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THE CRUSHING BITE OF TYRANNOSAURIDS

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Tyrannosaurids are a group of large meat eating theropod dinosaurs. Newly prepared material of *Gorgosaurus libratus*, *Tarbosaurus bataar*, and *Tyrannosaurus rex* provides additional knowledge of the structure and movement of the intramandibular jaw joint in the family. Paradoxically the theories of jaw movement and the fossil evidence in tyrannosaurids have not been comparable. It has been suggested that the joint had a wide range of movement to allow the gullet to expand, and to allow adjustment of the pitch and position of the mandibular teeth relative to the upper teeth (Maleev, 1974; Barsbold, 1983; Bakker et al., 1988; Molnar, 1991). A moveable joint suggested a feeding behaviour like lizards with a weak bite. On the other hand, the shortening and elevation of the skull in tyrannosaurids for insertion of powerful jaw muscles (Molnar and Farlow 1990), increased tooth robustness (Farlow et al., 1991), bite marks suggesting bone fragmentation (Erickson and Olson 1996), estimation of bite force from tooth-marked bone (Erickson et al., 1996), and bone fragments in coprolites (Chin et al. 1998) all suggests high bite force. Here we describe the intramandibular jaw joint and report on the discovery of the first completely preserved and fused supradentary/coronoid bones in three different tyrannosaurids. The fused supradentary/coronoid bone crosses the intramandibular jaw joint restricting its movement. This leads to a rigid lower jaw in tyrannosaurids that is a secondary specialization for a powerful crushing bite.

Institutional Abbreviations—BHI, Black Hills Institute, South Dakota, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; ZPAL, Institute of Palaeobiology, Academy of Sciences, Warszawa, Poland.

DISCUSSION

The lower jaw of theropods is often described as two segments loosely hinged together. The anterior segment consists of the dentary, splenial and supradentary, while the posterior consists of surangular, angular, coronoid, prearticular and articular (Bakker et al., 1988). The intramandibular joint between these two segments is one of the unique characters diagnosing Theropoda (Currie, 1997), and is moveable in many theropods.

The intramandibular jaw joint can be divided further into a dorsal and a ventral joint. In tyrannosaurids, the dorsal joint consists of the dentary anterolaterally, the surangular posterolaterally, the fused, saber-shaped supradentary/coronoid that covers the dentary and surangular medially, and the dorsal parts of the prearticular and splenial medial to the supradentary/coronoid (Figs. 1, 2). The posterodorsal part of the dentary has a long medial process and a shorter lateral one, and there is a deep pocket between them. The dorsolateral process, termed the intramandibular process by Currie and Zhao (1993), fits into a slot on the medial side of the surangular. The surangular has two anterodorsal processes, a large medial process, and a smaller lateral process. The long medial process fits deeply into the pocket between the pair of posterodorsal processes of the dentary, thereby restricting the medio-lateral movement between the two bones.

In *Tyrannosaurus* and *Gorgosaurus*, a well-preserved splenial is typically triangular. The medial side is smooth except for a ridge that forms a dorsolateral groove for the supradentary. This groove continues on the lateral side and forms a smooth area for the contact to the crescent-shaped area of the supradentary. The posterodorsal part of the splenial covers the anterodorsal margin of the prearticular.

Anteromedially, the supradentary 'blade' covers the basal portions of teeth 3–15 and the lateral surface has weak ridges that fit between the

teeth. Posterior to the tooth row, the supradentary has an elongate groove that fits over ridges on the intramandibular process of the surangular. The coronoid also fits closely in a groove in the surangular and a small posterior process wraps around the dorsomedial rim of the surangular. Medially the supradentary/coronoid has a large crescent-shaped area for contact with the dorsal part of the splenial. The large, flat medial surface of the coronoid is partially covered by the anterodorsal section of the prearticular.

The ventral part of the intramandibular joint involves the dentary anterolaterally, the angular posterolaterally and medially, the splenial anteromedially, and the prearticular posteromedially.

In *Tarbosaurus*, the posteroventral part of the dentary has an abrupt, square end, concave medially in transverse section where it meets the angular. Its posterior end articulates with a perfectly matched vertical ridge on the lateral surface of the angular. In *Tyrannosaurus* and *Gorgosaurus*, there is a smooth groove on the angular with no abutting ridge for the posteroventral end of the dentary. In all three taxa, the anteromedial groove for the posteroventral part of the splenial is deep.

