

ISSN 1759-0116 (Online)

# **ZooNova**

Occasional Papers in Zoology

Number 54, Pages 1 – 65

**THE TAXONOMICS OF THE LITHE BASAL  
EUTYRANNOSAUR GENERA AND SPECIES OF LATE  
MAASTRICHTIAN WESTERN NORTH AMERICA**

**Franco Sancarło and Gregory S. Paul**

Published on-line at [zoonova.afriherp.org](https://zoonova.afriherp.org)

Afriherp Communications, Greenford, United Kingdom

Date of publication: 24 September 2026

Copyright: Franco Sancarło and Gregory S. Paul 2026

*Digital copies are archived in <https://zenodo.org> and the British Legal Deposit Libraries  
(The British Library; National Library of Scotland; National Library of Wales; Bodleian  
Library, Oxford; University Library, Cambridge and the Library of Trinity College, Dublin)*

## The taxonomics of the lithe basal eutyranosaurus genera and species of late Maastrichtian western North America

LSID urn:lsid:zoobank.org:pub:85414D6C-544C-48CC-8E60-CF65B34F9CA8

Franco Sancarlo<sup>1</sup> and Gregory S. Paul<sup>2</sup>

<sup>1</sup> Via Carlo Alberto dalla Chiesa 8, San Giovanni Rotondo, 71013, Italia.

[franco.sancarlo.sgr@gmail.com](mailto:franco.sancarlo.sgr@gmail.com);

<https://orcid.org/0009-0009-9285-9755>

<sup>2</sup> 3100 St Paul St. 604, Baltimore MD, 21218, USA.

[GSP1954@aol.com](mailto:GSP1954@aol.com);

<https://orcid.org/0000-0002-4493-6092>

### ABSTRACT

In 1946 Gilmore observed that the Hell Creek Formation component of the larger TT-zone of the late Maastrichtian contained more tyrannosaur taxa than just titanic *Tyrannosaurus rex*, based on a small, ontogenetically mature skull with a higher tooth count than the tyrant lizard. Over four decades later the skull was assigned to its own genus, *Nanotyrannus lancensis*. Also tagged shortly after was the taxon *Stygivenator molnari*. At the last turn of the century it was contended that all TT-zone tyrannosaurs are adult or juvenile *T. rex*, a view that became accepted by many. Because of the unusual morphological alterations that this hypothesis requires, it was consequently proposed that during ontogeny *T. rex* experienced a peculiar fish like metamorphosis. This conservative analysis rejects radical ontogenetic speculations, in favour of *Tyrannosaurus* having shared much the same, usual amniote/diapsid conventional growth observed in its fellow tyrannosaurids and especially tyrannosaurins. Actual juvenile *Tyrannosaurus* specimens show the same tooth count and other osteological features observed in the adults, negating the need for the metamorphosis that is not observed in any amniotes; this option has become widely accepted. The most extensive tyrannosaur phylogenetic analysis to date confirms that the comparative anatomical analysis that most TT-zone mini tyrannosaurs possess a number of features that indicate they are not only not *Tyrannosaurus*, but represent an array of basal eutyranosaurus taxa that are neither *Nanotyrannus* nor *Stygivenator*, with high tooth counts, and at least in some examples elongated hands, prominent dentary grooves and other features. Two new taxa are correspondingly named at the species and/or genus-level, *Gilmoretyrannus lethaeus* and *Larsonvenator elegans*. These are postulated to represent at least in part the migration of basal eutyranosaurs from former Appalachia into the Laramidia region via the new Laralachia land bridge. The total number of tyrannosaur taxa now known to have inhabited the TT-zone for over 1 MA is seven species in five genera from multiple subfamilies, with a smaller portion of this collection extant at any given stratigraphic level.

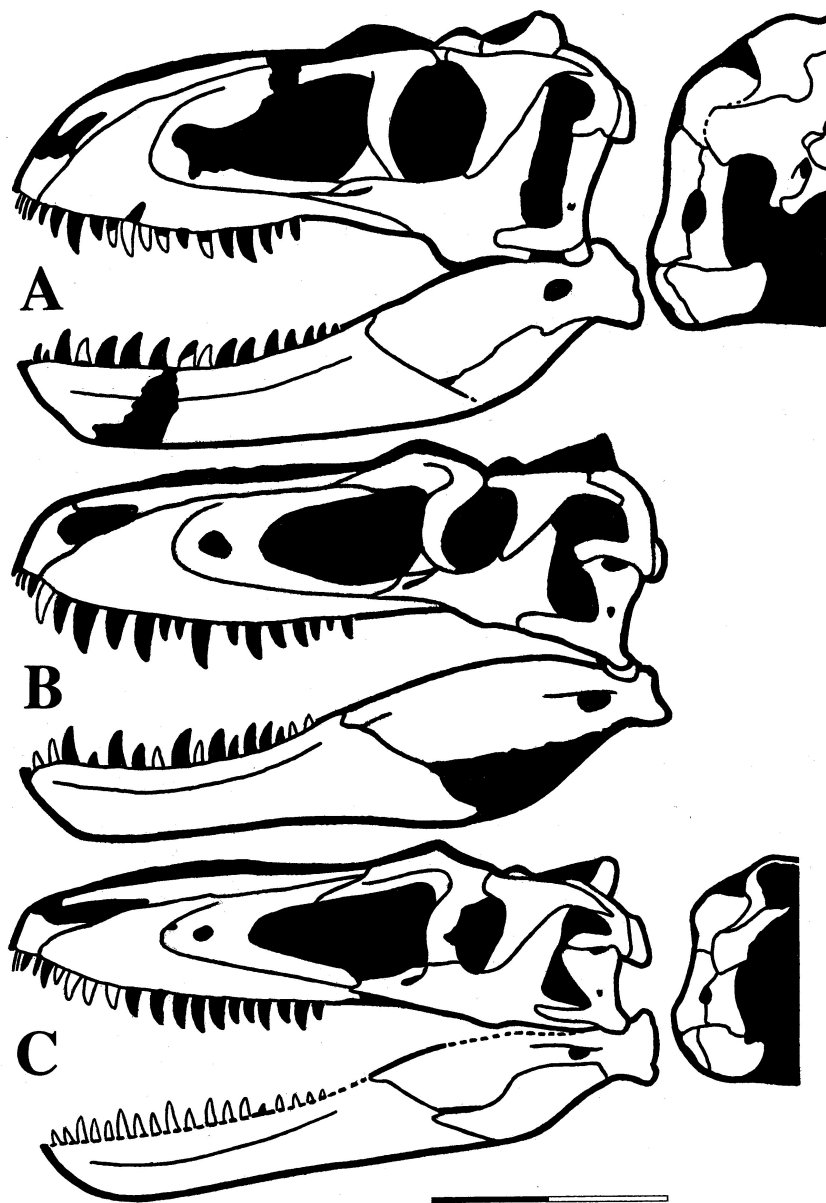
**Key words:** Dinosauria, Theropoda, tyrannosaur, *Tyrannosaurus*, *Nanotyrannus*, *Stygivenator*, Cretaceous, Laramidia.

### INTRODUCTION

The following is a brief overview of publications on the subject focusing on highlights pertinent to this analysis. Found in the latest Maastrichtian Hell Creek Formation, the gigantic avaped theropod *Tyrannosaurus rex*, then represented mainly by two semi-complete skulls and skeletons, was recognized after the prior turn of the century (Osborn 1905, 1906). During World War 2 another, much smaller tyrannosaur skull with a higher number of maxillary teeth, was found in the same formation (Figs. 1A, 2, 3H). Using standard comparative anatomy, Gilmore (1946) recognized that



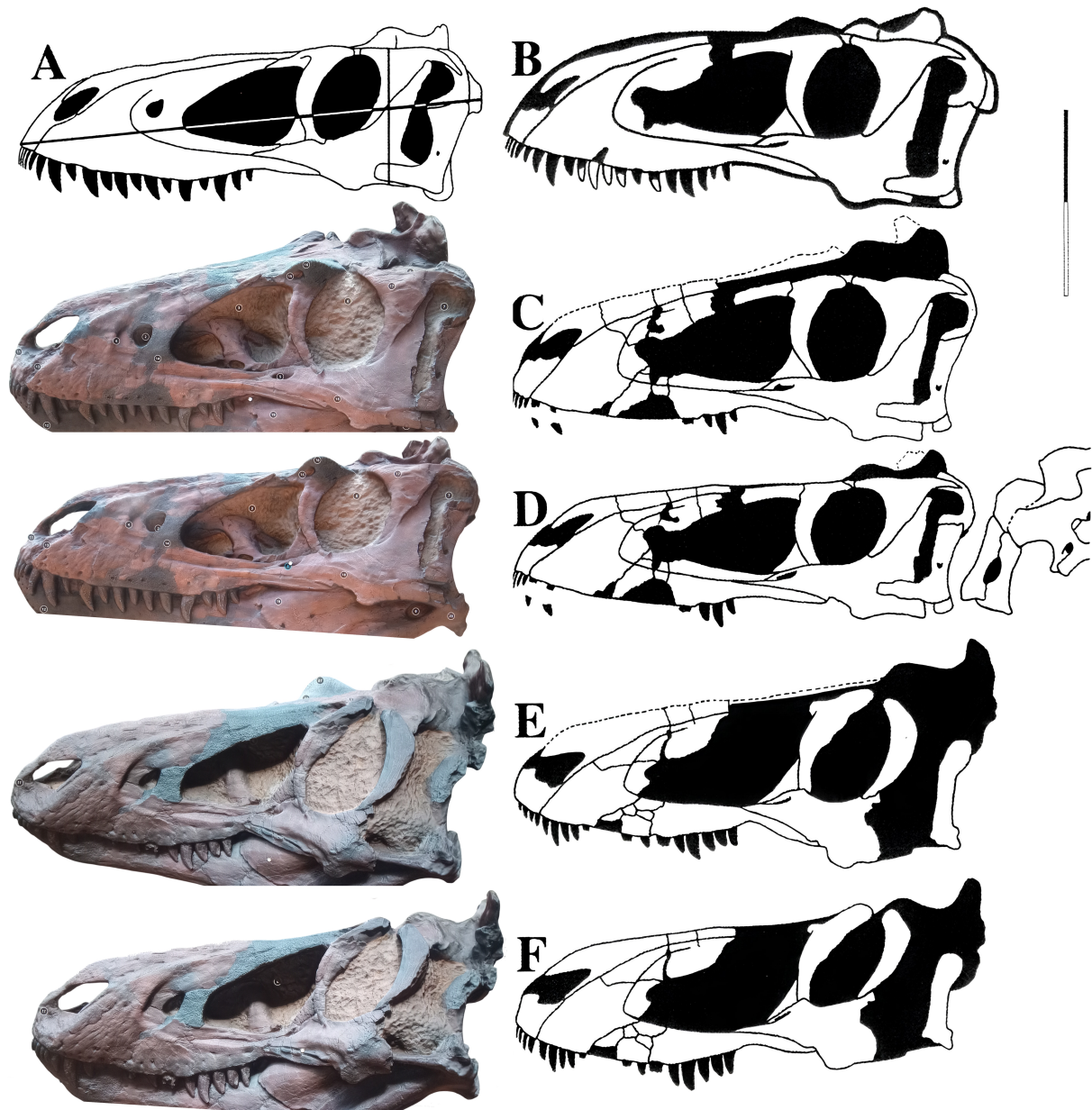
CMNH 7541 was a distinct taxon that he assigned to *Gorgosaurus lancensis*, effectively establishing the multiple tyrannosaur taxa hypothesis (MTTH) for TT-zone (sensu Paul *et al.*, 2022, Paul 2025a: includes Hell Creek, Lance, Denver, Ferris, Frenchmen, Scollard and Willow Creek Formations) tyrannosaurs, a view supported by Paul (1988). The same year Bakker *et al.* (1988) described CMNH 7541 as a new genus, *Nanotyrannus lancensis*, Larson (2008) concurred with the validity of the taxon. A detailed redescription of CMNH 7541 was skeptical of it being a *Tyrannosaurus* juvenile (Witmer & Ridgely 2010), in part because its tooth count is too high for it to be in the latter genus.



**FIGURE 1.** Known-bone profile-skulls of TT-zone baso-eutyranosaur holotypes in lateral and posterior views to approximate same scale, bar equals 250 mm. **A** *Nanotyrannus lancensis* CMNH 7541 holotype (see Fig. 2) adult, ~650 mm, lacrimal hornlet and anterior rami of squamosal-quadratojugal not preserved); **B** *Gilmoretyrannus lethaeus* BMRP 2002.4.1 holotype (subadult, ~685); **C** *Larsonvenator elegans* NCSM 40000 holotype (near adult, ~660).

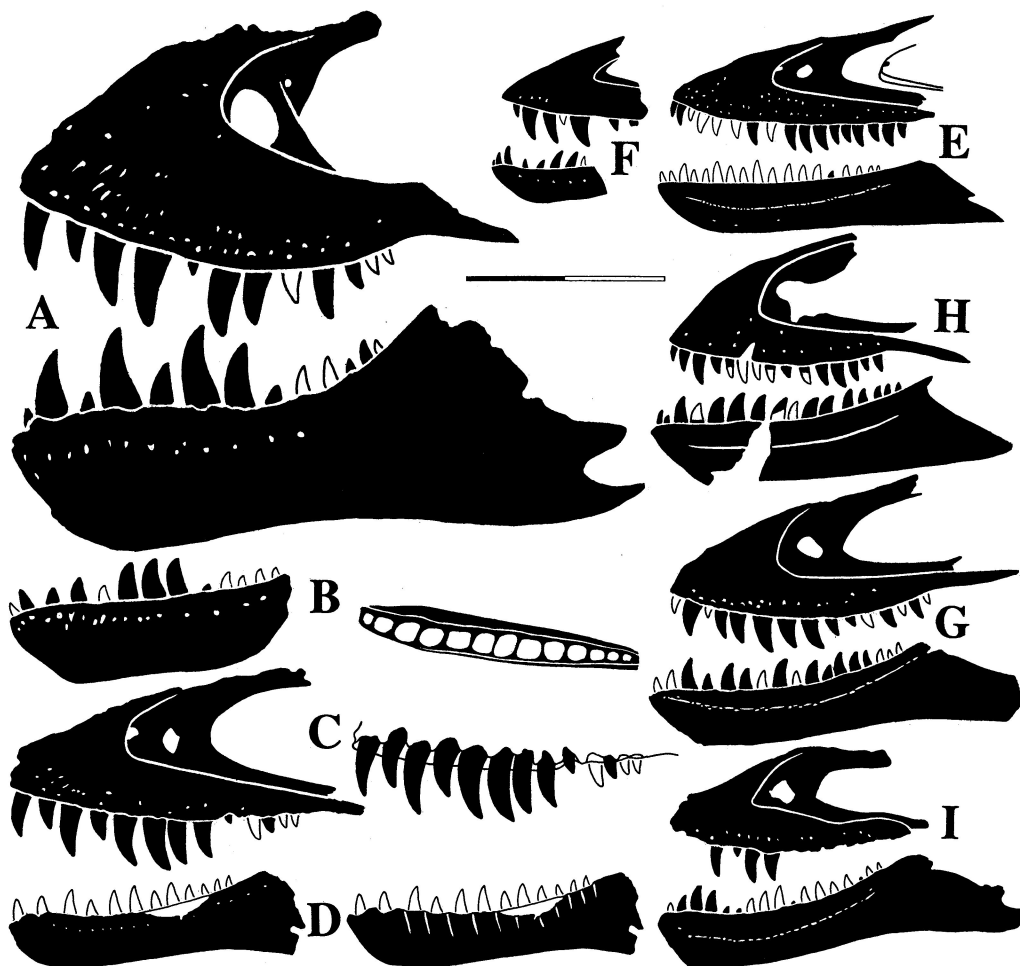
A broadly similar sized partial cranium from the Hell Creek (Fig. 3F; Molnar 1978), LACM 28471, was rendered *Aublysodon molnari* (Paul 1988; supported by Molnar & Carpenter 1989) and then

*Stygivenator molnari* (Olshevsky *et al.* 1995) – these were the first works to further increase the apparent diversity of TT-zone lesser sized (femur ~900 mm or less, ~ 2 tonnes or less) tyrannosaurs. Currie (2003a) continued to support the MTTH. Larson (2013a) argued that fairly complete, slender proportioned, many toothed BRMP 2002.4.1 (Figs. 1B, 3G, 4D) is a *Nanotyrannus lancensis* also of about the same size. That year, Larson (2013b) critically demonstrated that new Hell Creek and Lance Formation specimens, including the virtually complete, many toothed skull and skeleton NCSM 40000 of similar dimensions to the others (Figs. 1C, 3E, 4C, 7C), sports a manus as a long or longer than those of adult *Tyrannosaurus* (Fig. 5D,E), further effectively precluding their being juveniles of the latter.



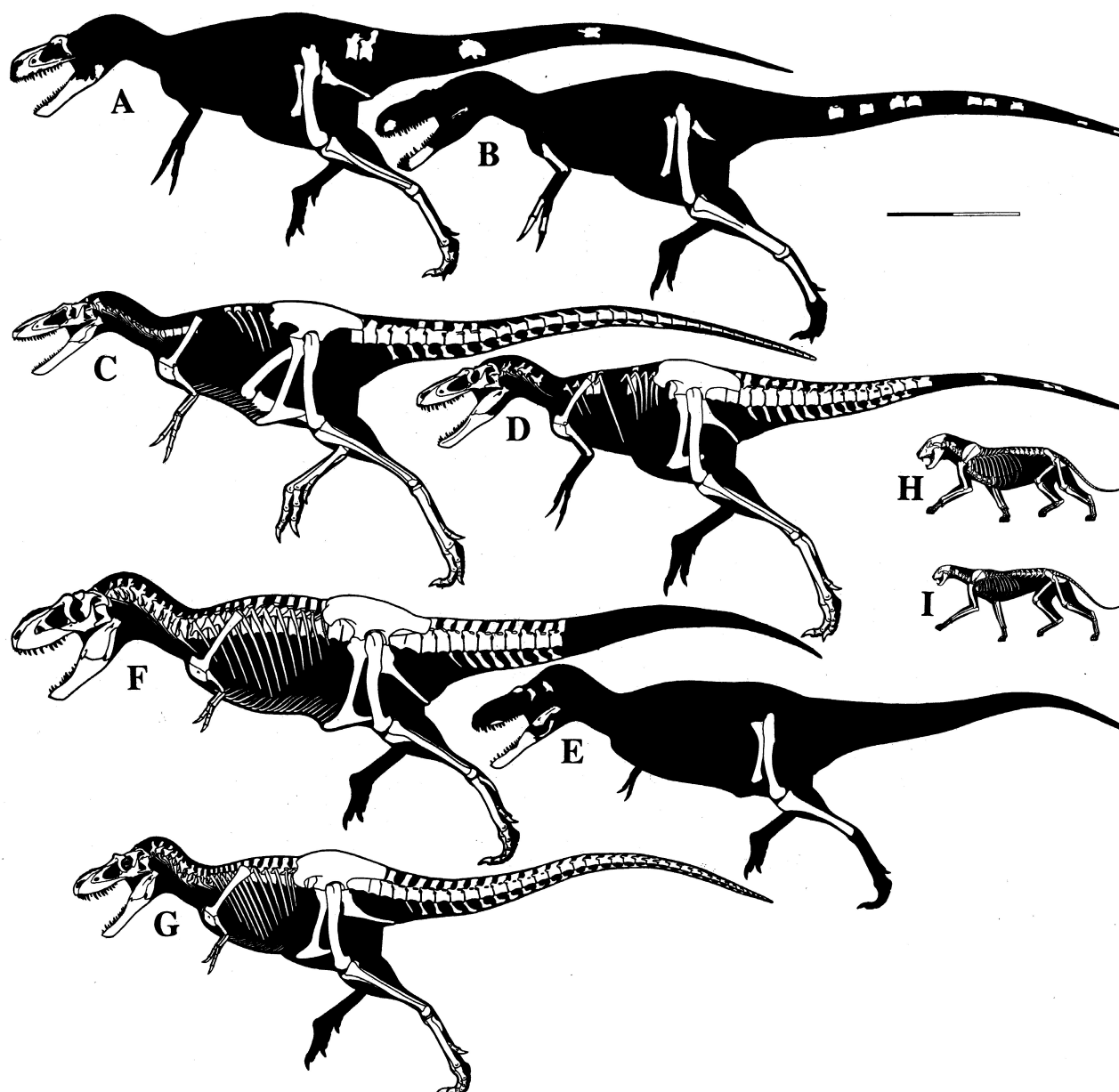
**FIGURE 2.** Images of *Nanotyrannus lancensis* holotype CMNH 7541 cranium to same scale, bar equals 250 mm. **A** Bakker *et al.* (1988) restoration with skull top perpendicular to viewer as per **D**, general height/length measurement dimensions indicated, H/L 0.29. **B** Known bone profile-skull restoration showing actual skull depth based primarily on **C**, H/L ~0.32. **C-F** scans (screen shots from Rogez 2021) on left, as preserved direct tracings on right with plaster lacrimal hornlets omitted and with missing bone in solid black, and breakage indicated (after scans in Fig. 4B,C in Witmer & Ridgely 2010), **C** & **D** left side, **E** & **F** right side reversed, **C** & **E** with sides of skull flat on to viewer to show actual depth of sides, **D** & **F** with skull top perpendicular to viewer, **D** includes posterior view (after Fig. 3B in Witmer & Ridgely 2010).

Schmerge & Rothschild (2016a,b) supported the placement of CMNH 7541 and BRMP 2002.4.1 outside *Tyrannosaurus* due to their possession of a prominent lateral dentary groove absent from adult and juveniles of the tyrant lizard (Fig. 3), the latter including Baby Bob. Jevnikar & Zanno (2021) observed that the growth of BRMP 2006.4.4 does not conform with it being a juvenile *Tyrannosaurus*, and Griffin *et al.* (2025) finding that CMNH 7541 is an adult.



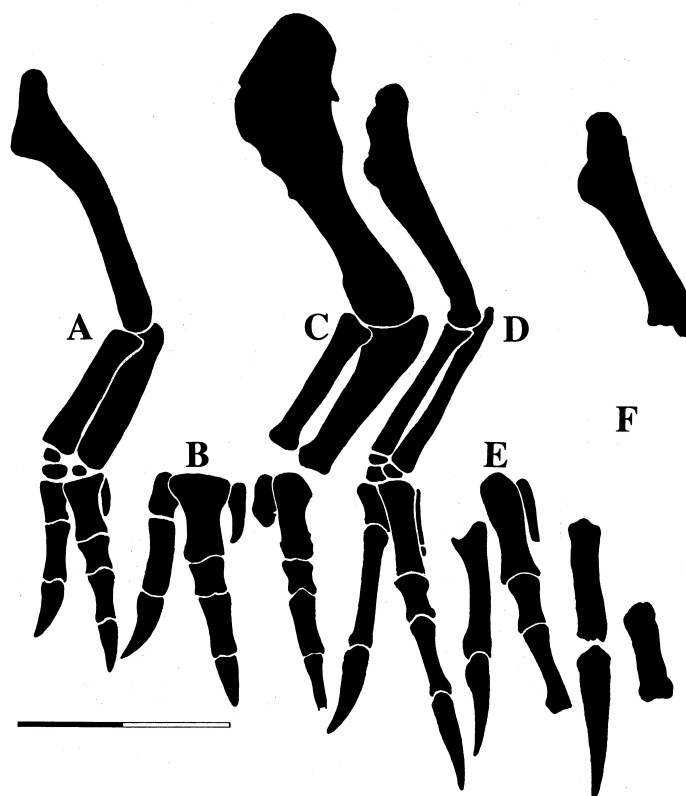
**FIGURE 3.** Known-bone profiles of TT-zone eutyranosaur maxillae and dentaries to same approximate scale, bar equals 200 mm, dimensions for E are approximate (derived in part from Fig. 8 in Paul 2025a with additions and/or alterations to B and D). Maxilla and/or dentary in left view (some reversed, some combined from both sides), known tooth positions lacking teeth or not visible by eye or published scans indicated by tooth outlines: **A**, *Tyrannosaurus rex* CMNH 9380 holotype (adult, 6.5 tonnes); **B** *Tyrannosaurus incertae sedis* BHI 6439 (juvenile, ~1, dorsal view of alveoli); **C** *Tyrannosaurus imperator?* KU 156375 (juvenile, ~800 kg); **D** *Tyrannosaurus incertae sedis* Baby Bob (juvenile, ~500, medial view of tooth sulci). Baso-eutyranosaurus: **E** *Larsonvenator elegans* NCSM 40000 holotype (near adult, ~600); **F** *Stygivenator molnari* LACM 28471 holotype (subadult? ~400); **G** *Gilmoretyrannus* BMRP 2002.4.1 holotype (subadult, 570); **H** *Nanotyrannus lancensis* holotype CMNH 7541 (adult, ~450); **I** *Gilmoretyrannus incertae sedis*, HRS 08 (subadult, ~450).

Extensive analyses by Longrich & Saitta (2024) and Paul (2025a, also 2024b) detailed reasons that most small-bodied TT-zone tyrannosaurs are not juvenile *Tyrannosaurus*, while a minority are. Those studies were the first to reveal that the non-*Tyrannosaurus* specimens preserve a taxonomically diverse set of non-tyrannosaurid baso-eutyranosaurus (eutyranosaurus with or likely to have had long forelimbs, excluding tyrannosaurids [and aliormanians], modified from Paul 2025a), and indicated some were outside *Nanotyrannus*.



**FIGURE 4.** Known/visible-bone profile-skeletals of predators to same scale, bar equals 1 m. **A** *Appalachiosaurus montgomeriensis* holotype RMM 6670 (femur length 786 mm, ~700 kg); **B** *Dryptosaurus aquilunguis* holotype ANSP 9995 (780, ~700); **C** *Larsonvenator elegans* holotype NCSM 40000 (near adult, 717, ~600); **D** *Gilmoretyrannus lethaeus* holotype BMRP 2002.4.1 (subadult, ~720, ~570) with lower forelimb proportions extrapolated from those of other baso-eutyrannosaurs with similarly long humeri; **E** *Tyrannosaurus incertae sedis* Baby Bob (juvenile, 645, ~670); **F** *Tarbosaurus* MgD-1/3 (juvenile, 700 mm, 850); **G** *Gorgosaurus libratus* TMP 1991.36.5000 (juvenile, 645, 590); **H** pantherine felid *Panthera* (immature, 30); **I** feline felid *Acinonyx* (immature, 20).

Paul (2024b, and formally in 2025a) was the first to diagnose NCSM 40000 outside that genus, and as a possible new genus. Paul (2024b, 2025a) further proposed that the exceptional diversity of TT-zone tyrannosaurs was due at least in part to a paleogeographically novel influx of long-handed baso-eutyrannosaurs from eastern North America over the just emerged Laralachia bridge that had reunited the long split continent. Later in 2025 Zanno & Napoli further demonstrated that CMNH 7541, BMRP 2002.4.1, NCMS 40000 and other specimens are basal eutyrannosaurs, concentrated in species of *Nanotyrannus* whose predecessors probably moved in from Appalachia.



**FIGURE 5.** Known-bone profiles of TT-zone tyrannosaurin and baso-eutyrranosaur forelimbs to same scale, bar equals 250 mm (modified from Fig. 9 in Paul 2025a except for **D**). **A** *Tyrannosaurus incertae sedis*, UCRC V1 (subadult); **B** *Tyrannosaurus regina*, MOR 980 (adult); **C** *Tyrannosaurus imperator* holotype FMNH PR 2081 (adult; placement of distal elements not certain); **D** *Larsonvenator elegans* holotype NCSM 40000 (subadult); **E** *Larsonvenator elegans?* Jodi (adult?); **F** *Dryptosaurus aquilunguis* holotype ANSP 9995 (placement of one distal element not certain).

The results of Raun *et al.* (2025a) imply that the growth of *Tarbosaurus* favours the MTTH. That more than one tyrannosaur taxon can share the same habitat, sometimes both gigantic, other cases very disparate in size, has been established (Russell 1970; Currie 2003a; Kurzanov 1976; Brusatte *et al.* 2009; Paul 2010, 2016, 2024a,b; Lu *et al.* 2014; Mo & Xing 2015; Brusatte & Carr 2016; Carr 2022; Zheng *et al.* 2024).

Paul (2016, 2024a,b, 2025a,b), Paul *et al.* (2022) and Longrich & Saitta (2024 tentatively) split mature *Tyrannosaurus rex* itself into multiple intragenera sibling species, adding *T. imperator* and *T. regina* (compare wider variation in *Tyrannosaurus* skulls compared to in other speciose tyrannosaurid genera, Figs. 6, 8). Zanno & Napoli (2025) offered that the basic premise may be correct. That gigantic *Tarbosaurus* appears to contain sibling species (Raun *et al.* 2025b) adds support for the MTTH.

