Zootaxa 3759 (1): 001–074
www.mapress.com/zootaxa/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3759.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:E9F2EADE-3745-468B-9344-1ECCA4C2EA22

ZOOTAXA

3759

Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth

CHRISTOPHE HENDRICKX[1,2] & OCTÁVIO MATEUS[1,2]
[1]*Universidade Nova de Lisboa, CICEGe, Departamento de Ciências da Terra, Faculdade de Ciências e Tecnologia, Quinta da Torre 2829-516 Caparica, Portugal. E-mail: christophe.hendrickx@hotmail.com*
[2]*Museu da Lourinhã, Rua João Luis de Moura 9 2530-158 Lourinhã, Portugal*

Magnolia Press
Auckland, New Zealand

Accepted by R. Benson: 27 Nov. 2013; published: 30 Jan. 2014

CHRISTOPHE HENDRICKX & OCTÁVIO MATEUS
Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth
(*Zootaxa* 3759)

74 pp.; 30 cm.

30 Jan. 2014

ISBN 978-1-77557-326-5 (paperback)

ISBN 978-1-77557-327-2 (Online edition)

FIRST PUBLISHED IN 2014 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: zootaxa@mapress.com

http://www.mapress.com/zootaxa/

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of contents

Abstract

Theropod dinosaurs form a highly diversified clade, and their teeth are some of the most common components of the Mesozoic dinosaur fossil record. This is the case in the Lourinhã Formation (Late Jurassic, Kimmeridgian-Tithonian) of Portugal, where theropod teeth are particularly abundant and diverse. Four isolated theropod teeth are here described and identified based on morphometric and anatomical data. They are included in a cladistic analysis performed on a data matrix of 141 dentition-based characters coded in 60 taxa, as well as a supermatrix combining our dataset with six recent datamatrices based on the whole theropod skeleton. The consensus tree resulting from the dentition-based data matrix reveals that theropod teeth provide reliable data for identification at approximately family level. Therefore, phylogenetic methods will help identifying theropod teeth with more confidence in the future. Although dental characters do not reliably indicate relationships among higher clades of theropods, they demonstrate interesting patterns of homoplasy suggesting dietary convergence in (1) alvarezsauroids, therizinosaurs and troodontids; (2) coelophysoids and spinosaurids; (3) compsognathids and dromaeosaurids; and (4) ceratosaurids, allosauroids and megalosaurids.

Based on morphometric and cladistic analyses, the biggest tooth from Lourinhã is referred to a mesial crown of the megalosaurid *Torvosaurus tanneri*, due to the elliptical cross section of the crown base, the large size and elongation of the crown, medially positioned mesial and distal carinae, and the coarse denticles. The smallest tooth is identified as *Richardoestesia*, and as a close relative of *R. gilmorei* based on the weak constriction between crown and root, the "eight-shaped" outline of the base crown and, on the distal carina, the average of ten symmetrically rounded denticles per mm, as well as a subequal number of denticles basally and at mid-crown. Finally, the two medium-sized teeth belong to the same taxon and exhibit pronounced interdenticular sulci between distal denticles, hooked distal denticles for one of them, an irregular enamel texture, and a straight distal margin, a combination of features only observed in abelisaurids. They provide the first record of Abelisauridae in the Jurassic of Laurasia and one of the oldest records of this clade in the world, suggesting a possible radiation of Abelisauridae in Europe well before the Upper Cretaceous.

Key words: Abelisauridae, Megalosauridae, *Torvosaurus*, *Richardoestesia*, teeth, cladistic, Theropoda, Portugal, Late Jurassic

Introduction

The Upper Jurassic of Portugal has yielded an important fauna of dinosaurs, one of the richest of Europe. Dinosaur bones and teeth have been collected for more than 140 years, mainly from two important paleontological sites both situated in the centre of Portugal (Rauhut 2000; Antunes & Mateus 2003). The first, Guimarota Mine, is constituted by several layers of limestone, sandstone, mudstone, marl and coal belonging to the Alcobaça Formation (Kimmeridgian; Helmdach 1971; Henkel & Krusat 1980; Schudack 2000; Kullberg *et al.* 2012). Exploration in the 1960s, and new excavations from 1972 to 1982, unearthed ornithischian and saurischian dinosaurs, mostly represented by isolated teeth (Zinke 1998; Rauhut 2000, 2001). The second, the Lourinhã region, is the richest area for dinosaur fossils in Portugal (Antunes & Mateus 2003). Bones, teeth, tracks, eggs and embryos of dinosaurs have been uncovered in several localities of the Lourinhã Formation Kimmeridgian-Tithonian in age (Antunes & Mateus 2003, Kullberg *et al.* 2012).

Most major clades of dinosaurs (ornithopods, thyreophorans, sauropodomorphs and theropods) are represented in the Upper Jurassic of Portugal, but theropods are the most diversified group of dinosaurs represented (Rauhut 2000; Mateus 2006). Material from the Guimarota Mine and the Lourinhã region has been referred to at least seven theropod taxa, including *Ceratosaurus dentisulcatus* (Mateus & Antunes 2000a; Mateus *et al.* 2006), *Torvosaurus tanneri* (Mateus & Antunes 2000b; Mateus *et al.* 2006; Malafaia *et al.* 2008), *Allosaurus europaeus* (Mateus *et al.* 2006), *Allosaurus fragilis* (Pérez-Moreno *et al.* 1999; Malafaia *et al.* 2007), *Lourinhanosaurus autunesi* (Mateus 1998), *Aviatyrannis jurassica* (Rauhut 2003), cf. *Compsognathus* sp. (Zinke 1998) and cf. *Archaeopteryx* sp. (Weigert 1995; Wiechmann & Gloy 2000). Also present are theropods belonging to Dromaeosauridae, Troodontidae and of uncertain affinities (cf. *Richardoestesia* sp. and cf. *Paronychodon* sp.; Zinke & Rauhut 1994; Zinke 1998; Mateus 2005). Moreover, theropod embryos and hatchlings, ascribed to *Lourinhanosaurus* (de Ricqlès *et al.* 2001; Mateus *et al.* 1998; Hendrickx & Mateus 2012), *Allosaurus* (Rauhut & Fechner 2005) and *Torvosaurus* (Araújo et al. 2013), were also collected in Portugal, and a diverse ichnological record is known (Mateus & Milàn 2010).

Theropod teeth are very common in the Lourinhã Formation, and some of them have been reported in the literature already. In the 1950s, several theropod teeth found at Porto das Barcas (Lourinhã Formation) near Lourinhã were briefly described by Lapparent & Zbyszewski (1957). The material was collected by Carlos Ribeiro during a geologic cross section on June 20, 1863, and those teeth seem to be the historically earliest dinosaur discovery in Portugal (Antunes & Mateus 2003). Identified by Lapparent & Zbyszewski (1957) as belonging to the species *Megalosaurus insignis* and the new taxon *Megalosaurus pombali*, these two taxa are however currently considered as invalid (Antunes & Mateus 2003; Holtz *et al.* 2004; Carrano *et al.* 2012). Later, Antunes (1990) mentioned the presence of a tooth fragment also attributed to the genus *Megalosaurus*. However, the first thorough study of theropod teeth from the Lourinhã area was made by Rauhut & Kriwet (1994), who described two large theropod teeth also found in Porto das Barcas, which they attributed cautiously to an indeterminate "carnosaur". Finally, Mateus (2005) and Mateus *et al.* (2006) mentioned and briefly described several theropod teeth from the Lourinhã Formation, recognizing the presence of *Ceratosaurus dentisulcatus* and the clades of Carcharodontosauridae and Troodontidae in this unit.

Although theropod teeth are rather simple structures, far less informative than mammal teeth (Longrich 2008; Han *et al.* 2011) or many other parts of the skeleton such as the quadrate (Hendrickx *et al.* 2012), a number of workers have successfully used theropod tooth morphology for taxonomic purposes (e.g., Currie *et al.* 1990; Fiorillo & Currie 1994; Rauhut & Werner 1995; Baszio 1997; Zinke 1998; Fiorillo & Gangloff 2001; Rauhut 2002; Sankey *et al.* 2002; Fanti & Therrien 2007; Larson 2008; Longrich 2008; Brinkman 2008; Sankey 2008; Soto & Perea 2008; Buckley *et al.* 2010; Larson *et al.* 2010; Ősi *et al.* 2010; Han *et al.* 2011; Larson & Currie 2013). Tooth measurements were first utilized by Currie *et al.* (1990) and Farlow *et al.* (1991) for systematic identification of theropod teeth, and later authors followed or modified this method to document isolated theropod teeth (e.g., Fiorillo & Currie 1994; Baszio 1997; Holtz *et al.* 1998; Sankey 2001; Sankey *et al.* 2002; Bakker & Bir 2004; Samman *et al.* 2005; Sankey 2008; Larson 2008; Han *et al.* 2011; Larson & Currie 2013; Torices *et al.* in press). Smith (2005) and Smith *et al.* (2005) were the first to successfully discriminate theropod teeth to the genus level based on a quantitative methodology and discriminant analyses. Such methodology was later followed by Smith & Vechia (2006), Smith & Lamanna (2006), Van der Lubbe *et al.* (2009), Torres-Rodríguez *et al.* (2010) and Ősi *et al.* (2010) to identify isolated teeth of theropods, and used in a slightly different way by Fanti & Therrien (2007), Larson (2008) and Larson & Currie (2013). The taxonomic utility of theropod teeth evaluated with cladistics tools has recently been investigated by Hwang (2007) who mostly focused on the enamel microstructure. Hwang (2007) performed a first cladistic analysis by using eight dental and 31 enamel characters coded in 52 dinosaur taxa, including 25 theropods, and combined their enamel based characters with the dataset of Makovicky *et al.* (2005). A same method was used by Cillari (2010) who performed a cladistic analysis using 19 dentition-based characters coded in 13 theropod taxa and 14 morphotypes of theropod teeth.

The present work aims to evaluate the systematic potential of theropod teeth and investigate the systematic palaeontology of four isolated theropod teeth chosen in the collection of the Museu of Lourinhã based on their completeness, particular shape and interesting features displayed (e.g., interdenticular sulci, transversal and marginal undulations, mesio-distal constriction of the crown). The systematic value of theropod teeth was assessed by following the methodology of Hwang (2007), i.e., performing a cladistic analysis on a data matrix including dentition-based characters only, and the taxonomic identification of the four teeth from Portugal was investigated by using the morphometric methodology of Smith *et al.* (2005). Our study is intended as a case study for identification of isolated theropod teeth, which previous studies have often failed to identify with any certainty (e.g., Maganuco *et al.* 2005; Ősi *et al.* 2010; Han *et al.* 2011; Torices *et al.* in press).

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; **AODF**, Australian Age of Dinosaurs Fossil, Winton, Queensland, Australia; **BYUVP**, Brigham Young University Vertebrate Paleontology, Provo, Utah, USA; **CM**, Carnegie Museum, Pittsburgh, Pennsylvania, USA; **DMNH**, Denver Museum of Natural History, Denver, Colorado, USA; **FMNH PR**, Field Museum of Natural History, Chicago, Illinois, USA; **FPDM**, Fukui Prefectural Dinosaur Museum, Katsuyama, Fukui, Japan; **HIII**, Henan Geological Museum, Zhengzhou, Henan Province, China; IGM, Institute of Geology, Ulaan Baatar, Mongolia; **LH PV**, Long Hao Institute of Geology and Paleontology, Hohhot, Nei Mongol, China; **MACN-CH**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MCF-PVPH**, Museo Municipal Carmen Funes, Paleontologia de Vertebrados, Plaza Huincul, Argentina; **MG GUI**, Museu Geológico (Guimarota collection), Lisbon, Portugal; **MIWG**, Dinosaur Isle, Isle of Wight Museum Services, Sandown, United Kingdom; **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; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **MNN**, Musée National du Niger, Niamey, Niger; **MPCA**, Museo Provincial Carlos Ameghino, Cipolletti, Río Negro, Argentina; **MSNM**, Museo di Storia Naturale di Milano, Milan, Italy; **MUCPv**, Museo de Ciencias Naturales de la Universidad Nacional de Comahue, Lago Barreales, Argentina; **MUCPv-CH**, Museo de Ciencias Naturales de la Universidad Nacional de Comahue, El Chocón collection, Villa El Chocón, Argentina; **MWC**, Museum of Western Colorado, Fruita (or Grand Junction), Colorado, USA; **NCSM**, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA; **NHM**, The Natural History Museum, London, United Kingdom; **NMC**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **OUMNH**, Oxford University Museum, Oxford, UK; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **SBA-SA**, Soprintendenza per i Beni Archeologici di Salerno Avellino Benevento e Caserta, Salerno, Italy; **SMA**, Sauriermuseum Aathal, Aathal, Switzerland; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **SMU**, Southern Methodist, University, Dallas, Texas, USA; **UA**, Université d'Antananarivo, Antananarivo, Madagascar; **UC**, University of Chicago Paleontological Collection, Chicago, USA; **UCMP**, University of California Museum of Paleontology, Berkeley, California, USA; **UCPC**, University of Chicago Paleontological Collection, Chicago, USA; **UMNH VP**, Utah Museum of Natural History, University of Utah, Salt Lake City, Utah, USA; **USNM VP**, United State National Museum Vertebrate Paleontology, Washington, District of Columbia, USA; **USNM**, United State National Museum Vertebrate Paleontology, Washington, District of Columbia, USA; **SGM**, Ministère de l'Énergie et des Mines, Rabat, Morocco.

Locality, geological and stratigraphical setting

The four teeth all come from the Lourinhã Formation near the town of Lourinhã. The Lourinhã Formation is 600 to 1100 meters thick and mostly appears along the cliffs bounding the Atlantic Ocean, 70 km North of Lisbon. The formation is delimited at its base by the Amaral Formation of Kimmeridgian age, comprising shallow marine sandstones and oolites, as well as a shallow marine carbonate shelf forming the contact with the Lourinhã

Formation. The Cretaceous continental clastic Torres Vedras Formation (or Group) lies unconformably above the Lourinhã Formation.

The Lourinhã Formation consists of continental deposits intercalated with some shallow marine deposits, corresponding to an alluvial fan and fluvio-deltaic environments punctuated by periodic marine transgressions (Kullberg *et al.* 2012; Hill 1988, 1989). Theropod teeth can be found in both Porto Novo and Santa Rita members of the Lourinhã Formation. For more information regarding the sedimentology on those two members, see Hill (1988, 1989).

Several authors (e.g., Manuppella 1996, 1998; Manuppella *et al.* 1999) have considered the Alcobaça Formation as being similar to the Lourinhã Formation. However, the latter is dated Upper Kimmeridgian-Tithonian in age and is therefore slightly younger and also more continental than the Alcobaça Formation (Mateus 2006). Nevertheless, both the Lourinhã and Alcobaça Formation of Portugal are comparable with the Morrison Formation of North America and the Tendaguru Beds in Tanzania as the three regions are Kimmeridgian-Tithonian in age and show similar ecosystems, all dominated by dinosaurs (Mateus 2006).

Methodology

Morphometrics. The description of teeth follows the dental nomenclature proposed by Smith & Dodson (2003). Both descriptive morphological characters and quantitative morphometric techniques were used to analyse and identify the four theropod teeth. Observations were made with a binocular microscope Leica MZ6 as well as a digital microscope AM411T-Dino-Lite Pro. Photographs were taken with a digital camera for the biggest teeth and the digital microscope for the smaller tooth.

The quantitative methodology was based on numerical data developed by Smith (2005) and Smith *et al.* (2005), and updated by Smith & Lamanna (2006), Smith & Dalla Vecchia (2006) and Smith (2007). Additional morphometric data of theropod teeth were collected from Canudo *et al.* (2006), Soto & Perea (2008), Sereno & Brusatte (2008), Molnar *et al.* (2009), Van der Lubbe *et al.* (2009), Torres-Rodríguez *et al.* (2010), Ősi *et al.* (2010) and Gianechini *et al.* (2011b). Morphometric measurements were also taken on many theropod teeth belonging to the palaeontological collections of 24 museums from Argentina, Europe and the United States. The data file is available at DRYAD (http://doi.org/10.5061/dryad.33tb2). Anatomical and morphometric abbreviations follow Smith *et al.* (2005).

Measurements and ratios proposed by Smith *et al.* (2005) were taken with a digital calliper and the following measurements were done: **AL**, apical length (in mm); **CBL**, crown base length, measured at the base of the crown from its mesialmost to its distalmost extension (excluding the carinae; in mm); **CBR**, crown base ratio, numerical value derived from dividing CBW through CBL (= labiolingual compression); **CBW**, crown base width, labiolingual extension of the crown at its base (in mm); **CH**, crown height, measured from the basodistal most point of the crown toward its tip (in mm); **CHR**, crown height ratio, numerical value derived from dividing CH through CBL; **DAVG**, average distal denticle density on 5 mm; **DA**, denticle density for distal apical serration, i.e., denticles per 5 mm at the most apical part of the distal carina; **DB**, denticle density for distal basal serration, i.e., denticles per 5 mm at the most basal part of the distal carina; **DC**, denticle density for distal mid-crown serration, i.e., denticles per 5 mm at the mid-crown part of the distal carina; **DSDI**, denticle size difference index, ratio between the number of denticles per 5 mm of the mesial and distal carinae, at mid-crown; **MA**, denticle density for mesial apical serration, i.e., denticles per 5 mm at the most apical part of the mesial carina; **MB**, denticle density for mesial basal serration, i.e., denticles per 5 mm at the most basal part of the mesial carina; **MC**, denticle density for mesial mid-crown serration, i.e., denticles per 5 mm at the mid-crown part of the mesial carina; **MAVG**, average mesial denticle density on 5 mm.

Cladistic analysis. A character-taxon data matrix of dentition-based characters (Appendix) was created and scored in 60 nonavian theropod taxa (Table 1) in order to evaluate the taxonomic potential of theropod dentitions and assess the phylogenetic relationship of the four teeth from the Lourinhã Formation. Teeth pertaining to most clades of nonavian theropods were examined and coded from first-hand observations (54 taxa, 90% of the dataset), high-resolution photographs (*Dilophosaurus* and *Scipionyx*), and by using full descriptions and illustrations of the teeth in the literature for six taxa (*Fukuiraptor*, *Australovenator*, *Jianchangosaurus*, *Erlikosaurus* and *Zanabazar*; Table 1). *Eoraptor lunensis*, considered to be a basal saurischian (Langer & Benton 2007), a basal theropod

(Nesbitt *et al.* 2009; Nesbitt 2011; Sues *et al.* 2011) or a basal sauropodomorph (Martinez *et al.* 2011; Sereno *et al.* 2013), was specified as the outgroup.

The data matrix encompasses 141 equally weighted morphological characters based on the morphology of the crown, root, mesial and distal carinae, denticles, interdenticular sulci ('blood grooves' *sensu* Currie *et al.* 1990, and 'caudae' *sensu* Abler 1992), crown ornamentations (i.e., transversal and marginal undulations, flutes, longitudinal grooves and ridges, etc.), and enamel texture and microstructure (see Appendix, Fig. A1-5 for illustrations of dentition-based characters). Characters related to the shape, size and number of teeth/alveoli of the premaxilla, maxilla and dentary were also included in the data matrix (Appendix). Seventy-four characters are derived from the literature, and 67 characters (47.5%) were revealed by descriptive work on the teeth and our personal observations. Due to the important variation of morphology between lateral and mesialmost dentition (i.e., the mesialmost dentition comprises the premaxillary teeth as well as mesialmost dentary teeth and, in some cases, maxillary teeth that share a morphology similar to those of premaxillary teeth), the dataset was divided into mesialmost and lateral teeth (Appendix). Among the 141 morphological characters, 81 are multistate characters, ten are continuous (characters related to CH, CHR, CBR, MC and DC for both mesialmost and lateral teeth) and three are meristic and concern the number of premaxillary, maxillary and dentary teeth. All 13 continuous and meristic characters were transformed into discrete characters of no more than five character states by assigning a specific range or value (Appendix), and ten multistate characters (characters 2, 4, 15, 17, 24, 25, 36, 53, 65 and 86) were ordered.

The systematic potential of theropod teeth was first evaluated by performing a cladistic analysis on the data matrix of dentition-based characters without the isolated teeth from the Lourinhã Formation. In order to constrain all major theropod clades and visualize the dentition-based synapomorphies for each theropod clade, a second analysis was performed on a supermatrix combining our dentition-based data matrix with six recent datasets on non-avian theropods based on the whole skeleton (Xu *et al.* 2009; Brusatte *et al.* 2010; Martinez *et al.* 2011; Senter 2011; Pol & Rauhut 2012; Carrano *et al.* 2012), and from which all teeth-related characters were removed. The resulting supermatrix includes 1972 characters with 65 treated as ordered (the data file is available at DRYAD: http://doi.org/10.5061/dryad.33tb2). The four isolated teeth from the Lourinhã Formation were then incorporated in the matrix and supermatrix in order to assess their phylogenetic relationship.

TNT v1.1 (Goloboff *et al.* 2008) was employed to search for most-parsimonious trees (MPTs). The matrix and supermatrix were analysed under the 'New Technology Search' with the 'driven search' option (TreeDrift, Tree Fusing, Ratchet, and Sectorial Searches selected with default parameters), and stabilizing the consensus twice with a factor of 75. The consistency and retention indices as well as the Bremer supports (Bremer 1994) were calculated using the "stats" and "aquickie" commands, respectively, and a bootstrap analysis was performed with the standard options.

Results

Cladistic analysis

The analysis of the data matrix of dentition-based characters including 60 theropod taxa yielded 10 most parsimonious trees (MPTs), in which the strict consensus trees (length = 681 steps; CI = 0.338, RI = 0.56) resulted in a few polytomies affecting clades of no more than three taxa (Appendix, Fig. A6–7). A similar topology was found when the four isolated teeth were incorporated (Fig. 1), and the cladistic analysis yielded 7 MPTs (length = 703 steps; CI = 0.331, RI = 0.564). Although the strict consensus trees did not recover the general topology of theropod classification with the usual major clades (e.g., Neotheropoda, Tetanurae, Avetheropoda, Coelurosauria), many theropod clades such as Ceratosauridae, Abelisauridae, Spinosauridae, Megalosauridae, Tyrannosauroidea and Therizinosauria were resolved, demonstrating some systematic potential of theropod teeth at approximately family level. As noted by Hwang (2007), dentition-based characters can be good at recovering individual clades, but not at resolving the relationship between those clades. This is obviously due to the large amount of convergence in theropod dentition, directly linked to diet, among a clade displaying the most variation of feeding strategies among dinosaurs (Rayfield 2005; Therrien *et al.* 2005; Zanno & Makovicky 2011).

TABLE 1. Teeth and tooth bearing bones of nonavian theropod specimens examined and included in this study.

Taxon - author	Specimens	Examined	Other photo credits	Literature used
Eoraptor lunensis Sereno *et al.* 1993	PVSJ 512	Y	Martín Ezcurra	Sereno *et al.* 1993; Martínez *et al.* 2011
Herrerasaurus ischigualastensis Reig 1963	PVSJ 053, 407, 605; MACN-CH 18.060	Y	Martín Ezcurra	Sereno and Novas 1994
Eodromaeus murphi Martínez *et al.* 2011	PVSJ 560, 561	Y		Martínez *et al.* 2011
Coelophysis bauri Cope 1887	CM 81765, 82931; AMNH 7223, 7224, 7227, 7228, 7229, 7231	Y		Rowe 1989; Buckley 2009
Dilophosaurus wetherilli Welles 1970	UCMP 37302, 37303, 77270	N	Martín Ezcurra; Steve Brusatte	Welles 1984
Ceratosaurus nasicornis Marsh 1884	USNM 4735; UMNH VP 5278 (= UUVP 155, 158, 674); MWC 1;	Y	Matthew Carrano; Roger Benson	Gilmore 1920; Madsen and Welles 2000; Bakker and Bir 2004
Genyodectes serus Woodward 1901	MLP 26-39	Y		Rauhut 2004
Berberosaurus liassicus Allain *et al.* 2007	MNHN Pt339	Y		
Noasaurus leali Bonaparte and Powell 1980	PVL 4061	Y		Bonaparte and Powell 1980; Candeiro 2007
Masiakasaurus knopfleri Sampson *et al.* 2001	FMNH PR 2182, 2183, 2201, 2221, 2453, 2471, 2476, 2696; UA 8680, 9091, 9128	Y	Matthew Carrano	Carrano *et al.* 2002; Carrano *et al.* 2011
Kryptops palaios Sereno and Brusatte 2008	MNN GAD1−1	Y		Sereno and Brusatte 2008
Rugops primus Sereno *et al.* 2004	MNN IGU1	Y		Sereno *et al.* 2004
Abelisaurus comahuensis Bonaparte and Novas 1985	MPCA 1, 5, 229, 267, 687, 689, 709	Y		Bonaparte and Novas 1985; Candeiro 2007
Aucasaurus garridoi Coria *et al.* 2002	MCF-PVPH 236	Y	Matthew Lamanna	Candeiro 2007
Indosuchus raptorius von Huene and Matley 1933	AMNH 1753, 1955, 1960	Y		Sampson *et al.* 1996
Skorpiovenator bustingorryi Canale *et al.* 2009	MMCN-PV 48	Y	Matthew Lamanna	Candeiro 2007; Canale *et al.* 2009
Majungasaurus crenatissimus Lavocat 1955	MNHN MAJ1; FMNH PR 114 2008, 2100, 2278; UA 8716	Y		Fanti and Therrien 2007; Smith 2007
Piatnitzkysaurus floresi Bonaparte 1979	PVL 4073; MACN-CH 895	Y	Matthew Carrano; Martín Ezcurra	Bonaparte 1986
Eustreptospondylus oxoniensis Walker 1964	OUMNH J.13558	Y		Sadleir *et al.* 2008
Dubreuillosaurus valesdunensis Allain 2002	MNHN 1998-13	Y		Allain 2002

......continued on the next page

TABLE 1. (Continued)

Taxon - author	Specimens	Examined	Other photo credits	Literature used
Afrovenator abakensis Sereno *et al.* 1996	UC UBA1	Y		Sereno *et al.* 1996
Duriavenator hesperis Waldman 1974	NHM R.332	Y		Benson 2008
Megalosaurus bucklandii Mantell 1827	OUMNH J.13505, J.13506; NHM R.8303, R.8305	Y		Benson *et al.* 2008; Benson 2009; Benson 2010
Torvosaurus tanneri Galton and Jensen 1979	BYUVP 2003, 4882, 9122 12817; ML 1100	Y	Matthew Carrano	Jensen 1985; Britt 1991; Bakker and Bir 2004
Baryonyx walkeri Charig and Milner 1986	NHM R.9951; ML 1190	Y		Charig and Milner 1997; Mateus *et al.* 2011
Suchomimus tenerensis Sereno *et al.* 1998	MNN GDF501, GDF502, G2-2, G5-1, G6, G22-7, G26-5, G34-1, G34-7, G34-12, G35-9, G43-5, G54-4, G67-1, G67-8, G69-5, G73-3, G74-1, G100-4, G232	Y	Roger Benson	Sereno *et al.* 1998
Irritator challengeri Martill *et al.* 1996/*Angaturama limai* Kellner and Campos 1996	SMNS 58022; AMNH 30230 (cast)	Y	Ricardo Araújo	Kellner 1996; Kellner and Campos 1996; Sues *et al.* 2002
Spinosaurus aegyptiacus Stromer 1915	MSNM V3976, V4047, V6422, V6424, V6865, V6896; NHM R.16420, R.16421	Y	Andrea Cau	Stromer 1915; Milner 2003; Dal Sasso *et al.* 2005; Hasegawa 2010
Sinraptor sp. Currie and Zhao 1993	IVPP 10600; ZDM T0024	N	Philip Currie	Currie and Zhao, 1993
Erectopus superbus Sauvage 1882	MNHN 2001-4	Y		Allain 2005
Allosaurus fragilis Marsh 1877	AMNH 600, 851; BYUVP 2028; MWC 5440; USNM 8335; UMNH VP 5427 10.093, 40.585; CM 1254, 11844, 21703; SMA 0005/02	Y	Steve Brusatte	Osborn 1912; Gilmore 1920; Madsen 1976; Chure 2000; Bakker and Bir 2004; Loewen 2009
Neovenator salerii Hutt *et al.* 1996	MIWG 6348; NHM R.10001	Y	Steve Brusatte; Roger Benson	Brusatte *et al.* 2008
Australovenator wintonensis Hocknull *et al.* 2009	AODF 604	N		Hocknull *et al.* 2009
Fukuiraptor kitadaniensis Azuma and Currie 2000	FPDM 9712203, 9712204 (+ many others)	N		Azuma and Currie 2000; Currie and Azuma, 2006; Molnar *et al.* 2009
Acrocanthosaurus atokensis Stovall and Langston 1950	NCSM 14345; SMU 74646	Y	Drew Eddy; Vince Shneider; Ricardo Araújo	Harris 1998; Currie and Carpenter 2000; Eddy and Clark 2011
Eocarcharia dinops Sereno and Brusatte 2008	MNN GAD7, GAD13, GAD14	Y	Juan Canale	Sereno and Brusatte 2008
Carcharodontosaurus saharicus Depéret and Savornin 1925	MNN GAD8, IGU5; SGM Din-1; UC PV6	Y		Stromer 1931; Sereno *et al.* 1996; Brusatte and Sereno 2007
Mapusaurus roseae Coria and Currie 2006	MCF-PVPH 108	Y	Matthew Lamanna	Coria and Currie 2006; Candeiro 2007

......continued on the next page

TABLE 1. (Continued)

Taxon - author	Specimens	Examined	Other photo credits	Literature used
Giganotosaurus carolinii Coria and Salgado 1995	MUCPv-CH-1; MUCPv 95	Y	Matthew Lamanna	Coria and Salgado 1995; Calvo and Coria 1998; Candeiro 2007
Proceratosaurus bradleyi von Huene 1926	NHM R 4860	Y		Rauhut *et al.* 2009
Eotyrannus lengi Hutt *et al.* 2001	MIWG 1997.550	Y		Hutt *et al.* 2001
Raptorex kriegsteini Sereno *et al.* 2009	LH PV18	Y		Sereno *et al.* 2009
Alioramus altai Brusatte *et al.* 2009a	IGM 100/ 1844	Y	Steve Brusatte	Brusatte *et al.* 2009a; Brusatte *et al.* 2012
Tyrannosaurus rex Osborn 1905	CM 9380; AMNH 5027; FMNH PR2081; NHM R.7994	Y	Mickey Mortimer	Osborn 1912; Molnar 1991; Brochu 2003; Smith 2005
Compsognathus longipes Wagner 1861	MNHN CNJ 79	Y	Karine Peyer	Stromer 1934; Ostrom 1978; Peyer 2006
Scipionyx samnicicus Dal Sasso and Signore 1998	SBA-SA 163760	N	Cristiano Dal Sasso	Dal Sasso and Maganuco 2011
Ornitholestes hermanni Osborn 1903	AMNH FARB 619	Y		Osborn 1903
Shuvuuia deserti Chiappe *et al.* 1998	IGM 100/977	Y		Chiappe *et al.* 1998
Jianchangosaurus yixianensis Pu *et al.* 2013	41HIII-0308A	N		Pu *et al.* 2013
Erlikosaurus andrewsi Perle, 1981	IGM 100/111	N		Clark *et al.* 1994
Buitreraptor gonzalezorum Makovicky *et al.* 2005	MPCA 245	Y		Makovicky *et al.* 2005; Gianechini *et al.* 2010
Velociraptor mongoliensis Osborn 1924	AMNH 6515	Y		Osborn 1924; Sues 1977; Barsbold and Osmolska 1999
Bambiraptor feinbergi Burnham *et al.* 2000	AMNH 001	Y		Burnham 2004
Dromaeosaurus albertensis Mathew and Brown 1922	AMNH 5356	Y		Colbert and Russel 1969; Currie *et al.* 1990; Currie 1995; Baszio 1997
Saurornitholestes langstoni Sues 1978	DMNH 22870	Y		Sues 1978; Currie *et al.* 1990; Baszio 1997
Tsaagan mangas Norell *et al.* 2006	IGM 100-1015	Y		Norell *et al.* 2006
Byronosaurus jaffei Norell *et al.* 2000	IGM 100/983	Y		Norell *et al.* 2000; Makovicky *et al.* 2003
Zanabazar junior Barsbold 1974	IGM 100/1	N		Norell *et al.* 2009
Troodon formosus Leidy 1856	DMNH 22337, 22837	Y		Currie 1987; Currie *et al.* 1990; Baszio 1997; Longrich 2008
Richardoestesia gilmorei Currie *et al.* 1990	NMC 343	N		Currie *et al.* 1990; Baszio 1997; Sankey *et al.* 2002; Longrich 2008; Larson and Currie 2013

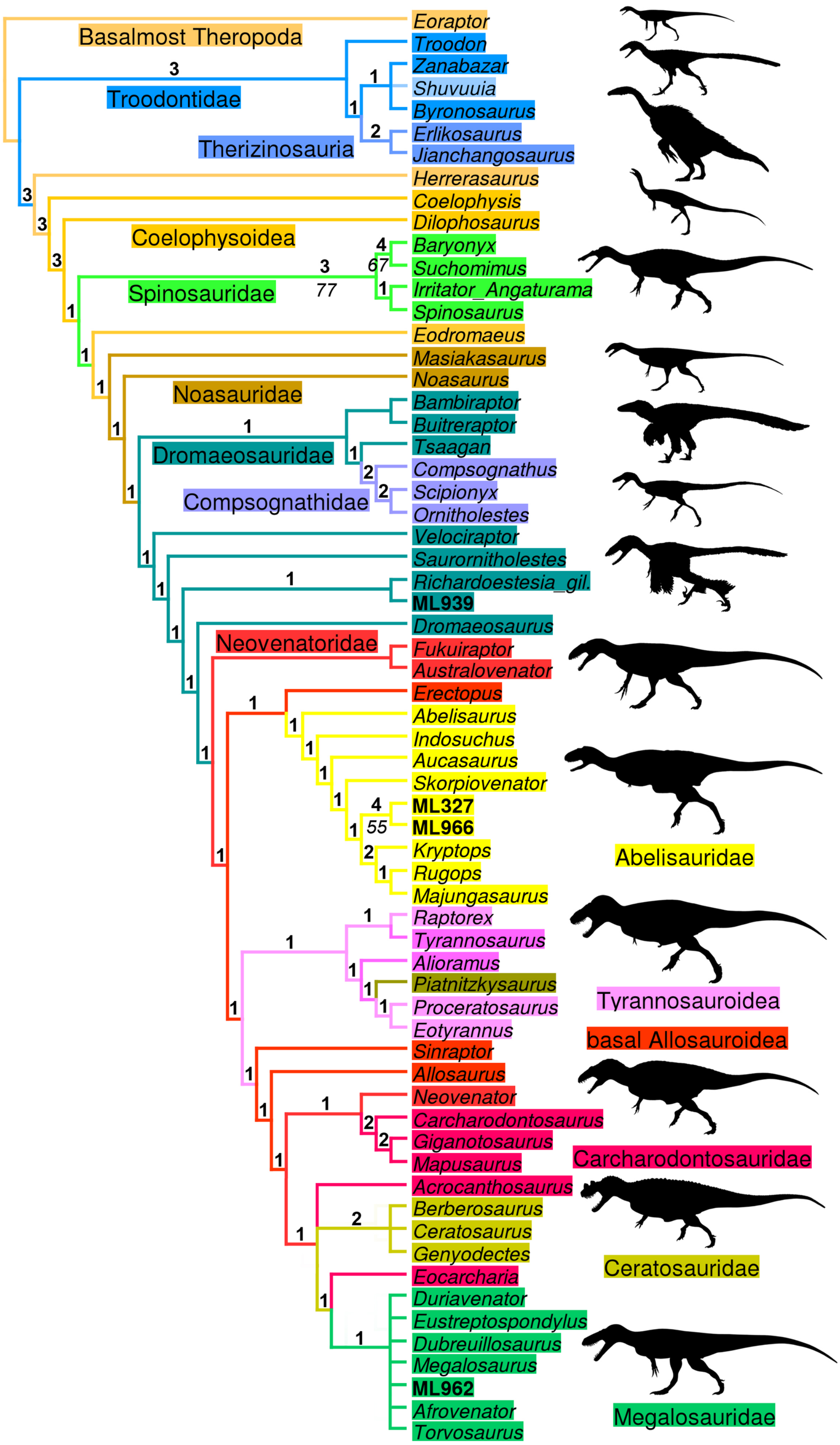


FIGURE 1. Strict consensus cladogram of seven most parsimonious trees recovered from analysis of dentition based characters. Initial analysis was a New Technology Search using TNT v.1.1 of a data matrix comprising 141 dentition-based characters for one outgroup (*Eoraptor*), 59 nonavian theropod taxa, as well as ML 327, ML 939, ML 962 and ML 966. Tree length = 703 steps; CI = 0.331; RI = 0.564. Bremer support values are in bold and bootstrap values are in italic. For silhouette attribution, see Appendix.

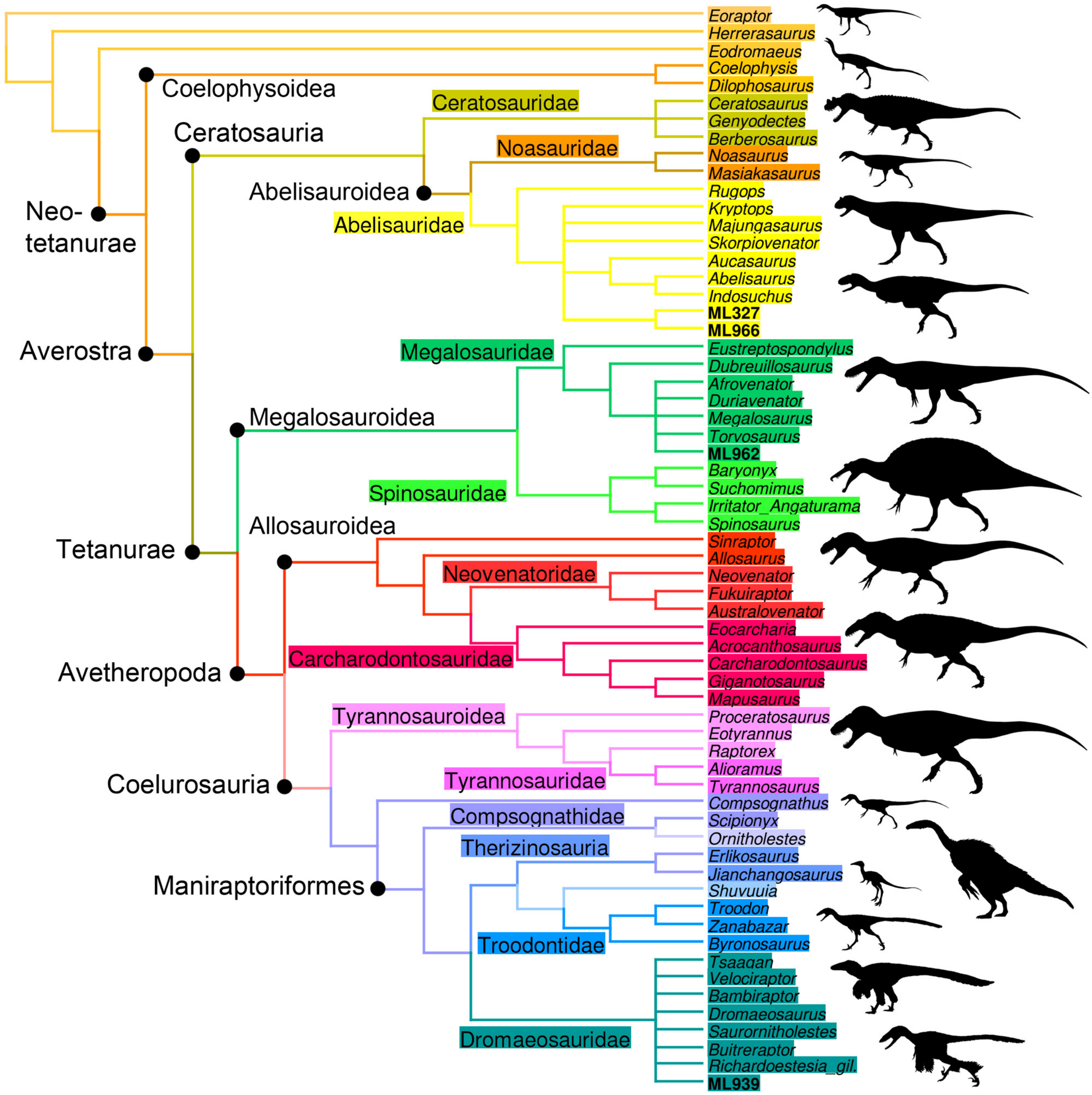


FIGURE 2. Strict consensus cladogram of 49 most parsimonious trees recovered from analysis of a supermatrix of 1972 discrete characters after the deletion of the two wildcard taxa *Erectopus* and *Piatnitzkysaurus*. The supermatrix includes a dentition-based datamatrix of 141 discrete characters and six recent datasets based on whole theropod skeleton (Xu *et al.* 2009; Brusatte *et al.* 2010; Martinez *et al.* 2011; Senter 2011; Pol and Rauhut 2012; Carrano *et al.* 2012). Initial analysis was a New Technology Search using TNT v.1.1 for one outgroup (*Eoraptor*), 57 non-avian theropod taxa and ML 327, ML 966, ML 939 (coded as lateral teeth), and ML 962 (coded as a mesialmost tooth). Tree length = 3552 steps; CI = 0.563; RI = 0.628. For silhouette attribution, see Appendix.

