Wear facets and enamel spalling in tyrannosaurid dinosaurs

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Numerous paleontologists have noted wear facets on tyrannosaurid lateral teeth over the past century. While several workers have proposed explanations for these features, there remains to this day no consensus concerning their etiology. Here we report on an examination of wear surfaces on these teeth from the Upper Cretaceous (mid-Campanian) Judith River Group of southern Alberta, Canada. This study reveals two distinct types of wear features on the labial and lingual sides of tyrannosaurid lateral teeth: irregular "spalled" surfaces and wear facets. The irregular spalled surfaces typically extend to the apex of the tooth, which evidently reflects flaking of enamel resulting from forces produced during contact between tooth and food. These surfaces are often rounded, presumably from antemortem wear following spalling. Wear striations on these surfaces are oriented heterogeneously. The wear facets, in contrast, occur on only one side of the tooth and are typically elliptical in outline and evince parallel wear striations. Similar patterns of parallel wear striations in extant mammals reflect tooth-tooth contact. We therefore propose that wear facets in tyrannosaurids were formed by repeated tooth-tooth contact between the lingual side of maxillary teeth and labial side of dentary teeth. It remains unclear whether this contact was serendipitous or adaptive, though it appears to be unusual for reptiles, as we have found no evidence for wear facets in extant varanids and crocodilians.

Key words: *Daspletosaurus*, *Gorgosaurus*, Tyrannosauridae, enamel spalling, wear facets, lateral teeth, diet.

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Introduction

Lambe (1917) noted wear surfaces on the side faces of tyrannosaurid lateral teeth from the Red Deer River deposits of western Canada. He wrote (p. 18): "as the upper teeth closed outside those of the mandible any wear, not on the point, would result from the contact of the inner surface of the upper teeth with the outer surface of the lower ones." Recent workers, have, however, challenged this assertion, suggesting that the shapes, locations, and incidences of tyrannosaurid wear surfaces are not indicative of tooth-tooth contact (Farlow and Brinkman 1994; Molnar 1998; Jacobsen 1996, 2003). Here we reevaluate this evidence by examining wear striations in tyrannosaurid lateral teeth in addition to the shapes and locations of their wear surfaces.

Background

Lambe's (1917) original assertions may have important implications for the mechanics of tyrannosaur biting. The maxillary and dentary teeth of most extant reptiles that we have studied do not come into regular contact when the mouth is closed. Lambe's (1917) interpretation, if correct, would imply that tyrannosaur maxillary and dentary teeth did come into direct opposition during feeding, suggesting a possible functional adaptation for food shearing, or at least, a unique jaw design compared with numerous living varanids and crocodilians examined.

Several researchers have, however, recently challenged the notion that wear features seen on tyrannosaurid teeth reflect repeated tooth-to-tooth contact (i.e., attrition). Farlow, cited in Abler (1992), suggested that these features are seen only on the lingual face. Farlow and Brinkman (1994), refined this notion with a large study of Judith River Formation tyrannosaurid teeth. Their observations suggested to them that there were indeed wear features on the labial faces of these teeth, but that these wear features (especially larger ones) were more frequent on the lingual faces. Farlow and Brinkman (1994) noted the discrepancy between their observations and those of Lambe (1917), but they did not offer an explanation for the observed pattern.

Molnar (1998) more recently cited Farlow's original comments (in Abler 1992) suggesting that tyrannosaurid tooth wear features only occur on lateral surfaces. Molnar wrote that this indicated that the wear features originally observed by Lambe (1917) could not have been caused by attrition. As Farlow and Brinkman (1994) noted, however, wear features are not uncommon on the labial sides of tyrannosaurid lateral teeth (albeit perhaps smaller on average than those on the lingual sides). This observation was confirmed by Jacobsen (2003), who also suggested that these features were more likely formed by interactions with food (abrasion) than by repeated tooth-tooth contact.

Occlusal mechanics and tooth wear

An understanding of the relationships between occlusal mechanics and tooth wear can surely help in choosing between competing hypotheses for the etiology of wear features on the lateral teeth of tyrannosaurids. Much work in this area has been done for mammals. Butler (1952) and Mills (1955, 1967) even devised a method for reconstructing occlusal mechanics for mammals by examining directions of microscopic striations on the facets formed by contact between upper and lower teeth during mastication. Mills (1955), for example, noted that for these striations "the overwhelming majority of them are parallel and therefore serve to indicate the direction of jaw movement which produced the facet in question".

