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A presentation of the current data on the exceptionally diverse non-tyrannosaurid eutyrannosaur and tyrannosaurini genera and species of western North America during the End Cretaceous North American Interchange

GREGORY S. PAUL
3100 St Paul St. 604, Baltimore MD, 21218 USA
GSP1954@aol.com; *https://orcid.org/0000-0002-4493-6092*

Abstract

Differences in proportions, anatomy, and species display features between specimens of all sizes from the latest Maastrichtian formations of the North American upper plains, greatly exceed those observed in other eutyrannosaur species, genera and subfamilies. The question is not whether more than one taxon was extant, but how many and at what ranks. Among the large *Tyrannosaurus*, early *T. imperator* retains the robust proportions, two lower functional incisors and postorbital boss features derived from earlier tyrannosaurids—the boss that includes highly atypical, large, long spindles not present in stratigraphically higher species. Among the latter, about half are robust *T. rex* specimens with single lower incisors, and are adorned by unique, very prominent "Mickey Mouse" postorbital display discs not previously observed in *Tyrannosaurus*. Contemporary *T. regina* skulls and skeletons are markedly more gracile, and lack either the postorbital spindles or discs. About half a dozen small remains are from juvenile specimens of *Tyrannosaurus* with the same tooth counts and lack of a prominent lateral dentary groove as the adults. Twice as many cannot be juveniles because their preserved hands are absolutely as large or larger than those of large adults—appendages do not atrophy with maturity in amniotes, and the feature excludes them from being tyrannosaurids. Furthermore, they have more teeth than adult specimens of *Tyrannosaurus*—tooth count reduction being abnormal or absent among growing reptiles. Growth arcs preserved in bone sections show these non-tyrannosaurids were growth slowing or ceasing subadults or adults, not rapidly increasing mass expansion expected in early ontogeny giants. The large-handed basal eutyrannosaurs are diverse, some but not necessarily all being *Nanotyrannus* or *Stygivenator*. Probably having evolved in Appalachia, the basal eutyrannosaurs were invading western North America (over the recently emerged land bridge), where they continued to evolve as they successfully competed with juvenile *Tyrannosaurus*. The result was an exceptionally diverse assemblage of tyrannosaurs at that end Cretaceous locality—caused by the rare ancient geographical event.

Keywords: Dinosauria, Theropoda, tyrannosaur, *Tyrannosaurus*, *Nanotyrannus*, *Stygivenator*, Cretaceous, Laramidia

Introduction

It has long been widely albeit not universally held that all the tyrannosaur specimens of all sizes from the TT-zone (*Tyrannosaurus–Triceratops* dominated Lancian formations of the American–Canadian upper plains region sensu Paul *et al*., 2022) constitute the one specific tyrannosaurid taxon, the celebrated *Tyrannosaurus rex* (Figs 1, 2A–I, P–R). This view has often been disputed by a number of researchers in two basic, but interrelated expressions. One is the matter of the number of *Tyrannosaurus* species represented by large remains that represent adults or close to that. In parallel many see all of the smaller tyrannosaur fossils as juvenile *T. rex*, while others propose that at least some were other taxa—among them *Nanotyrannus lancensis* and *Stygivenator molnari*—that may not even be tyrannosaurids, being basal eutyrannosaurs. The extensive reference histories of the varying views have been listed elsewhere including Paul *et al*. (2022), as well as Longrich & Saitta (2024) who revealed serious deficiencies in the hypothesis that all TT-zone tyrannosaurs big and little are one species, as do Griffen *et al*. (2024). In addition, Carr *et al*. (2022) argued against Paul *et al*. (2022) who proposed the two new gigantic TT-zone species *T. regina* and *T. imperator*. Paul *et al*. (2022) sparked an atypically intense reaction in the press as well as Carr *et al*. This is perplexing in that data and analysis of similar quality in recent work on cryptic intragenus species such as *Allosaurus* (Chure & Loewen, 2020; Danison *et al*., 2024) have been accepted with little or no discontent. Dalman *et al*. (2024) named a new giant late Campanian/early Maastrichtian species from the southwest United State *Tyrannosaurus mcraeensis*. Dalman *et al*. (2024) and Longrich & Saitta (2024) were provisionally favourable to multiple TT-zone *Tyrannosaurus* species, with the latter tentatively assigning some specimens to *T. imperator*.

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This analysis is a refinement and major expansion of Paul (2022) incorporating data and analysis that is necessary for work by others on the issue to proceed, with the addition of an extensive discussion and evaluation of the status of the small tyrannosaur TT-zone specimens. The result is a comprehensive examination of the data on hand for specimens of all dimensions. Because this is the first major study to assess and formally diagnose the taxonomy of all significant TT-zone tyrannosaurs at the same time, it enjoys the advantage of potential data reinforcement between the fossils of varying proportions. Also examined are related situations regarding Lancian and other pertinent tyrannosaurs from outside the TT-zone. The intent is to provide the latest data and analysis on hand on an active area of research and debate, so that it is available and can be considered and further processed by others.

Although not an exhaustive, in-depth review of past efforts, or a large-scale, original research project, this work is the most extensive look on the combined subjects to date, based on the data available to the author at this time. The results are only compatible with the existence of a number of tyrannosauroid taxa in the TT-zone among both adults and smaller specimens, as well as tyrannosaurins in the North American Campanian/Maastrichtian. Indeed, some items render the possibility of some of the lesser tyrannosaur material from the TT-zone being juvenile *Tyrannosaurus* biologically impossible. That while the evidence for large *Tyrannosaurus* being more than one species has become strong enough that the pressing question is not whether there were multiple species in the genus, but how many. These complex results allow aspects of the evolution of terminal Cretaceous tyrannosauroids in the context of major paleogeographic events to be discerned for the first time (Dow *et al*., 2024 being a recent example for another taxonomic group), an ability not allowed by the obsolete and evolutionarily simplistic wastebasket placement of everything in *T. rex*. Unprecedented comprehensive diagnoses for three late Maastrichtian *Tyrannosaurus* species are produced. These include early, robust as was normal for tyrannosaurids, two lower incisor toothed, broad interfenestral pillared *T. imperator* that sported a long low, spindle postorbital boss—this species may have descended from similarly adorned earlier *T.*? *mcraeensis*. Subsequently appearing in contemporary parallel in the latest per K/Pg Maastrichtian are robust *T. rex* with one functional incisor and high placed postorbital discs not seen in any other avepods, and atypically gracile *T. regina* with one incisor and modest sized display discs. At present, only one major giant *Tyrannosaurus* specimen, due to its lack of key diagnostic elements and stratigraphic data, cannot be placed. The implication by Longrich & Saitta (2024) that many of the small TT-zone tyrannosaurs are multiple species and even genera of gracile non-tyrannosaurid eutyrannosaurs is affirmed, with provisional diagnoses provided for *Nanotyrannus* and *Stygivenator*. That said, insufficient data on their anatomy and stratigraphy significantly limits the detailed work on the small graciles.

It is proposed that the high diversity of large to gigantic avepod theropods in the TT-zone is both the Mesozoic predatory dinosaurian norm, and the result of the reunification of the North American continent in the later Maastrichtian due to retreat of the interior seaway. Similar to the recent great American interchange between North and South America, the end Mesozoic North American interchange allowed a mixing of modest-sized eastern non-tyrannosaurids bearing relatively large arms with the titanic bodied, small-forelimbed tyrannosaurids that had been evolving on Laramidia and in Asia. The current evidence tends to favour *Tyrannosaurus* having evolved from earlier, over-sized local tyrannosaurids, rather than being an Asian import. Adequacy problems with a number of type specimens for the small graciles are discussed. Also considered are problems with palaeozoological procedures that have hindered the investigation of the systematics and evolution of TT-zone tyrannosaurs into this century. In particular, the criteria for determining dinosaur species have been highly inconsistent. Normal, scientifically proper procedures that have been utilized with little or no protest on other dinosaur taxa of late have been inconsistently considered inadequate when applied to TT-zone tyrannosaurs. Meanwhile, some arguments designed to force all the TT-zone tyrannosaurs into *T. rex* are themselves not scientific. This analysis refutes in nearly all regards those by Carr (2020) and Carr *et al*. (2022).

Because a number of significant TT-zone specimens have not been tagged with popular names that have graced most of them since the 1990s, such are proposed (see Table 1).

Institutional abbreviations

AMNH, American Museum of Natural History, New York; AWMM, Auckland War Memorial Museum, Auckland; BHI, Black Hills Institute, Hill City; BDM, Badlands Dinosaur Museum, Dickinson, BRMP, Burpee Museum of Natural History, Rockford; CM, Carnegie Museum of Natural History, Pittsburgh; CMN, Canadian Museum of Nature, Ottawa; CMNH, Cleveland Museum of Natural History, Cleveland; CURC, Chicago University Research Center, Chicago; DDM, Dinosaur Discovery Museum, Kenosha; DMNS, Denver Museum of Nature and Science, Denver; EM, Eastend Museum, Eastend. FMNH, Field Museum of Natural History, Chicago; GM, Ganzhou Museum, Ganzhou; HRS, Hanson Research Station, Newcastle; KU, Kansas University, Lawrence; LACM, Los Angeles County Museum, Los Angeles; LH, Long Hao Institute of Geology and Palaeontology,

TABLE 1. Skull ratios and related data for large *Tyrannosaurus* specimens, measurements in mm. Specimens approximately ordered by gross stratigraphic level in the TT-zone, and species assignments, to the degree possible, with robust, gracile or borderline as determined by overall skeletal analysis, largely based on results from Paul *et al*. (2022); results are plotted in Fig. 3K–N. Maxilla length/height ratios from Paul *et al*. (2022) and Supplementary Table 2), some corrections noted below for each ratio. All skull lengths are approximate and there are uncertainties about some; more readily measured femoral lengths provide generally more reliable comparative sizes of the individuals. Additional calculations (variation percentage, ratio ranges, ratio averages and medians) for the large specimens of each taxon are at the bottom of each taxon's data set. Abbreviations—postorbital boss prominence rankings; not prominent (NP), fairly prominent (FP), prominent (P), and very prominent (VP): nasal ridge rugosity ratings; smooth (S), fairly rough (FR), rough (R), very rough (VR), extra rough (ER): element is too incomplete in at least one dimension or otherwise not measurable or estimable (nm). New informal names are based on those of their discoverers.

	Species	Grac or Rob	Level	Skull Length	Femur Length	Maxilla L/D Ratio	Maxilla Fenestra Width	Min Pillar Width	MF/MP Ratio
NHMAD Stan	*T. reg.*	G	h	1470	1350	1.96	127l	33l	3.85
LACM23844 Harley Rex	*T. reg.*?	g?	h	1380	na	2.17	127r	32r	3.97
LACM150167 Thomas	*T. reg.*	G	h	1370	1181	2.11	99	20	4.95
USNM555000 Wankel	*T. reg.*	G	h	1360	1280	2.02	97l	23l	4.22
MOR980 Peck's-rex	*T. reg.*	G	h	1360	1232	2.26	116r	27r	4.3
TMP81.6.1 Black Beauty	*T. reg.*	G	h	1190	1210	2.19	103l 89r	27l 24r	3.76
RSMP2523.8 Scotty	*T. rex*	R	h	1610	1333	nm	118r	50r	2.36
CM9380 Barnum	*T. rex*	R	h	1360	1269	1.83	110l	33l	3.33
UWBM99000 Tufts-Love	*T. rex*	R	h	1300	na	1.88	124r	40r	3.1
Z-rex/Samson	*T. imp.*	R	l	1400	1343	1.87	97r	48r	2.02
FMNHPR2081 Sue	*T. imp.*	R	l or m	1470	1321	nm	112r	~51r	~2.2
MOR008 Bill	*T. imp.*?	?	na	1400	na	2.06	81r	25r	3.24
SDSM12047 Jennings	*T. imp.*	R	l	1400	na	nm	103l	48l	2.15
MB R91216 Tristan	*T. imp.*	R	l	1300	1220	nm	nm	nm	nm
RGM792.000 Trix	*T. imp.*	R	l	1300	1170	1.85	91l 125r	43l 48r	2.35
MOR1125 B-rex	*T. imp.*	R	l or m	1230	1150	1.88	98l	49l	2
AMNH5027 Brown	?	?	na	1370	na	1.97	115l 105r	38l 36r	2.98
UCMP118742	*T. rex*?	?	h	na	na	2.08	113r	44r	2.57
Range						1.83–2.26			2–4.95
Median						2.05			3.48
Average						2.00			3.03

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TABLE 1 (Continued)

	Lac Height	Min Lac Width	Lac H/B Ratio	Jugal Height	Jugal Width	Jugal H/B Ratio	Quadrat Height	Min Quadr Width	Quadrat H/B Ratio
NHMAD “S”	350l	51l	6.86	461l	139l	3.32	304l	63l	4.83
LACM23844 Harley	325r	57r	5.7	na	na	na	nm	nm	nm
LACM150167 Thomas	na	na	na		nm		301	71	4.24
USNM555000 Wankel	284l	55l	5.16	398r	119r	3.34	265r	66r	4.02
MOR980 Peck’s-rex	nm	nm	nm	nm	nm	nm	250r	52r	4.81
TMP81.6.1 B.B.	229l	32l	7.15	334r	100l 113r	3.14	199r	54r	3.69
RSMP2523.8 Scotty	372l	55l 55r	6.75	nm	nm	nm	278r	71l 70r	3.94
CM9380 Barnum	380l	80l	4.75	na	na	na	na	na	na
UWBM99000 T.-L.	310r	47r	6.6	397r	142r	2.8	na	na	na
Z-rex/Samson	338r	69r	4.9	408r	157r	2.6	nm	nm	nm
MOR008 Bill	378r	87r	4.34	nm	nm	nm	nm	nm	nm
FMNHPR2081 Sue	263l	70l	3.75	430r	135r	3.19	267l	70l	3.81
SDSM12047 Jennings	nm	nm	nm	nm	nm	nm	210l	61l	3.44
MBR91216 Tris	396l	81l	4.89	nm	nm	nm	nm	nm	nm
RGM792.000 Trix	280l 346r	55l 48r	6.15	400l 413r	130l 144r	2.97	208l 235r	55l 58r	3.92
MOR1125 B-rex	286l	47l	6.09	371l	142l	2.61	273l	59l	4.63
AMNH5027 Brown	318l 323r	56l 65r	5.25	438l	164l	2.67	274l 303r	58l 56r	5.06
UCMP118742	na	na	na	na	na	na	na	na	na
Range			3.75–7.2			2.6–3.34			3.44–5.06
Median			5.48			2.97			4.25
Average			5.6			2.96			4.22

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TABLE 1 (Continued)

	Species	Skull Length	Femur Length	Postorbital Boss Score	Postorbital Boss Rank	Postorbital Boss Shape	Nasal Ridge Score	Nasal Ridge Rank	Sex
NHMAD "S"	*T. reg.*	1470	1350	9	P	hat	8	R	M
LACM23844 Harley	*T. reg.*?	1400	na	3	NP		7	R	F
LACM150167 Thomas	*T. reg.*	1370	1181	2	NP		na	na	F?
USNM555000 Wankel	*T. reg.*	1360	1280	10	P		9	R	M?
MOR980 Peck's-rex	*T. reg.*	1360	1232	8	P		4	FR	M?
TMP81.6.1 B.B.	*T. reg.*	1190	1210	5	FP		1	FS	F
RSMP2523.8 Scotty	*T. rex*	Nr	1333	14	VP	knob disc	11	R	M
CM9380 Barnum	*T. rex*	1360	1269	na	na	na	na	na	?
UWBM99000 T.-L.	*T. rex*	1300	na	11	P	knob disc	14	VR	F?
Z-rex/Samson	*T. imp.*	1400	1343	6	P		6	R	F?
FMNHPR2081 Sue	*T. imp.*	1470	1321	15	VP	spindle	5	FR	M
MOR008 Bill	*T. imp.*?	1400	na	16	VP	spindle	15	FR	M
SDSM12047 Jennings	*T. imp.*	1400	na	13	P	~spindle	10	R	M?
MBR91216 Tris.	*T. imp.*	1300	1220	1	NP		2	FS	F
RGM792.000 Trix	*T. imp.*	1250	1170	12	P	spindle	12	VR	M?
MOR1125 B-rex	*T. imp.*	1230	1150	4	FP		3	FR	F
AMNH5027 Brown	?	1370	na	7	P		13	VR	?
UCMP118742	*T. rex*?	na	na	na	na		na	na	?

Hohhot; LL, The Manchester Museum, Manchester; MB, Museum fur Naturkunde, Berlin; MNHN, Museum national d'Histoire naturalle of Paris, Paris; MOR, Museum of the Rockies, Bozeman; MPC, Mongolian Palaeontological Center, Ulaanbaatar; MWC, Museum of Western Colorado, Fruita; NCMNS, North Carolina Museum of Natural Sciences, Raleigh; NHMAD, Natural History Museum Abu Dhabi, Abu Dhabi; NHMUK, Natural History Museum, London; PIN, Palaeontological Institute, Moscow; RGM, Rijksmuseum van Geologie en Mineralogie, Leiden; RMDRC, Rocky Mountain Dinosaur Resource Center, Colorado Springs; ROM, Royal Ontario Museum, Toronto; RSM, Royal Saskatchewan Museum, Regina; SDSM, Museum of Geology, South Dakota School of Mines and Technology, Rapid City; SM, Science Museum, St Paul; SMNH, Saskatchewan Museum of Natural History, Regina; TCM, The Children's Museum, Indianapolis; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller; TMT, Tate Museum, Casper; UCMP, University of California Museum of Palaeontology, Berkeley; UCRC, University of Chicago Research Collection, Chicago; UMNH, Utah Museum of Natural History, Salt Lake City; USNM, National Museum of Natural History, Smithsonian, Washington DC; UWBM, University of Washington Burke Museum of Nature and Culture, Seattle; UVALP, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton; YPM, Yale Peabody Museum, New Haven; ZPAL, Institute of Palaeontology, Polish Academy of Sciences, Warsaw.

Material and methods

In order to keep the main text reasonably compact, large and important portions of the study, including regarding methods and material, are in the Supplementary.

Informal eutyrannosaur taxonomic terminology

Non-tyrannosaurid eutyrannosaurs are generally shortened to baso-eutyrannosaurs. This includes medium sized North American eutyrannosaurs with long lower forelimbs and digits approaching, matching or exceeding in size those of adult *Tyrannosaurus*.

The competing hypotheses

That among the TT-zone tyrannosaurs of all dimensions "the everything is *Tyrannosaurus rex* hypothesis" (ETRH) is a simple paradigm. The competing "multiple tyrannosaur taxa hypothesis" (MTTH) is a much more complex proposition, containing many internal variants. One major subset of the MTTH is "the multiple *Tyrannosaurus* species hypothesis" (MTSH) in which the giants are more than one species of *Tyrannosaurus*, while all the small gracile remains are juveniles of those species. In another major subset of the MTTH "the multiple small taxa hypothesis" (MSTH) posits there is only *T. rex* regarding species among the giants, but some of the lesser sized graciles are not juveniles of that taxon. A subset of that is "the every small taxon is *Nanotyrannus lancensis* hypothesis" (ESTNLH)—paralleling the premise that all or at least the large TT-zone tyrannosaurs are *Tyrannosaurus rex*. The numerous small taxa hypothesis (NSTH) proposes that the grownups are all *T. rex*, but the small remains themselves represent multiple taxa, at least species of *Nanotyrannus*, perhaps multiple genera. The other major subset of the MTTH is "the multiple taxa at all sizes hypothesis" (MTASH) that posits that both the great and small TT-zone tyrannosaur fossils each contain multiple taxa.

In defence of the ETRH, Carr (2020) presented "the fish model of *Tyrannosaurus rex* growth hypothesis" (FMTRGH). The application of a radical metamorphosis stage observed in some teleosts such as salmon to growing TT-zone tyrannosaurs is an effort to explain why many of the small examples do not form the smooth ontogenetic anatomical continuum up to adult size observed in other tyrannosaur taxa, and in amniotes in general.

Hypotheses abbreviations

ETRH, everything is *Tyrannosaurus rex* hypothesis
FMTRGH, fish model of *Tyrannosaurus rex* growth hypothesis
MTTH, multiple tyrannosaur taxa hypothesis
MOTSH, multiple only *Tyrannosaurus* species hypothesis
MOSTH, multiple only small taxa hypothesis
ESTNLH, every small taxon is *Nanotyrannus lancensis* hypothesis
MSTH, multiple small taxa hypothesis
MTASH, multiple taxa at all sizes hypothesis

Methodology—the ordinary versus the extraordinary, the pressing need for biological plausibility, and what is null

A primary goal of this paper is to produce the most extensive yet presented character and proportional driven taxonomic diagnoses of all fossil TT-zone eutyrannosaur taxa that in coordination with stratigraphic placement—and within the current standard norms for designating palaeospecies—can be used to restore evolutionary patterns, and from that determine the taxa. Because sibling species within a genus are inherently closely related, anatomical grade and visual species identification features are the critical determinate of species status, rendering extensive phylogenetics and statistics unnecessary (as per Chure & Loewen, 2020; Danison *et al.*, 2024). The large *Tyrannosaurus* species are therefore determined via the detailed systematic differential character-based diagnoses made possible by this expanded examination, and gross stratigraphic placement from Paul *et al.* (2022; as in Chure & Loewen, 2020 and Danison *et al.*, 2024; additional references for similar standard diagnosis and stratigraphy based intragenus species work are in the Supplementary). When assessing whether or not small examples are juveniles of multi-tonne adults, growth related items are considered, including growth arcs, and compatibility with known normal amniote ontogeny. When these factors exclude their being growing *Tyrannosaurus*, the small graciles are character diagnosed at various taxonomic levels; stratigraphy is not an important factor due to lack of information. Also integrated into the work are important but neglected paleogeographic events underway near or at the TT-zone.

This analysis follows Paul *et al.* (2022) and Longrich & Saitta (2024) in considering *Tyrannosaurus* to be just another dinosaur. When assessing the potential status of species in the genus and other tyrannosaurs in the Lancian formations, one must proceed in the manner normal for prehistoric amniote systematics—in line with the treatment of the non-ionic *Allosaurus* by Chure & Loewen (2020) and Danison *et al.* (2024). Special treatment for *Tyrannosaurus* would be seriously unscientific and abnormal, a core principle of science being maximal consistency in procedures. The ordinary treatment is both in regards to the criteria used to determine the TT-zone tyrannosaurus taxa, and the biology of the taxon. The latter, such as the ontogeny of *Tyrannosaurus*, must be presumed to be normal for amniotes, dinosaurs and tyrannosaurs unless compelling, extraordinary evidence indicates otherwise. The ordinary treatment also applies to norms and measures used to assay taxa being no more or less strict that those generally applied in vertebrate palaeozoology. It follows that *T. rex* is widely considered an iconic dinosaur species (as noted in Paul *et al.*, 2022) must be and is totally ignored and has no influence of the analysis and conclusions. Note that this researcher has not inherently favoured the ETRH over the MTTH, provisionally supporting the first (Paul, 2008, 2010) when the data appeared to be tilted towards the former.

Ergo, species determination herein is based on the current preponderance of evidence for whatever hypothesis receives the most positive support. Retention of one species for a set of fossils is not parsimonious over multiple intragenus species, either possibility being basically viable until the question is properly tested.

It follows that the anatomical gauges used to assess *Tyrannosaurus* and other TT-zone tyrannosaur species need to be the same as those applied to other cases, with a broadly similar degree of variation used to determine whether the fossils are accommodated by one or more taxa—more variability cannot be allowed in a *Tyrannosaurus* species such as *T. rex* than in say *Tarbosaurus bataar*, *Gorgosaurus libratus*, *Allosaurus fragilis or A. jimmadseni*, or *Triceratops* species (Paul *et al*., 2022; Supplementary). Variability can be assayed quantitatively, for example, femoral robustness measured by bone length/shaft circumference ratio ranges in differing taxa, but also visually via the differences in shapes of display organs. Variation between species can be particularly minimal regarding intragenus sibling species that have just diverged. Complete nonoverlap of character possession between species is not necessary, especially between intragenus sibling species (Supplementary), but the less overlap there is the stronger the case for multispecificity.

The visual display organs that typically characterize species are of special importance in this work. The anatomical criteria used to determine the species recorded by large *Tyrannosaurus* remains are presented at length in the Supplementary (Engelman (2024) includes a similarly extensive supplement). That includes an extensive review of the species determination processes applied to TT-zone *Triceratops* in the seminal study by Scannella *et al*. (2014) in comparison to those used in Paul *et al*. (2022) and herein. Also considered in the Supplement is whether Carr (2020) prerebutted and Carr *et al*. (2022) successfully refuted Paul *et al*. (2022).

The application of methodological consistency over amniotes includes both that observed in adults, and during ontogeny. Growth patterns proposed for *Tyrannosaurus* need to be those typical of amniotes and not differ significantly from those of close relations. It follows that growth curves recorded in bones should show the proposed juveniles on a course to grow up into the much larger adults they are projected to become. As is standard procedure in palaeobiology, demanding automatic rejection are those scenarios that are at best implausible or even impossible for amniotes, unless extraordinary evidence indicates otherwise. The Supplementary contains a determination of whether Carr (2020) is in accord with the last necessity regarding his advocacy of the FMTRGH.

