

HETERODONTY IN *TYRANNOSAURUS REX*: IMPLICATIONS FOR THE TAXONOMIC AND SYSTEMATIC UTILITY OF THEROPOD DENTITIONS

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ABSTRACT—*Tyrannosaurus rex* possesses a heterodont dentition composed of three classes (premaxillary, maxillary, and dentary) and several sets. The maxilla contains mesial and distal sets and the dentary contains first dentary tooth (d1), mesial, and distal sets. Teeth were described with four size and two shape variables and several variables describing crown curvature and denticle size. The premaxillary teeth are derived structures with labiolingually oriented long axes, moderate mesial curvature, and mesiolingually and distolingually placed carinae that extend down the lingual faces. The mesial maxillary crowns are large, basally rounded, and moderately curved with mesiodistally oriented long axes. The mesial carinae begin at the apices and curve lingually to about the midcrown point and the distal carinae begin at the apices and extend down the labial sides of the distal faces. The distal maxillary crowns are larger than the premaxillary and smaller than the mesial maxillary and all but the most distal dentary teeth. They have labiolingually oriented long axes and have narrower basal widths than lengths. The carinae roughly define the mesiodistal axes of the crowns. The first dentary tooth is similar to those of the premaxilla. The mesial dentary teeth are similar to the mesial maxillary teeth and the distal dentary teeth are similar to those in the distal maxilla. This examination revealed that several putative systematic characters related to size and shape can be discerned from *T. rex* teeth, suggesting that useful dental characters may be more common within the Theropoda than has generally been presumed.

INTRODUCTION

The literature regarding non-avian theropods can be traced to Brooks (1763), but the description of *Megalosaurus* Buckland, 1824, constitutes their first technical treatment (Delair and Sarjeant, 2002). Since their discovery, discussions of osteology and systematics have often ignored the dentition, largely because theropod teeth are simple structures lacking easily identifiable features (see Farlow et al., 1991; Currie, 1997a; Sander, 1997). They are thus often dismissed as ‘typically theropod’ or as ‘laterally compressed blades’ (e.g., Dong et al., 1975; Bonaparte and Novas, 1985; Gao, 1992; Chen et al., 1998; Azuma and Currie, 2000). Most phylogenies include few dental characters (e.g., Holtz, 1994, 1998; Norell et al., 2001) and detailed tooth descriptions are generally restricted to taxa with distinctive dentitions (e.g., Charig and Milner, 1986; Pérez-Moreno et al., 1994; Sereno et al., 1996; Xu et al., 1999, 2002; Norell et al., 2000). Although the key characters uniting the Spinosaurinae are all related to the dentition (see Sereno et al., 1998; Sues et al., 2002), and such features have been important in studies of toothed birds, for most groups even works that describe the dentigerous bones in detail refer to the teeth themselves only briefly or omit discussion of them altogether (e.g., Bonaparte et al., 1990; Molnar, 1991). Studies of within-taxon theropod dental variation are virtually nonexistent.

Current interest in theropod systematics and a high frequency of tooth discovery makes the lack of a detailed knowledge base on dental morphology problematic. Some authors dismiss teeth as being too simple or homogenous to be systematically useful while others continue using them to erect new taxa (e.g., Carpenter, 1982; Antunes and Sigogneau-Russell, 1991; Okazaki, 1992; Chure, 1994; Nesov, 1995; Sankey, 2001), most of which are considered nomina dubia (e.g., see Holtz, 2004; Holtz et al., 2004). Moreover, most existing work has been conducted on isolated crowns referred to taxa on the basis of a priori assumptions of phylogenetic affinities. Outcomes from such studies must be viewed as approximations of the results that would be pro-

duced by using teeth of known taxonomy (Farlow et al., 1991), results that can only be obtained by examining teeth within jaws. Until studies of morphology and variation are conducted on the in-situ teeth of well-supported taxa, any inherent taxonomic or systematic utility possessed by these elements will go unrealized and the confused plethora of theropod tooth taxa and assemblages will continue to be bewildering (see Chure, 2001).

Here, for the first time, the dentition of a single theropod, *Tyrannosaurus rex* Osborn, 1905, is discussed in detail. The Tyrannosauridae consist of several well-supported North American and Asian forms (Carpenter, 1990, 1992; Holtz, 1994; Carr, 1999; Carr and Williamson, 2000; Brochu, 2002; Currie, 2003a). This species was selected because it has an interesting dentition, is known from multiple individuals, and has a well-studied anatomy that would be complemented by an examination of the dental apparatus (see Osborn, 1905, 1906, 1912, 1913, 1917; Carpenter, 1990, 1992; Molnar, 1991, 1998; Carr, 1999; Carr and Williamson, 2000, 2004; Brochu, 2002; Hurum and Sabath, 2003). As the functional aspects of *T. rex* teeth have been addressed elsewhere (Abler, 1992, 1999, 2001; Erickson, 1996; Molnar, 1998), the emphasis here is placed on morphology.

It is the paucity of obvious qualitative features that is the problem with theropod teeth. Such characters can occasionally be discerned in simple-toothed forms (e.g., Poyato-Ariza, 2003). However, quantitative analyses that have proved useful in studying mammalian dentitions (e.g., Korth, 1996; Polly, 1998a, b; Carrasco, 2000a, b) may be usefully applied to theropod teeth, relying more on numerical methods than is typical in dinosaur studies (Smith et al., 2005). This approach should facilitate systematic character selection as well as the rigorous discrimination of similar forms. This paper combines detailed descriptions and a quantitative examination of within- and between-taxon variability to assess potential characters.

Abbreviations for Variables—**AL**, apical length; **CA**, crown angle; **CA2**, crown angle corrected for size; **CBL**, crown base length; **CBR**, crown base ratio; **CBW**, crown base width; **CH**,

crown height; **CHR**, crown height ratio; **DA**, distal apical denticle density; **DAVG**, average distal denticle density; **DAVG2**, size adjusted average distal denticle density; **DB**, distal basal denticle density; **DC**, distal mid-crown denticle density; **MA**, mesial apical denticle density; **MAVG**, average mesial denticle density; **MB**, mesial basal denticle density; **MC**, mesial mid-crown denticle density. Following Smith and Dodson (2003), the abbreviations **d** (dentary), **mx** (maxillary), and **pm** (premaxillary) are used when referring to tooth positions and are followed by a numeral that indicates the specific tooth (e.g., mx3 refers to the third maxillary tooth).

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York; **BHI**, Black Hills Institute of Geological Research, Hill City, SD; **BMNH**, Natural History Museum, London; **CM**, Carnegie Museum of Natural History, Pittsburgh; **CMNH**, Cleveland Museum of Natural History; **FMNH**, Field Museum of Natural History, Chicago; **GIN**, Geological Institute, Mongolian Academy of Sciences, Ulan Bataar; **KUVP**, University of Kansas Natural History Museum, Lawrence; **LACM**, Los Angeles County Museum; **MBR**, Museum für Naturkunde der Humboldt Universität, Berlin; **MCZ**, Museum of Comparative Zoology, Harvard University; **MOR**, Museum of the Rockies, Bozeman; **NCSM**, North Carolina State Museum, Raleigh; **NIGP**, Nanjing Institute of Geology and Palaeontology, Nanjing, China; **OMNH**, Oklahoma Museum of Natural History, Norman; **ROM**, Royal Ontario Museum, Toronto; **SDSM**, South Dakota School of Mines, Rapid City; **SGM**, Ministère de l'Énergie et des Mines, Rabat, Morocco; **SMU**, Southern Methodist University, Dallas; **UCMP**, Museum of Paleontology, University of California at Berkeley; **UMNH**, Utah Museum of Natural History, Salt Lake City; **YPM**, Peabody Museum of Natural History, Yale University.

MATERIALS AND METHODS

Materials

Most known *T. rex* crania containing teeth were examined (Supplementary Data 1, available online at www.vertpaleo.org/jvp/JVPcontents.html). *Tarbosaurus* Maleev, 1955, was excluded as there is no consensus on its taxonomy and it appears to be a distinct species (Holtz, 2001; Hurum and Sabath, 2003; Carr and Williamson, 2004). Data from *Dilophosaurus* Welles, 1970; *Liliensternus* Welles, 1984; *Ceratosaurus dentisulcatus* Madsen and Welles, 2000 (? = *Ceratosaurus nasicornis* Marsh, 1884); *Masiakasaurus* Sampson et al. 2001; *Indosuchus*; *Majungatholus* Sues and Taquet, 1979; *Baryonyx* Charig and Milner, 1986; *Suchomimus* Sereno et al., 1998; *Allosaurus* Marsh 1877; *Acrocanthosaurus* Stovall and Langston, 1950; *Carcharodontosaurus* Stromer, 1931; *Gorgosaurus* Lambe, 1914; *Daspletosaurus* Russell, 1970; *Tyrannosaurus rex*; *Troodon* Leidy, 1856; *Sauromithoides junior* Barsbold, 1974; *Bambiraptor* Burnham et al., 2000; *Deinonychus* Ostrom, 1969a; *Dromaeosaurus* Matthew and Brown, 1922; and *Velociraptor* Osborn, 1924 were used to provide context for teeth of *Tyrannosaurus rex* within theropod dental morphospace (see Smith et al., 2005, for data).

Growth-related change is important in paleobiology (e.g., Currie, 2003b). However, as ontogeny in *Tyrannosaurus rex* is currently poorly understood, data were excluded from problematic specimens (see Molnar and Carpenter, 1989; Carr, 1999; Brochu, 2002; Carr and Williamson, 2004), such as LACM 28741 (*'Aublysodon'*) and CMNH 7541 (*'Nanotyrannus'*), to be dealt with separately. These specimens are likely juveniles of *T. rex* (see Carr, 1999; Holtz, 2001), and have been synonymized as such (Carr and Williamson, 2004). However, a consensus is lacking (see Currie, 2003a; Currie et al., 2003), and there are new data (J. Peterson, pers. comm., 2002) that merit consideration. I am not comfortable coding teeth as pertaining to *T. rex* unless there is

general agreement that they are such, nor is it wise to use data from a problematic specimen to support or refute a *T. rex* affinity for that individual. Therefore, I included only those data that are currently unquestioned as pertaining to *T. rex*. As tyrannosaurid taxonomy becomes clearer, the dentitions of problematic specimens should be compared against those of well-supported taxa. In the absence of this and in the absence of data for proven juvenile teeth for *T. rex*, discussions of ontogenetic change in its dentition are premature (e.g., Senter and Robins, 2003).

Measurements and Counts

Measurements were made directly with electronic calipers or on digital images using SigmaScan®. Denticles were counted with a Hensoldt-Wetzlar 8X lens possessing a mm-scale reticle. Data cases are averages of five replicate measurements (measurement repeatability was assessed by Smith, 2002). Data were included from teeth regarded as being fully erupted (teeth that are erupting, are reconstructed, or are not accessible because the specimen is on display were omitted). Orientation terminology (Fig. 1A) follows Smith and Dodson (2003). Studies of tyrannosaurid dentitions must pay particular attention to the premaxillary and first dentary teeth. The basal short axes of these crowns are mesiodistal rather than labiolingual in orientation (as in most theropods), and the long axes (sensu the basoapical axis in human incisors, see Minagi et al., 1999) are oriented labiolingually rather than mesiodistally (Fig. 1B, C).

The variables used in this article (Fig. 1D, E) were derived or discussed in detail by Smith et al. (2005); they are noted briefly here. Size was described using crown base length (CBL), crown base width (CBW), crown height (CH), and apical length (AL). CBL and CBW were measured in a horizontal plane referenced approximately to point B of Smith et al. (2005). Basal shape was described using the crown base ratio (CBR = CBW/CBL); crown "squatness" was assessed using the crown height ratio (CHR = CH/CBL). Apex displacement from the crown base center and crown curvature were described using the crown angle (CA).

Crown angle values were calculated using the Law of Cosines and solving for:

$$\theta = \arccos\left(\frac{a^2 + b^2 - c^2}{2ab}\right) \quad (1)$$

where a = CBL, b = AL, and c = CH.

Denticle size and spacing was quantified by determining the number of denticles per 5 mm of carina length (see Farlow and Brinkman, 1987), counted as close to the base, mid point, and apex as possible (see Chandler, 1990), thus generating the basal (MB and DB), mid-crown (MC and DC), and apical densities (MA and DA). For very small teeth (e.g., *Bambiraptor*), counts were taken over 2 mm and then adjusted to 5 mm after Farlow et al. (1991). Five counts of each variable were taken, the means of which yielded average densities for the mesial and distal carinae (MAVG, DAVG, after Chandler, 1990). The ratio of MAVG to DAVG generated the denticle size density index (DSDI), devised and discussed by Rauhut and Werner (1995).

Analyses

Statistical analyses were run with SPSS, SigmaStat®, and Stat-View and were illustrated using SigmaPlot®. Factors that might have a significant effect on the variability within the data were examined using analysis of variance (ANOVA). As biogeography (concept after Carrasco, 2000a, b; Lieberman et al., 2002) showed no significant effect on the observed variation (Smith et al., 2005) and sexing and aging of tyrannosaurs is problematic (Larson, 1994; Chapman et al., 1997; Galton, 1999), tooth position is the main factor that might account for a significant proportion of the observed variation. ANOVA was employed to test this hypothesis using variability profiles sensu Yablokov (1974)

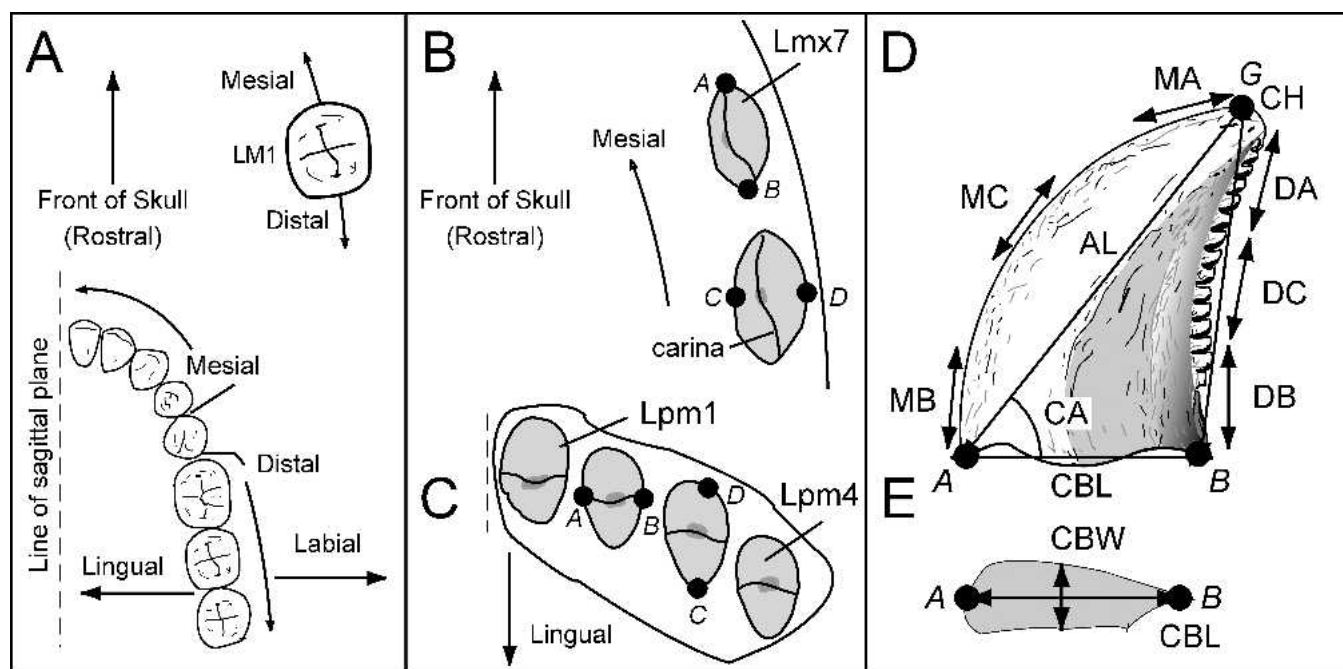


FIGURE 1. **A**, idealized human dental arcade, in palatal view, showing mesial, distal, labial, and lingual directions (modified from Smith and Dodson, 2003). **LM1**, left upper first molar. **B**, photo traces of AMNH 5027 Lmx7–8 (bones are schematic), showing mesiodistal orientations of crown long axes (points A–D were defined by Smith et al., 2005). **C**, photo trace of the premaxilla of AMNH 5027 (teeth are schematic) in palatal view showing labiolingual orientations of the crown long axes. **D**, *Saurornitholestes* Sues, 1978, crown in lateral view showing crown height (CH, measured from the apex to the base of the enamel (~between points G and B)); crown base length (CBL, measured along the mesiodistal axis of the crown at the base of the enamel, ~between points A and B); apical length (AL, measured between points A and G); crown angle (CA, angle GAB); mesial apical (MA), mesial mid-crown (MC), and mesial basal (MB) denticle densities (measured along the length of the mesial carina); distal apical (DA), distal mid-crown (DC), and distal basal (DB) denticle densities (measured along the length of the distal carina). **E**, the crown in D in basal view showing CBL and crown base width (CBW, measured perpendicular to CBL). Crown in D redrawn from Currie et al., (1990). Figure concept after Smith et al. (2005).

but modified after Smith (2002) to show positional variation within tooth rows (*sensu* Williamson, 1996). As the variables were compared with tooth position rather than with coefficients of variation (see Yablokov, 1974), raw data were analyzed instead of following Sokal and Braumann (1980). The results were examined using post-hoc tests that compared the means of the dependent variables with respect to tooth position: Fisher's PLSD (see Sokal and Rolf, 1995) and Tukey-Kramer (Kramer, 1956). Raw data were used for AL, CA, CBL, CBR, CBW, CH, CHR, MAVG, and DAVG. CA and DAVG were also compared after removing size as a confounding variable (see Marko and Jackson, 2001). Smith et al. (2005) log-transformed the data and ran a principal-components analysis. The data for DAVG were then regressed on PC1, which explained 84.4% of the observed variation; the residuals from these regressions constitute the size-corrected variables CA2 and DAVG2.

