

ON THE DENTARY IN THE FUKUI PREFECTURAL DINOSAUR MUSEUM OF *GORGOSAURUS LIBRATUS* (THEROPODA: TYRANNOSAURIDAE) FROM THE DINOSAUR PARK FORMATION (UPPER CRETACEOUS) OF ALBERTA, CANADA

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ABSTRACT

An isolated right dentary of the tyrannosaurid *Gorgosaurus libratus* in the Fukui Prefectural Dinosaur Museum found in the Dinosaur Park Formation in southern Alberta, Canada, is described. The referral of the dentary to *G. libratus* is based on several morphological features, including the lack of the posteroventral transitional point in the anterior step of the lingual bar, the foramen intermandibularis oralis overlaps ventrally the anterior terminus of the Meckelian groove, and the anterior terminus of the Meckelian groove contacts the posterior margin of the dentary symphysis. The excellent preservation of the dentary allows for detailed comparisons with other tyrannosaurids, especially with its close relative *Albertosaurus sarcophagus* with which *G. libratus* is often synonymized. The two taxa can be differentiated based on the overall morphology of the anterior step of the lingual bar, position of the foramen intermandibularis oralis with respect to the anterior terminus of the Meckelian groove, the posterior step of the Meckelian fossa, and the articulation facet and notch for the splenial. This work provides further support for recognizing *G. libratus* as a taxon distinct from and not a synonym of *Albertosaurus*.

Key words : *Gorgosaurus*, *Albertosaurus*, Albertosaurinae, Tyrannosauridae, Theropoda, Upper Cretaceous, Dinosaur Park Formation, Canada

INTRODUCTION

Tyrannosaurid dinosaurs were large-bodied predators, which, for most of the Campanian-Maastrichtian dominated the terrestrial ecosystems in Asia and North America (e.g., Russell, 1970; Currie, 2003; Holtz, 2004; Hone et al., 2011; Dalman, 2013). This highly specialized clade of carnivorous dinosaurs is characterized by massive skulls and short didactyl forelimbs (e.g., Osborn, 1905; Lambe, 1917; Brochu, 2003; Holtz, 2004). Since the discovery of the first skeleton of *Tyrannosaurus rex* over a century ago in the Lance Formation in Wyoming, several new taxa have been recovered from the Upper Cretaceous rocks throughout the western part of North America. Currently eight North American species have been identified representing two subclades: Albertosaurinae, which includes *Albertosaurus sarcophagus* and *Gorgosaurus libratus*, and Tyrannosaurinae, which includes *Bistahieversor sealeyi*, two species of the genus *Daspletosaurus*, *D. horneri* and *D. torosus*, *Lythronax argestes*, the highly controversial *Nanotyrannus lancensis*, *Nanuqsaurus*

hoglundi, *Teratophoneus curriei*, and *Tyrannosaurus rex*. Specimens currently assigned to *Daspletosaurus* and *Gorgosaurus* collected from the Campanian deposits of the Judith River and Two Medicine formations in Montana most likely represent new species (Currie et al. 2005; Stein and Triebold, 2013; Dalman and Lucas, 2015). Similarly, fragmentary specimens of tyrannosaurids recovered from the San Juan Basin in northwestern New Mexico, the Aguja and Javelina formations of Texas, and isolated teeth from the Corral de Enmedio and Lomas Coloradas formations of Sonora, Mexico most likely represent previously unrecognized taxa, which provide further support for the morphological and taxonomic diversity of these iconic predators (e.g., Jasinski et al., 2011; Lehman and Wick, 2012; Serrano-Brañas et al., 2014, 2017).

Although tyrannosaurids are the most studied carnivorous dinosaurs, their species-level taxonomy is still not clearly resolved. *Gorgosaurus* is one of the most commonly recovered tyrannosaurids in North America, and the majority of specimens have been found in the Campanian deposits of the Dinosaur Park Formation (76.9–75.8 Ma) in southwestern Alberta, Canada, and the Judith River (80–75 Ma) and the Two Medicine (83.5–74.9 Ma) formations in Montana, USA (Lambe, 1917; Currie, 2003, 2005; Dalman and Lucas, 2015). Among tyrannosaurids, *Gorgosaurus*

Received April 30, 2017. Accepted September 28, 2017.

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has most often been synonymized with *Albertosaurus* and referred to as *Albertosaurus libratus* (Russell, 1970; Carr, 1999, 2010; Carr and Williamson, 2000; Carr et al., 2017). In the past decade, new specimens of *Albertosaurus sarcophagus* and *Gorgosaurus libratus* have been recovered from the Upper Cretaceous of Alberta, Canada. These specimens allowed Currie (2003) to find numerous morphological features in the skull that clearly differentiate these taxa. In his study, however, Currie (2003) only briefly described the morphological features of the dentaries of *Albertosaurus* and *Gorgosaurus*.

This work presents the first detailed osteological description of an isolated dentary of *Gorgosaurus libratus* (FPDM-V 8062) found in the Dinosaur Park Formation in southwestern Alberta, Canada. FPDM-V 8062 was purchased by FPDM from a Japanese fossil collector who is now deceased. Detailed comparisons with the dentaries of *Albertosaurus sarcophagus* and other tyrannosaurids provide further evidence of the taxonomic distinctiveness of *A. sarcophagus* and *G. libratus*.

Institutional abbreviations

BHI: Black Hills Institute of Geological Research, Hill City, South Dakota, USA; **BMNH**: British Museum of Natural History, London, UK; **BMR**: Burpee Museum of Natural History, Rockford, Illinois, USA; **FPDM**: Fukui Prefectural Dinosaur Museum, Fukui, Japan; **IGM**: Institute of Geology (currently Institute of Paleontology and Geology), Ulaan Baatar, Mongolia; **NMMNH**: New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; **TMP**: Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UMNH**: Natural History Museum of Utah, Salt Lake City, Utah, USA; **ZCDM**: Zhucheng Dinosaur Museum, Zhucheng, China; **ZPAL**: Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland.

SYSTEMATICS

FPDM-V8062, a complete right dentary with teeth in the Fukui Prefectural Dinosaur Museum, is assigned to *Gorgosaurus libratus* based on several key characters, such as the lack of the posteroventral transitional point in the anterior step of the lingual bar, the foramen intermandibularis oralis overlaps ventrally the anterior terminus of the Meckelian groove, and the anterior terminus of the Meckelian groove contacts the posterior margin of the dentary symphysis. Furthermore, the surface of the inflection point where, the ventral and the anterior margins of the dentary meet, is strongly rugose and projects ventrally beyond the ventral margin of the dentary. The posterior step in the dentary is well defined, whereas the notch for the articulation with the splenial is diminutive. The anterior portion of the facet for the splenial is dorsoventrally wide.