Similarly to Hwang (2007: fig. 38), the basalmost dinosaur *Eoraptor* and derived coelurosaurs such as troodontids and therizinosaurs appear closely related based on dental characters. They have similar dentitions in both their morphology (i.e., small crowns, constriction occurring between crown and root; distal denticles hooked and inclined apically from the distal margin), and microstructure (Hwang 2007), and might therefore have shared a similar diet, most likely omnivory (including partial herbivory) or herbivory (e.g., Russell & Dong 1993; Holtz *et al.* 1998; Barrett 2000; Zanno & Makovicky 2011; Sereno *et al.* 2013). Coelophysoids and spinosaurids possess relatively similar dentitions to each other (i.e., premaxillary tooth-row posteriorly constricted, anterior maxillary teeth facing anterodorsally, fluted teeth in *Coelophysis* and spinosaurids, and terminal rosette of the dentary in

Dilophosaurus and spinosaurids), suggesting they also had close diets involving grapping small preys such as small crocodylomorphs, juvenile dinosaurs and fishes (e.g., Paul 1988; Charig & Milner 1997; Farlow & Holtz 2002; Holtz 2003; Therrien *et al.* 2005; Nesbitt *et al.* 2006; Milner & Kirkland 2007). A similar morphological convergence occurs between the dentitions of noasaurids, compsognathids and dromaeosaurids which probably fed on small to medium-sized preys (e.g., Carpenter 1998; Carrano *et al.* 2002; Dal Sasso & Maganuco 2011; Peyer 2006; Gignac *et al.* 2010). These theropods all bear small ziphodont (i.e., labio-lingually compressed crown in which both mesial and distal margins possess serrated carinae) teeth with large sometimes apically inclined distal denticles and, when present, smaller mesial serrations (e.g., Currie *et al.* 1990; Currie & Chen 2001; Rauhut *et al.* 2012; pers. obs.). The mesialmost teeth of these theropods also tend to lack mesial and, in some cases, distal serrations (e.g., Stromer 1934; Gianechini *et al.* 2011b; Dal Sasso & Maganuco 2011). Ceratosauridae, Megalosauridae, some basal allosauroids, Carcharodontosauridae and Tyrannosauroidea are nested in the same clade based on dental characters (Fig. 1), illustrating similar feeding strategies involving consumption of large preys (mostly dinosaurs) among these large, robust-skulled averostrans (e.g., Carpenter 1998; Farlow & Holtz 2002; Holtz 2003; Carpenter *et al.* 2005; Bakker & Bir 2005; Hone & Rauhut 2010). Their lateral teeth are indeed sometimes very similar as members of these clades possess large, elongated and labio-lingually compressed teeth with a distal carina bearing coarse symmetrical to asymmetrical chisel-like denticles with often deep and elongated interdenticular sulci (pers. obs.). The premaxillary and dentary teeth tend to be smaller than the maxillary dentition, and there is an overlap of the second and third premaxillary alveoli in these theropods. The lateral teeth of ceratosaurids, megalosaurids and allosauroids can also display the same crown structures: large transversal undulations (i.e., long mesio-distally oriented wrinkles on the crown; Brusatte *et al.* 2007) and short marginal undulations (i.e., pronounced mesio-distally oriented wrinkles adjacent to carinae) and a similar pattern of oriented texture of the enamel (pers. obs.; Appendix, Fig. A4F). Tyrannosaurid teeth also display similar crown ornamentations, but their lateral teeth are much stouter and the mesialmost teeth have a mesial carina displaced lingually, rather than mesially or labially (e.g., Molnar 1998; Smith 2005; Samman *et al.* 2005; Holtz 2003, 2004, 2008).

Due to the variability of their dentitions, Dromaeosauridae and Allosauroidea were recovered as polyphyletic according to dental characters. Indeed, the lateral teeth of the dromaeosaurids *Buitreraptor*, *Dromaeosaurus* and *Saurornitholestes* are quite distinct from those of other dromaeosaurids. Regarding their serrations, for instance, *Buitreraptor* lacks mesial and distal denticles (Gianechini *et al.* 2011b), whereas *Dromaeosaurus* bears subquadrangular denticles with a convex margin (Currie *et al.* 1990; Currie 1995), and *Saurornitholestes* possesses large and apically hooked denticles, reminiscent of those of Troodontidae (Currie *et al.* 1990). The differences among allosauroid dentitions are more subtle. Most allosaurid teeth are incrassate, strongly recurved distally and bear a sharply twisted mesial carina in some teeth of the lateral dentition (Madsen 1978; Bakker 1998; Holtz *et al.* 2004; pers. obs.). This contrasts with the strongly labio-lingually compressed crowns of Neovenatoridae (e.g., *Neovenator*, *Fukuiraptor* and *Australovenator*; Currie & Azuma 2006; Hocknull *et al.* 2009) and some Carcharodontosauridae (e.g., *Carcharodontosaurus*, *Mapusaurus*; Stromer 1931; Coria & Currie 2006; pers. obs.), and the weakly recurved teeth of Metriacanthosauridae and Carcharodontosauridae which possess a relatively straight mesial carina (e.g., Stromer 1931; Coria & Currie 2006; Brusatte & Sereno 2007; pers. obs.).

On the other hand, with their characteristic dentitions, ceratosaurids, abelisaurids, spinosaurids, megalosaurids, tyrannosauroids, compsognathids and therizinosaurs were found as monophyletic in this analysis (Fig. 1). Ceratosaurid teeth are characterized by larger mid-maxillary teeth when compared to anterior maxillary teeth and, in lateral teeth, a labial depression on the basal part of the crown, a distal carina extending to the cervix or just above it and a broad interdenticular space in between distal denticles (Bakker & Bir 2004; Rauhut 2004; pers. obs.). Their lateral teeth also have a braided texture (i.e., oriented enamel texture made of alternating sinuous ridges and grooves: Appendix, Fig. A4K) of the enamel (unlike the irregular enamel texture of most abelisauroid teeth), and the crown tend to be strongly labiolingually compressed, sometimes bearing well-visible transversal undulations and a distal carina strongly labially deflected. In addition, the labial surface adjacent to the distal and sometimes mesial carinae is often flat or concave in ceratosaurid lateral teeth (Rauhut 2004; pers. obs.).

Likewise, abelisaurid teeth are weakly recurved distally, so that their distal profile is either straight or even convex in lateral view, and many abelisaurids tend to have low crowns (or 'brachydont' *sensu* Smith *et al.* 2005; Smith 2007; pers. obs.), although elongated crowns can be borne by some abelisaurid taxa such as *Aucasaurus garridoi* (MCF-PVPH 236) and *Skorpiovenator bustingorryi* (MMCN-PV 48). The enamel surface texture of abelisaurid crowns is irregular (i.e., non-oriented enamel texture: Fig. A4J), unlike the braided or veined (sculptured) enamel texture of most neotheropod (pers. obs.). Abelisaurid alveoli are always mesio-distally oriented, even the mesialmost ones, and subrectangular in outline (e.g., Sereno *et al.* 2004; Sampson & Witmer 2007; Sereno & Brusatte 2008; pers. obs.), and their lateral crowns also possess mesial and distal carinae centrally positioned on the crown in mesial and distal views, respectively (Smith 2007). Both carinae always reach the cervix of the crown and the denticles often show a deep interdenticular sulcus and/or apex pointing apically. Their mesialmost teeth are also typical, as they have a concave surface adjacent to the mesial carina and sometimes marginal to the distal carina in the mesialmost tooth (Fanti & Therrien 2007; Smith 2007; pers. obs.).

Due to their highly specialized skull and dentition, adapted for piscivory (e.g., Taquet 1984; Charig & Milner 1997; Sereno *et al.* 1998; Dal Sasso *et al.* 2005; Hendrickx & Buffetaut 2008; Dal Sasso *et al.* 2009), several features of spinosaurid teeth have already been used as synapomorphies by many authors (e.g., Sereno *et al.* 1998; Holtz *et al.* 2004; Benson 2010; Mateus *et al.* 2011; Carrano *et al.* 2012). Their teeth are indeed highly diagnostic (in fact the most diagnostic among theropods; see Table 2) as all spinosaurids possess subcircular mesialmost and lateral crowns displaying flutes (i.e., subparallel longitudinal grooves separated by acute ridges) on the lingual and/or labial margin, minute denticles or no serrations at all on both mesial and distal carinae, and the enamel texture of *Spinosaurus* and baryonychines is deeply veined (or 'sculptured' *sensu* Hasegawa *et al.* 2010) and curves basally close to the carinae. Their spatulated premaxillae bear a minimum of six teeth. The posterior premaxillary teeth are significantly smaller than the anterior ones and the premaxillary tooth row extends anterior to the external naris. Moreover, the dentaries also form a terminal rosette, in which the anteriormost teeth are significantly larger than mid- and posterior dentary teeth (e.g., Stromer 1915; Charig & Milner 1997; Sereno *et al.* 1998).

Megalosaurid dentitions are mostly characterized by the low-number of maxillary and dentary teeth (<15 alveoli: pers. obs.). The mesialmost and lateral teeth of Megalosauridae can be distinguished from those borne by their related cousins (i.e., Ceratosauria, Allosauroidea, Tyrannosauroidea) based on many features, which will be thoroughly described elsewhere.

Tyrannosauroids can be differentiated from other theropods based mostly on the morphology of their mesialmost teeth. Indeed, the basal cross-section of the mesialmost crown is usually U-shaped (i.e., the mesial and distal carina are strongly displaced and face lingually or linguodistally; Appendix, Fig. A1I-J), the third and fourth premaxillary teeth are distinctively overlapping, and the posterior premaxillary teeth are significantly smaller than the anterior maxillary teeth (e.g., Paul 1988; Molnar 1998; Holtz 2004; Samman *et al.* 2005; Smith 2005). The mesialmost maxillary and dentary teeth of tyrannosauroids are also significantly smaller than the mid-maxillary and dentary teeth, respectively, and the crowns display an oriented enamel texture (although not present in some tyrannosaurids), contrary to most other coelurosaurs. Like noasaurids and some dromaeosaurids, the distal denticles are larger than the mesial ones in the lateral teeth (DSDI < 1.2) of basal tyrannosauroids and juvenile tyrannosaurids (Rauhut *et al.* 2012; Xu *et al.* 2004, 2006; Li *et al.* 2010; Carr & Williamson 2004).

In Compsognathidae, and convergently with *Ornitholestes*, the mesial and distal carinae of mesialmost teeth are absent or unserrated, and the lateral teeth do not bear mesial denticles, whereas the distal denticles disappear well beneath the apex of the crown (e.g., Currie & Chen 2001; Peyer 2006; Dal Sasso & Maganuco 2011; pers. obs.). Absence of mesial denticles in both mesialmost and lateral teeth and unserrated mesialmost teeth (in the first two mesialmost teeth at least) seem indeed to be a condition shared by all compsognathids but *Sinocalliopteryx gigas* (Currie & Chen 2001; Hwang *et al.* 2004; Ji *et al.* 2007; Chiappe & Göhlich 2011; Dal Sasso & Maganuco 2011). Therizinosaurs have a highly diagnostic dentition showing a superficial convergence with the teeth of basal sauropodomorphs and ornithischians (Zhao & Xu 1998; Barrett 2000; Barrett 2009; Pu *et al.* 2013). Therizinosaurs are indeed characterized by toothless premaxillae, an important constriction between root and crown, both mesial and distal carinae terminating well-above the cervix, pointed denticles oriented apically from the mesial and distal margins, and a subequal number of denticles at mid-crown and the apex (pers. obs.).

The cladistic analysis performed on the supermatrix of 60 taxa yielded nine most parsimonious trees (MPTs), the strict consensus of which (length = 3583 steps; CI = 0.546; RI = 0.604) displays a large polytomy affecting Avetheropoda (Appendix, Fig. A8a). A poorly resolved consensus tree (95 MPTs of length = 3607 steps; CI = 0.529; RI = 0.58) with an important polytomy was also found when incorporating the four isolated teeth to the supermatrix (Appendix, Fig. A8b). This is due to the wildcard taxa *Erectopus* (either found as a Ceratosauridae, a basal Tetanurae or a Megalosauroidea) and *Piatnitzkysaurus* (nested within the clade of Tetanurae or Megalosauroidea). The deletion of these two wildcard taxa in the first analysis allows constraining all major theropod clades, with the exception of Deinonychosauria (Appendix, Fig. A8). Indeed, due to the obvious convergence of their dentition (i.e., dentition showing constricted tooth with weak or no distal curvature, unserrated crown, carinae bearing large hooked/pointed denticles, and teeth sometimes set in an open groove; Russell & Dong 1993; Holtz *et al.* 2000; pers. obs.), Troodontidae are more closely related to *Shuvuuia* and Therizinosauria than to Dromaeosauridae. The cladistic analysis performed on the supermatrix of 58 taxa (isolated teeth excluded), and yielding 4 MPTs (length = 3529 steps; CI = 0.575; RI = 0.642), shows that only a few unambiguous (i.e., unique or non-homoplasious) dentition-based synapomorphies define theropods clades (Table 2; Appendix, Fig. A9). The large majority of dentition-based characters are homoplastic, demonstrating a high degree of convergence among theropod dentitions. Several clades of theropods such as Ceratosauridae, Abelisauroidea, Noasauridae, Abelisauridae, Megalosauroidea and Therizinosauria are characterized by a combination of ambiguous synapomorphies (i.e., homoplasious state changes), and only Coelophysoidea, Averostra, Spinosauridae, Avetheropoda, Tyrannosauroidea, non-tyrannosauroid Coelurosauria and Dromaeosauridae are defined by both ambiguous and unambiguous synapomorphic characters (Table 2; Appendix, Table A1). With six and three unambiguous synapomorphies, Spinosauridae and Averostra, respectively, are the best supported clades in term of dental characters, and the clade of Tyrannosauroidea only includes two unambiguous synapomorphies (Table 2).

TABLE 2. List of unambiguous (non-homoplasious) dentition-based synapomorphies by theropod clades for results of the cladistic analysis of the dentition-based dataset.

Clade	Synapomorphy
Coelophysoidea	Tooth row slightly constricted in the posterior part of the premaxilla (15:1).
Averostra	Anterior premaxillary alveoli labio-lingually oriented, posterior premaxillary alveoli mesio-distally oriented (3:1); less than 14 denticles per 5mm on the mesial carina in mesialmost teeth (51:2); less than 16 denticles per 5mm on the mesial carina in lateral teeth (84:3).
Spinosauridae	More than five premaxillary teeth (2:34); premaxillary tooth row anterior to external naris (14:1); maxillary alveoli subcircular in outline (23:2); mesial carina terminating well beneath the cervix in mesialmost teeth (50:2); flutes present on both labial and lingual sides in lateral teeth (107:2); deeply veined enamel texture in lateral teeth (117:2).
Spinosaurinae	Mesial margin of lateral crown slightly convex, almost straight, apex centrally positioned (69:1).
Avetheropoda	Outline of basal cross-section D-shaped or J-shaped in mesialmost tooth (41:3).
Carcharodontosaurinae	Mesial carina terminating well beneath the cervix in lateral teeth (80:2).
Tyrannosauroidea	Anteriormost dentary alveoli significantly smaller than mid- and posterior dentary alveoli (27:2); distal carina labially displaced and facing lingually or linguodistally in mesialmost teeth (48:2).
Therizinosauroidea	Toothless premaxilla (1:1); constriction between root and crown present in some lateral teeth (64:0).
Troodontidae	Anterior maxillary alveoli significantly smaller than posterior maxillary alveoli (18:2).
Dromaeosauridae	Labial depression extending along the basal half of the crown or more apically in lateral teeth (73:2).

When integrating the fourth isolated teeth and excluding the wildcard taxa *Erectopus* and *Piatnitzkysaurus*, the cladistic analysis performed on the supermatrix of 62 taxa yielded 49 MPTs and a well-resolved consensus tree (length = 3552 steps; CI = 0.563; RI = 0.628) that mirrors to a large degree the general classification of theropods (Fig. 2). The phylogenetic position of the four isolated teeth from the Lourinhã Formation will be discussed in the following sections after describing each of them thoroughly.

Systematic Palaeontology

Dinosauria Owen, 1842

Saurischia Seeley, 1887

Theropoda Marsh, 1881

Ceratosauria Marsh, 1884

Abelisauroidea Bonaparte, 1991

Abelisauridae Bonaparte & Novas, 1985

Gen. and sp. indet.

Referred material. ML 327 and ML 966 (Figs. 3–4).

Locality and horizon. Cliffs of Lourinhã, Lourinhã, Portugal. Lourinhã Formation, Kimmeridgian-Tithonian, Upper Jurassic.

Description. ML 327 lacks the lowermost part of the crown, a small piece of the mesial carina on the lingual face and a few denticles on the distal carina. However, the crown is well preserved and most of the denticles are intact. The apical part of the distal carina of ML 966 is also missing; otherwise this tooth is relatively well-preserved, with some part of the enamel cracked and missing.

Crown. The teeth are slightly elongated baso-apically (CHR of 1.58 in ML 327 and 1.95 in ML 966) and ziphodont in shape. Both crowns are only weakly curved distally, and the apex has been worn.

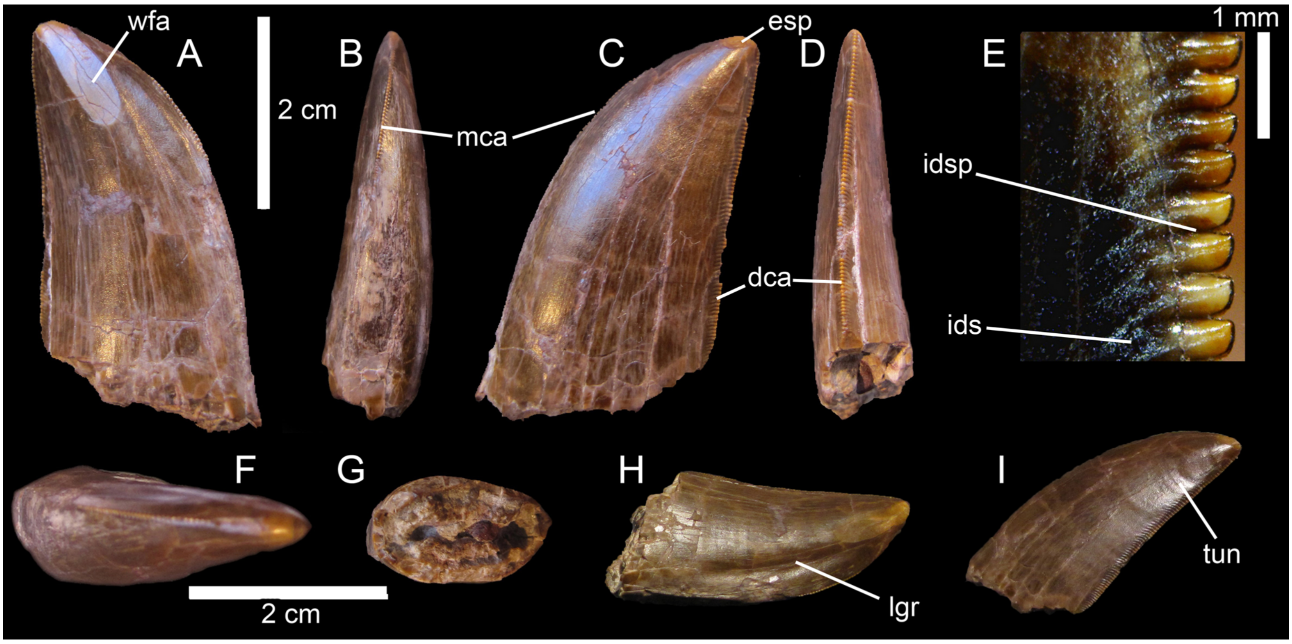


FIGURE 3. Isolated tooth (ML 327) of an Abelisauridae in lingual (A), mesial (B), labial (C), distal (D), apical (F), basal (G) and mesio-lingual (H) and labio-distal views. Apical denticles of the distal carina in labial view (E). Abbreviations: **dca**, distal carina; **esp**, enamel spalling; **ids**, interdenticular sulcus; **idsp**, interdenticular space; **lgr**, longitudinal groove; **mca**, mesial carina; **tun**, transversal undulation; **wfa**, wear facet.

In lateral view, the distal carina is slightly concave, almost straight. The axis passing through the basal part of distal carina is perpendicular to the transversal plane of the crown. The mesial margin of the crown is much more recurved than the distal margin and the curvature is more important apically than basally. The apex is not acute and pointed but slightly rounded. In ML 327, it shows a small spalling surface on the labial face and a large wear facet (Fig. 3A) corresponding to an elongated tongue-shaped surface bearing diagonal striations and inclined mesio-basally on the two-thirds of the lingual side. The spalling surface on the lingual side of the crown in ML 966 is rather subtriangular and only limited to the apex. Both mesial and distal carinae are serrated from the base to the tip of the crown. The lingual surface of ML 327 bears a prominent longitudinal depression on its mesial part, 4 mm from the mesial carina at the mid-crown. This narrow groove (Fig. 3H) of 1.5 mm width extends from around 8.5 mm above the cervix dentis (or neck of the tooth, here referred to as 'cervix' *sensu* Smith & Dodson 2003) and ends at a distance of 8 mm from the apex. The longitudinal depression roughly follows the curvature of the crown, is closer to the mesial carina at its basal and apical endings, and almost contacts the large wear facet apically. No longitudinal groove is present on the labial face of the crown in ML 327 and on both labial and lingual sides of the tooth in ML 966.

In mesial view, the mesial carina of both teeth is concave and inclined baso-lingually. The carina remains medially positioned on the tip of the crown but twists lingually towards the root more basally and extends mesio-lingually to the cervix (Figs. 3B and 4B). The crown apex remains straight and follows the general curvature of the crown. The lingual surface is slightly baso-apically sigmoid with the basal part of the crown concave and the apical one convex. On the other hand, the entire labial surface of the crown is strongly convex baso-apically. There is a flattened surface at the base of the mesial margin which is delimited lingually by the mesial carina in ML 327. This flattened surface, which appears above the cervix, extends on the first third of the crown. In ML 966 however, the surface at the base of the mesial margin is strongly convex.

In distal view, the distal carina is weakly sigmoid with a large bow oriented lingually along the basal two-thirds of the crown while the apical part of the distal carina is straight. The carina is slightly lingually positioned on the distal margin of the crown but moves medially at the tip.

In apical view, the tip of both crowns is distally positioned, with no curvature on the lingual or labial sides. The labial margin is globally convex but the distal surface is rather flattened or weakly convex. On the contrary, the surface adjacent to the distal carina on the lingual margin is rather slightly concave. In ML 327, the mesial part of the labial face is strongly convex whereas the mesial part of the lingual surface has a double curvature due to the presence of the longitudinal depression. In both teeth, the distal carina is angular whereas the mesial carina forms a low but pointed ridge which strongly displaces lingually towards the root.

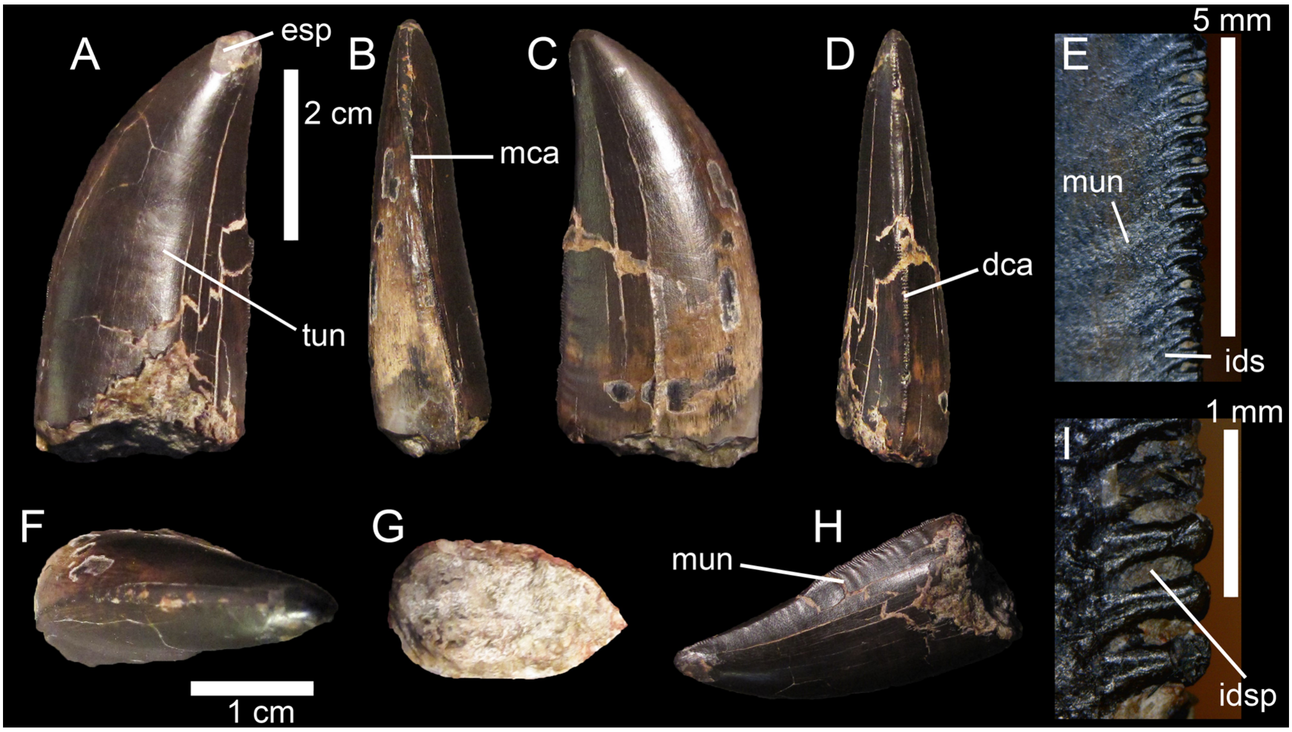


FIGURE 4. Isolated tooth (ML 966) of an Abelisauridae in lingual (A), mesial (B), labial (C), distal (D), apical (F), basal (G) and linguo-distal (H) views. Mid-crown denticles of the distal carina in lingual view (E, I). Abbreviations: **dca**, distal carina; **esp**, enamel spalling; **ids**, interdenticular sulcus; **idsp**, interdenticular space; **lgr**, longitudinal groove; **mca**, mesial carina; **mun**, marginal undulation; **tun**, transversal undulation.

In basal view, the cross-section outline of the crown base is elliptical and slightly lanceolate (i.e., mesial margin convex and distal margin pointed) in ML 327 (Fig. 3G) whereas ML 966 has a well-marked lanceolate outline of the crown base (Fig. 4G). In ML 327, the mesial part is roughly triangular in shape with the tip of the triangle pointed mesio-lingually whereas the mesial part of ML 966 is strongly subtriangular with the tip of the triangle medially positioned. In both crowns, the distal margin of the crown forms a semicircle. The distal margin bears the superficial ridge of the distal carina which is mesio-lingually positioned. The labio-lingual width of the base of the crown is bigger mesially (CBW of 10.69 in ML 327 and 12.94 in ML 966). With their rather flattened bases, the middles of the lingual and labial faces are almost parallel. The middle of the labial surface remains roughly flat towards the tip while the lingual surface becomes strongly convex apically. In ML 327, the dentine layer is thin (1 mm on the labial margin) and becomes thicker in the distal part of the crown (1.9 mm). Although the lingual margin has been damaged in this tooth, the pulp cavity seems to share the same lanceolate outline of the crown-base, but there is a weak labio-lingual constriction of the cavity 8 mm below the extremity of the distal carina.

Denticles. The mesial carina of ML 327 bears 11 denticles per 5 mm at the tip, 13 at the mid-crown and 20 near the cervix. In ML 966, the mesial carina shows 15 denticles at mid-crown, and 19 denticles at the base, the mesioapical denticles having been worn off. (Table 3). In both crowns, the denticles decrease in size towards the root at two-thirds of the crown and the most basal denticles are minute. In lateral view, the mesial denticles are longer baso-apically than mesio-distally, which give them a subrectangular (or 'cartouche-like' *sensu* Harris 1998) outline. Since the denticles are inclined towards the tip of the crown and the main axis of the denticle is not perpendicular to the mesial margin of the crown, the shape of the denticle is rather parallelogram-shaped. The external margin of the mesial denticles is rounded and sometimes asymmetrically convex, with the concavity positioned slightly apically. In both teeth, the lingual and labial surfaces of the denticles are convex and the interdenticular space is shallow. In mesial view, the denticles are not labio-lingually large, they are roughly chisel-like in shape but their external margin is rounded, and the main body of the denticles is almost cylindrical. There is no interdenticular sulcus between the mesial denticles in both teeth.

TABLE 3. Morphometric measurements of four isolated theropod teeth from the Lourinhã Formation of Portugal.

Specimen	ML 327	ML 966	ML 962	ML 939
Position	Isolated, lateral	Isolated, lateral	Isolated, mesial	Isolated, lateral
CBL	20.07	23.69	31.2	2.8
CBW	10.69	12.95	20.2	1
CH	31.76	46.41	85.8	5.1
AL	38.11	51.06	91.9	5.5
CBR	0.5326	0.5462	0.647	0.357
CHR	1.582	1.959	2.75	1.821
MA	11 (5mm)	?	?	?
MC	13 (5mm)	15 (5mm)	8 (5mm)	/
MB	20 (5mm)	19 (5mm)	/	/
DA	12 (5mm)	12 (5mm)	7 (5mm)	8 (1mm)
DC	11 (5mm)	14 (5mm)	8 (5mm)	9 (1mm)
DB	15 (5mm)	19 (5mm)	11 (5mm)	9 (1mm)
MAVG	14.66 (5mm)	16 (5mm)	8 (5mm)	?
DAVG	12.667 (5mm)	15 (5mm)	8.666 (5mm)	9.75 (1mm)
DSDI	1.14	1.06	0.931	?

The distal carina of ML 327 has 12 denticles per 5 mm at the apex, 13 at the mid-crown, and around 15 at the crown base (but not near the cervix, this part being missing) so that they are similar in size to mesial denticles (DSDI of 1.14). In ML 966, 14, 12 and 14 denticles per 5 mm can be observed at the apex, mid-crown and base of the crown, respectively, and this tooth also share a DSDI close to one (Table 3). Unlike the mesial denticles, the distal denticles of both crowns are longer mesio-distally than baso-apically, except in the apical denticles which are squared-like in shape, and the main axis of the denticles is perpendicular to the distal margin. In lateral view, some distal denticles of ML 327 show an external margin pointing slightly towards the tip of the crown (Fig. 3E), so that the apical margin of the denticles is weakly concave whereas the basodistal margin is strongly convex. In all other distal denticles of ML 327 and all distal denticles of ML 966, the external margin is asymmetrically convex, with the denticle apex slightly apically positioned (Fig. 4I). In both teeth, the labial and lingual surfaces of the denticle body are convex. The distal denticles also have a deeper interdenticular space than the mesial ones and their external margin is more acute, giving them a real chisel-like shape in distal view. In ML 327, the enamel layer is thicker than in the mesial denticles and, in both teeth, most of denticles show an elongated interdenticular sulcus diagonally oriented basally away from the denticles (Figs. 3E and 4E). These shallow grooves are parallel to each other and extend from the base of the interdenticular space and run on both labial and lingual faces of the crown. They are shorter in the apical denticles, and completely absent in the most apical one, both on the labial and lingual surface. Their inclination also tends to be reduced towards the root with interdenticular sulci being almost perpendicular to the distal margin in the basal denticles.

Surface. The enamel surface of both crowns is very well preserved and shows perfectly a granular and irregular texture on both lingual and labial faces. Besides the large longitudinal depression present on the lingual face, transversal and shallow undulations are present on both lingual and distal surfaces in ML 327 (Fig. 3I). On the labial face of this tooth, they form large parabolic furrows curving apically near the distal carina, disappearing on the mesial part of the labial face due to the strong curvature of the crown. On the lingual face of this crown, they are visible distally, near the distal carina, and also in the middle of the crown, in the mid-crown surface. The undulations are absent on both convex surface adjacent to the mesial carina and the longitudinal depression. Unlike the labial wrinkling, these undulations do not bent towards the tip of the crown near the carina. In ML 966, the transversal undulations are also clearly visible on both sides of the crown (Fig. 4A). They are particularly pronounced close to the distal carina on the labial margin where they also curve apically adjacent to the distal carina (Figs. 4E, H). As in ML 327, the transversal undulations are large, parabolic and shallow on the lingual side of the crown, and they do not curve toward the apex close to the carinae. In both teeth, these undulations are parallel and irregularly spaced and there are approximately 3 to 4 wrinkles per 5 mm on both faces of those crowns.

Discussion. Since the root is absent, ML 327 and ML 966 are most likely shed teeth. The labio-lingual compression of these moderately large teeth (CH > 30 mm), associated with serrated mesial and distal carinae and curvature of the tip distally, is a plesiomorphic condition seen in theropod dinosaurs. Among known large terrestrial Jurassic groups of vertebrates, this combination of characters is only seen in theropods.

Although ML 966 is slightly bigger than ML 327 (Table 3), both teeth can confidently be associated to the same taxon as they share the same outline, CBR, DSDI, and the following features: presence of well-developed interdenticular sulci pointing basally, transversal undulations on both labial and lingual faces, a mesial carina offset, strongly twisted lingually towards the root and reaching the cervix, a distal carina slightly sigmoid and lingually positioned, a lingual face baso-apically concave and a labial surface baso-apically sigmoid, and a lanceolate outline of the base-crown in cross-section. Nevertheless, some denticles of ML 327 differ from ML 966 as their external margins are pointing apically and are not asymmetrically convex on their entire distal margins. However, denticle recurvature can vary in tooth row (Fanti & Therrien 2007; see below). The interdenticular space of the distal denticles is wider in ML 966, and the crown is also slightly more elongated than ML 327 (CHR of 1.95 and 1.58) but elongation of the crown also varies greatly along the tooth row in theropods (e.g., *Ceratosaurus*, *Allosaurus*, *Proceratosaurus, Tyrannosaurus*).

One of the most striking features in these two isolated teeth is the presence of tenuous to well-marked transversal undulations ('enamel wrinckles' *sensu* Brusatte *et al.* 2007) on the crown. Thought to be a possible tetanuran synapomorphy (Brusatte *et al.* 2007), transversal undulations are present on the crown of many theropods, from basal to derived forms, as well as metriorhynchid crocodylomorphs (Andrade *et al.* 2010) and rauisuchian crurotarsans (Brusatte *et al.* 2009b), and this feature cannot therefore be considered as a reliable tool alone for identifying teeth. In theropods, they have indeed been observed in basalmost theropods such as *Sanjuansaurus gordilloi* (PVSJ 605) and *Eodromaeus murphi* (PVSJ 561), ceratosaurs such as *Ceratosaurus nasicornis* (USNM VP 4735), *Berberosaurus liassicus* (MNHN Pt369), *Genyodectes serus* (MLP 26–39), *Abelisaurus comahuensis* (MPCA 1, 229, 687), *Aucasaurus garridoi* (MCF-PVPH 236) and *Majungasaurus crenatissimus* (FMNH PR 2278), all non-Maniraptoriformes tetanurans (see Brusatte *et al.* 2007), and some deinonychosaurs like *Troodon formosus* (DMNH 22337) and *Dromaeosaurus albertensis* (AMNH 5356).

ML 966 also displays pronounced undulations adjacent to the distal carina. Short and marginal undulations close to carinae are a well-known feature of carcharodontosaurids teeth (Sereno *et al.* 1996; Coria & Currie 2006) as they appear on the teeth of *Carcharodontosaurus saharicus* (SGM Din-1; UC PV6), *Mapusaurus roseae* (MCF-PVPH 108) and *Giganotosaurus carolinii* (MUCPv-CH-1). However, marginal undulations have also been reported among non-carcharodontosaurid theropods such as the abelisaurid *Skorpiovenator bustingorryi* (Canale *et al.* 2009). They actually seem to be present in a large range of non-coelurosaur averostrans as they have also been noticed in other ceratosaurs such as *Ceratosaurus nasicornis* (USNM 4735), *Abelisaurus comahuensis* (MPCA 5) and *Majungasaurus crenatissimus* (FMNH 2100), megalosaurids like *Afrovenator abakensis* (UC UBA1), *Megalosaurus bucklandii* (NHM R.234; OUMNH J.23014) and *Torvosaurus tanneri* (ML 1100), spinosaurids such as *Baryonyx walkeri* (NHM R.9951), *Suchomimus tenerensis* (MNN G35-9), and *Irritator challengeri* (SMNS 58022), and other allosauroids like *Allosaurus fragilis* (USNM 8335), *Neovenator salerii* (MIWG 6348) and *Acrocanthosaurus atokensis* (NCSM 14345).

Both teeth also possess a slightly curved distal profile of the crown, with the apex of the teeth located just apical to the most distal point of the crown at the cervix. This feature was considered to be a potential synapomorphy for Abelisauridae by Smith (2007) as a straight or slightly curved distal profile of the crown exists in *Majungasaurus crenatissimus*, *Indosuchus raptorius*, *Rugops primus*, *Kryptops palaios, Aucasaurus garridoi* (Smith & Vechia 2006; Smith & Lamanna 2006; Smith 2007; Candeiro 2007; pers. obs.) and many indeterminate abelisaurids (e.g., UCPC 10; MNHN MRS 1619, MRS 1620). Although the distal profile of the crown displays a strong curvature in most other theropods (Ezcurra 2009; pers. obs.), a weak curvature of the distal profile can also occur in some teeth of basalmost theropods (PVSJ 512), ceratosaurids (USNM 4735; MLP 26-39), noasaurids (PVL 4061), allosauroids (SGM Din1; MCF-PVH 108.43), tyrannosauroids (MIWG 1997.550; USNM 12814; FMNH PR2081) and some coelurosaurs (Currie *et al.* 1990: fig. 8.5A; Sankey *et al.* 2002: fig. 4.10); therefore, the systematic utility of this feature requires association with other characters.

Nevertheless, the presence of strongly developed and elongated interdenticular sulci between distal denticles seems to be a condition genuinely shared by non-maniraptoriform averostrans. This feature has been observed in the abelisaurids *Kryptops palaios* (MNN GAD1−1) and *Majungasaurus crenatissimus* (FMNH PR 2100, 2278), the megalosauroid *Piatnitzkysaurus floresi* (PVL 4073), the megalosaurids *Megalosaurus bucklandi* (OUMNH J13506) and *Torvosaurus tanneri* (ML 1100), the carcharodontosaurids *Giganotosaurus carolinii* (MUCPv-CH-1) and *Mapusaurus roseae* (MCF-PVPH-108), and the tyrannosaurid *Tyrannosaurus rex* (FMNH PR2081). However, an irregular texture of the enamel (i.e., no specific orientation of the enamel wrinkling texture) seems to be present in most non-tetanurans theropods such as Coelophysoidea and Abelisauroidea, some tyrannosaurids and many primitive coelurosaurs, Compsognathidae and Deinonychosauria (pers. obs.). On the other hand, a braided/veined oriented texture of the enamel has been observed in Ceratosauridae, Megalosauroidea, Allosauroidea and Tyrannosauroidea and it is therefore unlikely that ML 327 and ML 966 belong to one of those clades.

A peculiar anatomical feature of ML 327 is also the presence of distal denticles with an apex pointing towards the tip, a feature present in the teeth of some abelisauroids such as *Masiakasaurus knopfleri* (FMNH PR 2221, 2296), *Kryptops palaios* (MNN GAD1−1), *Rugops primus* (MNN IGU1), *Majungasaurus crenatissimus* (FMNH PR 2008, 2100, 2278) and other abelisaurid taxa (e.g., MUCPv 482; MUCPv 641). Among large theropods like ceratosaurids, megalosauroids, allosauroids and tyrannosauroids, the denticles are symmetrically rounded or slightly asymmetrically convex in lateral view but never hooked apically (*contra* Bakker & Bir 2004 for ceratosaurids and allosaurids, and Smith 2007 for tyrannosaurids; Currie *et al.* 1990; Abler 1992; pers. obs.). Slightly to strongly hooked distal denticles can also be observed in the basal saurischian *Eoraptor lunensis* (e.g., third right premaxillary tooth; PVSJ 512) and many Troodontidae (e.g., Currie 1987; Currie *et al.* 1990; Holtz *et al.* 1998; Longrich 2008; pers. obs.) and Dromaeosauridae (e.g., Currie *et al.* 1990; Currie & Varricchio 2004; Baszio 1997; Longrich 2008; pers. obs.). Deinonychosaurs, however, possess either very large and well-separated serrations, as in troodontids and *Saurornitholestes*, or a number of denticles per five millimeters higher than 14 on the distal carina (Smith *et al.* 2005). Likewise, both dromaeosaurids and *Masiakasaurus* tend to have distal denticles larger to mesial serrations (Currie *et al.* 1990; Currie & Varricchio 2004; Norell *et al.* 2006; Longrich 2008; pers. obs.). To our knowledge, neither noasaurids nor deinonychosaurs display a combination of pronounced and elongated interdenticular sulci and short marginal undulations on the crown.

Interestingly, ML 966 lacks hooked denticles on the distal carina as all denticles are either symmetrically or asymmetrically convex. This would therefore suggest that apically recurved denticles might not be present in all teeth along the tooth row. Denticle recurvature seems indeed to vary in the dentition of *Majungasaurus crenatissimus* as strongly recurved denticles are present in lateral and mesial dentary teeth and slightly recurved to symmetrically rounded denticles exist in some lateral and premaxilla teeth (Fanti & Therrien 2007; pers. obs.).

The presence of an elongated and deep groove adjacent to the mesial carina on the lingual side of the crown in

ML 327 is another peculiar feature that, to our knowledge, has not been observed in any teeth belonging to a large theropod (crown with CH > 30 mm), and might therefore represent an autapomorphy. A concave surface adjacent to the mesial carina can be observed in the mesialmost teeth of many abelisaurids such as *Rugops primus* (MNN IGU1), *Indosuchus raptorius* (AMNH 1753) and *Majungasaurus crenatissimus* (FMNH PR 2100), but also in *Allosaurus fragilis* (AMNH 851), some tyrannosauroids such as *Proceratosaurus bradleyi* (NHM R 4860) and *Eotyrannus lengi* (MIWG 1997.550), and some dromaeosaurids like *Dromaeosaurus albertensis* (AMNH 5356). However, the surface adjacent to the mesial carina in ML 327 is convex and the concave area formed by the longitudinal groove is narrow. Longitudinal grooves running along the crown surface can also be observed in several theropod taxa such as *Scipionyx samniticus* (Dal Sasso & Maganuco 2011), *Buitreraptor gonzalezorum* and *Austroraptor cabazai* (Gianechini *et al.* 2011b), and there are two grooves separated by a large medial ridge (Gianechini *et al.* 2011a; Gianechini *et al.* 2011b; pers. obs.). Likewise, the mesial groove present in ML 327 cannot be confused with the large medial concavity ('supradental groove' of Gong *et al.* 2010) present on the crown of many theropods like *Orkoraptor burkei* (Novas *et al.* 2008) and *Sinornithosaurus* (Gong *et al.* 2010), or the numerous flutes visible on the teeth of *Coelophysis bauri* (Buckley 2009), *Masiakasaurus knopfleri* (Carrano *et al.* 2002), *Ceratosaurus nasicornis* (Madsen & Welles 2000), spinosaurids (e.g., Charig & Milner 1997; Sereno *et al.* 1998; Sues *et al.* 2002), *Paronychodon lacustris* (e.g., Cope 1876; Sankey *et al.* 2002; Baszio 1997; Sankey 2008) or *Velociraptor mongoliensis* (AMNH 6515).