MORPHOLOGY AND POSITIONAL VARIATION

Osborn's (1912) study remains the best prior treatment of *Tyrannosaurus* dentition, although other works have briefly discussed the teeth (e.g., Brochu, 2002; Hurum and Sabath, 2003). Osborn (1912) focused on CM 9380, AMNH 5027, 5117, 5866, and CM 9379. He reported a dental formula of 4 premaxillary, 12 maxillary, and 13–14 dentary teeth, for 58–60 total positions. Molnar (1991) found 4/11–12/? from these specimens and LACM 23844 and SDSM 12047. Currie et al. (2003) reported 4/11–12/12–14, but from which specimens these data came is not clear. Table 2 provides an updated list of tooth counts.

Theropods are not usually considered to be heterodont taxa, but this view is too simple (see Currie, 1987). *Tyrannosaurus rex*

in particular exhibits as much heterodonty (see Stromer, 1934) as do taxa acknowledged as having distinctive dentitions, such as *Eoraptor* Sereno et al., 1993, *Troodon*, and *Masiakasaurus*. Preliminarily, *T. rex* appears to be more heterodont than *Daspletosaurus* or *Albertosaurus*; it possesses tooth morphologies that we can regard as classes at the element level (see Peyer, 1968; Zhao et al., 2000) and as sets *sensu* Hungerbühler (2000) at the intra-element level. These sets differ in concept from the ontogenetic tooth families of Edmund (1969) and Osborn (1973). Broadly, *T. rex* follows the 'typical' theropod pattern (see Holtz and Osmólska, 2004) of 'recurved' crowns possessing longer base lengths than widths (Molnar and Carpenter, 1989). However, *T. rex* teeth are less curved than those of many theropods (an obvious exception to this are the dentitions of certain spinosaurids; see Sereno et al., 1998; Sues et al., 2002).

The Premaxillary Dentition

There are four teeth in all known premaxillae of *T. rex*, a feature that is robust for the Tyrannosauridae (see Osborn, 1905, 1906, 1912; Carpenter, 1990, 1992; Molnar, 1991; Brochu, 2002; Currie, 2003a; Hurum and Sabath, 2003). Premaxillary tooth count is constant for most theropods (see Lamanna, 1998). Currie (*pers. comm.*, 1998; see also Ji and Ji, 1997) noted a discrepancy in tooth count in a specimen of *Sinosauropteryx* Ji and Ji, 1996 (NIGP 127586), but the lack of variation in other theropods suggests that this might be a specimen-specific or taxon-specific anomaly (assuming the individuals all represent one species). Currie and Chen (2001) reported that preparation issues confound tooth counts in *Sinosauropteryx*. *Baryonyx* might possess

TABLE 1. *Tyrannosaurus rex* class-level comparisons for the nine principal variables used in this study. “*p* (Premaxilla)” = *p* values of ANOVAs for maxilla and dentary values against the premaxillary values; “*p* (Max-Dent)” = *p* values of ANOVAs between the maxilla and dentary values. “*S*(P)” and “*S*(M)” = indications of significance (*) or nonsignificance (-) at 95% for the ANOVAs.

Bone	Variable	Mean	Min.	Max.	St. Dev.	<i>p</i> (Premaxilla)	<i>p</i> (Max-Dent)	<i>S</i> (P)	<i>S</i> (M)	<i>n</i>
Premaxilla	CBL	31.41	27.38	36.06	2.666					9
Premaxilla	CBW	19.01	14.27	24.00	2.992					9
Premaxilla	CH	50.63	42.55	63.65	7.393					9
Premaxilla	AL	57.25	50.21	71.97	6.640					9
Premaxilla	CBR	.60	.52	.67	0.052					9
Premaxilla	CHR	1.61	1.42	1.77	1.607					9
Premaxilla	CA	85.44	84.59	86.38	0.715					9
Premaxilla	MAVG	9.9	9.1	10.8	0.568					9
Premaxilla	DAVG	9.9	8.4	11.0	0.831					9
Maxilla	CBL	40.37	18.96	54.88	8.807	.0059		*		59
Maxilla	CBW	27.90	12.83	41.59	6.885	.0004		*		57
Maxilla	CH	78.62	27.02	117.10	24.364	.0011		*		52
Maxilla	AL	86.21	32.14	138.94	26.201	.0016		*		52
Maxilla	CBR	.69	.57	.86	0.073	.0001		*		57
Maxilla	CHR	1.97	1.43	2.55	.269	.0005		*		52
Maxilla	CA	86.67	81.45	88.11	1.491	.0945		--		52
Maxilla	MAVG	9.1	6.8	13.4	1.316	.1135		--		49
Maxilla	DAVG	9.4	7.2	13.2	1.368	.3214		--		48
Dentary	CBL	36.05	15.01	52.07	9.586	.1487	.0089	--	*	62
Dentary	CBW	25.92	9.22	38.57	7.192	.0056	.1175	*	--	62
Dentary	CH	64.87	15.85	105.61	23.538	.0890	.0024	--	*	58
Dentary	AL	70.62	17.41	115.88	25.160	.1352	.0013	--	*	58
Dentary	CBR	.72	.56	.88	0.056	<.0001	.0450	*	*	62
Dentary	CHR	1.7	1.06	2.36	0.297	.1071	.0003	--	*	58
Dentary	CA	85.75	76.45	87.76	2.495	.6733	.0182	--	*	58
Dentary	MAVG	9.6	7.0	14.4	1.479	.5833	.0604	--	--	51
Dentary	DAVG	10.0	7.5	15.7	1.803	.8725	.0383	--	*	52

six left and seven right premaxillary teeth in BMNH R9951 (see Charig and Milner, 1997). However, Rpm6 and 7 appear to be crowded into one alveolus, suggesting that BMNH R9951 could also be anomalous. Such anomalies are common in mammals (P. Dodson, pers. comm., 2004) and should not affect the stability of theropod counts. It is also possible that tooth-count variation increases with decreasing crown size (J. D. Harris, pers. comm., 2004).

Crown Size—The premaxillary class is significantly smaller than the maxillary class in CBL, CBW, CH, and AL (Table 1, Fig. 2), as in other tyrannosaurids (Russell, 1970; Holtz, 2001; Currie, 2003a; Hurum and Sabath, 2003) and some ceratosaurs (Rauhut, 2004). There are trends of increasing size along the tooth row for CBL, CBW, CH, and AL (Fig. 2). The first tooth (mean pm1 CBL = 28.61 mm) is significantly smaller than that for pm3 (pm3 CBL = 33.96; ANOVA with pm1: $F = 2.92$, $p = .0346$), but the remaining teeth are not significantly different from each other in size. The fourth tooth is slightly smaller than pm3 in all size variables, but the differences are not significant. A similar decrease in size toward the premaxillary-maxillary suture (premaxilla-maxilla joint sensu Molnar, 1991) occurs in *Coelophysis* Cope, 1889, *Dilophosaurus*, and *Eoraptor* (Welles, 1984; Colbert, 1989; Sereno and Novas, 1993).

Crown Shape and Carina Morphologies—Theropod crown basal cross sections are often ovals that taper to points corresponding to the locations of the carinae (Fig. 1B). The basal long axis (generally oriented mesiodistally) can be twice the length of the short axis (usually oriented labiolingually). In the premaxilla of *T. rex* however, although the crown bases are narrow ovals, the long axes are oriented labiolingually (Fig. 1C). The labial faces are ovals that are convex toward the rostral end of the snout (Fig. 3A). The lingual faces form very weakly convex curves (e.g., AMNH 5027), which are more pronounced basally, creating a shallow wide ridge (contra Molnar and Carpenter, 1989); apically the faces are almost flat (Fig. 3B). The curves of the lingual faces flatten out proximal to the carinae, which are located at the mesiolingual and distolingual corners of the

TABLE 2. Premaxillary, maxillary, and dentary tooth counts of *Tyrannosaurus rex*.

Specimen	Element	Side	Positions
AMNH 5027	Premaxilla	Left	4
AMNH 5027	Premaxilla	Right	4
BHI 3033	Premaxilla	Left	4
BHI 3033	Premaxilla	Right	4
FMNH PR2081	Premaxilla	Left	4
FMNH PR2081	Premaxilla	Right	4
LACM 23844	Premaxilla	Right	4
AMNH 5027	Maxilla	Left	12
AMNH 5027	Maxilla	Right	12
BHI 3033	Maxilla	Left	11
BHI 3033	Maxilla	Right	11
CM 9380	Maxilla	Left	12
FMNH PR2081	Maxilla	Left	12
FMNH PR2081	Maxilla	Right	12
LACM 23844	Maxilla	Right	11
MOR 555	Maxilla	Left	12
MOR 1125	Maxilla	Right	12
SDSM 12047	Maxilla	Left	12
SDSM 12047	Maxilla	Right	12
UCMP 118742	Maxilla	Right	12
AMNH 5027	Dentary	Left	14
AMNH 5027	Dentary	Right	14
BHI 3033	Dentary	Left	13
BHI 3033	Dentary	Right	13
BMNH 5863	Dentary	Left	14
CM 9380	Dentary	Left	13
CM 9380	Dentary	Right	13
FMNH PR2081	Dentary	Left	13
FMNH PR2081	Dentary	Right	14
LACM 23844	Dentary	Right	11
LACM 23844	Dentary	Left	11
LACM 150167	Dentary	Right	12
MOR 1125	Dentary	Right	14
SDSM 12047	Dentary	Left	14
SDSM 12047	Dentary	Right	?15

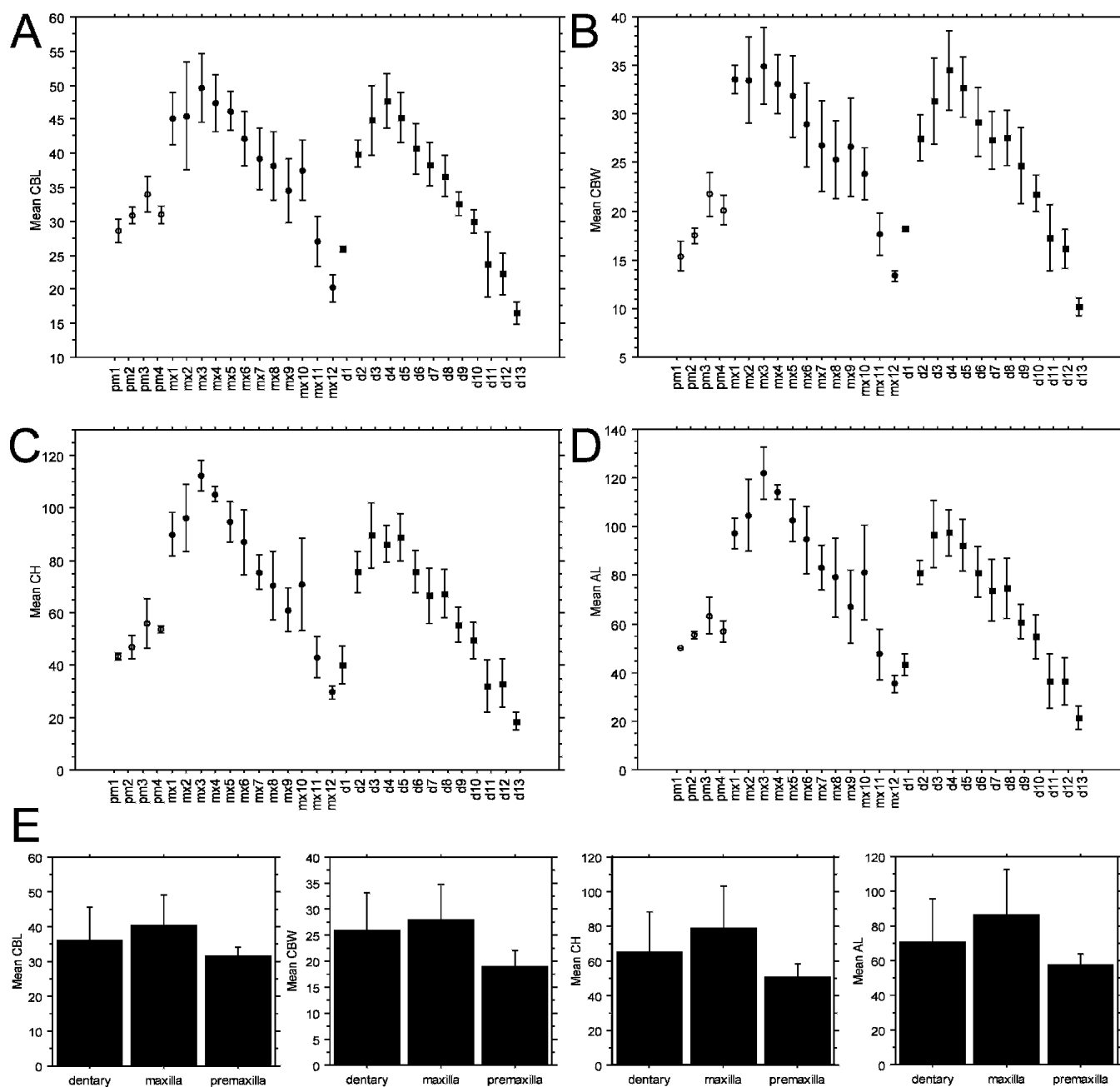


FIGURE 2. Crown size (in mm) variability profiles, with respect to tooth position, for CBL (A), CBW (B), CH (C), and AL (D) of *Tyrannosaurus rex*. E, crown size (CBL, CBW, CH, and AL, in mm) comparisons for *T. rex* tooth classes. See Supplementary Data 1, www.vertpaleo.org/jvp/JVPcontents.html, for data. Error bars = ± 1 standard deviation.

crowns. The flattening is more pronounced distal to pm1 where the very slightly convex mesial and distal faces curve into the lingual face.