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
THEROPODA Marsh, 1881
COELUROSAURIA von Huene, 1914

TYRANNOSAURIDAE Osborn, 1906
ALBERTOSAURINAE Currie et al., 2003
GORGOSAURUS LIBRATUS Lambe, 1914

Material.—FPDM-V8062, a complete right dentary with teeth, described here for the first time (Fig. 1).

Locality and age.—Dinosaur Provincial Park, southern Alberta, Canada. Upper Cretaceous (Campanian) Dinosaur Park Formation.

DESCRIPTION

Dentary.—The length of the preserved dentary FPDM-V8062 is 54 cm (Fig. 1). The dentary is mediolaterally thick along the tooth row; however, it gradually narrows at the posterior end. The dentary has 15 well-preserved teeth. Nearly all of the teeth are fully erupted, except for d5, d8, d11, and d14, which are partially erupted. The alveoli are nearly circular, except for alveolus 1, which is mediolaterally compressed and has an elliptical shape. The dorsoventral depth of the dentary is not uniform throughout its length. The dorsoventral depth of the dentary is 10 cm at alveolus 5 and increases more posteriorly, so that, it is 11 cm at alveolus 9 and, is 15 cm at alveolus 15.

The lateral surface of FPDM-V8062 is perforated by several mental foramina. The foramina are arranged in two parallel rows: alveolar and ventrolateral rows. Two anteriormost mental foramina in the alveolar row are situated directly ventral to the alveolar margin of the first alveolus. These foramina are nearly 1 cm apart from each other. The first foramen is approximately 0.5 cm ventral to the alveolar margin of the dentary, whereas the second foramen is 1 cm ventral to the alveolar margin, so that the

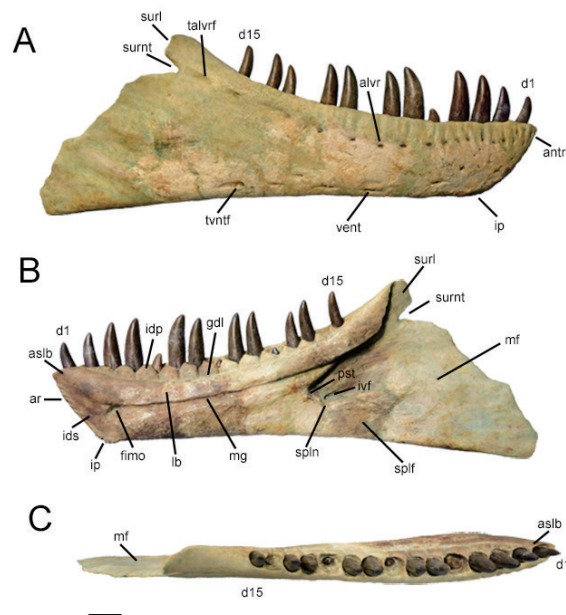


FIGURE 1. Right dentary of *Gorgosaurus libratus* (FPDM-V8062). **A**, lateral view; **B**, medial view; **C**, dorsal view. Abbreviations are shown in Appendix 1. Bar = 5 cm.

foramina are not parallel to the alveolar margin of the dentary. The third foramen is posteroventral to the second foramen, 1 cm apart from the latter and 2 cm ventral to the alveolar margin of the dentary. The consecutive mental foramina parallel the alveolar margin. At the level of alveoli 2 and 4, the foramina are tightly spaced, approximately 1 cm apart from each other and 2 cm ventral to the alveolar margin of the dentary. At the level of alveolus 5, the foramina become gradually larger and are more widely separated from each other. The distance between each consecutive foramen increases from 1.5 cm to 4 cm. In the posterior region, the foramina are situated within an elongate, fossa-like depression. At the level of alveolus 12, the fossa-like depression is 4 cm long and 0.5 cm wide. The two consecutive, more posterior fossae are 2 cm and 3 cm long, and 0.3 cm wide.

The ventral row of mental foramina in FPDM-V8062 parallels the alveolar row and the ventral margin of the dentary. The foramina are elongate and widely spaced. The lengths of the foramina are between 2 cm and 3 cm. The distalmost foramen is large and has a circular shape. Associated with this foramen is an elongate, shallow, fossa-like depression that is directly posterior to it. The fossa-like depression is 3.2 cm long and 1 cm wide.

Another row of mental foramina is situated on the anterior surface of the dentary. The row extends dorsoventrally, uninterrupted to the inflection point (= transition point of Carr et al., 2005) where the ventral and the anterior margins of the dentary meet. The foramina are large, circular and deep. A portion of the first anterodorsal foramen is visible in lateral view, whereas all other foramina in the series are only visible in anterior view. The inflection point is convex and projected ventrally.

The medial surface of the dentary is flat. The interdental plates are well preserved. The first interdental plate is entirely covered by the anterior step of the lingual bar (Dalman and Lucas, 2015; Fig. 2). Most of the second interdental plate is also covered by the lingual bar, with only a small posterior portion being visible. The third through seventh interdental plates are the tallest in the series. Their anterior and posterior surfaces are vertical and

parallel to each other. The dorsal surface of each interdental plate forms a low triangle; idp8 and idp9 have the same morphology as more anterior interdental plates, however, they are progressively smaller. Each consecutive interdental plate in the posterior region of the dentary, idp10 through idp15, gradually decreases in size but maintains a triangular shape. As in other tyrannosaurids, the interdental plates in FPDM-V8062 are unfused to each other; they flare out medially, and they are separated by a groove for the dental lamina ventral to the tooth row. In the anterior region of the dentary, the groove for the dental lamina curves anterodorsally, and, in the posterior region it curves posterodorsally.

In life, the interdental plates in tyrannosaurids and other non-avian theropods were covered by the ossified supradentary/coronoid (e.g., Molnar, 1991; Brochu, 2003; Currie, 2003; Hurum and Sabath, 2003; Dalman and Lucas, 2015). FPDM-V8062 does not preserve the supradentary. However, based on the overall height of the interdental plates and the outline of the dorsal surface of the lingual bar, the supradentary in FPDM-V8062 would likely have covered the posterior portion of the second interdental plate and all other interdental plates lingually. The first interdental plate and the anterior portion of the second interdental plate are covered by the anterior step of the lingual bar (Dalman and Lucas, 2015; Fig. 2). In FPDM-V8062, the dorsal surface of the anterior step of the lingual bar parallels the alveolar row (= tooth row). The dorsal surface of the step extends posteriorly and terminates directly anterior to the second alveolus. This terminal point is identified here as the posterodorsal transition point of the anterior step of the lingual bar. Directly posterior to the posterodorsal transition point, the lingual bar gently slopes ventrally and continues posteriorly and terminates approximately 8 cm posterior to alveolus 15.

