Variation in premaxillary tooth count and a developmental abnormality in a tyrannosaurid dinosaur

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Premaxillary tooth count tends to be stable amongst toothed dinosaurs, and most theropods have four teeth in each premaxilla. Only one case of bilaterally asymmetric variation is known in theropod premaxillary dentition, and there is no record of ontogenetic or individual variation in premaxillary tooth count. Based on these observations, a tyrannosaurid left premaxilla with three teeth (TMP 2007.20.124) is an interesting deviation and represents an unusual individual of *Daspletosaurus* sp. with a developmental abnormality. The lower number of teeth is coupled with relatively larger alveoli, each of which is capable of hosting a larger than normal tooth. This indicates that tooth size and dental count vary inversely, and instances of reduction in tooth count may arise from selection for increased tooth size. On the other hand, the conservative number of premaxillary teeth in most theropods implies strong developmental constraints and a functional trade-off between the dimensions of the premaxillary alveolar margin and the size of the teeth. In light of recent advances in the study of tooth morphogenesis, tooth count is a function of two parameters: dimensions of an odontogenic field for a tooth series, and dimensions of tooth positions. A probable developmental cause for the low tooth count of TMP 2007.20.124 is that the dimensions of the alveoli expanded by approximately a third during tooth morphogenesis. Numerical traits such as tooth count are difficult to treat in a phylogenetic analysis. When formulating a phylogenetic character, a potential alternative to simply counting is to rely on the morphological signature for developmental parameters that control the number of the element in question.

Key words: Dinosauria, Theropoda, Tyrannosauridae, tooth count, developmental regulation, Dinosaur Park Formation, Alberta, Canada.

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Introduction

Premaxillary tooth count is remarkably stable amongst toothed theropod dinosaurs, and an overwhelming majority of taxa have four teeth in each premaxilla. There are only six exceptions to this rule. *Pelecanimimus* and spinosauroids have six or seven premaxillary teeth (Perez-Moreno et al. 1994; Charig and Milner 1997; Rauhut 2003; Dal Sasso et al. 2005). *Allosaurus* and *Neovenator* each have five premaxillary teeth (Gilmore 1920; Madsen 1976; Hutt et al. 1996), whereas *Ceratosaurus* is unique in having just three (Gilmore 1920; Madsen and Welles 2000). *Torvosaurus* is also previously reported to have only three premaxillary teeth on each side (Galton and Jensen 1979), but it has the fourth tooth, which is pathological and covered by a rugose excrescence of bone (Britt 1991; Roger Benson personal communication 2009). In almost all theropods, there is no known individual or bilateral variation in the number of premaxillary teeth. An exception is the holotype of *Baryonyx*, which has six premaxillary teeth on the left side, and seven on the other (Charig and Milner 1997). No theropod is known to increase or decrease the number of premaxillary teeth in ontogeny, although most theropod taxa lack ontogenetic series of specimens. Amongst coelurosaurs with teeth, the premaxillary tooth count of four is universal, with the exception of the unusual *Pelecanimimus*. Tooth count does vary in maxillae and dentaries, notably in tyrannosaurids, both individually and bilaterally (Currie 2003a). These variations in tyrannosaurids most likely represent developmental plasticity near the back end of the tooth rows, but this is not the case in the front part in proximity of the premaxilla (rationale for this in Discussion).

Premaxillary tooth count is similarly stable in sauropods (Table 1). The count is universally four amongst sauropods, even in the sauropod *Nigersaurus* with its highly modified skull and dentition in which the dental battery houses more than five hundred teeth (Sereno et al. 2007). Because the tooth count is variable amongst prosauropods, the conservation of four premaxillary teeth is either retention of the presiomorphic archosaur condition or an independently acquired trait. The latter hypothesis is dependent on the paraphyly of prosauro-