The prearticular has several grooves and ridges for attachment to the surangular and angular. Two large notches on the prearticular completely lock the angular in *Tarbosaurus*, but not in *Gorgosaurus* and *Tyrannosaurus*. The prearticular and surangular are both fused to the articular in *Tarbosaurus*, but are free in *Tyrannosaurus*. In the latter, the splenial has a long ridge, ventrolaterally, for attachment to the dentary, and the most posterior part has ridges for the anteromedial groove of the angular.

The supradentary/coronoid is fused in the three tyrannosaurids studied to form a long saber-shaped bone medial to the dentary and the surangular. *Daspletosaurus* (TMP 94.143.1) seems to have had a supradentary/coronoid with the same shape. This is similar to the situation in *Monolophosaurus* (Zhao and Currie, 1993), *Dromaeosaurus* (Currie, 1995), and possibly the *Sinraptor* (Currie and Zhao, 1993). The supradentary is described in prosauropods, sauropods and ceratopsians (named intercoronoid by Brown and Schlaikjer, 1940). In the prosauropod *Plateosaurus*, the supradentary is of the same shape and position as in theropods, but remains unfused to the coronoid (Brown and Schlaikjer, 1940). The supradentary bone is also found in the sauropods *Brachiosaurus* and *Camarasaurus* (Berman and McIntosh, 1986). In ornithischia the supradentary bone is only described in some ceratopsians (*Protoceratops*, *Monoclonius* and *Triceratops*). It is small and placed medioventral to the tooth row. In *Protoceratops* it is fused to the coronoid in adult specimens (Brown and Schlaikjer, 1940).

In earlier reconstructions of tyrannosaurids (Bakker et al., 1988; Molnar, 1991), the transition between the anterior and posterior segments of the lower jaw was described as a hinge with possibility for movement between the two segments. The discovery of the fused supradentary/coronoid, bridging the two segments of the lower jaw, and the long anteromedial process of the surangular suggests that lateral movement (Bakker et al., 1988) to expand the gullet was not possible.

Another theory is that a ventral movement of the anterior segment of the lower jaw absorbed, or softened, impact during biting (Lucas, 1994). In *Tarbosaurus*, the dentary is locked into the angular, the latter is locked into the prearticular, which in turn is fused to the articular. This would not allow significant ventral movement of the anterior segment in relation to the posterior part of the lower jaw. In *Tyrannosaurus* and *Gorgosaurus*, some small additional movement may have been possible between the dentary and the angular, but it too would have been limited by the dorsal supradentary/coronoid bridge. The interlocking of

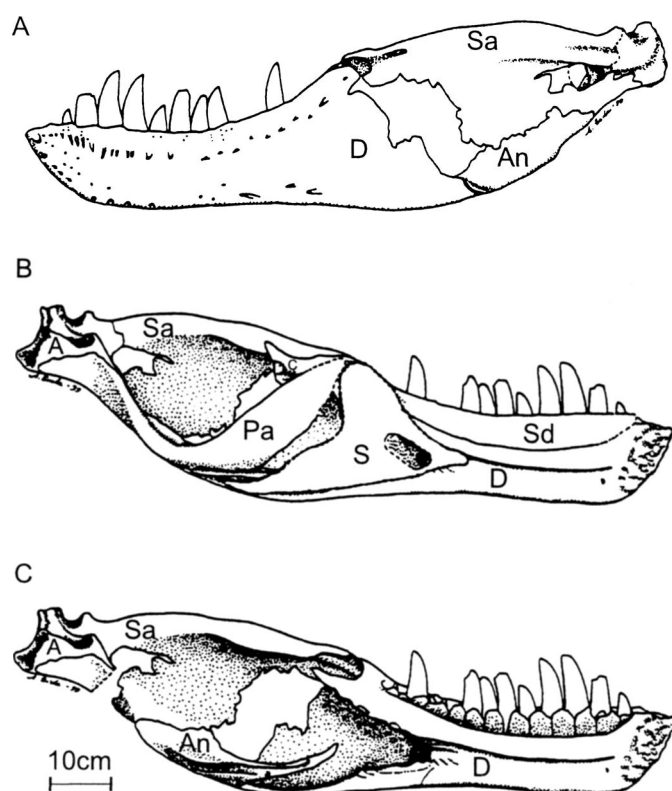


FIGURE 1. A–C, *Tarbosaurus bataar* ZPAL MgD-I/4, the lower jaw in lateral view (A), the lower jaw in medial view (B), the splenial bone reconstructed after ZPAL MgD-I/5, in medial view with the prearticular, splenial and supradentary/coronoid removed (C). **Abbreviations:** A, articular; An, angular; C, coronoid; D, dentary; Pa, prearticular; S, splenial; Sa, surangular; Sd, supradentary.

