH PV18) and Tyrannosaurus (CMNH 9380; NHMUK PV R.7994; FMNH PR.2081), the distal carina is strongly deflected labially in mesial teeth as well as in the mesial half of the lateral (i.e., ‘transitional’) dentition. In tyrannosauroids, the carina is significantly labially displaced in most dentary teeth (C.H. personal obs.).

Mesial and lateral dentitions. A strongly deflected distal carina towards the labial side of the crown also occurs in the mesial teeth in: the non-averostran saurischians Dilophosaurus (UCMP 37302), Eoraptor (PVJS 512) and Ischisaurus (MACN 18.060); the megalosauroid Monolophosaurus (IVPP 84019); the neovenatorid Fukuiraptor (Currie and Azuma, 2006, figure 1SA-B); the carcharodontosaurids Acrocanthosaurus (NCSM 14345), Giganotosaurus (MUCPv-CH-1), Mapusaurus (MCF-PVPH 108), and Tyran notitan (MEF-PV 1156); and the dromaeosaurids Linheraptor (IVPP V16923), Richardoestesia (Currie et al., 1990), Sauornitholestes (TMP 88.121.39) and Sinornithosaurus (IVPP V12811). A strong labial displacement of the distal carina was also noticed in some lateral teeth of: the basal ceratosaur Sait riovenator (Dal Sasso et al., 2018, figure 5L) and Berberosaurus (MNHN To 369); the abelisaurid Arcovenator (MHNA.PV.2011.12.187); the piatnitzkysaurids Marshosaurus (UMNH VP 7824) and Piatnitzkysaurus (MACN 895); the neovenatoridsa Megaraptor (MUCPv 595), Neovenator (MIWG 6348) and Orkoraptor (MPM-Pv 3457); as well as Ornitholestes (AMNH 619).

Remarks and synapomorphy. The distal carina of mesial and lateral teeth is displaced lingually and not labially in the basal sauropodomorph Eoraptor (PVJS 512). The distal carina is centrally-positioned on the crown or only weakly displaced labially in the whole dentition of Abelisauridae, Eodromaeus (PVJS 561), Lili stenurus (MB R.2175), Megalosauridae, Noasaurus (PVL 4061), Sanjuansaurus (PVJS 605) and Spinosa uridae, in the lateral dentition of Carcharodontosauridae, and possibly the whole dentition of non-dromaeosaurid neocoe lurosaurids (C.H. personal obs.). The strong
labial displacement of the distal carina is a synapomorphy of Tyrannosauroidea for both mesial and lateral teeth. Given the presence of strongly labially displaced distal carina in at least the lateral dentition of basal ceratosaurs (i.e., Saltrosaurus, Berberosaurus) and the whole dentition of ceratosaurids (n.b., the strongly displaced distal carina in both basal ceratosaurs and ceratosaurids result from the poorly convex, almost flat, labial surface of the crown, which appears to characterize all non-abelisaurid ceratosaurs; C.H. personal obs.), this dental feature is also a possible synapomorphy of the clade Ceratosauria. A centrally positioned or weakly displaced distal carina on the crown is a here considered a synapomorphy of Abelisauridae and Megalosauroidea for the whole dentition, and Carcharodontosauria for lateral teeth.

**Functional morphology.** A gripping function was suggested by Reichel (2012) for the mesial maxillary and dentary dentitions of *Tyrannosaurus*, which have crowns with a strongly labially deflected distal carina. Such placement of the distal carina, combined with the centrally positioned or lingually twisted mesial carina, causes the anterior area of the jaw to make wide cuts on the prey and consequently wide-open wounds (Reichel, 2012). Crowns with labially deflected distal carinae were accompanied by the en echelon arrangement of the mesial maxillary teeth in *Tyrannosaurus*, which prevented the meat from slicing forward (Reichel, 2012). Conversely, the mesial and distal carinae are centrally positioned and on the same sagittal plane in more distal crowns, providing a slicing function to these teeth (Reichel, 2012).

**Hooked denticles**

The presence of distal denticles with an apex pointing towards the tip (Figure 14) is a feature present in the teeth of the basal sauropodomorph *Eoraptor* (e.g., third right premaxillary tooth; PVSJ 512; Figure 14.1), an isolated tooth possibly belonging to the neotheropod *Gojirasaurus* (Carpenter, 1997; Griffin, 2019) and many abelisaurids such as *Kryptops* (MNN GAD1-1; Sereno et al., 2004), *Majungasaurus* (FMNH PR.2008, 2100, 2278; Fanti and Therrien, 2007; Figure 14.3), *Masiakasaurus* (FMNH PR.2221, 2296; Figure 14.2) and *Rugops* (MNN IGU1). Mesial and distal hooked denticles can also be observed in some therizinosaurids such as *Alxasaurus* (Russell and Dong, 1993; IVPP V88402; Figure 14.6), *Beipiaosaurus* (Liao and Xu, 2019), *Eshanosaurus* (IVPP V11579; Figure 14.5), *Jianchangosaurus* (Pu et al., 2013, figure 4E, F) and *Notrhonychus* (Kirkland and Wolfe, 2001). Some dromaeosaurids are well known to possess apically hooked denticles (e.g., Currie et al., 1990; Currie, 1995; Larson, 2008; Longrich, 2008), yet they are only present in the eudromaeosaurians *Atrociraptor* (TMP 1995.166.01; Currie and Varricchio, 2004; Figure 14.7) and *Saurornitholestes* (Currie et al., 1990; Sankey, 2001). Finally, some anchiornithines like *Caihong* (Hu et al., 2018) and several derived troodontines such as *Saurornithoides* (Norell et al., 2009), *Sinornithoides* (Currie and Dong, 2001b), *Troodon* (e.g., Currie, 1987; Currie et al., 1990; Holtz et al., 1998; Longrich, 2008; Figure 14.8) and *Zanabazar* (Norell et al., 2009) also display apically hooked denticles (Makovicky et al., 2003). Among basal tetanurans, the distal denticles of some maxillary and dentary teeth (dt7 of MACN-CH 895; mx13 of PVL 4073; Figure 14.4) and an isolated lateral tooth associated with the holotype of *Piatnitzkysaurus* (PVL 4073) are strongly asymmetrically convex to apically hooked. However, the external margin of distal denticles in other maxillary and isolated lateral teeth of the holotypic and referred material of *Piatnitzkysaurus floresi* (e.g., mx11 of PVL 4073 and all maxillary and isolated teeth of MACN-CH 895) is symmetrically to slightly asymmetrically convex (C.H. personal obs.), showing some variation in the curvature of the external margin in the distal denticles in this taxon.

**Remarks and synapomorphy.** The morphology of denticles with apically hooked external margin varies significantly among theropods. In some *Masiakasaurus* teeth, the hooked denticles are mesiodistally narrow and differ from the more subquadrangular denticles of abelisaurids and dromaeosaurids. Likewise, denticles with hooked external margins are usually apically inclined in therizinosaurids, sometimes almost apicobasally oriented on the carinae. Nevertheless, many therizinosaur taxa do not bear genuinely hooked denticles but rather pointed denticles perpendicular to the crown margin, as in *Eshanosaurus* (IVPP V11579; Zhao and Xu, 1998), or apically inclined and/or vertically oriented denticles, as seen in *Beipiaosaurus* (Xu et al., 1999; Liao and Xu, 2019), *Erlikosaurus* (Clark et al., 1994) and *Jianchangosaurus* (Pu et al., 2013). This is also the case in troodontidae, which tend to have particularly large, bulbous, and widely separated denticles. Given this morphology, troodontid denticles strongly differ from the small numerous and asymmetrically convex or parallelogram-shaped denticles (Figure 14.7) of dromaeosaurids (n.b., based on this differ-
ence, the isolated teeth AMNH 8518 and DMNH 22870 referred to a dromaeosaurid and Saurornitholestes, respectively, are here identified as belonging to Troodon). Hooked denticles are clearly seen in Pectinodon (Longrich, 2008), Sinornithoides (Currie and Dong, 2001b), Troodon (Currie, 1987; Currie et al., 1990; Holtz et al., 1998; Ryan et al., 1998; Longrich, 2008) and some troodontid teeth from France (Vullo et al., 2007; Vullo and Néraudeau, 2010) and Central Asia (Averianov and Sues, 2007). Many troodontid taxa such as Linhevenator (Xu et al., 2011a), Pectinodon (Longrich, 2008), Sauornithoides, Zanabazar (Norell et al., 2009), and teeth of indeterminate Troodontidae from France (Vullo and Néraudeau, 2010), Uzbekistan (Averianov and Sues, 2007) and India (Goswami et al., 2013) also show large denticles either with a pointed or a parabolic and rounded external margin. Variation in dentine sizes and morphologies may, however, be positional, as proposed by Longrich (2008) for Pectinodon bakkeri.

In many theropod clades such as ceratosaurids, megalosaurids, allosaurids and tyrannosaurids, the denticles are symmetrically rounded or asymmetrically convex in lateral view (Currie et al.,
tion of denticles, the hooked denticles and overall denticle morphologies of the troodontid crown. This indicates that, like the archosaurian reptiles, which have likely converged morphologically as a result of selection to perform a similar function. Consequently, abelisauroids were probably able to handle struggling prey and processing bones as part of their diet, a hypothesis that requires to be tested with FEA techniques in the future.

Small number of denticles on the carina

Farlow et al. (1991) demonstrated that denticle density decrease allometrically with basal crown length and height in theropods, a rule that can certainly apply to most theropods with ziphodont (D’Amore and Blumenschine, 2012) and pachyodont dentition such as tyrannosaurids (Carr and Williamson, 2000), but not to folidont and conodont theropods. Indeed, some folidont theropods like therizinosaurs have small crowns with particularly coarse denticles (Clark et al., 2004) whereas others with conodont teeth like baryonychines have comparatively large crowns with minute denticles (Mateus et al., 2011; see next section; D’Amore and Blumenschine, 2012). A small number of denticles (here arbitrarily defined as less than 15 denticles on the crown) along the whole carina characterizes many troodontids such as Dalianosaurus (Shen et al., 2017a), Linhevenator (Xu et al., 2011a), Pectinodon (Carpenter, 1982; Larson and Currie, 2013), Saurornithoides (Norell et al., 2009), Sinornithoides (Curie and Dong, 2001b), Sinusonasus (IVPP V11527), Troodon (Leidy, 1856; Russell, 1948; Currie, 1987) and Zanabazar (Norell et al., 2009). This feature is also present in most therizinosaurs such as Alxasaurus (Russell and Dong, 1993), Beipiaosaurus (Xu et al., 1999; Liao and Xu, 2019), Elikosaurus (MPC-D 100-111; Clark et al., 1994), Eshanosaurus (Xu et al., 2001), Jianchangosaurus (Pu et al., 2013), Nothronychus (Kirkland and Wolfe, 2001) and Segnosaurus (MPC-D 100-80). A carina bearing few denticles is, however, not restricted to these two clades, as this dental feature can also be found in some lateral teeth of the basal oviraptorosaur Incisivosaurus (IVPP V13326), and the dromaeosaurids Microraptor (IVPP V13475; Hwang et al., 2002, figure 5) and Paronychodon (Currie et al., 1990), which has been interpreted as being a tooth morphotype of Richardoestesia by Longrich (2008) and as a pathological specimen of already known dromaeosaurid and troodontid taxa (Hwang, 2005). Some crowns of Saurornitholestes appear to have less than 15 denticles on the carina (Currie et al., 1990; Baszio, 1997; Larson and Currie, 2013) but the quantitative data gathered by Larson and Currie (2013) indicates that the large
majority of Sauornitholestes teeth have much more than 15 denticles on the crown.

**Remarks and synapomorphy.** Embryonic or juvenile theropods tend to bear few coarse denticles such as the theropod embryos tentatively ascribed to *Lourinhanosaurus* (Araújo et al., 2013), the hatchling *Scipionyx* (Dal Sasso and Maganuco, 2011), and the posthatching *Sciuromimus* (Rauhut et al., 2012). The presence of crowns with less than 15 denticles on the carina is a synapomorphy of Therizinosauridae among Therizinosauroidea (sensu Zanno, 2010a), and Troodontidae more derived than *Sinovenator* (Appendix 6.16 for lateral teeth).

**Functional morphology.** In mature individuals, strongly constricted subsymmetrical crowns bearing relatively few large pointed denticles seem to be adapted to an omnivorous diet including plant material at least partially. Therizinosaur teeth are convergent with those of basal sauropodomorphs and iguanas (Barrett, 2000). Indeed, both possess relatively few and large pointed denticles on the carinae, mesial and distal carinae not reaching the cervix, and a convex margin of the crown, a tooth morphology that is correlated with omnivorous diets (Barrett, 2000). Troodontids with large apically hooked denticles on the distal carina have also been interpreted as omnivorous, as well as insectivorous based on the convergent dentition with iguanids and bat-eared fox, respectively (Varricchio, 1997; Holtz et al., 1998; Zanno et al., 2009). Holtz et al. (1998) suggested that the large denticles of troodontids and therizinosaurs would sever larger-sized and/or more resistant structures such as plant fibers. However, a predominantly carnivorous diet in troodontids has been inferred by other authors due to interdenticular sulci and sharp and hooked denticles (Currie and Dong, 2001b; Zanno and Makovicky, 2011; see previous sections on dentition type and hooked denticles). According to Currie et al. (1990), the large denticles of troodontids would slice through soft material and bones. Few troodontids actually possess sharply pointed and hooked serrations, and the denticles of *Linhenевator* (Xu et al., 2011a), *Pectinodon* (Carpenter, 1982; Larson and Currie, 2013), *Sauornithoides* and *Zanabazar* (Norell et al., 2009) rather display a rounded external margin. However, the presence of ziphodont lateral crowns and distally recurved pointy folidont teeth showing a weak constriction in the dentition of these troodontids support the fact that they fed predominantly on meat. Interestingly, large denticles are typically associated with a constricted crown, as illustrated with *Microraptor*, the only established dromaeosaurid possessing a small number of denticles on the crown and a constriction at the crown base. This suggests that *Microraptor* had an atypical diet among dromaeosaurids, which are usually considered as unquestioned carnivores (Norell and Makovicky, 2004; Zanno and Makovicky, 2011). The peculiar dentition of *Microraptor* seems to support a diverse diet, in which gut contents already revealed remains of mammals (Larsson et al., 2010), enantiornithine birds (O’Connor et al., 2011), and fish (Xing et al., 2013b). *Microraptor* and troodontids with denticulated teeth share the same heterodont lateral dentition made of weakly constricted teeth and a few distally denticulated crowns in the distal portion of the jaw (Hwang et al., 2002). It is, therefore, likely that derived troodontids bearing crowns with a small number of denticles were opportunistic carnivores feeding on a large variety of small prey items. As already mentioned in the previous section on hooked denticles, it was revealed that troodontids with coarse denticles likely favored small and softer prey with thinner bones (Torices et al., 2018).

