



Article

Taxonomic Status of *Nanotyrannus lancensis* (Dinosauria: Tyrannosauroidae)—A Distinct Taxon of Small-Bodied Tyrannosaur

Nicholas R. Longrich ^{1,*}  and Evan T. Saitta ² ¹ Department of Life Sciences, University of Bath, Claverton Down, Bath BA2 7AY, UK² Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, USA; evansaitta@gmail.com

* Correspondence: nrl22@bath.ac.uk

Abstract: Tyrannosaurs are among the most intensively studied and best-known dinosaurs. Despite this, their relationships and systematics are highly controversial. An ongoing debate concerns the validity of *Nanotyrannus lancensis*, interpreted either as a distinct genus of small-bodied tyrannosaur or a juvenile of *Tyrannosaurus rex*. We examine multiple lines of evidence and show that the evidence strongly supports recognition of *Nanotyrannus* as a distinct species for the following reasons: 1. High diversity of tyrannosaurs and predatory dinosaurs supports the idea that multiple tyrannosaurids inhabited the late Maastrichtian of Laramidia; 2. *Nanotyrannus* lacks characters supporting referral to *Tyrannosaurus* or Tyrannosaurinae but differs from *T. rex* in >150 morphological characters, while intermediate forms combining the features of *Nanotyrannus* and *T. rex* are unknown; 3. Histology shows specimens of *Nanotyrannus* showing (i) skeletal fusions, (ii) mature skull bone textures, (iii) slow growth rates relative to *T. rex*, (iv) decelerating growth in their final years of life, and (v) growth curves predicting adult masses of ~1500 kg or less, showing these animals are subadults and young adults, not juvenile *Tyrannosaurus*; 4. growth series of other tyrannosaurids, including *Tarbosaurus* and *Gorgosaurus*, do not show morphological changes proposed for a *Nanotyrannus*–*Tyrannosaurus* growth series, and deriving *Tyrannosaurus* from *Nanotyrannus* requires several changes inconsistent with known patterns of dinosaur development; 5. Juvenile *T. rex* exist, showing diagnostic features of *Tyrannosaurus*; 6. Phylogenetic analysis suggests that *Nanotyrannus* may lie outside Tyrannosauridae. Tyrannosaur diversity before the K-Pg extinction is higher than previously appreciated. The challenges inherent in diagnosing species based on fossils mean paleontologists may be systematically underestimating the diversity of ancient ecosystems.

Keywords: dinosauria; Theropoda; Tyrannosauroidae; *Nanotyrannus lancensis*; *Tyrannosaurus rex*

Citation: Longrich, N.R.; Saitta, E.T. Taxonomic Status of *Nanotyrannus lancensis* (Dinosauria: Tyrannosauroidae)—A Distinct Taxon of Small-Bodied Tyrannosaur. *Foss. Stud.* **2024**, *2*, 1–65. <https://doi.org/10.3390/fossils2010001>

Academic Editor: Federico Agnolin

Received: 4 November 2023

Revised: 18 December 2023

Accepted: 21 December 2023

Published: 3 January 2024



Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

1.1. The Tyrannosaurs, the Most Iconic of All Dinosaurs

The first small, primitive tyrannosaurs evolved in the Late Jurassic of Laurasia and then diversified in the early Cretaceous [1]. Initially, tyrannosaurs were largely subordinate to larger-bodied megalosauroid and allosauroid [2,3] predators. However, by the end of the Cretaceous, tyrannosaurs became larger and more specialized [1,4,5], evolving giant forms with massive skulls and reduced forelimbs. Tyrannosaur evolution culminated in the late Maastrichtian, with the appearance of the giant *Tyrannosaurus rex* [4,6,7]. *T. rex* was among the last of the tyrannosaurs and the largest tyrannosaur, perhaps the largest terrestrial predator of all time.

Tyrannosaurs are among the best-known and most intensively studied groups of dinosaurs [1,4,5]. Dozens of skeletons are known, representing almost thirty species [1,4,5]. Of these, far and away the most well-known, intensively studied species is *Tyrannosaurus rex*. Multiple studies have examined the evolution [1,4,5], development [8–10], locomotion [11],

feeding [12–15], and systematics [9,16–19] of *T. rex*. It is one of the most well-known fossil organisms, and probably more thoroughly studied than most living species.

Despite this, much remains unknown. Remarkably, one of the most fundamental problems—how many tyrannosaur species are represented by fossils assigned to *Tyrannosaurus*—remains highly controversial. Among the most persistent issues concerns whether the latest Maastrichtian tyrannosaurs of western North America represent one species, showing remarkable variation through development, or whether small specimens represent a distinct lineage of small-bodied tyrannosaurs. This issue is of interest because this basic problem—classifying fossils into species—underpins our efforts to understand the evolution and extinction of fossil species, their geographic ranges, their growth, and their biology. That such a well-known, intensively studied animal remains so controversial is remarkable, and raises fundamental questions about the reliability of the taxonomies forming the foundation of paleontology.

1.2. Abbreviations

AMNH, American Museum of Natural History, New York, NY, USA; BHI, Black Hills Institute of Geological Research, Hill City, SD, USA; BMNH, British Museum of Natural History, London, UK; BMRP, Burpee Museum of Natural History, Rockford, IL, USA; CM, Carnegie Museum, Pittsburgh, PA, USA; CMNH, Cleveland Museum of Natural History, Cleveland, OH, USA; DDM, Dinosaur Discovery Museum, Kenosha, WI, USA; FMNH, Field Museum of Natural History, Chicago, IL, USA; LACM, Natural History Museum, Los Angeles, CA, USA; KU, University of Kansas, Lawrence, Kansas; MOR, Museum of the Rockies, Bozeman, MT, USA; NHMUK, York Natural History Museum, London, England; NMMNH New Mexico Museum of Natural History and Science, Albuquerque, NM, USA; PIN, Paleontological Institute, Russian Academy of Science, Moscow, Russia; RSM, Royal Saskatchewan Museum, Eastend, Saskatchewan, Canada; SDSM, South Dakota School of Mines and Technology, Rapid City, SD, USA; HRS, Hanson Research Station, Newcastle, WY, USA; TMM, Texas Memorial Museum, Austin, TX, USA; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; UCMP, University of California Berkeley, Berkeley, CA, USA; UMNH, University of Utah Museum of Natural History; USNM, United States National Museum, Smithsonian Institution, Washington, DC, USA; UWBM, University of Washington Burke Museum, Seattle, Washington, DC, USA; UWGM, Geology Museum, Madison, WI, USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

1.3. *Tyrannosaurus rex*

Historically, a single tyrannosaur species has been recognized from the latest Maastrichtian of western North America, *Tyrannosaurus rex*. Named by Henry Fairfield Osborn in 1905 [6], *T. rex* has a convoluted history (Table 1). Like many dinosaurs discovered in the ‘Dinosaur Rush’ of the late 19th and early 20th centuries, it was part of the ‘Bone Wars’, the scientific rivalry between Othniel Charles Marsh and Edward Drinker Cope [20], although it would not be well-known or studied in detail until many years later.

Among the first discoveries that can be referred to as *Tyrannosaurus* is an isolated fourth metatarsal, USNM 2110, collected by J. B. Hatcher in 1890 from the late Maastrichtian-aged Lance Formation of Wyoming [20]. Later that year, Marsh named the fossil as an ornithomimid, *Ornithomimus grandis* [21]. Two years later, in 1892, Cope collected a pair of huge vertebrae from the Hell Creek Formation of South Dakota, which he described and named *Manospondylus gigas* [22]. Both animals, being giant tyrannosaurs, probably belong to *Tyrannosaurus* but are not diagnostic to species level, so these names are considered invalid.

Table 1. Taxonomy of *Tyrannosaurus* and late Maastrichtian Tyrannosaurini.

Taxon	Publication	Specimen	Status
<i>Ornithomimus grandis</i>	Marsh 1890 [21]	USNM 2110	<i>Tyrannosaurus</i> indet.
<i>Manospondylus gigas</i>	Cope 1892 [22]	AMNH 3982	<i>Tyrannosaurus</i> indet.
<i>Dynamosaurus imperiosus</i>	Osborn 1905 [6]	AMNH 5866/BMNH R7995	<i>Tyrannosaurus rex</i>
<i>Tyrannosaurus rex</i>	Osborn 1905 [6]	AMNH 973/CM 9380	<i>Tyrannosaurus rex</i>
<i>Albertosaurus megagracilis</i>	Paul 1988 [23]		<i>Tyrannosaurus</i> indet.
<i>Dinotyrannus megagracilis</i>	Olshevsky 1995 [24]		<i>Tyrannosaurus</i> indet.
<i>Tyrannosaurus "x"</i>	Larson 2008 [16]	AMNH 5027	<i>T. rex</i> or <i>T. imperator</i> ?
<i>Tyrannosaurus imperator</i>	Paul et al. 2022 [18]	FMNH PR 2081	<i>T. rex</i> or <i>T. imperator</i> ?
<i>Tyrannosaurus regina</i>	Paul et al. 2022 [18]	USNM 555000	<i>Tyrannosaurus</i> indet.

A few years later, Barnum Brown collected a pair of tyrannosaur skeletons for the American Museum of Natural History in New York. The first, AMNH 5866 (sold to the British Museum, now BMNH R7995), was collected in 1900 from the Lance Formation of Wyoming. He collected the second, AMNH 973 (sold to the Carnegie Museum, now CM 9380), in 1902 from the uppermost Hell Creek Formation of Montana [20].

In 1905, Osborn described the first skeleton, AMNH 5866, as *Dynamosaurus imperiosus*, and the second, AMNH 973, as *Tyrannosaurus rex* [6]. Following further preparation and study, Osborn concluded in 1906 that the two animals were “generically if not specifically identical” [25]. Because *Dynamosaurus* and *Tyrannosaurus* were published in the same paper, ICZN rules let Osborn, as the first reviser, choose which name to retain. Unsurprisingly, he retained the now-iconic name *Tyrannosaurus rex* [25].

Since Osborn, *Tyrannosaurus* has generally been considered to contain a single species [4,5,9,17,19], *T. rex*. However, even setting aside the controversial specimens later assigned to *Nanotyrannus*, significant differences exist between specimens unambiguously assigned to *Tyrannosaurus* [16,18]. The possibility of multiple species has been raised several times [16,18].

Larson [16] cites a communication with Bakker as the source of this idea and, following Bakker, proposed that *T. rex* could be divided into *T. rex* and “*T. x*”, which differed in subtle details such as the shape of the second dentary tooth, tooth count, and the size of the lacrimal pneumatic foramen. Recently, Paul et al. [18] recognized three species of *Tyrannosaurus*: *T. rex*, *T. imperator*, and *T. regina*; these do not neatly conform to the *T. rex* and *T. “x”* of Larson, given that Larson [16] considered the holotype of *T. imperator*, FMNH PR 2081, the famed Sue specimen, to represent *T. rex*. The existence of multiple species is plausible, given the extensive variation seen in the genus [16,18] and the existence of species-level turnover within the Hell Creek Formation [26], but it remains controversial [19]. We consider this hypothesis viable but in need of further study.

1.4. *Nanotyrannus*

The systematics of late Maastrichtian tyrannosaurs were further complicated by the naming of *Gorgosaurus lancensis*, later renamed *Nanotyrannus lancensis*, from the late Maastrichtian beds that produced *T. rex*. In 1942, a field party from the Cleveland Museum of Natural History discovered a small tyrannosaur skull (Figure 1) in the Hell Creek Formation of Montana [27]. The skull, CMNH 7541, was described and named by Charles Gilmore in a paper published posthumously in 1946 [27].

The skull differs markedly from *Tyrannosaurus* in its proportions (Figure 2). Gilmore compared the animal to *Gorgosaurus libratus* from the Campanian of Canada and, noting similarities, argued that the skull was referable to *Gorgosaurus* [27]. He described the skull as a distinct species, *Gorgosaurus lancensis*, primarily based on the long period of time separating the two [27]. Since then, the status of *Nanotyrannus* has proven controversial.

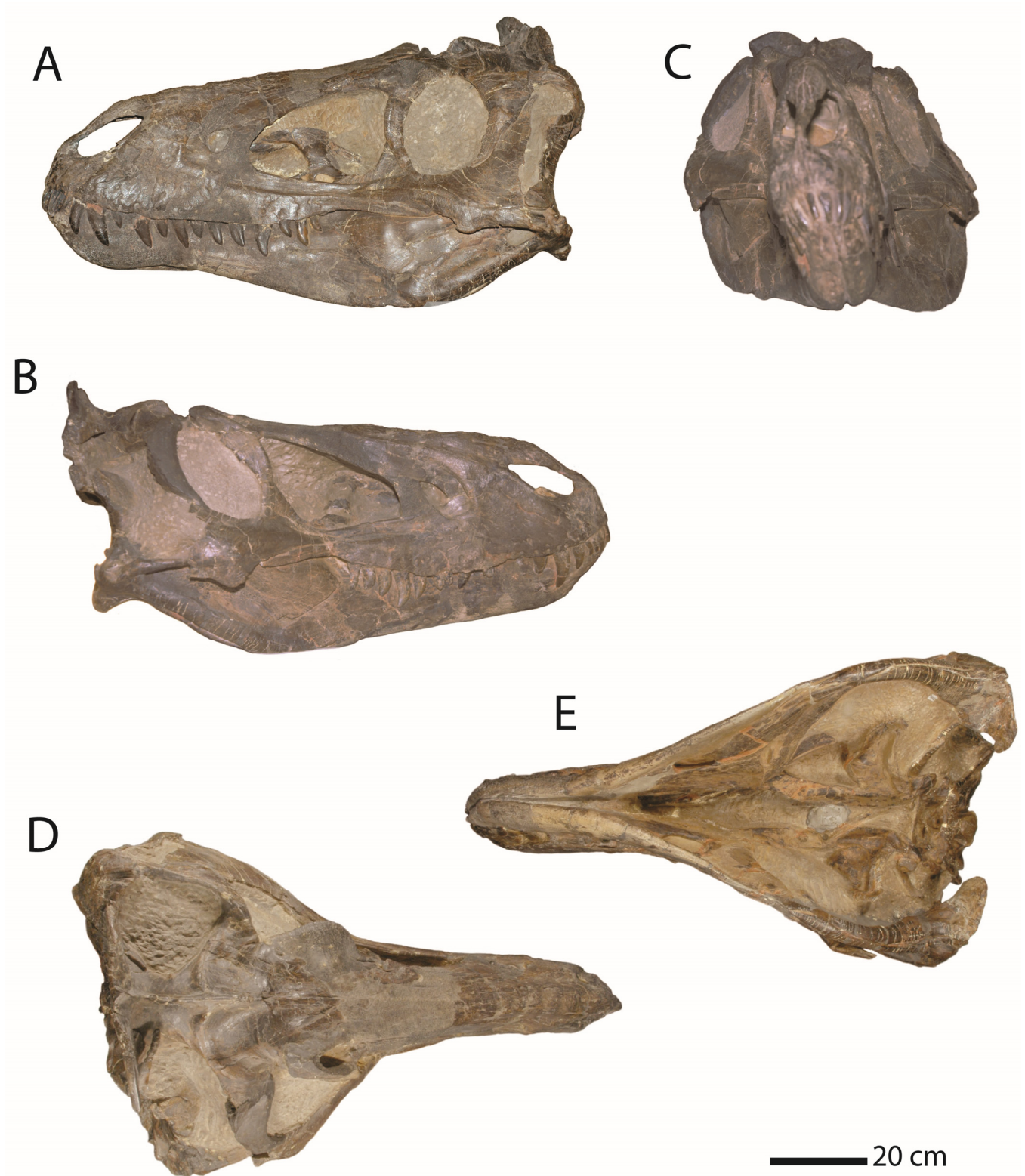


Figure 1. Holotype of *Nanotyrannus lancensis*, CMNH 7541. In (A), left lateral view; (B), right lateral view; (C), anterior view; (D), dorsal view; (E), ventral view. Scale = 20 cm.



Figure 2. Comparison of *Nanotyrannus lancensis* CMNH 7541 (A,C) and *Tyrannosaurus* AMNH 5027 (B,D) (not to scale).

Rozhdestvensky [28], based on a growth series of *Tarbosaurus*, suggested that *Gorgosaurus lancensis* might represent a juvenile *T. rex* [28], while Russell [29] regarded *G. lancensis* as an adult.

A paper by Bakker, Williams, and Currie in 1988 [30] would support Gilmore's recognition of the animal as a distinct species. Bakker and colleagues, however, argued that *Gorgosaurus lancensis* was not only distinct from *T. rex* but distinct from *Gorgosaurus* and represented a deeper diverging lineage of tyrannosaur [30]. This would put it outside of Tyrannosauridae as currently defined (i.e., *Tyrannosaurus rex* + *Albertosaurus sarcophagus*). If so, CMNH 7541 would represent a non-tyrannosaurid member of Tyrannosauroidae. Accordingly, Bakker et al. created a new genus, renaming CMNH 7541 *Nanotyrannus lancensis* [30].

The taxonomy of *Nanotyrannus* is further complicated by the discovery of a small tyrannosaur near Jordan, Montana [23,31,32]. The "Jordan theropod" has unserrated premaxillary teeth with a chisel-shaped tip, similar to those described as *Aublysodon* by Leidy [33] from the Campanian of Montana. Molnar and Carpenter referred the Jordan theropod to *Aublysodon* [32]. Paul (1988) described the Jordan theropod as a new species of *Aublysodon*, *Aublysodon molnari* [23]. It was later named as a distinct genus, *Stygivenator*, by Olshevsky [24]. *Stygivenator molnari* is similar to the type of *Nanotyrannus* in overall morphology, raising the possibility that it is synonymous with *Nanotyrannus* (in which case it also could be a juvenile *T. rex*). However, there are subtle, potentially significant differences in the shape of the teeth, maxillae, and dentaries (see Discussion).

Subsequently, Carpenter [34] suggested that the holotype of *Nanotyrannus lancensis* might be immature and, following Rozhdestvensky, interpreted it as a juvenile *T. rex*. Further study by Carr [9] agreed with Rozhdestvensky and Carpenter's identification of the animal as immature. Evidence for immaturity comes from the existence of striated texture of the surficial bone, [9] which is typical of young, rapidly growing dinosaurs, including extant birds [35,36] (but see below).

In recent years, the interpretation of *Nanotyrannus* as a juvenile *Tyrannosaurus* has been widely adopted [4,5,7,37,38] but not universally accepted. Critically, we will argue, it is unclear that these animals are in fact juveniles, or that they show features referable to *T. rex*. Carr identified 13 characters in the *Nanotyrannus* type that supposedly support referral to *T. rex* [9]. These characters are problematic because many (if not all) are widely distributed in Tyrannosauridae [39] or appear to be absent from *Nanotyrannus* (see Discussion).

Meanwhile, others have contested the referral to *Tyrannosaurus*. Currie [39] suggested that the difference in tooth count between the animals is of taxonomic significance, arguing that theropods do not show large changes in tooth count over ontogeny. Larson [40] provided the most comprehensive case for recognizing *Nanotyrannus* as distinct, cataloging characters potentially differentiating the two [16]. He also argued that a new and larger animal showing the *Nanotyrannus* morphology, the "Jane" specimen [41], represented an adult of the species [40]. Larson [42] also reported a new skeleton, part of the "Dueling Dinosaurs", noting features such as elongated forelimbs, suggesting *Nanotyrannus* was distinct from *T. rex* [42].

Witmer and Ridgely [43,44] noted extensive differences between the holotypes of *Nanotyrannus* and *Tyrannosaurus*. They found many characters difficult to ascribe to ontogeny but remained agnostic about the taxon's validity [44]. Schmerge and Rothschild [45] noted a lateral groove on the dentary as potentially supporting *Nanotyrannus* as distinct, a conclusion disputed by Brusatte et al. [43].

Woodward et al. [46] sectioned bones of putative *Nanotyrannus*, including "Jane" and "Petey" BMRP 2006.4.4, interpreting them as juveniles of *Tyrannosaurus*. They noted that the bones lack an external fundamental system, a characteristic of old, slow-growing adults, and argued the histology is consistent with the animals representing juvenile *Tyrannosaurus*. However, a more recent analysis suggested that the growth trajectory of the second animal, BMRP 2006.4.4, could not be linked to the growth curves of *T. rex* [47].

Finally, Carr [10] attempted to synthesize the known data to assemble specimens assigned to *Nanotyrannus* and *Tyrannosaurus* into a hypothetical 'growth curve'.

The taxonomy of *Nanotyrannus* is, therefore, as complicated as that of *T. rex* (Table 2), and its status currently remains unresolved: was *Nanotyrannus* a juvenile of *Tyrannosaurus* or a distinct lineage of tyrannosaur (Figure 3)?

Table 2. Current taxonomy of *Nanotyrannus lancensis* and *N. lancensis*-like fossils.

Taxon	Publication	Specimen	Status
<i>Gorgosaurus lancensis</i>	Gilmore, 1946 [27]	CMNH 7541	<i>Nanotyrannus lancensis</i> or <i>Tyrannosaurus</i> (?)
<i>Albertosaurus lancensis</i>	Paul, 1988 [23]	CMNH 7541	<i>Nanotyrannus lancensis</i> or <i>Tyrannosaurus</i> (?)
<i>Nanotyrannus lancensis</i>	Bakker et al., 1988 [30]	CMNH 7541	<i>Nanotyrannus lancensis</i> or <i>Tyrannosaurus</i> (?)
<i>Aublysodon molnari</i>	Paul, 1988 [23]	LACM 28471	<i>Nanotyrannus lancensis</i> , <i>Stygivenator molnari</i> , or <i>Tyrannosaurus</i> (?)
<i>Stygivenator molnari</i>	Olshevsky, 1995 [24]	LACM 28471	<i>Nanotyrannus lancensis</i> , <i>Stygivenator molnari</i> , or <i>Tyrannosaurus</i> (?)

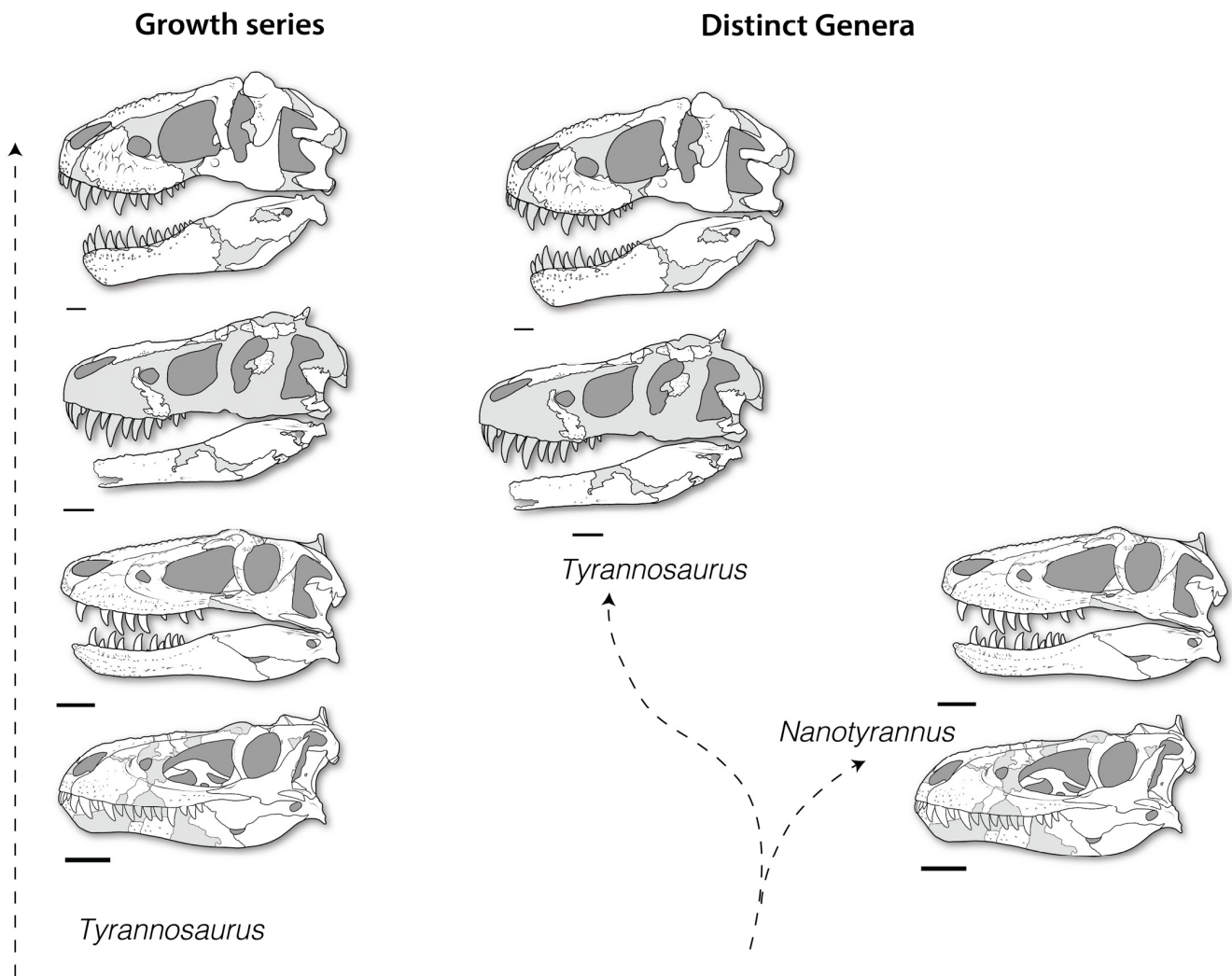


Figure 3. Competing hypotheses. *Nanotyrannus* as either juveniles of *Tyrannosaurus* or as a distinct lineage of small-bodied tyrannosaur. Scale = 10 cm.

1.5. Purpose and Approach of This Paper

The debate over *Nanotyrannus* has been considered resolved by some, but important questions remain. Our goal here is to synthesize all available evidence concerning the taxonomic status of *Nanotyrannus*. Rather than focusing on a single line of evidence, such as a growth series or histology, our approach is to synthesize multiple different lines of evidence to provide a robust inference.

A single line of argumentation and analysis, even one that appears conclusive, could be incorrect due to biases or errors in the data. It could also arrive at incorrect conclusions due to errors in the analysis of the data, choice of models used, or interpretation. It is less likely that multiple lines of evidence will independently point to the wrong conclusions, an approach referred to as triangulation of conclusions. As Galileo argued, ‘two truths can never contradict each other’, i.e., all lines of evidence are necessarily consilient with the correct hypothesis and must agree with each other.

We consider the following lines of evidence:

1. *Patterns of diversity in Tyrannosauridae and other predators.* The frequent coexistence of two species of tyrannosaur suggests that this pattern is the rule; the existence of a distinct taxon alongside *Tyrannosaurus* is expected from known patterns of dinosaur diversity.

2. *Morphological differences between Nanotyrannus and Tyrannosaurus and lack of intermediates.* The hypothesis that the animals represent a growth series of a single species predicts intermediate forms linking the two. However, dozens of characters in almost every skull bone distinguish *Nanotyrannus* and *Tyrannosaurus*, while no intermediate forms are known.
3. *Developmental patterns seen in other tyrannosaurs.* The hypothesized synonymy of *Nanotyrannus* and *Tyrannosaurus* suggests that *Nanotyrannus* will resemble the juveniles of other tyrannosaur species. However, the major changes in morphology proposed for the *Nanotyrannus*–*Tyrannosaurus* growth series are not seen in tyrannosaurs such as *Tarbosaurus* and *Gorgosaurus*, arguing against ontogeny as an explanation for morphological differences.
4. *Adult specimens referable to Nanotyrannus.* The hypothesis that *Nanotyrannus* is a juvenile *Tyrannosaurus* predicts that all *Nanotyrannus* will show features associated with immaturity, including immature bone texture and lack of fusion between skeletal elements. Histology is also predicted to show *Nanotyrannus* specimens rapidly growing to reach adult sizes on the order of ~8000 kg. *Nanotyrannus* specimens instead show patterns of bone fusion and bone texture consistent with maturity, are slow growing compared to maximal growth rates of *T. rex*, and show a pattern of decelerating growth in their final years of life, consistent with fairly mature animals. Reconstructed growth curves predict small adult body mass (<2000 kg, more likely ~900–1500 kg).
5. *Juvenile tyrannosaurs showing diagnostic features of T. rex.* The hypothesized *Nanotyrannus*–*Tyrannosaurus* growth series requires that small specimens showing features of *Tyrannosaurus* do not exist. A juvenile skull, slightly larger than *Nanotyrannus*, and a juvenile frontal, smaller than the holotype, represent juveniles of *Tyrannosaurus*.
6. *Phylogenetic analysis of Nanotyrannus.* If *Nanotyrannus* is a juvenile *Tyrannosaurus*, then phylogenetic analysis with ontogenetically variable characters removed should cause *Nanotyrannus* to cluster with *Tyrannosaurus*. The morphology of *Nanotyrannus* instead places it outside of Tyrannosaurinae and Tyrannosauridae, even when restricting analysis to characters known to be stable during ontogeny.

2. Materials and Methods

2.1. Clustering Analysis

To study patterns of morphological variation, we added a series of specimens of *Nanotyrannus* and *Tyrannosaurus* to a character–taxon matrix, coded for 158 morphological characters chosen as potentially differentiating *Nanotyrannus* from *Tyrannosaurus* (Supplementary Information S1); body size (estimated skull length > 1 m) was also added as a character. UPGMA clustering analysis was run in PAUP* 4.10 b10 [48] to create a tree that joins specimens where branch length is proportional to character difference. A second UPGMA analysis was conducted using the character–taxon matrix of Carr [10] with hypothetical “embryo” and “adult” removed. The two datasets were also analyzed using principal coordinates analysis (PCoA), which is used instead of PCA because of its ability to handle missing data.

2.2. Histology and Growth Curves

Midshaft femoral LAG numbers (periosteum arbitrarily assigned a half-LAG value to reflect an incomplete record of annual growth) and circumferences for Sue (FMNH PR 2081) and Petey (BMRP 2006.4.4) were obtained from Cullen et al. [49]. The periosteal circumference was derived from Campione et al. [50] for Sue, and Figure S2C of Woodward et al. [46] using the measurement tool in Adobe Photoshop (v. 25.0.0) for Petey. For Jane (BMRP 2002.4.1), LAG numbers were obtained from Woodward et al. [46] and either left uncorrected or corrected for split multi-LAGs (as in Cullen et al. [49]), reducing the number of LAGs counted from nine to six. Given the incomplete transverse section of the midshaft femur in Jane, LAG distance from the endosteal surface was first measured in Photoshop using Figure 4A in Woodward et al. [46]. Then, the half width (i.e., radius) of the femur at

midshaft at death (i.e., including medullary cavity and cortex on one side) was measured as 43.5 mm from Figure S2A in Woodward et al. [46]. LAG spacing was then used to back-estimate femoral width at the time of deposition of each previous LAG (i.e., femoral radius at death was subtracted by the difference in the radii between the periosteum and the final most LAG from the endosteum, and so on towards the interior LAGs). The LAG circumference was then estimated by approximating the midshaft femoral cross section as a circle (i.e., double femur radius at a given LAG times π). Masses at each LAG were calculated from the circumference data using Equation (7) of Campione et al. [50] for bipeds without correction for the non-circular cross-section. Logistic, Gompertz, logarithmic, and von Bertalanffy growth models were fit to each specimen in R (version 4.1.1). See Supplementary Information S2 for curves and mass estimates (Supplementary Information S2), and Supplementary Information Data for data and Supplementary Information Code for code.

The Zuri pubis (HRS081514), was analyzed similarly, by measuring the LAG spacing from the cortical bone in the pubis thin section shown in Figure 3 of Griffin [51] in Photoshop. Next, the growth record of the pubis' radius was back estimated by scaling and aligning the narrow region of the thin section shown in Figure 3 to the entire transverse section in Figure 6 of Griffin [51] and then obtaining the radius of the pubis at the time of death that was parallel to the measured LAG spacing. Models were fit to the data in R.

2.3. Phylogenetic Analysis

We coded *Nanotyrannus lancensis* into two previously published character–taxon matrices [1,52] using a composite coding of CMNH 7541, BMRP 2002.4.1, LACM 28471, and the HRS material (Supplementary Information S3, Supplementary Information S4). Coding focused on the skull because the postcrania of BMRP 2002.4.1 are mounted and neither BMRP 2002.4.1 nor BMRP 2006.4.4 are described. Phylogenetic analysis was run in equal-weights parsimony using PAUP* 4.10 b10 [48] (a single character, character 504, was assessed to be potentially redundant and excluded). A second set of analyses was conducted using only ontogenetically stable characters, i.e., characters coding the same in *Tarbosaurus* adults [53], subadults [34], and young juveniles [54]. “*Raptorex kriegsteini*” was excluded from analysis because it appears to represent a juvenile tyrannosaurine, most likely *Tarbosaurus* [55].

3. Results

3.1. Diversity Patterns of Tyrannosaurs and Apex Predators

The first argument for recognizing *Nanotyrannus* as a distinct taxon is that tyrannosaurids achieved high diversity in the latest Cretaceous (Table 3) and that well-sampled dinosaurian assemblages typically had several large predator species. This point is far from conclusive, but it is an important starting point in considering the evidence. All else being equal, we should expect multiple tyrannosaurs to exist in the latest Maastrichtian of North America, and arguments for the existence of a distinct taxon should, therefore, be considered carefully.

Tyrannosaurs were diverse in the Late Cretaceous of Laurasia [4,39,52,56–62]. Small tyrannosaurs of the Cenomanian [63] and Turonian [64,65] were replaced by large-bodied tyrannosaurs by the Campanian [52,57]. Multiple lineages evolved, including the gracile Albertosaurinae [66] and robust Tyrannosaurinae [56]. Tyrannosaurs also show endemism; distinct taxa occur up and down the Western Interior from Mexico [62] and the American Southwest [52,56,58,59] north into the Northern Great Plains [61,67] and the High Arctic [68], implying high speciation rates.

Strikingly, several well-sampled assemblages supported two distinct tyrannosaurid taxa. The Dinosaur Park Formation assemblage of southern Canada included at least two species, the gracile *Gorgosaurus libratus* [66] and the larger and more robust *Daspletosaurus* [67]; similarly, *Gorgosaurus* and *Daspletosaurus* coexist in the Judith River Formation [69]. The Nemegt Formation of Mongolia was home to the small and gracile *Alioramus* [70] and the larger, more robust *Tarbosaurus* [53]. Although many formations contain just one species, these formations are generally poorly sampled, producing either

a handful of diagnostic remains, or often, a single diagnostic specimen, so their low diversity may be due to sampling. The Horseshoe Canyon Formation is perhaps the only well-sampled formation in western North America to have a single tyrannosaur [71]. While our sample of faunas is limited and imperfect, it appears that, as often as not, multiple tyrannosaurs coexisted.

Other theropods show similar patterns. Multiple abelisaurids coexisted in the late Maastrichtian of Morocco [72], the Campanian-Maastrichtian La Colonia Formation of Argentina [73], and the Maastrichtian Lameta Formation of India [74–77]. Several large carnivores coexisted in the Cenomanian Kem Kem beds of Morocco [78,79] and the Cenomanian Candeleros Formation of Argentina [80,81]. The Late Jurassic of North America had four medium to giant carnivores—*Marshosaurus*, *Torvosaurus*, *Allosaurus*, and *Ceratosaurus*. *Torvosaurus*, *Allosaurus*, and *Ceratosaurus* co-occur in the Late Jurassic of Europe, and high diversity is also seen in the Late Jurassic of East Africa [82].

Similar patterns occur in mammals and marine vertebrates. Mammalian apex predators are small relative to dinosaurs, but in North America, saber-toothed *Smilodon* coexisted with American lions, dire wolves [83], and the cheetah-like *Miracinonyx* [84], and these would have been joined by puma and jaguars [85]. In Europe, saber-toothed cats coexisted with cave lions and hyenas [83]. In Africa, as recently as 1.5 Ma, the saber-toothed cats *Dinofelis* and *Homotherium*, lions, leopards, cheetahs, and hyenas coexisted [86]. The more depauperate predator communities of modern ecosystems are likely due to human-induced [87] megafaunal extinctions and give a biased picture of terrestrial predator diversity.

Similarly, marine ecosystems typically have multiple species of apex predators. Several species of large, predatory mosasaurs coexisted in the Maastrichtian [88,89], and the giant shark *Otodus megalodon* coexisted with the predatory whale *Livyatan* [90]. Modern marine ecosystems, meanwhile, have two different large apex predators, great whites [91] and orcas [85], as well as smaller apex predators, such as false killer whales and leopard seals [85].

It is also common for clades of predators to show size disparity. Felids range from 1.1–1.6 kg (*Prionailurus rubiginosus*) to over 300 kg (*Panthera tigris*) [85], and canids range from 1.0–1.5 kg (*Vulpes zerda*) to 80 kg (*Canis lupus*); mustelids range from 25–250 g (least weasel, *Mustela niveleris*) to a maximum of 32 kg (wolverine, *Gulo gulo*) [85]. Among varanids, masses range from 16.3 g (Dampier Peninsula monitor, *Varanus sparnus*) to 80 kg (Komodo dragon, *Varanus komodoensis*) [92]. Among birds [93], falcons range from 43 g (black-thighed falconet, *Microhierax fringillarius*) to 1.75 kg (Gyr falcon, *Falco rusticolus*); hawks range from 93 g (Pearl Kite, *Gampsonyx swainsonii*) to 8.2 kg (Cape Griffon, *Gyps coprotheres*). Many of these size ranges were still larger in the Pleistocene prior to the elimination of larger members of these clades by humans.