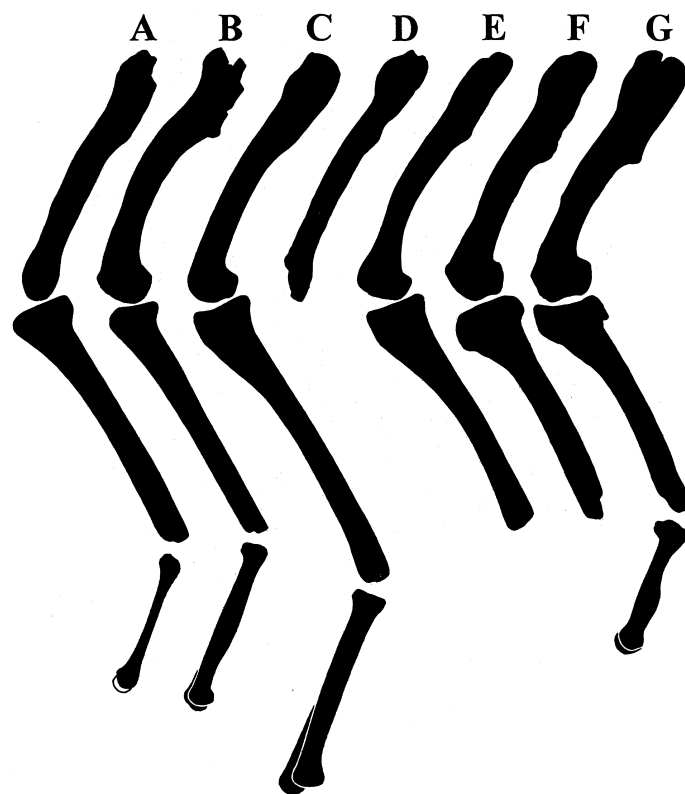
The fossil growth series of *Tarbosaurus* fossils (Fig. 6A-H; also see Paul 2024a,b skeletal illustrated entries on the taxon) inspired Rozhdestvensky (1965) to suggest that CMNH 7541 may have been a juvenile *Tyrannosaurus* in a one sentence portion of a footnote that lacks any analysis. Had the inconsistent tooth counts between the American mini tyrannosaur and the tyrant lizard been contrasted with the steadier tooth numbers in the Asian terror lizard been noted and used to dismiss *N. lancensis* as a juvenile, then the ETRH may have never arisen. Carpenter (1992) further speculated that *Nanotyrannus* (Figs. 1-3, 9) is a juvenile *T. rex* (Figs 3, 4, 9, 10) again without regard to the former's high number of teeth. In 1999 Carr established the modern everything is *T. rex* hypothesis (ETRH). It was based in part on an incorrect claim of tooth reduction in growing *Gorgosaurus libratus*. Despite that error being quickly corrected by Currie (2003a,b), studies

focused directly on the ontogenetic segment of the ETRH that support the thesis include Carr & Williamson (2004), Brusatte & Carr (2016), Brusatte *et al.* (2016), Woodward *et al.* (2020), Voris *et al.* (2025), culminating in an extensive study by Carr (2020).



**FIGURE 6.** Known-bone profile-skulls of Nemegt complex tyrannosaurs to same scale, bar equals 1 m (from Fig. 2 in Paul 2025a except for I which is from Paul, 2024a,b). Some skulls reversed, and/or both sides used to complete restoration. *Tarbosaurus* ontogenetic series: **A** PIN 551-1 (mature, ~4.5 t); **B** MgD-1/4 (mature, ~3.5); **C** PIN 551-3 (immature, 2.5); **D** PIN 553-1 (juvenile, ~1.5); **E** MgD-1/3 (juvenile, 850 kg); **F** PIN 552-2 (juvenile, 600); **G** LHP V18 (*Raptorex kriegsteini* holotype) (juvenile, 75); **H** MPC-D107/7 (juvenile, ~75); **I** *Alioramus* MPC-D 100/1844 holotype (subadult, ~250).

Faced with the problems posed by the exceptionally radical ontogenetic changes in *T. rex* required if all the highly anatomically diverse TT-zone lesser tyrannosaur fossils are included in one taxon as he assumed in the paper (as noted by Paul 2022), Carr (2020) engaged in the speculation that the species experienced a sudden ontogenetic metamorphosis that would be unique among known amniotes. This recently devised version of the ETRH was often presented as the widely accepted modern paradigm that therefore requires refutation to lose its privileged status, the above citations show that the number of researchers who presented studies that concentrate on the TT-zone data regarding the ETRH versus the MTTH was actually broadly similar. In any case, in the combined data and analysis wake of Longrich and Saitta (2024), Paul (2025a) and then Zanno & Napoli (2025) and Griffin *et al.* (2026), it appears that the full blown ETRH no longer has publicly confirmed absolutist adherents, varying forms of the MTTH now being operative. This includes Carr in Hernandez-Luna *et al.* (2026). Woodward *et al.* (2026) took a relatively neutral stance on the issue. The inherently rigid ETRH had been effectively discouraging research into TT-zone tyrannosaur diversity – which is why the first paper to take a large data set based look at the question of mature *Tyrannosaurus* species was Paul *et al.* (2022) followed by Paul (2025a) -- the MTTH does the opposite. So the ascendancy of the latter hypothesis has opened to field to innovative, cutting edge research on the issues with a vigor not see before. It is not just *T. rex* anymore.



**FIGURE 7.** Known-bone profiles of late Campanian to late Maastrichtian Appalachia and TT-zone eutyrranosaur hindlimbs reproduced to same femur length to facilitate visual comparisons of femoral shaft curvatures and element length ratios. **A** *Dryptosaurus aquilunguis* holotype ANSP 9995 (femur 780 mm long, tibia 760 mm, metatarsus ~410); **B** *Appalachiosaurus montgomeriensis* holotype RMM 6670 (786, 762, ~480); **C** *Larsonvenator elegans* holotype NCSM 40000 (near adult, 717, 820, 560); **D** *Gilmoretyrannus lethaeus?* BMRP 2006.4.4 (774); **E** *Tyrannosaurus incertae sedis* Baby Bob (juvenile, 645, 605); **F** *Tyrannosaurus incertae sedis* USNM 6183 (subadult, 990, 885); **G** *Tyrannosaurus imperator* holotype FMNH PR208 (adult, 1321, 1143, 671).

Paul (2025a) provisionally placed BMRP 2002.4.1, NCSM 40000 and other TT-zone specimens in the previously named genera *Nanotyrannus* and *Stygivenator*. Zanno and Napoli. (2025) considered only *Nanotyrannus* to be viable and sank *Stygivenator* which was not analyzed separately, while including in the prior genus the closely related new intragenus sibling species *N. lethaeus*. This was accepted in Hernandez-Luna *et al.* (2026). Longrich *et al.* (2026a), reinstated *Stygivenator molnari*, and offered the new combination *Stygivenator lethaeus*. Fresh hatched juvenile *Tyrannosaurus* remains described by Longrich *et al.* (2026b) confirmed that juveniles of the tyrannosaurid were distinctive from contemporary baso-eutyrranosaur. Initiated by the senior author to test the resulting questions, this review paper – no new specimens are introduced -- focuses on determining whether or not the mini tyrannosaurs of the TT-zone are all juvenile *T. rex*, if not how many taxa the non-*Tyrannosaurus* specimens represent, examine if they are the same taxa as late Cretaceous tyrannosaurs from Appalachia, and if any can be diagnosed on phylogenetic and gradistic grounds sufficient to confirm old or require new generic and/or specific titles. By doing so, the diversity of the resident fauna can be better determined. Related items involving the origins and diversity of the TT-zone dinosaur predators are considered. This is achieved by presenting and then parsimoniously following the critical aspects of actual, ordinary, observed amniote-diapsid-tyrannosaur-tyrannosaurin ontogeny, rather than more speculative hypotheses. This sets the needed conventional standards for addressing the problem moving forward. The largest tyrannosaur character matrix phylogenetic analysis to date is conducted (Figs 11-14). Some aspects of speciation in mature

*Tyrannosaurus* are touched upon, but this is not a major subject herein and persons are referred to Paul (2025a) for an extensive examination of that subject.

AMNH, American Museum of Natural History, New York; ANSP, The Academy of Natural Sciences, Philadelphia; BDM, Badlands Dinosaur Museum, Dickinson; BHI, Black Hills Institute, Hill City; BRMP, Burpee Museum of Natural History, Rockford; CMN, Canadian Museum of Nature, Ottawa; CMNH, Cleveland Museum of Natural History, Cleveland; DINO, Dinosaur National Monument, Vernal; DDM, Dinosaur Discovery Museum, Kenosha; DMNS, Denver Museum of Nature and Science, Denver; FMNH, Field Museum of Natural History, Chicago; HRS, Hanson Research Station, Newcastle; KU, Kansas University, Lawrence; LACM, Los Angeles County Museum, Los Angeles; MOR, Museum of the Rockies, Bozeman; MPC, Mongolian Palaeontological Center, Ulaanbaatar; NCSM, North Carolina Museum of Natural Sciences, Raleigh; NHMAD, Natural History Museum Abu Dhabi, Dubai; PIN, Palaeontological Institute, Moscow; RMM, Red Mountain Museum, Birmingham; RSM, Royal Saskatchewan Museum, Regina; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller; UCMP, University of California Museum of Palaeontology, Berkeley; UCRC, University of Chicago Research Collection, Chicago; USNM, National Museum of Natural History, Smithsonian, Washington DC.

## MATERIAL AND METHODS

### Issues and discourse addressed versus referenced

This analysis is not a comprehensive review of all intricate aspects of the subjects covered. It is intended to address specific issues. As such detailed discussions of many issues that have been addressed in-depth elsewhere of late (as per Paul *et al.* 2022; Longrich and Saitta 2024; Paul 2025a; Zanno & Napoli 2025) are not repeated, the prior analyses being cited when they pertain.

### Phylogenetics

A total of 753 characters and 42 taxa were used in this study (see Phylogenetic Cladograms and Character Matrix below). In order to focus on relationships within the tyrannosauroids, the large nontyrannosauroid *Allosaurus* is used as the outgroup. Of the characters, 394 are derived from Voris *et al.* (2020, 1–394), with modifications applied to characters 31, 261, 263, and 369; 199 from Dalman *et al.* (2024, 395–594), with a modification applied to character 240; 135 from Zanno & Napoli (2025, 595–728), with modifications applied to characters 237 and 290; and 15 from Larson (2013b, 729–743), while an additional 11 new derived characters are proposed below (744–753), some of which are from Paul *et al.* 2022 and Paul 2025a, including characters assigned to three TT-zone species – some character states are partly overlapping as per other species such as those of *Triceratops* (Paul 2025a). A number of the characters are used to help diagnose the systematics of the groups and species. In order to not prejudice their taxonomic placements, CMNH 7541, BM BMRP 2002.4.1 HRS 08, LACM 28471 and NCMS 40000 are scored separately. The analyses were conducted using TNT version 1.6 (Goloboff & Morales, 2023) using the New Technology search and Traditional Search, with the trees graphically refined using Mesquite version 4.03 (Maddison & Maddison, 2026), (Figs. 11–14). Subsequently, six analyses were performed on TNT using maximum parsimony according to the Guoyi script (Zhang, 2025) with extended implied weighting, equal weighting, 4 with implied weighting at  $k = 3, 6, 12, 24$ . The results were finally refined in WinClada version 1.00.08 (Nixon, 2002). Finally, a Bayesian analysis was performed using the program MrBayes version 3.2.7a (Ronquist *et al.*, 2012), the results of which were subsequently graphically refined using Mesquite.

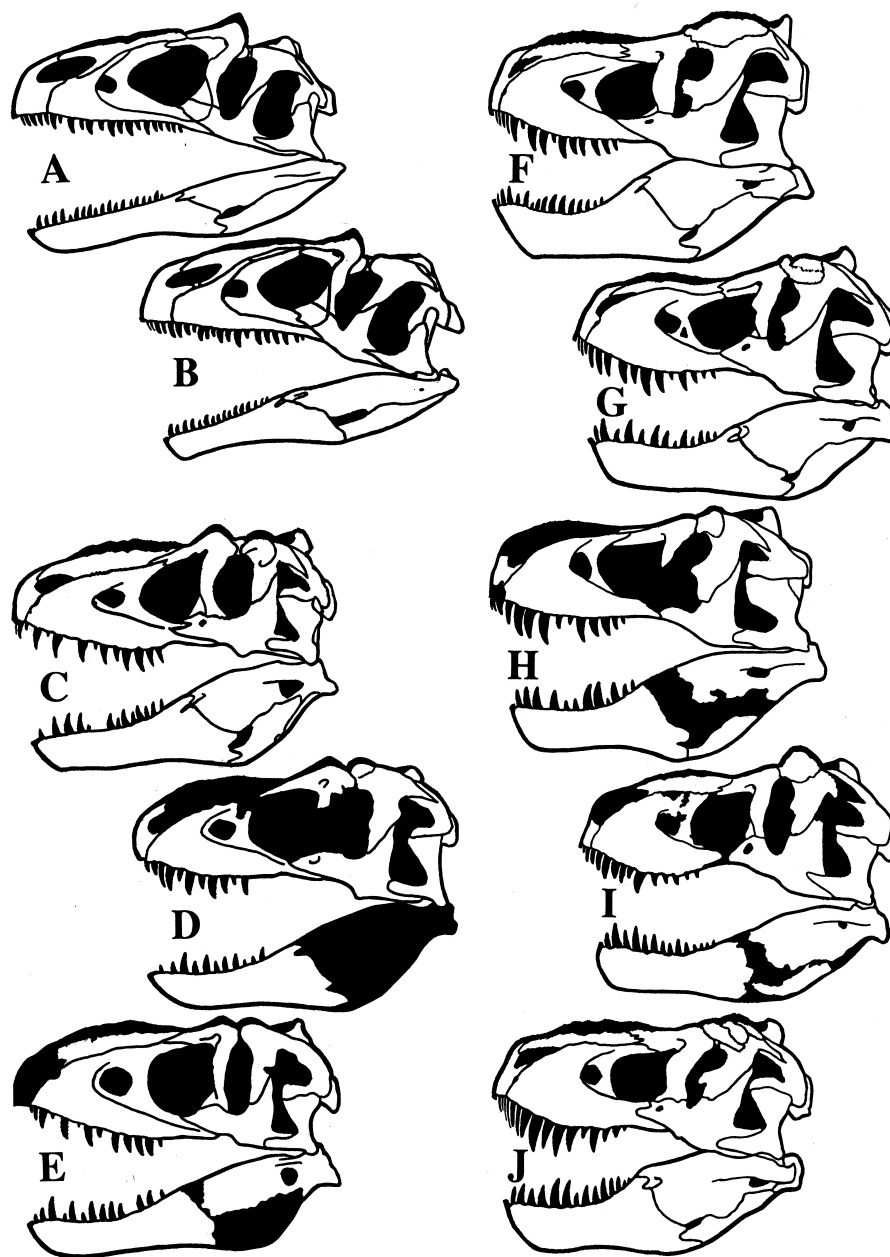


Due to substantial data gaps in the TT-zone baso-eutyrannosaur fossils the results are somewhat tenuous in terms of their intrarelationships, and relative to the Appalachian baso-eutyrannosaurs. The phylogenetic results need to be supplemented by other aspects of their form and function.

### Critical diagnoses factors

With taxonomy being a combination of clade plus grade, the latter plays a key role in taxonomic determinations when diagnosing genera and species (Mihlbacher 2008; Carpenter 2010; Mader 2010; Knutsen 2012; Carr *et al.* 2017; Chure & Loewen 2020; Johnson *et al.* 2020; Larramendi *et al.* 2020; Paul *et al.* 2022; Danison *et al.* 2024; Sanchez-Fenollosa *et al.* 2024; Paul 2025a,b). Grade differences are the result of the functional differences that help assess higher level taxonomic distances between species. If two species consistently cladistically score and phylogenetically position as sibling taxa, that does not automatically mean they are in the same genus. Grade criteria expressed as diagnoses also apply, as does the probability of ghost taxa between them due to the gaps in the fossil record. For example, within equids *Plesippus* and *Equus* are close generic relatives to one another (Barrón-Ortiz *et al.* 2019), but are distinguishable from each other at the genus level on gradistic grounds. Within each genus are sibling species that are diagnosable despite being very close relations that in some cases inhabit the same habitats. Similar situations apply in other cases, such as the rhinocerotids *Diceros bicornis* and *Ceratotherium simum* (Liu *et al.* 2021). It is becoming increasingly apparent that intragenera species are more common than had been realized: *Loxodonta* now includes two species (Grubb *et al.* 2000), *Giraffa* four (IUCN 2025), small *Canis* are increasingly speciose (Koepfli *et al.* 2015). The probability that this cryptic species factor applies to fossil taxa, tyrannosaurids included, is being increasingly recognized of late (Paul *et al.* 2022; Napoli *et al.* 2023; Longrich & Saitta 2024; Stock *et al.* 2024; Griffin *et al.* 2025; Paul 2025a, Zanno & Napoli 2025; Raun *et al.* 2025b). Within eutyrannosaurs being sibling taxa in mini-clades does not necessarily demand they be a united genus if gradistic differentiation is deemed sufficient, as per *Alioramus* and *Qianzhousaurus*, *Bistahieversor* and *Jinbeisaurus* and, *Albertosaurus* and *Gorgosaurus*, and *Teratophoneus* and *Lythronax* (Figs 11-14; Brusatte & Carr 2016; Dalman *et al.* 2024; Longrich & Saitta 2024; Voris *et al.* 2025; Zanno & Napoli 2025).

Assessing generic and specific status is not just a matter of scoring characters. It is also one of holistic visual comparative anatomy (Paul 2025a). For instance, Voris *et al.* (2025) cited the presence of one attribute on one TT-zone *Tyrannosaurus* dentary, MOR 008, as negating the placement of “*T.*” *mcraeensis* outside the former taxon. Aside from the MOR 008 dentary being too damaged to determine the bone’s shape (Paul 2025a), the “*T.*” *mcraeensis* element is so distinctive in overall form from those of TT-zone fossils (Fig. 4C in Dalman *et al.* 2024) that it is clearly a distinct, probably more basal, taxon. More generally, in this analysis the degree of difference in overall shape and morphological profiles and proportions of individual superficial bones in the adult crania of accepted avetheropod genera, including those that are multispecific (Fig. 8), are compared to the total anatomical configurations of TT-zone non-*Tyrannosaurus* mature skulls (Fig. 1). This follows the practical procedure whereby visual anatomical comparisons are used to help distinguish taxa, as per bird watching (Peterson, 1934). Likewise, local native animal identification is usually in good accord with Linnean determinations (Paul 2025a and references therein). In standard taxonomic principle gradistic variation within each of a set of genera, especially when closely related, needs to be about the same. *Tyrannosaurus* contains at least as much osteological variability as multispecific *Daspletosaurus* (Fig. 8C-E versus F-J) because the former is at least as multispecific. Ergo, if differentiation in the TT-zone baso-eutyrannosaur skulls exceeds that observed within the other avetheropod genera, then the former represent multiple genera. If not, then they are not different genera.



**FIGURE 8.** Known-bone profile-skulls of avetheropod avepod adults or close to it, reproduced to same length to facilitate intra and inter genera visual comparisons from Paul (2024b, 2025a, see Fig. 2B,D,E,G,I in latter reference for same scale reproductions of F-J, as well as additional *Tyrannosaurus* skulls). **A** *Allosaurus jimmadseni* holotype DINO 11541; **B** *Allosaurus fragilis* DINO 2560; **C** *Daspletosaurus torosus* holotype CMN 8506; **D** *Daspletosaurus wilsoni* (or *horneri*) holotype BDM 107; **E** *Daspletosaurus horneri* holotype MOR 590; **F** *Tyrannosaurus imperator* holotype FMNH PR208; **G** *Tyrannosaurus regina* NHMAD 2020.00001; **H** *Tyrannosaurus regina* LACM 150167; **I** *Tyrannosaurus rex* RSM2523.8; **J** *Tyrannosaurus incertae sedis* AMNH 5027.

### The time and niche factors

Evidence has grown that dinosaur species were prone to turning over rapidly, with species typically not lasting more than a few hundreds of thousands of years (Paul 2010, 2016, 2024a,b; 2025a,b; Scannella *et al.* 2014; Fowler 2017; Mallon 2017; Chure and Loewen 2020; Paul *et al.* 2022; Danison *et al.* 2024; Holmes *et al.* 2026). The same works also often found that large predators can

exhibit considerable diversity at the same level in a particular formation, with the multiplicity often increasing with decreasing size. A factor in the fast and diverse evolution of dinosaur taxa may have a genetic basis due to high chromosome numbers that are still present in the species prolific birds (O'Connor *et al.* 2018). The rapid, r-strategy reproduction of giant avepods depositing large numbers of rather small eggs may have also favoured swift evolution and diversification. It is therefore presumed herein that if fossils are separated by more than a few hundred thousand years that they are probably different species, unless strong comparative anatomical evidence indicates otherwise. The latter includes near identical morphology of overlapping elements. Nor can it be presumed that incomplete specimens found at the same stratigraphic level of a formation from a given family or superfamily are those of one species—unless found in very close association without duplications -- rather than being from more than one taxon on niche exclusion grounds. The situation needs to be tested via the degree of anatomical variation that is extant within the ancient habitat; if it is too extensive to be accommodated by one or two species or genera, then a higher taxonomic count is viable and may be required. Observed anatomical variation establishes taxonomic diversity, not expectations of niche availability. Consisting of multiple species, genera can last over long stratigraphic periods. In western North America the probable presence of a small tyrannosaur taxon was demonstrated some time ago (Lehman & Wick 2012). The possibility that a substantial number of cryptic tyrannosaur species existed in their formations, and are preserved among the fossils collected from the sediments, is very substantial (Paul *et al.* 2022, Longrich and Saitta, 2024; Stock *et al.* 2024; Griffin *et al.* 2025; Paul 2025a; Zanno & Napoli 2025; Raun *et al.* 2025b). TT-zone sediment deposition lasted over 1 Ma, stratigraphic levels of the specimens under consideration when known and not are from Paul *et al.* (2022), Paul (2025a), Zanno & Napoli (2025) and Roberts *et al.* (2026) -- examination of the LACM 28471 collection records did not provide adequate information pertaining to its level, that will require large scale stratigraphic work on private property that may not be currently possible.

### Critical emphasis on actual amniote ontogenetic biology

The comparative anatomy is combined with basic ontogenetic norms and principles to produce a parsimonious null hypothesis for the work on TT-zone tyrannosaurs as discussed in this section. The degree to which standard realistic ontogenetics is detailed and employed in this study is unprecedented concerning TT-zone eutyrranosaur (building upon Longrich & Saitta 2024, Paul 2025a; Zanno & Napoli 2025). This is in contrast to Carr (2020); in order to try to fit all TT-zone specimens of all sizes into *T. rex*, Carr contends that *Tyrannosaurus* underwent a rapid, dramatic metamorphosis that among items included a significant reduction in numbers of teeth. Among vertebrates, metamorphosis is limited to fish and amphibians, not having been observed among amniotes, tyrannosaurids included (Currie 2003a,b; Longrich & Saitta 2024; Paul 2025a; Yun *et al.* 2025; Zanno & Napoli 2025). Juveniles within a species, and between closely related species, tend to be very similar in form, especially in early ontogeny (Paris *et al.* 2008; Laudet 2011; Napoli 2024). As growth occurs, variation at any life stage may remain minimal, as within nondomestic *Equus* species, and within *Dromaius novaehollandiae*. That appears to be the norm among nonavian dinosaurs including tyrannosaurins (Mallon 2017; Mallon & Hone 2024). Or variability may increase dramatically, as in species of *Homo* and *Otis*. Major adult differentiation is generally associated with sexual dimorphism. To put it another way, variation within a given species when present occurs with maturity, juveniles do not start out diverse and lose the variability as they grow up. In Reptilia/Sauropsida tooth counts nearly always remain stable with growth, or less often increase (Witmer & Ridgely 2010; Larson 2013b; Brown *et al.* 2015; Napoli 2024). Tooth loss with maturity is rare, being limited to captorhinid basal sauropsids (Haridy *et al.* 2018), fully marine ichthyosaurs that reduce teeth to a nonfunctional level (Dick & Maxwell 2015; Paul 2025a), and

some ceratosaurian basal avepod theropods that underwent a radical transformation from predaceous toothed juveniles to herbivorous beaked adults while they retained the alveoli (Wang *et al.* 2017; Paul 2024a, b; Zanno & Napoli 2025). Ontogenetic tooth loss does not occur in predaceous terrestrial reptiles, including *Gorgosaurus* and *Tarbosaurus* (Rozhdestvensky 1965; Currie 2003a; Longrich & Saitta 2024; Paul 2025a), and claims of such in *Alioramus* are unsubstantiated (Longrich & Saitta 2024; Paul 2025a). Tooth loss with ontogeny in synapsids is not particularly pertinent to this analysis, that remote group relative to diapsids undergoing a very different evolutionary path regarding dental adaptations (Benton 2014; Bertin *et al.* 2018; LeBlanc *et al.* 2018).

*Tarbosaurus* ontogeny is of critical importance in setting the parsimonious null hypothesis standard for assessing the ontogeny of its close relative. It was a similarly robust, gigantic fellow tyrannosaurin, the closest in form and function to the tyrant lizard yet known. These predators are so alike that they have sometimes been considered at least potentially congeneric (Maleev 1955; Rozhdestvensky 1965; Paul 1988, 2008, 2010, 2016, 2024a; Carpenter 1992; Carr 1999, 2020, 2022, 2025; Hernandez-Luna *et al.* 2026). *Tarbosaurus* osteological ontogeny is well documented (Fig. 6A-H; Rozhdestvensky 1965; Carpenter 1992; Longrich & Saitta 2024; Paul 2020, 2016, 2024a,b, 2025a; Yun *et al.* 2025). Regarding the latter, Yun *et al.*'s (2025) extensive study on the cranial ontogeny of *Tarbosaurus* casually suggests that the growth patterns they observed generally parallel those of *Gorgosaurus* and *Tyrannosaurus*. This was not verified by applying the same methodologies to the American tyrannosaurids. Nor was the dramatic, sudden mid-growth metamorphosis proposed by Carr (2020) for *T. rex* observed in *T. bataar* (Longrich & Saitta 2024; Paul 2025a). Also not considered by Yun *et al.* (2025) was the data and analysis presented by proponents of the MTTH, including the major new works by Longrich and Saitta (2024) and Paul (2025a). As a result, issues concerning tooth counts and form, lateral dentary grooves and other critical items were not addressed.

It is concluded that the similarities in growth between the two tyrannosaurins Yun *et al.* (2025) commented on were only of the broadest nature, often related to increasing robustness with size, not verification that the atypical ETRH version of *Tyrannosaurus* growth closely matches that actually present in *Tarbosaurus*. To the contrary, viewed parsimoniously that two taxa that are so similar in form, function and presumably genetics experienced dramatically different ontogenies is sufficiently low that it must be *a-priori* assumed that the growth of the sister taxa was very similar unless additional evidence indicates otherwise. That means that showing otherwise has the major burden of evidence upon it. During the entire observed ontogeny from under 100 kg to over 4 tonnes of *Tarbosaurus* there is nothing out of the amniote/diapsid routine (Rozhdestvensky 1965; Carpenter 1992; Paul 2024a,b; Raun *et al.* 2025a; Yun *et al.* 2025). It shows a persistently consistent morphology that starts with basic features retained in the adults. These include a stable tooth count, absence of a long prominent dentary groove and diminutive forelimbs and manus that are about two thirds femur length at any growth stage, and a smooth allometric growth arc with no sudden metamorphic proportional and morphological alterations – *Tarbosaurus* always looked like *Tarbosaurus* as it matured.

The degree of ontogenetic niche partitioning that occurred in *Tarbosaurus* was correspondingly modest, consisting largely of an allometric increase in robustness and moderate decrease in relative limb length, striking alterations to body form related to dramatic changes in predation are not observed. And immature *Tarbosaurus* are readily distinguishable from non*Tarbosaurus* lesser sized taxa that lived in the same habitat (Fig. 6E-H versus 6I). That the maturation of the Nemegt tyrannosaurin was entirely normal bolsters it as a model to apply to its very close relation *Tyrannosaurus*. It follows that to convincingly establish that growth in the so similar *Tyrannosaurus*

was dramatically outside the ordinary tarbosaur pattern is inherently nonparsimonious, and demands exceptional positive evidence that such was the case. This conventional standard should have always been the norm in this field of research, and that it has not among so many researchers has been a failing of dinosaurology. For the first time the conservative, parsimonious, null hypothesis analytical technique that needs to be applied to the ontogenetic-taxonomic status of TT-zone like tyrannosaurs is comprehensively listed in Table 1.

**TABLE 1.**

---

**Conventional, parsimonious criteria for examining and restoring growth in fossil amniotes, including TT-zone eutyranosaurs --**

- Close correspondence in growth patterns with those of close relations, which in this case is albertosaurs and especially tarbosaurids, which include the below standard amniote/diapsid features.
- Juveniles of a single species will be highly similar in core characteristics and are visual predecessors of their adult form -- this requires consideration of all TT-zone tyrannosaur fossils below two tonnes estimated live mass in order to assay all the variation they contain.
- No sudden fish style metamorphosis including limb atrophy.
- Reptilian tooth counts are always in a narrow range, and do not decrease with increasing size down to the adult counts.
- Growth as recorded by bone rings is very likely to follow a fairly smooth arc peaking in mass accumulation in the teens.
- In the case of exceptionally powerfully built *Tyrannosaurus*, its juveniles should be at least about as robustly built in dentition, skull and skeleton than are the young of the nearly as hefty *Tarbosaurus*, if not more so.