On the basis of the combination of several important features in ML 966 and ML 327, a large crown (CH > 30 mm), an almost straight distal profile of the tooth, transversal and short marginal undulations on the crown, denticles with strongly developed interdenticular sulci, a DSDI close to one, an irregular enamel texture and the presence of apically pointed denticles on the distal carina in ML 327, these two teeth are assigned to a member of the Abelisauridae. Within this clade, ML327 and ML 966 only differ from other abelisaurids by having a strongly twisted mesial carina. However, this feature is also present in some basal abelisaurids such as *Abelisaurus* (MPCA 685). Also, ML 327 has a labially displaced distal carina which contrasts with the centrally positioned carina on the distal margin of the crown of abelisaurids (pers. obs.).

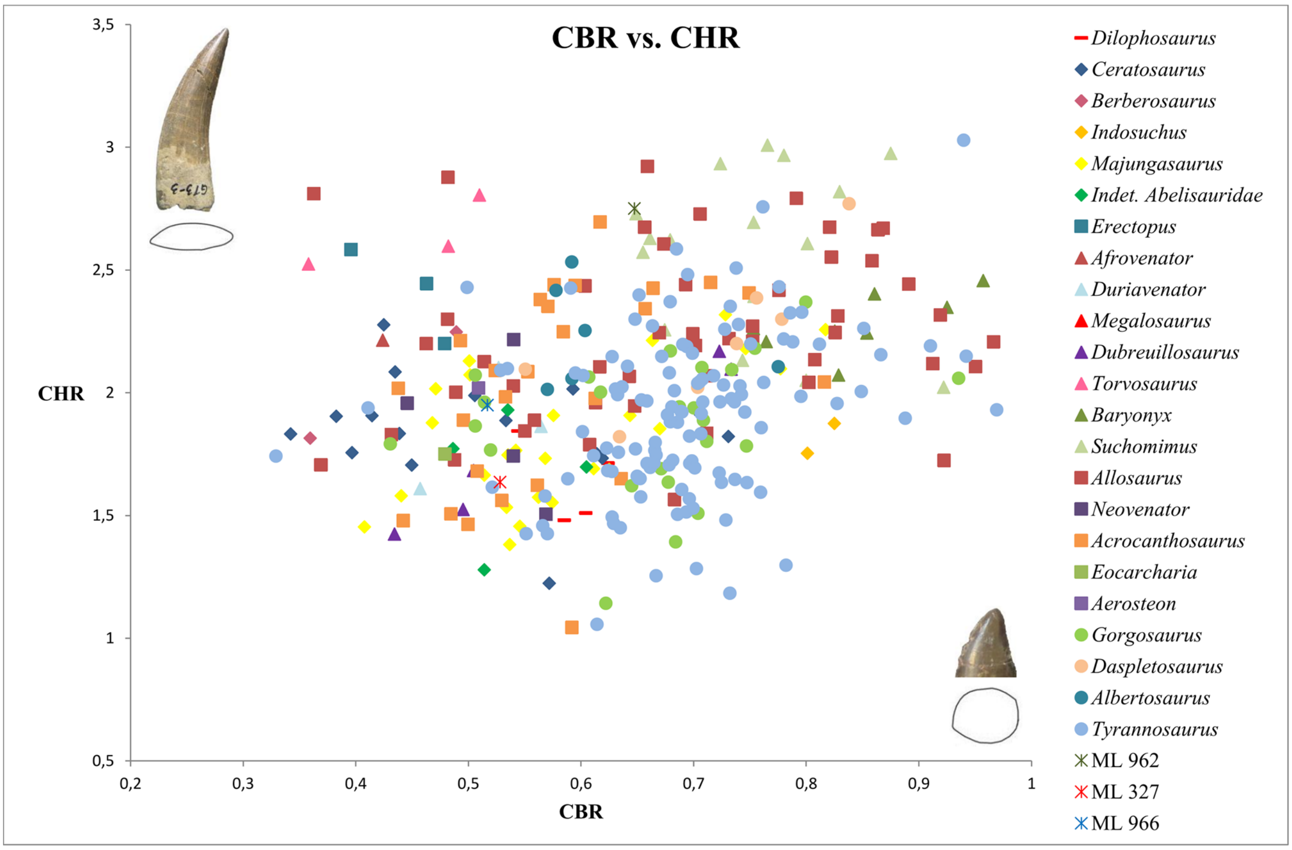


FIGURE 5. Plots of CBR versus CHR of ML 962, ML 327, ML 966 and 23 theropod taxa comprising the data set. For reasons of clarity, only taxa with CBR of less than 1 were considered.

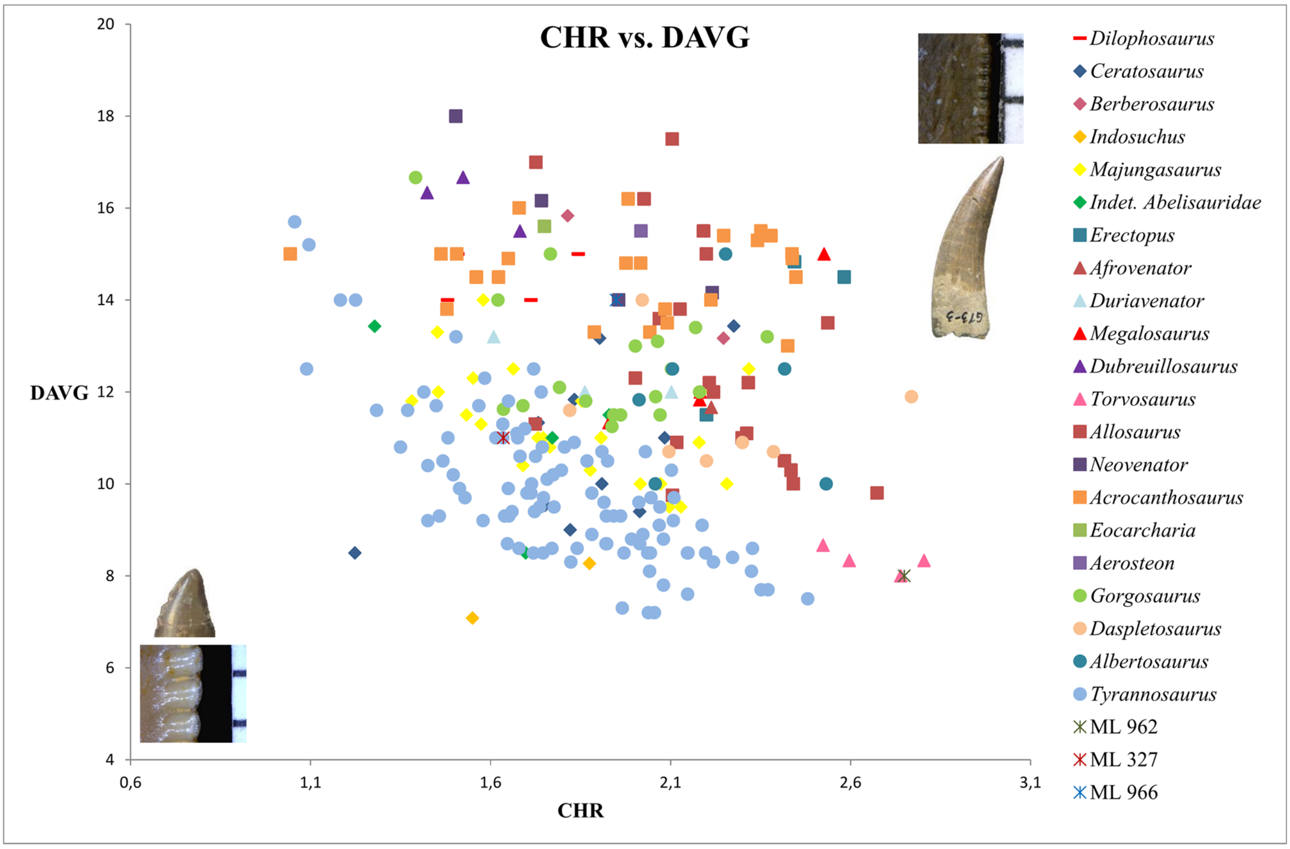


FIGURE 6. Plots of CHR versus DAVG of ML 962, ML 327, ML 966 and 21 theropod taxa comprising the data set. For reasons of clarity, only taxa with serration of less than 20 denticles were considered.

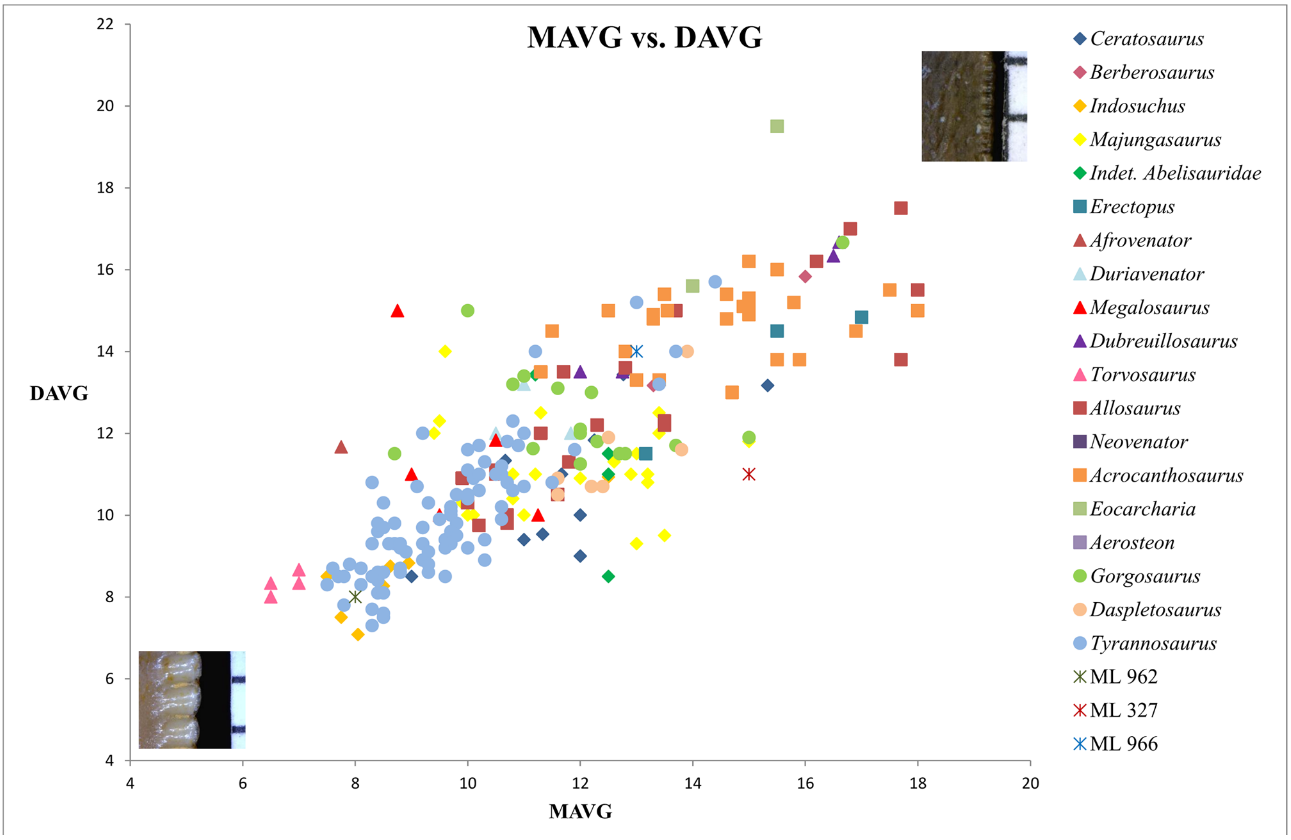


FIGURE 7. Plots of MAVG versus DAVG of ML 962, ML 327, ML 966 and 19 theropod taxa comprising the data set. For reasons of clarity, only taxa with serration of less than 20 denticles were considered.

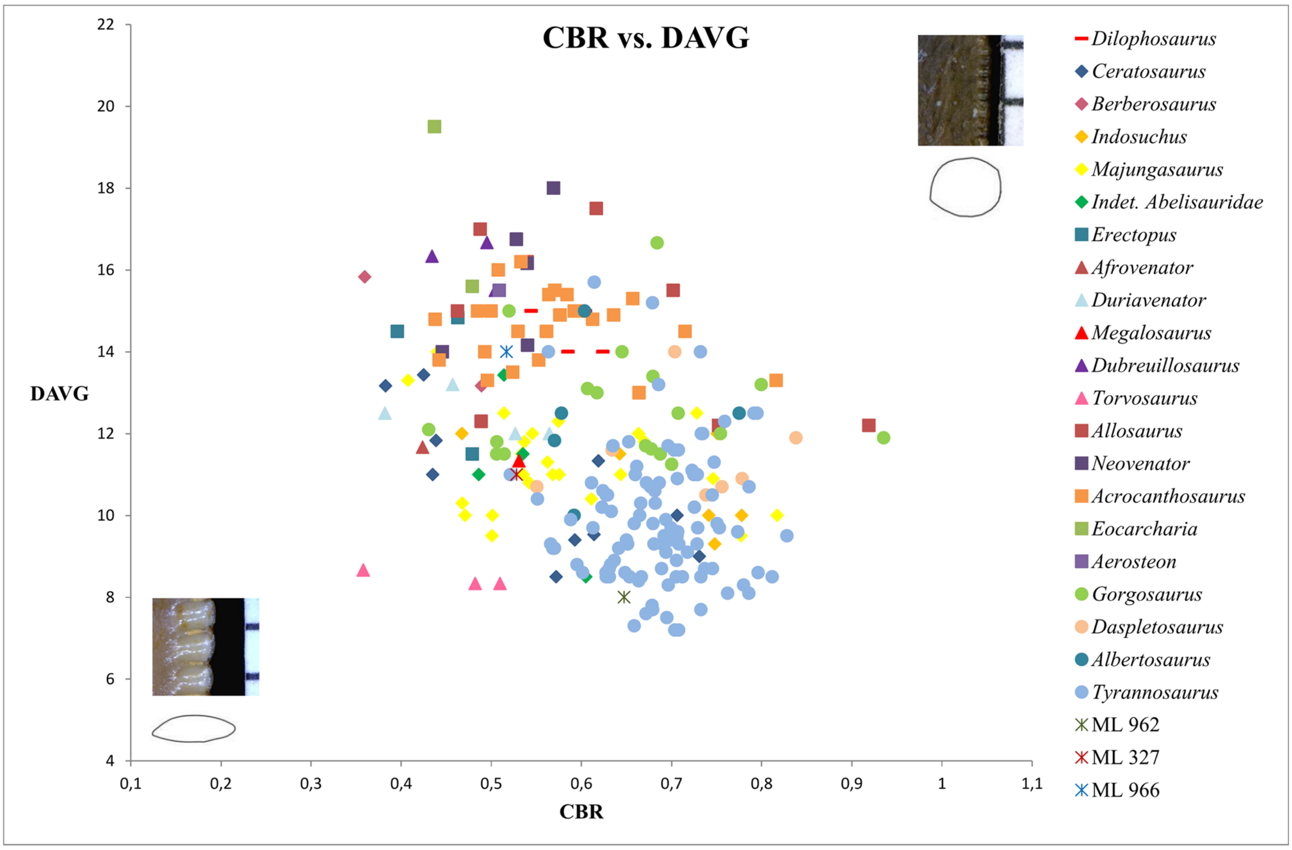


FIGURE 8. Plots of CBR versus DAVG of ML 962, ML 327, ML 966 and 21 theropod taxa comprising the data set. For reasons of clarity, only taxa with serration of less than 22 denticles were considered.

Bivariate plots of CBR and CHR reveal that ML 966 and ML 327 mainly occupy the same area of values as Abelisauridae (*Majungasaurus* + indeterminate abelisaurids), *Ceratosaurus*, *Allosaurus*, *Acrocanthosaurus* and *Gorgosaurus* teeth (Fig. 5). However, bivariate plots with MAVG or DAVG clearly show that the two teeth possess smaller mesial and distal denticles than any abelisaurids represented, with a number of denticles per five mm situated among the values of *Allosaurus*, *Acrocanthosaurus* and *Berberosaurus* (Figs 6–8). The number of denticles per five mm of ML 966 and ML 327 are indeed situated between 13 to 16, a higher number than in *Majungasaurus*, *Indosuchus*, *Rugops* and UCPC 10 (Smith 2007; Sereno & Brusatte 2008; pers. obs.) but comparable to that of the most basal abelisaurid *Kryptops* (Sereno & Brusatte 2008) and *Abelisaurus* (pers. obs.).

Due to the relatively important labiolingual compression of the base crown (CBR close to 0.5), ML 966 and ML 327 are most likely lateral teeth and have therefore been coded as such in our datasets. When the two isolated teeth are included in the dentition-based data matrix, the resulting consensus tree of the cladistic analysis retrieved both teeth together in a well-supported clade (Bremer support of 4) nested among abelisaurid theropods (Fig. 1). Both isolated teeth form the sister taxon of a clade encompassing the abelisaurids *Rugops*, *Kryptops* and *Majungasaurus*, and the monophyletic group formed by ML 966, ML 327 and these three abelisaurids is supported by two ambiguous synapomorphies: the long and well-developed interdenticular sulci of basal and mid-crown denticles on the distal carina (char. 105 and 106). When incorporated into the supermatrix, the cladistic analyses resulted in a poorly resolved consensus tree in which ML 327 and ML 966 were found as sister-taxa among the clade of Abelisauridae (Appendix, Fig. A10). The deletion of the wildcard taxa *Erectopus* and *Piatnitzkysaurus* resulted in a better resolved consensus tree in which ML 327 and ML 966 are still nested in the same clade within Abelisauridae (Fig. 2).

Tetanurae Gauthier, 1986

Megalosauroidea Fitzinger, 1843

Megalosauridae Fitzinger, 1843

***Torvosaurus tanneri* Galton & Jensen, 1979**

Referred material. ML 962 (Fig. 9).

Locality and horizon. Cliffs of Praia da Area Branca North, Praia da Area Branca, Lourinhã, Portugal. Bombaral Member, Lourinhã Formation, Tithonian, Upper Jurassic.

Description. ML 962 is an elongated tooth lacking the mesial part of the tip. Although most of the mesial and distal denticles are damaged and missing, their bases are still present so that it was possible to count the number of denticles basally, apically and at the mid-crown.

Crown. The tooth is particularly large, (CH of 85 mm) and the general shape of the tooth resembles the 'typical' blade-like theropod tooth by being labiolingually compressed, distally curved and having serrated carinae. However, the base is particularly narrow mesio-distally (CBL of 31.5 mm) and quite large labio-lingually (CBW of 20.2 mm) so that the crown-base has an ovoid cross-section (CBR of 0.64).

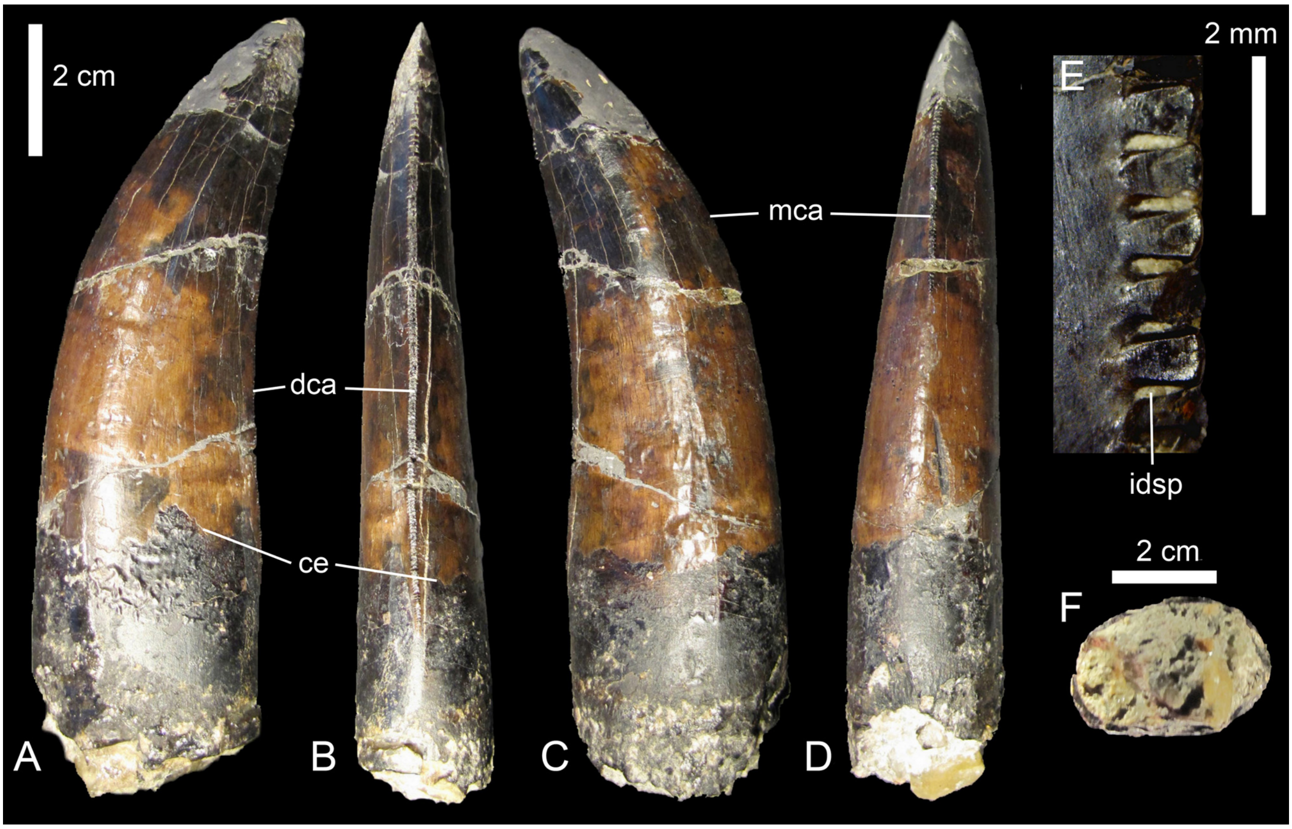


FIGURE 9. Isolated tooth of *Torvosaurus tanneri* (ML 962) in labial (A), distal (B), lingual (C), mesial (D) and basal (F) views. Apical denticles of the distal carina in labial view (E). Abbreviations: **ce**, cervix; **dca**, distal carina; **idsp**, interdenticular space; **mca**, mesial carina.

In lateral view, the mesial and distal margins of the root and basal half of the crown are roughly straight whereas the distal half of the crown is bent distally. The curvature of the crown is larger mesially than distally and the base of the crown is slightly larger than the mid-crown mesio-distally.

In distal view, the distal carina is medially positioned, slightly curved and bowed labially. The carina bears denticles all along the crown edge, from the preserved tip of the crown to the cervix.

In mesial view, the mesial carina, on the other hand, appears at the mid-crown, approximately 30 mm from the cervix, the basal part of the crown remaining smooth and rounded (Fig. 9D). The carina is labially positioned and weakly offset apically but slightly curves lingually towards the root, becoming medially positioned on the mesial margin of the crown. Both lingual and labial surfaces are baso-apically concave and the root surface remains almost straight.

In apical view, the tip is weakly labio-lingually oriented and medially positioned on the crown. The mesial carina forms just a low ridge whereas the distal carina is more acute, and bends lingually towards the root.

In cross section, the basal crown is elliptical (Fig. 9F) with both mesial and distal parts rounded. The labial face shows a short flattened surface in its centre whereas the lingual margin is weakly convex. Both labial and lingual surfaces are strongly mesio-distally convex all along the crown. The dentine layer is thin (0.6 mm in the lingual part) and its thickness is greater on the distal part of the crown (1.7 mm), the mesial part being absent. The length of the pulp cavity is 17.8 mm labio-lingually and around 28 mm mesio-distally.

Denticles. The mesial carina has 8 denticles at the mid-crown, and the number of denticles near the apex is unknown due to the missing part of tip of the crown (Table 3). The size of the denticles decreases towards the root from approximately the two-thirds of the crow, a tendency also observable on the distal carina but on a much longer distance.

The distal carina bears around 7 denticles per 5 mm at the apex, 8 at the mid-crown and 11 at the base of the crown, the latter being minute near the cervix. The biggest denticles can be found 20 mm below the apex of the crown and are the only denticles entirely preserved on the apical part of the distal carina. They are chisel-like in shape, mesio-distally longer than baso-apically and their main axis is perpendicular to the distal margin (Fig. 9E). A transversal section of the denticles would reveal a triangular shape as their bases are labio-lingually large and their tips are angular.

The labial and lingual surfaces of both mesial and distal denticles are slightly convex or completely flattened baso-apically, and only their basal and apical borders are rounded and curved to form the limits of the interdenticular spaces. The latter are deep and narrow and often filled with sediments. Their width tends to decrease towards the tip of the denticles which is slightly wider baso-apically than the base.

The external margin of mesial and distal denticles is symmetrically and slightly convex and does not point towards the tip of the crown. The denticle surface is covered by enamel, but the layer of enamel has disappeared in the middle of several denticles surfaces. This might, however, be due to erosion rather than initial wear. A few other denticles are also preserved on the basal part of the distal carina. They are quite different from the apical denticles by having a much more rounded external margin. The denticles are symmetrically rounded in lateral view and their labial and lingual surfaces are strongly convex. The interdenticular space is shallower and also slightly wider than in the apical denticles.

The mesial and distal denticles differ in their elongation; the few preserved denticles on the mesial carina are longer baso-apically than mesio-distally. The interdenticular space of mesial denticle is narrow and deep and the external margin of the denticle is slightly convex, almost flat.

Short interdenticular sulci appear between the distal denticles, but not in the most apical and basal ones. These shallow grooves running on both labial and lingual surfaces of the crown are inclined towards the root and more pronounced on the lingual face. They are, however, totally absent between the mesial denticles.

Surface. The crown surface is rugged and shows many irregularities. Possibly due to erosion and wear, the enamel texture of the crown is completely smooth and does not show any microscopic sculpturing. Two large transversal undulations appear on both labial and lingual surface of the basal part of the crown, but those deep structures do not correspond to the numerous and shallow transversal undulations illustrated by Brusatte *et al.* (2007) and might be due to deformation.

Discussion. Since most of the root is missing and the pulp cavity is excavated and filled with sediment, we interpret ML 962 as a shed tooth (Bakker & Bir 2004). A very large and fairly straight crown showing a labio-lingually compression, distinct serrations on mesial and distal carinae, and a slight curvature of the tip distally is a combination of characters observed in theropod dinosaurs only (Buffetaut & Ingavat 1986), especially in the Upper Jurassic of Portugal (pers. obs.).

With a crown height of more than eight centimetres (CH of 85.8 mm), ML 962 is a large crown belonging to a particularly large theropod. Although size is a plastic feature and must be used carefully for systematic purpose, this feature has already been demonstrated to be useful for discriminating teeth of different theropod taxa (Smith 2005; Smith *et al.* 2005; Han *et al.* 2011). Indeed, to our knowledge, crowns of more than eight centimetres are only borne by non-coelurosaur averostrans and derived Tyrannosauroidea, as they can be found in Ceratosauridae

(*Ceratosaurus*, *Genyodectes*), Megalosauroidea (e.g., *Torvosaurus* and *Spinosaurus*), Allosauroidea (e.g., *Carcharodontosaurus*, *Mapusaurus*, *Giganotosaurus*) and Tyrannosauridae (e.g., *Tyrannosaurus*, *Tarbosaurus*).

The denticles of ML 962 are also particularly coarse and an average of 8 denticles per 5 mm on both carinae is a condition present in particularly large basal tetanurans. Such feature can indeed be observed in Megalosauridae (Rauhut & Werner 1995; Smith 2007; pers. obs.), Carcharodontosaurinae (Rauhut & Werner 1995; Veralli & Calvo 2004; Corria & Currie 2006; pers. obs.) and Tyrannosauridae (Rauhut & Werner 1995; Smith 2005; pers. obs.). To our knowledge, less than 9 denticles on both mesial and distal carinae is a feature absent in basal Megalosauroidea (e.g., *Piatnitzkysaurus*), some Megalosauridae (e.g., *Eustreptospondylus*, *Dubreuillosaurus*), non-carcharodontosaurine Allosauroidea (e.g., *Allosaurus*, *Neovenator*, *Acrocanthosaurus*), and all Ceratosauridae and Spinosauridae (pers. obs.). *Indosuchus raptorius* (AMNH 1753, 1955, 1960) is the only abelisaurid possessing less than 8 denticles per 5 mm on both carinae but the teeth are typical of abelisaurids as their crowns are low and weakly recurved distally. It is therefore unlikely that ML 962 belongs to one of these groups of theropods.

With an elliptical outline of the crown base in cross-section (CBR of 0.6) and a strong elongation, ML 962 is also very peculiar. In most carnivorous theropods, the lateral teeth are usually strongly medio-laterally flattened, giving a lenticular or lanceolate outline of the base crown in cross-section, and an elliptical outline of the crown base is usually present in mesialmost teeth, i.e., the premaxillary and mesialmost teeth of the dentary and maxilla (pers. obs.). Among basal tetanurans except Spinosauridae (which possess conical and fluted crowns along the tooth row), an ovoid subcircular outline of the crown base can clearly be observed in mesialmost teeth of megalosaurids such as *Duriavenator hesperis* (NHM R.332), *Dubreuillosaurus valesdunensis* (MNHN 1998-13) and *Torvosaurus tanneri* (Britt 1991) and allosauroids like *Acrocanthosaurus atokensis* (NCSM 14345) and *Giganotosaurus carolinii* (MUCPv-CH-1; Candeiro 2007). Some tetanurans like *Acrocanthosaurus*, *Giganotosaurus* and *Tyrannosaurus* can also have an ovoid cross-section of the base crown more distally in the jaws (Smith 2005; Candeiro 2007; pers. obs.). Nevertheless, the lateral teeth of those theropods are much more massive and incrassate, the labiolingual width of the crown base being sometimes equal or larger than its mesiodistal length in Tyrannosauridae, giving them the typical 'banana' shape (Smith 2005; pers. obs.). We therefore interpret ML 962 as a mesialmost tooth of a basal tetanuran.

This large crown also possesses a mesial carina medially positioned on the mesial margin of the crown, running slightly diagonally and terminating at the mid-crown, well above the cervix. Among mesialmost teeth of tetanurans, such a combination of features can be observed in Megalosauridae such as *Torvosaurus tanneri* (BYUVP 2003), *Duriavenator hesperis* (NHM R.332) and *Dubreuillosaurus valesdunensis* (MNHN 1998-13) as well as the carcharodontosaurid *Acrocanthosaurus atokensis* (NCSM 14345). In Allosauridae and Tyrannosauroidea, the mesial carina extends to the cervix of the crown, or very close to it, and either twists lingually like in *Allosaurus fragilis* (AMNH 851; CM 21703; SMA 0005/02) and *Proceratosaurus bradleyi* (Rauhut *et al.* 2010) or faces entirely lingually in more derived tyrannosauroids, giving the typical D-shape cross-section of the base-crown (Smith 2005; Sereno *et al.* 2009; pers. obs.). The distal carina of ML 962 is also centrally positioned on the distal margin of the crown, a feature visible in the mesialmost teeth of megalosaurids such as *Eustreptospondylus oxoniensis* (OUMNH J.13558), *Dubreuillosaurus valesdunensis* (MNHN 1998-13) and *Duriavenator hesperis* (NHM R.332). On the other hand, the distal carina of mesialmost teeth of carcharodontosaurids such as *Acrocanthosaurus atokensis* (NCSM 14345) and *Giganotosaurus carolinii* (MUCPv-CH-1) is slightly to strongly displaced labially on the distal margin of the crown (a similar feature is found in *Genyodectes* and *Dromaeosaurus* for instance; Currie *et al.* 1990; Rauhut 2004; pers. obs.), so that the mesial and distal carinae are not aligned on a same plan like in megalosaurid theropods (pers. obs.). It is, therefore, more likely that ML 962 belongs to Megalosauridae than Carcharodontosauridae.

Among Megalosauridae, a very large and strongly elongated crown (CHR > 2.5) with large chisel-like and symmetrically rounded denticles (less than 9 denticles on the distal carina) seems to be a combination of characters only seen in *Torvosaurus* (pers. obs.). The general shape and outline of ML 962 also resemble very much those of one probable *Torvosaurus tanneri* shed tooth illustrated by Jensen (1985: fig. 5e) and the first dentary tooth of *Torvosaurus* (BYUVP 2003). These two teeth share with ML 962 same curvature and elongation as well as a lateral face that is particularly convex. In addition, the outline of the basal crown seems to fit with the mesialmost dentary alveoli of *Torvosaurus* (Britt 1991: fig. 3f), the premaxillary alveoli being more elongated mesio-distally (or labio-lingually for the first alveolus).

Both morphological and cladistic analyses support the identification of ML 962 to the taxon *Torvosaurus*.

Bivariate plots of MAVG and DAVG (Fig. 7) show that ML 962 possesses the same number of denticles per five mm as *Carcharodontosaurus*, *Tyrannosaurus* and *Indosuchus*, and close values of denticles as *Torvosaurus*. However, bivariate plots of CHR and DAVG clearly illustrates the same values of ML 962 and *Torvosaurus* teeth (Fig. 6), on the opposite of bivariate graphs with CBR, as CBR values of ML 962 and *Torvosaurus* teeth are significantly different (Figs. 5, 8). This can be explained by the absence of mesial teeth of *Torvosaurus* in our dataset. As it has been mentioned previously, mesialmost teeth of many theropods are usually labiolingually thicker than lateral teeth, and this is clearly the case in *Torvosaurus* and Megalosauridae in which mesialmost teeth have an elliptical to rounded cross-section at the crown base instead of a lenticular outline typically present in the lateral teeth of these taxa. Following this observation, characters on mesialmost teeth were only coded in ML 962 in our data matrix.

The cladistic analysis performed on the datamatrix of dentition-based characters recovered ML 962 as a megalosaurid theropod, forming a polytomy with all members of this clade (Fig. 1). This lack of resolution can be explained by the absence of mesialmost teeth in *Afrovenator* and *Megalosaurus*, and the little information collected from mesialmost dentition of *Eustreptospondylus*, *Duriavenator* and *Torvosaurus* in our dataset. A similar position within the megalosaurid clade was found when the cladistic analysis was performed on the supermatrix, but ML 962 forms a polytomy with the megalosaurids *Torvosaurus*, *Megalosaurus*, *Afrovenator* and *Duriavenator* that bear large teeth (Fig. 2, Appendix Fig. A10).

Following the results of both cladistic and morphological analyses, we identify ML 962 as a mesial tooth, perhaps a dentary tooth, belonging to the species *Torvosaurus tanneri*. Material of *Torvosaurus tanneri* are not rare in the Kimmeridgian—Tithonian of Europe and North America and have been reported several times in the Lourinhã Formation previously (Mateus & Antunes 2000b; Mateus 2005; Mateus *et al.* 2006). Therefore, this referral to *Torvosaurus* is consistent both stratigraphically and biogeographically.

Neotetanurae Sereno *et al.*, 1994

Coelurosauria von Huene, 1914

Dromaeosauridae Matthew & Brown, 1922

***Richardoestesia* Currie *et al.*, 1990**

***Richardoestesia* aff. *R. gilmorei* Currie *et al.*, 1990**

Referred material. ML 939 (Fig. 10).

Locality and horizon. Cliffs of Valmitão South, Lourinhã, Portugal. Amoreira-Porto Novo Member, Lourinhã Formation, Late Kimmeridgian, Upper Jurassic.

Description. The crown is entirely preserved but shows an important spalled surface extending on the apical part of the mesial margin of the tooth. A small piece and some denticles of the distal carina are missing but most of them are intact and well-preserved. The tooth only preserved the basal part of the root.

Crown. The crown is small (CH of 5.1 mm), slightly elongated (CBH of 1.82) and strongly compressed labio-lingually (CBR of 0.5; Table 3). The tip is strongly recurved distally and the apex is pointed, mostly due to the wear facet. The mesial carina is missing and might have been worn on the tip of the crown. The distal carina is serrated and bears denticles from the cervix to the apex.

In lateral view, the crown is straight along the basal part, then abruptly curves distally at two-thirds of its height at an angle of 55° to the vertical, forming an acute backward tip. The most basal part of the crown is slightly constricted mesio-distally, but the constriction only occurs on the mesial margin of the crown, the distal margin being straight along the first fourth of the crown. The distal carina is universally concave, but the carina curves above the straight basal margin, and the distal part of the carina is straight. The mesial margin is convex above the cervix only on the basal half of the crown, the other half remaining flat due to the wear facet. A convex surface delimited by a longitudinal groove mesially and a flattened or slightly concave surface distally appears on both lingual and labial faces. This large mesial ridge follows the same curvature of the crown and its mesio-distal width decreases towards the tip. It starts one-third of the way from the base of the crown on the labial face and from the apical part of the root on the lingual surface. Both lingual and labial grooves are narrow and reach the wear facet at the tip.

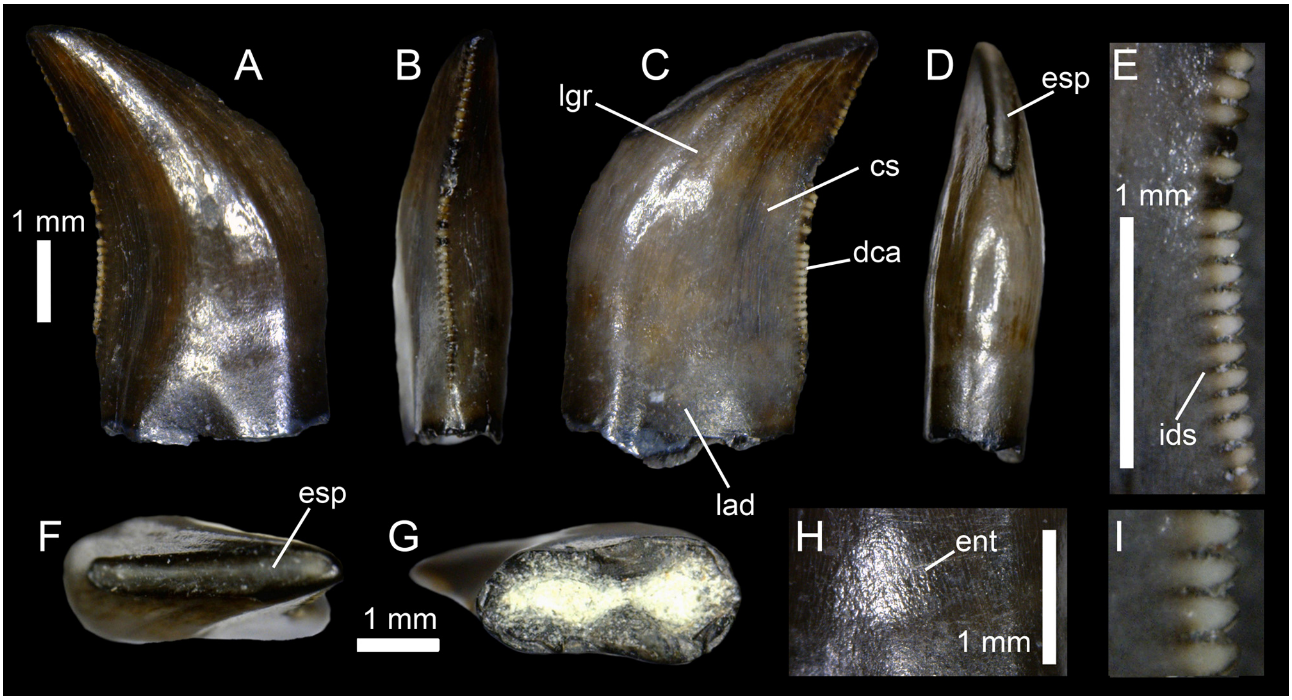


FIGURE 10. Isolated tooth (ML 939) of *Richardoestesia* aff. *R. gilmorei* in lingual (A), distal (B), labial (C), mesial (D), apical (F) and basal (G) views. Mid-crown denticles of the distal carina in labial (E, I) views, and enamel texture in lingual (H) view. Abbreviations: **cs**, concave surface; **dca**, distal carina; **ent**, enamel texture; **esp**, enamel spalling; **ids**, interdenticular sulcus; **lad**, labial depression; **lgr**, longitudinal groove.

In mesial view the crown tip is straight and curves neither labially nor lingually. Both labial and lingual faces are weakly convex and the crown-base width is slightly narrower than the mid-crown width. The crown remains, however, strongly compressed labio-lingually all along its height, and the crown width slightly decreases from the mid-crown to the tip.

In distal view, the most basal part of the serrated carina is straight and vertical but then curved all along the rest of the crown with the bow directed lingually. The distal carina is slightly oriented labially (we regarded the labial face of the crown as the face towards which the distal carina was displaced, at it is almost always the case in theropods; pers. obs.), and the labial face adjacent to the carina is flat whereas the lingual surface near the carina is concave.

In apical view, the basal part of the mesial margin is strongly convex and the wear facet situated on the distal part forms a narrow flat surface revealing the enamel and the dentine layers. In basal view, the crown-base forms an "eight-shaped" in cross section (Fig. 10G) due to the basal concavity on both labial and lingual side of the crown. The concave surface on the lingual face is shallow, triangular in shape and extends on one-third of the crown whereas the one on the labial face is slightly deeper and ends at the cervix level. The mesial part of the crown is labio-lingually wider (1.2 mm) than the distal part (1 mm). The dentine layer is thicker in the centre of both labial and lingual sides, giving an even well-pronounced "eight-shaped" to the pulp cavity, thinner distally.

Denticles. Only the distal carina is preserved and serrated, and the morphology of the denticles varies along the carina. With 10 denticles per 1 mm basally and at the mid-crown and 9 apically, the denticles slightly increase in size near the apex. The basal denticles are longer mesio-distally than baso-apically. In lateral view, they are tongue-shaped with their external margin strongly convex, parabolic and symmetrically rounded or slightly pointing towards the tip of the crown (Fig. 10I), giving them an asymmetrical outline. Although the basal denticles become mesio-distally shorter towards the root and the mid-crown, they share a same baso-apical width than denticles at mid-height of crown. On the other hand, the apical denticles are short and baso-apically larger than the basal ones. The most apical denticles are cartouche-shaped with their external margin symmetrically or asymmetrically convex. These denticles are also mesio-distally short and just form a small symmetrical bump at the apex in lateral view. In apical view, the lingual and dorsal surfaces of the body of the denticles are convex, and the denticle tip is chisel-like in shape.