Some studies have described dental wear striations in dinosaurs that suggested mastication as well (Weishampel 1984; Fiorillo 1991a, 1995, 1997, 1998; Weishampel and Norman 1989; Upchurch and Barrett 2000; Barrett 2001; Rybczynski and Vickaryous 2001). These studies have focused on presumed herbivorous species. Weishampel (1984), for example, noted that, as with mammals, hadrosaurs have parallel striations on facets likely reflecting the direction of precise tooth-tooth occlusion during chewing.

So where do the wear surfaces on tyrannosaurids fit in with this? Do tyrannosaurid lateral teeth show evidence of dental attrition suggesting repeated, precise contact between upper and lower dentitions during feeding, or is some other phenomenon responsible for the wear features observed by so many researchers? While Abler (1992) did note some parallel striations on tyrannosaurid lateral teeth, he also reported considerable striation orientation heterogeneity, suggesting "nonorthal movement either by the predator or the prey" (Abler 1997: 742).

Here we argue that feature shape and location, and striation orientation suggest that there are actually two different types of wear surfaces on the sides of tyrannosaurid lateral teeth: spalled surfaces resulting from antemortem enamel flaking, and attritional facets caused by tooth-tooth contact during feeding. While spalled surfaces are common in living reptiles, we found no attritional facets on a large sample of extant varanid, and crocodilian teeth. This suggests a degree of tooth-tooth contact during feeding in tyrannosaurids (whether selected for or fortuitous) beyond that of observed extant reptiles.

Institutional abbreviations.—MCZ, Museum of Comparative Zoology at Harvard University, Cambridge, MA, USA; SAM, South African Museum, Cape Town, South Africa; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

Materials and methods

In this study we examined lateral teeth of tyrannosaurids housed at the Royal Tyrrell Museum of Palaeontology. These teeth are from the Upper Cretaceous (mid-Campanian) age Oldman and Dinosaur Park formations, Judith River Group of southern Alberta, Canada (Eberth et al. 2001; Currie 2003). Two tyrannosaurid species are currently recognized from these mid-Campanian formations, *Daspletosaurus torosus* and *Gorgosaurus libratus* (Currie 2003). While the isolated teeth likely represent these taxa, they cannot be differentiated with confidence and are identified as Tyrannosauridae indet. (Philip J. Currie, personal communication 2003). Molds and casts were prepared, as part of a larger study, for 150 specimens (both isolated teeth and those in maxillae and dentaries) that appeared to preserve antemortem microwear following the procedures described by Teaford (1988). We also examined an extant baseline series of crocodilian and varanid lateral teeth at the Florida Museum of Natural History. Specimens included *Alligator mississippiensis* (n = 16), *Caiman crocodilus* (n = 23), *Crocodylus acutus* (n = 9), *Varanus olivaceus* (n = 24), *Varanus komodoensis* (n = 5), *Varanus niloticus* (n= 6), and *V. salvator* (n = 3).

Positions and shapes of wear surfaces were noted on the extant and fossil specimens. High resolution casts were then prepared using conventional microwear procedures (Rose 1983; Ungar 1996). Specimens were cleaned with cotton swabs soaked in acetone. High resolution molds were then made using President's Jet (ColtPne Corp) polyvinylsiloxane dental impression material, and tooth replicas were prepared using Epotek 301 (Epoxy Technology Inc.) epoxy. This procedure produces casts that preserve microwear surfaces true to a fraction of a micron (Beynon 1987). Tooth replicas were examined for antemortem microscopic wear using a binocular light microscope.

Table 1. Examples of tyrannosaurid lateral teeth with wear facets containing large parallel striations. All of these specimens are from the Judith River Group of western Canada.