Within predator clades, diversity tends to be higher towards the lower end of the mass range; that is, there are fewer species of big cats than small cats, fewer wolves than foxes, many small weasels and ferrets, and just one wolverine [85]. The reasons for these patterns are unknown, but they imply higher speciation rates at low mass, higher extinction at large size, or both. In light of this, one would expect the diversity of small tyrannosaurs to be higher than for large tyrannosaurs.

Table 3. Diversity of Tyrannosauroida in the latest Cretaceous (Campanian-Maastrichtian) of Laramidia, Appalachia, and Asia.

Taxon	Age	Formation	Locality	Describer
Dryptosauridae				
<i>Dryptosaurus aquilunguis</i>	Late Maastrichtian	Hornerstown Formation	New Jersey, USA	[94]
<i>Appalachiosaurus montgomeriensis</i> (?)	Early Campanian	Demopolis Formation	Alabama, USA	[95]

Table 3. Cont.

Taxon	Age	Formation	Locality	Describer
Alioraminae				
<i>Alioramus altai</i>	Maastrichtian	Nemegt Formation	Mongolia	[96]
<i>Alioramus remotus</i>	Maastrichtian	Nemegt Formation	Mongolia	[97]
<i>Qianzhousaurus sinensis</i>	Maastrichtian	Nanxiong Formation	China	[98]
Albertosaurinae				
<i>Albertosaurus sarcophagus</i>	Early Maastrichtian	Horseshoe Canyon Formation	Alberta, Canada	[6]
<i>Gorgosaurus libratus</i>	Late Campanian	Dinosaur Park Formation	Alberta, Canada	[66]
Tyrannosaurinae				
<i>Thanatotheristes degrootorum</i>	Early Campanian	Foremost Formation	Alberta, Canada	[57]
<i>Daspletosaurus torosus</i>	Middle Campanian	Oldman Formation	Alberta, Canada	[29]
<i>Daspletosaurus wilsoni</i>	Middle Campanian	Judith River Fm.	Montana, USA	[60]
<i>Daspletosaurus</i> sp.	Late Campanian	Dinosaur Park Formation	Alberta, Canada	[39]
<i>Daspletosaurus horneri</i>	Late Campanian	Two Medicine Fm.	Montana, USA	[61]
<i>Dynamoterror dynastes</i>	Early Campanian	Menefee Fm.	New Mexico, USA	[99]
<i>Labocania anomala</i>	Late Campanian	La Bocana Roja Formation	Baja California, Mexico	[62]
<i>Lythronax argestes</i>	Early Campanian	Wahweap Formation	Utah, USA	[56]
<i>Teratophoneus curriei</i>	Late Campanian	Kaiparowits Formation	Utah, USA	[58]
<i>Bistahieversor sealeyi</i>	Late Campanian	Kirtland Formation	New Mexico, USA	[59]
<i>Nanuqsaurus hoglundi</i>	Middle Maastrichtian	Prince Creek Fm.	Alaska, USA	[68]
<i>Shanshanosaurus huoyanshanensis</i>	Late Cretaceous	Subashi Formation	Xinjiang, China	[100]
<i>Tarbosaurus bataar</i>	Maastrichtian	Nemegt Formation	Mongolia	[101]
<i>Zhuchengtyrannus magnus</i>	Campanian	Hongtuya Formation, Wangshi Group	Shandong, China	[102]
<i>Tyrannosaurus rex</i>	Late Maastrichtian	Hell Creek, Lance, Frenchman, Scollard, North Horn Fms	Alberta and Saskatchewan, Canada; Montana, Wyoming, North Dakota, South Dakota, Colorado, Utah, USA	[6]

Extraordinary claims require extraordinary evidence, but the existence of multiple large predators in the late Maastrichtian of North America would be ordinary. It would be extraordinary to find a single, giant predator and no smaller species. In light of other dinosaur faunas, modern mammal communities, and marine faunas, niche partitioning between large predators is the rule. In no known ecosystem—dinosaurian, mammalian, terrestrial, or marine—did a single, giant species of predator dominate. If *T. rex* was the only tyrannosaurid in the ecosystem, then this leaves a remarkable gap in size between *T. rex*, approaching [103] or exceeding [104] 8000–9000 kg in mass, and the dromaeosaurs *Dakotaraptor steini* [105] and *Acheroraptor temertyorum* [106], which were more than an order of magnitude smaller.

3.2. Morphology of *Nanotyrannus* and *Tyrannosaurus*

The two hypotheses make different predictions about the morphology of *Nanotyrannus* specimens and *Tyrannosaurus* specimens. Both hypotheses predict that the two will show distinct forms—either a distinct *Nanotyrannus* morphology and a distinct *Tyrannosaurus*

morphology or a distinct juvenile *Tyrannosaurus* and adult *Tyrannosaurus* morphology. If *Nanotyrannus* is a juvenile, however, the *Nanotyrannus* morphology and *Tyrannosaurus rex* morphology must be linked by intermediate forms [107]. These intermediates should show character states intermediate between the *Tyrannosaurus* state and the *Nanotyrannus* state and/or mosaicism, with mixtures of juvenile *Nanotyrannus* characters and adult *T. rex* characters. If, however, *Nanotyrannus* is a distinct taxon, such intermediates will be nonexistent; variation should be discrete, not continuous.

3.2.1. Characters Differentiating *Nanotyrannus* and *Tyrannosaurus*

The following list of 158 characters (Table 4) is assembled from previous studies of *Nanotyrannus*, including the original description by Gilmore [27], as well as Bakker et al. [30], Witmer and Ridgely [43], Larson [40], Schmerge and Rothschild [45] phylogenetic analyses by Loewen et al. [56] and Brusatte and Carr [1], and new characters found during this study. The number of characters differentiating the two is remarkable. Diagnostic characters occur in every bone in the skull examined; multiple characters typically diagnose each bone. Even more striking is the absence of clear intermediate fossils linking the two morphotypes: tyrannosaurs either exhibit the *Nanotyrannus* character states or the *Tyrannosaurus* character states but never combinations of these states, strongly arguing that they represent two distinct species.

This list is not comprehensive. Some characters were subtle or variable and so excluded pending further study. The list also focuses on cranial characters because casts, specimens, and descriptions are more readily available, but the postcrania also show marked differences, which require more study. Selected characters are illustrated (Figures 4–13) but are not meant to exhaustively catalog all diagnostic characters found.

Character List: Characters differentiating *Nanotyrannus* and *Tyrannosaurus*. Ontogenetically stable characters = †, Ontogenetically labile characters = *. *Nanotyrannus* characters are plesiomorphies unless denoted otherwise.

Table 4. Morphological characters differentiating *Nanotyrannus* and *Tyrannosaurus*.

Premaxilla	
1.	Premaxilla, anterior margin of premaxilla sloped posterodorsally in lateral view (<i>Nanotyrannus</i>) versus vertically oriented (<i>Tyrannosaurus</i>) †;
2.	Premaxilla, ventral margin distinctly upturned in lateral view (<i>Nanotyrannus</i>) or horizontal (<i>Tyrannosaurus</i>) † (<i>autapomorphy</i>).
3.	Premaxilla, articulated premaxillae form a long, narrow U in dorsal or ventral view (<i>Nanotyrannus</i>) or very short, and broad transversely (<i>Tyrannosaurus</i>);
4.	Premaxilla, subnarial process faces anterolaterally (<i>Nanotyrannus</i>) or anteriorly (<i>Tyrannosaurus</i>) †;
Maxilla	
5.	Maxilla, sculpture of maxilla weakly developed, simple rugosity (<i>Nanotyrannus</i>) or forming ridges and deep depressions on lateral surface of maxilla (<i>Tyrannosaurus</i>) *;
6.	Maxilla, subnarial fossa and foramen exposed in lateral view (<i>Nanotyrannus</i>) or obscured in lateral view (<i>Tyrannosaurus</i>) †;
7.	Maxilla, maxillae narrow in dorsal view (<i>Nanotyrannus</i>) versus muzzle broad in dorsal view (<i>Tyrannosaurus</i>);
8.	Maxilla, maxilla long and low, more than twice as long as tall (<i>Nanotyrannus</i>), versus short and tall (<i>Tyrannosaurus</i>) †;
9.	Maxilla, ventral margin of maxilla weakly convex or straight (<i>Nanotyrannus</i>), or strongly curved, projecting strongly downwards relative to jugal process (<i>Tyrannosaurus</i>) *;
10.	Maxilla, nasal closely approaches anterodorsal margin of antorbital fossa (<i>Nanotyrannus</i>) or maxilla broadly separates nasal from antorbital fossa (<i>Tyrannosaurus</i>) *;
11.	Maxilla, antorbital fossa shallow (<i>Nanotyrannus</i>) or deep (<i>Tyrannosaurus</i>) †;
12.	Maxilla, promaxillary fenestra visible in lateral view (<i>Nanotyrannus</i>) or concealed in lateral view (<i>Tyrannosaurus</i>) †;

Table 4. Cont.

13. Maxilla, accessory antorbital fenestra small and does not reach anterior end of antorbital fossa (*Nanotyrannus*) versus large and reaches anterior end of antorbital fossa (*Tyrannosaurus*) †;
14. Maxilla, accessory antorbital fenestra lies well above ventral margin of antorbital fossa (*Nanotyrannus*) versus ventrally positioned (*Tyrannosaurus*) †;
15. Maxilla, antorbital fossa with a broad rim beneath the antorbital fenestra (*Nanotyrannus*) versus antorbital fossa with a very narrow exposure along the posteroventral margin of the antorbital fenestra (*Tyrannosaurus*) †;
16. Maxilla, broad posterodorsal process of maxilla extends posterodorsally and defines a wide antorbital fossa above antorbital fenestra and under the nasals (*Nanotyrannus*) versus very narrow contribution to antorbital fossa below nasals (*Tyrannosaurus*) †;
17. Maxilla, antorbital fenestra with a narrow U- or V-shaped anterior margin (*Nanotyrannus*) versus a broadly U-shaped or squared-off anterior margin (*Tyrannosaurus*) †;
18. Maxilla, promaxillary recess small (*Nanotyrannus*) or greatly enlarged (*Tyrannosaurus*);
19. Maxilla, deep recess on medial surface of maxilla above maxillary fenestra absent (*Nanotyrannus*) or present (*Tyrannosaurus*);
20. Maxilla, sinus on medial surface of maxilla posterodorsal to maxillary fenestra, small and shallow (*Nanotyrannus*) or deep and extensive (*Tyrannosaurus*);
21. Maxilla, internal antorbital fossa weakly developed (*Nanotyrannus*) or extensive (*Tyrannosaurus*);
22. Maxilla, articulation for vomer and palatal shelves lies ventrally (*Nanotyrannus*) or elevated well above interdental plates (*Tyrannosaurus*);
23. Maxilla, occlusal pits weakly developed or absent (*Nanotyrannus*) or well-developed and prominent on inside of maxilla (*Tyrannosaurus*);
24. Maxilla extends caudally under orbit (*Nanotyrannus*) or only as far as beneath the lacrimal bar (*Tyrannosaurus*) *;
25. Maxilla, maxilla-palatine contact straight (*Nanotyrannus*) strongly curved (*Tyrannosaurus*).

Nasals

26. Nasals, nasal premaxillary processes wide in dorsal view (*Nanotyrannus*) or narrow where they approach and clasp premaxillae (*Tyrannosaurus*) †;
27. Nasals, nasals narrow (*Nanotyrannus*) versus transversely broad (*Tyrannosaurus*) †;
28. Nasals, nasals relatively flat and low in lateral view (*Nanotyrannus*) versus strongly arched transversely and tall in lateral view (*Tyrannosaurus*) *;
29. Nasals, nasals broad posteriorly where they contact the frontals (*Nanotyrannus*) versus narrow and strongly tapered posteriorly where they contact the frontals (*Tyrannosaurus*) *;
30. Nasals, nasals form a relatively smooth contact with maxillae (*Nanotyrannus*) versus a strongly interdigitating contact with notches fitting into the maxillae (*Tyrannosaurus*) *;
31. Nasals, nasals flat posteriorly (*Nanotyrannus*) or with a dorsal depression or groove, and lateral edges of nasals upturned to contribute to nasolacrimal ridge (*Tyrannosaurus*) †.

Lacrimal

32. Lacrimal, lacrimal L-shaped in lateral view, anterior and ventral rami diverging at approximately a right angle (*Nanotyrannus*) or anterior and ventral rami diverging at an acute angle in lateral view (*Tyrannosaurus*) *;
33. Lacrimal, anterior process similar to ventral process in length (*Nanotyrannus*) or anterior process much shorter than ventral process (*Tyrannosaurus*) †;
34. Lacrimal, lacrimal with a low, crescent-shaped lacrimal horn (*Nanotyrannus*) or lacrimal horn reduced to a low, broad rugosity (*Tyrannosaurus*) †;
35. Lacrimal, lacrimal horn mediolaterally narrow and with a narrow apex (*Nanotyrannus*) or strongly inflated and a transversely broad, rounded apex (*Tyrannosaurus*) *;
36. Lacrimal, lacrimal horn with a broad, strongly emarginated pneumatic excavation with multiple large foramina (*Nanotyrannus*) versus reduced pneumatic excavation with a small foramen (*Tyrannosaurus*) *;
37. Lacrimal, broad development of antorbital fossa on base of lacrimal ventral ramus (*Nanotyrannus*) versus anteroposteriorly narrow exposure of antorbital fossa (*Tyrannosaurus*);
38. Lacrimal, orbital bar strongly curved (*Nanotyrannus*) versus relatively straight (*Tyrannosaurus*) †;
39. Lacrimal, bone T-shaped in lateral view, with a large posterior process (*Nanotyrannus*) or L-shaped, with a short posterior process (*Tyrannosaurus*) *;

Table 4. Cont.

-
40. Lacrimal, lacrimal with low medial flange (*Nanotyrannus*) or prominent medial flange (*Tyrannosaurus*);
 41. Lacrimal, medial surface with a small foramen in antorbital fossa (*Nanotyrannus*) or enlarged pneumatic opening in the antorbital fossa (*Tyrannosaurus*);
 42. Lacrimal, large, shallow depression on medial surface of lacrimal (*Nanotyrannus*) or small deep fossa (*Tyrannosaurus*).

Frontals

43. Frontals, frontals participate in orbital margin (*Nanotyrannus*) or excluded from orbit by postorbital-lacrimal contact (*Tyrannosaurus*) †;
44. Frontals, frontal table long and narrow in dorsal view (*Nanotyrannus*) versus short and wide (*Tyrannosaurus*) †;
45. Frontal, short contribution of frontal to sagittal crest, with parietal forming most of the crest (*Nanotyrannus*) or long frontal contribution to sagittal crest (*Tyrannosaurus*) †;
46. Frontals, supratemporal fossae short (*Nanotyrannus*) versus very long (*Tyrannosaurus*) *;
47. Frontals, frontals broad anteriorly between lacrimals (*Nanotyrannus*) versus strongly constricted between lacrimals (*Tyrannosaurus*) †;
48. Frontals, supratemporal fossa with a concave anterior margin (*Nanotyrannus*) or S-shaped margin of supratemporal fossae, being strongly extended forward medially (*Tyrannosaurus*);
49. Frontals, distinct downflex of supratemporal fossae relative to frontal table absent (*Nanotyrannus*) or present, and supratemporal fossae distinctly sloped downward relative to (*Tyrannosaurus*) †;
50. Frontals, frontal-postorbital suture shallow in lateral view (*Nanotyrannus*) or dorsoventrally extensive (*Tyrannosaurus*) †.

Parietal

51. Parietal, nuchal crest in posterior view with pointed dorsolateral corners (*Nanotyrannus*) or broadly rounded (*Tyrannosaurus*);
52. Parietal, posterior surface of nuchal crest with broad ridge (*Nanotyrannus*) or a sharp, narrow, well-defined ridge (*Tyrannosaurus*);
53. Parietal, parietal nuchal crest straight in dorsal view (*Nanotyrannus*) or arcuate, projecting back along midline and wrapping forward laterally (*Tyrannosaurus*).

Postorbital

54. Postorbital, postorbital with a rudimentary postorbital boss (*Nanotyrannus*), versus a massive, dorsoventrally extended postorbital boss (*Tyrannosaurus*) *;
55. Postorbital, jugal process anteroposteriorly narrow (*Nanotyrannus*) versus anteroposteriorly broad (*Tyrannosaurus*) *;
56. Postorbital, suborbital flange rudimentary (*Nanotyrannus*) versus expanded and constricting orbit (*Tyrannosaurus*) *;
57. Postorbital, straight contact with the jugal (*Nanotyrannus*) versus jugal contact strongly convex (*Tyrannosaurus*) *;
58. Postorbital, squamosal process narrow and splintlike (*Nanotyrannus*) or a dorsoventrally deep, triangular structure (*Tyrannosaurus*) *;
59. Postorbital, main body of postorbital shallow (*Nanotyrannus*) or dorsally extended above squamosal process (*Tyrannosaurus*) *;
60. Postorbital, anterior end of postorbital shallow (*Nanotyrannus*) or deep and massive where it contacts frontals and lacrimals (*Tyrannosaurus*) *;
61. Postorbital, anterior end of postorbital projects anteriorly (*Nanotyrannus*) hooked downward anteriorly (*Tyrannosaurus*);
62. Postorbital, fossa on medial surface of postorbital present (*Nanotyrannus*) or absent (*Tyrannosaurus*).

Jugal

63. Jugal, antorbital fossa extends beneath lacrimal (*Nanotyrannus*) or lies largely anterior to ventral process of lacrimal (*Tyrannosaurus*) *;
 64. Jugal, body of jugal narrow anteriorly beneath lacrimal (*Nanotyrannus*) versus dorsoventrally expanded relative to depth beneath orbit (*Tyrannosaurus*) †;
 65. Jugal, jugal with a wide, shallowly concave orbital margin (*Nanotyrannus*) versus jugal contribution to orbit a deep, narrow notch (*Tyrannosaurus*) *;
 66. Jugal, jugal with a small pneumatic opening at the corner of the antorbital fossa (*Nanotyrannus*) versus a large dorsally positioned one (*Tyrannosaurus*) *;
-

Table 4. Cont.

-
67. Jugal, pneumatic recess shallow (*Nanotyrannus*) or deeply excavating the jugal (*Tyrannosaurus*)*;
 68. Jugal, notch for postorbital small (*Nanotyrannus*) or enlarged to receive a broad ventral process of the jugal (*Tyrannosaurus*)*;
 69. Jugal, postorbital process anteroposteriorly narrow where it contacts postorbital (*Nanotyrannus*) or anteroposteriorly broad (*Tyrannosaurus*);
 70. Jugal, narrow articulation for the postorbital (*Nanotyrannus*) or contacts postorbital via a broadly overlapping lap joint (*Tyrannosaurus*);
 71. Jugal, quadratojugal ramus short (*Nanotyrannus*) versus elongate (*Tyrannosaurus*) †;
 72. Jugal, posterior ramus extends horizontally (*Nanotyrannus*) or dorsal margin deflected upwards (*Tyrannosaurus*) †.

Quadratojugal

73. Quadratojugal, forms an anteroposteriorly short contact with squamosal (*Nanotyrannus*) versus a broad squamosal contact (*Tyrannosaurus*);
74. Quadratojugal, anterior process of quadratojugal narrow (*Nanotyrannus*) versus deep (*Tyrannosaurus*);
75. Quadratojugal, dorsal margin concave (*Nanotyrannus*) straight or convex (*Tyrannosaurus*);
76. Quadratojugal, quadratojugal anterior ridge narrow and tapers distally (*Nanotyrannus*) or massive and extends to end of quadratojugal (*Tyrannosaurus*);
77. Quadratojugal, pneumatic foramen pierces lateral surface of quadratojugal (*Nanotyrannus*) or pneumatic foramen absent (*Tyrannosaurus*) (autapomorphy);
78. Quadratojugal, posterior process extends posteriorly (*Nanotyrannus*) or posterodorsally to wrap onto posterior face of quadrate (*Tyrannosaurus*);
79. Quadrate, quadratojugal pneumatic foramen present (*Nanotyrannus*) or absent (*Tyrannosaurus*) †.

Squamosals

80. Squamosals, caudal ends of squamosals do not extend far past parietal in dorsal view (*Nanotyrannus*) versus squamosals project strongly posterior to parietals in dorsal view (*Tyrannosaurus*);
81. Squamosal, ventral fossa of squamosal bounded anteriorly by a narrow bar of bone (*Nanotyrannus*) or a broad, shallow shelf (*Tyrannosaurus*);
82. Squamosal, anterior lamina does not extend forward (*Nanotyrannus*) or extends forward to anterior end of squamosal (*Tyrannosaurus*);
83. Squamosal, ventral fossa lacks a pneumatic recess (*Nanotyrannus*) or pneumatic recess present in the roof of the ventral fossa (*Tyrannosaurus*);
84. Squamosal, quadratojugal process forming a narrow point anteriorly (*Nanotyrannus*) or a broad rounded or subrectangular tip (*Tyrannosaurus*).

Vomer

85. Vomer, vomer narrow anteriorly (*Nanotyrannus*) or transversely expanded (*Tyrannosaurus*);
86. Vomer, distal end dorsoventrally expanded (*Nanotyrannus*) or low (*Tyrannosaurus*);
87. Vomer, proximal end dorsoventrally expanded (*Tyrannosaurus*).

Palatine

88. Palatine, dorsal process of palatine lacks posterior expansion (*Nanotyrannus*) or bears a large, broad posterior expansion (*Tyrannosaurus*);
89. Palatine, neck of dorsal process projects anterodorsally (*Nanotyrannus*) or dorsally (*Tyrannosaurus*)*;
90. Palatine, anterior prong of dorsal process long and slender (*Nanotyrannus*) or short and robust (*Tyrannosaurus*);
91. Palatine, pneumatic fossae small (*Nanotyrannus*) or enlarged (*Tyrannosaurus*);
92. Palatine, body weakly inflated (*Nanotyrannus*) or strongly inflated (*Tyrannosaurus*);
93. Palatine, anteroventral process slender (*Nanotyrannus*) or proportionately short and broad (*Tyrannosaurus*).

Ectopterygoid

94. Ectopterygoid, opening of pneumatic recess a thin slot (*Nanotyrannus*) or a large aperture (*Tyrannosaurus*);
 95. Ectopterygoid, posterior edge of pneumatic recess flat (*Nanotyrannus*) or bounded by a distinct lip (*Tyrannosaurus*);
-

Table 4. Cont.

-
96. Ectopterygoid, jugal process lacks a pneumatic foramen (*Nanotyrannus*) or with a large pneumatic foramen (*Tyrannosaurus*);
 97. Ectopterygoid, ectopterygoid weakly expanded (*Nanotyrannus*) strongly inflated (*Tyrannosaurus*).

Braincase

98. Supraoccipital, subrectangular (*Nanotyrannus*) forked dorsally (*Tyrannosaurus*);
99. Exoccipitals, paroccipital processes taper in posterior view (*Nanotyrannus*) or distally broad (*Tyrannosaurus*);
100. Exoccipitals, paroccipital processes extend laterally (*Nanotyrannus*) versus posterolaterally (*Tyrannosaurus*);
101. Parasphenoid, rostrum long, slender and triangular in lateral view (*Nanotyrannus*) or proportionately short, deep and rectangular in shape (*Tyrannosaurus*)*;
102. Basioccipital with prominent depressions ventrolateral to the occipital condyle and extending onto the basal tubera in posterior view (*Nanotyrannus*) or absent (*Tyrannosaurus*);
103. Basioccipital, basal tubera separated by a deep, narrow notch (*Nanotyrannus*) versus a shallow, wide notch (*Tyrannosaurus*);
104. Basioccipital, basal tubera wider than basispterygoid processes and extremely wide relative to skull width (*Nanotyrannus*) or as wide or narrower than basispterygoid processes (*Tyrannosaurus*) (autapomorphy);
105. Basisphenoid, basisphenoid recess, faces posteroventrally (*Nanotyrannus*) or strongly directed posteriorly (*Tyrannosaurus*).

Dentary

106. Dentary, anteroventral margin of dentary symphysis rises up at a shallow angle (*Nanotyrannus*) versus rises up steeply (*Tyrannosaurus*);
107. Dentary, anterior end of dentary shallow (*Nanotyrannus*) or distinctly expanded relative to midlength (*Tyrannosaurus*);
108. Dentary, symphysis weakly developed (*Nanotyrannus*) or massive facet where dentaries contact (*Tyrannosaurus*);
109. Dentary, symphysis ends beneath fourth tooth (*Nanotyrannus*) or third (*Tyrannosaurus*);
110. Dentary, interdental plates weakly developed, tapering dorsally (*Nanotyrannus*) or large and broad, covering much of the tooth roots (*Tyrannosaurus*) †;
111. Dentary, first two alveoli small (*Nanotyrannus*), or first alveolus small (*Tyrannosaurus*) †;
112. Dentary, lingual bar covers first alveolus (*Nanotyrannus*) or first two alveoli (*Tyrannosaurus*);
113. Dentary, dentary groove present and well-defined (*Nanotyrannus*) or reduced/absent (*Tyrannosaurus*);
114. Dentary, neurovascular foramina in small pits (*Nanotyrannus*) or set in deep grooves (*Tyrannosaurus*);
115. Dentary, ventral margin bowed (*Nanotyrannus*) or straight (*Tyrannosaurus*);
116. Dentary, neurovascular foramina lie low on dentary (*Nanotyrannus*) or high on dentary (*Tyrannosaurus*);
117. Dentary, toothrow straight or weakly curved in dorsal view (*Nanotyrannus*) versus bowed outwards anteriorly in dorsal view to create a broad, U-shaped jaw (*Tyrannosaurus*);
118. Dentary, weakly expanded posteriorly (*Nanotyrannus*) versus strongly expanded posteriorly to about twice its minimum depth (*Tyrannosaurus*);
119. Dentary, lingual bar similar in depth anteriorly and posteriorly (*Nanotyrannus*) versus narrow and tapered posteriorly relative to the anterior of the toothrow (*Tyrannosaurus*);
120. Dentary, facet for articulation with splenial below Meckelian fossa weakly developed (*Nanotyrannus*) or large, very broad contact surface (*Tyrannosaurus*);
121. Dentary, Meckelian fossa narrow and V-shaped anteriorly (*Nanotyrannus*) or broad and U-shaped (*Tyrannosaurus*);
122. Dentary, contact with surangular straight (*Nanotyrannus*) or strongly concave (*Tyrannosaurus*);
123. Dentary, weak notch of angular process (*Nanotyrannus*) or very strong forking of angular process (*Tyrannosaurus*).

Posterior Mandible

124. Splenial, mylohyoid foramen long and low (*Nanotyrannus*) or short and tall (*Tyrannosaurus*);
 125. Angular, posteroventral margin strongly convex (*Nanotyrannus*) or relatively straight (*Tyrannosaurus*);
 126. Prearticular, weakly bowed (*Nanotyrannus*) or strongly bowed (*Tyrannosaurus*);
-

Table 4. *Cont.*

-
127. Prearticular, midshaft flattened, plate-like (*Nanotyrannus*) or rounded, width and height subequal (*Tyrannosaurus*);
 128. Surangular, groove and enlarged foramen absent (*Nanotyrannus*) or present (*Tyrannosaurus*);
 129. Surangular, lateral shelf short (*Nanotyrannus*) or elongate, extending about half the length of the surangular (*Tyrannosaurus*);
 130. Surangular, shallow below surangular foramen (*Nanotyrannus*) versus very deep below surangular foramen (*Tyrannosaurus*);
 131. Surangular, long and low (*Nanotyrannus*) or short and deep (*Tyrannosaurus*) *;
 132. Surangular, coronoid process weakly developed (*Nanotyrannus*) or tall and anteroposteriorly expanded (*Tyrannosaurus*);
 133. Surangular, surangular shelf thin (*Nanotyrannus*) or thick and massive (*Tyrannosaurus*);
 134. Surangular, surangular foramen lies just anterior to condyle (*Nanotyrannus*) or well anterior to condyle (*Tyrannosaurus*);
 135. Articular, subrectangular medial projection in caudal view (*Nanotyrannus*) or articular smoothly rounded and semicircular to crescentic in posterior view (*Tyrannosaurus*).

Dentition

136. Dentition, premaxillary teeth procumbent (*Nanotyrannus*) or project vertically down (*Tyrannosaurus*) † (autapomorphy);
137. Dentition, premaxillary tooth apices blunt and chisel-like (*Nanotyrannus*) versus sharp and pointed (*Tyrannosaurus*) †;
138. Dentition, premaxillary teeth unserrated in adults (*Nanotyrannus*) versus serrated (*Tyrannosaurus*) † (autapomorphy);
139. Dentition, premaxillary teeth subequal in size (*Nanotyrannus*) or first tooth small relative to successive teeth (*Tyrannosaurus*) †;
140. Dentition, number of dentary teeth: 13 (0), 14 (1), 15 (2), 16 (3), 17 (4) †;
141. Dentition, number of maxillary teeth: 11 (0), 12 (1), 13 (2), 14 (3), 15 (4) †;
142. Dentition, maxilla with a small, incisiform first tooth (*Nanotyrannus*) or maxilla with large and pointed first tooth (*Tyrannosaurus*) †;
143. Dentition, maxillary and dentary teeth laterally compressed and with rectangular bases (*Nanotyrannus*) versus broad and ovate (*Tyrannosaurus*) *;
144. Dentition, anterior teeth of maxilla and dentary not markedly enlarged relative to more posterior teeth (*Nanotyrannus*) or caniniform teeth in anterior maxilla and dentary (*Tyrannosaurus*) †;

Postcrania

145. Scapula, broad shaft relative to coracoid articulation (*Nanotyrannus*) or narrow neck and very broad coracoid expansion, about three times width of shaft just above the acromion (*Tyrannosaurus*);
146. Coracoid, short and wide (*Nanotyrannus*) or tall, height about equal to width across scapular facet (*Tyrannosaurus*);
147. Humerus, proximal head small and ellipsoidal (*Nanotyrannus*) or massive, bulbous, and proximally projecting (*Tyrannosaurus*);
148. Humerus, internal tuberosity small, well-differentiated, and distally placed (*Nanotyrannus*) or large, poorly differentiated, and proximally placed (*Tyrannosaurus*);
149. Manus, manual unguals large (*Nanotyrannus*) or highly reduced (*Tyrannosaurus*);
150. Ilium, blade long and low (*Nanotyrannus*) or tall (*Tyrannosaurus*);
151. Ilium, blade with a straight dorsal margin (*Nanotyrannus*) versus convex (*Tyrannosaurus*);
152. Pubis, pubic boot slender (*Nanotyrannus*) deep in lateral view (*Tyrannosaurus*);
153. Femur, femur with large accessory trochanter (*Nanotyrannus*) or a small accessory trochanter (*Tyrannosaurus*);
154. Femur, femoral head elevated (*Nanotyrannus*) versus weakly elevated (*Tyrannosaurus*);
155. Femur, fourth trochanter small (*Nanotyrannus*) versus massive (*Tyrannosaurus*);
156. Tibia, cnemial crest long and narrow, tapering and triangular in profile (*Nanotyrannus*) or proportionately short and broad, with a squared-off end (*Tyrannosaurus*);
157. Metatarsus, shaft of metatarsal III straight (*Nanotyrannus*) or twisted in anterior view (*Tyrannosaurus*);
158. Metatarsal III, ventral surface of MT III with a narrow keel (*Nanotyrannus*) or a broad ventral tubercle or 'pillar' (*Tyrannosaurus*);

Body Size

159. Small size (estimated skull length ≤ 90 cm) or large (>90 skull length);
-

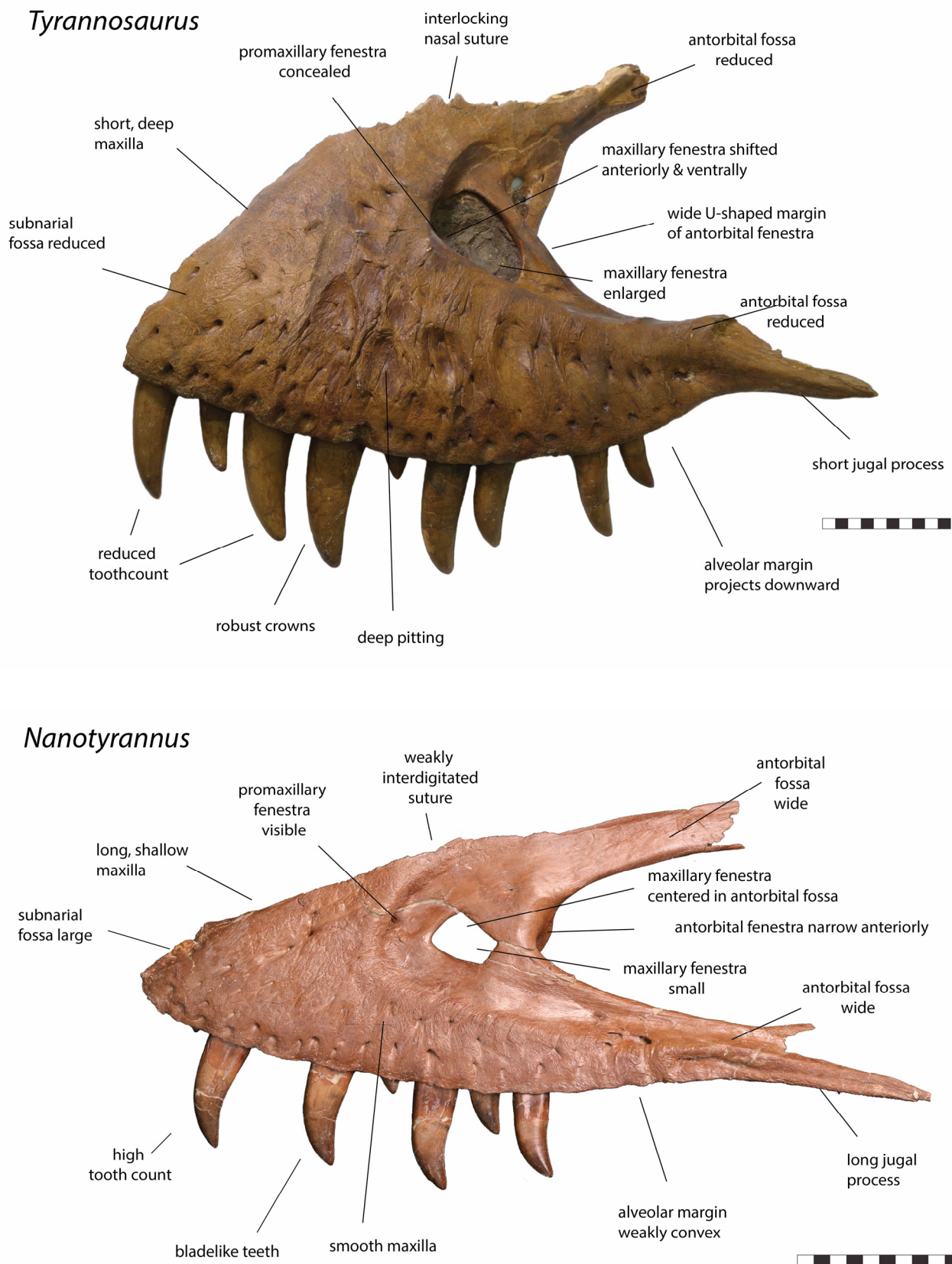


Figure 4. Left maxilla of *Tyrannosaurus rex* CM 9380 and right maxilla (reversed) of *Nanotyrannus* BMRP 2002.4.1 in lateral view, showing anatomical characters differentiating the two. Scale = 10 cm.