The lingual bar is elongate with a flat medial surface, underlying the interdental plates and overlying the Meckelian groove. Overall length of the lingual bar is 43 cm. In the anterior region, the lingual bar is slightly flared and dorsoventrally deep and shallow throughout most of the anteroposterior length. The

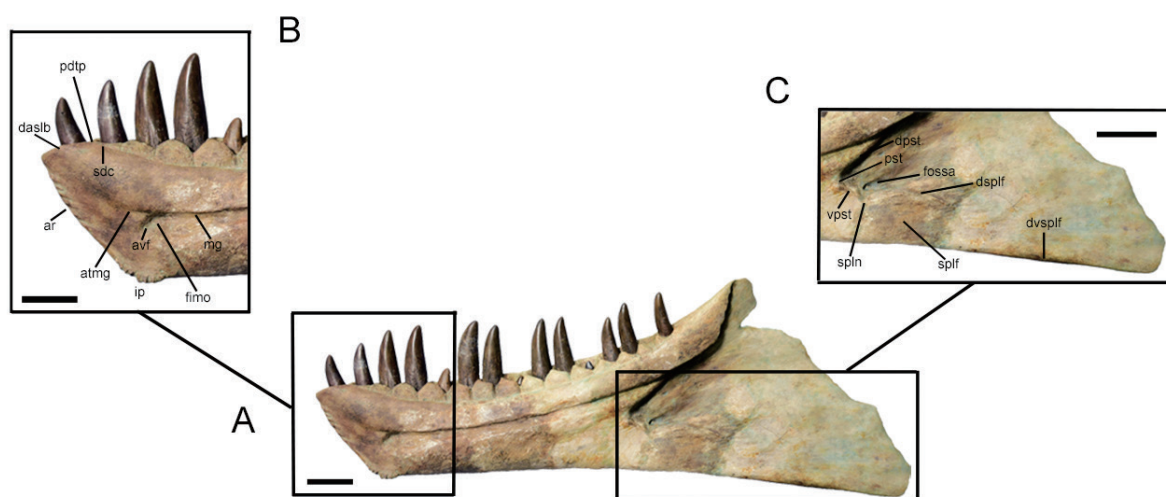


FIGURE 2. Right dentary of *Gorgosaurus libratus* (FPDM-V8062). A, medial view; B, close up of the anterior end in medial view; C, close up of the posterior end in medial view. Abbreviations are shown in Appendix 1. Bar = 5 cm.

posterior portion of the lingual bar (= lappet of Brusatte et al., 2012) covers the dorsal portion of the Meckelian fossa medially. The medial prong for the articulation with the surangular is not preserved, whereas the lateral prong is preserved and nearly complete. A sharp notch separates the lateral prong from the dorsal margin of the Meckelian fossa.

The anteroventral surface of the lingual bar is slightly inclined anterodorsally and makes direct contact with the interdental symphysis and with the dorsal portion of the foramen intermandibularis oralis (Fig. 2). For most of its anteroposterior length, the ventral surface of the lingual bar is straight. As a result, the dorsal and the ventral surfaces of the lingual bar are parallel to each other.

Directly ventral to the lingual bar is the Meckelian groove. It is an elongate and well-defined feature. The anterior portion of the Meckelian groove at the level of alveoli 2 through 6 is situated at the mid-height of the dentary. At the level of alveoli 10 through 15, the Meckelian groove is inclined posterodorsally, so that it is dorsal to the mid-height of the dentary. Throughout its length the Meckelian groove has a uniform dorsoventral depth of approximately 0.5 cm. At the level of alveolus 3, the Meckelian groove contacts directly the foramen intermandibularis oralis (Fig. 2). Anterior to the foramen, a small terminal end of the Meckelian groove at the level of alveolus 2 extends anteriorly and contacts the posterior margin of the dentary symphysis. The posterior end of the Meckelian groove terminates at the level of alveolus 14 and directly dorsal to the posterior step for the contact with the splenial. The posterior step emerges from the posterodorsal surface of the ventral portion of the dentary and laterally envelops the intermandibular vascular foramen (Fig. 2). The anterior end of the step is concave and situated at the level of alveolus 12. The ventral portion of the step is significantly shorter than the dorsal one. It slopes posteroventrally and terminates at the level of alveolus 13. Directly ventral to it is a shallow notch for the articulation with the splenial (Fig. 2). The anterior and ventral portions of the notch form a 90° angle. A single, well-defined intermandibular vascular foramen is situated slightly dorsal to the ventral portion of the posterior step (Fig. 2). The foramen is circular and deep. A characteristic fossa-like structure is associated with the foramen. The fossa slightly flares posteriorly and merges with the Meckelian fossa. The surface of the Meckelian fossa is smooth and flat.

A flat articular facet for the splenial extends along the ventral margin of the Meckelian fossa (Fig. 2). The facet is extensive at the anterior end. Its dorsal surface is strongly convex and dorsoventrally wide. The convexity extends approximately 8 cm and terminates at the level of and posterior to alveolus 15. Immediately posterior to this level, the facet becomes significantly narrower.

Anteriorly, the ventral and the anterior margins of the dentary meet at the inflection point ventral to the level of alveoli 2 and 3 and brace the dentary symphysis medially (Fig. 2). In this region, the dentary is convex and strongly rugose. The rugosity extends anteroposteriorly along the convex surface of the inflection point. Along its anteroventral margin the rugosity consists of several

short and well-defined grooves and ridges. The medial surface of the inflection point is slightly raised.

The dentary symphysis in FPDM-V8062 is long and, flat and has an elliptically-shaped smooth surface, which terminates posteroventrally at the level of alveolus 3 (Fig. 2). Along the anteromedial margin of the dentary symphysis extends a characteristic rugosity. The rugosity consists of short grooves and ridges, which are parallel to each other. However, this rugosity does not extend throughout the entire length of the anteromedial margin of the dentary symphysis. It originates nearly 1 cm ventral to the anteriormost end of the anterior step of the lingual bar and terminates at the level anterior to the foramen intermandibularis oralis (Fig. 2). The remaining portion of the anterior margin of the dentary symphysis between the terminal end of the rugosity and the inflection point is smooth.

A single foramen intermandibularis oralis is present at the level of alveolus 4 (Fig. 2). The foramen overlaps ventrally the anterior portion of the Meckelian groove. However, it does not contact the dentary symphysis. Instead, a characteristic fossa anteroventral to the foramen and associated with it contacts the posterior margin of the dentary symphysis.