The interdenticular sulci of basal denticles are absent or very short. When present, they are shallow and straight, extending perpendicular to the distal margin on the labial and lingual faces from between the denticles. The interdenticular sulci are totally absent in the apical denticles. The interdenticular space of distal denticles is narrow, slightly larger in the apical denticles, and usually filled with sediment.

Surface. The enamel texture of the crown surface is irregular and shows finely wrinkled non-oriented structures on both sides (Fig. 10H). Except for the presence of those microscopic sculptures, there is no other ornamentations on the crown surface.

Discussion. ML 939 is interpreted as a shed tooth as it lacks most of the root and the pulp cavity is slightly excavated.

The presence of a basal constriction between the crown and root has been observed in basal most theropods like *Eoraptor lunensis* (Sereno *et al.* 1993) and many coelurosaurs such as the tyrannosauroid *Proceratosaurus* (Rauhut *et al.* 2010), the compsognathid *Compsognathus* (Zinke & Rauhut 1994), the ornithomimosaur *Pelecanimimus* (Pérez-Moreno *et al.* 1994), alvarezsaurids (Perle *et al.* 1993), basal oviraptorosaurs (Osmólska *et al.* 2004), therizinosaurs (e.g., Russell & Dong 1993; Zhao & Xu 1998; Kirkland *et al.* 2005), troodontids (e.g., Currie *et al.* 1990; Baszio 1997; Norell *et al.* 2000; Currie & Dong 2001; Sankey *et al.* 2002; Averianov & Sues 2007), the dromaeosaurids *Microraptor* (Xu *et al.* 2000), and many basal avialans such as *Archaeopteryx* and *Cathayornis* (Hou 1997; Feduccia 2002).

Nevertheless, the presence of an eight-shape outline of the crown-base in cross-section is a common feature of many deinonychosaurs such as *Saurornitholestes* (Currie *et al.* 1990; Sankey *et al.* 2002), *Tsaagan* (Norell *et al.* 2006), *Pyroraptor* (Allain & Taquet 2000; Gianechini *et al.* 2011b), *Buitreraptor* (Gianechini *et al.* 2011b) and the enigmatic theropod *Richardoestesia gilmorei* (Currie *et al.* 1990). With perhaps the exception of *Berberosaurus* (MNH Pt339), the base crown of non-maniraptoriform theropods like coelophysoids, ceratosaurs, megalosauroids, allosauroids and most of tyrannosauroids can be subcircular, ovoid, elliptical, lenticular or bean-shaped but not eight-shaped (pers. obs.). This also seems to be the case in more derived coelurosaurs such as Compsognathidae (e.g., Zinke 1998: fig. 2; Dal Sasso & Maganuco 2011: fig. 44 to 48), therizinosaurs (Clark *et al.* 1994: fig. 12; Zhao & Xu 1998: fig. 1), Oviraptorosaurs (Balanoff *et al.* 2009: fig. 2-7) and perhaps *Ornitholestes hermanni* (AMNH 619). The latter possesses a median concave surface on the labial surface of some crowns, but does not seem to have any on the lingual one, giving a bean-shaped outline of the crown base in cross section (pers. obs.). The tyrannosaurid *Alioramus altai* (IGM 100-1844) and the neovenatorid *Orkoraptor burkei* (Novas *et al.* 2008; Benson *et al.* 2010) are two exceptions; the latter possesses a particularly developed median depression on both labial and lingual sides of the crown. To our knowledge, it represents the second non-coelurosaurian theropods with an eight-shaped cross section of the crown (the other one being *Berberosaurus*), and other neovenatorids such as *Neovenator* (MIWG 6348), *Aerosteon* (Sereno *et al.* 2008), *Fukuiraptor* (Azuma & Currie 2000; Currie & Azuma 2006; Molnar *et al.* 2009) and *Australovenator* (Hocknull *et al.* 2009) do not display this peculiarity. An eight-shaped outline of the base crown was also reported in the coelophysoid *Liliensternus* by Gianechini *et al.* 2011 (Fig. 3c). Nevertheless, based on the crown morphology of this taxon, it is more likely that the eight-shaped outline corresponds to a cross section in the root rather than at the base-crown. ML 939 has a low crown with small denticles and a mesiodistal constriction at the base and therefore contrasts with the elongated teeth of Neovenatoridae and Tyrannosauridae which bear large denticles and never show a mesio-distal constriction at the base crown (pers. obs.). Therefore, it is unlikely that this shed tooth belongs to a non-maniraptoriform theropod.

ML 939 serrations are particularly minute and the distal carina bears nine to ten denticles per one millimetre. Among deinonychosaurs, such condition only exists, to our knowledge, in the taxa *Richardoestesia gilmorei* and *Richardoestesia isosceles* (e.g., Currie *et al.* 1990; Sankey 2001; Sankey *et al.* 2002; Baszio 1997; Sankey 2008; Larson 2008; Larson & Currie 2013) but the dental morphology of the latter (i.e., teeth with no constriction, straight to slightly recurved, crown subtriangular in outline) strongly differs with that of ML 939. The external margins of the denticles are symmetrically rounded or slightly curved towards the tip of the crown, and the basal and mid-crown denticles have similar size on the distal carina, two conditions shared by *Richardoestesia gilmorei* (Currie *et al.* 1990 fig. 8.4; Baszio 1997; Larson 2008). Although the presence of a longitudinal groove mesially positioned on the crown has never been noticed in *Richardoestesia gilmorei*, this feature seems to be present in some specimens assigned to this species (see Baszio 1997: Plate IV fig. 47; Sankey *et al.* 2002: fig. 5 n°6), and longitudinal grooves have already been observed in the genus *Richardoestesia* (Currie *et al.* 1990; Sankey 2001; Rauhut 2002). Nevertheless, several differences exist between ML 939 and the teeth of the holotype of *Richardoestesia gilmorei*, namely, the presence of interdenticular sulci and mesio-distally elongated distal denticles, and the absence of a mesial carina reaching the cervix in ML 939. Although the mesial serration are usually restricted to the apicalmost part of the crown in *R. gilmorei*, the mesial carina always reaches the cervix in this taxon (Derek Larson pers. comm.).

With a strongly labiolingually compressed profile of the crown, ML 939 was coded as a lateral tooth. The cladistic analysis performed on the dentition-based dataset recovered ML 939 as a close relative of *Richardoestesia gilmorei* (Fig. 1). The clade encompassing those two taxa is defined by two ambiguous synapomorphies: a weak constriction occurring at the base crown (characters 63) and subequal number of distal denticles basally and at the mid-crown (character 99). The analysis performed on the supermatrix recovered it as a Dromaeosauridae along with *Richardoestesia* (Fig. 2; Appendix, Fig. A10).

Richardoestesia gilmorei is a common species in the Late Cretaceous of Northern America and teeth belonging to this taxon, or referred to it, have been found in the Santonian Milk River Formation, the Campanian Belly River Group, the Campanian-Maastrichtian Horseshoe Canyon Formation, and the Maastrichtian Scollard Formation of Alberta, the Frenchman Formation of Saskatchewan (Canada), the Hell Creek Formation of Montana and the Lance Formation of Wyoming (e.g., Currie *et al.* 1990; Baszio 1997; Longrich 2008; Sankey 2008; Larson 2008; Larson *et al.* 2010; Larson & Currie 2013). Given the results of the cladistic analysis, *R. gilmorei* likely belongs to Dromaeosauridae than any other theropod clade.

Small theropod teeth from the Upper Jurassic of Portugal have already been assigned with caution to the genus *Richardoestesia* by Zinke (1998). Nevertheless, they strongly differ from ML 939 by being extremely elongated and weakly recurved, resembling the elongated and subtriangular teeth assigned to *Richardoestesia* sp. by Baszio (1997), and *Richardoestesia isosceles* by Sankey (2001). Following the cladistic analysis and the diagnosis of teeth belonging to *Richardoestesia* sp. (and *R. gilmorei* in particular) given by Currie *et al.* (1990), Baszio (1997) and Longrich (2008), and since the presence of teeth similar to those of *Richardoestesia isosceles* has already been reported in the Late Jurassic of Portugal (Zinke 1998), ML 939 is ascribed to the possible dromaeosaurid *Richardoestesia*, which extends the stratigraphic range of the taxon back to the Jurassic. ML 939 is similar to *R. gilmorei* teeth in many aspects, but this taxon has only been recorded in the Late Cretaceous of North America, more than 90 million years after the Jurassic/Cretaceous boundary. We therefore consider that ML 939 belongs to a close relative of *Richardoestesia gilmorei*.

Discussion

Results of both cladistic and morphometric analyses indicate that ML 327 and ML 966 belong to a member of the Abelisauridae, representing the earliest record of this clade in Laurasia and the first record of abelisaurids in the Kimmeridgian-Tithonian.

Abelisauridae have often been considered as one of the dominant terrestrial predators in most Gondwanan landmasses during the Cretaceous (Carrano & Sampson 2008). Their presence is now attested in the Jurassic of Gondwana as a newly described abelisaurid, *Eoabelisaurus mefi*, comes from the Middle Jurassic of Argentina, extending the lineage of this clade by more than 40 million years (Pol & Rauhut 2012). Abelisaurid teeth have also been reported in the Middle Jurassic of the Mahajanga basin of Madagascar by Maganuco *et al.* (2005).

With the exception of *Eoabelisaurus* and Middle Jurassic abelisaurids from Madagascar, the oldest records of Abelisauridae come from the Hauterivian-Barremian of Argentina (Rauhut *et al.* 2003) and the Aptian-Albian of Niger (Sereno & Brusatte 2008) as all other potential abelisaurid remains from the Middle and Late Jurassic of Gondwana and Laurasia pertained to Abelisauroidea (e.g., Rauhut 2005; Allain *et al.*2007; Carrano & Sampson 2008; Ezcurra & Agnolín 2012). Some hind limb elements from the Tendaguru Beds of Tanzania (Kimmeridgian—Tithonian) might however pertain to an abelisaurid (Rauhut 2011). In the Morrison Formation, a humerus and a proximal tibia were assigned to the basal ceratosaur *Elaphrosaurus* (Galton 1982; Chure 2001), however the tibia resembles isolated abelisauroid tibiae from Tendaguru and may attest the presence of Abelisauroidea in the Western Hemisphere in the Upper Jurassic (Rauhut 2005; Carrano & Sampson 2008). Abelisauroid taxa seems however to be particularly rare elements of the Morrison Formation fauna (Rauhut 2005). In Europe, abelisauroid remains are scarce as well and Abelisauridae have only been collected from the Upper Cretaceous of France (Buffetaut *et al.* 1988; Le Loeuff & Buffetaut 1991; Carrano & Sampson 2008; Tortosa *et al.* 2010). The two abelisaurid teeth discovered in the Late Jurassic of Portugal therefore indicate a first radiation of this clade in the European archipelagos well before the Late Cretaceous.

With Allosauridae, Ceratosauridae, Megalosauridae, Tyrannosauroidea, Compsognathidae, Dromaeosauridae and Archaeopterygidae previously documented, the theropod fauna of the Lourinhã Formation included elements specific to Europe (*Compsognathus* and *Archaeopteryx*) and also those known in Northern America (*Allosaurus*, *Ceratosaurus*, *Torvosaurus*, *Richardoestesia*). The presence of Abelisauridae adds for the first time a typical Gondwanan element to the large diversity of the Laurasian theropods in the Late Jurassic of the Iberian Peninsula. As it was already suggested by Buffetaut (1989) and Le Loeuff (1991) for Cretaceous theropods, the European Jurassic theropod fauna may have been a mixture of Gondwanan and Laurasian elements where the typical Gondwanan abelisaurids are in minority.

ML 939 assigned to *Richardoestesia* aff. *R. gilmorei* supports the presence of the taxon *Richardoestesia* and the clade of Dromaeosauridae back to the Upper Jurassic in Europe, as it was previously suggested (e.g., Zinke 2000; Van der Lubbe *et al.* 2009). Dromaeosaurids and the lineage leading to the genus *Richardoestesia* likely originated in Laurasia in the Middle to Late Jurassic while the temporary regional uplift around the Callovian/Oxfordian transition created the temporary opportunity of land gateways between North America and the Iberian Meseta.

Conclusions

The description and identification of four theropod teeth from the Lourinhã Formation provide additional information on the Late Jurassic dinosaur fauna of the Iberian Peninsula and the biogeographical and stratigraphic distribution of Abelisauridae. Based on both morphological and cladistic analyses using a new data matrix of 141 characters on teeth, two isolated teeth have been successfully identified as belonging to an Abelisauridae, one to the megalosaurid *Torvosaurus tanneri*, and one as a close relative of the enigmatic coelurosaur *Richardoestesia gilmorei*, increasing the already high diversity of predatory dinosaurs living in the Kimmeridgian–Tithonian of Southern Europe. If these referrals are correct, theropods from the Upper Jurassic of Europe are now represented by Ceratosauridae, Abelisauridae, Megalosauridae, Allosauridae, Tyrannosauroidea, Compsognathidae, Deinonychosauria and Avialae, corresponding to a mixture of Laurasian and Gondwanan elements.

Although materials of *Torvosaurus tanneri* and a close relative of *Richardoestesia* have already been identified in the Upper Jurassic of Portugal, an abelisaurid is here reported for the first time in the Lourinhã Formation. This represents the first record of Abelisauridae in the Late Jurassic of Laurasia and one of the oldest records in the globe, revealing a first radiation of this clade in Europe back to the Jurassic.

As previously noted by Smith *et al.* (2005) and more recently by Han *et al.* (2011), this study also shows that morphometric data, combined with numerous anatomical characters on teeth, proves to be useful in order to clarify the phylogenetical position of isolated theropod teeth. Although many dentition-based characters are homoplastic, several theropod clades such as Ceratosauridae, Abelisauridae, Spinosauridae, Megalosauridae and Tyrannosauroidea have distinctive teeth, characterized by a combination of features that were not taken into consideration previously. This provides tools for the identification of isolated theropod teeth, often more common than bones, therefore allowing expanding our knowledge about the geography and chronology of theropod taxa, as demonstrated in this case for abelisaurids. This is particularly encouraging for future research on theropod dentition and, thereby, additional information regarding the size and shape of crown, carinae, denticles and enamel texture and microstructure remain to be collected on teeth of many theropod taxa. Moreover, the dentition of a large number of theropod dinosaurs is usually briefly described, sometimes even avoided, and detailed descriptions of premaxillary, maxillary and dentary teeth of many well-preserved theropods such as *Ceratosaurus*, *Torvosaurus*, *Allosaurus* and *Sinraptor* still need to be done and would greatly facilitate the assignment of isolated teeth to specific clades or taxa.

Acknowledgements

The authors would like to thank Derek Larson (Uni. Toronto) who helped coding the dentition of *Richardoestesia gilmorei* based on its personal observation of the holotype, as well as Ricardo Araújo (SMU), Steve Brusatte (Uni. Edinburgh), Nicolai Christiansen (Milan, Italy), Azzurra Cillari, and Mickey Mortimer for useful information regarding coding character and theropod dentition. Teeth of many nonavian theropods were examined in several institutions all over the world and access to the material was possible thanks to Louis Jacobs (SMU), Dale Winkler (SMU), Anthony Fiorillo (DMNH), Paul Sereno (Uni. Chicago), Peter Makovicky (FMNH), William Simpson (FMNH), Matthew Lamanna (CMNH), Amy Henrici (CMNH), Matthew Carrano (NMNH), Michael Brett-Surman (NMNH), Sandra Chapman (NHM), Paul Barrett (NHM), Paul Jeffery (OUMNH), Stephen Hutt (MIW), Ronan Allain (MNHN), Rainer Schoch (SMNS), Hans-Jacob Siber (SMA), Christiano Dal Sasso (MSNM), Alejandro Kramarz (MACN), Fernando Novas (MACN), Ruben Barbieri (MPCA), Leonardo Salgado (MUCPv), Juan Ignacio Canale (MUCPv-CH), Rodolfo Coria (MCF-PVPH), Cecilia Succar (MCF-PVPH), Jorge Calvo (CePaLB), Ricardo Martínez (PVSJ), Carl Mehling (AMNH), Mark Norell (AMNH), David Krauze (SBU), Joseph Groenke (SBU), Paul Brinkman (NCSM), Lindsay Zanno (NCSM) and Jorge Sequeira (LNEG). Photographs of theropod teeth were kindly shared by Martín Ezcurra (LMU), Matthew Lamanna (CMNH), Matthew Carrano (NMNH), Steve Brusatte (Uni. Edinburgh), Emanuel Tschopp (UNL), Mattia Antonio Baiano, Drew Eddy (Uni. Texas), Roger Benson (Uni. Oxford), Ricardo Araújo (SMU), Vince Shneider (NCSM), Karin Peyer (MNHN), Juan Canale (MUCPv-CH) and Andrea Cau (MGG), and the authors would like to address their sincere thanks to all of these people. Morphometric data on theropod teeth were generously communicated by Carlos Roberto Candeiro (UFB), Lisa Buckley (Uni. Alberta), James Farlow (IPFW), Julia Sankey (CSU), Federico Fanti (MGPGC) and Steven Sweetman (Uni. of Portsmouth) and many missing papers on theropod dentition were kindly sent by Cristiano Dal Sasso (MSNM), Andrea Cau (MGG), Steve Brusatte (Uni. Edinburgh) and Mickey Mortimer. We acknowledge the use of the Willi Hennig Society edition of TNT for the cladistic analysis and Phylopic for the theropod silhouettes, and thank Scott Hartman and Funkmonk for accepting to use their artworks. Comments on an early version of the manuscript by Derek Larson (Uni. Toronto), Steve Brusatte (Uni. Edinburgh) and Roger Benson (Uni. of Oxford) considerably improved the quality of the paper. Many thanks to G. A. Martin who provided corrections of spelling mistakes. This research was supported by the Fundação para a Ciência e a Tecnologia (FCT) scholarship SFRH/BD/62979/2009 (Ministério da Ciência, Tecnologia e Ensino superior, Portugal) and the European Science Foundation (ESF). C.H. dedicates this paper to J. Hendrickx for his support in the visit of collections all over the world, and to the memory of J. Ernst.

References

Abler, W.L. (1992) The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals. *Paleobiology*, 18, 161–183.

Allain, R. (2002) Discovery of a megalosaur (Dinosauria, Theropoda) in the middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. *Journal of Vertebrate Paleontology*, 22, 548–563. http://dx.doi.org/10.1671/0272-4634(2002)022[0548:domdti]2.0.co;2

Allain, R. (2005) The enigmatic theropod dinosaur *Erectopus superbus* (Sauvage 1882) from the Lower Albian of Louppy-le-Chateau. *In*: Carpenter, K. (Ed.), *The Carnivorous Dinosaurs*. Indiana University Press, Bloomington, pp. 72–86.

Allain, R. & Taquet, P. (2000) A new genus of Dromaeosauridae (Dinosauria, Theropoda) from the Upper Cretaceous of France. *Journal of Vertebrate Paleontology*, 20, 404–407. http://dx.doi.org/10.1671/0272-4634(2000)020[0404:angodd]2.0.co;2

Allain, R., Tykoski, R., Aquesbi, N., Jalil, N.-E., Monbaron, M., Russell, D. & Taquet, P. (2007) An abelisauroid (Dinosauria: Theropoda) from the Early Jurassic of the High Atlas Mountains, Morocco, and the radiation of ceratosaurs. *Journal of Vertebrate Paleontology*, 27, 610–624. http://dx.doi.org/10.1671/0272-4634(2007)27[610:aadtft]2.0.co;2

Antunes, M.T. (1990) Dinossauros de Sesimbra e Zambujal - Episódios de há cerca de 140 milhões de anos. *Sesimbra Cultural*, 0, 12–14.

Antunes, M.T. & Mateus, O. (2003) Dinosaurs of Portugal. *Comptes Rendus Palevol*, 2, 77–95. http://dx.doi.org/10.1016/s1631-0683(03)00003-4

Araújo, R., Castanhinha, R., Martins, R.M.S., Mateus, O., Hendrickx, C., Beckmann, F., Schell, N. & Alves, L.C. (2013) Filling the gaps of dinosaur eggshell phylogeny: Late Jurassic Theropod clutch with embryos from Portugal. *Scientific*

Reports, 3, 1924.
http://dx.doi.org/10.1038/srep01924
Averianov, A.O. & Sues, H.-D. (2007) A new troodontid (Dinosauria: Theropoda) from the Cenomanian of Uzbekistan, with a review of troodontid records from the territories of the Former Soviet Union. *Journal of Vertebrate Paleontology*, 27, 87–98.
http://dx.doi.org/10.1671/0272-4634(2007)27[87:antdtf]2.0.co;2
Azuma, Y. & Currie, P.J. (2000) A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. *Canadian Journal of Earth Sciences*, 37, 1735–1753.
http://dx.doi.org/10.1139/e00-064
Bakker, R.T. (1998) Brontosaur killers: late Jurassic allosaurids as sabre-tooth cat analogues. *Gaia*, 15, 145–158.
Bakker, R.T. & Bir, G. (2004) Dinosaur crime scene investigations: Theropod behavior at Como Bluff, Wyoming, and the evolution of birdness. *In*: Currie, P.J., Koppelhus, E.B., Shugar, M.A. & Wright, J.L. (Eds.), *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds*. Indiana University Press, Bloomington, pp. 301–342.
Barrett, P.M. (2000) Prosauropod dinosaurs and iguanas: speculations on the diets of extinct reptiles. *In*: Sues, H.-D. (Ed.), *Evolution of Herbivory in Terrestrial Vertebrates*. Cambridge University Press, Cambridge, U.K.; New York, pp. 42–78.
Barrett, P.M. (2009) The affinities of the enigmatic dinosaur *Eshanosaurus deguchiianus* from the Early Jurassic of Yunnan Province, People's Republic of China. *Palaeontology*, 52, 681–688.
http://dx.doi.org/10.1111/j.1475-4983.2009.00887.x
Barsbold, R. (1974) Saurornithoididae, a new family of small theropod dinosaurs from central Asia and North America. *Palaeontologia Polonica*, 30, 5–22.
Barsbold, R. & Osmólska, H. (1999) The skull of *Velociraptor* (Theropoda) from the late Cretaceous of Mongolia. *Acta Palaeontologica Polonica*, 44, 189–219.
Baszio, S. (1997) Systematic palaeontology of isolated dinosaur teeth from the latest Cretaceous of south Alberta, Canada. *Courier Forschungsinstitut Senckenberg*, 196, 33–77.
Benson, R., Carrano, M. & Brusatte, S. (2010) A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften*, 97, 71–78.
http://dx.doi.org/10.1007/s00114-009-0614-x
Benson, R.B.J. (2008) A redescription of '*Megalosaurus*' *hesperis* (Dinosauria, Theropoda) from the Inferior Oolite (Bajocian, Middle Jurassic) of Dorset, United Kingdom. *Zootaxa*, 1931, 57–67.
Benson, R.B.J. (2009) An assessment of variability in dinosaur remains from the Bathonian (Middle Jurassic) of Stonesfield and New Park Quarry, UK and taxonomic implications for *Megalosaurus bucklandii* and *Iliosuchus incognitus*. *Palaeontology*, 52, 857–877.
http://dx.doi.org/10.1111/j.1475-4983.2009.00884.x
Benson, R.B.J. (2010) A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society*, 158, 882–935.
http://dx.doi.org/10.1111/j.1096-3642.2009.00569.x
Benson, R.B.J., Barrett, P.M., Powell, H.P. & Norman, D.B. (2008) The taxonomic status of *Megalosaurus bucklandii* (Dinosauria, Theropoda) from the Middle Jurassic of Oxfordshire, UK. *Palaeontology*, 51, 419–424.
http://dx.doi.org/10.1111/j.1475-4983.2008.00751.x
Bonaparte, J.F. (1979) Dinosaurs: A Jurassic assemblage from Patagonia. *Science*, 205, 1377–1379.
http://dx.doi.org/10.1126/science.205.4413.1377
Bonaparte, J.F. (1986) Les dinosaures (carnosaures, allosauridés, sauropodes, cétiosauridés) du Jurassique Moyen de Cerro Cóndor (Chubut, Argentina). *Annales de Paléontologie (Vert.-Invert.)*, 72, 247–289.
Bonaparte, J.F. (1991) The Gondwanian theropod families Abelisauridae and Noasauridae. *Historical Biology*, 5, 1–25.
http://dx.doi.org/10.1080/10292389109380385
Bonaparte, J.F. & Novas, F.E. (1985) *Abelisaurus comahuensis*, n.g., n.sp., Carnosauria del Crétacico Tardio de Patagonia. *Ameghiniana*, 21, 259–265.
Bonaparte, J.F. & Powell, J.E. (1980) A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Coelurosauria-Carnosauria-Aves). *Mémoires de la Société Géologique de France, Nouvelle Série*, 139, 19–28.
Bremer, K. (1994) Branch support and tree stability. *Cladistics*, 10, 295–304.
http://dx.doi.org/10.1111/j.1096-0031.1994.tb00179.x
Brinkman, D.B. (2008) The structure of Late Cretaceous (late Campanian) nonmarine aquatic communities: a guild analysis of two vertebrate microfossil localities in Dinosaur Provincial Park, Alberta, Canada. *In*: Sankey, J.T. & Baszio, S. (Eds.), *Vertebrate Microfossil Assemblages.* Indiana University Press, Bloomington, pp. 33–60.
Britt, B.B. (1991) Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. *Brigham Young University Geology Studies*, 37, 1–72.
Brochu, C.A. (2003) Osteology of *Tyrannosaurus Rex*: Insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology*, 22, 1–138.
http://dx.doi.org/10.1080/02724634.2003.10010947
Brusatte, S., Carr, T. & Norell, M. (2012) The osteology of *Alioramus*, a gracile and long-snouted tyrannosaurid (Dinosauria:

Theropoda) from the Late Cretaceous of Mongolia. *Bulletin of the American Museum of Natural History*, 366, 1–197. http://dx.doi.org/10.1206/770.1
Brusatte, S.L. & Sereno, P.C. (2007) A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. *Journal of Vertebrate Paleontology*, 27, 902–916. http://dx.doi.org/10.1671/0272-4634(2007)27[902:ansocd]2.0.co;2
Brusatte, S.L., Benson, J.B., Carr, T.D., Williamson, T.E. & Sereno, P.C. (2007) The systematic utility of theropod enamel wrinkles. *Journal of Vertebrate Paleontology*, 27, 1052–1056. http://dx.doi.org/10.1671/0272-4634(2007)27[1052:tsuote]2.0.co;2
Brusatte, S.L., Benson, R.B.J. & Hutt, S. (2008) The osteology of *Neovenator salerii* (Dinosauria: Theropoda) from the Wealden Group (Barremian) of the Isle of Wight. *Palaeontographical Society Monographs*, 162, 1–75. http://dx.doi.org/10.1080/02724630903416092
Brusatte, S.L., Butler, R.J., Sulej, T. & Niedźwiedzki, G. (2009b) The taxonomy and anatomy of rauisuchian archosaurs from the Late Triassic of Germany and Poland. *Acta Palaeontologica Polonica*, 54, 221–230. http://dx.doi.org/10.1073/pnas.0906911106
Brusatte, S.L., Carr, T.D., Erickson, G.M., Bever, G.S. & Norell, M.A. (2009a) A long-snouted, multihorned tyrannosaurid from the Late Cretaceous of Mongolia. *Proceedings of the National Academy of Sciences*, 106, 17261–17266. http://dx.doi.org/10.1073/pnas.0906911106
Brusatte, S.L., Norell, M.A., Carr, T.D., Erickson, G.M., Hutchinson, J.R., Balanoff, A.M., Bever, G.S., Choiniere, J.N., Makovicky, P.J. & Xu, X. (2010) Tyrannosaur paleobiology: New research on ancient exemplar organisms. *Science*, 329, 1481–1485. http://dx.doi.org/10.1126/science.1193304
Buckley, L.G. (2009) Individual and ontogenetic variation in theropod dinosaur teeth: a case study of *Coelophysis bauri* (Theropoda: Coelophysoidea) and implications for identifying isolated theropod teeth. Unpublished MSc thesis, University of Alberta, Alberta, 109 pp.
Buckley, L.G., Larson, D.W., Reichel, M. & Samman, T. (2010) Quantifying tooth variation within a single population of *Albertosaurus sarcophagus* (Theropoda: Tyrannosauridae) and implications for identifying isolated teeth of tyrannosaurids. *Canadian Journal of Earth Sciences*, 47, 1227–1251. http://dx.doi.org/10.1139/e10-029
Buffetaut, E. (1989) Archosaurian reptiles with Gondwanan affinities in the Upper Cretaceous of Europe. *Terra Nova*, 1, 69–74. http://dx.doi.org/10.1111/j.1365-3121.1989.tb00328.x
Buffetaut, E. & Ingavat, R. (1986) Unusual theropod dinosaur teeth from the Upper Jurassic of Phu Wiang, northeastern Thailand. *Revue de Paléobiologie*, 5, 217–220.
Buffetaut, E., Méchin, P. & Méchin-Salessy, A. (1988) Un dinosaure théropode d'affinités gondwaniennes dans le Crétacé supérieur de Provence. *Comptes Rendus de l'Académie des Sciences Paris, Série II*, 306, 153–158.
Burnham, D.A. (2004) New information on *Bambiraptor feinbergi* (Theropoda: Dromaeosauridae) from the Late Cretaceous of Montana. *In*: Currie, P.J., Koppelhus, E.B., Shugar, M.A. & Wright, J.L. (Eds.), *Feathered Dragons: Studies on the Transition from Dinosaurs to Birds*. Indiana University Press, Bloomington, pp. 67–111.
Burnham, D.A., Derstler, K.L., Currie, P.J., Bakker, R.T., Zhou, Z. & Ostrom, J.H. (2000) Remarkable new birdlike dinosaur (Theropoda: Maniraptora) from the Upper Cretaceous of Montana. *The Paleontological Institute, The University of Kansas*, 13, 1–14.
Calvo, J.O. & Coria, R. (1998) New specimen of *Giganotosaurus carolinii* (Coria and Salgado 1995), supports it as the largest theropod ever found. *Gaia*, 15, 117–122.
Canale, J.I., Scanferla, C.A., Agnolin, F.L. & Novas, F.E. (2009) New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften*, 96, 409–414. http://dx.doi.org/10.1007/s00114-008-0487-4
Candeiro, C.R.A. (2007) Padrões morfológicos dos dentes de Abelisauroidea e Carcharodontosauridae (Theropoda, Dinosauria) do Cretáceo da América do Sul. Unpublished Ph.D. dissertation, Universidade Federal do Rio de Janeiro, Rio de Janeiro, 208 pp.
Canudo, J.I., Ruiz-Omeñaca J.I., Aurell M., Barco J.L. & Cuenca-Bescos, G. (2006) A megatheropod tooth from the late Tithonian-lower Berriasian (Jurassic-Cretaceous transition) of Galve (Aragon, NE Spain). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 239, 77–99.
Carpenter, K. (1998) Evidence of predatory behavior by carnivorous dinosaurs. *Gaia*, 15, 135–144.
Carpenter, K., Sanders, F., McWhinney, L.A. & Wood, L. (2005) Evidence for predator-prey relationships. *In*: Carpenter, K. (Ed.), *The Carnivorous Dinosaurs*. Bloomington, Indiana, pp. 325–350.
Carr, T.D. & Williamson, T.E. (2004) Diversity of late Maastrichtian Tyrannosauridae (Dinosauria: Theropoda) from western North America. *Zoological Journal of the Linnean Society*, 142, 479–523. http://dx.doi.org/10.1111/j.1096-3642.2004.00130.x
Carrano, M.T. & Sampson, S.D. (2008) The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, 6, 183–236. http://dx.doi.org/10.1017/s1477201907002246

Carrano, M.T., Benson, R.B.J. & Sampson, S.D. (2012) The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, 10, 211–300.
http://dx.doi.org/10.5479/si.00810266.95.1

Carrano, M.T., Loewen, M.A. & Sertich, J.J.W. (2011) New materials of *Masiakasaurus knopfleri* Sampson, Carrano, and Forster 2001, and implications for the morphology of the Noasauridae (Theropoda: Ceratosauria). *Smithsonian Contributions to Paleobiology*, 95, 1–53.
http://dx.doi.org/10.5479/si.00810266.95.1

Carrano, M.T., Sampson, S. & Forster, C. (2002) The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, 22, 510–534.
http://dx.doi.org/10.1671/0272-4634(2002)022[0510:toomka]2.0.co;2

Charig, A.J. & Milner, A.C. (1986) *Baryonyx*, a remarkable new theropod dinosaur. *Nature*, 324, 359–361.
http://dx.doi.org/10.1038/324359a0

Charig, A.J. & Milner, A.C. (1997) *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum*, 53, 11–70.

Chiappe, L.M. & Göhlich, U.B. (2010) Anatomy of *Juravenator starki* (Theropoda: Coelurosauria) from the Late Jurassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*, 258, 257–296.
http://dx.doi.org/10.1127/0077-7749/2010/0125

Chiappe, L.M., Norell, M.A. & Clark, J.M. (1998) The skull of a relative of the stem-group bird *Mononykus*. *Nature*, 392, 275–278.
http://dx.doi.org/10.1038/32642

Chure, D.J. (2000) A new species of *Allosaurus* from the Morrison Formation of Dinosaur National Monument (Utah-Colorado) and a revision of the theropod family Allosauridae. Unpublished Ph.D. dissertation, Columbia University, New York, New York, 964 pp.

Chure, D.J. (2001) The second record of the African theropod *Elaphrosaurus* (Dinosauria, Ceratosauria) from the Western Hemisphere. *Neues Jahrbuch fur Geologie und Palaontologie-Monatshefte*, 2001, 565–576.

Cillari, A. (2010) *Teeth of Theropoda (Dinosauria, Saurischia): morphology, function and classification*. Unpublished Ph.D. dissertation, Scienze della Terra, Sapienza Universit di Roma, 193 pp.

Clark, J.M., Perle, A. & Norell, M. (1994) The skull of *Erlicosaurus andrewsi*, a late Cretaceous "Segnosaur" (Theropoda, Therizinosauridae) from Mongolia. *American Museum Novitates*, 3115, 1–39.

Colbert, E.H., Russell, D.A. & Matthew, W.D. (1969) The small Cretaceous dinosaur *Dromaeosaurus*. *American Museum Novitates*, 2380, 1–49.

Cope, E.D. (1876) Descriptions of some vertebrate remains from the Fort Union beds of Montana. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 28, 248–261.

Cope, E.D. (1887) The dinosaur genus *Coelurus*. *American Naturalist*, 21, 367–369.

Coria, R.A. & Currie, P.J. (2006) A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas*, 28, 71–118.

Coria, R.A. & Salgado, L. (1995) A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature*, 377, 224–226.
http://dx.doi.org/10.1038/377224a0

Coria, R.A., Chiappe, L.M. & Dingus, L. (2002) A new close relative of *Carnotaurus sastrei* Bonaparte 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology*, 22, 460–465.
http://dx.doi.org/10.1671/0272-4634(2002)022[0460:ancroc]2.0.co;2

Currie, P.J. (1987) Bird-like characteristics of the jaws and teeth of troodontid theropods (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology*, 7, 72–81.
http://dx.doi.org/10.1080/02724634.1987.10011638

Currie, P.J. (1995) New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). *Journal of Vertebrate Paleontology*, 15, 576–591.
http://dx.doi.org/10.1080/02724634.1995.10011250

Currie, P.J. & Azuma, Y. (2006) New specimens, including a growth series, of *Fukuiraptor* (Dinosauria, Theropoda) from the Lower Cretaceous Kitadani Quarry of Japan. *Journal of the Paleontological Society of Korea*, 22, 173.

Currie, P.J. & Carpenter, K. (2000) A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas*, 22, 207–246.
http://dx.doi.org/10.2307/2421859

Currie, P.J. & Chen, P. (2001) Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Canadian Journal of Earth Sciences*, 38, 1705–1727.
http://dx.doi.org/10.1139/e01-050

Currie, P.J. & Dong, Z.M. (2001) New information on Cretaceous troodontids (Dinosauria, Theropoda) from the People's Republic of China. Results from the Sino−Canadian Dinosaur Project. Part 3. *Canadian Journal of Earth Sciences*, 38, 1753–1766.
http://dx.doi.org/10.1139/e01-065

Currie, P.J. & Varricchio, D.J. (2004) A new dromaeosaurid from the Horseshoe Canyon Formation (upper Cretaceous) of Alberta, Canada. *In*: Currie, P.J., Koppelhus, E.B., Shugar, M.A. & Wright, J.L. (Eds.), *Feathered Dragons: Studies on the*

Transition from Dinosaurs to Birds. Indiana University Press, Bloomington, pp. 112–132.
http://dx.doi.org/10.1017/s0016756805300434

Currie, P.J. & Zhao, X.-J. (1993) A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, 30, 2037–2081.
http://dx.doi.org/10.1139/e93-179

Currie, P.J., Rigby, J.K. Jr. & Sloan, R.E. (1990) Theropod teeth from the Judith River Formation of southern Alberta, Canada. *In*: Carpenter, K. & Currie, P.J. (Eds.), *Dinosaur Systematics: Approaches and Perspectives*. Cambridge, Cambridge University Press, pp. 107–125.
http://dx.doi.org/10.1017/cbo9780511608377.011

Dal Sasso, C. & Maganuco, S. (2011) *Scipionyx samniticus* (Theropoda: Compsognathidae) from the Lower Cretaceous of Italy: osteology, ontogenetic assessment, phylogeny, soft tissue anatomy, taphonomy and palaeobiology. *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 37, 1–281.
http://dx.doi.org/10.1080/08912963.2012.654705

Dal Sasso, C. & Signore, M. (1998) Exceptional soft-tissue preservation in a theropod dinosaur from Italy. *Nature*, 392, 383–387.
http://dx.doi.org/10.1038/32884

Dal Sasso, C., Maganuco, S. & Cioffi, A. (2009) A neurovascular cavity within the snout of the predatory dinosaur *Spinosaurus*. *First International Congress on North African Vertebrate Palaeontology 25-27 May 2009,* Marrakech Morocco, pp. 22–23.

Dal Sasso, C., Maganuco, S., Buffetaut, E. & Mendez, M.A. (2005) New information on the skull of the enigmatic theropod *Spinosaurus*, with remarks on its size and affinities. *Journal of Vertebrate Paleontology*, 25, 888–896.
http://dx.doi.org/10.1671/0272-4634(2005)025[0888:niotso]2.0.co;2

De Andrade, M., Young, M.T., Desojo, J.B. & Brusatte, S.L. (2010) The evolution of extreme hypercarnivory in Metriorhynchidae (Mesoeucrocodylia: Thalattosuchia) based on evidence from microscopic denticle morphology. *Journal of Vertebrate Paleontology*, 30, 1451–1465.
http://dx.doi.org/10.1080/02724634.2010.501442

de Ricqlès, A., Mateus, O., Antunes, M.T. & Taquet, P. (2001) Histomorphogenesis of embryos of Upper Jurassic theropods from Lourinhã (Portugal). *Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science*, 332, 647–656.
http://dx.doi.org/10.1016/s1251-8050(01)01580-4

Depéret, C. & Savornin, J. (1925) Sur la découverte d'une faune de vertébrés albiens à Timimoun (Sahara occidental). *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences Paris*, 181, 1108–1111.

Eddy, D.R. & Clarke, J.A. (2011) New information on the cranial anatomy of *Acrocanthosaurus atokensis* and its implications for the phylogeny of Allosauroidea (Dinosauria: Theropoda). *PLOS ONE*, 6, e17932.
http://dx.doi.org/10.1371/journal.pone.0017932

Ezcurra, M.D. (2009) Theropod remains from the uppermost Cretaceous of Colombia and their implications for the palaeozoogeography of western Gondwana. *Cretaceous Research*, 30, 1339–1344.
http://dx.doi.org/10.1016/j.cretres.2009.08.004

Ezcurra, M.D. & Agnolín, F.L. (2012) An abelisauroid dinosaur from the Middle Jurassic of Laurasia and its implications on theropod palaeobiogeography and evolution. *Proceedings of the Geologists' Association*, 123, 500–507.
http://dx.doi.org/10.1016/j.pgeola.2011.12.003

Fanti, F. & Therrien, F. (2007) Theropod tooth assemblages from the Late Cretaceous Maevarano Formation and the possible presence of dromaeosaurids in Madagascar. *Acta Palaeontologica Polonica*, 52, 155–166.

Farlow, J.O. & Holtz Jr, T.R. (2002) The fossil record of predation in dinosaurs. *Paleontological Society Papers*, 8, 251–266.

Farlow, J.O., Brinkman, D.L., Abler, W.L. & Currie, P.J. (1991) Size, shape, and serration density of theropod dinosaur lateral teeth. *Modern Geology*, 16, 161–198.

Feduccia, A. (2002) Birds are dinosaurs: simple answer to a complex problem. *The Auk*, 119, 1187–1201.
http://dx.doi.org/10.1642/0004-8038(2002)119[1187:badsat]2.0.co;2

Fiorillo, A.R. & Currie, P.J. (1994) Theropod teeth from the Judith River Formation (Upper Cretaceous) of south-central Montana. *Journal of Vertebrate Paleontology*, 14, 74–80.
http://dx.doi.org/10.1080/02724634.1994.10011539

Fiorillo, A.R. & Gangloff, R.A. (2001) Theropod teeth from the Prince Creek Formation (Cretaceous) of northern Alaska, with speculations on Arctic dinosaur paleoecology. *Journal of Vertebrate Paleontology*, 20, 675–682.
http://dx.doi.org/10.1671/0272-4634(2000)020[0675:ttftpc]2.0.co;2

Fitzinger, L. (1843) *Systema reptilium. Fasciculus primus: Amblyglossae*. Apud Braumüller and Seidel Bibliopolas, Vienna, 106 pp.

Galton, P.M. & Jensen, J.A. (1979) A new large theropod dinosaur from the Upper Jurassic of Colorado. *Brigham Young University Geology Studies*, 26, 1–12.