**Normal *Tyrannosaurus* growth recorded by actual juveniles of the genus --**

- There is a close correspondence with the normal amniote-diapsid-tyrannosaurid growth pattern of its fellow tyrannosaurin *Tarbosaurus*.
- As far as is known the juveniles are both highly similar to one another, and are fairly robust, clear cut antecedents of their adult form.
- There is no sudden fish style metamorphosis, including atrophy of the manus.
- Dental counts are always in a narrow range, and do not experience a highly atypical decrease with increasing size down to the adult counts.
- There is not a shift from a prominent lateral dentary groove to little or none.
- A diversion from a standard growth S-curve is not involved.
- There is nothing radical or abnormal from ontogenetic norms.

**Aberrant improbable or impossible growth associated with and required by the ETRH --**

- A highly abnormal and divergent from the normal ontogeny of amniotes, diapsids, and tyrannosaurids that is drastically different from that of fellow tyrannosaurin *Tarbosaurus*, that is otherwise so similar it potentially qualifies as congeneric with *Tyrannosaurus* according to Carr.
  - Lack of a compelling explanation for the above when it does not occur elsewhere, other tyrannosaurids and tyrannosaurins included.
  - A unique or close to it divergence in dental and cranial attributes among juveniles of a given growth stage, covered over by neglecting the fossils that qualify as juvenile *Tyrannosaurus*.
  - A sudden metamorphosis of the type seen among some fish, but not amniotes.
  - A very rare contraction and decrease of reptilian tooth counts not seen in beakless predaceous theropods, tyrannosaurids and tyrannosaurins included.
  - Growth irregular, involving peculiar slow-downs among pre/teens.
-

It follows that if substantial osteological and dental differences are present between lesser sized individual TT-zone tyrannosaurs at given size and potential stages, then they represent multiple taxa. In that case, those specimens that most closely match the features of adult *Tyrannosaurus* are the juveniles of that genus and its species. If growth was slowing at smaller sizes according to the spacing of LAG in preteen and teen aged individuals, then the possibility of their being a juvenile of the fast-growing tyrant lizard giant is low at best. If anatomical variation within the fossils that do not qualify as immature *Tyrannosaurus* is itself extensive, then they very probably represent multiple taxa at least at the species level, and possibly higher depending on the degree of variation -- if some of those specimens possess non-tyrannosaurid features such as long hands then they likely lie outside that family. The prior methods are entirely conservative and normal in nature. Doing anything outside those conventional procedures constitute at best radical propositions and hypotheses that require abundant positive evidence to support them. Building on prior work most recently by Longrich and Saitta (2024), Paul (2025a) and then Zanno & Napoli (2025), this study goes further to describe and apply these reasonable principles than any to date. These routine methods need to be adhered to as much as possible in all future work on the subject.

### Notes on *Tyrannosaurus* species

There are two subsections contained within the ETRH. One focuses on the number of taxa preserved in the smaller specimens, and the other addresses how many species there are among the adults. Regarding the latter, Hernandez-Luna *et al.* (2026) tentatively support the general concept of speciose TT-zone adult *Tyrannosaurus* and cite Paul (2025a). When Hernandez-Luna *et al.* 2026 repeat criticisms of the dental factors presented in Paul *et al.* (2022) that had been initially raised by Carr *et al.* (2022), they neglect that Paul (2025a) refuted many of the arguments in the former. This includes the use of a specific ratio by Paul *et al.* (2022, and Paul 2025A) to divide the anterior dentary tooth proportions, because Carr (2020) had also used a specific arbitrary ratio for a similar comparative anatomy purpose. Although the absolute measurement values by Carr *et al.* (2022) and Carr (2025) differ from those of Larson (2008), Paul *et al.* (2022) and Paul (2025a), the similar relative sizes of the left dentary 2<sup>nd</sup> and 3<sup>rd</sup> tooth positions (as measured by alveoli and/or tooth base diameter depending on what is available) of the *T. rex* CM 973 holotype (Fig. 3A) is affirmed, as is the smaller dimensions of the 1<sup>st</sup> position. The results confirm the derived condition of only one small tooth at the anterior end of a CMNH 9380 dentary that had been rare in the lower TT-zone, and then become dominant in the upper. Carr *et al.* (2022) and Carr (2025) show that the situation regarding the right dentary differs, with the 2<sup>nd</sup> position shorter than the 3<sup>rd</sup>. However, the overall cross-sectional area of the 2<sup>nd</sup> position appears to be substantially greater than that of the 1<sup>st</sup> in Figure 25B in Carr (2025). That suggests that the 2<sup>nd</sup> tooth, which is not preserved, could have been markedly larger than is the preserved, slender incisiform at the tip of the element. That possibility favours at least a partial presence of the derived *Tyrannosaurus* condition (see Fig. 3 in Paul *et al.* 2022) in the holotype of the type species.

The tooth position length ratio system used by Larson (2008), Paul *et al.* (2022) and Paul (2025a) may have limits. A comparison of the cross sectional areas of dentary positions 1-3 in the *Tyrannosaurus* fossil sample could provide superior comparative results, but would be very difficult to produce due to practical logistical issues. In any case, citing one or a few exceptions to a larger pattern of character distribution as refuting its entire diagnostic utility in taxonomic work is not automatically definitive. As a consequence that intragenera species are so similar to one another, the diagnostic characters of sibling taxa often show overlap (Paul *et al.* 2022; Paul 2025a), as per the species of *Triceratops* (Scannella *et al.* 2014; contra the contention otherwise by Carr *et al.* 2022 and Yun 2026). Because biological evolution is irregular, not precise, there being divergence in the proportions of the right and left tooth positions in CM 9380 is not sufficient to negate the strong

general trend of reduction of two small anterior dentary teeth down to one over time in *Tyrannosaurus* (Paul *et al.* 2022; Paul 2025a; the stratigraphic factor continuing to be disregarded by Hernandez-Luna *et al.* 2026). All the more so because the change is in tune with other, time related changes in the osteology of the genus that indicate it was speciating over time.

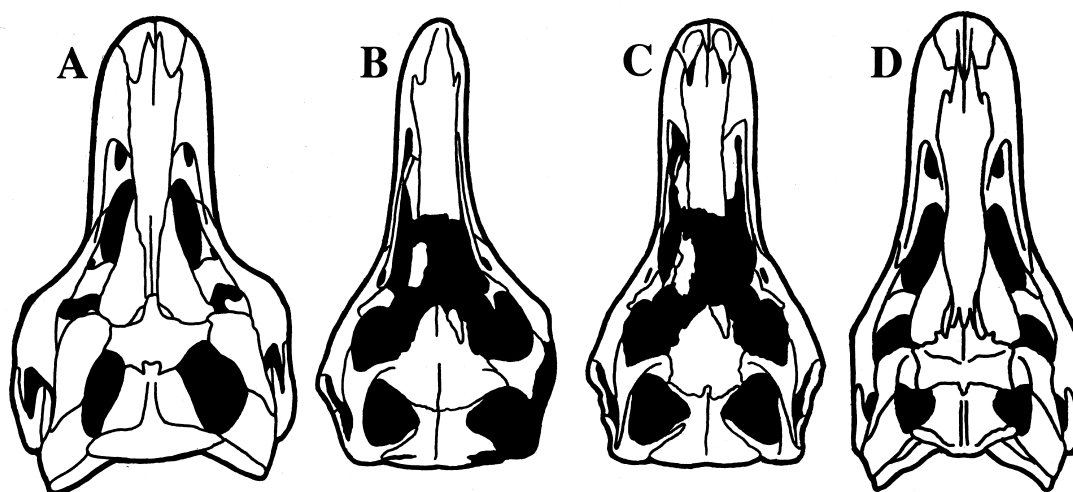
Use of a single anatomical attribute to broadly assess species status is inherently limited. As per Yun (2026) who concludes that variation in TT-zone tyrant lizard maxillae is within the range present within a single species. Because Yun (2026) does not examine and establish parameters for the amount of variation present within specimens of other accepted tyrannosaur sibling species, his results do not meet the minimum standards of comparative testing and are not verified. Indeed, the amount of differentiation observable in the maxillae figured by Yun (2026) is very high, as is observed herein and in Paul *et al.* (2022) and Paul (2025a). Nor does Yun (2026) consider the very large and important variability of the interfenestral pillar documented in Paul (2025a). Carr *et al.* (2022), Carr (2025), Hernandez-Luna *et al.* 2026 and Yun (2026) do not meet the extensive rigorous criteria detailed in Paul *et al.* (2022) and Paul (2025a) for refuting multispecific TT-zone *Tyrannosaurus*. To refute the large data set based results of Paul *et al.* (2022) and Paul (2025) requires showing that cumulative variation in TT-zone *Tyrannosaurus* crania and postcrania is less than observed in other intragenera species, if the variation is similar then multiple sibling species is at least viable if not superior, and the latter applies if the variation is greater. Variation in *Tyrannosaurus* femur/length to shaft circumference of at least 80% maximum size is about twice as high as observed in the exceptionally large collection of measured femora representing a single dinosaur species (Hennig 1925).

The opinion that the pro-ETRH Carr (2020) constituted a rebuttal of MTTH Paul *et al.* (2022) has been additionally damaged by the widely acknowledged rebuttal of the ETRH it advocated. Further reinforcing intragenera sibling species is the readily visible greater variation in cranial anatomy, especially the very different postorbital bosses and interfenestral pillar, of *Tyrannosaurus* (Figs. 8F-J, 10B,C,E) compared to other avipods including specimens of *Tarbosaurus* (Fig. 6A-H; Paul 2025a), and species of *Daspletosaurus* (Fig. 8C-E) and *Allosaurus* (Fig. 8A,B). It is worth noting that the proportional means being used to distinguish intra *Tarbosaurus* sibling species (Raun *et al.* 2025b) are broadly similar in nature to those utilized for the same purpose for *Tyrannosaurus*, and may be less extensive and stratigraphically correlated. If in the future earlier *T. imperator* is accepted as distinct from *T. rex* while contemporary *T. regina* is not (as implied by Longrich & Saitta 2024), that continues to treat *T. rex* as a special species that suddenly at the very end of the Mesozoic evolved unprecedented proportional and display diversity than seen prior in other tyrannosaur and dinosaur species (Paul *et al.* 2022; Paul 2025a). The presence of a robust and a gracile tyrannosaurid taxa in the same level of a formation being comparatively normal leaves it the parsimonious probability. Note that two giant tyrannosaurid, probably tyrannosaurins, taxa appear to be present in the same quarry from the Hongtuya Formation (Hone *et al.* 2011).

Voris *et al.* (2025) propose that the flat ventral margin of the “*T.*” *mcraeensis* holotype dentary is also observed in *Tyrannosaurus* specimen MOR 008, contradicting a taxonomic separation at least at the species level. However, like many elements of the MOR 008 skull, the postero-ventral corner of the preserved dentary is heavily fragmented and includes restoration work (Paul, pers. observation). Because its atypical profile compared to other *Tyrannosaurus* is dubious it cannot be used to negate a well-founded taxonomic distinction presented by Dalman *et al.* (2024, that may be at the genus level, Paul 2025a). If Voris *et al.* (2025) are correct that “*T.*” *mcraeensis* is more contemporary with TT-zone *Tyrannosaurus* than thought by Dalman *et al.* (2024, then the giant tyrannosaur/s of the southwest appear to have retained into the later Maastrichtian, the geographic differentiation common to western North America in the late Cretaceous.

## Specimens and work thereon

Specimens of modest dimensions under consideration are USNM 6183 (Hatcher), UCRC V1, LACM 23845 (*Dinotyrannus megagracilis* holotype), BHI 6439 (Nicklas), KU 156375 (Laurel), UCMP 84133, MOR 1189. Baby Bob, DMNS Teen Rex which can be at least provisionally assigned to *Tyrannosaurus* according to following references and work herein, and BMRP 2002.4.1 (Jane, *Gilmoretyrannus lethaeus* holotype) & 2006.4.4, (Petey), CMNH 7541 (*Nanotyrannus lancensis* holotype), DDM 344.1 (Tom), FNMH PR2411, HRS 08 (Zuri), 15001, Jodi, KU 155809 (Maddy), LACM 28471 (*Stygivenator molnari* holotype), MOR 6625 (Chomper), NCSM 40000 (Bloody Mary, ex BHI 6437, NCMNSBM in Paul, 2025a), RSM P2347.1, TMP 80.16.425 that at least probably lie outside the genus (Figs 1, 2, 3B-I, 4C-E, 7C-E, 9B, 10G,H; Gilmore 1946; Molnar 1978; 1980; Bakker *et al.* 1988; Paul 1988, 1998 Fig. 3C, 2025; Olshevsky *et al.* 1995; Larson 2008, 2013a, b; Schmerge & Rothschild 2016a,b; Burnham *et al.* 2018; Paul *et al.* 2022; Longrich & Saitta 2024; Zanno & Napoli 2025; Woodward *et al.* 2026; Hernandez-Luna *et al.* 2026; Longrich *et al.* 2026a). That many of these specimens have not been described is not critical to taxonomic work, such being common in paleontological systematic work (as per the treatment of BMRP 2002.4.1 by Zanno & Napoli 2025). Tooth socket counts not in the literature are based on direct examination and/or high quality photographs. Preservation of these specimens ranges from essentially complete to very fragmentary, with the *Tyrannosaurus* being towards the latter end of the preservation spectrum. None of these specimens indicate individuals below a few hundred kilograms, unlike *Tarbosaurus* juveniles of less than 100 kg (Fig. 6G,H; Paul 2024a, b). The putative non-Tyrannosaurus remains are broadly similar in size (Figs. 1, 3E-I, 4C,D), precluding major ontogenetically driven shape reformation as being responsible for the extensive variation that is present. Also precluded is strong sexual dimorphism in such immature individuals. With the TT-zone having been deposited over 1+ MA (Paul *et al.* 2022 and refs. therein; Zanno & Napoli 2025) this is not an issue regarding subfamilies and genera that can easily last that long, but can be for species. Fragmentary post-hatchling TT-zone eutyranosaur fossils have been assigned to *Tyrannosaurus* by Longrich *et al.* (2026a). Appalachian baso-eutyranosaurus date from the late Campanian (*Appalachiosaurus*, Carr *et al.* 2005) to the late Maastrichtian (*Dryptosaurus*, Carpenter *et al.* 1997; Gallagher 2023).



**FIGURE 9.** Known-bone profile-skulls of eutyranosaurus in dorsal view reproduced to same midline length to facilitate intergenera visual comparisons. **A** *Tyrannosaurus* AMNH 5027; **B** *Nanotyrannus* holotype CMNH 7541 as preserved from 3-D scan, extent of preserved elements aided by Figures 3A, 4D in Witmer and Ridgely (2010); **C** CMNH 7541 as restored by Carr (1999); **D** *Daspletosaurus* holotype CMN 8506.



The cranium only *N. lancensis* (Gilmore 1946) and *S. molnari* (Paul 1988) were named on incomplete materials when the TT-zone tyrannosaur fossil record was sparse. It has since become extensive, allowing new holotypes to be based on specimens that are largely complete regarding both the cranium and postcranium. It is strongly recommended that high skull-skeletal fossil completeness be a strict requirement for any future new tyrannosaur taxa from the TT-zone complex of formations. This is in accord with Paul *et al.* (2022) and Paul (2025a) in which the new *Tyrannosaurus* species were likewise founded only on specimens possessing sufficient diagnostic skull-skeletal features including orbital display in association with skull and skeletal proportions including the diagnostically critical complete femur, and basic stratigraphic levels were known – classic AMNH 5027 for instance is an unsuitable holotype on some of these grounds.

This being a review paper that does not introduce new fossil remains, no specimen illustrated herein has not been previously documented by published images, which are not repeated herein (as per photograph free Carr 2020 who did not document any of the ~1800 characters scored in numerous specimens with images, the near photograph free Yun 2026 who did not personally examine the specimens he sampled and in some cases used drawings rather than photographs, and Zanno & Napoli 2025 rediagnosed *N. lancensis* without including images of CMNH 7541, and few of undescribed BMRP 2002.4.1 that they designate the holotype of *N. lethaeus*). Use of profile (rather than shaded or photographic) images has the advantage of maximizing visual comparisons of critical shape and proportional differences. They also have the advantage of being able to present more direct plan views of the anatomy of skulls whose actual depth/length proportions may be obscured in photographs of complex topography crania. Those in Figures 3, 5, 6, 10 are derived in part from Paul (2025a) as noted in captions, with modification and additions.

Illustrations and restorations (Figs. 1-10) were produced following standard procedures for generating technical paleoillustrations that are as meticulous as possible, and are based on personal examination, scans, photographs and illustrations, including those in Gilmore (1946), Witmer and Ridgely (2010), Larson (2013a), Longrich & Saitta (2024) and Zanno & Napoli (2025). Bones have been carefully traced from source images -- any who disagree with their accuracy need to demonstrate each of the errors with measurements and/or comparative images – the first alone can be confusing and misleading. AI was not used in producing the illustrations. Elements including teeth from one side are often used to fill in those missing from the other. What bones are or are not known is not always clear, many postcranial elements of the complete NCSM 40000 are concealed for the long term. None of the baso-eutyrannosaur skulls restored (Fig. 1) are complete, fully articulated and undistorted, so all require considerable restoration. Occasional subtle differences between skull elements in different figures are due to elements from different specimens and/or sides being used. The left sides that are restored are often compromises to varying degrees that naturally result from combining right with left elements to obtain an average. Because of these factors, all intraskull restored dimensional ratios are approximations to varying degrees – total skull length is premaxilla tip to tip of paroccipital wing (Fig. 2A); temporal box length is latter to anterior edge of lacrimal preorbital bar; rostrum length is latter to premaxilla tip; rostrum height is measured at the anterior end of the antorbital fossa; general skull height is measured at the postorbital bar vertical sans any ventral jugal cornual rugosity (Fig. 2A); dentary length is anterior tip to posterior edge at intermandibular fenestra; dentary depth is at mid length; posterior mandible height is maximum depth at about mid length. Profile-skeletons that are based on fragmentary specimens involve extensive extrapolation and cross-scaling from related taxon. For example, the shape and size of the cranium of the Appalachia *Dryptosaurus* dimensionally stems from the depth of its dentary applied to that of its baso-eutyrannosaur relation *Appalachiosaurus* (Fig. 4A,B). The body

form of the modest sized USNM 555000 is downsized to accommodate the remains of the large juvenile LACM 23845 (Fig. 10D,G).

BMRP 2002.4.1 (Figs. 1B, 3G, 4D) has yet to be described -- Zanno & Napoli (2025) proceeded to diagnose it as the holotype of a new species before that work has been presented (by Carr). Longrich *et al.* (2026a) moved the new species to another genus without figuring 2002.4.1. Parts of the specimen have been extensively imaged in the technical literature (Larson 2013a; Longrich & Saitta 2024; Zanno & Napoli 2025) and elsewhere, many measurements have not been published. The skull elements appear little distorted, but are disarticulated, the absence of the frontals and braincase precludes an accurate dorsal view restoration. The lateral view presents fairly typical eutyrannosaur proportions. General height/total length is a moderately low  $\sim 0.24$ . Rostrum height/total length also is a moderately low  $\sim 0.21$ . Rostrum/temporal box length is a long  $\sim 1.65$ . Dentary height/length is  $\sim 0.16$ , but that value is on the low side because the mid dentary is vertically pinched relative to the ends. Skull HRS 08 is missing too much of the temporal region and posterior mandible to be reliably restored for these skull shape and proportional needs, what is known appears to have a similar general shape to BMRP 2002.4.1 (including the profiles of the dentary and maxilla, although the anterior antorbital fossa profile of the latter is distinctive (Fig. 3G,I).

NCSM 40000 (Fig. 1C) has been technically extensively documented, measured and diagnosed in a major paper as within *N. lancensis* by Zanno & Napoli (2025), who then used it to partly characterize the taxon. Paul (2025a) had provisionally diagnosed it as a probable new taxon, possibly a species within *Stygivenator*. NCSM 40000 is further available as images in various locations. The accessioned and published specimen therefore meets all modern standards for further taxonomic analysis, rendering it even more available for holotype designation than was BMRP 2002.4.1. Damaged by amateur excavation before professionals arrived, NCSM 40000 is undergoing long term preparation, and extensive soft tissues obscure much of the presacral series and thorax, so the profile-skeletal (Fig. 4C) is the most that can be generated for the foreseeable future. Images utilized are Figures 2, 5 and Extended Data Figures 1, 2 from Zanno & Napoli (2025) supplemented by online photographs, measurements are from their Table SI.1.5. The cross scaling of the detached rostral and temporal sections of the cranium in Zanno and Napoli's (2025) Extended Data Figure 3 is in good general accord with those present in online photographs showing the skull in its sediment block.

In Extended Data Figure 3c,e in Zanno and Napoli's (2025 the two images are not exactly the same scale, c being reproduced  $\sim 4$  larger than e). Breakage of the lacrimals in the region of the dorsal hornlets tilted the roof elements anterior to them, giving the illusion of a flexed skull at mid-length. The false curve has been removed, leaving the skull straight in lateral profile. The correction also shows the hornlets have the normal single peak. Because both sides of the NCSM 40000 cranial temporal box are somewhat distorted and damaged (EDFig. 3 in Zanno & Napoli 2025), the compromises resulting from using right and left elements leaves the exact shape and dimensions of the orbit uncertain, but it was rather small relative to the skull. That said, the generally good similarity of the shape and proportions of elements from the different sides do not appear to record serious dorso-ventral cranial crushing. The temporal region is skewed somewhat to the right dorsally (EDFig. 3b,d in Zanno & Napoli 2025), but not to the degree of seriously impacting the similar depths and configurations of the lateral surfaces. The length/height ratio of the fossil's temporal box, is replicated in the restoration. The maxillae are very similar in their low height and acute triangular shape, any difference not being sufficient to significantly alter the profile of the shallow, sharp rostrum, which is a close match on both sides as seen in Extended Data Figure 3c,e in Zanno & Napoli (2025), especially when the differing scales of the two images are adjusted as noted above. The rim of the right anterior antorbital fenestra is a little shallower and more sharp

angled than the left (Fig. 3E). The former condition is seen in the articulated skull image in Zanno & Napoli (EDFig. 3a). The discrepancy may be the result of right/left asymmetry and/or minor dorso-ventral crushing, the left version is used in the final restorations. The elongated alioramin-like (Paul 2010, 2016, 2024a,b; Brusatte *et al.* 2012) cranial configuration is similar to that present in EDFig. 3a in Zanno & Napoli (2025) as well as online photographs of the skull in the sediment block. The fore versus aft sections ratios are inherently approximate because of the detachment of the fore and aft sections precludes precision. The slightly ventrally disarticulated premaxillae are moved dorsally a little to bring their ventral margins correctly in the same line as those of the maxillae. Although the dentaries are tightly articulated with the rostrum, a short portion of the right dentary's dorsal edge exposed with a tooth in place indicates their depth.

The maximum total length of the NCSM 40000 restoration is a little shorter than in EDFigure 3a and Table SI.1.5 in Zanno & Napoli (2025) entirely because of the proper close application of the paroccipital wing to the posterior surface of the squamosal. General height/total length is a shallow  $\sim 0.22$ . Total skull length/rostrum height is a very shallow 0.19 to 0.2, the detachment of the front and aft halves precludes a tighter value. Rostrum/temporal box length is a long 1.65 to 1.85, again the detachment of the front and aft halves precludes a tighter value. Dentary height/length appears to be consistently shallow with a minimum of  $\sim 0.16$ . Temporal box/posterior mandible height is low at  $\sim 1.35$ . Posterior mandible height/total skull length is a shallow  $\sim 0.17$ . How reliably the cranium can be restored in dorsal view is not clear.

The largely albeit not entirely complete and significantly damaged CMNH 7541 (Figs. 1A, 2, 9B) can be restored in lateral view, although doing so faces numerous issues due to the missing bone elements, combined with sometimes perplexing distortions seen in the photographs and scans in Witmer & Ridgely (2010). The deformation is so extensive that the right and left sides look like they could be from different animals. Even so, the basic dimensions of the orbital regions are intact, including large orbits and jugals. Judging from Gilmore's (1946) text, the specimen is a single block including the tightly articulated mandibles, in which case the basic original length is preserved. So while the mid maxillae are fragmented and much of the skull roof is absent (Fig. 2C-F; Fig. 4 in Witmer and Ridgely 2010), this has little apparent effect on the overall length of the cranium. Witmer and Ridgely (2010) praised the original restoration work. The general shapes of the maxillae and antorbital fossae are preserved, particularly their antero-posteriorly short, vertically tall and correspondingly blunt proportions.

A rotatable 3-D scan (Fig. 2C,F left row; Rogez 2021) has been used to determine the actual lateral view proportions. Differences in apparent proportions of the overall cranium and elements are unusually substantial. This is because the temporal box is dorso-ventrally flattened because it is strongly splayed out ventrally relative to the roof on both sides (Fig. 2C-F; Figs. 2B,C, 3A,B, 4A,D-F in Witmer & Ridgely 2010). As a result the aft half of the skull appears shallower than it actually is when the skull roof top is posed perpendicular to the viewer (as in Pl. 1 in Gilmore 1946; Fig. 8.8 in Larson 2008; Figs 1, 3B,C in Witmer & Ridgely 2010; Fig. 3A,B in Longrich & Saitta 2024).

Illustrations of the skull have been prone to be correspondingly too shallow, especially aft, with a general height to length ratio of 0.28-0.295 (Bakker *et al.* 1988 as shown in Fig. 2A; Carr 1999; Paul 2024b; Longrich & Saitta 2025). The excessive beam of the lower temporal box is a major factor in the additional variations between photographs, because small differences in camera angles, distances and lenses are exaggerated in the resulting images. Correctly restoring the true lateral view as accurately as possible was achieved by rotating the 3-D scan until the sides were flat onto the viewer (Fig. 2C,E). If anything, the right side is deeper than the left. The actual depth of the temporal box on both sides is about a fifth greater than when seen in standard pseudo lateral views (Fig 2C,E versus D,F).

The final restoration is based primarily on the left side, with some content from the right. This work reveals that the skull was distinctly deep both fore and aft, more so than the norm for eutyrannosaurs of this size (Fig. 1A). The frontoparietal, sagittal and occipital crests are also exceptionally vertically prominent. The quadrates and quadratojugal have been pushed forward and somewhat medially, shortening the lateral temporal fenestra. This distortion was corrected to allow room for the anterior rami of the quadratojugal and squamosal, which lengthens the skull ~4%. Even with the correction, the lateral temporal fenestra appears antero-posteriorly shorter than the eutyrannosaurs norm, in association with the usually tall postorbital and post temporal fenestra bars. The posterior view (Fig. 1A) is de-distorted (from Fig. 2D) to show the post temporal bar properly subvertical. The mandible is primarily after Figure 15C in Witmer and Ridgely (2010); because the lower jaw is severely jammed up into the skull (far more than possible in life, p. 34 in Paul 2024b, and to the degree that the teeth have been pushed postero-ventrally) its massive depth has not been previously realized. That is in part because most side view images of the preserved right dentary are not flat on to the element, as it correctly is in Witmer and Ridgely (2010), and properly rotated online scans. The position of the detached anteriormost dentary relative to the rest of the lower jaws is not certain. General height/total length is a deep ~0.32 – to arrive at a 0.29 value would require lengthening the cranium by nearly a tenth, or 100 mm. Rostrum height/total length also is a deep ~0.27. Rostrum/temporal box length is a short ~1.45. Dentary height/dentary length is a deep ~0.18. Temporal box/posterior mandible height is a high ~1.4. Posterior mandible height/total skull length is a deep ~0.22. Because CMNH 7541 has been asymmetrically distorted in a complex manner, and extensive dorsal cranial elements are missing (Fig. 9B), it proved impractical to reliably restore its configuration in dorsal view (Paul 2025a; Zanno & Napoli 2025).

The very narrow CMNH 7541 rostrum appears to be laterally compressed an uncertain amount (but Longrich & Saitta 2024 disagree). Carr's (1999) restoration of the rostrum as broader than preserved (Fig. 9C) is as plausible if not probable, as it is unconfirmable. Carr's viable version is more similar in proportions to that of *Daspletosaurus* than *Tyrannosaurus* (Fig. 9A,D), so the reasonable restored dorsal dimensions do not particularly favour the specimen being within the tyrant lizard (Paul 2025a and then Zanno & Napoli 2025). Because any effort to restore CMNH 7541 in dorsal aspect produces an arbitrary rather than scientifically score-able and diagnosable result, the item cannot be used for phylogenetic or gradistic assessments as explained by Paul (2025a) and then Zanno & Napoli (2025). The absence of a prefrontonasal processes of the frontals observed by Voris *et al.* (2025) may be due to the large break of this skull at this position (Fig. 6B in Carr 1999; Fig. 3B in Witmer & Ridgely 2010) leading to the loss of the small and delicate processes (see Fig. 5C in Carr 1999), and cannot be reliably scored as a character either. Longrich & Saitta (2024) note that Carr (Fig. 6 in 1999 in which the lateral restorations do not entirely match each other, Fig. 12 in 2020) appears to have restored the skull in a manner that makes it look more like *Tyrannosaurus* than it actually is, including premaxillary teeth that are too vertical, a snout tip that is too broad U-shaped in dorso-ventral view, and a maxillary fenestra that is placed too far anteriorly, especially in one version.