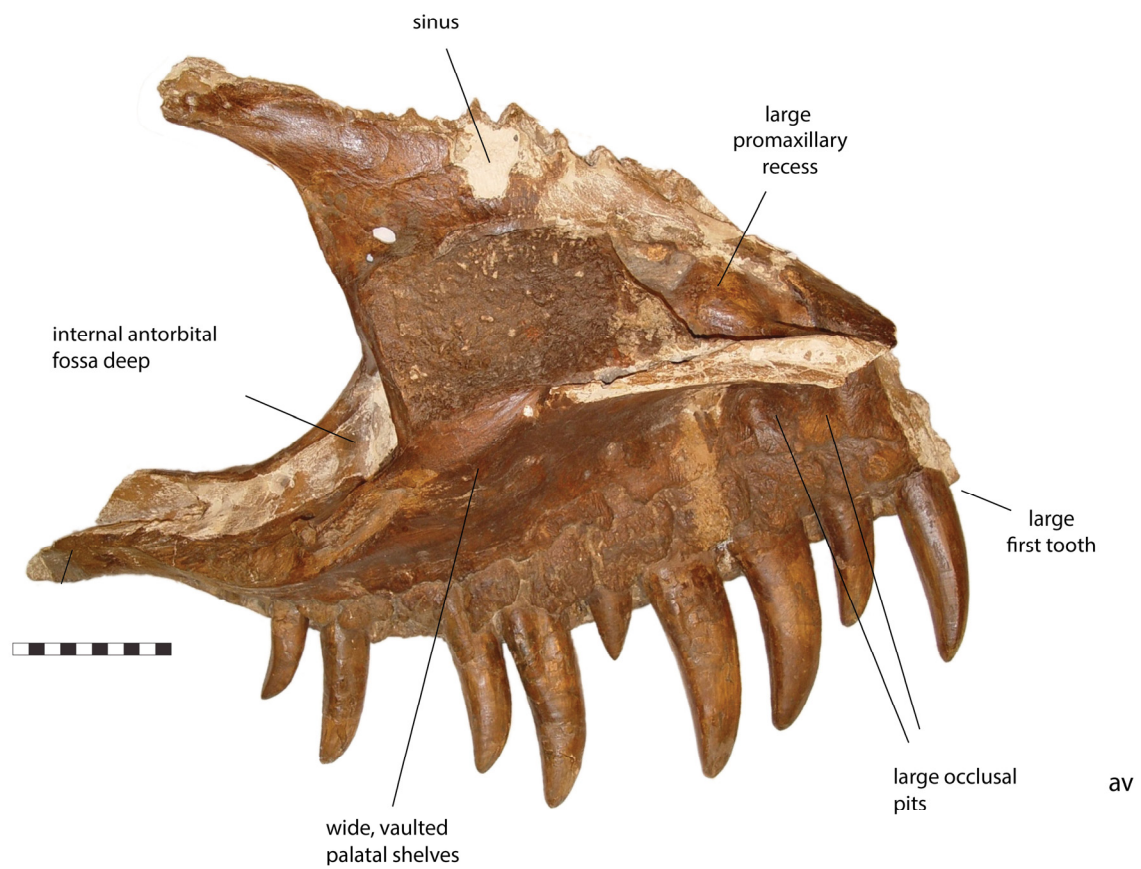
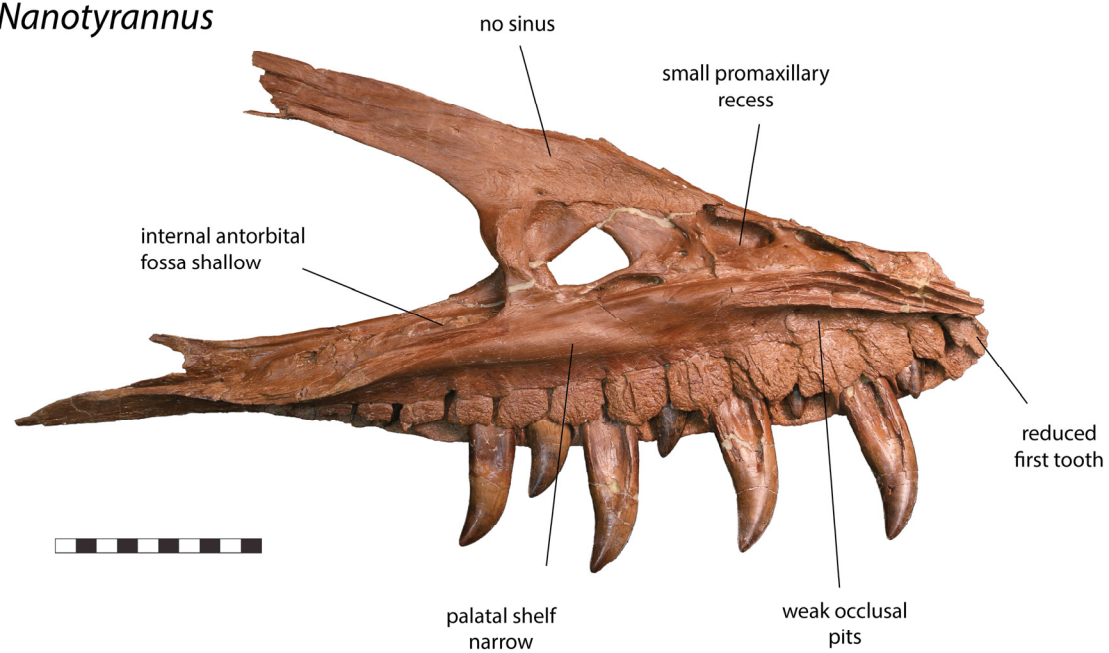
Tyrannosaurus*Nanotyrannus*

Figure 5. Left maxilla of *Tyrannosaurus rex* CM 9380 and right maxilla (reversed) of *Nanotyrannus* BMRP 2002.4.1, medial view, showing anatomical characters differentiating the two. Scale = 10 cm.

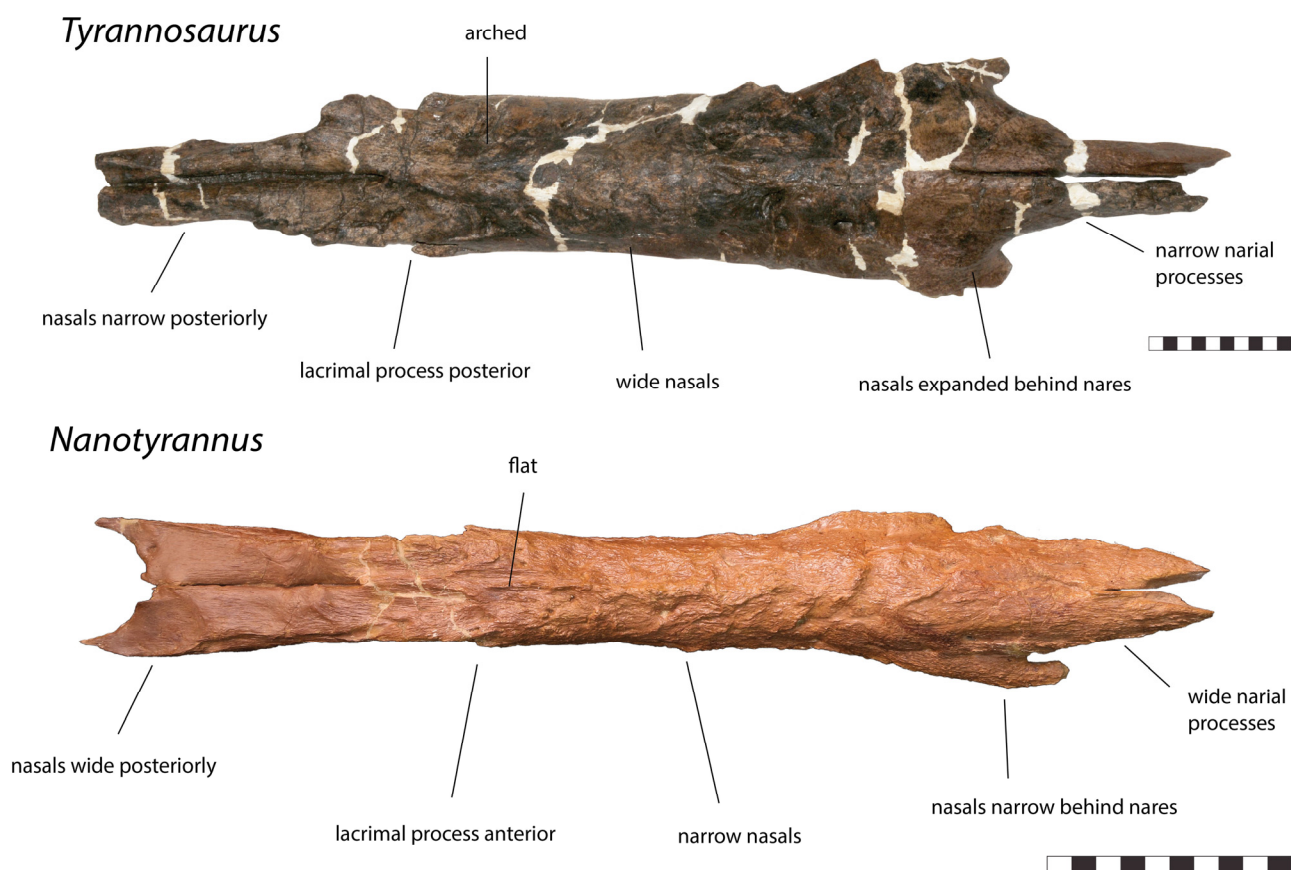


Figure 6. Nasals of *Tyrannosaurus* RSM P2523.8 and nasals of *Nanotyrannus* BMRP 2002.4.1, dorsal view, showing anatomical characters differentiating the two. Scale = 10 cm.

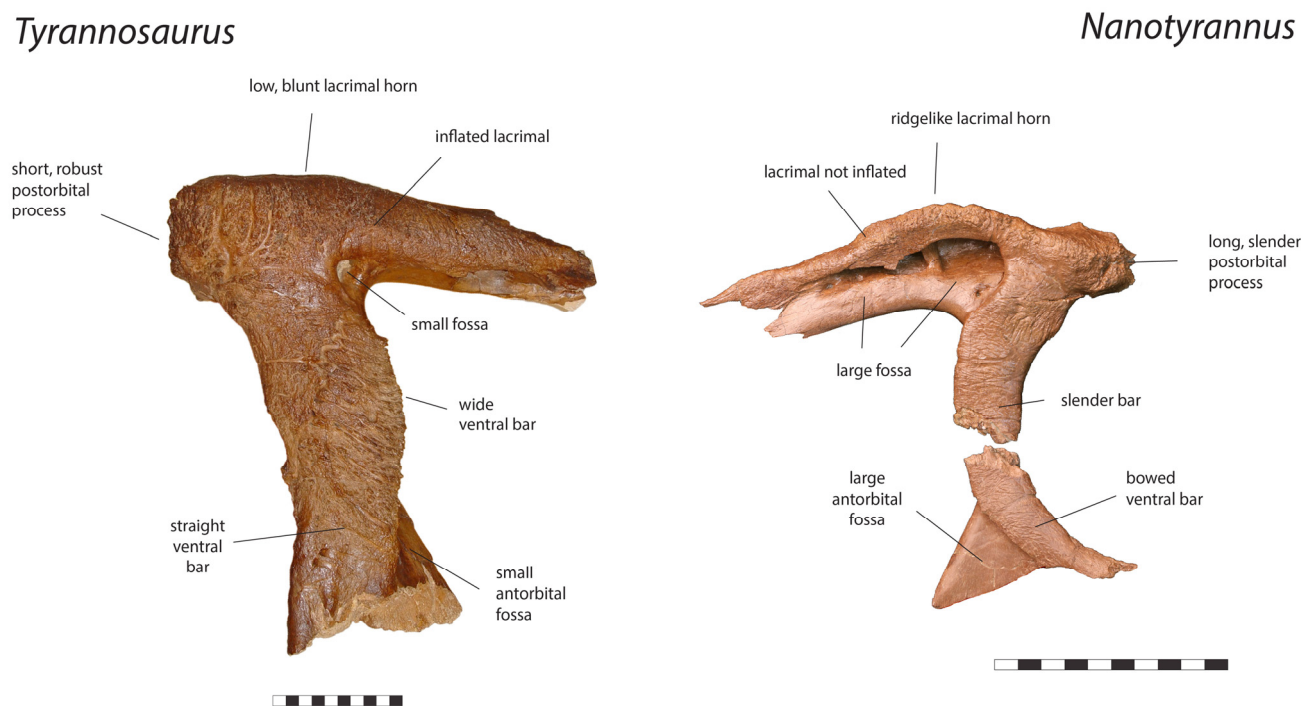


Figure 7. Right lacrimal of *Tyrannosaurus rex* holotype CM 9380 and left lacrimal *Nanotyrannus* BMRP 2002.4.1, lateral view, showing anatomical characters differentiating the two. Scale = 10 cm.

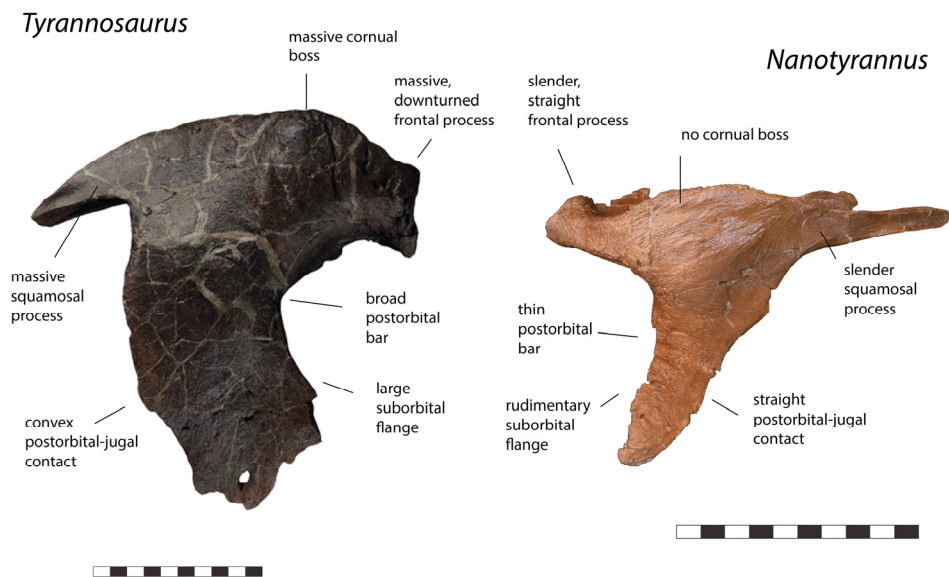


Figure 8. Right postorbital of *Tyrannosaurus rex* LACM 150167 and left postorbital *Nanotyrannus* BMRP 2002.4.1 in lateral view, showing anatomical characters differentiating the two. Scale = 10 cm.

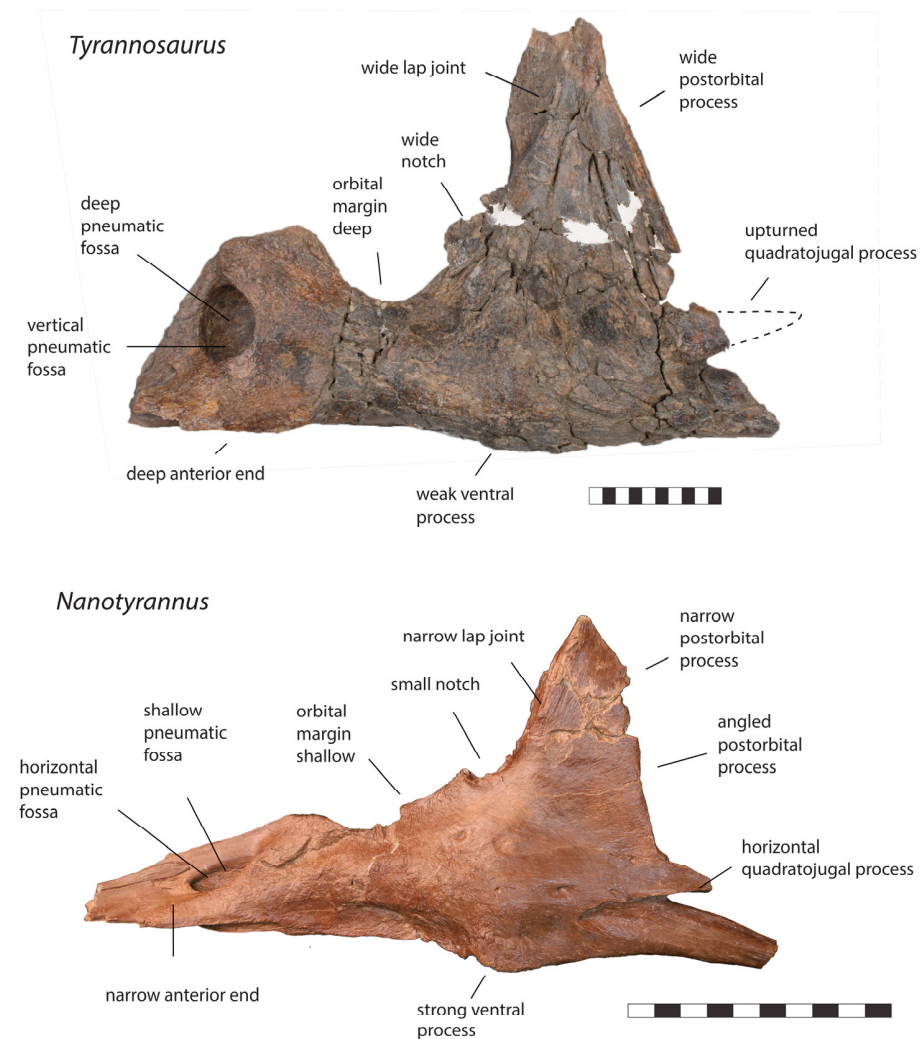


Figure 9. Left jugal of *Tyrannosaurus* RSM P2523.8 and left jugal of *Nanotyrannus* BMRP 2002.4.1 in lateral view, showing anatomical characters differentiating the two. Scale = 10 cm.

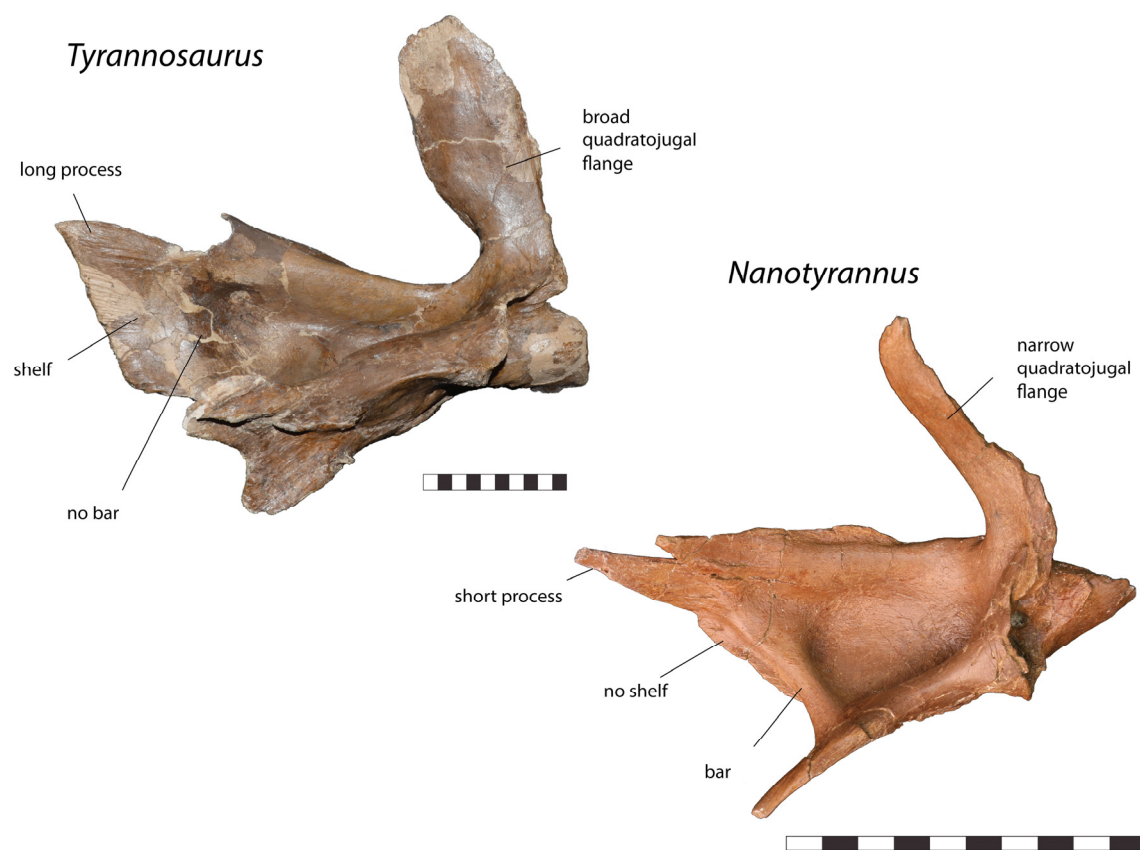


Figure 10. Right squamosal of *Tyrannosaurus* CM 9380 and left squamosal (reversed) *Nanotyrannus* BMRP 2002.4.1 in ventral view, showing anatomical characters differentiating the two. Scale = 10 cm.

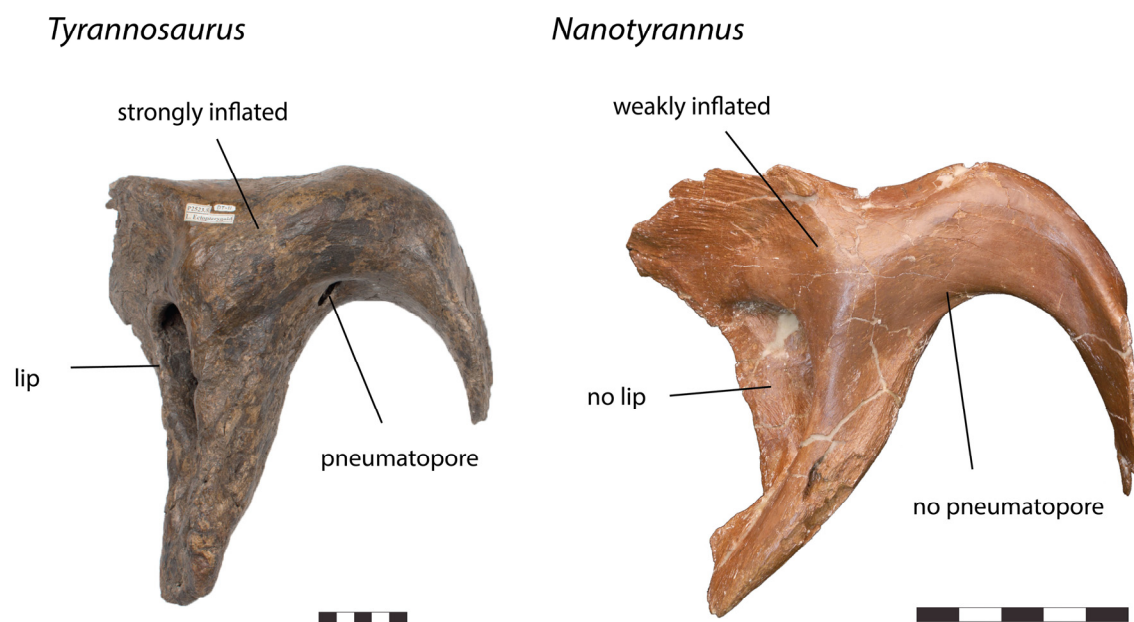


Figure 11. Left ectopterygoid of *Tyrannosaurus* RSM P2523.8 and right ectopterygoid (reversed) of *Nanotyrannus* BMRP 2002.4.1 in lateral view, showing anatomical characters differentiating the two. Scale = 5 cm.

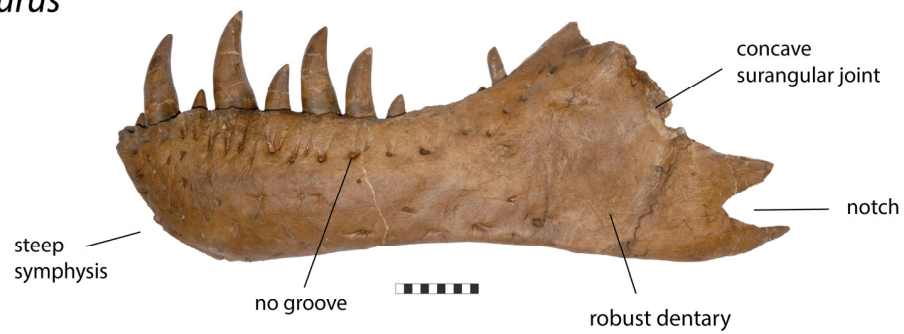
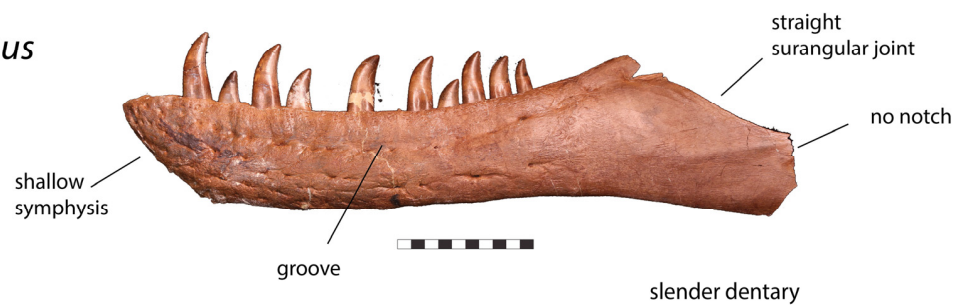
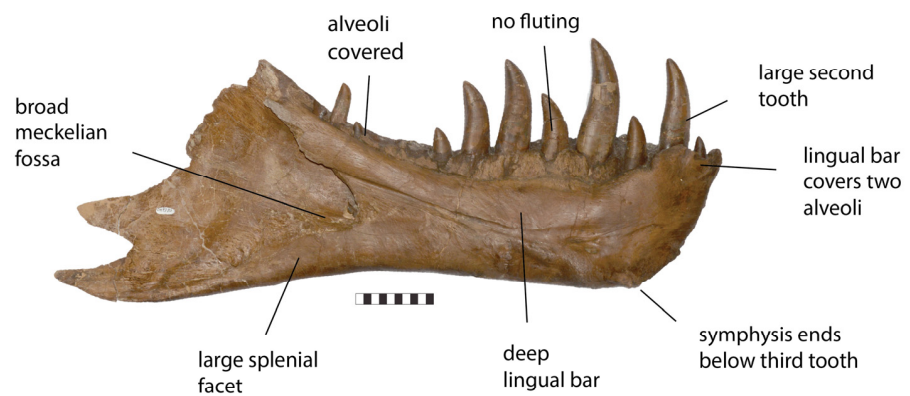
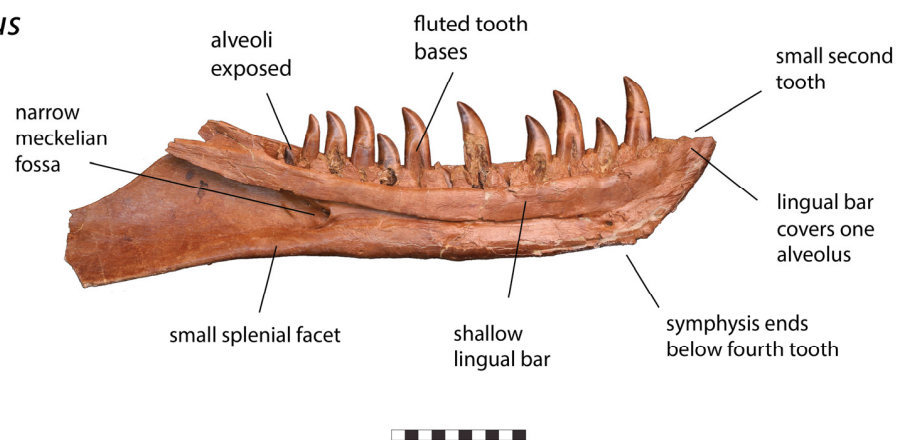
Tyrannosaurus*Nanotyrannus**Tyrannosaurus**Nanotyrannus*

Figure 12. Left dentary of *Tyrannosaurus rex* CM 9380 and right dentary (reversed) *Nanotyrannus* BMRP 2002.4.1 in lateral (**top**) and medial (**below**) views, showing anatomical characters differentiating the two. Scale = 10 cm.

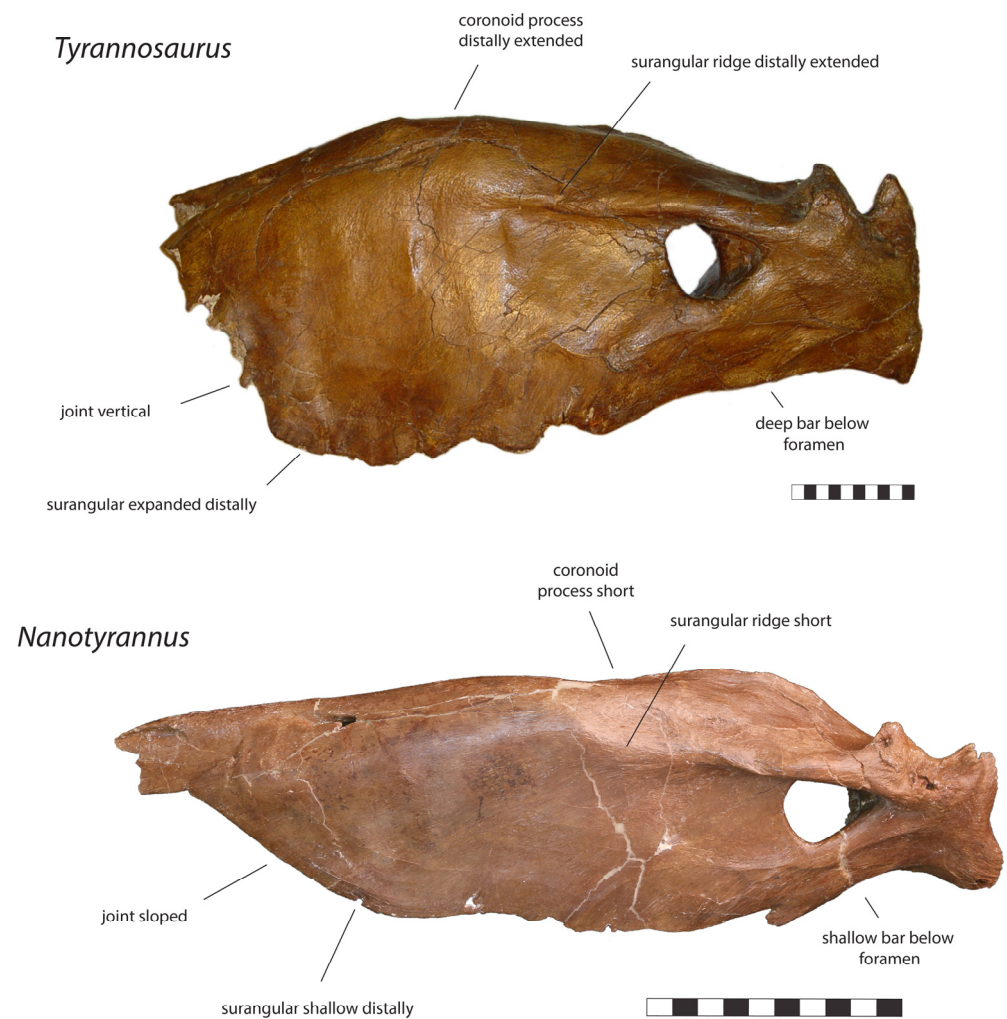


Figure 13. Left surangular of *Tyrannosaurus* CM 9380 and right surangular (reversed) *Nanotyrannus* BMRP 2002.4.1 in lateral views, showing anatomical characters differentiating the two. Scale = 10 cm.

We were able to assess just over half of these characters (80/158) for their stability over the course of development in Tyrannosaurini by examining their expression in juvenile *Tarbosaurus* [54] versus adult *Tarbosaurus* [53,101] (or for the frontals, juvenile versus adult *Tyrannosaurus*: see below). Not all characters are known for juveniles of *Tarbosaurus*, and a handful of the characters that diagnose *Tyrannosaurus* do not occur in *Tarbosaurus*, but of the 50% of characters that could be assessed, just under half (36 characters, 45%) changed over ontogeny, and slightly more than half (44 characters, 55%) were stable, being visible in young juveniles and adults. It is possible that some characters scored here as ontogenetically stable are absent in very young *T. rex*, but they do not change over the ranges of size relevant to the *Nanotyrannus* problem. Characters related to the premaxilla, maxilla, and dentition tended to be stable; characters related to the orbit, cranial ornament, and skull roof tended to show ontogenetic change.

This is meant to be a preliminary study; more specimens and a more thorough analysis of the problem are required. However, if some differences could conceivably be explained by ontogeny, not all can be. Furthermore, there is the issue of whether the distribution of characters in the specimens is consistent with this hypothesis.

3.2.2. Character Distribution and Clustering Analysis

The hypothesis that the *Nanotyrannus* morphology and the *Tyrannosaurus* morphology represent endpoints of a “growth series” makes a testable prediction about the distribution

To visualize these patterns, we performed a clustering analysis. We analyzed the morphological data using a UPGMA clustering analysis (Figure 14) using PAUP* 4.10 b10 to analyze a matrix of 158 anatomical characters coded for *Nanotyrannus* and *Tyrannosaurus*. Because a UPGMA tree shows branch lengths as proportional to similarity, it serves to visualize the overall difference between the specimens. If the two represent a growth series, they should form a continuum. Instead, specimens show two discrete clusters, consistent with two separate lineages. A similar pattern (Figure 15) emerges using principle coordinates analysis (PCoA).

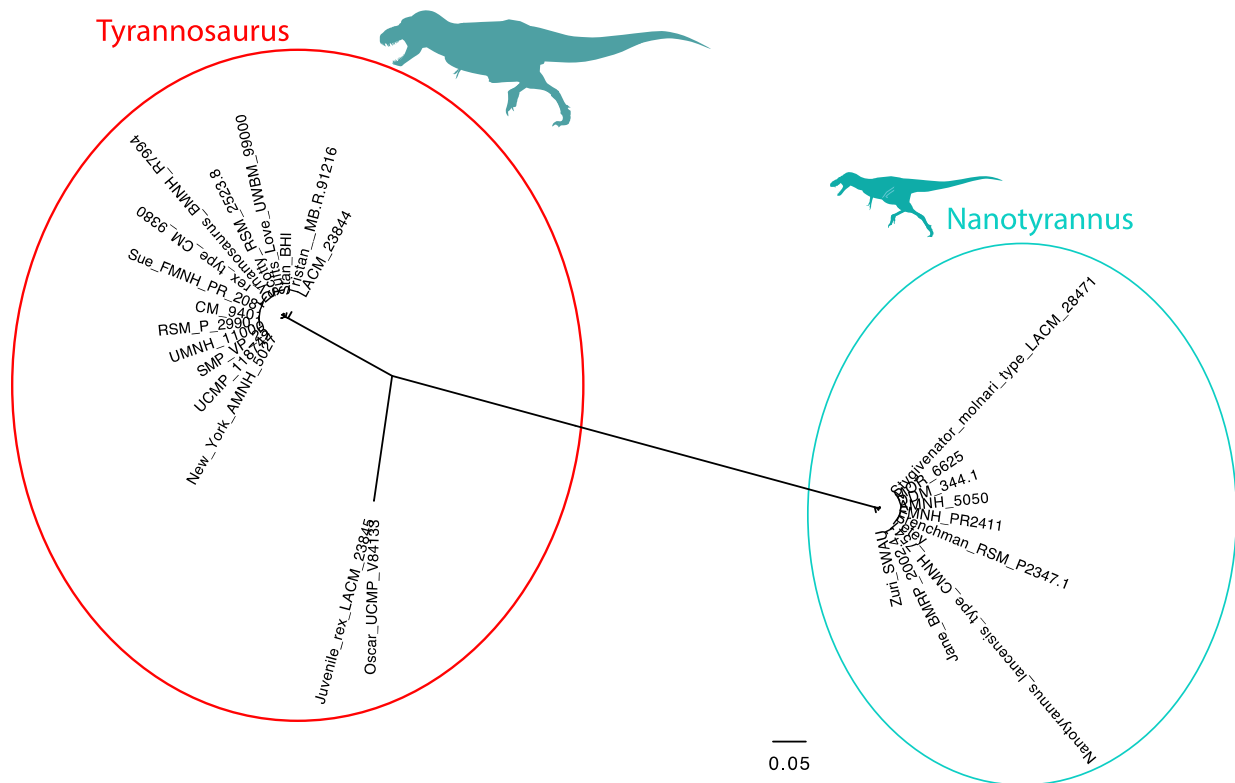


Figure 14. Unweighted pair group with arithmetic mean (UPGMA) tree showing distinct clustering of *Tyrannosaurus* and *Nanotyrannus*, with no intermediate morphotypes using characters identified in this study (Supplementary Information S2). Of 158 potentially diagnostic morphological characters, almost all are invariant, exclusively found in either *Nanotyrannus* or *Tyrannosaurus*.