Also requiring run-of-the-mill treatment is the number of species of large land predators expected to be present in a given Mesozoic–Cenozoic habitat. If it were typical for there to be just one, then the ETRH would be favoured. But the norm is for more than one to be present, with the size typically 1–10 tonnes in the Jurassic–Cretaceous, especially in the latter period (Paul, 1988, 2010, 2016, 2024a, b; Paul *et al*., 2022; Paterna & Cau, 2022; Dalman *et al*., 2024; Longrich & Saitta, 2024). This often involves multiple avepod families. But in the late Late Cretaceous, tyrannosauroids were the only big avepods extant in North America and eastern Asia, so any multiple habitat-sharing taxa had to be from that clade. In some cases, the multiple tyrannosaur taxa in a given fauna show substantial size differentiation (*i.e*., *Tarbosaurus/Alioramus*). In other cases, two taxa are similarly gigantic (*Gorgosaurus/Daspletosaurus* which exhibit a subtle respectively gracile/robust differentiation), or both are modest in size (*Qianzhousaurus/Asiatyrannus*). The high possibility if not probability of unnamed, same size, anatomically cryptic sibling intraspecies in North American tyrannosaur genera other than *Tyrannosaurus* has seen support in recent investigations (Paulina-Carabagal *et al*. (2021) for *Daspletosaurus*, Napoli *et al*. (2023) for *Gorgosaurus* and Stock *et al*. (2024) for *Albertosaurus*). The possibility of the long extant TT-zone *Tyrannosaurus* being multispecific is similarly substantial.

Also requiring consideration is if a reconnection of two major land areas previously isolated by a marine water barrier has recently occurred in the region of interest. Such has a significant probability of increasing the diversity of both previously separated faunas, especially close to the new isthmus. This applies at the genus level and above, it being unlikely that a given genus would dwell on both sides of a saltwater barrier prior to its being readily crossable.

Of related major importance in species determination is the evolutionary speciation time factor as recorded by stratigraphic placement. Dinosaur genera were often prone to rapid evolution (Ryan & Evans, 2005; Gates *et al*., 2012; Scannella *et al*., 2014; Paul, 2016, 2024a, 2024b; Fowler, 2017; Mallon, 2019; Stock *et al*., 2024; Mallon *et al*., 2025), a tendency that appears to have been driven in part by the genetic flexibility of the clade retained in birds, leading to their high speciation rates (O'Connor *et al*., 2018). Possible exceptions, as proposed by Son *et al*. (2024), are comparatively infrequent. If the fossils of a genus extend over a few hundred thousand years, the likelihood that they represent more than one species becomes increasingly high to the degree that it becomes the most parsimonious hypothesis.

Rather than the null hypothesis automatically favouring the ETRH, the high number of species inherent to all genera that have existed (as per Gourvennec (2012) who criticizes the over splitting of palaeogenera), the high number of taxa of large predators normal in a given habitat at a given time, plus the high rate of speciation in long lasting dinosaur bearing formations, means that it is the MTTH that enjoys the parsimony edge. And all the more so if a mixing of previously distinct faunas is underway because of the emergence of a new land bridge near the location of interest. Exactly that had just occurred in regard to the TT-zone with the end Cretaceous withering of the interior seaway. The MTTH does not require extraordinary evidence, ordinary data will do. It follows that it is up the ETRH proponents to do what they have not yet done, provide the extensive set of positive evidence needed to establish that the tyrant lizard king was the sole large TT-zone predator despite the ongoing North American Interchange happening at that time and location, without deploying extraordinary hypotheses to try to overcome major inconsistencies of the ETRH.

In the tradition of forceful scientific discourse Carr *et al.* (2022) is often sharply rhetorically critical of the procedures and results of Paul *et al.* (2022). This work adopts the same modus operandi and tone in kind, the intent being to best reveal and discuss when necessary possible serious issues with the ETRH, with additional emphasis on its subpremise, the FMTRGH.

Methodological parameters list

Based on the above methodological principles, the parameters for determining intragenus sibling species among adults and juveniles versus different taxa between small and large members of a clade found in roughly contemporary habitats, are listed below (see Supplementary for further discussion on the criteria and parameters for supporting or refuting the ETRH or the MTTH).

MS (multiple species, supports at least one version of MTTH). Situation favours or establishes the multiple taxa hypothesis.

SS (single species, supports ETRH). Situation favours or establishes the one taxa hypothesis.

This is a general set of rules for palaeospecies determination, how the TT-zone tyrannosauroids in particular fit into each of them according to this study is indicated with a (T).

MS (T). Adult fossils of a genus show substantial variations in morphology including proportions comparable to those that distinguish intragenus species, especially of visual display structures.

MS (T). Adult fossils of a genus show substantial variations in morphology including proportions comparable to those that distinguish intragenus species, that markedly exceed the divergences observed in other members of the clade whether they be species, or the entire rest of the group.

SS. Adult fossils of genus show very little variation in morphology, including proportions and visual display structures.

MS (T). Adult fossils of a genus are present over a long geological period, a few hundred thousand years or more.

MS (T, between *T. imperator* and higher stratigraphic species). Adult fossils of a genus show substantial variations in morphology including proportions comparable to those that distinguish intragenus species, especially of visual display structures, and the differences correlate to a substantial degree with differing stratigraphic levels. Even if the variation does not exceed that seen within species from a given narrow time zone, change over time is indicative of speciation over time.

MS (T, between *T. rex* and *regina*). Adult fossils of a genus show substantial variations in morphology including proportions comparable to those that distinguish intragenus species, especially of visual display structures, that do not tend to correlate with stratigraphic level, when the anatomical divergences markedly exceed those observed in other species within the clade such as family level whether they be species, or the entire rest of the group.

MS or SS. Adult fossils of a genus show substantial morphological variations that do not exceed those present in species, and do not tend to correlate with stratigraphic level, in which case the variations may reflect sibling species, or intraspecies variation such as subspecific, sexual dimorphism, or individual variance.

MS (T). Substantial morphological variations tend to sort out into clusters, with each cluster distinguished from the others by a largely consistent set of characteristics not usually present in the others. It is not necessary that the clusters show no overlap, although the more nonoverlap the greater the evidence for speciation.

MS (T). Adult fossils of a genus show substantial morphological variations that tend to sort out into clusters, with each cluster distinguished from others by a largely consistent set of characteristics not usually present in the others, and the clusters in at least some cases correlate with differing stratigraphic levels.

MS or SS. Substantial morphological variations tend to sort out into clusters, with each cluster distinguished from the others by a largely consistent set of characteristics not usually present in the others, and do not tend to correlate with stratigraphic level, in which case the variations may reflect sibling species, or intraspecific variation such as sexual dimorphism.

MS (T). A major interchange of previously isolated faunas is underway in the territory, at least temporarily boosting the local diversity of taxa.

SS. An interchange of previously isolated faunas is not underway in the territory, so the local diversity of taxa has not been boosted.

SS. If small individuals of a clade show a gradual size related change in morphology grading smoothly into larger adults without any abrupt, major transitions in form over a short segment, and intermediates between the early juvenile and late adult forming a continuum, it is at least possible if not probable that the former are juveniles of the latter, especially when present in the same stratigraphic level.

MS (T). If small individuals of a clade show a sharp divergence in morphology relative to larger adults that would require an abrupt, major transition in form over a short segment of growth than it is highly improbable that the former are juveniles of the latter. This is all the truer if the degree of change is not observed in other amniotes, especially close relations of the subjects.

MS (T). If small individuals of a clade have one or more significant skeletal elements that are absolutely larger than those of larger adults this essentially proves that the former are not juveniles of the latter, shrinkage of elements not being documented among amniotes; only extensive compelling evidence otherwise can overturn this conclusion.

MS (T). If small individuals of a clade have higher maxillary and dentary tooth counts than do adults, then the former cannot be the juveniles of the latter. This is all the truer if small examples with the same tooth counts as the adults are also present.

SS (T). If small individuals of a clade have the same tooth counts as the adults, then it is at least possible if not probable that the former are the juveniles of the latter.

MS. If small individuals of a clade have external fundamental system outer bone layer, then this essentially proves the former are not juveniles of larger adults.

MS (T). If small individuals of a clade show a rapid decline in bone growth zone widths while well short of the size of the adults the former are very probably subadults of a distinct species rather than being juveniles of the larger adults, the greater the size difference the more likely this is to be true.

SS. If small individuals of a clade show an increase in bone growth zone widths while entering the expected rapid phase of growth, they are very probably juveniles of larger adults.

MS (T). If the above forms of evidence for juvenile status of small individuals of a clade are substantial or better, the greater the phylogenetic remoteness from the adult members of the clade the greater the probability of the former not being juveniles of the latter.

Fossil material

The author has seen a large number of the Late Cretaceous North American and Asian tyrannosauroid fossils considered herein over the years. Images of the remains not directly documented by this researcher are either in the technical literature, or popular publications and online postings. All the currently or once privately held specimens utilized herein have appeared in the technical literature (including Larson, 2008, 2013a; Hutchinson *et al*., 2011; Schmerge & Rothschild, 2016b; Paul *et al*., 2022; Carr *et al*., 2022). The lecture by Carr *et al*. (2022) against the use of such specimens in Paul *et al*. (2022) who were far from unique in doing so, followed by their use of the same specimens in an effort to refute Paul *et al*. (2022), is hypocritical and removes the authority of those authors to criticize such practices.

The number of large—at least 80% the size of the largest specimens—*Tyrannosaurus* specimens examined for purposes of diagnosing the species by Paul *et al*. (2022) and herein is now 38, with 32 stratigraphically correlated. The only giant *Tyrannosaurus* skull and skeleton described in extensive detail in a modern publication is FMNH PR2081 (Brochu, 2003). Molnar (1991) did extensive work on the skull of LACM23845, and (Persons *et al*., 2019) provided a significant look at the skull and skeleton of RSM2523.8. Although useful, the descriptions of CMNH9380 (ex AMNH973) and AMNH5027 (Osborn, 1905, 1906, 1912, 1916) are dated. Otherwise, the major *Tyrannosaurus* remains (USNM555000, NHMADS (ex BHI3033), MB.R.91216, RGM792.000, UWBM99000, MOR008, 980, MOR1125, MOR1128, SDSM12047, RTMP1981.6.1, LACM150167) that are in some cases analysed in numerous technical publications including this one, have not been studied and described in detail if at all. So, examining undescribed TT-zone tyrannosaur material, sometimes with the only available images in the popular milieu, is the norm in the technical literature. High quality, multiple view photographs of the LACM150167 cranial elements were made available by the institution for analysis and the first restoration of the skull (Fig. 2E).

While Paul *et al*. (2022) paid only incidental attention to smaller TT-zone tyrannosaurs, this paper includes an extensive investigation of these fossils.

The *Nanotyrannus* holotype skull has received significant examination (Witmer & Ridgley, 2010). The *Stygivenator molnari* and *Dinotyrannus megagracilis* holotypes were covered by Molnar (1978, 1980). Regarding the only two good TT-zone small tyrannosaur skulls-skeletons, neither BMRP002.4.1 nor the even more complete NCMNSBM (Bloody Mary, new specimen number not yet assigned, ex BHI6437) have been detailed. The most extensive examination of the former is Larson (2013b), but it is not a full description and lacks measurements of the elements that were figured. A skeletal restoration of BMRP2002.4.1 has been executed based on photographs and illustrations of mounted casts and other data (Fig. 1G). It is not possible to produce

FIGURE 1. TT-zone tyrannosaurini and baso-eutyrannosaur known-bone profile-skeletals and skulls to same scale, bar equals 2 m, with skulls revised to varying extents from versions in Paul *et al.* (2022, Fig. 1) with particular attention directed to accurate postorbital bosses, arrows point to those of large presumed mature males (MM) of the three species. *Tyrannosaurus* profile-skeletals: **A**, Upper TT-zone *T. rex* holotype CM9380 (6.5 tonnes). **B**, Upper TT-zone *T. rex* RSM2523.8 (mature, male? 7.8). **C**, Upper TT-zone *T. regina* NHMADS (ex BHI3033) (mature, male?, 7.5); **D**, Upper TT-zone *T. regina* holotype USNM555000 (immature? male? 6.1). **E**, Lower TT-zone *T. imperator* holotype FMNHPR2081 (mature, male? 7.8). **F**, TT-zone level unknown *T.* incertae sedis AMNH5027, preservation of ribs uncertain. Baso-eutyrannosaur skeletal: **G**, *Nanotyrannus*? incertae sedis BMRP2002.4.1 (530 kg).

such for NCMNSBM because much of the fossil remains under matrix in the published lateral view photographs, which do provide good views of the skull, forelimbs and hindlimbs (the partial skeletal of the specimen in Paul (2024b) is a provisional image for general illustrative purposes). One of the photographs includes a scale bar that was laid next to the forelimb, along with a cast of the arm of FMNHPR2081 that confirmed the scale for the appendage. Even so the proportional ratios for the two specimens are not exact.

The proportional measurements data used in this study are in part those employed in Paul *et al.* (2022), which focused on the robustness versus gracility of skull and skeletal elements. The techniques used for measuring the proportions of the maxilla, dentary, ilium, humerus, femur and metatarsals are presented in Figure 8.9 in Larson (2008). None of these measurements were challenged by Carr *et al.* (2022) and were utilized by them. In this work four new cranial measurements of the 17 large *Tyrannosaurus* skulls are added (Table 1), the techniques are illustrated in Supplement Figure 8. The obtained values are from direct measurements, or from photographs of specimens taken by myself, provided to me, or published or posted. Illustrations of postorbital bosses are traced from photographs gathered under similar circumstances. Digital scanning of the display structures may improve the results, that will require a major future project, and the often-large differences are sufficient to be delineated by the methods used herein. Anteroposterior dimensions of the bases of anterior dentary teeth, largely from Larson (2008) and especially Paul *et al.* (2022), on a given side are from either the teeth themselves, or the alveoli which are usually barely larger (further discussion including criticisms by Carr *et al.* (2022) is in the Supplement). In any case it is the ratios which are of importance regarding the elements' dimensions, not direct comparisons of the absolute measurements. Skull illustrations are direct tracings of photographs and technical illustrations,

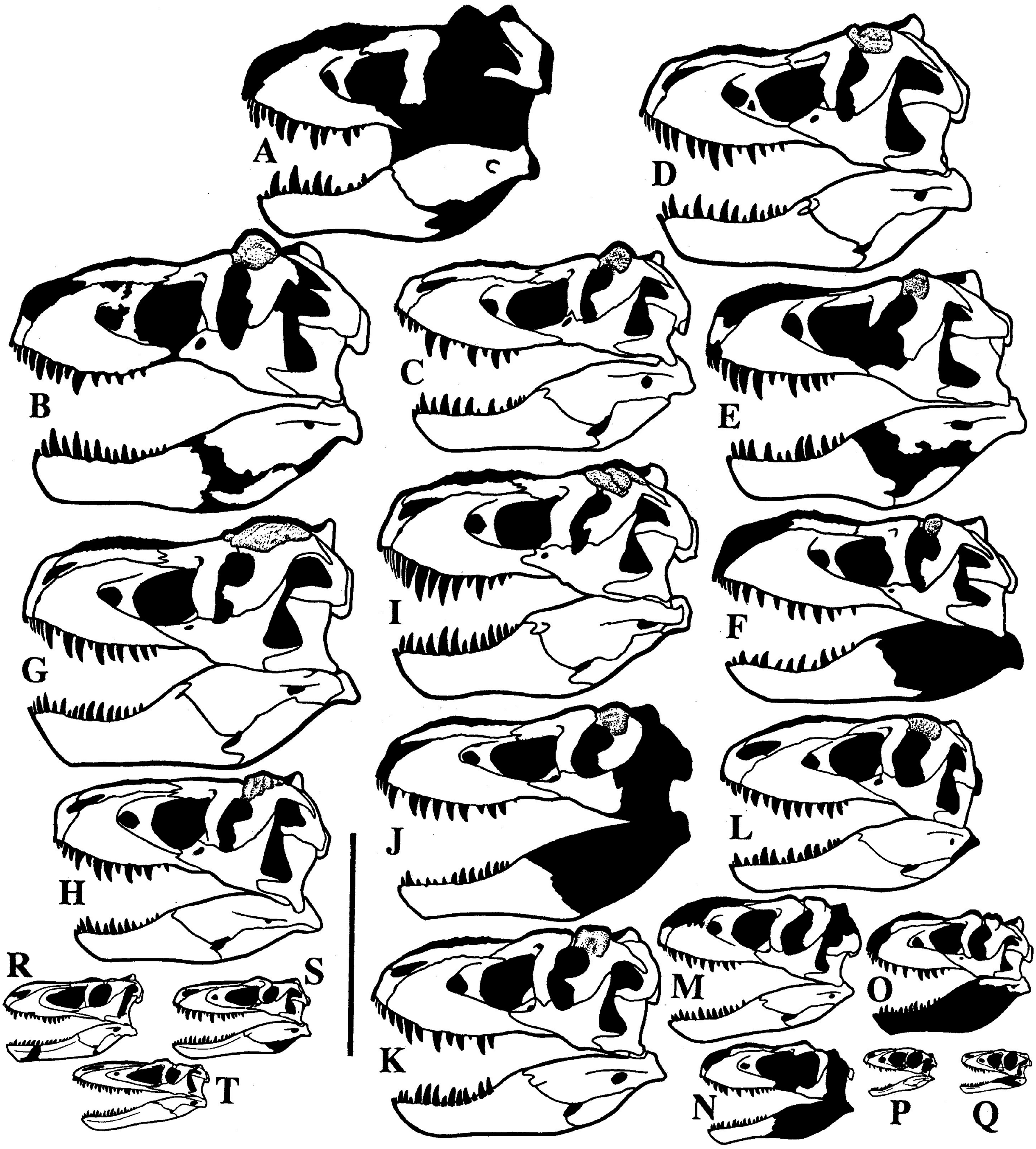

FIGURE 2. Tyrannosaurini and TT-zone baso-eutyrannosaur known bone skulls, usually positioned to decreasing ontogenetic size *in Tyrannosaurus* and *Tarbosaurus* respectively, to same scale, bar equals 1 m, dimensions for Q and R are approximate, postorbital bosses of large specimens stipple shaded. Some skulls reversed, and/or both sides used to complete restoration. *Tyrannosaurus*: **A**, Upper TT-zone *T. rex* holotype CM9380. **B**, Upper TT-zone *T. rex* RSM2523.8 (mature, male?). **C**, Upper TT-zone *T. rex* UWBM99000 (immature? female?). **D**, Upper TT-zone *T. regina* NHMAD "S" (ex BHI3033). **E**, Upper TT-zone *T. regina* LACM150167 (immature female?). **F**, Upper TT-zone *T. regina* holotype USNM555000 (immature? male?). **G**, Lower TT-zone *T. imperator* holotype FMNHPR2081 (MM 7.8). **H**, lower TT-zone *T. imperator* MOR1125 (immature? female). **I**, TT-zone level unknown *T.* incertae sedis AMNH5027. *Tarbosaurus*. **J**, *T. bataar* holotype PIN551-1 (mature). **K**, MgD-1/4 (mature). **L**, *T. efremovi* holotype PIN551-3 (immature). **M**, PIN553-1 (juvenile). **N**, MgD-1/3 (juvenile). **O**, PIN552-2 (juvenile). **P**, *Raptorex kriegsteini* holotype LHPV18 (juvenile). **Q**, MPC-D107/7 (juvenile). TT-zone baso-tyrannosaurs: **R**, lower TT-zone *Nanotyrannus lancensis* holotype CMNH7541 (subadult). **S**, TT-zone level uncertain *N.*? incertae sedis BMRP2002.4.1 (subadult). **T**, TT-zone level uncertain *Stygivenator*? incertae sedis NCMNSMB (subadult).

the severely dorso-ventrally crushed FMNHPR2081is heavily restored. It is often difficult to accurately measure or restore the actual dimensions of skulls because of distortion, and because many are reconstructions assembled from multiple disarticulated elements of varying completeness, so the skull lengths listed in Table 1 are sometimes approximations and using them for direct statistical comparisons to the dimensions of elements is problematic. Procedures for producing high fidelity profile-skeletals and using them to estimate body masses (Fig. 1) for tyrannosaurids and other tetrapods are detailed in Paul (1988, 1997, 2016, 2019; Larramendi *et al*., 2021). The results are somewhat lower than those in Longrich & Saitta (2024) that uses a different methodology for mass estimation.

The measurements for all the elements sampled have been converted into ratios and stratigraphically correlated to the extent possible (Table 1; Supplementary Table 2), and the results graphically plotted (Fig. 3) to help reveal any resulting evolutionary patterns over time (as per Fig. 1 in Scannella *et al*., 2014). The relative prominence of cranial display structures is comparatively rated by reproducing photographs to a same ornament bearing element anteroposterior length and cross comparing and ordering them until a progressive increase in the degree of prominence was placed in a series that could then be approximately numerically ranked (Table 1). The forms of the bosses are stratigraphically correlated in the text to reveal any patterns of evolution over time. Raw femur measurements are graphically plotted to allow visual comparison of variations of the proportions between *Tyrannosaurus* and other tyrannosaurid taxa.

The results of the collective analysis for large *Tyrannosaurus* fossils are tabulated towards the end of the section on species of that genus.

Stratigraphy

The stratigraphy determined by methods used in Larson (2008), Carr (2020) and Paul *et al*. (1922) for large *Tyrannosaurus* fossils and some other TT-zone non-*Tyrannosaurus* fossils is reutilized herein. As explained by Paul *et al*. (2022 and refs therein, also Eberth & Kamo, 2019; Mallon *et al*., 2025), all Canadian formations are high in the TT-zone. None of Paul *et al*. (2022) geological data was actually refuted by Carr *et al*. (2022), some of it being the same as in Carr (2020). The placements are lower, middle and high TT-zone, that being adequate for the purposes of *Tyrannosaurus* species determination as detailed in Paul *et al*. (2022) and the Supplementary (contra Carr *et al*. (2022), Carr *et al*. (2017), Chure & Loewen (2020), Danison *et al*. (2024) apply similar quality gross stratigraphy for *Allosaurus* and *Daspletosaurus* species respectively, and Mallon *et al*. (2025) for Canadian *Triceratops*). Of the 38 large *Tyrannosaurus* fossils considered, 32 are stratigraphically located. Stratigraphic data is poor or absent for most juvenile *Tyrannosaurus* (USNM6183, UCRCV1, BHI6439, KU156375, Baby Bob) and non-*Tyrannosaurus* specimens. Concerning the latter, NCMNABM and Jodi are from the lower Hell Creek (Larson, pers. comm.). BMRP2002.4.1 is from high in the Hell Creek according to Henderson & Harrison (2008), but the formation is very thin at that location and the fossil's geological placement awaits further testing. LACM28471 is from the same ranch but not same location as are high placed 23844 and 23845 (LACM records), because the property is large it is not certain if the *S. molnari* is from the same level of the Hell Creek Formation. Canadian RSMP2347.1 is upper TT-zone. No data is accessible for BMRP2006.4.4, DDM344.1, FNMHPR2411, HRS08, 15001, KU155809, MOR6625. Improving the stratigraphic data for the TT-zone tyrannosaur fossils scattered over many states and provinces in multiple formations—some of which have upwards sloping proceeding easterly bottoms due to the regression of the remnant of the interior seaway over geotime—will require many years if not decades, this study works with what is currently available.

Bone growth ring measurements and annual mass gains

Data for hindlimb bone growth zone thickness in tyrannosaurids is from Horner & Padian (2004), Cullen *et al*. (2020), Woodward *et al*. (2020) and Therrien *et al*. (2023). When complete sections (as per Fig. 2c in Cullen *et al*., 2020; Fig. S2 in Woodward *et al*., 2020) are not available, the femur or tibia bone centre to the surface of the cortex radius was calculated from external measurements directly or from images of the element; data for the full cortex of MOR1128 is not available at this time. Double and triple rings are taken to represent one annulus (as per Longrich & Saitta, 2024)—this presumption is supported by the irregular presence of such multi-lines between bones of the same tyrannosaur specimen, and within a bone (as per Fig. 2c in Cullen *et al*., 2020). Restoring standard from hatching/birth to maturity growth curves usually involves extensive assumptions and extrapolations involving extrapolating lost inner rings and not yet deposited outer layers. To avoid that this study is limited to approximating and comparing mass gains per annum documented by preserved rings. This process starts with volumetric mass estimates for USNM555000, FMNHPR2081 and BMRP2002.4.1 (Fig. 1D, E, G). The relationship of circumference of femora and tibiae relative to body mass is highly variable in TT-zone eutyrannosaurs because of the high divergence in robust versus gracile *Tyrannosaurus* femora which represent differing taxa and/or sexes, and strong size related allometry some of which is due to ontogeny. Each bone radius was used to estimate corresponding femur or tibia length, which was then used to restore body mass (further details on procedures with Supplementary: Table 1). Because of significant data gaps inherent to the process the results are highly provisional except for the values based on the last stages of growth for a given specimen.