The conspicuous differences in the vertical versus the longitudinal dimensions of the elements of the skulls that are presented in Figure 1 support the variations in their restored overall length/depth ratios. The CMNH 7541 quadratojugal is tall, the vertical height approaching the horizontal distance between the anterior tip of the maxilla and its antorbital fossa. The shorter BMRP 2002.4.1 quadratojugal is just ~80% the length of the anterior maxilla, in line with a shallower cranium. The even shorter quadratojugals of NCSM 40000 are about three quarters the anterior maxilla length, in accord with its exceptionally low cranial profile vis-à-vis the other specimens. The lower height to length of the maxilla also contributes to its very shallow skull. To stretch the *Nanotyrannus* cranium

to match the lower profiles of the others would require large arbitrary space gaps between the fragments of the maxillae that are not preserved in the fossil.

The first small incisoriform of LACM 28471 is interpreted as a displaced last premaxillary tooth rather than a “premaxillariform” maxillary tooth, as proposed by Carr & Williamson (2004) and Zanno & Napoli (2025, Supplementary Information 1). This element likely originates from the premaxilla, which is partially preserved and shows visible alveoli (Molnar, 1978; Olshevsky *et al.*, 1995; Ford, 2005, pers. comm.; personal observation), and was subsequently broken and glued into its current position. A re-examination of Molnar (1978) supports this interpretation. Consequently, this would indicate the presence of only one maxillary incisoriform tooth per side, rather than two.

The *Appalachiosaurus montgomeriensis* holotype RMM 6670 skull restoration (Fig. 4A) is little different from that of Carr *et al.* (2025). The incomplete elements preclude ratio calculations, but the general boxy proportions appear more like that of CMNH 7541 than the very elongated NCSM 40000. Zanno & Napoli assigned undescribed KU 156375 to *N. lancensis* without presenting photographs or other images.

Produced via standard consistent comparative techniques (Paul 1988, 2024a,b, Larramendi *et al.* 2021), volumetric mass estimates for specimens as preserved, or projected for adults, are derived in part from mass and growth stage data in Paul (2024b, 2025a), Zanno & Napoli (2025) and Griffin *et al.* (2025), with modifications herein. As per the diapsid-dinosaur norm (Paul 1988, 2024a,b), articulated tyrannosaur skeletons preserve the trunk ribs swept postero-ventrally (as per Fig. 2 in Zanno & Napoli 2025), which significantly reduces the volume of the trunk compared to restorations showing the chest ribs vertical or swept ventro-anteriorly (contra the mounted skeleton scans in Hutchinson *et al.* 2011). The latter incorrectly inflates the volume/mass of the restoration. So do restorations showing the gastralia basket bowed convex ventrally; such represents the subject distended by gorging on a carcass, or post-mortem bloating as is commonly preserved in the fossils. Profiles are restored in the healthy lean-hungry condition suitable for flesh eaters on the hunt, with empty hollow bellies, and the minimal fat deposits that maximize speed performance and agility in pursuit predators. Use of bone circumferences for mass estimation has higher +/- errors; mass/circumference ratios can differ considerably within species due to sexual, individual and other variations, even more between species, yet more between genera. Nor can circumference based estimates take into account dimensional differentiations present in actual fossil skeletons. Using circumferences led Zanno & Napoli (2025) to estimate that BMRP 2002.4.1 was ~18% heavier than NCSM 40000, this result is not sufficiently dependable for comparative size work because of the inherent +/- error. The pelvis and tail of the latter appear larger than that of the former (Fig. 4C,D) – the two specimens have similar sized limbs – and the volumetric method favours 40000 being at least as weighty as 2002.4.1. Because the latter was not as far along in its growth (Paul 2025a; Zanno & Napoli 2025) the adult mass of its species was probably substantially higher than that of NCSM 40000, as per their systematic diagnoses -- with Jodi about 10% longer than the *L. elegans* holotype (Fig. 5D,E) its mass should have been about a third higher.

### Systematic analysis and diagnoses

Systematic diagnoses for assessing North American Campanian/Maastrichtian baso-eutyranosaur and TT-zone tyrannosaurid taxonomics are based largely on Paul (2025a) which are in part based on previous efforts referenced therein, plus Longrich & Saitta 2024) and Zanno & Napoli (2025), with further additions and revisions following the characters employed in the phylogenetic matrix (see above and Phylogenetic Cladograms and Character Matrix). The diagnoses are differential cumulative character compilations for each taxon that when combined with some distinctive characters/apomorphies (indicated with an\*) are intended to detect and describe gradistic separation

of genera and species. Some characters known from only some members of a group are listed as general attributes of that group, with exceptions noted in the genus or species diagnoses when such is known to be the case. Because the number of *Tyrannosaurus* intragenera species is not a focus of this study, that taxon is diagnosed only at the genus level, with an emphasis on characters known to be present in juvenile remains. Diagnostic characters are sometimes overlapping non-bimodal between taxa at a given level, and not entirely consistent within taxon as per Maisch (2008), Maxwell (2012), Scannella *et al.* (2014), MacDonald & Currie (2018), Harvati & Ackermann (2022), Paul *et al.* (2022), Carr *et al.* (2022), Longrich & Saitta (2024). A few specimens have been reassigned or their status modified relative to Paul (2025a). Because the cumulative evidence presented in this analysis finds that some small TT-zone tyrannosaur fossils are not juvenile *Tyrannosaurus*, and as near adults they possessed adult attributes, their anatomical characteristics can be used to taxonomically define and diagnose them differentially from adult tyrannosaurins (Bakker *et al.* 1988; Larson 2008, 2013a, b; Schmerge & Rothschild 2016a,b; Longrich & Saitta 2024; Paul 2025a; Zanno & Napoli 2025). Synonyms for taxa are included only when specifically pertinent. Proportional data is contained in the Specimens and work thereon section of Materials and Methods, and the comparative figures of the specimens.

## SYSTEMATIC PALAEOLOGY

### North America baso-eutyrranosaur general

**Character attributes.** 1-2 tonnes, at least fairly gracile; anterior margin of premaxilla sloped dorsoposteriorly, ventral margin anteriorly upturned, form narrow U or V in dorso/ventral view, subnasal process faces anterolaterally, subnasal foramen absent, nasals narrow except broad where contact frontals, transversely fairly flat, contact with maxilla fairly smooth, maxilla long and low, ventral margin gently convex, antorbital fossa shallow, accessory antorbital fenestra small and does not contract rim of antorbital fossa, interfenestral pillar always broad, antorbital fossa rim broad along lower edge of antorbital fenestra, promaxillary recess small, posterodorsal process long and robust, posterodorsal process posteriorly elongated, deep medial recess above antorbital fenestra absent, medial sinus above antorbital fenestra small and shallow, medial antorbital fossa weakly developed, palatal shelves not elevated, lacrimal more T shaped with long posterodorsal projection, subtriangular hornlet present, antorbital fossa contribution deep, frontals participate in orbit rim, long and narrow in dorsal view although broad between lacrimals, contribute to short portion of sagittal crest, supratemporal fossa short, parietal nuchal crest broad, postorbital main body shallow, boss is subtle subcircular, knob-like discs limited to the frontal process that do not project above the dorsal rim of the skull, jugal process narrow and lacks orbital flange, jugal contact fairly straight, jugal anterior wing shallow, orbital margin long and gently curved, antorbital fossa contribution shallow, pneumatic recess shallow, quadratojugal process short, quadratojugal jugal process shallow: squamosal not large, ventral fossa lacks pneumatic recess, quadratojugal lateral foramen present, tip of quadratojugal process not squared off, abducens nerve nearly intersects pituitary fossa so sinus cavernosus, ascending diverticulum of anterior rostral tympanic recess present, condylotuberal crests strong, subsellar sinus extends into cultriform process, vomer anteriorly narrow and deep, palatine anterior processes long and slender, pneumatic fossa small, body weakly inflated, ectopterygoid pneumatic opening is a thin slot, dentary shallow, fairly straight in dorsal view, symphysis weak, long and prominent lateral groove usually present, interdental plates weakly developed, surangular contact slopes strongly anterodorsally, surangular shallow, lateral shelf short and not prominent, premaxillary teeth procumbent, lack serrations, atypically blunted, 15–16 maxillary and 16–17 dentary teeth that are bladed, anteriormost maxillary tooth incisiform; proatlantal arches strap-like; scapula blade neck not especially narrow, glenoid fossa extends onto lateral surface of scapula, humerus head not massive, forelimb often if not always elongated

distally, especially manus, so forelimb is about same length as femur or greater, and manus absolutely larger than those of adult tyrannosaurines; ilium shallow, dorsal rim fairly straight, anteroventral prong hook shaped, pubic boot gracile, femur fourth trochanter weakly developed, tibia cnemial crest gracile, rounded.

### **Genus *Appalachiosaurus* Carr *et al.*, 2005**

**Type species.** *Appalachiosaurus montgomeriensis* Carr *et al.*, 2005

**Holotype.** RMM 6670.

**Diagnosis.** 700 kg; Rostrum deep, subrectangular because of maxilla and anterior fossa boundaries forming an angle over 30 degrees, promaxillary fenestra not visible in lateral view; dentary tip not upcurved; 15 maxillary teeth, 7 teeth anterior to anterior end of antorbital fossa; femoral shaft strongly bowed; femur and tibia similar in length, metatarsus not highly elongated.

**Locality and horizon.** Late Campanian, lower Demopolis, Alabama.

### **Genus *Dryptosaurus* Marsh, 1887**

**Type species.** *Dryptosaurus aquilunguis* Cope, 1866

**Holotype.** ANSP 9995.

**Diagnosis.** 700 kg; manual digit 1 claw very large, humerus/femur ratio 0.375, manual phalanx 1-2/femur ratio 0.22 and forelimb probably longer than femur; femoral shaft nearly straight\*, femur and tibia similar in length, metatarsus not highly elongated.

**Locality and horizon.** Late/st Maastrichtian, upper New Egypt, New Jersey.

### **Genus *Nanotyrannus* Bakker *et al.*, 1988**

**Type species.** *Nanotyrannus lancensis* Gilmore, 1946

**Holotype.** CMNH 7541.

**Diagnosis.** ~500 kg; Mature skull fairly deep, subrectangular because of deep, blunt rostrum with maxilla and anterior fossa boundaries forming an angle over 30 degrees, 8 teeth anterior to anterior end of antorbital fossa, promaxillary fenestra not visible in lateral view, orbit large, jugal large and tall\*, quadratojugal tall, lateral temporal fenestra tall, jugal ventral cornual boss prominent, postorbital dorsal prong absent, frontoparietal peak prominent, quadratojugal-quadrato foramen large, paroccipital processes subhorizontal and distal ventral edge pendant, anterior palatine recess forms discrete pneumatic sinus extending anteriorly into maxillary process of palatine, dentary tip not upcurved and has prominent chin, dentary deep, posterior mandible deep, two small anterior dentary incisorforms, 15 maxillary and 16 dentary teeth, maxillary teeth neither large nor strongly recurved.

**Locality and horizon.** Late Maastrichtian, lower? Hell Creek, Montana.

### **Genus *Gilmoretyrannus* gen. nov.**

LSID urn:lsid:zoobank.org:act:1F0259D1-7F2B-4405-85A4-222ABFC9A490

**Etymology.** In honor of Charles W. Gilmore for recognizing the existence of multiple tyrannosaur taxa in the TT-zone, and Peter Larson for his extensive research on the hypothesis.

**Type species.** *Gilmoretyrannus lethaeus* Zanno & Napoli, 2025

= *Nanotyrannus lancensis* in Larson, 2013b

= *Nanotyrannus lethaeus* (Zanno & Napoli, 2025) Bakker *et al.* 1988

**Holotype.** BMRP 2002.4.1

**Potential referred specimens.** BMRP 2006.4.4? HRS 08?, HRS 15001?

**Diagnosis.** ~1 tonne; skull fairly shallow, subrectangular, 6 teeth anterior to anterior end of antorbital fossa, promaxillary fenestra not visible in lateral view, maxillary fenestra large, maxillary

flange weak, orbit not large, jugal, quadratojugal and lateral temporal fenestra not tall, dorsal prong present on squamosal process of postorbital, anterior palatine recess forms open fossa, anterior buttress on jugal process of palatine present, dentary tip not upcurved and has prominent chin, dentary moderately deep, posterior mandible moderately deep, probably 1 small anterior dentary incisiform, 15 maxillary and 17 dentary teeth, maxillary teeth fairly large and not strongly recurved; axial neural spine narrow and sharp tipped in lateral view, distinctly crenulated along entire anterior rim, single pleurocoel on axial centrum, caudal vertebrae apneumatic; entepicondyle of humerus subvertical in distal view, humerus/femur ratio ~0.38; strongly dorsally convex margin of posterior portion of pubic boot, pubic shaft bowed posteriorly, tibia markedly longer than femur, metatarsus very elongated.

**Locality and horizon.** Hell Creek, Lance, upper? TT-zone; Montana, Wyoming.

**Tribe Larsonvenatorini tribus nov.**

LSID urn:lsid:zoobank.org:act:477AB186-CF96-41A6-A58A-DF8069DE6EE6

**Type genus.** *Larsonvenator*

**Diagnosis.** Skull subtriangular because of sharp rostrum with maxilla and anterior fossa boundaries acute at an angle of ~30 degrees\*, dentary chinless and upcurved\*.

**Genus** *Stygivenator* Olshevsky, Ford & Yamamoto, 1995

**Type species.** *Stygivenator molnari* Paul, 1988

**Holotype.** LACM 28471

**Diagnosis.** 5 teeth anterior to anterior end of antorbital fossa, promaxillary fenestra not visible in lateral view, maxillary teeth large and strongly recurved except for one anterior small incisoriform, lateral dentary groove absent; height of the largest anterior maxillary tooth equals or even surpasses the depth of the dentary at its location\*.

**Locality and horizon.** Late Maastrichtian, upper? Hell Creek; Montana.

**Genus** *Larsonvenator* gen. nov.

LSID urn:lsid:zoobank.org:act:AEE95A79-81A9-4AC4-9B19-EA29404D22BC

**Etymology.** In honor of Peter Larson for his extensive research on the TT-zone tyrannosaur taxa great and small.

**Type species.** *Larsonvenator elegans* sp. nov.

LSID urn:lsid:zoobank.org:act:414AADD8-9888-4BDD-B19D-6A1012A0F333

=*Nanotyrannus lancensis* in Zanno & Napoli 2025

=*Stygivenator molnari* in Longrich & Saitta 2024

=*Stygivenator* sp. In Paul 2025a

**Etymology.** *elegans* meaning elegant in Latin.

**Holotype.** NCSM 40000 (ex BHI 6437).

**Provisional referred specimen.** Jodi.

**Diagnosis.** 700 kg; skull very shallow, 8 teeth anterior to anterior end of antorbital fossa, promaxillary fenestra visible in lateral view, maxillary fenestra small, orbit small\*, jugal not tall, quadratojugal short, lateral temporal fenestra short, postorbital dorsal prong absent, frontoparietal peak low, quadratojugal-quadratoquadrate foramen small, paroccipital processes slope lateroventrally and distal ventral edge straight, anterior palatine recess forms discrete pneumatic sinus extending anteriorly into maxillary process of palatine, dentary shallow, posterior mandible shallow, 16-17\* maxillary teeth are neither large nor strongly recurved, 2 small anterior incisiforms, 17-18 dentary teeth; height of the largest anterior maxillary tooth do not surpasses the depth of the dentary at its location; axial neural spine broad in lateral view, anterior rim poorly crenulated, two or more pleurocoels set in fossa on axial centrum\*, infraprezygapophyseal pneumatic recesses on anterior



proximal caudal vertebrae, caudal count 35; bulbous supraradiocondylar ridge and pronounced craniomedially projecting entepicondyle on humerus, pubic shaft straight, boot has straight anterodorsal, posterodorsal and ventral margins, humerus/femur ratio 0.39, manual phalanx I-1/femur ratio 0.22 and forelimb longer than femur, very elongated manual phalange I-1 markedly longer than those of adult *Tyrannosaurus*, as are manual claws, remnant phalange on manual digit 3; femoral shaft strongly bowed; tibia markedly longer than femur, metatarsus very elongated.

**Locality and horizon.** Late Maastrichtian, lower Hell Creek; Montana.

### **Subfamily Tyrannosaurinae Osborn, 1906**

#### **Tribe Tyrannosaurini Olshevsky, Ford & Yamamoto, 1995**

**Diagnosis.** 4+ tonnes, robust; rostrum deep, anterior margin of premaxilla vertical, ventral margin flat, form broad U in dorso/ventral view, subnarial process faces anteriorly, subnarial foramen present, nasals broad except narrow where contact frontals, transversely arched, contact with maxilla irregular, maxilla deep, ventral margin strongly convex, antorbital fossa deep, premaxillary fenestra not visible in lateral view, accessory antorbital fenestra fairly large and contracts rim of antorbital fossa, interfenestral pillar breadth variable, antorbital fossa rim narrow along lower edge of antorbital fenestra, promaxillary recess large, posterodorsal process short and slender, posterodorsal process posteriorly abbreviated, deep medial recess above antorbital fenestra present, medial sinus above antorbital fenestra large and deep, medial antorbital fossa well developed, palatal shelves elevated, lacrimal more L shaped with short posterodorsal projection, hornlet very shallow or absent, antorbital fossa contribution shallow, frontals do not participate in orbit rim, short and broad in dorsal view although narrow between lacrimals, contribute to long portion of sagittal crest, supratemporal fossa long, frontoparietal peak prominent, parietal nuchal crest is a ridge, postorbital main body deep, bosses highly variable in size and shape, jugal process broad and has often prominent orbital flange, jugal contact convex ventrally, jugal anterior wing deep, orbital margin short and strongly in cut, antorbital fossa contribution deep, pneumatic recess deep, jugal ventral cornual boss prominent, quadratojugal process fairly long, quadratojugal jugal process fairly deep, quadratojugal lateral foramen absent, intra quadratojugal-squamosal fenestra absent, squamosal large, ventral fossa has pneumatic recess, tip of quadratojugal process squared off, paroccipital processes subhorizontal and distal ventral edge pendant, abducens nerve does not nearly intersect pituitary fossa so sinus not cavernosus, ascending diverticulum of the anterior tympanic recess absent, condylotuberal crests strong, subsellar sinus extends into cultriform process, vomer anteriorly broad, palatine anterior processes short and robust, pneumatic fossa large, body inflated, ectopterygoid pneumatic opening is large; dentary tip not upcurved and has prominent chin, dentary deep, laterally bowed in dorsal view, symphysis well developed, prominent lateral groove absent, interdental plates well developed, surangular contact subvertical, posterior mandible deep, lateral shelf long and prominent, premaxillary teeth vertical, serrated, crowns not blunted, 11–13 maxillary and 12–15 dentary teeth at all growth stages, anteriormost maxillary tooth nonincisiform; proatlantal arches triradiate, caudal count 40+, mid-posterior centra not elongated, transverse processes expanded posteriorly, proximal haemal arches vertically elongate, mid haemal arches deeply curved; scapula blade neck slender, glenoid fossa does not extend onto lateral surface of scapula, forelimb very reduced\*, manus especially, to about two thirds femur length, humerus/femur ratio -0.27-.034, manual phalanx 1-2/femur ratio 0.053-0.96, mature manus absolutely smaller than those of at least some adult baso-eutyranosaurs, first manual phalanx of digit 1 not elongated, no phalanges on manual digit 3; ilium deep, dorsal rim dorsally arched, anteroventral prong weakly developed, pubic boot large; pubic shaft fairly straight, femoral shaft strongly bowed, femur fourth trochanter well developed, tibia cnemial crest large, squared off, tibia not elongated relative to femur even in juveniles, metatarsus not strongly elongated.

**Genus *Tyrannosaurus* Osborn, 1905**

= *Dinotyrannus* Olshevsky, Ford & Yamamoto, 1995

**Diagnosis.** 7.5 tonnes\*; 4-5 teeth anterior to anterior end of antorbital fossa, presence of anterodorsal process on anterior ramus of lacrimal that projects into nasal, dorsal lacrimals nearly meet at midline\*, sublunate in dorsal shape partly because lateral swelling on supraorbital process is absent\*, quadratojugal foramen absent, quadratojugal-quadratojugal foramen small, vomer sometimes has anterior spear point, contact with premaxilla not as extensive, anterior prong shallow, deep ventral flange absent, dentary lacks significant lateral groove, 11–12 maxillary and 12–14 dentary teeth at all growth stages, two (*T. imperator*) or one (*T. rex*, *T. regina*) small anterior dentary incisiforms, sometimes very large teeth robust; axial neural spine broad in lateral view, caudal count 42-43; humerus/femur ratio ~0.3; phalanx 1-2/femur ratio ~0.6; pubic boot massive.

**Type species *Tyrannosaurus rex* Osborn, 1905**

**Holotype.** CM 9380.

**Referred specimens.** As per Paul (2025a)

**Diagnosis.** As per Paul (2025a).

**Locality and horizon.** Latest Maastrichtian, upper and possibly middle Hell Creek and Lance, Ferris, Denver, Frenchman, Willow Creek, lower Scollard; Montana, Colorado, Dakotas, Wyoming, Alberta, Saskatchewan.

*Tyrannosaurus imperator* Paul *et al.*, 2022

**Holotype.** FMNH PR2081.

**Referred specimens.** As per Paul (2025a).

**Diagnosis.** As per Paul (2025a).

**Locality and horizon.** Late Maastrichtian, lower, lower middle and possibly middle Hell Creek and Lance, Laramie, Arapahoe; Montana, Dakotas, Wyoming, Colorado.

*Tyrannosaurus regina* Paul *et al.*, 2022

**Holotype.** USNM 555000 (MOR 555).

**Referred specimens.** As per Paul (2025a).

**Diagnosis.** As per Paul (2025a).

**Locality and horizon.** Latest Maastrichtian, upper and possibly middle Hell Creek and Lance, Ferris, Denver, Frenchman, Willow Creek, lower Scollard, lower North Horn?; Montana, Colorado, Dakotas, Wyoming, Alberta, Saskatchewan.

## RESULTS AND DISCUSSION

### Phylogenetics

The phylogenetic results (Figs. 11-14) are broadly similar to other recent efforts in general aspects, with the same taxa placing as either noneutyranosaur baso-tyranosauroids or as eutyranosauroids, and among the latter as baso-eutyranosauroids versus tyrannosaurids (Lu *et al.* 2014; Brusatte & Carr 2016; Carr *et al.* 2017; Dalman *et al.* 2024; Longrich & Saitta 2024; Voris *et al.* 2025; Zanno & Napoli 2025; Hernandez-Luna *et al.* 2026; Longrich *et al.* 2026a). Within each of these major groups relative placements of specific genera are often somewhat different than in the past efforts, these items are not a primary focus of this study.

Focusing in on the results that are most pertinent herein, the placement of the Appalachian *Appalachiosaurus* and long armed *Dryptosaurus* holotypes at or near the base of eutyranosauroids is as per the usual pattern. The new results agree with the positions of CMNH 7541, BMRP 2002.4.1,

HRS 08, LACM 28471 and NCSM 40000 outside short armed tyrannosaurids as per Longrich & Saitta (2024) and Zanno & Napoli (2025), contrary to the ETRH. This pattern obviously works against any one of these specimens being juvenile *Tyrannosaurus*. With the novel characters including those related to the limbs of the baso-eutyranosaurs incorporated, and LACM 28471 processed on its own, it scores as outside *Nanotyrannus* (contra Zanno & Napoli 2025). The latter as the holotype skull alone is basal relative to BMRP 2002.4.1, HRS 08, and NCSM 40000, with the last allied with similarly sharp snouted LACM 28471 (contra Zanno & Napoli 2025). *Nanotyrannus* does not share 5 synapomorphies with the clade containing BMRP 2002.4.1, LACM 28471 and NCSM 40000, and additionally does not share 4 synapomorphies with the Larsonventorini. The siting of CMNH 7541 in a clade with BMRP 2002.4.1, HRS 08, LACM 28471 and NCSM 40000 may be an artifact of the absence of postcrania with the *Nanotyrannus* holotype as further discussed below, it may be a short legged dryptosaur. BMRP 2002.4.1 and HRS 08 appear to form a clade.

Forming their own clade are sharp snouted *Alioramus* and *Qianzhousaurus* (Lu *et al.* 2014; Brusatte & Carr 2016; Carr *et al.* 2017; Dalman *et al.* 2024; Longrich & Saitta 2024; Zanno & Napoli 2025). Our results have them at the base of the clade that includes tyrannosaurids, similar to Carr *et al.* (2017), Dalman *et al.* (2024) and Longrich & Saitta (2024), the other studies place them well up in the family. If the new results are correct then the clade may be a sister family to tyrannosaurids. These results and alternative possibilities cannot be currently further tested via the nature of the Asian gracile's forelimbs because of those appendages being absent, but their not being especially close relatives of the North American baso-eutyranosaurs is indicated by features of their skulls and dentition. The results of the New Technology search with standard setting search equivalent to the strict consensus tree position *T. ? mcræensis* directly basal to TT-zone *Tyrannosaurus*, which is agreeable with its being at the base of the latter genus, or outside it on anatomical gradistic grounds (as noted above). In the traditional search the most parsimonious results have *T. ? mcræensis* basal to the rest of the tyrannosaurin including the Asian taxa, in which case it is not a *Tyrannosaurus* according to standard definitions of the species (but see comments below). Highly robust, spindle bossed *T. imperator* comes out as basal to later *T. rex* and *T. regina* with their derived single slender anterior dentary teeth, the exceptional gracility and lack of prominent orbital boss indicates *T. regina* is not within contemporary *T. rex* (Paul *et al.* 2022; Paul 2025a). Because the *Tyrannosaurus* species do not fall into a straightforward stratigraphic series their evolution via simple anagenesis is ruled out, the details of how *T. regina* and *T. rex* are interrelated is not clear.

### The actual juvenile *Tyrannosaurus* fossils

The study of *Tyrannosaurus* ontogeny has been seriously limited -- and the survival of the ETRH seemingly enhanced - by the absence of a fairly complete skull and skeleton below a subadult femur length of substantially below 1250 mm and 6 tonnes (Fig. 10A-F) if the CMNH, BMRP, HRS, LACM and NCSM fossils are excluded from the genus; unlike the substantial growth series for *Gorgosaurus* (Fig. 11 in Paul, 2025a) and *Tarbosaurus* (taxon entries in Paul 2024,a,b). But that does not mean there are not juvenile tyrant lizard fossils. As a collective USNM 6183, UCRC V1, LACM 23845, BHI 6439, KU 156375, UCMP 84133, MOR 1189, Baby Bob, and DMNS Teen Rex – the last being the most complete among the collection including the skull – possess the youthful attributes anticipatory of final adult form expected in medium sized juveniles of giant adult *Tyrannosaurus*. Among these are low maxillary and dentary tooth counts of 12–13 fairly robust teeth, anterior maxilla and antorbital fossa fairly deep, frontal not elongated, dentary robust, prominent lateral dentary groove lacking, femur about the same length as the tibia which is normal in juvenile albertosaurs and tarbosaurus of similar dimensions (Fig. 3B-D; Schmerge & Rothschild 2016a,b; Longrich & Saitta 2024, Paul 2025a; Raun *et al.* 2025a; Zanno & Napoli 2025). These

remarkable remains show little variation between them. Zanno & Napoli (2025) placed KU 156375 in *N. lancensis*, but it has a *Tyrannosaurus* grade low tooth count (Fig. 3C; Burnham *et al.* 2018).

The true pre/teen tyrant lizard fossils further show that basic attributes of the mighty tyrant lizard were already in place early in ontogeny, the juveniles being miniature proto *Tyrannosaurus*, stoutish in their few teeth and their bones, well on their way to becoming yet more so when mature. Even recently hatched *Tyrannosaurus* were miniatures of the genus (Longrich *et al.* 2026b). Dramatic changes in form with growth to adapt to ontogenetic shifts in niche partitioning did not happen beyond that seen in growing albertosaurs and, even more telling, in the fellow tyrannosaurin tarbosaur in which the young are similar in core attributes to their adult morphology (Figs. 4F, 6A–H; Longrich & Saitta 2024; p. 163 in Paul, 2024b; Figs. 11 in Paul, 2025a, Yun *et al.* 2025; Raun *et al.* 2025a; Zanno & Napoli 2025).