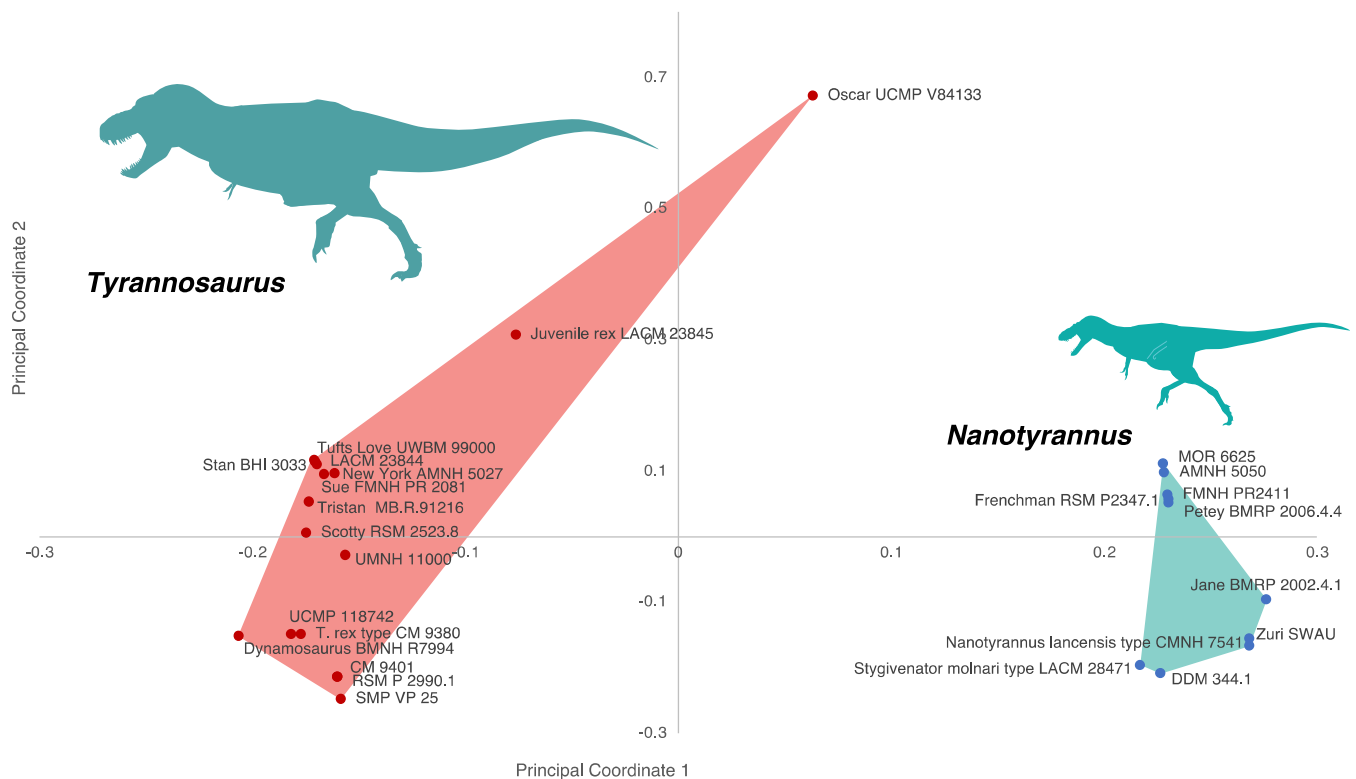


Figure 15. Principal coordinates analysis (PCoA) showing discrete clusters of *Tyrannosaurus* and *Nanotyrannus* using characters identified during this study (Supplementary Information S2). The first principal coordinate explains 60.138% of the variation and drives most of the separation between *Tyrannosaurus* and *Nanotyrannus*; the second explains 10.921% of the variation.

The discrete clusters found here are not a result of our choice of characters but reflect the highly dissimilar anatomy of the fossils. This can be shown by repeating the same analysis using the dataset of Carr [10]. This character–taxon dataset is meant to capture ontogenetic changes but recovers a similar pattern to the one found with our dataset. This pattern is seen with UPGMA analysis (Figure 16) and PCoA (Figure 17). The lone exception is BMRP 2006.4.4, which clusters with *Tyrannosaurus rex*. This does not seem to result from a strong character signal because (i) the animal lacks cranial material, (ii) the femur was not coded, and (iii) the matrix includes a very large number of subtle characters of the pedal phalanges which (as the material has not been described) we could not verify, but which may drive this pattern. We suspect the placement of BMRP 2006.4.4 is a coding artifact, but further study of the characters and material is needed.

Again, variation is discrete; the *Tyrannosaurus* morphs cluster to the exclusion of the *Nanotyrannus* morphs without intermediates. This pattern is consistent with two distinct evolutionary lineages rather than a growth series.

Finally, we studied the variation of a discrete, multi-state character, tooth count, versus size (Figure 18), using dentary tooththrow length as a size proxy [40]. *Nanotyrannus* has more teeth than *Tyrannosaurus*. Although tooth count has been hypothesized to change as the animals grow, when the *Tyrannosaurus* tooth count is plotted against tooththrow length, the slope is almost horizontal, with no clear correlation between tooththrow length and maxillary tooth count ($R^2 = 0.0123$) or dentary tooth count ($R^2 = 0.0077$). This suggests that tooth count, while variable between individuals, does not change markedly as animals grow. *Nanotyrannus* shows a slight increase in tooth count with size, but the sample size is small. These results suggest that the difference in tooth count between *Nanotyrannus* and *Tyrannosaurus* does not result from differences in size and age of the animals.

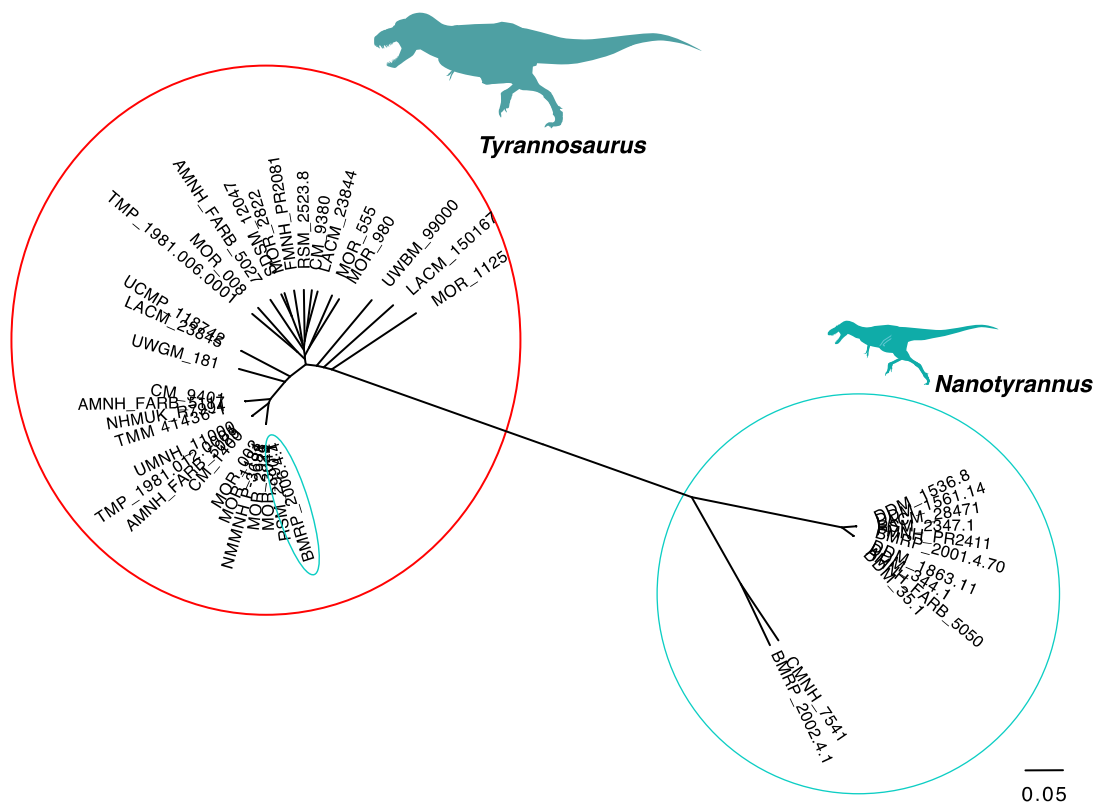


Figure 16. Unweighted pair group with arithmetic mean (UPGMA) tree showing distinct clustering of *Tyrannosaurus* and *Nanotyrannus*, using the Carr [10] dataset.

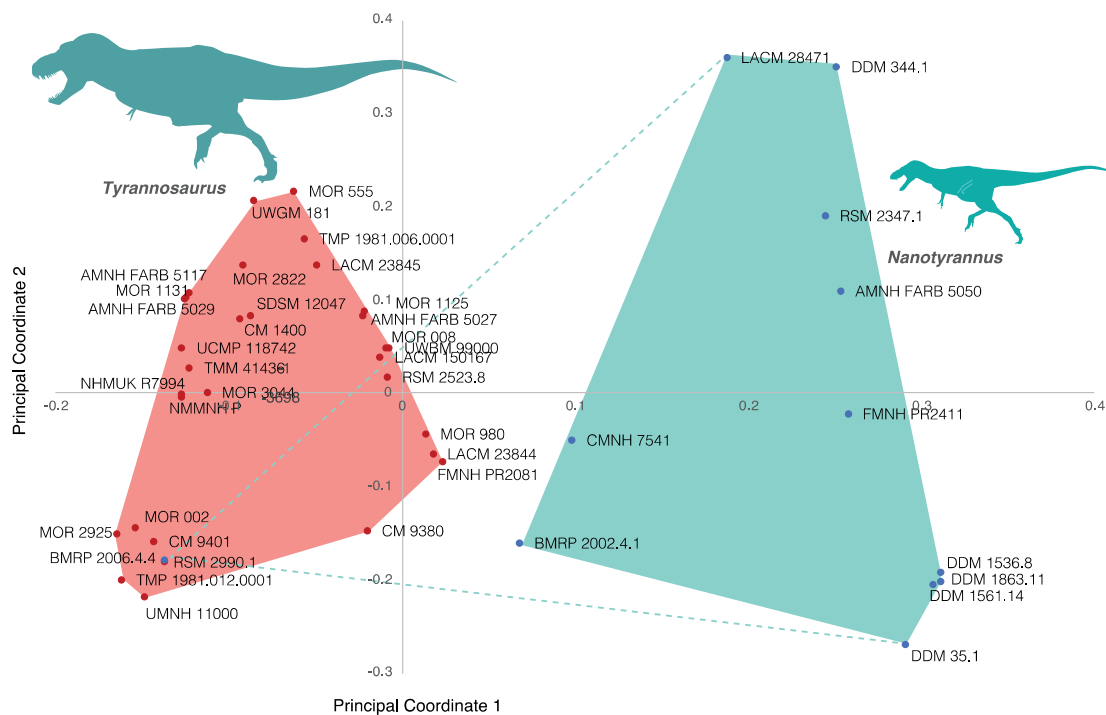


Figure 17. Principal coordinates analysis (PCoA) showing the first two principal coordinates using the Carr [10] dataset. *Tyrannosaurus* and *Nanotyrannus* form discrete clusters with the exception of *Nanotyrannus* BMRP 2006.4.4, which lacks cranial material. The first principal coordinate explains 29.348% of the variation; the second principal coordinate explains 6.1163%.

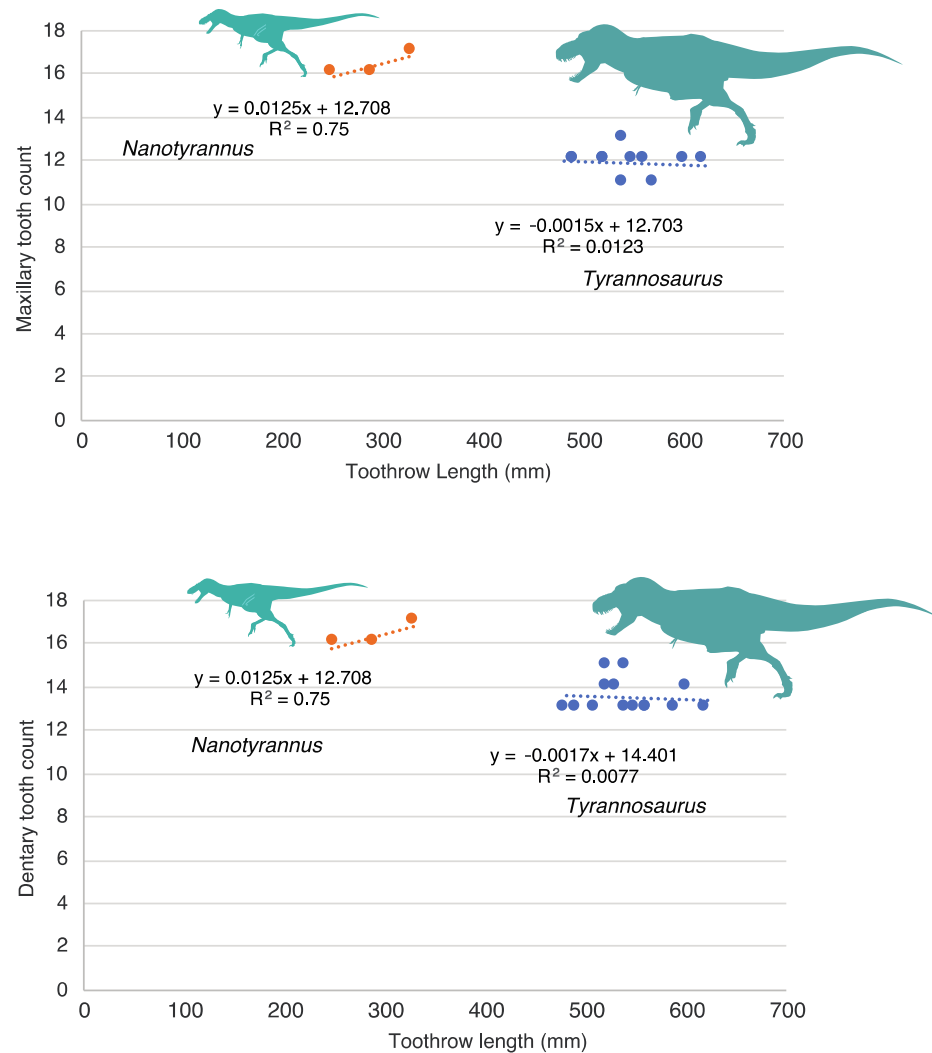


Figure 18. Tooth count versus dentary tooththrow length in *Nanotyrannus* and *Tyrannosaurus*. Top, maxillary tooth count versus dentary tooththrow length; bottom, dentary tooth count versus dentary tooththrow length. Tooth count shows no correlation with tooththrow length in *Tyrannosaurus*, suggesting that tooth count does not change with size. Data from Larson [40] and maxilla HRS 0438.

3.3. *Nanotyrannus* Morphology Inconsistent with Predicted Morphology of Juvenile *Tyrannosaurinae*

The hypothesized “growth series” linking *Nanotyrannus* to *Tyrannosaurus* can be tested by comparing it with the growth series of other tyrannosaurids, especially tyrannosaurines. If *Nanotyrannus* is a juvenile of *Tyrannosaurus*, and its distinctive morphology is the result of immaturity, then features of *Nanotyrannus* are predicted to occur in juveniles of other tyrannosaurs. If *Nanotyrannus* is a distinct taxon, then these features will be absent. We argue that juveniles of other tyrannosaurs do not conform to the “growth series” proposed for *Tyrannosaurus* [10].

A young juvenile of *Tarbosaurus bataar*, a close relative of *Tyrannosaurus*, is known [54]. In several features—posteriorly wide nasals, a gracile postorbital, a slender dentary, and lack of the suborbital process of the orbit—the animal resembles *Nanotyrannus*. This means some features seen in *Nanotyrannus* could conceivably be juvenile characters, but these features do not necessarily mean that the animals are juvenile since they occur in adults of tyrannosaurids such as *Alioramus* [70,96].

However, the juvenile *Tarbosaurus* skull differs from that of *Nanotyrannus* in many ways while resembling adult *Tarbosaurus* and *T. rex* (Figure 19). Features shared with *Tarbosaurus*

and *T. rex* (but not *Nanotyrannus*) include the tall and deep maxilla, the narrow rim of the antorbital fossa, an anteriorly placed maxillary fenestra, a large maxillary fenestra, limited contribution of the lacrimal to the antorbital fossa, weak curvature of the ventral ramus of the lacrimal, an anteriorly expanded jugal, and a broad base of the jugal postorbital process.

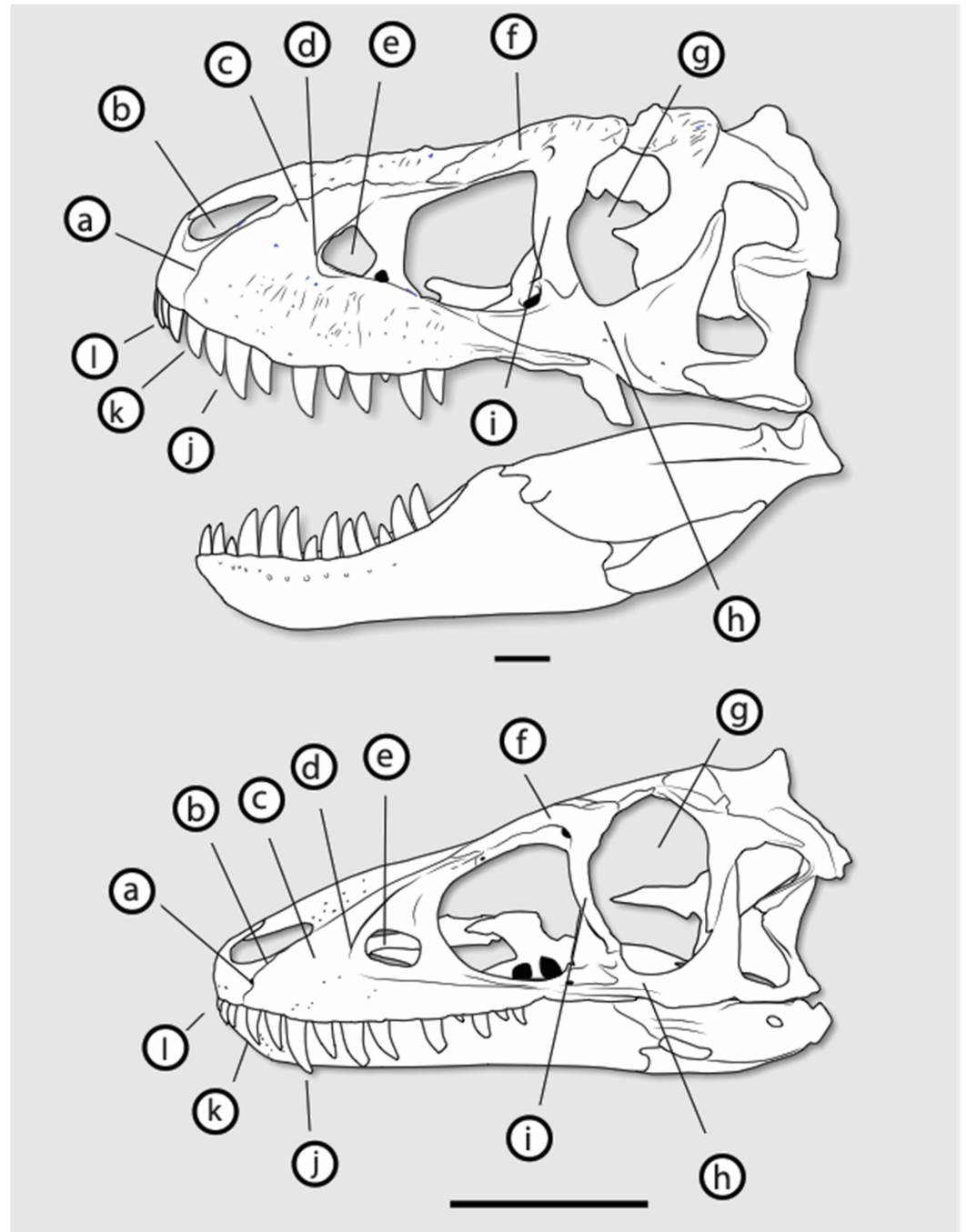


Figure 19. Ontogenetically stable characters in juveniles and adults of *Tarbosaurus* (Tyrannosaurini). Characters: (a) promaxillary fenestra concealed, (b) narial process of premaxilla faces anteriorly, (c) maxilla relatively short and tall, (d) promaxillary fenestra concealed in lateral view, (e) maxillary fenestra positioned anteriorly and ventrally, (f) lacrimal horn low, (g) orbit tall, (h) jugal narrow below orbit, (i) weakly curved orbital bar of lacrimal, (j) large anterior maxillary teeth, (k) first maxillary tooth large, (l) premaxillary teeth with pointed apices and serrated. Scale = 10 cm.

These features appear early in the ontogeny of *Tarbosaurus* and would presumably occur early in the ontogeny of *Tyrannosaurus*. The absence of these features in absolutely larger *Nanotyrannus* specimens is difficult to explain in terms of ontogeny unless *Tyrannosaurus* had a pattern of development unlike that of *Tarbosaurus* (Figure 20).

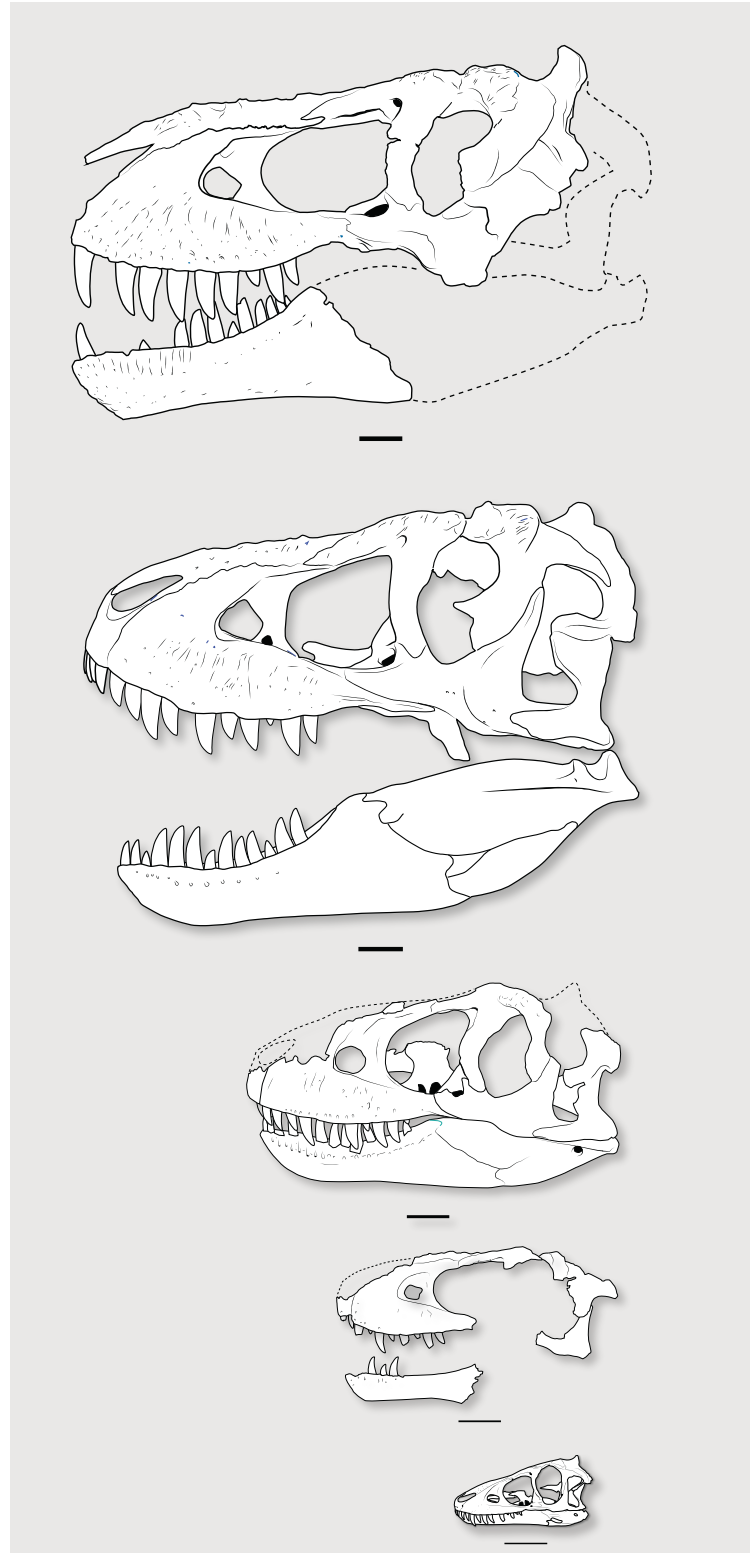


Figure 20. Growth series of *Tarbosaurus*. Top to bottom: PIN 551-1 [108], ZPAL MgD-I/4 [53], PIN 553-1 [108], PIN 552-2 [108]. Scale = 10 cm.

Some features of Tyrannosaurinae, especially those related to the skull ornamentation, orbits, and skull roof, appear to develop late, but others appear in even the youngest specimens (Figures 19 and 20). At least some tyrannosaurine features would be expected in *Nanotyrannus* if it was a juvenile tyrannosaurine, but few, if any, are present.

Juveniles are also known for *Gorgosaurus libratus*, including skulls [109,110] and isolated elements [9]. Juveniles are remarkably similar to adult *Gorgosaurus*, particularly in the shape of the maxilla, antorbital fenestra, antorbital fossa, and maxillary fenestra, implying that *Gorgosaurus* did not undergo radical changes in skull anatomy as it grew. Neither do juvenile *Gorgosaurus* exhibit *Nanotyrannus*-like characters such as the expanded antorbital fossa, procumbent premaxillary teeth, or a pneumatized quadratojugal. Growth patterns in *Gorgosaurus*, therefore, argue against *Nanotyrannus*' morphology being the result of immaturity.

For *Nanotyrannus* to be a juvenile *Tyrannosaurus*, *Tyrannosaurus* would have had to have a radically different development pattern than *Tarbosaurus* or *Gorgosaurus*. This is not impossible; ontogeny evolves. However, it is more parsimonious to treat *Nanotyrannus* and *Tyrannosaurus* as distinct species.

Finally, the proportions of the manus in the two animals are inconsistent with *Nanotyrannus* developing into *Tyrannosaurus* (Figure 21). Despite coming from much smaller animals, approximately 5–6 m in length (versus 12 m or more in *Tyrannosaurus*), manual phalanges of BMRP 2006.4.4 and HRS 15001 are significantly larger than those of even very large *Tyrannosaurus*, FMNH PR 2081. While allometric growth is possible, with the manus becoming proportionately smaller, the proportions seen in *Nanotyrannus* require the manus and claws to become absolutely smaller—for bone to be resorbed and elements reduced in length—as the animal matures. We are unaware of any amniote that develops in this fashion. Another problem is that the tip of the vomer is deeper in *Nanotyrannus* than in *Tyrannosaurus*; this would require the end of the vomer to shrink or be resorbed [40].

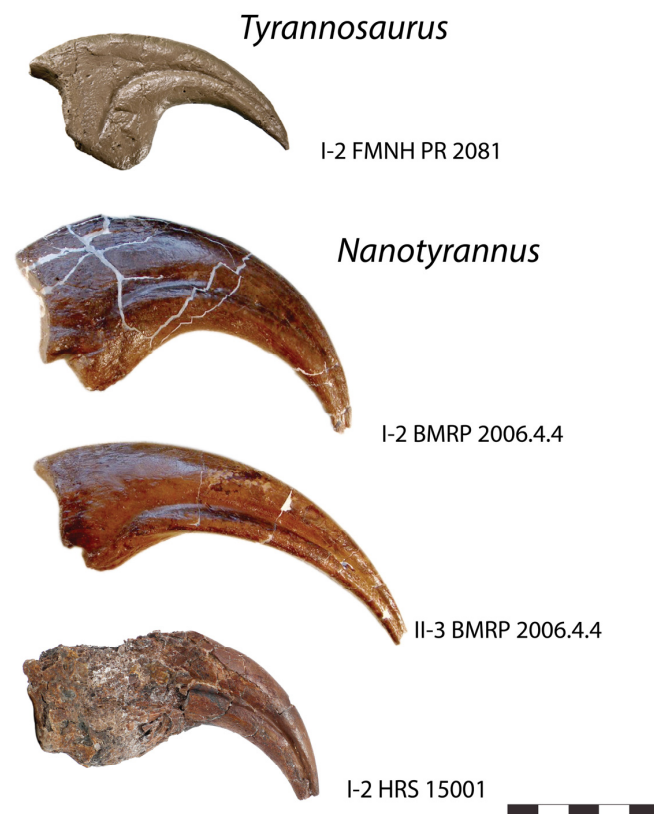


Figure 21. Manual unguals of *Tyrannosaurus* and *Nanotyrannus*, shown to scale; small *Nanotyrannus* specimens have absolutely larger unguals than much larger *Tyrannosaurus*. Scale = 5 cm.

Larson [40] also notes that patterns of pneumaticity are stable in birds as they grow, which makes differences in the presence and position of pneumatic foramina, such as the maxillary fenestra (Figure 4), difficult to explain.

3.4. Histology Supports Existence of Mature *Nanotyrannus*

3.4.1. Use of Histology to Test the Two Hypotheses

If *Nanotyrannus* is a juvenile of *Tyrannosaurus*, then all individuals showing the *Nanotyrannus* morphology must be immature relative to *Tyrannosaurus*. Bone histology can be used to infer the age and maturity of fossils, either to estimate absolute age (i.e., years of age) or relative maturity (e.g., young, rapidly growing juveniles and subadults, slower growing young adults versus old adults with slowed/ceased growth). The study of histology encompasses all aspects of bony tissue development, not simply thin sections and growth lines. To assess whether animals putatively identified as *Nanotyrannus* represent juveniles of *T. rex* or a distinct, small-bodied tyrannosaur taxon, maturity can be assessed in at least five distinct ways:

- (i) Patterns of skeletal fusion;
- (ii) Bone surface texture;
- (iii) Presence/absence of an external fundamental system (EFS);
- (iv) Patterns of annual growth rates, either in terms of measures of bone deposition or kilograms of mass;
- (v) Predicted adult mass, extrapolated from growth curves.

Nanotyrannus individuals show skeletal fusion and rugose facial bone, suggesting they were approaching maturity. Histology shows that *Nanotyrannus* individuals lack an external fundamental system, meaning that they are not old adults, but they show annual growth rates suggesting maturity. They also have predicted adult masses strongly suggestive of a distinct, small-bodied taxon rather than of juveniles of the giant *Tyrannosaurus*.

3.4.2. Skeletal Fusion

In vertebrates, composite elements such as the skull, vertebrae, shoulder girdle, sacrum, and pelvis may fuse late in development when growth slows. In crocodilians, centra and neural arches of vertebrae typically fuse late in life [111]. In ceratopsids, skull elements and their associated osteoderms fuse late in development [107]. Which elements fuse and the sequence of fusion can vary from taxon to taxon and even individual to individual [107]. Furthermore, some skull elements fuse early in ontogeny. The parietal bones, for example, are fused even in very young individuals in ceratopsids [112] and tyrannosaurids [54,113], and nasals are fused even in very young tyrannosaurids [54,113]. Therefore, not all fusions signal maturity. Some elements, however, only fuse in large individuals, suggesting their fusion correlates with skeletal maturity.

The scapula and coracoid fuse appear to fuse late in many dinosaurs, including *Herrerasaurus* [114], Abelisauridae [115], and at least some dromaeosaurs, including *Velociraptor mongoliensis* [116] and *Achillobator giganticus* [117]. Fusion of the scapulocoracoid also occurs in tyrannosaurs. Partial scapulocoracoid fusion is seen in *Albertosaurus sarcophagus* [71]; complete fusion is seen in a large *T. rex* [7] and a *Tyrannosaurus* from the Naashoibito member of the Kirtland Formation [118].

In some theropods, the pelvis shows partial or complete fusion in large individuals. The pubis and ilium fuse in the microraptorine *Hesperonychus elizabethae* [119]; the ilium, ischium, and pubis fuse in Coelophysoidea [120], Abelisauridae [121–123], and Ornithomimidae [124–127]. Fusion of the pubis and ischium also occurs in a large individual of *T. rex* [7]; the pubes and ischia are fused in *Daspletosaurus* UALVP 52981.

While not all skeletal fusions are correlated with maturity, fusion of the vertebrae, pectoral girdle, and pelvic girdle do seem to correlate with maturity. Strikingly, a number of fusions occur in *Nanotyrannus* BMRP 2002.4.1 [40]. These include fusion or partial fusion of neural arches to centra, fusion of the scapulocoracoid, and fusion of the ilium, pubis, and ischium [40]. This degree of skeletal fusion is consistent with the animal being a

nearly full-sized subadult or early adult [40]. Further study of skeletal fusion patterns is needed for tyrannosaurs (and dinosaurs more generally), but evidence from skeletal fusions suggests that *Nanotyrannus* are not juveniles of *Tyrannosaurus*.

3.4.3. Surface Texture

In many dinosaurs, the adult skull bones take on a rugose to gnarled surface texture and may develop sculpturing. In chasmosaurine ceratopsians, for example, juveniles and subadults have smooth, striated skull bones. In adults, the bone takes on a gnarled texture, resembling tree bark, often with extensive, high-relief rugosity [107,128,129] and grooves for blood vessels. The appearance of rugose bone texture can be used as a rough proxy for maturity in Ceratopsidae. Striated bone is not seen in the very oldest individuals but is seen in very large individuals of *Torosaurus* [107], showing that it persists relatively late in subadults and young adults.

A similar pattern is seen in tyrannosaurids. In *Gorgosaurus*, nasals [9], maxillae [9], and postorbitals [110] are relatively smooth in juveniles, and become more rugose in subadults and adults. A similar pattern occurs in postorbitals of *Daspletosaurus* [110]. Young *Tarbosaurus* show weak sculpturing of the maxilla, while nasals and lacrimals are almost smooth [54]; smooth facial bones are seen in another juvenile tyrannosaurine, the holotype of “*Raptorex kriegsteini*” [113], likely a juvenile *Tarbosaurus* [55]. Adults have highly rugose facial bones [101].

These patterns are hard to quantify or characterize objectively, but overall, it appears that rugosity of facial elements increases as animals mature, providing a rough proxy for maturity. As in Ceratopsidae, striated bone persists relatively late in ontogeny, being seen in subadult *Alioramus* [70], young adult *Gorgosaurus* [109], and in the types of the tyrannosaurines *Bistahieversor* [59] and *Thanatotheristes* [110]. Although the presence of striated bone may show that an animal has not ceased growing entirely, its presence in relatively large young adults suggests that it cannot be used to identify animals as juveniles.

In the smallest *Nanotyrannus* specimen, LACM 28471, the surface of the maxillae and nasals is smooth, with little sculpture. However, in the larger *N. lancensis* holotype, CMNH 7541 (Figure 22), much of the nasals, maxillae, and the anteroventral surface of the dentary are rugose, as are the lateral surface of the lacrimal, the descending process of the postorbital, and the jugal ventral surface. Striated bone occurs inside the antorbital fossa, on the dentary’s dorsolateral surface, and the dorsal part of the jugal. The specimen, therefore, shows a mixture of textures, as expected for a subadult or young adult.



Figure 22. Facial bone rugosity in the *Nanotyrannus lancensis* holotype CMNH 7541. (A), nasal in left lateral view, (B), right maxilla, (C), right dentary. Scale = 5 cm.

In Jane (BMRP 2002.4.1), the maxillae, lacrimals, postorbitals, nasals, and the tip of the dentary are highly rugose and covered with grooves, sculpturing, and gnarled bone (Figure 23); striated bone is found on the antorbital fossa of the maxilla and lacrimal, the posterior end of the nasal, and the posterior end of the dentary. These bone textures suggest a subadult or young adult. The Zuri specimens show highly rugose sculpturing on the maxilla, nasals, lacrimals, and dentary tip. The maxilla of KU 155809 is also highly rugose. Meanwhile, the nasals of LACM 23845, the smallest definitive *Tyrannosaurus* skull, show weak sculpturing.

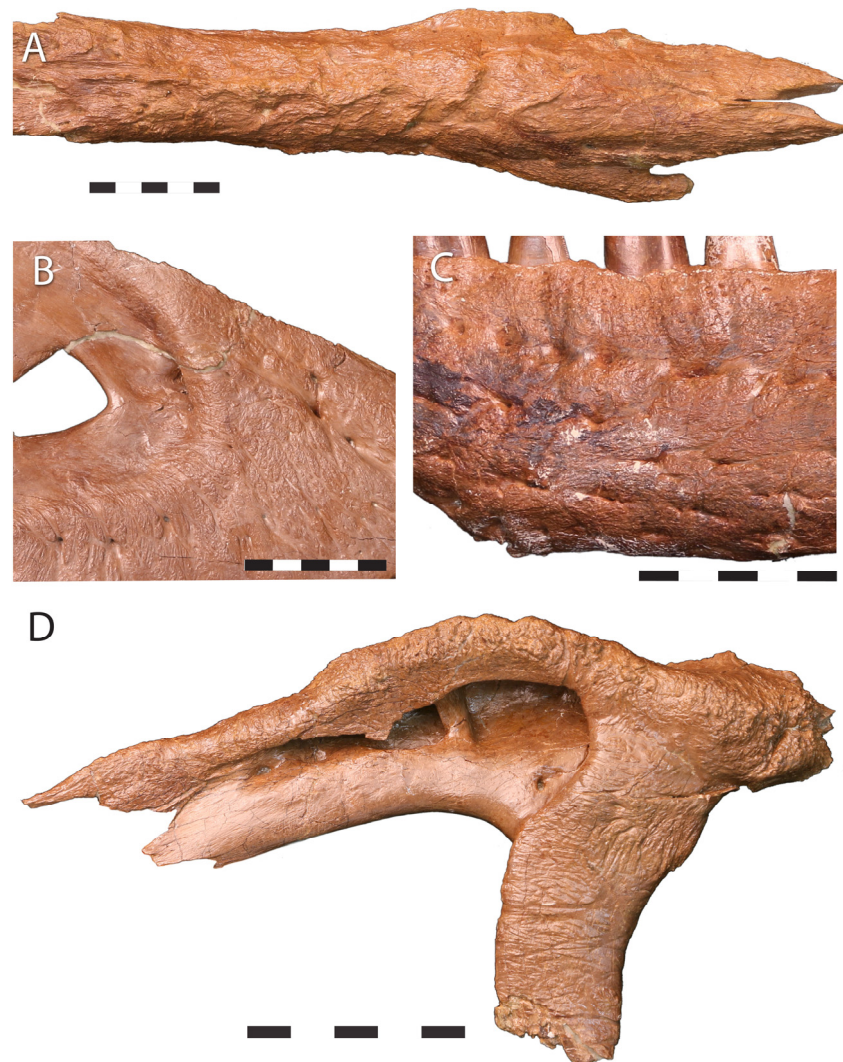


Figure 23. Facial bone rugosity in Jane BMRP 2002.4.1. (A), nasals, (B) right maxilla, (C), left dentary, (D), left lacrimal. The facial bones are extensively sculptured, similar to the condition seen in large *Tyrannosaurus rex*. Scale = 5 cm.