Systematic analysis and diagnoses

Paul *et al.* (2022) found that many large TT-zone *Tyrannosaurus* fossils sorted into three diagnosable character clusters that indicated subtle but significant evolution that further indicated the presence of three intragenus species, based largely on proportional patterns linked partly to stratigraphic level. Laying out some of the basic diagnostic parameters of the species formed the foundations for the subsequent discovery of additional features that reinforce the specific segregation, to the extent that the differences are no longer subtle—to put it another way, if not for the analysis of Paul *et al.* (2022) the progress described in this work would not have been possible.

The below revised diagnoses are for TT-zone non-*Tyrannosaurus* specimens, and Asian and North American derived tyrannosaurins, and are differential between those taxa, they are not in regard to other tyrannosauroids. 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), Supplementary (for more information see further discussions below). A few specimens have been reassigned or their status modified relative to Paul *et al.* (2022). As detailed in the Supplement, ETRH driven Carr *et al.*'s (2022) diagnosing *Tarbosaurus bataar* and *Tyrannosaurus rex* at the genus rather than the specific level produced unreliable results. This effort is more focused on species diagnosis as is possible.

Characters used are only those this researcher is reasonably confident of being both accurate and applicable to the questions at hand, the tabulation is not exhaustive (for a more extensive character set see Longrich & Saitta, 2024). 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). Within the diagnoses, characters that distinguish TT-zone non-*Tyrannosaurus* taxa from juvenile *Tyrannosaurus* of similar size are indicated by #. Within the *Tyrannosaurus* diagnoses the following applies: MGE, most gracile example/s in the genus; MRE, most robust example/s in the genus. Cumulative sets of character differences largely distinguish the *Tyrannosaurus* species from one another, the observed autapomorphies in a particular species relative to the other *Tyrannosaurus* species are indicated by *. Because the relationships between the often fragmentary and/or not yet well described specimens small TT-zone remains are often obscure, the diagnoses are sometimes for informal collectives. The immediately below systematics for Tyrannosaurini rests on the existence of three *Tyrannosaurus* species, a version incorporating only two species in the genus is added at the end for reasons later explained in the analysis. A few synonyms are noted specific to purposes of this study.

TT-zone eutyrannosaurs

Character attributes: Medium sized, gracile; rostrum elongated; anterior margin of premaxilla sloped dorsoposteriorily, ventral margin anteriorly upturned, form narrow U or V in dorso/ventral view, subnarial process faces anterolaterally; 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, tip of quadratojugal process not squared off; 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, 15–16 maxillary and 16–17 dentary teeth that are bladed; two functional anterior dentary incisiforms; vertebrae gracile; scapula blade neck not especially narrow; humerus head not massive; distal forelimb elongated, especially manus so forelimb is about same length as femur or greater, and manus absolutely larger than those of adult tyrannosaurins; ilium shallow, dorsal rim fairly straight, anteroventral prong hook shaped; pubic boot gracile; femur fourth trochanter weakly developed; tibia cnemial crest gracile, rounded; distal hindlimb elongated with tibia markedly longer than femur.

Informal Nanotyrannos
Informal diagnosis: Anterior maxilla moderately elongated, it and anterior fossa moderately deep; pneumatic lateral foramen on quadratojugal; anterior dentary not upcurved.

Systematic palaeontology

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

Type species. *Nanotyrannus lancensis* Gilmore, 1946

Holotype. CMNH7541.

Diagnosis. Rostrum fairly deep, anterior maxilla not strongly elongated, antorbital fenestra and orbit large; temporal region broad; surangular short; 15 maxillary and 16 dentary teeth.

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

Nanotyrannus sp/s.?

Diagnosis. Rostrum fairly shallow, anterior maxilla more elongated; antorbital fenestra and orbit not large; surangular long; 15 maxillary and 17 dentary teeth.

Potential specimens: BMRP2002.4.1, 2006.4.4? HRS08, 15001?

Locality and horizon. Hell Creek, Lance, levels not documented; Montana, Wyoming.

Informal stygivenators

Informal diagnosis. Anterior maxilla and anterior fossa boundary sharply triangular; anterior dentary strongly upcurved.

Genus *Stygivenator* Olshevsky & Ford, 1995

Type species. *Stygivenator molnari* Paul, 1988

Holotype. LACM28471

Diagnosis. Anterior maxilla not highly elongated, maxillary teeth large.

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

Stygivenator sp.

Material. Potential specimens, NCMNSBM (ex BHI6437), Jodi.

Diagnosis. Rostrum including anterior maxilla highly elongated, dentary extremely elongated, surangular and angular reduced; first manal phalanx of digit 1 very elongated, twice as long as that of adult tyrannosaurins; remnant phalange on manal digit 3.

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

Subfamily Tyrannosaurini Olshevsky & Ford, 1995

Diagnosis. Rostrum massive; anterior margin of premaxilla vertical, ventral margin flat, form broad U in dorso/ventral view, subnarial process faces anteriorly; nasals broad except narrow where contact frontals, transversely arced, contact with maxilla irregular; maxilla deep, ventral margin strongly convex, antorbital fossa deep, 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, 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, quadratojugal process fairly long; quadratojugal jugal process fairly deep, no pneumatic lateral foramen on quadratojugal; squamosal large, ventral fossa has pneumatic recess, tip of quadratojugal process squared off; vomer anteriorly broad; palatine anterior processes short and robust, pneumatic fossa large, body inflated; ectopterygoid pneumatic opening is large; dentary deep, laterally bowed in dorsal view, symphysis well developed, lateral groove #usually absent, interdental plates well developed, surangular contact subvertical; surangular deep, lateral shelf long and prominent; premaxillary teeth vertical, 11–13 maxillary and 12–15 dentary teeth at all growth stages; forelimb very reduced, manus especially, to about two thirds femur length, and manus absolutely smaller than those of adult nanotyrannos, first manal phalanx of digit 1 not elongated, no phalanges on digit 3; ilium deep, dorsal rim dorsally arced, anteroventral prong weakly developed; pubic boot large; femur fourth trochanter well developed; tibia cnemial crest large, squared off; distal hindlimb elongated only in juveniles.

Genus *Tarbosaurus* Maleev, 1955
Olshevsky & Ford 1995 *Jenghizkhan*?
Sereno *et al.* 2002 *Raptorex*

Diagnosis. Temporal region breadth well under twice that of rostrum and less than half the length of skull, orbits and lateral face of jugal do not face substantially anteriorly; nasal is well over half length of skull and strongly domed; anterodorsal process on anterior ramus of lacrimal absent; interfenestral pillar broad; lacrimals do not nearly meet at midline and lateral swelling on supraorbital process of lacrimal is present; vomer has extensive contact with premaxilla, anterior prong deep, ventral flange deep; dentary lacks lateral groove except is short and weak in very small juveniles; 12–13 maxillary and 14–15 dentary teeth at all growth stages, usually or always two slender functional anterior incisiform dentary teeth, large teeth not as robust; pubic boot moderate in size, lower hindlimb elements longer relative to femur.

Type species? *Tarbosaurus bataar* Maleev, 1955

Maleev, 1955 *Tyrannosaurus bataar*
Maleev, 1955 *T. efremovi*?
Sereno *et al.* 2002 *Raptorex kriegsteini*

Holotype. PIN551-1.

Referred specimens: As listed in Hurum & Sabath (2003).

Diagnosis. Gigantic and robust at 4–5 tonnes; interfenestral pillar broad, postorbital bosses are fairly subtle subcircular, knob-like discs limited to the frontal process that do not project well above the dorsal rim of the skull; femur robust as per relative to general tyrannosaurid curve.

Locality and horizon. Early Maastrichtian, Nemegt; Mongolia.

Genus *Tyrannosaurus* Osborn, 1905

Olshevsky & Ford, 1995 *Dinotyrannus*

Diagnosis. Temporal region about twice as broad as rostrum and over half the length of skull, orbits and lateral face of jugal face substantially anteriorly; nasal a little over half length of skull and not as strongly domed; presence of anterodorsal process on anterior ramus of lacrimal that projects into nasal; lacrimals nearly meet at midline, sublunate in dorsal shape partly because lateral swelling on supraorbital process is absent; postorbital bosses highly variable in size and shape; vomer sometimes has anterior spear point, contact with premaxilla not as extensive, anterior prong shallow, deep ventral flange absent; dentary lacks lateral groove; 11–12 maxillary and 12–14 dentary teeth at all growth stages, one or two slender functional anterior incisiform dentary teeth, sometimes very large teeth robust; pubic boot massive; lower hindlimb elements not highly elongated relative to femur even in juveniles.

Tyrannosaurus? *mcraeensis* Dalmna *et al.*, 2024

Holotype. NMMNHP-3698.

Diagnosis. Gigantic at 6–8 tonnes; postorbital boss is low, somewhat horizontally extended, does not project much above dorsal rim of the skull; posterior dentary not deep, two slender functional anterior incisiform dentary teeth.

Locality and horizon. Latest Campanian or early Maastrichtian, Hall Lake; New Mexico.

Tyrannosaurus imperator Paul *et al.*, 2022

Holotype. FMNHPR2081.

Referred specimens: BHI4182, 6248?, AMNH3892, MBR.91216, KU156375?, MOR1125, 1128, RGM792.000, SDSM12047, TCM2001.90.1, TMTv2222, MOR008?

Diagnosis. Gigantic at 6–8 tonnes; very robust, always or usually so regarding maxilla all being more robust than *T. regina* but not all *T. rex*, interfenestral pillar (MRE) all being more robust than for *T. rex* and especially *T. regina*, lacrimal (MRE), postorbital process of jugal (MRE), quadratojugal (MRE), dentary, humerus, ilium (MRE) all being more robust than for *T. rex* and *T. regina*, metatarsals 2 and 4, with length/circumference ratios of 2.4 or less for the femur (MRE); posterior dentary deep, usually two slender functional anterior incisiform dentary teeth; very rugose nasals sometimes present; postorbital bosses are sometimes large, prominent horizontally extended spindles that extend posteriorly to close to or on the anterior squamosal process, do not project much above dorsal rim of the skull presumably among males (tall discs not present), antero-medial processes can be fairly well developed.

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

Type species *Tyrannosaurus rex* Osborn, 1905

Holotype. CM9380 (ex AMNH973).

Referred specimens: BHI6230, 6233, 6435, 6436, UWBM99000, RSM2523.8, BHI4100?, NHMUKR7994?, UCMP118742?.

Diagnosis. Gigantic at 6–8 tonnes; generally robust, but overall less so than *T. imperator*, always or usually so regarding maxilla (MRE) all being more robust than for *T. regina* but not for all *T. imperator*, interfenestral pillar all being more robust than for *T. regina* while being more gracile than for *T. imperator*, postorbital process of jugal all being more robust than for *T. regina* but not all *T. imperator*, quadratojugal, dentary (MRE), and in some cases metatarsals, with length/circumference ratios of 2.4 or less for the femur; posterior dentary deep; usually one slender functional anterior incisiform dentary tooth and no examples with a truly small second dentary tooth yet observed; very rugose nasals sometimes present; postorbital bosses are sometimes prominent subcircular, knob-like discs limited to the frontal process that project well above the dorsal rim of the skull presumably among males (low spindles not present), antero-medial processes weakly developed.

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 regina Paul *et al.*, 2022

Holotype. USNM555000 (MOR555).

Referred specimens: MOR980, LACM23844, 150167, LL12823, NHMADS (ex BHI3033), TMP81.6.1, UMNH11000?.

Diagnosis. Gigantic at 6–8 tonnes; generally gracile, more so than *T. rex* and much more than *T. imperator*, always or usually so regarding maxilla (MGE) all more gracile than *T. rex* or *T. imperator*, interfenestral pillar (MGE) all more gracile than *T. rex* or especially *T. imperator*, lacrimal (MGE), postorbital process of jugal (MGE) all more gracile than *T. rex* but not all *T. imperator*, quadratojugal (MGE), dentary (MGE), humerus (MGE), ilium all more gracile than *T. imperator*, femur gracile relative to scaling norm for tyrannosaurids with length/circumference ratios of 2.4 or higher; posterior dentary deep; one slender functional anterior incisiform dentary tooth and no examples with a truly small second dentary tooth yet observed; very rugose nasals not yet observed, postorbital bosses do not project much above dorsal rim of the skull, do not often extend onto squamosal process, are sometimes hat shaped presumably among mature males (low spindles or tall discs not present).

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.

Tyrannosaurus incertae sedis

Robusts of uncertain or middle TT-zone stratigraphic position that are probably *T. Imperator* or *T. rex*. BHI6231, 6232, 6242, USNM6183; of uncertain proportions and high stratigraphic placement that are probably *T. rex* or *T. regina*—AWMMIL2022.9,

BHI6249, DMNS2827, LACM23845; MOR009, 46028-1, TMP81.12.1; insufficient proportional and/or stratigraphic information for a species assignment—AMNH5027, 30564, BHI6439, CM1400, UCMP84133, UCRCV1, Baby Bob. Upper Javelina remains of unnamed species probably in the genus—TMM41436-1, 46028-1.

Eutyrannosauria incertae sedis

Material. DDM344.1, FMNPR2411, MOR6625, RMDRC2002.MT-001, RSM2347.1, 2990.1.

Incorporating Only Two Species of TT-zone Tyrannosaurus

These diagnoses of adult TT-zone *Tyrannosaurus* are for just two species arbitrarily assuming that *T. regina* is a junior synonym of *T. rex*, see further discussion below.

Tyrannosaurus imperator Paul *et al.*, 2022

Holotype. FMNHPR2081.

Referred specimens: BHI4182, 6248?, AMNH3892, KU156375?, MBR.91216, MOR1125, 1128, RGM792.000, SDSM12047, TCM2001.90.1, TMTv2222, MOR008?.

Diagnosis. Gigantic at 6–8 tonnes; very robust, usually two slender functional anterior incisiform dentary teeth; postorbital bosses are sometimes large, prominent horizontally extended spindles that extend posteriorly to close to or on the anterior squamosal process, do not project much above dorsal rim of the skull presumably among males (tall discs not present).

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

Tyrannosaurus rex Osborn, 1905

Paul, 1988 *T. megagracilis*
Paul *et al*., 2022 *T. regina*

Holotype. CM9380.

Referred specimens: BHI4100, 6230, 6233, 6249, 6435, 6436, NHMADS, LACM23484, 150167, 23485, DMNS2827, LL12823, MOR009, 980, NHMUKR7994, RSM2523.8, TMP81.6.1, 81.12.1, UCMP118742. USNM555000, UWBM99000, UMNH11000?.

Diagnosis. Gigantic at 6–8 tonnes; robust to gracile, usually one slender functional anterior incisiform dentary tooth and no examples with a truly small second dentary tooth yet observed; postorbital bosses in a few cases are prominent subcircular, disc-like knobs limited to the frontal process that project well above the dorsal rim of the skull presumably among males (low spindles not present).

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, Utah?, Alberta, Saskatchewan.

Tyrannosaurus incertae sedis

Material. Robusts of uncertain stratigraphic position that are probably *T. Imperator* or *T. rex*—BHI6231, 6232, 6242, USNM 6183; insufficient proportional and/or stratigraphic information for a species assignment—AMNH5027, 30564, AWMM-IL2022.9, CM1400, RMDRC2002.MT-001, TMM41436-1, 46028-1, UCMP84133.

Results

The Large TT-zone *Tyrannosaurus* Fossils

The principles and methods discussed above for using differing anatomical characteristics to assess intragenus sibling species as preserved as adults or close are applied in this section to the 38 large (~80% largest observed adult size, Paul *et al*. 2022) *Tyrannosaurus* specimens examined in this work. Much of the Supplement includes additional observations on the criteria for determining intragenus species, the reasons Carr (2020) and Carr *et al*. (2022) did not properly test the question of *Tyrannosaurus* species, why the results of Paul *et al*. (2022) and herein are probably comparable in effectiveness to those of Scannella *et al*. (2014), and numerous other aspects of the *Tyrannosaurus* diversity question.

The Daspletosaurus sibling species standard

The close, possibly ancestral *Tyrannosaurus* relative *Daspletosaurus* is unusual among tyrannosaurid genera in being widely considered to consist of multiple species on anatomical and stratigraphic grounds that evolved over a period of ~1.5 Ma (Carr *et al*., 2017; Paulina-Carabagal *et al*., 2021; Warshaw & Fowler, 2022; Paul, 2024a, 2024b; Scherer & Voiculescu-Holvad, 2024; Warshaw *et al*., 2024; Scherer, 2025). This is so despite the small sample size of half a dozen or so fairly complete adult specimens, and the absence of quantitative statistical analysis, the species being designated mainly on the basis of qualitative diagnoses. The discussions on the matter have focused on the associated hypothesis of anagenesis and to a lesser extent the number of species, monospecificity for the genus is not being advocated. The separation of *T. torosus*, *T. horneri* and possibly *T. wilsoni* is anatomically justified by their distinctive cranial display features discussed below combined with time separations. Otherwise, the diagnoses are somewhat problematic because of insufficient illustrative or quantitative documentation of the differentiation of some characters in the different species, the possibility that some differences are random divergences due to the small sample size, disagreements in the specific diagnostic features among papers discussing the matter, and the issue of sexual dimorphism not being discussed. Although meeting palaeotaxonomic norms, the criteria for showing that *Daspletosaurus* was speciose are not particularly high. The subtle visual variability between the species is not greater than present in *Tyrannosaurus* (compare Fig. 13 in Warshaw & Fowler, 2022 and Fig. 4 in Warshaw *et al*., 2024 to Fig. 2A–I herein).

Taxonomic implications. There is not a need for the totality of data and analysis supporting species within TT-zone adult *Tyrannosaurus* to be any better than that for its tyrannosaurid relation the span of the palaeotemporal existence of which was comparable (and Carr *et al*. (2017) did not provide detailed stratigraphy, the data in the other papers is not precise and somewhat inconsistent due to data limitations and disagreements), the sample size is much less, the character documentation somewhat problematic, and for which no statistical analysis has been presented. Opponents of multispecies *Tyrannosaurus* who accept such for *Daspletosaurus* must explain why the anatomical and stratigraphic data is inadequate for the more commonly preserved former over the latter. It is therefore of taxonomic procedural concern that Carr *et al*. (2022) did not consider the modest standards for the designation of the new tyrannosaurid intragenus *Daspletosaurus* species by Carr *et al*. (2017) in their examination of *Tyrannosaurus* species (same regarding species within *Allosaurus* as per Chure & Loewen, 2020, see Supplementary).

Additional quantitative proportional cranial data

Carr *et al*. (2022) protest the inability of Paul *et al*. (2022) to place at the species level four largely or entirely complete skulls, although they conceded that the current display status of AMNH5027 hinders its assessment.

Paul *et al*. (2022) found that two major nondental cranial features, the length/depth ratios of the largest and primary tooth bearing skull bones the maxilla and dentary, are compatible with an increase towards gracility and/or variation with time in the genus. Four vertical bars the width of which can be measured provide additional data on the dorso-ventral strength of 17 *Tyrannosaurus* skulls with which to further test the species question—the interfenestral pillar of the maxilla, the lacrimal, the postorbital process of the jugal, and the posterior ramus of the quadratojugal (Table 1; Fig. 2A–I; Supplfig. 8). These bars help resist the intense biting force of the giant predator's titanic jaws (Gignac & Erickson, 2017).

The hourglass shaped interfenestral pillar separates the small maxillary fenestra at the anterior end of the antorbital fossa from the much larger antorbital fenestra that fills most of the fossa. The width of the bar at its anteroposterior narrowest is visually highly and distinctively variable in *Tyrannosaurus*; the width of the bar at its base tends to correlate with that at its midpoint. The stoutness of the pillar is most readily assessed by comparing its width to that of the antorbital fossa it helps contain—the combined size of this complex is fairly consistent relative to the rest of the skull. The pillar is relatively broad in the lower TT-zone *T. imperator*. All of those specimens cluster tightly together—the value for the holotype is an approximation due to damage to the skull, that it is broad is indicated by its wide base. All pillars in skulls assignable to *T. regina* have slender interfenestral pillars, much more so than yet observed in any *T. imperator*. Those of *T. rex* are intermediate in breadth, all being more robust than *T. regina*, and slenderer than any *T. imperator*, so there is no observed overlap in the sample between the three species, which equals two cases of bimodality in the current sample. The variation in robustness with more recent time is, as often observed in *Tyrannosaurus* elements, substantial, very much so being about five times as great in high placed skulls than it is in the earlier examples. As a result of the above the shift from robustness in the low TT-zone to much more gracility later in time is very strong. The robustness versus gracility of the entire maxilla broadly parallels that of the pillar it contains in that those of *T. regina* always being shallower than those of *T. rex*, as well as *T. imperator*. In both these comparisons of strength the maxillae of *Tyrannosaurus* provide some of the best evidence for three over two or one species (Fig. 3J, K).

The preorbital bar formed by the arced, narrow lacrimal is more difficult to assess in part because it has a complex twisted shape along its long vertical axis, and its minimal anteroposterior diameter must be carefully assessed to not under measure the minimum width. With that caveat, the thickest lacrimal bar is present in *T. imperator*, and thinnest bars belong to *T. regina* always have a thin bar, so while there is extensive overlap there is a trend towards more gracility with stratigraphic height, but not towards more variation—although a decrease is not observed (Fig. 3L).

The strength of the postorbital bar is best measured by the breath of the sharply triangular, plate like ascending process of the jugal at the level of its ventral most articulation with the postorbital, that being compared to the total height of the jugal to generate the ratio. Note that the width can look narrower than it is in direct lateral view images of skulls because the lateral surface of the jugal is directed somewhat anteriorly in the genus, because the narrow snout flares laterally to the much broader temporal region at this location. Again, the most robust examples are early *T. imperators*, the most gracile are late *T. regina*s (Fig. 3M). As with the maxillary pillar, the *T. reg*ina bars are always less robust than those of *T. rex*, although the sample of the latter is one. There is extensive overlap with *T. imperator*, even so an overall trend towards more gracility with time exist, yet no trend towards more variation. Most of the same pattern applies to the strongly embayed quadratojugal, which likewise does not decrease in variation with later time (Fig. 3N). Interestingly, TMP81.6.1 shows the greatest breadth among the *T. regina* in its aft two bars, while having slender anterior bars, showing a mosaic pattern in the taxon.

A visual survey indicates that the interfenestral pillar of the maxilla is normally robust in earlier large North American and Asian tyrannosaurids (Fig. 2J–L; Maleev, 1955, 1974; Rozhdestvensky, 1965; Russell, 1970; Currie, 2003a; Hurum & Sabath, 2003; *Carr & Williamson*, 2010; Carr *et al*., 2011, 2017*;* Brusatte *et al*., 2012; Lu *et al*., 2014), so thick maxillary bars is another example of the retention of the general ancestral tyrannosaurid condition in early *T. imperator*, along with its robustness the femur especially, and two incisiform dentary teeth (Paul *et al*., 2022)—the pillar is not as broad in TMM41436-1. And the exceptional gracility of the maxillary pillar and femur of *T. regina* are very atypical adaptations that appear late in the family and genus. It is notable that the basic pattern with all the vertical skull bars is in tune with the overall changes in robustness during the evolution of and within *Tyrannosauru*s, with the advent of exceptional gracility seeing the skull becoming more lightly constructed. This is most clearly seen as the maxilla overall becomes shallower, the interfenestral bar becomes more delicate, but the same applies to a fair extent in the rest of the supporting bars. This reinforces the evidence that a

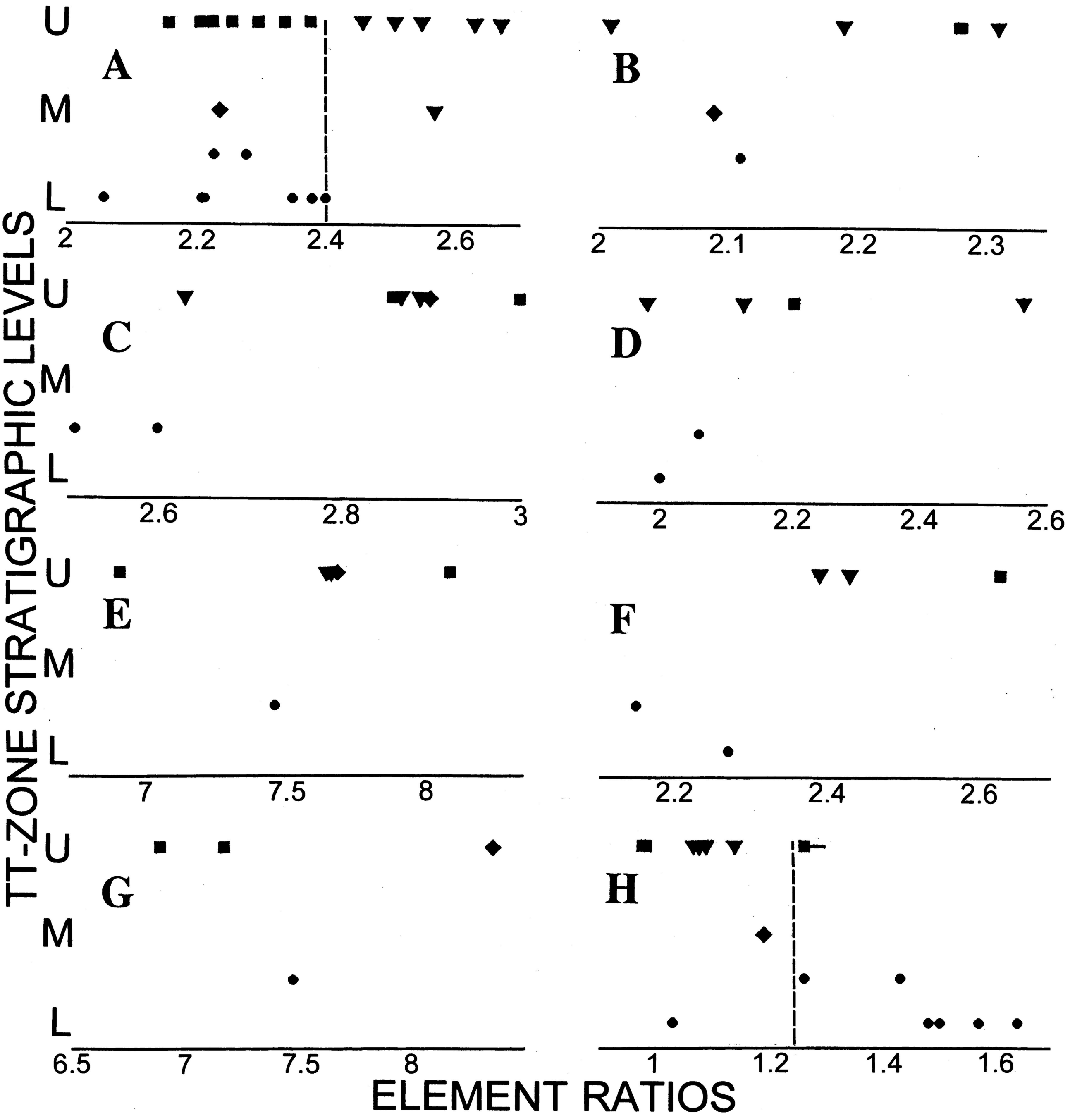

FIGURE 3. Element ratios for large *Tyrannosaurus rex* (squares), *T. regina* (inverted triangles) *T. imperator* (circles) and *T.* incertae sedis (diamonds) specimen at differing stratigraphic levels (lower L, middle M, upper U) in the TT-zone; specimens that may be from either the upper lower or lower middle T-zone are plotted between the lower and middle levels. For **A–G**, **I–N** increasingly bone gracility is to the right, for **H** increasing 2nd incisor robustness is the left. Data from Table 1 and Supplementary Table 2. **A**, Femur length/minimum circumference, divisions at 2.4 between robusts and graciles indicated by vertical dashed line. **B**, Humerus length/min. circle. **C**, Ilium length/depth. **D**, Metatarsal 2 length/min. circle. **E**, Metatarsal 2 length/min. diameter. **F**, Metatarsal 4 length/min. circle. **G**, Metatarsal 4 length/min. diameter. **H**, Dentary teeth/alveoli 2/3 (possibly 3/4 if 1 is no longer functional) anteroposterior base diameters, division at 1.25 between one and two incisors indicated by vertical dashed line (horizontal line indicate different value of Carr *et al.*, 2022). **I**, Dentary length/depth. **J**, Maxilla length/depth. **K**, Maxillary fenestra length/interfenestral pillar min. width. **L**, Lacrimal height/min. width. **M**, Jugal height/postorbital process width. **N**, Quadratojugal height/min. width.