the posterior part of the coronoid to the dorsal rim of the surangular would also have prevented mediolateral and dorsoventral movement. Ridges on the ventrolateral side of the supradentary fit between the teeth, suggesting that movement of the supradentary relative to the teeth was not possible. The dentary, supradentary/coronoid and splenial may have been able to move dorsally relative to the back of the jaw, but such rotation must have been slight because the inter-fingering of the coronoid-surangular suture is complex and firm.

A very different joint, also termed the intramandibular jaw joint, is present in the extinct mosasaurs and snakes (Lee et al., 1999). The dorsal part of the joint consists of flexible connective tissue and a bony articulation is only present ventrally between the splenial and angular. The joint was restricted to mostly mediolateral movement (horizontal flexion). In these groups, the joint appears to be an adaptation for using the dentition in the capture (grasping) of large prey, rather than for mastication and crushing.

The dentary in anguimorph lepidosaurs that have an intramandibular jaw joint is proportionally shorter than in those that lack this joint (McDowell and Bogert, 1954; Sereno and Novas, 1993). A grasping bite was probably used in members of Abelisauridae (Theropoda) possessing short dentaries and intramandibular jaw joints that allowed large movements of the anterior segment in relation to the back of the jaw (Bonaparte et al., 1990). The dentaries of tyrannosaurids and sinraptorids are relatively long compared to those of Abelisauridae. Because the tyrannosaurid lower jaw was rigid with little movement at the intramandibular joint, they are better suited for delivering crushing bites. Fusion of the coronoid and supradentary, elongation of the medial process of the surangular, and the presence of high interlocking ridges and deep grooves on the articular and prearticular are all secondary adaptations to a relatively rigid lower jaw in tyrannosaurids. It is not surprising that they generated the strongest bite forces known (Erickson et al., 1996).

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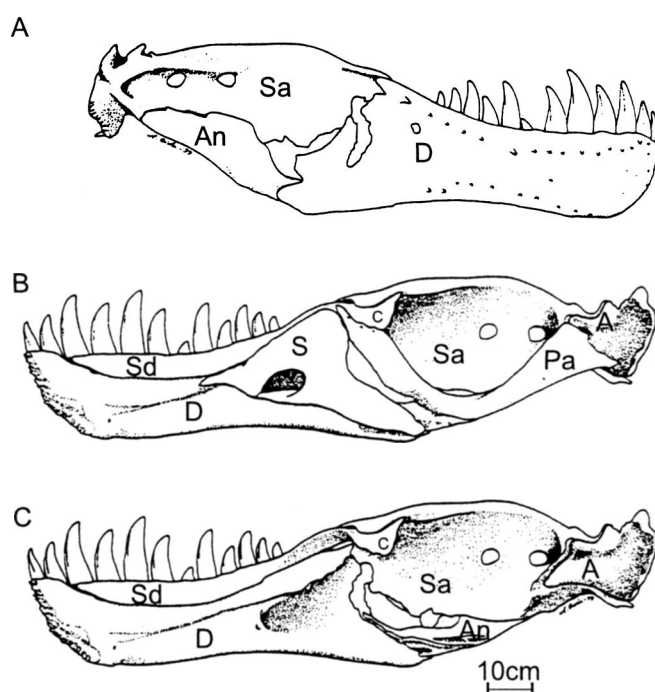


FIGURE 2. A–C, *Tyrannosaurus rex* BHI-3033, the lower jaw in lateral view (A), medial view (B), and in medial view with the prearticular and splenial removed (C). Abbreviations as for Figure 1.

son for making the specimens of *Tarbosaurus* and *Tyrannosaurus* available for our study. Thanks to Hans Arne Nakrem, Bjørn Lund, Øyvind Enger and Tomasz Sulej for their skillful preparation and casting of the *Tarbosaurus* specimen. We are also thankful to Thomas R. Holtz, Gregory M. Erickson and Christopher A. Brochu for their thorough reviews. This work was supported by the Norwegian Research Council (grant no. 122898/410).

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