**Large number of denticles on the carina**

Minute denticles relative to tooth size (i.e., more than 250 denticles along the distal carina) are found in the dentition of the baryonychines *Baryonyx* (150–300 denticles on the carinae; ~35 de/5mm; NHMUK PV R.9951; ML 1190; Figure 15.1) and *Suchomimus* (100–280 denticles on the carinae; ~35 de/5mm; e.g., UC G67-1, G22-7, G34-12; Figure 15.2) on both carinae and, due to their large size, some lateral teeth of the carcharodontosaurid *Acrocanthosaurus* (80–270 denticles on the carinae; ~15 de/5mm; NCSM 14345; Smith et al., 2005).

**Remarks and synapomorphy.** A distal carina with a large number of denticles (i.e., more than 200 denticles) is also present in some particularly apico-basally long lateral crowns of the ceratosaurid *Ceratosaurus* (~15 de/5mm; ML 865, 1151; Smith et al., 2005) and the tyrannosaurid *Tyrannosaurus* (~10 de/5mm; Smith, 2005). Regardless of the tooth dimension, theropods with particularly small denticles, i.e., more than 6 denticles per millimeter on the distal carina, include non-neotheropod saurischians such as *Aorun*, Baryonychinae, Coelophysis, Compsognathidae, Eodromaeus, Eoraptor, *Falcarius*, Liliensternus, Noasauridae, Ornitholestes, Proceratosaurus, Richardoestesia, Saurornitholestes (including *Sauornitholestes*), *Sinovenator* and *Velociraptor* (Smith et al., 2005;
Zanno, 2010b; Rauhut et al., 2012; Larson and Currie, 2013; Choiniere et al., 2014a; C.H. personal obs.). The presence of a large number of minute denticles (more than 25 de/5mm for crowns of more than 4 cm) along both carinae is a synapomorphy of Baryonychinae (Appendix 6.16 for mesial and lateral teeth).

**Functional morphology.** The presence of minute denticles in large baryonychine teeth seems to be correlated with the increase in robustness of the crown (Charig and Milner, 1997). It may also result from the simplification of teeth that were mostly used to impale prey rather than slicing their flesh, evolving towards unserrated crowns in Spinosaurinae (Charig and Milner, 1997; Buffetaut, 2011; Gianechini et al., 2011b). This dental simplification is also present in other theropods such as *Compsognathus*, in which many teeth have lost serrations. The reversed condition occurred in Therizinosauria and Troodontidae, in which the basal forms bear minute denticles that increase in size in more derived taxa. Minute denticles are not suitable for the ‘rip and grip’ cutting action of medium-sized serrations of most non-avian theropods and might function in a similar way to unserrated teeth (Farlow et al., 1991; Charig and Milner, 1997).

**Sporadic variation of denticle size**

Random variation of denticle size along denticulated carina (Figure 15.1-2) has been observed in the baryonychines *Baryonyx* (NHMUK PV R.9951, ML 1190; Mateus et al., 2011; Figure 15.1) and *Suchomimus* (MNN G26-5b; Figure 15.2), and was thought to be restricted to Baryonychinae (Mateus et al., 2011). This dental feature is, however, present on the mesial carina of an isolated mesial tooth of *Nuthetes* (NHMUK PV R.15871 B), teeth referred to *Richardoestesia isosceles* (Larson, 2008) and some dentary crowns of the therizinosaurid *Segnosaurus*. In the latter, one small denticle is bounded by two large ones (Zanno et al., 2016, figure 3A).

**Remarks and synapomorphy.** In spinosaurids, a sporadic variation of denticle size is much more developed in *Baryonyx* and occurs along the whole carinae in this taxon. In *Suchomimus*, most denticles gradually change in size along the carinae and the basal part of the carina only displays this sporadic change of denticle size. Such a feature most likely results from the reduction of denticle dimension in Spinosauridae, which occurred throughout the evolution of this clade. In Spinosaurinae, the carina is unserrated, yet it does not correspond to a smooth and regularly shape ridge. In lateral view, the carinae of *Irritator* and *Spinosaurus* are ‘beaded’ (sensu Sues et al., 2002; Figure 15.3) and sculptured (Figure 15.4), respectively (Sues et al., 2002; Hasegawa et al., 2010), thus witnessing the vestigial presence of small denticles along the carinae. The sporadic variation of denticle size observed in *Segnosaurus* is, here, interpreted as an abnormality caused by trauma (see above). A sporadic variation of denticle size along the carinae.
is synapomorphic for Baryonychinae (Appendix 6.17).

**Bilobate denticles**

Thought to be an autapomorphy of the carcharodontosaurids *Acrocanthosaurus* (SMU 74646) and *Carcharodontosaurus* (UCRC PV6); the possible metriacanthosaurid *Erectopus* (MNHN 2001-4; Figure 16.3), and the tyrannosaurid *Tyran-nosaurus* (FMNH PR.2081, mx10; Figure 16.4). They also appear to be present in the abelisaurids *Abelisaurus* (MPCA 5) and *Aucasaurus* (MCF-PVPH 236; Figure 16.1), although the double convexity may result from the external margin being slightly worn out. Bilobate denticles have also been observed on the teeth of non-theropod dinosaurs such as the rauisuchid *Postosuchus* (R. Molnar, personal commun., 2017).

**Remarks and synapomorphy.** Bilobate denticles seem to be malformations possibly resulting from trauma. Yet, they have not been observed in any non-averostran theropods and Maniraptorniformes and may, therefore, correspond to a tooth trait change due to genetic factors influencing denticle morphology, a hypothesis that requires further testing. We, however, do not consider the presence of bilobate denticles as an apomorphic feature of a certain clade or taxon.

**Size difference between mesial and distal denticles**

Distal larger than mesial denticles. Long thought to characterize the dentition of Dromaeosauridae, and therefore used as a primary feature to identify dromaeosaurid teeth (e.g., Rauhut and Werner, 1995; Sweetman, 2004; Vullo et al., 2007; Lubbe et al., 2009), the difference in size between mesial and distal is widespread among other clades. Subtle differences in size may occur between mesial and distal denticles, and we consider there is a significant size variation between the mesial and distal denticulated carinae when the denticle size index (DSDI) is higher than 1.2 or lower than 0.9. The arbitrary value of 1.2 to explain the much larger size of distal denticles compared to the mesial ones, was proposed by Rauhut et al. (2010) and corresponds to more than six mesial denticles for five distal serrations. A DSDI higher than 1.2 was measured in the lateral dentition of: the non-averostran neotheropods *Dracoraptor* (NMW 2015.5G), *Dracovenator* (BP/1/5243; Yates, 2005), and *Dilophosaurus* (Welles, 1984; Smith et al., 2005; UCMP 37302), but not *Sinosaurus triassicus* (IVPP V34; = *Dilophosaurus* sinensis according to Xing et al., 2013a); the noasaurids *Noasaurus* (PV 4061) and *Masiakasaurus* (e.g., UA 9091; FMNH PR.2201, 2211, 2696; Figure 17.1); the abelisaurids *Arcovenator* (MHNA.PV.2011.12.15; R.234) and possibly *Torvosaurus* (ML 1100); the carcharodontosaurids *Acrocanthosaurus* (SMU 74646) and *Carcharodontosaurus* (UCRC PV6); the possible metriacanthosaurid *Erectopus* (MNHN 2001-4; Figure 16.3), and the tyrannosaurid *Tyran-nosaurus* (FMNH PR.2081, mx10; Figure 16.4).
MHNA.PV.2011.12.187) and Majungasaurus (Fanti and Therrien, 2007); and the pteranodonid Marshosaurus (Madsen, 1976; UMNH 6368; Figure 17.2) and Piatnitzkysaurus (PVL 4043; MACN-CH 895), but not Condorraptor (Rauhut, 2005). A difference in size between mesial and distal denticles was also measured in a few teeth of: the baryonychines Baryonyx (NHMUK PV R.9951) and Suchomimus (UC G26-5; UC G67-1); the mesial dentition of Acrocanthosaurus (NCSM 14345) and Ceratosaurus (UMNH VP 5278), and in some lateral teeth of Allosaurus (e.g., UMNH VP 6189, UMNH VP 5841). Most crowns of these taxa appear, however, to have a DSDI close to 1 (C.H. personal obs.).

As noted by Rauhut et al. (2010), this condition is widespread among basal Tyrannosauroidea and can be observed in Dilong (Xu et al., 2004), Eotyrannus (Hutt et al., 2001; MIWG 1997.550, mx1 with DSDI of 1.5, isolated lateral crown with DSDI of 1.35; contra Sweetman, 2004; Figure 17.3), Guanlong (Xu et al., 2006), Proceratosaurus (Rauhut et al., 2010), Stokesosaurus (UMNH VP 6368), Timurlengia (Averianov and Sues, 2012) and Xiongguanlong (Li et al., 2010). The proceratosaurid Yutyrannus (ELDM V1001) has mesial and distal denticles of the same size at mid-crown, whereas the tyrannosaurid Nanotyrannus, a possible juvenile of Tyrannosaurus (e.g., Carr, 1999; Carr and Williamson, 2004; see Larson, 2013 for a different opinion), shows a DSDI higher than 1.2 in most teeth (Carr and Williamson, 2004).

Among non-tyrannosaurid coelurosauria, a DSDI higher than 1.2 was also measured in the teeth of the basal coelurosauria Bicentenaria (MPCN-Pv 866) and Zululong (IVPP V15912, pre-maxillary tooth), as well as the therizinosaurids Falcarius (UMNH VP 14528 Ldt?) and Nothronychus (Hedrick et al., 2015). Nonetheless, no size discrepancy between mesial and distal denticles was noticed in the dentition of Eoraptor (Zanno et al., 2016, figure 4), Eshanosaurus (IVPP V11579), Segnosaurus (Zanno et al., 2016), and the maxillary teeth of Falcarius (UMNH VP 14545). The majority of eudromaeosaurians such as the microraptorines Changyuvaraptor (Han et al., 2014), Graciliaptor (Xu and Wang, 2004), Sinornithosaurus (Xu and Wu, 2001) and Tianyuraptor (Zheng et al., 2010), the dromaeosaurines Achillobator (Perle et al., 1999), Atrociraptor (Currie and Varricchio, 2004), Dakotaraptor (DePalma et al., 2015) and Utahraptor (BYU-VP 18075), the velociraptorines Acheroiraptor (Evans et al., 2013), Bambiraptor (Burnham, 2004), Deinonychus (Ostrom, 1969; Figure 17.4), Linheraptor (IVPP V16923), Sauornitholestes (Currie et al., 1990), and Velociraptor (Barsbold and Osmolska, 1999), and the European dromaeosaurines Nuthetes (Milner, 2002) and Pyroraptor (Allain and Taquet, 2000) also have a DSDI higher than 1.2. In Troodontidae, the lateral teeth of Zanabazar (Barsbold, 1974) and some isolated crowns assigned to Troodon also display such difference in denticle size between the mesial and distal carinae (Currie, 1987, figure 5k, m). Mesial denticles significantly smaller than distal denticles were also noted in the basal neotheropod Liliensternus (Smith et al., 2005), but both carinae bear denticles of relatively similar size in this taxon (Cilardi, 2010; C.H. personal obs.).

Mesial larger than distal denticles. Mesial denticles are significantly larger than distal denticles (DSDI < 0.9) at mid-crown in some lateral teeth of: the basal sauropodomorph Eoraptor (PVSJ 512); the megalosaurids Afrovenator (UC UBA 1), Duriavenator (NHMUK PV R.332), Megalosaurus (NHMUK PV R.234; Milner, 2002), and Torvosaurus (ML 148); the carcharodontosaurids Acrocan-
Remarks and synapomorphy. A significant difference in size between mesial and distal denticles, with the mesial serrations being significantly smaller than the distal ones, was acquired independently in Abelisauridae, Dilophosauridae, Dromaeosauridae, Noasauridae, Piatnitzkysauridae, and Tyrannosauroidea, and teeth bearing distal denticles significantly bigger than the mesial ones are considered as synapomorphic for the clades Coelurosauria, Noasaurinae, and Piatnitzkysauridae (Appendix 6.19 for lateral teeth). Likewise, the presence of some lateral teeth with mesial denticles significantly larger than distal ones was convergently acquired by large-sized megalosaurus, carcharodontosaurids, and tyrannosaurs, as well as the dromaeosaurid *Dromaeosaurus*. Functional morphology. According to Fowler et al. (2011a), the reduction of mesial denticles would enhance the piercing function of the tooth. However, this functional hypothesis has never been tested. Distal denticles significantly larger than mesial ones are typically present in small-sized meat-eating theropods (i.e., Noasauridae, basal Tyrannosauroidea, and Eudromaeosauria). The mesial and distal denticles are subequal in size in *Utahraptor* (Kirkland et al., 1993) and only slightly smaller on the mesial carina in *Achillobator* (Perle et al., 1999), the two largest dromaeosaurids. Piatnitzkysauridae and derived Abelisauridae appear to be the only medium-sized theropods showing a clear difference in size between mesial and distal serrations, with mesial denticles being significantly smaller than the distal ones. Mesial denticles larger than distal denticles tend to be present in particularly large-sized theropods such as megalosaurus, carcharodontosaurids and tyrannosaurs. Consequently, functional or developmental factors, or a combination of both, seem to come into play for the establishment of this condition in such disparate theropod clades with possibly similar feeding strategies.