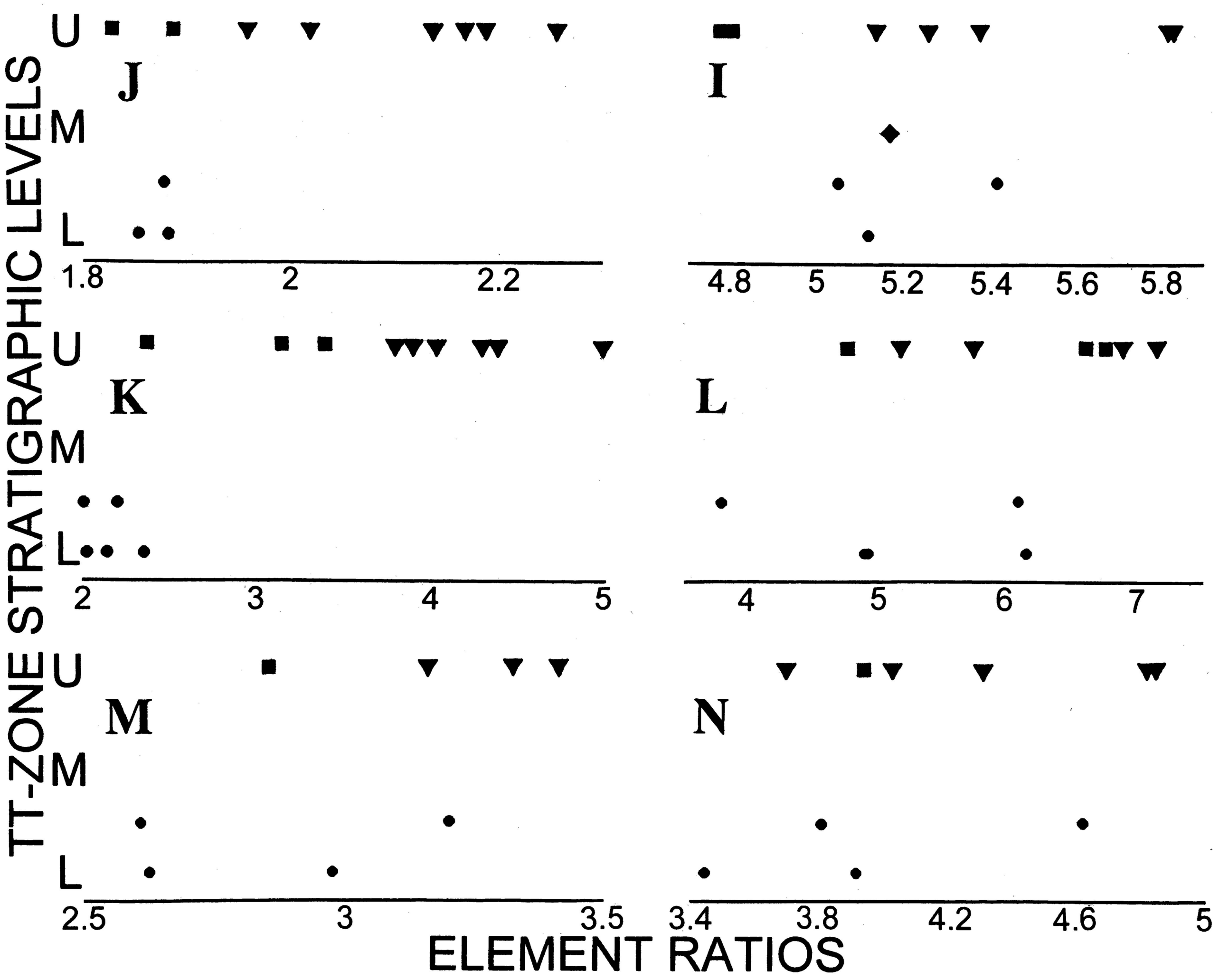

FIGURE 3. (Continued) Element ratios for large *Tyrannosaurus rex* (squares), *T. regina* (inverted triangles) *T. imperator* (circles) and *T.* incertae sedis (diamonds) specimen at differing stratigraphic levels (lower L, middle M, upper U) in the TT-zone; specimens that may be from either the upper lower or lower middle T-zone are plotted between the lower and middle levels.

population of late *Tyrannosaurus* were reducing the strength factors of the head and body—the gracile femora are below the general tyrannosaurid curve as discovered by Paul *et al.* (2022)—in the genus characterized by its overall massiveness. And this shift included the snout in an animal know for the power of its bite that apparently exceeded that seen in any other known land predator. This constitutes a major and consistent trend that is not readily explained by individual variation, dimorphism, or ontogeny.

The observed cranial strength patterns fit that predicted by three rather than two or one species. All known low TT-zone robust *T. imperator* sport interfenestral bars broader than those of latter gracile *T. regina*, and all contemporary robust *T. rex* have bars thicker than those of *T. regina*, with even the fairly stout *T. rex* interfenestral pillars not overlapping with those of the earlier robust *T. imperator*. The situation is not as clear cut with the other measures including the dentary, but in all cases, it is *T. regina* that is most lightly constructed, in all but one it is *T. imperator* is the strongest, and in the maxilla *T. regina* is always deeper than that of *T. rex*.

With the expansion of the cranial data set the observed patterns are now sufficient to place all but one of the large *Tyrannosaurus* skulls and skeletons, a few of which had been taxonomic floaters, in one of the three named species at least tentatively. Like the ratio for its pillar, the length/depth ratio of the maxilla of RGM792.000 of 1.85 is in the robust zone, as is its femur, reinforcing its placement in low TT-zone *T. imperator* (Fig. 1A, J, K; Table 1; Supplementary Table 2). A similar maxillary ratio for UWBM99000 indicates that the high TT-zone specimen is a *T. rex*, as does the broad interfenestral pillar it contains. The thick pillar of the high placed UCMP118742 maxilla favors placement in *T. rex*. LACM23844 is borderline regarding its maxilla, dentary and lacrimal. and looks robust in a metatarsal, but the slender interfenestral pillar implies it is a *T. regina*. The low maxilla and exceptionally slender pillar of LACM150167 firmly reaffirms its position in *T. regina*. Species identification of the prior is aided by their known stratigraphic placements. The last item is not yet true of MOR008 the skull of which is not complete, the proportions of the maxilla are borderline, and the important limb elements are not on hand. The robust interfenestral bar and dentary, and two incisiform teeth are compatible with and suggestive of *T. imperator* status.

The new characters have been added to the revised and expanded diagnoses for the three species in the systematic palaeontology section.

Taxonomic implications. Repeated variation in the strength of primary vertical strength bars in *Tyrannosaurus* crania records yet more and surprising strength reduction as the genus evolved over the last hundreds of millennia of the Mesozoic. Of the four bars, the evidence provided by the maxilla's interfenstral pillar shows the strongest and most clear-cut trends and appears to move away from the robust ancestral tyrannosaurid condition. The patterns observed in the pillar and the other three bars favours a speciose over a monospecific genus, and three over two taxa. The evidence provided by the vertical bars is in tune with the overall skew towards slenderer and derived proportions observed in a number of other parts of the skull and skeleton in late *Tyrannosaurus*, *T. regina* especially, way from the ancestral condition, with *T. rex* retaining the most of the older anatomy. All three species gain new specimen members. The ability to place all but one *Tyrannosaurus s*kull (see below) in one of the three species removes the—spurious in its theoretical basis—objection to the multispecies hypothesis by Carr *et al.* (2022).

Consider that LACM150167 was assigned to *T. regina* in Paul *et al.* (2022) based on its gracile postcrania and stratigraphic placement. During submission of this study the author obtained high resolution photographs of the skull elements. In the measurements the specimen again scores as a gracile *T. regina*, with the interfenestral pillar being the slenderest yet observed. The verification of the Paul *et al.* (2022) placement of the specimen (also see work on its postorbital bosses below) with the new data reinforce the soundness of the anatomical-statistical foundations of the three species hypothesis.

Many more than just two features separate/d the three species

In order to try to preclude claims that just two characters distinguish the species, as Carr *et al.* (2022) did anyway, Paul *et al.* (2022) explicitly states immediately before the systematic diagnoses that "the species diagnoses incorporate the cumulative proportions of six elements in addition to the femur". The diagnoses specifically state that is expressed as a matter of general robustness or gracility, which includes the maxilla, dentary, humerus, ilium, femur, and two metatarsals. Only the dentary does not show a plain trend towards gracility with later time, although there is no example of any low geologically placed strongly gracile element. The three holotypes possess all or nearly all of the 7 pertinent elements. Also observe that all those elements show a clear pattern of little variation low in the TT-zone to more variable higher up. This was documented in the data tables and visually in Figure 6 in Paul *et al.* (2022, repeated and expanded in Fig. 3 herein). Also note that metatarsals as well as femora were illustrated in Figure 2 in Paul *et al.* (2022). The paper used only one specific robusticity ratio for defining the species, 2.4 for the femur, because that is the only practical way to produce a value that can be readily applied, the individuals all having some internal variation in robustness, and the massive proximal hindlimb element being most commonly preserved intact. In addition to the robustness of important elements, the condition of the anteriormost dentary teeth were utilized, so the total number of elements and characters examined was 8 in Paul *et al.* (2022). The inaccurate claim that the study works with just two characters should not have been stated, and must never be repeated.

In part to make clearer the number of characters being used to characterize *Tyrannosaurus* species, the taxonomic diagnoses are more explicitly stated in the systematic palaeontology section, the number now being a dozen.

The quantitative speciation pattern

With the addition of the above new four skull characters, the number of ratio based measures cranial and postcranial characters used to help track *Tyrannosaurus* speciation and diagnose the species is now a dozen incorporating 11 elements, although the two metatarsals are part of the united tarsometatarsus complex. The results include the following.

In all 6 cranial robusticity plots the most gracile ratio is that of a *T. regina* (Fig. 3I–N). As explained in the Supplement none of the *Triceratops s*pecies shows such consistency of proportional cranial variation extremities.

In 9 ratios the most gracile condition is observed in *T. regina* (Fig. 3A, B, D, I–N).

In only 2 plots (Fig. 3B, D) is a *T. regina* the most robust overall, but in those plots the sample is on the small side, especially for *T. imperator*.

T. imperator is never the most gracile in any element or ratio (Fig. 3A–G, I–N). None of the *Triceratops* species shows such consistency of proportional cranial and postcranial variation extremities.

In 6.5 items the most robust or the two incisor tooth condition is seen in *T. imperator* (Fig. 3A, C, F, K–N)—the 0.5 applies to one of the unavoidably divided (see Paul *et al*., 2022) metatarsal measurements.

In 7 plots and 5 elements all *T. regina* are more gracile than any *T. imperator*, exhibiting nonoverlapping bimodality between the two taxa (Fig. 3A, C, E, F, J, K).

In 4 elements all *T. regina* are more gracile than any *T. rex* among high stratigraphic level specimens, exhibiting nonoverlapping bimodality between the two taxa despite the possibility of hybridization (Fig. 3A, J, K, M).

In no element is *T. regina* always more robust than is its contemporary taxon.

As a result of the above, in 10 elements and 12 plots (Fig. 3A–G, J–N) there is an overall trend, from minor to strong, toward greater gracility progressing geologically upwards. Trends towards increasing robusticity have not been discovered.

There are 5 cases of nonoverlapping bimodal separation between at least two species (Fig. 3A, C, J, K, M).

11 measurements in crania and postcrania favour actuality of robust and gracile morphs in generally good accord with femoral robustness (Fig. 3A–D, F, G, I–N).

In 8 and 10 plots elements there is in increase in variation within a given element from modest to many folds progressing upwards (Fig. 3A–G, I–K). Only in dentary teeth is there a decrease in variation (Fig. 3H).

The proportions of at least the femur, the maxillary interfenestral bar, and the anterior dentary teeth shift significantly away from the ancestral tyrannosaurid condition of robust proportions or two incisiform teeth.

Taxonomic implications. The above quantitative work exceeds that in some noncontroversial recent examinations of intragenus palaeospecies (as per Chure & Loewen, 2020; Danison *et al*., 2024; Carr *et al*., 2017; other references in the Supplementary), others can further explore the statistical implications of the data set.

Highly divergent postorbital sexual display bosses support three species, each dimorphic and give T. rex *a distinctive new look*

Why and how cranial display features are especially critical to scientific species identification is detailed in the Supplement. Bony tyrannosaurid cranial displays were modestly developed, consisting of a long, low, irregular central ridge at the midline confluence of the paired nasals, short if present at all ridges of varying shapes on the top bars of the lacrimals, and variable bosses on the dorsal postorbital (Paul, 2010, 2016, 2024a, b). The bosses are considered to consist of the cornual prominence that projects distinctly off of the general surface of the postorbital, gentle rugosities that closely conform to the main topography of the postorbital in a few specimens such as MOR55555 are not included. The lack of similarly significant, consistent divergences among *Tyrannosaurus* nasal and lacrimal rugosities and bosses are discussed in the Supplement.

16 of 17 large *Tyrannosaurus* skulls bear preserved cornual bosses on the dorsal postorbital, with 7 now assigned to *T. imperator* including the holotype, 6 to *T. regina* including the holotype, and 2 to *T. rex* sans the holotype (Figs 1B–F; 2B–I, 4A–P, 5 in which the bosses are stratigraphically placed, 6). In these specimens there is a very large divergence in the prominence and form of the postorbital bosses, to a degree not seen within and even between some other tyrannosaurid genera (Figs 2J–L, 4T, U). This conspicuous lack of species-specific consistency in the genus is a contributor to the skulls of the tyrant saurian looking unusually variable compared to other tyrannosaurid species (Paul *et al*., 2022, Supplementary Information), a point that has never been explained in the context of all the skulls being those of only the tyrant lizard king without royal siblings.

Differences in supraorbital displays have been used to help diagnose intragenera sibling species of the close *Tyrannosaurus* relation *Daspletosaurus*, with the widely accepted *D. horneri* apparently bearing smaller structures than earlier *D. torosus* that may have had larger ornaments than later *D. wilsoni* ((Fig. 4Q–U; Warshaw & Fowler, 2022; Scherer & Voiculescu-Holvad, 2024; Warshaw *et al*., 2024; Scherer, 2025). There has yet to be a systematic effort to assess and compare the form and development of *Tyrannosaurus* cranial bosses in order to tease out their systematic implications. That is because within the simplistic hypothesis of one species the pattern appears chaotic, and therefore due to random, inexplicable individual variation, combined with ontogeny and perhaps dimorphism—Carr (2020) does not describe or score the postorbital bosses in the needed detail, and Carr *et al*. (2022) make no effort the examine the conspicuous ornaments. Also, the timing of this effort is fortuitous. It was only fairly recently that two new skulls with atypical postorbital bosses became available. So, attempts to systematically sort out the taxonomic implications of the bosses coincidently became feasible only during the period when this researcher was working on the problem of *Tyrannosaurus* species starting in 2010, and was made possible by the advent of the data and results in Paul *et al*. (2022) and immediately above, which allowed the assignment of most skulls to species. As a result, the assignment of 15 of the skulls to stratigraphic levels combined with the above work placing 16 crania in the species serendipitously led to the revelation of a pattern that, in this first detailed examination of the

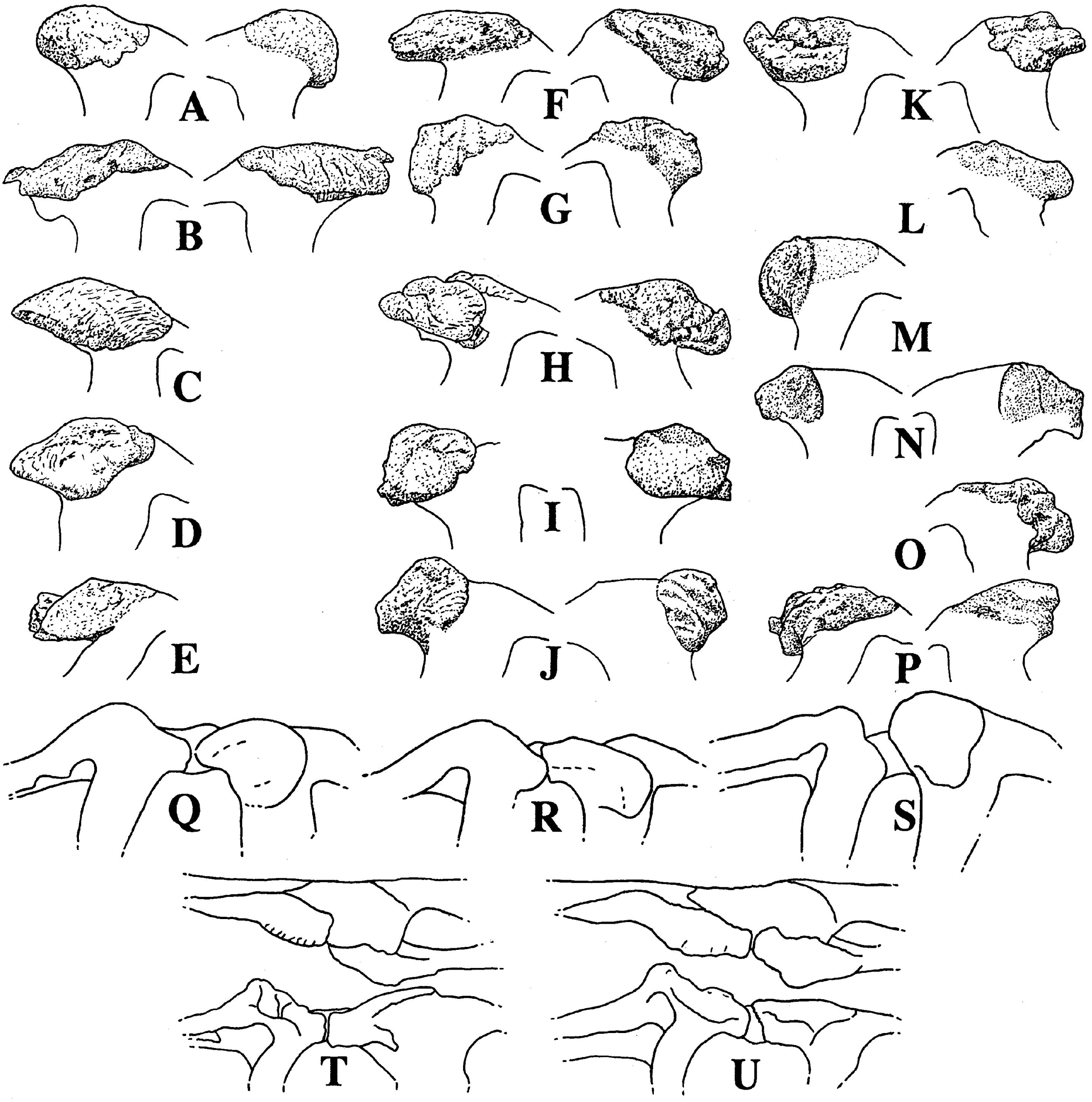

FIGURE 4. North American tyrannosaurid orbital displays as preserved. TT-zone *Tyrannosaurus* species left and/or right postorbital cornual bosses in lateral view, presented at an approximate constant skull size, in each species the specimens are presented in order of general decreasing size of the individuals (for most of these specimens' bosses at same scale and placed at their stratigraphic levels see Fig. 5). Lower TT-zone *T. imperator*: **A**, Samson. **B**, FMNHPR2081. **C**, MOR008. **D**, SDSM12047. **E**, HMNMB.R.91216. **F**, RGM792.000. **G**, MOR1125. **H**, *T.* incertae sedis, AMNH5027. Upper TT-zone *T. rex*: **I**, RSMP2523.8. **J**, UWBM99000. Upper TT-zone *T. regina*: **K**, NHMADS. **L**, LACM23844. **M**, USNM555000. **N**, LACM150167. **O**, MOR980. **P**, TMP81.6.1, *Daspletosaurus* species left lacrimal and postorbital display structures in lateral view to same length. **Q**, *D. torosus*, CMN8506. **R**, *D. wilsoni*, BDM107. **S**, *D. horneri*, MOR590, albertosaurin left lacrimal and postorbital display structures in lateral (bottom row) and dorsal (top row) views to same length. **T**, *Gorgosaurus libratus*, TMP91.36.500. **U**, *Albertosaurus sarcophagus*, TMP81.10.1.

supraorbital bosses of the genus, demonstrates species level differentiation between the taxa. And suggests that the species were probably internally dimorphic. The possession of such display organs is in line with the evidence for intraspecific combat recorded on the skulls of the genus (Brown *et al.*, 2022).

Being predators wherein both sexes lacked a need for well-developed cranial weapons for defence that can also be used for displays purposes, significant sexual dimorphism in skull ornamentation is a high possibility in these dinosaurs. It is presumed that if there is significant variation in the size and form of *Tyrannosaurus* cranial displays in a given species, that the bigger and more ornate expressions are those of males as per the null hypothesis—it being improbable that males exhibited parental care (Paul, 2008, 2016, 2024a, b) as do male cassowaries whose crests are smaller than those of females in absolute although not necessarily relative size (Green *et al*., 2022; Supplementary).

The varying development of the postorbital boss was approximated by laying out photographs of all sufficiently well-preserved left and right examples, which tend to be reasonably consistent in their configuration between the two sides of given individuals (Fig. 4A, B, F–K, N, P). That the lefts and rights of the specimens are so uniform on individuals indicates that their shapes and sizes were significantly genetically controlled as expected for display structure intended to visually segregate species in order to inhibit cross species reproduction. The images were replicated to a consistent posterior skull height to facilitate comparisons of degrees of development. The images were then re/positioned relative to one another in a gradistic manner from least prominent to most so, until an order was arrived at, and each specimen was scored from 1 to 15. These results are very approximate because although differing degrees of prominence are very real—the boss of MBR.91216 (Fig. 4E) is clearly much less enlarged than that of MOR008 (Fig. 4C)—the fine gradations involve a degree of judgement, which are impacted by differing lighting in the images, as well as extensive differences in the form of the bosses, and other factors. Possibly 3-D scanning of the fossils can be used to obtain better results in the future. The quantitative results were used to produce the following ratings; not prominent (NP), fairly prominent (FP), prominent (P), very prominent (VP). There are multiple examples of each grade, at different levels of the TT-zone.