Striated surface textures associated with growth occur in the holotype of *Nanotyrannus lancensis* CMNH 7541 and in BMRP 2002.41. However, striated bone is seen in subadults or young adults of other tyrannosaurs [57,59,70,109]. Overall, bone textures suggest a degree of maturity in these animals, suggesting they are subadults or young adults of a distinct taxon, not juveniles of *Tyrannosaurus*.

3.4.4. External Fundamental System

The external fundamental system, or EFS, is an outermost band of very slow-growing bone with multiple, closely spaced lines of arrested growth (LAGs). It is deposited as

growth rates slow and plateau late in life. An EFS can be used as an indicator of the cessation of significant growth and the attainment of maximum body size in a highly mature animal.

The existence of an EFS would be strong evidence that an animal was old and had effectively stopped growing. The absence of an external fundamental system would suggest that the animal had yet to achieve full adult size. It would mean the animal was not an old adult; however, given that the EFS appears late in life, as the animal attains maximum size [8,49,130], it would not preclude the possibility that an animal was a young adult just short of full size.

Three putative *Nanotyrannus*, BMRP 2002.4.1, BMRP 2006.4.4, and HRS 081514, have been sectioned and lack an EFS [46,51]. This shows these animals are not old adults but does not preclude the possibility that these animals are young adults. In *T. rex*, individuals are nearly full size before establishing an external fundamental system. Sue, FMNH PR 2081, grew to an estimated 7930 kg before establishing an EFS [49,50], then died at 8223 kg [50], adding only around 300 kg (i.e., <4% increase) after the appearance of the EFS. BMRP 2002.4.1, BMRP 2006.4.4, and HRS 081514 may represent young adults.

3.4.5. Growth Rates

Lines of arrested growth (LAGs) record changes in bone circumference and diameter over time (Figure 24). Assuming that such lines develop annually, as is commonly done in paleohistology, it becomes possible to reconstruct growth rates by using measured and estimated circumferences either reported in or calculated from published data [46,49,50] to estimate mass [50] at various points in the individual's lifespan. By converting femoral circumferences into body mass estimates [50], one can estimate changes in mass in terms of kilograms per year (Table 5). Note that Jane's femur is incomplete, so the circumference was approximated as a circle using LAG spacing from the endosteum and using femur width (Supplemental Material).

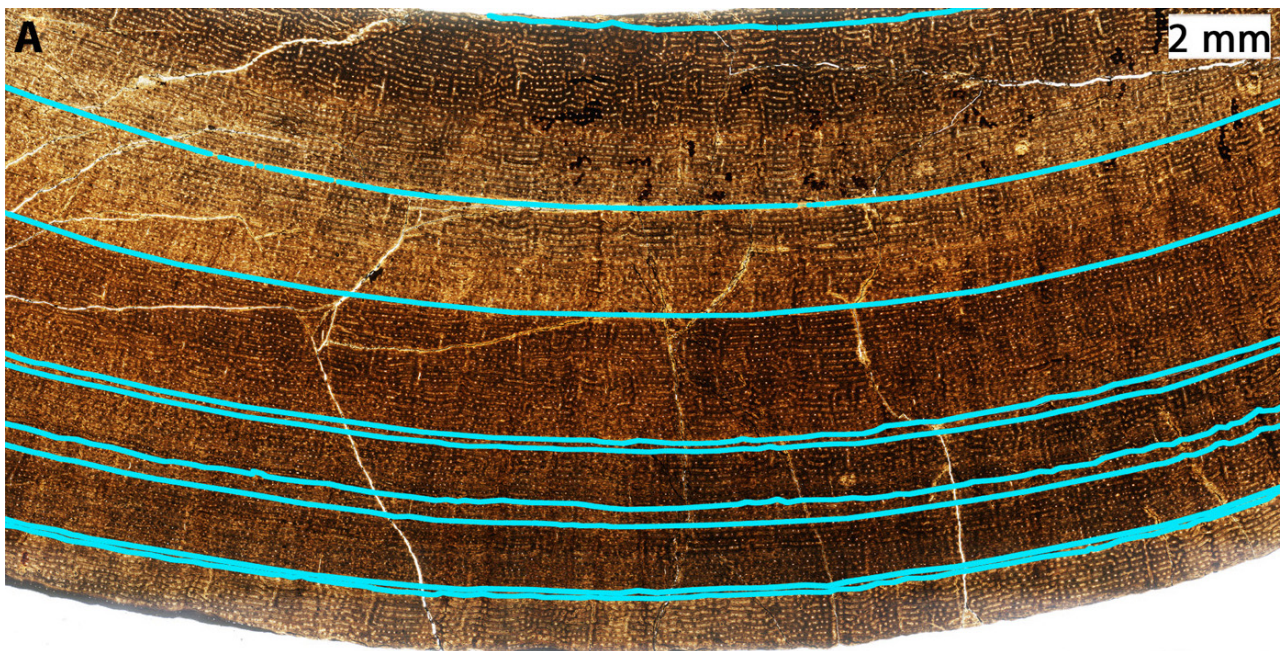


Figure 24. Cont.

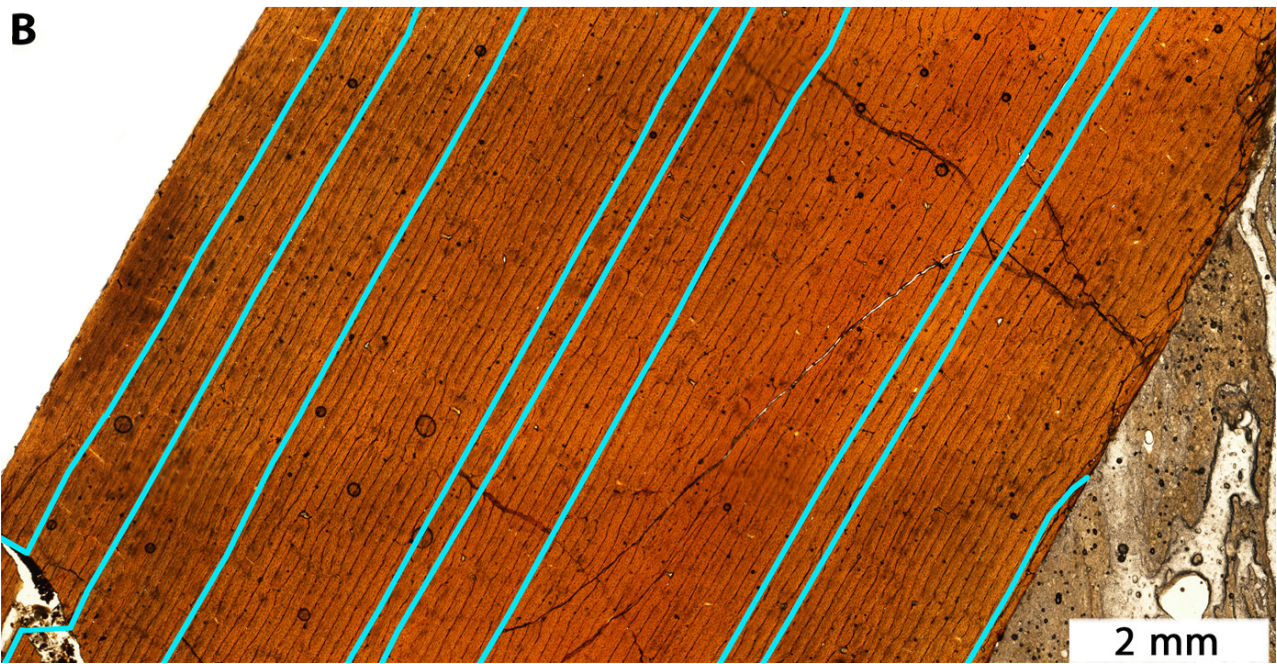


Figure 24. Thin sections of the femur of (A), BMRP 2002.4.1 (“Jane”) and (B), BMRP 2006.4.4 (“Petey”). An external fundamental system (EFS) is absent, but lines of arrested growth or LAGs (blue) become closer toward the outer edge of the bone, showing decelerating growth. Modified from [46]. Note that some LAGs are likely split (multi-LAGs) and do not represent a full year of growth.

Table 5. LAG data, body mass, and growth rate estimates rounded to the nearest kg for Sue (FMNH PR 2081), Petey (BMRP 2006.4.4), and Jane (BMRP 2002.4.4) based on femoral circumferences, including corrected values for Jane based on a split multi-LAG interpretation [49]. Campione et al. [50] estimate Sue’s mass at death (i.e., after LAG #23) as 7377 kg after applying a correction for non-circular femoral cross-section. Hutchinson et al. [104] estimate Jane’s mass at death (i.e., after LAG #9) as 954 kg based on 3D modeling. See Supplemental File for equations used in calculations. Note that LAG #1 and the periosteum do not record a full year of growth. Periosteum is assigned a LAG pseudo-number of +0.5 after the final LAG, indicating that death could have occurred at any point after the last yearly marker was deposited while assigning an age at the midpoint of that final year. Jane required estimation of LAG/periosteum circumferences from LAG spacing and femoral width due to the incomplete cross-section of the femur midshaft. (1) LAG (or periosteum) distance from endosteum is measured at the time of death, (2) femoral width at midshaft (including medullary cavity) is measured at time of death and back estimated using LAG spacing, (3) femoral circumference derived from femoral width at a given year is approximated as a circular cross-section. Data sources: Campione et al. [50]; Cullen et al. [49]; Woodward et al. [46].

Specimen	Nickname	Taxon	LAG No.	Circumference (mm)	Mass (kg) (Campione et al., 2014), Equation (7))	Mass Increase from Previous LAG (kg)
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	1	338.7	1924	NA
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	2	387	2777	853
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	3	415.7	3382	605
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	4	440.3	3962	580
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	5	459.7	4461	500
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	6	485.5	5185	724
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	7	511.1	5973	788

Table 5. Cont.

Specimen	Nickname	Taxon	LAG No.	Circumference (mm)	Mass (kg) (Campione et al., 2014), Equation (7))	Mass Increase from Previous LAG (kg)
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	8	527.1	6503	529
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	9	542.8	7050	547
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	10	551.6	7369	319
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	11	559.3	7656	287
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	12	564.9	7869	213
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	13	565.7	7900	31
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	14	566.5	7931	31
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	15	567.4	7965	35
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	16	568.2	7996	31
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	17	569	8027	31
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	18	569.8	8059	31
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	19	570.7	8094	35
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	20	571.5	8125	31
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	21	572.3	8156	31
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	22	573.1	8188	31
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	23	574	8223	35
FMNH PR 2081	Sue	<i>Tyrannosaurus</i>	Periosteum	579	8422	199
BMRP 2006.4.4	Petey	<i>Nanotyrannus</i>	1	148.4	198	NA
BMRP 2006.4.4	Petey	<i>Nanotyrannus</i>	2	165.9	269	71
BMRP 2006.4.4	Petey	<i>Nanotyrannus</i>	3	194.7	419	149
BMRP 2006.4.4	Petey	<i>Nanotyrannus</i>	4	214.5	547	128
BMRP 2006.4.4	Petey	<i>Nanotyrannus</i>	5	223.6	613	66
BMRP 2006.4.4	Petey	<i>Nanotyrannus</i>	6	229.4	658	45
BMRP 2006.4.4	Petey	<i>Nanotyrannus</i>	7	234.8	701	44
BMRP 2006.4.4	Petey	<i>Nanotyrannus</i>	Periosteum	244.7	786	84
BMRP 2002.4.4	Jane	<i>Nanotyrannus</i>	1	195.9	426	NA
BMRP 2002.4.4	Jane	<i>Nanotyrannus</i>	2	218.4	575	149
BMRP 2002.4.4	Jane	<i>Nanotyrannus</i>	3	231.8	677	102
BMRP 2002.4.4	Jane	<i>Nanotyrannus</i>	4	247.3	809	132
BMRP 2002.4.4	Jane	<i>Nanotyrannus</i>	5	248.6	820	11
BMRP 2002.4.4	Jane	<i>Nanotyrannus</i>	6	255.3	884	63
BMRP 2002.4.4	Jane	<i>Nanotyrannus</i>	7	257.7	906	23
BMRP 2002.4.4	Jane	<i>Nanotyrannus</i>	8	265.7	986	79
BMRP 2002.4.4	Jane	<i>Nanotyrannus</i>	9	266.6	995	9
BMRP 2002.4.4	Jane	<i>Nanotyrannus</i>	Periosteum	273.2	1064	69
BMRP 2002.4.4	Jane (corrected)	<i>Nanotyrannus</i>	1	195.9	426	NA
BMRP 2002.4.4	Jane (corrected)	<i>Nanotyrannus</i>	2	218.4	575	149
BMRP 2002.4.4	Jane (corrected)	<i>Nanotyrannus</i>	3	231.8	677	102
BMRP 2002.4.4	Jane (corrected)	<i>Nanotyrannus</i>	4	248.6	820	144

Table 5. Cont.

Specimen	Nickname	Taxon	LAG No.	Circumference (mm)	Mass (kg) (Campioni et al., 2014), Equation (7))	Mass Increase from Previous LAG (kg)
BMRP 2002.4.4	Jane (corrected)	<i>Nanotyrannus</i>	5	257.7	906	86
BMRP 2002.4.4	Jane (corrected)	<i>Nanotyrannus</i>	6	266.6	995	88
BMRP 2002.4.4	Jane (corrected)	<i>Nanotyrannus</i>	Periosteum	273.2	1064	69

Juvenile tyrannosaurs have high maximal growth rates, approaching [8] or exceeding 800 kg/y in *Tyrannosaurus*. Immature *Tyrannosaurus*, particularly juveniles weighing ~1000–2000 kg, are predicted to have high growth rates as they enter their exponential growth phase. If *Nanotyrannus* is a distinct, small-bodied tyrannosaur, then it will have much lower growth rates at this size, comparable to growth curves modeled for small-bodied tyrannosaurids such as *Gorgosaurus* or *Albertosaurus* [8]. However, if the two taxa are synonymous, then specimens the size of BMRP 2002.4.1 and BMRP 2006.4.4 should be in their rapid, exponential growth phase—especially if one assumes that they have entered their teenage years [46].

Narrow spacing of LAGs (Figure 24), especially towards the periosteum, shows low growth rates in putative *Nanotyrannus* specimens (Figure 25, Table 5). Growth rates do not exceed 150 kg/year for the last few years of life and can be less than 50 kg/year. This rejects the hypothesis that these are young, rapidly growing *T. rex*, which achieved peak growth rates exceeding 800 kg/y based on the estimates from FMNH PR2081 (Table 5).

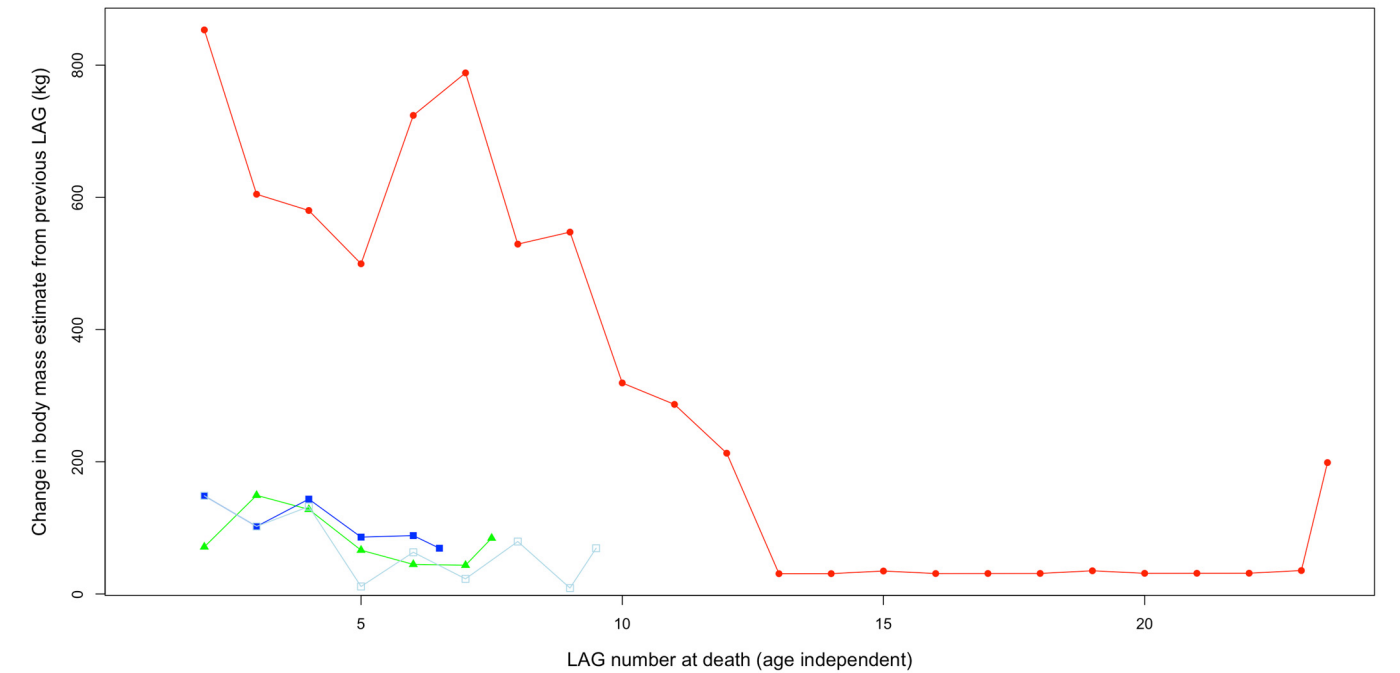


Figure 25. Changes in estimated body mass from previous LAG as preserved in the femurs of Sue (red, circles), Petey (green, triangles), and Jane BMRP 2002.4.1, corrected for possible split multi-LAGs as in Cullen et al. [49] (dark blue, solid squares) and uncorrected as in Woodward et al. [46] (light blue, open squares), at the time of death. Periosteum included here as the final half LAG. LAG 1 excluded here because (1) it is a partial record of growth due to medullary cavity remodeling and bone resorption and (2) because Jane’s incomplete femur and Sue’s core sampling (rather than a complete transverse section) exclude easy measurement/estimation of endosteal circumference. An EFS is readily apparent in the last decade or so of Sue’s life. See the Supplemental Material for plots that exclude the periosteum.

3.4.6. Growth Trends

Growth rates change over time. Growth accelerates until roughly the middle of life in symmetric logistic and asymmetric Gompertz growth models as commonly applied to dinosaurs [8,131–133] then decelerates. Growth finally slows and almost stops in the last few years of life, reaching asymptotic growth. Based on their size (and even their approximated age from prior studies [46]), if the animals assigned to *Nanotyrannus* are juvenile *T. rex*, then they should show increasing growth rates (i.e., exponential growth) as they approach the rapid, protracted growth spurt at the middle of the tyrannosaur life cycle at around 1000–4000 kg [8]. If they are subadults or adults of a distinct, small-bodied species, they would be expected to show decelerating or ceased growth.

Growth rates in *Nanotyrannus* show a general trend of deceleration in their final years of life. These trends resemble those seen in mature *T. rex* as growth begins to plateau just before it establishes an EFS. These patterns are strongly suggestive of relatively mature animals, either late-stage subadults or early adults, not rapidly growing juveniles.

Estimated maximum size. It is possible to fit various kinds of growth curves to estimated masses [133], which can be extrapolated and used to predict the mass that a given individual would have achieved at full size. This approach can be used to test whether *Nanotyrannus* specimens would have grown to the enormous sizes (~8000 kg) seen in *T. rex*. If the putative *Nanotyrannus* were juveniles of *T. rex*, then their predicted adult masses should be on the order of 5000–10,000 kg, as in *T. rex*. If they are subadults or young adults of small-bodied tyrannosaurs, then their predicted adult masses should be much lower.

A caveat is that, when fitting a growth model to a year-by-year growth record from a single individual rather than to mass-age data from separate individuals, the assumption of independence of data is violated, making these pseudo-regression analyses (and making the calculation of confidence/prediction intervals moot). These models are nevertheless useful in extrapolating adult masses when individuals die prior to reaching full size. This is because, although extrapolation is always highly uncertain in science, we are limited to the growth record preserved in the femora; speculation that growth rates could have exponentially increased had these putative *Nanotyrannus* specimens lived longer is, therefore, a weaker argument than the use of adult size estimates from these pseudo-regressions. We prefer the admittedly high uncertainty of extrapolation modeled on empirical evidence to speculation (i.e., one could speculate that any number of changes in growth rate or morphology might have occurred post-mortem since such speculation is unbounded by fossil evidence).

Growth curves using asymptotic logistic, Gompertz, and von Bertalanffy models predict fully adult masses (Figure 26) on the order of perhaps ~700–1100 kg for BMRP 2006.4.4 and ~1200–2100 kg for BMRP 2002.4.1 (when corrected for split multi-LAGs [49]). Non-asymptotic logarithmic models can achieve higher masses since they have no upper limit, but these predicted masses still fall far short of *T. rex* (Figure 27) and are closer to that of *Albertosaurus*. These estimates are, in the context of comparison with *T. rex*, also roughly consistent with mass estimates at the time of death for BMRP 2002.4.1 derived from 3D modeling [104]. Mass estimates are not available for the Zuri specimen (HRS 081514) because the pubis was sectioned rather than the femur. However, plotting the growth of this specimen using data from Griffin [51] shows slow growth and growth deceleration rather than rapid, accelerating growth (Figure 28); it was apparently near full size when it died.

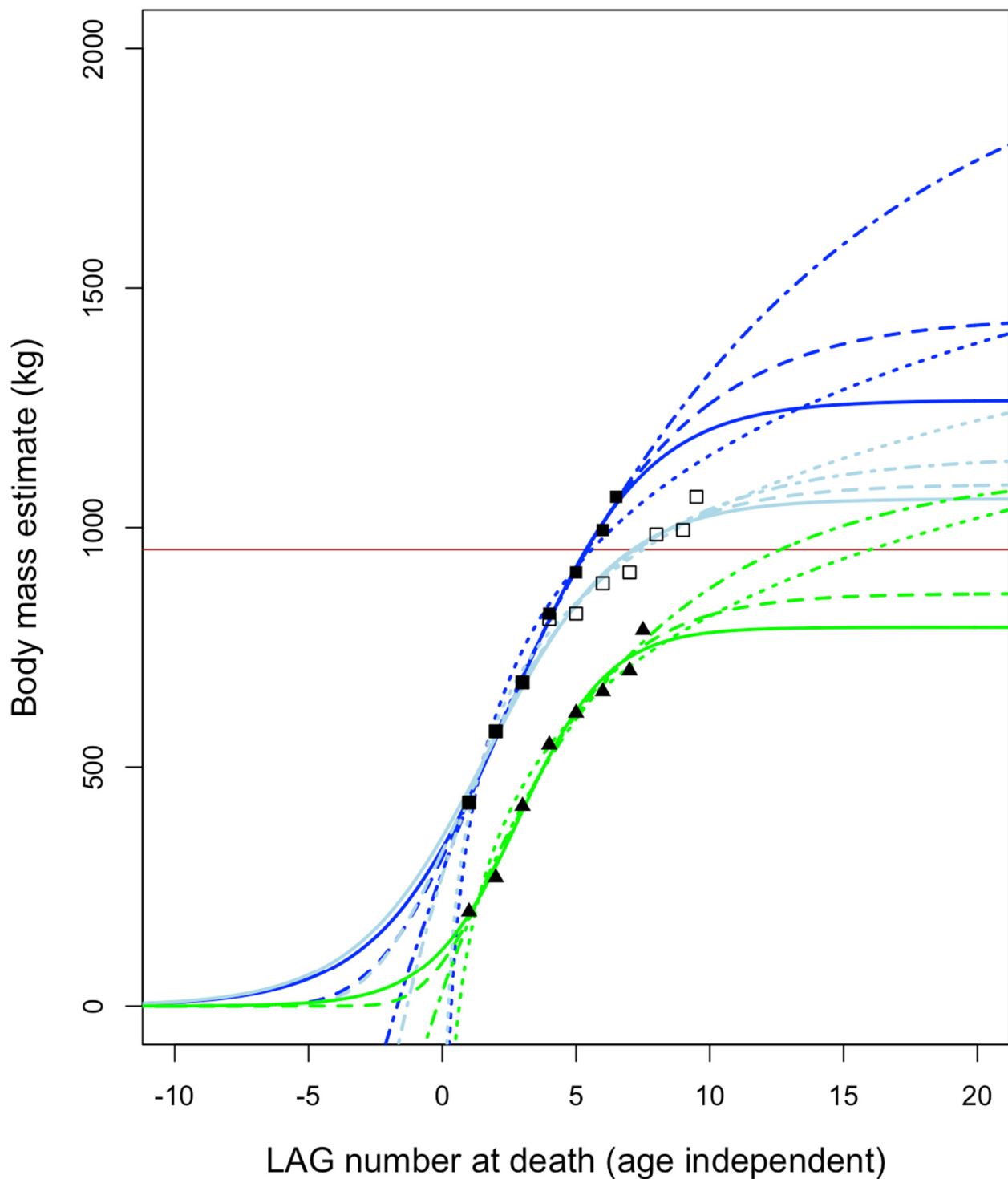


Figure 26. Age-independent growth curves for *Nanotyrannus* BMRP 2006.4.4 Petey (green, triangles) and Jane, the latter both corrected (dark blue, solid squares) for split multi-LAGs as in Cullen et al. [49] and uncorrected (light blue, open squares) as in Woodward et al. [46]. LAG #1 and the periosteum (arbitrarily assigned a half-year value) are included in the regressions. Four models are fit to each specimen: logistic (solid), Gompertz (dashed), logarithmic (dotted), and von Bertalanffy (dot-dash). Horizontal line is the mass estimate at the time of death for Jane from Hutchinson et al. [104] using 3D modeling. Results are similar to those deriving from regressions that exclude LAG #1 and the periosteum (Supplemental Material).

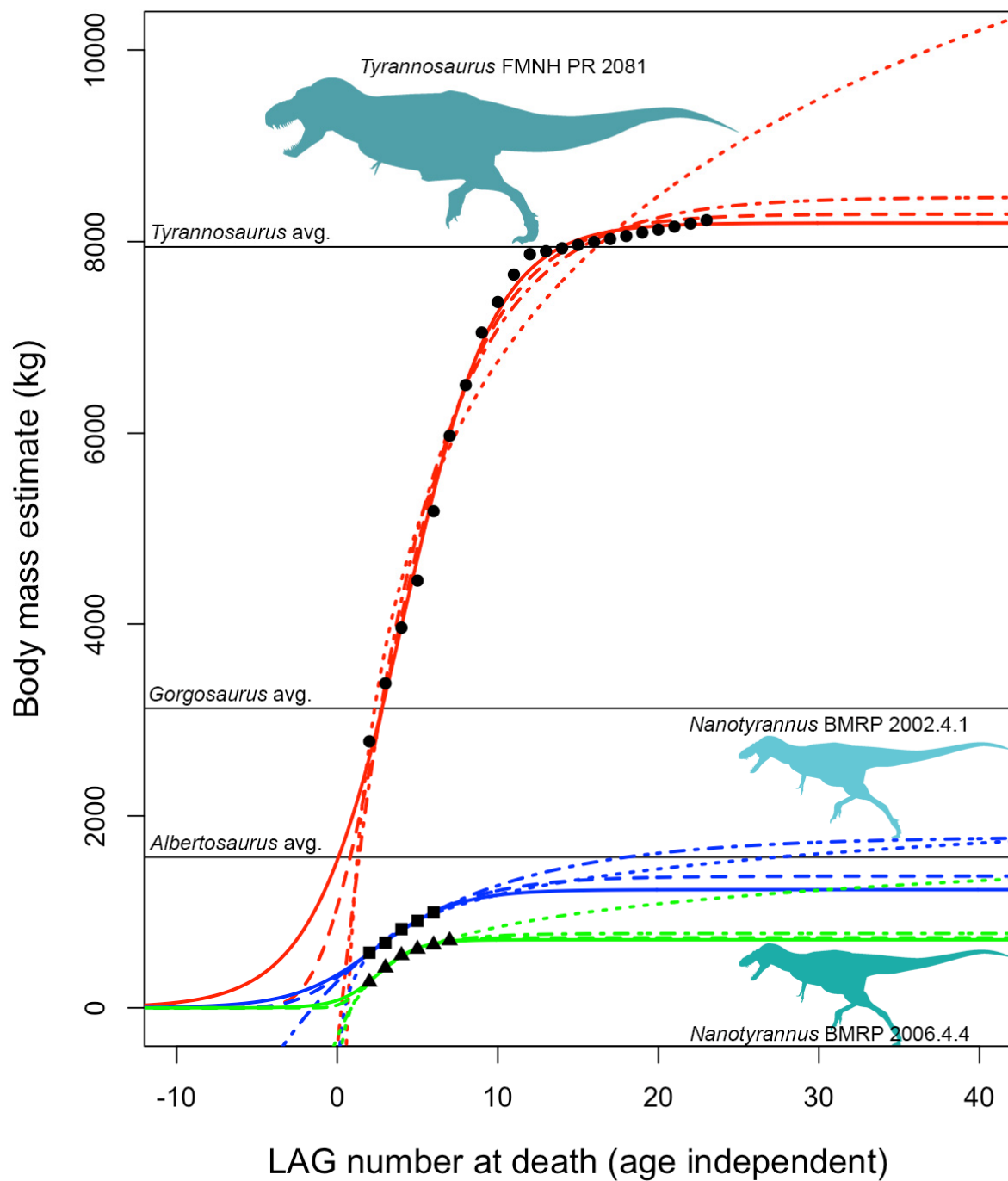


Figure 27. Age-independent growth curves for a large, old *Tyrannosaurus*, Sue FMNH PR 2081 (red, circles), and two *Nanotyrannus*, Petey BMRP 2006.4.4 (green, triangles) and Jane BMRP 2002.4.1 (dark blue, squares), corrected for split multi-LAGs as in Cullen et al. [49]. LAG #1 and the periosteum are not included in the regressions shown here. Four different growth models are fit to each specimen: logistic (solid), Gompertz (dashed), logarithmic (dotted), and von Bertalanffy (dot—dash). Horizontal black lines are asymptotic masses derived from logistic regressions of multiple individuals (i.e., multiple specimens used in the regression, with each specimen assigned a single mass and age at death) from Longrich et al. (in review) and are presented in decreasing order as follows: *Tyrannosaurus*, *Gorgosaurus*, *Albertosaurus*. Results are similar to those deriving from regressions that include LAG #1 and the periosteum (Supplemental Material).

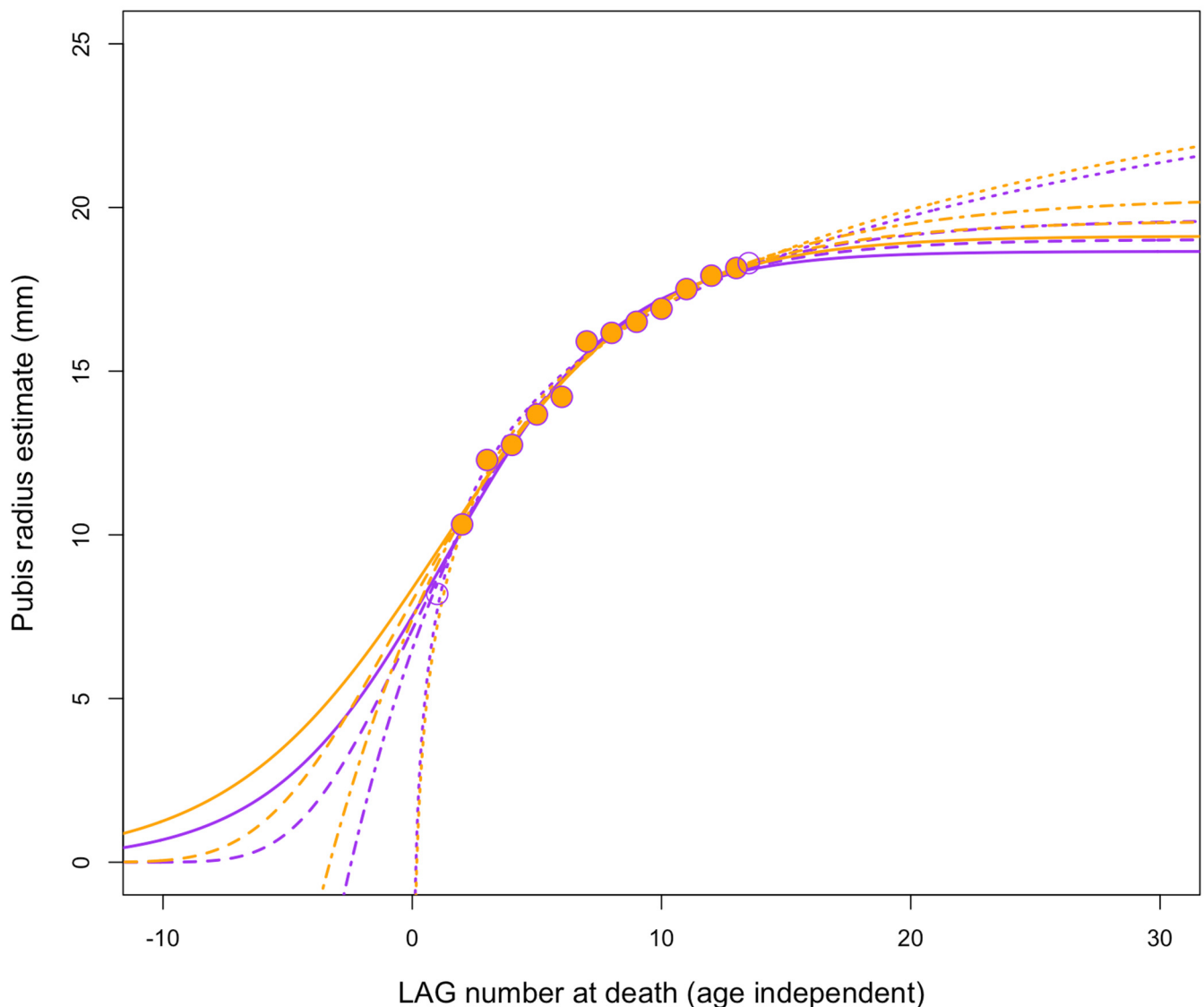


Figure 28. Growth record from Zuri (HRS 081514) pubis, with radius back-estimated from LAG spacing [51]. Models including the periosteum and LAG 1 are in purple; excluding the periosteum and LAG 1 are in orange. Four different growth models are fit under both conditions: logistic (solid), Gompertz (dashed), logarithmic (dotted), and von Bertalanffy (dot-dash).

All mass estimates for adult *Nanotyrannus* are far below those expected for *T. rex* (Figure 27), which is predicted to hit ~8000 kg or more depending upon the model and mass estimates used. Growth trajectories of BMRP 2002.4.1 and BMRP 2006.4.4 are, therefore, inconsistent with their identification as juvenile *Tyrannosaurus rex*, even under a variety of growth models and initial conditions during curve fitting (Supplemental Material). Our estimates instead suggest that they represent a distinct, small-bodied taxon. Although it is conceivable that young *Tyrannosaurus* sometimes showed slow growth rates due to sickness, lack of food, or other stresses, it is unlikely that all three individuals sectioned would exhibit similar growth anomalies; it is more likely that they exhibit typical growth rates for their taxon.

Another alternative hypothesis for this variation in growth trajectories, while assuming taxonomic synonymy, would be that the putative *Nanotyrannus* specimens are members of the smaller sex in *T. rex*. While it is reasonable to assume that Sue is fairly representative of average adult *T. rex* size for its sex (i.e., as far as fossil discovery approximates random sampling of the population of *T. rex*), the magnitude of hypothetical body mass dimorphism

between Sue and the *Nanotyrannus* specimens from at least the asymptotic models (Supplemental Material) would be implausible. This hypothetical dimorphism would exceed those estimated or observed in other non-avian [134] and avian [93] dinosaurs, highly sexually dimorphic mammals such as sperm whales [135], and would only be comparable to the most extreme examples of sexual dimorphism in extant tetrapods (e.g., southern elephant seals [136,137]).