Catalog number	Taxon	Side of tooth
TMP 66.31.104	Tyrannosauridae indet.	lingual
TMP 79.14.1027	Tyrannosauridae indet.	lingual
TMP 79.14.1040	Tyrannosauridae indet.	lingual
TMP 80.16.864	Tyrannosauridae indet.	lingual
TMP 80.16.934	Tyrannosauridae indet.	labial
TMP 80.44.6	Tyrannosauridae indet.	lingual
TMP 81.18.126	Tyrannosauridae indet.	lingual
TMP 81.22.28	Tyrannosauridae indet.	lingual
TMP 82.19.422	Tyrannosauridae indet.	lingual
TMP 84.36.2	Tyrannosauridae indet.	lingual
TMP 85.6.130	Tyrannosauridae indet.	lingual
TMP 87.36.295	Tyrannosauridae indet.	lingual
TMP 94.12.602	*Gorgosaurus torosus*	lingual

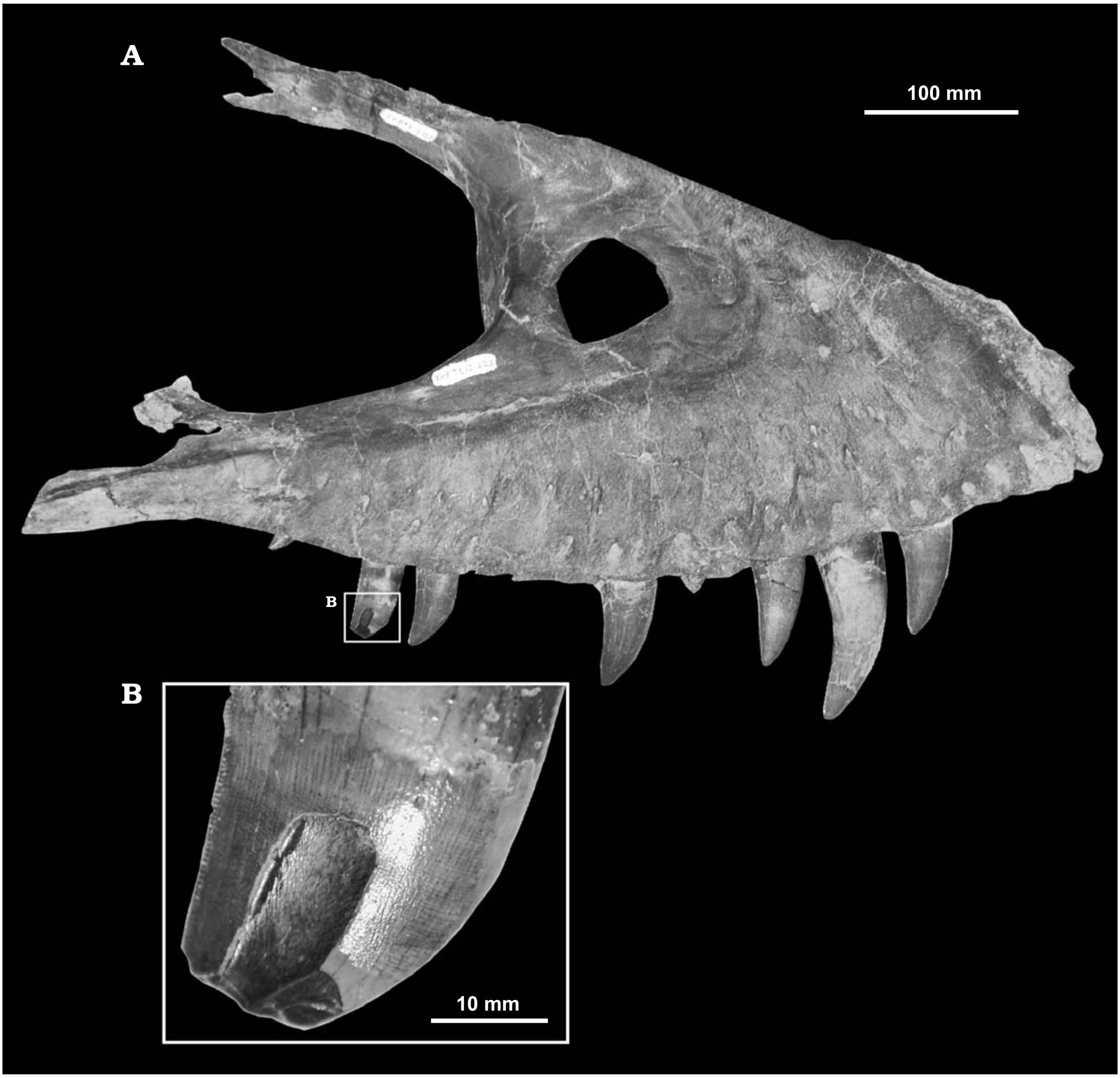

Fig. 1. Lateral view of *Daspletosaurus torosus* maxilla TMP 97.12.223 (**A**) and expanded view of a tooth with a spalled surface (**B**).