Galton, P.M. (1982) *Elaphrosaurus*, an ornithomimid dinosaur from the upper jurassic of north America and Africa. *Paläontologische Zeitschrift*, 56, 265–275.
http://dx.doi.org/10.1007/bf02988803

Gauthier, J.A. (1986) Saurischian monophyly and the origin of birds. *In*: Padian, K. (Ed.), *The origin of birds and the evolution of flight. Memoirs of the California Academy of Science*, 8, pp. 1–55.
Gianechini, F.A., Agnolín, F.L. & Ezcurra, M.D. (2011a) A reassessment of the purported venom delivery system of the bird-like raptor *Sinornithosaurus*. *Paläontologische Zeitschrift*, 85, 103–107. http://dx.doi.org/10.1007/s12542-010-0074-9
Gianechini, F.A., Makovicky, P.J., Apesteguía, S. (2011b) The teeth of the unenlagiine theropod *Buitreraptor* from the Cretaceous of Patagonia, Argentina, and the unusual dentition of the Gondwanan dromaeosaurids. *Acta Palaeontologica Polonica*, 56, 279–290. http://dx.doi.org/10.4202/app.2009.0127
Gignac, P.M., Makovicky, P.J., Erickson, G.M. & Walsh, R.P. (2010) A description of *Deinonychus antirrhopus* bite marks and estimates of bite force using tooth indentation simulations. *Journal of Vertebrate Paleontology*, 30, 1169–1177. http://dx.doi.org/10.1080/02724634.2010.483535
Gilmore, C.W. (1920) Osteology of the carnivorous Dinosauria in the United State National museum: with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bulletin of the United States National Museum*, 110, 1–159. http://dx.doi.org/10.5479/si.03629236.110.i
Goloboff, P.A., Farris, J.S. & Nixon, K.C. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, 24, 774–786. http://dx.doi.org/10.1111/j.1096-0031.2008.00217.x
Gong, E., Martin, L.D., Burnham, D.A. & Falk, A.R. (2010) The birdlike raptor *Sinornithosaurus* was venomous. *Proceedings of the National Academy of Sciences*, 107, 766–768. http://dx.doi.org/10.1073/pnas.0912360107
Han, F., Clark, J.M., Xu, X., Sullivan, C., Choiniere, J. & Hone, D.W.E. (2011) Theropod teeth from the Middle-Upper Jurassic Shishugou Formation of Northwest Xinjiang, China. *Journal of Vertebrate Paleontology*, 31, 111–126. http://dx.doi.org/10.1080/02724634.2011.546291
Harris, J.D. (1998) A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. *New Mexico Museum of Natural History and Science Bulletin*, 13, 1–75.
Hasegawa, Y., Tanaka, G., Takakuwa, Y. & Koike, S. (2010) Fine sculptures on a tooth of *Spinosaurus* (Dinosauria, Theropoda) from Morocco. *Bulletin of Gunma Museum of Natural History*, 14, 11–20.
Helmdach, F.F. (1971) Stratigraphy and ostracod-fauna from the coalmine Guimarota (Upper Jurassic). *Memórias dos Serviços Geológicos de Portugal* (N.S.), 17, 41–88.
Hendrickx, C. & Buffetaut, E. (2008) Functional interpretation of spinosaurid quadrates (Dinosauria: Theropoda) from the Mid-Cretaceous of Morocco. *56th Annual Symposium of Vertebrate Palaeontology and Comparative Anatomy. Dublin (September 2nd-6th 2008)*, pp. 25–26.
Hendrickx, C. & Mateus, O. (2012) Ontogenetical changes in the quadrate of basal tetanurans. *In:* Royo-Torres, R., Gascó, F. & Alcalá, L. (Eds.), *10th Annual Meeting of the European Association of Vertebrate Palaeontologists. ¡Fundamental!*, pp. 101–104.
Hendrickx, C., Araújo, R. & Mateus, O. (2012) The nonavian theropod quadrate: systematic usefulness, major trends and phylogenetic morphometrics analysis. *72nd Annual Meeting Society of Vertebrate Paleontology, Raleigh, USA. (October 17-20 2012)*, *Program and Abstracts*, 110 pp.
Henkel, S. & Krusat, G. (1980) Die Fossil-Lagerstätte in der Kohlengrube Guimarota (Portugal) und der erste Fund eines Docodontiden-Skelettes. *Berliner geowissenschaftliche Abhandlungen A*, 20, 209–216.
Hill, G. (1988) *The sedimentology and lithostratigraphy of the Upper Jurassic Lourinhã Formation, Lusitanian Basin, Portugal*. Unpublished Ph.D. dissertation, The Open University, England, 292 pp.
Hill, G. (1989) Distal alluvial fan sediments from the Upper Jurassic of Portugal: controls on their cyclicity and channel formation. *Journal of the Geological Society, London*, 146, 539–555. http://dx.doi.org/10.1144/gsjgs.146.3.0539
Hocknull, S.A., White, M.A., Tischler, T.R., Cook, A.G., Calleja, N.D., Sloan, T. & Elliott, D.A. (2009) New Mid-Cretaceous (Latest Albian) Dinosaurs from Winton, Queensland, Australia. *PLOS ONE*, 4, e6190. http://dx.doi.org/10.1371/journal.pone.0006190
Holtz Jr, T.R. (2003) Dinosaur predation: evidence and ecomorphology. *In*: Kelley, P.H., Kowalewski, M. & Hansen, T.A. (Eds.), *Predator—Prey Interactions in the Fossil Record*. Topics in Geobiology. Springer US, pp. 325–340. http://dx.doi.org/10.1007/978-1-4615-0161-9_14
Holtz Jr, T.R. (2004) Tyrannosauroidea. *In*: Weishampel, D.B., Dodson, P. & Osmólska, H. (Eds.), *The Dinosauria. Second Edition*. Berkeley/Los Angeles/London, pp. 111–136.
Holtz Jr, T.R. (2008) A critical reappraisal of the obligate scavenging hypothesis for *Tyrannosaurus rex* and other tyrant dinosaurs. *In*: Larson, P.L. & Kenneth, C. (Eds.), *Tyrannosaurus rex, the Tyrant King*. Indiana University Press, Bloomington, pp. 371–396.
Holtz, T.R. Jr., Brinkman, D.L. & Chandler, C.L. (1998) Denticle morphometrics and a possibly omnivorous feeding habit for the theropod dinosaur *Troodon*. *Gaia*, 15, 159–166.
Holtz, T.R. Jr., Molnar, R.E. & Currie, P.J. (2004) Basal Tetanurae. *In*: Weishampel, D.B., Dodson, P. & Osmólska, H. (Eds.), *The Dinosauria*, Second Edition. University of California Press, Berkeley, pp. 71–110.
Hou, L. (1997) *Mesozoic Birds of China*. Phoenix Valley Bird Park, Lugu Hsiang, Taiwan, 137 pp.

Hutt, S., Martill, D.M. & Barker, M.J. (1996) The first European allosaurid dinosaur (Lower Cretaceous, Wealden Group, England). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 1996, 635–644.

Hutt, S., Naish, D., Martill, D.M., Barker, M.J. & Newbery, P. (2001) A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England. *Cretaceous Research*, 22, 227–242. http://dx.doi.org/10.1006/cres.2001.0252

Hwang, S.H. (2007) *Phylogenetic patterns of enamel microstructure in dinosaur teeth*. Unpublished Ph.D. dissertation, Columbia University, New York, 274 pp.

Hwang, S.H., Norell, M.A., Ji, Q. & Keqin, G. (2004) A large compsognathid from the Early Cretaceous Yixian Formation of China. *Journal of Systematic Palaeontology*, 2, 13–30. http://dx.doi.org/10.1017/s1477201903001081

Jensen, J.A. (1985) Uncompahgre dinosaur fauna: A preliminary report. *The Great Basin Naturalist*, 45, 710–720.

Ji, Q., Ji, S., Lü, J. & Yuan, C. (2007) A new giant compsognathid dinosaur with long filamentous integuments from Lower Cretaceous of Northeastern China. *Acta Geologica Sinica*, 81, 8–15.

Kellner, A.W.A. (1996) Remarks on Brazilian dinosaurs. *Memoirs of the Queensland Museum*, 39, 611–626.

Kellner, A.W.A. & Campos, D.A. (1996) First Early Cretaceous theropod dinosaur from Brazil with comments on Spinosauridae. *Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen*, 199, 151–166.

Kirkland, J.I., Zanno, L.E., Sampson, S.D., Clark, J.M. & DeBlieux, D.D. (2005) A primitive therizinosauroid dinosaur from the Early Cretaceous of Utah. *Nature*, 7038, 84–87. http://dx.doi.org/10.1038/nature03468

Kullberg, J.C., Rocha, R.B., Soares, A.F., Rey, J., Terrinha, P., Azerêdo, A.C., Callapez, P., Duarte, L.V., Kullberg, M.C., Martins, L., Miranda, J.R., Alves, C., Mata, J., Madeira, J., Mateus, O., Moreira, M. & Nogueira, C.R. (2012) A Bacia Lusitaniana: estratigrafia, paleogeografia e tectónica. *In*: Dias, R., Araújo, A., Terrinha, P. & Kullberg, J.C. (Eds.), *Geologia de Portugal no contexto da Ibéria*. Escolar Editora, pp. 989–1141.

Langer, M.C. & Benton, M.J. (2006) Early dinosaurs: a phylogenetic study. *Journal of Systematic Palaeontology*, 4, 309–358. http://dx.doi.org/10.1017/s1477201906001970

Lapparent, A.F. de & Zbyszewski, G. (1957) Les dinosauriens du Portugal. *Mémoires du Service géologique du Portugal*, 2, 1–63.

Larson, D.W. (2008) Diversity and variation of theropod dinosaur teeth from the uppermost Santonian Milk River Formation (Upper Cretaceous), Alberta: a quantitative method supporting identification of the oldest dinosaur tooth assemblage in Canada. *Canadian Journal of Earth Science*, 45, 1455–1468. http://dx.doi.org/10.1139/e08-070

Larson, D.W. & Currie, P.J. (2013) Multivariate analyses of small theropod dinosaur teeth and implications for paleoecological turnover through time. *PLOS ONE*, 8, e54329. http://dx.doi.org/10.1371/journal.pone.0054329

Larson, D.W., Brinkman, D.B. & Bell, R. (2010) Faunal assemblages from the upper Horseshoe Canyon Formation, an early Maastrichtian cool-climate assemblage from Alberta, with special reference to the *Albertosaurus sarcophagus* bonebed. *Canadian Journal of Earth Sciences*, 49, 1159–1181. http://dx.doi.org/10.1139/e10-005

Lavocat, R. (1955) Sur une portion de mandibule de théropode provenant du Crétacé supérieur de Madagascar. *Bulletin du Muséum National d'Histoire Naturelle*, 27, 256–259.

Le Loeuff, J. (1991) The Campano-Maastrichtian vertebrate faunas from southern Europe and their relationships with other faunas in the world; palaeobiogeographical implications. *Cretaceous Research*, 12, 93–114. http://dx.doi.org/10.1016/s0195-6671(05)80019-9

Le Loeuff, J. & Buffetaut, E. (1991) *Tarascosaurus salluvicus* nov. gen., nov. sp., dinosaure théropode du Crétacé Supérieur du sud de la France. *Géobios*, 24, 585–594. http://dx.doi.org/10.1016/0016-6995(91)80022-r

Leidy, J. (1856) Notice of remains of extinct reptiles and fishes, discovered by Dr. F.V. Hayden in the Bad Lands of the Judith River, Nebraska Territory. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 8, 72–73.

Li, D., Norell, M.A., Gao, K.Q., Smith, N.D. & Makovicky, P.J. (2010) A longirostrine tyrannosauroid from the Early Cretaceous of China. *Proceedings of the Royal Society B: Biological Sciences*, 277, 183–190. http://dx.doi.org/10.1098/rspb.2009.0249

Loewen, M.A. (2010) Variation in the Late Jurassic theropod dinosaur *Allosaurus*: Ontogenetic, functional, and taxonomic implications. Unpublished Ph.D. dissertation, The University of Utah, Utah, 326 pp.

Longrich, N. (2008) Small theropod teeth from the Lance Formation of Wyoming, USA. *In*: Sankey, J.T. & Baszio, S. (Eds.), *Vertebrate Microfossil Assemblages*. Indiana University Press, Bloomington, pp. 135–158.

Madsen, J.H. (1976) *Allosaurus fragilis*: a revised osteology. *Utah Geological Survey Bulletin*, 109, 1–163.

Madsen, J.H. & Welles, S.P. (2000) *Ceratosaurus* (Dinosauria, Theropoda): a revised osteology. *Utah Geological Survey, Miscellaneous Publication*, 00–2, 1–80.

Maganuco, S., Cau, A. & Pasini, G. (2005) First description of theropod remains from the Middle Jurassic (Bathonian) of Madagascar. *Atti della Società italiana di scienze naturali e del museo civico di storia naturale di Milano*, 146, 165–202.

Makovicky, P.J., Apesteguía, S. & Agnolín, F.L. (2005) The earliest dromaeosaurid theropod from South America. *Nature*, 437,

1007–1011.
http://dx.doi.org/10.1038/nature03996
Malafaia, E., Dantas, P., Ortega, F. & Escaso, F. (2007) Nuevos restos de *Allosaurus fragilis* (Theropoda: Carnosauria) del yacimiento de Andrés (Jurásico Superior; centro-oeste de Portugal). *Cantera Paleontológica*, 1, 255–271.
Malafaia, E., Ortega, F., Silva, B. & Escaso, F. (2008) Fragmento de un maxilar de terópodo de Praia da Corva (Jurásico Superior. Torres Vedras, Portugal). *Palaeontologica Nova. SEPAZ*, 8, 273–279.
Mantell, G.A. (1827) Illustrations of the geology of Sussex: A general view of the geological relations of the South-Eastern part of England, with figures and descriptions of the fossils of Tilgate Forest. Lupton Relfe, London. 92 pp.
Manuppella, G. (1996) Carta geológica de Portugal 1/50 000. Folha 30-A, Lourinhã. *Instituto Geológico e Mineiro*.
Manuppella, G. (1998) Geologic data about the «Camadas de Alcobaça» (Upper Jurassic) North of Lourinhã, and facies variation. *Memórias da Academia de Ciências de Lisboa*, 37, 17–24.
Manuppella, G., Antunes, M.T., Pais, J., Ramalho, M.M. & Rey, J. (1999) Notícia explicativa da folha 30-A Lourinhã. *Instituto Geológico e Mineiro*, 1–83.
Marsh, O.C. (1881) Classification of the Dinosauria. *American Journal of Science*, 23, 241–244.
http://dx.doi.org/10.2475/ajs.s3-23.133.81
Marsh, O.C. (1884) Principal characters of American Jurassic dinosaurs. Part VIII. The Order Theropoda. *American Journal of Science*, 27, 329–340.
http://dx.doi.org/10.2475/ajs.s3-27.160.329
Martinez, R.N., Sereno, P.C., Alcober, O.A., Colombi, C.E., Renne, P.R., Montañez, I.P. & Currie, B.S. (2011) A basal dinosaur from the dawn of the dinosaur era in southwestern Pangaea. *Science*, 331, 206.
http://dx.doi.org/10.1126/science.1198467
Mateus, I., Mateus, H., Antunes, M.T., Mateus, O., Taquet, P., Ribeiro, V. & Manuppella, G. (1998) Upper Jurassic theropod dinosaur embryos from Lourinhã (Portugal). *Memórias da Academia das Ciências de Lisboa*, 37, 101–110.
Mateus, O. (1998) *Lourinhanosaurus antunesi*, a new Upper Jurassic allosauroid (Dinosauria: Theropoda) from Lourinhã (Portugal). *Memórias da Academia de Ciências de Lisboa*, 37, 111–124.
Mateus, O. (2005) Dinossauros do Jurássico Superior de Portugal, com destaque para os saurísquios. Dissertação de Doutoramento. Unpublished Ph.D. dissertation, Universidade Nova de Lisboa, Lisboa, 375 pp.
Mateus, O. (2006) Late Jurassic dinosaurs from the Morrison Formation, the Lourinhã and Alcobaça Formations (Portugal), and the Tendaguru Beds (Tanzania): a comparison. *Paleontology and Geology of the Upper Jurassic Morrison Formation*, 36, 223–231.
Mateus, O. & Antunes, M.T. (2000a) *Ceratosaurus* sp. (Dinosauria: Theropoda) in the Late Jurassic of Portugal. 31st International Geological Congress, Abstract Volume, Rio de Janeiro, Brazil, 1 pp.
Mateus, O. & Antunes, M.T. (2000b) *Torvosaurus* sp. (Dinosauria: Theropoda) in the Late Jurassic of Portugal. *In*: *Libro de resúmenes, I Congresso Ibérico de Paleontología-XVI Jornadas de la Sociedad Española de Paleontología*. pp. 115–117.
Mateus, O. & Milàn, J. (2010) A diverse Upper Jurassic dinosaur ichnofauna from central-west Portugal. *Lethaia*, 43, 245–257.
http://dx.doi.org/10.1111/j.1502-3931.2009.00190.x
Mateus, O., Araújo, R., Natário, C. & Castanhinha, R. (2011) A new specimen of the theropod dinosaur *Baryonyx* from the early Cretaceous of Portugal and taxonomic validity of *Suchosaurus*. *Zootaxa*, 2827, 54–68.
Mateus, O., Walen, A. & Antunes, M.T. (2006) The large theropod fauna of the Lourinhã Formation (Portugal) and its similarity to the Morrison Formation, with a description of a new species of *Allosaurus*. *In*: Foster, J.R. & Lucas, S.G. (Eds.), *Paleontology and Geology of the Upper Jurassic Morrison Formation.* New Mexico Museum of Natural History and Science Bulletin, 36, pp. 123–129.
Matthew, W.D. & Brown, B. (1922) The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. *Bulletin of the American Museum of Natural History*, 46, 367–385.
Milner, A.C. (2003) Fish-eating theropods: a short review of the systematics, biology and palaeobiogeography of spinosaurs. *Journadas Internacionales sobre paleontologiá de Dinosaurios y su Entoro*, 2, 129–138.
Milner, A.R. & Kirkland, J.I. (2007) The case for fishing dinosaurs at the St. George Dinosaur Discovery site at Johnson Farm. *Utah Geological Survey Notes*, 39, 1–3.
Molnar, R.E. (1991) The cranial morphology of *Tyrannosaurus rex*. *Palaeontographica Abteilung A*, 217, 137–176.
Molnar, R.E. (1998) Mechanical factors in the design of the skull of *Tyrannosaurus rex* (Osborn, 1905). *Gaia*, 15, 193–218.
Molnar, R.E., Obata, I., Tanimoto, M. & Matsukawa, M. (2009) A tooth of *Fukuiraptor* aff. *F. kitadaniensis* from the Lower Cretaceous Sebayashi Formation, Sanchu Cretaceous, Japan. *Bulletin of Tokyo Gakugei University, Division of Natural Sciences*, 61, 105–117.
Nesbitt, S.J. (2011) The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History*, 352, 1–292.
http://dx.doi.org/10.1206/352.1
Nesbitt, S.J., Smith, N.D., Irmis, R.B., Turner, A.H., Downs, A. & Norell, M.A. (2009) A complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. *Science*, 326, 1530–1533.
http://dx.doi.org/10.1126/science.1180350
Nesbitt, S.J., Turner, A.H., Erickson, G.M. & Norell, M.A. (2006) Prey choice and cannibalistic behaviour in the theropod *Coelophysis*. *Biology Letters*, 2, 611–614.

http://dx.doi.org/10.1098/rsbl.2006.0524
Norell, M.A., Clark, J.M., Turner, A.H., Makovicky, P.J., Barsbold, R. & Rowe, T. (2006) A new dromaeosaurid theropod from Ukhaa Tolgod (Ömnögov, Mongolia). *American Museum Novitates*, 3545, 1–51.
http://dx.doi.org/10.1206/0003-0082(2006)3545[1:andtfu]2.0.co;2
Norell, M.A., Makovicky, P.J. & Clark, J.M. (2000) A new troodontid from Ukhaa Tolgod, Late Cretaceous, Mongolia. *Journal of Vertebrate Paleontology*, 20, 7–11.
http://dx.doi.org/10.1671/0272-4634(2000)020[0007:anttfu]2.0.co;2
Norell, M.A., Makovicky, P.J., Bever, G.S., Balanoff, A.M., Clark, J.M., Barsbold, R. & Rowe, T. (2009) A review of the Mongolian Cretaceous dinosaur *Saurornithoides* (Troodontidae: Theropoda). *American Museum Novitates*, 3654, 1–63.
Novas, F.E., Ezcurra, M.D. & Lecuona, A. (2008) *Orkoraptor burkei* nov. gen. et sp., a large theropod from the Maastrichtian Pari Aike Formation, Southern Patagonia, Argentina. *Cretaceous Research*, 29, 468–480.
http://dx.doi.org/10.1016/j.cretres.2008.01.001
Osborn, H.F. (1903) *Ornitholestes hermanni*, a new compsognathoid dinosaur from the Upper Jurassic. *Bulletin of the American Museum of Natural History*, 19, 459–464.
Osborn, H.F. (1905) *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bulletin of the American Museum of Natural History*, 21, 259–265.
Osborn, H.F. (1912) Crania of *Tyrannosaurus* and *Allosaurus*. *Memoirs of the American Museum of Natural History. New Series*, 1, 1–30.
Osborn, H.F. (1924) Three new Theropoda, *Protoceratops* zone, central Mongolia. *American Museum Novitates*, 144, 1–12.
Ősi, A., Apesteguia, S. & Kowalewski, M. (2010) Non-avian theropod dinosaurs from the Early Late Cretaceous of central Europe. *Cretaceous Research*, 31, 304–320.
http://dx.doi.org/10.1016/j.cretres.2010.01.001
Osmólska, H., Currie, P.J., Barsbold, R. (2004) Oviraptorosauria. *In*: Weishampel, D.B., Dodson, P. & Osmólska, H. (Eds.), *The Dinosauria*, Second edition. University of California Press, Berkeley, Los Angeles, and London, pp. 517–606.
http://dx.doi.org/10.1017/s001675680624305x
Ostrom, J.H. (1978) The osteology of *Compsognathus longipes* Wagner. *Zitteliana*, 4, 73–118.
Owen, R. (1842) Report on British fossil reptiles. Part II. *Reports of the British Association for the Advancement of Science*, 11, 60–204.
Paul, G.S. (1988) *Predatory Dinosaurs of the World: A Complete Illustrated Guide*. Simon and Schuster. 464 pp.
Pérez-Moreno, B.P., Chure, D.J. , Pires, C., Marques da Silva, C., dos Santos, V., Dantas, P., Póvoas, L., Cachão, M., Sanz, J.L. & Galopim de Carvalho, A.M. (1999) On the presence of *Allosaurus fragilis* (Theropoda, Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. *Journal of the Geological Society of London*, 156, 449–452.
http://dx.doi.org/10.1144/gsjgs.156.3.0449
Pérez-Moreno, B.P., Sanz, J.L., Buscalioni, A.D., Moratalla, J.J., Ortega, F. & Rasskin-Gutman, D. (1994) A unique multitoothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature*, 370, 363–367.
http://dx.doi.org/10.1038/370363a0
Perle, A. (1981) [A new segnosaurid from the Upper Cretaceous of Mongolia] (in Russian). *Joint Soviet–Mongolian Paleontological Expedition, Transactions*, 8, 45–55.
Perle, A., Norell, M.A., Chiappe, L.M. & Clark, J.M. (1993) Flightless bird from the Cretaceous of Mongolia. *Nature*, 362, 623–626.
http://dx.doi.org/10.1038/362623a0
Peyer, K. (2006) A reconsideration of *Compsognathus* from the upper Tithonian of Canjuers, southeastern France. *Journal of Vertebrate Paleontology*, 26, 879–896.
http://dx.doi.org/10.1671/0272-4634(2006)26[879:arocft]2.0.co;2
Pol, D. & Rauhut, O.W.M. (2012) A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. *Proceedings of the Royal Society B: Biological Sciences*, 279, 3170–3175.
http://dx.doi.org/10.1098/rspb.2012.0660
Pu, H., Kobayashi, Y., Lü, J., Xu, L., Wu, Y., Chang, H., Zhang, J. & Jia, S. (2013) An unusual basal therizinosaur dinosaur with an ornithischian dental arrangement from Northeastern China. *PLOS ONE*, 8, e63423.
http://dx.doi.org/10.1371/journal.pone.0063423
Rauhut, O.W.M. (2000) The dinosaur fauna from the Guimarota mine. *In*: Martin, T. & Krebs, B. (Eds.), *Guimarota – A Jurassic Ecosystem*. Verlag Dr. Friedrich Pfeil, Munich, pp. 75–82.
Rauhut, O.W.M. (2001) Herbivorous dinosaurs from the Late Jurassic (Kimmeridgian) of Guimarota, Portugal. *Proceedings of the Geologists' Association*, 112, 275–283.
http://dx.doi.org/10.1016/s0016-7878(01)80007-9
Rauhut, O.W.M. (2002) Dinosaur teeth from the Barremian of Uña, Province of Cuenca, Spain. *Cretaceous Research*, 23, 255–263.
http://dx.doi.org/10.1006/cres.2002.1003
Rauhut, O.W.M. (2003) A tyrannosauroid dinosaur from the Upper Jurassic of Portugal. *Palaeontology*, 46, 903–910.
http://dx.doi.org/10.1111/1475-4983.00325

Rauhut, O.W.M. (2004) Provenance and anatomy of *Genyodectes serus*, a large-toothed ceratosaur (Dinosauria: Theropoda) from Patagonia. *Journal of Vertebrate Paleontology*, 24, 894–902.
http://dx.doi.org/10.1671/0272-4634(2004)024[0894:paaogs]2.0.co;2
Rauhut, O.W.M. (2005) Post−cranial remains of “coelurosaurs” (Dinosauria, Theropoda) from the Late Jurassic of Tanzania. *Geological Magazine*, 142, 97–107.
http://dx.doi.org/10.1017/s0016756804000330
Rauhut, O.W. (2011) Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). *Special Papers in Palaeontology*, 86, 195–239.
Rauhut, O.W.M. & Fechner, R. (2005) Early development of the facial region in a non-avian theropod dinosaur. *Proceedings of the Royal Society B: Biological Sciences*, 272, 1179–1183.
http://dx.doi.org/10.1098/rspb.2005.3071
Rauhut, O.W.M. & Kriwet, J. (1994) Teeth of a big theropod dinosaur from Porto das Barcas (Portugal). *Berliner Geowissenschaftliche Abhandlungen E*, 13, 179–186.
Rauhut, O.W.M. & Werner. C. (1995) First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). *Paläontologische Zeitschrift*, 69, 475–486.
http://dx.doi.org/10.1007/bf02987808
Rauhut, O.W.M., Cladera, G., Vickers-Rich, P. & Rich, T.H.V. (2003) Dinosaur remains from the Lower Cretaceous of the Chubut Group, Argentina. *Cretaceous Research*, 24, 487–97.
http://dx.doi.org/10.1016/s0195-6671(03)00067-3
Rauhut, O.W.M., Milner, A.C. & Moore-Fay, S. (2010) Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward 1910) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society*, 158, 155–195.
http://dx.doi.org/10.1111/j.1096-3642.2009.00591.x
Rayfield, E.J. (2005) Aspects of comparative cranial mechanics in the theropod dinosaurs *Coelophysis*, *Allosaurus* and *Tyrannosaurus*. *Zoological Journal of the Linnean Society*, 144, 309–316.
http://dx.doi.org/10.1111/j.1096-3642.2005.00176.x
Reig, O.A. (1963) La presencia de dinosaurios saurisquios en los “Estratos de Ischigualasto” (Mesotriásico Superior) de las provincias de San Juan y La Rioja (República Argentina). *Ameghiniana*, 3, 3–20.
Rowe, T. (1989) A new species of the theropod dinosaur *Syntarsus* from the Early Jurassic Kayenta Formation of Arizona. *Journal of Vertebrate Paleontology*, 9, 125–136.
http://dx.doi.org/10.1080/02724634.1989.10011748
Russell, D.A. & Dong Z-M. (1993) The affinities of a new theropod from the Alxa Desert, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences*, 30, 2107–2127.
http://dx.doi.org/10.1139/e93-183
Sadleir, R., Barrett, P.M. & Powell, H.P. (2008) The anatomy and systematics of *Eustreptospondylus oxoniensis*, a theropod dinosaur from the Middle Jurassic of Oxfordshire, England. *Monograph of the Palaeontographical Society, London*, 160, 1–82.
http://dx.doi.org/10.1080/02724630903413206
Samman, T., Powell, G.L., Currie, P.J. & Hills, L.V. (2005) Morphometry of the teeth of western North American tyrannosaurids and its applicability to quantitative classification. *Acta Palaeontologica Polonica*, 50, 757.
Sampson, S.D., Carrano, M.T. & Forster, C.A. (2001) A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. *Nature*, 409, 504–506.
http://dx.doi.org/10.1038/35054046
Sampson, S.D., Krause, D.W., Dodson, P. & Forster, C.A. (1996) The premaxilla of *Majungasaurus* (Dinosauria: Theropoda), with implications for Gondwanan paleobiogeography. *Journal of Vertebrate Paleontology*, 16, 601–605.
http://dx.doi.org/10.1080/02724634.1996.10011350
Sankey, J.T. (2001) Late Campanian southern dinosaurs, Aguja Formation, Big Bend, Texas. *Journal of Paleontology*, 75, 208–215.
http://dx.doi.org/10.1666/0022-3360(2001)075%3C0208:lcsdaf%3E2.0.co;2
Sankey, J.T. (2008) Diversity of Latest Cretaceous (late Maastrichtian) small theropods and birds: teeth from the Lance and Hell Creek Formations, USA. *In*: Sankey, J.T. & Baszio, S. (Eds.), *Vertebrate Microfossil Assemblages*. Indiana University Press, Bloomington, pp. 117–134.
Sankey, J.T., Brinkman, D.B., Guenther, M. & Currie, P.J. (2002) Small theropod and bird teeth from the Late Cretaceous (late Campanian) Judith River Group, Alberta. *Journal of Paleontology*, 76, 751–763.
http://dx.doi.org/10.1666/0022-3360(2002)076%3C0751:stabtf%3E2.0.co;2
Sauvage, H.E. (1882) Recherches sur les reptiles trouvés dans le Gault de l'Est du bassin de Paris. *Bulletin de la Société Géologique de France*, 2, 1–41.
Schudack, M. (2000) Ostracods and charophytes from the Guimarota beds. *In*: Martin, T. & Krebs, B. (Eds.), *Guimarota - A Jurassic ecosystem*. Verlag Dr. Friedrich Pfeil, München, pp. 33–36
Seeley, H.G. (1887) On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London*, 43, 165–171.

http://dx.doi.org/10.1098/rspl.1887.0117
Senter, P. (2011) Using creation science to demonstrate evolution 2: morphological continuity within Dinosauria. *Journal of Evolutionary Biology*, 24, 2197–2216.
http://dx.doi.org/10.1111/j.1420-9101.2011.02349.x
Sereno, P.C. & Brusatte, S.L. (2008) Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation of Niger. *Acta Palaeontologica Polonica*, 53, 15–46.
http://dx.doi.org/10.4202/app.2008.0102
Sereno, P.C. & Novas, F.E. (1994) The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology*, 13, 451–476.
http://dx.doi.org/10.1080/02724634.1994.10011525
Sereno, P.C., Beck, A.L., Dutheil, D.B., Gado, B., Larsson, H.C.E., Lyon, G.H., Marcot, J.D., Rauhut, O.W.M., Sadleir, R.W., Sidor, C.A., Varricchio, D.D., Wilson, G.P. & Wilson, J.A. (1998) A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science*, 282, 1298–1302.
http://dx.doi.org/10.1126/science.282.5392.1298
Sereno, P.C., Dutheil, D.B., Larochene, M., Larsson, H.C.E., Lyon, G.H., Magwene, P.M., Sidor, C.A., Varricchio, D.J. & Wilson, J.A. (1996) Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science*, 272, 986–991.
http://dx.doi.org/10.1126/science.272.5264.986
Sereno, P.C., Forster, C.A., Rogers, R.R. & Monetta, A.M. (1993) Primitive dinosaur skeleton from Argentina and the early evolution of Dinosauria. *Nature*, 361, 64–66.
http://dx.doi.org/10.1038/361064a0
Sereno, P.C., Martínez, R.N. & Alcober, O.A. (2013) Osteology of *Eoraptor lunensis* (Dinosauria, Sauropodomorpha). *Journal of Vertebrate Paleontology*, 32, 83–179.
http://dx.doi.org/10.1080/02724634.2013.820113
Sereno, P.C., Martinez, R.N., Wilson, J.A., Varricchio, D.J., Alcober, O.A. & Larsson, H.C.E. (2008) Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *PLOS ONE*, 3, e3303.
http://dx.doi.org/10.1371/journal.pone.0003303
Sereno, P.C., Tan, L., Brusatte, S.L., Kriegstein, H.J., Zhao, X. & Cloward, K. (2009) Tyrannosaurid skeletal design first evolved at small body size. *Science*, 326, 418–422.
http://dx.doi.org/10.1126/science.1177428
Sereno, P.C., Wilson, J.A., Larsson, H.C.E., Dutheil, D.B. & Sues, H.-D. (1994) Early Cretaceous dinosaurs from the Sahara. *Science*, 266, 267–271.
http://dx.doi.org/10.1126/science.266.5183.267
Sereno, P.C., Wilson, J.A. & Conrad, J.L. (2004) New dinosaurs link southern landmasses in the Mid–Cretaceous. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271, 1325–1330.
http://dx.doi.org/10.1098/rspb.2004.2692
Smith, J.B. (2005) Heterodonty in *Tyrannosaurus rex*: implications for the taxonomic and systematic utility of theropod dentitions. *Journal of Vertebrate Paleontology*, 25, 865–887.
http://dx.doi.org/10.1671/0272-4634(2005)025[0865:hitrif]2.0.co;2
Smith, J.B. (2007) Dental morphology and variation in *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, 27, 103–126.
http://dx.doi.org/10.1671/0272-4634(2007)27[103:dmavim]2.0.co;2
Smith, J.B. & Dalla Vecchia, F.M. (2006) An abelisaurid (Dinosauria: Theropoda) tooth from the Lower Cretaceous Chicla Formation of Libya. *Journal of African Earth Sciences*, 46, 240–244.
http://dx.doi.org/10.1016/j.jafrearsci.2006.05.007
Smith, J.B. & Dodson, P. (2003) A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology*, 23, 1–14.
http://dx.doi.org/10.1671/0272-4634(2003)23[1:apfast]2.0.co;2
Smith, J.B. & Lamanna, M. C. (2006) An abelisaurid from the Late Cretaceous of Egypt: implications for theropod biogeography. *Naturwissenschaften*, 93, 242–245.
http://dx.doi.org/10.1007/s00114-006-0092-3
Smith, J.B., Vann, D.R. & Dodson, P. (2005) Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. *The Anatomical Record Part A*, 285, 699–736.
http://dx.doi.org/10.1002/ar.a.20206
Soto, M. & Perea, D. (2008) A ceratosaurid (Dinosauria, Theropoda) from the Late Jurassic–Early Cretaceous of Uruguay. *Journal of Vertebrate Paleontology*, 28, 439–444.
http://dx.doi.org/10.1671/0272-4634(2008)28[439:acdtft]2.0.co;2
Stovall, J.W. & Langston, Jr. W. (1950) *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. *The American Midland Naturalist*, 43, 696–728.
http://dx.doi.org/10.2307/2421859
Stromer, E. (1915) Wirbeltier-Reste der Baharije- Stufe (unterstes Cenoman). 3. Das original des theropoden *Spinosaurus*

aegyptiacus nov. gen. nov. spec. *Abhandlungen der Königlichen Bayerischen Akademie der Wissenschaften, Mathematisch- Physikalische Klasse*, 28, 1–32.

Stromer, E. (1931) Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. *Abhandlungen der Bayerischen Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Abteilung*, 9, 1–31.

Stromer, E. (1934) Die Zähne des *Compsognathus* und Bemerkungen über das Gebiss der Theropoda. *Centralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B*, 4, 74–85.

Sues, H.-D. (1978) A new small theropod dinosaur from the Judith River Formation (Campanian) of Alberta Canada. *Zoological Journal of the Linnean Society*, 62, 381–400. http://dx.doi.org/10.1111/j.1096-3642.1978.tb01049.x

Sues, H.-D., Frey, E., Martill, D.M. & Scott, D.M. (2002) *Irritator challengeri*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology*, 22, 535–547. http://dx.doi.org/10.1671/0272-4634(2002)022[0535:icasdt]2.0.co;2

Sues, H.-D., Nesbitt, S.J., Berman, D.S. & Henrici, A.C. (2011) A late-surviving basal theropod dinosaur from the latest Triassic of North America. *Proceedings of the Royal Society B: Biological Sciences*, 278, 3459–3464. http://dx.doi.org/10.1098/rspb.2011.0410

Taquet, P. (1984) Une curieuse spécialisation du crâne de certains dinosaures carnivores du Crétacé: le museau long et étroit des spinosauridés. *Comptes-rendus des séances de l'Académie des sciences. Série 2, Mécanique-physique, chimie, sciences de l'univers, sciences de la terre*, 299, 217–222.

Therrien, F., Henderson, D.M. & Ruff, C.B. (2005) Bite me: biomechanical models of theropod mandibles and implications for feeding behavior. *In*: Carpenter, K. (Ed.), *The Carnivorous Dinosaurs.* Indiana University Press, Bloomington, pp. 179–237.

Torices, A., Currie, P.J., Canudo, J.I. & Pereda-Suberbiola, X. (in press) Theropod dinosaurs from the Upper Cretaceous of the South Pyrenees Basin of Spain. *Acta Palaeontologica Polonica*. http://dx.doi.org/10.4202/app.2012.0121

Torres-Rodríguez, E., Montellano-Ballesteros, M., Hernández-Rivera, R. & Benammi, M. (2010) Dientes de terópodos del Cretácico Superior del Estado de Coahuila, México. *Revista Mexicana de Ciencias Geológicas*, 27, 72–83.

Tortosa, T., Buffetaut, E., Dutour Y. & Cheylan, G. (2010) Abelisaur remains from Provence (Southeastern France): phylogenetic and paleobiogeographic implications. *Mésogée*, 66, 55.

Van der Lubbe, T., Richter U. & Knötschke, N. (2009) Velociraptorine dromaeosaurid teeth from the Kimmeridgian (Late Jurassic) of Germany. *Acta Palaeontologica Polonica*, 54, 401–408. http://dx.doi.org/10.4202/app.2008.0007

Veralli, C. & Calvo, J.O. (2004) Dientes de terópodos carcharodontosáuridos del Turoniano superior-Coniaciano inferior del Neuquén, Patagonia, Argentina. *Ameghiniana*, 4, 587–590.

von Huene, F.R. (1914) Das natürliche System der Saurischia. *Zentralblatt für Mineralogie, Geologie und Paläontologie Abteilung B*, 5, 154–158.

von Huene, F.R. & Matley, C.A. (1933) The Cretaceous Saurischia and Ornithischia of the Central provinces. *Memoirs of the Geological Survey of India, New Series*, 21, 1–74.

Wagner, A. (1861) Neue Beiträge zur Kenntnis der urweltlichen fauna des lithographischen Schiefers; V. *Compsognathus longipes* Wagner. *Abhandlungen der Bayerischen Akademie der Wissenschaften*, 9, 30–38.

Waldman, M. (1974) Megalosaurids from the Bajocian (Middle Jurassic) of Dorset. *Palaeontology*, 17, 325–339.

Walker, A.D. (1964) Triassic reptiles from the Elgin Area: *Ornithosuchus* and the origin of carnosaurs. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 248, 53–134. http://dx.doi.org/10.1098/rstb.1964.0009

Weigert, A. (1995) Isolierte zähne von cf. *Archaeopteryx* sp. aus dem Oberen Jura der Kohlengurbe Guimarota (Portugal). *Neues Jahrbuch fur Geologie und Palaontologie Monatshefte*, 9, 562–576.

Welles, S.P. (1970) *Dilophosaurus* (Reptilia, Saurischia), a new name for a dinosaur. *Journal of Paleontology*, 44, 989.

Welles, S.P. (1984) *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. *Palaeontographica Abteilung A*, A185, 85–180.

Wiechmann, M.F. & Gloy, U. (2000) Pterosaurs and urvogels from the Guimarota mine. *In*: Martin, T. & Krebs, B. (Eds.), *Guimarota. A Jurassic Ecosystem*. Verlag Dr. Friedrich Pfeil, Munich, pp. 83–86.

Wilkinson, M. (1994) Common cladistic information and its consensus representation: Reduced Adams and reduced cladistic consensus trees and profiles. *Systematic Biology*, 43, 343–368.

Woodward, A.S. (1901) On some extinct reptiles from Patagonia, of the genera *Miolania*, *Dinilysia*, and *Genyodectes*. *Proceedings of the Zoological Society of London*, 70, 169–184. http://dx.doi.org/10.1111/j.1469-7998.1901.tb08537.x

Xu, X., Clark, J.M., Forster, C.A., Norell, M.A., Erickson, G.M., Eberth, D.A., Jia, C. & Zhao, Q. (2006) A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature*, 439, 715–718. http://dx.doi.org/10.1038/nature04511

Xu, X., Clark, J.M., Mo, J., Choiniere, J., Forster, C.A., Erickson, G.M., Hone, D.W.E., Sullivan, C., Eberth, D.A., Nesbitt, S., Zhao, Q., Hernandez, R., Jia, C., Han, F. & Guo, Y. (2009) A Jurassic ceratosaur from China helps clarify avian digital

homologies. *Nature*, 459, 940–944.
http://dx.doi.org/10.1038/nature08124

Xu, X., Norell, M.A., Kuang, X., Wang, X., Zhao, Q. & Jia, C. (2004) Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature*, 431, 680–684.
http://dx.doi.org/10.1038/nature02855

Xu, X., Zhou, Z. & Wang, X. (2000) The smallest known non-avian theropod dinosaur. *Nature*, 408, 705–708.

Zanno, L.E. & Makovicky, P.J. (2011) Herbivorous ecomorphology and specialization patterns in theropod dinosaur evolution. *Proceedings of the National Academy of Sciences*, 108, 232–237. http://dx.doi.org/10.1073/pnas.1011924108

Zanno, L.E., Gillette, D.D., Albright, L.B. & Titus, A.L. (2009) A new North American therizinosaurid and the role of herbivory in 'predatory' dinosaur evolution. *Proceedings of the Royal Society B: Biological Sciences*, 276, 3505–3511.
http://dx.doi.org/10.1098/rspb.2009.1029

Zhao, X. & Xu, X. (1998) The oldest coelurosaurian. *Nature*, 394, 234.