A number of theropods exhibit positional variation with respect to carina placement. *Tyrannosaurus rex* exhibits dramatic changes in this feature along the maxillary and dentary tooth rows, but virtually none within the premaxilla: the carinae are all located at the corners of the teeth, as in other tyrannosaurids (Russell, 1970; Currie, 2003a). In labial view, the denticles are often just visible along the mesial and distal edges of the labial faces. The carinae start from lingual points on the apices and extend basally along the mesial and distal faces to the bases, exhibiting slight labial convexity. They cross the apices with a

surface expression of one carina wrapping over the tip rather than two distinct carinae, although each is discussed separately here. The mesial carinae are $\sim 2\text{--}5$ mm shorter than the distal and often do not extend to the bases. Both carinae in pm3 of BHI 3033 terminate before reaching the base. Often premaxillary mesial carinae of *T. rex* are slightly shorter than the distal carinae, so it might be possible to discriminate left and right crowns by identifying the distal carina. Similar morphologies occur in the premaxillae of other tyrannosaurids (Russell, 1970; Carr, 1999; Currie, 2003a), leading to the premaxillary crowns being referred to as ‘incisiform,’ ‘U-shaped,’ or ‘D-shaped in cross section’ (see Russell, 1970; Currie et al., 1990; Carpenter, 1992; Holtz, 1994, 1998; Carr, 1999; Ford and Chure, 2001; Brochu, 2002; Currie,

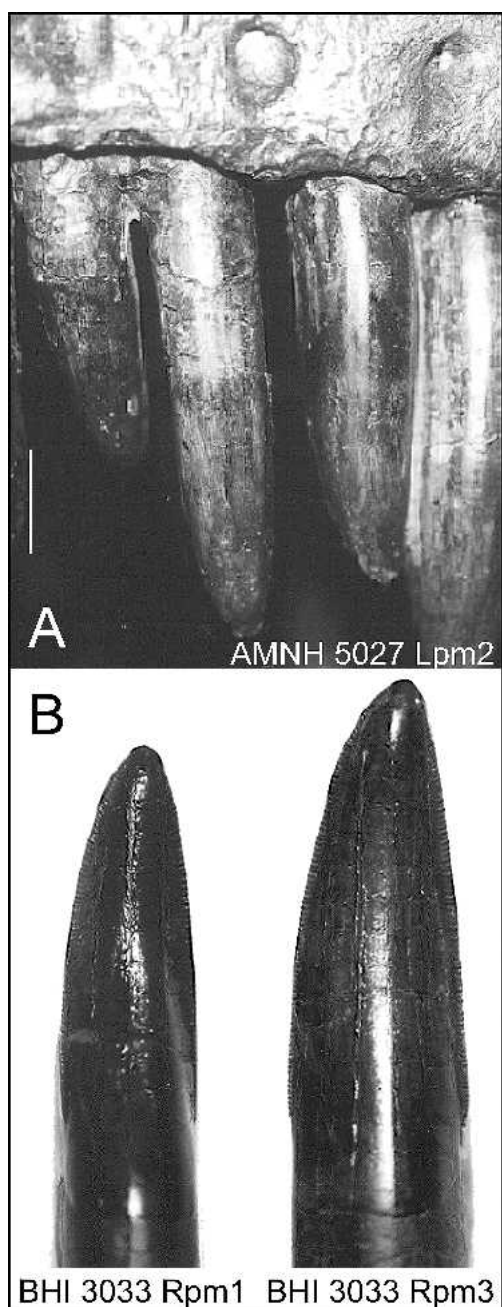


FIGURE 3. Premaxillary crown morphologies in *Tyrannosaurus rex*. **A**, Lpm2 of AMNH 5027 in labial view. **B**, Rpm1 and Rpm3 of BHI 3033 in lingual view. Scale bar equals 5 mm.

2003a; Carr and Williamson, 2004). Given the convexity of the lingual face and the oval shapes of the crown bases, these descriptors are somewhat inaccurate, but do get the general meaning across (at least colloquially; better descriptions might be desired when using this feature as a systematic character).

Although theropod teeth in general tend to be more circular mesially and more bladelike distally (see Smith et al., 2005), *T. rex* exhibits a reverse trend. The premaxillary teeth are significantly more blade-like than those in the maxilla or dentary (Table 1, Fig. 4A). This might be initially surprising, but *T. rex* premaxillary crown bases are very elongate. The first two teeth are significantly less circular than are than pm3 and 4 (pm2 CBR = 0.57; pm3 = 0.64, $F = 14.06$, $p = .0128$). The premaxillary

teeth are more 'squat' than in the maxilla or dentary (Table 1, Fig. 4B). Along the tooth row, the crowns become increasingly, but not significantly, more elongated (CHR values of 1.52, 1.52, 1.64, and 1.74, from p1–pm4, respectively).

The rostral end of the snout in *T. rex* is more squared off than in many theropods (Fig. 5A), so that the tooth row curves away from the midline. This, along with the derived crown shapes, produces the distinctive tyrannosaurid premaxillary dentition. Carina placement and lingual face morphology in *T. rex* are similar to those of pm1 of *Allosaurus* (e.g., YPM 1333 and 4933, MOR 693, and UMNH 1251) and pm1–3 in *Majungatholus* (e.g., FMNH PR2100). In all three taxa the carinae form the mesial and distal edges of the lingual faces in lingual view (Figs. 5B–D). However, this resemblance of *Allosaurus* and *Majungatholus* premaxillary teeth with those of *T. rex* is only valid mesially. By the distal ends of the tooth rows in both of these taxa, the crowns are distinctly different from the premaxillary condition in *T. rex*. By pm4 in *Allosaurus* (YPM 1333), the mesial carina, in mesial view, begins at the apex and curves lingually such that it forms the lingual edge of the mesial face at about the mid-crown point. In pm5 the distal carina essentially defines the distal keel of the crown, showing only a very slight labial convexity along its length.

Crown Curvature—That crown curvature is taxonomically variable in theropods has been suggested (Gilmore, 1920; Russell, 1970; Madsen, 1976). Within-taxon variation takes the form of increasingly curved crowns along the length of the tooth row (see Smith 2002), often accompanied by a decrease in size (Chandler, 1990). However, some taxa, such as *Spinosaurus* Stromer, 1915, and *Irritator* Martill et al., 1996, exhibit very little mesial curvature (see Sues et al., 2002). This curvature can be seen indirectly in the CA data generated by equation (1). In general, CA values closer to 90° indicate more centrally positioned apices, a condition that usually correlates with less curved mesial profiles. Lower CA values usually correlate with more strongly curved mesial profiles. In *T. rex*, curvature decreases from pm1–4 (Fig. 4C), but the differences are not significant (mean CA values of 84.7°, 85.1°, 85.9°, and 85.9° from pm1–4). The CA values in the premaxillary dentition versus those in the maxilla and dentary are also not significant (Table 1, Fig. 4C).

Denticles—The mesial premaxillary denticles range in size from ~9–11/5 mm (Table 1), with a weak trend of increasing size along the tooth row (Fig. 6A), although differences between adjacent teeth are mostly not significant. Premaxillary MAVG values are not significantly larger than those of the maxillary or dentary teeth (Table 1). In examining the components from which MAVG is generated, the MA data range from 8.4–10.9/5 mm, the MC data from 7–9.5/5 mm, and the MB data from 9–12.5/5 mm. There is no significant size trend along the tooth row in the apical denticles, but the mid-crown denticles show a very weak increasing trend. The MB data show no clear trends. The apical mesial denticles (10.3/5 mm) are significantly smaller than those of the maxilla (7.9/5 mm, $p < .0001$) and dentary (8.5/5 mm, $p = .0245$), but the mid-crown and basal denticles are not. Overall, the components of MAVG and DAVG mimic the trends illustrated in Figure 6. As Smith (2002) provided variability plots of these variables and they are not substantially more informative for understanding the dentition of *T. rex*, MA, MC, MB, DA, DC, and DB plots have been omitted here. The distal denticles display similar patterns of variation to that seen in MAVG data (Fig. 6B); premaxillary DAVG values are not significantly different in size from those of the maxilla or dentary (Table 1). The apical distal denticles (10.3/5 mm) are significantly smaller than those of the maxilla (8.3/5 mm, $p = .0003$), but not those of the dentary (9.4/5 mm, $p = .0890$). There are no significant differences in size between the dentigerous bones of *T. rex* for the mid-crown or basal distal denticles.

When premaxillary DSDI data are examined for *T. rex*, posi-

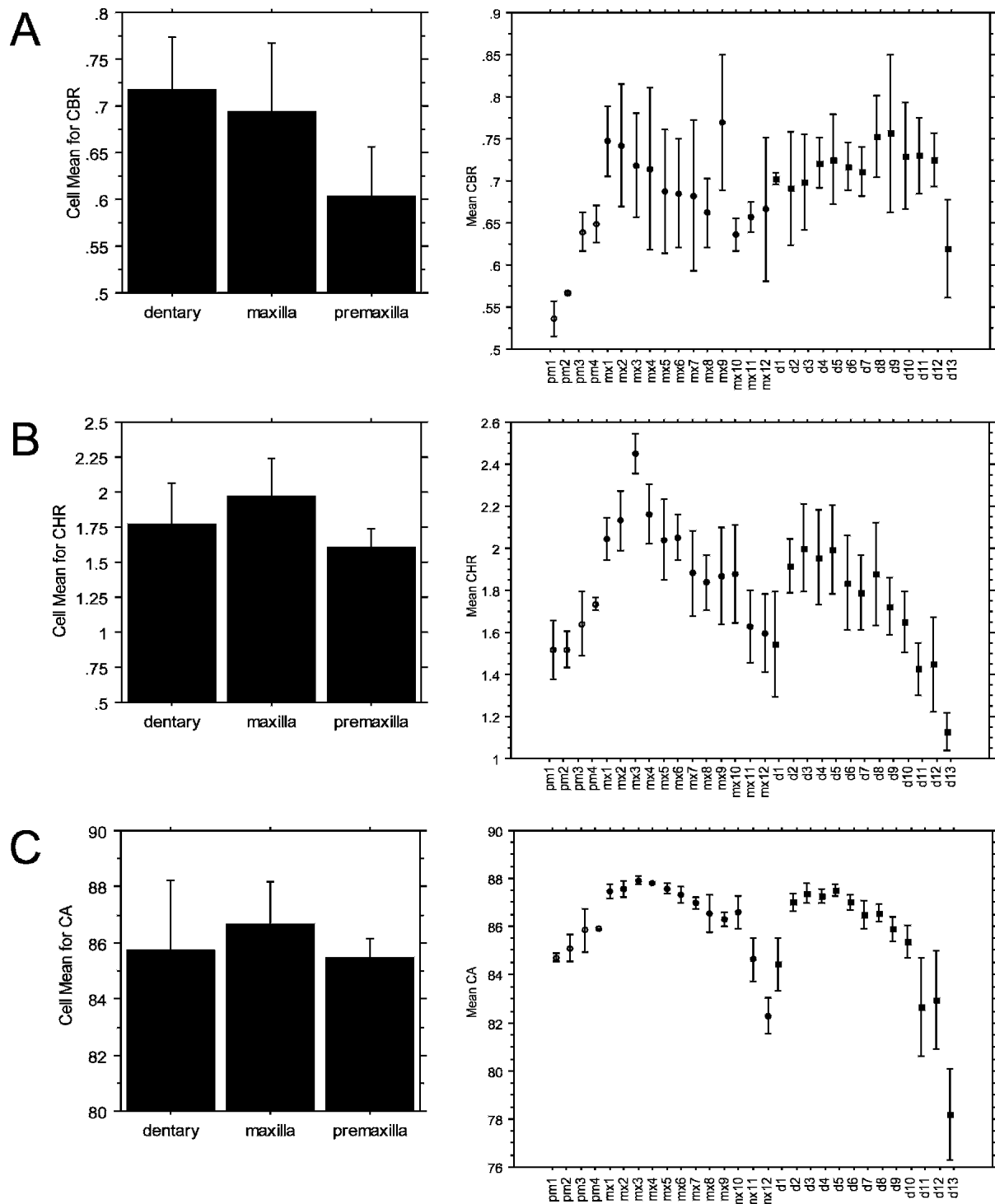


FIGURE 4. Crown shape comparisons and variability profiles, with respect to tooth position, for CBR (A), CHR (B), and CA (C) of *Tyrannosaurus rex*. See methods for units. See Supplementary Data 1, www.vertpaleo.org/jvp/JVPcontents.html, for data. Error bars equal ± 1 standard deviation.

tional variation in the denticles largely disappears (Fig. 6C). The range of premaxillary DSDI variation is well within the range of DSDI variability for the mouth as a whole. Indeed, while there is some noise within the data, there is little positional influence for this feature in any of three tooth classes. Thus, DSDI does not appear to be particularly useful in examining *T. rex* teeth. However, the lack of positional variation suggests that DSDI data might have some systematic utility.

The Maxillary Dentition

The maxillary class of *T. rex* contains an average of 12 teeth, including the largest in the dental arcade and some of the smallest (Fig. 2). It is significantly larger than the premaxillary and dentary classes in CBL, CH, and AL and significantly larger than the premaxillary class in CBW (Table 1). Indeed, mx3 and mx4 are large enough that it might be possible to distinguish them

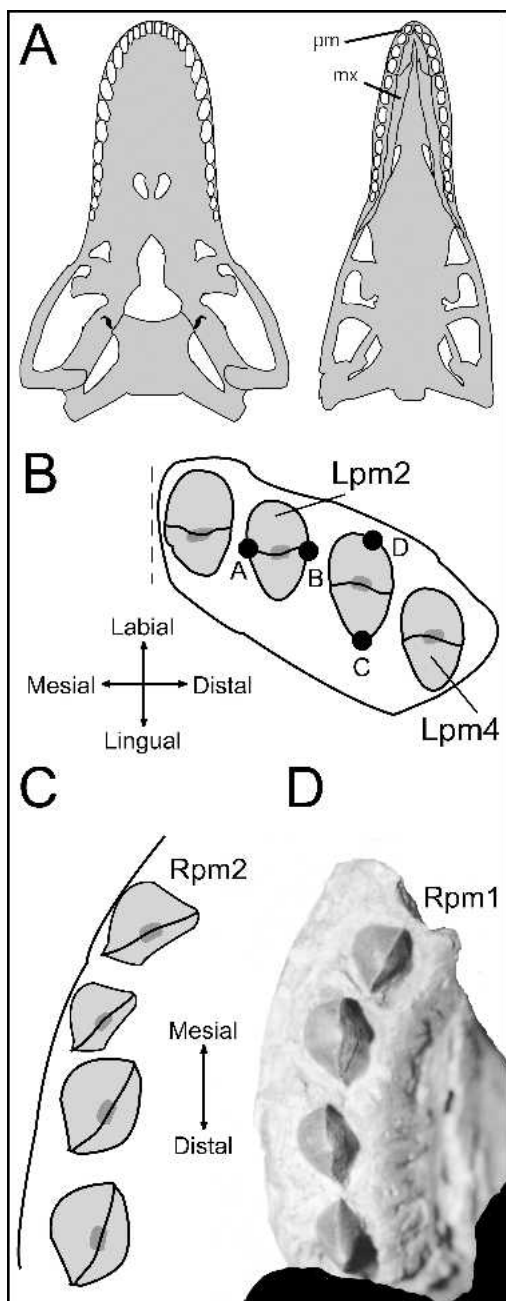


FIGURE 5. Premaxillary tooth morphology in *Tyrannosaurus rex*. **A**, idealized skulls of *T. rex* and *Dromaeosaurus* in palatal view, showing variation in snout shape (after Molnar, 1998, and Currie, 1995). **B**, photo trace of AMNH 5027 in palatal view showing labiolingual crown long-axis orientations (teeth are schematic; dashed line is sagittal plane). **C**, photo trace of *Allosaurus* (YPM 1333) in palatal view, showing morphology and carinae of Rpm2–5. **D**, right premaxilla of *Majungatholus* (FMNH PR 2100) in occlusal view.

from dentary crowns using CH (mx3: 111.30 mm; mx4: 105.34 mm versus d4: 90.14 mm). The teeth in the maxillary dentition are different from those in the premaxillary class in terms of shape and size. Crown size and shape change enough within the maxilla that the dentition can be discussed in terms of two distinct sets.