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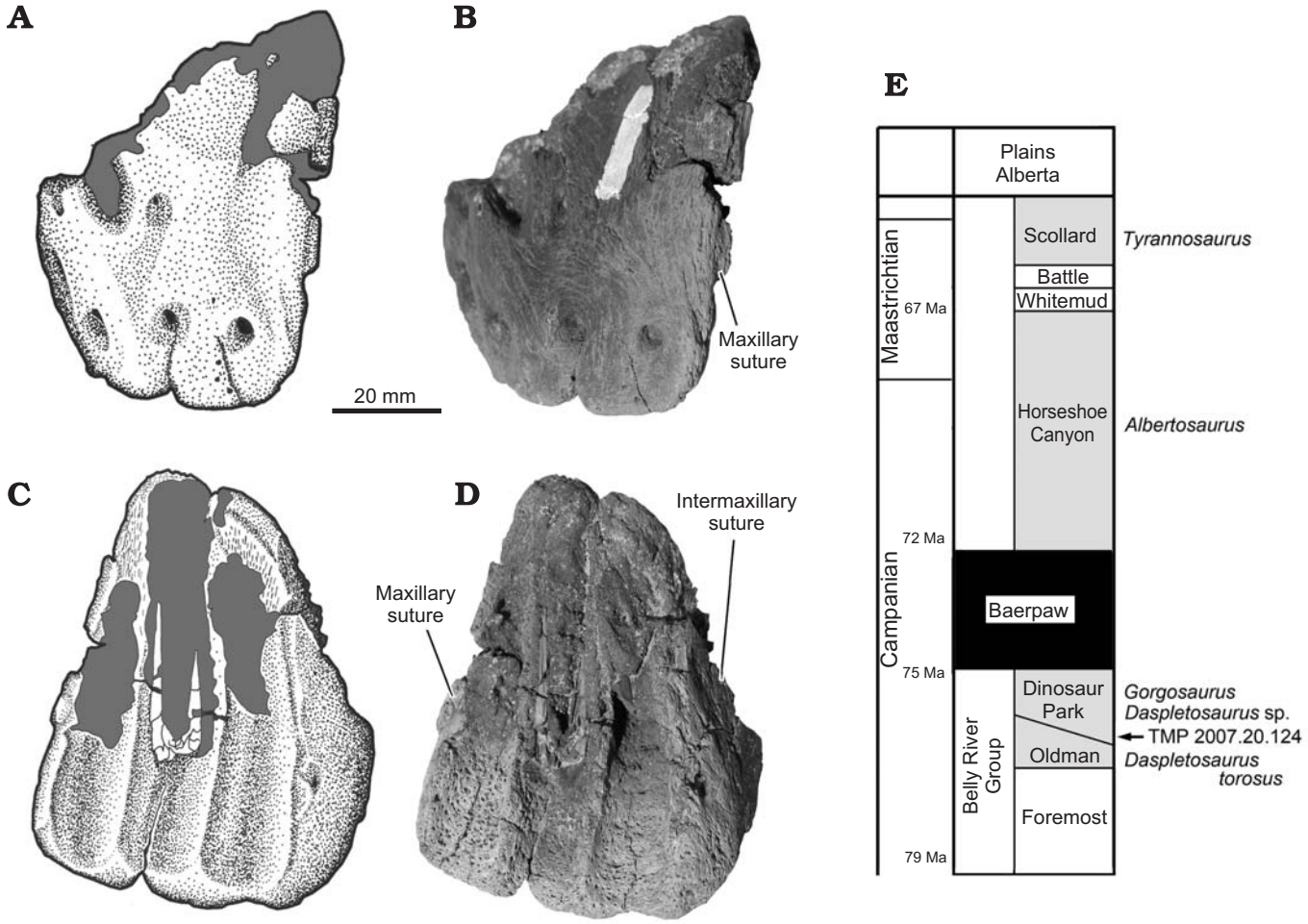

Fig. 1. **A**–**D**. A left partial tyrannosaurid premaxilla with three alveoli, from the Dinosaur Park Formation (Campanian), Alberta, Canada; TMP 2007.124.20; in lateral (**A**, **B**) and posteromedial (**C**, **D**) views; illustrations (**A**, **C**) and photographs (**B**, **D**). **E**. Stratigraphic column showing succession of tyrannosaurids during the Upper Cretaceous of Alberta, Canada. Shaded units indicate occurrence of tyrannosaurids identifiable down to generic level.

pods. Ornithischians repeatedly evolved edentulous premaxillae that are correlated with the presence of extensive beaks. The tooth count is more variable across clades, but an important trend in the currently available data is that the lack of premaxillary teeth in stegosaurs, ankylosaurs, iguanodonts and ceratopsids is not preceded by sequential loss. This is also true for the lineages of edentulous theropods (e.g., ornithomimosaurs and oviraptorids). In summary, premaxillary tooth count is relatively stable within major clades of dinosaurs, regardless of a wide variety of snout morphology. This conservatism suggests that premaxillary tooth count in dinosaurs is a trait under strong developmental regulation.

Based on these observations, a left tyrannosaurid premaxilla with three alveoli (TMP 2007.20.124) is an interesting deviation. This provides the first evidence that the premaxillary tooth count varies in tyrannosaurids, and a second exception from the four-tooth "rule" in coelurosaurs in addition to the unusual *Pelecanimimus*. It is common across vertebrates that tooth count morphologically distinguishes species from one another. Therefore, plasticity in tooth count provides an opportunity to understand the developmental background for discrete morphological variation. This paper addresses the developmental and functional implications of three premaxillary teeth in tyrannosaurids and explores the developmental mechanisms that may account for tooth count variation.

