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Citation for published version:

Brusatte, S, Carr, TD, Williamson, TE, Holtz, TR, Hone, DWE & Williams, S 2016, 'Dentary groove morphology does not distinguish 'Nanotyrannus' as a valid taxon of tyrannosauroid dinosaur. Comment on: "Distribution of the dentary groove of theropod dinosaurs: implications for theropod phylogeny and the validity of the genus *Nanotyrannus* Bakker et al., 1988"', *Cretaceous Research*, vol. 65, pp. 232-237. <https://doi.org/10.1016/j.cretres.2016.02.007>

Digital Object Identifier (DOI):

[10.1016/j.cretres.2016.02.007](https://doi.org/10.1016/j.cretres.2016.02.007)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Cretaceous Research

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Dentary groove morphology does not distinguish ‘*Nanotyrannus*’ as a valid taxon of tyrannosauroid dinosaur. Comment on: “Distribution of the dentary groove of theropod dinosaurs: implications for theropod phylogeny and the validity of the genus *Nanotyrannus* Bakker et al., 1988”

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ABSTRACT: There has been considerable debate about whether the controversial tyrannosauroid dinosaur '*Nanotyrannus lancensis*' from the uppermost Cretaceous of North America is a valid taxon or a juvenile of the contemporaneous *Tyrannosaurus rex*. In a recent Cretaceous Research article, Schmerge and Rothschild (2016) brought a new piece of evidence to this discussion: the morphology of the dentary groove, a depression on the lateral surface of the dentary that houses neurovascular foramina. They argued that an alleged '*Nanotyrannus*' specimen, which possesses a groove, cannot be referable to *Tyrannosaurus rex*, which they considered as lacking the groove, and they hypothesized that '*Nanotyrannus*' is closely related to albertosaurine tyrannosauroids, which also are said to possess the groove. However, we show that the groove is a widespread feature of tyrannosauroids that is present in *T. rex* and many other specimens, and that it is an ontogenetically variable feature that changes from a sharp, deeply-impressed groove to a shallower sulcus as an individual matures. As a result, the presence or absence of a dentary groove does not clarify the validity of '*Nanotyrannus*' or its phylogenetic position among tyrannosauroids. We consider it most parsimonious that '*Nanotyrannus*' specimens belong to juvenile *T. rex*.

1) Introduction

In a recent *Cretaceous Research* article, Schmerge and Rothschild (2016) argued that the controversial tyrannosauroid dinosaur ‘*Nanotyrannus lancensis*’ from the uppermost Cretaceous of North America is a valid taxon, as originally proposed by Bakker et al. (1988). There has been considerable debate recently about the affinities of ‘*Nanotyrannus*’, with some authors considering it a distinct taxon (e.g., Currie, 2003; Larson, 2013), but most tyrannosauroid specialists regarding its holotype skull (CMNH 7541) and other possibly referred specimens (e.g., BMRP 2002.4.1) as belonging to juveniles of the contemporaneous *Tyrannosaurus rex* (e.g., Carr, 1999; Brochu, 2003; Carr and Williamson, 2004; Holtz, 2004; Brusatte et al., 2010; Brusatte and Carr, 2016). These latter authors have recognized differences between purported ‘*Nanotyrannus*’ specimens (which are clearly juveniles based on bone histology and possession of characters seen in the early growth stages of other tyrannosauroids: Carr, 1999; Erickson, 2005) and large specimens of *T. rex*, but explain them as ontogenetically variable features that changed as juveniles grew into massive, deep-skulled, strong-biting adults.