In most adult eutyrannosaurs there is little variation in preserved postorbital display structures, consisting of a subtle, semi-lunate form with the convex arc directed anteroventrally, limited to the frontal process of the postorbital, and not projecting much if at all above the rim of the skull. They rate NP and perhaps at most FP. This is true of the species of *Alioramus*, *Qianzhousaurus*, *Teratophoneus*, *Gorgosaurus*, *Albertosaurus*, *Daspletosaurus* and *Tarbosaurus*, both between and within the species (Figs 2J–Q, S, T, 4Q–U; Maleev, 1955, 1974; Rozhdestvensky, 1965; Russell, 1970; Currie, 2003a; Hurum & Sabath, 2003; *Carr & Williamson*, 2010; Carr *et al*., 2011, 2017*;* Brusatte *et al*., 2012; Lu *et al*., 2014). Notably, the basal North American tyrannosaurin *T*.? *mcraeensis* is well off the tyrannosaurid norm in having a more elongated, including posteriorly, irregular boss (Dalman *et al*., 2024). This was a harbinger of taxonomically informative things to come regarding North American tyrannosaurins.

Among TT-zone *Tyrannosaurus* the most developed orbital bosses are always present on very large specimens, but some large individuals do not have VP or even P/FP bosses, with one having an NP boss (Figs 1B–E, 2B–I, 5, 6). This indicates that although ontogeny of course played a role in the degree of development of the display structures, it was more complicated than just that. *T. imperator* bosses range from NP to VP, *T. regina* from NP to P, and the two *T. rex* are P or VP. All rankings are found at differing levels of the TT-zone.

Among the lower TT-zone *T. imperator* documented female MOR1125 (Schweitzer *et al*., 2016) is a medium

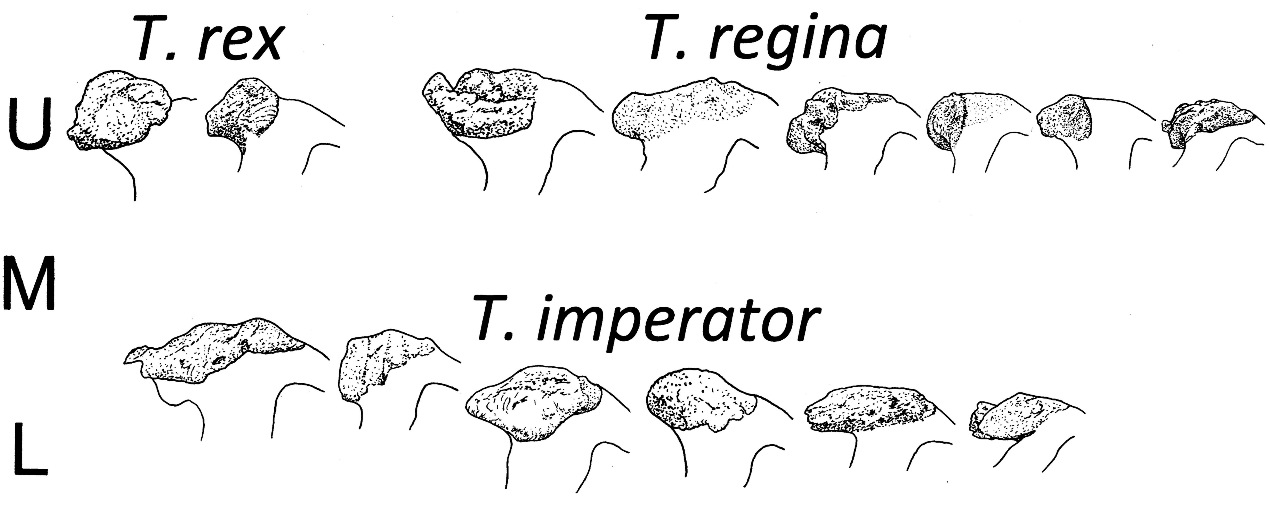

FIGURE 5. Left (some reversed) postorbital bosses as preserved in lateral view of *Tyrannosaurus t*o same approximate scale, arranged by species in accordance with their gross level in the TT-zone, presented in order of general decreasing size of the individuals. For specimen identification of each specimen refer to Figure 4.

sized robust that was reproductive but not fully mature, and it has an FP protuberance (Figs 2H, 4G, 5, 6D). Having an even less prominent boss, similar sized MBR.91216 (Figs 4E, 5) is another candidate for a female, although immature male is also possible. Although very large, and with a P boss, that of Samson (Figs 4A, 5) is relatively short, leaving open the possibility it was a fully mature female. The rest of the very large individuals with big spindle bosses are probably mature males (Figs 4B–D, F, 5). In *T. regina* 3 large specimens have P bosses (Figs 4K, M, O, 5, 6C, F), but another only a NP (Figs 4L, 5), suggesting the first are mature males and the later a mature female. Meanwhile the more modest sized TMP81.6.1's FP boss and LACM150167's NP boss (Figs 4N, P, 5) imply there were females. For *T. rex* that very large RSMP2523.8 has a somewhat more prominent boss than less massive UWBM99000 favors the former being a fully grown male (Figs 2B, C, 5, 6B, E), the latter a female with immature male also possible.

If all upper TT-zone *Tyrannosaurus* are the one species *T. rex*, with the robusts and graciles each representing a sex, then it would be expected that as the species evolved from lower TT-zone *Tyrannosaurus*, the specimens with prominent postorbital bosses—probably males—would end up limited to one morph or the other. If instead they are two sympatric species, then some skulls of both the robust and the gracile species are predicted to exhibit prominent bosses. Note that this result is not dependent on sample size because what is on hand establishes the lack of correlation between the postorbital bosses and skeletal build predicted by one species in the high TT-zone in favour of two. The apparent preserved pattern in which both robusts and graciles have both poorly and well-developed postorbital display structures is instead most accord with the latter circumstances.

Yet stronger and more compelling support for the three species hypothesis is found in the distinctive and varying shapes of the bosses. The simple monospecific hypothesis predicts there should be just one basic type of boss distributed evenly through the TT-zone in the genus, perhaps with some dimorphic variation found between robusts and graciles. If instead the display structures change with time while remaining consistent in form at a given time, then this indicates anagenetic evolution into new species. *i.e.*, two chronospecies predicts a more complex scheme with at least two differing boss morphologies stratigraphically separated. In a yet more complicated situation three species would be indicated by at least three differing boss forms. The latter state of affairs is operative. A number of low TT-zone *Tyrannosaurus*, the *T. imperator* holotype most of all, have very distinctive, anteroposteriorly long and low, spindle shaped postorbital prominences that extend from the lacrimal contact back to nearly or all the way onto the anterior section of the squamosal process of the postorbital, these do not project much above the dorsal edge of the skull (Figs 1E, 2G, 4B–D, F, 5, 6A). Atypical for tyrannosaurids in general, such bosses are not yet known from the high TT-zone (Fig. 5), and all the specimens that have the spindles are assignable to lower TT-zone, robust *T. imperator*. On the skull roof small medially oriented anteromedial projections of the postorbital prominences are oriented towards the skull midline, but are far from contacting one another. In very sharp visual contrast, two high TT-zone specimens exhibit very different, vertically prominent, semi-circular knob/disc shaped bosses that project well above the dorsal rim of the skull, and are limited to the frontal process of the postorbital, with a large space between the posteriormost edge of the protuberance and the squamosal process (Figs 1B, 2B, C, 4I, J, 5, 6B, E; fig. 12 in Persons *et al*., 2019). There are not significant anteromedial projections of the prominences. These similarly exceptional "Mickey Mouse" knob bosses of RSMP2523.8 and UWBM99000 (Figs 1B, 4I, J) reinforce their placement in the same species, that being *T. rex*—that the two skulls especially the latter are fairly new is a factor in their remarkable shaped bosses not being recognized earlier, the absence of postorbitals in the *T. rex* holotype may have hindered appreciation of this anatomical situation to date. No low TT-zone specimens have such orbital projections in shape, elevation, or extreme anterior placement (Fig. 5)—for that matter no other tyrannosaurid, or theropod, has such idiosyncratic eye-catching postorbital displays. *T. regina* bosses are much less dramatic, none having either the full spindle or disc shape, and not particularly large (Figs 1C, 2D–F, 4K–P, 5, 6C, F). Posterior extent is irregular. The largest and presumably most mature and probably male *T. regina* has bosses that have something of a brimmed hat in a picture appearance (Figs 1C, 4K). In at least some cases the anteromedial projections are well developed like those of *T. imperator*.

Of interest is the postorbital boss of the gigantic non TT-zone *Tyrannosaurus* from the late Maastrichtian North Horn Formation, NMNNHP-3698 (Sampson & Loewen, 2005). With the horizontally short, subcircular boss being limited to the frontal process of the postorbital it is clearly not the *T. imperator* type. Nor does it have the exceptionally prominent *T. rex* form. It is most similar to *T. regina*, and favours the presence of the species in Utah.

Differences between the shapes of *Tyrannosaurus* ornament bosses were often far from subtle and would have been readily visible to the living archosaurs. As discussed in the Supplements section on determining palaeospecies, it is very probable that the keratin sheathes covering dinosaur postorbital bosses moderately expanded and enhanced the ornaments' size while largely replicating their bony cores. This presumption is applied

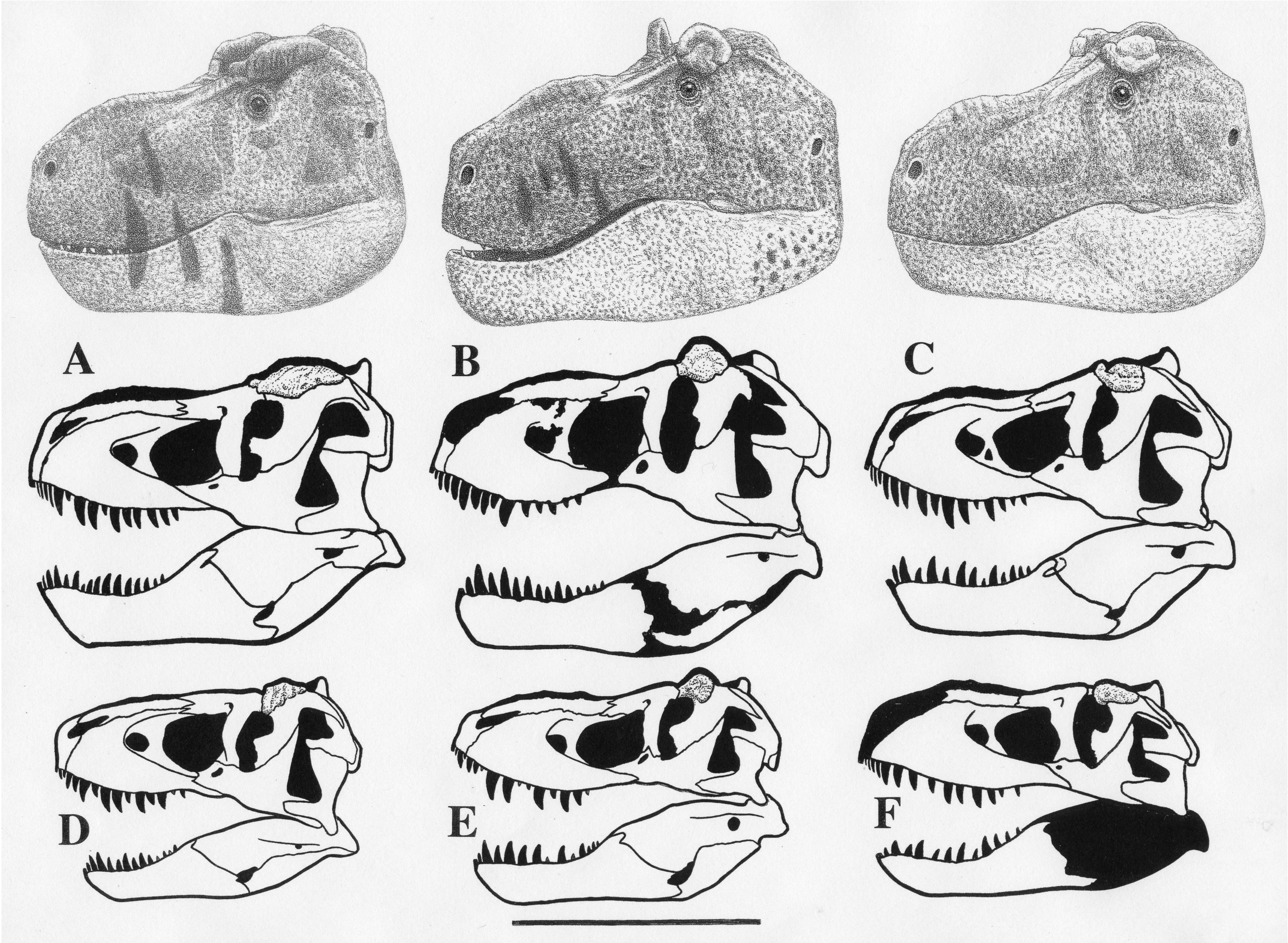

FIGURE 6. Adult and subadult *Tyrannosaurus* head restorations and/or known bone profile-skulls as preserved to same scale, bar equals 1 m. Restored bosses carefully proportioned in size relative to skull, and in shape, after being enlarged a modest amount with reconstructed keratin sheaths, scales and color patterns speculative, ornament color patterns kept simple to emphasize surface topographic differences. Adults: **A**, Lower TT-zone *T. imperator*, holotype FMNHPR2081 (male?). **B**, Upper TT-zone *T. rex*, RSM2523.8 (male?). **C**, Upper TT-zone *T. regina*, NHMADS (exBHI3033) (male?). Immature: **D**, *T. imperator*, MOR1125 (female). **E**, *T. rex*, UWBM99000 (female?). **F**, *T. regina*, holotype USNM555000 (male?).

to life restorations of *Tyrannosaurus* heads representing large males of each of the three species (Fig. 6). Lacking examples other than the prior, the possibility that the bosses bore much larger soft coverings that dramatically altered their form is too low to warrant serious consideration much less illustration. Even if such occurred it is very unlikely that the coverings of such very different bone foundations happened to coincide to produce the same final external appearance between the morphotypes and stratigraphic horizons.

As a result of this analysis, what was orderless in the context of monospecific *Tyrannosaurus* without stratigraphic examination is now a strong pattern of evolving species specific ornamentation distinguishing four species, three of them from the TT-zone, two of them contemporaries. Large, probably male individuals of each TT-zone species sport bosses distinctive from the other two taxa. The boss was a modestly developed, horizontally elongated structure in at the latest early Maastrichtian *T.*? *mcraeensis*, making it already distinctive from the tyrannosaurid standard. The basal American tyrannosaurin anteroposteriorly elongated cornual boss were more visually filled out spindles in basal *T. imperator*. In latter *T. rex* the bosses are very optically different, anteriorly limited, vertically elevated subcircular discs in the shape of elevated knobs, in coexistent *T. regina* the bosses remain more horizontally elongated and/or lower and readily distinguishable by late *Tyrannosaurus* eyes (Fig. 6). That there is considerable variation in boss topography within at least two of the species (Figs 4A–G, K–O, 5) is fully in line with the similar intraspecific divergences seen in species display structures in a host of species (Supplementary), including the tremendous differences in brow horn length and orientation in *T. horridus* (Supplfig. 7A–G), and the tusks within proboscidean species, and the perpetual search for atypical trophy antlers by hunters. While *Tyrannosaurus* boss shape divergences in the best developed examples of larger TT-zone specimens the three taxa are broadly similar to those that distinguish the males of modern sibling species, they in their numerous considerable differentiations exceed the simpler and lesser variations normal between the sexes of extant species. That means that sex based dimorphism is not as explanatory as is speciation. And just as dimorphism is not a viable simple hypothesis for robust versus gracile proportions because the latter are absent in the low TT-zone, the absence of anteriorly placed knob bosses in any known low TT-zone skulls currently excludes the possibility of dimorphism between the bosses of *T. imperator* and those of later *Tyrannosaurus*. And while sexual differentiation within a single species predicts that the robusts should share one basic form of boss and graciles the other configuration, that early and later robusts instead have strikingly different cornuals rejects that hypothesis and is fully in line with species evolution. That the differing bosses of upper TT-zone sympatric *Tyrannosaurus* were dimorphic is also improbable because that condition should result in differing sizes of otherwise fairly similar display structures in the sexes with those on males being larger, not in the dramatically different knob versus hat shapes that are examples par excellence of the divergent anatomical topographies that evolve as species specific visual cues. Nor is how only a quarter of the high placed skulls bear the prominent knobs in line with an expected 50/50 male/female ratio. To the above can be added the lack of precedence in tyrannosaurids species for differing postorbital display bosses between the sexes.

If well developed, prominent postorbital bosses of distinctive shapes are male display characters then it is expected that females would lack such, at least in terms of size. It is therefore notable that among lower TT-zone *Tyrannosaurus* the known female, MOR1125 (Figs 2H, 4G, 5, 6D), lacks the full developed spindle that appears to have visually distinguished male *T. imperator* (Figs 2B, 4B, 5, 6A). If the upper TT-zone *Tyrannosaurus* females are also robusts then the specimens that bear the most visually attention getting bosses should be graciles, but the two that have such displays are robusts that are probable males. The modest size of the knob boss on the modest sized and potentially female UWBM99000 (Figs 2C, 4J, 5, 6E) is most compatible with *T. rex* being robusts that bore the supraorbital discs whether male or female, leaving them visually distinct from more gracile *T. regina* that lacked the distinct display knobs of its contemporary. If the inferior hypothesis that *T. regina* is a junior synonym of *T. rex* is accepted, then presumably the latter with their tall bosses are robust males and the former gracile females in a peculiar pattern not observed in other tyrannosaurids or dinosaurs.

Because other known tyrannosaurids do not bear postorbital bosses similar to those of *Tyrannosaurus*, each of the types embellishing the tyrant king, queen and emperor qualify as an autapomorphies both among the family, and within the genus.

A complex statistical shape analysis of the bosses is beyond the capability of this work if it is possible at all, but the distribution of *Tyrannosaurus* boss morphology is bimodal in that no member of the genus from low in the TT-zone has the elevated discs of RSMP2523.8 and UWBM99000, nor does any documented high placed example have the spindles of RSMP2523.8, MOR008, or RGM792.000, and no specimens assigned to *T. rex* or *T. imperator* have a boss like that of NHMADS.

The profile-skeletals in Figure 1 and the skulls in Figures 2 and 6 are the first set to show all of the best *Tyrannosaurus* skeletons and a number of skulls with preserved postorbitals accurately sporting their varying supraorbital display structures. Aside from necessitating a significant revision in the appearance of *Tyrannosaurus* and its species *T. rex* especially (Supplementary), the skeletals help show that the species, males in particular, would have been easy to tell apart when living animals with a quick visual glance, as is further indicated by life restorations of the species heads (Fig. 6). *Tyrannosaurus* shows markedly stronger differentiation in bone based species specific features than are present in within other multispecies genera of eutyrannosaurs (Figs 2H–J, P–R, 4Q–S), other theropods (Paul, 2010, 2016, 2024a, b) *Allosaurus* species being as example, *Varanus*, *Panthera* and *Canis* (Supplfigs 2–4), *Stenopterygius* and *Pliosaurus* (Maisch, 2008; Maxwell, 2012 Knutsen, 2012), and comparable to herbivores such as *Triceratops* in terms of the nasal horn differentiation that is a major critical species marker in that genus (Supplfig. 7 and species diagnoses in the Supplementary), as well as some mammalian ungulates (Nowak, 1991).

The bosses confirm the species identifications of three skulls that had not been species placed in Paul *et al.* (2022), but were by additional skull proportions above—that further eliminates the objections by Carr *et al.* (2022) regarding this matter.

The inherently very weak alternatives if only the species *T. rex* is preserved, demands an incoherent level of extreme individual variation, which lacks logical evolutionary cogence as selective forces somehow happen to produce a significant pattern over time that is entirely in accord with and evidence for species divergence in three taxa. It further leaves the notable cornual boss of *T.*? *mcraeensis* without an evolutionary context vis-à-vis other tyrannosaurids versus TT-zone *Tyrannosaurus*. The degree to which the anatomical/stratigraphic patterns observed with the current specimens do or do not hold up as new specimens come on line will help test the cranial display hypothesis presented in this analysis. Also potentially pertinent is preliminary notice of divergent final growth and size patterns in *Tyrannosaurus* that do not conform with stratigraphy or robustness, and that this may represent cryptic sexual dimorphism (Jevnikar & Zanno, 2021). It will be interesting to see to what degree that evidence conforms to the above not at all cryptic results.

Continuing to pose an interesting outlier is AMNH5027 (Figs 1F, 2I, 4H). Its P grade postorbital bosses do not fit readily into the topology of any of the other variants. The main boss is anteriorly placed somewhat like those of *T. rex*, yet are somewhat more horizontally long, and feature a projecting lip along the orbital edge, while the boss narrows down to a ridge atop the dorsal rim of the postorbital. The bosses do not project well above the dorsal rim of the skull as in *T. rex*, the anteromedial projections are present. The bosses are somewhat more similar to those of *T. regina*, but remain distinctive. Rediagnosing the species by forcing *T. regina* into *T. rex* (systematic palaeontology section alternative) does not aid in the placement of 5027 (see Supplementary for further discourse on this specimen).

The new characters have been added to the revised and expanded diagnoses for the three species in the systematic palaeontology section, which now incorporate 13 diagnostic characters. That compares to 7 for two *Allosaurus* species (Chure & Loewen, 2020; but see Supplementary) and less for another species of the genus (Danison *et al*., 2024).

Taxonomic implications. Opposite the simple and fairly consistent supraorbital display arrangement predicted by the monospecificity of the ETRH, correlating the highly variable topography of *Tyrannosaurus* preorbital bosses with stratigraphy and species reveals the anatomically and stratigraphically complex pattern that is the hallmark of the identification and diagnosis of sibling species. Of the modest but effective level expected in closely related predators lacking garish display ornamentation. If *Tyrannosaurus* had the same constancy in boss configuration seen in most other tyrannosaurs that would not be evidence for monospecificity because that the uniformity is the norm within multispecies genera and even between genera. Instead, the genus shows if anything more cornual variability than is known in *Daspletosaurus* which is consistently considered to include a series of species that can be visually identified by their differing cranial displays. The sheer amount of cornual boss variation in the genus compared to other tyrannosaur or for that matter theropod genera is on its own strong evidence for intragenus species of *Tyrannosaurus*. This is all the truer because the variability occurs in the manner expected in, and best explained by, three TT-zone species in the MTTH, with the differing configurations of the bosses reinforcing the assignments of the skulls to specific species based on other anatomical and stratigraphic parameters. What once did not make sense now does, and the long noticed but never explained variability of *Tyrannosaurus* skulls is readily explained as due to their representing different species. Explained is the evolution of North American tyrannosaurin display bosses starting with the Campanian/Maastrichtian boundary Texas species. Now provisionally identifiable to the species level is the North Horn *Tyrannosaurus.* The criticism of the MTTH that differing species exclusive display features are absent in *Tyrannosaurus* is now falsified, that belief being the result of the failure to rigorously test the status of *T. rex* with the substantial data that is available. To put it another way, not thinking that multiple species of *Tyrannosaurus* exist, lacking incentive to look for evidence otherwise ETRH proponents have not directed attention to the information openly visible among the orbital bosses of the genus, despite or perhaps because of their obvious high variability. The already strong preponderance of evidence for three over two over one species is correspondingly greatly enhanced by the identification of species discrimination visual devices in each of the taxa based on that data. Which also allows provisional identification of sexes within the three species (these being listed in Table 1). With species identification displays being a classic defining attribute of that taxonomic level, the bosses alone establish that *Tyrannosaurus* was not just *T. rex*. The cranial displays of the predator of *Triceratops* (see Happ, 2008) are about as definitive in determining the species of *Tyrannosaurus* as are the display horns of the ceratopsid as shown by Scannella *et al*. (2014; see Supplementary). The hypothesis of 3 species, with all the graciles being in one of them, has made it possible to tease out these patterns, something the one species proposition is incapable of. Assuming 1 species, or 2 chronospecies, obscures the dimorphism because it fails to explain why both robust and gracile specimens sometimes brandish well developed orbital displays while others less so.

Paul *et al*. (2022) missed the opportunity to describe the relationship of the supraorbital bosses to the species of *Tyrannosaurus*. Because Carr *et al*. (2022) focuses on criticizing Paul *et al*. (2022) rather than go beyond to investigate the broader situation, they did too. That Paul *et al*. (2022) laid the foundations for exploring multispecific *Tyrannosaurus* made these novel results serendipitously possible. LACM150167 was first assigned to *T. regina* in Paul *et al*. (2022) based on its postcranial measurements and stratigraphic placement, the skull proportions discussed above supporting the placement. High resolution photographs of the postorbitals obtained during submission of this work show that it has the subtle bosses expected of a gracile *T. regina* (Fig. 4N) This further verification of the Paul *et al*. (2022) placement of the specimen strengthens the anatomical-statistical foundations of the three species hypothesis.

With the addition of the postorbital boss the number of elements used to assay *Tyrannosaurus* species is a dozen, which is within palaeotaxonomic norms (Supplementary).