Zinke, J. (1998) Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal). *Paläontologische Zeitschrifte*, 72, 179–189.
http://dx.doi.org/10.1007/bf02987825

Zinke, J. & Rauhut, O.W.M. (1994) Small theropods (Dinosauria, Saurischia) from the Upper Jurassic and Lower Cretaceous of the Iberian Peninsula. *Berliner geowiss, Abh. (E)*, 13, 163–177.

APPENDIX

Character list

The full set of 141 dentition-based characters is listed here. 74 characters are derived from the literature and the original and sometimes previous usages of the character are indicated by citations (with the corresponding character number) in parentheses. 67 characters (47.5%) were revealed by our personal observation of the dentition of more than hundred theropod taxa. Among the 81 multistate characters, 71 were left unordered such as the elongation and thickness of the tooth, the extension of the carinae along the crown, and the development of interdenticular sulci, due to the variability of these features along the tooth row. Therefore, only characters with obvious evolutionary continuity were ordered and concern the overlap of the first and second premaxillary alveoli (char. 4), the constriction of the premaxillary tooth rows (char. 15), the posterior extension of the tooth row relative to the orbit (char. 24), and the size of the crown (char. 36 and 65) and denticles (char. 53 and 86), i.e. there must be a theropod bearing moderately large teeth/denticles between two closely related taxa with one having very small crowns (CH < 10 mm)/denticles (> 250 denticles on the carinae), and another possessing very large teeth (CH > 60 mm)/denticles (< 15 denticles on the carinae).

Characters related to the number of teeth borne by the premaxilla (char. 2), the maxilla (char. 17) and the dentary (char. 25) were also ordered. According to Miyashita *et al.* (2010), characters based on tooth count do not accurately reflect true phylogenetic signal as tooth count varies ontogenetically, intraspecifically and even between the left and right jaws of a same individual. Nevertheless, the number of premaxillary teeth is for instance remarkably stable among theropods (Miyashita *et al.* 2010; pers. obs.), and a large number of closely related theropod taxa share the same number of teeth borne by the maxilla (e.g., non-carcharodontosaurid allosauroids) and dentary (e.g., megalosaurids). Likewise, the ontogenetical variation of the number of maxillary and dentary teeth, and suggested by Carr (1999) for tyrannosaurids, was questioned by Currie (2003) and refuted by Tsuihiji *et al.* (2011). Furthermore, the tooth counts typically varies of one or two teeth between the left and right jaws of a same individual (Currie 2003). Although the tooth count variation seems to exceed two teeth for the maxilla or the dentary in some taxa (e.g., *Ceratosaurus nasicornis*, *Tyrannosaurus rex*; Carrano and Sampson 2008; Brusatte *et al.* 2012), the character states of our datamatrix regarding the maxillary and dentary tooth count corresponds, in most cases, to a range of two teeth or more, and we therefore assume that there must be a theropod with an intermediate tooth count between a more primitive one with two teeth less and a more derived with two teeth more. Given the results of the cladistic analysis, this assumption is coherent with the evolution of maxillary and dentary tooth count for most theropod clades, except perhaps for baryonychine and spinosaurine Spinosauridae that may have followed two different path in the evolution of their dentition.

Some characters concern the curvature of the labial and lingual sides of the crown, and the presence of ornamentations on their surface. The labial and lingual sides of a theropod tooth can be identified thanks to the position and orientation of the mesial and distal carinae. The mesial carina, when curving towards the base of the crown, always twists towards the lingual side, whereas the distal carina, when deflected from the centre of the distal margin, is displaced labially in the large majority of theropods. Furthermore, there is typically a centrally positioned depression on the lingual side of the root which can extends on the basal part of the crown in many taxa. If this depression appears on both labial and distal sides of the crown, the lingual depression is usually deeper than the labial one (pers. obs.).

Two characters are related to the outline of the crown base in cross-section. This feature is particularly important in mesialmost teeth which have a typical cross-section outline in many theropod clades. The following figure illustrates the different outlines and the associated terms used in this paper. Because theropod teeth morphology varies through ontogeny (Araújo *et al.* 2013), some dentition-based characters are only coded in mature (i.e., sub-adult and adult) individuals. They concern the crown size (CH), the average number of denticles (per 5 mm) on the mesial and distal carinae, and the size of the denticles along the carinae for both mesialmost and distal dentition. Indeed, embryo and hatchling individuals have logically smaller crowns with smaller denticles, as well as larger denticles at the base of the crown (pers. obs.).

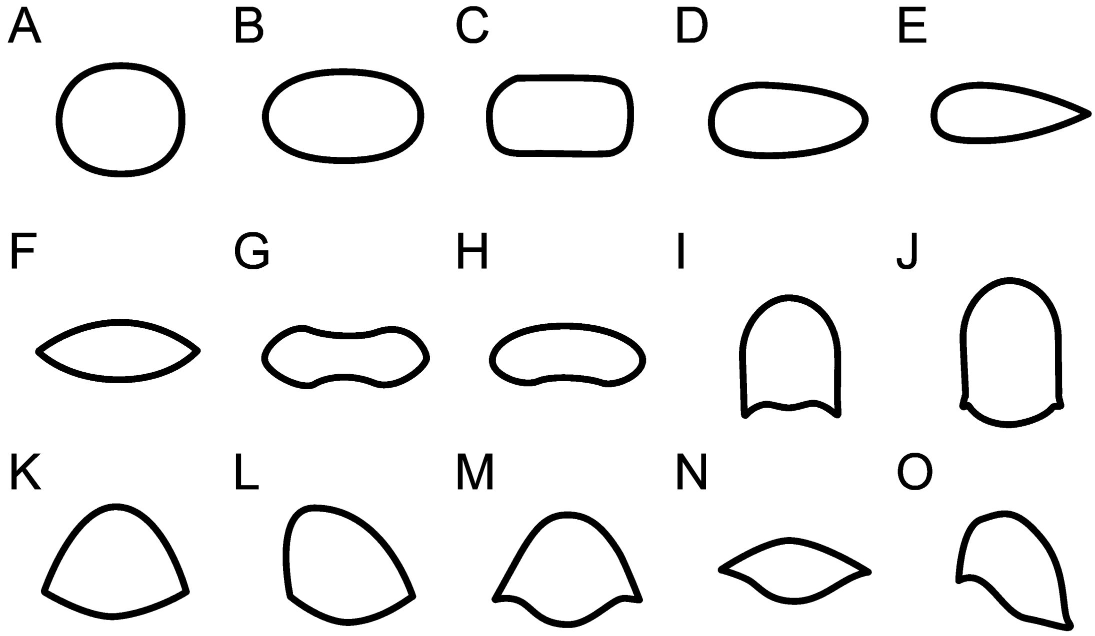


FIGURE A1. Cross-section outlines of the base crown at the cervix in nonavian theropods. **A.** subcircular; **B**. elliptical; **C.** subrectangular; **D.** oval; **E.** lanceolate; **F.** lenticular; **G.** eight-shaped; **H.** bean-shaped (reniform); **I–J.** U-shaped; **K–L.** D-shaped; **M–N.** 'Flying-saucer' shape; **O.** J-shaped.

I. PREMAXILLA ALVEOLI/TEETH

1. Premaxillary teeth (Russel and Dong 1993 #2): (0) present; (1) absent.
2. Number of premaxillary teeth (or alveoli; Modified from Harris 1998 #47; Sereno *et al.* 1998 #19; **Ordered**): (0) 3; (1) 4; (2) 5; (3) 6; (4) 7.
3. Premaxillary alveoli, direction of main axis of elongation in palatal view (**New**; Unordered): (0) all alveoli mesio-distally oriented; (1) anterior alveoli labio-lingually oriented, posterior alveoli mesio-distally oriented; (2) all alveoli labio-lingually oriented.
4. Premaxillary alveoli, overlap of the first and second alveoli in palatal view (**New**; **Ordered**): (0) absent; (1) present, partial; (2) present, complete.
5. Premaxillary alveoli, overlap of the second and third alveoli in palatal view (**New**): (0) absent; (1) present.
6. Premaxillary alveoli, overlap of the third and fourth alveoli in palatal view (**New**): (0) absent; (1) present.
7. Premaxillary teeth (or alveoli), size (Modified from Holtz *et al.* 2004 #261; Unordered): (0) all approximately equal in size; (1) posterior teeth (or alveoli) smaller than anterior teeth (or alveoli); (2) anterior teeth (or alveoli) smaller than posterior teeth (or alveoli).
8. Anterior premaxillary teeth (or alveoli), size (**New**; Unordered): (0) significantly smaller than the first six anterior <u>maxillary</u> teeth (or alveoli); (1) subequal in size than the first six anterior <u>maxillary</u> teeth (or alveoli); (2) significantly larger than the first six anterior <u>maxillary</u> teeth (or alveoli).
9. Posterior premaxillary teeth (or alveoli), size (Modified from Holtz 2001 #15; Unordered): (0) significantly smaller than the first six anterior <u>maxillary</u> teeth (or alveoli); (1) subequal in size than the first six anterior <u>maxillary</u> teeth (or alveoli).
10. First premaxillary tooth (or alveolus), size (Modified from Sereno *et al.* 1998 #38; Unordered): (0) subequal in size than second tooth (or alveolus); (1) significantly smaller than second tooth (or alveolus); (2) significantly bigger than second tooth (or alveolus).
11. Second premaxillary tooth (or alveolus), size (Modified from Currie 1995 #4; Unordered): (0) subequal in size than third (and fourth) premaxillary tooth (or alveolus); (1) significantly smaller than third (and fourth) tooth (or alveolus); (2) significantly larger than third (and fourth) tooth (or alveolus).
12. Posteriormost premaxillary tooth (or alveolus), size (**New**; Unordered): (0) subequal in size than more anterior teeth (or alveoli); (1) significantly smaller than more anterior teeth (or alveoli); (2) significantly larger than more anterior teeth (or alveoli).
13. Distal premaxillary alveoli, shape in palatal view (**New**): (0) oval to subcircular; (1) subrectangular.
14. Premaxillary tooth row, posterior extension (position of posteriormost premaxillary tooth; Modified from Sereno 1999 #36): (0) aligned (ventral) to external naris; (1) anterior to external naris.

15. Premaxillary tooth row, posterior part in palatal view (**New**; **Ordered**): (0) unconstricted; (1) slightly constricted; (2) strongly constricted, terminal rosette of premaxilla.
16. Subnarial gap (i.e., posterior part of premaxillary alveolar margin unedentelous, resulting in an interruption of the upper tooth row; Modified from Gauthier 1986; Welles 1984; Rowe 1989; Rowe and Gauthier 1990; Sereno 1999 #34): (0) absent; (1) present.

II. MAXILLA ALVEOLI/TEETH

17. Number of maxillary teeth (or alveoli; Modified from Perle *et al.* 1993; **Ordered**): (0) >19; (1) 18–19; (2) 16–17; (3) 15; (4) 10–14; (5) 1–9.
18. Anterior maxillary teeth (or alveoli), size (Modified from Zanno *et al.* 2009 #340; Unordered): (0) subequal in size than posterior teeth (or alveoli); (1) significantly larger than posterior maxillary teeth (or alveoli); (2) significantly smaller than posterior maxillary teeth (or alveoli).
19. Mid-maxillary teeth (or alveoli), mesiodistal length: (**New**): (0) subequal in size than anteriormost maxillary teeth (or alveoli); (1) significantly larger than anteriormost maxillary teeth (or alveoli).
20. First maxillary alveolus, size (Modified from Sereno *et al.* 1998 #38): (0) significantly smaller than second tooth (or alveolus); (1) subequal in size than second tooth (or alveolus).
21. First maxillary alveolus opens (Rowe 1989): (0) ventrally; (1) anteroventrally.
22. Maxillary teeth, inclination (**New**): (0) pointing ventrally; (1) pointing ventro-laterally.
23. Maxillary alveoli, shape in palatal view (**New**; Unordered): (0) oval to lenticular; (1) subrectangular; (2) circular.
24. Maxillary tooth row, posterior extension (i.e., position of posteriormost tooth; Modified from Gauthier 1986; Harris 1998 #3; Holtz 1998 #133; Rauhut 2003 #70; **Ordered**): (0) posterior to the anterior rim of orbit; (1) aligned (ventral) to the anterior rim of orbit; (2) anterior to the anterior rim of the orbit, posterior to the anteroventral rim of the antorbital fenestra; (3) aligned to the anteroventral rim of the antorbital fenestra; (4) anterior to the anteroventral rim of the antorbital fenestra.

III. DENTARY ALVEOLI/TEETH

25. Number of dentary teeth (or alveoli; Modified from Senter 2002 #22; Carrano *et al.* 2002 #59; **Ordered**): (0) > 25; (1) 18–25; (2) 15–17; (3) < 15.
26. Dentary alveoli in dorsal view (Currie 1987 #24): (0) well-separated; (1) merged to form a paradental groove.
27. Anteriormost dentary teeth (or alveoli), size (Modified from Russell and Dong 1993; Unordered): (0) subequal in size than mid- and posterior dentary teeth (or alveoli); (1) significantly larger than mid- and posterior dentary teeth (or alveoli); (2) significantly smaller than mid- and posterior dentary teeth (or alveoli).
28. First dentary tooth (or alveolus), size in comparison to second and third dentary alveoli (Modified from Gauthier 1986 #36 and Harris 1998 #48. Based on Holtz *et al.* 2004 #213 and Sereno *et al.* 2004 #71): (0) subequal in size; (1) first tooth (or alveolus) substantially smaller.
29. Mid-dentary teeth (or alveoli), size (Modified from Pérez-Moreno *et al.* 1994): (0) subequal in size than anterior <u>maxillary</u> teeth (or alveoli); (1) significantly smaller than anterior <u>maxillary</u> teeth (or alveoli).
30. Enlarged fanglike anterior dentary tooth (that inserts into a notch between the premaxilla and maxilla; Clark *et al.* 1994): (0) absent; (1) present.
31. Terminal rosette of dentary, number of teeth (or alveoli; **New**; Unordered): (0) terminal rosette absent; (1) four teeth (or alveoli); (2) five teeth (or alveoli).
32. Anterior dentary teeth (**New**): (0) facing dorsally; (1) procumbent, facing anterodorsally.

VI. PALATAL TEETH

33. Palatal teeth on the pterygoid (Sereno 1999 #107): (0) present; (1) absent.

V. MESIALMOST TEETH

Crown

34. Mesialmost teeth, constriction between root and crown (Modified from Martin *et al.* 1980; Hou *et al.* 1996; Currie 1987; Unordered): (0) absent; (1) constriction important, base of crown occupying 85% or less of largest crown width; (2) constriction weak, base of crown occupying more than 85% of largest crown width.
35. Mesialmost teeth, constriction between root and crown along the tooth row (**New**): (0) present in some teeth; (1) present in all teeth.
36. Mesialmost teeth, crown height (CH in centimetres) in subadult/adult (**New**; **Ordered**): (0) CH ≤ 1; (1) $1 < \text{CH} \leq 6$; (2) CH > 6.
37. Mesialmost teeth, labiolingual compression of the crown (CBR = CBW/CBL; Modified from Sereno *et al.* 1998 #17; Charig and Milner 1997; Unordered): (0) CBR ≤ 0.75, oval to lenticular; (1) weak, $0.75 < \text{CBR} < 1.2$, tooth subcircular; (2) teeth labiolingually elongated, CBR > 1.2.
38. Mesialmost teeth, baso-apical elongation of the crown (CHR = CH/CBL; **New**; Unordered): (0) strongly elongated, CHR > 3; (1) important, $2.5 < \text{CHR} \leq 3$; (2) normal, $2 < \text{CHR} \leq 2.5$; (3) weak, CHR ≤ 2.
39. Mesialmost teeth, crown recurvature (lingually or distally; Modified from Sereno *et al.* 1998 #35; Unordered): (0) present, strongly recurved; (1) present, slightly recurved; (2) absent, tooth crown straight and apex centrally positioned or almost centrally positioned.

40. Mesialmost teeth, distal margin of the crown in lateral view (Modified from Canale *et al.* 2009 #5 (Smith 2007; Unordered): (0) mainly concave; (1) straight; (2) mainly convex.
41. Mesialmost teeth, outline of basal cross-section of the crown in the mesialmost tooth (Modified from Bakker *et al.* 1988 #22; Unordered): (0) subcircular, ovoid or elliptical; (1) lanceolate, with acute and well-developed distal carina and mesial margin convex; (2) 'Flying-saucer' shape, with labial margin convex and lingual margin biconcave; (3) D-shaped or J-shaped, with lingual margins strongly convex and labial margins convex or sigmoid; (5) U-shaped, with mesial and distal margin subparalell and lingual margin planar or weakly convex; (6), lenticular, with acute and well-developed distal and mesial carinae
42. Mesialmost teeth, concave surface adjacent to the carina: (**New**; Unordered): (0) absent; (1) on the <u>labial</u> surface and adjacent to the <u>distal</u> carina; (2) on the <u>lingual</u> surface and adjacent to <u>both carinae</u>; (3) on the <u>lingual</u> surface and adjacent to the <u>mesial carina only</u>; (4) on the <u>lingual</u> surface and adjacent to the <u>distal</u> carina only.

Carinae

43. Mesialmost teeth, mesial carina (**New**): (0) absent; (1) present.
44. Mesialmost teeth, mesial carina (Modified from Senter *et al.* 2004 #20): (0) non-serrated; (1) serrated.
45. Mesialmost teeth, distal carina (**New**): (0) serrated; (1) non-serrated.
46. Mesialmost teeth, mesial carina (**New**; Unordered): (0) not twisted at all; (1) twisted, curves onto the lingual surface.
47. Mesialmost teeth, mesial carina (Modified from Currie 1995 #2; Unordered): (0) facing mesially; (1) facing mesiolabially or labially; (2) facing mesiolingually; (3) facing entirely lingually.
48. Mesialmost teeth, distal carina (**New**; Unordered): (0) centrally positioned on the crown and facing distally or labiodistally; (1) labially displaced and facing distally or labiodistally; (2) labially displaced and facing lingually or linguodistally.
49. Mesialmost teeth, axis passing through both carinae at mid-crown (**New**; Unordered): (0) sub-parallel to long axis of skull; (1) diagonally oriented from long axis of skull; (2) perpendicular to long axis of skull.
50. Mesialmost teeth, mesial carina, and if serrated, basalmost serration of the mesial carina (Modified from Benson 2009 #89; Unordered): (0) terminates well-above the cervix; (1) extends to the cervix or just above it; (2) terminates well beneath the cervix.

Denticles

51. Mesialmost teeth, average number of denticles per five mm on mesial carina at two-thirds of the crown (MC) in subadult/adult (Modified from Russel and Dong 1993 #20; Unordered): (0) > 19; (1) 14–19; (2) 9–13; (3) 1–8.
52. Mesialmost teeth, average number of mid-crown denticles per five mm on distal carina (DC) in subadult/adult (Modified from Russel and Dong 1993 #20; Unordered): (0) > 19; (1) 14–19; (2) 9–13; (3) 1–8.
53. Mesialmost teeth, denticle size (except in embryos and hatchlings; **New**; **Ordered**): (0) minute denticles, more than 250 denticles along the crown; (1) normal in height, between 15 to 250 denticles along the crown; (2) very larges denticles, less than 15 denticles along the crown.
54. Mesialmost teeth, denticles on mesial carina (Modified from Norell *et al.* 2001 #88; Unordered): (0) rounded and symmetrically convex; (1) rounded and asymmetrically convex; (2) strongly hooked/pointed, denticles with a tip pointing apically.
55. Mesialmost teeth, denticles on distal carina (Modified from Senter *et al.* 2004 #23; Unordered): (0) rounded and symmetrically convex; (1) rounded and asymmetrically convex; (2) strongly hooked/pointed, denticles with a tip pointing apically.
56. Mesialmost teeth, size of mesial denticles relative to distal denticles (i.e., DSDI; Rauhut and Werner 1995; Unordered): (0) mesial and distal denticles of same size, 0.8 < DSDI <1.2; (1) mesial denticles larger than distal ones, DSDI < 0,8 (2) distal denticles larger than mesial ones, DSDI > 1,2.
57. Mesialmost teeth, denticles contiguous over tip (Modified from Harris 1998 #45): (0) present; (1) absent.
58. Mesialmost teeth, interdenticular sulci (Modified from Benson 2009 #90; Unordered): (0) absent; (1) present, short; (2) present, long and well-developed.

Ornamentations

59. Mesialmost teeth, flutes (i.e., subparallel longitudinal grooves separated by acute ridges) on the crown (Modified from Sereno *et al.* 1998 #18; Charig and Milner 1997; Unordered): (0) absent; (1) present on the lingual surface only; (2) present on both labial and lingual surfaces; (3) present on the labial surface only.
60. Mesialmost teeth, longitudinal groove on the labial and/or lingual side of the crown (**New**; Unordered): (0) absent; (1) present, a single groove centrally positioned; (2) present, a single groove mesially positioned.
61. Mesialmost teeth, elongated, large, longitudinal and rounded ridge, different from acute ridges of fluted surface, on the lingual side of the crown (**New**; Unordered): (0) absent; (1) present, a single ridge centrally positioned; (2) present, two ridges or more.
62. Mesialmost teeth, basal striations, different of flutes, on both lingual and labial surfaces of the crown (**New**): (0) absent; (1) present.

VI. LATERAL TEETH

Crown

63. Lateral teeth, constriction between root and crown (Modified from Martin *et al.* 1980; Hou *et al.* 1996; Currie 1987; Unordered): (0) absent; (1) constriction important, base of crown occupying 85% or less of largest crown width; (2)

constriction weak, base of crown occupying more than 85% of largest crown width.

64. Lateral teeth, constriction between root and crown along the tooth row (**New**): (0) present in some teeth; (1) present in all teeth.
65. Lateral teeth, height of the largest crown (CH in centimetres) in subadult/adults (**New**; **Ordered**): (0) CH $\leq$ 1; (1) 1 < CH $\leq$ 6; (2) CH > 6.
66. Lateral teeth, labiolingual compression of the crown (CBR = CBW/CBL; **New**; Unordered): (0) important, CBR $\leq$ 0.5, tooth strongly flattened; (1) normal, 0.5 < CBR $\leq$ 0.75; (2) weak, CBR > 0.75, tooth incrassate or subcircular.
67. Lateral teeth, baso-apical elongation of the crown (CHR = CH/CBL; **New**; Unordered): (0) weak, CHR $\leq$ 1.5; (1) normal, 1.5 < CHR $\leq$ 2.5; (2) important, CHR > 2.5.
68. Lateral teeth, distal margin of crown in lateral view (**New**; Unordered): (0) strongly concave; (1) slightly concave, roughly straight, or straight, apex positioned at the same level as distal profile; (2) convex, apex positioned mesial to mesial profile; (3) weakly sigmoid, basal half concave and apical half convex.
69. Lateral teeth, mesial margin of crown in lateral view (**New**): (0) strongly convex; (1) slightly convex, almost straight, apex centrally positioned.
70. Lateral teeth, mesiodistal curvature of the labial surface of the crown (**New**): (0) convex; (1) surface centrally positioned on the crown roughly flattened.
71. Lateral teeth, concave surface adjacent to carinae all along the crown (**New**; Unordered): (0) absent; (1) present on labial surface and adjacent to distal carina; (2) present on lingual surface and adjacent to distal carina; (3) present on the labial surface and adjacent to both mesial and distal carinae; (4) present on lingual surface and adjacent to both mesial and distal carinae.
72. Lateral teeth, outline of basal cross-section of the crown (**New**; Unordered): (0) subcircular; (1) lenticular or lanceolate; (2) elliptical or bean-shaped (i.e., longitudinal depression centrally positioned on one side only); (3) 8-shaped (i.e., longitudinal depression centrally positioned on both lingual and labial margins); (4) subrectangular.
73. Lateral teeth, basoapical extension of labial depression (i.e., centrally positioned depression on the basolabial surface) on the crown: (**New**; Unordered): (0) labial depression absent; (1) restricted to the crown base; (2) extends along the basal half of the crown or more apically.

Carinae

74. Lateral teeth, mesial carina (**New**): (0) present; (1) absent.
75. Lateral teeth, mesial carina (Modified from Currie 1995 #2): (0) centrally positioned on mesial margin or slightly twisted lingually towards the base; (1) sharply twisted lingually.
76. Lateral teeth, mesial carina (Modified from Senter *et al.* 2004 #20): (0) serrated; (1) non-serrated.
77. Lateral teeth, distal carina (**New**): (0) present; (1) absent.
78. Lateral teeth, distal carina (**New**): (0) serrated; (1) non-serrated.
79. Lateral teeth, extension of mesial carina relative to distal carina (**New**): (0) mesial carina extends at the same level or terminates more apically than the distal carina; (1) mesial carina extends more basally than the distal carina.
80. Lateral teeth, mesial carina, and if serrated, basalmost serration of the mesial carina (Modified from Benson 2009 #89; Unordered): (0) terminates around mid-height of crown or more apically; (1) extends to base of crown or slightly above the cervix; (2) terminates well beneath the cervix.
81. Lateral teeth, distal carina, and if serrated, basalmost serration of the distal carina (Modified from Benson 2009 #89): (0) extends to the cervix or just above it; (1) terminates well beneath the cervix; (2) terminates well-above the cervix.
82. Lateral teeth, profile of the distal carina on the crown in distal view (**New**): (0) straight or very slightly bowed; (1) strongly bowed or sigmoid.
83. Lateral teeth, position of distal carina on the crown in distal view (**New**): (0) centrally positioned, crown subsymmetrical; (1) strongly labially deflected on the distal margin, crown asymmetrical.

Denticles/serrations

84. Lateral teeth, average number of denticles per five mm on mesial carina at two-thirds of the crown (MCA) in subadult/adult (Modified from Russel and Dong 1993 #20; Unordered): (0) > 44; (1) 30–44; (2) 16–29; (3) 9–15; (4) < 9.
85. Lateral teeth, average number of mid-crown denticles per five mm on distal carina (DC) in subadult/adult (Modified from Russel and Dong 1993 #20; Unordered): (0) > 44; (1) 30–44; (2) 16–29; (3) 9–15; (4) < 9.
86. Lateral teeth, denticle size on a single carina (except in embryos and hatchlings; **New**; **Ordered**): (0) minute denticles, more than 250 denticles; (1) normal in height, between 20 to 250 denticles; (2) very larges denticles, less than 20 denticles.
87. Lateral teeth, shape of denticles on mesial carina in lateral view (Modified from Norell *et al.* 2001 #88; Unordered): (0) symmetrically convex; (1) asymmetrically convex; (2) hooked/pointed.
88. Lateral teeth, shape of denticles on distal carina in lateral view (Senter *et al.* 2004 #23; Unordered): (0) symmetrically convex; (1) asymmetrically convex; (2) hooked/pointed.
89. Lateral teeth, shape of mesial margin of rounded denticles on mesial carina in lateral view (**New**): (0) parabolic; (1) subrectangular, with flattened surface.
90. Lateral teeth, shape of distal margin of rounded denticles on distal carina in lateral view (**New**; Unordered): (0) parabolic; (1) subrectangular, with flattened surface; (2) semi-circular.
91. Lateral teeth, shape of denticles at two-thirds of the crown (MC-MA) on mesial carina in lateral view (**New**; Unordered): (0) longer basoapically than mesiodistally, vertical subrectangular; (1) as long mediodistally as basoapically,

subquadrangular; (2) longer mediodistally than basoapically, horizontal subrectangular.

92. Lateral teeth, shape of mid-crown denticles (DC) on distal carina in lateral view (**New**; Unordered): (0) as long mediodistally than basoapically, subquadrangular; (1) longer mediodistally than basoapically, horizontal subrectangular; (2) longer basoapically than mesiodistally, vertical subrectangular.
93. Lateral teeth, denticle size along the carinae (Mateus *et al.* 2011): (0) regular, gradual change in denticle size; (1) irregular, sporadic change in denticle size.
94. Lateral teeth, biconvex apical denticles (i.e., biconvex external margin of denticle) on mesial carina in lateral view (**New**): (0) absent; (1) present.
95. Lateral teeth, orientation of mesiodistal axis of apical denticles on mesial carina in lateral view (**New**): (0) perpendicular to mesial margin; (1) inclined apically from mesial margin.
96. Lateral teeth, orientation of mesiodistal axis of mid-crown denticles on distal carina in lateral view (**New**): (0) perpendicular to distal margin; (1) inclined apically from distal margin.
97. Lateral teeth, average number of denticles on mesial carina (**New**; Unordered): (0) higher number of denticles basally than at the mid-crown; (1) lower number of denticles basally than at the mid-crown; (2) subequal number of denticles basally than at the mid-crown.
98. Lateral teeth, average number of denticles on mesial carina (**New**; Unordered): (0) higher number of denticles apically than at the mid-crown; (1) lower number of denticles apically than at the mid-crown; (2) subequal number of denticles apically than at the mid-crown.
99. Lateral teeth, average number of denticles on distal carina (except in embryos and hatchlings; **New**; Unordered): (0) higher number of denticles basally than at the mid-crown; (1) subequal or lower number of denticles basally than at the mid-crown.
100. Lateral teeth, average number of denticles on distal carina (**New**; Unordered): (0) higher number of denticles apically than at the mid-crown; (1) lower number of denticles apically than at the mid-crown; (2) subequal number of denticles apically than at the mid-crown.
101. Lateral teeth, size of mesial denticles relative to distal denticles (i.e., DSDI; Rauhut and Werner 1995; Unordered): (0) mesial and distal denticles of same size, 0.8 < DSDI <1.2; (1) mesial denticles larger than distal ones, DSDI < 0,8 (2) distal denticles larger than mesial ones, DSDI > 1,2.
102. Lateral teeth, distal denticles on the apex (Harris 1998 #45): (0) contiguous over tip, or very close to the apex; (1) distal denticles disappear well beneath the apex.
103. Lateral teeth, interdenticular space between mid-crown denticles on the distal carina (**New**): (0) narrow, less than one third of the denticle width; (1) broad, more than one third of the denticle width.
104. Lateral teeth, interdenticular sulci between apical denticles on the mesial carina (Modified from Benson 2009 #90; Unordered): (0) absent; (1) present, short and poorly developed; (2) present, long and well-developed.
105. Lateral teeth, interdenticular sulci between mid-crown denticles on the distal carina (Modified from Benson 2009 #90; Unordered): (0) absent; (1) present, short and poorly developed; (2) present, long and well-developed.
106. Lateral teeth, interdenticular sulci between basalmost denticles on the distal carina (Modified from Benson 2009 #90; Unordered): (0) absent; (1) present, short and poorly developed; (2) present, long and well-developed.

Ornamentations and texture

107. Lateral teeth, flutes (i.e., subparallel longitudinal grooves separated by acute ridges) on the crown (Modified from Sereno *et al.* 1998 #18; Charig and Milner 1997; Unordered): (0) absent; (1) present on the lingual surface; (2) present on both labial and lingual surfaces.
108. Lateral teeth, average number of flutes on the crown (**New**; Unordered): (0) 1–7; (1) >7
109. Lateral teeth, large transversal undulations on the crown in some teeth (Holtz 1998 #131; Unordered): (0) absent; (1) present, tenuous; (2) present, well visible.
110. Lateral teeth, large transversal undulations on the crown in some teeth when present (**New**): (0) present, just a few; (1) present, numerous and closely packed.
111. Lateral teeth, marginal undulations (i.e., short undulations adjacent to carinae) in some teeth (Modified from Currie and Carpenter 2000 #42; Brusatte *et al.* 2007; Unordered): (0) absent; (1) present and short, the mesiodistal elongation is less than twice the space separating each undulations; (2) present and elongated, the mesiodistal elongation is longer than twice the space separating each undulations.
112. Lateral teeth, marginal undulations in some teeth (**New**; Unordered): (0) present and shallow, only visible with light; (1) present and pronounced, well visible in lateral view.
113. Lateral teeth, marginal undulations in some teeth (**New**; Unordered): (0) present only on the mesial side of the crown; (1) present only on the distal side of the crown; (2) present on both mesial and distal sides.
114. Lateral teeth, marginal undulations in some teeth (**New**; Unordered): (0) present and mesio-distally oriented; (1) present and diagonally oriented.
115. Lateral teeth, longitudinal groove on the labial and/or lingual surface of the crown (**New**; Unordered): (0) absent; (1) present, a single groove centrally positioned; (2) present, a single groove adjacent to mesial carina; (3) present, two grooves.
116. Lateral teeth, elongated longitudinal and rounded ridge (different from acute ridges of fluted surface) on the lingual surface of the crown (**New**; Unordered): (0) absent; (1) present, a single ridge centrally positioned; (2) present, two or three

ridges.

117. Lateral teeth, enamel surface texture (**New**; Unordered): (0) smooth or irregular (non-oriented) texture; (1) braided (oriented) texture, not clearly visible with light; (2) braided (oriented) texture, clearly visible with light; (2) deeply veined texture.
118. Lateral teeth, oriented enamel surface texture (**New**): (0) remains baso-apically oriented or slightly curved basally close to the carinae; (1) strongly curved basally close to the carinae.

VII. ENAMEL MICROSTRUCTURE

119. Enamel microstructure, enamel tubules (Hwang 2007 #12; Unordered): (0) absent or rare; (1) common only in BUL and/or inner potion of enamel; (2) common and extend throughout entire enamel thickness; (3) extremely common and forming an integral structural component of enamel.
120. Enamel microstructure, predominant enamel type (Hwang 2007 #13; Unordered): (0) parallel crystallites; (1) basal unit layer (BUL); (2) columnar.
121. Enamel microstructure, predominant enamel type, percentage of enamel thickness (Hwang 2007 #14): (0) ≥ 75%; (1) < 75%.
122. Enamel microstructure, number of enamel types present in schmelzmuster (Hwang 2007 #15; Unordered): (0) one; (1) two; (3) four.
123. Enamel microstructure, number of different module types present in schmelzmuster (Hwang 2007 #16; Unordered): (0) one; (1) two.
124. Enamel microstructure, boundary between first and second enamel types from the EDJ (Hwang 2007 #17): (0) parallel to EDJ; (1) jagged, varies in distance from EDJ.
125. Enamel microstructure, boundary between second and third enamel types from the EDJ (Hwang 2007 #18): (0) parallel to EDJ; (1) jagged, varies in distance from EDJ.
126. Enamel microstructure, basal unit layer (BUL; Hwang 2007 #19): (0) present; (1) absent.
127. Enamel microstructure, basal unit layer (BUL; Hwang 2007 #20): (0) poorly developed; (1) well-developed, with distinct planes of separation between adjacent units.
128. Enamel microstructure, basal unit layer (BUL), maximum unit diameter (Hwang 2007 #21): (0) < 10 µm; (1) ≥ 10 µm.
129. Enamel microstructure, basal unit layer (BUL; Hwang 2007 #22; Unordered): (0) < 25% of total enamel thickness; (1) 25–50% of total enamel thickness; (2) ≥ 50% of enamel thickness.
130. Enamel microstructure, incremental lines (Hwang 2007 #23; Unordered): (0) absent; (1) faint, poorly defined; (2) well-defined.
131. Enamel microstructure, incremental lines (Hwang 2007 #24; Unordered): (0) present in one section of the schmelzmuster only; (1) present in more than one section of the schmelzmuster but not throughout entire schmelzmuster; (2) present throughout entire schmelzmuster.
132. Enamel microstructure, columnar units closest to the EDJ, shape of units in cross-sections (Hwang 2007 #27; Unordered): (0) polygons with sharp corners and more than 4 sides; (1) subcircular or polygons with rounded corners and more than 4 sides; (2) triangles and/or rectangles with sharp corners.
133. Enamel microstructure, columnar units closest to the EDJ (Hwang 2007 #28): (0) extend straight and unbroken to the OES or to within 20 µm below the OES; (1) end, split, or are interrupter less than two-thirds of the distance from the EDJ to OES.
134. Enamel microstructure, columnar units closest to the EDJ, maximum unit diameter (Hwang 2007 #29): (0) < 15 µm; (1) ≥ 15µm.
135. Enamel microstructure, columnar units closest to the OES (Hwang 2007 #33): (0) no dominant direction of orientation, planes of separations equally well-developed in all directions; (1) distinct longitudinal orientation, planes of separation better developed in an apicobasal (longitudinal) direction.
136. Enamel microstructure, ratio of thickest enamel type in schmelzmuster divided by second thickest enamel type (Hwang 2007 #39): (0) > 7; (1) 1.3 to 7; (2) 1 to 1.3.

VIII. ROOT

137. Root, shape in lateral view (**New**): (0) with subparallel margins; (1) with convex margins, root significantly larger than base crown.
138. Root, distal shape in lateral view (Sereno *et al.* 1998 #21; Charig and Milner 1997): (0) broad; (1) strongly tapered.
139. Root, outline of mid-root in cross section (**New**; Unordered): (0) oval to subcircular; (1) 8-shaped (i.e., longitudinal depression centrally positioned on both lingual and labial margins); (2) bean-shaped (i.e., longitudinal depression centrally positioned on one side only).
140. Root, form of the unerupted tooth fossa (i.e., lingual depression hosting the unerupted tooth) in lingual view (**New**): (0) deep and well-delimited depression; (1) shallow concavity.
141. Root, transversal undulations below the cervix (**New**): (0) absent; (1) present.

Character dependency

All characters are treated as independent. Although some character states are repeated for mesialmost teeth and lateral teeth, their dependence is strongly limited due to the large amount of variation between mesialmost teeth (i.e., premaxillary teeth and mesialmost dentary teeth) and lateral teeth (pers. obs.). In fact, mesialmost teeth tend to be either shorter or longer and usually labio-lingually thicker than lateral teeth. In addition, they also tend to lack of serrations or bearing denticles on the distal carina only, whereas lateral teeth have serrated mesial and distal keels in most carnivorous theropods. The number of denticles on both carinae in mesialmost teeth and lateral teeth can also be different in some taxa (e.g., *Ceratosaurus*, *Dubreuillosaurus*, *Duriavenator*, *Allosaurus*). Likewise, both mesial and distal carinae can strongly variate in position and orientation when compared to those of lateral teeth. The best example is the 'Flying-saucer' shape, D-shaped, J-shaped or U-shaped outline of mesialmost crowns at their base in Abelisauridae, basal Allosauroidea, Tyrannosauridae and some dromaeosaurids, which contrast with the tear-drop/lenticular outline of lateral teeth in those taxa. Finally, mesialmost teeth can display several crown features like flutes (e.g., *Ceratosaurus*, *Scipionyx*, *Velociraptor*), basal striations (e.g., *Herrerasaurus*, *Proceratosaurus*) or longitudinal grooves (*Allosaurus*, *Raptorex*) that can be totally absent in lateral teeth (pers. obs.).