Schmerge and Rothschild (2016) bring a new piece of evidence to the debate: the morphology of the dentary groove, a depression that extends anteroposteriorly across part of the lateral surface of the dentary and houses neurovascular foramina below the tooth alveoli. Based on the distribution of this feature, they argue that the alleged ‘*Nanotyrannus*’ specimen BMRP 2002.4.1, which possesses a groove, cannot be referable to *Tyrannosaurus rex*, which is said to lack this feature. They furthermore hypothesize that ‘*Nanotyrannus*’ is not particularly closely related to *Tyrannosaurus rex*, but groups with the albertosaurine tyrannosaurids (*Albertosaurus* and *Gorgosaurus*), which also are said to possess the groove. These interpretations hinge on

Schmerge and Rothschild's (2016) correct identification of the groove in tyrannosauroid specimens, their assertion that the groove is not an ontogenetically variable feature, and their contention that a single anatomical feature can be a 'key' characteristic for elucidating phylogenetic relationships.

In this response, we challenge these points. We show that the groove is a widespread feature of tyrannosauroids, and that it is ontogenetically variable. As a result, the presence or absence of a dentary groove does not clarify the validity of '*Nanotyrannus*' or its phylogenetic position among tyrannosauroids.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, NY, USA; **BMRP**, Burpee Museum of Natural History, Rockford, IL, USA; **BYU**, Brigham Young University, Provo, Utah, USA; **CMN**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **CMNH**, Cleveland Museum of Natural History, Cleveland, OH, USA; **FMNH**, Field Museum of Natural History, Chicago, IL, USA; **IGM**, Institute of Geology, Ulaan Baatar, Mongolia; **LH**, Long Hao institute of Geology and Paleontology, Hohhot, China; **MOR**, Museum of the Rockies, Bozeman, Montana, USA; **NMMNHS**, New Mexico Museum of Natural History and Science, Albuquerque, NM, USA; **PIN**, Paleontological Institute, Moscow, Russia; **RMM**, Red Mountain Museum, McWane Center, Birmingham, Alabama, USA; **ROM**, Royal Ontario Museum, Toronto, Ontario, Canada; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **ZCDM**, Zhucheng Dinosaur Museum, Shandong, China; **ZPAL**, Instytut Paleobiologii PAN, Warsaw, Poland.

2) The dentary groove as a phylogenetic character

Schmerge and Rothschild (2016:26) insinuate that the dentary groove had yet to be ‘anatomically defined’ and only recently had been included in phylogenetic character datasets, beginning with the tyrannosauroid-specific study of Brusatte et al. (2010). However, this is incorrect. There is a long legacy of phylogenetic characters relating to the dentary groove, and it has appeared in several iterations of the Theropod Working Group (TWiG) dataset, a 20+ year project that has conducted increasingly larger and more inclusive analyses of theropod phylogeny (e.g., Norell et al., 2001: character 73; Turner et al., 2007: character 71; Turner et al., 2012: character 69; Brusatte et al. 2014:, character 69). Part of this confusion stems from our (Brusatte and Carr’s) error in not attributing the historical usage of this character in our 2010 study.

The TWiG character was inspired by Currie’s (1987) description of the derived bird-like theropod *Troodon*, in which he noted that the primary neurovascular foramina on the lateral dentary were set into a groove. Additional comparisons by the TWiG team revealed that nearly all troodontids had this morphology, in which the neurovascular foramina are embedded into a sharp, dorsoventrally shallow, deeply impressed groove that is more pronounced across the middle and posterior regions of the dentary but becomes much more shallowly impressed as it dissipates anteriorly, in the symphyseal region and underneath the first several alveoli. This differs from the condition in other theropods, which early versions of the TWiG dataset described as having ‘superficial’ neurovascular foramina.

Later TWiG studies revealed that some dromaeosaurids (*Buitreraptor*, *Austroraptor*, *Shanag*), some early birds (e.g., *Pengornis*, *Yanornis*), the basal alvarezsauroid *Haplocheirus*, and some basal tyrannosauroids (*Guanlong*, *Proceratosaurus*, *Sinotyrannus*, *Yutyranus*) also possessed the deep groove of troodontids. This led Brusatte et al. (2010) to include the character

in their tyrannosauroid-specific dataset, which was later merged into the larger TWiG dataset by Brusatte et al. (2014). In doing so, Brusatte et al. (2010) redefined the character states so that they were more descriptive. The primitive ‘superficial’ condition, seen in most theropods, was defined as one in which the foramina are ‘distinct or set into a shallow groove posteriorly’. The derived condition, seen in troodontids and the handful of other theropods mentioned above, was defined as one in which the foramina are ‘set into a deep and sharp groove across the middle and posterior regions of the dentary’.