DISCUSSION

Russell (1970), in his revision of the North American tyrannosaurids, synonymized *Albertosaurus* and *Gorgosaurus*. At the time, Russell (1970) was unable to find any morphological differences between these genera because of the lack of well-preserved specimens. However, the discovery of new specimens of *Albertosaurus* and *Gorgosaurus* in the past decade allowed Currie (2003) to find many morphological features in the skulls of these genera that clearly differentiate them. In his study, Currie (2003), however, only briefly described the morphological features of the dentaries of *Albertosaurus* and *Gorgosaurus* as well as those of other tyrannosaurids. Despite a detailed osteological description by Currie (2003), especially of *Albertosaurus* and *Gorgosaurus*, some other workers continued to synonymize these genera (e.g., Carr, 1999, 2010; Carr and Williamson, 2000, 2010; Carr et al., 2011, 2017). Both genera are classified as members of the Subfamily Albertosaurinae. Holtz (2004) suggested that *Appalachiosaurus montgomeriensis* (Carr et al., 2005) may also be a member of Albertosaurinae. *Albertosaurus* was a slightly larger and more robust animal than *Gorgosaurus* (Currie, 2003). When compared with other tyrannosaurids, *Albertosaurus* and *Gorgosaurus* have narrower skulls in the posterior region, and more numerous pits in the ventral surfaces of the maxillary palatal shelves for the accommodation of the dentary teeth than do tyrannosaurines (Currie, 2003). The occipital condyle is oriented ventrally in *Albertosaurus* and *Gorgosaurus*, but not to the same degree as in the tyrannosaurines (Currie, 2003). Finally, both genera have a single pneumatic foramen (pneumatopore) in the palatine, a morphological feature they share with *Appalachiosaurus montgomeriensis* and *Bistahieversor sealeyi*, whereas the derived tyrannosaurines (e.g., *Tyrannosaurus rex*) have two pneumatic foramina (Carr et al., 2005; Carr and

Williamson, 2010).

The referral of the isolated right dentary, FPDm-V8062, to *Gorgosaurus libratus* is supported by several morphological features and also by its stratigraphic position. *Gorgosaurus* is found exclusively in the Campanian deposits in the Dinosaur Park Formation, whereas *Albertosaurus* is found in the late Campanian and early Maastrichtian deposits of the Horseshoe Canyon Formation (Currie, 2003, 2005; Eberth and Currie, 2010; Bell and Currie, 2014). FPDm-V8062 can be differentiated from the dentaries of its closest relative, *Albertosaurus sarcophagus*, based on the following characters. In *A. sarcophagus*, the anterior step of the lingual bar is diminutive, especially its dorsal surface that parallels the alveolar row (Fig. 3). The posterodorsal transition point of the anterior step of the lingual bar is not well defined. As a result, the supradentary in *A. sarcophagus* covers the posterior portion of the first alveolus/interdental plate, whereas in *G. libratus* it does not reach the first alveolus/interdental plate. Furthermore, the foramen intermandibularis oralis in *A. sarcophagus* is ventral to the anterior terminus of the Meckelian groove, whereas in *G. libratus* the foramen overlaps the Meckelian groove ventrally. In both taxa the anterior terminus of the Meckelian groove contacts the posterior margin of the dentary symphysis. However, *A. sarcophagus* lacks the characteristic anterior fossa associated with the foramen intermandibularis oralis, whereas in *G. libratus* the fossa contacts the posterior margin of the dentary symphysis.

The lingual bar in *Albertosaurus sarcophagus* is dorsoventrally wider than it is in *Gorgosaurus libratus* and not flared in the anterior region. Interestingly, the flaring of the anterior lingual bar is absent in juvenile, subadult and adult individuals of *A. sarcophagus* (Fig. 4). In *G. libratus*, the flaring of the anterior end of the lingual bar is present in individuals of all ontogenetic stages (Fig. 4).

The posterior step in the dentaries of *Albertosaurus sarcophagus* and *Gorgosaurus libratus* is situated ventral to the Meckelian groove (Figs. 2 and 3). In both taxa, the posterior step is diminutive. In *A. sarcophagus*, however, it is not as widely open as in *G. libratus*. In contrast, the notch for the articulation with the splenial is much better defined in *A. sarcophagus* than in *G. libratus* (Figs. 2 and 3). In *A. sarcophagus* the notch is elongate, narrow, and nearly parallels the Meckelian groove. Also, in *A. sarcophagus* a shallow depression-like structure is directly ventral to this notch, whereas in *G. libratus* this depression is absent (Figs. 2 and 3).

The facet for the articulation with the splenial in *Gorgosaurus libratus* is extensive, whereas it is an elongated structure, and its dorsal margin parallels the ventral margin of the dentary in *Albertosaurus sarcophagus* (Figs. 2 and 3). However, one exception is the isolated dentary TMP 1999.55.170, assigned to *G. libratus* by Currie (2003), from the Dinosaur Park Formation (Fig. 5). In TMP 1999.55.170, the facet for the articulation with the splenial closely resembles in overall morphology that of *G. libratus* (Fig. 2). However, there are several morphological features present in TMP 1999.55.170 that are different from *Gorgosaurus*, such as relatively high tooth count (17), the anterior step of the lingual bar covers two instead of one alveolus, and the foramen intermandibularis is situated directly at the anterior terminus of the Meckelian groove (Fig. 5), which is characteristic of *Daspletosaurus*. Therefore, it is very likely that the TMP 1999.55.170 dentary was misidentified and most likely belongs to a tyrannosaurine tyrannosaurid, probably *Daspletosaurus*, and not *Gorgosaurus*.

Among tyrannosaurids, the alioramines exhibit dentary morphology similar to that of the albertosaurines. The holotype of *Alioramus altai*, a member of Alioramini, includes exceptionally well-preserved dentaries. The dentaries of *A. altai* were described