Distal denticles significantly larger than mesial ones, in fact, appear to be a common feature of juvenile tyrannosaurs, with DSDIs decreasing progressively throughout ontogeny in at least *Tyrannosaurus* (Carr and Williamson, 2004). A significant difference between mesial and distal denticles has for instance been observed in the transitional dentition (i.e., teeth at the transition between the mesial and lateral dentition) of an immature specimen of *Daspletosaurus* (TMP 1994.143.01), the premaxillary, maxillary and dentary dentitions of a juvenile *Tarbosaurus* (Tsuihiji et al., 2011), and the lateral dentition of the juvenile tyrannosaurine *Shanshanosaurus* (Currie and Dong, 2001a). In the young specimens of *Daspletosaurus*, the carinae of the premaxillary teeth are unserrated (TMP 1994.143.1; Currie, 2003) and show the beaded condition seen in *Irritator* (Figure 15.3). Transitional teeth in this taxon have a more distal and, in some cases, poorly delimited mesial denticles and much larger and well-differentiated distal denticles.

**Straight to convex distal profile**

Although a straight or convex distal margin of the crown is the most common condition in conodont and foliodont teeth, most ziphodont and pachydont teeth are usually slightly to strongly concave distally (Ezcurra, 2009; C.H. personal obs.). A straight or slightly curved distal profile was considered to be a synapomorphy for Abelisauridae by Smith (2007) as this feature is present in the crowns of *Aucasaurus*, *Indosuchus*, *Majungasaurus*, *Rugops*, *Kryptops* (Smith and Lamanna, 2006; Smith and Dalla Vecchia, 2006; Candeiro, 2007; Smith, 2007; C.H. personal obs.), and many indeterminate abelisaurids (e.g., UCPC 10; MNHN MRS1619, MRS1620). However, a straight or slightly concave curvature of the distal profile also occurs in the basalmost sauropodomorph *Eoraptor* (PVSJ 512), the ceratosaurs *Ceratosaurus* (USNM 4735) and *Genyodectes* (MLP 26-39), the noasaurids *Noasaurus* (PVL 4061), the allosaurid *Allosaurus* (NHFO 455), the metriacanthosaurs *Sinraptor* (IVPP 10600) and *Yangchuanosaurus* (CV 00215), the carcharodontosaurids *Carcharodontosaurus* (SGM Din1) and *Mapusaurus* (MCF-PVH 108.43), the basal pantyrranosaurian *Eotyrannus* (MIWG 1997.550), and some coelurosaurs such as *Paronychodon* (Currie et al., 1990, figure 8.5A) and *Zapsalis* [Sankey et al., 2002, figure 4.10; n.b., *Zapsalis* corresponds to ‘Dromaeosaurus’ morphotype A of Longrich (2008), ?*Dromaeosaurus* morphotype A of Sankey et al. (2002) and Sankey (2008), and Dromaeosaurinae morphotype A of Larson (2008)]. A straight distal margin of the crown is also present in pachydont teeth of some tyrannosaurs such as *Gorgosaurus.*
A sigmoid outline of the distal margin of the crown, with the basal half slightly concave and the apical half weakly convex, is typical of carcharodontosaurid lateral teeth and can be observed in Carcharodontosaurus (SGM Din-1) and Giganotosaurus (MUCPv CH1). Among non-avian theropods, a convex distal profile of the crown is visible in some Abelisauridae, Alvarezsauria, Ceratosauridae, Carcharodontosaurus, Fukuivenator, Ornithomimosauria, Oviraptorosauria, Therizinosauria and Spinosauridae.

**Remarks and synapomorphy.** Given the wide distribution of a straight or convex distal profile, this feature cannot be used solely to identify teeth and therefore the synapomorphy proposed by Smith (2007) cannot be supported. However, a convex distal profile of the crown is a rare condition in ziphodont teeth and is only present, to our knowledge, in Abelisauridae and a few lateral teeth of Carcharodontosaurus (Stromer, 1931, figure 2) and Ceratosaurus, in which the feature is considered to be apomorphic. A slightly convex and almost straight mesial profile is seen in Alvarezsauridae/Parvicursorinae, Fukuivenator, Ornithomimosauria, Therizinosauria and some Spinosauridae, whereas all other theropods display a strongly convex mesial profile. The presence of some lateral crowns with a straight distal profile is here considered to be synapomorphic for Ceratosauria, Spinosauridae, and Paraves, whereas a convex distal profile of the crown is a synapomorphy of Maniraptora.

**Flutes**

**Whole dentition.** Flutes are well-known to characterize the dentition of spinosaurids, as they are present on at least some of the mesial and lateral crowns in all known spinosaurid species (e.g., Charig and Milner, 1997; Taquet and Russell, 1998; Sereno et al., 1998; Sues et al., 2002; Dal Sasso et al., 2005; Sales and Schultz, 2017; Figure 18.5). Besides Spinosauridae, the basal theropod Tawa (GR 241; Figure 18.1), juvenile individuals of the coelophysid Coelophysis (Buckley and Currie, 2014), the noasaurid Masiakasaurus (Carrano et al., 2002; Figure 18.4), and an undescribed metriacanthosaurid (ZLTJ 0115) appear to be the only non-avian theropods bearing fluted mesial and lateral teeth. All preserved premaxillary, maxillary, and dentary teeth seem to be fluted on both sides in Tawa (GR 241). Flutes are restricted to the anterior portion of the maxilla and dentary in juvenile individuals of Coelophysis, as they are present on the labial surface of the crown up to the fifth maxillary and third dentary teeth in RTMP 1984.63.1-1 and to the first maxillary and sixth dentary teeth in NMMNH P-42200 (Buckley and Currie, 2014). In Masiakasaurus, flutes have been observed on the lingual surface of most in situ dentary teeth. They are present in Ldt1 (3 flutes) of FMNH PR 2471 and Rdt4 (5 flutes) and Rdt6 (1 flute) of UA 8680. The latter also seems to have a single flute on the labial surface of the crown, whereas the partially erupted tooth Ldt4 of FMNH PR 2471, of which the apex can only be seen, does not show any fluting.

In Spinosauridae, flutes are present on the lingual surface of all premaxillary teeth of Baryonyx (with the possible exception of the pm1, in which the lingual surface of Lpm1 is badly preserved and hidden by matrix) but absent in Lmx5, the only lateral tooth preserved in situ (NMMUK PV R.9951). Nine out of 14 isolated teeth from the mesial and lateral dentitions (which are impossible to distinguish in Spinosauridae) have flutes, suggesting that at least some lateral teeth were also fluted in Baryonyx. In Suchomimus, flutes can be seen on the labial surface of Lpm2, Lpm3 and mx19 but are absent on both labial and lingual sides of Rmx10 in MNN GDF501. Fluted crowns are also present in the posterior portion of the maxilla of the juvenile specimen MNN G232, and in the central portion of a dentary in MNN G74-1. All preserved maxillary teeth of Irritator (SMNS 58022) are fluted. For the gigantic snout (MSNM V4047) referred to Spinosaurus, most but not all premaxillary and maxillary teeth are fluted, with flutes being numerous, closely packed and mesiodistally narrow in the largest crowns (i.e., Rpm3, Lmx2, L and Rmx3 and Lmx4). Flutes are essentially restricted to the lingual surface in Baryonyx (Charig and Milner, 1997; n.b., only a single tooth bears several flutes on the lingual side and a single flute on the labial surface; C.H. personal obs.) and present on both sides in most Suchomimus and all Suchosaurus crowns. All preserved teeth of Irritator appear to be fluted on both labial and lingual sides (Sues et al., 2002), and most Spinosaurus teeth have flutes on both sides as well.

**Mesial dentition.** Flutes restricted to the mesial dentition are present in the ceratosaurid Ceratosaurus (e.g., Madsen and Welles, 2000; UMNH VP 5278; Figure 18.3), the compsognathid Scipionyx (Dal Sasso and Maganuco, 2011; Figure 18.7) and the dromaeosaurid Velociraptor (AMNH 6515; Figure 18.10). While flutes have only been observed on the lingual and labial surface of a single pre-
maxillary tooth of *Scipionyx* (Lpm5) and *Velociraptor* (L and Rpm1), respectively, they are present on the lingual surface of all premaxillary and at least the first two dentary teeth of *Ceratosaurus* (UMNH VP 5278).

**Lateral dentition.** Flutes are visible in the lateral dentition of the non-averostran neotheropod *Sinosaurus triassicus* (IVPP V34) in labial view, showing the transverse undulations at the base of the crown; 3, First left and right premaxillary teeth of the ceratosaurid *Ceratosaurus nasicornis* (UMNH VP 5278) in lingual view; 4, Third right dentary tooth of the noasaurid *Masiakasaurus knoepleri* (UA 8680) in lingual view; 5, Isolated tooth of the baryonychine *Suchosaurus cultridens* (= Baryonyx walkeri?; NHMUK PV R.36536) in lingual view; 6, Second right maxillary tooth of the basal pantyrrannosaurian *Dilong paradoxus* (IVPP V14242) in labial view (n.b., an apparent labial concavity delimited by two faint longitudinal ridges results from a lightning effect); 7, Fifth left premaxillary tooth of the comp-sognathid *Scipionyx samniticus* (SBA-SA 163760) in lingual view (reprinted with permission from Dal Sasso and Maganuco (2011), courtesy of Cristiano Dal Sasso & Simone Maganuco, © Soprintendenza Archeologia, Belle Arti e Paesaggio per le Province di Caserta e Benevento); 8, Seventh or eight? right maxillary tooth of the dromaeosaurid *Microraptor* sp. (IVPP 2008.5) in labial view; 9, Fourth left maxillary tooth of the dromaeosaurid *Sinornithosaurus mil- lenii* (IVPP V12811) in labial view; 10, First right premaxillary tooth of the dromaeosaurid *Velociraptor mongoliensis* (AMNH 6515) in labial view. Abbreviation: tun, transverse undulation. Scale bars equal 1 cm (1–2, 4), 1 mm (3, 5–8).

**FIGURE 18.** Fluted teeth in non-avian Theropoda. 1, Fifth? left maxillary tooth of the basal theropod *Tawa hallae* (GR 241) in lingual view (courtesy of Sterling Nesbitt); 2, Fourth? left maxillary tooth of the non-averostran neotheropod *Sinosaurus triassicus* (IVPP V34) in labial view, showing the transverse undulations at the base of the crown; 3, First left and right premaxillary teeth of the ceratosaurid *Ceratosaurus nasicornis* (UMNH VP 5278) in lingual view; 4, Third right dentary tooth of the noasaurid *Masiakasaurus knoepleri* (UA 8680) in lingual view; 5, Isolated tooth of the baryonychine *Suchosaurus cultridens* (= Baryonyx walkeri?; NHMUK PV R.36536) in lingual view; 6, Second right maxillary tooth of the basal pantyrrannosaurian *Dilong paradoxus* (IVPP V14242) in labial view (n.b., an apparent labial concavity delimited by two faint longitudinal ridges results from a lightning effect); 7, Fifth left premaxillary tooth of the comp-sognathid *Scipionyx samniticus* (SBA-SA 163760) in lingual view (reprinted with permission from Dal Sasso and Maganuco (2011), courtesy of Cristiano Dal Sasso & Simone Maganuco, © Soprintendenza Archeologia, Belle Arti e Paesaggio per le Province di Caserta e Benevento); 8, Seventh or eight? right maxillary tooth of the dromaeosaurid *Microraptor* sp. (IVPP 2008.5) in labial view; 9, Fourth left maxillary tooth of the dromaeosaurid *Sinornithosaurus mil- lenii* (IVPP V12811) in labial view; 10, First right premaxillary tooth of the dromaeosaurid *Velociraptor mongoliensis* (AMNH 6515) in labial view. Abbreviation: tun, transverse undulation. Scale bars equal 1 cm (1–2, 4), 1 mm (3, 5–8).
(2014), such ontogenetic variation may indicate different diets between juvenile and mature individuals, with young *Coelophysis* primarily eating arthropods and fish. This ontogenetic pattern can also be observed in the basal pantyrannosaurian *Dilong* as the crowns of IVPP V14243 are not fluted whereas the specimen IVPP V14242, which represents an earlier ontogenetic stage than IVPP V14243 (Xu et al., 2004), clearly bears several fluted teeth.