Institutional abbreviation.—CMNH, Cleveland Museum of Natural History, Cleveland, Ohio, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

Systematic palaeontology

Theropoda Marsh, 1881
Coelurosauria von Huene, 1914
Tyrannosauridae Osborn, 1906
Genus *Daspletosaurus* Russell, 1970
cf. *Daspletosaurus* sp.
Fig. 1.

Material.—TMP 2007.20.124, a partial left premaxilla.

Description.—TMP 2007.20.124 is a left tyrannosaurid premaxilla, based on the angle between the alveolar margin and

Table 1. Summary of premaxillary tooth count in dinosaurs. The tooth count of four is independently conserved in theropods and sauropods. Ornithischians repeatedly evolved edentulous premaxillae. The ornithischians with premaxillary teeth tend to lack alveoli in the anterior part of the element where kelatinous sheath form a beak ("partly" in the "edentulous" column). There is no positive evidence for sequential loss of teeth into edentulous premaxilla.

Clade	Tooth count	Note	Edentulous	Sources
Theropoda	3–7 or 0	majority have four premaxillary teeth	partly or entirely	Cited in text
Prosauropoda	3–6	four or five in most taxa; 5–6 in *Plateosaurus*	–	Galton and Upchurch (2004a)
Sauropoda	4	all sauropods have four	–	Upchurch et al. (2004); Sereno et al. (2007)
Basal Ornithischia	6	the count based on *Lesothosaurus*	partly	Sereno (1991)
Basal Thyreophora	5	the count based on *Emausaurus* and *Scelidosaurus*	partly	Norman et al. (2004)
Stegosauria	7 or 0	*Huayangosaurus* (7)	partly or entirely	Sereno and Dong (1992); Galton and Upchurch (2004b)
Ankylosauria	8, 6, or 0	*Silvisaurus* (8), *Cedarpelta* (6), *Sauropelta*, and *Struthiosaurus*	partly or entirely	Nopcsa (1929); Eaton (1960); Coombs (1971); Carpenter et al. (2001)
Basal Ornithopoda	5, 3 or 2	five in most taxa; 3 in *Heterodontosaurus*, and 2–3 in *Abrictosaurus*	partly	Galton (1974); Weishampel and Witmer (1990); Norman et al. (2004)
Iguanodontia	0	all with edentulous premaxilla	entirely	Norman (2004); Horner et al. (2004)
Pachycephalosauria	3	three where premaxilla is known	partly	Maryańska et al. (2004)
Ceratopsia	3, 2, or 0	*Archaeoceratops*, *Liaoceratops*, and *Yinlong* (3); *Protoceratops* (2)	partly or entirely	Brown and Schlaikjer (1940); Dong and Azuma (1997); Xu et al. (2002, 2006)

Table 2. Measurements on and proportions of the tyrannosaurid premaxillae stored at TMP, not including the specimens on display. Arc length was measured by a tape measure, and the others were by a caliper. All measurements in mm. Abbreviations: A1, mesiodistal diameter of first alveolus; A2, mesiodistal diameter of second alveolus; A3, mesiodistal diameter of third alveolus; A4, mesiodistal diameter of fourth alveolus; ACL, arc length (outside the curvature) of alveolar margin; AM, mean mesiodistal alveolus diameter; A/ACL, sum of mesiodistal alveolar diameters divided by the arc length.

Taxon	Specimen number	ACL	A1	A2	A3	A4	AM	AM/ACL
Gorgosaurus libratus	TMP 2005.12.69	36	7.1	6.65	6.75	7.25	6.94	0.193
Daspletosaurus sp.	TMP 1994.143.1	42	–	8.65	6.4	–	7.53	0.179
Gorgosaurus libratus	TMP 1992.36.1014	50.5	11	10.5	–	–	10.75	0.213
Gorgosaurus libratus	TMP 1999.33.1	52	13.8	8	12.6	10.7	11.28	0.217
Gorgosaurus libratus	TMP 2005.9.9	53	13.9	9.55	10.55	8.5	10.63	0.2
cf. *Daspletosaurus* sp.	TMP 2007.20.124	55	14.45	13.45	11.4	–	13.1	0.238
Tarbosaurus bataar	TMP 2000.50.5	57	9.7	10.5	10.35	13.9	11.11	0.195
Gorgosaurus libratus	TMP 1986.36.116	60	11.75	10.5	10.35	11.2	10.95	0.183
Daspletosaurus sp.	TMP 1985.62.1	71	15.45	14.2	16	13.7	14.84	0.209
Daspletosaurus torosus	TMP 2001.36.1	75	13	14	12.5	12.15	12.91	0.172
Daspletosaurus sp.	TMP 1992.36.636	76	14.7	15.7	14.8	15.6	15.2	0.2
Daspletosaurus torosus	TMP 2001.36.1	78	13.7	13.8	12	12.8	13.08	0.168