Results

Observations of wear surface shapes, locations and wear patterning on the tyrannosaurid teeth suggest two different types of features, each with different etiologies. These include spalled surfaces (Figs. 1, 2), and occlusal facets (Figs. 3, 4).

Wear feature shapes and locations.—Spalled surfaces tend to be short and squat, with proximal edges irregular or perpendicular to the long axis of the tooth (Figs. 1, 2). These surfaces are found on all sides of the tooth, are conchoidal in nature, and typically extended to the apex. The edges of these surfaces are often rounded, presumably by antemortem wear. Spalled surfaces were common in both tyrannosaurids and extant reptiles, especially crocodilians. The wear surface described by Farlow and Brinkman (1994) for a specimen of *Varanus komodoensis* (MCZ 24907) fits the criteria for this type.

Wear facets, in contrast, tend to be elongated and elliptical in shape, and follow the long axis of the tooth (Figs. 3, 4; Table 1). They vary in size from relatively small areas to much larger surfaces, with edges abutting anterior and posterior serrated keels. These are uniformly flat, and are found on labial or lingual surfaces of teeth—but not on both—and not on mesial or distal surfaces. These facets cut well into the

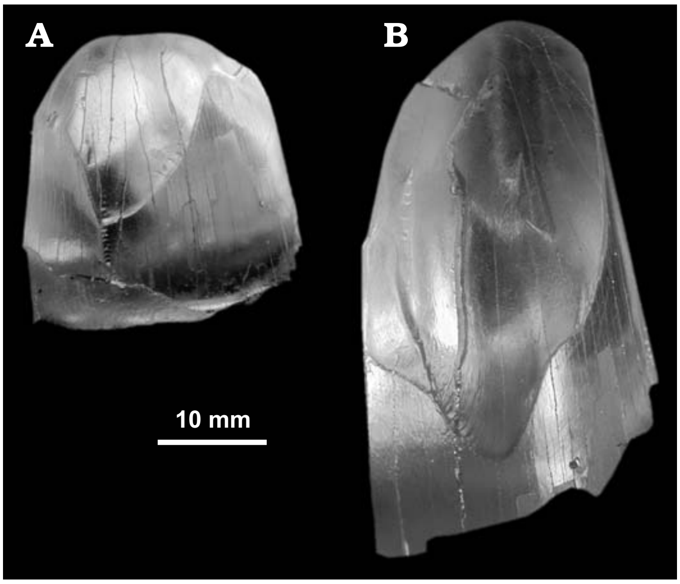

Fig. 2. Examples of additional tyrannosaurid lateral teeth with spalled surfaces. **A**. TMP 79.14.775. **B**. TMP 66.11.94.