3.5. Existence of Juvenile *Tyrannosaurus* Refutes Identification of *Nanotyrannus* as Juvenile *Tyrannosaurus*

The hypothesis that *Nanotyrannus* is a juvenile *Tyrannosaurus* predicts that the two forms should not overlap in size; that is, all *Nanotyrannus* will be small, and all *Tyrannosaurus* will be big. No small *Tyrannosaurus* should exist. Conversely, if *Nanotyrannus* is a distinct species, then small juveniles of *Tyrannosaurus*—approaching the size of *Nanotyrannus* or smaller—must exist. Juvenile dinosaurs tend to be extremely rare; however, potential juveniles of *Tyrannosaurus* are known, including a partial skull.

The smallest unambiguous *Tyrannosaurus* skeleton known is LACM 28345 [17]. This specimen exhibits diagnostic features of *T. rex*, including broad, posteriorly tapering nasals, short nasal processes of the frontals, loss of the cornual process of the lacrimal, a reduced antorbital fossa of the lacrimal, and reduced exposure of the antorbital fossa on the maxilla [17].

The skull of LACM 28345 is an estimated 800 mm long. This is 40% longer than the holotype of *Nanotyrannus lancensis* (CMNH 7541) [30], which measures 570 mm [44] but only about 12% larger than the estimated skull length for Jane BMRP 2002.4.1, which measures ~710 mm. LACM 28345 is unfortunately incomplete but exhibits the *Tyrannosaurus* morphology in almost all characters for which it can be coded [17].

Although it is conceivable that the differences in morphology seen could rapidly develop as the animals mature at this size, it seems unlikely. The apparent absence of smaller *Tyrannosaurus* has been considered evidence that *Nanotyrannus* represents a juvenile *T. rex*. However, isolated specimens document individuals comparable to or smaller than *Nanotyrannus* in size.

One such specimen is UCMP V84133 from the Hell Creek Formation (Figure 29). The specimen is a small right frontal. It differs from the frontals of the *Nanotyrannus lancensis* holotype CMNH 7541 and DDM 334.1 [27,30,44] in several respects (Figure 30). First, the nasal process is narrow, half the width of the frontal or less; the nasal processes are more than half the width of the frontal in *Nanotyrannus*. Second, the lacrimal is broadly extended inward to constrict the skull table and inserts into deep depressions on the lateral surface of the frontal, approaching the condition seen in *T. rex* [7,138]. Third, the orbital margin is not visible, with the postorbital and the lacrimal contacts approaching one another so they would have contacted, excluding the frontal from the orbit.

Furthermore, the postorbital process is dorsoventrally extended, again resembling *T. rex*; this feature is absent in *Tarbosaurus* and is, therefore, an autapomorphy of *Tyrannosaurus* [139]. The posterior end of the frontal is deflected downward relative to the skull table, another feature characteristic of *T. rex*. The bone is dorsoventrally thickened, a feature of tyrannosaurids. The frontals also become thinner where the sagittal crust approaches the midline, showing the development of the double-ridge condition characterizing *T. rex* [17]. None of these features are seen in *Nanotyrannus* [44].

Although the frontal differs from adult specimens of *Tyrannosaurus rex* in its shape and proportions, it can be connected with other specimens to form a growth series (Figure 30), suggesting it represents a young *T. rex*.

The paired frontals would have been about 80 mm across, suggesting an animal about 60% larger than the smallest known *Tarbosaurus* [54], implying a skull length of around 465 mm—significantly smaller than the type specimen of *Nanotyrannus*. Assuming skull length was around 12% of body length, this would imply a total length of ~4 m.

Phylogenetic analysis of this specimen (Figure 31) recovers it as a derived tyrannosaurine, but unresolved with respect to *Tyrannosaurus*, *Tarbosaurus*, and *Zhuchengtyrannus*. This is consistent with its referral to *Tyrannosaurus rex*. This result is recovered in the dataset derived from Dalman et al. [52,56,64] and also the dataset of Brusatte and Carr [1,64].

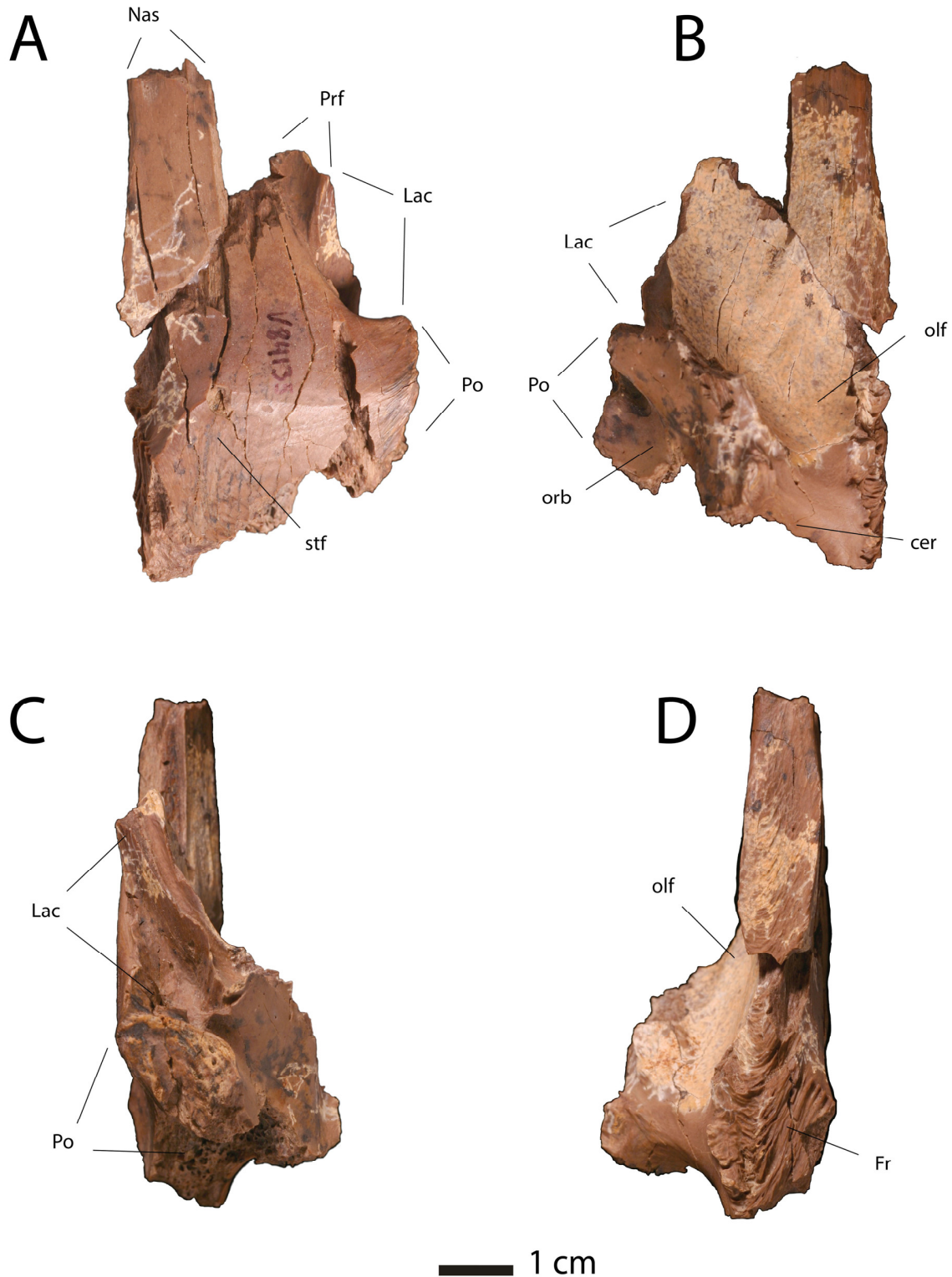


Figure 29. Frontal of juvenile *Tyrannosaurus* UCMP V84133 in (A), dorsal, (B), ventral, (C), lateral, and (D), medial view. Abbreviations: cer, cerebral fossa; Fr, frontal facet; Lac, lacrimal; Nas, nasal; olf, olfactory tract; orb, orbital fossa; Po, postorbital facet; Prf, prefrontal facet, stf, supratemporal fossa.

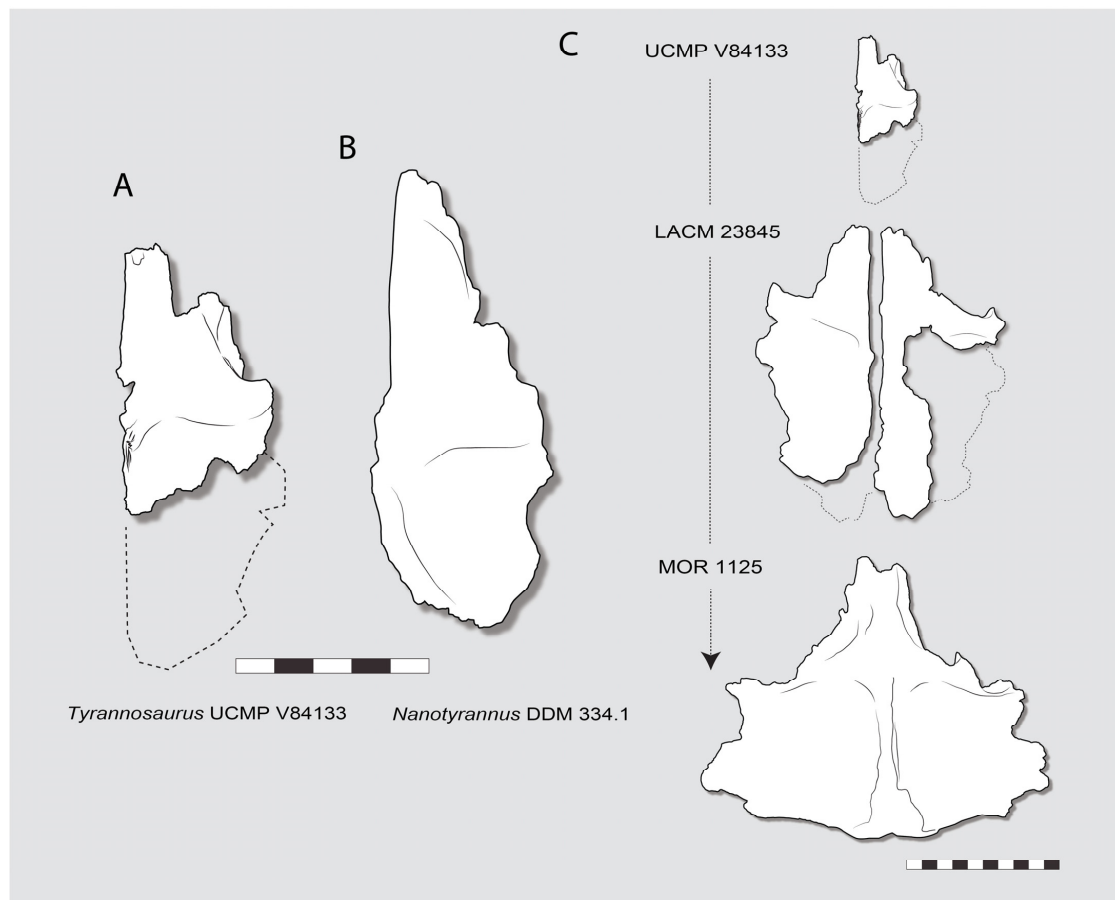


Figure 30. (A,B), frontals of juvenile *Tyrannosaurus* compared with *Nanotyrannus* DDM 334.1 (Scale bar = 5 cm); (C), growth series connecting UCMP V84133 *Tyrannosaurus* juvenile to the larger juvenile LACM 23845 and, finally, adult MOR 1125. Scales = 5 cm (A,B); 10 cm (C).

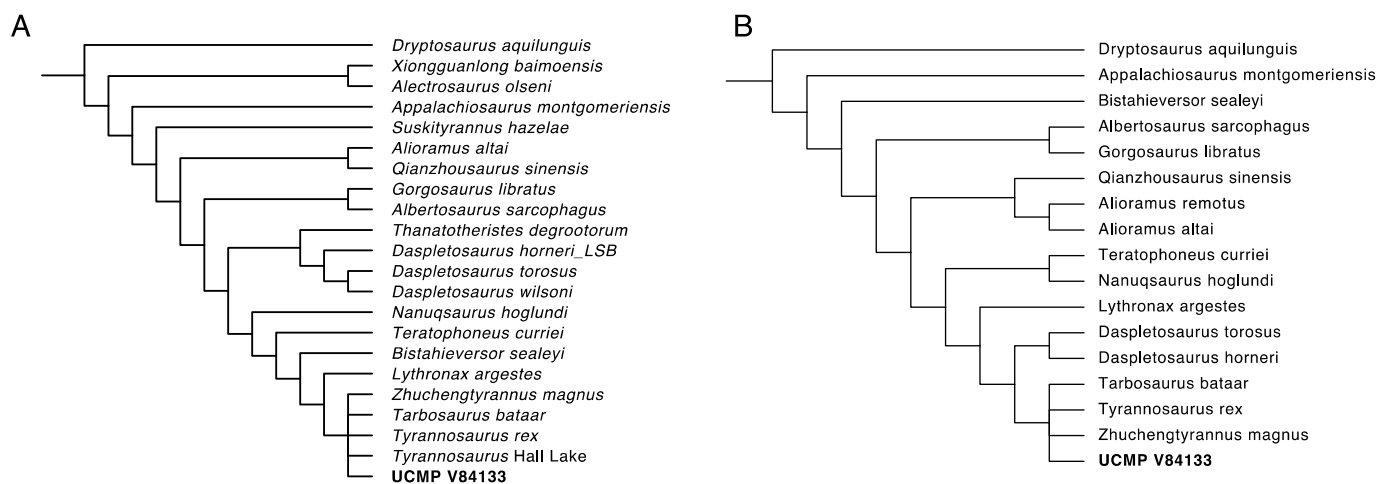


Figure 31. Phylogenetic analysis of the isolated frontal UCMP V84133. (A), analyzed using the Dalman et al. dataset [52], strict consensus of 14 trees (Tree length = 1787; Consistency index (CI) = 0.3788; Retention index (RI) = 0.7484) and (B) the dataset based on Brusatte and Carr [1,64], strict consensus of 105 trees (Tree length = 760; Consistency index (CI) = 0.5592; Retention index (RI) = 0.8149).

3.6. Phylogenetic Analysis Suggests *Nanotyrannus* Is Not a Member of Tyrannosauridae

If *Nanotyrannus* is not *Tyrannosaurus*, then what is it? Gilmore [27] concluded that *Nanotyrannus lancensis* was a species of *Gorgosaurus*. This would place it in the family Tyrannosauridae, in the subfamily Albertosaurinae.

Bakker et al. [30], however, argued *Nanotyrannus* lay outside of the split between Tyrannosaurinae and Albertosaurinae, and represented a primitive side-branch of tyrannosaurs. This puts *Nanotyrannus* outside of Tyrannosauridae (depending on the precise definition used). This hypothesis was not tested using a morphological phylogenetic analysis. Surprisingly, little attempt has been made to test the phylogenetic position of *Nanotyrannus* since the work of Bakker et al.

We added *Nanotyrannus* to a previously published character–taxon matrix by Loewen et al. [56], updated by Wolfe et al. [64] and Dalman et al. [52], and ran a phylogenetic analysis using equal weights parsimony under PAUP* 4.10 b10 [48]. The analysis recovered the two most parsimonious trees (Figure 32).

These results corroborate Bakker et al. in recovering *Nanotyrannus* just outside the Tyrannosaurinae–Albertosaurinae split, although our analysis differs from theirs in placing Alioraminae in a more basal position, below *Nanotyrannus*. We found almost no character support for the placement of *Nanotyrannus* in Tyrannosaurinae or Tyrannosauridae. Although characters can change through ontogeny, the near-total absence of any *T. rex*-like features in animals exceeding 1000 kg is striking.

We repeated our phylogenetic analysis using another dataset, the Brusatte and Carr matrix [1], updated by Wolfe et al. [64]. This matrix produces similar results (Figure 33). *Nanotyrannus* emerges below Alioraminae but with Albertosaurinae further down the tree. This would make *Nanotyrannus* a basal member of the Tyrannosaurinae. We note, however, numerous discrepancies between specimens and codings in this matrix, particularly miscodes that appear to force *Bistahieversor* outside of Tyrannosauridae. This raises issues of whether the backbone of the tree is properly reconstructed; we suspect that the first topology better reflects tyrannosauroid phylogeny.

Because derived features appear late in ontogeny, immature animals may be artificially pushed down the tree, as seen by the inclusion of “*Raptorex kriegsteini*”, a juvenile tyrannosaurine [55] in phylogenetic analysis [113]. We, therefore, undertook a second series of analyses, with *Nanotyrannus* only coded for characters that are ontogenetically stable in tyrannosaurines, i.e., present both in young juveniles and adults. As discussed above, we assess ontogenetically stable characters as characters that are coded identically in juveniles [54] and adults [53] of *Tarbosaurus baatar*.

When this is done, *Nanotyrannus* still emerges as a non-tyrannosaurid (Figure 34), with an identical position as found in the previous pair of analyses. This is because those characters of *Tyrannosaurus*, Tyrannosaurinae, and even Tyrannosauridae that are predicted to be present even in very young *Tyrannosaurus* (based on their occurrence in *Tarbosaurus*) are conspicuously absent in *Nanotyrannus*, causing it to fall outside of Tyrannosauridae. Unless *Tyrannosaurus* developed in a way completely unlike *Tarbosaurus* (or any tyrannosaurid), these results refute the idea that *Nanotyrannus* is a juvenile *Tyrannosaurus*.

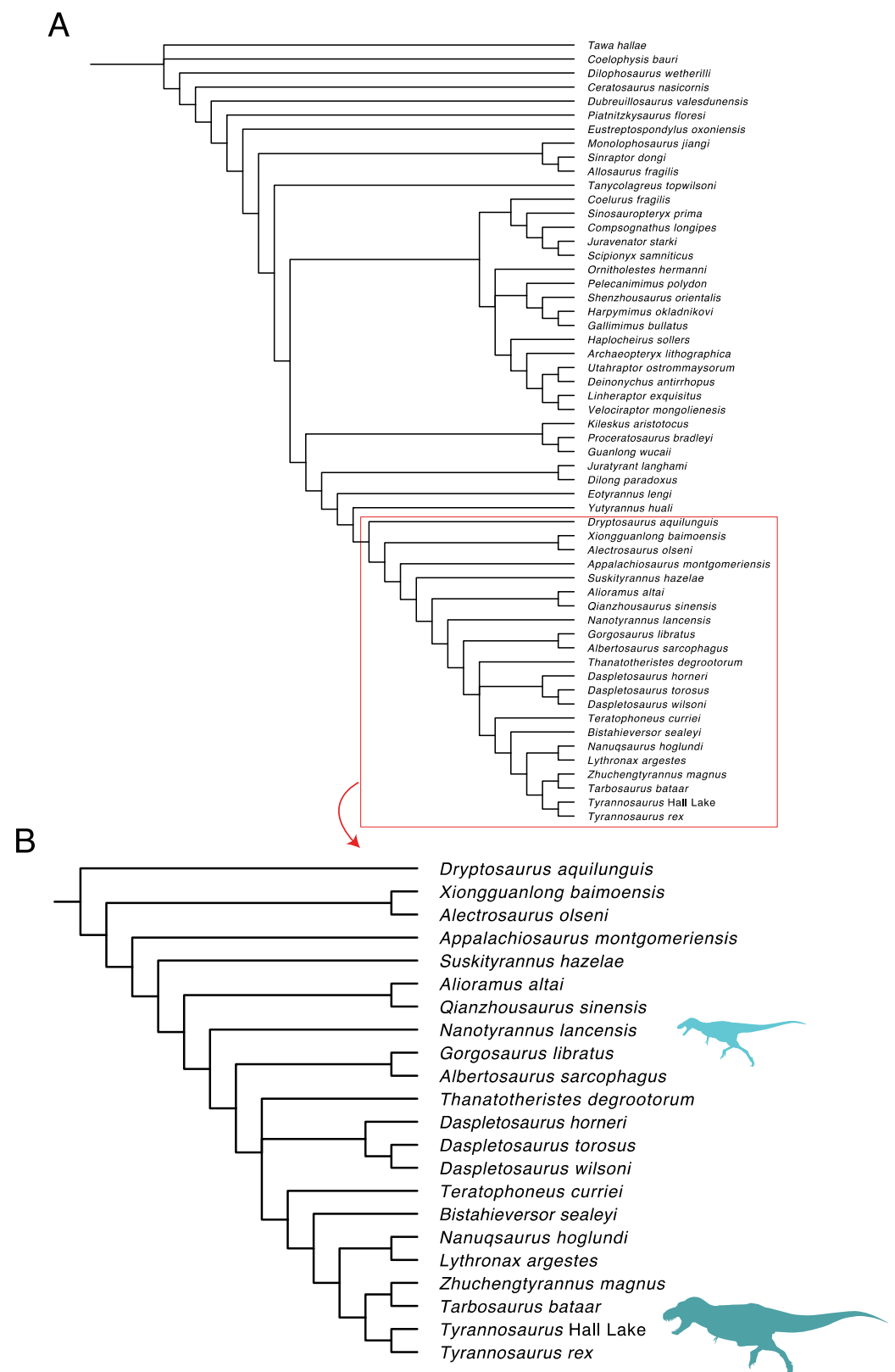


Figure 32. (A) Phylogenetic placement of *Nanotyrannus* as a non-tyrannosaurid member of Tyrannosauoidea based on equal-weight parsimony *Nanotyrannus* based on the Dalman et al. matrix [52] (Tree length = 1808; Consistency index (CI) = 0.3744; Retention index (RI) = 0.7492); (B) closeup focused on derived tyrannosauroids.

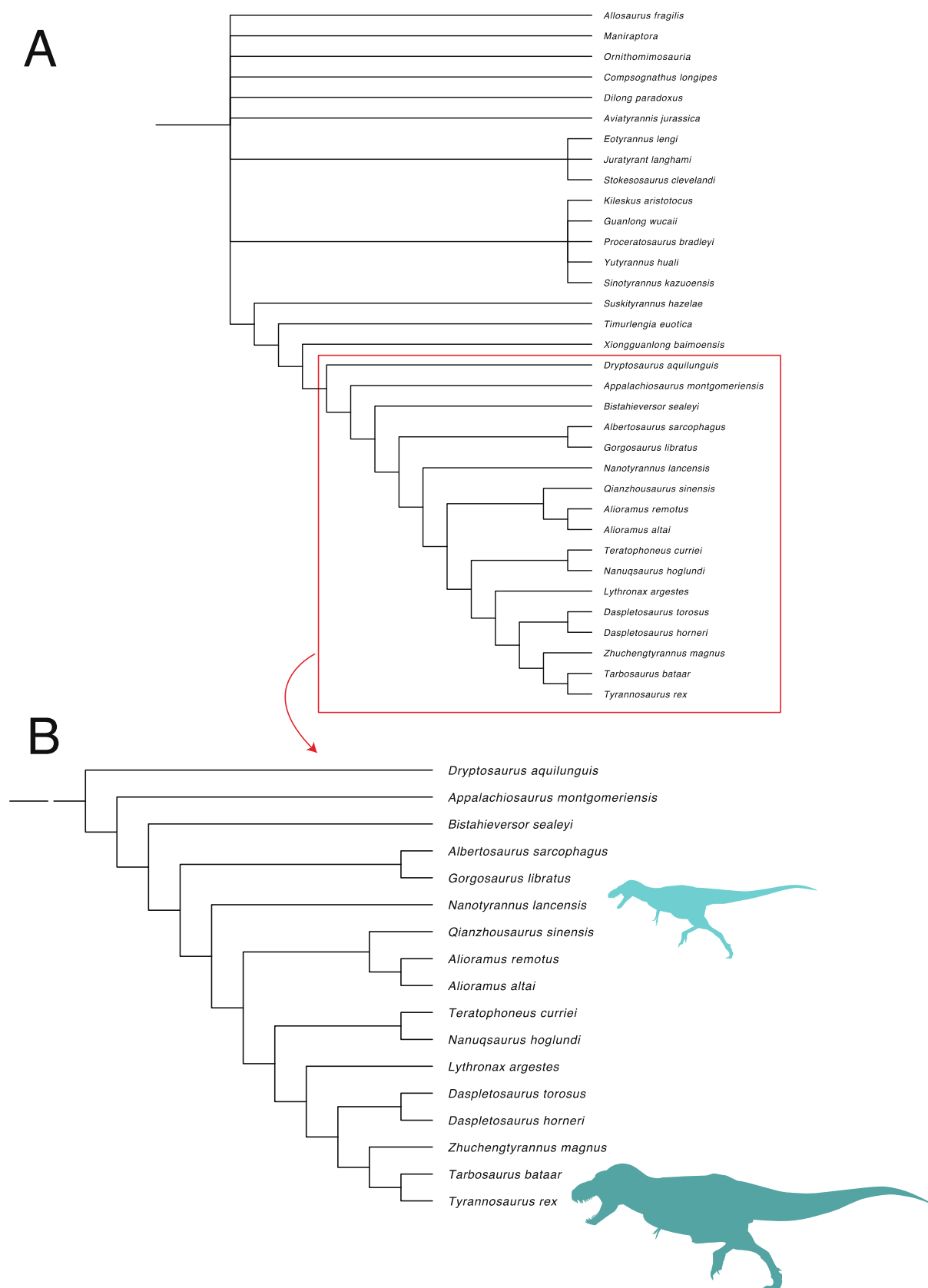


Figure 33. (A) Phylogenetic placement of *Nanotyrannus* based on the Brusatte and Carr matrix [1], updated by Wolfe et al. [64]. Strict consensus of 21 trees (Tree length = 778; Consistency index (CI) = 0.5463; Retention index (RI) = 0.8084) (B) closeup focused on derived tyrannosauroids.

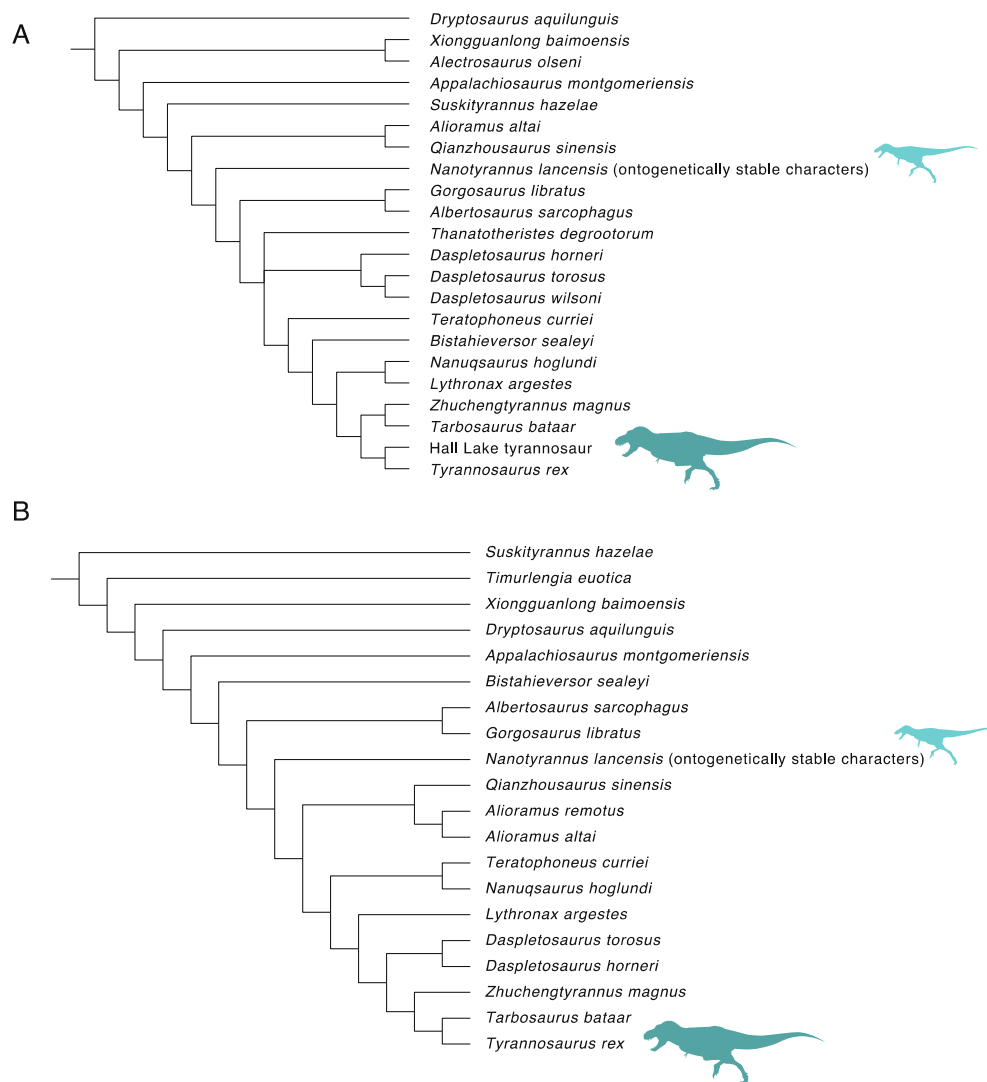


Figure 34. Phylogenetic analysis using only ontogenetically stable characters using (A) the Dalman et al. matrix [52], strict consensus of 2 most-parsimonious trees (Tree length = 1793, Consistency index (CI) = 0.3776, Retention index (RI) = 0.7484) and (B) the Brusatte and Carr matrix [1,64], strict consensus of 21 trees (Tree length = 767; Consistency index (CI) = 0.5541; Retention index (RI) = 0.8119).

4. Discussion

4.1. Summary of Evidence for the Validity of *Nanotyrannus*

All available evidence is consistent with the identification of *Nanotyrannus* as a distinct species of small-bodied tyrannosaur rather than a juvenile *T. rex*.

First, the high diversity of predators in many dinosaur-dominated ecosystems, and terrestrial and marine ecosystems in general, suggests that more than one tyrannosaur should exist in the late Maastrichtian of the Western Interior.

Second, extensive morphological differences separate *Nanotyrannus* and *Tyrannosaurus* (158 characters identified here), but no clear intermediate specimens exist. A discrete pattern of variation exists; all specimens conform either to the *Nanotyrannus* morphology or the *Tyrannosaurus* morphology. Further sampling could reveal intermediates, but since the 'growth series' hypothesis was originally proposed [17], new fossils have reinforced this pattern, with *Nanotyrannus* and *Tyrannosaurus* forming discrete clusters rather than a continuum as predicted by the 'growth series' hypothesis. We found no characters supporting the referral of *Nanotyrannus* to *Tyrannosaurus* or even Tyrannosaurinae.

Third, morphological changes seen during ontogeny in other tyrannosaurs [9,54,101,109] are inconsistent with the ‘growth series’ hypothesis [10,17]. The “growth series” requires changes in tooth morphology, an increase in tooth number, changes in the shape of the antorbital fossa and accessory antorbital fenestra, and elongation of the rostra. Such changes are not seen in *Tarbosaurus*. Instead, tyrannosaurine features are evident in small *Tarbosaurus* [54] and would be expected in much larger *Nanotyrannus* specimens (Figure 19). Subadult *Tarbosaurus* is largely identical to the adult [34]. For *Nanotyrannus* to represent a juvenile *T. rex* would require that *Tyrannosaurus* have to have a radically different ontogeny than other tyrannosaurs. Although ontogeny can evolve, it is more parsimonious to assume that *Nanotyrannus* is not part of the *T. rex* ontogenetic series. Several changes required—including loss of the ventral flange of the vomer, and the reduction of the manual phalanges—seem to defy known patterns of amniote skeletal development.

Fourth, histology suggests that specimens of *Nanotyrannus* are subadults or young adults of a small-bodied tyrannosaur. Large *Nanotyrannus* individuals show skeletal fusions, adult bone texture on facial bones, relatively slow growth, and decelerating growth, and their growth curves predict adult body masses of ~1200–2100 kg (BMRP 2002.4.1) and ~700–1100 kg (BMRP 2006.4.4), below the mass of adult *T. rex*. The higher mass estimates are biologically unrealistic because they depend on models (logarithmic and von Bertalanffy) in which growth is at a maximum at hatching and then decelerates. Histological studies show that dinosaur growth follows an S-curve, with absolute growth rates being low early on, accelerating, then decelerating [8]. The most realistic models are, therefore, logistic and Gompertz curves, which suggest adult masses of <1500 and <900 kg for these animals. Regardless of the model employed, none of the specimens sectioned show growth patterns consistent with growing to the large sizes achieved by *Tyrannosaurus*. Although it is not impossible that juvenile *T. rex* might show unusual patterns such as a growth deceleration, perhaps due to poor food availability, all *Nanotyrannus* specimens that have been thin-sectioned show these growth patterns. This suggests it is a real phenomenon, not an artifact.

Fifth, a small frontal, UCMP V84133, shows diagnostic features of *T. rex* in an animal smaller than the *Nanotyrannus lancensis* type. The identification of a young juvenile of *T. rex*—even a single bone of a single individual—definitively rejects the hypothesis that the two are the same species.

Last, phylogenetic analysis recovers *Nanotyrannus* as a non-tyrannosaurid. Character evidence supports a basal position in the tree, with little evidence for affinities with Tyrannosaurinae or even Tyrannosauridae. This result is robust, being recovered even when restricted to a limited subset of ontogenetically invariant characters.

Although any single line of evidence can potentially be contested, the consilience between all lines of evidence, each supporting the distinctiveness of *Nanotyrannus*, is striking. The absence of evidence either that *Nanotyrannus* represents a juvenile or of features allowing referral to *T. rex* is equally striking. The simplest explanation that fits the facts—what we know about dinosaur diversity, the morphology of the fossils, the development of tyrannosaurs, the histology of the individuals, and the existence of small *T. rex*—is that *Nanotyrannus* is a distinct taxon. Based on the characters identified above, we suggest that at least 11 specimens can either be referred to as *Nanotyrannus* or represent close relatives of *Nanotyrannus* (Table 6) although just how many species they represent remains unclear.

Table 6. Specimens of *Nanotyrannus*.

Specimen	Identification	Formation	Locality	Notes
CMNH 7541	<i>Nanotyrannus lancensis</i>	Hell Creek	Montana	<i>Nanotyrannus lancensis</i> holotype skull; subadult or young adult
AMNH 5050	aff. <i>Nanotyrannus</i>			Partial dentary

Table 6. Cont.

Specimen	Identification	Formation	Locality	Notes
BMRP 2002.4.1	<i>Nanotyrannus lancensis</i> (or aff <i>Stygivenator</i> ?)	Hell Creek	Montana	“Jane”; skull and skeleton, young adult
BMRP 2006.4.4	cf. <i>Nanotyrannus</i>	Hell Creek	Montana	“Petey”; partial post-cranial skeleton young adult
FMNH PR 2411	cf. <i>Nanotyrannus</i>	Hell Creek	South Dakota	lacrima
HRS specimen	<i>Nanotyrannus lancensis</i> (or aff <i>Stygivenator</i> ?)	Lance	Wyoming	“Zuri”; partial skull and skeleton, young adult; HRS 08423, 08502, 08607, 08486, 08496,
RSM P2347.1	aff. <i>Nanotyrannus</i>	Frenchman Formation	Saskatchewan	Maxilla
KU 155809	<i>Nanotyrannus lancensis</i> (or aff <i>Stygivenator</i> ?)	Hell Creek	Montana	Skull and partial skeleton
LACM 28471	<i>Nanotyrannus lancensis</i> (or <i>Stygivenator molnari</i>)	Hell Creek	Montana	<i>Stygivenator lancensis</i> holotype; partial skull, juvenile
MOR 6625	aff. <i>Nanotyrannus</i>			Partial jaws
DDM 344.1	aff. <i>Nanotyrannus</i>			Frontal
“Dueling Dinosaurs”	<i>Nanotyrannus lancensis</i> (or <i>Stygivenator molnari</i> ?)	Hell Creek	Montana	Skull and skeleton (Larson, 2013b)

4.2. Critique of Previous Work Synonymizing *Nanotyrannus* and *Tyrannosaurus*

The seminal work identifying *Nanotyrannus* as a juvenile *Tyrannosaurus* is that of Carr 1999 [9], although it to a degree builds on arguments made by Carpenter [34]. Carr’s conclusion rests on two claims: first, that the holotype of *Nanotyrannus lancensis* CMNH 7541 is a juvenile, and second, that it shows diagnostic features of *Tyrannosaurus*. We argue that neither claim is supported by the evidence.

First, Carr [9] argues that striated bone can be used to infer relative age in tyrannosaurs and that it is correlated with rapidly growing juveniles. As discussed, striated bone persists until late in ontogeny in tyrannosaurids; for example, young adults of *Gorgosaurus libratus* have striated bone [109]. Striated bone indicates that an animal has not ceased growing, not that it is a young juvenile. Carr also argues that features of *Nanotyrannus* are consistent with those seen in juvenile tyrannosaurs [9]; this may be true but as discussed above similar features are seen in primitive tyrannosaurs such as *Alioramus* [70] and could represent the adult morphology of a primitive tyrannosaur.

Second, Carr [9] lists thirteen characters supposedly shared by *Nanotyrannus* and *Tyrannosaurus* and supporting synonymy. We had difficulty verifying these observations. Of these characters, most, if not all, are either shared by a broader range of tyrannosaurs (Table 7) (and are, therefore, not diagnostic of *Tyrannosaurus*) or else do not appear to be shared by *Tyrannosaurus* and *Nanotyrannus*.