the interpremaxillary suture, which is more than 50° (Fig. 1). The angle is 60°, and is comparable to that of immature tyrannosaurines (63° in TMP 1994.143.1 *Daspletosaurus* sp.), but larger than that of albertosaurines (35° and 47° in TMP 1991.36.500 and TMP 1999.33.1, *Gorgosaurus libratus*). Because of abrasion, it lacks the supranarial and subnarial processes, and most of the medial surface, including the interdental plates, is missing. The arc length along the complete alveolar margin is 20% larger than that of a juvenile *Daspletosaurus* sp. (TMP 1994.143.1) and about as large as that of an adult *Gorgosaurus libratus* (TMP 2005.9.9) (Table 2; ACL). When in its life position, the premaxilla is relatively short anteroposteriorly and wide lateromedially, just as in those of similar-sized tyrannosaurids. The narial fossa is partially preserved. The interpremaxillary suture is a flat surface that extends along the medial edge of the anterior wall of the first alveolus. The interdental plates are missing, but two ridges clearly mark the boundaries between the three teeth. The partially preserved, smooth surface along the posterior edge of the bone is part of the maxillary suture. The texture is unlike the pitted, spongy alveolar surface. The three alveoli are variable in size (Table 2). The first alveolus is the largest, and the next two alveoli are successively smaller. The three alveoli gradually taper dorsally, following the external bone

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profile. There is no indication of a space for an extra alveolus anywhere along the alveolar margin.

Stratigraphic and geographic range.—Dinosaur Park Formation, Belly River Group (Campanian, Cretaceous); 5 m above the boundary with the underlying Oldman Formation. Denhart Coulee, southern Alberta, Canada.

Discussion

Taxonomic affinity.—Two tyrannosaurid taxa are known from the Dinosaur Park Formation: the albertosaurine *Gorgosaurus libratus* and the tyrannosaurine *Daspletosaurus* sp. (Currie 2003a; Fig. 1E). TMP 2007.20.124 is identified as cf. *Daspletosaurus* sp. based on the greater relative width of the premaxilla in its life position, as determined by the angle between the interpremaxillary suture and the alveolar margin in ventral view. Even though the width of a tyrannosaurid premaxilla is influenced by allometry, the premaxillary width can be differentiated between albertosaurines and tyrannosaurines (Currie 2003a; Carr and Williamson 2004). Carr and Williamson (2004) used the "narrow" width to distinguish albertosaurines from tyrannosaurines, but they did not provide objective, quantitative criteria to define "narrow." In this paper, a "wide" premaxilla typical of tyrannosaurines is defined as one in which all the premaxillary teeth are visible in anterior view. That is, each of the teeth after the first one is not overlapped for more than a third of its width by the sequentially more anterior tooth. This visibility criterion applies to immature specimens of tyrannosaurines (TMP 1994.143.1, *Daspletosaurus* sp.; CMNH 7514, *Nanotyrannus lancensis*), but may differ in specimens with aberrant tooth counts. TMP 2007.20.124 is still interpreted as "wide" because the angle between the interpremaxillary suture and the alveolar margin is comparable to that of tyrannosaurines (50–80°).

TMP 2007.20.124 possibly represents a new tyrannosaurid taxon because it deviates from the remarkably conservative condition of four premaxillary teeth amongst theropods. However, it is not warranted to assume a distinct taxon based only on the tooth count of a single element, regardless of how unusual. No other potentially diagnostic character is seen in the specimen, and there is no way to test the possibility of bilateral asymmetry, as is the case for *Baryonyx* (Charig and Milner 1997). Furthermore, the Dinosaur Park Formation is an extremely well-sampled stratigraphic unit from which more than thirty associated skulls and skeletons of tyrannosaurids have been collected, all unambiguously identified either as *Daspletosaurus* or *Gorgosaurus* (Currie 2003a, 2005). The discovery of another distinct large tyrannosaurid theropod is unlikely from this formation. Unless supported by further evidence, TMP 2007.20.124 is best identified as *Daspletosaurus* sp., the only tyrannosaurine from the formation.