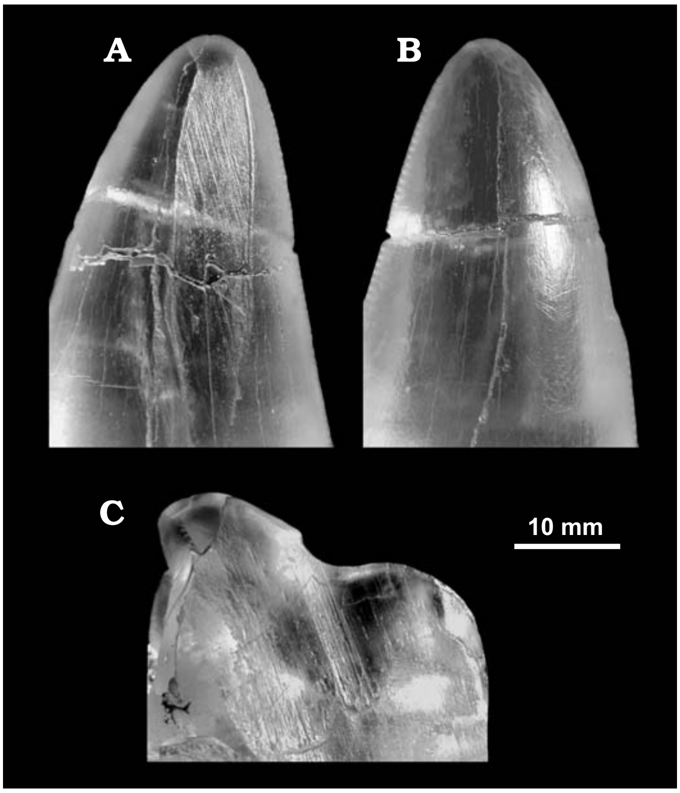

Fig. 3. Tyrannosaurid lateral tooth with parallel striations on wear facet (**A**, **B**) compared to wear striations on the P4 carnassial facet of an African lion, *Panthera leo* (**C**). **A**, **B**. Opposite sides of TMP 80.16.864. **C**. SAM 36975.

dentine, and subsequent smoothing of exposed enamel edges is common. Such wear facets are often seen on tyrannosaurid teeth, but, in no case did we see them on any of the extant specimens examined.

Striation orientation.—Wear striations within the spalled surfaces are microscopic and oriented heterogeneously in a manner indistinguishable from that in adjacent surfaces of the tooth. Striations tend to be broader within the spalled dentine surfaces than in adjacent enamel, which likely relate to differences in hardness of the two dental tissues.

Wear striations within wear facets, in contrast, are much larger (usually visible to the naked eye) and oriented homogeneously (see Fig. 3). These apparently antemortem wear striations are typically offset about 15 degrees from the long axis of the facet, being more apical on the mesial side of the facet and more basal on the distal side. These striations are usually confined to the wear surface, though they occasionally extend onto the adjacent enamel where facets are small. The sizes, densities and orientational homogeneity of these striations are comparable to those found in mammalian attritional facets. Figure 3 shows attritional striations in a lion carnassial occlusal facet and those in a tyrannosaurid lateral tooth for comparison. This pattern was not seen on wear surfaces of any of the extant specimens examined.

Smaller, microscopic striations were also found within tyrannosaurid tooth facets. Some of these were parallel with the larger striations, but others were more heterogeneously oriented. These smaller striations were present on all sides of the tooth. Indeed, many of the labial and lingual surfaces of isolated teeth that lack both spalling and faceting preserve such small, heterogeneously oriented striations.

A few teeth lacking facets or spalls also evince marked striation orientation homogeneity, with large parallel striations on one side of the tooth. Microwear patterning on these surfaces resembles that on facets, and is offset from the long-axis of the tooth by about 15 degrees. The shapes of these wear surfaces suggest that they may be "pre-facets", resulting from attritional wear, but not to the extent of facet formation. This, when considered along with specimens showing variable facet sizes, may provide insight into the process of facet formation.

Finally, surfaces that show the shapes and positioning expected of an attritional facet occasionally lack parallel striations (e.g., Fig. 4). We suspect that these may be altered attritional facets. This pattern is as would be expected if an opposing tooth was shed, and the facet surface was subsequently worn by tooth-food abrasion, particularly where these surfaces preserve the smaller, heterogeneously oriented striations.

Discussion

Lambe (1917) suggested that wear surfaces found on the sides of lateral teeth of tyrannosaurids resulted from tooth-tooth contact during feeding. More recent works have suggested that these surfaces must have a different etiology (Farlow and Brinkman 1994; Molnar 1998; Jacobsen 2003). For example, Farlow and Brinkman (1994) note the presence of wear on the inner sides of tyrannosaurid and Komodo dragon dentary teeth. Because the tyrannosaurid and varanid maxillary dental