Table 7. Characters reported by Carr [9] as supporting referral of *Nanotyrannus* to *Tyrannosaurus* and assessment made here.

Character	Assessment
(1) Nasal processes of the premaxillae tightly appressed throughout their entire length	Not diagnostic of <i>Tyrannosaurus</i> ; present in <i>Tarbosaurus</i> , <i>Bistahieversor</i> , <i>Daspletosaurus</i>
(2) Restricted exposure of the jugal within the antorbital fenestra	Not diagnostic of <i>Tyrannosaurus</i> ; present in <i>Gorgosaurus libratus</i>

Table 7. Cont.

Character	Assessment
(3) Antorbital fossa reaches the nasal suture caudodorsally	Not diagnostic of <i>Tyrannosaurus</i> ; present in <i>Gorgosaurus libratus</i> , <i>Alioramus altai</i>
(4) Transversely broad jugal pneumatic recess	Not shared by <i>Tyrannosaurus</i> and <i>Nanotyrannus</i> ; recess broad in <i>Tyrannosaurus</i> , narrow in <i>Nanotyrannus</i>
(5) Elongate frontal sagittal crest	Not shared by <i>Tyrannosaurus</i> and <i>Nanotyrannus</i> ; frontal sagittal crest short in <i>Nanotyrannus</i>
(6) Strongly divergent and short basal tubers	Not shared by <i>Tyrannosaurus</i> and <i>Nanotyrannus</i> ; basal tubera more elongate in <i>Nanotyrannus</i> than <i>Tyrannosaurus</i>
(7) Rostroventrally-oriented caudal occipital plate	Not shared by <i>Tyrannosaurus</i> and <i>Nanotyrannus</i> ; caudally oriented in <i>Tyrannosaurus</i> , faces posteroventrally in <i>Nanotyrannus</i>
(8) Shallow subcondylar recess	Not shared by <i>Tyrannosaurus</i> and <i>Nanotyrannus</i> ; subcondylar recess well-developed in <i>Nanotyrannus</i>
(9) Rostroventrally deep basisphenoid plate and rostrocaudally-restricted basisphenoid recess	Not shared by <i>Tyrannosaurus</i> and <i>Nanotyrannus</i> ; anteroposteriorly narrow basisphenoid recess in <i>Tyrannosaurus</i> ; anteroposteriorly wide basisphenoid recess in <i>Nanotyrannus</i>
(10) Inflated ectopterygoid	Not shared by <i>Tyrannosaurus</i> and <i>Nanotyrannus</i> ; ectopterygoid weakly inflated in <i>Nanotyrannus</i>
(11) Strongly convex rostral plate of the surangular	Not diagnostic of <i>Tyrannosaurus</i> ; seen in <i>Daspletosaurus</i>
(12) Transversely narrow snout and broad temporal region relative to other tyrannosaurids	Not shared by <i>Tyrannosaurus</i> and <i>Nanotyrannus</i> ; snout narrow in <i>Nanotyrannus</i> and broad in <i>Tyrannosaurus</i> ; temporal region broader in <i>Tyrannosaurus</i>
(13) Deep mandible relative to other tyrannosaurids	Not diagnostic of <i>Tyrannosaurus</i> ; seen in <i>Tarbosaurus</i> , <i>Bistahieversor</i> , <i>Daspletosaurus</i> ; absent in some specimens of <i>Nanotyrannus</i>

For example, the closely appressed nasal processes of the premaxilla and narrow jugal exposure in the antorbital fenestra are interpreted as a diagnostic feature of *Tyrannosaurus*, but these features occur in other tyrannosaurids. The skull shapes are not similar, either. The broad, *T. rex*-like muzzle illustrated for the holotype of *Nanotyrannus lancensis* by Carr (1999) is not present; the snout as preserved is very narrow as in *Gorgosaurus* and alioramins [98], not like the broad rostrum of *T. rex* and *Tarbosaurus*. This does not appear to be an artifact of crushing; other *Nanotyrannus* specimens have narrow nasals and lack the broad palatal shelves and vomers associated with the broad rostrum of *Tyrannosaurus*. Neither is the temporal region of the skull in *Nanotyrannus* unusually broad relative to skull length [30]. We suggest the evidence presented by Carr is insufficient to support the referral of *Nanotyrannus* to *Tyrannosaurus* or even Tyrannosaurinae. We concede that more detailed character analysis is required, but we were unable to confidently identify characters in *Nanotyrannus* that are shared with *Tyrannosaurus* but not with other tyrannosaurids. We argue that Carr (1999) fails to show either that the type is a juvenile, or that it exhibits features supporting referral to *Tyrannosaurus*.

In a subsequent paper, Carr and Williamson [17] assemble *Nanotyrannus* and *Tyrannosaurus* skulls into a “growth series”. However, simply because large and small animals can be assembled into a series does not demonstrate it is a growth series; if different species are arranged by size, what emerges is a size series, which assumes (rather than proves) that they are a single species. Furthermore, the very large number of characters identified as separating small *T. rex* from *Nanotyrannus* in this series [17] is inconsistent with a gradual change over the course of development in a single species.

Finally, Carr [10] attempted to reconstruct growth in *Tyrannosaurus* and argued that 21 distinct growth stages could be identified, identified by ‘synontomorphies’. Carr’s [10] analysis of *T. rex* growth begins by taking for granted the assumption that *Nanotyrannus* is synonymous with *T. rex*. By forcing all these specimens into a single growth trajectory, Carr [10] is forced to conclude that *T. rex* showed extremely unusual growth.

As shown above, a large number of differences separate *Nanotyrannus* and *Tyrannosaurus* without clear intermediates, such that this requires a massive, extremely rapid gain in novel character states between the *Nanotyrannus* form and the *Tyrannosaurus* morphotype. Carr notes that in this model, “sharp boundaries between categories are seen at the subadult and adult categories” and concludes that most of these changes occurred within two years, a pattern not seen in other tyrannosaurs or other dinosaurs. To account for this unusual observation, Carr argues, “The extreme number of changes at the transition between juveniles and subadults shows that the ontogeny of *T. rex* exhibits secondary metamorphosis, analogous to the abrupt ontogenetic changes that are seen at sexual maturity among teleosts”; that is, that *Tyrannosaurus* underwent a sudden change similar to that seen among certain fish, e.g., Pacific Salmon, *Onchorhynchus* spp., which change their skull and body shape on entering freshwater to breed. We are unaware of any amniote that develops in this way. It seems far simpler to assume that the two are distinct species.

Another problem is the use of cladistics as a model for interpreting development. Carr’s “ontogram” model may be inappropriate for studying patterns of ontogenetic variation because the assumptions of cladistic analysis do not match the way animals grow. Cladistic analysis assumes that there is a single, correct tree—there is a single true evolutionary history of the clade analyzed described by a branching diagram, with gains and losses of characters along its branches.

The problem is that ontogeny is not a single coordinated hierarchy; there are many sources of variation with respect to size and morphology other than age. Carr suggests that size decouples from maturity among adults [10], but ontogeny is even more complex than this. Individual variation, developmental plasticity because of environmental factors, and sex are all common factors that can drastically lower the nearly perfect correlation between size, age, and morphology that Carr concludes. A cladistic analysis that assumes a single growth trajectory may simply be an inappropriate way to model growth, which can show considerable variation. It might serve to roughly order individuals in an objective and repeatable way [107] but not to identify a large number of distinct growth stages.

The attempt to force the data to conform to a model—rather than to let the patterns emerge from the data—is perhaps best seen in Figure 12 of Carr [10]. The plot of age versus mass for 31 specimens results from forcing specimens onto the best-fit regression calculated by Erickson et al. [8]. These specimens do not all have estimated ages and masses measured, and those used in the regression analysis of Erickson et al. [8] have their estimates presented incorrectly in order to place them precisely onto the regression line. Few empirical datasets will look like this, as no organisms grow identically from individual to individual due to variations in sex, genetics, and life history. The resulting curve and “growth series” are an attempt to force the data to a model, not to test whether the data fit the model; it is a hypothesis, not a result.

4.3. Affinities of *Nanotyrannus*-like Dinosaurs

A question raised by the removal of *Nanotyrannus* from *Tyrannosaurus* is whether all of the small tyrannosaurs from Hell Creek represent the same species or even the same lineage. Overall, the morphology of the animals is very similar, as shown by their codings in the character–taxon matrix (Supplementary Information S2); however, almost all of the characters shared by the *Nanotyrannus* type and referred specimens are plesiomorphies, and so do not necessarily support the monophyly of these individuals.

Several characters appear to be derived, however. These include (i) the upturned premaxilla, (ii) the procumbent premaxillary teeth (perhaps correlated/redundant with the first character, (iii) unserrated premaxillary teeth, and (iv) the pneumatic foramen of the

quadratojugal. These characters suggest that *Nanotyrannus* and specimens referred to it form a clade to the exclusion of other tyrannosaurs. Whether these animals all represent a single species or even a single genus remains unclear.

A high degree of variability exists within both *Tyrannosaurus* and *Nanotyrannus*. Within *T. rex*, differences exist in the arrangement of the dentary teeth and the structure of the lacrimal, which is more L-shaped in the holotype and certain specimens and more hooked in others. The holotype of *T. rex* also has a very straight squamosal, a feature shared with a large *Tyrannosaurus* from the Frenchman Formation [103] but not a number of other specimens [6,7]. Insofar as the morphological differences tend to be associated, that would support the idea that more than one species of *Tyrannosaurus* exists [16,18], especially given the existence of distinct species of *Triceratops* [140,141]. However, further work is needed to support or reject the existence of distinct species.

Similarly, a high degree of variation is seen in specimens referred to *Nanotyrannus* [142]. The type of *Stygivenator molnari* differs from the type of *Nanotyrannus lancensis* in several ways. The anterior end of the antorbital fossa is narrow [17], the maxilla is long and low, and the tip of the mandible hooks upwards. These same features are seen in the “Dueling Dinosaurs” tyrannosaur found in association with a *Triceratops* [142], although they are approached in Jane (BMRP 2002.4.1) and Zuri. This raises the possibility that specimens referred to as *Nanotyrannus* represent two distinct lineages, *Nanotyrannus lancensis* and *Stygivenator* (or *Nanotyrannus*) *molnari*. Again, further work and more fossils are needed to corroborate or reject this possibility.

The existence of *Nanotyrannus* as a distinct tyrannosaur lineage implies that other members of the lineage might exist in North America. A potential relative of *Nanotyrannus* is NMMNH P-25049 from the Kirtland Formation of New Mexico [59] (NRL pers. obs.; J. Sertich pers. comm. 2023). NMMNH P-25049 lacks features allowing referral to *Bistahieversor* but resembles *Nanotyrannus* in having a longirostrine skull, low and rounded lacrimal horns, a dentary groove, and a low nasal weakly interlocking with the maxilla. NMMNH P-25049 also resembles juvenile *Gorgosaurus* [109], but the broad dorsal and ventral margins of the antorbital fossa, the shape of the orbit, and the dentary groove are overall more similar to *Nanotyrannus*.

Other potential *Nanotyrannus*-like theropods are represented by premaxillary teeth identified as “*Aublysodon*”. *Aublysodon* is a tooth taxon originally described by Joseph Leidy [33] from the Campanian-aged Judith River Formation of Montana. *Aublysodon* teeth are distinctive in being unserrated with blunt, chisel-shaped tips. Similar teeth occur in the Dinosaur Park Formation of Alberta [143]. These teeth could represent *Nanotyrannus*-like animals, but juvenile *Gorgosaurus* [109] are described as having unserrated premaxillary teeth [39], while those of adults are serrated [39]. Furthermore, Currie et al. [143] note that *Aublysodon* in Dinosaur Park are invariably small individuals, suggesting these teeth may be juvenile albertosaurines.

4.4. Weaknesses in the Hypothesis

We argue that the weight of the evidence favors *Nanotyrannus* as distinct, but some evidence appears inconsistent with this hypothesis. The absence of *Nanotyrannus* individuals with an external fundamental system is curious. We suggest this may be a sampling effect since many large dinosaurs are actually still-growing subadults rather than old adults with growth cessation [8,144]. If so, a specimen of *Nanotyrannus* will eventually be discovered with an EFS.

It may be that few individuals live long enough to form an EFS. Strikingly, none of the *Gorgosaurus* sampled by Erickson [8] had an EFS, and only one individual among each of the *T. rex*, *Albertosaurus*, and *Daspletosaurus* samples sectioned had an EFS. A study of life history and mortality in *Albertosaurus* suggests that perhaps 5% of all individuals lived beyond 20 years [145], with the EFS forming at 22 years in one *Albertosaurus* [8]. A rarity of old *Nanotyrannus* might be expected if most tyrannosaurs died young.

Another issue concerns the rarity of small *T. rex*. We maintain that LACM 23845 represents such a juvenile, however. The estimated skull length of this animal (80 cm) is barely larger than that of BMRP 2002.4.1 (est. 71 cm), about 113% the length of this animal. The minor difference in size seems inconsistent with the radically different morphology seen in BMRP 2002.4.1 and LACM 23845. Furthermore, the frontal described here (UCMP V84133) appears to come from a very small *T. rex*, with a skull around 45–50 cm in length. The rarity of young *T. rex* may reflect the rarity of juvenile dinosaurs in general; juveniles are rare even for common dinosaurs like *Triceratops* [112], and small dinosaurs in general tend to be rare [119]. This may be due to taphonomic biases; in particular, small animals are more likely to be consumed by predators and scavengers. Young *T. rex*, less than 3–4 m in length, may have been swallowed in a few bites, or whole, by adults, and would not become fossils.

4.5. Systematics and The Evolution of Development

Evolution often proceeds by terminal addition or subtraction of characters, i.e., new features tend to be added or subtracted late in development rather than early. This may be because mutations appearing early are more likely to be harmful or lethal; sexually selected features also tend to appear late [146].

Evolution via the terminal addition of characters is known as peramorphosis. In peramorphosis, new stages or features are added to the end of the ancestral development sequence, often by elaborating and extending existing development trajectories. For example, in *Triceratops*, derived features, including orbital horns, elongation of the frill, and elongation of the rostrum, are absent in young individuals [112,147], as are fusions between skull elements [107], but develop later in life. The result of the late development of these features is that juvenile *Triceratops* resemble primitive ceratopsids such as *Protoceratops* [148]. Peramorphosis seems to explain the evolution of a number of features in Tyrannosaurinae. The keyhole-shaped orbit, massive lacrimal boss and cornual boss, and modifications of the skull roof, such as the narrow frontal–nasal contact, are absent in the youngest tyrannosaurines [54] but develop in older juveniles and subadults [53]. However, primitive tyrannosauroids such as *Alioramus* [70] retain the primitive condition even as adults and, therefore, resemble the juveniles of Tyrannosaurinae. Because of this, it is illogical to assume that *Nanotyrannus* must be a juvenile because it lacks features associated with adulthood in Tyrannosaurinae.

Terminal addition can force juveniles down the tree when included in a phylogenetic analysis because they have not yet developed the late-appearing, derived features to place them with their clade. An example is a small tyrannosaurid described as “*Raptorex kriegsteini*” [113]. “*Raptorex*” is an immature [55,149] tyrannosaurid from the Nemegt of Mongolia [55]. It shows features seen in adults of primitive tyrannosaurs, including a large orbit, slender lacrimal and postorbitals, and a frontal participating in the orbit. As a result, it emerges basally in phylogenetic analyses [1,56,113]. However, several features—the short and tall maxilla, pointed premaxillary teeth, the large and anteroventrally located maxillary fenestra, and anterior expansion of the jugal—suggest affinities with Tyrannosaurinae, specifically *Tarbosaurus*.

We concede that the terminal addition of characters could cause *Nanotyrannus* to slip down the tree if it were a young juvenile. However, there is no evidence that the morphology of the specimens here is, in fact, the result of immaturity. *Nanotyrannus* specimens show no trend toward the acquisition of *Tyrannosaurus*-like features as they become larger and older. Crucially, features associated with immaturity in derived Tyrannosaurinae such as *Tarbosaurus* cannot be assumed to be juvenile; that is, features associated with juveniles in one lineage cannot be assumed to be associated with immaturity in another lineage because developmental patterns evolve. Finally, when we exclude ontogenetically variable features, *Nanotyrannus* still emerges as a basal tyrannosauroid, not a tyrannosaurid.

Another developmental mechanism complicating systematics is the terminal deletion of characters. Various terms are used for this, including paedomorphosis, or neoteny, where juvenile traits are

retained in adults. In chimpanzees and Neanderthals, for example, a rounded cranium and small orbital ridges are juvenile characters, but these features are typical of adult *Homo sapiens* due to neoteny [150]. Birds retain characteristics of juvenile theropods [151]. Paedomorphosis is a common means by which development evolves new morphologies. It is conceivable that *Nanotyrannus* is a paedomorphic tyrannosaurid. In at least one feature, it appears to be paedomorphic: whereas basal tyrannosauroids have serrated premaxillary teeth [152], *Nanotyrannus* lacks serrations on the premaxillary teeth, as in embryonic tyrannosaurs [153]. Assuming *Nanotyrannus* is a juvenile because it resembles juvenile tyrannosaurids is like assuming that a *Homo sapiens* skull is immature because it resembles a young Neanderthal child. One species “juvenile features” can be the adult morphology of another species.

4.6. Implications

Systematics can be seen as a battle between ‘splitters’, who tend to recognize a large number of species, and ‘lumpers’, who tend to recognize few. Both are important because sometimes scientists err in failing to recognize distinct species and other times, they mistake differences between individuals, males and females, or adults and juveniles as species-level differences. Ideally, through lumping and splitting, we arrive at a better understanding of life’s diversity.

Different systematic philosophies have prevailed at different times. The history of *Nanotyrannus* is interesting as part of a broader history of conflicting taxonomic practices in paleontology. Cope and Marsh, who helped found vertebrate paleontology in North America, were famous, if not notorious, for naming species based on incomplete fossils, as with “*Ornithomimus grandis*” [21] and “*Manospondylus gigas*” [22]. Their approach could charitably be described as entrepreneurial and exuberant—with many new fossils and new taxa to name, their strategy seems to have been to stake a claim on as many species as possible and let others clean up problems that emerged later. Alternatively, one could view it as a competition driven by personal vanity.

Unlike Marsh and Cope, Gilmore was a more cautious worker. Gilmore would describe a number of dinosaur species, almost all of which—*Thescelosaurus neglectus* [154], *Chirostenotes pergracilis* [155], *Bactrosaurus johnsoni* [156], *Alectrosaurus olsoni* [156], and *Alamosaurus sanjuanensis* [157]—are considered valid. One, *Brachyceratops montanensis* [158], is an indeterminate juvenile of a horned dinosaur, possibly *Achelousaurus* or *Einosaurus* [129]. Gilmore’s approach reflects a more conservative, thorough approach to paleontological taxonomy that prevailed after the more exuberant days of Marsh and Cope, probably in part because of the problems that came from trying to navigate the maze of names left behind by those two. In this light it is striking that Gilmore chose to recognize *Nanotyrannus lancensis* as distinct from *Tyrannosaurus*; the species results not from the early excesses of the Bone Wars, but was named as paleontology entered a more cautious, conservative phase. The recognition of *Nanotyrannus* as a distinct genus by Bakker et al. [30], in turn, represents a swing of the pendulum back towards recognizing more species and genera. Several things drive this trend toward recognizing new species.

First, we simply have more fossils as time progresses, which gives us a better understanding of patterns of variation. The large number *Tyrannosaurus* specimens [10,159], for example, including highly complete skulls and skeletons, provide context for diagnosing other species and provide a better understanding of patterns of intraspecific variation (or at least intrageneric variation [18]). Bonebeds of dinosaurs [160–162] are particularly useful in understanding growth and variation since they preserve large numbers of individuals from a small area and a brief period of time, recording population-level variation without the confounding factors of evolution across space or time.

Juveniles and growth series of closely related animals like *Tarbosaurus* [34,53,54,101,139,163] and *Gorgosaurus* [9,109,110] also shed light on patterns of development in tyrannosaurs. Similarly, the discovery of juveniles of other kinds of dinosaurs, such as *Protoceratops* [148]

and *Triceratops* [112,147], is critical to understanding which features are labile and subject to change over ontogeny and which are stable—that is, which features are diagnostic.

Furthermore, cladistic methodologies, although not without problems, make it possible to interpret fossils in an evolutionary framework [1,56,64]. Even where fossils are incomplete or subtly different, if they can be shown to lie on a distinct branch of the evolutionary tree, justification may exist for the recognition of new species.

We have also come to a better understanding of dinosaur evolution, recognizing that dinosaurs show high levels of species turnover through time [160,161] and high levels of endemism [161,162]. Few dinosaur species were widespread or long-lived. These patterns are not unique to dinosaurs; mammals show endemism [164], lizards [165,166] and plants show marked turnover [167,168]. Turnover and endemism seem to be the rule for dinosaurs and other extinct species.

And arguably, paleontologists have simply gotten better at recognizing distinct species—certainly, one would hope that two centuries of experience have taught us something. This is not to say that we should be incautious in naming or recognizing species, but we should recognize that countless dinosaurs and other animals existed over the millions of years that these lineages roamed Earth, that they can be hard to tell apart, and are often distinguished by subtle features.

Recognizing these species is complicated by the biases of the fossil record. Vertebrates are relatively rare in the fossil record; complete remains are especially rare. Focusing on skulls and skeletons gives us a large amount of information per specimen but at the cost of having few specimens to work with. Focusing on incomplete remains, such as isolated teeth, jaws, and bones, provides a larger sample size, but incomplete remains have fewer informative characters.

Furthermore, telling fossil species apart is simply difficult. Modern species are often diagnosed by characters that are not, or are rarely, preserved in the fossil record. Consider a pair of extant birds—the raven, *Corvus corax*, and the American crow, *Corvus brachyrhynchos*. Ravens can be distinguished from crows by their larger size, bigger bill, long throat feathers, gray neck feathers (in the juvenile), long and tapered wings, pointed tail, a hoarse call, soaring flight, and a tendency to associate in small groups [169]. Of these characters, only the larger size and longer beak would commonly preserve as fossils. Given this, the differences between *C. corax* and *C. brachyrhynchos* might easily be mistaken for intraspecific variation, with only fossils to work with. Features diagnosing species are often subtle. Species evolve not to be identifiable by human beings but to be identifiable by each other, using clues like color, songs, and scents. Biologists often struggle to discriminate species on the basis of morphology and undercount species. In recent years, DNA has revealed the existence of cryptic species. For example, the Sacred Crocodile, *Crocodilus suchus*, was long thought to be synonymous with the Nile Crocodile, *C. niloticus*, by scientists (although ancient Egyptians and 19th-century taxonomists recognized the two as separate) until DNA showed the species was distinct [170]. Similarly, African elephants were put into a single species, *Loxodonta africana*, until genomics resurrected the species *L. cyclotus* [171]. Genomics has revealed new species of baleen whale [172,173] and giraffe [174]. Even when working with extant animals, discriminating species is difficult.

We argue that the trend toward splitting in paleontology represents a broad pattern in science towards the recognition of more species, notwithstanding a number of recent attempts to synonymize genera. Some of these synonymies seem plausible, e.g., the synonymy of the flat-headed pachycephalosaurs *Ornathotholus* and *Homalocephale* as juveniles (or females) of the dome-headed pachycephalosaurs *Stegoceras* [175] and *Prenocephale* [176], respectively. Others, such as the synonymization of *Torosaurus* and *Triceratops* [177], sinking *Stygimoloch* into *Dracorex* [178], or (as we argue here) the synonymization of *Nanotyrannus* and *Tyrannosaurus*, are not supported by the available evidence. Overall, the number of dinosaur species continues to increase, driven by collecting, but also by splitting of known fossils into new species and genera [52,162,179,180].

The debate between splitting and lumping is not a mere philosophical issue, an arbitrary human decision in the way Osborn arbitrarily chose the name *Tyrannosaurus* over *Dynamosaurus*. The recognition of a species is an evolutionary hypothesis; it suggests that a period of evolution and reproductive isolation separates the populations that the fossils in question are drawn from. The recognition of a species is fundamentally a hypothesis about the course of evolution; names merely reflect these hypotheses [181], and so how we choose to name species affects how we reconstruct past diversity.

Logically, at any given point we may accurately estimate a group's diversity, overestimate diversity, or underestimate it. It seems likely that we are significantly underestimating fossil diversity. For many reasons—because species are often distinguished by subtle differences and are hard to tell apart, because paleontologists tend to work with small sample sizes, and because the development, variation, and sexual dimorphism of fossil groups are poorly understood—we may be underestimating fossil diversity as a whole.

If there is one thing the modern world and the fossil record tell us, it is that evolution tends to increase diversity over time, slowly increasing the total number of lineages. Such increases are temporarily interrupted by turnover events or mass extinctions [182], which depress diversity, at which point it tends to increase again [182]. Evolution also causes anagenesis [26], such that lineages that fail to go extinct slowly turn into new species over time. Species speciate, splitting into multiple descendant lineages—it is a fundamental pattern in evolution [181]. We should expect to find large numbers of species in the fossil record, and given the limits of the fossil record, we almost certainly underestimate fossil diversity. This matters because many of the problems we are interested in as paleontologists and evolutionary biologists—changes in diversity, mass extinction, diversity gradients, endemism, and the drivers of these patterns—require an accurate understanding of the number of species.

It is remarkable that the systematics of an animal as famous, as well-known, and as intensively studied as *Tyrannosaurus* have remained so incompletely understood and controversial. This emphasizes how little we really know about past diversity. If we still do not understand *T. rex*, what else do we not understand? There is a great deal we do not know, and may never know, about the life of the past.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/fossils2010001/s1>: Supplementary Information S1, Character-Taxon matrix for clustering analysis; Supplementary Information S2, Growth Curves and Asymptote Estimates; Supplementary Information S3, Character-taxon Matrix for Phylogenetic Analysis 1; Supplementary Information S4, Character-Taxon Matrix for Phylogenetic Analysis 2. See also Supplementary Data, data for histology analysis, and Supplementary Code, code for histological analysis.

Author Contributions: Conceptualization, N.R.L.; methodology, N.R.L. and E.T.S.; writing—original draft preparation, N.R.L. and E.T.S.; writing—review and editing, N.R.L. and E.T.S.; visualization, N.R.L. and E.T.S. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: All data are available in the paper or the supporting data.

Acknowledgments: Thanks for discussions to Bhart-Anjan Bhullar, Art Chadwick, Tom Cullen, Phil Currie, Brian Curtice, Jacques Gauthier, Pete Larson, Mark Loewen, Pete Makovicky, Greg Paul, Joe Sertich, Sam Shepard, Eric Snively, Jared Voris, Larry Witmer, Jared Wood and Darla Zelenitzsky. We thank H. Woodward Ballard for sharing high-resolution files for the supplemental figures in Woodward et al. [46], Larry Witmer for photos of the *Nanotyrannus lancensis* holotype, Matt Lamanna for photos of the *Tyrannosaurus rex* holotype, Scott Persons for photos of RSM 2523.8, Pete Larson for photos of FMNH PR2411 and *Tyrannosaurus*, and Andrey Atuchin for images of the *Tarbosaurus* holotype. Thanks to Tetsuto Miyashita, Phil Currie, Matt Lamanna, and Larry Witmer for the photographs. Thanks to T. Cullen for helpful discussions of histology. Thanks to the Black Hills Institute and the Burpee Museum for specimen access. Finally, thanks to the three reviewers for their constructive reviews of the manuscript. Andrey Atuchin skilfully drew the line drawings for *Nanotyrannus* and *Tyrannosaurus* skulls.

Conflicts of Interest: The authors declare no conflicts of interest.

References

- Brusatte, S.L.; Carr, T.D. The phylogeny and evolutionary history of tyrannosauroid dinosaurs. *Sci. Rep.* **2016**, *6*, 20252. [\[CrossRef\]](#)
- Zanno, L.E.; Makovicky, P.J. Neovenatorid theropods are apex predators in the Late Cretaceous of North America. *Nat. Commun.* **2013**, *4*, 2827. [\[CrossRef\]](#)
- Brusatte, S.L.; Benson, R.B.; Hutt, S. The osteology of *Neovenator salerii* (Dinosauria: Theropoda) from the Wealden group (Barremian) of the Isle of Wight. *Paleontogr. Soc. Monogr.* **2008**, *162*, 1–75.
- Holtz, T.R. Tyrannosauroida. In *The Dinosauria*, 2nd ed.; Weishampel, D.B., Dodson, P., Osmolska, H., Eds.; University of California Press: Berkeley, CA, USA, 2004; pp. 111–136.
- Brusatte, S.L.; Norell, M.A.; Carr, T.D.; Erickson, G.M.; Hutchinson, J.R.; Balanoff, A.M.; Bever, G.S.; Choiniere, J.N.; Makovicky, P.J.; Xu, X. Tyrannosaur paleobiology: New research on ancient exemplar organisms. *Science* **2010**, *329*, 1481–1485. [\[CrossRef\]](#)
- Osborn, H.F. *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bull. Am. Mus. Nat. Hist.* **1905**, *35*, 733–771.
- Brochu, C.A. Osteology of *Tyrannosaurus rex*: Insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *J. Vertebr. Paleontol. Mem.* **2003**, *7*, 1–138. [\[CrossRef\]](#)
- Erickson, G.M.; Makovicky, P.J.; Currie, P.J.; Norell, M.A.; Yerby, S.A.; Brochu, C.A. Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature* **2004**, *430*, 772–775. [\[CrossRef\]](#)
- Carr, T.D. Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria). *J. Vertebr. Paleontol.* **1999**, *19*, 497–520. [\[CrossRef\]](#)
- Carr, T.D. A high-resolution growth series of *Tyrannosaurus rex* obtained from multiple lines of evidence. *PeerJ* **2020**, *8*, e9192. [\[CrossRef\]](#)
- Hutchinson, J.R.; Garcia, M. *Tyrannosaurus* was not a fast runner. *Nature* **2002**, *415*, 1018–1021. [\[CrossRef\]](#)
- DePalma, R.A.; Burnham, D.A.; Martin, L.D.; Rothschild, B.M.; Larson, P.L. Physical evidence of predatory behavior in *Tyrannosaurus rex*. *Proc. Natl. Acad. Sci. USA* **2013**, *110*, 12560–12564. [\[CrossRef\]](#)
- Longrich, N.R.; Horner, J.R.; Erickson, G.M.; Currie, P.J. Cannibalism in *Tyrannosaurus rex*. *PLoS ONE* **2010**, *5*, e13419. [\[CrossRef\]](#)
- Erickson, G.M.; Van Kirk, S.D.; Su, J.; Levenston, M.E.; Caler, W.E.; Carter, D.R. Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones. *Nature* **1996**, *382*, 706–708. [\[CrossRef\]](#)
- Chin, K.; Tokaryk, T.T.; Erickson, G.M.; Calk, L.C. A king-sized theropod coprolite. *Nature* **1998**, *393*, 680–682. [\[CrossRef\]](#)
- Larson, P.L. Variation and Sexual Dimorphism in *Tyrannosaurus rex*. In *Tyrannosaurus rex, the Tyrant King*; Larson, P.L., Carpenter, K., Eds.; Indiana University Press: Bloomington, IN, USA, 2008; pp. 103–128.
- Carr, T.D.; Williamson, T.E. Diversity of late Maastrichtian Tyrannosauridae (Dinosauria: Theropoda) from western North America. *Zool. J. Linn. Soc.* **2004**, *142*, 479–523. [\[CrossRef\]](#)
- Paul, G.S.; Persons, W.S.; Van Raalte, J. The Tyrant Lizard King, Queen and Emperor: Multiple Lines of Morphological and Stratigraphic Evidence Support Subtle Evolution and Probable Speciation Within the North American Genus *Tyrannosaurus*. *Evol. Biol.* **2022**, *49*, 156–179. [\[CrossRef\]](#)
- Carr, T.D.; Napoli, J.G.; Brusatte, S.L.; Holtz, T.R.; Hone, D.W.; Williamson, T.E.; Zanno, L.E. Insufficient Evidence for Multiple Species of *Tyrannosaurus* in the Latest Cretaceous of North America: A Comment on “The Tyrant Lizard King, Queen and Emperor: Multiple Lines of Morphological and Stratigraphic Evidence Support Subtle Evolution and Probable Speciation Within the North American Genus *Tyrannosaurus*”. *Evol. Biol.* **2022**, *39*, 327–341.
- Breithaup, B.H.; Southwell, E.H.; Matthews, N.A. *Dynamosaurus imperiosus* and the earliest discoveries of *Tyrannosaurus rex* in Wyoming and the West. *New Mex. Mus. Nat. Hist. Sci. Bull.* **2006**, *35*, 257–258.
- Marsh, O.C. Description of new dinosaurian reptiles. *Am. J. Sci.* **1890**, *39*, 81–86. [\[CrossRef\]](#)
- Cope, E.D. Fourth note on the Dinosauria of the Laramie. *Am. Nat.* **1892**, *26*, 756–758.
- Paul, G.S. *Predatory Dinosaurs of the World*; Simon and Schuster: New York, NY, USA, 1988; p. 464.
- Olshevsky, G. The origin and evolution of the tyrannosaurids. *Kyoryugaku Saizensen* **1995**, *9*, 92–119.
- Osborn, H.F. *Tyrannosaurus*, Upper Cretaceous carnivorous dinosaur (second communication). *Bull. Am. Mus. Nat. Hist.* **1906**, *22*, 281–296.
- Scannella, J.B. Anagenesis in *Triceratops*: Evidence from a newly resolved stratigraphic framework for the Hell Creek Formation. *Cincinnati Mus. Cent. Sci. Contrib.* **2009**, *3*, 148–149.
- Gilmore, C.W. A new carnivorous dinosaur from the Lance Formation. *Smithson. Misc. Collect.* **1946**, *106*, 1–19.
- Rozhdestvensky, A.K. Growth changes in Asian dinosaurs and some problems of their taxonomy. *Paleontol. Zhurnal* **1965**, *3*, 95–109.
- Russell, D.A. Tyrannosaurs from the Late Cretaceous of Western Canada. *Natl. Mus. Nat. Sci. Publ. Palaeontol.* **1970**, *1*, 1–34.
- Bakker, R.; Williams, M.; Currie, P.J. *Nanotyrannus*, a new genus of pygmy tyrannosaur, from the latest Cretaceous of Montana. *Hunteria* **1988**, *1*, 1–30.
- Molnar, R. A new theropod dinosaur from the Upper Cretaceous of central Montana. *J. Paleontol.* **1978**, *52*, 73–82.
- Molnar, R.E.; Carpenter, K. The Jordan theropod (Maastrichtian, Montana, USA) referred to the genus *Aublysodon*. *Geobios* **1989**, *22*, 445–454. [\[CrossRef\]](#)
- Leidy, J.F. Remarks on a jaw fragment of *Megalosaurus*. *Proc. Phila. Acad. Nat. Sci.* **1868**, *20*, 197–200.