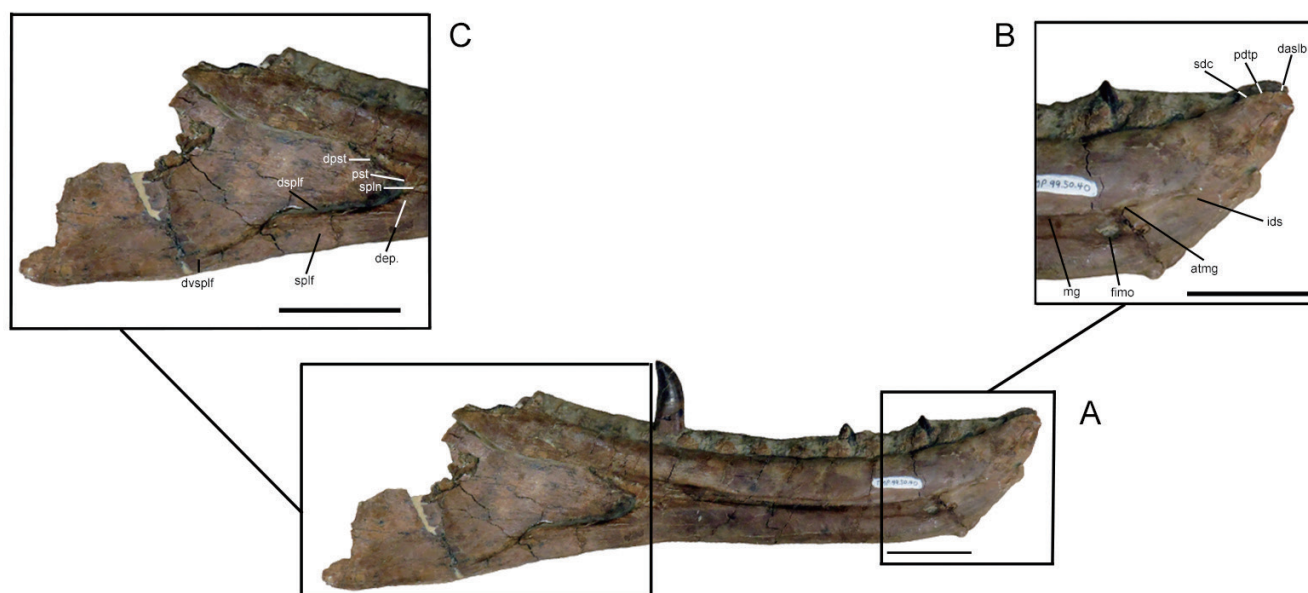


FIGURE 3. Left dentary of *Albertosaurus sarcophagus* (TMP 1999.50.40). A, medial view; B, close up of the anterior end in medial view; C, close up of the posterior end in medial view. Abbreviations are shown in Appendix 1. Bar = 5 cm.

previously by Brusatte et al. (2012). However, some of the morphological features here described were not mentioned previously for this taxon (Fig. 6). The anterior step of the lingual bar in *A. altai* closely resembles that of *Gorgosaurus libratus*, but differs from that of *Albertosaurus sarcophagus*. The step is diminutive and covers only the first alveolus/interdental plate. As in *G. libratus*, the anterior step of the lingual bar in *A. altai* has the posterodorsal transitional point, and its dorsal surface parallels the alveolar row. The dorsoventral width of the lingual bar in *A. altai* seems uniform throughout its length. The anterior terminal end of the Meckelian groove directly contacts the foramen intermandibularis oralis, but does not contact the posterior margin of the dentary symphysis. At the level of alveolus 11, the Meckelian groove begins to widen dorsoventrally and continues to widen as it progresses posteriorly. In both *A. sarcophagus* and *G. libratus*, the Meckelian groove is a narrow structure. However, in isolated juvenile dentaries of *A. sarcophagus* (TMP 2007.007.0001) and of *G. libratus* (TMP 86.144.01; Fig. 7), the posterior portion of the Meckelian groove is slightly wider than the anterior end, suggesting that the wider posterior end of the

Meckelian groove is a juvenile characteristic. Indeed, Brusatte et al. (2012) referred the holotype specimen of *A. altai* (IGM 100/1844) to a juvenile.

The posterior step in the dentary of *A. altai* is well defined (Fig. 6). It lies directly on the long axis of the Meckelian groove. The dorsal and ventral surfaces of the step are angled slightly. In contrast, in *Albertosaurus sarcophagus*, the dorsal surface of the step is angled, whereas the ventral surface nearly parallels the posterior end of the Meckelian groove. In *Gorgosaurus libratus*, the ventral surface of the step is strongly angled. However, in an isolated dentary of *G. libratus* (TMP 1983.36.134), the ventral surface of the posterior step parallels the Meckelian groove (Fig. 8). This indicates that this feature is variable and may also change during ontogeny.

The notch for the articulation with the splenial is well defined in *Alioramus altai* (Fig. 6). It is a short and narrow structure that is aligned with the ventral margin of the Meckelian groove. In contrast, in *Albertosaurus sarcophagus* and *Gorgosaurus libratus*, the notch is diminutive and is ventral to the Meckelian groove. The facet for the articulation with the splenial in *A. altai* closely

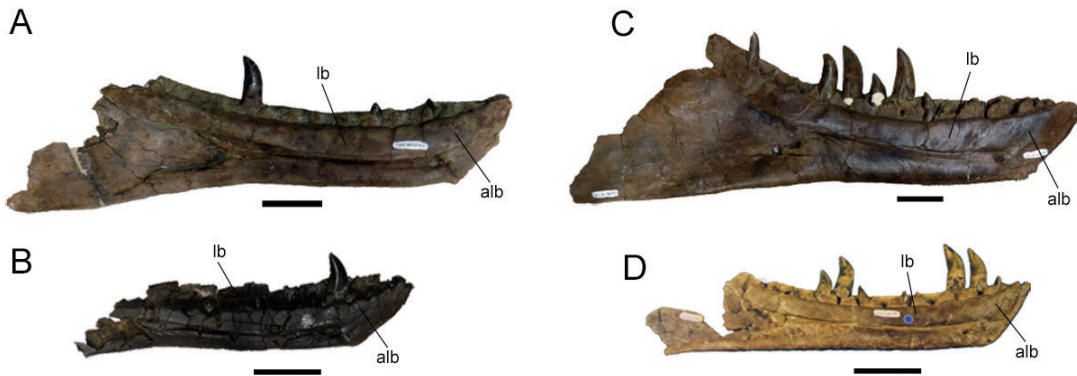


FIGURE 4. Dentaries of albertosaurinae tyrannosaurids in medial view. **A**, *Albertosaurus sarcophagus* (subadult) (TMP 1999.50.40); **B**, *Albertosaurus sarcophagus* (juvenile) (TMP 2007.007.0001); **C**, *Gorgosaurus libratus* (adult) (TMP 1983.36.134) (right dentary reversed); **D**, *Gorgosaurus libratus* (juvenile) (TMP 1986.144.01) (right dentary reversed). Abbreviations are shown in Appendix 1. Bar = 5 cm.

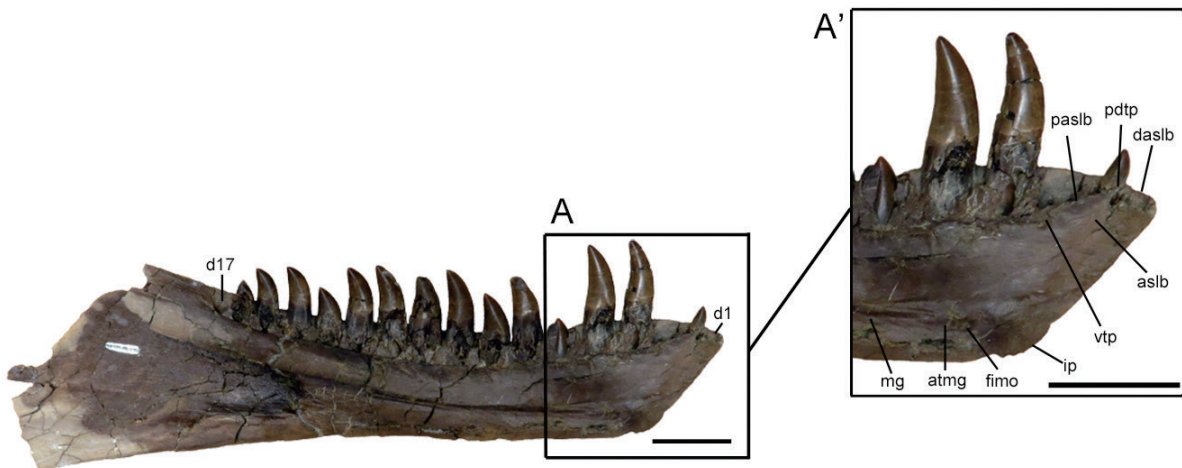


FIGURE 5. Left dentary (TMP 1999.55.170) previously assigned to *Gorgosaurus libratus*. **A**, medial view; **A'**, close up of the anterior end in medial view. Abbreviations are shown in Appendix 1. Bar = 5 cm.