To put it another way, the amniote and tyrannosaurin growth pattern, and what is known of *Tyrannosaurus* juvenile fossils, mean that if some of those specimens were close to complete, the resulting series of same scale profile-skeletal growth series should be much like that of its close tyrannosaurin tarbosaur kin (as restored for Baby Bob in Figs. 4E, 10H). To recap, not required is the drastic divergences from regular amniote/diapsid growth courses forced by the ETRH (Table 1). Those divergences consisting of an exceptional degree of intraspecific anatomical variation within the juvenile population, followed by a similarly remarkable reduction in anatomical variation with growth that involves an extraordinary, nonamniote metamorphosis associated with a sudden transformation in morphobiology, a highly atypical diapsid tooth count contraction in variation via reduction – that in giants whose adult jaws are exceptionally long with plenty of space for lots of teeth -- nor irregular growth curves. *Tyrannosaurus* always looked like *Tyrannosaurus* as it matured, its growth was, as expected, fully within the amniote routine as per its sister taxon *Tarbosaurus* (Figs. 4F, 6A–H). There is not actual, positive evidence otherwise. The conservative, parsimonious, null hypothesis cannot be other than these youthful *Tyrannosaurus* fossils completely remove and entirely contradict the need or desire of the ETRH to force all lesser sized TT-zone tyrannosaur fossils into *Tyrannosaurus*. Also rendered moot is the Voris *et al.* (2025) observation of possible asymmetrical loss of one tooth in an adult *Tyrannosaurus*, since it would not have had many more teeth when young in any case (see Paul 2025a and Zanno & Napoli 2025; nor has the situation in other adult tyrannosaurids been documented to see if it differs from *Tyrannosaurus*).

Automatic assignment of juvenile *Tyrannosaurus* to *T. rex* should be avoided; the fragmentary condition of all the true juveniles of the genus, and limited stratigraphic information, precludes placing a number of the specimens in a particular tyrant king species (Paul 2025a). One of the exceptions is KU 156375. From the middle Hell Creek (Burnham *pers. comm.*), that, and its very broad interfenestral pillar, supports assignment of an apparent TT-zone juvenile *Tyrannosaurus* maxilla (Fig. 3C) to a late appearing *T. imperator* on a tentative basis. From higher in the zone, Baby Bob (Burnham *pers. comm.*), LACM 23845, RSM P2347 (Paul 2025a), and FMNH PR 4920 (Longrich *et al.* 2026b) are candidates for being juvenile *T. rex* or *T. regina*, further assignments not being practical (Paul 2025a) -- while LACM 23845 had potential as a taxon type if what is known of the fossil had proven highly distinctive from other TT-zone tyrannosaurins (as had been thought by Paul, 1988), it is too fragmentary and immature to be utilized as a type regarding the subtler differences between adult sibling intragenera species of *Tyrannosaurus* (Paul *et al.* 2022, Paul 2025a). With a number of undoubted juvenile *Tyrannosaurus* fossils on hand, the next question is whether all similar sized TT-zone tyrannosaur remains are also juveniles of the genus, or are so divergent from tyrant lizard juveniles and adults that they must be a different taxon or taxa?

**The subadult and adult non-*Tyrannosaurus* TT-zone fossils**

As a collective BMRP 2002.4.1 & 2006.4.4 1, CMNH 7541, DDM 344.1, FNMH PR2411, HRS 08, 15001, Jodi, KU 155809, LACM 28471, MOR 6625, NCSM 40000, RSM P2347.1 and TMP 80.16.425 possess attributes that dramatically differentiate and preclude them from being juvenile *Tyrannosaurus* and even tyrannosaurids (Fig. 11-14). Among them are long forelimb elements that in absolute measure are distally about as large or larger than those of adult *Tyrannosaurus*, maxillary and dentary tooth counts exceeding 12 and 14 respectively, teeth more bladed, sharper, more subtriangular anterior maxillae and antorbital fossae, frontal elongated, lack of subnarial foramen, intra quadratojugal-squamosal fenestra, quadratojugal foramen and prominent long lateral dentary groove present, caudal count markedly lower than tyrannosaurins, femur markedly shorter than tibia, metatarsus almost as long as adult *Tyrannosaurus* (Figs. 1, 3E-I, 4C,D, 7C; Table 1; Gilmore 1946; Bakker *et al.* 1988; Currie 2003; Larson 2008, 2013a,b; Schmerge & Rothschild 2016a,b; Longrich & Saitta 2024; Paul 2025a; Zanno & Napoli 2025). The delicate, skull and skeleton of shallow headed, long armed and gracile legged BMRP 2002.4.1, and the even more extremely shallow alioramin style headed NCSM 40000, could hardly be more different from the markedly more massive juvenile of similar overall dimensions of the tyrannosaurin closet to form and function of *Tyrannosaurus* (Fig. 4C,D,F). For the slender forms to have grown into a *Tyrannosaurus* would have required them to dramatically morph in osteological anatomy with growth in a manner common in nonamniotes, but not yet observed in amniotes. With their extra gracile form included exceptionally elongated distal hindlimbs, the likes of NCMA 40000 and BMRP 2002.4.1 are outside the growth series of even the relatively lightly constructed albertosaurs, much less the heftier tyrannosaurins (Fig. 4C,D,G). It is apparent that very lithe American fossils are not the latter or the juveniles of any giant morphotype, or even tyrannosaurids. With their not even being in the same family, it is less anatomically and developmentally logical to assert that the lithe TT-zone eutyrranosaur non-tyrannosaurids are juvenile *Tyrannosaurus* that should have appeared as suggested in Figure 3F, than would be proposing that felid fossils uncovered in the same deposits of ultra-gracile *Acinonyx* fossils were young *Panthera* (Fig. 4H,I). Or using alioramin remains to help restore the growth of tarbosaurus (Fig. 6).

The ETRH proposes that a single taxon was a superpredator that well fulfilled all tyrannosaur predatory niches in its habitat from delicate hatchlings of few kilograms through exceptionally gracile teens up to 7 plus tonne adults. Because the latter were such massive forms the taxon was effectively precluded from this all-encompassing role. Being on a growth trajectory to mature robusticity the juveniles had to always be on the heftier side of growing juvenile proportions to get to the stout adult condition as they remained in accord with the biological limitations of amniote/reptile growth. Because juvenile *Tyrannosaurus* could not be optimized for tyrannosaur style predation at any stage of immaturity, they were open to competition from mini eutyrranosaur that were better adapted to be hunters at modest dimensions.

The ETRH scenario being inherently unrealistic, the above specimens being so contrary in their attributes to being juvenile giant tyrannosaurins, and there being little if any actual anatomical or histological positive evidence that they are juvenile *Tyrannosaurus*, arguments otherwise have been comparatively radical, ad-hoc attempts to explain away the non-*Tyrannosaurus* features the long hands and too many teeth among them, Such being in accord with the ETRH because such might not be entirely biologically impossible, even if it is so far out of accord with other amniotes and/or reptiles and tyrannosaurids that it is extremely improbable at best. The few efforts to produce positive ETRH evidence from the specimens have failed. The seemingly *Tyrannosaurus* like anterior frontals of CMNH 7541 (Voris *et al.* 2025) are attributable to distortion and breakage of the fossil (Paul 2025a; Zanno & Napoli 2025). Their being so dramatically different from the authentic

juvenile *Tyrannosaurus* fossils of about the same size means the cited specimens cannot be fast-growing tyrant lizards as confirmed by their bone rings. Not only do juveniles not show so much morphological variation within a species or even within a genus, forcing all lesser TT-zone tyrannosaurs into one such taxon requires a sharp reduction in osteological variation with maturity, the opposite of the ontogenetic pattern in organisms. This includes the tooth reduction from as high as 17 to as low as 11 that is not seen in nonmarine, nonbeaked diapsids. The effort by Carr (2020) to selectively use the observations of Brown *et al.* (2015) to defend tooth loss in maturing *Tyrannosaurus* was contrary to the actual results of the latter paper (Longrich & Saitta 2024; Napoli 2024; Paul 2025a; Zanno & Napoli 2025). Supporters of the ETRH have to date evaded addressing these issues by ignoring the existence of the actual *Tyrannosaurus* juveniles (as per Carr 2020; 2025). Nor is sexual dimorphism an explanation for the variation among juveniles. Placing all these variants in *T. rex* would be broadly similar to squeezing all Nemegt tyrannosaurs great and small including *Alioramus* (Fig. 6I) into *T. bataar* when only some of the diverse lessers (Fig. 6D-H) are juveniles of that giant tyrannosaurin (Fig. 6A-C), these being easy to identify because they are visibly younger versions of their parents with which they share common characteristics.

If all the mini TT-zone tyrannosaur specimens were conventionally consistent in morphological form, then the ETRH would be the parsimonious null hypothesis, but that is not the case. Instead, the long forelimbs, manus especially (Figs. 4C, 5D-F) exclude the collection from tyrannosaurids, phylogenetically placing them as basal eutyranosaurs (Longrich & Saitta 2024; Paul 2025a; Zanno & Napoli 2025). To press all lesser TT-zone tyrannosaurs into *Tyrannosaurus* other than its true juveniles has been an outlier premise that strongly violates the principle null parsimony, and must be rejected. There never has been a paleozoological need for the modern ETRH, and there has never been actual positive evidence for it, the premise resting on perplexing efforts to explain away fatal defects of the hypothesis with increasingly questionably elaborate and thus extraordinary speculations not backed up by the necessary extraordinary evidence, and in some cases are errant (see Longrich & Saitta 2024 and Paul 2025a for further discussion). Instead, the remarkable degree of variation within the TT-zone non-*Tyrannosaurus* is itself so high that multiple taxa at least the species level and probably higher are indicated.

Carr has engaged in an ironic paradox. Although not always direct about it, he continues to be favour *Tarbosaurus* as a junior synonym of *Tyrannosaurus* (Carr 1999, 2020, 2022, 2025; in Hernandez-Luna *et al.* 2026 the synonymization is most explicit). A genus requires limited gradistic variation in the species it contains throughout ontogeny. Because that is the situation, the congeneric hypothesis is plausible (if the taxa shared a recent, presumably Asian common ancestor which may or may not be correct; Dalman *et al.* 2024; Paul 2025a; Longrich *et al.* 2026a; also a possible *Tyrannosaurus* in this context is *Zhuchengtyrannus*, particularly if it is intermediate to *Tarbosaurus* and *Tyrannosaurus* as implied by Dalman *et al.* 2024, also see Longrich *et al.* 2026a). But if *Tyrannosaurus* featured a growth pattern as far different from the conventional course observed in *Tarbosaurus* that has been proffered by Carr, then they a priori are poor candidates for being the same genus. Carr (2025) casually assumes that CM 7541, BMRP 2002.4.1, FMNH PR2411 and LACM 28471 are juvenile *T. rex* without citing the extensive new work of Longrich & Saitta (2024) and Paul (2025a) indicating otherwise, risking contaminating his comparative anatomy of the taxon.

### Growing up not to be *Tyrannosaurus*

The ETRH compatible smooth *Tyrannosaurus* growth curve in Figs. 12, 22-25 in Carr (2020) was based on Erickson *et al.* (2004), that has been obsolesced by Woodward *et al.* (2026). Although including CMNH 7541, and BMRP 2002.4.1 and 2006.4.4, the plot was not based on actual,

smoothly continuous growth ring sequences from the specimens, Instead the fossils actual bone histologies do not conform to the errant curve (Longrich & Saitta 2024; Paul 2025a; Zanno & Napoli 2025; Woodward *et al.* 2026). The MTTH in contrast predicts that modest sized baso-eutyranosaur growth markedly diverged from that of juvenile *Tyrannosaurus* of the same size, as the former slowed down and terminated growth entering maturity, while the latter accelerated mass gains at the middle of their growth cycle. Potentially complicating the issue is that reptilian and avian LAG may be deposited more than once a year in many cases (Paul 2012, Chinsamy & Pereyra, 2026). This factor can mean a faster rate of growth than indicated by ring counts, but should not impact comparative patterns of growth. The results of Cullen *et al.* (2020), Woodward *et al.* (2020, 2026), Jevnikar & Zanno (2021), Longrich & Saitta (2024), Paul (2025a) and then Zanno & Napoli (2025) have found that the BRMP duo experienced a decrease in the pace of growth going into their teens that parsimoniously is most and biologically entirely compatible with their being subadults that would not exceed a tonne. And CMNH 7541 was adult at about half a tonne according to Griffin *et al.* (2025; confirming Gilmore 1946; Bakker *et al.* (1988)), while 600 kg NCMS 40000 was nearly grown up (Zanno & Napoli 2025). Because these results are entirely compatible with and strongly supportive of the MTTH, that the growth data correspondingly affirms the latter means it is the conventional, parsimonious null conclusion.

Having analyzed the largest yet sample of *Tyrannosaurus* specimens to restore the taxon's growth, Woodward *et al.* (2026) proceed to speculate that those TT-zone tyrannosaur fossils that fall out of the normal curve of the genus may – if it happens they are in the taxon -- experienced atypical disruptions, or alternative courses, as somehow erratic juveniles of the tyrant lizard. This is done by combining all the remains in a *Tyrannosaurus rex* species complex. This would be like combining the growth data of all Nemegt tyrannosaurs including *Alioramus* into a *Tarbosaurus bataar* species complex. With the latter venture unlikely to be conducted, the question arises why it was done with the TT-zone remains, and the utility of doing so is not apparent. If not for the ETRH having been widely adopted, it is doubtful the *T. rex* species complex would have been proposed, it now coming across as obsolete and improbable thesis in search of a theoretical home. It is a nonparsimonious and therefore weak ad hoc hypothesis that meets no particular current need. There not being any, much less compelling, morphological evidence that any of the slow growth specimens were *Tyrannosaurus* in the first place. Only if the latter were true would it be necessary to consider and perhaps accept their early slowing growth as within *Tyrannosaurus* bounds, and try to produce explanations for the diversion from the taxon's norm. Ascribing the similar growth of the BMRP pair to similar conditions within their common habitat (Woodward *et al.* 2026) does not explain NCMS 40000 and CMNH 7541 sharing the same attributes, they being from different environments. That the preserved growth of little DDM 35 is within the curve of small *Tyrannosaurus* is not informative because it died before the growth curve divergence of the maturing baso-eutyranosaurs. Combining the course of maturation from different species to restore growth at genus level is inherently problematic (Paul 2025a), but sibling species of the same adult size have a good chance if not probability of being similar. The fitting of all the actual *Tyrannosaurus* sample into a single coherent curve (Longrich *et al.* 2026b; Woodward *et al.* 2026) is therefore not necessarily incompatible with the speciose *Tyrannosaurus* hypothesis, that neither predicting nor requiring a differentiation between the similar sized sibling species in this factor. Although irregular growth in *Tyrannosaurus* may be biologically plausible, that there is no actual evidence of such within fossils anatomically assignable to the genus or any of its species, leaves the Woodward *et al.* (2020, 2026) hypothesis a paleoosteological stretch that is as entirely unnecessary, as it is inferior to the conservative MTTH null alternative.

### The many lesser-sized TT-zone baso-eutyrranosaur taxa

In the wake of the new consensus that many or most mini TT-zone tyrannosaurs are not *Tyrannosaurus* or even Tyrannosauridae (as per Longrich & Saitta 2024; Paul 2025a; then Zanno & Napoli 2025; Hernandez-Luna *et al.* 2026, Longrich *et al.* 2026a), a number of taxonomic questions ensue that shall be discussed in this section.. Are they all *N. lancensis*, or do they record a larger number of taxa? If the latter is operative, how many genera and/or species do they represent? Are any of the remains requiring assignment to previously named taxa, or new names? The last question is dependent in part on TT-zone fossils not always being synonymous with the tyrannosaurs of Appalachia. What sub/family or sub/families do the fossils belong to, and do any necessitate new names?

A distinctive feature of Tyrannosauridae is the very small size of their two fingered forelimbs, including the manus (Figs. 4F, 10). It follows that any tyrannosaurs that possess larger fore appendages are very probably not tyrannosaurids, instead being more basal eutyrranosaur (see Phylogenetic Cladograms and Character Matrix section below). That is assumed to be the case herein for the TT-zone non-*Tyrannosaurus* specimens, at least some or all of which probably had larger hands at least relatively and in some cases absolutely than the great tyrant lizard (Larson 2013; Paul *et al.* 2022; Longrich & Saitta 2024; Paul 2025a; Zanno and Napoli 2025). In any case, the focus of this study is on comparative genus and species status over exact phylogenetic position, the latter appearing to be undeterminable at this time due to limited data.

With it clear that most non-*Tyrannosaurus* like specimens are also too different from juvenile and adult *Tyrannosaurus* to be such, it has sometimes been presented that they themselves all reside on one taxon, presumably *Nanotyrannus* at least at the genus level, if not *N. lancensis* specifically (Larson 2008 2013a,b; Zanno & Napoli 2025). This is uncomfortably similar to placing all giant TT-zone *Tyrannosaurus* in *T. rex*, the synonymies need to be shown to be the superior hypothesis. If the non-*Tyrannosaurus* fossils all show a tight osteological similarity, then the every small taxon is *Nanotyrannus lancensis* hypothesis (ESTNLH) is correct. If otherwise, then the multiple small taxa hypothesis (MSTH) is operative, it being a viable possibility in view of the presence of more than one mini tyrannosaur in Asian faunas at least on occasion. That the degree of anatomical diversity that is detailed in this study being a good deal higher among 1 tonne or less TT-zone tyrannosaurs than within the species of *Tyrannosaurus* which helps show that most of the former are not juveniles of the latter, further favours substantial taxonomic diversity among the lessers. If anything, the greater osteological variation in the smaller tyrannosaurs is likely to reflect even more species and even generic separation that observed in the one genus *Tyrannosaurus*, within which the amount of inconsistency is compatible only with intragenera sibling species. The MSTH is correspondingly highly viable. The next question is whether there is substantial confirmatory evidence in its favour.

Visual examination of the profile cranials (Figs. 1, 3E-I) and skeletal (Fig. 4C,D) of the TT-zone baso-eutyrranosaur readily reveals the manifest morphological divergences between them that is detailed in the systematic diagnoses. There is more differentiation between the skulls than seen in skulls of all three adult *Tyrannosaurus* species combined (Fig. 8F-J). Nor do multispecific *Allosaurus* (Fig. 8A,B), or *Daspletosaurus* (Fig. 8C-E), contain such variation. Among the complete TT-zone baso-eutyrranosaur crania, that of NCSM 40000 is particularly and strikingly distinctive in its low profile, long, shallow, pointed rostrum including a pointed anterior end of the maxillary fossa and fenestra, shallow dentary with an upcurved, chinless tip, reduced posterior mandible complex, and a high tooth count. Also distinctive are the peculiar proportions of its small skulled long legged skeleton as seen in Figure 4C. There is more divergence in these fossils than is seen among the likes of *Corythosaurus* and *Lambeosaurus* (Suppl Fig. 4 in Paul 2025a, also 2024a),



*Centrosaurus* and *Styracosaurus* (Paul 2024a), within *Canis*, *Panthera*, *Metarhinus* (SupplFigs. 2, 3 in Paul 2025a), and is broadly similar to or exceeds that dividing sister genera such as *Ceratotherium* and *Diceros*, or *Plesippus* and *Equus*. Placement of NCSM 40000 in the same genus as either CMNH 7541 or BRMP 2002.4.1 is not viable on basic gradistic grounds, the anatomical differentiations between the specimens exceeding those observed in other dinosaur genera.

Within the context of the baso-eutyranosaur cranial gestalt, the gracile and delicate NCSM 40000 versus tall, stout and blockish CMNH 7541 are sharply divergent in overall configuration and numerous details (Figs. 1A,C, 2, 3E,H). Those include the much more prominent dorsal crests of the 7451 temporal box, a conspicuous ventral jugal boss, the promaxillary fenestra not visible from the side, larger quadratojugal-quadrato fenestra, more horizontal paroccipital process, larger orbit, dentary chin, less teeth and other items cited in the diagnoses. The differences are so dramatic that they indicate major functional differences in predatory actions, and visual display at the aft skull roof.

Being clearly distinguished by phylogenetic scoring and positioning (Figs. 11-14), it is questionable whether such can be contained in a subfamily, it is well beyond the species or genus norm. What NCSM 40000 osteologically is easily most similar to the perhaps slightly smaller *S. molnari* holotype (Figs. 3E,F; Longrich & Saitta 2024; Paul 2025a), with them phylogenetically plotting as sister taxa (Figs. 11-14). Being only a rostrum, anterior dentary and a few other minor elements, LACM 28471 is a quite poor holotype bordering on *nomen dubium* status (which Zanno & Napoli 2025 think it is; Longrich *et al.* 2026a consider it valid).

Placing other specimens in *S. molnari* or *Stygivenator* risks rendering the genus and species wastebasket taxa. Even so, there is a sufficient diagnostic differentiation between LACM 28471 and NCSM 40000 to assess if they appear to be the same taxon or not. They share the same unusually sharp pointed anterior maxillae and antorbital fossae, and upcurved, chinless dentary tips not present in other TT-zone baso-eutyranosaurs (Fig. 3G-I). These features readily exclude both of them from the squarish nosed *Nanotyrannus* anatomical mold, barring them from inclusion in that genus (contra Zanno & Napoli 2025).

It follows that, regardless of its qualifications as a type, LACM 28471 should not be subsumed into *Nanotyrannus* without presenting strong comparative evidence of its taxonomic compatibility gradistic and otherwise (as per Longrich *et al.* 2026a), and the specimen consequently needs to be scored separately in phylogenetic analyses. *Stygivenator*'s enlarged, hooked teeth (Fig. 3F,H; condition confirmed by Ford *pers. comm.*) render its placement in *Nanotyrannus* all the more gradistically untenable.

The distinctive shared features do indicate that NCSM 40000 and LACM 28471 are closely related members of the same distinct subclade, and Paul (2025a) tentatively placed them in the same genus. There are, however, marked differences between the two that further indicate they are not intragenera sibling species. In 28471 just five tooth sockets are anterior to the anterior end of the antorbital fossa, for 40000 it is eight. The crooked maxillary teeth of *S. molnari* are much larger and more recurved (Fig 3F). NCSM 40000 sports two small incisiform teeth at the anterior end of the maxilla, LACM 28471 one. The promaxillary fenestra is laterally visible in one but not the other. Unusual for baso-eutyranosaurs, LACM 28471 lacks evidence of having the dentary groove that is so prominent in NCSM 40000 and other TT-zone baso-eutyranosaurs, although its presence posteriorly cannot be ruled out with that section of the element not preserved. These differences are too extensive and major to be contained in a dinosaur species, all the more so since sexual dimorphism has not been shown to exist on such a scale in a dinosaur taxon, including predatory (as noted in Paul *et al.* 2022 and refs. therein; Paul 2025a). Nor are such extensive divergences present

within tyrannosaur genera, matching or exceeding for example that between *Albertosaurus* and *Gorgosaurus* or *Tyrannosaurus* and *Tarbosaurus* (Fig. 2 in Paul 2025a), or within *Daspletosaurus* (Fig. 6C-E) or *Tyrannosaurus* (Fig. 8F-J), as well as *Allosaurus* (Fig. 8A,B).

In any case, assigning the superb NCSM 40000 fossil to the at least near *nomen dubium* that is the fragmentary LACM 28471 is itself problematic, all the more so because if the latter specimen were more complete it likely would show yet more differences with NCSM 40000. And the possibility that there is a substantial time difference between the fossils is itself systematically significant. Nor is it plausible to assign the extreme form that is NCSM 40000 with its low, stretched snouted, small orbit, exceptionally high tooth count and other items to any other known TT-zone taxon on grade grounds alone. The flawed type CMNH 7541 included. Contrary to Longrich and Saitta (2024), Paul (2025a), and Zanno & Napoli (2025), because it does not fit well into any available binomial taxon to the degree that researchers cannot agree which it belongs in, NCSM 40000 requires its own genus and species, *Larsonvenator elegans*. Whether it and *Stygivenator molnari* were contemporaries, or separated by time, is not yet certain; the latter is more probable than not. Being diagnostic, *Stygivenator molnari* is retained for the time being at least. These taxa are sufficiently allied with one another, and distinctive from other TT-zone baso-eutyrannosaurs – the exceptionally acutely sharp anterior maxilla being a distinctive apomorphy relative to other late Maastrichtian North American baso-eutyrannosaurs (that were perhaps paralleled in Asian tyrannosaurs (Fig. 6I) -- that they can form a subfamily tagged after the much more complete fossil of the two, Larsonvenatorini. That awaits assignment as the family level circumstances are sorted out as discussed below.

Lacking any postcrania, and having suffered significant cranial damage, CMNH 7541 is a deficient holotype bordering on a *nomen dubium* (most so regarding issues regarding potential *Tyrannosaurus* species and their names, Paul *et al.* 2022; Paul 2025a) - it is somewhat better in this regard than LACM 28471, but not by a lot. The lack of postcrania is an especially critical phylogenetic and taxonomic deficiency of the mini tyrannosaur. Lacking such, it cannot be ruled out that the specimen is a *Dryptosaurus* or relative which has a straight shafted femur that is about the same length as the robust tibia (Figs. 4B, 7A; Carpenter *et al.* 1997; Brusatte *et al.* 2015), or a close relation.

That *Nanotyrannus* falls out closest to the Appalachia baso-eutyrannosaurs among the TT-zone specimens (Figs. 11-14) elevates this possibility. In contrast NCSM 40000, BRMP 2002.4.1 and possibly BMRP 2006.4.4 have to be dismissed as dryptosaurs because they have elongated tibiae and metatarsals, and/or more bowed femora (Figs. 4B-D, 7C,D). Assigning these and other specimens to ambiguous *Nanotyrannus* in view of this large data gap is correspondingly problematic and best avoided unless harder evidence indicates otherwise, and the evidence on hand does not indicate otherwise. Likewise, if the 7451 maxilla is so distorted that its true shape cannot be determined as Zanno & Napoli (2025) hint, then its taxonomic utility is further undermined, and placing numerous other specimens in the taxon is all the more problematic, risking making *Nanotyrannus* a wastebasket taxon if other specimens are placed in it. So while using the extreme graciles to characterize and diagnose the postcrania of *Nanotyrannus* may hit the mark, it is at significant risk of being seriously errant.

Although CMNH 7541 and BRMP 2002.4.1 are less extremely divergent from one another than either is from the larsonvenatorins, the differences are still extensive; of the two the *N. lancensis* skull is deeper and shorter snouted, the orbit is much larger, the jugal is much larger and the quadratojugal and lateral temporal fenestra taller and perhaps shorter fore-and-aft, the teeth are smaller, and there apparently are two more teeth anterior to the anterior end of the antorbital fossa, the mandible is more robust, and the dentary is squarer tipped than BRMP 2002.4.1 (Figs 1A,B,

3G,H). The status of the intra-quadratojugal-squamosal fenestra is not clear in *N. lancensis*, although it is very likely to have had the condition. Its prominent ventral jugal cornual boss, a potential visual taxon identification feature similar to that seen in many tyrannosaurids, is distinctive from the much less developed processes of BMRP 2002.4.1, and HRS 08, as well as sharp snouted NCSM 40000 and LACM 28471.

The extensive phylogenetic work has BMRP 2002.4.1 distinct from more basal *Nanotyrannus*, and nearer larsonvenatorins. Zanno & Napoli (2025) are correct that CMNH 7451 and BMRP 2002.4.1 are not the same taxon, which they distinguished at the sibling species level of *N. lancensis* and *N. lethaeus*. But BMRP 2002.4.1 is gradistically and it follows functionally set well between CMNH 7451 and NCSM 40000. And the differences between the first two – again -- exceed those present within other tyrannosaur genera, being gradistically comparable to those that distinguish *Albertosaurus* from *Gorgosaurus*, and exceeding those observed in *Daspletosaurus* or *Tyrannosaurus* (Fig. 8C-J), or *Allosaurus* (Fig. 8A,B). Longrich *et al.* (2026a) justifiably consider BMRP 2002.4.1 to be outside the low quality *Nanotyrannus* type, but their placing it in also deficient *Stygivenator* is not viable either (compare Fig. 3F to G). Ergo, the well preserved BMRP 2002.4.1 needs its own genus, and is therefore the holotype of *Gilmoretyrannus lethaeus*. HRS 08 (Fig. 3I) is more similar to the latter in the modest size of its jugal and quadratojugal relative to the maxilla than to *N. lancensis*, and is a sister specimen with BMRP 2002.4.1, and is tentatively referred to at least that genus. That the configuration of the HRS 08 antorbital fossa is distinctive may indicate it was a distinct species, but naming it such is not yet warranted. KUVF 155809 is from very low in the Hell Creek (Burnham, *pers. comm.*), whether it is similarly stratigraphically placed with *Nanotyrannus* or *Larsonvenator* is not apparent at this time. Lacking postcrania in one case, nor can it be determined if these form a subfamily. Whether they are such or not, rounder snouted, square jawed *Nanotyrannus* and *Gilmoretyrannus* are easily distinguished and diagnosed at the genus and even higher level from the sharp nosed, relatively chinless larsonvenatorins, BMRP 2002.4.1 and its cohort being differentiated from NCSM 40000 and LACM 28471 by the large sets of details in the differential diagnoses. The difference in that case is at least as great as it is between *Tyrannosaurus* and *Daspletosaurus* (Fig. 8F-J versus C-E). With NCSM 40000 removed from *Nanotyrannus* the diagnoses of the latter genus and its species are significantly altered and more specific from those in Zanno & Napoli (2025). Due to the great morphological variability found in TT-zone baso-eutyrranosaur, their placement in one genus does not enjoy parsimony or null status.