Developmental abnormality.—TMP 2007.20.124 provides the first evidence that the premaxillary tooth count can vary in tyrannosaurids. The loss of one tooth position is not due to breakage of the specimen because the maxillary suture is still preserved. Neither does the low tooth count represent post-natal modification or a pathological condition, because the specimen lacks an alveolus filled with bone, and because there is no abnormal bone texture. The size differences between the alveoli are also minor. It is therefore unlikely that any one of the alveoli expanded to incorporate another alveolus at some stage of development. Past bibliographic reviews of theropod palaeopathology (Tanke and Rothschild 2002; Rothschild and Tanke 2005) do not include observations of theropod premaxilla tooth count variation due to pathological conditions. The low tooth count is not attributable to ontogenetic variation either. A juvenile specimen of *Daspletosaurus* (TMP 1994.143.1, 10 years old, 496 kg estimated body mass; Erickson et al. 2004) is smaller than TMP 2007.20.124 in size, but clearly has four premaxillary teeth on both premaxillae as in all other specimens of *Daspletosaurus*. This means that the premaxillary tooth count neither increases nor decreases in *Daspletosaurus* under normal conditions. Thus, the low premaxillary tooth count in TMP 2007.20.124 represents a case of abnormal tooth development. Under this hypothesis, it is unlikely that the number of the premaxillary teeth is subject to developmental plasticity under normal conditions, because no other tyrannosaurid premaxilla is known to have more than or less than four teeth. The three complete alveoli with no trace indicating the fourth precludes post-natal modification to the number of the premaxillary teeth. Thus, the three-tooth state may be interpreted as a developmental abnormality due to an error during odontogenesis. Further analysis of this character requires a brief review of tooth morphogenesis and discussion for a developmental model to explain tooth count variation.

Developmental models for tooth count variation.—Using mice, Kavanagh et al. (2007) demonstrated that inhibitory signals from a developing tooth bud successively regulate development of the next tooth. Under this model, prolonged or accelerated development of a tooth bud changes the proportions of molars that subsequently develop, and results in variation in the number and relative size of the teeth (Fig. 2A). A long history of morphological works on mammal dentition lends support for this model. Most importantly, teeth that develop later have lower heritabilities for size or are more variable in size and shape (Lundström 1948; Bader 1965; Bader and Lehman 1965; Guthrie 1965; Sofaer et al. 1971a; Gingerich and Winkler 1979). This is because the last tooth to develop must accommodate fluctuations in size growth of earlier developing teeth. Indeed, if the teeth that develop earlier end up being relatively larger, the ones that develop later tend to compensate for this by reducing their relative size (Gruneburg 1951; Grewal 1962; Van Valen 1962; Gould and Garwood 1969; Sofaer 1969; Sofaer et al. 1971a, b) Recently, Laffont et al. (2009) and Renaud et al. (2009) provided positive evidence for the cascading effect of molar proportions in voles and mice. These observations