Crown Size—The mesial set (mx1–mx3) consists of very large crowns (see Molnar, 1991) with oval bases and moderate mesial curvature (Figs. 2A–D). The first tooth is not ‘small’ as in *Gor-*

gosaurus and *Daspletosaurus* (Currie, 2003a). Rather, mx1 is one of the largest crowns in the mouth, as in *Tarbosaurus* (Hurum and Sabath, 2003). True, mx1 is the smallest member of the mesial maxillary set, but it is roughly the same size as the largest crown in the dentary (mx1 CH: 90.04 mm; d4 CH: 90.14 mm). Crown size increases from mx1–mx3. There is an inflection point at ~mx4 beyond which size decreases to the end of the tooth row. It is between mx3 and mx4, on the basis of size, that the break between the mesial and distal sets was placed. The distal set (mx4–mx12) mostly contains smaller teeth with rather straight distal curvature profiles and long base lengths as compared to widths (although mx4 and 5 are large teeth). In the mesial set, mx1 is significantly smaller than mx3 in CH and AL (mx3 CH: 111.30 mm, p .0030). These are the only significant differences in size in the mesial set. In the distal set, size decreases from mx4–mx12 for all size variables (recognized by Osborn, 1912). As in the premaxilla, few teeth are significantly larger than adjacent crowns but the mesial teeth in the set are significantly larger than the more distal crowns (mx5 CBL: 46.19 mm; mx7 CBL: 39.17 mm, p .0065). A noticeable outlier is mx10, which is significantly taller than mx11 (mx10 CH: 70.98; mx11 CH: 42.98, p .0004). The reason this tooth is an outlier is because Lmx10 of SDSM 12047 is larger (CH: 91.27 mm) than Rmx10 of FMNH PR2081 (CH: 61.04 mm), or Rmx10 of MOR 1125 (CH: 88.82 mm). The tooth does not appear to be anomalous, however, as SDSM 12047 has a number of very large crowns (Supplementary Data 1).

Crown Shape and Carina Morphologies—The mesial maxillary tooth bases are more circular than the distal crowns (Fig. 4A), as in most tyrannosaurids (Brochu, 2002), but few of the adjacent teeth are significantly different from each other. The maxillary teeth become increasingly elongated along the mesial set (mx3 is the most elongated crown in the mouth) and become increasingly ‘squat’ distally (Fig. 4B). The most distal maxillary teeth are roughly equivalent in CHR to ~d9.

In the maxilla, the carinae, which in the premaxilla are situated at the linguomesial and linguodistal corners of the crowns, are in more obvious mesiodistal positions. In the first maxillary teeth, carina morphologies, orientations, and positions all begin to change, becoming increasingly mesiodistally positioned along the tooth row (Fig. 7). By the middle of the row, the teeth have distinctly different shapes than those in the premaxilla, and have carina positions that remain fairly constant to the end of the tooth row.

The change in morphology from pm4 to mx1 is more dramatic than those between mx1 and the rest of the mesial set. Although mx1 might be described as a transitional form between the two tooth types, it is more similar in form to the maxillary than the premaxillary dentition. If the premaxillary crowns are described as ‘incisiform’ sensu Brochu (2002) and Russell (1970), then using this terminology for mx1 (as for *Daspletosaurus* and *Gorgosaurus*; see Carr, 1999; Currie, 2003) in *Tyrannosaurus rex* is clearly inaccurate. The basal long axis of pm4 is roughly labiolingual with respect to the upper jaw and the mesial and distal faces are almost flat (Fig. 8). However, in mx1 the mesial face is narrow and curved (convex rostrally) and the labial and lingual faces are more elongate and flat than in the premaxilla. The carina that is at the linguomesial corner of pm4 is positioned on mx1 such that, in lingual view, its base is at the middle of the lingual face; the carina situated at the linguodistal corner of pm4 is, in labial view, located in the distal third of the labial face (Fig. 8).

As maxillary position increases, what was the linguomesial carina on pm4 becomes increasingly mesially positioned on the lingual face; it is clearly recognizable as the mesial carina by mx2. The linguodistal carina of pm4 simultaneously becomes increasingly distally located on the labiodistal faces of the maxillary teeth. It is recognizable as the distal carina in mx1 (Figs. 9A, B). The second and third maxillary teeth possess the ‘classic’ image

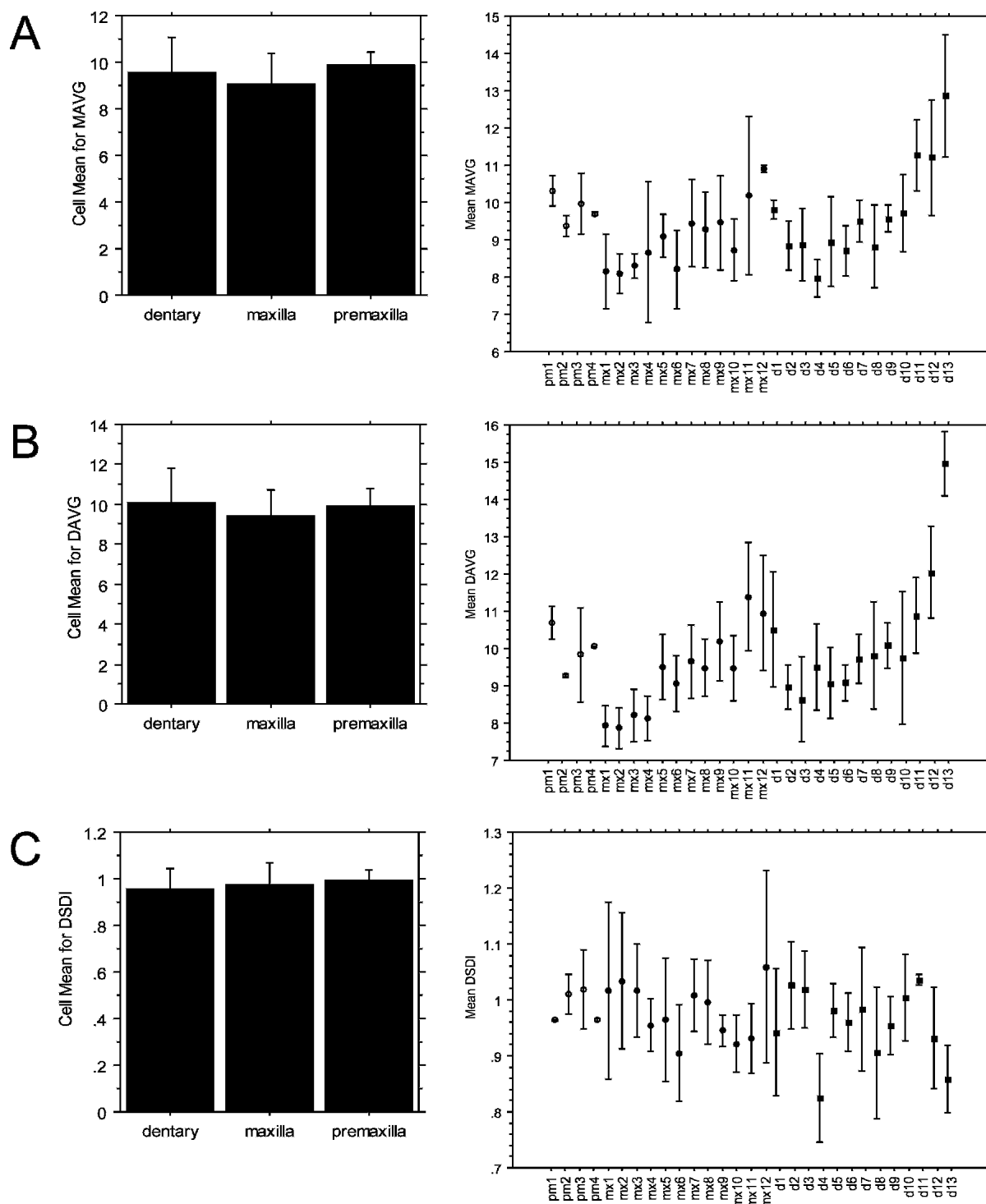


FIGURE 6. Dentine size comparisons and variability profiles, with respect to tooth position, for MAVG (A), DAVG (B), and DSDI (C) of *Tyrannosaurus rex*. See methods for units. See Supplementary Data 1, www.vertpaleo.org/jvp/JVPcontents.html, for data. Error bars equal ± 1 standard deviation.

of crowns of *T. rex* (e.g., FMNH PR2081). The mesial carinae, in mesial view, start at the middle of the apex and curve lingually such that at the base of the crown, they are completely on the lingual sides of the bases. They terminate slightly apical from the crown bases where the distal carinae extend to the bases of the enamel. Similar morphologies occur in *Gorgosaurus* and *Appalachiosaurus* Carr et al., 2005. The mesial carina is variably

placed in mx3. In mesial view, it is located on the lingual side of the apex and largely forms the lingual edge of the mesial face at its terminus ~20 mm apical from the base of the enamel (BHI 3033), or it is more labially placed (AMNH 5027, Fig. 9C).

Distally, crown shapes do not change dramatically except for size and length/width relationships, and the carinae are more parallel with the basal long axes. While the mesial teeth are more

rounded than those distally, the overall shapes of mx5–6 are not that dissimilar from the overall shapes of mx11–12 (Fig. 10). The labiolingual faces of the more mesial teeth (mx4–6) are more rounded (e.g., CM 9380, FMNH PR2081, SDSM 12047), while

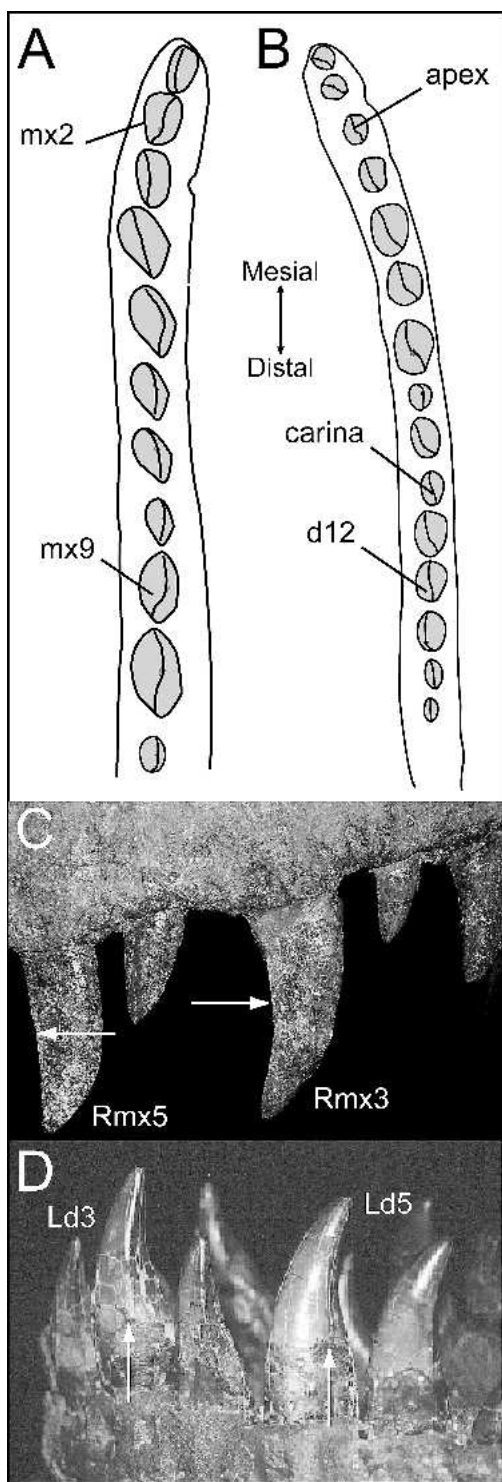


FIGURE 7. Positional variation in carina placement and orientation of *Tyrannosaurus rex*. Right maxilla (A) and left dentary (B) in palatal view (composite photo traces of AMNH 5027). C, the mesial right maxillary dentition of LACM 23844 in labial view (arrows indicate distal carinae, which are forming the distal edges of the labial faces of the teeth by mx3). D, the mesial left dentary dentition of FMNH PR2081 in labial view (arrows indicate distal carinae).

these faces in mx7–8 (e.g., MOR 555, SDSM 12047) are ‘subparallel’ and just slightly convex. The mesial faces are round in all of the teeth (more strongly so in the distal teeth), but the distal faces of the mesial teeth are more rounded than they are distally. In Lmx9 of BHI 3033, the distal face is basically flat and slopes from the labial edge of the face towards the carina (Fig. 10).

In a mesial view of mx4 and mx5 (e.g., AMNH 5027), the mesial carinae begin at the apices and extend basally in the middle or labial thirds of the faces in a slight labial curve, terminating ~20 mm apical from the bases (Fig. 10). In distal view, the distal carinae begin just lingual from the apices and extend basally in the lingual quarters of the distal faces. In mx6, the mesial carina begins at the apex and almost immediately begins to curve lingually. This twist becomes slightly sharper at its base. The carina terminates ~25 mm apical from the base of the enamel. The carina does not ‘fade’ into the mesial face, but rather terminates in a final small denticle. This occurs in all of the observed *T. rex* specimens except for MOR 1125, where several mesial carinae appear to continue past where the denticles terminate (e.g., cf. Lmx2). The mesial carinae in Lmx7–8 of MOR 555 extend basally in the midline of the mesial faces in mesial view; they begin curving lingually ~25 mm basally from the apices (Fig. 10). In Lmx7, this twist is stronger basally and, in mesial view, the carina terminates ~9 mm apically from the base in the lingual quarter of the mesial face. In Lmx6 of BHI 3033, the mesial carina does not appear to have a substantial lingual curve for ~25 mm basally from the apex, although the carina is difficult to observe as this crown is not fully erupted. In both Lmx6 and Lmx7 of MOR 555 and CM 9380, the distal carinae, in distal view, begin at the apices and extend basally in the distal faces, terminating just labial to the midline at the bases. In Lmx7 of MOR 555, the distal carina appears to extend to the enamel base, although poor preservation confounds the observation. The mesial carina of Lmx8 clearly terminates ~22–24 mm from the base of the mesial face. In mesial view, it starts from the apex in the middle of the mesial face and extends basally in the face, but there is a slight lingual curve ~11 mm apically from its terminus. In distal view, the distal carina starts at the apex in the middle of the face and extends basally, curving slightly labially at the base. The labial and lingual faces of mx7–8 are basically flat and parallel to each other. In Lmx9 of BHI 3033, the mesial carina begins at the apex and curves labially toward the base, ending at about the crown midpoint. This labial curve is more distinct in Lmx9 of MOR 555, where the carina extends basally in the middle of the face for ~23 mm before kinking lingually, continuing for ~13 mm and ending. In distal view of Lmx9 in BHI 3033 and Lmx8 of MOR 555, the distal carinae start just labial to the apices and extend basally in the lingual quarters of the faces to the bases of the enamel (Fig. 10). However, in Lmx10 of SDSM 12047, the distal carina is located several mm more labially. In BHI 3033, there is a slight lingual curve that starts at about the crown midpoint and continues to the base. In MOR 555, the curve begins closer to the apex. Distal to mx9, the carinae are roughly aligned with the mesiodistal axes of the crowns, but are not as closely tied to the long axes as they are in some other theropods (e.g., *Deinonychus*).