Zanno & Napoli (2025) focus on cladistics and particular characters to sort out taxonomic assignments, such as NCSM 40000 (and its well-developed anterior palatine pneumatic chamber) and the *S. molnari* holotype being within *N. lancensis* that both are markedly divergent in basic form from. They do so without seeming to consider the overall anatomical configurations of the fossils' remains in order to assess the total gradistic differentiations that are also critical to generic assignments. They logically exclude BMRP 2002.4.1 from the quite different *N. lancensis*, but they then illogically place NCSM 40000 in that species even though it is clearly even more anatomically divergent from CMNH 7451 than is 2002.4.1. This study further finds that characters that Zanno & Napoli (2025) consider markers of genera, instead characterize a more general sub/family level, judging from the more limited degrees of variations observed in other Late Cretaceous tyrannosaur genera. Features of this type may include the openings present in baso-eutyrranosaur quadratojugals, as future research may determine.

Despite the much smaller fossil sample size relative to the dozens of known *Tyrannosaurus* specimens, substantially more baso-eutyrranosaur taxa are observed in the TT-zone, including genera, than among the tyrant lizard. The latter being limited to the one genus *Tyrannosaurus* in spite of it including significant species grade diversity (Figs. 8F-J, 10; Paul *et al.* 2022; Paul 2025a;

provisionally Longrich & Saitta 2024; Zanno & Napoli 2025). This does not arise from our propensity to automatically split specimens based on minor individual or subgeneric variations – after all Paul (2025a) places dozens of specimens in *Tyrannosaurus*, and about a dozen of them each in the three named species. The conclusion stems from their simply being more gradistic and functional diversity contained in the limited baso-eutyranosaur remains than the entirety of the giants' combined fossil collective. Comparing Figure 1 to Figure 8F-J, the *Tyrannosaurus* crania are more consistent in overall profile and dimensions of the major elements, including the jugal and quadratojugal. Differences in that genus focus on the postorbital bosses which are exceptionally divergent species specific display features of the tyrant lizard (Paul 2025a). Even if all *Tyrannosaurus* specimens are squeezed into just *T. rex*, the much greater differentiation between its contemporary baso-eutyranosaurs in the same formations indicates they were more taxonomically diverse. As the future sample of baso-eutyranosaurs gradually expands it can be expected that many of the specimens will be assigned to the designated taxa. In any case, predator diversity being normally higher among smaller examples in a given habitat, it is not surprising this is proving true in the TT-zone. Aside from their being intrinsically taxonomically necessary, the new names are designed to help redirect researchers from, as has been the habit, of over-focusing on *Nanotyrannus* as being the go to name for all or most of the lesser TT-zone tyrannosaur fossils that are not *Tyrannosaurus*. With the MSTH heavily favoured over the ESTNLH, there are now four diagnosable genera in that collection of remains.

A question is whether any of the TT-zone lesser taxa are synonymous with similar residents of Appalachia. It is very improbable that any late Maastrichtian baso-eutyranosaur belonged to the same species as late Campanian *Appalachiosaurus montgomeriensis* (Figs. 4A, 7B) it having lived about 11 Ma years earlier (Carr *et al.* 2005). Being in the same genus is less improbable, although still a stretch. In any case, the tibia of the holotype is about the same length of the femur (Carr *et al.* 2005), unlike *Gilmoretyrannus* and *Larsonvenator* in which the tibia is markedly longer than the femur (Figs. 4C,D, 7C). This effectively excludes the two new genera from sharing the same genus as the older eastern avepod. Being a contemporary of the TT-zone fauna, and sporting a long manus, *Dryptosaurus aquilunguis* is a candidate for being conspecific or congeneric with western late Maastrichtian baso-eutyranosaurs. However, the nearly straight femoral shaft, and/or low tibia/femur ratio of ANSP 9995 (Figs. 4B, 7A), indicate larsonvenatorins and *Gilmoretyrannus* (Figs. 4C,D, 7C,D) are not its close relations. Conversely, the exceptionally large *Dryptosaurus* thumb claw, and a more robust forelimb, add to its separation from *Gilmoretyrannus* and *Larsonvenator* (Figs. 5D-F, 11-14). Whether postcrania absent *Nanotyrannus lancensis* with its skull distinct from other regional tyrannosaurs, and nearly headless ANSP 9995 are the same taxon at least at the subfamily level, and possibly down to species, is up for taxonomic grabs. They share a lateral dentary groove. But the fragmentary nature of ANSP 9995 may qualify it as a *nomen dubium* for taxonomic purposes while CMNH 7541 is not much better. Further remains of these taxa are required to resolve these issues. As it is, the possibility of the synonymy at the family or below level is additional reason to be cautious about emphasizing *Nanotyrannus* as the central taxon of the non-*Tyrannosaurus* TT-zone fossils. And the possibility that some western tyrannosaurs are within an eastern species or genus consequently cannot be ruled out.

The high diversity taxonomic and otherwise of the TT-zone baso-eutyranosaurs reinforces that these are not the anatomically uniform specimens expected if they were juvenile *Tyrannosaurus*. To put it another way, with CMNH 7541, NCMS 40000 and BRMP 2002.4.1, *et al.* too different from one another to be placed in the same species or even genus as sub/adults, they cannot be placed as juveniles within a united taxon.

## Family troubles

*Dryptosaurus* has its own family Dryptosauridae, the foundation of which is weak in view of the fragmentary specimen it is based upon (Fig. 4B) – a situation that is not likely to improve in the near future if ever because of the limited exposures of the New Egypt Formation. Zanno & Napoli (2025) placed the two *Nanotyrannus* species in their own family, Nanotyrannidae. This is plausible if *Nanotyrannus* had elongated distal hindlimbs, but problematic because of the adequacy concerns with the skull only holotype, and because it therefore cannot be ruled out that it is a dryptosaurid at this time. If that ever happens Nanotyrannidae will be subsumed into Dryptosauridae (a similar result is seen in the Bayesian tree, Fig 14). That possibility has the possibility of being tested by the finding at some point of more complete CMNH 7541 type postcrania in the extensive TT-zone deposits. The ability of phylogenetics to deal with the situation is limited because *Dryptosaurus* cannot be scored for critical cranial characters. And the postcranial attributes of *N. lancensis* cannot be reliably scored either. Our results (Figs. 11–14) suggest but do not establish that *Nanotyrannus* is not in the same family as other TT-zone mini tyrannosaurs. Until the fossil data base is improved, there is no good resolution for the north American baso-eutyrannosaur family problem (as noted by Paul 2025a). It is possible that both families are valid, in which case Larsonvenatorini is likely under Nanotyrannidae. And/or Larsonvenatorini may need to be elevated to sub or full family status. Because *Gilmoretyrannus* is at least gradistically quite distinct from all other genera its higher level status is indeterminate. In view of these currently recalcitrant paleotaxonomic vexations, this analysis does not set up and diagnose baso-eutyrannosaur families, and Larsonvenatorini is a taxonomic floater among baso-eutyrannosaurs at this time. This is similar to some other intrinsically ambiguous dinosaur sub/family conundrums, such as those afflicting titanosaurs, as per Utetitaninae (Paul 2025b).

## Where did so many TT-zone baso-eutyrannosaurs come from? And why did they do so well?

In the ETRH, the origin of known TT-zone tyrannosaurs has simply been that of *Tyrannosaurus*. With the MTHH widely accepted, the circumstances were much more complicated in evolutionary-diversity-geographic terms. The TT-zone was inhabited by a host of mini baso-eutyrannosaur taxa of about a tonne or less when adult, dwelling alongside elephant sized tyrannosaurid species. The number of the latter is three in one genus (Paul *et al.* 2025; Paul 2025a, two are named in Longrich & Saitta 2024; number not specified Zanno & Napoli 2025), the lessers number four for a combined seven species, in five genera. In that case, the tyrannosaur diversity within the habitat was on the high side compared to other tyrannosaur dominated faunas. That when the diversity of TT-zone herbivorous ornithischians appears to have been lower than prior in the region (Fowler 2017; Paul 2010, 2016, 2024a,b). But that tendency cannot be used to reliably assess the diversity of the predatory fauna, which can only be achieved via the degree of morphological variation observed in the comparative anatomy of the fossil population. Because it was common for Mesozoic dinosaur bearing formations and dinosaurs faunas to include more than one giant avepod including tyrannosaurids, multiple species of TT-zone *Tyrannosaurus* is a norm rather than requiring special explanation. It is the multiplicity of the smaller taxa as per the MTHH that is indicated in their exceptional variation that may appear atypical among tyrannosaurs, for which there is usually one identified lesser taxon in a given habitat (Brusatte *et al.* 2009, 2016; Lu *et al.* 2014; Brusatte & Carr 2016; Paul 2010, 2016, 2024a,b). That the TT-zone has been exceptionally heavily prospected since the late 1800s is a factor in its exceptionally high observed tyrannosaur diversity. And it is not as though all the TT-zone tyrannosaurs shared the same paleohabitat. The possibility of graciles migrating into the region from multiple directions may be a factor. The TT-zone consists of seven formations laid down over considerable time and territory. The large number of named taxa appears to reflect discreet sampling of a diverse sets of baso-eutyrannosaur populations over that time and

space. Although the details remain obscure, while lower Hell Creek *Nanotyrannus lancensis* and *Larsonvenator elegans* may or may not have lived in the same time and place, neither probably dwelled alongside *Stygivenator molnari* and *Gilmoretirannus lethaeus*, which in turn may or may have not been within the same given fauna at the same time. There are no cases to date of more than one tyrannosaur taxon being found in the same quarry; shifting territorial ranges at small and large scales differing habitat/niche preferences, and the like may have reduced real world competition among species that are found in the same gross formation level. Note that restorations of specific TT-zone habitats should avoid portraying taxa that were unlikely to have been contemporaneous; potentially lower Hell Creek *N. lancensis* and *L. elegans* might have encountered one another, *G. lethaeus* was probably not yet extant.

All that said, a nontypical causal explanation for the systematic diversity anomaly is called for. That appears to be an exceptional regional geological-geographic event that was underway during the later portion of the Maastrichtian. The reunification after tens of millions of years of the North American continent resulted from the emergence of the Laralachia (Paul 2024b, 2025a) land bridge as the interior seaway withdrew (a hypothesis later supported by Zanno & Napoli 2025). Basal eutyranosaurs, at least some bearing an elongated manus, had been evolving in Appalachia. The new route west allowed them to invade Laramidia and intermingle with its short-armed tyrannosaurids. The degree to which late Maastrichtian baso-eutyranosaur taxa were direct imports from Appalachia, or had evolved into new taxa since crossing the bridge, cannot be resolved with the data on hand. It is possible that not all the invaders were from eastern North America, some may have moved in from Asia via Beringia. Alioramin skulls are in particular similar to those of larsonvenatorins, sharing a distinctive sharp snout and upcurved, chinless anterior dentary (compare Figs. 1C to 6I). The sparsity of information on the dimensions of alioramin forelimbs stands in the way of settling this possibility to the degree that reliable phylogenetic results cannot be obtained, and whether the Asian examples were tyrannosaurids or basal to the family. For these modest-sized predators to make their way across the high latitude bridge would have been easier than for the giant tyrannosaurins. In those circumstances the unusual high diversity is yet better explained by immigration into the TT-zone faunas from multiple directions.

From wherever they came, the resulting intermixing in the TT-zone appears to have gone well for the new residents, with their fossils outnumbering those of juvenile *Tyrannosaurus* by half or more again; it is possible that the former were suffering higher mortality rates. Relative to the derived tyrannosaurids, baso-eutyranosaurs retained the more common theropod condition of substantial arms and hands in lieu of a massive head (Scherer *et al.* 2026). Sporting long jaws bearing many bladed teeth, more mobile, much longer arms and hands that approached those of some allosaurids in length (Paul 2024b), and longer legs, baso-eutyranosaurus should have been better adapted for filling the role of medium-sized predators than were relatively clunky juvenile tyrant lizards. The latter being compromise medium-sized predator niche giant *Tyrannosaurus* in-waiting, hampered by their severely reduced arms, fewer, blunter teeth, and shorter lower legs when it came to pursuing and dispatching smaller game.

Not yet known is whether western tyrannosaurids successfully moved into Appalachia in the later Maastrichtian, as did large ceratopsids (Farke & Phillips, 2017). It is also possible that baso-eutyranosaurs whose Appalachian ancestors had earlier headed and settled in the west, then underwent speciation and perhaps beyond in their new home, and subsequently returned in part to Appalachia, *Dryptosaurus* being a possible example. Ergo, it cannot be simply assumed that late Maastrichtian eastern region tyrannosaur clan evolved entirely in place, the situation may have been more complicated. Returning to the Amero-Canadian west, having initially resulted of the novel geographic situation of the later Maastrichtian, the atypically high TT-zone tyrannosaur diversity

might have proved temporary over deep time. What cannot be known is how baso-eutyranosaurs versus tyrannosaurids would have fared proceeding beyond 66 MA had the K/Pg extinction not occurred.

### How did grownup *Tyrannosaurus* become gigantic?

Despite apparently being under intense competitive pressure by markedly more numerous baso-eutyranosaurs, enough juvenile *Tyrannosaurus* managed to grow up to sustain the populations of the genus. Paul *et al.* (2022) proposed that the rapid appearance of multiple species of an elephant sized tyrannosaurid genus in late Maastrichtian western North America, was due to the appearance of the Laramidia land bridge suddenly enormously expanding the resource base for the great predators. The food base expansion then further allowing the coexistence of larger contemporary robust and gracile tyrannosaurid species than the rhino-sized albertosaur/daspletosaur examples present earlier on the narrow Laramidia peninsula. Paul (2025a) noted the apparent previous existence of oversized tyrannosaurids on Laramidia as early as the Campanian ((Stein & Triebold 2013, Dalman *et al.* 2024; Longrich *et al.* 2026a), the early existence of “*T.*” *mcraeensis* has been challenged (Voris *et al.*, 2025). The size evolution question remains open.



**FIGURE 10.** Known-bone profile-skeletals of TT-zone adult and juvenile *Tyrannosaurus* to same scale, bar equals 2 m, arrows point to postorbital bosses of large presumed mature males (modified from Fig. 1 in Paul, 2025a). **A** Upper TT-zone *T. rex* holotype CM 9380 (ex AMNH 973) (6.5 tonnes); **B** Upper TT-zone *T. rex* RSM 2523.8 (mature, male? 7.8); **C** Upper TT-zone *Tyrannosaurus regina* NHMAD 2020.00001 (ex BHI 3033, NHMAD S in Paul, 2025a) (mature, male?, 7.5); **D** Upper TT-zone *Tyrannosaurus regina* holotype USNM 555000 (immature? male? 6.1); **E** Lower TT-zone *Tyrannosaurus imperator* holotype FMNH PR2081 (mature, male? 7.8); **F** TT-zone level unknown *Tyrannosaurus incertae sedis* AMNH 5027 (7), preservation of ribs uncertain; **G** upper TT-zone *Tyrannosaurus rex* or *T. regina* LACM 23845 (juvenile, 2); **H** level uncertain *Tyrannosaurus incertae sedis* Baby Bob (juvenile 650 kg).

**Restoring *Tyrannosaurus* developmental ontogeny**

As explained by Jevnikar and Zanno (2020). Paul et al. (2022), Longrich and Saitta (2024), Paul (2025a), Zanno & Napoli (2025), Longrich et al. (2026b) and Woodward *et al.* (2026), the common practice of using lesser TT-zone baso-eutyranosaurs as models, the *Gilmoretyrannus lethaeus* holotype most commonly, for restoring the teen years of *Tyrannosaurus* is as errant as using coyotes to do the same with wolves, or bobcats for pumas, and the like (Fig. 4H,I; contra results of Paul 2008; Hutchinson *et al.* 2011; Snively et al. 2019; Carr 2020; Woodward *et al.* 2020). Only juvenile specimens that can be confidently assigned to the tyrant lizard should be used to examine and restore its maturation factors such as growth curves and rates and interruption, shifts in locomotion and agility, predatory habits and niche partition, mental acuity, etc. as they achieved adult status (Figs. 3A-D, 4E, 7E-G, 10). Unfortunately, the fragmentary nature of such fossils to date (Figs. 3B-D, 4E, 10G,H, Fig. 29 in Longrich & Saitta 2024) – Teen Rex may fill that gap -- as well as most being non-accessioned, inhibits such efforts compared to *Gorgosaurus* and *Tarbosaurus* ontogeny. The latter is therefore the most suitable robust tyrannosaurin for this field of analysis at this time.

**The lithe baso-eutyranosaur taxa were not functional equivalents to one another**

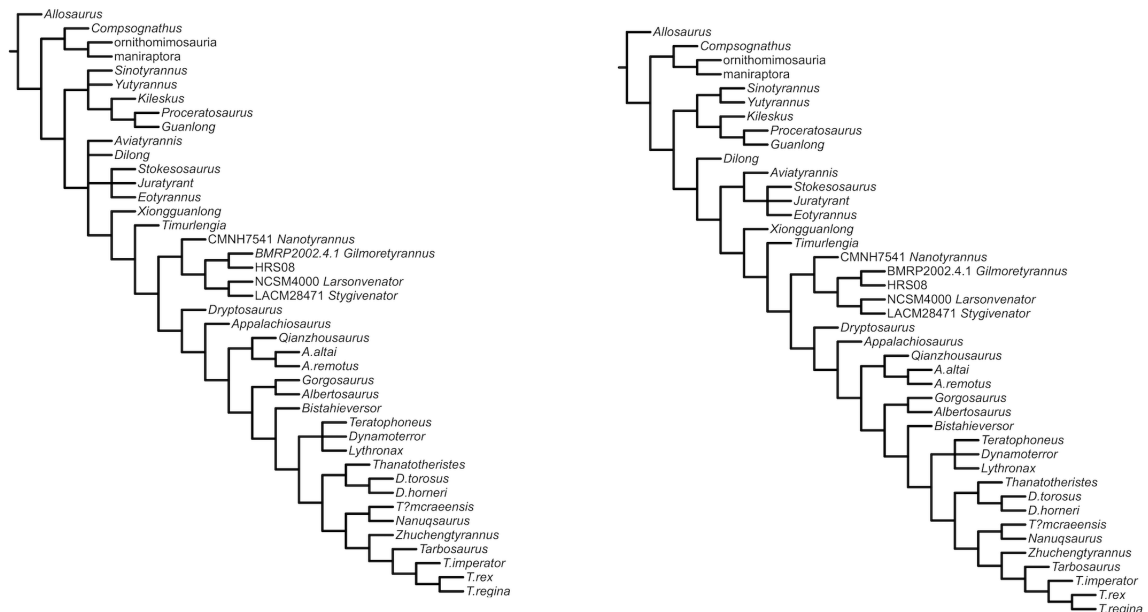
Not only are the small eutyranosaurs of the TT-zone not useable for examining *Tyrannosaurus* ontogeny other than for disparate comparative purposes, it is necessary to not presume they are functionally uniform among themselves. The opposite is true, the divergences in the *Nanotyrannus* and *Larsonvenator* skulls (Fig. 1A,B) are extensive to the degree of being adaptatively extreme. Far from studying them as a functional unit, the baso-eutyranosaurs need to be analyzed as distinct genera and probably higher in the normal manner, with *Nanotyrannus* apparently robust headed from purposes of high predation, and *Larsonvenator* as lightly structured for markedly different hunting and feeding modes. The same principle applies to examining growth patterns and other factors -- see where the data leads rather than assume where it will.



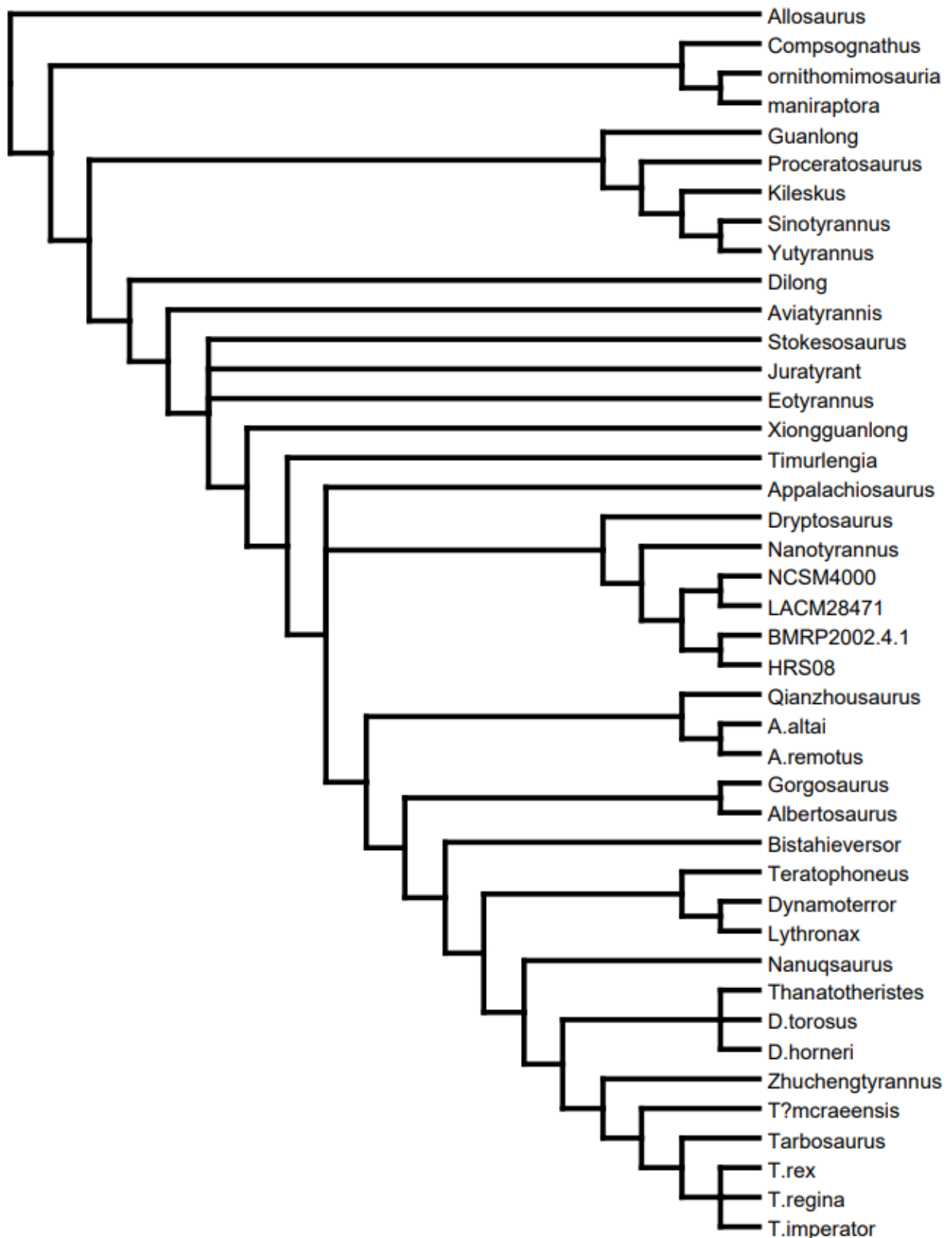




**FIGURE 12.** Results of phylogenetic analysis under maximum parsimony, showing strict consensus tree inferred under implied-weights. From right to left, to top to bottom. K=3, K=6, K=12, K=24.



**FIGURE 13.** Results of phylogenetic analysis under maximum parsimony. From right to left, strict consensus tree inferred under equal-weight, strict consensus tree inferred under extended implied-weight.



**FIGURE 14.** Results of phylogenetic analysis under Bayesian inference. Summary statistics for partitions with frequency  $\geq 0.10$  in at least one run: Average standard deviation of split frequencies = 0.012827. Maximum standard deviation of split frequencies = 0.041428. Average PSRF for parameter values (excluding NA and  $>10.0$ ) = 1.00. Maximum PSRF for parameter values = 1.025. the result seems to supports Nanotyrannidae as a junior synonym of Dryptosauridae.

**Characters from the analyses of Voris *et al.* 2020 (1-394)**

1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105, 106, 107, 108, 109, 110, 111, 112, 113, 114, 115, 116, 117, 118, 119, 120, 121, 122, 123, 124, 125, 126, 127, 128, 129, 130, 131, 132, 133, 134, 135, 136, 137, 138, 139, 140, 141, 142, 143, 144, 145, 146, 147, 148, 149, 150, 151, 152, 153, 154, 155, 156, 157, 158, 159, 160, 161, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 174, 175, 176, 177, 178, 179, 180, 181, 182, 183, 184, 185, 186, 187, 188, 189, 190, 191, 192, 193, 194, 195, 196, 197, 198, 199, 200, 201, 202, 203, 204, 205, 206, 207, 208, 209, 210, 211, 212, 213, 214, 215, 216, 217, 218, 219, 220, 221, 222, 223, 224, 225, 226, 227, 228, 229, 230, 231, 232, 233, 234, 235, 236, 237, 238, 239, 240, 241, 242, 243, 244, 245, 246, 247, 248, 249, 250, 251, 252, 253, 254, 255, 256, 257, 258, 259, 260, 261, 262, 263, 264, 265, 266, 267, 268, 269, 270, 271, 272, 273, 274, 275, 276, 277, 278, 279, 280, 281, 282, 283, 284, 285, 286, 287, 288, 289, 290, 291, 292, 293, 294, 295, 296, 297, 298, 299, 300, 301, 302, 303, 304, 305, 306, 307, 308, 309, 310, 311, 312, 313, 314, 315, 316, 317, 318, 319, 320, 321, 322, 323, 324, 325, 326, 327, 328, 329, 330, 331, 332, 333, 334, 335, 336, 337, 338, 339, 340, 341, 342, 343, 344, 345, 346, 347, 348, 349, 350, 351, 352, 353, 354, 355, 356, 357, 358, 359, 360, 361, 362, 363, 364, 365, 366, 367, 368, 369, 370, 371, 372, 373, 374, 375, 376, 377, 378, 379, 380, 381, 382, 383, 384, 385, 386, 387, 388, 389, 390, 391, 392, 393, 394.

Modified characters:

31) Maxillary interfenestral pillar is broad (0); moderately broad (1); narrow (2) (Paul 2025a)

261) Dentition, dentary dentition, dentary tooth count: less than 12(0), 12-15 (1); 16-18(2); 19 or more (3) (Paul 2025a; this study results)

263) Dentition, maxillary dentition, maxillary tooth count: less than 11 (0); 11-13 (1); 14-17 (2); 18 or greater (3) (Paul 2025a; this study results)

369) Tibia, length relative to the femur: 1.05 or greater (0); less than 1.00 (1; 1.00-1.05 (2) (this study results).

**Characters from the analysis of Dalman *et al.* 2024 (395-642)**

3, 10, 11, 12, 15, 23, 25, 26, 27, 28, 30, 44, 45, 46, 48, 50, 51, 53, 54, 55, 56, 58, 65, 72, 74, 75, 76, 77, 78, 82, 83, 86, 87, 88, 91, 92, 93, 99, 100, 101, 102, 107, 113, 116, 118, 119, 120, 125, 127, 128, 129, 130, 133, 134, 135, 137, 138, 139, 148, 150, 163, 164, 167, 172, 173, 174, 175, 176, 177, 179, 186, 187, 189, 190, 191, 193, 197, 199, 200, 207, 214, 224, 230, 232, 236, 239, 240, 241, 242, 246, 247, 248, 250, 251, 258, 259, 261, 263, 264, 265, 267, 269, 270, 271, 272, 273, 274, 275, 278, 279, 280, 281, 282, 284, 285, 286, 288, 289, 294, 295, 309, 314, 319, 320, 321, 322, 323, 336, 337, 338, 339, 340, 347, 348, 352, 353, 354, 355, 356, 357, 358, 359, 360, 361, 362, 368, 369, 370, 371, 373, 374, 375, 376, 397, 415, 424, 425, 431, 434, 438, 440, 444, 445, 447, 448, 450, 456, 457, 465, 466, 468, 469, 470, 472, 473, 474, 475, 476, 477, 478, 479, 480, 482, 485, 487, 488, 491, 492, 493, 496, 497, 498, 499, 501, 502, 504, 506, 507, 508.

Modified characters:

240) anterior dentary shape: dentary tip not upcurved (0); is strongly upcurved (1) (this study results).

**Characters from the analysis of Zanno & Napoli 2025 (643-843)**

9, 12, 13, 14, 15, 18, 24, 25, 35, 39, 40, 41, 46, 47, 55, 56, 57, 59, 60, 62, 63, 64, 72, 74, 77, 78, 79, 81, 82, 83, 95, 98, 99, 102, 111, 113, 114, 122, 123, 125, 134, 141, 142, 147, 148, 152, 153, 154,

155, 157, 159, 160, 163, 164, 165, 168, 187, 188, 192, 202, 203, 204, 212, 214, 218, 221, 233, 237, 249, 255, 256, 258, 259, 265, 266, 267, 268, 269, 270, 271, 278, 279, 282, 285, 290, 298, 306, 308, 312, 319, 328, 330, 332, 334, 335, 341, 342, 343, 344, 345, 347, 348, 349, 350, 356, 357, 358, 361, 363, 364, 366, 383, 403, 404, 406, 408, 410, 411, 413, 421, 422, 426, 427, 428, 429, 430, 431, 432, 434, 437, 440, 441.