Among tyrannosauroids, the derived, deeply impressed, troodontid-style groove is present only in the basal clade Proceratosauridae. It is absent in all other tyrannosauroids, and is scored that way in the Brusatte et al. (2010, 2014) datasets, and in the recently published update of our tyrannosauroid dataset (Brusatte and Carr 2016). That is not to say that other tyrannosauroids do not have any type of groove on the dentary, just that they do not possess the distinctive troodontid-style condition. Indeed, many of them have shallower grooves that fall into the ‘superficial’ category.

Schmerge and Rothschild (2016), on the other hand, consider some derived tyrannosauroids like *Albertosaurus*, *Gorgosaurus*, *Dryptosaurus*, and putative specimens of ‘*Nanotyrannus*’ to possess what they consider as a ‘dentary groove’. Their concept of a dentary groove is much more inclusive than the strictly-defined feature in the TWiG dataset, and seems to be a catch-all that combines the troodontid condition (as seen in proceratosaurids) and the more shallow grooves that are commonly seen in other tyrannosauroids (see below).

3) Dentary grooves are widespread among tyrannosauroids

We prefer to distinguish between troodontid-style grooves and shallow grooves using the TWiG definitions, and will continue to do so in our phylogenetic analyses (e.g., Brusatte and Carr, 2016). However, in the following discussion, we employ Schmerge and Rothschild's (2016) more inclusive definition of a 'dentary groove', considering it as any longitudinal depression on the lateral surface of the dentary that includes a series of neurovascular foramina underneath the tooth row. Schmerge and Rothschild (2016) identify this type of groove in the BMRP 2002.4.1 skull of '*Nanotyrannus*', and also in *Albertosaurus*, *Gorgosaurus*, *Dryptosaurus*, and proceratosaurids. However, they consider it absent in all other tyrannosauroids, including *Bistahieversor*, *Alioramus*, *Tarbosaurus*, and *Tyrannosaurus*. In most cases these assessments were based on examination of published photographs, mostly of holotype specimens only, as Schmerge and Rothschild (2016:27) wanted to 'avoid controversy as to taxonomic assignment'.

In fact, a neurovascular groove on the lateral surface of the dentary is widespread among tyrannosauroids, although often it is shallow or even very shallow (particularly anteriorly in the symphyseal region) and can easily be missed in photographs. Contra to Schmerge and Rothschild (2016), it is present in specimens of *Raptorex* (LH PV18; Sereno et al., 2009: fig. 1), *Appalachiosaurus* (RMM 6670; Carr et al. 2005: fig. 12), *Bistahieversor* (Fig. 1G-H; NMMNHS P-27469, P-25049; Carr and Williamson, 2010: fig. 1), *Alioramus* (IGM 100/1844; Brusatte et al., 2012: fig. 32), *Teratophoneus* (BYU 9398; Carr et al., 2011: fig. 2; Loewen et al. 2013: fig. 3), *Daspletosaurus* (Fig. 1E-F; MN 8506; TMP 1994.143.001; Currie, 2003: fig. 33), *Tarbosaurus* (Fig. 1A-B; e.g., PIN 551-2/1, 551-12/1, 4216/3, 4216/1; ZPAL MgD-I/75, I/5), and *Tyrannosaurus* (Fig. 1C-D; e.g., CMN 9380; MOR 008; AMNH FARB 5027; Osborn, 1912: pl. 1, although we do concur with Schmerge and Rothschild [2016] that some *Tyrannosaurus* specimens like FMNH PR 2081 have such a shallow groove that it is essentially absent). We

have personally observed and studied all of these specimens, and photographs of some of the more salient ones are shown in Figure 1. The groove is also present on the tyrannosaurids *Lythronax* (Loewen et al., 2013: fig. 2) and *Zhuchengtyrannus* (ZCDM V0031; Hone et al., 2011: fig. 3), which were not considered by Schmerge and Rothschild (2016).