In contrast to the condition in some theropods (e.g., *Allosaurus*, *Deinonychus*, *Dromaeosaurus*), the mesial maxillary teeth of *T. rex* (e.g., MOR 008, AMNH 5027) are not set in the jaw with their long axes lined up mesiodistally. Instead, there is an angle of ~30° between the crown long axes and the alveolar margin of the maxillae, away from the premaxillary symphysis (Fig. 11). This en echelon tooth emplacement results in the apices not lining up in particular along a mesiodistal line (see discussion). The characteristic occurs in *Acrocanthosaurus* and *Majungatholus*, but does not appear to occur in *Gorgosaurus* or *Daspletosaurus*. It varies within *T. rex*, being more clearly observed in

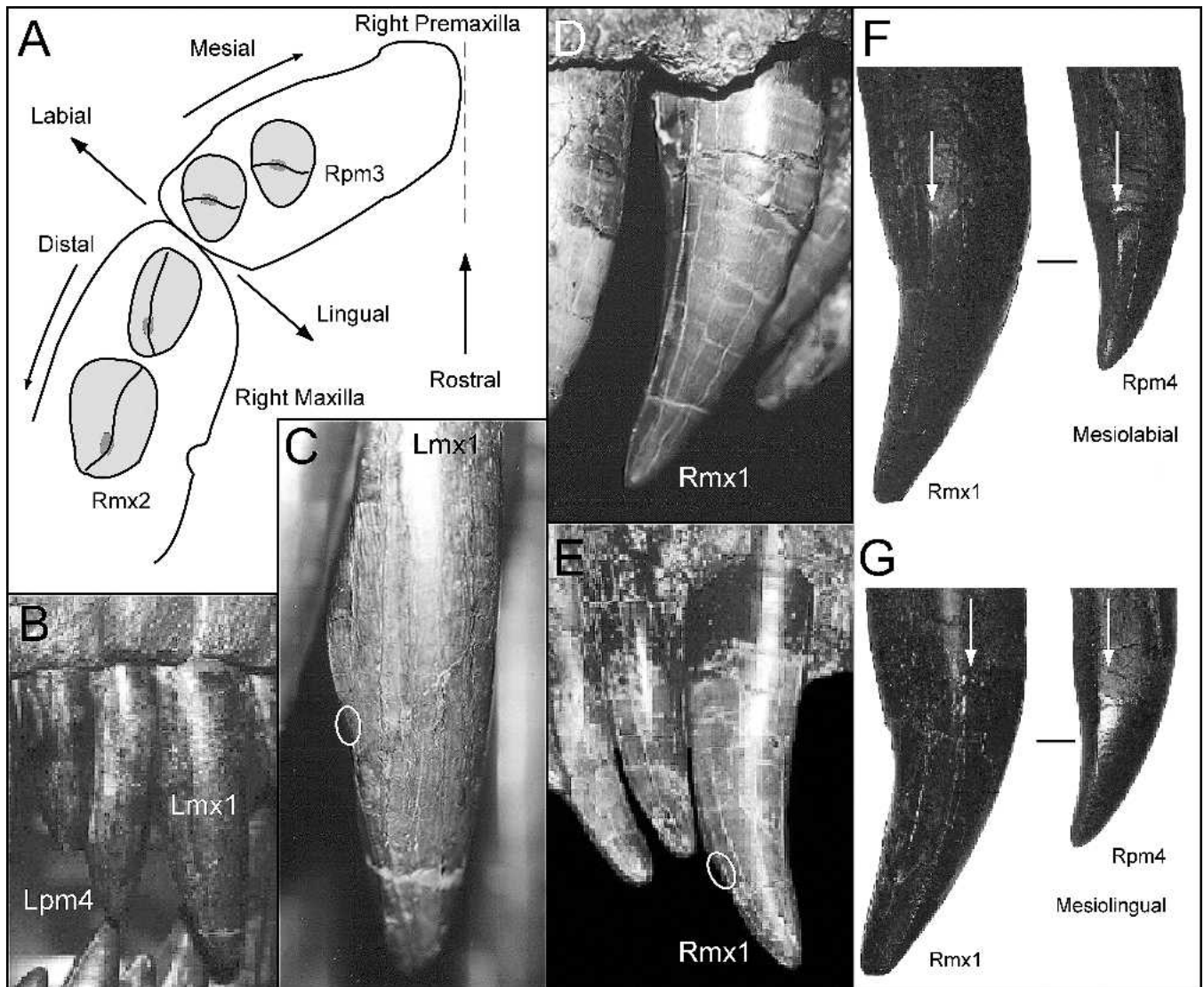


FIGURE 8. Morphologies of pmx4 and mx1 in *Tyrannosaurus rex*. **A**, photo traces of distal right premaxilla and mesial right maxilla in palatal view (AMNH 5027); note differences between the classes. **B**, Lpm4 and Lmx1 (AMNH 5027) in mesiolabial view. **C**, mx1 (AMNH 5027) in mesial view; note the mesial carina visible on the lingual edge (circle). **D**, Rmx1 of FMNH PR2081 in labial view; note sizes of mx1 and pm4, the flattened shape of the lingual face of pm4, and the placement of the carinae (circle). **E**, Rmx1 of FMNH PR2081 in lingual view; note sizes of mx1 and pm4, the flattened shape of the lingual face of pm4, and the placement of the carinae (circle). **F**, Rpm4 and Rmx1 of BHI 3033 in mesiolabial view; note size differences, carina placement (arrows), and the slight increase in mesial curvature in mx1 (scale bars equal 1 cm). **G**, the teeth in mesiolingual view (image reflected).

AMNH 5027 and FMNH PR2081 than in SDSM 12047. It can be seen in the left mesial alveoli of FMNH PR2081 in figure 4a and the CT data of Brochu (2002). Brochu (2002) also reveals that while the tooth bases are angled $\sim 40^\circ$ away from the sagittal plane (in MOR 008 and FMNH PR2081), the crowns themselves twist slightly so as to be more or less in a mesiodistal orientation (seen in Rmx3 and Rmx5 of FMNH PR2081). This is in contrast to the situation in *Majungatholus* and *Acrocanthosaurus*, where the crowns do not twist and the teeth actually angle away from the midline.

Crown Curvature—Distally in the maxilla, apices become increasingly displaced from where they would be located in true cones, accompanied by an increase in curvature (Fig. 4C). Mean crown angle values are fairly constant ($\sim 88^\circ$) in the mesial set (mx1–mx5), although mx5 (87.6°) and mx6 (87.3°) are slightly different. They decrease slightly across the mesial part of the distal set to mx10 (86.6°), and then drop to mx12 (82.3°). The CA

data reflect the moderate increase in mesial curvature in the maxilla and the dramatic increase in the last few teeth. In the distal maxilla, the mesial faces rise with very gentle curves apically from the base (the basal portions of some of the faces are almost straight), to or just apical to the mid crown. Here the slopes become more sharply curved. The first maxillary crown possesses a straighter mesial profile (similar to those of the mesial premaxilla) than do the rest of the mesial-set teeth. Unlike in other taxa, (e.g., *Deinonychus*, *Allosaurus*), the distal profiles become more straightened in the distal maxilla rather than simply increasing in curvature.

Denticles—There is a weak trend in decreasing denticle size along the maxillary tooth row for both carinae (Fig. 6). The trend correlates with the increase in crown size observed across the maxilla and is expected given the relationship between tooth and denticle size (Farlow et al., 1991). Mean densities range from 6.8–13.4/5 mm (MAVG) and from 7.2–13.2/5 mm (DAVG). For

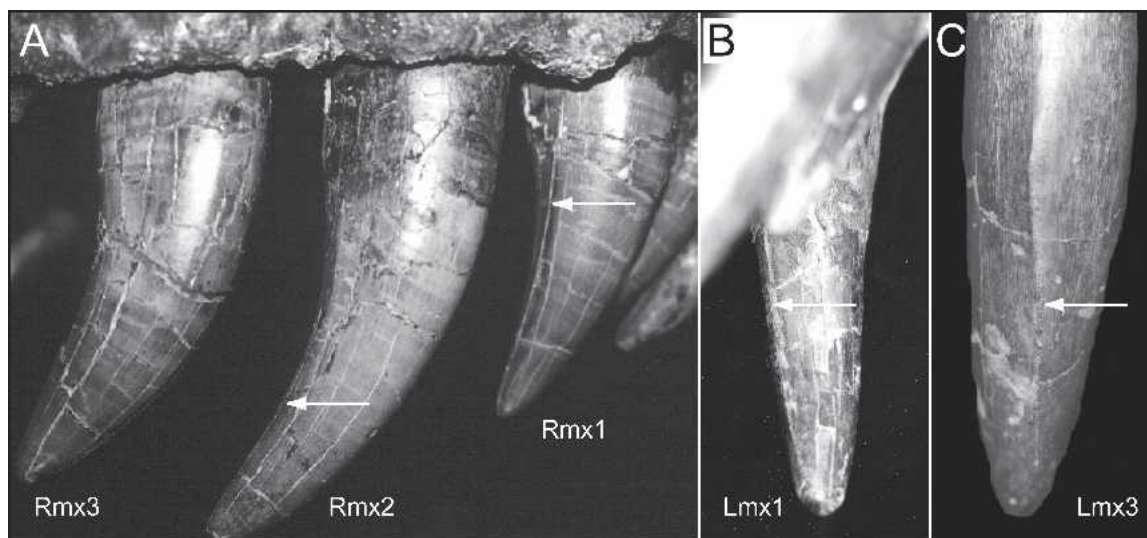


FIGURE 9. Mesial set morphology in *Tyrannosaurus rex*. **A**, Rmx1–3 of FMNH PR2081 in labial view. **B**, Lmx1 of SDSM 12047 in distal view. **C**, Lmx3 of AMNH 5027 in mesial view. Arrows show carinae.

both carinae, position is a significant factor in explaining the observed variation, but there is no significant separation, in either carina, between the mesial and distal sets. Contrary to the reports of Molnar and Carpenter (1989) and Carr and Williamson (2004), there is no significant difference in denticle size between the mesial and distal carinae (MAVG = 9.1/5 mm; DAVG = 9.4/5 mm, $p = .3470$). The DSDI data roughly mirror the MAVG and DAVG numbers (Fig. 6C), but, as in the premaxilla, tooth position only slightly influences DSDI variation in the maxilla.

Tooth position is not a significant factor in MA, MC, or MB variation. The MC and MB data mirror the MAVG data and there is a decrease in MA size mesially. Position within the tooth row is significant in explaining the observed variation in DA, DC, and DB, all of which decrease in size distally.

The Dentary Dentition

There are 12–14 dentary teeth in *T. rex* (Table 2). As in the maxilla, tooth size and shape variation is qualitatively greater than for many theropods (Currie, 1997a, b). There are several distinct morphologies within the dentary class, and it is possible to divide the dentition into three sets on the basis of size and gross morphology: a set containing d1, a mesial dentary set (d2–d4), and a distal dentary set (d5–d14).

Crown Size—The dentary contains very large crowns as well as the smallest in the mouth. Tooth position has a significant effect on the observed variation in size. There is an increase in size from d1 to d4 and then a decrease from ~d5 to d13 (Fig. 2). The first tooth is significantly smaller in terms of CBL, CBW, CH, and AL than the teeth mesial to ~d9 (e.g., d1 CBL = 25.9 mm; d2 CBL = 39.9 mm, $p < .0001$; d9 CBL = 32.56, $p = .0268$). Carr and Williamson (2004) reported that d1 in tyrannosaurids is the smallest tooth in the dentary. This is not the case in *T. rex* (contrary to Carr and Williamson's results, this is also not true for dromaeosaurids) as the last dentary teeth are significantly smaller than d1 (Fig. 2; e.g., d1 CBW = 18.2 mm; d13 CBW = 10.2 mm, $p = .0089$).

The teeth of the mesial dentary set are significantly larger than d1. The CBL difference between d1 and d2 is 14 mm, so although they are similar in morphology and carina orientations (see below), size might be enough to distinguish d2 from d1 (the difference is not obvious in AMNH 5027 but is in FMNH PR2081). It

should also be difficult to confuse the mesial-set teeth with those in the premaxilla as the size and morphologies of the sets are different. In terms of CBL and CBW, d4 is the largest tooth in the dentary. This crown is designated as the last tooth in the mesial set because it marks an inflection point beyond which size decreases to the end of the tooth row in CBL, CBW, and AL (Fig. 2). The fifth tooth is not significantly different from d4 or in some cases d3, but for all size variables, d5 is smaller than d4. There is heterodonty within the distal set, but the changes are subtle and the teeth become increasingly smaller to the end of the tooth row. Distal to d7, the distal set teeth are significantly smaller than those in the mesial set. The thirteenth and fourteenth dentary teeth are the smallest in the mouth of *T. rex* (d12 CBL = 22.29 mm; d13 CBL = 16.53 mm, $p = .0485$).

Crown Shape and Carina Morphologies—Tooth position does not have a significant effect on CBR variation in the dentary and there are no real trends of basal shape across the tooth row (Fig. 4A), although d13 is an outlier that is significantly more lance shaped than the more mesial teeth. There is a trend towards increasingly squat teeth (Fig. 4B) and tooth position is significant for CHR. There is a significant difference in 'squatness' between d1 and the mesial dentary set. The mesial-set teeth exhibit similar degrees of elongation. Distal to d4, the teeth become increasingly 'squat.' The most distal teeth possess significantly lower CHR values than those in the rest of the mouth (d12 = 1.45; d13 = 1.23, $p = .0366$).