Modified characters:

237) Dentary, rostral margin, shape, lateral view: chinless rounded (0); sharp chinned (1) (Zanno and Napoli 2025)

290) Axial centrum, pleurocoels, number: 1 (0); 2 or more (1) (Zanno and Napoli 2025)

Character extracted from Larson (2013b)

729) Antorbital fossa: (0) – Very shallow; (1) – Shallow; (2) – Deep; (3) – Very deep

730) Ventral antorbital maxillary ridge meets jugal: (0) – No; (1) – Yes

731) Vomer expansion: (0) – Laterally; (1) – Dorsoventrally

732) Posterior dorsal quadratojugal notch: (0) – No; (1) – Yes

733) Central dorsal quadratojugal notch: (0) – No; (1) – Yes

734) Quadrate-squamosal articulation: (0) – Single; (1) – Double; (2) – More than 2

735) Cranial nerve V-2 bounded by: (0) – Maxilla; (1) – Maxilla and premaxilla

736) Fourth maxillary tooth length/width (at base of crown): (0) – More than 2; (1) – Less than 2

737) Fourth dentary tooth length/width (at base of crown): (0) – More than 1.4; (1) – Less than 1.4

738) Anterior squamosal pneumatic foramina: (0) – Absent; (1) – Small; (2) – Large; (3) – Very large

739) Lateral lachrymal pneumatic foramina: (0) – Very small; (1) – Small; (2) – Large

740) Medial lachrymal pneumatic foramina: (0) – No; (1) – Yes

741) Jugal pneumatic foramina: (0) – Anterolateral facing; (1) – Dorsolateral facing; (2) – Absent

742) Fused pelvis No (0) Yes (1)

743) Lateral component of glenoid Absent (0) Present(1).

### **An additional 10 new derived characters are proposed below (744-753):**

744) Intra quadratojugal–squamosal fenestra: present (0); absent (1) (Zanno and Napoli 2025)

745) Skull deep, subrectangular because of blunt rostrum with maxilla and anterior fossa boundaries forming an angle over 30 degrees (0); subtriangular because of sharp rostrum with maxilla and anterior fossa boundaries acute at an angle of ~30 degrees or less (1)

746) Maxillary: maxillary tooth before antorbital fossa less than 3 (0); 3–4 (1); 5–6 (2); 7–8 (3); greater than 8 (4)

747) Metatarsus not highly elongated, with proportions similar to *Tyrannosaurus* (0); highly elongated, with proportions similar to *Gilmoretyrannus* (1).

748) Femur: robust with a length/circumferences ratio below 2.4(0); gracile with a length/circumferences above 2.4 (1) (Paul *et al.* 2022)

749) Lateral dentary groove entirely absent or poorly developed (0); well-developed (1)

750) Forelimb longer than femur (0); shorter than femur (1)

751) Quadratojugal, vertical height in lateral view: very tall, the vertical height being about the same as the horizontal distance between the anterior tip of the maxilla and its antorbital fossa (0); is just ~80% the length of the anterior maxilla, in line with a shallower cranium (1); about three quarters of the length of the anterior maxilla, in accord with its exceptionally low cranial profile (2)

752) Quadratojudal-quadrate foramen small 0); large (1)

753) Axis neural spine anterior rim fairly smooth (0); well crenulated (1) (Zanno and Napoli 2025)

T.rex 1111002111112220011101121011101112?0?01102121111021121010211112010?/?1?  
102010021102211111011?1110121101211011031100021001111112111013?

12111111111101111100312123201111111101111101101111111111111211101111100201111111  
101111111111111120110112221211011121111121211102011111011111111021110121111111111  
110212110111111111112101111101011010000112111111211111212211121111111111111121  
1100000000111111000011021??  
01010111220101211101220211101011202111211111201110110201110011112111010011111101  
111112202222010211121100010011101101000000101110000000100110210122110022211221112  
101102111201112001011301121110011010?0?011200111110111002?10311010111112021210?  
1011010211110111001111110111111?01?000011101?010?001012010?110101?  
10011030000111131100010200001001  
T.regina 111100211112220011101121011101112?0?01102121111021121010211112010??1?  
102010021102211111011?1110121101211011011100021001111112111013?  
1211111111110111110031212320111111111011111011011111111111112111101111100201111111  
1011111111111111201101122212110111211111212111020111110111111110211110121111111111  
11021211011111111111210111110101110100001121111112111112122111211111111111111121  
1100000000111111000011021??  
01010111220101211101220211101011202111211111201110110201110011112111010011111101  
111112202222010211121100010011101101000000101110000000100110210122110022211221112  
101102111201112001011301121110011010?0?011200111110111002?10311010111112021210?  
1011010211110111001111110111111?01?000011101?010?001012010?110101?  
10011030000111131100010211001001  
T?mraeensis 1?????  
2????????????????????????????????????????????????????????????????????????????????  
????012110???0110002100??  
1111211101????????????????????????????????????????????????????????????????????  
????????????????1?111120110????????????????????????????1??  
10????????????????????????????????????????????????????????????????????????????  
????????????????????????????????????????????????????????????????????????????1??  
0101020????????????????????????????????????????01100?111??111????????  
10201121????????????????????????????????????????????????????????????????????  
1131????????????????????????????????1000?1????????????????????0?????1????????  
1????????????????????????????????????????????????????????????????????0???  
T.imperator 111100211112220011101121011100112?0?01102121111021121010211112010??1?  
102010021102211111011?1110121101211011021100021001111112111013?  
1211111111110111110031212320111111111011111011011111111111112111101111100201111111  
101111111111111101101122212110111211111212111020111110111111110211110121111111111  
11021211011111111111210111110101110100001121111112111112122111211111111111111121  
1100000000111111000011021??  
0101011122010121110122021110101120211121111120111011020111001111211101011111101  
111112202222010211121100010011101101000000101110000000100110210122110022211221112  
101102111201112001011301121110011010?0?011200111110111002?10311010111112021210?  
1011010211110111001111110111111?01?000011101?010?001012010?110101?  
10011030000111131100010200001001  
Timurlengia 00????????????????00?01?????20??10??1?0?001?1?  
0101????????????????????????????????????????????????????????????????????  
????0?0?????01??21001??1????????????????????????02?0201?01001000?0?001000??  
0111?????????1??11??01?????????2?20??1?0????????????  
00011????????????????????????????  
00????????????????????????????????????????????????????????1????????????????11?

1????????????????

0????????????????????????????????????????????????????????????????????????????????????

0??1??????00?0????0????????????????????????????????????????????????????????00??????10????

00-01????????????????????????????????????10???111?0?0??????1????1?????0011????

0????????????????????????????????????????????????????????????????????????????1???????

*Aviatyrannis*

0????????????????????????????????????????????????????????????????????????????????????

????????????????????????????????????????????????????????????????????????????????????

????????????????????????????????????????????????????????????????????????????????????

????????????????????????????????????????????????????????????100?0000010000011101??????0???

11????????????????????????????????????????????????????????????????????????????????

????????????????????????????????????????????????????????????????????????????????

????????????????10????

1????????????????????????????????????????????????????????????????????????????????

????????????????????????????????????????????????????????????????????????????

0????????????????????????????????????????????????????????

*Sinotyrannus* 0???12??????10?1?1?1110?0?0?00????0?1?0?0???????

1????????????????????????????????????????????????????????????????????????????????

????????????????????????????????????????????????????????????????????????????????

10????????????????????????????0?01????????????????????????????????????????????

00?100?0?1010001000????????????????????????????????????????????????????????1?

0010101?1????????????????????????????????????????????????????????????????????011?

0????????????????????????????????????1?1????????????????????

00????????????????????????????????????0???

1200????????????????????????????????????????????????????????????????????

1????????????????????1????????????????2?????0????????1???????

*A. altai* 00010011?11???????

0000001111120010111110100111102112101110101201111000021011210111101011100011001010

1220001000000010011001112011113201111011111011101102100112111110101??

101110011011101000110121111011111101101111001111011100101110121211110??

100000????3?2000001000100011110?11011?21011111????????????????????10?111101?

0110100??????????21?111?11111211???00?1111?11?010010010?0001??

001011011--110101111100101000021010000101121200110111110101011010110000112?

100010010101101101101121000101????0010001101101???0?0???11????????????

122110011??122111210110??1120???00000000?

010001000-01-10001100010010001100000101000000??2?111101000?100001111?20?????

111111?10??????????????????0???10-1???0001?0????2?????01??????111101??

*A. remotus* 000?0????1??????????0?????????1?0?1?0?001????2??2?0111?1???

0????????????????????????????????????????????00000?1001?0??11??1?1?3??10?1?01???1????

01???1001?2111110101????????????????1101211?1011?1111011?1?1???0?????01?????0??

1?121?????????????????0?

1????????????????????????????????????????????????????????????????????????????

????????????????????1????????????????????0?10????1101???1???0??????????00?0?

01??????????11????????????????????????10?01?????110011?1?21??????????

0????????????????????????????????????????????????????????00?????1??????0?

01??????0???110?21?????10????????10100000?????????????????0111?

1????????????????????????????????????????0????????????????????111?0????



D.torusus  
1111001101011220011100020001111012002111022011110211210102111120111100112110121112  
111111111?111012010121000101111001100101?11211111321211110111111011?  
0111211112211111101010110111001100111110011?1211110111111?1011111111111???

11101211011011222111101112?1100212111101000111101111110211110?????1?111111?  
212111?11111?111121011110101101?00011211111121111?12210?2?1111?111111?11?1??  
00111100000111001011021--01210101220001110000220211001011212000201111??  
101011120011000111100001011111111011101102221010111211000100111011??  
0000001011100000001000?02101221100?21122111210110211120?  
21100000021011010000-01-0-0013010101?21110221010101100111121111101?01?000?  
11111111????1101???11????112010-1001?1?01?10021?101???1????????20100?11?  
12100010100001101  
Appalachiosaurus 1??1?0????????????000001001??100100?01?01001111???1200101?1?1?  
001101?002?01010????1?0?  
0????????????????????????????????????????????????????????????????????????????  
000000010100010?00????????????????????????????????????11?110?01?1????????20?1????2?  
2?1?2????????????????????????????????0????????????????????????????????????????  
1??????12111?111110????21111111110110?0??????0?01?00?010-?1---1?1?  
1001110????????????????????2?????11????????????????????00101001010?  
10110????????????????0????????????????????0????????0110?  
2211002211022111210110001120101100?0?0??110?0000-0?-100?????  
1100--????????????????????????????00?01????20????10?1????????????????????  
11?????1?01111000??1????????01???0?00?1????  
Bistahieversor 1?0?0011010111200110000010?101100210101?0100111102??  
200101011010011001102000010?02110??1000000?00?0001210001011100010001000001??10?  
31111110??1??1021101102100122111110101?00000?010001110?????1???11?111111?101?  
1110110011?1?1111100?011001212101100112?1?0?2?2??120?????111????????????????  
0111111????????????????????????????????????????????111?1????1111011111?  
1100010000010?11111001011021--0121010?220101110012302110010101121012111112010?  
011020111001111?  
0010101111111011111220222010111121100????????????????????????????????  
1????????????????????????000001?01001000????-0-011110110110211101201??10?  
00010111011211?1001?010?011011?10?????  
101????????????????????????????????????????11?11??1?1201???01?0?1?01?  
Drypto 1????????????????????????????????  
00????????????????????????????????????????????????????????????????????????  
????????????????????????????????????????????????????????????????????????  
??????????0?0??1212?1?1????????????1?00????????????????????????  
10100?????1?????11????????????????????1??????12?????????1012??2?01111?????  
1????????????????0?  
0????????????????????????????????????????????????????????????????????  
0?????????11110????????0????????????00????????????0??1??  
2110011110221112101?0???010000????  
0????????????????????????????????????????????????????????????1??11?????  
1??????????0????????????00?00?1?11111??????????????????????0?1?0??  
Kileskus 0???12?????110111200100??0?00?000?00?0000?0?000??  
000????????????????????????????????????????????????????????????????????  
????????????????????????????????????????????????????????????????????  
?????????0100010?????????????  
20????????????????????????????????????????????????????????????????  
????????????????????000?????0??????0???1?00?  
01100????????????????????????????????????????????????????????????

[illegible]

00?00000?0000101000?0?????????????????02001?0?0100?0?0010?0?????????????01001??  
100?1?010002?00?11??0?0?10101000100000010000000001000000????????000000110000001???  
0??0100001000?0??0?0001110??10?00010?0000??011?0000000000010000??01?00?????????  
10001100101100110-00100-0110000001000100000000-0-022001000011010111000010010000111  
???00100100010011011101001111000000021100010001001???000000101010000000100000110?  
21110001???021112101?010100000000000000??1200101???00-10110000-0??0?  
1000---??-0-0-????0?00?00?1????????00--???-0????1?01????????????????0??0??1??  
0????????????????????1100000010001??1020111?20?  
Eotyrannus 0??0?0?????11?100101110????????????????00?0?0?1???????2?01010000?101001?  
001??1??0??000?00?0????????????????????0????????????????????????????????00011?1???  
0????????????????????????????001????0?00?0????????????????????????????????????000?  
10000?02110100??????????2?2??0?010??00?0?0??00??1?0??????????00??011011011??  
0000??00?11????????????11????????????????????????????????01??000?001?00?????????  
000011001010-01--010100????????????????????????????????????????????????????????  
0??????01?0??10??????02??11?0?0??????1?0?100011?0?????????????  
00000001000????????????????10?????????0101010000000?0?0??12????1????00-10??????  
0?????????????????-??0-????????????????00--10??????11?100?????0?0??11??1?1?  
1?????????????0-????1????1??????0?????1?1??0???  
Terathoponeus 1?????1??1?????????000010??1?????0?11?01001??102?1??????????2?  
011100102?01010??201010?0??????0??0121?1??101000200?1011??0?1013112111101011?  
101110120211111011111?1?1?????????????????????1?0121111?11110102011?11?1?0011?1?1??  
0100?011?01222?1??111??1??????01100?0??????11?11?102??????????111????1?  
0211111011?????????10??1?10101?1?0000?121111112?11101112111211?11?111??????????  
110001111011??00101102??????010112000111100123021100101011??00?  
01111120111011020111001111??01?101111111??111122022200011?121??0??  
0011101101000000101110000000100?10210122110022211?21?1????????????????10000002??  
10????0?????????11010100001?1110?????1??00011111121?0?????????0?????  
1?????????????????0??1??0-????????????111?10????????????3??000??02010?101??0??1?  
Nanuqsaurus 0????????????????????????????????????  
2????????????????????????????????????????????????????????????????????????????  
?????????????????1?011??1111?21011100??  
1????????????????????????????????????????????????????????110?10?  
10????????????????????????????????????????????????????????????????????????  
????????????????????????????????????????????????????????????????????0?  
0????????????????????????????????????1012?  
02????????????????????????????????????????1?????  
01????????????????????????????????????????????????????????????????????????  
?????????????10?2????????????????????????????????????????????1?1?11?????????  
1????????????????????????????????????????????????????????????????????????  
0?????

Dynamoterror

1????????????????????????????????????????????????????????????????????????  
????????????????????????????????????????????????????????????????1?0?2??11?1??  
1????????????????????????????????????????????????????????????????????????  
????????????????????????????????????????????????????????????????????????  
????????????????????????????????????1????011????????????????????????1??1?  
00????????????????????????????????????????????????????????????????????????  
????????????????????????????????????????????????????????????????????????

011110111?100010?00?011????010201??01311110200

Nanotyrannus 1011000?01???12????10000?0000?1003?0101?11001??10???2?00001?00?  
00?????????0?0????1???01???0010001000020000?00000000?10000?1???001?11??11???011???0?  
0???0?????????011110101011010?????????????111111101111011011?????????????11111?  
110??111??21???001??????  
211021210????????????????????????????????????????????????????????????????????????????????  
????????????????????????????????????????????????????????????????01000???2110?00001??10001?110?????011?10?  
112202110010111121111??111110?0???1110110001111??01??00000? ??????1113?2011110001111?  
11?0????????????????????????????????????????????????????????????????????????????????????  
100?????????0?0???0100?????????0???1101---?0?00? ??????11111110??1001?????????????  
0011?????????????????????????????????????????????????????????????0111100000201??102?0???01?  
BMRP2002.4.1 0?01000?01???12???2?10010?000101002?0111?11001?1102???2?000????11?  
011110110??01010?0?11?000?00010001000?10000?000000?0?00000?10?001?12??11??  
01?????0???0????????????????????????????????????????????????????????????????????????????????  
01111?0101?1111221???0?????????2?112120021?1?1?1000?????2110?????????111111?  
0011?????????????????10?101?111?0001?01100011????100?2111?1???1?????0?11111?111?11????  
00?0????21110?00001???10001?001??1110011?????????????????111?2111??1?  
1?????????????????????????????????00000? ??????????????11110?????1?11?0??10110?????0000?0001?  
10000000100?0?0210?21???011?????????????00? ??????1001?0?  
11110000010101010011000010100011100---130001011111?????????????000101?????????????  
001100?11?010??11?11???????????10??1?101111100101000011110000201110021111?1?1  
HRS080?0???0?0???????????10010?000101??2???11?02001??102?12?0?0?0?1?  
20?????????????????????????????010?0?0???????10001?  
0????????????????????????????????????????????????????????????????????????????????????  
?????????????????????????????011110101011?????????????????????1?  
00????????????????????????????????????????????????????????????????????????????????????  
?????????????????????????????0?0?0?????????????1???1??01??  
0?????????????????????????????2?111?????????????????????????????????0000??  
0????????????????????????????????????????????????????????????????????????????????????  
?????????????????00??11100?010??10100110?????????011?0?0????????????????????????  
01?????????????1?????????????????????????????????????????????????????00?????00? ??????0??1?  
1???  
LACM28471 ?????0???????120???00?????????????????111100?????012?1?????  
1????????????????????????????????????????????????????????????????????????????????????  
????????????????????????????????????????????????????????????????????????????????????  
1???????????????????????11?1?  
00????????????????????????????????????????????????????????????????????????????????????  
?????????????????????????????0?????????????0001??  
100?????????????????????????????????????????????????????????????????????????????????010?  
0????????????????????????????  
0?????????????????????????????????????????????????????????????????????????????????0?????21??  
00????110100????????????????????????????????????????????????????????????????????  
011?????????????????????????????????????????????????????0?????01???????11??????  
Lythronax 1????0???1?????????00000?0010?10??10?01101001?1102112?011001?1?  
0???????????????????????1???001010?02010121010?0?????????????????????????????1?11?11?1?  
1011?0120211?1?11?111?????????????????????????????????????????????????????????0?1?????1?????  
01?0?1222?211?????1???????1?0????????????????????????????????  
1?????????????????????????????????0?????????121111?11?????????????????11?111?1?????  
0??11?00111111??000011021--01210?????????????11012?????????????

2111211????????????????????????????????1????1011111111????11112202222010201?????  
0????????????????????????????????????????021????????????211?21?1?????0?1112011????1002?110?  
10?01101011000--????????01101????????011110212121????01????011111?????????  
1????????????????????????????????????10????????1????????????????1???0?00?0?0?  
Xiongguanlong 0001000000?1102001?????0?0???1?0?00?01?0?001?0?01???1?0001010??  
0000????01?0100??000?0?0?0?????0?0?011000?0?0?00?0110000??0000?21?111110100?  
010?1?????100?10?1111?0??10?0?100????????????001002?00110?0000?10?  
1????????????????????????????????????????2?2??100?0??  
00001001000110000010????????????????????????????????????????110?101????001111?  
0????????????????????111100120????????????????????????????????00011?0010?1011---00100-0???001??  
000010000?000-1?12200000101111????0100000100010000??  
00????????????????????????????????1000100010011????????????????????????????????  
2110022????2????????????????????????0?00???10???00???1-0-001000????????1101---?01010-????  
0??1?11?1???1????????????????????0?01001?-????????????????????01????1????????????21?  
00000?001?0?111?11??2?0  
maniraptora ?000000000?000000?00000000?000?00100?00?000011100?0000000001000000??  
1???0?00000?01000?01?00???0?0000000000000?0?0010?0010000?00001000001010010?000????  
00?00000000000?0?00??0?000?0001000?0?0?0000002?1?000?1000?010000?00000000??  
00000000000000000001?0000000?0000000?0?01000000?00?100001?111100?1000?  
00000000000010000000000000000?000000000000??100001100??  
011000000000100001000000100000000000??00????11100?000010-00—1000—  
00---1---1-1-001-0?0???-?031?00000000--111?0111001?0?1?0--01?  
01000100-0010000-100--0-0-001000?0?20010?00000?  
00210010111110101111120101102111110?012111?10211201000000000000000?  
1????????????0?????000?000000000000000?010?0?0?000010?001?001000010?00?000000????  
001000000102011100000101010002010?0000010000000121????0??0102011??1111010.

## CONCLUSION

Based on straightforward comparative anatomy and conventional ontogeny, and a large scale phylogenetic matrix, the 1946 Gilmore Hypothesis established that the TT-zone was inhabited by multiple tyrannosaur taxa. This conservative conclusion likely would have remained the established paradigm, especially had it been reinforced by Rozhdestvensky in 1965. In 1999 Carr contended otherwise, based on a critical ontogenetic tooth count error (which may have stemmed in part from an excessive tooth count for juvenile *G. libratus* AMNH 5664 in Bakker *et al.* 1988). Given that mistake, the radical, nonparsimonious speculations necessary to sustain the ETRH, and the presentation of fossils that directly contradict the opinion years ago, it is perplexing why it was such a popular theory. Instead, the fossil and the paleogeographic data show that the TT-zone experienced an incursion of one tonne or less basal eutyranosaurs of likely eastern heritage that were apparently successfully competing with the resident juvenile *Tyrannosaurus*. In the future, tyrannosaurin ontogeny needs to follow the solid principles established in this decade by Longrich and Saitta (2014), Paul (2025a), Zanno & Napoli (2025) and herein. Rather than just one titanic taxon lasting over 1 MA, identifiable TT-zone species and genera from a few hundred kilograms to 8 tonnes over that span currently number seven and five respectively, with none likely to have been extant over that entire period. With the onset of the compelling MTTH papers over the last two years, study of the TT-zone tyrannosaurus has been released and opened to complex alternative possibilities that are inherently difficult to resolve. With the ongoing sudden displacement of the ETRH with the MTTH as the paradigm, the question is not if there were multiple species and genera in the TT-zone – as well as other tyrannosaur habitats -- but how many and at what

systematic level. And what it means in paleozoological regards. The already late Gilmore would never know how prescient his 1946 hypothesis was, and we are honored to have named one of the pertinent genera in recognition of his achievement in dinosaurology.

## ACKNOWLEDGMENTS

Thanks go to those noted in Paul *et al.* (2022) and Paul (2025a), as well as to Davide Mandorlo for his help in the phylogenetic analysis, Tracy Ford giving us other images and information on LACM 28471, Leonardo Natale (student at the “Accademia di Belle Arti” of Foggia) for his help on editing some images. Also of considerable assistance have been Robert Telleria, and the 3 anonymous reviewers. And finally, we thank editors Lynn Raw and Andrew Whittington for their advice.

## REFERENCES

- Bakker, R.T., Currie, P.J. & Williams, M. 1988.** *Nanotyrannus*, a new genus of pygmy tyrannosaur, from the Latest Cretaceous of Montana. *Hunteria*, 1:1–30. <https://zenodo.org/records/1037529>
- Barrón-Ortiz, C.I., Avilla, L.S., Jass, C.N., Bravo-Cuevas, V.M., Machado, H. & Mothé, D. 2019.** What is *Equus*? Reconciling taxonomy and phylogenetic analyses. *Frontiers in Ecology and Evolution*, 7: 343. <https://doi.org/10.3389/fevo.2019.00343>.
- Benton, M. J. 2014.** *Vertebrate Palaeontology*. Wiley-Blackwell.
- Bertin, T.J.C., Thivichon-Prince B., LeBlanc, A.R.H., Caldwell, M.W. & Viriot, L. 2018.** Current perspectives on tooth implantation, attachment, and replacement in Amniota. *Frontiers in Physiology*, 9: 1630. <https://doi.org/10.3389/fphys.2018.01630>.
- Brochu, C.A. 2003.** Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology*, 22 (7): 1–138. <https://doi.org/10.1080/02724634.2003.10010947>.
- Brown, C.M., VanBuren, C.S., Larson, D.W., Brink, K.S., Campione, N.E., Vavrek, M.J. & Evans, D.C. 2015.** Tooth counts through growth in diapsid reptiles: implications for interpreting individual and size-related variation in the fossil record. *Journal of Anatomy*, 226: 322–333. <https://doi.org/10.1111/joa.12280>.
- Brusatte, S.L., Benson, R.B.J. & Norell, M.A. 2011.** The anatomy of *Dryptosaurus aquilunguis* (Dinosauria: Theropoda) and a review of its tyrannosauroid affinities. *American Museum Novitates*, 3717: 1–53. <https://doi.org/10.1206/3717.2>.
- Brusatte, S.L. & Carr, T.D. 2016.** The phylogeny and evolutionary history of tyrannosauroid dinosaurs. *Scientific Reports*, 6: 1–8. <https://doi.org/10.1038/srep20252>.
- Brusatte, S.L., Carr, T.D., Erickson, G.M. & Norell, M.A. 2009.** A long-snouted, multihorned tyrannosaurid from the Late Cretaceous of Mongolia. *Proceedings of the National Academy of Sciences*, 106: 17261–17266. <https://doi.org/10.1073/pnas.0906911106>.
- Brusatte, S.L., Carr, T.D. & Norell, M.A. 2012.** The osteology of *Alioramus*, a gracile and long-snouted tyrannosaurid from the Late Cretaceous of Mongolia. *Bulletin of the American Museum of Natural History*, 366: 1–197. <https://doi.org/10.1206/770.1>.
- Brusatte, S.L., Carr, T.D., Williamson, T.E., Holtz, T.R., Hone, W.E. & Williams, S.A. 2016.** Dentary groove morphology does not distinguish “*Nanotyrannus*” as a valid taxon of tyrannosauroid dinosaur. Comment on: “Distribution of the dentary groove of theropod dinosaurs: Implications for theropod phylogeny and the validity of the genus *Nanotyrannus* Bakker *et al.*, 1988”. *Cretaceous Research*, 65: 232–237. <https://doi.org/10.1016/j.cretres.2016.02.007>.



- 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. (2010) Tyrannosaur paleobiology: new research on ancient exemplar organisms. *Science*, 329(5998): 1481–1485. <https://doi.org/10.1126/science.1193304>.
- Burnham, D.A., Atkins-Weltman, K.L. & Jevnikar, E.M. 2018. A new juvenile *Tyrannosaurus rex* from the Hell Creek Formation of eastern Montana provides insights into cranial and dental ontogeny. *Society of Vertebrate Paleontology 78<sup>th</sup> Annual Meeting*, 99.
- Carpenter, K. 1992. Tyrannosaurids of Asia and North America. pp. 250–268. In: Mateer, N.J. & Peiji, C. (Eds), *Aspects of Nonmarine Cretaceous Geology*. China Ocean Press.
- Carpenter, K. 2010. Species concept in North American stegosaurs. *Swiss Journal of Geosciences* 103: 155–162. <https://doi.org/10.1007/s00015-010-0020-6>.
- Carpenter, K., Russell, D.A., Baird, D. & Denton, R. 1997. Redescription of the holotype of *Dryptosaurus aquilunguis* from the Upper Cretaceous of New Jersey. *Journal of Vertebrate Paleontology*, 17: 561–573. <https://doi.org/10.1080/02724634.1997.10011003>.
- Carr, T.D. 1999. Craniofacial ontogeny in tyrannosaurid dinosaurs. *Journal of Vertebrate Paleontology*, 19: 497–523. <https://doi.org/10.1080/02724634.1999.10011161>.
- Carr, T.D. 2020. A high-resolution growth series of *Tyrannosaurus rex* obtained from multiple lines of evidence. *PeerJ*, 8: e9192. <https://doi.org/10.7717/peerj.9192>.
- Carr, T.D. 2022. A reappraisal of tyrannosauroid fossils from the Iren Dabasu Formation, Inner Mongolia, People's Republic of China. *Journal of Vertebrate Paleontology*, 42(5): e2199817. <https://doi.org/10.1080/02724634.2023.2199817>.
- Carr, T.D. 2025. Observations on the skull of the type specimen of *Tyrannosaurus rex* Osborn, 1905. *All Earth*, 37: 1–66. <https://doi.org/10.1080/27669645.2025.2539638>.
- Carr, T.D., Napoli, J.G., Brusatte, S.L., Holtz, T.R., Hone, D.W., Williamson, T.E. & Zanno, L.E. 2022. 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 evidence support subtle evolution and probable speciation within the North American genus *Tyrannosaurus*”. *Evolutionary Biology*, 49: 327–341. <https://doi.org/10.1007/s11692-022-09573-1>.
- Carr, T.D., Varricchio, D.J., Sedlmayr, J.C., Roberts, E.M. & Moore, J.R. 2017. A new tyrannosaur with evidence for anagenesis and crocodile-like facial sensory system. *Scientific Reports*, 7: 4494s. <https://doi.org/10.1038/srep44942>.
- Carr, T.D. & Williamson, T.E. 2004. Diversity of late Maastrichtian Tyrannosauridae from western North America. *Zoological Journal of the Linnean Society*, 142: 479–523. <https://doi.org/10.1111/j.1096-3642.2004.00130.x>.
- Carr, T.D., Williamson, T.E. & Schwimmer, D.R. 2005. A new genus and species of tyrannosauroid from the Late Cretaceous Demopolis Formation of Alabama. *Journal of Vertebrate Paleontology*, 25: 119–143. [https://doi.org/10.1671/0272-4634\(2005\)025\[0119:ANGASO\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2005)025[0119:ANGASO]2.0.CO;2).
- Chinsamy, A. & Pereyra, M. 2026. Stochastic growth marks in *Crocodylus niloticus*. *Scientific Reports*, 16: 1811. <https://doi.org/10.1038/s41598-025-31384-5>.
- Chure, D.J. & Loewen, M.A. 2020. Cranial anatomy of *Allosaurus jimmdaseni*, a new species from the lower Morrison Formation of western North America. *PeerJ*, 8: e7803. <https://doi.org/10.7717/peerj.7803>.
- Cullen, T.M., Canale, J.I., Apesteguía, S., Smith, N.D., Hu, D.Y. & Makovicky, P.J. 2020. Osteohistological analyses reveal diverse strategies of theropod body-size evolution. *Proceedings of the Royal Society B*, 287: 2020–2258. <https://doi.org/10.1098/rspb.2020.2258>.