Individual, ontogenetic and dimorphic causes do not explain the variations in Tyrannosaurus *fossils*

Paul *et al*. (2022) carefully examined the alternative explanations for the condition of *Tyrannosaurus* and found that they all failed to explain the degree and pattern of the variation in proportions and teeth as well as speciation. The study agreed with Carr (2020) that growth was not the cause for reasons detailed in both papers. Nor is likely that histological analysis will change that conclusion when some *Tyrannosaurus* femora that are less than three quarters the length of the longest femur are more robust than the latter (Supplfig. 12B). Another reason differences in ontogeny and size cannot be a solution is because the dimensions of the largest specimens from the three basic levels and three species are very similar. All are large individuals with femurs of 1100 to 1350 mm, and the largest specimens in all three levels and species sport femora of 1320 to 1350 mm, with estimated masses that vary by only a few hundred kilograms (Fig. 1B, C, E). Sexual dimorphism was not the cause because the ratio between robusts and graciles is well off 50/50 within a substantial sample, and because only robusts have been documented to be present early in the TT-zone—Carr *et al*. (2022) did not integrate these important factors into their paper. The same issues pertain to the stratigraphic separation between morphotypes of the postorbital bosses. If the changes over time resulted from genetic drift, then that is what can create new sibling species. The variation in the genus is not random over time as it would have to be to be plausibly attributable to individuality, so the latter does not provide a compelling, positive, evolutionary explanation for the shifts. Why would individual variation result in a difference in femur robustness in one tyrannosaurid species that exceeds that seen in all previous members of the family combined? All the more so when variation in basal *Tyrannosaurus* is in the tyrannosaurid norm, and the variation according to the data on hand only appears in the upper TT-zone, and is skewed away from the ancestral condition? Likewise, how does intraspecific wandering explain the differences in postorbital bosses that are exactly the type that evolve to minimize interspecific reproduction? Attempts to use individual variation to explain the highly peculiar observed pattern will be ad-hoc opinion without scientific value.

Taxonomic implications. The evolution of variation in *Tyrannosaurus* dimensions in the crania teeth included and the postcrania away from the long standing tyrannosaurid ancestral conditions quickly to a derived status unique among tyrannosaurids is fully compatible with, and can only readily be logically explained by, selective genetics driven speciation.

The variation factor

The taxonomic story of *Tyrannosaurus* that had not been fully appreciated and deeply examined is the exceptional degree of variation in the genus, and all the more its change over time. In terms of display bosses, skull and skeletal robustness, and incisiform teeth. Such extensive variation has not been observed in other theropod species, and is not coherently explicable as the result of individual, ontogenetic, or sexual difference within a species, all the more so because there appears to be a strong stratigraphic segregation between important aspects of the variability. The exceptional variation in *Tyrannosaurus* via-a-vis earlier tyrannosaurids is probably not the result of a large sample size because it is smaller than for the other tyrannosaurids, and because the outliers in gracility on the one hand (NHMADS) and robustness (BHI6248) were discovered fairly early (Larson, 2008) when the sample size of the genus was markedly smaller than it is now.

Taxonomic Implications. No attempt to render the placement of all specimens in one species the superior hypothesis can succeed unless it is convincingly explained how two incisiforms and spindle bosses are known from the low TT-zone only, and graciles and knob or hat bosses only from high in the zone, and why so much quantitative inconsistency in so many regards is not observed in other tyrannosaurid species.

One, two, three or more species?

In view of the long time span over which *Tyrannosaurus* lived during which many other dinosaur genera underwent speciation, and the observed, significant changes in anatomy, the question is less likely to be whether *Tyrannosaurus* was multispecific, but how many species are represented by the TT-zone fossils. The shift in incisiform tooth count and the expansion in proportional variation with the advent of gracility strongly indicates at least two species. As explained in Paul *et al*. (2022) if the upper TT-zone specimens are one taxon then the onset of the expanded variation relative to early tyrannosaurids *T. imperator* included is the evidence of the novel reproductive shift that would mark a new chronospecies. But that hypothesis is inferior to two late species because such strong dimorphism had not been seen in prior tyrannosaurid species, *T. imperator* included, by a factor of two. If instead the upper TT-zone *Tyrannosaurus* remained all robust that too would favor chronospecies, as would all high placed specimens being gracile, and a lack of major variation in postorbital boss form in the very last *Tyrannosaurus* would indicate chronospecies. That the evidence instead indicates there is atypically high variation in high TT-zone *Tyrannosaurus* is most compatible with separation into two taxa of robust and gracile form as had been observed in earlier tyrannosaurids inhabiting the same ecospace. That is even more probable because that variation is entirely due to the swift shift to gracility away from what had been the long lasting tyrannosaurid norm, impacting even the bar separating the preorbital fenestrae, which best fits the adaptative speciation model. Also consider that if heavily built *T. imperator* is valid, then the separation from that is greater in distance vis-a-vis gracile *T. regina* than it is compared to stouter *T. rex*, so *T. regina* is an anatomical divergence driven species. Aside from the femur the maxilla (in both overall dimensions and the pillar dimensions) produces the strongest bone results in support of 3 species. To that add that the varying configurations of the postorbital bosses in combination with stratigraphic factors is most in line with sexual dimorphism within three species.

In order to test two chronospecies versus three species *T. imperator* and *T. rex* were diagnosed, with *T. regina* arbitrarily subsumed into the contemporary *T. rex* in the systematic palaeontology section. The result was the dramatic reduction of the diagnostic characters down to the anterior dentary teeth and the orbital bosses. The separation between the two paleospecies remains fully valid, just one character being sufficient for the purpose (see Supplementary), and the species grade display structures being especially definitive. But all the many differentials between the species regarding robustness and display features, and the exceptional anatomical and statistical variation in the high TT-zone fossils compared to the much more uniform *T. imperator* including the unprecedented shift to gracility, is disappeared without logical scientific justification. And the sharp reduction of the character list is contrary to those who favor large numbers of characters separating species. Statistically awkward is that only two of the many *T. rex* skulls have the knob supraorbital bosses that help diagnose the species, when many of the *T. imperators* have the spindles that characterize that taxon. So two chronospecies, although well superior to *T. rex* alone, is markedly inferior to three species characterized by a host of features. This exercise reinforces the need for all studies that designate palaeospecies to incorporate species systematic diagnoses to help test the favoured hypothesis.

Taxonomic implications. With ontogeny, random individuality and dimorphism falling short in explaining the changing circumstances of the giant avepod progressing from the lower TT-zone to high in the formations, a single species is scientifically inferior to two, and two is inferior to three. AMNH5027 may hint at yet more.

The geotime factor

The exact time span of the TT-zone is not known, but was probably considerable, in the area of 1.5 million years (see Paul *et al*., 2022 and references therein) that allows plenty of time for speciation at the sibling level. This favours via parsimony and evolutionary probabilities speciation of *Tyrannosaurus* over the formation of the formations—such appearing to have occurred regarding three serial species of *Triceratops* over the same time period (Scannella *et al*., 2014; Paul, 2010, 2016, 2024a; Fowler, 2017; Mallon *et al*., 2025), and *Daspletosaurus* and *Albertosaurus* as previously discussed.

Taxonomic implications. An absence of evidence of changing morphology among *Tyrannosaurus* specimens from the lower to upper TT-zone could negate the time factor, but the available anatomical evidence instead favours species level changes in display structures and cranial, dental and postcranial proportions progressing toward the top of the zone.

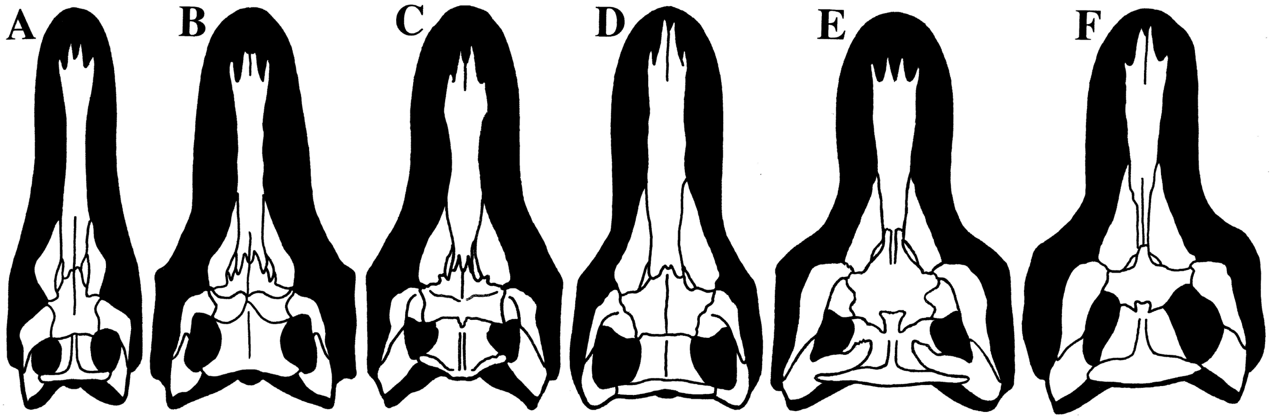

FIGURE 7. Same skull length comparisons of tyrannosaurid cranial dorsal elements (white bones over black profile of entire skull) to contrast the exceptional width of the postorbitals relative to the preorbital elements in *Tyrannosaurus*. **A**, *Qianzhousaurus* GM F10004. **B**, *Gorgosaurus*, UALVP10. **C**, *Daspletosaurus*, CMN8506. **D**, *Tarbosaurus*, MgD-1/4. **E**, *T. imperator*, FMNHPR2081. **F**, *T.* incertae sedis, AMNH5027.

What Tyrannosaurus *species bosses and diagnoses reveal about the ancestry and evolution of the genus*

The diagnosis of basal *Tyrannosaurus* in the form of *T. imperator* with a spindle boss is of phylogenetic importance because it is very unlike those of earlier and more basal tyrannosaurines *Daspletosaurus* and *T. bataar*, or any other eutyrannosaurs which all share a fairly standard subtle disc boss (Figs 2H–J, P–R, 4P, Q). That indicates early *Tyrannosaurus* were not retaining a general tyrannosaurid ancestral condition at least vis-a-via those genera in this particular regard. The issue has been illuminated by the postorbital boss of *T.*? *mcraeensis*, its having a distinctive, low, somewhat elongated display structure (Dalman *et al*., 2024) that looks like an ideal antecedent of that of *T. imperator* spindle. And *T.*? *mcraeensis* has—like other non-*Tyrannosaurus* tyrannosaurids (Paul *et al*., 2022)—the basal *Tyrannosaurus* (*T. imperator*) condition of two small anterior dentary teeth (ratio between 3rd and 2nd teeth 1.35; Fig. 6 in Gillette *et al*., 1986; Fig. 3 in Dalman *et al*. 2024). It is therefore possible that the ancestry of the TT-zone tyrannosaurid genus lies in or near *T.*? *mcraeensis*. Also of interest is that the *Tyrannosaurus* boss most like the earlier tyrannosaurines is the late *T. rex*, although its extra prominent boss is more derived and may have evolved independently.

Why are *Tyrannosaurus* cornual bosses so different from those of other tyrannosaurids including the other tyrannosaurin *Tarbosaurus*, and from one another in a way not seen in other tyrannosaurid taxa, including *Tarbosaurus*? A major driving factor in the evolution of the unusually high diversity of postorbital display bosses in *Tyrannosaurus* is likely to have been the dramatic broadening of the temporal box in the genus relative to other eutyrannosaurs (Fig. 7). Expanded in order to greatly boost the closing power of the jaw musculature by enlarging the volume of the portion of the skull containing the pertinent muscles (Gignac & Erickson, 2017), the lateral expansion of the aft skull had the side effect of laterally elongating the postorbital so that it was transversally much broader than the lacrimal to a degree not seen in other tyrannosaurids. That incidentally rendered the postorbital boss much more visible when the head was viewed from the front than in other tyrannosaurids. That in turn placed exceptional visual emphasis on the now uniquely conspicuous *Tyrannosaurus* bosses, subjecting them to more sexual selective pressure than previously seen in the family, resulting in a greater variety of shapes.

The resulting posterolaterally prominent *T.*? *mcraeensis* and even more so *T. imperator* bosses may have remained *the Tyrannosaurus* standard, but for the latest Maastrichtian *T. rex*/*T. regina* speciation event. In other cases when two tyrannosaurids shared the same habitat they were different genera, as per *Gorgosaurus*/*Daspletosaurus*, and *Alioramus*/*Tarbosaurus*, so overall anatomical divergences were apparently sufficient for species differentiation without much in the way of orbital boss differentiation. When *Tyrannosaurus* evolved new and contemporary species the two expressions of the genus were so similar in general head and body form that selective forces compelled the evolution of distinctive orbital displays for purposes of species identification.

Taxonomic implications. Because the ETRH pays no particular attention to the highly variable configuration of the postorbital bosses that it regards of little or no importance, the theory lacks practical use in determining the ancestry and evolution of the TT-zone giants. The multiple species thesis does pay very close attention to those critical display items, and therefore advances the analysis of its phylogeny relative to the rest of the tyrannosaurids and within the genus.

Tyrannosaurid species turnover pattern

As per many dinosaur clades, including other giant north American tyrannosaurids, speciation in *Tyrannosaurus* best fits into the common dinosaur rapid turner over mode as indicated by significant anatomical changes in about a million years of less, in tune with contemporary ceratopsids and most hadrosaurs. This differs from the pattern that may apply to some other dinosaurs, such as some *Psittacosaurus* species which remained little changed over extended periods according to Son *et al*., (2024).

The taxonomy picture for large Tyrannosaurus

The current preponderance of evidence is heavily on the side of evolutionary speciation in TT-zone *Tyrannosaurus*. Specimens lower in the zone retain ancestral conditions including robust femora, usually two lower incisiforms, a broad interfenestral pillar, and a long, low orbital boss that is distinctive from all other tyrannosaurids including other TT-zone *Tyrannosaurus*, with the notable exception of the potentially ancestral *T.*? *mcraeensis*. *T. imperator* has a uniquely long low spindle postorbital display boss that is not present in any other tyrannosaurids including *T. regina* and *T. rex*, and the latter has derived, atypically prominent “Mickey Mouse” postorbital discs not present in any other tyrannosaurids including *T. regina* and *T. imperator.* And the last retains the ancestral condition of two dentary incisors and robust elements while *T. rex* and *T. regina* have a derived condition of one large incisor, while the last is remarkably skeletally gracile for such a giant. Offering no positive evidence to explain this diversity over 1.5 million years, the ETRH can only proffer a level of anatomical divergence that changes over time that is well beyond that observed in other species including among tyrannosaurs. Because efforts to actively

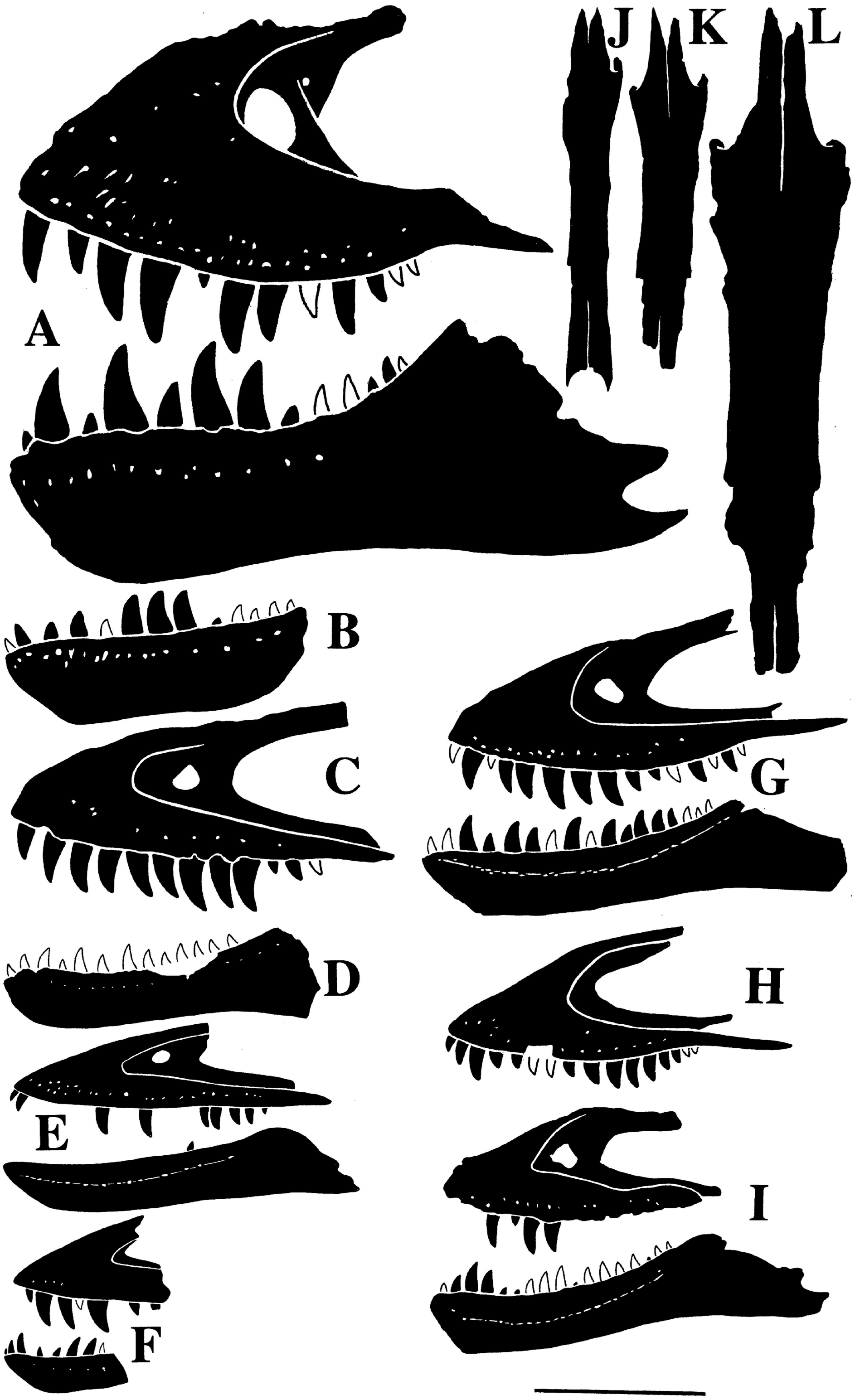

FIGURE 8. TT-zone eutyrannosaur skull elements as preserved to same scale, bar equals 200 mm, dimensions for **E** are approximate. Maxilla and/or dentary in left view (some reversed, some combined from both sides), tooth positions lacking teeth indicated by tooth outlines, tooth count for **H** not yet known: *Tyrannosaurus*: **A**, *T. rex*, holotype CMNH9380 (adult, 6.5 tonnes). **B**, *T.* incertae sedis, BHI6439 (juvenile, ~1). **C**, *T. imperator*? KU156375 (juvenile, ~800 kg). **D**, *T.* incertae sedis Baby Bob (juvenile, ~500). Basotyrannosaurs: **E**, *Stygivenator*? incertae sedis, NCMNSBM (subadult, ~450?). **F**, *S. molnari*, holotype LACM28471 (subadult, ~400). **G**, *Nanotyrannus*? incertae sedis, BMRP2002.4.1 (subadult, 530). **H**, *N. lancensis*, holotype CMNH7541 (subadult, ~450). **I**, *N.*? incertae sedis, HRS08 (subadult, ~450). Nasals in dorsal view: **J**, *N.*? incertae sedis BMRP 2002.4.1 (subadult, 530); **K**, *T.* incertae sedis LACM 23845 (juvenile, ~1.7 t). **L**, *T. rex*, RSMP2523 (adult, 7.8).

refute the MTTH have failed in part because of the lack of actual evidence for the ETRH, they are now obsolete. If the cumulative data were so in line with speciation regarding any dinosaur genus other than the celebrated *Tyrannosaurus*, *T. rex* specifically, the results would find wide acceptance. That the results of Paul *et al*. (2022) led to such a sharp reaction is indicative of procedural problems in dinosaurology. If the not so iconic *Allosaurus* and *Daspletosaurus* with little contention includes sibling intragenus species due to crude stratigraphic separation combined with a few minor character differences with little if anything in the way of visual display and proportional differentiation, and no supporting statistical or phylogenetic work, then why not the same regarding *Tyrannosaurus* that exhibits at least as much if not more display and proportional divergences? That has yet to be explained by ETRH defenders, and there is no compelling reason to think it can be.

The Lithe TT-zone *Eutyrannosaur* Fossils

Having explored the situation with the species of the great *Tyrannosaurus*, this section takes a look at the lesser remains that may or may not have grown up to become tyrant lizards. The multiple questions include whether all of the graciles are juvenile *Tyrannosaurus* or not, and if the latter is supported whether the non-*Tyrannosaurus* can all be simply placed in the one genus or species *Nanotyrannus lancensis*, or if that itself is a wastebasket taxon that cannot accommodate multiple taxa. Also open to question is whether any non-*Tyrannosaurus* are tyrannosaurids and/or more basal eutyrannosaurs. Some issues with the Carr (2020) analysis on this subject are discussed in the Supplementary.

What are juvenile Tyrannosaurus, *and what are not*

As documented by the systematic palaeontology section and the ensuing analysis, the question is not whether any TT-zone gracile tyrannosaurus are not juvenile *Tyrannosaurus*, but which are not, and which are (Figs 1G, 2R–T, 8B–K, 9D,E, 10).

Small TT-zone tyrannosaurids that qualify as being juvenile *Tyrannosaurus* due to the character possessions and/or combination of maxillary and dentary teeth counts being limited to 12–13, teeth being robust, a fairly deep anterior maxilla and antorbital fossa, elongated frontal, a robust dentary, lack of a lateral dentary groove, a robust femur and a tibia only a little longer than the femur include USNM6183, UCRCV1, LACM23845 (*Dinotyrannus megagracilis* holotype), BHI6439, KU156375, UCMP84133, and Baby Bob (Fig. 8B–D; Lipkin *et al*., 2007; Schmerge & Rothschild, 2016a, b; Burnham *et al*., 2018; Paul *et al*., 2022; Longrich & Saitta, 2024). All these specimens are fragmentary. That, combined with inadequate knowledge of *Tyrannosaurus* species' growth patterns which may have been similar over much of the curve, precludes both their being useful in helping discern the intragenus species, or placing most of the specimens in a particular tyrant king species. The exception is KU156375, its very broad interfenestral pillar favors assignment of the only known TT-zone juvenile *Tyrannosaurus* maxilla (Fig. 8C) to *T. imperator* on a tentative basis. Otherwise, the only potential means of currently assigning specimens is by stratigraphic placement. An unambiguous juvenile *Tyrannosaurus* from the low TT-zone is probably a *T. imperator*. Those from high in the strata are either *T. rex* or *T. regina*. Lack of vertical placement information for most of the specimens bars their species assignments. The high TT-zone location of LACM23845 favors it being a juvenile *T. rex* or *T. regina*; its assignment to the latter over the former by Paul *et al*. (2022) being plausible but speculative, it is now more conservatively considered *Tyrannosaurus* incertae sedis.

Small TT-zone tyrannosauroids that do not qualify as being juvenile *Tyrannosaurus* due to forelimb elements that in absolute measure are about as large or larger than those of adult *Tyrannosaurus*, maxillary teeth counts exceeding 13, bladed teeth, a sharp, subtriangular anterior maxilla and antorbital fossa, elongated frontals, presence of a long lateral dentary groove, and a tibia markedly longer than the femur include BMRP2006.4.4 and 2002.4.1, CMNH7541, DDM344.1, FNMHPR2411, HRS08, 15001, Jodi, KU155809, LACM28471 (*Stygivenator molnari* holotype), MOR6625, NCMNSBM (Bloody Mary, no specimen number yet assigned), ex BHI6437, and RSMP2347.1 (Figs 1G, 8E–J, 9D, E, 10; Gilmore, 1946; Russell, 1970; Molnar, 1978, 1980; Bakker *et al*., 1988; Paul, 1988; Larson, 2008, 2013a, b; Schmerge & Rothschild, 2016a, b; Paul *et al*., 2022; Longrich & Saitta, 2024). TT-zone non-*Tyrannosaurus* fossils outnumber juvenile *Tyrannosaurus* about two to one, and include more complete remains. Specimens at least provisionally assignable to either *Nanotyrannus* or to *Stygivenator* appear similar in number, but that conclusion is highly provisional, and half the non-*Tyrannosaurus* remains are not assignable on the available information.

Taxonomic implications. Aside from the basic issue of whether or not the lesser TT-zone tyrannosaurs are juvenile tyrant lizards, if they are not there is the question how many taxa they themselves constitute. Although there are not the quality juvenile *Tyrannosaurus* fossils known for *Gorgosaurus* and *Tarbosaurus*, there is a substantial set of juvenile *Tyrannosaurus* remains that overlap in size with those of other morphotypes that provide the decisive anatomical data set needed to test the lesser size end of the MTTH versus the ETRH (contra otherwise by Paul (2008, 2010), Carr (2022)). With these TT-zone fossils on hand, we shall start with the most critical factor to examine the issue.