As in the maxilla, the location and orientation of the carinae change with position from mesial to distal in the dentary (Fig. 7B, D). Osborn (1912) reported that the basolingual surfaces of the teeth have a pronounced concavity that is wider root apically (sensu Smith and Dodson, 2003) than basally, where it tapers to a foramen for the dental artery. This structure is obvious in some *T. rex* teeth, but it is not always congruent with the dental foramina. Mesially, crown shape is distinct from that of the distal set; d1 in particular resembles the premaxillary class more than the dentary sets (Fig. 12). The labial face of d1 is convex rostrally and the mesial and distal faces are flattened and elongated. However, unlike in the premaxilla, the basal long axis of d1 is mesio-distally oriented. The tooth is more conical than are those in the premaxilla. The lingual face is more rounded than in the premaxilla, although apically it is very similar to that of the premaxillary crowns. The carinae are linguomesially and linguodistally

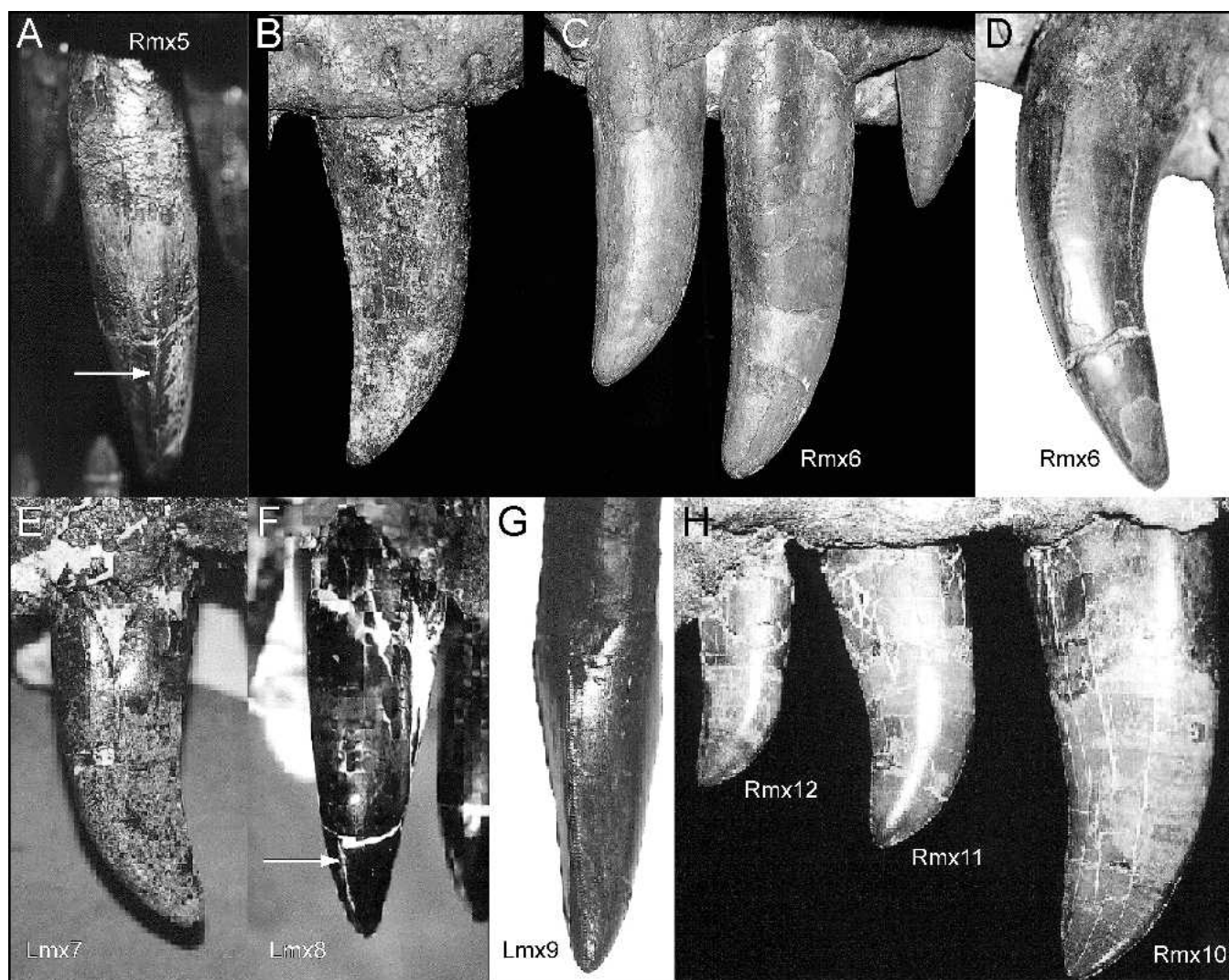


FIGURE 10. Distal set morphology in *Tyrannosaurus rex*. **A**, Rmx5 of AMNH 5027 in mesial view. **B**, Rmx5 of LACM 23844 in labial view. **C**, Lmx5–7 of CM 9380 in lingual view. **D**, Rmx6 of SDSM 12047 in lingual view. **E**, Lmx7 of MOR 555 in labial view. **F**, Lmx8 of MOR 555 in mesial view. **G**, Lmx9 of BHI 3033 in distal view. **H**, Rmx10–12 of FMNH PR2081 in labial view.

positioned, although the bases are more labially positioned than in the premaxilla. Molnar (1978) and Carr and Williamson (2004) noted this general morphology in the putative juvenile specimen of *T. rex*, LACM 28741.

The second crown (the first in the mesial set) is a transitional form between d1 and the more distal dentary teeth (Fig. 13). Osborn (1912) noted correctly that the mesial crowns distal to d1 are morphologically dissimilar from the premaxillary teeth, and recognized that the dentary series changed in a similar manner to the maxilla, with the carinae changing from the labial and lingual surfaces mesially to the mesial and distal surfaces distally. The mesial carina of d2 is positioned mesially as compared to that of d1. It begins at the apex and extends basally along the lingual edge of the mesial face, such that denticles can be seen on the lingual edge in mesial view. The distal carina of d2 remains close to where it is in d1, such that its base is located in the distal quarter of the labial face. By d3, the mesial carina is positioned such that it in mesial view, it begins just lingual to the apex and extends basally in the lingual quarter of the mesial face. The distal carina is located such that its base is in the distal quarter of the labial face, similar to that of d2. Carina orientations in d4 are very similar to d3. The labial faces of the mesial set are almost

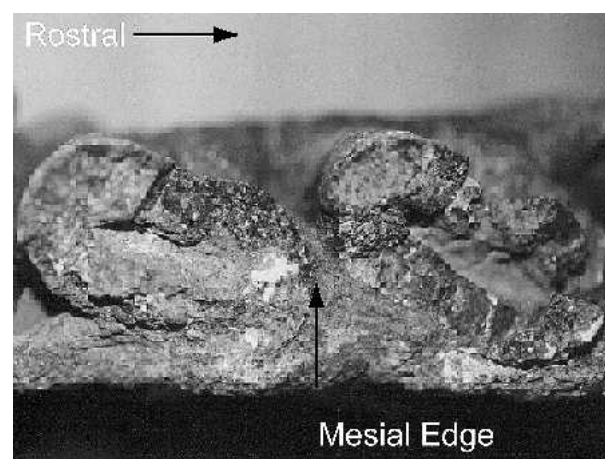


FIGURE 11. Maxillary teeth (?5–7) of *Tyrannosaurus rex* (MOR 008) in apical view; note orientation with respect to lateral side of the bone (crowns are broken; view is of the cross sections of the teeth).

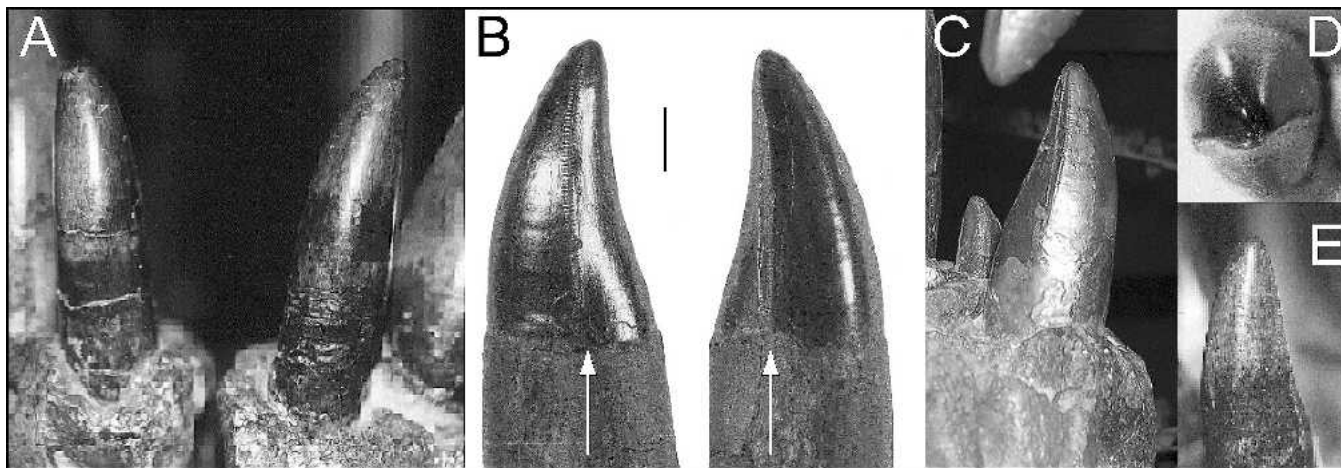


FIGURE 12. Morphology of d1 in *Tyrannosaurus rex*. **A**, first dentary teeth of AMNH 5027 in labial view. **B**, Rd1 of BHI 3033 in mesial and distal views. **C**, Rd1 of CM 9380 in mesial view. **D**, Rd1 of BHI 3033 in occlusal view. **E**, Ld1 of AMNH 5027 in distolabial view.

flat (e.g., BHI 3033, FMNH PR2081, and MOR 008), while the lingual faces are slightly convex.

In the distal set, carina orientations become increasingly mesiodistally aligned, the long axes of which largely parallel the edge of the dentary (Figs. 7B, 14). Mesially in the set (d5–d8), the teeth resemble the mesial maxillary teeth, except that they are narrower. The distal-most teeth (>d12) are different from all other *T. rex* crowns; they are small, very narrow, and have strongly curved mesial curvature profiles and almost straight distal profiles that in some cases (Ld13 of BHI 3033) angle toward the apex. Even in the last few teeth, however, the mesial carinae exhibit a basal lingual twist and the distal carinae are labially placed (e.g., Rd13 of LACM 150167).

As in the maxilla and in *Acrocanthosaurus*, but in contrast to the condition in *Albertosaurus*, *Allosaurus*, and *Gorgosaurus*, the mesial dentary teeth (e.g., MOR 008, AMNH 5027) are not set in the jaw with their long axes lined up mesiodistally. Rather, the crowns are oriented such that there is an angle of $\sim 30^\circ$ between the long axes and the alveolar margin. Thus, the apices do not line up with each other along the tooth row and the surface area the teeth can contact during a bite is greater in *T. rex* than it is in other tyrannosaurids such as *Gorgosaurus* (see discussion).

Crown Curvature—As in the maxilla, curvature increases across the dentary and position is a significant factor in explaining the observed variation (Fig. 4C). The CA for d1 (84.44°) is significantly different from pm1 using CBW, it is not distinct from pm1 in terms of apex displacement ($\text{pm1} = 84.72^\circ$, $p = .7154$). However, pm1 has a more strongly curved mesial profile than does d1 (Fig. 15). As the crowns become more elongated in the mesial dentary, their apices become more centrally positioned and there is a weak trend of increasing CA in the set (Fig. 4C). However, in the distal set, CA values decrease steadily to the end of the row. The last dentary teeth have the most displaced apices in the dentition (d13 CA = 78.17° ; d12 = 82.93° , $p < .0001$).

Denticles—As in the rest of the mouth, denticle sizes in the dentary are reciprocals of crown size, and denticle density increases distally along the tooth row (Fig. 6). Mesial densities range from 7–14.4/5 mm and distal densities range from 7.5–15.7/5 mm; d4 has the largest mesial denticles (7.8/5 mm) and d3 has the largest distal denticles (8.8/5 mm). The distal dentary teeth have the smallest denticles in the entire dentition (d13 DAVG: 14.9/5 mm; d12: 12/5 mm, $p = .0006$). Contrary to Carr and Williamson (2004), there is no significant difference in denticle

size between the mesial and distal carinae (MAVG = 9.6/5 mm; DAVG = 10/5 mm, $p = .5100$). The DSDI data for the dentary (Fig. 6C) exhibit a similar trend to that observed in the maxilla; DSDI values do not increase or decrease substantially along the tooth row.

NON-POSITIONAL VARIATION

Apical Denticles—Carinae can be isolated or can cross the apex as one entity. For theropods with ‘single’ carinae, the denticles can terminate prior to or can cross the apex. This latter condition, apical denticulation, has been described in *Acrocanthosaurus*, *Alectrosaurus* Gilmore, 1933, *Dryptosaurus* Marsh 1877, *Eotyrannus* Hutt et al., 2001, *Neovenator* Hutt et al., 1996, and *Ricardoestesia* Currie et al., 1990, and is considered unusual (see Harris, 1998; Hutt et al., 2001). However, I have observed it in *Majungatholus*, *Allosaurus*, *Carcharodontosaurus*, tyrannosaurids, and dromaeosaurids, a distribution similar to that reported by Currie and Carpenter (2000). I agree with these authors that apical denticulation in and of itself is not a particularly useful character. However, recording whether or not the denticles cross the carinae (with possible taphonomic modification acknowledged) in theropod descriptions is still useful as I suspect that possession of apical denticulation is likely to be the plesiomorphic theropod state, while a lack of apical denticles is the derived condition.

Crown Ornamentation—‘Enamel wrinkles’ are considered diagnostic for carcharodontosaurids (see Stromer, 1931; Sereno et al., 1996; Chure et al., 1999). Evaluating the distribution of the feature is beyond the scope of this paper, but observations made during this study indicate that the distribution of ‘enamel wrinkles’ extends beyond *Carcharodontosaurus* and *Giganotosaurus* Coria and Salgado, 1995, as similar structures occur in tyrannosaurids (including *T. rex*), allosaurids, *Dromaeosaurus* (AMNH 5356), and (very weakly) in *Irritator* (SMNS 58022). They are more strongly developed and exhibit slightly different morphologies in *Carcharodontosaurus* (SGM Din-1) as compared to other theropods, but ‘enamel wrinkles’ (broadly defined) are not restricted to this group, especially as there is no consensus as to what exactly constitutes an ‘enamel wrinkle.’

Split Carinae—This feature and its implications were discussed by Erickson (1995) and will not be restated here. Rather, as Erickson’s (1995) work focused on an assemblage of shed tyrannosaurid teeth, I will simply note the instances of in situ split carinae observed during this study. The first occurs in Rd2

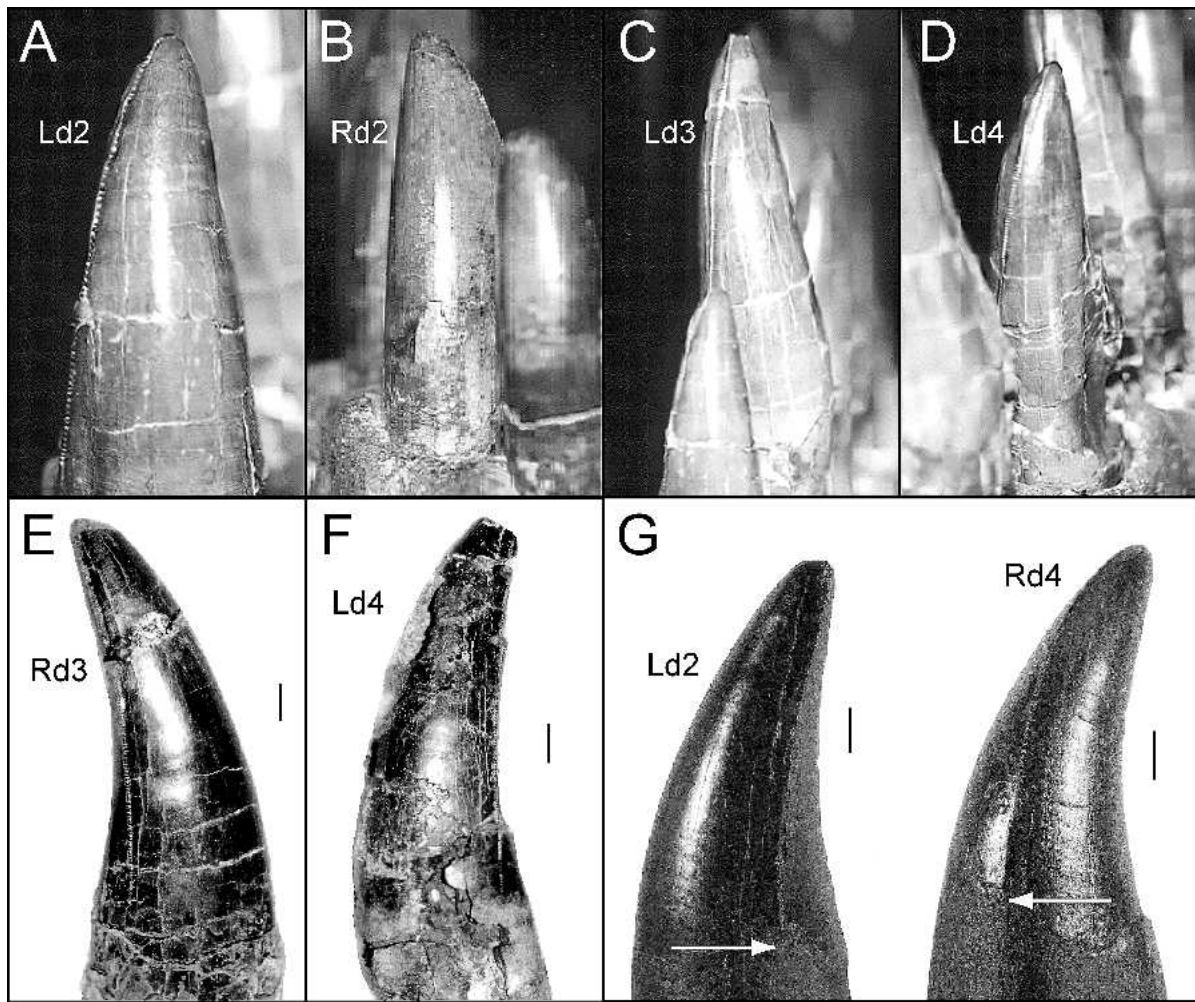


FIGURE 13. Mesial dentary set morphology in *Tyrannosaurus rex*. Ld2 of FMNH PR2081 (A), Rd2 of AMNH 5027 (B), Ld3 (C), and Ld4 (D) of FMNH PR2081, all in mesial view. E, Ld2 and Rd4 of BHI 3033 in labial and lingual views (arrows mark ends of distal (Ld2) and mesial (Rd4) carinae).

of SDSM 12047, where an additional mesial carina occurs on the mesial face. It begins ~12–13 mm from the apex, ~1–2 mm labial of center, and extends down the labial quarter of the face. It is denticulate along its entire length; the denticles are smaller than those on the principal carina (~10/5 mm apically; ~9/5 mm basally). The second occurs in CM 1400, a partial left maxilla from the Lance Formation of Wyoming (see McIntosh, 1981). This bone possesses six complete alveoli and preserves four teeth. The third tooth back from the rostral margin (Lmx3?) has a secondary carina labial to the principal keel apically on the crown. These are the only instances of in situ split carinae in *T. rex* that I have observed. A third possible occurrence exists on the basal margin of the distal carina of Ld2 on BMNH R5863. However, there is a crack in the crown enamel between the two serrated ridges and it is possible that the crack runs through the distal carina, separating it and giving it the appearance of being split.