Illustration of states of dentition-based characters

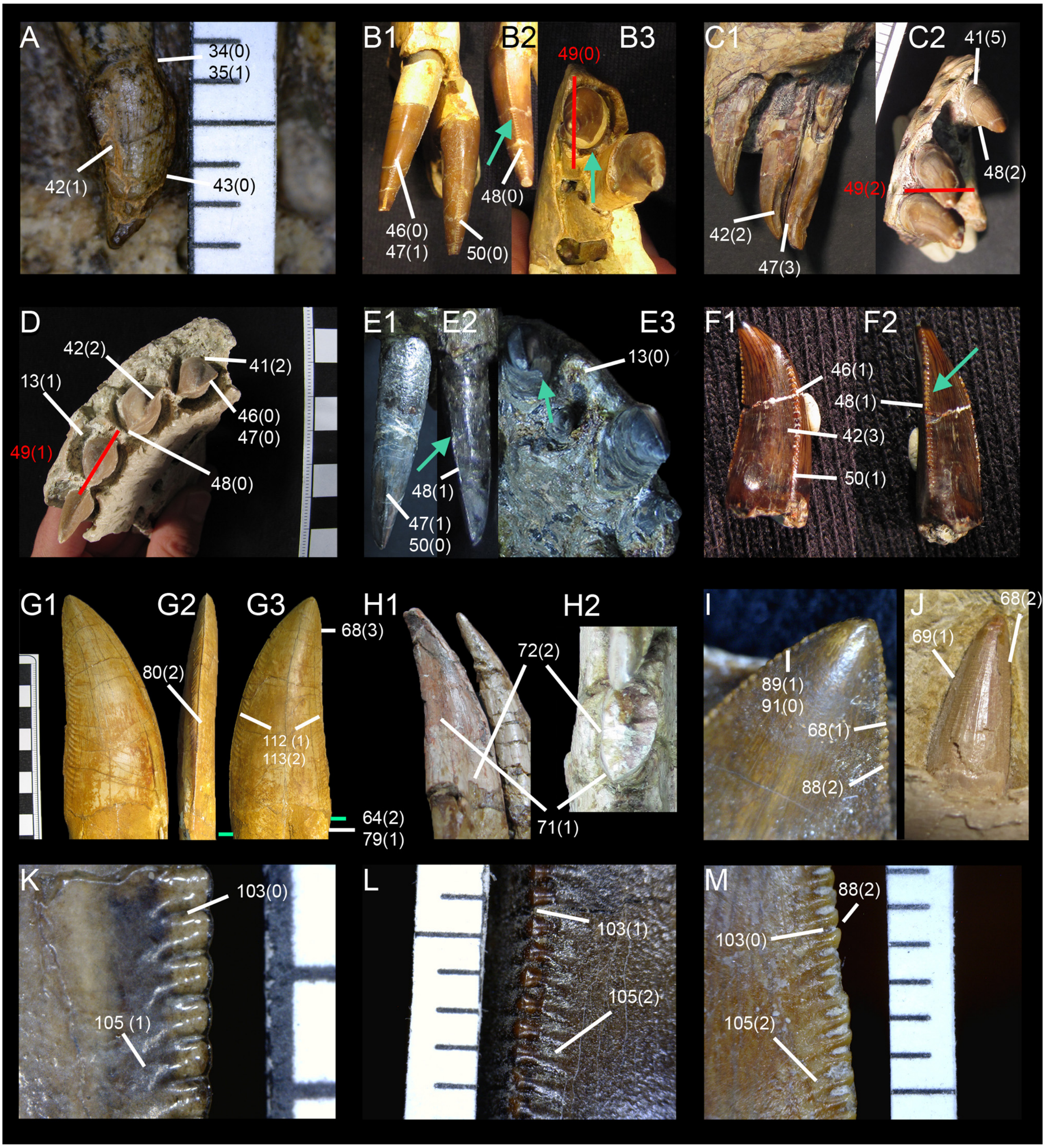
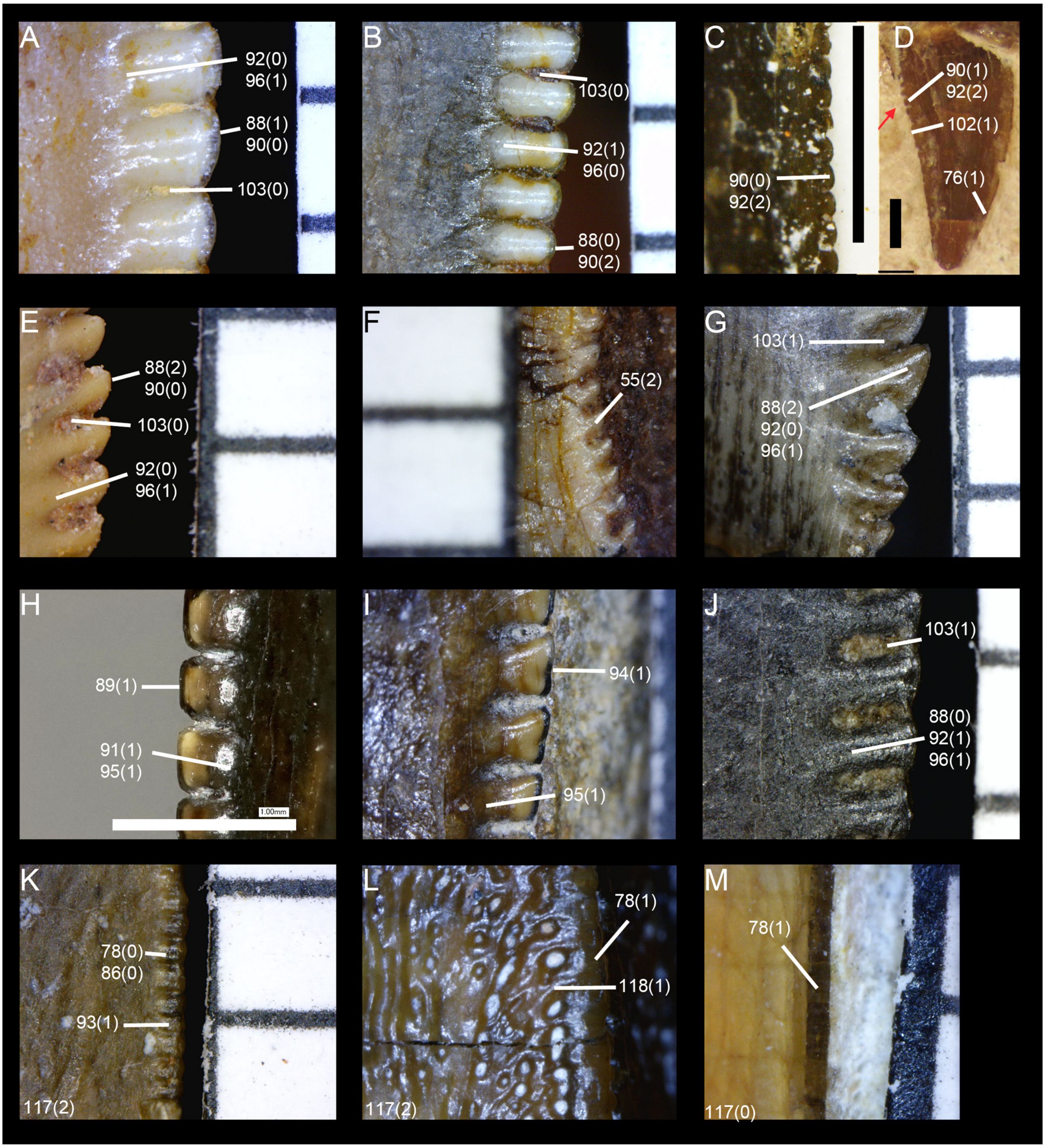


FIGURE A2. States of dentition-based characters. **A.** Fourth right premaxillary tooth of *Eoraptor lunensis* (PVSJ 512) in lateral view lacking a mesial carina (char. 43:0), displaying a concave area present on the labial side of the crown and adjacent to the distal carina (char. 42:1), and having an important constriction between root and crown at both mesial and distal margins (char. 35:1), giving a lanceolate shape to one of the premaxillary teeth (char. 34:0). **B.** First and second left premaxillary teeth of *Dubreuillosaurus valesdunensis* (MNHN 1998-13) in anterior (B1) and palatal (B3) views, and second left premaxillary tooth in posterior view (B2) showing a non-twisted (char. 46:0) mesial carina, facing labially (char. 47:1) and terminating well-above the cervix (char. 50:0), as well as a distal carina facing distally (char. 48:0). The axis passing through both carinae at mid-crown in *Dubreuillosaurus* mesialmost teeth is subparallel to long axis of the skull (char. 49:0). The distal carinae, designated by the green arrows, are centrally positioned on the crown and not displaced labially. **C.** Premaxillary teeth of *Raptorex kriegsteini* (LH PV18) in medial (C1) and palatal (C2) views showing the U-shaped outline of mesialmost crowns (char. 41:5), the concave area adjacent to both carinae (char. 42:2), the mesial and distal carinae facing lingually (char. 47:3; char. 48:2), and the axis passing through both carinae at mid-crown in mesialmost teeth that is perpendicular to long axis of skull (char. 49:2). **D.** Right premaxilla of *Majungasaurus crenatissimus* (FMNH PR 2100) in palatal view displaying the subrectangular alveoli (char. 13:1), a 'flying-saucer'-shaped outline of the mesialmost teeth (char. 41:2), a concave area present on the lingual side of the crown and adjacent to both carina (char. 42:2), a non-twisted mesial carina (char. 46:0) facing mesially (char. 47:0), a distal carina facing distally (char. 48:0), and an axis passing through both carinae at mid-crown in mesialmost teeth medio-laterally oriented from long axis of skull (char. 49:1). **E.** First premaxillary tooth of *Acrocanthosaurus atokensis* (NCSM 14345) in anterior (E1) and posterior (E2) views and premaxillary teeth in palatal view (E3) showing the oval alveoli (char. 13:0), and the mesial carina facing labially (char. 47.1) and terminating well-above the cervix (char. 50:0). Unlike *Dubreuillosaurus valesdunensis*, the distal carina, pointed by the green arrows, is here strongly displaced labially (char. 48:1). **F.** Isolated premaxillary crown of *Dromaeosaurus albertensis* (AMNH 5356) in lingual (F1) and distal (F2) views showing the concave area on the lingual side of the crown and adjacent to the mesial carina only (char. 42:3), and the strongly twisted mesial carina (char. 46:1) terminating at the level of the cervix (char. 50:1). Like *Acrocanthosaurus*, the distal carina, designated by the green arrow, is strongly displaced labially (char. 48:1). **G.** Isolated lateral tooth of *Carcharodontosaurus saharicus* (UC PV6) in lingual (G1), mesial (G2) and labial (G3) views showing the weak constriction between root and crown at the lateral margin (char. 64:2), the weakly sigmoid distal profile of the crown due to the convex apical half of the tooth (char. 68:3), the pronounced and well-visible marginal undulations (char. 112:1) adjacent to both carinae (char. 113:2), and the mesial carina terminating well beneath the cervix (char. 80:2) and extending further basally than the distal carina (char. 79:1; the basal extension of carinae are represented by green bars). **H.** Lateral teeth of *Genyodectes serus* (MLP 26-39) in linguodistal (H1) and apical (H2) views showing the concave surface adjacent to the distal carina (char. 71:1) and the wide mesiodistally concave area on the basal part of the labial margin of the crown and giving a bean-shape outline of the cross-section (char. 72:2). **I.** Tenth left maxillary tooth of *Rugops primus* (MNN IGU1) in labial views showing the slightly concave, roughly straight distal margin of the crown (char. 68:1), the apically hooked denticles on the distal carina (char. 88:2), and the parabolic margin of apical denticles on the mesial carina (char. 89:1), having a vertical subrectangular shape (char. 91:0). **J.** Maxillary tooth of *Irritator challengeri* (SMNS 58022) in labial view showing the convex, almost straight mesial (char. 69:1) and distal (char. 68:2) margins of the crown. **K.** Mid-crown denticles on the distal carina of the first left maxillary crown of *Erectopus superbus* (MNHN 2001-4) in lateral view showing the narrow interdenticular space (char. 103:0), and the short interdenticular sulci (char. 105:1) in between the denticles. **L.** Mid-crown denticles on the distal carina of the height right maxillary tooth of *Tyrannosaurus rex* (FMNH PR 2081) in laterodistal view showing the broad interdenticular space (char. 103:1) and the well-developed interdenticular sulci (char. 105:2) in between the denticles. **M.** Mid-crown denticles on the distal carina of the third right maxillary tooth of *Majungasaurus crenatissimus* (FMNH PR 2278) in lateral view showing the apically hooked denticles (char. 88:2), the narrow interdenticular space (char. 103:0), and the well-developed interdenticular sulci (char. 105:2).



A
92(0)
96(1)
88(1)
90(0)
103(0)
B
103(0)
92(1)
96(0)
88(0)
90(2)
C
90(0)
92(2)
D
90(1)
92(2)
102(1)
76(1)
E
88(2)
90(0)
103(0)
92(0)
96(1)
F
55(2)
G
103(1)
88(2)
92(0)
96(1)
H
89(1)
91(1)
95(1)
1.00mm
I
94(1)
95(1)
J
103(1)
88(0)
92(1)
96(1)
K
78(0)
86(0)
93(1)
117(2)
L
78(1)
118(1)
117(2)
M
78(1)
117(0)

FIGURE A3. States of denticle-based characters. **A.** Mid-crown denticles on the distal carina of an isolated tooth of *Carcharodontosaurus saharicus* (UC unlabelled) in lateral view showing the asymmetrically convex (char. 88:1) and parabolic (char. 90:0) margin of subquadrangular (char. 92:0) and apically inclined (char. 96:1) denticles, as well as a narrow interdenticular space (char. 103:0). **B.** Mid-crown denticles on the distal carina of an isolated tooth of *Afrovenator abakensis* (UC unlabelled) in lateral view showing the symmetrically convex (char. 88:0) and semi-circular (char. 90:2) margin of horizontal subrectangular (char. 92:1) denticles, perpendicular to mesial margin (char. 96:0), as well as a narrow interdenticular space (char. 103:0). **C.** Distal denticles of the fourth left maxillary tooth of *Eodromaeus murphi* (PVSJ 561) in lateral view displaying the mid-crown denticles vertically subrectangular in shape (char. 92:2) and having a convex external margin (char. 90:0) on the distal carina. **D.** Third left maxillary tooth of *Scipionyx samniticus* in lateral view displaying an unserrated mesial carina (char. 76:1), mid-crown denticles vertically subrectangular in shape (char. 92:2) and having a flattened margin (char. 90:1) on the distal carina, and a serrated distal carina extending well-beneath the crown apex (char. 102:1). **E.** Mid-crown denticles on the distal carina of an isolated tooth belonging to an indeterminate abelisaurid (MUCPv 482) in lateral view showing apically hooked denticles (char. 88:2) with a parabolic margin (char. 90:0), subquadrangular in shape (char. 92:0) and apically inclined (char. 96:1) from the distal margin, as well as a narrow interdenticular space between the denticles (char. 103:0). **F.** Mid-crown denticles on the distal carina of the third right premaxillary tooth of *Eoraptor lunensis* (PVSJ 512) in lateral view showing the apically hooked denticles (char. 55:2). **G.** Basal and mid-crown denticles on the distal carina of an isolated tooth of *Troodon formosus* (DMNH 22837) in lateral view showing subquadrangular (char. 92:0), apically hooked and strongly variable in size (char. 88:2) denticles, apically inclined (char. 96:1) from the distal margin, as well as a broad interdenticular space (char. 103:1) between them. **H.** Apical denticles on the mesial carina of an isolated tooth of *Acrocanthosaurus atokensis* (SMU 74646) in lateral view showing the subquadrangular (char. 91:1) and apically inclined (char. 95:1) denticles with a flattened margin (char. 89:1). **I.** Apical denticles on the mesial carina of an isolated lateral crown belonging to *Megalosaurus bucklandi* (NHM R234, tooth in matrix) in lateral view showing the apically inclined (char. 95:1) and biconvex denticles (char. 94:1). **J.** Mid-crown denticles on the distal carina of the ninth right maxillary tooth of *Allosaurus fragilis* (AMNH 851) in lateral view showing the symmetrically convex (char. 88:0), horizontal subrectangular (char. 92:1) and apically inclined (char. 96:1) denticles, as well as the broad interdenticular space (char. 103:1). **K.** Mid-crown denticles on the distal carina of an isolated tooth of *Suchomimus tenerensis* (MNN G73-3) in lateral view showing the serrated carina (char. 78:0) with minute denticles (char. 86:0) of irregular size along the carina (char. 93:1) and a veined enamel texture (char. 117:2). **L.** Distal carina at mid-crown in an isolated tooth of *Spinosaurus aegyptiacus* (MSNM V6422) in laterodistal view showing an unserrated carina (char. 78:1) and a deeply veined enamel surface texture (char. 117:2) curving basally in the vicinity of the carina (char. 118:1). **M.** Distal carina at mid-crown of a maxillary tooth of *Irritator challengeri* (SMNS 58022) in lateral view showing an unserrated carina (char. 78:1) and the smooth enamel surface texture (char. 117:0).

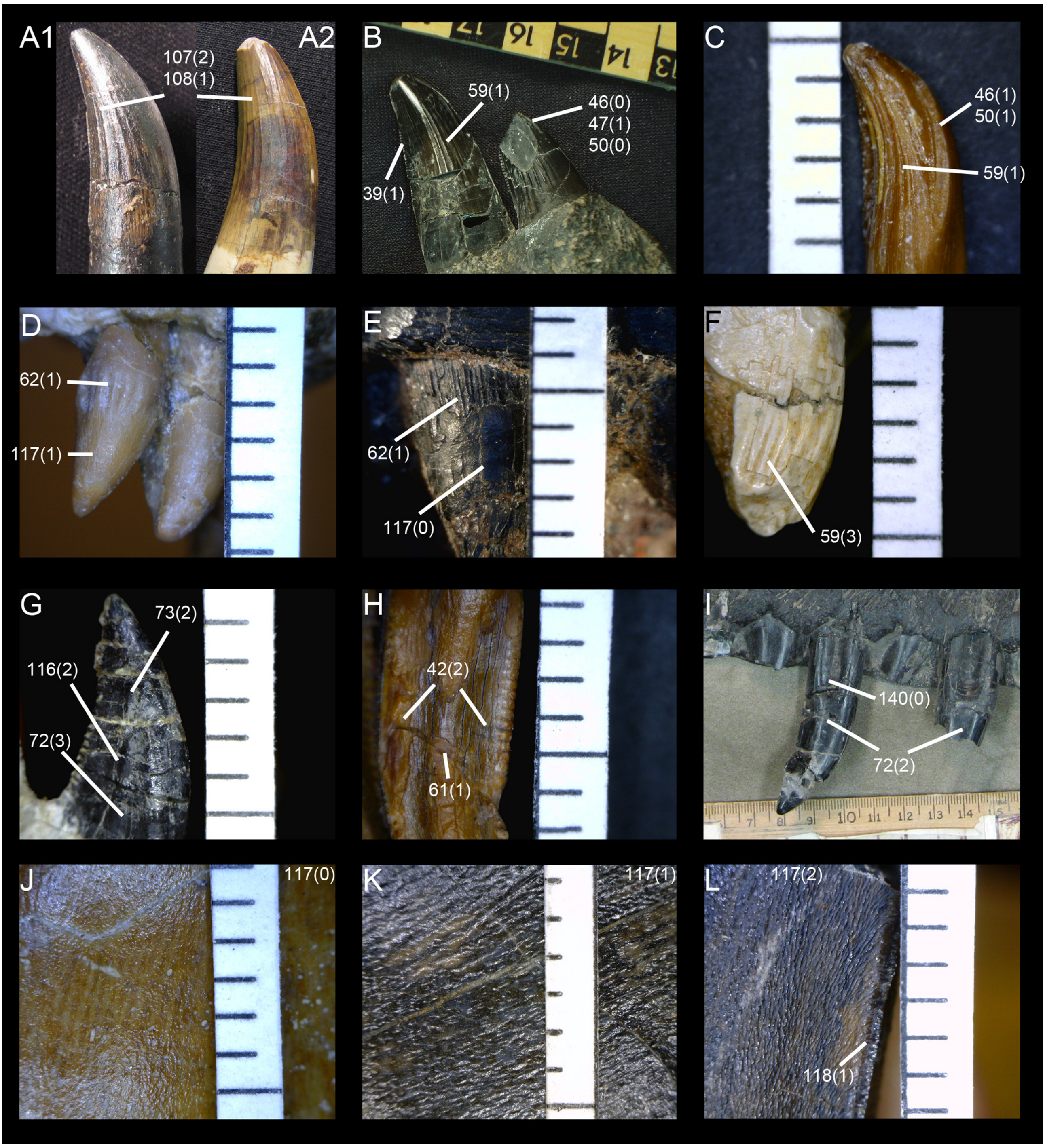

A1
107(2)
108(1)
A2
B
59(1)
46(0)
47(1)
50(0)
39(1)
C
46(1)
50(1)
59(1)
D
62(1)
117(1)
E
62(1)
117(0)
F
59(3)
G
73(2)
116(2)
72(3)
H
42(2)
61(1)
I
140(0)
72(2)
J
117(0)
K
117(1)
L
117(2)
118(1)

FIGURE A4. States of crown structure-based characters. **A.** Isolated teeth of *Baryonyx walkeri* (A1, NHM R9951) and *Suchomimus tenerensis* (A2, MNN G48-9) in lateral view displaying less than ten flutes (char. 108:1) present on both labial and lingual side of the crown (char. 107:2) in those taxa. **B.** First and second left dentary teeth of *Ceratosaurus nasicornis* (formerly *C. dentisulcatus*; UMNH VP 5278 = UUVP 158) in lingual view showing the weak recurvature of these mesialmost crowns (char. 39:1), the untwisted mesial carina (char. 46:0) facing mesio-labially (char. 47:1) and terminating well-above the tooth-cervix (char. 50:0), and the fluted crown, only present on the lingual side of the tooth (char. 59:1). **C.** Isolated mesialmost tooth of *Masiakasaurus knopfleri* (FMNH PR 2696, small tooth) in mesio-lingual view displaying the twisted mesial carina (char. 46:1) extending to the tooth cervix (char. 50:1), as well as the flutes present only on the lingual side of the tooth (char. 59:1). **D.** First right premaxillary tooth of *Proceratosaurus bradleyi* (NHM R 4860) in labial view displaying the short longitudinal furrows/striations present at the base of the crown (char. 62:1) and the braided enamel surface texture of the crown (char. 117:1). **E.** Tenth left maxillary tooth of *Herrerasaurus ischigualastensis* (PVSJ 407) in lateral view showing the longitudinal furrows/striations present at the base of the crown (char. 62:1; also present on the mesialmost teeth of *H. ischigualastensis* = *Ischisaurus cattoi*, MACN 18.060), and the irregular/non-oriented enamel surface texture of the crown (char. 117:0). **F.** First right premaxillary tooth of *Velociraptor mongoliensis* (AMNH 6515) in labial view showing the flutes present on the labial side of the crows (char. 59:3). **G.** Fifth left maxillary tooth of *Bambiraptor feinbergi* (AMNH 30556) in labial view displaying the wide mesiodistally concave area on the basal part of the crown extending along two-thirds of the crown (char. 73:2) and giving the 8-shaped cross-section of the base crown (char. 72:3), and the two elongated, longitudinal and rounded ridges present on the lingual side of the crown as well (char. 116:2). **H.** Third right premaxillary tooth of *Raptorex kriegsteini* (LH PV18) in lingual view showing the two concave areas on the lingual side of the crown and adjacent to both carinae (char. 42:2) and the central and longitudinal ridge on the crown (char. 61:1). **I.** Sixth and eight left maxillary teeth of *Allosaurus fragilis* (UMNH VP 5393) in medial view displaying the deep and well delimited unerupted tooth fossa (char. 140:0) and the wide mesiodistally concave area on the basal part of the crown and present on the lingual side of the tooth, giving the bean-shape cross-section of the base crown (char. 72:2) in this specimen (photo courtesy shared by Stephen Brusatte). **J.** Enamel texture of the sixth right maxillary crown of *Majungasaurus crenatissimus* (FMNH PR 2278) in lateral view showing the irregular non-oriented enamel surface texture (char. 117:0). **K.** Enamel texture of the second right maxillary tooth of *Acrocanthosaurus atokensis* (NCSM 14345) in lateral view showing the regular, oriented braided enamel surface texture of the crown (char. 117:1). **L.** Enamel texture of an isolated tooth of *Baryonyx walkeri* (NHM R9951) in lateral view showing the deeply veined enamel surface texture of the crown (char. 117:2), strongly curved basally close to the carina (char. 118:1).

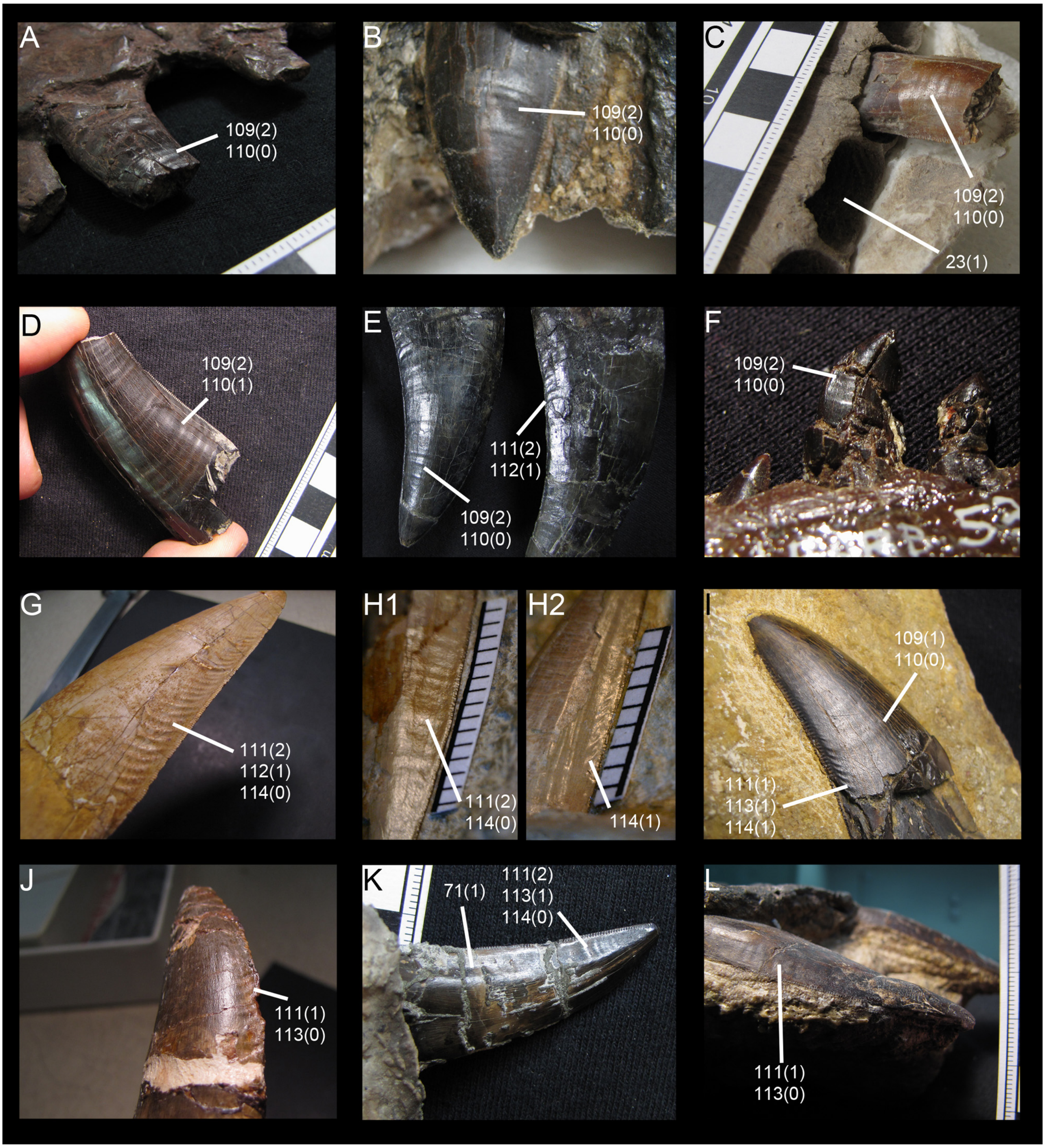

A
109(2)
110(0)
B
109(2)
110(0)
C
109(2)
110(0)
23(1)
D
109(2)
110(1)
E
111(2)
112(1)
109(2)
110(0)
F
109(2)
110(0)
G
111(2)
112(1)
114(0)
H1
111(2)
114(0)
H2
114(1)
I
109(1)
110(0)
111(1)
113(1)
114(1)
J
111(1)
113(0)
K
71(1)
111(2)
113(1)
114(0)
L
111(1)
113(0)

FIGURE A5. States of crown undulation-based characters and distribution of transversal and marginal undulations in nonavian Theropoda. **A.** Fifth? left maxillary tooth of *Herrerasaurus ischigualastensis* (formerly *Sanjuansaurus gordilloi*, PVSJ 605) in lateroventral view displaying the well-visible (char. 109:2) but few (char. 110:0) transversal undulations on the crown. **B.** Fifth or sixth left maxillary tooth of *Ceratosaurus nasicornis* (USNM 4735) in labial view displaying the well-visible (char. 109:2) but few (char. 110:0) transversal undulations on the crown. **C.** Second left maxillary tooth of *Majungasaurus crenatissimus* (FMNH PR 2278) in medioposterior view displaying the well-visible (char. 109:2) but few (char. 110:0) transversal undulations on the crown, as well as the subrectangular maxillary alveoli (char. 23:1). **D.** Isolated lateral tooth of *Megalosaurus bucklandii* (OUMNH J.29866) in lateral view displaying the well-visible (char. 109:2) and numerous and closely packed (char. 110:1) transversal undulations on the crown. **E.** Fifth and sixth right maxillary teeth of *Acrocanthosaurus atokensis* (NCSM 14345) in lateral view displaying the well-visible (char. 109:2) but few (char. 110:0) transversal undulations, that cannot be confused with the pronounced (char. 112:1) and mesiodistally elongated (char. 111:2) marginal undulations adjacent to the distal carina. **F.** Eighth left maxillary tooth of *Dromaeosaurus albertensis* (AMNH 5356) in medial view showing the well-visible (char. 109:2) but few (char. 110:0) transversal undulations on the crown. **G.** Isolated lateral tooth of *Carcharodontosaurus saharicus* (UC unnumbered) in laterodistal view showing the elongated (char. 111:2), pronounced (char. 112:1) and mesio-distally oriented (char. 114:0) marginal undulations adjacent to the distal carina. **H.** Mesial margin of a left maxillary tooth in labialo-mesial view (H1) and distal margin of a right maxillary tooth in labialo-distal view (H2) of *Irritator challengeri* (SMNS 58022) displaying the elongated (char. 111:2) and mesio-distally oriented (char. 114:0) marginal undulations adjacent to the mesial carina, and the diagonally oriented marginal undulations (char. 114:1), adjacent to the distal carina. **I.** Isolated lateral tooth of *Megalosaurus bucklandi* (OUMNH J.23014) in latero-distal view displaying the tenuous (char. 109:2) and few (char. 110:0) transversal undulations on the crown, as well as the short (char. 111:1) and diagonally oriented (char. 114:1) marginal undulations, adjacent to the distal carina only (char. 113:1). **J.** Isolated lateral tooth of *Afrovenator abakensis* (UC UBA1) in latero-mesial view displaying the short (char. 111:1) marginal undulations, adjacent to the mesial carina only (char. 113:0). **K.** Isolated lateral tooth of *Neovenator salerii* (MIWG 6348) in labial view displaying the concave surface adjacent to the distal carina (char. 71:1), the elongated (char. 111:2), mesio-distally oriented (char. 114:0) marginal undulations, adjacent to the distal carina only (char. 113:1). **L.** Fourth left maxillary tooth of *Ceratosaurus nasicornis* (USNM 4735) in mesial view showing the short (char. 111:1) marginal undulations adjacent to the mesial carina only (char. 113:0).

Datamatrix of dentition based characters

nstates 5
xread
141 64
Eoraptor
010100000000?000110000?02???????0100[01][12]100[01][01]10000101012[12]1100000[12]00?[01]10?[13]?00000000?012
210[01]00000001--001000000-0-0---0000??????????????????????
Herrerasaurus
0100000000000000110000002000100010-10[23]10000-0--0---01-0-?000010-
1[012][01][01]000[02]0000000?000221000[01]100000-???0?10000-200---0000??????????????????????
Eodromaeus
01???????????000410?000?30??10000?????????????????????????????0-
0[01]2000110[01]0000010000[01]1[01]0000[01]000020000?00000-100---0010??????????????????????
Coelophysis
010?00000000001101011000001 0?10010-00[012]10000-0--0---01-0-0030000-
[01][01][01]000[13]00000000[01]0??[01][01]100[01]0100000-000000000[03]00-0---001000011--1---0------?????
Dilophosaurus
01[01]100200101002141111001 20[01]11110?0-10[01]00001101???01110000000000-
111000[34]1[01]00000010002310000[01]100000?0?20?0000-0-0---00?0??????????????????00100
Ceratosaurus
00111-0000000000[34]1110001[23]001100010-10[23][12]000[01]1001100[23][23]10000010000-
[12][01]1[012]01[34]?[01]000000100133100[01]011001[01]0[12]0[02]00100[02]0-
2010[01]0001022021000110202000000100
Genyodectes
0111110000000000??11000?30011000?0-20[012]0000110011 00221000?000000-
1[01]1[01]01[34]2[01]00000000[01]13310[01]0010001[01]-2020010[01]00-210---0010??????????????????????
Berberosaurus
???0-10100123100000 00?01331[01][01]???1001?-
1020?10000-200---0010??????????????????????
Noasaurus

????????????????4101000??0-
01[01]1000100000001000121000000000000?2?2?00000-0-0---0000????????????????????????
Masiakasaurus
0?11???1?0???????10?000?30000001?210[12][01]10221[01]01011100100[02]0010000-
[01][01][12]0000100000001001[12]210[012][01]000000[01]00002000000-200---0010??????????????????00110
Kryptops
??????????????????0?001???????????????????????????????????????0-
1?110001000000000100?231[01]2[01]0000001?0?000022?0-0-0---0000??????????????????0????
Rugops
0100000?1?001000?111001?????????????0???2?11??00??????????????0-
1[01]?[12]000100000001000[23]310200000001?0?000000?0-0-0---0000???????????????????????
Abelisaurus
01?000???????000????00????????????0-103[12][12]221100???12210[12]00200000-
1[01][01]1000100000001?00331[01][12]0010011100000000100-1010100000??????????????????????
Aucasaurus
01?000??1?00?00041010011???????????????????????????????????????0-
1[01][01]1000100000001000331[01][12][01]01[01]011100?00000000-200---0000??????????????????0?0??
Indosuchus
0100000110001000400100l??0?10000?0-1[01]3[12][12][23][23]110[01]0011[23][23]1??0?000000-
?[01]?[12]0001000000010?0331??????????0???0??0110-0-0---0000???????????????????????
Majungasaurus
010000011[01]0010002111001120010000l0-103[12][12][23][23]110[01]0011221[12]200200000-
1[01][01][12]000100000001000[34]31[12]2000[01]000100000001220-20101000002202100011010200000?????
Skorpiovenator
01???????????000110?00?1?????????0-10222?[23]1100???1?11???0000000-
10[01][12]00[01]10000000101033l0?0?11001[01]0?0?0?00000-0-20200000??????????????????????
Erectopus
????????????????????000???????????????????????????????????????0-
10[12]00121000000001000331 00[01]0110100000000000100-1[01]0---0000???????????????????????
Piatnitzkysaurus
????????????????1?00000??0???000??????????????????????????????0-
1110010100000000[01]10331000[02][01]10000000000001[12]0-[12]1201000[01]0??????????????????00110
Eustreptospondylus
011110?0000?0000????000?30011000???1??10?0110?100022100?0100000-
11?0000100000000???[34]3100[01]0000000??00000??0-0-0---0010???????????????????????
Afrovenator
????????????????4101000 2??????????????????????????????????????0-20100021000000000110431[01][01][01]2010?00-
0010001110-0-10000010??????????????????0?1?0
Dubreuillosaurus
0111100000000000410100023001100010-10210001100100022l000?000000-
1[01]0000010000000000100221[01][01][01]0000000-0010000110-0-0---0010??????????????????000?0
Duriavenator
0?11???0?0??00???101000??0010000?0-?02??1?110?100?[23]3100?0?00000-
1[01]100001?00000001??3310[01][01]00101[01]0-1010000110-[01]00---0010??????????????????00?10
Megalosaurus
0???????????????41010002300100001??????????????????????????????0-
[12][01]1000010000000001[01]0331[01][01][01][02]010100-1000001[12][12]0-2110[12][01]0010???????????????????????
Torvosaurus
0111100100010000410100023 0??10001??20???0011001000331???0?00000-
20200001000000001[01]0441[01][01][01]0110?00-10100[01]1220-2[01]10100010??????????????????00210
Baryonyx
0[34]11101100110120?100102?0011111010-11[12]1000110010020000000010000-
12100000000000[012]1[01]011[01]00[01][01]21110002020000000[12]00-10100021??????????????????01011
Suchomimus
041110110011012001001022001111l?10-???100011001002000000000[12]0000-
1[12][12]000000000000[012]1[01]0[12][12][01]00[01][01]1010002202000000[12]00-
10[12][01]0021???????????????????????
Irritator_Angaturama
0410001??0210121?????022?0??????1?????????????????????????????0-12[12]01000000010101100-----------------------210-
101[01]0000???????????????????????
Spinosaurus

0312[01]01101210121410011232011111[12]110-?[01]??1001010100[12]--------20000-[12][12][12]01000000101010[01]100------
------------------220-0---0021???????????????????????
Sinraptor
011110201002000030010002200?100010-1?[123]1[12]2311012011?21000??00000-
[12]?1[01]00[01][23]100000000003310[01]00110?000000001?[02]?0-210---0010??????????????????00?00
Allosaurus
02111001100000000300100022000100010-1[01][12]00[23][23]11012111221[01][01]0000[01][02]00-
[12][012][12]0000200[01]0000[01]1[01]1[23][23]1[01][01]001100110000011[12][12]0-
20201[01]00002202110011111200000000
Neovenator
02111120112000003100000??00110001?????????????????????????????0-111001[12]2000000011[01]3[23]11100110010-
0000011110-2[01]20100010??????????????????00211
Fukuiraptor
????????????????????000??0?1?0?0?0-1[01]?0030110121?1[01]110[01]0??00000-
[01][01][012]00??1?000000[01]010[23][23]0[01][01]000[01]0?0000000002220-[12]020?000????????????????????????
Australovenator
????????????????????????1001?000?0-1[01][23]00?311012??1?[12]1????00000-
1[01]1001[12]?000000000?[01]331?[01]?00[01]0??0-000001???0-??????001???????????????????????
Acrocanthosaurus
0111110000000000310100022001100010-[12][01][12]100011001100[12]210000000000-
[12][01][012]0000?0000000[01]11[01][23]3[01]001[01]110111010[12]0010[01]00-
2[01]2[01]100010???????????????????????
Eocarcharia
????????????????310?000???0-
101[03]00020000000011[01]321[01][01]0[02][12]10110-101[01]001110-100---0010???????????????????????
Carcharodontosaurus
????????????????40010002?0?1?000??????????????????????????????20201[13]00010000012110[34][34]1110010011[01]00
00[01]001[01][01]0-[01]021200010??????????????????00110
Giganotosaurus
01111101111?0000??0?000?2001?00010-
?1?1100110[01]1111221?00?10000202[01][12][03]00010000000[12]110[34][34]1[01][01]001[01]00000000001[12]220-
[12]0[12]0200010??????????????????00[12]10
Mapusaurus
????????????????4101000??0???000?0-
11[23]1000110[01]?1??221??000000020[12][01][01][013]00010000000[12]110[34][34]1[01][01]0011000000000001[12]220-
0-[12][01]200010??????????????????[01]0[12]10
Proceratosaurus
01111100000000[01]0011100?2102110011100?[23]103[03]110122[12]00010020000010-
1?[01]0000[13][01]0[01]000000[01]11[12]1000000000000002000[01][01]0-0-0---0010???????????????????????
Eotyrannus
0121110000000000??10001??0210000?0-1211[01]4311013221[12][12]10000100000-
111[01]0001000000000[01]02[23]10000000000000002000110-0-0---0010???????????????????????
Raptorex
01211100000000004001000220211000010-?2[01]104211003221??10020000100-
?[01]100[01]0000[01]0000[01]0[01]1??100[01][02]1[01]0000000000000100-100---0010??????????????????0?100
Alioramus
????????????????21110002102110001?????????????????????????????0-
?[01][01]00[01]0[13]10[01]0000[01]011??10000110001000000000100-210---0010??????????????????00100
Tyrannosaurus
01221100000000000411100023021000010-223[01]04[02]11003221[23][23]10000000[01]00-
[12][12][12][01]000000[01]0000[01]001[34][34]100001[01]0100020200122?0-2[01]0---001022021101---0-0111200000
Compsognathus
01????00????00?210?00?2100?100010-0?3[012]0?00-1-------------00000-0[01][12]00000?1--0[01]--2??-0--0-[01]-20--0--
00-10-000-0-0---0000??????????????????10?00
Scipionyx
02?100-11122?001510000?23001100010-??2000?0-1-------------10000-??[012][01]0?0?11--01--[02]??-??-0-0-[02]0--0--?0-
10-000-0-0---0000???????????????????????
Ornitholestes
011100121021?0004101000230001000110[01]?210300-1-------------00000-0110000211--0[01]--200-00-0-0-00--0---0-10-
000-0-0---0010???????????????????????
Shuvuuia
???????????????000100?401000000?1100?22000-1-------------00?0210012000001--00--------------------------0-0-0---000-

??????????????????0?0??
Jianchangosaurus
1---------------0---00?20000-000?21102100411000000 1?22??000?0011021[12]0?[03]00000000020033222000000 11-2-
20010000-0-0---000-?????????????????010?0
Erlikosaurus
1---------------0???00?30010?00110-0022100110000 00??2??000000011020200000000000200??2[02][02]00020011-2-
20010000-0-0---000-??????????????????0?0??
Tsaagan
011100210021?000400?00?2[23]001000010-1?3[01][01]000-0--0---01-0-0000?00-1?1[01]0?0311--01--000-21-0-0-10--0--
00-00-000-0-0---0000???????????????????????
Velociraptor
011000110?21?000[34]10?00?2[23]001100010-00310301101201?001?02?030?00-
001[01]0?1?2[01]000000000121000000[01]0000?0022000000-0-0---0[012]00100110-00000-----1?????
Bambiraptor
01??00?????00004???00?230?10000??????????0-0--?---??-?-??0???0-
0[01]1000[01]32[01]0000000001[12]10[01]0001000[01]??002010000-0-0---0[02]1000000--1---12-----?????
Dromaeosaurus
0???000?10000000500100023001000010-1[01][12][01]033110121111111000100000-
[01]11000[01]3[12]010000[01]001[23]2100000[01]000100000000100-100---0000201110-000112----2?????
Saurornitholestes
01?????????????0????????20???000?0-0221033[01]10121111[12]1[01][12]20100000-
[01]02[01]00[12]0[12][01][01]0000[01]000[12][12][12]22[12]-01000[01]00002010000-0-0---0000211110-00020-----100100
Buitreraptor
?????????????????????002?0??0000??????????????????????????????0-0[01][01]000[01]321--1-----------------------------0-0-0-
--[13][12]00??????????????????1?1?0
Byronosaurus
0101000110?00000021100?30100?000?1000211010-1-------------0000[12]00[12][12][01]0?[01][24][01]1--1---------------------
--------0-0-0---[13][12]0000000--1---22-----?????
Zanabazar
0101000000000000[01]2110004010010001110031 1[35]?0-1-------------0000[12]10[12][01][01]0?1[13]?[01]01000?000-32-2-
0-000-1--22-1[01]0000-000---2000??????????????????????
Troodon
01??????????????????000?010000001210121050[01][01]0000?13322200000002101[01][01]00[134]1[01][01]0[01]0001000[
34][34][12]22[12]00[01]001100000010000-100---0000110110-00020-----100110
Richardoestesia_gilmorei
????????????????????????10?????????????????????????????????????2?001[01]0023[12]00[01]0000000[12][12]101000[02]00
0[01]0010[02]000000-0-0---000-200110-010112----0?????
ML962
????????????????????????????????0-
20100001100?0?0331?00?10000???
ML327
???0-
1111000100100001?1134112[01]011001000000?00220-100---2010??????????????????????
ML966
???0-
11110001001000?1?1033111[01]01100100?000?10220-1010110010??????????????????????
ML939
??2-001000[12]31???0000000?01?[01]?2?100?0-
010?00?100-0-0---2000????????????????????1??
;
ccode + 1 3 14 16 23 24 35 52 64 85;
;
proc/;

Supermatrix of dentition based characters combined with 6 other datasets

The data file is available at DRYAD: http://doi.org/10.5061/dryad.33tb2.

Results of the cladistic analyses

Cladistic analysis on the dentition based datamatrix (isolated teeth excluded) and list of synapomorphies and autapomorphies for each clade.