In some of these cases, we are considering the same specimens as Schmerge and Rothschild (2016) but our observations are at odds (e.g., *Raptorex*, *Appalachiosaurus*, *Bistahieversor*, *Alioramus*, *Teratophoneus*). The most likely explanation is that all Schmerge and Rothschild (2016) scored all of these taxa based on figures in published literature, which often do not clearly convey the extent and morphology of shallow grooves. In other cases, however, our disagreements have to do with Schmerge and Rothschild's (2016) strategy of targeting holotypes or small samples of taxa known from many specimens. For example, they score *Tarbosaurus* as lacking the groove based on a photograph of a single specimen (MPC-D 107/7) with either an absent or very shallow groove, whereas we have examined numerous other specimens in the Warsaw (ZPAL) and Moscow (PIN) collections that have grooves of varying morphology, from very shallow to deeply impressed (Fig. 1A-B). Therefore, by looking primarily at holotypes rather than larger hypodigms, Schmerge and Rothschild (2016) minimize the chance of recognizing variation in this trait. To effectively demonstrate this trait exists in only one state within a species (i.e., that it does not vary by ontogeny, sexual dimorphism, individual variation, or other causes), one needs to examine a larger number of individuals.

Our identification of a dentary groove in a wide variety of tyrannosauroids, including *Tyrannosaurus rex*, falsifies two main conclusions of Schmerge and Rothschild (2016): that the presence of a groove differentiates 'Nanotyrannus' from *T. rex*, and that the groove is unusually shared between 'Nanotyrannus' and albertosaurines (*Albertosaurus* and *Gorgosaurus*) to the

exclusion of other taxa. Instead, the groove is a common character of tyrannosauroids, and indeed theropods in general, that all of these taxa plesiomorphically retain from their distant ancestors. Simple presence or absence of a groove appears to have no bearing on tyrannosauroid phylogeny, although as discussed above, the presence of a troodontid-style deep, sharp groove is a proceratosaurid synapomorphy (Brusatte et al. 2010, 2014; Brusatte and Carr 2016).

4) Dentary grooves are ontogenetically variable in tyrannosauroids

Schmerge and Rothschild (2016:31) also argue that the dentary groove is an ontogenetically invariant feature in tyrannosauroids, meaning that juveniles and adults of the same taxon would have the same condition (presence or absence of the groove). This is based on two points: 1) their identification of the groove as absent in juvenile, subadult, and adult specimens of *Tyrannosaurus rex*, and 2) a philosophical argument that a ‘dramatic change’ like ‘metamorphosis’ would be needed to explain the loss of the groove as an individual matured, because the groove corresponds to a system of nerves that they assume to be developmentally conservative.

In fact, the morphology of the groove is highly ontogenetically variable in tyrannosauroids, and in some taxa clearly changes from a deeply-inset and pronounced structure in juveniles to a shallow and sometimes nearly indistinguishable sulcus in adults. This can be seen in the growth series of two tyrannosauroids. A remarkably preserved juvenile specimen of *Tarbosaurus* that died at two or three years of age has a deep, well-pronounced dentary groove (Tsuihiji et al., 2011: fig. 3). Much larger, subadult and adult *Tarbosaurus* retain dentary grooves, but they are much more shallowly impressed (Fig. 1A-B; PIN 551-2/1, 551-12/1,

4216/3, 4216/1; ZPAL MgD-I/75, I/5). In the same vein, a juvenile *Bistahieversor* specimen has a deep groove across the middle and posterior portion of its dentary, which approaches the troodontid-condition in having well-defined dorsal and ventral margins that completely enclose the neurovascular foramina (Fig. 1G; NMMNHS P-25049; Carr and Williamson, 2010: fig. 1B). An adult, by contrast, has a much shallower groove that is better defined ventrally than dorsally. The neurovascular foramina are larger and channel upwards, breaching the dorsal margin of the groove and thus making the groove appear as a less discrete structure (Fig. 1H; NMMNHS P-27469; Carr and Williamson, 2010: fig. 1A).