Denticle Curves—Theropod denticle morphology has recently begun to be addressed (Currie et al., 1990; Slaughter et al., 1994; Baszio, 1997; Holtz, 1998; Holtz et al., 1998). Chisel-shaped denticles are said to be distinctive dromaeosaurid characters (Currie et al., 1990), pointed denticles that hook apically have been cited as characteristic for tyrannosaurids (Currie et al., 1990; Abler, 1992) and for troodontids (Currie, 1987). In reality,

denticle morphology has only been examined at very basic levels (e.g., Currie et al., 1990) and variation in denticle shapes has not yet been examined. The true taxonomic and systematic utility of denticle shapes is currently unknown and applications of these shapes are premature. It might be profitable in the future to mathematically model the curved shapes of denticles as was discussed by Smith et al. (2005) for crown curvature profiles.

DISCUSSION

Teeth of *T. rex* possess several theropod plesiomorphies, including 'sharp' and 'not closely packed' crowns (Gauthier, 1986) with serrated carinae (Holtz, 1998) and significant curvature (Serenio et al., 1998). However, accounting for positional variation, *T. rex* displays features distinct from the teeth of other tyrannosaurids and non-tyrannosaurids that might hold promise for taxonomy and systematics. It is important to assess the distribution of these features within the Theropoda to gauge systematic potential (as is true for non-dental traits), and the strength of the analysis presented here is reduced without detailed comparisons of other dentitions. The discussion must begin somewhere, however, and the length of this article illustrates that the process of accounting for variation in theropod dentitions is involved enough to make the simultaneous study of nu-

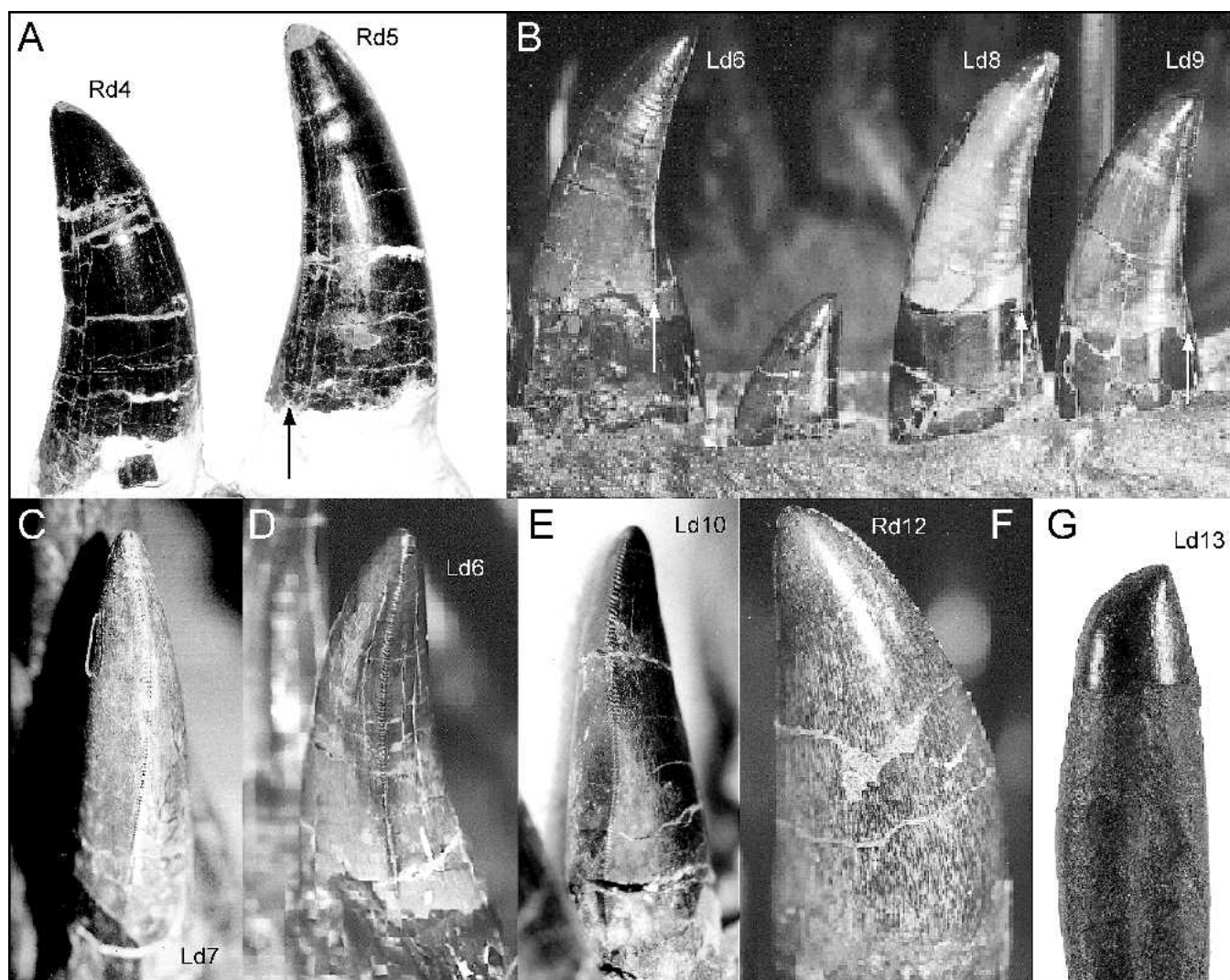


FIGURE 14. Distal dentary set morphology in *Tyrannosaurus rex*. **A**, Rd4–5 of SDSM 12047 in labial view (arrow indicates carina location). **B**, Ld6–9 of FMNH PR2081 in labial view. **C**, Ld7 of BMNH R5863 in mesial view. **D**, Ld6 of FMNH PR2081 in distal view. **E**, Ld10 of SDSM 12047 in mesial view. **F**, Rd12 of AMNH 5027 in labial view. **G**, Ld13 of BHI 3033 in labial view.

merous taxa impractical, especially those with heterodont dentitions. The discussion of putative characters given below is thus a very preliminary step that awaits detailed examinations of the dental arcs of other theropod species.

Placing Teeth in Alveoli

A stepwise discriminant analysis using squared Mahalanobis distances was run to study the prospect of correlating teeth with alveoli. The analysis was run in the same manner as those in Smith et al. (2005) and used AL, CA2, CBL, CBR, CH, CHR, CBW, and DAVG2 (see Smith et al., 2005, for data). The analysis succeeded in correctly classifying 41% of the teeth with the correct alveolus, not a good result. It is possible that sample size (116 valid teeth) is to blame. If so, the result is discouraging as this is a larger sample than is likely to be obtained for most theropods for the foreseeable future. However, results improve when tooth class, rather than position, is used as a factor (Table 3). In this analysis, 67% of the teeth were correlated with the correct bone. As it is difficult to discriminate *T. rex* maxillary and dentary crowns using visual inspection, these results offer some

promise as to the future potential of being able to correlate teeth with alveoli, especially as more data are added to the standard.

Taxonomy and Systematics

Tooth Count—Lamanna (1998) found that premaxillary tooth count varies little within theropod species and is a robust character. The present work and all consulted sources agree that *T. rex* possesses the theropod plesiomorphy of four premaxillary teeth (Holtz, 1998). In general, maxillary and dentary counts are weak characters, except that high counts are synapomorphic for certain taxa, such as ornithomimids and some spinosaurids (but see Holtz, 2001; Currie, 2003a). Tyrannosaurids possess too much intraspecific variation in maxillary and dentary tooth counts for these features to be systematically useful (Lamanna, 1998).

Tooth Emplacement—The en echelon emplacement of crowns that occurs in the lateral dentitions of some theropods (Fig. 11) is intriguing and it is tempting to interpret this feature in a systematic sense. A difference between the trend of the bone and the crowns' basal long axes would result in the cutting of a wider swath during a bite than with teeth that line up along the

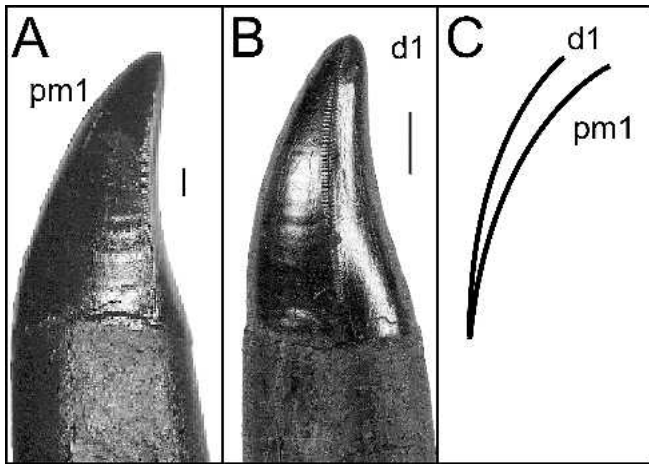


FIGURE 15. Curvature profiles in pm1 and d1 of *Tyrannosaurus rex*. **A**, Lpm1 of BHI 3033 in mesial view. **B**, Ld1 of BHI 3033 in labiodistal view. **C**, Mesial profiles derived from A and B, scaled to the same size. Scale bars equal 1 cm.

trend of the bone, as occurs in some modern reptiles (see Auffenberg, 1981). This wider swath might serve to increase the efficiency with which a theropod could tear meat from a prey animal and as such there is likely to be a strong functional aspect to this feature. The en echelon emplacement of lateral teeth appears to be restricted to certain theropods and might represent a derived condition. The distribution of this feature within the Theropoda is curious, however (e.g., *Acrocanthosaurus*, *Giganotosaurus*, *Majungatholus*, *T. rex*), and warrants additional study.

Tooth Size—Dental size features are not common in theropod phylogenetic analyses. Indeed, basal width is the only common theropod tooth size character (narrow crown bases are considered plesiomorphic for the Theropoda, Holtz, 2001). While size features must be handled carefully if they are to be examined in a systematic light, *T. rex* crowns are generally so much larger than those of other theropods in terms of CBL and CH that these features might be useful if compared with other metrics (e.g., limb lengths, Currie, 1998). Such appears to be the case for CBW. Although teeth of *Carcharodontosaurus* are similar in size to teeth of *T. rex* (Figs. 16A, C, D), *T. rex* crowns are substantially wider (Fig. 16B). In fact, *T. rex* might well have the widest teeth of any theropod, a feature affected less by position than some of the other variables (Fig. 2). Large basal width thus might ultimately prove to be a viable autapomorphy of *Tyrannosaurus*. Holtz (2001) erected a similar character (79: incassate crowns: cross section greater than 60% wide labiolingually as long mesiodistally). In examining the data here, Holtz's character (79) holds up for *T. rex* and *Daspletosaurus*, but is not robust for *Gorgosaurus*. Currie et al. (2003) discounted Holtz's character 79 with the argument that base width is allometric and juvenile

tyrannosaurids should possess ziphodont 'lateral' teeth. This is entirely possible, but Currie et al. (2003) did not support the hypothesis. There was no discussion of the data nor were juvenile crowns identified within the dataset. Although postulated juvenile crowns identified as cf. *T. rex* are known (pers. obs.; see also Currie et al., 1990), none of these has been conclusively shown to pertain to *T. rex* because there are currently no proven juvenile skulls of *T. rex*. For *T. rex* at least, the dentition of which differs from other tyrannosaurids in several ways, the lack of definitive juvenile data makes hypotheses regarding the 'juvenile condition' of the teeth of this animal speculative. The spread of the data reported by Currie et al. (2003:fig. 1) does not demonstrate that juvenile tyrannosaurids have ziphodont teeth, nor does it demonstrate that *T. rex* lacks a distinct CBW condition (various taxa possess aspects of their teeth that depart from clean linear relationships, see Farlow et al., 1991; Holtz et al., 1998).

Carr and Williamson (2004), Carr et al. (2005), and Currie (2003a) reported that a 'small' mx1 is a tyrannosaurid character. Qualitatively, mx1 in *Daspletosaurus* and *Gorgosaurus* is smaller than the mesial maxillary dentition (see Carr, 1999; Currie, 2003a). In *T. rex*, however, although mx1 is the smallest crown in the mesial maxillary set, it is not 'small' with respect to the rest of the dentition. Indeed, mx1 is significantly larger than most of the maxillary teeth and almost the entire dentary class (Fig. 2), a feature recognized by Osborn (1912). A 'small mx1' is not a synapomorphy of the Tyrannosauridae, nor does it unite the Tyrannosaurinae sensu Currie (2003b) as the condition occurs in *Daspletosaurus*, but not in *T. rex* or in *Tarbosaurus*; this merits investigation given the relationships recovered by Holtz (2001) versus those obtained by Currie et al. (2003). Also intriguing is the fact that CMNH 7541 appears to possess a 'small mx1.' If additional material of '*Nanotyrannus*' continues to support the possession of this feature, it might have implications for the taxonomic validity of this taxon. LACM 12471 also possesses a 'small mx1,' which might have implications for the hypothesis of Carr and Williamson (2004) that this specimen represents a juvenile *T. rex*. Even if tooth size in the maxilla of *T. rex* increases with positive allometry (Currie, 2003b), there is little reason to believe that mx1 would respond differently during growth than the rest of the maxillary class, especially as it is possible that theropod teeth exhibit small amounts of ontogenetic change (see Currie et al., 1990). As such, given the normal caveats related to sample size, the disproportionately small sizes of mx1 in some tyrannosaurids are probably real features; while not a tyrannosaurid synapomorphy, it might still be useful in helping to recover relationships within the clade.

Carr and Williamson (2004) reported that d1 in tyrannosaurids is 'subconical' in shape and is the smallest tooth in the dentary. Their precise definition of 'subconical' is difficult to ascertain, but as discussed above, the morphology of d1 in *T. rex* is certainly different from the rest of the dentary teeth and indeed is similar to the premaxillary dentition. However, although d1 is similar in size to d11 (Fig. 2), it is significantly larger than the distal teeth of both the dentary and the maxilla (d12–d14; mx12). For at least *T. rex*, then, a 'small' d1 is not a viable character.