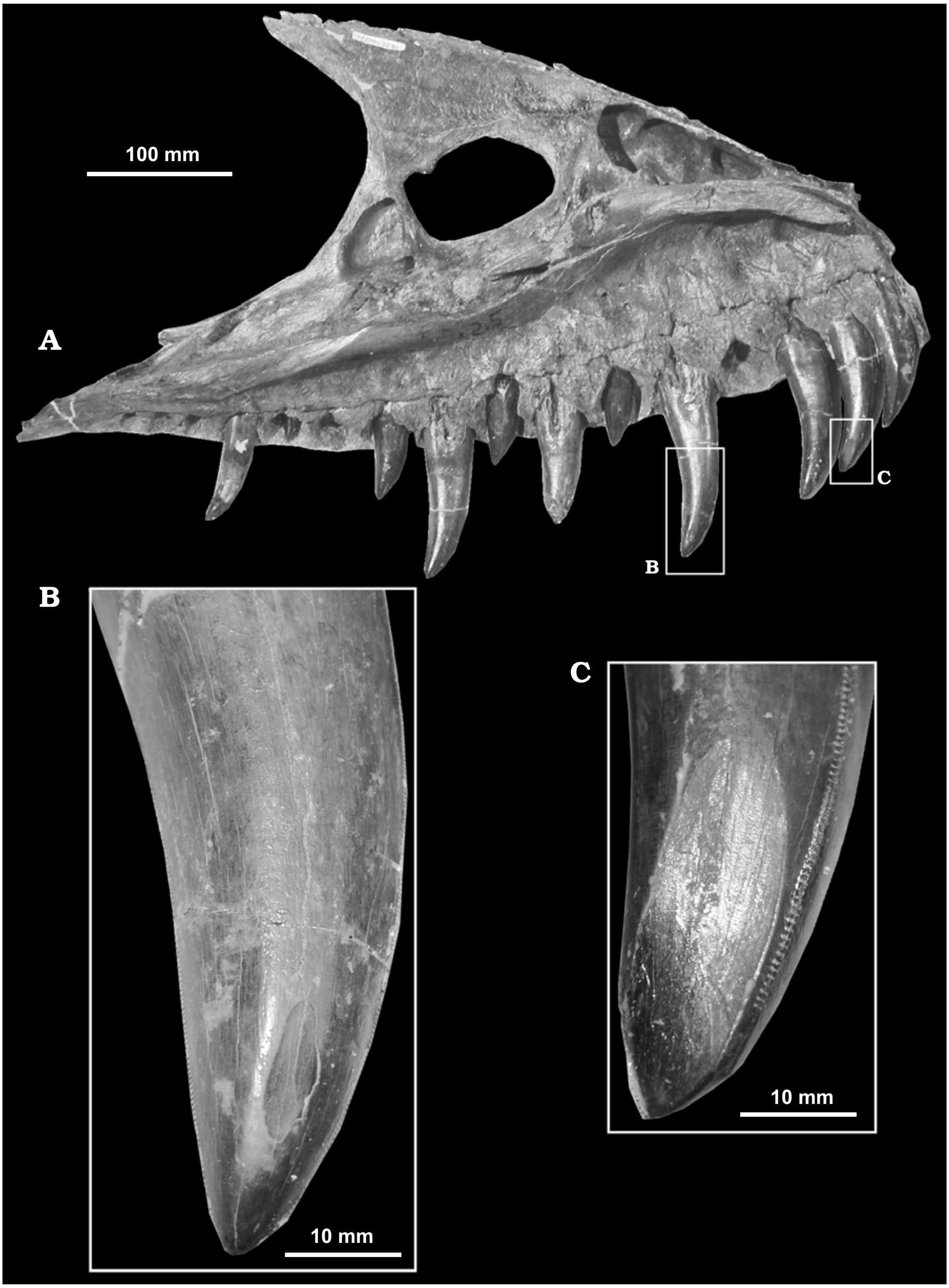

Fig. 4. Medial view of *Daspletosaurus torosus* maxilla TMP 2001.36.01 (**A**) and expanded views of teeth with elliptical wear facets (**B**, **C**).

arcades are wider than the dentary dental arcade, upper teeth should rest outside of lower teeth when the jaw is closed, and wear facets should generally occur on the inner surfaces of maxillary teeth and outer surfaces of dentary teeth.

We suggest that the confusion stems from the probability that there are at least two independent factors causing wear surfaces on tyrannosaurid lateral teeth: antemortem enamel spalling with subsequent surface smoothing due to wear; and attrition due to regular contact between the lingual surfaces of maxillary teeth and the labial surfaces of dentary teeth.

Antemortem enamel spalling.—Spalled surfaces are uneven at their edges, typically conchoidal, concave or convex in relation to the surrounding enamel surface, and tend to extend to the apex of the tooth. They appear as if enamel flakes were splayed off the underlying dentine surfaces. This seems to have occurred before death in most cases because rough edges of the spalled surfaces have evidently been smoothed by antemortem wear. Similarities in microwear striation orientations between the spalled surface and adjacent enamel support the idea that enamel flakes splayed off during life, as suggested for microwear on chipped tooth surfaces in other studies (Ungar and Grine 1991).