The number of flutes on the labial or lingual surface of the crown ranges from one to eight in juvenile *Coelophysis* (Buckley, 2009, figure 4.3, 4.4 and 4.5), four to seven in the mesial dentition of *Ceratosaurus* (4–6 flutes in L/Rpm1-3 and 4–5 in Ldt1-2 of UMNH VP 5278; Figure 18.3), two to five in the mesial crowns of *Masiakasaurus* (3–4 in average; UA 8680, FMNH PR 2182, 2471, 2696; Figure 18.4), and three in a single maxillary crown of *Sinosaurs* (IVPP V34; Figure 18.2). In spinosaurids, we counted four to eight flutes in *Baryonyx* (6–7 in average; NHMUK PV R.9951), ten to 12 in *Suchosaurus cultridens* (NHMUK PV R.3308, R.4702, and R.36536; Figure 18.5), two to 10 in *Suchomimus* (6–7 in average; UC G26-5, G34-7, UC G67-1), and five to 10 in *Irritator* (7–8 in average; SMNS 58022). The highest number of flutes in theropods is seen in the unserrated crowns of some spinosaurines, with up to 17 flutes in *Sinoplosaurus* (IVPP V4793.2) and *Siamosaurus* (TF 2043), and 20 flutes in the largest maxillary crowns of *Spinosaurs* (Lmx2 of MSNM V4047). In averostrans, there are four to six, possibly more in the undescribed metriacanthosaurid ZLJ 0115, 12 to 13 flutes in *Dilong* (Rmx2 and 4 of IVPP 14242; Figure 18.6), two or three in *Scipionyx* (Dal Sasso and Maganuco, 2011, figure 45; Figure 18.7), four or five in *Microraptor* (IVPP 2008.5; Figure 18.8), eight or nine in *Sinornithosaurus* (Rmx4 of IVPP V12811; Figure 18.9), and around three to six flutes in the first premaxillary teeth of *Velociraptor* (AMNH 6515; Figure 18.10). Fluted mesial and lateral teeth are a synapomorphy of Spinosauridae (Sereno et al., 1998), whereas fluted lateral teeth are here considered as synapomorphic for Microraptorinae (Appendix 6.21).

**Functional morphology.** The presence of flutes, usually on conical teeth, is common in piscivorous tetrapods such as crocodiles (Longrich, 2008), mosasaurs, plesiosaurs (Massare, 1987) and pterosaurs (e.g., Kellner and Tomida, 2000; Andres et al., 2010). Longitudinal ridges bounding flutes are present in a large array of tooth morphologies associated with different diets in marine reptiles (Massare, 1987). Plesiosaurid teeth with long slender conidont crowns and flutes delimited by low longitudinal ridges suggest that they were used to pierce soft prey, whereas the straight and robust cones with flutes delimited by prominent ridges were used for grasping prey with a hard exterior in ichthyosaurs. Likewise, the longitudinal and sharp ridge bounding each flute of large pliosaurs is probably a cutting edge used for tearing fleshy prey (Massare, 1987). Therefore, the presence of flutes on the crown may have a broad and general function in animals with disparate tooth morphologies and teeth adapted to different diets. Flutes most likely have some piercing and gripping function, allowing the sharp ridges to pierce the skin and broadening the flesh as the tooth penetrates the prey body, and keeping slippery prey in the mouth (Sues et al., 2002). Fluted crowns, which appear to be more difficult to pull out compared to non-fluted crowns given that the contact area between the meat and the teeth is larger, may have prevented the struggling prey from rotating and also helped to resist its movements (Kouzuma S. and Kamiya M., personal comm., 2017).

**Transverse undulations**

Although thought to be a possible tetanuran synapomorphy (Brusatte et al., 2007), transverse undulations (Figure 19) are present in the crowns of many non-avian theropods, from basal to derived forms. These are present in: the basalmost saurischians *Ichisaurus* (MACN 18.060), *Eodromaeus* (PVSJ 561) and *Sanjuansaurus* (PVSJ 605; Figure 19.1); the basal theropods *Dracoraptor* (NMW 2015.5G) and *Dracoovenator* (BP/1/5243); the basal ceratosaur *Berberosaurus* (MNHN To 369); the ceratosaurid *Ceratosaurus* (USNM 4735) and *Genyodectes* (MLP 26-39; Figure 19.2); the noasaurid *Masiakasaurus* (FMNH PR.2221, 2476; Figure 19.3), and the abelisaurids *Aucasaurus* (MCF-PVPH 236; Figure 19.4) and *Majungasaurus* (FMNH PR.2278). As noted by Brusatte et al. (2007), transverse undulations are widespread among basal tetanurans and have been observed in: the megalosauroid *Monolophosaurus* (IVPP V84019; Brusatte et al., 2010a; Figure 19.5); the ptiaptzatkysaurids *Marshosaurus* (DMNS 3718; Figure 19.6) and *Piatnitzkysaurus* (PVL 4073; MACN CH 895); the megalosaurids *Duriaenator* (NHMUK PV R.332) and *Megalosaurus* (NHMUK PV R.8303; OUMNH J13505); the spinosaurid *Baryonyx* (NHMUK PV R.9951; ML 1190); the allosaurids *Acrocanthosaurus* (NCSM 14345), *Allosaurus* (AMNH 851; NHFO 455; UMNH VP5841;
Figure 20.7), Concavenator (Cuesta et al., 2018), Neovenator (MIWG 6348), Giganotosaurus (MUCPv-CH-1; Figure 19.7), and Sinraptor (IVPP 10600); the tyrannosaurids Alioramus (MPC-D 100-1844; Brusatte et al., 2012), Dilong (IVPP V11979), Guanlong (IVPP ZHU14532), Gorgosaurus (USNM 12814), Teratophoneus (UMNH VP 16690; Figure 20.10) and Tyrannosaurus (FMNH PR 2081); and the basal coelurosaur Ornitholestes (AMNH 619) and Zuolong (Choiniere et al., 2010a). Among neocoelurosaurids, they are present in: the therizinosaurs Falcarius (UMNH VP 14545; Figure 19.8) and Segnosaurus (MPC-D 100-80); the dromaeosaurids Atrociraptor (TMP 1995.166.01; Figure 19.9), Deinonychus (YPM 5232), Dromaeosaurus (Smith, 2005; AMNH 5356), Saurognathus (TMP 1988.212.39, 1994.12.844), Utahraptor (BYU 1249) and an inde-terminate velociraptorine (DMNH unnumbered); and the troodontid Troodon (DMNH 22337; Figure 19.10).

Remarks and synapomorphy. Transverse undulations are not restricted to the crown as they have also been observed on the root of various averostrans such as Aucasaurus (MCF-PVPH 236), Allosaurus (UMNH VP 1251, 5841), Baryonyx (NHMUK PV R.9951), Neovenator (MIWG 6348), Sauornitholestes (TMP 1988.121.39), Zuolong (Choiniere et al., 2010a) and an immature specimen of Daspletosaurus (TMP 1994.143.1). Transverse undulations may be genuinely absent in the dentition of Alveoresauridae, Compsognathidae, Halszkaraptorinae, Microraptorinae, Ornithomimidae, Oviraptorosauria, Scansoriopterygidae and Enunlagiinae, given that they are not observed in these clades. Likewise, enamel undu-
lations (i.e., transverse and marginal undulations) have not been observed in the teeth of any coelophysoids, and these theropods may also lack these dental features. Due to the wide distribution of these crown ornamentations in non-avian theropods, enamel undulations have to be used in concert with other dental features in order to assign teeth to more restricted theropod clades. Nevertheless, the presence of numerous and closely packed transverse undulations seems to be restricted to the crowns of non-neocoeurosaur avetheropods such as Allosauroidea, Ceratosauridae, Megalosauridae, Piatnitzkysauridae and Tyrannosauridae, as well as some dromaeosaurs like Deinonychus and Saurornitholestes (C.H. personal obs.). Transverse undulations are here considered to be synapomorphic for Avetheropoda (Appendix 6.22).

**Functional morphology.** Transverse undulations may have served to minimize suction when the tooth was pulled out of the flesh (Currie and Azuma, 2006), to help strengthen the crown during feeding (Brusatte, 2012), or may simply be a byproduct of growth (Brusatte et al., 2007). Transverse undulations in large meat-eating theropods are not necessarily homologous to those in taxa such as *Troodon* and *Dromaeosaurus*, and may differ in their development and origin. Transverse undulations are also present in many other tetrapods, including pliosaurids (Zverkov et al., 2018), mosasaurs (Buffetaut and Bardet, 2012), metriorhynchid crocodylomorphs (De Andrade et al., 2009), and several other theropod clades.

**FIGURE 20.** Marginal undulations in the teeth of non-avian Theropoda. 1, Fifth left maxillary tooth of the ceratosaurid *Ceratosaurus nasicornis* (UMNH VP 5278; reversed) in lingual view; 2, Second left maxillary tooth of the noasaurid *Masiakasaurus knoepferi* (FMNH PR.2696) in labiodistal view; 3, Second left maxillary tooth of the abelisaurid *Majungasaurus crenatissimus* (FMNH PR 2100) in basolinguinal view; 4, Second right maxillary crown of the megalosaurid *Monolophosaurus jiangi* (IVPP 84019) in labial view; 5, Isolated lateral tooth of the piatnitzkysaurid *Piatnitzkysaurus floresi* (MACN 895) in linguodistal view; 6, Isolated lateral tooth of the spinosaurid *Suchomimus tenerensis* (MNN G51) in labiodistal view; 7, Sixth left maxillary tooth of the allosaurid *Allosaurus* sp. (UMNH VP 9168) in labial view and showing both the marginal and transverse undulations on the crown; 8, Distalmost isolated tooth of the carcharodontosaurid *Mapusaurus roseae* (MCF-PVPH-108.103) in basolabial view; 9, Isolated mesial tooth of the basal pantyrranosaurian *Aviatyrannis jurassica* (MG27801 D90) in labial view; 10, Isolated lateral tooth of the pantyrranosaurian *Teratophoneus curriei* (UMNH VP 16690) in basolabial view, showing both the marginal and transverse undulations. Abbreviation: tun, transverse undulation. Scale bars equal 1 cm (1, 3–8), 5 mm (10), 1 mm (2, 9).
Marginal undulations

Short and marginal undulations close to the carinae are a well-known feature of carcharodontosaurid teeth (Sereno et al., 1996; Coria and Currie, 2006) as they appear on the crowns of *Carcharodontosaurus* (SGM Din-1; UC PV6; MNN IGU6), *Concavenator* (Cuesta et al., 2018), *Giganotosaurus* (MUCPv-CH-1), *Mapusaurus* (MCF-PVPH 108; Figure 20.8) and *Tyrannotitan* (Canale et al., 2015). Marginal undulations (Figure 20) have also been reported in the abelisaurid *Skorpiovenator* (Canale et al., 2009) and are present in a large range of non-neoceleurosaur avetheropods: the ceratosaurs *Abelisaurus* (MC 5, MC 687), *Ceratosaurus* (USNM 4735; Figure 20.1), *Chenanisaurus* (Longrich et al., 2017), *Majungasaurus* (FMNH 2100; Figure 20.3) and *Masiakasaurus* (FMNH PR.2182; Figure 20.2), the megalosaurid *Monolophosaurus* (IVPP V84019; Figure 20.4); the piatnitzkysaurids *Marshosaurus* (DMNS 3718) and *Piatnitzkysaurus* (PVL 4073; MACN 895; Figure 20.5); the megalosaurids *Afrovenator* (UC UBA1), *Megalosaurus* (NHMUK PV R.234; OUMNH J.23014), and *Torvosaurus* (ML 500; Hendrickx et al., 2015c); the spinosaurids *Baryonyx* (NHMUK PV R.9951), *Irritator* (Sues et al., 2002; Figure 15.3), *Suchomimus* (MNN G35-9; Figure 20.6) and an indeterminate spinosaurine from Brazil (Medeiros, 2006); the pantyrranosaurians *Avi-tyrannnis* (MG 27801 D90; Figure 20.9), *Daspletosaurs* (NHMUK PV R.4863), *Lythronax* (UMNH VP 20200), *Teratophoneus* (UMNH VP 16690; Figure 20.10), and *Tyranosaurus* (Brusatte et al., 2007); and many non-carcharodontosaurine allosaurs such as *Acrocanthosaurus* (NCSM 14345), *Allosaurus* (e.g., USNM 8335; UMNHP VP 5837, 6113, 7436; Figure 20.7), *Fukuiraptor* (FPDM 9712204; Azuma and Currie, 2000, figure 4 bottom right), *Neovenator* (MIWG 6348) and *Sin-raptor* (IVPP V10600).

Remarks and synapomorphy. In most theropods, marginal undulations usually extend mesiodistally on the crown, and are typically elongated and parabolic, with the part adjacent to the carina curving apically. However, marginal undulations of some theropods can be short, broad, and mesiodistally straight, as seen adjacent to the mesial carina of *Afrovenator* (MNN UBA1), *Ceratosaurus* (USNM 4735; Hendrickx et al., 2015c, figure A5.L), *Masiakasaurus* (FMNH PR.2182) and *Tyranosaurus* (TMP 1981.006.01). They can also be strongly diagonally-oriented, as observed in some teeth of *Irritator* (Sues et al., 2002, figure 5), *Masiakasaurus* (FMNH PR.2696; Figure 20.2), *Monolophosaurus* (IVPP V84019; Figure 20.4), *Megalosaurus* (OUMNH J.23014), *Suchomimus* (MNN G51; Figure 20.6), and an indeterminate spinosaurid (Medeiros, 2006). Numerous and extremely pronounced marginal undulations on both mesial and distal sides of the crown have only been identified in *Carcharodontosaurus saharicus* and seem to be autapomorphic to this taxon among theropods (Brusatte and Sereno, 2007). The marginal undulations of other carcharodontosaurids such as *Acrocanthosaurus*, *Carcharodontosaurus iguidensis*, *Concavenator*, *Giganotosaurus*, *Mapusaurus* and *Tyranosaurus* are present but not as pronounced and numerous as those visible in the teeth of the neotype of *Carcharodontosaurus saharicus* (Brusatte and Sereno, 2007; C.H. personal obs.). Some *Allosaurus* lateral crowns also show numerous and particularly pronounced marginal undulations, yet they are mesiodistally shorter and restricted to the distal carina of the crown (Figure 20.7).

Marginal undulation is a more widespread feature than previously thought in non-avian theropods, and the presence of marginal undulations is here considered to be a synapomorphy of Tetanurae (Appendix 6.23). Yet, we cannot entirely dismiss the hypothesis that this feature is convergently present in several clades of theropods as it might have a particular functional role that converged after the split of the various theropod clades possessing it. Interestingly, marginal undulations are present only in large-sized theropods with the exception of *Masiakasaurus* and *Avi-tyranninis*.