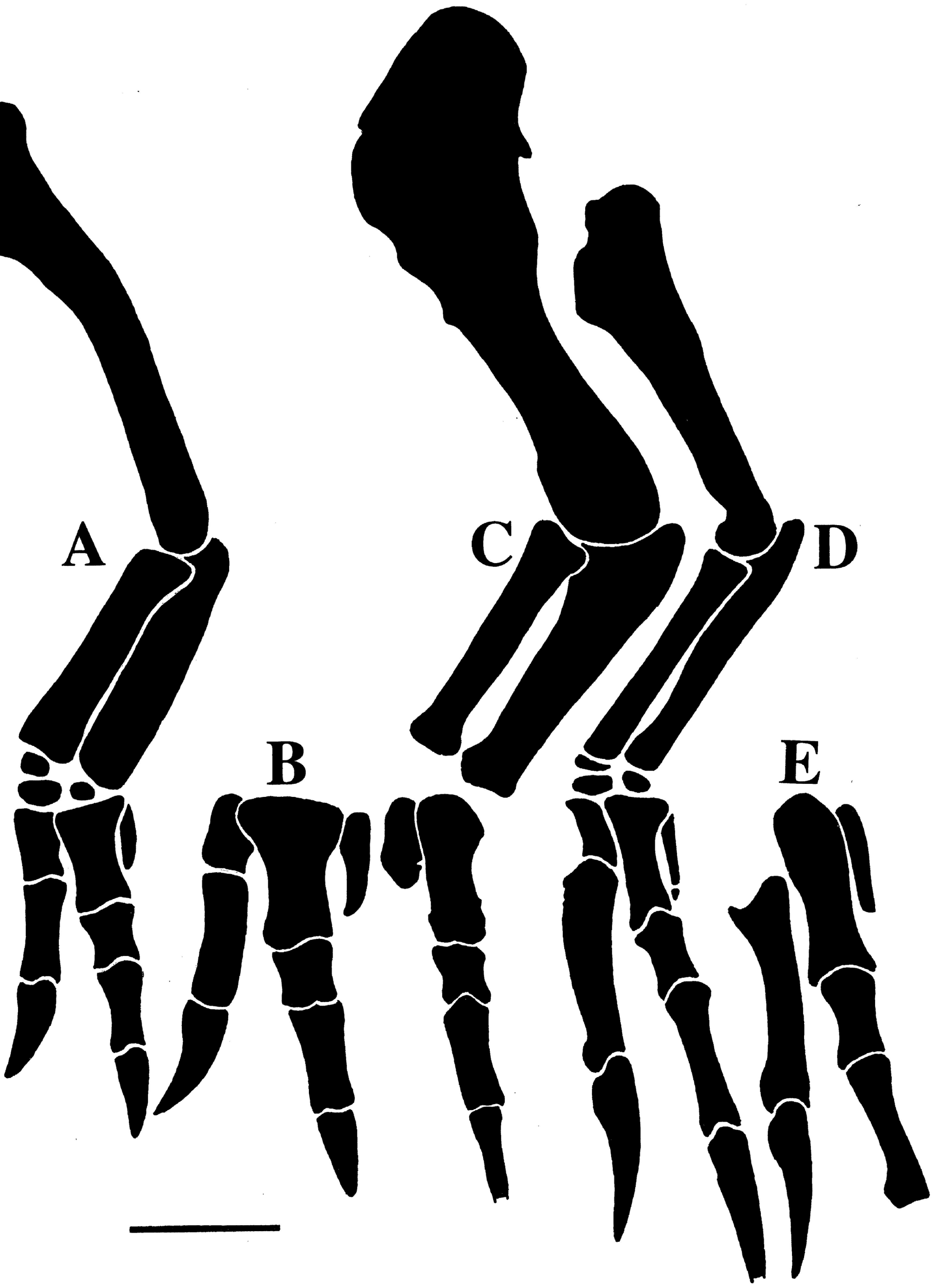

FIGURE 9. TT-zone tyrannosaurini and baso-eutyrannosaur forelimbs as preserved to same scale, bar equals 100 mm (element profiles and measurements from photographs with metric rulers for all but **C** (Brochu, 2003), official measurements await formal descriptions). **A**, *Tyrannosaurus* incertae sedis, UCRCV1 (subadult). **B**, *T. regina*, MOR980 (adult). **C**, *T. imperator*, holotype FMNHPR208 (adult; placement of distal elements not certain). **D**, *Stygivenator*? incertae sedis, NCMNSBM (subadult). **E**, Baso-eutyrannosaur Jodi (subadult).

The critical forelimb and manus size factor

This analysis of the non/juvenile status of small TT-zone tyrannosauroids that do not readily fit into the *Tyrannosaurus* growth pattern starts with a factor that disproves their being juveniles of the genus that, although known for years, yet has gone ignored by many, Larson (2013a) and Longrich & Saitta (2024) being exceptions. No known amniote undergoes a reduction in the absolute size of limb elements as they mature, resulting in the adults having a shorter appendage than when they were younger, such radical metamorphosis being limited to invertebrates and nonamniote vertebrates (Longrich & Saitta, 2024). No dinosaur, avepod, or tyrannosauroid growth series (Fig. 11), including that of the gigantic tyrannosaurin *Tarbosaurus* (p. 163 in Paul, 2024b). exhibits such an abnormal ontogenetic size decrease. Such as not been observed in

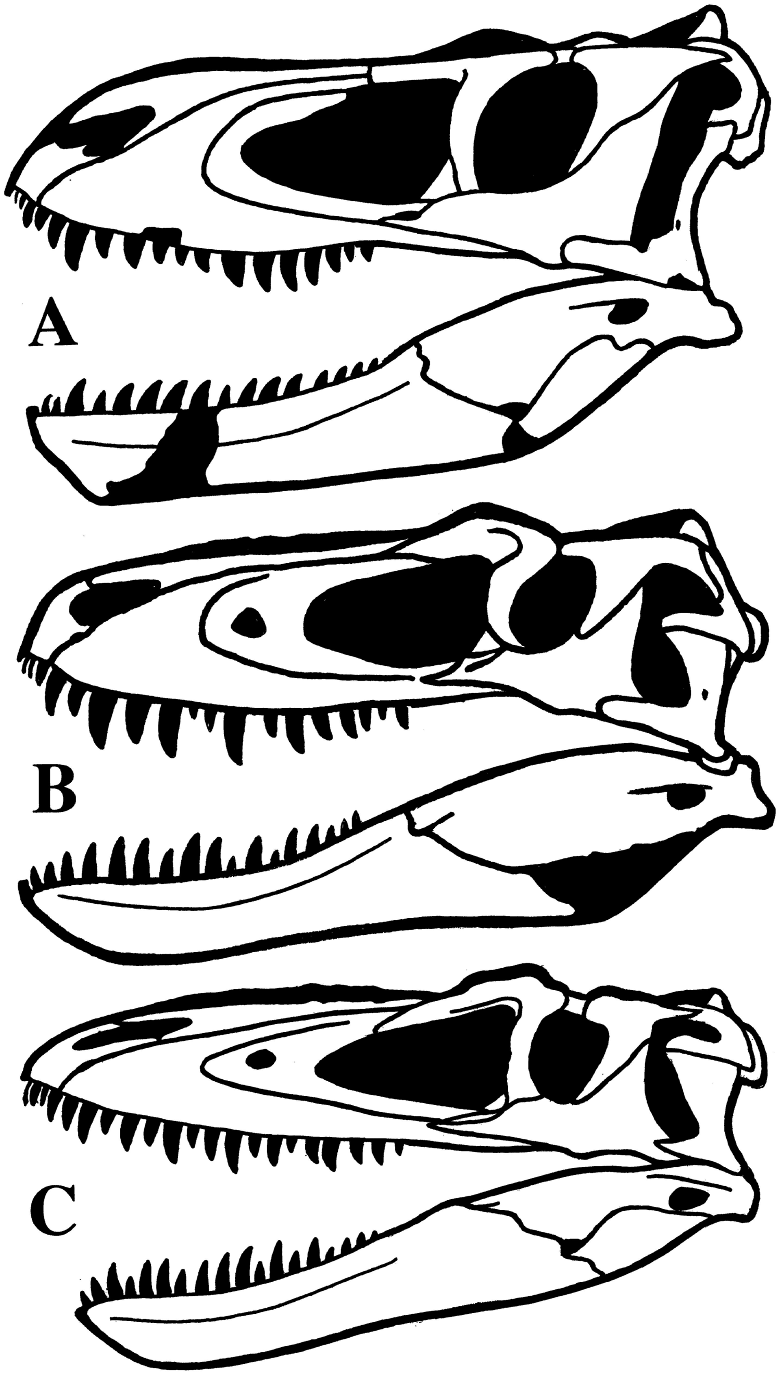

FIGURE 10. Subadult TT-zone nontyrannosaurid tyrannosaurid skulls as preserved to approximate same scale, bar equals 0.5 m. **A**, *Nanotyrannus lancensis*, CMNH7541 holotype (lacrimal hornlet not preserved). **B**, *N.*? incertae sedis, BMRP2002.4.1. **C**, *Stygivenator*? incertae sedis, NCMNABM.

other avepods with severely atrophied distal forelimbs (Wang *et al*., 2017; Liberona *et al*., 2019; Guinard, 2020; Canale *et al*., 2022)—the small manal claws of juvenile hoatzins atrophy during ontogeny, but the manus overall smoothly increases in size and configuration up to the adult condition without dimensional reversals. Nor is there evidence of significant variation in the size and form of the appendage in *Tyrannosaurus* (Figs 1A, D, E, 9A–C). Advocates of *T. rex* as the only TT-zone species have not cited an example of an amniote that exhibits appendage atrophy with maturity. It therefore must be concluded that the possibility that *Tyrannosaurus* alone among all known amniotes may have experienced such a strange and inexplicable absolute withering of its arms with maturity is in practical biological terms zero. In which case small TT-zone graciles that have forelimb elements about as large and larger than those of adult *Tyrannosaurus* cannot be its juveniles. The far simpler and much more plausible explanation for the big armed TT-zone tyrannosaurs is that they were immigrants from eastern North America where the pertinent baso-eutyrannosaur clade had evolved.

It follows that because small TT-zone tyrannosaur specimens BMRP2006.4.4, HRS15001, Jodi, and NCMNSBM (Fig. 9D, E) have manal elements as large or larger than those of adult *Tyrannosaurus* (Fig. A–C in Paul,1924) they are barred from being members of that genus, (Larson, 2013a; Longrich & Saitta, 2024). The elongation of TT-zone non-tyrannosaurids arms is due largely to that of the radius-ulna and especially the manus, the humerus is not especially long. For example, the humerus/femur ratio of NCMNSBM the hand length of which matches those of adult *Tyrannosaurus* is over a third, only modestly higher than the 0.26–0.3 ratio observed in adults (CMNH9380; FMNHPR2081; USNM555000). At a quarter the femur length, the NCMNSBM radius is relatively up to twice as long as those of the giants at 0.09 to 1.12 (FMNHPR2081; USNM555000). Finger 2 of NCMNSBM is about half femur length, compared to just 0.24 in *Tyrannosaurus* (USNM555000). The thumb phalanx is literally about twice as long as that of gigantic FMNHPR2081 of nearly two times larger over all body dimensions; postulating reabsorption of such a slender bone down to half juvenile length with maturity is an incongruous hypothesis. The total length of the Bloody Mary forelimb exceeds that of the femur; adult *Tyrannosaurus* arms are about two thirds femur length. The impressive—for end Cretaceous tyrannosaurs—size of the small individuals' hands is regarding their length, most of the phalanges are relatively much slenderer than those of *Tyrannosaurus*, although their absolute breadths may be more comparable. In the face of the irrevocable manus evidence the non-*Tyrannosaurus* status of the pertinent specimens is settled, the rest of the analysis is confirmatory.

The situation regarding the other probable non-*Tyrannosaurus* TT-zone specimens is obscure due to absence of lower forelimb and manal elements, or the absence of other postcranial elements to compare them to. The humerus/femur ratio BMRP2002.4.1 is much less than that of NCMNSBM. That the length of the former's humerus is roughly comparable to or a little longer than that of the generally smaller NCMNSBM suggests BMRP2002.4.1. was not a relatively big armed as Bloody Mary, but the very large manal elements of otherwise similar BMRP2006.4.4 indicate that 2002.4.1 was bigger armed than the great *Tyrannosaurus*.

That the manus proportions of NCMNSBM and Jodi differ, the 1st digit phalanx of the first is much longer relative to metacarpal 2 than that of the latter (Fig. 9D, E), may suggest they are not the same species.

Among near tyrannosaurid tyrannosauroids outside the TT-zone, the one with sufficient preserved forelimb material to assay is *Dryptosaurus*. Its elongated arms, manus especially (Carpenter *et al*., 1997; Brusatte *et al*., 2011), imply a close relationship to the long armed TT-zone baso-eutyrannosaurs.

Taxonomic implications. Large hands disprove the ETRH regarding many of the small bodied fossils, and indicate that the graciles that have them are not even tyrannosaurids much less tyrannosaurins.

Tyrannosaurus *was not a teleost: implausibly sudden transformations and character disparities*

The amniote norm is for juveniles to grow into adults without sudden, radical, metamorphosis style transitions in form during growth, a smoother continuation being typical. This is observed in documented dinosaur growth series, including avepods, including tyrannosaurids, among the latter the gigantic tyrannosaurin *Tarbosaurus* (Figs 2H–O, 11; Paul, 2010, 2016, 2024b, p. 163; Longrich & Saitta, 2024). At any given stage the skulls of the Asian giant are a modest modification from the earlier growth stage, forming a progressive continuum with no disruptions much less sudden dramatic transformations. Same applies to the fossils *of Gorgosaurus libratus* (Fig. 11). Paul (2008) noted that assuming, as I did at the time, that *T. rex* was the only tyrannosaur species in its habitat, that it experienced a unique and odd shape shift during ontogeny. Witmer & Ridgley noted the ontogenetic improbabilities of growing CMNH7541 into a *Tyrannosaurus*. Larson (2013b) showed that the anterior vomer of CMNH7541 is deeper in absolute measure than that of adult *Tyrannosaurus*, another biologically impractical need for reabsorption forced by the just *T. rex* hypothesis (Longrich & Saitta, 2024).

The largely to entirely complete CMNH7541, BMRP2002.4.1 and NCMNSBM do not have the anatomical appearance of a juvenile *Tyrannosaurus* in the manner that relatively similar sized TMP2009.12.14, TMP1991.36.5000 and AMNH5664 do of grown up *Gorgosaurus*, or PIN 552-2, MgD-1/3 and PIN553-1 of *Tarbosaurus* (Figs 1, 2, 8, 9, 10, 11). In albertosaurins and tarbosaurs the youngsters look like gracile versions of what they are going to become, like horse foals (the pattern even applies within breeds—lanky thoroughbred foals look like they are on stick stilts, young Belgian work horses not so much).

In contrast, same scale comparisons of cranial elements of the pertinent TT-zone juvenile tyrannosaur specimens fail to show a smooth series (Fig. 8). Despite being similar in size, the nasal of BMRP2002.4.1 is much narrower than the similar sized bone of the juvenile *Tyrannosaurus* LACM23845 which is proportionally fairly similar to that a markedly larger adult of the genus (Fig. 8J–L). The juvenile *Tyrannosaurus* BHI6439 dentary is much more robust in all dimensions than is that of the broadly similar sized BMRP2002.4.1, the former

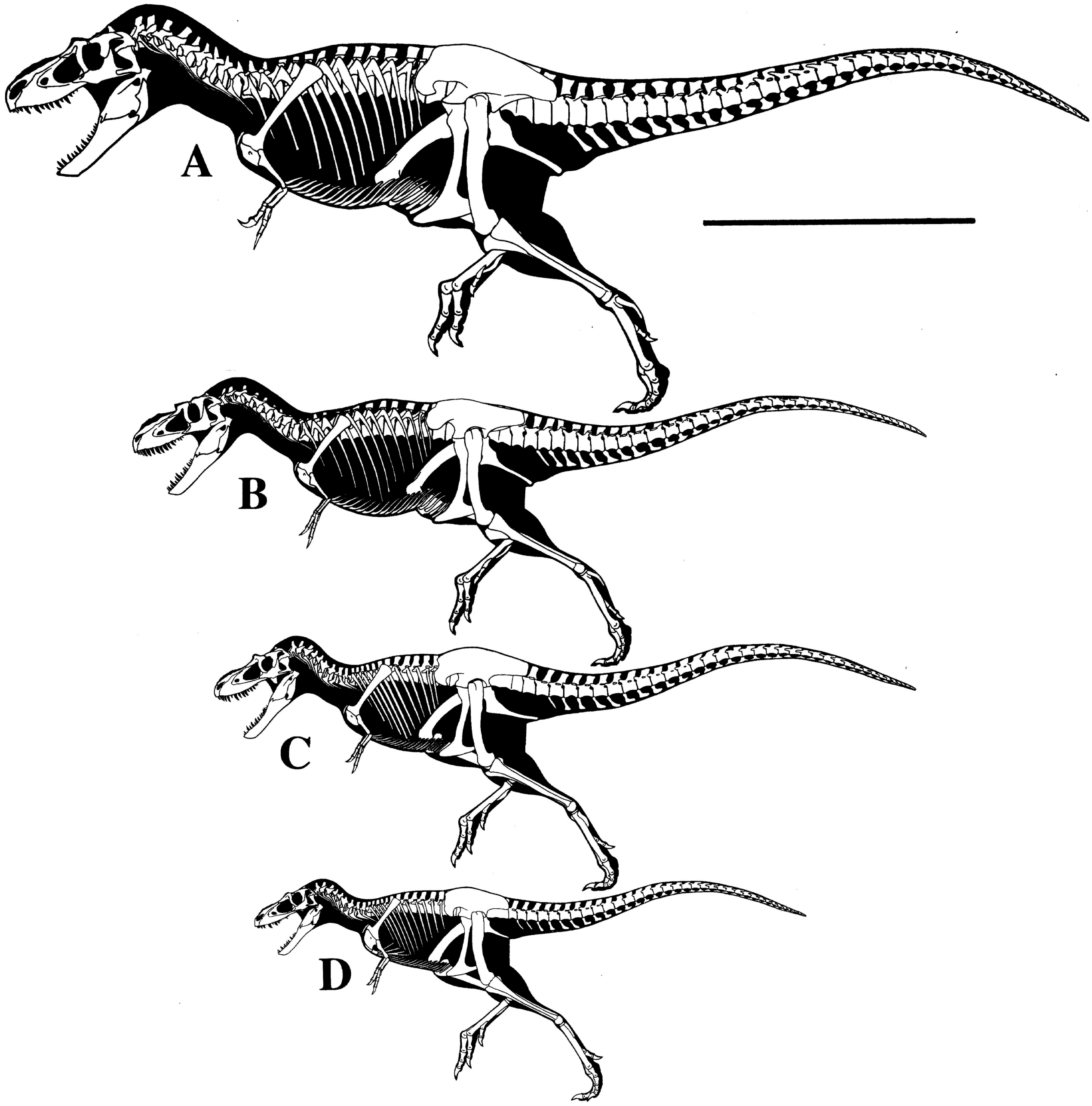

FIGURE 11. Growth series of Dinosaur Park *Gorgosaurus* profile-skeletals to same scale, bar equals 2 m. **A**, AMNH5458. **B**, AMNH5664. **C**, TMP1991.36.5000. **D**, TMP2009.12.14.

lacks any sign of the lateral groove on the latter, and the 13 robust teeth of BHI6439 are very different from the 17 blades of Jane. Getting the former from BMRP2002.4.1 is at best an extreme ontogenetic stretch not seen in other tyrannosaurids. Even worse for the only *T. rex* hypothesis is that while gracile, immature *Tyrannosaurus* Baby Bob that is smaller than BMRP2002.4.1 and about the same size as the *Nanotyrannus* holotype and HRS08, BB has the *Tyrannosaurus* condition of much fewer and more robust teeth, and lacks the lateral groove of the dentary (Fig. 8D; Larson, 2013a; Schmerge & Rothschild, 2016a, b; Longrich & Saitta, 2024). BB cannot be part of the same growth series as sometimes larger, sometimes similar sized, and sometimes smaller BMRP2002.4.1, CMNH7541, LACM28471 or NCMNSBM. The last two specimens sport sharply triangular "Stygi" anterior maxillae and antorbital fossae, and upcurved dentary tips, that are distinctive from both the juvenile *Tyrannosaurus*, as well as the "Nano" morphology of BMRP2002.4.1, CMNH7541, and HRS08.

Viewing the skulls in their entirety produces the same result (Fig. 2). Unlike the growing *Tarbosaurus* crania that blend into one another with only modest alterations with maturity, NCMNSBM is drastically different in form from even similar sized BMRP2002.4.1 and CMNH7541, much less the larger *Tyrannosaurus* skulls with it shares no diagnostic features with aside from being a derived tyrannosauroid. In addition, all those skulls do not share a similar form with similar sized *Tarbosaurus* juveniles. Concurrence in appearance is to be expected among the juveniles of two close relatives that share a similar growth size span. That they do not is further indication that the lithe TT-zone tyrannosaurs were not young tyrannosaurins.

Not implausible is that the elongated distal hindlimbs of gracile TT-zone tyrannosaurs could mature into the less distally elongated legs of adult *Tyrannosaurus*. such being observed in albertosaurins and tarbosaurs (Figs 1, 11; Paul, 2024a, b). But an apparently lower femur/tibia ratio of Baby Bob appears to show that the tyrant lizard started out less lithe limbed than the TT-zone non-tyrannosaurid eutyrannosaurs.

Taxonomic implications. Recognizing the profound multiple morph shifts with growth required by his proposed growth series, Carr (2020) could have reconsidered his conclusions. Instead, trying to conform the fossils to the ETRH, and unable to cite examples of amniotes that experience such remarkable ontogenetic alterations, Carr (2020) proposed the extreme, highly non-parsimonious, nonamniote fish model of *Tyrannosaurus rex* growth hypothesis in which the species underwent an abnormal metamorphosis upon sexual maturity. Just how drastic and correspondingly implausible was illuminated by his citing teleost fish as ontogenetic analogues. But T*yrannosaurus* was not a fish, and the possibility that it experienced nonamniote growth is too improbable to be considered a sound scientific concept unless all the data unambiguously supports such (as first pointed out by Longrich & Saitta, 2024). Which the data does not, showing that *Tyrannosaurus* fossils have a growth pattern normal for tyrannosaurids specifically and amniotes broadly. As it is, the Carr hypothesis has the appearance of being a convoluted, extraordinary theory in search of arguments to try to support the single species premise, rather than a plausible much less parsimonious theory based on the data on hand. I do not accuse Carr of enforcing a desired result, but raise the point to state clearly that use of extraordinary hypotheses has the potential to be abused and should raise alarms for reviewers of future taxonomic work.

Lateral dentary groove

Lateral dentary grooves are common but far from universal in avepods, including tyrannosauroids (Brusatte *et al*., 2010, 2016; Schmerge & Rothschild (2016a, b) who provide extensive discussion and photographic documentation of the feature and absence of same; Carr, 2020; Longrich & Saitta, 2024). For the purposes of this study lateral dentary grooves are readily visible, well defined elongated, slender depressions that extend along a considerable length of a dentary, containing a number of small foramina that in at least some portions are not closely spaced. Faux grooves can result from the close spacing of a high number of the foramina sulci.

Tyrannosaurins lack well developed grooves. The contention by Brusatte *et al*. (2016) that adult and juvenile *Tarbosaurus* have them are not supported by the data. Their Fig. 1A, B indicates that the lines are at best weakly developed in adults. Same is true in the image of the very small juvenile in Fig. 4B in Tsuihiji *et al*. (2011) in which the groove is weak and short—that the same sized *Raptorex* and *Bagaraatan* (Fig. 1A, B in Slowiak *et al*., 2024) holotypes have the same distinctive topography strongly indicates they are both juvenile *Tarbosaurus* (Fowler *et al*., 2011)—that Slowiak *et al*. (2024) do not recognize that this feature helps subsume *Bagaraatan* into *Tarbosaurus* is because of the imprecise analysis of tyrannosaur dentary grooves by themselves and Brusatte *et al*. (2016). Nor do prominent grooves appear in the array of larger juveniles and adults described by Maleev (1955, 1974), Rozhdestvensky (1965) and Hurum & Sabath (2003). Also lacking well-formed lines are any unambiguous *Tyrannosaurus* of any ontogenetic stage (Larson, 2013a; Schmerge & Rothschild, 2016a, 2016b; Longrich & Saitta, 2024). The supposed adult dentary grooves indicated in Fig. 1C, D in Brusatte *et al*. (2016) are not visible, in some cases what may appear to be such being an illusion formed by closely spaced foramina. An examination of images of all adult *Tyrannosaurus* skulls failed to produce a single example of the existence of the groove in a manner at all comparable to those seen in the small tyrannosauroids that do have them (also contra Carr, 2020). Nor is the line present on the two juvenile *Tyrannosaurus* dentaries BHI6943 and the half-sized BB (Schmerge & Rothschild, 2016a, b). A prominent lateral groove is consistently present in albertosaurins adult and immature (Schmerge & Rothschild, 2016a, 2016b; Brusatte *et al*., 2016). As far as is known the lateral groove is consistently developed during ontogeny in a given late Cretaceous tyrannosauroid species, the only exception being weak development in small juveniles. Major intraspecific variation whether individual, sexual or otherwise has not been observed.