Tooth Shape—'Incisiform' premaxillary crowns with linguomesially and linguodistally placed carinae are generally considered to be derived for tyrannosaurids (see Carpenter, 1982; Bakker et al., 1988; Molnar and Carpenter, 1989; Chandler, 1990; Currie et al., 1990; Abler, 1992; Farlow and Brinkman, 1994; Carr, 1999; Carr and Williamson, 2000; Sankey, 2001; Carr and Williamson, 2004). The condition is real, although some other theropods (e.g., dromaeosaurids) also possess premaxillary features that are similar to what occurs in tyrannosaurids (pers. obs.; see also Molnar, 1978; Molnar and Carpenter, 1989; Holtz, 1998). There might be an alternative to coding premaxillary crowns as simply "D-shaped in cross section," to better distinguish the tyrannosaurid condition. In contrast to other theropods, tyranno-

TABLE 3. Classification results for *T. rex* tooth/bone DFA. 67% of original group cases correctly classified.

Actual	Predicted			Total
	Premaxilla	Maxilla	Dentary	
Premaxilla <i>n</i>	8	0	1	9
Maxilla	10	27	12	49
Dentary	5	10	42	57
Premaxilla %	88.8	0	11.1	100
Maxilla	20.4	55.1	24.5	100
Dentary	8.8	17.5	73.7	100

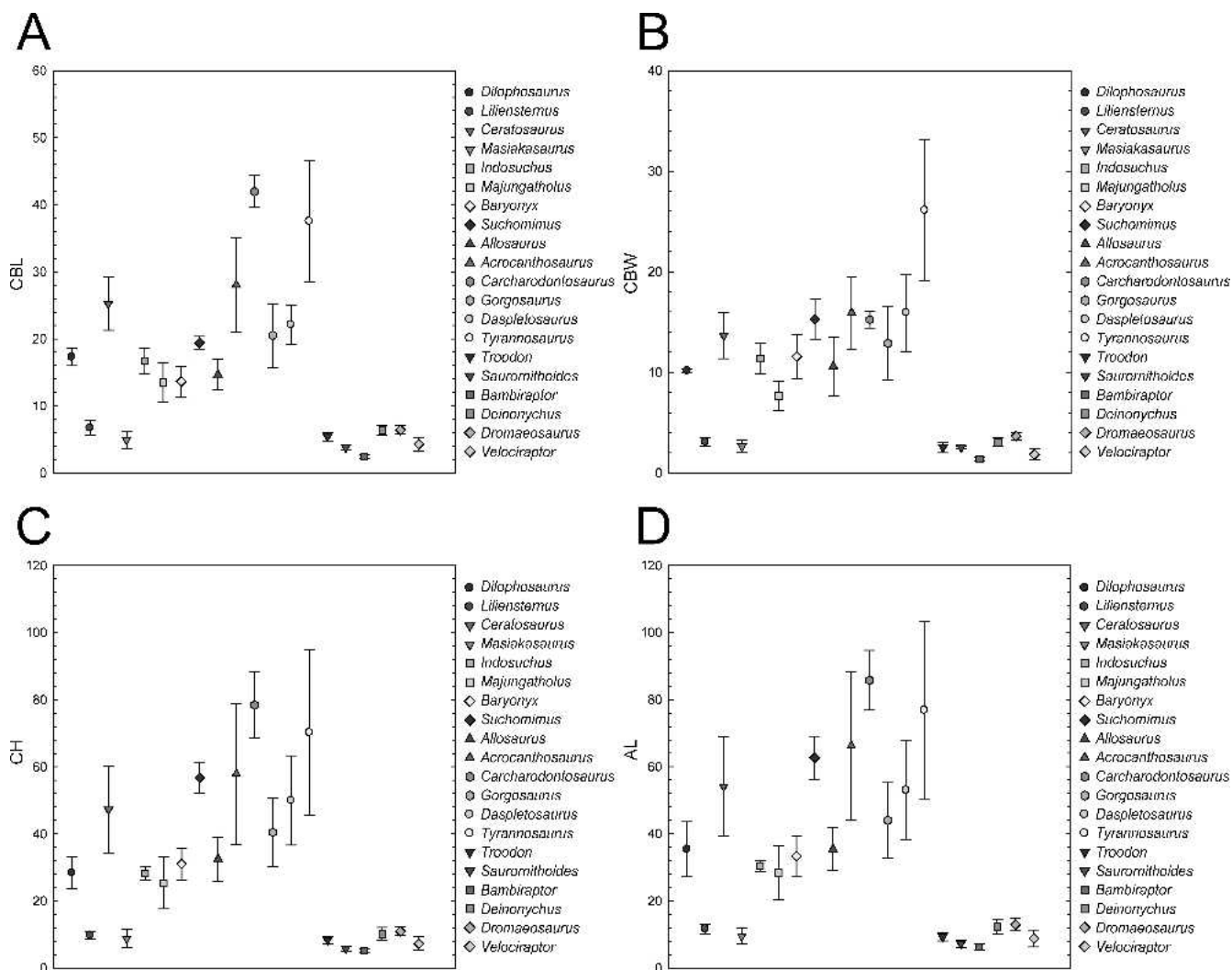


FIGURE 16. Between-taxon comparisons of CBL (A), CBW (B), CH (C), and AL (D) for the theropods examined in this study (data from Smith et al., in press). Units are mm. Error bars equal ± 1 standard deviation.

saurid premaxillary basal long axes are labiolingually oriented, with carinae that are positioned at the linguomesial and linguo-distal corners of the crown. In the premaxillary dentitions of *Allosaurus* and some other taxa, the long axes are not strictly labiolingual and the placement of the carinae is more complicated. As such, tyrannosaurid premaxillary mesiodistal axes are distinctly shorter than those of other theropods; this is a derived condition of the clade (see Fig. 5).

As with crown size, an 'incisiform' mx1 has been described as a tyrannosaurid synapomorphy (Carr, 1999; Currie, 2003a; Carr and Williamson, 2004), occurring in *Gorgosaurus* and *Daspletosaurus* as well as in problematic specimens such as LACM 28471 and FMNH PR2211 (e.g., Molnar, 1978; Carr and Williamson, 2004). However, the premaxillary teeth of *T. rex* and other tyrannosaurids have also been referred to as 'incisiform' in shape (e.g., Russell, 1970; Holtz, 1998; Brochu, 2002). In *T. rex*, mx1 is morphologically distinct from the more distal teeth and from the premaxillary class. The difference in shape is more dramatic between mx1 and the premaxillary class than it is between mx1 and the rest of the maxillary series; mx1 does not possess the same morphology as the premaxillary crowns and the term incisiform cannot be used in the same sense for both pm4 and mx1 in *T. rex*. The long axis of mx1 is mesiodistally oriented and is longer than

the labiolingual axis. The mesial carina extends down the lingual side of the mesial face, which is the homologue to the labial face in the premaxilla. This is not the morphology of mx1 in *Daspletosaurus* or in *Gorgosaurus* and it is distinctly different from the premaxillary condition in *T. rex*. I would argue that there is no single good term for the morphology of mx1 in *T. rex* and that this crown is best described as a transitional form between the premaxillary and the maxillary classes, but one that is decidedly more similar to the maxillary condition. Using 'incisiform' in the same sense for both morphologies is not appropriate; if an 'incisiform' mx1 occurs in *Gorgosaurus* and *Daspletosaurus*, then the condition that actually occurs in *T. rex* is a lack of an incisiform mx1. CMNH 7541, the holotype of *Nanotyrannus*, and LACM 28471 both possess an 'incisiform' mx1 sensu Carr (1999). If 'incisiform' is describing the same morphologies in these non-*T. rex* taxa, then the presence of an 'incisiform' mx1 in CMNH 7541 and LACM 28471 might argue for the distinction of these specimens from *T. rex* and against the juvenile *T. rex* hypotheses advocated by Carr (1999) and Carr and Williamson (2004); this would be curious because the evidence offered by these authors is very compelling.

Carina Lengths—In *T. rex*, the mesial carinae terminate above the crown bases and the distal carinae extend to the bases.

Currie and Dong (2001) reported that the mesial carinae of maxillary teeth extend to the crown bases, but the results presented here refute this hypothesis. Shortened maxillary carinae occur in several theropods (e.g., *Gorgosaurus*, *Acrocanthosaurus*). Carr and Williamson (2004) reported that this condition is typical of tyrannosaurids except *Daspletosaurus*. In *T. rex* it is possible to interpret this feature as a trend of decreasing mesial carina length along the maxillary tooth row; in the distal crowns the mesial carinae terminate ~25 mm above the bases of the enamel. Carina length cannot be used to discriminate a maxillary crown versus one from the dentary, but the fact that some theropods do not appear to possess shortened maxillary carinae (e.g., *Velociraptor*) suggests that this feature holds some taxonomic utility.

Denticles—Since denticle and tooth sizes generally scale together (Chandler, 1990; Farlow et al., 1991; Baszio, 1997), denticle size would seem unlikely to be useful in taxonomy or systematics. However, few tests have been done and denticle sizes are occasionally considered to be taxonomically diagnostic (Molnar and Carpenter, 1989). Chandler (1990) reported that the taxonomic value of serration densities had not been assessed prior to her work because of a lack of diagnostic specimens (Carr, 1999, and I have had similar problems). Assessing the utility of denticles has been further hampered because existing published data are often calculated from a single tooth or as an average of several crowns (e.g., Barsbold, 1983; Currie, 1995;

Azuma and Currie, 2000; Currie and Carpenter, 2000; Hutt et al., 2001). There is sometimes no distinction made concerning from which carina or even which tooth measurements come (e.g., Barsbold, 1983; Hurum and Sabath, 2003). Chandler's (1990) lamentation over a lack of data reflected the additional problem that denticle densities have virtually never been reported in such a way as to facilitate a detailed examination of their variability.

Denticle sizes alone do a poor job of discriminating most theropods (Figs. 17A, B). Rauhut and Werner (1995) devised DSDI to improve this situation, but the results are mixed (Fig. 17C). It discriminates poorly overall, but *Deinonychus* is significantly different from *Dromaeosaurus*, two taxa with otherwise very similar teeth (see Currie et al., 1990). This is mostly due to differences in MAVG between these taxa. There are other potentially useful tooth and denticle relationships as well. Troodontids and dromaeosaurids have derived teeth (Holtz, 1998, 2001) with significantly larger distal than mesial denticles (contrary to Carr and Williamson [2000; 2004], this is not typical of tyrannosaurids, at least where *T. rex* is concerned) and some spinosaurids have unusually small denticles for the size of the teeth. DAVG and DSDI values do not illustrate these characteristics well, but some resolution comes from using the size corrected DAVG2 (Fig. 17D). Mean DAVG2 values below ~.5 might be significant for troodontids and above .5 might be a synapomorphy for baryonychines. A tooth/denticle size index might thus

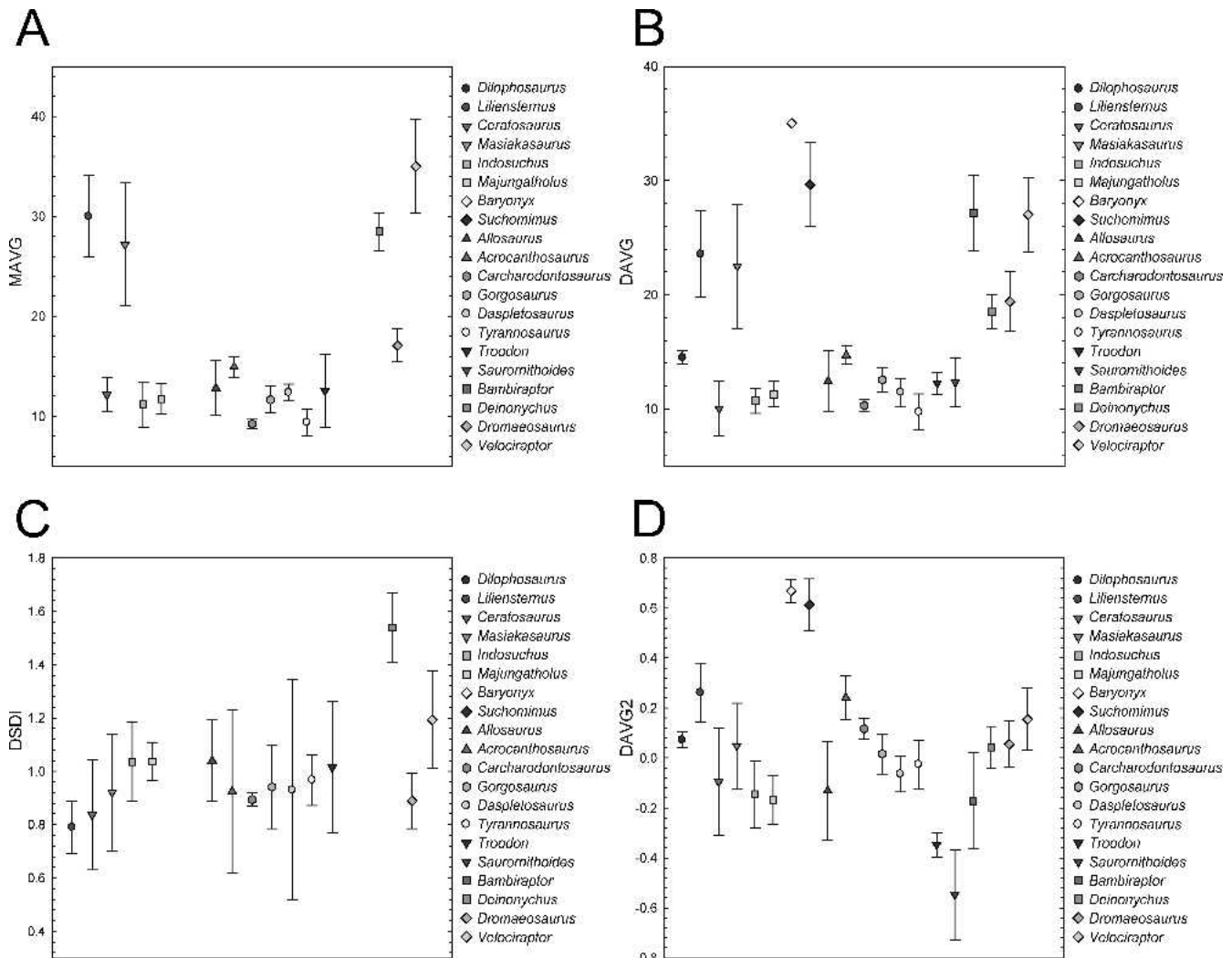


FIGURE 17. Between-taxon comparisons of MAVG (A), DAVG (B), DSDI (C), and DAVG2 (D) for the theropods examined in this study (data from Smith et al., in press). See methods for units. Error bars equal ± 1 standard deviation.

generate a useful theropod character. Although devising this is beyond the scope of this paper, the concept has been qualitatively discussed previously by Sereno et al. (1998) and was explored by Farlow et al. (1991). Denticle size should be explored further.

Summary

Theropod teeth are simple structures, but this work has shown that there can be useful information contained within theropod dentitions if they are studied in detail, by combining qualitative descriptions with quantitative methods. With the dental anatomy and variation of a common theropod documented, we might ultimately expect additional systematic information to come from teeth. Also, a standard now exists against which to compare putative teeth of *T. rex*. It should now be possible to examine assemblages of isolated crowns from Upper Cretaceous rocks in western North America and identify teeth of *T. rex* within these assemblages. Descriptions of other dentitions should facilitate the inclusion in theropod phylogenetic analyses of additional dental information, facilitate the taxonomic identification of isolated teeth, and aid in assessing the validity of 'tooth taxa,' benefiting all biogeographical and paleoecological research conducted in terrestrial Mesozoic rocks.

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