Interdenticular sulci

Elongated interdenticular sulci. Thought to be restricted to Allosauroidea and Tyrannosauroidea ('Carnosauria' sensu Gauthier, 1986; Rauhut and Kriwet, 1994) or to represent an abelisaurid synapomorphy (Smith, 2007), interdenticular sulci (Figure 21), in fact, occur in many other theropod clades. Strongly developed and elongated sulci have been observed in the abelisaurids *Chenanisaurus* (Longrich et al., 2017), *Kryptops* (MNPP GAD1–1), and *Majungasaurus* (FMNH PR.2100, 2278; Figure 21.2) and the non-spinosaurid megalosaurids *Megalosaurus* (OUMNH J13506; Figure 21.4), *Piatnitzkysaurus* (PVL 4073; Figure 21.3) and *Torvosaurus* (Hendrickx and Mateus, 2014b). In avetheropods, they are also present in the allo-
sauroids Allosaurus (UMNH VP 6499, 10393; Figure 21.6), Fukuiraptor (Azuma and Currie, 2000), Giganotosaurus (MUCPv-CH-1; Figure 21.7), Mapusaurus (MCF-PVPH-108) and Sinraptor (IVPP 10600; Figure 21.5), and the tyrannosaurids Albertosaurus (TMP 1999.50.40), Daspletosaurus (TMP 1994.143.1) and Tyrannosaurus (FMNH PR.2081; Figure 21.8). In non-paravian maniraptoriforms, they have only been observed in the basal therizinosaur Falcarius (UMNH VP 14528; Figure 21.9).

Short interdenticular sulci. Poorly-developed interdenticular sulci are widespread among non-neocoeleosaur theropods as they have been noticed in the basal theropod Tawa (GR 241), and almost all allosauroids, ceratosaurs (Figure 21.1), megalosauroids, piatnitzkysaurids (including Condorraptor; contra Rauhut, 2005) and tyrannosauroids (e.g., Currie et al., 1990; Azuma and Currie, 2000; Fanti and Therrien, 2007; Hendrickx and Mateus, 2014a; Hendrickx et al., 2015c; C.H. personal obs.). In paravians, they have also been observed in the microraptorine specimen IVPP V13476 (Xu and Li, 2016), the eudromaeosaurians Deinonychus (YPM 5232; Figure 21.10), Saurornitholestes (Currie et al., 1990) and Dromaeosaurus (AMNH 5356; Currie et al., 1990; Larson, 2008), as well as some troodontids (Currie and Dong, 2001b; Sankey, 2008, figure 3.13 and 3.21) such as Troodon (NHMUK PV R.12568).

Remarks and synapomorphy. Interdenticular sulci have not been seen in herrerasaurids, coelophysoids, dilophosaurids, noasaurids, spinosaurids, several abelisaurids such as Rugops (MNN

FIGURE 21. Well-developed interdenticular sulci in non-avian Theropoda. 1, Distal carina of the eighth left maxillary tooth of the ceratosaurs Ceratosaurus nasicornis (UMNH VP 5278; image upside down) in lateral view; 2, Distal carina of the sixth right maxillary tooth of the abelisaurid Majungasaurus crenatissimus (FMNH PR.2278; image upside down) in lateral view; 3, Distal carina of an isolated lateral tooth of the piatnitzkysaurid Piatnitzkysaurus floresi (PVL 4073) in lateral view; 4, Distal carina of an isolated lateral tooth of the megalosaurid Megalosaurus bucklandi (NHMUK PV R.234) in labial view; 5, Distal carina of an isolated lateral tooth of the metriacanthosaurid Sinraptor dongi (IVPP V10600) in lateral view; 6, Distal carina of an isolated tooth of the allosaurid Allosaurus sp. (UMNH VP 6177) in lateral view, also showing the transverse undulations at the crown base; 7, Distal carina of an isolated lateral tooth of the carcharodontosaurid Giganotosaurus carolinii (MUCPv CH1 L2) in lateral view; 8, Distal carina of the fifth right maxillary tooth of the tyrannosaurid Tyrannosaurus rex (FMNH PR.2081; image upside down) in lateral view; 9, Distal carina of a right mid-dentary tooth of the basal therizinosaur Falcarius utahensis (UMNH VP 14528) in labial view; 10, Distal carina of the last? right dentary tooth of the dromaeosaurid Deinonychus antirrhopus (YPM 5232) in labial view. Scale bars equal 1 mm.
infectious bite, distributing stresses from the base of venomous theropod, hosting septic bacteria for an entry of venom in a possible infectious or venomous delivery systems. It is, nonetheless, possible that interdenticular sulci had a combination of several or all of these functions in some theropods.

Functional morphology. Interdenticular sulci have been noticed in several theropods by many authors (Currie et al., 1990; Abler, 1992; Buscalioni et al., 1996; Smith, 2007; Benson, 2009), but none provided functional implications for these structures. Interdenticular sulci may play several roles such as helping the entry of venom in a possible venomous theropod, hosting septic bacteria for an infectious bite, distributing stresses from the base of the denticle, or preventing suction when the crown was pulled out of the flesh. The first hypothesis is supported by the presence of interdenticular sulci on the crown of the venomous Komodo dragon (D’Amore and Blumenschine, 2009), representing a rare example of an extant animal showing these sulci. The teeth of the Komodo dragon do not have any venom-delivering systems, unlike the hollow teeth of snakes or the apicobasally long grooves on the crowns of helodermatid lizards (Fry et al., 2009). Instead, its crowns are smooth and lack any dental features besides short interdenticular sulci and plicidentine (i.e., the radial infolding of the dentine layer of the basal portion of the crown, present in some fish, amphibians, and varanoids; e.g., Peyer, 1968; Kearney et al., 2006; Maxwell et al., 2011), so that the venom seems to enter via deep wounds when lacerating the prey items (Fry et al., 2009). Therefore, interdenticular sulci of Varanus komodoensis and theropods may help venom to be administrated during biting.

The second hypothesis was proposed by Abler (1997, 1999) for the deep interdenticular space (‘cella’ sensu Abler, 1992, 1999) present in between tyrannosaurid denticles. Abler (1992, 1999) suggested that these interdenticular spaces would trap grease and food debris that functioned as receptacles for septic bacteria, becoming the source of a lethal infection when biting. Pathogenic bacteria have also been reported in the saliva of the Komodo dragon (Auffenberg, 1981; Montgomery et al., 2002), and interdenticular sulci may help the proliferation and entering of these toxic bacteria within the prey. Fry et al. (2009), however, note that no compelling evidence supports the presence of pathogenic bacteria in the saliva of Varanus komodoensis, a hypothesis supported by Goldstein et al. (2013) based on captive Komodo dragons. Yet, Tehrani et al. (2008) and Vikrant and Verma (2014) have reported septic effects of varanid bites, and pathogenic bacteria might, therefore, be present and possibly hosted within interdenticular sulci of the crowns of wild varanids.

Interdenticular sulci may also serve as stress-distributing structures as they re-orient the stresses at the base of the denticle towards the middle of the crown, thus preserving the integrity of the denticle under high-stress regimes. Contrasting with the disparate morphology of hooked denticles among different theropod clades, interdenticular sulci are similar, possibly homologous, in Ceratosauridae, Megalosauroidea, Allosauroidea, Tyrannosauroida, Therizinosauria and Paraves. Given that these theropods were faunivorous, herbivorous or omnivorous, this condition favors the idea that interdenticular sulci are stress-dissipation or suction reduction structures, rather than specialized infectious or venomous delivery systems. It is, nonetheless, possible that interdenticular sulci had a combination of several or all of these functions in some theropods.

Longitudinal ridges

Mesial dentition. A longitudinal ridge centrally positioned on the lingual surface of the crown and delimited by two concave surfaces is typical of tyrannosaurid mesial teeth (Carr and Williamson, 2004). This feature has been observed in the pantyrannosaurs Albertosaurus (Carr and Williamson, 2004), Appalachianosaurus (Carr et al., 2005), Daspletosaurus (Lehman and Carpenter, 1990; TMP 1994.143.01), Gorgosaurus (Cillari, 2010), Nanotyrannus (Carr and Williamson, 2004; n.b., the small-sized Lmx1 of LACM 28471 displaying a U-shaped cross-section and a medial ridge is here considered to be a premaxillary tooth; Molnar, 1978; contra Carr and Williamson, 2004), Raptorex (Sereno et al., 2009; LH PV18; Figure 22.2), Timurlengia (Averianov and Sues, 2012), Tyrannosaurus (Smith, 2005; MOR 1125), Xiongguanlong (Li et al.,
2010; Figure 11.4) and an indeterminate tyrannosaurid from the Cenomanian of Utah (Zanno et al., 2019). A discrete ridge also occurs on the lingual side of the mesial premaxillary teeth in the basal tyrannosauroids Dinosaur (IVPP V11979, V14243) and Proceratosaurus (Lpm2; NHMUK PV R.4860). In Proceratosaurus, the median ridge seems, however, to be a byproduct of the numerous basal striations extending on the basal half or basal two-thirds of the lingual surface of the crowns. This median ridge is absent in the proceratosaurid Guanlong (IVPP V14531; contra Sereno et al., 2009) as well as some basal pantyrannosaurs such as Aviatyrannis (MG 2781 D90 and D172) and Eotyrannus (MIWG 1997.550). Outside Tyrannosauroidea, one or several longitudinal ridges can be seen on the lingual surfaces of some premaxillary teeth of the basal coelurosaur Fukuiraptor (Azuma et al., 2016), and the microraptorines Sinornithosaurus (IVPP V12811) and some specimens of Microraptor (IVPP V13320, 2008.5). Likewise, a mesiodistally wide and centrally positioned convexity delimited by two concavities adjacent to the carinae on the lingual surface of some premaxillary crowns of Allosaurus (YPM-PU 14554) can also be considered as a longitudinal ridge.

**Lateral dentition.** Two longitudinal ridges delimiting the lingual depression are observable on the lingual surface of some lateral teeth of Orkoraptor (Novas et al., 2008; Figure 22.1). One, two or several longitudinal ridges delimiting grooves of irregular width and orientation are present on the crowns of the basal therizinosaur Falcarius (Zanno, 2010a) and many paravians. In Falcarius, a single centrally positioned longitudinal ridge running along the whole crown height can be observed on the lingual surface of the first maxillary tooth of UMN VP 14545 and several mid-dentary teeth (Zanno, 2010b, figure 2L; Button et al. (2017), supplemental figure S2B). In dromaeosaurids, they have been noticed in Bambiraptor (AMNH 30556; Figure 22.3), Buitreraptor (Gianechini et al., 2011b; MPCA 245), Changyuraptor (Han et al., 2014, figure 3b), Linheraptor (IVPP V16923), Microraptor (IVPP 2008.5), Richardoestesia (Longrich, 2008; Sankey, 2008), Saurornitholestes (Baszio, 1997; Sankey, 2008), Velociraptor (AMNH 6515), and Zapsalis (Larson, 2008; Longrich, 2008; Larson and Currie, 2013), as well as Acheroraptor, in which they are numerous and particularly well-visible (Evans et al., 2013; Figure 22.4). They are also present in some troodontids such as cf. Pectinodon (Sankey, 2008; Larson and Currie, 2013), Troodon (Currie, 1987, figure 5S; Sankey, 2008) and the indeterminate paravians and tooth-based taxa Eurychodon (Antunes and Sigogneau-Russell, 1991) and Paronychodon (Currie et al., 1990; Zinke and Rauhut, 1994; Baszio, 1997; Larson, 2008; Sankey, 2008). In the ziphodont teeth of troodontids, a prominent median ridge appears to be present on the lingual surface of some maxillary crowns in Xixiasaurus (Lü et al., 2010, figure 3A1) and is visible on the labial surface of the some maxillary teeth in Byronosaurus (Makovicky et al., 2003; Figure 6.3). Faint longitudinal ridges delimiting shallow and narrow grooves were reported by Choiniere et al.
(2014b) on the largest crowns of the lateral dentition in the basal alvarezsauroid Haplocheirus, yet we could not observe this feature.

**Remarks and synapomorphy.** The presence of one or several ridges extending diagonally or parallel to the crown margins on the labial and/or lingual surface of the crown is a possible synapomorphy of Paravians. Among tyrannosaurs, a median longitudinal ridge on the lingual surface of mesial teeth is a synapomorphy of a clade encompassing Timurlengia and more derived tyrannosauroids (Brusatte et al., 2016; Appendix 6.25 for mesial teeth). This feature seems to be absent in more basal tyrannosauroids such as Aviatyrannus, Eotyrannus, Guanlong and Proceratosaurus, with the exception of Dilong which is here considered as autapomorphic. The longitudinal ridges in dromaeosaurids seem to be a genuine diagnostic feature (Evans et al., 2013) that could be apomorphic for some dromaeosaurid clades.

**Functional morphology.** Prominent ridges delimiting deep grooves dorsal to the plicidentine are present on the crown of the possibly venomous Varanus (Megaalania) priscus (Fry et al., 2009, figure 3), which also possesses a ziphodont dentition. These ridges are similar to those observed in Bambiraptor, Buitreraptor and Velociraptor which delimit the labial depression on the crown. These structures may have helped venom to enter in the prey flesh. Other authors proposed that the labial and lingual depressions in the lateral dentition of Sinornithosaurus were related to venom delivery (Gong et al., 2010, 2011). The dentition of the possibly venomous Varanus priscus is, to our knowledge, the closest analogue to the dromaeosaurid condition in terms of tooth type (i.e., ziphodont), denticle morphology and crown ornamentation (i.e., longitudinal ridges/grooves). Based solely on the fact that Varanus and some dromaeosaurids show some morphological convergence (and not on other anatomical features proposed by Gong et al. (2010, 2011) such as a ‘subfenestral fossa’ housing an ascinar venom gland), it is plausible that some theropods may have been venomous animals. For a different opinion, see Gianechini et al. (2011a).