The ontogenetic trend from a deeply impressed to a shallow and indistinct groove is also seen in three taxa that were discussed by Schmerge and Rothschild (2016). First, in *Gorgosaurus*, a taxon they consider as possessing the groove, juveniles have sharp and well-defined grooves whereas adults have less discrete and shallower grooves just like those of adult *Tarbosaurus* and *Bistahieversor* (Fig. 1I-J; juvenile condition: TMP 1986.144.0001 and ROM 1247, adult condition: CMN 2120). Second, the trend is seen in *Albertosaurus* (juvenile condition: TMP 1986.064.0001, adult condition: TMP 1999.050.0021). It is also worth noting that some non-ontogenetic variation is also seen in *Abertosaurus* and *Gorgosaurus*, as some adults have a deep groove like that of juveniles (TMP 2000.045.0084, AMNH FARB 5458, respectively). Third, although Schmerge and Rothschild (2016) argue that no specimens of *T. rex* possess the groove, we disagree and instead identify *T. rex* as undergoing the same ontogenetic trajectory as other tyrannosauroids. Our observations show that a groove is seen on the left side of the juvenile specimen LACM 28471, contra to Schmerge and Rothschild (2016), but heavy damage to the external bone surface obscures its depth, easily making it appear absent in photographs. There is also a groove in adult *T. rex* specimens (Fig. 1C-D; AMNH FARB 5027;

CM 9380; MOR 008), which is shallow, weakly inset, and houses large foramina that course dorsally, just as in other adult tyrannosaurids. The well-defined grooves of the two purported ‘*Nanotyrannus*’ specimens (CMNH 7541; BMRP 2002.4.1) are thus expected for juvenile *T. rex* filling an ontogenetic gap between the very small LACM 28471 and adults.

The dentary groove, therefore, can be added to the list of features that are ontogenetically variable in large-bodied tyrannosauroids, which have been outlined in detail by Carr (1999) and Carr and Williamson (2004). Many of these other ontogenetic transformations in skull shape, robusticity, ornamentation, and sinuses are much more extreme than a shallowing of the neurovascular groove on the dentary, so there is no need to invoke biologically implausible mechanisms like metamorphosis to explain the latter. With that said, *T. rex* did undergo a major transformation as it grew from a tiny hatchling into a multi-ton, 13-meter-long, bone-crunching adult (Erickson et al., 2004). Subtle alterations in its neurovascular ornamentation were some of the least impressive changes as *T. rex* and other tyrannosauroids matured.

5) Key characters and phylogenetic analysis

Even if Schmerge and Rothschild (2016) were correct and ‘*Nanotyrannus*’ and *T. rex* had different conditions of the dentary groove, it is unclear what this difference would mean systematically and phylogenetically. A common dictum of modern phylogenetics is that all possible relevant evidence should be used to construct a phylogenetic hypothesis—the ‘total evidence’ approach (e.g., Kluge, 1989). Individual characters can have patchy distributions between (and within) taxa, so it is the weight of total character evidence that is the best test of phylogenetic relationships.