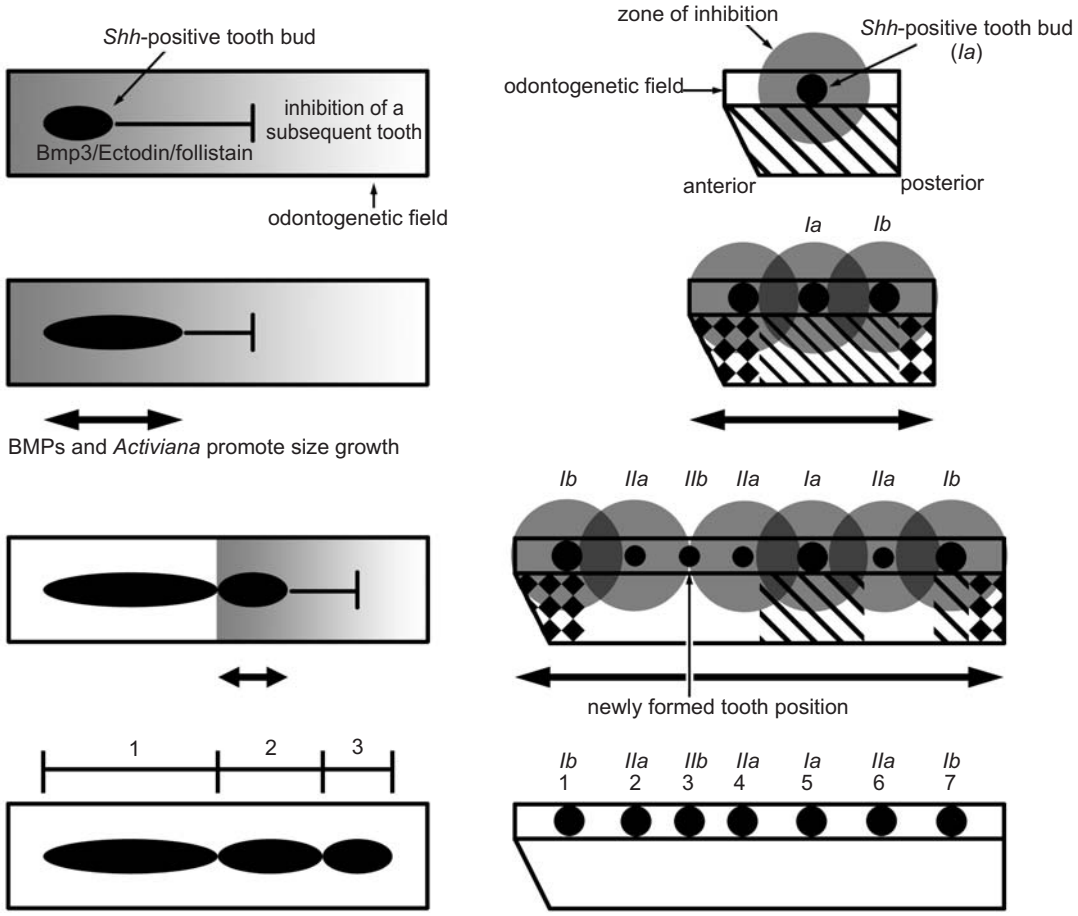

Fig. 2. Diagrams that represent developmental models to explain regulation of tooth count. **A**. The inhibitory cascade model (Kavanagh et al. 2007) in which a developing tooth successively inhibits subsequent ones in a hypothetical mammal. **B**. The zone of inhibition model (Osborn 1971, 1978, 1998; Kulesa et al. 1996) in which a tooth develops outside the sphere of inhibition around an already developing tooth in a hypothetical reptile. Roman numerals show the sequence of tooth site formation, whereas Arabic numerals indicate the spatial order of tooth positions. The inhibitory cascade model explains regulation of tooth size, whereas the zone of inhibition model deals with spatial regulation of tooth positions. The pattern of tooth formation is spatially and temporarily sequential in the inhibitory cascade model (applicable to mammals), but does not have to be spatially sequential in the zone of inhibition model (applicable to mammals and non-mammals alike).

demonstrate that the dimensions of a tooth position are regulated separately from the dimensions of an odontogenic field, and that changes in tooth size alter the proportions of the teeth and eventually lead to tooth count variation. Renvoisé et al. (2009) used the molar dimensions in arvicolines to reject proportional reduction in molar size predicted by the inhibitory cascade model. However, proportional reduction in tooth size is only possible if the inhibitory signals proportionally accumulates from one tooth to next, and if relative dimensions of the odontogenic field remains constant between animals under comparison. In other words, a cascade of inhibitory signals can create teeth of identical size if the signals proportionally decrease in expression levels from one tooth to the next.

Outside Mammalia, there is evidence for shared regulatory pathways and similar regulatory mechanisms for tooth size and an odontogenic field (Smith 2003; Streelman et al. 2003; Fraser et al. 2004, 2006a, 2009). But tooth patterning is more complicated in non-mammalian vertebrates, partly because primary tooth position patterning must translate into continuous replacement pattern (Fraser et al. 2006b; Huysseune and Witten 2006), and partly because teeth do not necessarily form in an apparent sequential manner. In alligators, for example, primary tooth positions are established anterior and posterior to the first tooth bud, and secondary tooth positions are set in between some of the primary ones (Westergaard and Ferguson 1986, 1987, 1990). To interpret this, Osborn (1971, 1978) postulated a zone of inhibition around a developing tooth bud, coupled with growth of an entire odontogenic field (Kulesa et al. 1996; Osborn 1998). That is, a tooth bud can only develop outside the sphere of a threshold concentration of inhibitors around an already developing tooth bud (Fig. 2B). Growth of the odontogenic field allows adjacent teeth to form outside the zone of inhibition. Under this model, a zone of inhibition morphologically manifests itself in the space that each tooth position occupies.

Developmental implications.—These developmental insights are useful in the interpretation of tooth count variation. In tyrannosaurid theropods, tooth count varies intraspecifically