The grooved teeth present in Unenlagiinae may indicate fish-eating behavior, since these dromaeosaurids lived in proximity to fluvial systems (Gianechini et al., 2011b). However, the teeth of piscivorous tetrapods such as crocodiles, marine reptiles, pterosaurs and spinosaurids are fluted and do not possess wide longitudinal grooves bounded by one or two poorly delimited ridges. Based on the tooth morphology, a piscivorous lifestyle of dromaeosaurid theropods, although evidenced in Microraptor (Xing et al., 2013b), is therefore poorly supported in Unenlagiinae.

**Longitudinal grooves**

The presence of longitudinal grooves on the crown, which differ from lingual/labial depressions, flutes and concave surfaces, is poorly documented in theropods and may suggest the scarcity of this feature among these dinosaurs. A longitudinal groove on the mesiolingual surface of the crown has been noted in the lateral tooth of an abelisaurid (Hendrickx and Mateus, 2014a). Several authors have noted a groove in the vicinity of the mesial carina on the lingual surface of the mesial teeth. This is, for instance, the case in the paravians Linhevenator (Xu et al., 2011a), Sinornithosaurus (Xu and Wu, 2001) and Urbacodon (Averianov and Sues, 2007). Yet, they better correspond to a mesiodistally narrow and well-delimited concave surface and are here reported in the section on J-shaped cross-section. A similar groove can be observed in some mesial teeth of the metriacanthosaurid Sinraptor (IVPP V10600) and the allosaurid Allosaurus (UMNH VP 1251). Longitudinal grooves have also been observed on the crowns of Byronosaurus (Makovicky et al., 2003), as well as Austroraptor and Buitreraptor by Gianechini et al. (2011b), yet they result from the longitudinal ridges delimiting them, and we only consider the presence of ridges in Austroraptor, Buitreraptor, and Byronosaurus. An indeterminate tyrannosaurid from the Cenomanian of Utah also presents the particularity of having a longitudinal groove centrally positioned on the lingual side of a single mesial isolated crown (Zanno et al., 2019). Like these authors, who regard this dental feature as autapomorphic, we did not observe such groove in the mesial dentition of any other theropods. Finally, faint longitudinal grooves are present on the apex of a crown of Mononykus.

**Basal striations**

Basal striations, forming short parallel grooves extending apicobasally on the crown base, have been reported in herrerassaurids (Hendrickx and Mateus, 2014a) and the basal tyrannosaurid Proceratosaurus (Rauhut et al., 2010; Appendix 6.27). In the herrerassaurids Herrerassaurus (PVSJ 407; mx10) and Ischisaurus (MACN 18.060; pm1), which may represent the same taxon (Novas, 1992), these striations are numerous, closely packed, and restricted to some teeth. Although
they likely result from taphonomic or anthropogenic factors in *Herrerasaurus* (they appear as scratches extending randomly apicobasally on the crown base and could correspond to striations from a layer of glue), basal striations appear to be genuinely present in the first premaxillary tooth of *Ischisaurus* where they, however, seem to be restricted to the root. These closely packed basal striations resemble and might be homologous to the plicidentine. A thorough investigation on the histology of teeth presenting such basal striations is, however, required to support this hypothesis.

Unlike herrerasaurids, basal striations form wide longitudinal depressions on the labial and/or lingual surfaces of most mesial teeth in *Proceratosaurus* (Rauhut et al., 2010). These basal striations do most likely not result from taphonomic processes given that they are restricted to the mesial dentition (pm1 to 3, dt1 and 3) and are present on undeformed teeth with well-preserved denticles and enamel surface texture (C.H. personal obs.). Apicobasally oriented striations at the base of the crown have also been noted in Spinosauridae by Mateus et al. (2011) but these basal striations could not be observed in any spinosaurid examined first hand.

**Irregular and smooth enamel texture**

With the exception of Spinosauridae, the crown enamel texture is rarely detailed in the theropod literature and we, therefore, rely on our own observations to explore this feature’s distribution among non-avian theropods. An irregular non-oriented or smooth texture of the enamel (Figure 23) is present in most non-tetanuran saurischians, including *Eoraptor* (PVSJ 512), *Herrerasaurus* (PVSJ 407; Figure 23.1), *Ischisaurus* (MACN 18.060), *Saltrovenator* (Dal Sasso et al., 2018), *Sinosaurus* (IVPP V34) and most abelisauroids [e.g., *Limusaurus*; Wang et al.’s (2017a) data matrix] like *Abelisaurus*, *Aucasaurus* (Figure 23.2), *Chenanisaurus* (Longrich et al., 2017), *Kryptops*, *Majungasaurus* and *Noasaurus* (C.H. personal obs.). An irregular or smooth texture has also been observed in most non-dromaeosaurid neocoelurosaur such as *Compsoognathus* (MNHN CNJ 79), *Scipionyx* (SBA-SA 163760), *Nqwebasaurus* (AM 6040), *Pelecanimimus* (LHC 7777), *Alcasaurus* (IVPP V88860), *Beipiaosaurus* (IVPP V11559), *Etliksaurus* (MPC-D 100-111), *Shuvuuia* (MPC-D 100-977), *Caudipteryx* (IVPP V12430), *Almas* (MPC-D 100-1323), an unnamed basal troodontid (MPC-D 100-1128), *Byronosaurus* (MPC-D 100-983), *Troodon* (DMNH 22337; 22837), *Epidexipteryx* (IVPP V15471) and *Archaeopteryx* (11th specimen). In dromaeosaurids, this type of enamel texture has also been seen in *Buitreraptor* (MPCA 245), *Velociraptor* (AMNH 6515), *Tsaagan* (MPC-D 100-1015) and in the lateral dentition of *Dromaeosaurus* (AMNH 5356). Among non-neocoelurosaur tetanurans, an irregular texture of the enamel was observed in *Erectopus* (MNHN 2001-4), *Sinraptor dongi* (IVPP 10600) and *S. hepingensis* (ZDM T0024) as well as *Irritator* (SMNS 58022). Based on our observation, the latter does not appear to display the deeply veined texture of other spinosaurids (we could not identify the granular texture observed by Sues et al. (2002) in any maxillary tooth of *Irritator*). An irregular texture is also present in the crowns of some *Tyrannosauridae* such as *Tyrannosaurus* (FMNH PR.2081; Figure 23.4) and *Zhuchengtyrannus* (ZCDM V0031). This pattern of enamel texture has also been identified in some *Allosaurus* teeth (NHFO 455; Figure 23.3), the other crowns displaying a more oriented texture. In fact, *Allosaurus* appears to show a transitional condition between metriacanthosaurids with

**FIGURE 23.** Irregular enamel texture of non-avian Theropoda. 1. Tenth left maxillary tooth of the herrerasaurid *Herrerasaurus ischigualastensis* (PVSJ 407) in labial view; 2. Isolated tooth of the abelisaurid *Aucasaurus garridoi* (MCF-PVPH-236) in lateral view; 3. Second premaxillary tooth of the allosaurid *Allosaurus jimmadseni* (NHFO 455) in labial view; 4. Tenth maxillary tooth of the tyrannosaurid *Tyrannosaurus rex* (FMNH PR.2081) in labial view.
a non-oriented irregular enamel texture and the Allosauria (i.e., Allosauridae + Neovenatoridae + Carcharodontosauridae) with an oriented texture of the enamel. The presence of a smooth or irregular enamel surface texture is considered to be synapomorphic for Abelisauroidea, Metriacanthosauridae, and Neocoeleurosauria (Appendix 6.28).

**Braided enamel texture**

A braided texture of the enamel, defined by alternating and interweaving grooves and sinuous ridges apicobasally oriented on the crown and never converging (Hendrickx et al., 2015c; Figure 24), is present in non-neocoeleurosaur Neotheropoda, and can be observed in basal tetanurans such as *Monolophosaurus* (IVPP V84019), non-spinosaurid Megalosauroidae (e.g., *Afrovenator*, *Dubreuillosaurus*, *Eustreptospondylus*, *Megalosaurus*, *Piatnitzkysaurus*, *Torvosaurus*), Allosauria (e.g., *Acrocanthosaurus*, *Allosaurus*, *Carcharodontosaurus*, *Eocarcharia*, *Giganotosaurus*, *Mapusaurus*, *Megalosaurus*, *Piatnitzkysaurus*, *Teratosaurus*; Figure 24.2), Tyrannosauroidea (e.g., *Albertosaurus*, *Allosaurus*, *Ceratosaurus*, *Genyodectes*, *Lythronax*, *Proceratosaurus*, *Raptorex*, *Teratophoneus*, *Tyrannosaurus*; Figure 24.3) the basal coelurosaurs *Bicentenaria* (MPCA 866), *Juravenator* (JME Sch 200), *Ornitholestes* (AMNH 619) and *Zuolong* (IVPP V15709), and the basal alvarezsauroid *Aorun* (IVPP V15709). Such texture is also present in the basal saurischian *Eodromaeus* (PVSJ 561), the basal theropod *Dracovenator* (BP/1/5243), the non-averostran neotheropods *Coelophysis* (CMNH 81765), *Dracoraptor* (Martill et al., 2016, figure 9A-B), and *Megapnosaurus rhodesiensis* (USNM unnumbered), and non-abelisaurid ceratosaurs (e.g., *Berberosaurus*, *Ceratosaurus*, *Genyodectes*; Figure 24.1). An oriented texture has also been identified in the basal neotheropod *Dilophosaurus* sinensis (the ‘longitudinal striations in the enamel’ of Xing 2012), the therizinosaur *Segnosaurus* (MPC-D 100-80), the dromaeosaurs *Atrociraptor* (TMP 1995.166.01), *Bambiraptor* (AMNH 30556), *Deinonychus* (YPM 5232 612), and *Saurornitholestes* (TMP 1994.12.844), and some mesial teeth of *Dromaeosaurus* (AMNH 5356; Figure 24.4) and *Masiakasaurus* (FMNH PR.2182, 2471). It is unknown whether a braided enamel texture is the ancestral condition in theropods, but the presence of such oriented pattern of the enamel is here considered synapomorphic for the clade Microraptorinae + Eudromaeosauria (Appendix 6.28).

**Veined and anastomosed enamel texture**

**Veined enamel texture.** A veined texture of the enamel is made of deep alternating grooves and long sinuous and/or dichotomized ridges obliquely or apicobasally oriented and converging basomesially or basodistally on the crown (Hendrickx et al., 2015d). It can be seen in the baryonychines *Baryonyx walkeri* (NHMUK PV R.9951; ML 1190; Figure 25.1) and *Suchomimus tenerensis* (SMNS 58022) is smooth or displays an irregular pattern (Figure 21.3).

**Anastomosed enamel texture.** An anastomosed enamel surface texture, which consists of multiple ridges dividing and reconnecting in an irregular way, is present in *Spinosaurus aegyptiacus* (USNM unnumbered), and the basal alvarezsauroid *Aorun* (IVPP V15709). Such texture is also present in the basal saurischian *Eodromaeus* (PVSJ 561), the basal theropod *Dracovenator* (BP/1/5243), the non-averostran neotheropods *Coelophysis* (CMNH 81765), *Dracoraptor* (Martill et al., 2016, figure 9A-B), and *Megapnosaurus rhodesiensis* (USNM unnumbered), and non-abelisaurid ceratosaurs (e.g., *Berberosaurus*, *Ceratosaurus*, *Genyodectes*; Figure 24.1). An oriented texture has also been identified in the basal neotheropod *Dilophosaurus* sinensis (the ‘longitudinal striations in the enamel’ of Xing 2012), the therizinosaur *Segnosaurus* (MPC-D 100-80), the dromaeosaurs *Atrociraptor* (TMP 1995.166.01), *Bambiraptor* (AMNH 30556), *Deinonychus* (YPM 5232 612), and *Saurornitholestes* (TMP 1994.12.844), and some mesial teeth of *Dromaeosaurus* (AMNH 5356; Figure 24.4) and *Masiakasaurus* (FMNH PR.2182, 2471). It is unknown whether a braided enamel texture is the ancestral condition in theropods, but the presence of such oriented pattern of the enamel is here considered synapomorphic for the clade Microraptorinae + Eudromaeosauria (Appendix 6.28).
raptorosaur *Incisivosaurus gauthieri* (IVPP 13326). Such a pattern of the enamel texture has only been observed in these taxa and may correspond to an autapomorphy of *Spinosaurus* and *Incisivosaurus*. In spinosaurids, veined and anastomosed enamel textures are characterized by their strong basal curvature adjacent to the carinae (Hasegawa et al., 2010; Mateus et al., 2011), a feature that is not present in other theropods with a braided enamel texture of the crown (C.H. personal obs.).

**Functional morphology and synapomorphy.** We hypothesize that a veined and anastomosed texture of the enamel was developed in crowns subjected to particularly high mechanical stresses during feeding, a hypothesis which requires to be properly tested with tools like FEA. Spinosaursids are known to be at least partially piscivorous (e.g., Taquet, 1984; Charig and Milner, 1997; Ibrahim et al., 2014; Sales and Schultz, 2017), hunting on fish with hard scales like those of the actinopterygian *Scheenstia*, whose remains were found in the stomach region of *Baryonyx* (Charig and Milner, 1997). The coarse, complex and multiridged enamel may have conveyed particularly high resistance to the crowns, which were capable to resist high apicobasal stresses when piercing the scaly skins of fish. The same can be said for the putative herbivorous *Incisivosaurus*, whose premaxillary teeth show a strong similarity with the incisors of several mammalian lineages such as rodents (Xu et al., 2002a). Some rodents are known to use their elongated incisors for gnawing (Ungar, 2010) and if the dentition of *Incisivosaurus* does not support such a feeding strategy (i.e., the anteriormost dentary portion is edentulous and the lateral dentition includes minute and labiolingually compressed folidont teeth unadapted for chewing), this basal oviraptorosaur likely used its premaxillary teeth to cut through particularly hard plant material. The presence of a deeply veined and/or anastomosed enamel surface texture is synapomorphic for *Spinosauridae* (Appendix 6.28).