Schmerge and Rothschild (2016) do conduct a broader phylogenetic analysis, by including the BMRP 2002.4.1 skull of '*Nanotyrannus*' in the cladistic dataset of Brusatte et al. (2010). Although this exercise is much preferable to arguments based on single characters, the methodology of Schmerge and Rothschild (2016) has its flaws. First, they scored '*Nanotyrannus*' based on cranial characters only (except for a single character relating to the forelimbs), even though there are ample postcranial data for BMRP 2002.4.1. Second, the phylogenetic dataset of Brusatte et al. (2010) was designed to test the relationships of taxa using adult specimens. It includes many ontogenetically variable characters, and because of the complex interplay between ontogeny and phylogeny, it scores taxa for the adult condition. In unavoidable cases, taxa without known adult specimens are included in the dataset, the best example being *Raptorex*. However, although it possesses numerous features of derived tyrannosaurines, *Raptorex* falls out as a basal non-tyrannosaurid, which is surely the result of the juvenile condition of holotype (see discussion in Fowler et al., 2011, and a similar case concerning juvenile *Tarbosaurus* in Tsuihiji et al., 2011). In that regard, the placement of '*Nanotyrannus*' as phylogenetically distant from *T. rex* in Schmerge and Rothschild's (2016) analysis is most likely an artifact of its juvenile status. This is how we would interpret the results of Schmerge and Rothschild's (2016) analysis, as it follows our interpretation of the placement of the juvenile *Raptorex* in our published studies (Brusatte et al. 2010; Brusatte and Carr 2016).

Phylogenetic analyses can only determine the relationships among taxa. They cannot, on their own, determine if two specimens belong to the same species, although they can provide topologies that are consistent or inconsistent with such a hypothesis. The ultimate arbiter of whether '*Nanotyrannus*' is a distinct species is whether it possesses unique diagnostic features that are not seen in *Tyrannosaurus rex*, particularly *T. rex* specimens of the same size and

ontogenetic stage of the purported '*Nanotyrannus*' material. Schmerge and Rothschild (2016:31) state that Larson (2013) identified 'more than 30 other skeletal characters as evidence' to separate '*Nanotyrannus*' and *T. rex*. However, as has been shown by Carr (1999) and Carr and Williamson (2004), the vast majority of these features are ontogenetically variable, and therefore not reliable indicators of taxonomic separation. The monographic description of BMRP 2002.4.1 and its inclusion in a phylogenetic analysis that minimizes the effects of ontogenetic variation, both of which are underway by one of us (TDC) and have been presented in abstract form (Carr et al., 2015), will go a long way in clarifying the systematics of the long-controversial '*Nanotyrannus*'.

6) Conclusions

Contrary to Schmerge and Rothschild (2016), neurovascular grooves on the lateral surface of the dentary are common features among tyrannosauroids, and they become more shallowly inset and less distinct during ontogeny. The groove in one putative specimen of '*Nanotyrannus*' does not differentiate it from *T. rex* or link it to albertosaurines. Rather, the pronounced condition of the groove is entirely consistent with the identification of this specimen as a juvenile *T. rex*. We reaffirm that the most parsimonious explanation of all observations is that '*Nanotyrannus*' is not a pygmy tyrannosaur, but a young *T. rex* that has yet to grow into its adult frame.

Acknowledgements

We thank the many curators who have allowed us to study tyrannosauroid specimens in their care, Lindsay Zanno for helpful comments in review, and the editor, Eduardo Koutsoukos, for entertaining our response. SLB is supported by a Marie Curie Career Integration Grant EC630652.

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Fig. 1. Lateral views of tyrannosauroid dentaries with a lateral groove (indicated by arrows). (A) *Tarbosaurus bataar*, PIN 4216/3 (image reversed); (B) *Tarbosaurus bataar*, PIN 551-2/1; (C) Adult *Tyrannosaurus rex*, MOR 008 (image reversed); (D) Adult *Tyrannosaurus rex*, AMNH FARB 5027 (cast); (E) Juvenile *Daspletosaurus torosus*, TMP 1994.143.0001; (F) Adult *Daspletosaurus torosus*, CMN 8506 (image reversed); (G) Juvenile *Bistahieversor sealeyi*, NMMNHS P-25049 (image reversed); (H) Adult *Bistahieversor sealeyi*, NMMNHS P-27469; (I) Juvenile *Gorgosaurus libratus*, ROM 1247 (image reversed); (J) Adult *Gorgosaurus libratus*, CMNN 2120. Scale bars equal 10 cm. Scales not available for A-C because these photographs were taken of specimens on display behind glass.