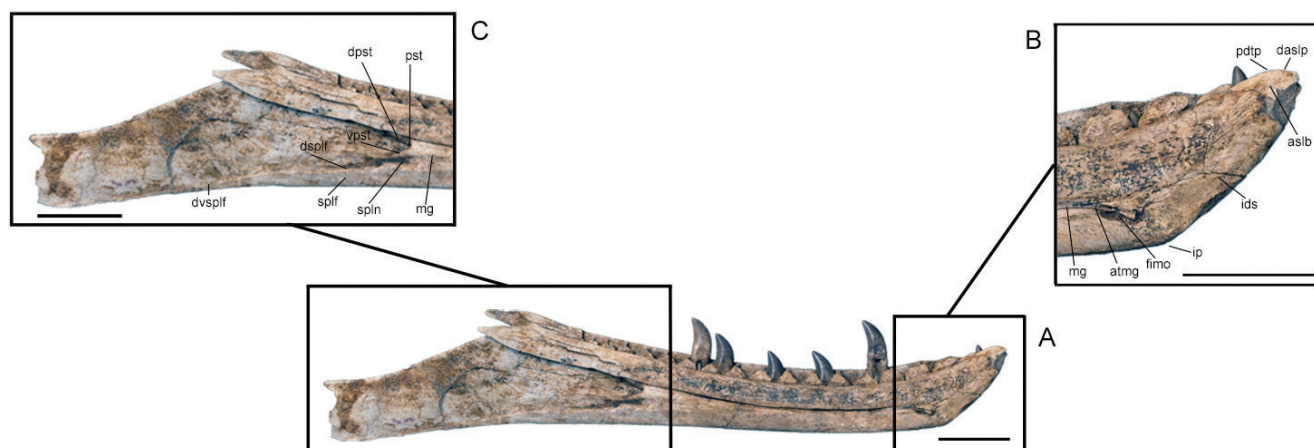


FIGURE 6. Left dentary of *Alioramus altai* (IGM 100/1844). **A**, medial view; **B**, close up of the anterior end in medial view; **C**, close up of the posterior end in medial view. Abbreviations are in Appendix 1. Bar = 5 cm.

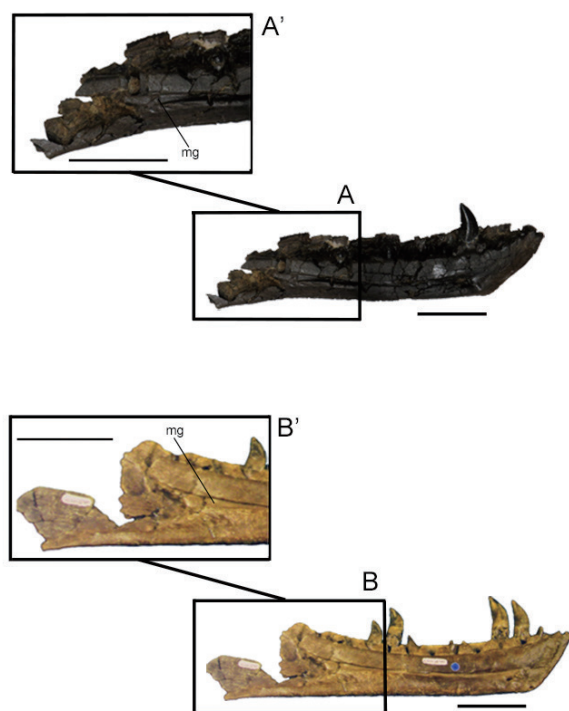


FIGURE 7. Dentaries of juvenile albertosaurinae tyrannosaurids. **A**, *Albertosaurus sarcophagus* (TMP 2007.007.0001); **B**, *Gorgosaurus libratus* (TMP 1986.144.01) (right dentary reversed). Abbreviations are in Appendix 1. Bar = 5 cm.

resembles that of *A. sarcophagus*. It is elongated, and its dorsal margin parallels the ventral margin of the dentary.

The various morphological features in the dentaries of tyrannosaurines differ from those of *Albertosaurus* and *Gorgosaurus* and from *Alioramus*. They also differ among taxa. The anterior step of the lingual bar in all known tyrannosaurines, such as *Bistahieversor*, *Daspletosaurus*, *Lythronax*, *Nanotyrannus*, *Nanuqsaurus*, *Teratophoneus*, *Tarbosaurus*, *Tyrannosaurus* and

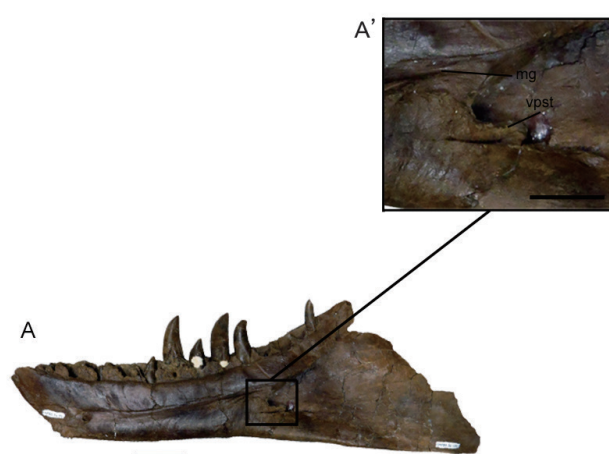


FIGURE 8. Right dentary of *Gorgosaurus libratus* (TMP 1983.36.134). **A**, medial view; **A'**, close up of the posterior area in medial view. Abbreviations are in Appendix 1. Bar = 5 cm.

Zhuchengtyrannus, has both transitional points: posterodorsal and ventral (Dalman and Lucas, 2015). The anterior step of the lingual bar in some taxa is diminutive and covers only the first alveolus/interdental plate (e.g., *Bistahieversor* and *Nanotyrannus*; Fig. 9), whereas in other taxa the step is pronounced and covers the first and the second alveoli/interdental plates (e.g., *Daspletosaurus*, *Lythronax*, *Tarbosaurus*, *Tyrannosaurus*, and *Zhuchengtyrannus*; Fig. 10). Furthermore, among tyrannosaurines the posterior surface (towards the mouth) of the anterior step of the lingual bar, particularly in *Tyrannosaurus rex*, is vertical, giving it a nearly square-shaped appearance (Dalman and Lucas, 2015), whereas in all other taxa the posterior surface of the step is angled. The dentaries of derived tyrannosaurines such as *Tarbosaurus* and *Tyrannosaurus* lack the notch for the articulation with the splenial, but they possess the posterior step (Fig. 11), which is present in albertosaurines, alioramines, and in other less derived tyrannosaurines.