**Procumbent, laterocumbent and retrocumbent teeth**

**Procumbency in the premaxilla.** Procumbent teeth (i.e., anterior inclination of the teeth; opposite of decumbent teeth, i.e., teeth with no inclination) are visible in the premaxilla of the basal sau-rischian *Daemonosaurus* (Sues et al., 2011), the basal coelurosaur *Ornitholestes* (Figure 26.1), the basal oviraptorosaur *Similicaudipteryx* (Li et al., 2018, figure S3f), the scansoriopterygids *Epidexipteryx* (Zhang et al., 2008; Figure 26.2) and *Yi* (Xu et al., 2015b), in some specimens of the basal avian *Archaeopteryx* (Rauhut et al., 2018), and to a lesser degree in the basal theropod *Dracovenator* (Yates, 2005). Based on the inclination of the alveoli, procumbent premaxillary teeth were also likely present in the noasaurid *Masiakasaurus* (Carrano et al., 2011) and the basal tetanuran *Chilesaurus* (SNGM-1935). Although the premaxillary teeth of the oviraptorosaur *Caudipteryx* were thought to be procumbent by Ji et al. (1998), the first right premaxillary tooth preserved in-situ in IVPP V12430 points ventrally, suggesting that the premaxillary teeth of *Caudipteryx* were decumbent.

**Procumbency in the maxilla.** Anteroventrally inclined teeth are present in the mesial maxillary teeth of many non-averostran neotheropods such as *Coelophysis* (Colbert, 1989), *Dilophosaurus* (Welles, 1984; Figure 26.4), *Syntarsus* 'kayentakatae' (Rowe, 1989), and *Zupaysaurus* (Ezcurra, 2007), the basal neotheropod *Dilophosaurus* 'sinensis' (ZLJT 0057), all *Spinosauridae* (Charig and Milner, 1997; Taquet and Russell, 1998; Sereno et al., 1998; Dal Sasso et al., 2005) that possess a
sigmoid alveolar margin of the upper jaw (Figure 26.3), and in the basal neocoeolurosaur *Ornitholestes hermanni* (AMNH 619; reversed) in lateral view; 2, Procumbent premaxillary and dentary teeth of the right rostrum of the scansoriopterygid *Epidexipteryx hui* (IVPP V15471; reversed) in lateral view; 3, Hypothetical procumbent mesial maxillary teeth of the left maxilla of the spinosaurid *Baryonyx walkeri* (NHMUK PV R.9951) in lateral view; 4, Hypothetical procumbent mesial maxillary teeth of the right maxilla of the non-averostran neotheropod *Dilophosaurus wetherilli* (UCMP 37303; reversed) in lateral view; 5, Procumbent mesial dentary teeth of the left dentary of the noasaurid *Masiakasaurus knopfleri* (FMNH PR 2471) in lateral view; 6, Procumbent mesial dentary teeth of the right dentary of the proceratosaurid *Proceratosaurus bradleyi* (NHMUK PV R.4860; reversed) in lateral view. Scale bars equal 1 cm (1–2, 5), 2 cm (6), and 5 cm (3, 4).

**FIGURE 26.** Procumbent teeth in non-avian Theropoda. 1, Procumbent premaxillary teeth of the right rostrum of the basal neocoeolurosaur *Ornitholestes hermanni* (AMNH 619; reversed) in lateral view; 2, Procumbent premaxillary and dentary teeth of the right rostrum of the scansoriopterygid *Epidexipteryx hui* (IVPP V15471; reversed) in lateral view; 3, Hypothetical procumbent mesial maxillary teeth of the left maxilla of the spinosaurid *Baryonyx walkeri* (NHMUK PV R.9951) in lateral view; 4, Hypothetical procumbent mesial maxillary teeth of the right maxilla of the non-averostran neotheropod *Dilophosaurus wetherilli* (UCMP 37303; reversed) in lateral view; 5, Procumbent mesial dentary teeth of the left dentary of the noasaurid *Masiakasaurus knopfleri* (FMNH PR 2471) in lateral view; 6, Procumbent mesial dentary teeth of the right dentary of the proceratosaurid *Proceratosaurus bradleyi* (NHMUK PV R.4860; reversed) in lateral view. Scale bars equal 1 cm (1–2, 5), 2 cm (6), and 5 cm (3, 4).

sigmoid alveolar margin of the upper jaw (Figure 26.3), and in the basal coelurosaur *Ornitholestes* (AMNH 619). Procumbency has also been noted in the first maxillary tooth of the compsognathid *Scipionyx* (Dal Sasso and Maganuco, 2011) and the noasaurid *Masiakasaurus* (Carrano et al., 2002, 2011). An anteroventrally inclined lateral dentition has been observed in the maxilla of the basal tetanuran *Chilesaurus* (Novas et al., 2015, figure 2a), the basal ornithomimosaur *Nqwebasaurus* (Choiniere et al., 2012), the basal oviraptorosaur *Similicaudipteryx* (Li et al., 2018, figure S3f), the scansoriopterygid *Epidexipteryx* (Zhang et al., 2008) and some specimens of *Archaeopteryx* (Rauhut et al., 2018). *Chilesaurus* and *Nqwebasaurus*’ procumbency may, however, result from diagenetic factors (Choiniere et al., 2012). Procumbent mesial maxillary teeth is a synapomorphy for Spinosauridae (Appendix 6.30)

**Procumbency in the dentary.** Strongly procumbent teeth are seen in the anteriormost part of the dentary of the basal saurischian *Daemonosaurus* (Sues et al., 2011), the coelophysoids *Coelophysis* (NMMNH p42200; DMNS 39022; CM 81765),
Megapnosaurus (Raath, 1977), the basal neotheropod Liliensternus (MB R.2175), the noasaurid Masiakasaurus (Carrano et al., 2002; Figure 26.5), the spinosaurid Spinosaurus (NHMUK VP R.16421), adult individuals of the dromaeosaurid Utahraptor (UMNH VP 20501; Kirkland et al., 2016, figure 9B) and the troodontid Daliansaurus (Shen et al., 2017a, figures 3 and 4A). Among Tyrannosauroidea, the proceratosaurid Proceratosaurus (Rauhut et al., 2010; Figure 26.6) and a single specimen of the basal pantyrranosaurian Dilong (IVPP V11979) also show this condition. Procumbent mesial dentary teeth are present, yet to a lesser degree (i.e., teeth less labiobasally inclined), in the basal saurischian Herrerasaurus (Sereno and Novas, 1994), the megalosaurid Duriavenator (Benson, 2008) and the tyrannosaurids Alberlosaurus, Daspletosaurus, Tarbosaurus and Tyrananosaurus (Bakker et al., 1988; Carr and Williamson, 2004). Slightly procumbent mesialmost dentary teeth have also been observed in the basal maniraptoriform Ornitholestes (AMNH 619), the alvarezsaurid Haplocheirus (Choiniere et al., 2010b), the basal oviraptorosaur Incisivosaurus (Balanoff et al., 2009), and the dromaeosaurids Sinornithosaurus (Xu and Wu, 2001), possibly Sauornitholestes (TMP 88.121.39), and some Microraptor specimens (BMNH PH881; Xing et al., 2013b). In the basal tetanuran Chilesaurus (Novas et al., 2015), the ornithomimosaur Shenzhouaurus (Ji et al., 2003), the basal oviraptorosaur Similicaudipteryx (Li et al., 2018, figure S3f), and the scansoriopterygids Epidexipteryx (Zhang et al., 2008; Figure 26.2) and Yi (Xu et al., 2015b), the whole dentition of the dentary is slightly to strongly procumbent. If the mandibular procumbency in Similicaudipteryx and Epidexipteryx clearly results from the downturned symphyseal region of the dentary, that seen in Chilesaurus might possibly be due to diagenetic factors.

Laterocumbency. Theropod teeth can also be strongly inclined laterally/labially within the tooth-bearing bones (C.H. personal obs.), a condition here referred to as laterocumbent (Figure 27). Laterocumbent premaxillary and maxillary teeth seem to be synapomorphic for the Spinosaurinae as this condition is seen in Angaturama (USP GP/2T-5), Irritator (SMNS 58022) and Spinosaurus (MSNM V4047; Figure 27.1). The teeth of other spinosaurid taxa such as the baryonychine Baryonyx are decumbent or procumbent. A laterocumbent dentition is also present in some rhamphorhynchid (e.g., Rhamphorhynchus; Bonde and Leal, 2015), ornithocheirian (e.g., Ornithocheirus; Rodrigues and Kellner, 2013, figures 4-6, 11-14) and ctenochasmatid pterosaurs (e.g., Ctenochasma; Jouve, 2004) as well as in many plesiosaurs such as cryptoclidids (e.g., Cryptoclidus; Brown and Cruickshank, 1994, figure 5) and plesiosaurids (e.g., Morturneria, Aristonectes; O’Keefe et al., 2017).

Retrocumbency. Some theropods have posteriorly/distally inclined crowns along the jaws, a condition here referred to as retrocumbent. The apex of fully erupted retrocumbent teeth is strongly distally offset from the distal margin of the crownbase. Retrocumbent premaxillary teeth are present in juvenile individuals of Limusaurus (Wang et al., 2017a, figure 2A and B) as well as Eoraptor (PVSJ 512), Juravenator (Chiappe and Göhlich, 2010, figure 10A) and several basalmost neotheropods such as Dilophosaurus (Welles, 1984, figure 4), Dracovenator (BP/1/5278), ‘Syrantsus’ kayentakatae (Tykoski, 1998, figure 6) and some Coelophysis specimens (e.g., NMMNH p42200) due to the

**FIGURE 27.** Laterocumbent and retrocumbent teeth in non-avian Theropoda. 1, Laterocumbent teeth (teeth facing ventrolabially) in the maxillae of the spinosaurid Spinosaurus aegyptiacus (MSNM V4047) in palatal view; 2, retrocumbent teeth (distally inclined teeth) in the cranium of the dromaeosaurid Deinonychus antirrhopus (YPM 5232) in labial view. Scale bars equal 10 cm (1) and 2 cm (2).
slight posteroventral inclination of the premaxilla. Retrocumbent maxillary teeth have been observed in the coelophysoid Panguraptor (You et al., 2014, figure 2), the megalosaurid Sciurumimus (Rauhut et al., 2012), the dromaeosaurids Atrociraptor, Bambiraptor, and Deinonychus (Figure 27.2), and an undescribed dromaeosaurine (UC uncatalogued) from the Ulansuhai Formation of Inner Mongolia (Watanabe and Sereno, 2010). The retrocumbent premaxillary and maxillary teeth seen in one specimen of Sinovenator (IVPP V12615; Xu et al. 2002b, figure 1a) are here interpreted as resulting from diagenetic factors given that the cranial dentition is clearly decumbent in the undescribed specimen of Sinovenator IVPP V12632.

**Functional morphology.** Procumbent mesial teeth are common in piscivorous animals including crocodiles, fish, and pterosaurs (Xing et al.,
A forward-projecting mesial tooth arrangement seems to be adapted for the prehension of small prey such as invertebrates and small vertebrates such as fish (Carrano et al., 2002). In coelophysoids and spinosaurids, procumbent maxillary teeth result from the sigmoid ventral margin of the maxilla and are suitable for gripping small to moderate-sized prey transversally through slashing bites (Charig and Milner, 1997; Therrien et al., 2005). The sigmoid margin of the upper jaw, present in many crocodylomorphs, would also have enhanced the ability for holding prey and/or tearing (Charig and Milner, 1997; Therrien et al., 2005). The sigmoid margin of the upper jaw, present in many crocodylomorphs, would also have enhanced the ability for holding prey and/or tearing their flesh (Russell and Wu, 1997). Bakker and colleagues (1988) suggested that the mesialmost procumbent dentary teeth of tyrannosaurids allowed to bite a chunk of bone and flesh off a prey's body part that was gently curved such as the rib-cage and abdominal wall when the head was moving forward. In ornithomimosaurs with mesially inclined teeth like *Nqwebasaurus* and *Shenzhousaurus*, in which a herbivorous diet has been inferred (Makovicky et al., 2004; Zanno and Makovicky, 2011; Choiniere et al., 2012), procumbency is most likely adapted for the prehension of vegetation, perhaps for branch raking/stripping as suggested for other saurischians like *Diploodon* (e.g., Barrett and Upchurch, 1994; Upchurch and Barrett, 2000). The procumbency seen in the lateral dentition of ornithomimosaurs and other maniraptoriforms may also result from a trophic shift from carnivory to herbivory (Zanno and Makovicky, 2011; Choiniere et al., 2012). Laterocumbent and retrocumbent teeth conversely enable to firmly hold and keep small struggling and/or slippery prey such as lizards and fish, or to keep a firm and immobile bite when teeth are deeply inserted into the flesh of a larger prey item.