34. Carpenter, K. Tyrannosaurids (Dinosauria) of Asia and North America. In *Aspects of Nonmarine Cretaceous Geology*; Mateer, N.J., Chen, P.-J., Eds.; China Ocean Press: Beijing, China, 1992; pp. 250–268.
35. Tumarkin-Deratzian, A.R. Evaluation of long bone surface textures as ontogenetic in centrosaurine ceratopsids. *Anat. Rec.* **2009**, *292*, 1485–1500. [[CrossRef](#)] [[PubMed](#)]
36. Tumarkin-Deratzian, A.R.; Vann, D.R.; Dodson, P. Bone surface texture as an ontogenetic indicator in long bones of the Canada goose *Branta canadensis* (Anseriformes: Anatidae). *Zool. J. Linn. Soc.* **2006**, *148*, 133–168. [[CrossRef](#)]
37. Holtz, T.R., Jr. The phylogeny and taxonomy of the Tyrannosauridae. In *Mesozoic Vertebrate Life*; Tanke, D.H., Carpenter, K., Eds.; Indiana University Press: Bloomington, IN, USA, 2001; pp. 64–83.
38. Brusatte, S.L.; Carr, T.D.; Williamson, T.E.; Holtz, T.R., Jr.; Hone, D.W.; Williams, S.A. 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”. *Cretac. Res.* **2016**, *65*, 232–237.
39. Currie, P.J. Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. *Acta Palaeontol. Pol.* **2003**, *48*, 191–226.
40. Larson, P. The case for *Nanotyrannus*. In *Tyrannosaurid Paleobiology*; Parrish, J.M., Molnar, R.E., Currie, P.J., Koppelhus, E.B., Eds.; Indiana University Press: Bloomington, IN, USA, 2013; pp. 15–53.
41. Henderson, M.D.; Harrison, W.H. Taphonomy and environment of deposition of juvenile tyrannosaurid skeleton from the Hell Creek Formation (latest Maastrichtian) of southeastern Montana. In *Tyrannosaurus rex, the Tyrant King*; Indiana University Press: Bloomington, IN, USA, 2008; pp. 82–90.
42. Larson, P. The Validity of *Nanotyrannus lancensis* (Theropoda, Lancian—Upper Maastrichtian of North America). In Proceedings of the Society of Vertebrate Paleontology, Los Angeles, CA, USA, 30 October–2 November 2013.
43. Witmer, L.M.; Ridgely, R.C. New insights into the brain, braincase, and ear region of tyrannosaurs (Dinosauria, Theropoda), with implications for sensory organization and behavior. *Anat. Rec.* **2009**, *292*, 1266–1296. [[CrossRef](#)]
44. Witmer, L.M.; Ridgely, R.C. The Cleveland tyrannosaur skull (*Nanotyrannus* or *Tyrannosaurus*): New findings based on CT scanning, with special reference to the braincase. *Kirtlandia* **2010**, *57*, 61–81.
45. Schmerge, J.D.; Rothschild, B.M. Distribution of the dentary groove of theropod dinosaurs: Implications for theropod phylogeny and the validity of the genus *Nanotyrannus* Bakker et al., 1988. *Cretac. Res.* **2016**, *61*, 26–33. [[CrossRef](#)]
46. Woodward, H.N.; Tremaine, K.; Williams, S.A.; Zanno, L.E.; Horner, J.R.; Myhrvold, N. Growing up *Tyrannosaurus rex*: Osteohistology refutes the pygmy “*Nanotyrannus*” and supports ontogenetic niche partitioning in juvenile *Tyrannosaurus*. *Sci. Adv.* **2020**, *6*, eaax6250. [[CrossRef](#)]
47. Jevnikar, E.; Zanno, L. Bimodal trajectories and unresolved early growth stages in *Tyrannosaurus rex* growth. In Proceedings of the Society of Vertebrate Paleontology 2021 Annual Meeting, Minneapolis, MN, USA, 3–7 November 2021; p. 151.
48. Swofford, D.L. *PAUP *. Phylogenetic Analysis Using Parsimony (* and Other Methods)*; 4.0b10; Sinauer Associates: Sunderland, MA, USA, 2002.
49. Cullen, T.M.; Canale, J.I.; Apesteguía, S.; Smith, N.D.; Hu, D.; Makovicky, P.J. Osteohistological analyses reveal diverse strategies of theropod dinosaur body-size evolution. *Proc. R. Soc. B* **2020**, *287*, 20202258. [[CrossRef](#)]
50. Campione, N.E.; Evans, D.C.; Brown, C.M.; Carrano, M.T. Body mass estimation in non-avian bipeds using a theoretical conversion to quadruped stylopodial proportions. *Methods Ecol. Evol.* **2014**, *5*, 913–923. [[CrossRef](#)]
51. Griffin, C. Using osteohistology to determine the taxonomic validity of the Late Cretaceous dinosaur *Nanotyrannus lancensis* Bakker et al, 1988 (Theropoda: Tyrannosauridae). In Proceedings of the The Research and Scholarship Symposium, Cedarville, OH, USA, 16 April 2014.
52. Dalman, S.G.; Loewen, M.A.; Pyron, R.A.; Jasinski, S.E.; Malinzak, D.E.; Lucas, S.G.; Fiorillo, A.R.; Currie, P.J.; Longrich, N.R. A giant tyrannosaur from the Campanian–Maastrichtian of southern North America and the evolution of tyrannosaurid gigantism. *Sci. Rep.* **2024**, in press.
53. Hurum, J.H.; Sabath, K. Giant theropod dinosaurs from Asia and North America: Skulls of *Tarbosaurus bataar* and *Tyrannosaurus rex* compared. *Acta Palaeontol. Pol.* **2003**, *48*, 161–190.
54. Tsuihiji, T.; Watabe, M.; Tsogtbaatar, K.; Tsubamoto, T.; Barsbold, R.; Suzuki, S.; Lee, A.H.; Ridgely, R.C.; Kawahara, Y.; Witmer, L.M. Cranial osteology of a juvenile specimen of *Tarbosaurus bataar* (Theropoda, Tyrannosauridae) from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia. *J. Vertebr. Paleontol.* **2011**, *31*, 497–517. [[CrossRef](#)]
55. Fowler, D.W.; Woodward, H.N.; Freedman, E.A.; Larson, P.L.; Horner, J.R. Reanalysis of “*Raptorex kriegsteini*”: A juvenile tyrannosaurid dinosaur from Mongolia. *PLoS ONE* **2011**, *6*, e21376. [[CrossRef](#)]
56. Loewen, M.A.; Irmis, R.B.; Sertich, J.J.; Currie, P.J.; Sampson, S.D. Tyrant dinosaur evolution tracks the rise and fall of Late Cretaceous oceans. *PLoS ONE* **2013**, *8*, e79420. [[CrossRef](#)] [[PubMed](#)]
57. Voris, J.T.; Therrien, F.; Zelenitsky, D.K.; Brown, C.M. A new tyrannosaurine (Theropoda: Tyrannosauridae) from the Campanian Foremost Formation of Alberta, Canada, provides insight into the evolution and biogeography of tyrannosaurids. *Cretac. Res.* **2020**, *110*, 104388. [[CrossRef](#)]
58. Carr, T.D.; Williamson, T.E.; Britt, B.B.; Stadtman, K. Evidence for high taxonomic and morphologic tyrannosauroid diversity in the Late Cretaceous (Late Campanian) of the American Southwest and a new short-skulled tyrannosaurid from the Kaiparowits Formation of Utah. *Naturwissenschaften* **2011**, *98*, 241–246. [[CrossRef](#)]

59. Carr, T.D.; Williamson, T.E. *Bistahieversor sealeyi*, gen. et sp. nov., a new tyrannosauroid from New Mexico and the origin of deep snouts in Tyrannosauroida. *J. Vertebr. Paleontol.* **2010**, *30*, 1–16. [\[CrossRef\]](#)
60. Warshaw, E.A.; Fowler, D.W. A transitional species of *Daspletosaurus* Russell, 1970 from the Judith River Formation of eastern Montana. *PeerJ* **2022**, *10*, e14461. [\[CrossRef\]](#)
61. Carr, T.D.; Varricchio, D.J.; Sedlmayr, J.C.; Roberts, E.M.; Moore, J.R. A new tyrannosaur with evidence for anagenesis and crocodile-like facial sensory system. *Sci. Rep.* **2017**, *7*, 1–11. [\[CrossRef\]](#)
62. Molnar, R.E. A distinctive theropod dinosaur from the Upper Cretaceous of Baja California (Mexico). *J. Paleontol.* **1974**, *48*, 1009–1017.
63. Zanno, L.E.; Tucker, R.T.; Canoville, A.; Avrahami, H.M.; Gates, T.A.; Makovicky, P.J. Diminutive fleet-footed tyrannosauroid narrows the 70-million-year gap in the North American fossil record. *Commun. Biol.* **2019**, *2*, 64. [\[CrossRef\]](#) [\[PubMed\]](#)
64. Nesbitt, S.J.; Denton Jr, R.K.; Loewen, M.A.; Brusatte, S.L.; Smith, N.D.; Turner, A.H.; Kirkland, J.I.; McDonald, A.T.; Wolfe, D.G. A mid-Cretaceous tyrannosauroid and the origin of North American end-Cretaceous dinosaur assemblages. *Nat. Ecol. Evol.* **2019**, *3*, 892–899. [\[CrossRef\]](#) [\[PubMed\]](#)
65. Brusatte, S.L.; Averianov, A.; Sues, H.-D.; Muir, A.; Butler, I.B. New tyrannosaur from the mid-Cretaceous of Uzbekistan clarifies evolution of giant body sizes and advanced senses in tyrant dinosaurs. *Proc. Natl. Acad. Sci. USA* **2016**, *113*, 3447–3452. [\[CrossRef\]](#) [\[PubMed\]](#)
66. Lambe, L.M. On a new genus and species of carnivorous dinosaur from the Belly River Formation of Alberta, with a description of the skull of *Stephanosaurus marginatus* from the same horizon. *Ott. Nat.* **1914**, *28*, 13–20.
67. Currie, P.J. Theropods, including birds. In *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed*; Currie, P.J., Koppelhus, E.B., Farlow, J.O., Eds.; Indiana University Press: Bloomington, IN, USA, 2005; pp. 367–397.
68. Fiorillo, A.R.; Tykoski, R.S. A diminutive new tyrannosaur from the top of the world. *PLoS ONE* **2014**, *9*, e91287. [\[CrossRef\]](#) [\[PubMed\]](#)
69. Carr, T.D. Significant Geographic Range Extension for the Sympatric Tyrannosaurids *Albertosaurus Libratus* and *Daspletosaurus Torosus* from the Judith River Formation (Late Campanian) of Northern Montana. In Proceedings of The Society of Vertebrate Paleontology 2018 Annual Meeting, Albuquerque, NM, USA, 17–20 October 2018.
70. Brusatte, S.L.; Carr, T.D.; Norell, M.A. The osteology of *Alioramus*, a gracile and long-snouted tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. *Bull. Am. Mus. Nat. Hist.* **2012**, *2012*, 1–197. [\[CrossRef\]](#)
71. Mallon, J.C.; Bura, J.R.; Schumann, D.; Currie, P.J. A problematic tyrannosaurid (Dinosauria: Theropoda) skeleton and its implications for tyrannosaurid diversity in the Horseshoe Canyon Formation (Upper Cretaceous) of Alberta. *Anat. Rec.* **2020**, *303*, 673–690. [\[CrossRef\]](#)
72. Longrich, N.R.; Isasmendi, E.; Pereda-Suberbiola, X.; Jalil, N.-E. New fossils of Abelisauridae (Dinosauria: Theropoda) from the upper Maastrichtian of Morocco, North Africa. *Cretac. Res.* **2023**, *152*, 105677. [\[CrossRef\]](#)
73. Gasparini, Z.; Sterli, J.; Parras, A.; O’Gorman, J.P.; Salgado, L.; Varela, J.; Pol, D. Late Cretaceous reptilian biota of the La Colonia Formation, central Patagonia, Argentina: Occurrences, preservation and paleoenvironments. *Cretac. Res.* **2015**, *54*, 154–168. [\[CrossRef\]](#)
74. Novas, F.E.; Chatterjee, S.; Rudra, D.K.; Datta, P. *Rahiolisaurus gujaratensis*, n. gen. n. sp., a New Abelisaurid Theropod from the Late Cretaceous of India. In *New Aspects of Mesozoic Biodiversity*; Bandyopadhyay, S., Ed.; Springer: Berlin/Heidelberg, Germany, 2010; pp. 45–62.
75. Wilson, J.A.; Sereno, P.C.; Srivastava, S.; Bhatt, D.K.; Khosla, A.; Sahni, A. A new abelisaurid (Dinosauria, Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India. *Contrib. Mus. Paleontol. Univ. Mich.* **2003**, *31*, 1–42.
76. Chatterjee, S. *Indosuchus* and *Indosaurus*, Cretaceous carnosaur from India. *J. Paleontol.* **1978**, *52*, 570–580.
77. Huene, F.R.; Matley, C.A. The Cretaceous Saurischia and Ornithischia of the Central provinces. *Palaeontol. Indica (New Ser.) Mem. Geol. Surv. India* **1933**, *21*, 1–74.
78. Cau, A.; Dalla Vecchia, F.M.; Fabbri, M. A thick-skulled theropod (Dinosauria, Saurischia) from the Upper Cretaceous of Morocco with implications for carcharodontosaurid cranial evolution. *Cretac. Res.* **2013**, *40*, 251–260. [\[CrossRef\]](#)
79. Sereno, P.C.; Dutheil, D.B.; Iarochene, M.; Larsson, H.C. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science* **1996**, *272*, 986. [\[CrossRef\]](#) [\[PubMed\]](#)
80. Calvo, J.O.; Rubilar-Rogers, D.; Moreno, K. A new Abelisauridae (Dinosauria: Theropoda) from northwest Patagonia. *Ameghiniana* **2004**, *41*, 555–563.
81. Coria, R.A.; Salgado, L. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* **1995**, *377*, 224–226. [\[CrossRef\]](#)
82. Mateus, O. Late Jurassic dinosaurs from the Morrison Formation (USA), the Lourinha and Alcobaça formations (Portugal), and the Tendaguru Beds (Tanzania): A comparison. *New Mex. Mus. Nat. Hist. Sci. Bull.* **2006**, *36*, 223–231.
83. Van Valkenburgh, B.; Hayward, M.W.; Ripple, W.J.; Meloro, C.; Roth, V.L. The impact of large terrestrial carnivores on Pleistocene ecosystems. *Proc. Natl. Acad. Sci. USA* **2016**, *113*, 862–867. [\[CrossRef\]](#)
84. Barnett, R.; Barnes, I.; Phillips, M.J.; Martin, L.D.; Harington, C.R.; Leonard, J.A.; Cooper, A. Evolution of the extinct Sabretooths and the American cheetah-like cat. *Curr. Biol.* **2005**, *15*, R589–R590. [\[CrossRef\]](#)
85. Nowak, R.M. *Walker’s Mammals of the World*, 6th ed.; JHU Press: Baltimore, MD, USA, 1999.
86. Bibi, F.; Kiessling, W. Continuous evolutionary change in Plio-Pleistocene mammals of eastern Africa. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, 10623–10628. [\[CrossRef\]](#) [\[PubMed\]](#)

87. Diamond, J. *The Third Chimpanzee: The Evolution and Future of the Human Animal*; Harper Perennial: New York, NY, USA, 1992.
88. Bardet, N.; Falconnet, J.; Fischer, V.; Houssaye, A.; Jouve, S.; Pereda-Suberbiola, X.; Perez-García, A.; Rage, J.-C.; Vincent, P. Mesozoic marine reptile palaeobiogeography in response to drifting plates. *Gondwana Res.* **2014**, *26*, 869–887. [[CrossRef](#)]
89. Longrich, N.R.; Jalil, N.-E.; Khaldoune, F.; Yazami, O.K.; Pereda-Suberbiola, X.; Bardet, N. *Thalassotitan atrox*, a giant predatory mosasaurid (Squamata) from the Upper Maastrichtian Phosphates of Morocco. *Cretac. Res.* **2022**, *140*, 105315. [[CrossRef](#)]
90. Lambert, O.; Bianucci, G.; Post, K.; De Muizon, C.; Salas-Gismondi, R.; Urbina, M.; Reumer, J. The giant bite of a new raptorial sperm whale from the Miocene epoch of Peru. *Nature* **2010**, *466*, 105–108. [[CrossRef](#)] [[PubMed](#)]
91. Hart, J.L. *Pacific Fishes of Canada*; Fisheries Research Board of Canada Bulletin: Ottawa, IL, USA, 1973; Volume 180, p. 741.
92. Doughty, P.; Kealley, L.; Fitch, A.; Donnellan, S.C. A new diminutive species of *Varanus* from the Dampier Peninsula, western Kimberley region, Western Australia. *Rec. West. Aust. Mus.* **2014**, *29*, 128–140. [[CrossRef](#)]
93. Dunning, J.B. *Handbook of Avian Body Masses*, 2nd ed.; CRC Press: Boca Raton, FL, USA, 2007; p. 672.
94. Cope, E.D. Discovery of a gigantic dinosaur in the Cretaceous of New Jersey. *Proc. Acad. Nat. Sci. Phila.* **1866**, *18*, 275–279.
95. Carr, T.D.; Williamson, T.E.; Schwimmer, D.R. A new genus and species of tyrannosauroid from the Late Cretaceous (middle Campanian) Demopolis Formation of Alabama. *J. Vertebr. Paleontol.* **2005**, *25*, 119–143. [[CrossRef](#)]
96. Brusatte, S.L.; Carr, T.D.; Erickson, G.M.; Bever, G.S.; Norell, M. A long-snouted, multihorned tyrannosaurid from the Late Cretaceous of Mongolia. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 17251–17266. [[CrossRef](#)]
97. Kurzanov, S. New carnosaur from the Late Cretaceous of Nogon—Tsav, Mongolia. *Sovmest. Sov. Mong. Paleon Tologičeskaâ Eksped. Tr.* **1976**, *3*, 93–104.
98. Lü, J.; Yi, L.; Brusatte, S.L.; Yang, L.; Li, H.; Chen, L. A new clade of Asian Late Cretaceous long-snouted tyrannosaurids. *Nat. Commun.* **2014**, *5*, 3788. [[CrossRef](#)]
99. McDonald, A.T.; Wolfe, D.G.; Dooley, A.C., Jr. A new tyrannosaurid (Dinosauria: Theropoda) from the Upper Cretaceous Menefee Formation of New Mexico. *PeerJ* **2018**, *6*, e5749. [[CrossRef](#)]
100. Currie, P.J.; Zhiming, D. New information on *Shanshanosaurus huoyanshanensis*, a juvenile tyrannosaurid (Theropoda, Dinosauria) from the Late Cretaceous of China. *Can. J. Earth Sci.* **2001**, *38*, 1729–1737. [[CrossRef](#)]
101. Maleev, E.A. New carnivorous dinosaurs from the Upper Cretaceous of Mongolia. *Dokl. Akad. Nauk. SSSR* **1955**, *104*, 779–782.
102. Hone, D.W.; Wang, K.; Sullivan, C.; Zhao, X.; Chen, S.; Li, D.; Ji, S.; Ji, Q.; Xu, X. A new, large tyrannosaurine theropod from the Upper Cretaceous of China. *Cretac. Res.* **2011**, *32*, 495–503. [[CrossRef](#)]
103. Persons IV, W.S.; Currie, P.J.; Erickson, G.M. An older and exceptionally large adult specimen of *Tyrannosaurus rex*. *Anat. Rec.* **2020**, *303*, 656–672. [[CrossRef](#)]
104. Hutchinson, J.R.; Bates, K.T.; Molnar, J.; Allen, V.; Makovicky, P.J. A computational analysis of limb and body dimensions in *Tyrannosaurus rex* with implications for locomotion, ontogeny, and growth. *PLoS ONE* **2011**, *6*, e26037. [[CrossRef](#)]
105. DePalma, R.A.; Burnham, D.A.; Martin, L.D.; Larson, P.L.; Bakker, R.T. The first giant raptor (Theropoda: Dromaeosauridae) from the Hell Creek Formation. *Paleontol. Contrib.* **2015**, *14*, 1–16.
106. Evans, D.C.; Larson, D.W.; Currie, P.J. A new dromaeosaurid (Dinosauria: Theropoda) with Asian affinities from the latest Cretaceous of North America. *Naturwissenschaften* **2013**, *100*, 1041–1049. [[CrossRef](#)]
107. Longrich, N.R.; Field, D. *Torosaurus* is not *Triceratops*: Ontogeny in Chasmosaurine Ceratopsids as a Case Study in Dinosaur Taxonomy. *PLoS ONE* **2012**, *7*, e32623. [[CrossRef](#)]
108. Maleev, E.A. Giant carnosours of the family Tyrannosauridae. *Jt. Sov. Mong. Paleontol. Exped.* **1974**, *1*, 132–191.
109. Voris, J.T.; Zelenitsky, D.K.; Therrien, F.; Ridgely, R.C.; Currie, P.J.; Witmer, L.M. Two exceptionally preserved juvenile specimens of *Gorgosaurus libratus* (Tyrannosauridae, Albertosaurinae) provide new insight into the timing of ontogenetic changes in tyrannosaurids. *J. Vertebr. Paleontol.* **2021**, *41*, e2041651. [[CrossRef](#)]
110. Voris, J.T.; Zelenitsky, D.K.; Therrien, F.; Currie, P.J. Reassessment of a juvenile *Daspletosaurus* from the Late Cretaceous of Alberta, Canada with implications for the identification of immature tyrannosaurids. *Sci. Rep.* **2019**, *9*, 1–10. [[CrossRef](#)] [[PubMed](#)]
111. Brochu, C.A. Closure of neurocentral sutures during crocodylian ontogeny: Implication for maturity assessment in fossil archosaurs. *J. Vertebr. Paleontol.* **1996**, *16*, 49–62. [[CrossRef](#)]
112. Goodwin, M.B.; Clemens, W.A.; Horner, J.R.; Padian, K. The smallest known *Triceratops* skull: New observations on ceratopsid cranial anatomy and ontogeny. *J. Vertebr. Paleontol.* **2006**, *26*, 103–112. [[CrossRef](#)]
113. Sereno, P.C.; Tan, L.; Brusatte, S.L.; Kriegstein, H.J.; Zhao, X.; Cloward, K. Tyrannosaurid skeletal design first evolved at small body size. *Science* **2009**, *326*, 418–422. [[CrossRef](#)] [[PubMed](#)]
114. Sereno, P.C. The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. *J. Vertebr. Paleontol.* **1994**, *13*, 425–450. [[CrossRef](#)]
115. Burch, S.H.; Carrano, M.T. An articulated pectoral girdle and forelimb of the abelisaurid theropod *Majungasaurus crenatissimus* from the Late Cretaceous of Madagascar. *J. Vertebr. Paleontol.* **2012**, *32*, 1–16. [[CrossRef](#)]
116. Norell, M.A.; Makovicky, P.J. Important features of the dromaeosaurid skeleton II: Information from newly collected specimens of *Velociraptor mongoliensis*. *Am. Mus. Novit.* **1999**, *3282*, 1–45.
117. Perle, A.; Norell, M.A.; Clark, J.M. A new maniraptoran theropod *Achillobator giganticus* (Dromaeosauridae) from the Upper Cretaceous of Burkhan, Mongolia. *Dep. Geol. Natl. Univ. Mong. Ulaanbaatar* **1999**, *101*, 1–105.
118. Jasinski, S.E.; Sullivan, R.M.; Lucas, S.G. Taxonomic composition of the Alamo Wash local fauna from the Upper Cretaceous Ojo Alamo Formation (Naashoibito Member), San Juan Basin, New Mexico. *New Mex. Mus. Nat. Hist. Sci. Bull.* **2011**, *53*, 216–265.

119. Longrich, N.R.; Currie, P.J. A microraptorine (Dinosauria-Dromaeosauridae) from the Late Cretaceous of North America. *PNAS* **2009**, *106*, 5002–5008. [[CrossRef](#)] [[PubMed](#)]
120. Raath, M.A.; Carpenter, K.; Currie, P.J. Morphological variation in small theropods and its meaning in systematics: Evidence from *Syntarsus*. In *Dinosaur Systematics: Perspectives and Approaches*; Currie, P.J., Carpenter, K., Eds.; Cambridge University Press: Cambridge, UK, 1990; pp. 91–105.
121. Iori, F.V.; de Araújo-Júnior, H.I.; Tavares, S.A.S.; da Silva Marinho, T.; Martinelli, A.G. New theropod dinosaur from the Late Cretaceous of Brazil improves abelisaurid diversity. *J. South Am. Earth Sci.* **2021**, *112*, 103551. [[CrossRef](#)]
122. Pol, D.; Rauhut, O.W. A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. *Proc. R. Soc. B: Biol. Sci.* **2012**, *279*, 3170–3175. [[CrossRef](#)] [[PubMed](#)]
123. Cerroni, M.A.; Baiano, M.A.; Canale, J.I.; Agnolín, F.L.; Otero, A.; Novas, F.E. Appendicular osteology of *Skorpiovenator bustingorryi* (Theropoda, Abelisauridae) with comments on phylogenetic features of abelisaurids. *J. Syst. Palaeontol.* **2022**, *20*, 1–32. [[CrossRef](#)]
124. Macdonald, I.; Currie, P.J. Description of a partial *Dromiceiomimus* (Dinosauria: Theropoda) skeleton with comments on the validity of the genus. *Can. J. Earth Sci.* **2019**, *56*, 129–157. [[CrossRef](#)]
125. Osborn, H.F. Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. *Bull. Am. Mus. Nat. Hist.* **1917**, *35*, 733–771.
126. Yao, X.; Sullivan, C.; Tan, Q.; Xu, X. New ornithomimosaurian (Dinosauria: Theropoda) pelvis from the Upper Cretaceous Erlian Formation of Nei Mongol, North China. *Cretac. Res.* **2022**, *137*, 105234. [[CrossRef](#)]
127. Xu, L.; Kobayashi, Y.; Lü, J.; Lee, Y.-N.; Liu, Y.; Tanaka, K.; Zhang, X.; Jia, S.; Zhang, J. A new ornithomimid dinosaur with North American affinities from the Late Cretaceous Qiupa Formation in Henan Province of China. *Cretac. Res.* **2011**, *32*, 213–222. [[CrossRef](#)]
128. Brown, C.M.; Russell, A.P.; Ryan, M.J. Pattern and transition of surficial bone texture of the centrosaurine frill and their ontogenetic and taxonomic implications. *J. Vertebr. Paleontol.* **2009**, *29*, 132–141. [[CrossRef](#)]
129. Sampson, S.D.; Ryan, M.J.; Tanke, D.H. Craniofacial ontogeny in centrosaurine dinosaurs (Ornithischia: Ceratopsidae): Taxonomic and behavioral implications. *Zoological J. Linn. Soc.* **1997**, *121*, 293–337. [[CrossRef](#)]
130. Horner, J.R.; de Ricqlès, A.; Padian, K. Variation in dinosaur skeletochronology indicators: Implications for age assessment and physiology. *Paleobiology* **1999**, *25*, 295–304. [[CrossRef](#)]
131. Erickson, G.M.; Tumanova, T.A. Growth curve of *Psittacosaurus mongoliensis* Osborn (Ceratopsia: Psittacosauridae) inferred from long bone histology. *Zool. J. Linn. Soc.* **2000**, *130*, 551–566. [[CrossRef](#)]
132. Griebeler, E.M.; Klein, N.; Sander, P.M. Aging, maturation and growth of sauropodomorph dinosaurs as deduced from growth curves using long bone histological data: An assessment of methodological constraints and solutions. *PLoS ONE* **2013**, *8*, e67012. [[CrossRef](#)]
133. Erickson, G.M. On dinosaur growth. *Annu. Rev. Earth Planet. Sci.* **2014**, *42*, 675–697. [[CrossRef](#)]
134. Saitta, E.T.; Stockdale, M.T.; Longrich, N.R.; Bonhomme, V.; Benton, M.J.; Cuthill, I.C.; Makovicky, P.J. An effect size statistical framework for investigating sexual dimorphism in non-avian dinosaurs and other extinct taxa. *Biol. J. Linn. Soc.* **2020**, *131*, 231–273. [[CrossRef](#)]
135. Ralls, K.; Mesnick, S. Sexual Dimorphism. In *Encyclopedia of Marine Mammals*; Elsevier: Amsterdam, The Netherlands, 2009; pp. 1005–1011.
136. Laws, R.M. *The elephant seal (Mirounga leonina, Linn.): I. Growth and age*; HMSO: London, UK, 1953; p. 62.
137. McCann, T.S.; Fedak, M.A.; Harwood, J. Parental investment in southern elephant seals, *Mirounga leonina*. *Behav. Ecol. Sociobiol.* **1989**, *25*, 81–87. [[CrossRef](#)]
138. Molnar, R.E. The cranial morphology of *Tyrannosaurus rex* *Palaeontographica*. *Abt. A Paläozoologie Stratigr.* **1991**, *217*, 137–176.
139. Yun, C.-G.; Peters, G.F.; Currie, P.J. Allometric growth in the frontals of the Mongolian theropod dinosaur *Tarbosaurus bataar*. *Acta Palaeontol. Pol.* **2022**, *67*, 601–615. [[CrossRef](#)]
140. Forster, C.A. Species resolution in *Triceratops*: Cladistic and morphometric approaches. *J. Vertebr. Paleontol.* **1996**, *16*, 259–270. [[CrossRef](#)]
141. Scannella, J.B.; Fowler, D.W.; Goodwin, M.B.; Horner, J.R. Evolutionary trends in *Triceratops* from the Hell Creek Formation, Montana. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 10245–10250. [[CrossRef](#)]
142. Pringle, H. Selling America's fossil record. *Science* **2014**, *343*, 364–367. [[CrossRef](#)]
143. Currie, P.J.; Rigby, K.J.; Sloan, R.E. Theropod teeth from the Judith River Formation of southern Alberta, Canada. In *Dinosaur Systematics: Perspectives and Approaches*; Currie, P.J., Carpenter, K., Eds.; Cambridge University Press: Cambridge, UK, 1990; pp. 107–125.
144. Hone, D.W.; Farke, A.A.; Wedel, M.J. Ontogeny and the fossil record: What, if anything, is an adult dinosaur? *Biol. Lett.* **2016**, *12*, 20150947. [[CrossRef](#)]
145. Erickson, G.M.; Currie, P.J.; Inouye, B.D.; Winn, A.A. Tyrannosaur life tables: An example of nonavian dinosaur population biology. *Science* **2006**, *313*, 213–217. [[CrossRef](#)]
146. Darwin, C. *The Descent of Man and Selection in Relation to Sex*; Murray: London, UK, 1871.
147. Horner, J.R.; Goodwin, M.B. Major cranial changes during *Triceratops* ontogeny. *Proc. R. Soc. B* **2006**, *273*, 2757–2761.
148. Brown, B.; Schlaikjer, E.M. The structure and relationships of *Protoceratops*. *Ann. N. Y. Acad. Sci.* **1940**, *40*, 133–266. [[CrossRef](#)]
149. Carr, T.D. A reappraisal of tyrannosauroid fossils from the Iren Dabasu Formation (Coniacian–Campanian), Inner Mongolia, People's Republic of China. *J. Vertebr. Paleontol.* **2022**, *42*, e2199817. [[CrossRef](#)]

150. De Beer, G.R. *Embryos and Ancestors*, 2nd ed.; Clarendon Press: Oxford, UK, 1951; p. 159.
151. Bhullar, B.-A.S.; Marugán-Lobón, J.; Racimo, F.; Bever, G.S.; Rowe, T.B.; Norell, M.A.; Abzhanov, A. Birds have pedomorphic dinosaur skulls. *Nature* **2012**, *487*, 223–226.
152. Naish, D.; Cau, A. The osteology and affinities of *Eotyrannus lengi*, a tyrannosauroid theropod from the Wealden Supergroup of southern England. *PeerJ* **2022**, *10*, e12727. [[CrossRef](#)]
153. Funston, G.F.; Powers, M.J.; Whitebone, S.A.; Brusatte, S.L.; Scannella, J.B.; Horner, J.R.; Currie, P.J. Baby tyrannosaurid bones and teeth from the Late Cretaceous of western North America. *Can. J. Earth Sci.* **2021**, *58*, 756–777.
154. Gilmore, C.W. A new dinosaur from the Lance Formation of Wyoming. *Smithson. Misc. Collect.* **1913**, *61*, 1–5.
155. Gilmore, C.W. A new coelurid dinosaur from the Belly River Cretaceous of Alberta. *Can. Geol. Surv. Bull.* **1924**, *38*, 210639511.
156. Gilmore, C.W. On the dinosaurian fauna of the Iren Dabasu Formation. *Bull. Am. Mus. Nat. Hist.* **1933**, *67*, 23–78.
157. Gilmore, C.W. A new sauropod dinosaur from the Ojo Alamo Formation of New Mexico. *Smithson. Misc. Collect.* **1922**, *72*, 1–9.
158. Gilmore, C.W. A new ceratopsian dinosaur from the Upper Cretaceous of Montana, with note on *Hypacrosaurus*. *Smithson. Misc. Collect.* **1914**, *63*, 1–10.
159. Larson, N.L.; Larson, P.L.; Carpenter, K. One hundred years of *Tyrannosaurus rex*: The skeletons. *Tyrannosaurus Rex Tyrant King* **2008**, *1*, 1–56.
160. Mallon, J.C.; Evans, D.C.; Ryan, M.J.; Anderson, J.S. Megaherbivorous dinosaur turnover in the Dinosaur Park Formation (upper Campanian) of Alberta, Canada. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2012**, *350–352*, 124–138. [[CrossRef](#)]
161. Sampson, S.D.; Loewen, M.A.; Farke, A.A.; Roberts, E.M.; Forster, C.A.; Smith, J.A.; Titus, A.L. New horned dinosaurs from Utah provide evidence for intracontinental dinosaur endemism. *PLoS ONE* **2010**, *5*, e12292. [[CrossRef](#)]
162. Longrich, N.R. *Titanoceratops ouranos*, a giant horned dinosaur from the Late Campanian of New Mexico. *Cretac. Res.* **2011**, *32*, 264–276. [[CrossRef](#)]
163. Hanai, T.; Tsuihiji, T. Description of tooth ontogeny and replacement patterns in a juvenile *Tarbosaurus bataar* (Dinosauria: Theropoda) using CT-scan data. *Anat. Rec.* **2019**, *302*, 1210–1225. [[CrossRef](#)]
164. Longrich, N.R.; Striber, J.; Wills, M.A. Severe extinction and rapid recovery of mammals across the Cretaceous-Paleogene boundary, and the effects of rarity on patterns of extinction and recovery. *J. Evol. Biol.* **2016**, *29*, 1495–1512. [[CrossRef](#)]
165. Gao, K.-Q.; Fox, R.C. Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from Western Canada. *Bull. Carnegie Mus. Nat. Hist.* **1996**, *33*, 1–107. [[CrossRef](#)]
166. Longrich, N.R.; Bhullar, B.-A.S.; Gauthier, J. Mass extinction of lizards and snakes at the Cretaceous-Paleogene boundary. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 21396–21401. [[CrossRef](#)]
167. Sweet, A.R.; Braman, D.R. Cretaceous–Tertiary palynofloral perturbations and extinctions within the *Aquilapollenites* Phytogeographic Province. *Can. J. Earth Sci.* **2001**, *38*, 249–269. [[CrossRef](#)]
168. Johnson, K.R. Megaflora of the Hell Creek and lower Fort Union Formations in the western Dakotas: Vegetational response to climate change, the Cretaceous-Tertiary boundary event, and rapid marine transgression. *Geol. Soc. Am. Spec. Pap.* **2002**, *361*, 329–391.
169. Sibley, D.A. *The Sibley Guide to Birds*; Knopf: New York, NY, USA, 2000; p. 545.
170. Hekkala, E.; Shirley, M.H.; Amato, G.; Austin, J.D.; Charter, S.; Thorbjarnarson, J.; Vliet, K.A.; Houck, M.L.; Desalle, R.; Blum, M.J. An ancient icon reveals new mysteries: Mummy DNA resurrects a cryptic species within the Nile crocodile. *Mol. Ecol.* **2011**, *20*, 4199–4215. [[CrossRef](#)] [[PubMed](#)]
171. Rohland, N.; Reich, D.; Mallick, S.; Meyer, M.; Green, R.E.; Georgiadis, N.J.; Roca, A.L.; Hofreiter, M. Genomic DNA sequences from mastodon and woolly mammoth reveal deep speciation of forest and savanna elephants. *PLoS Biol.* **2010**, *8*, e1000564. [[CrossRef](#)] [[PubMed](#)]
172. Rosel, P.E.; Wilcox, L.A.; Yamada, T.K.; Mullin, K.D. A new species of baleen whale (*Balaenoptera*) from the Gulf of Mexico, with a review of its geographic distribution. *Mar. Mammal Sci.* **2021**, *37*, 577–610. [[CrossRef](#)]
173. Wada, S.; Oishi, M.; Yamada, T.K. A newly discovered species of living baleen whale. *Nature* **2003**, *426*, 278–281. [[CrossRef](#)]
174. Fennessy, J.; Bidon, T.; Reuss, F.; Kumar, V.; Elkan, P.; Nilsson, M.A.; Vamberger, M.; Fritz, U.; Janke, A. Multi-locus analyses reveal four giraffe species instead of one. *Curr. Biol.* **2016**, *26*, 2543–2549. [[CrossRef](#)]
175. Schott, R.K.; Evans, D.C.; Goodwin, M.B.; Horner, J.R.; Brown, C.M.; Longrich, N.R. Cranial Ontogeny in *Stegoceras validum* (Dinosauria: Pachycephalosauria): A Quantitative Model of Pachycephalosaur Dome Growth and Variation. *PLoS ONE* **2011**, *6*, e21092. [[CrossRef](#)]
176. Longrich, N.R.; Sankey, J.T.; Tanke, D.H. *Texacephale langstoni*, a new genus of pachycephalosaurid (Dinosauria: Ornithischia) from the upper Campanian Aguja Formation, southern Texas, USA. *Cretac. Res.* **2010**, *31*, 274–284. [[CrossRef](#)]
177. Scannella, J.; Horner, J.R. *Torosaurus* Marsh, 1891 is *Triceratops*, Marsh, 1889 (Ceratopsidae: Chasmosaurinae) synonymy through ontogeny. *J. Vertebr. Paleontol.* **2010**, *30*, 1157–1168. [[CrossRef](#)]
178. Horner, J.R.; Goodwin, M.B. Extreme cranial ontogeny in the Upper Cretaceous dinosaur *Pachycephalosaurus*. *PLoS ONE* **2009**, *4*, 27626. [[CrossRef](#)] [[PubMed](#)]
179. Longrich, N.R. *Mojoceratops perifania*, a new chasmosaurine ceratopsid from the Late Campanian of Western Canada. *J. Paleontol.* **2010**, *84*, 681–694. [[CrossRef](#)]

180. van der Reest, A.J.; Currie, P.J. Troodontids (Theropoda) from the Dinosaur Park Formation, Alberta, with a description of a unique new taxon: Implications for deinonychosaur diversity in North America. *Can. J. Earth Sci.* **2017**, *54*, 919–935. [[CrossRef](#)]
181. Darwin, C.R. *The Origin of Species*; John Murray: London, UK, 1859.
182. Raup, D.M.; Sepkoski, J.J., Jr. Mass extinctions in the marine fossil record. *Science* **1982**, *215*, 1501–1503. [[CrossRef](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.