The position of the foramen intermandibularis oralis in tyrannosaurines varies among taxa. For example, in some taxa (e.g., *Bistahieversor*, *Daspletosaurus*, *Lythronax*, *Teratophoneus*, and *Tyrannosaurus*) the foramen intermandibularis oralis is at the anterior terminus of the Meckelian groove, whereas in

Tarbosaurus and *Zhuchengtyrannus* it is ventral to the anterior terminus of the Meckelian groove (Dalman and Lucas, 2015).

The shape of the interdental plates in tyrannosaurines also varies among taxa. In *Daspletosaurus* and *Lythronax*, the interdental plates are triangular in shape, whereas in *Tarbosaurus*,

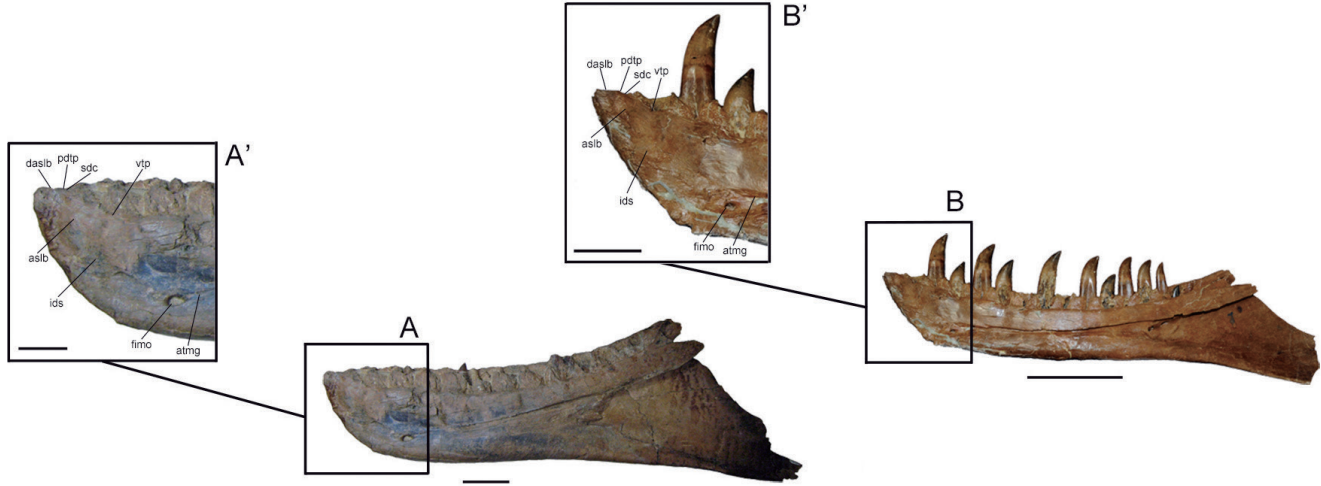


FIGURE 9. Dentaries of tyrannosaurine tyrannosaurids in medial view. **A**, *Bistahieversor sealeyi* (NMMNH P-27469); **A'**, close up of the anterior end of the dentary; **B**, *Nanotyrannus lancensis* (BMR P2002); **B'**, close up of the anterior end of the dentary. Abbreviations are in Appendix 1. Bar = 5 cm.

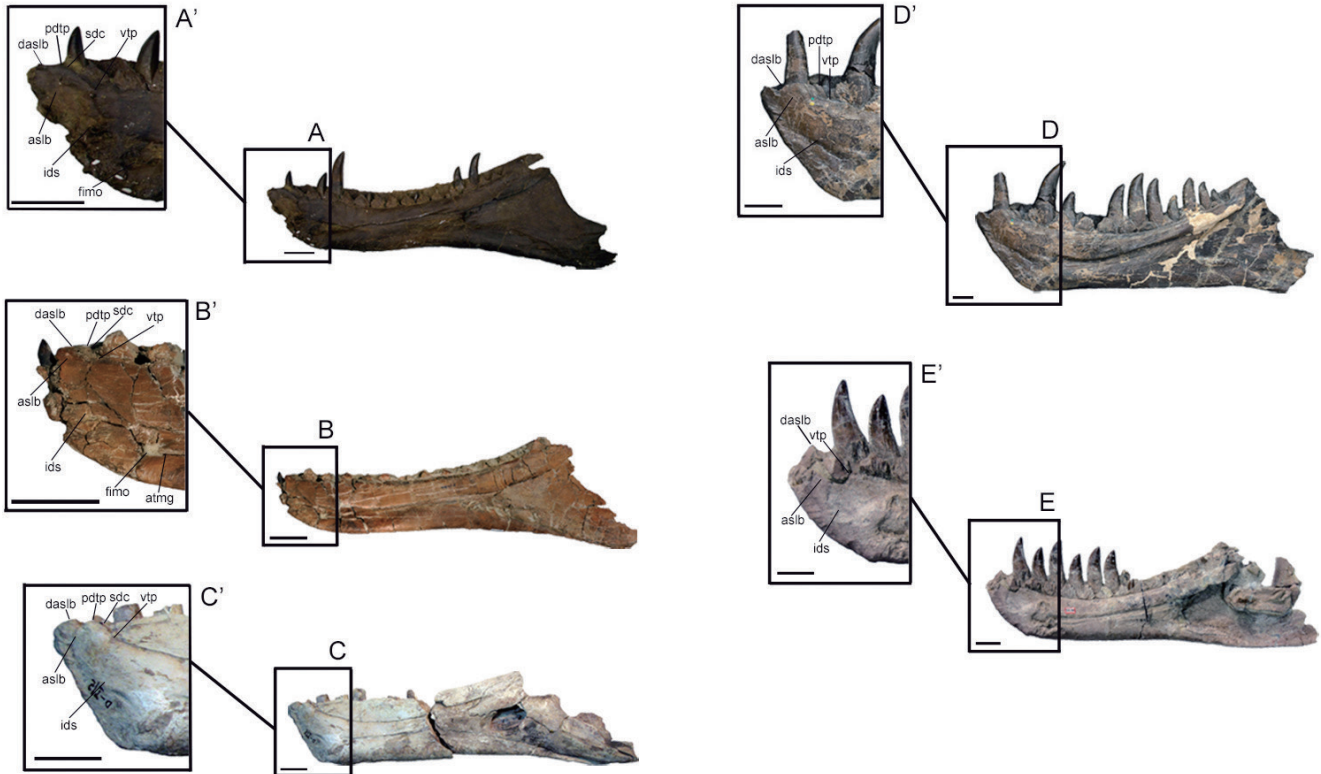


FIGURE 10. Dentaries of tyrannosaurine tyrannosaurids in medial view. **A**, *Daspletosaurus torosus* (TMP 2001.36.1); **A'**, close up of the anterior end of the dentary; **B**, *Lythronax argestes* (UMNH VP 20200); **B'**, close up of the anterior end of the dentary; **C**, *Tarbosaurus bataar* (ZPAL MgD-I/5); **C'**, close up of the anterior end of the dentary; **D**, *Tyrannosaurus rex* (BMNH R7994); **D'**, close up of the anterior end of the dentary; **E**, *Zhuchengtyrannus magnus* (ZCDM V0031); **E'**, close up of the anterior end of the dentary. Abbreviations are in Appendix 1. Bar = 5 cm.