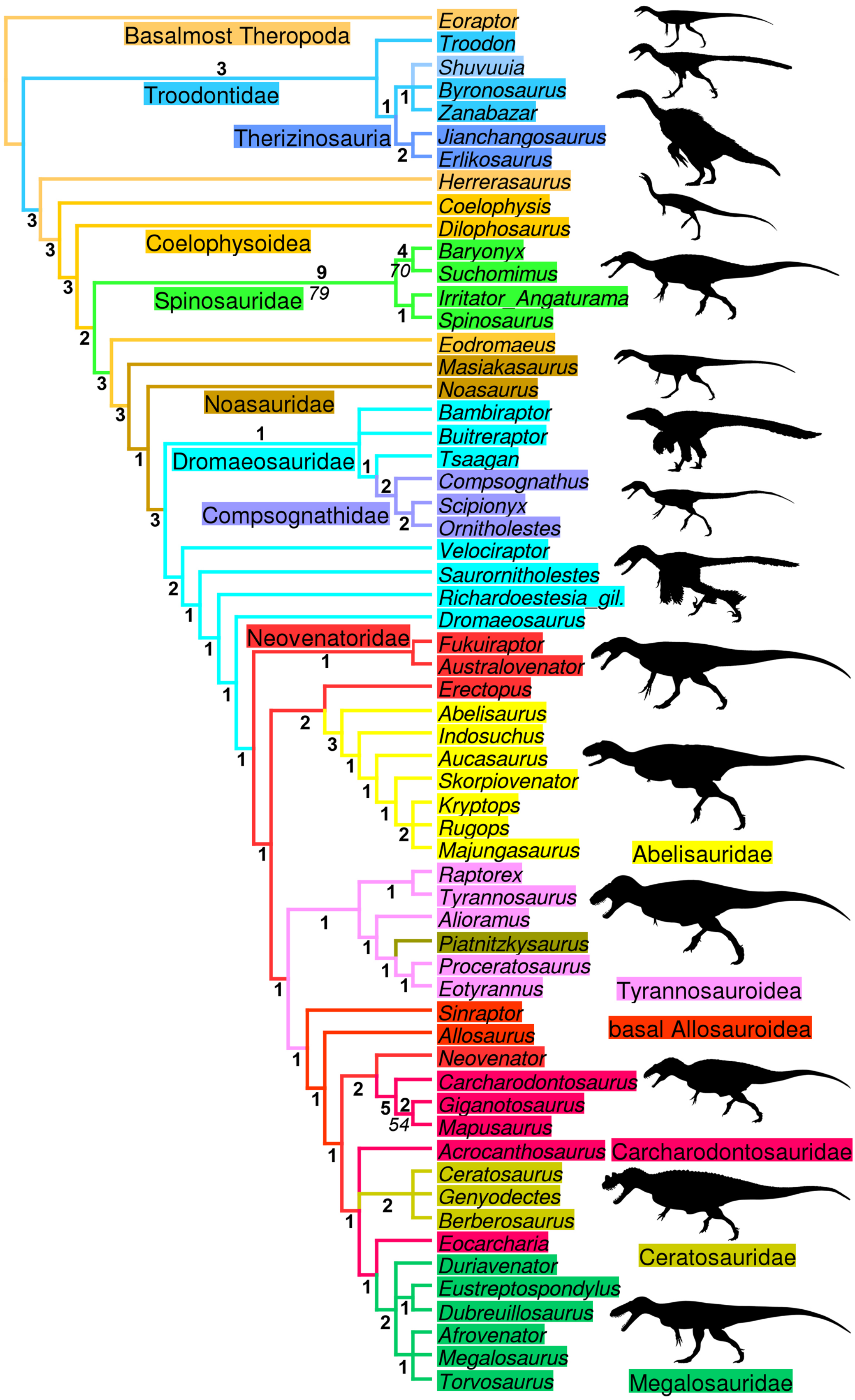

Basalmost Theropoda
Troodontidae
Therizinosauria
Coelophysoidea
Spinosauridae
Noasauridae
Dromaeosauridae
Compsognathidae
Neovenatoridae
Eoraptor
Troodon
Shuvuuia
Byronosaurus
Zanabazar
Jianchangosaurus
Erlikosaurus
Herrerasaurus
Coelophysis
Dilophosaurus
Baryonyx
Suchomimus
Irritator_Angaturama
Spinosaurus
Eodromaeus
Masiakasaurus
Noasaurus
Bambiraptor
Buitreraptor
Tsaagan
Compsognathus
Scipionyx
Ornitholestes
Velociraptor
Saurornitholestes
Richardoestesia_gil.
Dromaeosaurus
Fukuiraptor
Australovenator
Erectopus
Abelisaurus
Indosuchus
Aucasaurus
Skorpiovenator
Kryptops
Rugops
Majungasaurus
Abelisauridae
Raptorex
Tyrannosaurus
Alioramus
Piatnitzkysaurus
Proceratosaurus
Eotyrannus
Tyrannosauroidea
Sinraptor
Allosaurus
basal Allosauroidea
Neovenator
Carcharodontosaurus
Giganotosaurus
Mapusaurus
Acrocanthosaurus
Carcharodontosauridae
Ceratosaurus
Genyodectes
Berberosaurus
Ceratosauridae
Eocarcharia
Duriavenator
Eustreptospondylus
Dubreuillosaurus
Afrovenator
Megalosaurus
Torvosaurus
Megalosauridae

FIGURE A6. Strict consensus cladogram of 10 most parsimonious trees recovered from the analysis of a data matrix of dentition based characters. Initial analysis was a New Technology Search using TNT v.1.1 of a data matrix comprising 141 characters for one outgroup (*Eoraptor*) and 59 nonavian theropod taxa. Tree length = 681 steps; CI = 0.338; RI = 0.56. Bremer support values are in bold and bootstrap values are in italic.

Attribution of silhouettes for Figure 1, Figure 2 and Figure A6.

All theropod silhouettes in figures 1, 2 and A6 have been downloaded from phylopic.org. All images are under a Creative Commons Attribution-NonCommercial-ShareAlike 3.0 Unported License unless stated otherwise.
- Basalmost Theropoda (*Eoraptor* and *Herrerasaurus*): Scott Hartman
- Coelophysoidea: Funkmonk (Public Domain)
- Ceratosauridae: Scott Hartman
- Noasauridae: Scott Hartman
- Abelisauridae (two silhouettes): Scott Hartman
- Megalosauridae: Scott Hartman
- Spinosauridae: Scott Hartman
- Basal Allosauroidea/Neovenatoridae: Scott Hartman
- Carcharodontosauridae: Scott Hartman
- Tyrannosauridae: Scott Hartman
- Compsognathidae: Scott Hartman
- *Shuvuuia*: FunkMonk (Public Domain)
- Therizinosauria: Scott Hartman
- Troodontidae: Scott Hartman
- Dromaeosauridae: Scott Hartman and Funkmonk (Public Domain)

FIGURE A7. Strict consensus cladogram of 10 most parsimonious trees recovered from analysis of dentition based characters, with each nodes numbered (see the list of synapomorphies for each clades below). Initial analysis was a New Technology Search using TNT v.1.1 of a data matrix comprising 141 dentition-based characters for one outgroup (*Eoraptor lunensis*) and 59 nonavian theropod taxa. Tree length = 681 steps; CI = 0.338; RI = 0.56.

Cladistic analysis on a supermatrix with theropod taxa (ML teeth excluded).

Eoraptor
No autapomorphies

Herrerasaurus
Char. 4: 1 --> 0
Char. 62: 0 --> 1
Char. 71: 3 --> 0
Char. 109: 0 --> 2

Eodromaeus
Char. 33: 1 --> 0
Char. 67: 1 --> 2
Char. 71: 0 --> 1
Char. 84: 1 --> 0
Char. 97: 0 --> 2
Char. 109: 0 --> 1

Coelophysis
Char. 17: 1 --> 0
Char. 25: 2 --> 0
Char. 59: 0 --> 3

Dilophosaurus
Char. 10: 0 --> 1
Char. 19: 0 --> 1
Char. 39: 1 --> 0
Char. 52: 0 --> 1
Char. 85: 1 --> 3
Char. 92: 0 --> 1
Char. 101: 0 --> 2
Char. 140: 1 --> 0

Ceratosaurus
Char. 2: 1 --> 0
Char. 59: 0 --> 1
Char. 80: 0 --> 1
Char. 111: 0 --> 1

Genyodectes
Char. 36: 1 --> 2
Char. 39: 1 --> 0
Char. 92: 1 --> 0
Char. 98: 1 --> 2
Char. 1010: 0 --> 1

Berberosaurus
Char. 71: 34 --> 2
Char. 72: 2 --> 3

Noasaurus
Char. 68: 0 --> 1
Char. 99: 0 --> 2

Masiakasaurus
Char. 28: 1 --> 0
Char. 32: 0 --> 1
Char. 34: 0 --> 2
Char. 41: 0 --> 2
Char. 42: 0 --> 2
Char. 48: 0 --> 1
Char. 83: 0 --> 1
Char. 109: 0 --> 2

Kryptops
Char. 84: 3 --> 2
Char. 104: 0 --> 2

Rugops
No autapomorphies

Abelisaurus
Char. 58: 0 --> 2
Char. 111: 0 --> 1

Aucasaurus
Char. 109: 0 --> 2

Indosuchus
Char. 106: 0 --> 1

Majungasaurus
Char. 87: 0 --> 12
Char. 104: 0 --> 1
Char. 109: 0 --> 2
Char. 111: 0 --> 1

Skorpiovenator
Char. 17: 2 --> 1
Char. 38: 3 --> 2
Char. 52: 2 --> 1
Char. 82: 0 --> 1
Char. 111: 0 --> 2
Char. 113: 1 --> 2

Erectopus
Char. 70: 0 --> 1
Char. 71: 0 --> 2

Piatnitzkysaurus
Char. 70: 0 --> 1
Char. 111: 0 --> 2

Eustreptospondylus
Char. 58: 0 --> 1
Char. 100: 1 --> 0

Afrovenator
Char. 71: 0 --> 2
Char. 90: 0 --> 2
Char. 98: 1 --> 0
Char. 113: 1 --> 0

Dubreuillosaurus
Char. 84: 3 --> 2
Char. 85: 3 --> 2

Duriavenator
Char. 29: 1 --> 0
Char. 41: 0 --> 1

Megalosaurus
Char. 29: 1 --> 0
Char. 100: 1 --> 0

Torvosaurus
Char. 67: 1 --> 2
Char. 85: 3 --> 4
Char. 91: 0 --> 1
Char. 105: 1 --> 2
Char. 106: 1 --> 2
Char. 139: 1 --> 2

Baryonyx
Char. 91: 1 --> 2
Char. 92: 0 --> 1
Char. 94: 0 --> 1

Suchomimus
Char. 97: 0 --> 2

Irritator_Angaturama
Char. 4: 1 --> 0
Char. 117: 2 --> 0

Spinosaurus
Char. 4: 1 --> 2
Char. 10: 0 --> 1
Char. 22: 0 --> 1
Char. 24: 2 --> 3

Sinraptor
Char. 7: 0 --> 2
Char. 12: 0 --> 2
Char. 40: 0 --> 12
Char. 73: 0 --> 1
Char. 105: 1 --> 02
Char. 1010: 0 --> 1

Allosaurus
Char. 2: 1 --> 2
Char. 8: 0 --> 1
Char. 28: 1 --> 0
Char. 39: 1 --> 0
Char. 83: 0 --> 1
Char. 96: 0 --> 1
Char. 117: 1 --> 0
Char. 131: 0 --> 1
Char. 139: 1 --> 0

Neovenator
Char. 2: 1 --> 2
Char. 7: 0 --> 2
Char. 20: 1 --> 0
Char. 66: 0 --> 1
Char. 70: 0 --> 1
Char. 71: 0 --> 12
Char. 139: 1 --> 2
Char. 141: 0 --> 1

Fukuiraptor
Char. 42: 3 --> 0
Char. 86: 1 --> 0

Australovenator
Char. 103: 0 --> 1

Acrocanthosaurus
Char. 89: 0 --> 1
Char. 96: 0 --> 1

Eocarcharia
Char. 85: 3 --> 2
Char. 104: 0 --> 1

Carcharodontosaurus
Char. 18: 1 --> 0
Char. 79: 0 --> 1
Char. 92: 1 --> 0
Char. 94: 0 --> 1
Char. 103: 1 --> 0
Char. 112: 0 --> 1

Giganotosaurus
Char. 40: 0 --> 1
Char. 58: 0 --> 1

Mapusaurus
No autapomorphies

Proceratosaurus
Char. 32: 0 --> 1
Char. 34: 0 --> 1
Char. 36: 1 --> 0
Char. 41: 4 --> 3
Char. 50: 1 --> 0
Char. 51: 2 --> 0
Char. 52: 2 --> 0

Char. 56: 0 --> 2
Char. 62: 0 --> 1

Eotyrannus
Char. 29: 1 --> 0
Char. 58: 0 --> 1

Raptorex
Char. 56: 0 --> 2
Char. 109: 2 --> 1

Alioramus
Char. 73: 0 --> 1
Char. 96: 0 --> 1

Tyrannosaurus
Char. 4: 1 --> 2
Char. 25: 2 --> 3
Char. 29: 1 --> 0
Char. 94: 0 --> 1
Char. 98: 0 --> 2
Char. 100: 0 --> 2
Char. 103: 0 --> 1
Char. 104: 0 --> 2
Char. 105: 1 --> 2
Char. 139: 1 --> 0

Compsognathus
Char. 8: 1 --> 0
Char. 17: 4 --> 2
Char. 25: 3 --> 1

Scipionyx
Char. 2: 1 --> 2
Char. 10: 0 --> 1
Char. 12: 1 --> 2
Char. 16: 0 --> 1
Char. 17: 4 --> 5
Char. 20: 1 --> 0
Char. 39: 1 --> 0
Char. 59: 0 --> 1

Ornitholestes
Char. 8: 1 --> 2
Char. 28: 1 --> 0
Char. 34: 0 --> 1
Char. 41: 0 --> 3
Char. 117: 0 --> 1

Shuvuuia
Char. 18: 2 --> 0
Char. 39: 1 --> 2
Char. 40: 1 --> 2
Char. 66: 12 --> 0
Char. 68: 01 --> 2

Jianchangosaurus
Char. 36: 0 --> 1
Char. 42: 0 --> 4

Erlikosaurus
Char. 27: 0 --> 1
Char. 32: 0 --> 1
Char. 39: 1 --> 2
Char. 67: 1 --> 0
Char. 92: 0 --> 2

Tsaagan
Char. 7: 1 --> 2
Char. 18: 1 --> 0
Char. 36: 0 --> 1
Char. 65: 0 --> 1

Velociraptor
Char. 29: 0 --> 1
Char. 59: 0 --> 3
Char. 100: 0 --> 2
Char. 129: 2 --> 0

Bambiraptor
Char. 103: 0 --> 1
Char. 117: 0 --> 1

Dromaeosaurus
Char. 17: 4 --> 5
Char. 25: 2 --> 3
Char. 54: 0 --> 1
Char. 66: 0 --> 1
Char. 75: 0 --> 1
Char. 83: 0 --> 1
Char. 96: 0 --> 1
Char. 121: 0 --> 1
Char. 136: 0 --> 2

Saurornitholestes
Char. 37: 0 --> 2
Char. 55: 0 --> 12
Char. 67: 1 --> 2
Char. 72: 3 --> 0
Char. 87: 0 --> 2
Char. 88: 0 --> 2
Char. 89: 0 --> 12
Char. 103: 0 --> 1
Char. 120: 0 --> 1
Char. 121: 0 --> 1

Buitreraptor
Char. 77: 0 --> 1
Char. 115: 0 --> 13
Char. 116: 0 --> 12

Byronosaurus
Char. 8: 0 --> 1
Char. 9: 0 --> 1
Char. 35: 1 --> 0
Char. 42: 0 --> 1
Char. 64: 1 --> 0
Char. 72: 0 --> 24
Char. 77: 0 --> 1
Char. 115: 0 --> 13
Char. 116: 0 --> 12

Zanabazar
Char. 38: 2 --> 3
Char. 41: 0 --> 35
Char. 71: 0 --> 1
Char. 72: 0 --> 13
Char. 115: 0 --> 2

Troodon
Char. 37: 0 --> 1
Char. 41: 0 --> 5
Char. 50: 0 --> 1
Char. 51: 1 --> 3
Char. 72: 0 --> 1
Char. 89: 0 --> 12
Char. 109: 0 --> 1
Char. 119: 0 --> 1
Char. 120: 0 --> 1
Char. 126: 1 --> 0

Richardoestesia_gil.
Char. 25: 2 --> 1
Char. 63: 0 --> 2
Char. 71: 1 --> 2
Char. 88: 0 --> 1
Char. 92: 1 --> 02
Char. 99: 0 --> 1

Node 61
Char. 55: 2 --> 0
Char. 63: 2 --> 0
Char. 65: 0 --> 1
Char. 91: 0 --> 1
Char. 96: 1 --> 0

Node 62
No synapomorphies

Node 63
Char. 15: 12 --> 0
Char. 21: 1 --> 0
Char. 25: 2 --> 3
Char. 30: 1 --> 0
Char. 65: 1 --> 0
Char. 91: 1 --> 0

Node 64
Char. 8: 0 --> 1
Char. 11: 0 --> 2
Char. 24: 1 --> 2
Char. 51: 1 --> 0
Char. 71: 3 --> 0

Node 65
Char. 12: 0 --> 1
Char. 17: 1 --> 4
Char. 24: 0 --> 1

Char. 28: 0 --> 1
Char. 43: 0 --> 1

Node 66
Char. 15: 0 --> 1
Char. 21: 0 --> 1
Char. 30: 0 --> 1
Char. 85: 2 --> 1
Char. 117: 0 --> 1

Node 67 - Ceratosauridae
Char. 19: 0 --> 1
Char. 70: 0 --> 1
Char. 71: 0 --> 34
Char. 81: 1 --> 0
Char. 82: 1 --> 0
Char. 83: 0 --> 1
Char. 105: 1 --> 0

Node 68
Char. 9: 1 --> 0
Char. 49: 1 --> 0
Char. 50: 1 --> 0
Char. 98: 0 --> 1
Char. 100: 0 --> 12

Node 69
Char. 6: 0 --> 1
Char. 41: 2 --> 0
Char. 42: 3 --> 0
Char. 47: 2 --> 1

Node 70
Char. 81: 0 --> 1
Char. 95: 0 --> 1

Node 71
Char. 72: 1 --> 2
Char. 103: 0 --> 1

Node 72
Char. 5: 0 --> 1
Char. 8: 1 --> 0
Char. 29: 0 --> 1
Char. 109: 1 --> 2

Node 73
Char. 41: 3 --> 2
Char. 51: 1 --> 2
Char. 52: 1 --> 2
Char. 71: 1 --> 0
Char. 91: 0 --> 1

Node 74
Char. 72: 3 --> 1
Char. 73: 2 --> 0
Char. 85: 2 --> 3

Node 75
Char. 84: 1 --> 3
Char. 105: 0 --> 1
Char. 109: 0 --> 1

Node 76
Char. 129: 2 --> 1
Char. 130: 0 --> 1
Char. 136: 1 --> 0

Node 77
Char. 42: 0 --> 3
Char. 48: 0 --> 1
Char. 51: 0 --> 1
Char. 52: 0 --> 1

Node 78
Char. 41: 0 --> 3
Char. 66: 1 --> 0
Char. 71: 0 --> 1
Char. 126: 1 --> 0

Node 79
Char. 72: 1 --> 3
Char. 73: 0 --> 2
Char. 80: 1 --> 0
Char. 92: 0 --> 1

Node 80
Char. 117: 1 --> 0

Node 81
Char. 29: 1 --> 0
Char. 85: 1 --> 2
Char. 101: 0 --> 2

Node 82
Char. 91: 1 --> 0
Char. 95: 1 --> 0

Node 83
Char. 17: 4 --> 2
Char. 94: 1 --> 0

Node 84
Char. 105: 1 --> 0

Node 85
Char. 109: 1 --> 0

Node 86 - Abelisauridae
Char. 68: 0 --> 1
Char. 88: 0 --> 2
Char. 95: 0 --> 1
Char. 96: 0 --> 1

Node 87
Char. 80: 0 --> 1
Char. 94: 0 --> 1

Node 88
Char. 17: 2 --> 1
Char. 106: 0 --> 1

Node 89
Char. 17: 34 --> 2
Char. 25: 2 --> 1
Char. 82: 0 --> 1
Char. 1010: 0 --> 1

Node 90 - Tyrannosauroidea
Char. 6: 0 --> 1
Char. 9: 1 --> 0
Char. 27: 0 --> 2
Char. 37: 0 --> 2
Char. 41: 2 --> 4
Char. 48: 01 --> 2
Char. 49: 1 --> 2
Char. 66: 0 --> 1

Node 91
Char. 92: 1 --> 0
Char. 94: 1 --> 0

Node 92 - Megalosauridae
Char. 17: 3 --> 4
Char. 72: 2 --> 1
Char. 91: 1 --> 0
Char. 95: 1 --> 0

Node 93
Char. 103: 1 --> 0

Node 94
Char. 65: 1 --> 2
Char. 104: 0 --> 1
Char. 111: 0 --> 1

Node 95 - Baryonychinae
Char. 5: 0 --> 1
Char. 11: 2 --> 1
Char. 25: 2 --> 0

Node 96 - Spinosauridae
Char. 2: 1 --> 34
Char. 14: 0 --> 1
Char. 20: 1 --> 0
Char. 23: 0 --> 2
Char. 47: 0 --> 1
Char. 66: 1 --> 2
Char. 81: 0 --> 1
Char. 107: 0 --> 2
Char. 117: 1 --> 2

Node 97 - Spinosaurinae
Char. 69: 0 --> 1
Char. 76: 0 --> 1
Char. 78: 0 --> 1

Node 98
Char. 10: 0 --> 1
Char. 87: 0 --> 1
Char. 88: 0 --> 1

Node 99
Char. 39: 1 --> 0

Node 100 - Carcharodontosaurinae
Char. 17: 3 --> 4
Char. 63: 0 --> 2
Char. 65: 1 --> 2
Char. 72: 2 --> 1
Char. 80: 0 --> 2
Char. 113: 1 --> 2

Node 101
Char. 95: 1 --> 0
Char. 105: 1 --> 2
Char. 106: 01 --> 2

Node 102
Char. 92: 1 --> 0
Char. 101: 0 --> 2
Char. 109: 2 --> 0

Node 103
Char. 42: 3 --> 2
Char. 46: 1 --> 0
Char. 72: 1 --> 0

Node 104
Char. 29: 0 --> 1
Char. 45: 0 --> 1
Char. 81: 0 --> 2
Char. 85: 2 --> 0
Char. 102: 0 --> 1

Node 105
Char. 73: 2 --> 1
Char. 78: 0 --> 1

Node 106
Char. 43: 1 --> 0
Char. 74: 0 --> 1
Char. 137: 0 --> 1

Node 107
Char. 9: 0 --> 1
Char. 38: 3 --> 2

Node 108
Char. 45: 0 --> 1
Char. 74: 0 --> 1

Node 109
Char. 71: 3 --> 0
Char. 100: 0 --> 2
Char. 139: 1 --> 0

Node 110
Char. 25: 2 --> 0
Char. 53: 1 --> 2
Char. 64: 0 --> 1
Char. 84: 2 --> 3
Char. 85: 2 --> 3
Char. 87: 0 --> 2
Char. 88: 0 --> 2
Char. 95: 0 --> 1

Node 111 - Therizinosauria
Char. 1: 0 --> 1
Char. 43: 0 --> 1
Char. 63: 2 --> 1
Char. 81: 0 --> 2

FIGURE A8. A. Strict consensus cladogram of nine most parsimonious trees recovered from the analysis of a supermatrix including a dentition-based datamatrix and six recent datasets based on whole theropod skeleton (i.e., Xu *et al.* 2009; Brusatte *et al.* 2010; Martinez *et al.* 2011; Senter 2011; Pol and Rauhut 2012; Carrano *et al.* 2012). Initial analysis was a New Technology Search using TNT v.1.1 of a supermatrix comprising 1972 characters for one outgroup (*Eoraptor*) and 59 non-avian theropod taxa. Tree length = 3583 steps; CI = 0.546; RI = 0.604. **B**. Strict consensus cladogram of four most parsimonious trees recovered from the analysis of a supermatrix after the deletion of the two wildcard taxa *Erectopus* and *Piatnitzkysaurus*. Tree length = 3529 steps; CI = 0.575; RI = 0.642.

Unambiguous and ambiguous dentition based synapomorphies and autapomorphies from a cladistic analysis on the supermatrix (ML teeth excluded)

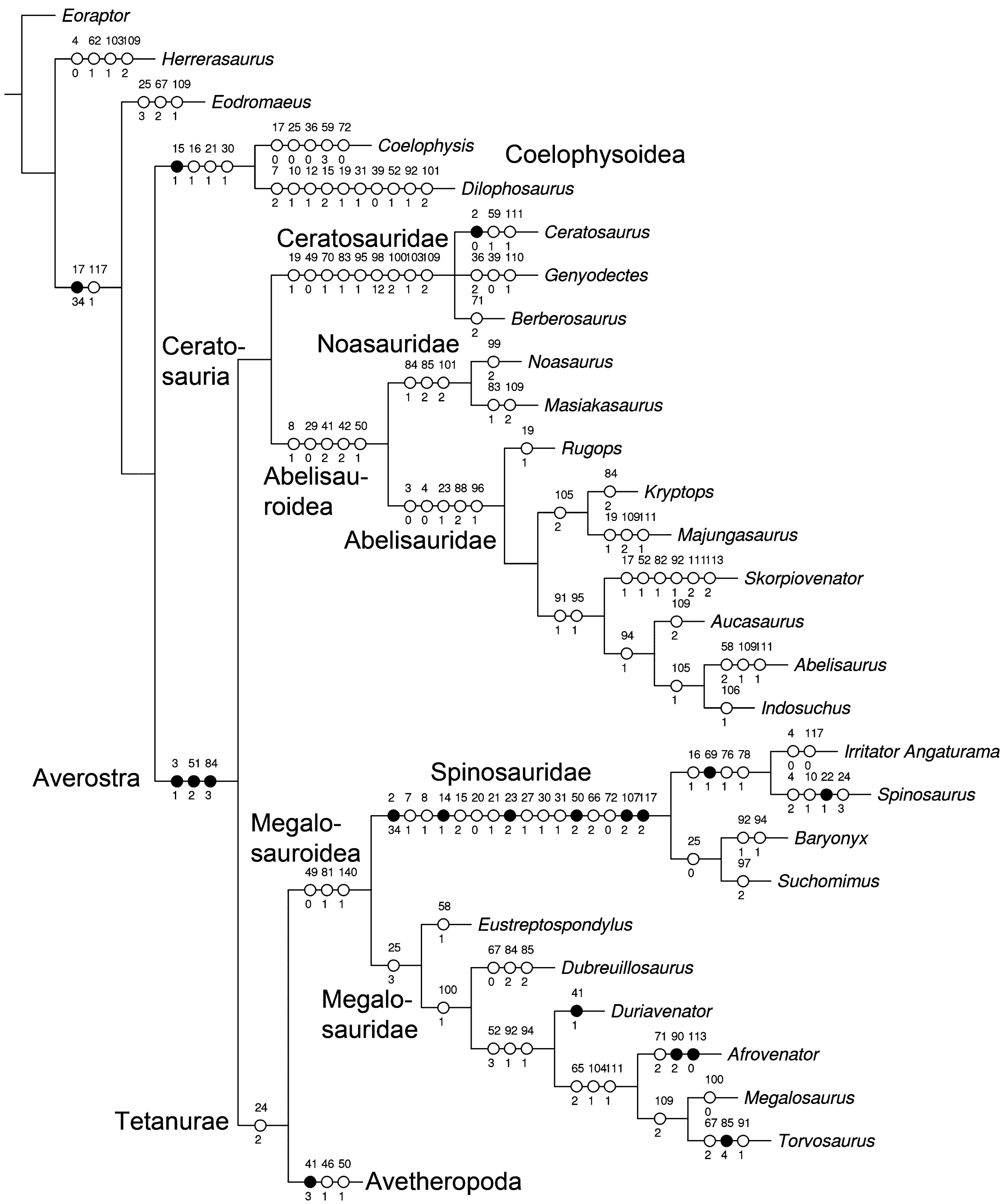


FIGURE A9a. Strict consensus cladogram of six most parsimonious trees recovered from the analysis of a supermatrix including a dentition-based datamatrix and six recent datasets based on whole theropod skeleton (i.e., Xu *et al.* 2009; Brusatte *et al.* 2010; Martinez *et al.* 2011; Senter 2011; Pol and Rauhut 2012; Carrano *et al.* 2012). The consensus tree was obtained after the deletion of the wildcard taxa *Erectopus* and *Piatnitzkysaurus*. Initial analysis was a Ratchet (Island Hopper) analysis using WinClada 1.00.08 of a supermatrix comprising 1972 characters for one outgroup (*Eoraptor*) and 57 non-avian theropod taxa. Tree length = 3507 steps; CI = 0.57; RI = 0.64. The same topology was obtained with TNT v.1.1 with a New Technology Search that yielded four MPTs (Tree length = 3529 steps; CI = 0.575; RI = 0.642). The unambiguous and ambiguous dentition based synapomorphies are represented by black and white circles, respectively, and the character number and character state associated with each synapomorphy are above and below the circles, respectively.

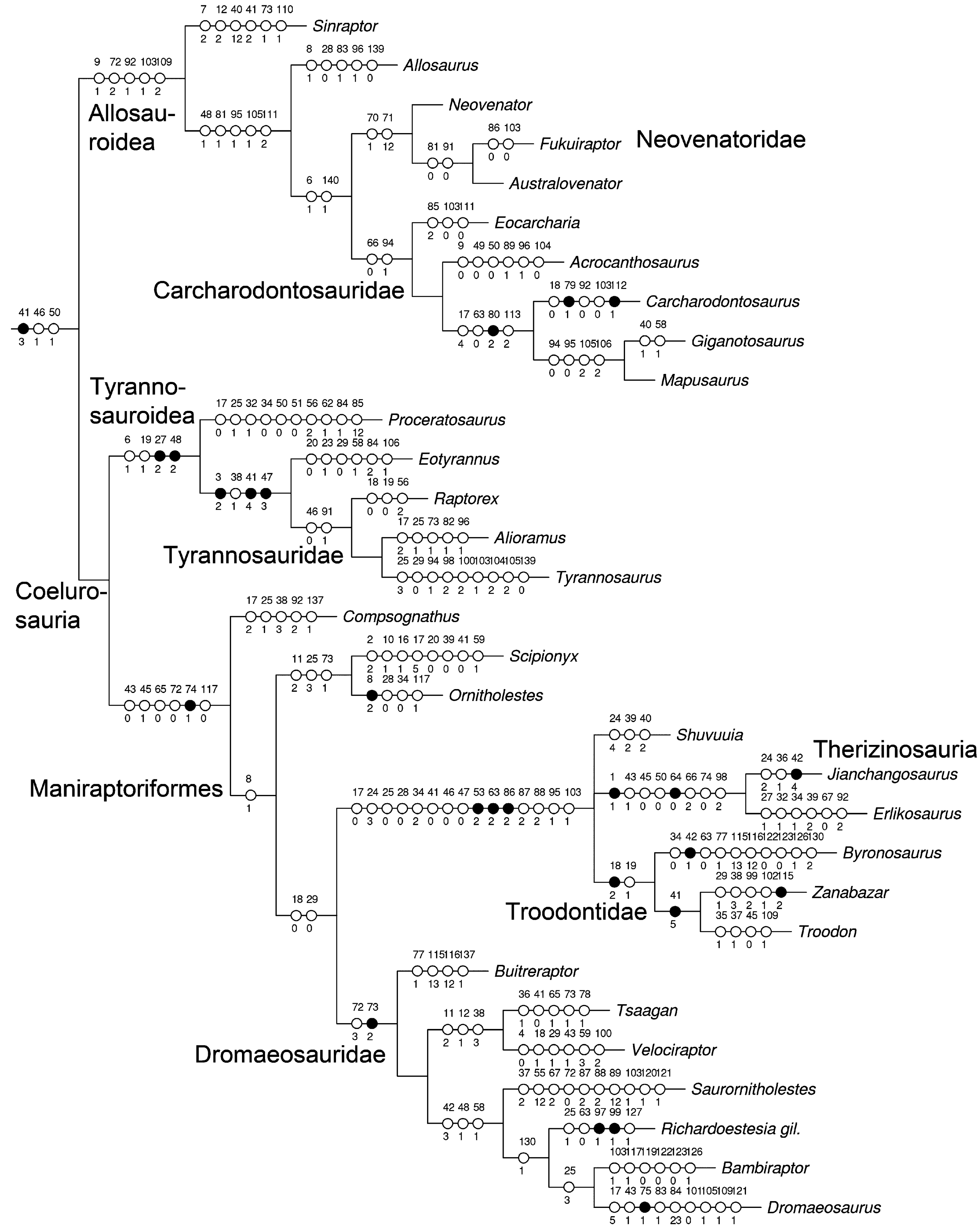


FIGURE A9b. (Continued)

TABLE A1. List of ambiguous and unambiguous dentition-based synapomorphies by theropod clades for results of the cladistic analysis of the dentition-based dataset.

Clade	Synapomorphies
Coelophysoidea	**Unambiguous:** Premaxillary tooth row slightly constricted (15:1). **Ambiguous:** subnarial gap in the premaxilla (16:1); first maxillary alveoli open anteroventrally (21:1); enlarged fanglike anterior dentary tooth (30:1).
Averostra	**Unambiguous:** anterior premaxillary alveoli labio-lingually oriented, posterior premaxillary alveoli mesio-distally oriented (3:1); less than 14 denticles per 5mm on the mesial carina in mesialmost teeth (51:2); less than 16 denticles per 5mm on the mesial carina in lateral teeth (84:3).
Ceratosauridae	**Ambiguous:** Mid-maxillary teeth (or alveoli) significantly larger than anteriormost maxillary teeth (19:1); axis passing through both carinae at mid-crown sub-parallel to long axis of skull in mesialmost teeth (49:0); surface centrally positioned on the crown roughly flattened in lateral teeth (70:1); distal carina strongly labially deflected on the distal margin in lateral teeth, crown asymmetrical (83:1); mesial denticles inclined apically in lateral teeth (95:1); subequal or lower number of denticles apically than at the mid-crown on the mesial carina in lateral teeth (98:12); subequal number of denticles apically than at the mid-crown on the distal carina in lateral teeth (100:2); interdenticular space between distal denticles broad, more than one third of the denticle width, in lateral teeth (103:1); large and well-visible transversal undulations on the crown in some lateral teeth (109:2).
Noasauridae	**Ambiguous:** 30-44 denticles per 5mm on mesial carina in lateral teeth (84:1); 16-29 denticles per 5mm on distal carina in lateral teeth (85:2); distal denticles larger than mesial ones in lateral teeth (101:2).
Abelisauridae	**Ambiguous:** Premaxillary alveoli mesio-distally oriented (3:0); no overlap of the first and second premaxillary alveoli (4:0); subrectangular maxillary alveoli (23:1); hooked distal denticles in lateral teeth (88:2); distal denticles inclined apically in lateral teeth (96:1).
Tetanurae	**Ambiguous:** Maxillary tooth row anterior to the anterior rim of the orbit, posterior to the anteroventral rim of the antorbital fenestra (24:2).
Megalosauroidea	**Ambiguous:** Axis passing through both carinae at mid-crown sub-parallel to long axis of skull in mesialmost teeth (49:0); distal carina terminating well beneath the cervix in lateral teeth (81:1); unerupted tooth fossa corresponding to a shallow concavity in the root of lateral teeth (140:1).
Spinosauridae	**Unambiguous:** More than five premaxillary teeth (2:34); premaxillary tooth row anterior to external naris (14:1); maxillary alveoli subcircular in outline (23:2); mesial carina terminating well beneath the cervix in mesialmost teeth (50:2); flutes present on both labial and lingual in lateral teeth (107:2); deeply veined enamel texture in lateral teeth (117:2). **Ambiguous:** Posterior premaxillary alveoli smaller than anterior premaxillary alveoli (7:1); anterior premaxillary teeth subequal in size than the first six anterior maxillary teeth (8:1); strongly constricted premaxillary tooth row (15:2); first maxillary alveolus significantly smaller than second alveolus (20:0); first maxillary alveolus opens anteroventrally (21:1); anteriormost dentary alveoli significantly larger than mid- and posterior dentary alveoli (27:1); enlarged fanglike anterior dentary tooth (30:1); four teeth within the terminal rosette of dentary (31:1); labiolingual compression of the crown weak, CBR > 0.75, tooth of the lateral dentition incrassate (66:2); subcircular outline of basal cross-section of the crown in lateral teeth (72:0).
Megalosauridae	**Ambiguous:** Less than 15 dentary teeth (25:3).
Avetheropoda	**Unambiguous:** Outline of basal cross-section D-shaped or J-shaped, with lingual margins strongly convex and labial margins convex or sigmoid, in the crown of mesialmost tooth (41:3). **Ambiguous:** Mesial carina twisted, curves onto the lingual surface in mesialmost teeth (46:1); mesial carina extends to the cervix or just above it in mesialmost teeth (50:1).
Allosauroidea	**Ambiguous:** Posterior premaxillary alveoli subequal in size than the first six anterior maxillary alveoli (9:1); outline of basal cross-section of the crown elliptical or bean-shaped in lateral teeth (72:2); mid-crown denticles on distal carina longer mediodistally than basoapically and with horizontal subrectangular outline (92:1); interdenticular space between mid-crown denticles on the distal carina broad, more than one third of the denticle width (103:1); large transversal undulations well-visible on the crown in some lateral teeth (109:2).

......continued on the next page

TABLE A1. (Continued)

Clade	Synapomorphies
Neovenatoridae	**Ambiguous:** Surface centrally positioned on the crown roughly flattened on the labial side of lateral teeth (70:1); concave surface adjacent to carinae all along the crown present on labial and lingual surface and adjacent to distal carina (71:12).
Carcharodontosauridae	**Ambiguous:** labiolingual compression of the crown important, CBR ≤ 0.5, lateral tooth strongly flattened (66:0); biconvex apical denticles present in lateral teeth (94:1).
Tyrannosauroidea	**Unambiguous:** Anteriormost dentary alveoli significantly smaller than mid- and posterior dentary alveoli (27:2); distal carina labially displaced and facing lingually or linguodistally in mesialmost teeth (48:2). **Ambiguous:** overlap of the third and fourth premaxillary alveoli (6:1); mid-maxillary alveoli significantly larger than anteriormost maxillary alveoli (48:2).
Therizinosauroidea	**Unambiguous:** Toothless premaxilla (1:1); constriction between root and crown present in some lateral teeth (64:0).
Troodontidae	**Unambiguous:** Anterior maxillary alveoli significantly smaller than posterior maxillary alveoli (18:2). **Ambiguous:** mid-maxillary teeth significantly larger than anteriormost maxillary teeth (19:1).
Dromaeosauridae	**Unambiguous:** labial depression extends along the basal half of the crown or more apically in lateral teeth (73:2). **Ambiguous:** outline of basal cross-section of the crown 8-shaped in lateral teeth (72:3).

Cladistic analysis on a supermatrix with theropod taxa (ML teeth included).

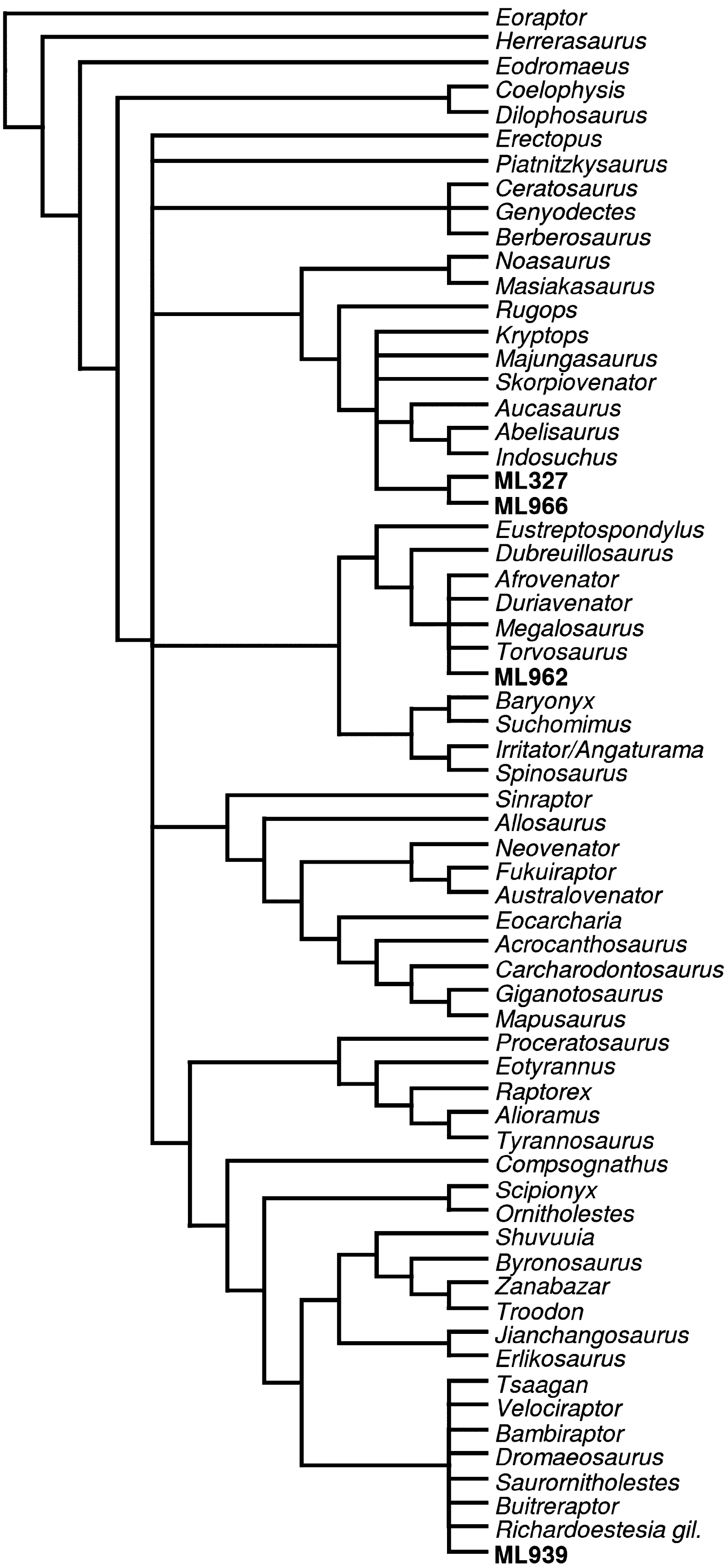


FIGURE A10. Strict consensus cladogram of 96 most parsimonious trees recovered from the analysis of a supermatrix including a dentition-based datamatrix and six recent datasets based on whole theropod skeleton (i.e., Xu *et al.* 2009; Brusatte *et al.* 2010; Martinez *et al.* 2011; Senter 2011; Pol and Rauhut 2012; Carrano *et al.* 2012). Initial analysis was a New Technology Search using TNT v.1.1 of a supermatrix comprising 1972 characters for one outgroup (*Eoraptor*), 59 non-avian theropod taxa and ML 327, ML 966, ML 939 (coded as lateral teeth), and ML 962 (coded as a mesialmost tooth). Tree length = 3607 steps; CI = 0.529; RI = 0.58.