There is a growing body of evidence that tyrannosaurids bit down to the bones of their prey (e.g., Fiorillo 1991b; Erickson and Olson 1996; Erickson et al. 1996; Jacobsen 1998; Meers 2002; Jacobsen 2003) and at least one bone rich tyrannosaurid coprolite (Chin et al. 1998) has been discovered. Thus, perhaps enamel spalling reflects traumatic events that occurred as bones (or other hard-objects) were crushed. Alternatively, enamel failure might have resulted from repeated, lower magnitude forces during food processing. The study of the sizes and shapes of spalled surfaces may lead to insights into the vectors and magnitudes of forces that caused them. Further, dental microwear analyses underway may reveal aspects of the material properties of foods eaten by these therapods.

Attritional facets.—Attritional facets, in contrast, tend to be elliptical in shape with smoother margins. These are always found on only one side of a lateral tooth, and never on the mesial or distal surfaces. These facets are variable in size, but take the contour expected by repeated contact with an opposing tooth. Wear striation patterns are comparable to those seen on extant mammalian occlusal facets, and suggest repeated tooth-tooth contact in one direction, with opposing teeth shearing past one another like scissor blades. Differences between the pattern on wear surfaces and adjacent enamel indicate that facet wear is antemortem and not the result of taphonomic damage. While it has been suggested that these wear facets may be related to tooth-food contact (e.g., Molnar 1998), the consistency in orientation (approximately 15 degrees from the long axis of the facet) of the relatively large parallel striations, and the fact that these striations match the expected direction of a vertically-oriented bite (see Molnar 1988: fig. 15) and tooth-tooth contact makes an attrition explanation more likely.

While Farlow (cited in Abler 1992) suggested that these elliptical wear features occur only on the lingual surfaces of lateral teeth, Farlow and Brinkman (1994) noted that wear features are not uncommonly found on lateral tooth labial surfaces. Because the maxillary dental arcade is broader than the mandibular arcade, if these wear surfaces result from attrition, they should normally occur on the lingual surfaces of maxillary teeth and labial surfaces of opposing dentary teeth.

This is not easy to evaluate using isolated teeth because of continued difficulties distinguishing upper left teeth from lower rights, and upper right teeth from lower lefts (Tanya Samman and Philip J. Currie, personal communication 2003). Further, differential shedding times between maxillary and dentary teeth would limit occurrences of complementary facets.

Still, those specimens in maxillae and dentary bones that we observed to have attritional facets always fell into the expected pattern, and isolated teeth never showed facets on both sides. In fact, facet locations may actually allow us to identify lateral teeth to quadrant if these facets only occur on the labial surfaces of lower teeth and lingual surfaces of upper ones (Lambe 1917).

Further, the attritional wear pattern on these teeth suggests a sequence of facet development, from parallel striations prior to marked faceting, to small facets, to large facets abutting denticulate keels. Though opposing surfaces abutting denticulate keels would provide an effective shearing mechanism (like a pair of scissors with serrated blades), it remains unclear whether this reflects natural selection for honing or merely fortuitous tooth-tooth contact. It is compelling, however, that attritional facets were not observed at all in the comparative baseline series of extant reptiles. There is evidently something unique about the fit between tyrannosaurid maxillary and dentary dental arcades that allows, at least on occasion, for such tooth-tooth contact.

So, how common was this phenomenon? Postmortem damage to tyrannosaurid tooth surfaces and resulting obliteration of antemortem microwear make it difficult to assess actual percentages of occurrence of occlusal facets using striation orientation criteria. Still, it is evident that more specimens lack occlusal facets than possess them. Also, tyrannosaurids evidently lacked the masticatory muscle differentiation and temporomandibular joint morphology necessary for precise chewing movements seen in mammals, and regular tooth replacement would have made it more difficult to produce precise occlusal relationships (e.g., see Ungar and Beaupre 1999).

In sum then, while some of the wear features on tyrannosaurid lateral teeth are evidently attritional facets similar to those seen in mammals and some herbivorous dinosaurs, these theropods most probably did not chew their food. Still, tooth-tooth contact may have allowed efficient slicing or perhaps even honing, whether fortuitous or a result of genetic adaptation. Further study of these specimens by conventional dental microwear analysis will hopefully cast further light on tyrannosaurid feeding behaviors.

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