- Currie, P.J. 2003a. Cranial anatomy of tyrannosaurids from the Late Cretaceous of Alberta. *Acta Palaeontologica Polonica*, 48: 191–226.
- Currie, P.J. 2003b. Allometric growth in tyrannosaurids from the Upper Cretaceous of North America and Asia. *Canadian Journal of Earth Sciences*, 40: 651–665. <https://doi.org/10.1139/e02-083>.
- 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. 2024. A giant tyrannosaur from the Campanian-Maastrichtian of southern North America and the evolution of tyrannosaurid gigantism. *Scientific Reports*, 13: 22124. <https://doi.org/10.1038/s41598-023-47011-0>.
- Danison, A., Wedel, M., Barta, D., Woodward, H., Flora, H., Lee, A. & Snively, E. 2024. Chimerism in specimens referred to *Saurophaganax maximus* reveals of new species of *Allosaurus*. *Vertebrate Anatomy Morphology Palaeontology*, 12: 81–114. <https://doi.org/10.18435/vamp29404>.
- Dick, D.G. & Maxwell, E.E. 2015. Ontogenetic tooth reduction in *Stenopterygius quadriscissus*: negative allometry, changes in growth rate, and early senescence of the dental lamina. *PLOS One*, 10(11): e0141904. <https://doi.org/10.1371/journal.pone.0141904>.
- Erickson, G.M., Makovicky, P.J., Currie, P.J., Norell, M.A., Yerby, S.A. & Brochu, C.A. 2004. Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature*, 430: 772–775. <https://doi.org/10.1038/nature02699>.
- Farke, A.A. & Phillips, G.E. 2017. The first reported ceratopsid dinosaur from eastern North America. *PeerJ*, 5: 3342. <https://doi.org/10.7717/peerj.3342>.
- Ford, T.L. 2005. Ghost lineages, paleogeographic and temporal distribution of Tyrannosaurids. "The Origin, Systematics, and Paleobiology of Tyrannosauridae" by Burpee Museum of Natural History and Northern Illinois University. <https://doi.org/10.13140/RG.2.2.20196.63360>.
- Fowler, D.W. 2017. Revised geochronology, correlation, and dinosaur stratigraphic ranges, correlation, and dinosaur stratigraphic ranges of the Santonian–Maastrichtian formations of the Western Interior of North America. *PLOS One*, 12: e0188426. <https://doi.org/10.1371/journal.pone.0188426>.
- Gallagher, W.B. 2023. An unusual theropod specimen from the late Maastrichtian of New Jersey. *The Anatomical Record*, 306: 1757–1761. <https://doi.org/10.1002/ar.25114>.
- Gilmore, C.W. 1946. A new carnivorous dinosaur from the Lance formation of Montana. *Smithsonian Miscellaneous Collections*, 106: 1–19.
- Griffin, C.T., Bugos, J., Poust, A.W., Morris, Z.S., Sombathy, R.S., D’Emic, M.D., O’Connor, P.M., Petermann, H., Fabbri, M. & Colleary, C. 2026. A diminutive tyrannosaur lived alongside *Tyrannosaurus rex*. *Science*, 391(6782): 300–305. <https://doi.org/10.1126/science.adx8706>.
- Goloboff, P.A. & Morales, M.A. 2023. TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel, Cladistics. *The Willi Hennig Society*, 39 (2): 144–153. <https://doi.org/10.1111/cla.12524>.
- Grubb, P., Groves, C.P., Dudley, J.P. & Shoshani, J. 2000. Living African elephants belong to two species: *Loxodonta africana* and *Loxodonta cyclotis*. *Elephant*, 2: 1–4. <https://doi.org/10.22237/elephant/1521732169>.
- Haridy, Y., LeBlanc, A.R.H. & Reisz, R.R. 2018. The Permian reptile *Opisthodontosaurus carrolli*: A model for acrodont tooth replacement and dental ontogeny. *Journal of Anatomy*, 232: 371–382. <https://doi.org/10.1111/joa.12754>.

- Harvati, K. & Ackermann, R.R. 2022** Merging morphological and genetic evidence to assess hybridization in western Eurasian late Pleistocene hominins. *Nature Ecology & Evolution*, 6: 1573–1585. <https://doi.org/10.1038/s41559-022-01875-z>.
- Hennig, E. 1925.** *Kentrurosaurus aethiopicus* – Die Stegosaurier-Funde vom Tendaguru, Deutsch-Ostafrika. *Palaeontographica*, Suppl, 7: 101–254.
- Hernandez-Luna, C.A., Hendrickx, C., Marin-Leyva, A.H. & Reisz, R.R. 2026.** The dentition of tyrannosaurid theropods: a review. *Discover Geoscience*, 4: 96. <https://doi.org/10.1007/s44288-026-00454-0>.
- Holmes, R.B., Jordan, C., Ryan, M.J. & Evans, D.C. 2026.** New information on the holotype of “*Chasmosaurus*” *russelli* necessitates the establishment of a new genus to receives the species. *Canadian Journal of Earth Sciences*, 63: 1–20. <https://doi.org/10.1139/cjes-2025-0031>.
- Hone, D.W.E., Wang, K., Sullivan, C., Zhao, X., Chen, Shu., Li, D., Ji, S., Ji, Q. & Xu, X. 2011.** A new large tyrannosaurine theropod from the Upper Cretaceous of China. *Cretaceous Research*, 32(4): 495–503. <https://doi.org/10.1016/j.cretres.2011.03.005>.
- Hutchinson, J.R., Bates, K.T., Molnar, J., Allen, V. & Makovicky, P.J. 2011.** A computational analysis of limb and body dimensions in *Tyrannosaurus rex* with implications for locomotion, ontogeny, and growth. *PLOS one*, 6: e26037. <https://doi.org/10.1371/journal.pone.0026037>.
- IUCN SSC. 2025.** An evaluation of the taxonomic states of the giraffe. *Giraffe and Okapi Specialist Group*, 1–55.
- Jevnikar, E.M. & Zanno, L.E. 2021.** Bimodal trajectories and unresolved early growth stages in *Tyrannosaurus rex* growth. *Society of Vertebrate Paleontology 81<sup>st</sup> Annual Meeting*, 150–151.
- Johnson, M., Young, M.T. & Brusatte, S.L. 2020.** Emptying the wastebasket: A historical and taxonomic revision of the Jurassic crocodylomorph *Steneosaurus*. *Zoological Journal of the Linnean Society*, 189: 428–448. <https://doi.org/10.1093/zoolinnean/zlaa027>.
- Knutsen, E.M. 2012.** A taxonomic revision of the genus *Pliosaurus*. *Norwegian Journal of Geology*, 92: 259–276.
- Koepfli, K.P., Pollinger, J., Godinho, R., Robinson, J., Lea, A., Hendricks, S., Schweizer, R.M., Thalmann, O., Silva, P., Fan, Z., Yurchenko, A.A., Dobrynin, P., Makunin, A., Cahill, J.A., Shapiro, B., Álvares, F., Brito, J.C., Geffen, E., Leonard, J.A., Helgen, K.M., Johnson, W.E., O’Brien, S.J., Van Valkenburgh, B. & Wayne, R.K. 2015.** Genome-wide Evidence Reveals that African and Eurasian Golden Jackals Are Distinct Species. *Current Biology*, 25(16): 2158–2165. <https://doi.org/10.1016/j.cub.2015.06.060>.
- Kurzanov S.M. 1976.** A new carnosaur from the Late Cretaceous of Nogon-Tsav, Mongolia. *The Joint Soviet-Mongolian Paleontological Expedition Transactions*, 3: 93–104.
- Larramendi, A., Paul, G.S. & Hsu, S. 2021.** Review and reappraisal of the specific gravities of present and past multicellular organisms, with an emphasis on vertebrates, particularly pterosaurs and dinosaurs: *The Anatomical Record*, 304: 1833–1888. <https://doi.org/10.1002/ar.24574>.
- Larramendi, A., Zhang, H. Palombo, M.R. & Ferretti, M.P. 2020.** The evolution of *Palaeoloxodon* skull structure: Disentangling phylogenetic, sexually dimorphic, ontogenetic, and allometric morphological signals. *Quaternary Science Review*, 229: 1–22. <https://doi.org/10.1016/j.quascirev.2019.106090>.
- Larson, P. 2008.** Variation and sexual dimorphism in *Tyrannosaurus rex*. pp. 103–130. In: Larson, P. & Carpenter, K. (Eds), *Tyrannosaurus rex: The Tyrant King*. Indiana University Press. <https://doi.org/10.2979/5139.0>.
- Larson, P. 2013a.** The validity of *Nanotyrannus lancensis*. *Society of Vertebrate Paleontology 73<sup>rd</sup> Annual Meeting*, 159.

- Larson, P. 2013b.** The case for *Nanotyrannus*. pp. 15–53. In: Parrish, J.M., Molnar, R.E., Currie, P.J. & Koppelhus, E.B. (Eds), *Tyrannosaurid Paleobiology*. Indiana University Press.
- Laudet, V. 2011.** The origins and evolution of vertebrate metamorphosis. *Current Biology*, 21: R726–R737. <https://doi.org/10.1016/j.cub.2011.07.030>.
- LeBlanc, A.R.H., Brink, K.S., Whitney, M.R., Abdala, F., & Reisz, R.R. 2018.** Dental ontogeny in extinct synapsids reveals a complex evolutionary history of the mammalian tooth attachment system. *Proceedings of the Royal Society B*, 285: 1–9. <https://doi.org/10.1098/rspb.2018.1792>.
- Lehman T.M. & Wick, S.L. 2012.** Tyrannosauroid dinosaurs from the Aguja Formation of Big Bend National Park, Texas. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 103: 471–485. <https://doi.org/10.1017/S1755691013000261>.
- Liu, S., Westbury, M.V., Dussex, N., Mitchell, K.J., Sinding, M.S., Heintzman, P.D., Duchêne, D.A., Kapp, J.D., von Seth, J., Heiniger, H., Sánchez-Barreiro, F., Margaryan, A., André-Olsen, R., De Cahsan, B., Meng, G., Yang, C., Chen, L., van der Valk, T., Moodley, Y., Rookmaaker, K., Bruford, M.W., Ryder, O., Steiner, C., Bruins-van Sonsbeek, L.G.R., Vartanyan, S., Guo, C., Cooper, A., Kosintsev, P., Kirillova, I., Lister, A.M., Marques-Bonet, T., Gopalakrishnan, S., Dunn R.R., Lorenzen, E.D., Shapiro, B., Zhang, G., Antoine, P.O., Dalén, L. & Gilbert, M.T.P. 2021.** Ancient and modern genomes unravel the evolutionary history of the rhinoceros family. *Cell*, 184(19): 4874–4885.e16. <https://doi.org/10.1016/j.cell.2021.07.032>.
- Loewen M.A, Irmis R.B, Sertich J.J, Currie P.J. & Sampson S.D. 2013.** Tyrant dinosaur evolution tracks the rise and fall of Late Cretaceous oceans. *PLoS One*, 8(11):e79420. <https://doi.org/10.1371/journal.pone.0079420>.
- Longrich, N.R. & Saitta, E.T. 2024.** Taxonomic status of *Nanotyrannus lancensis*—a distinct taxon of small-bodied tyrannosaur. *Fossil Studies*, 2: 1–25. <https://doi.org/10.3390/fossils2010001>.
- Longrich, N.R., Dalman, S., Lucas, S.G. & Fiorillo, A.R. 2026a.** A large tyrannosaurid from the Late Cretaceous of North America. *Scientific Reports*, 16: 8371. <https://doi.org/10.1038/s41598-026-38600-w>.
- Longrich, N.R., Makovicky, P.J., Tokaryk, T., Cooper, D.M.L., Saitta, E.T., Erickson, G.M., Szekely, T. & Snively, E. 2026b.** Hatchlings of *Tyrannosaurus rex* and the evolution of dinosaur reproductive strategies. *Biology*, 15: 1909. <https://10.3390/biology15131090>.
- Macdonald, I. & Currie, P.J. 2018.** Description of a partial *Dromiceiomimus* (Dinosauria: Theropoda) skeleton with comments on the validity of the genus. *Canadian Journal of Earth Sciences*, 56: 129–157. <https://doi.org/10.1139/cjes-2018-0162>.
- Maddison, W.P. and Maddison, D.R. 2026.** Mesquite: a modular system for evolutionary analysis. Version 4.03. <https://www.mesquiteproject.org>.
- Mader, B.J. 2010.** A species-level revision of the North American brontotheres *Eotitanops* and *Palaeosyops*. *Zootaxa*, 2339: 1–43. <https://doi.org/10.11646/zootaxa.2339.1.1>.
- Maisch, M.W. 2008.** Revision der Gattung *Stenopterygius* Jaekel, 1904 emend. Von Huene, 1922 aus dem unteren Jura Westeuropas. *Palaeodiversity*, 1: 227–271.
- Maleev, Y. 1955.** New carnivorous dinosaurs from the Upper Cretaceous of Mongolia. *Doklady Academy of Sciences USSR*, 104: 779–782.
- Mallon, J.C. 2017.** Recognizing sexual dimorphism in the fossil record: lessons from nonavian dinosaurs. *Paleobiology*, 43: 495–507. <https://doi.org/10.1017/pab.2016.51>.
- Mallon, J.C. & Hone, D.W. 2024.** Estimation of maximum body size in fossil species: A case study using *Tyrannosaurus rex*. *Ecology and Evolution*, 14: e11658. <https://doi.org/10.1002/ece3.11658>.



- Marsh, O.C. 1887.** Notice of a new and gigantic dinosaur. *The American Journal of Science and Arts*, 79: 87–88. <https://doi.org/10.2475/ajs.s3-14.79.87>.
- Maxwell, E.E. 2012.** New metrics to differentiate species of *Stenopterygius* from the Lower Jurassic of southwestern Germany. *Journal of Paleontology*, 86: 105–115. <https://doi.org/10.1666/11-038.1>.
- Mihlbacher, M.C. 2008.** Species taxonomy, phylogeny, and biogeography of the Brontotheriidae. *Bulletin of the American Museum of Natural History*, 311: 1–475. [https://doi.org/10.1206/0003-0090\(2008\)501\[1:STPABO\]2.0.CO;2](https://doi.org/10.1206/0003-0090(2008)501[1:STPABO]2.0.CO;2).
- Molnar, R.E. 1978.** A new theropod dinosaur from the Upper Cretaceous of central Montana. *Journal of Paleontology*, 52: 73–82.
- Molnar, R.E. 1980.** An albertosaur from the Hell-Creek formation of Montana. *Journal of Paleontology*, 54: 102–108.
- Molnar, R.E. & Carpenter, K. 1989.** The Jordan theropod referred to the genus *Aublysodon*. *Geobios*, 22: 445–454. [https://doi.org/10.1016/S0016-6995\(89\)80098-1](https://doi.org/10.1016/S0016-6995(89)80098-1).
- Napoli, J.G. 2024.** Resolving the “ontogeny problem” in vertebrate paleontology. *bioRxiv*, 10.25.620216. <https://doi.org/10.1101/2024.10.25.620216>.
- Napoli, J.G., Powers, M.J., Ruebenstahl, A.A., Voris, J.T., Green, T.L., Turner, A.H., Flynn, J.J., Currie, P.J. & Norell, M.A. 2023.** Cryptic species in the theropod fossil record. *Society of Vertebrate Paleontology 83<sup>rd</sup> Annual Meeting*, 319.
- Nixon, K.C. 2002.** WinClada, ver. 1.00.08. Published by the author, Ithaca, NY, USA.
- O’Connor, R.E., Romanov, M.N., Kiazim, L.G., Barrett, P.M., Farré, M., Damas, J., Ferguson-Smith, M., Valenzuela, N., Larkin, D.M. & Griffin, D.K. 2018.** Reconstruction of the diapsid ancestral genome permits chromosome evolution tracing in avian and non-avian dinosaurs. *Nature Communications*, 9: 1883. <https://doi.org/10.1038/s41467-018-04267-9>
- Olshevsky, G., Ford, T.L. & Yamamoto, S. 1995.** The origin and evolution of the tyrannosaurids, Part 2. *Dino Frontline*, 6: 75–99.
- Osborn, H.F. 1905.** *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bulletin of the American Museum of Natural History*, 21: 259–265.
- Osborn, H.F. 1906.** *Tyrannosaurus*, Upper Cretaceous carnivorous dinosaur (Second Communication). *Bulletin of the American Museum of Natural History*, 22: 281–296.
- Paris, M. & Laudet, V. 2008.** The history of a developmental stage: metamorphosis in chordates. *Genesis*, 46: 657–672. <https://doi.org/10.1002/dvg.20443>.
- Paul, G.S. 1988.** *Predatory Dinosaurs of the World*. Simon & Schuster, 110–113.
- Paul, G.S. 1998.** Limb design, function and running performance in ostrich-mimics and tyrannosaurus. *Gaia*, 15: 257–270.
- Paul, G.S. 2008.** The extreme lifestyles and habits of the gigantic tyrannosaurid superpredators of the Late Cretaceous of North America and Asia. pp. 307–352. In: Larson, P. & Carpenter, K. (Eds), *Tyrannosaurus rex: The Tyrant King*. Indiana University Press.
- Paul, G.S. 2010.** *The Princeton Field Guide to Dinosaurs*. Princeton University Press, 1–320. <https://doi.org/10.1515/9781400836154>.
- Paul, G.S. 2012.** Evidence for avian-mammalian aerobic capacity and thermoregulation in Mesozoic dinosaurs. pp. 818–871. In: Brett-Surman, M.K., Holtz, T.R. & Farlow, J. O. (Eds), *The Complete Dinosaur*. Indiana University Press.
- Paul, G.S. 2016.** *The Princeton Field Guide to Dinosaurs 2<sup>nd</sup> ed.* Princeton University Press, 1–360. <https://doi.org/10.1515/9781400883141>.
- Paul G.S. 2022.** *The Princeton Field Guide to Mesozoic Sea Reptiles*. Princeton University Press, 1–208. <https://doi.org/10.1515/9780691241456>.

- Paul, G.S. 2024a.** *The Princeton Field Guide to Dinosaurs 3<sup>rd</sup> ed.* Princeton University Press, 1–384. <https://doi.org/10.1515/9780691253336>.
- Paul, G.S. 2024b.** *The Princeton Field Guide to Predatory Dinosaurs.* Princeton University Press, 1–256. <https://doi.org/10.1515/9780691253336>.
- Paul, G.S. 2025a.** A presentation of the current data on the exceptionally diverse non-tyrannosaurid eutyrranosaur and tyrannosaurini genera and species of western North America during the End Cretaceous North American Interchange. *Mesozoic*, 2: 85–138. <https://doi.org/10.11646/mesozoic.2.2.1>.
- Paul, G.S. 2025b.** Stratigraphic and anatomical evidence for multiple titanosaurid dinosaur taxa in the late Late Cretaceous of southwestern North America. *Geology of the Intermountain West*, 12: 201–220. <https://doi.org/10.31711/giw.v12.pp201-220>.
- Paul, G.S., Persons, W.S. & Van Raalte, J. 2022.** The tyrant lizard king, queen and emperor: Multiple lines of evidence support subtle evolution and probable speciation within the North American genus *Tyrannosaurus*. *Evolutionary Biology*, 49: 156–179. <https://doi.org/10.1007/s11692-022-09561-5>.
- Peterson, R.T. 1934.** *A Field Guide to the Birds.* Houghton Mifflin.
- Raun, G.S., Sharpe, H.S. & Currie, P.J. 2025a.** The apple doesn't fall far from the tree: *Tarbosaurus* has stable discrete characters through ontogeny. *The Society of Vertebrate Paleontology 85<sup>th</sup> Meeting Abstracts*, 516.
- Raun, G.S., Sharpe, H.S., Powers, M.J. & Currie, P.J. 2025b.** Who was the ruler of Maastrichtian Mongolia? Taxonomic revision of *Tarbosaurus* provides insight into tyrannosaurid diversity of central Asia. *Canadian Society of Vertebrate Paleontology 11<sup>th</sup> Annual Meeting Abstracts*, 37.
- Roberts, E.M., Hendrix, M.S., Ramezani, J. Clyde, W.C., Zippi, P., Hodgson, S. Yuleridge, V. & Zanno, L.E. 2026.** High precision CA-ID-TIMS U-Pb zircon age for the “Dueling Dinosaurs” locality, with implications for regional correlation, basal age and duration of the Hell Creek Formation, Montana. *PLOS One*, 21: e0328861. <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0328861>.
- Rogez, B. 2021.** *Nanotyrannus*. <https://sketchfab.com/3d-models/nanotyrannus-young-t-rex-d2b1ea71dbea4c6e90ec93f046066cb2>.
- Rozhdestvensky, A.K. 1965.** Growth changes in Asian dinosaurs and some problems of their taxonomy. *Paleontologicheskii Zhurnal*, 1965: 95–109. <http://reptilis.net/DML/2020Dec/pdf09xDkFG82J.pdf>.
- Russell, D.A. 1970.** Tyrannosaurs from the Late Cretaceous of western Canada. *National Museum of Natural Sciences Publications in Paleontology*, 1: 1–34.
- Sanchez-Fenollosa, S., Escaso, F. & Cobos, A. 2024.** A new specimen of *Dacentrurus armatus* Owen, 1875 from the Upper Jurassic of Spain and European stegosaurian diversity. *Zoological Journal of the Linnean Society*, 203: zlae074. <https://doi.org/10.1093/zoolinnean/zlae074>.
- Scannella, J.B., Fowler, D.W., Goodwin, M.B. & Horner, J.R. 2014.** Evolutionary Trends in *Triceratops* from the Hell Creek Formation, Montana. *Proceedings of the National Academy of Sciences*, 111: 10245–10250. <https://doi.org/10.1073/pnas.1313334111>.
- Scherer, C.R., Steell, E. & Upchurch, P. 2026.** Drivers and mechanisms of convergent forelimb reduction in non-avian theropod dinosaurs. *Proceedings of the Royal Society B: Biological Sciences*, 293: 20260528. <https://doi.org/10.1098/rspb.2026.0528>
- Schmerge, J.D. & Rothschild, B.R. 2016a.** Distribution of the dentary groove of theropod dinosaurs: Implications for theropod phylogeny and the validity of the genus *Nanotyrannus*

- Bakker *et al.* 1988. *Cretaceous Research*, 61: 26–33. <https://doi.org/10.1016/j.cretres.2015.12.016>.
- Schmerge, J.D. & Rothschild, B.R. 2016b. When a groove is not a groove: Clarification of the appearance of the dentary groove in tyrannosauroid theropods and the distinction between *Nanotyrannus* and *Tyrannosaurus*. Reply to Comment on: “Distribution of the dentary groove of theropod dinosaurs: Implications for theropod phylogeny and the validity of the genus *Nanotyrannus* Bakker *et al.* 1988”. *Cretaceous Research*, 65: 238–243. <https://doi.org/10.1016/j.cretres.2016.04.015>.
- Sereno, P., Tan, L., Brusatte, S.L., Kriegstein, H.J., Zhao, X. & Cloward, K. 2009. "Tyrannosaurid skeletal design first evolved at small body size". *Science*, 326: 418–422. <https://doi.org/10.1126/science.1177428>.
- Snively, E., O'Brien, H., Henderson, D.M., Mallison, H., Surring, L.A., Burns, M.E., Holtz, T.R., Russell, A.P., Witmer, L.M., Currie, P.J., Hartman, S.A. & Cotton, J.R. 2019. Lower rotational inertia and larger leg muscles indicate more rapid turns in tyrannosaurids than in other large theropods. *PeerJ*, 7: e6432. <https://doi:10.7717/peerj.6432>
- Stein, W.W. & Triebold, M. 2013. Preliminary analysis of a sub-adult tyrannosaurid skeleton from the Judith River Formation of Petroleum County, Montana. pp. 55–77. In: Parrish, J.M., Molnar, R.E., Currie, P.J. & Koppelhus, E.B. (Eds), *Tyrannosaurid Paleobiology*. Indiana University Press, Bloomington.
- Stock, J.C., Powers, M.J., Coppock, C., Raun, G.S., Sharpe, H.S., Henry, S., Jared, T., Napoli, J.G. & Currie, P.J. 2024. New species of *Albertosaurus* from a distinct stratigraphic unit of the Horseshoe Canyon Formation corresponding to faunal and climatic changes. *The Society of Vertebrate Paleontology 84<sup>th</sup> Meeting Abstracts*, 518–519.
- Voris, J.T., Therrien, F., Zelenitzky, D.K. & Brown, C.M. 2020. "A new tyrannosaurine from the Campanian Foremost Formation of Alberta, Canada, provides insight into the evolution and biogeography of tyrannosaurids". *Cretaceous Research*, 110: 104388. <https://doi.org/10.1016/j.cretres.2020.104388>.
- Voris, J.T., Zelenitzky, D.K., Kobayashi, Y., Modesto, S.P., Therrien, F., Tsutsumi, H., Chinzorig, T. & Tsogtbaatar K. 2025. A new Mongolian tyrannosauroid and the evolution of Eutyrannosauria. *Nature*, 642(8069): 973–979. <https://doi.org/10.1038/s41586-025-08964-6>.
- Wang, S., Stiegler, J., Amiot, R., Wang, X., Du, G.-H., Clark, J.M. & Xu, X. 2017. Extreme ontogenetic changes in a ceratosaurian theropod. *Current Biology*, 27: 144–148. <https://doi.org/10.1016/j.cub.2016.10.043>.
- Witmer, L.M. & Ridgely, R.C. 2010. The Cleveland tyrannosaur skull (*Nanotyrannus* or *Tyrannosaurus*): New findings based on CT scanning, with special reference to the braincase. *Kirtlandia*, 57: 61–81.
- Woodward, H.N., Myhrvold, N.P. & Horner, J.R. 2026. Prolonged growth and extended subadult development in the *Tyrannosaurus rex* species complex revealed by expanded histological sampling and statistical modeling. *PeerJ*, 14: e20469. <https://doi.org/10.7717/peerj.20469>.
- Woodward, H.N., Tremaine, K., Williamson S.A., Zanno, L.E., Horner, J.R. & Myhrvold, N. 2020. Growing up *Tyrannosaurus rex*: Osteohistory refutes the pygmy “*Nanotyrannus*” and supports ontogenetic niche partitioning in juvenile *Tyrannosaurus*. *Science Advances*, 6: eaax6250. <https://doi.org/10.1126/sciadv.aax6250>.
- Yun, C-G. 2026. Geometric and linear morphometric approaches to establish taxonomic identity of a controversial tyrannosaurid maxilla specimen. *Lethaia*, 60: 1–10. <https://doi.org/10.18261/let.60.2.2>.

- Yun, C.G., Delcourt, R. & Currie, P.J. 2025.** Allometric growth and intraspecific variation of the craniomandibular bones of *Tarbosaurus bataar*: a geometric morphometric approach. *Lethaia*, 58: 1–28. <https://doi.org/10.18261/let.58.4.6>.
- Zanno, L.E. & Napoli, J.G. 2025.** *Nanotyrannus* and *Tyrannosaurus* coexisted at the close of the Cretaceous. *Nature*, 648: 357–367. <https://doi.org/10.1038/s41586-025-09801-6>.
- Zhang G. 2025.** guoyi.run: one-step TNT script for maximum parsimony phylogenetic analysis. *Zootaxa*, 5642: 96–98. <https://doi.org/10.11646/zootaxa.5642.1.10>.
- Zheng, W., Jin, X., Xie, J. & Du, T. 2024.** The first deep-snouted tyrannosaur from Upper Cretaceous Ganzhou City of southeastern China. *Scientific Reports*, 14, 16276. <https://doi.org/10.1038/s41598-024-66278-5>.

**Received:** 11 February 2025

**Accepted for publication:** 10 June 2026