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and bilaterally in the maxillae and dentaries. Amongst specimens of *Gorgosaurus*, for example, the maxillary tooth count varies from thirteen to fifteen, and bilateral variation may exist by a difference of one additional tooth on either side (Currie 2003a). In these animals, maxillary tooth row length is highly correlated with maxillary length (Currie 2003b), suggesting consistent spatial regulation of the odontogenic field. At the same time, correspondence of anterior alveolus positions with other morphological landmarks within maxillae (Miyashita 2008) indicates that the sizes of the teeth and of their zones of inhibition are also controlled. As such, putting teeth of given sizes along the alveolar margin lines up the alveoli in predictable positions. Posteriorly along the tooth row, however, the accumulation of small errors in regulation of tooth sizes and the zones of inhibition, plus perhaps slight difference in dimensions of the odontogenic field between right and left sides, would leave either enough or too little room for the last few teeth. At this stage, any presumptive tooth potential outside the field would be aborted. The net result is bilateral asymmetry and intraspecific variation in tyrannosaurid maxillary tooth count. Such hypothesised compensatory interaction is consistent with the mammalian trend of shifting molar proportions. Sofaer (1973) explains the mammalian compensatory interaction that teeth are genetically too large for the element in which they develop, and therefore modulate their proportions and number to fit in it. A compensatory interaction between the regulatory parameters offers a simpler explanation for tooth count variation than assuming that developmental regulation acts directly upon the determination of each tooth position. Although the zone of inhibition and tooth size cannot be decoupled for most dinosaurs with their teeth being closely packed together, the widely spaced dentition of the theropod *Archaeornithoides* (Elżanowski and Wellnhofer 1993) and the heterodont premaxillary dentition of spinosaurid theropods (Charig and Milner 1997; Dal Sasso et al. 2005) demonstrate that these traits can be independent.

As for premaxillary dentition in dinosaurs, less plasticity in tooth count is expected than for maxillary or dentary dentitions, simply because the relatively smaller dimensions of the alveolar margin of the premaxilla would leave little room for the accumulation of perturbations to include or exclude an extra tooth. A taxonomic difference in premaxillary tooth count must be a rare consequence of significant alterations to one or more of the regulatory properties to create or remove a tooth position. These predictions accurately describe the trends of premaxillary tooth count in dinosaurs (Table 1). Odontogenic fields of the premaxilla and maxilla are independent from each other (Westergaard and Ferguson 1990), partly because a tooth never develops across the boundary between the premaxilla and maxilla. In tyrannosaurids, the anterior borders of the maxillae serve as posterior walls of the last premaxillary alveoli (Currie 2003a). Also in tyrannosauroids, premaxillary teeth equal each other in size but are smaller than maxillary teeth, which suggests that relative size of the teeth is regulated independently between premaxilla and maxilla.

TMP 2007.20.124 has the largest alveolar dimensions relative to premaxillary size among all the tyrannosaurid premaxillae listed in Table 2 (Fig. 3). The sizes of the alveoli in TMP 2007.20.124 are comparable to those of TMP 2001.36.1, one of the largest specimens of *Daspletosaurus*, whereas the length of the premaxillary alveolar margin measured is approximately 30% smaller than that in TMP 2001.36.1. Because all alveoli in TMP 2007.20.124 are similar in size to each other, it is possible that the first three premaxillary tooth positions grew relatively large and eventually "pushed" the potential fourth tooth outside the odontogenic field of the premaxilla at an early stage in the development. The implication is that the low premaxillary tooth count of TMP 2007.20.124 is a result of an abnormal increase in tooth size, rather than to a change in relative dimensions of the odontogenic field or to an inconsistent regulation on tooth size along the tooth row. By simple calculation, a zone of inhibition a third larger could alter the tooth count to three from four (Fig. 4), which roughly coincides with relative size of premaxillary alveoli in TMP 2007.20.124 compared to other tyrannosaurids. When a mean alveolar diameter is corrected for length of the alveolar margin, TMP 2007.20.124 has a diameter 1.23 times the average of those in four-toothed tyrannosaurid premaxillae (Table 2: mean alveolus diameter/ premaxillary arc length). In contrast, the premaxillary tooth count of seven in *Pelecanimimus* is attributed to the relatively small size of the teeth (Perez-Moreno et al. 1994), which could be a consequence of decreased expression of the inhibitor. Finally, a test for cascading effect and compensatory interaction in tooth size regulation in dinosaurs must meet three predictions: (i) tooth count co-varies with relative dimensions of the tooth-bearing portion of the alveolar margin and/or the relative size of the alveoli taken