**Partial and complete edentulism**

**Premaxilla.** Among toothed theropods, partially edentulous premaxillae combined with toothed maxillae and dentaries is an autapomorphic condition of juvenile individuals of the noasaurid *Limusaurus* (Wang et al., 2017a, figure 2A and B), in which a single premaxillary tooth erupts in the posterior part of the premaxilla. Fully edentulous premaxillae with dentulous maxillae and dentaries are shared by Therizinosaurs such as *Erlikosaurus* (Clark et al., 1994; Lautenschlager et al., 2014; Figure 28.2) and *Jianchangosaurus* (Pu et al., 2013). Toothed premaxillae with edentulous maxillae and dentaries characterize the basal oviraptorosaur *Caudipteryx* (Ji et al., 1998; Zhou et al., 2000; Figure 28.5) whose teeth are restricted to the anterior portion of the premaxilla. Although premaxillary teeth were revealed to be present in an *Avimimus* specimen (Watabe et al., 2000), the premaxilla is edentulous in all specimens of this taxon (Funston et al., 2016; Tsuihiji et al., 2017; Funston personal comm. 2019). An edentulous premaxilla is synapomorphic for Ornithomimosauria more derived than *Pelecanimimus*, Therizinosauroidae and Caenagnostothoeida (Appendix 6.32).

**Maxilla.** An edentulous anterior portion of the maxilla is present in the therizinosaurs *Erlikosaurus* (Lautenschlager et al., 2014) and in ontogenetic stage II of *Limusaurus* (Wang et al., 2017a, figure 2B). An edentulous posterior portion of the maxilla (i.e., tooth row extending only on the anterior 75%, or anterior portion of the maxilla) can be seen in ontogenetic stage II of *Limusaurus* (Wang et al., 2017a, figure 2B), and the basal ornithomimosaur *Ngwebasaurus* (Choiniere et al., 2012) and *Pelecanimimus* (Pérez-Moreno et al., 1994). Such condition is also seen in the alvarezsaurid *Shuvuuia* (Chiappe et al., 1998), the therizinosaur *Erlikosaurus* (MPC-D 100-111), the oviraptorosaur *Similicaudipteryx* (Li et al., 2018, figure S3f), many jinfengopterygine and troodontine troodontids such as MPC-D 100-1128, IVPP V20378, *Almas*, *Byronosaurus*, *Gobivenator*, *Saurornithoides* and *Zanabazar* (Pei et al., 2017b), and the scansoriopterygids *Epidexipteryx* (IVPP V15471) and *Yi* (Xu et al., 2015b). A toothless posterior portion of the maxilla is a synapomorphy of Ornithomimosauria, whereas an edentulous maxilla is synapomorphic for Ornithomimosauria more derived than *Pelecanimimus*, and the oviraptorosaur clade gathering *Caudipteryx* and *Caenagnostothoeida* (Appendix 6.33).

**Dentary.** Edentulous premaxillae and maxillae, combined with toothed dentaries, are present in the basal ornithomimosaur *Harpymimus* (Kobayashi and Barsbold, 2005, *Hexing* (Jin et al., 2012) and *Shenzhousaurus* (Ji et al., 2003; Figure 28.3). The absence of teeth in the anteriormost part of a dentulous dentary has been recorded in *Eoraptor* (Sereno et al., 2013), therizinosauroids (*Beipiaosaurus*, *Erlikosaurus*, *Neimongosaurus*, *Segnosaurus*; Zanno et al., 2016; Liao and Xu, 2019; Figure 28.2), basal oviraptorosaurs (*Incisivosaurus*, *Protarchaeopteryx*, *Similicaudipteryx*; Zanno and Makovicky, 2011) and juvenile individuals of *Limusaurus* (Wang et al., 2017a, figure 2A and B). An edentulous anteriormost portion of the dentary was also noted in Alvarezsauridae by Longrich et al. (2009). Although possible, the source used by these authors (i.e., Suzuki et al., 2002) does not seem to provide this information, and the
missing anterior extremity of the dentary of *Shu-
vuua* (Dufaeu, 2003), the only alvarezsaurid pre-
serving in situ teeth in the anterior portion of the
mandible, does not allow to confirm this statement
either. The posterior portion of the dentary is
devoid of teeth (i.e., more than 25% of the poste-
rior portion of the dentary is toothless) in onto-
getic stage II of *Limusaurus* (Wang et al., 2017a,
figure 2B), the basal ornithomimosaurs *Harpymi-
numus* (Kobayashi and Barsbold, 2005), *Hexing*
(Jin et al., 2012) and *Shenzhousaurus* (Ji et al., 2003;
Figure 28.3), the oviraptorosaur *Similicaudipteryx*
(Li et al., 2018, figure S3f), and possibly all scanso-
riopterygids (e.g., IVPP V15471; STM 31-2; Zhang
et al., 2002, figure 1b). An edentulous posterior
portion of the dentary is synapomorphic for Ornit-
homimosauria more derived than *Pelecanimimus*,
whereas a toothless anterior most portion of the
dentary is a synapomorphy of Oviraptorosauria
and Therizinosauroidae (Appendix 6.33). The ovi-
raptorosaur clade gathering *Caudipteryx* and Caen-
nagnathoidea share the apomorphic feature of
having an edentulous dentary (Appendix 6.34).

**Complete edentulism.** Toothless non-avian ther-
ropods are restricted to three clades, namely: Cerat-
osauria with the noasaurid *Limusaurus* (Xu et al.,
2009; Figure 28.1), Ornithomimosauria with all
ornithomimidoids (Kobayashi and Barsbold, 2005;
Makovicky et al., 2010; Lee et al., 2014b; Figure
28.4), and Oviraptorosauria with all caenagna-
thoids (*Avimimus* + Caenagnathidae + Oviraptor-
dae, sensu Qiu et al., 2019; Figure 28.6). In *Limus-
aurus*, however, teeth are borne by hatching
and juvenile individuals and disappear throughout
ontogeny (Wang et al., 2017a). Palatal teeth have
been retained by the basal sauropodomorphs
*Eoraptor* (Sereno et al., 2013) and *Bariolestes*
(Müller et al., 2018) as well as the putative non-
neotheropod theropod *Eodromaeus* (Martínez et
al., 2011; Baron et al., 2017; Müller et al., 2018,
fourth phylogenetic analysis). Theropods more
derived than *Eodromaeus*, therefore, have an
dentulous pterygoid. If *Eodromaeus* is, however,
a non-theropod saurischian, as recently recovered
by Langer et al. (2017) and Müller et al. (2018,
first and fifth phylogenetic analyses), a toothless ptery-
goid is synapomorphic to theropods. As for the rest
of the jaw, a fully edentulous skull is synapomor-
phic for Ornithomimoidea and Caenagnathoidea.

**Functional morphology.** Tooth loss and edentul-
ism in theropods have been recently investigated
by Zhou and Li (2009), Davit-Béal et al. (2009),
Louchart and Viriot (2011), Zanno and Makovicky
(2011), Lautenschlager et al. (2013), Meredith et
al. (2014), Bhullar et al. (2016), Wang et al.
(2017b), Erickson et al. (2017) and Yang and
Sander (2018). The classical reasons for the origin
of edentulism are related to developmental eco-
my and for food acquisition. Davit-Béal et al.
(2009) pointed out that in tetrapods the loss of
teeth (or enamel) was preceded by the progressive
replacement of an anatomical identity that allowed
food uptake and oral processing (e.g., beak,
baleen, ever-growing teeth, known as hyspel-
odonty. Such anatomical entities are called by the
authors as secondary tools). Positive selection of
these secondary tools led to relaxed functional
constraints on the teeth evolution. However, vari-
ous other hypotheses have been proposed. Namely,
Zhou and Li (2009) while describing the
basal bird toothless *Zhongjianomis yangi* related
its edentulism to the selective pressure for weight
reduction. However, this hypothesis seems to lack
much support as not only teeth represent a minor
proportion of head weight, but also many other
dentulous clades are characterized by large body
masses (e.g., ornithomimosauria, turtles and
whales).

According to Lautenschlager et al. (2013) who
focused on Therizinosauria, large-scale dietary
changes were a trigger to specializations we see in
the masticatory apparatus of raptorial and theropods including tooth loss as in birds, their
descendants. Through FEA of biomechanical mod-
els of *Erlikosaurus*, the authors have concluded
that a keratinous rhamphotheca was capable of
dissipating stresses and strains generated by mus-
cle action during jaw adduction. Along these lines,
Zanno and Makovicky (2011) causally related par-
tial to complete edentulism to herbivory. However,
they argue that efficient oral processing is a nega-
tive selective factor for edentulism (Wings and
Sander, 2007; Zanno and Makovicky, 2011), as
various other herbivorous dinosaur clades actually
developed dental batteries. In order to understand
if edentulism aroused convergently in two or more
modern bird lineages, Meredith et al. (2014) ana-
lyzed for the presence of inactivating mutations on
six dentine- and enamel-forming genes in multiple
bird clades and a crocodilian outgroup. All enamel-
and dentine-forming genes were, in fact, deacti-
vated in all bird lineages but present in the croco-
dilian outgroup, pointing towards a single deactivation of these genes in the common ances-
tor to all birds.

In another study, Wang et al. (2017a) studied
nearly 20 specimens of the unorthodox ceratosau-
rian species *Limusaurus inextricabilis* concerning
its developmental morphological patterns. The juvenile *Limusaurus* possesses fully toothed jaws, but the teeth are completely lost in adults. This rare example of radical ontogenetic edentulism happens through an unusual mechanism, compared to Cretaceous ornithurine birds and other theropods. The teeth are lost on the anterior and posterior portions of the jaws coupled with tooth loss by the absence of replacement teeth eruption. The authors hypothesize that the early cessation of tooth replacement in *Limusaurus* may have resulted from the regression of successional lamina. Wang et al. (2017a) also point out to heterochronic mechanisms for the retardation and eventual truncation of tooth development, as exemplified by *Limusaurus*. In a follow-up paper, Wang et al. (2017b) provide evidence for the hypothesis of vestigialization of alveoli as part of a process towards edentulism. Caenagnathid oviraptorosaurs and the Cretaceous bird genus *Sapeornis* show a system of vestiges that connects via foramina with a dorsally closed canal homologous to alveoli, which exemplifies an evolutionary stage more advanced than that in *Limusaurus*. The authors further substantiate the hypothesis that heterochrony plays a crucial role in the progressively earlier postnatal and embryonic truncation of odontogenesis. Eventually, the absence of teeth leads to the development of a secondary tool: a keratinous beak.

More recently, Erickson et al. (2017) developed a new approach to determine incubation periods in fossil non-avian dinosaurs by counting the number of growth lines in fossil embryonic teeth of two ornithischian dinosaurs: *Hypacrosaurus* and *Protoceratops*. The estimated incubation periods of these ornithischians were close to those of reptiles (i.e., long incubation periods), contrasted with those of birds, which last for only 11-85d. It is noteworthy that this approach could be tested on other dinosaurs closer to the bird lineage (e.g., *Torvosaurus*; Araújo et al., 2013). Yang and Sander (2018) suggested that the incubation period is a selection factor for edentulism or, in other words, the selection for tooth loss was a side effect of the selection for fast embryo growth and thus shorter incubation. This hypothesis, however, lacks the support of experimental evidence.

**CONCLUSIONS**

By investigating the distribution of dental features in non-avian theropods, this study reveals that isolated theropod teeth can be better diagnosed at ‘family’ and ‘sub-family’ level clades than genus-level taxa based on qualitative data. The dentition of theropod dinosaurs is highly homoplasmatic: there is a morphological convergence among distantly related clades that have adopted similar dietary preferences. Nonetheless, dental characters often provide useful grouping information, and the isolated crowns of a few taxa such as *Majungasaurus*, *Piatnitzkysaurus* and *Acrocanthosaurus* provide sufficiently distinct morphologies to be used as high-precision biostratigraphic markers.

Crown ornamentations and enamel surface texture and microstructure are the least homoplasmatic dental features possibly because they are less prone to evolve than other dental features under similar evolutionary pressures. A mesial dentition bearing a longitudinal ridge, a mesial carina spiraling or reaching the cervix, an unserrated distal carina and the cross-sectional outline in mesial teeth as well as fluted lateral teeth, lateral crown height and a basal constriction at the cervix in the lateral dentition are the dental characters that provide the most important grouping information. On the other hand, procumbent teeth, the mesial and distal denticle morphology, a labially deflected distal carina, a significant difference in size between mesial and distal denticles, interdenticular sulci and transverse and marginal undulations provide particularly little grouping information. Yet, a combination of these dental features can certainly refine the identification of isolated teeth up to the genus level for some taxa.

Major evolutionary transitions in the dentition of theropod dinosaurs occurred with the emergence of Spinosauridae, Allosauroidea, Tyrannosauroidea and Maniraptoriformes. These dental transitions are functionally linked to an anteroposterior shortening of the premaxillae in allosauroids and tyrannosaurs, and to a switch in dietary preferences towards piscivory and herbivory in spinosaurids and maniraptoriforms, respectively. Although dental characters have high levels of homoplasy, for some large datasets they are no more or less reliable, on average, than other character systems. This argues for their continued inclusion into phylogenetic datasets for theropod dinosaurs. Moreover, the functional implications of tooth features allow for the more nuanced study of their homoplasy in a comparative biology framework.

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APPENDICES

The appendix files are available as PDFs at this url: https://palaeo-electronica.org/content/2019/2806-dental-features-in-theropods.

APPENDIX 1.

List of the 200 non-avian saurischian taxa included in this study and silhouette acknowledgments.

APPENDIX 2.

Dentition-based character list.

APPENDIX 3.

Phylogenetic character dataset.

APPENDIX 4.

CI and RI values.

APPENDIX 5.

Distribution of all 145 apomorphic dental characters.

APPENDIX 6.

Distribution of the 34 dental character

APPENDIX 7.

Prior use and scorings of dental characters in the most recent phylogenetic analyses.

APPENDIX 8.

Zipped file containing spreadsheets are available at this url: https://palaeo-electronica.org/content/2019/2806-dental-features-in-theropods.

T-tests and Mann-Whitney U-tests using ci and ri values for each dental character. (ci_ri_dental_characters.xlsx)

Ci and ri values for each dental character. (ci_ri_dental_characters_past3.xlsx)

Dentition-based datamatrix and dentition-based datamatrix combined with datasets on the whole skeleton. (teeth_characters_mesquite.xlsx)