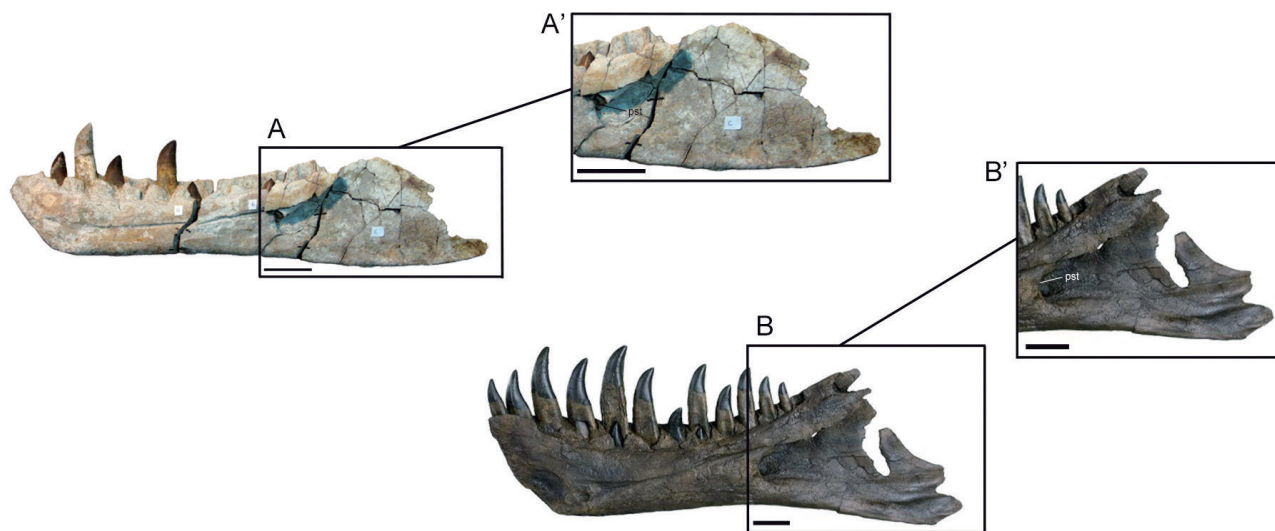


FIGURE 11. Dentaries of tyrannosaurinae tyrannosaurids in medial view. **A**, *Tarbosaurus bataar* (ZPAL MgD-I/1); **A'**, close up of the posterior end of the dentary; **B**, *Tyrannosaurus rex* (BHI 3033); **B'**, close up of the posterior end of the dentary. Abbreviations are in Appendix 1. Bar = 5 cm.

Tyrannosaurus, and *Zhuchengtyrannus* the interdental plates are large and rectangular (Figs. 9, 10). Furthermore, the anterior end of the lingual bar in tyrannosaurines is more strongly flared than it is in albertosaurines and especially in *Gorgosaurus libratus*.

CONCLUSIONS

The dentary of *Gorgosaurus libratus* is similar to that of *Albertosaurus sarcophagus* and in some respects to other tyrannosaurids, especially the alioramines. In this research, the dentary of *G. libratus* was described in detail, and its comparison with its closest relative, *A. sarcophagus*, shows several morphological features upon which these taxa are differentiated. Furthermore, the dentary of *Alioramus altai* shares many morphological features with both *A. sarcophagus* and *G. libratus*, suggesting a closer affinity with these taxa than with tyrannosaurines. This research supports the distinctiveness of *G. libratus*.

ACKNOWLEDGMENTS

We thank Dr. Teppei Sonoda (Fukui Prefectural Dinosaur Museum) for access to the specimen and the permission to study it. We thank Daniel Brinkman (Yale Peabody Museum of Natural History) and Kate Wellspring (formerly at Beneski Museum of Natural History) for access to specimens. We are grateful to Steve L. Brusatte, Philip J. Currie, David W. E. Hone, Jørn H. Hurum, Steven E. Jasinski, Mark A. Loewen, and Lawrence M. Witmer for sharing photographs of specimens and the permission to use them in our study. The paper benefited also from reviews by W. Scott Persons IV (University of Alberta) and Takanobu Tsuihiji (The University of Tokyo).

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APPENDIX 1

Anatomical Abbreviations

alb, anterior lingual bar; **alvr**, alveolar row of mental foramina; **antr**, anterior row of mental foramina; **ar**, anterior rugosity; **aslb**, anterior step of the lingual bar; **atmg**, anterior terminus of the Meckelian groove; **avf**, anteroventral fossa associated with the foramen intermandibularis oralis; **d1**, **d15**, **d17**, dentary tooth position; **daslb**, dorsal surface of the anterior step of the lingual bar; **dpst**, dorsal surface of the posterior step; **ds**, dentary symphysis; **dsplf**, dorsal margin/surface of the splenial facet; **dvspflf**, dorsoventral depth of the posterior portion of the splenial facet; **fimo**, foramen intermandibularis oralis; **fossa**, fossa

associated with intermandibular vascular foramen; **gdl**, groove for dental lamina; **idp**, interdental plate; **ip**, inflection point of the dentary; **ivf**, intermandibular vascular foramen; **lb**, lingual bar; **mf**, Meckelian fossa; **mg**, Meckelian groove; **paslb**, posterior surface (towards the mouth) of the anterior step of the lingual bar; **pdtp**, posterodorsal transition point of the anterior step of the lingual bar; **pst**, posterior step; **sd**, supradentary contact; **splf**, splenial facet; **spln**, splenial notch; **surl**, lateral prong for articulation with surangular; **surnt**, articular notch between lateral and medial prongs for articulation with surangular; **talvrf**, posterior terminal alveolar mental foramen; **tvntf**, posterior terminal mental foramen; **vent**, ventral row of mental foramina; **vtp**, ventral transition point of the anterior step of the lingual bar; **vpst**, ventral surface of the posterior step.