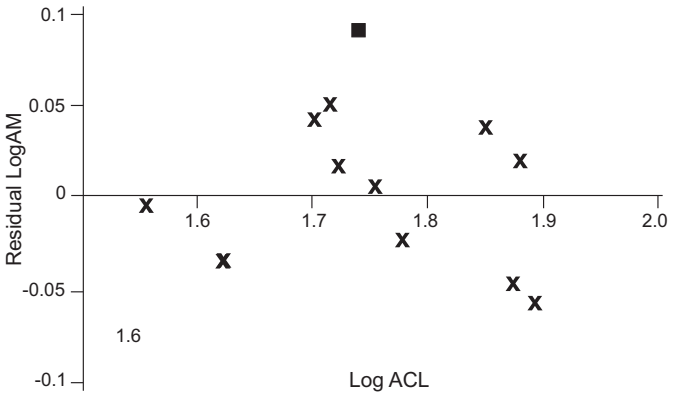

Fig. 3. A residual plot of diameters of premaxillary aliveoli relative to the alveolar dimensions. TMP 2007.20.124 (indicated by a square) has larger premaxillary alveoli relative to other tyrannosaurid specimens with four premaxillary teeth (indicated by X; see Table 2). A major reduced axis regression is computed for the four-toothed specimens (n = 11) in bivariate plot of log-transformed mean alveolus diameter against log-transformed premaxillary arc length ($y = 0.975x - 0.671$; $R = 0.941$; $R^2 = 0.886$). TMP 2007.20.124 does not fall in the range of variation in the residual plot, which suggests that it deviates from the normal tyrannosaurid trend. Abbreviations: ACL, arc length (outside the curvature) of alveolar margin; AM, mean mesiodistal alveolus diameter.

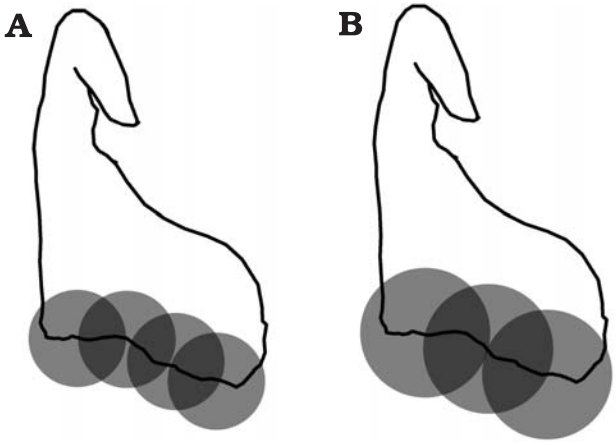

Fig. 4. Hypothetical zones of inhibition during premaxillary odontogenesis in tyrannosaurids. The outline represents a tyrannosaurid premaxilla in posteromedial view. **A**. A normal four-toothed premaxilla of a tyrannosaurid. **B**. TMP 2007.20.124 with only three premaxillary teeth. A zone of inhibition is a third larger in TMP 2007.20.124 than in a normal tyrannosaurid premaxilla, excluding the fourth tooth position from the alveolar margin.

together but not individually; (ii) the teeth and the alveoli show higher covariance in size and shape between adjacent ones than between those spaced widely apart along the series; and (iii) the last developing tooth and alveolus in the series are more variable in relative size and shape than the earlier ones. Although these predictions await quantitative tests, the relatively large tooth size and low tooth count in TMP 2007.20.124 provides qualitative support for tooth count as a function of relative tooth size. Also consistent with the first prediction is the association of a high premaxillary tooth count of seven with either small teeth (*Pelecanimimus*) or an elongate premaxillary alveolar margin (spinosaurids) in theropods.

Phylogenetic implications.—It is always an issue how to treat numerical traits such as tooth count and number of vertebrae in phylogenetic analysis, because implicit character weighting is an inevitable consequence of assigning a character state to continuous variation. All but one major character set for phylogenetic analysis of tyrannosaurids is free of characters based on tooth count (Holtz 2001, 2004; Carr 2004; Carr and Williamson in Brusatte et al. 2009; Sereno et al. 2009; as opposed to Currie et al. 2003). These characters do not accurately reflect true phylogenetic signals, not only because tooth count is variable individually, but also because tooth count is a function of size regulation of both an odontogenic field and tooth positions. Therefore, variation in tooth count should be assessed using a morphological signature for alteration in each parameter. Relative dimensions of an odontogenic field and relative tooth size may be difficult to determine. A more indirect alternative is to use a combination of particular positions of teeth relative to other landmarks. For example, a sixth maxillary tooth position coincides with the anterior margin of an antorbital fossa in all tyrannosaurids and in the basal tyrannosauroids *Dilong* and *Raptorex*, but not in another basal tyrannosauroid (*Guanlong*).

Functional implications.—The lower number of tooth positions and the sizes of the alveoli in TMP 2007.20.124 show that the premaxillary teeth were relatively larger, and presumably mechanically more resistant. However, the otherwise consistent presence of four teeth in tyrannosaurids suggests that the selective advantage of larger premaxillary teeth, if any, is limited. The conservatism in theropod premaxillary tooth count may imply that four is the functionally optimal number for premaxillary teeth. Lack of functional morphological studies on relatively small, lateromedially wide tyrannosaurid premaxillary teeth restrains the authors from exploring a functional implication of the larger premaxillary teeth.

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