Almost all of the small TT-zone dentaries that lack the other attributes characteristic of *Tyrannosaurus* exhibit a readily visible lateral groove, even when the same size or larger than the young tyrant lizard jaws that entirely lack the feature. Because such an inconsistent pattern of conspicuous grooves being present or not in similar sized juveniles of other avepods, tyrannosauroids included, has neither been documented nor makes apparent functional or ontogenetic sense, the disparity of this condition in the TT-zone tyrannosaurs constitutes excellent evidence that they are not contained within genus, much less species. So does that in other avepods, tyrannosauroids included, the degree of development of the groove does not significantly fluctuate much less disappear at varying growth stages. The attempts to conclude otherwise are weak efforts to wave away the compelling taxonomic implications of the telling ontogenetic evidence. A notable exception to the presence of groves among the non-*Tyrannosaurus* assemblage is the *Stygivenator* holotype, which lacks the feature (Schmerge & Rothschild, 2016a, b). This is not good evidence that LACM28471 is a baby *Tyrannosaurus* (contra Schmerge & Rothschild, 2016a, 2016b), the attribute often being absent in tyrannosaurids, and the specimen being similar in many ways to NCMNSBM the groove of which is very prominent. It is more likely that the two specimens, while probably within a non-tyrannosaurid subclade, do not belong to the same species and perhaps genus despite their other likenesses.

Taxonomic implications. There is no evidence that lateral dentary grooves undergo major alterations with growth in tyrannosauroids, and actual *Tyrannosaurus* juveniles lack them as do their parents, so prominent grooves preclude many small TT-zone tyrannosaurs from being juvenile tyrant lizards. The status of the feature also has diagnostic value between the non-*Tyrannosaurus* tyrannosauroids.

Head shape

One item that does appear to ally a small TT-zone tyrannosaur with *Tyrannosaurus* is the seemingly laterally very narrow snout contrasting with a very broad temporal region of the *Nanotyrannus* holotype, resulting in strongly forward facing orbits, those being classic characteristics of the tyrant lizard (Fig. 7E, F) not observed in other tyrannosaurids, even *Tarbosaurus* (Fig. 7D; the very narrow rostrum restored in Fig. 1 of Hurum & Sabath (2003) is refuted by the much broader snout of the articulated GIN107/1 in their Fig. 15, and the taxon's holotype lacks the great fore-aft disparity, pers. observ.). If anything, the condition appears more extreme as apparently preserved in CMNH7541 (Witmer & Ridgely, 2010) than it is in adult *Tyrannosaurus*, which if correct actually complicates an ontogenetic connection because the more developed condition would be expected to develop with maturity. But CMNH7541 has been asymmetrically distorted in a complex manner, and elements are missing, to the extent that this palaeoillustrator is not able to reliably restore its configuration in dorsal view. That the skull length/occipital widths ratio is about a fifth less in CMNH7541 than in *Tyrannosaurus* AMNH5027 indicates that the overall temporal breadth of the former has been exaggerated by post-mortem splaying of the ventral temporal region. Further complicating the situation that other pertinent skulls do not appear to have the broad aft skull, but the BMRP2002.4.1 skull has not been sufficiently described to restore in dorsal view, and it is disarticulated. Meanwhile the very narrow CMNH7541 rostrum appears to be laterally compressed an uncertain amount (but Longrich & Saitta (2024) disagree). The last researchers 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.

It has always struck this paleoartist that when viewed via neural processing pattern recognition visual mode (see Supplementary), the CMNH7541 skull simply does not look like those of the small juveniles of any other tyrannosaurids, lacking their elegant gracile lines (Figs 2K–R, 10). For that matter it does not look much like that of the also subadult BMRP2002.4.1, much less ultra-gracile headed alioramins. This may be partly due to the post burial distortion, but even taking that into account it may reflect that *Nanotyrannus lancensis* was not a young juvenile, but a subadult of a taxon whose mature cranial proportions were mimicking those of larger tyrannosaurid taxa. If so, it is possible if not probable status as a distinct species relative to other non-*Tyrannosaurus* TT-zone fossils is enhanced. Also true is that BMRP2002.4.1 and NCMNSBM do not look much like one another in the way the young *Gorgosaurus* skulls do, or those of *Tarbosaurus*. Indeed, NCMNSBM is an extreme bioform with its ultra long and low skull created by its extremely long rostrum and dentary, even alioramins don't quite match it. It has the morphological gestalt of a distinct taxon. All this adds up to the possibility if not probability that these and CMNH7541 are the remains of three different taxa. The observed pattern is in accord with the suggestions by Paul (2016, 2024a, b) and in more depth by Longrich & Saitta (2024) that the TT-zone fossils represent at least three genus level taxa, which if correct could sort out at the genus level into gigantic *Tyrannosaurus* alongside medium-sized *Nanotyrannus* and *Stygivenator*, if not more taxa.

Taxonomic implications. As jaguars do look like leopards, the strongly visually differing skulls of TT-zone tyrannosaurs favour the MTTH over the ETRH, and help delineate multiple taxa in the tyrannosauroids.

Ontogeny

The smoothly sigmodal growth curve of Figure 12 in Carr (2020) obtained by forcing all TT-zone tyrannosauroids into *T. rex* is a contrivance constructed in accord with the paper's explicitly stated ETRH assumption of conspecificity (Supplementary). The calculated ages at death of specimens of varying sizes covering over a

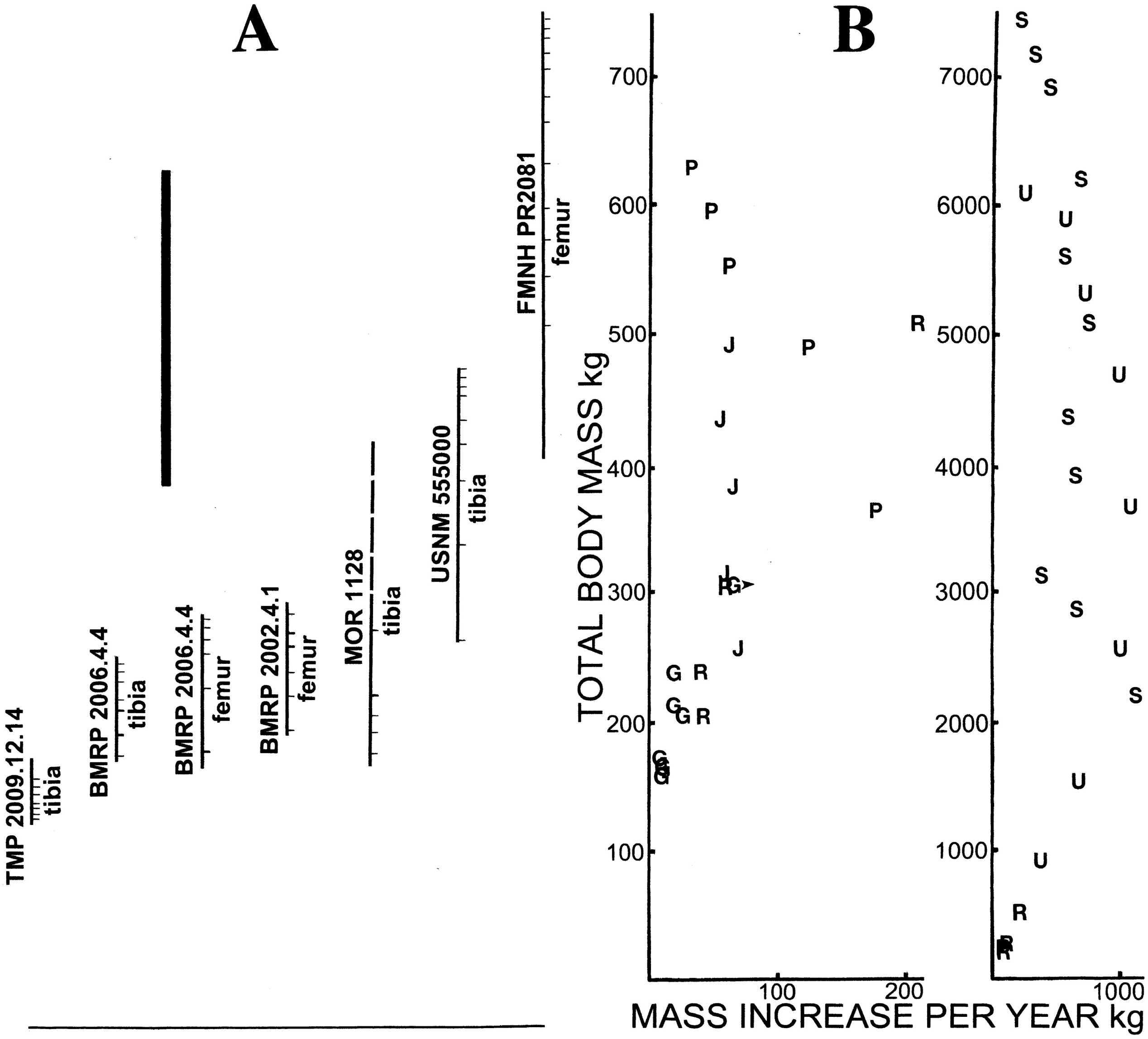

FIGURE 12. Late Cretaceous Laramidia eutyrannosaur growth patterns. **A**, spacing of femur and tibia cortex lines of arrested growth and growth zones of juvenile to adult Late Cretaceous North American eutyrannosaurs to same scale, bar equals 30 mm. Center of bones represented by horizontal line at base of figure, multiple lines indicated by thicker bars, MOR1128 cortex without documented growth marks indicated by dashed line. **B**, Growth per year (assuming annuli are that) as a function of total mass achieved that year, left plot smaller mass range up to 700 kg including non*Tyrannosaurus*, right plot entire mass range *Tyrannosaurus* only because other arcs too small to be plotted at this scale; G, juvenile *Gorgosaurus libratus*, TMP20009.12.14; J, subadult *Nanotyrannus*? BMRP2002.4.1; P, subadult *Nanotyrannus*? BMRP2006.4.4; R, robust, low TT-zone, immature *Tyrannosaurus imperator*, MOR1128; S, robust, low TT-zone, fully mature *Tyrannosaurus imperator*, holotype FMNHPR2081; U, gracile, high TT-zone, subadult *Tyrannosaurus regina*, holotype USNM555000.

million years was simplistically plotted as a function of body mass at death to form the curve, an invalid procedure because it maximized the possibility of creating a false impression of growth continuity within a single species (Longrich & Saitta, 2024). In no case was the growth curve of a small TT-zone specimen actually calculated based on empirical observation of bone growth, none being available at the time. The risk of generating a misleading impression has proven true, with growth curves based on femoral cross-sections of BMRP2002.4.1 and 2006.4.4 showing they had undergone a period of rapid mid growth mass gains, followed by the increasingly strong slow down observed in subadults that would complete maturation at about a sixth or less the bulk of adult *Tyrannosaurus* (Longrich & Saitta, 2024; also see Jevnikar & Zanno, 2021, as well as Cullen *et al*., 2020). Bone ring and other analysis of the hyoid of CMNH7541 indicates that it was fully adult (Griffin *et al*., 2024). Large avepods apparently experienced relatively smooth growth arcs (Erickson *et al*., 2004; Horner & Padian, 2004, Myhrvold, 2013; Cullen *et al*., 2020; Longrich & Saitta, 2024), rather than the more irregular growth observed in basal sauropodomorphs (Botho *et al*., 2022).

A direct presentation of the spacing of growth zones and the resulting mass growth per annum/total mass ratios (Fig. 12A, B; Supplementary: Table 1) verifies the results and conclusions of Longrich & Saitta (2024). Gigantic *Tyrannosaurus* FMNHPR2081 and especially USNM555000 follow the expected arc of low yearly gains when small, very large at rapid mid growth, and declining with maturity that was fully reached by the larger FMNHPR2081 (Erickson *et al*., 2004; Horner & Padian, 2004, Myhrvold, 2013; Cullen *et al*., 2020; Longrich & Saitta, 2024). Smaller MOR1128 begins with very low yearly mass additions when at a total mass in the low hundreds of kilograms, but increasing to substantial on the same initial projected normal growth arc as USNM555000, additional data is lacking for the former. Notably, the small juvenile *Gorgosaurus* (Fig. 12A) that also was on a growth trajectory to becoming a gigantic adult was increasingly putting on the kilograms in an arc similar to that—but perhaps a little less—than the MOR1128 *Tyrannosaurus* when at about the same size.

The growth patterns of BMRP2002.4.1 and 2006.4.4 are sharply different from those of similar sized juvenile *Tyrannosaurus*. The thickness of the growth zones is thinning with distance from the bone centre in the former at the same stage that they are becoming broader as juvenile *Tyrannosaurus* are heading towards becoming gigantic. This is especially true of BMRP2006.4.4, neither it nor BMRP2002.4.1 are on the giant tyrannosaur growth arc—the lesser slowdown of the latter implies it is not as close to maturity as broadly similar sized 2006.4.4. When approximately half a tonne *Tyrannosaurus* MOR1128 is boosting mass by a couple hundred kilograms a year, BMRP2002.4.1 and 2006.4.4 are adding only a sixth or less as much, so they were taking many years longer to grow that same amount as a young *Tyrannosaurus* at this same size. Entirely out of accord with the accelerating growth and massive at this size needed to become a multitonne adult tyrannosaurid in a limited time period, this has all the hallmarks of these graciles being subadults whose growth is deaccelerating as they near maturation, perhaps in the upper hundreds of kilograms or about a tonne (in broad accord with Longrich & Saitta, 2024). Histological evidence indicates that CMNH7541 had already reached full adulthood at about half a tonne (Griffin *et al*., 2024). The discordant growth observed in BMRP2002.4.1 and 2006.4.4 on the one hand versus MOR1128 on the other caused Woodward *et al*. (2020) to postulate that growth within *T. rex* was highly irregular in accord with the ETRH, instead the divergent growth patterns refute the ETRH—if bone microstructure showed that BMRP2002.4.1 and 2006.4.4 were on the same growth arc as juvenile *Tyrannosaurus* that would constitute significant evidence that they were the same taxon. Because the patterns are instead very discordant the opposite is solidly established. The smooth sigmodal *Tyrannosaurus* growth curve of Carr (2020) is correspondingly fictional.

When producing future growth bone microstructure growth studies researchers are encouraged to include uniform, same scale ring spacing charts and yearly body mass increases as a function of body mass in a given year as per Figure 12. That will make direct visual comparison comparisons easier, and provide more straightforward growth arcs that minimize the number of assumptions that need to be made.

The absence to date of superficial terminal growth deposits in any medium sized TT-zone tyrannosaurs is not definitive evidence that they are small juveniles far from completion of growing up to be mighty *Tyrannosaurus* (contra Carr, 1999, 2020; Woodward *et al*., 2020). Such as so far been identified in only one *Tyrannosaurus* specimen (FMNHPR2081), and has not yet been observed in any of the gracile Asian tyrannosaurs (Longrich & Saitta, 2024).

Bakker *et al*. (1988), Larson (2013b) and Longrich & Saitta (2024) have detailed the evidence from postcranial and/or cranial bone suturing and surface topography indicating that BMRP2002.4.1, CMNH7541 and HRS08 were approaching maturity at a modest size, rather than being small and young juveniles of adults massing at least ten times more (contra Carr, 1999, 2020). That smaller LACM28471 shows a more profound juvenile condition is compatible with it being the young of a moderate sized taxon as well as an enormous one.

Taxonomic implications. There is no positive evidence that the manner of growth recorded by bone tissues of at least some TT-zone non-*Tyrannosaurus* is compatible with them growing up to be tyrant lizards, instead the fossil evidence shows they did not do so. Trying to force the growth curves of BMRP2002.4.1 and 2006.4.4 to be in tune with that of growing *Tyrannosaurus* would make scientific sense only if the anatomical evidence strongly favoured their being juvenile tyrant lizards. Because the circumstances are the opposite, trying to reconcile the growth patterns is not parsimonious and therefore neither informative nor necessary (see Supplementary for further discussion).

Dentition

Putting all TT-zone tyrannosaurs in *T. rex* requires that maxillary and dentary tooth counts significantly declined with maturity in many (Fig. 8G–I) but not all (Fig. 8B–D) examples (Carr, 1999, 2020—although the latter also places a peculiar emphasis on an increase in maxillary tooth numbers with age—Carr *et al*., 2017, 2022). Such a dramatic yet inconsistent shift in simple tooth counts with ontogeny has not been observed in any other predatory avepod species starting with basal Triassic examples in studies over many decades, including other tyrannosaurs (Rozhdestvensky, 1965; Maleev, 1974; Madsen, 1976; Colbert, 1989; Currie, 2003a,b; Hurum & Sabath, 2003; Reinhart *et al*., 2009; Larson, 2013a, 2013b; Tsuihiji *et al*., 2011; Burnham *et al*., 2018; Longrich & Saitta, 2024), and age related consistency in tooth numbers in large taxa appears to be the diapsid norm (Brown *et al*., 2015, which Carr (2020) cites while appearing to deliberately ignore its actual contradictory implications for the ETRH (further discussion in the Supplementary); Larson (2013b) refutes claims by Carr (1999) that prior studies found declining tooth numbers in growing reptiles). A rare case of real change in tooth numbers with growth is in a basal archosauromorph taxon sporting an *increasingly* very large number of teeth (Ezcurra & Butler, 2015). Teeth can be lost in favour of a beak during a major ontogenetic shift from juvenile predation to adult herbivory (Wang *et al*., 2017), this is not pertinent to the consistently predaceous tyrannosaurs. Foster *et al*. (2022) claim there was a tooth numbers reduction in gracile Asian aliormini, but this is based on a comparison of three skulls of varying sizes from three different species, and therefore has no positive evidentiary applicability on the issue of tooth ontogeny within a single species. Carr *et al*. (2017) cite a back and forth changes in maxillary tooth count in two species of growing *Daspletosaurus*, but in both cases there is not a consistent growth trend one way or another in just three specimens each, and the small shifts may represent individual variations. The myth of tooth loss being normal in avepods is incorrect and never should be repeated unless actual evidence to the contrary is produced. It follows that the higher tooth counts of BMRP2002.4.1, CMNH7541, HRS08, and NCMNSBM relative to both bigger adult *Tyrannosaurus*, and to similar sized actual juvenile *Tyrannosaurus*, is potent evidence that the former are distinct taxa from the tyrant lizard (Larson, 2013b; Burnham *et al*., 2018; Longrich & Saitta, 2024). This is even truer because there are true *Tyrannosaurus* juveniles—BHI6439, KU156375, Baby Bob—with the same numbers of teeth as the adults. That removes the need for the higher tooth count specimens to be forced into the role of *Tyrannosaurus* juveniles, and removes the possibility of the former being the latter, such inconsistent tooth counts during growth of a species being as out of norms as declining numbers.

A similar situation applies to tooth morphology. Juvenile *Tyrannosaurus* sport atypically robust teeth like their parents, contrary to the more typically avepodan gracile blades present in similar sized BMRP2002.4.1, CMNH7541, HRS08, LACM28471, and NCMNSBM (Bakker *et al*., 1988; Larson, 2008, 2013a, b; Burnham *et al*., 2018; Longrich & Saitta, 2024). That is contrary to the comparatively convoluted thesis that the bladed teeth of the latter specimens are attributes of young *Tyrannosaurus* as contended by Carr (1999, 2020).

Taxonomic implications. The postulated shift in tooth counts in growing *Tyrannosaurus* flies in the face of what is known about reptilian dental ontogeny including among tyrannosauroids and tyrannosaurins.

Other items

That the pneumatic foramen present on the lateral surface of the quadratojugal of *Nanotyrannus* is also present on some other tyrannosaurs (Carr *et al*., 2017) does not negate it from being a character that helps distinguish it and diagnose it from *Tyrannosaurus* which lacks it (Larson, 2013b; Longrich & Saitta, 2024). The condition of this character in NCMNSBM is not yet known. Larson (2013a) noted the presence of a remnant outer finger digit on the latter specimen that aside from not being present in *Tyrannosaurus*, is a basal condition that indicates that this gracile dinosaur is not a tyrannosaurid.

Phylogenetics and diagnoses

Because most TT-zone gracile eutyrannosaur specimens are subadults their character states can be used for purposes of phylogenetic investigation. A number of phylogenetic analyses based on this premise have favoured the existence of at least one non-*Tyrannosaurus* taxon in the TT-zone (Bakker *et al*., 1988; Schmerge & Rothschild, 2016a; Longrich & Saitta, 2024). Further work in this area is beyond the scope of this study, and would not produce critically different results—in any case such work is limited by the fragmentary remains of many of the medium sized fossils and the absence of thorough descriptions of the more complete examples.

Taxonomic implications. The taxa are readily diagnosed because, even in consideration of the just cited limitations, they specimens are both so distinctive from one another, and cluster into types that share common features not seen in the others.

The actual anatomical ontogenetic development of Tyrannosaurus—T. rex *and otherwise*

Although genuine juvenile *Tyrannosaurus* fossils are limited, they and basic amniote ontogeny are sufficient to indicate that their lower arms and hands were always absolutely smaller than those of their parents and shorter than the femur, the low tooth count of the genus was fairly stable during growth, that the teeth were not thin blades in juveniles, that a prominent dentary groove did not exist at any stage or was at most weak in very small juveniles, and while their skulls and skeletons were much more gracile than the adults, the limbs may have not been as much so as with contemporary baso-eutyrannosaurs. Not yet known is the breadth of their temporal regions.

The End Cretaceous North American Interchange

The persistent late Mesozoic Bering land bridge between Asia and North America has long been a major topic of discussion concerning the evolution of Ameroasian tyrannosauroids. Much less addressed has been the reconnection of western and eastern North America as the anterior seaway withdrew in the Maastrichtian. This is surprising in view of it being known that the Appalachia predator fauna was dominated by a set of large albeit not gigantic baso-eutyrannosaurs represented by *Appalachiosaurus* and *Dryptosaurus*, and there should have been important interaction between them and the Laramidia tyrannosaurids as it became possible for their populations to directly interact after tens of millions of years of saltwater separation. A location that would have been a focus of interchange driven interactions was the TT-zone because it very near to and may in part have been part of the new Laralachia land bridge (Fig. 1B in Gates *et al*., 2012). This failure to attend to this major geographical/evolutionary event has been propelled by the wide acceptance of the ETRH, in which there simply are no nontyrannosaurid eutyrannosaurs in the TT-zone for reasons at best unclear. Also involved has been the casual assumption that the eastern non-tyrannosaurids with their long arms were archaic forms unable to compete with more sophisticated western tyrannosaurids once the two types met. In contrast the MTTH at the genus level and above is fully compatible with and predicted by the North American faunal interchange.

Taxonomic implications. That two distinctive tyrannosauroid faunas had just been rendered geographically free to intermix near and in the TT-zone means that the MTTH is the easily the parsimonious null hypothesis. In comparison the ETRH lacks a ready explanatory power for why only one species was in the region when its juveniles were not specifically adapted to being medium sized predators, in a locale open to an influx of Appalachian tyrannosauroids that were fully adapted for the role of middle-sized hunters. For the ETRH to survive it has to be shown that all medium size TT-zone tyrannosaur fossils show such a consistent anatomy with one another and the adults that there is no doubt they were *Tyrannosaurus rex* juveniles. And that without extraordinary hypotheses such as nonamniote metamorphosis needing to be invoked to try to explain away the major anatomical differences that do exist. Reconnection of large land masses being a palaeozoologically rare and therefor extraordinary event, the intermixing of many taxa resulting from the North American Interchange is predicted to have resulted in an unusually large number of tyrannosaur taxa in the TT-zone, which is verified by the comparative anatomical data.

The taxonomy picture for lithe TT-zone tyrannosaurs

The ETRH cannot be operative because some of its supposed juveniles have hands larger than those of adult *Tyrannosaurus*, which is not possible in amniotes and is thus not observed in any other dinosaurs including *Tarbosaurus*. The contention that all TT-zone tyrannosaur fossils are just one species or even one genus is not only not parsimonious, it cannot be possible. The opposing hypothesis that some of the small specimens are not juveniles of *T. rex* is not at all extraordinary (Paul *et al*., 2022; Longrich & Saitta, 2024). That is because the presence of more than one set of adult and juvenile predatory taxa in the same level of the same formation is the dinosaurian norm, that that situation applies to tyrannosaurs sharing the same habitat when as was always true no other large bodied avepod clades was present, such was sometimes expressed as one of the two tyrannosaur taxa being much smaller and more gracile than the giant, and because the TT-zone was right at the centre of the novel mixing of long divergent western and eastern faunas. It follows that multiple tyrannosaur types being at the site for an extended geological period is to be expected.

As it is, there are a number of TT-zone tyrannosaurid specimens smaller than the adults that do exhibit the attributes expected of juvenile *Tyrannosaurus*; including looking like juveniles of the famed genus, expanding outer bone growth zones that blend smoothly into the subadult growth curves, bone textures and fusion states of small juveniles, robust lateral teeth limited to 12–13? in the upper and lower jaws, a fairly deep anterior maxilla and antorbital fossa, a lack of a lateral dentary groove, a robust dentary and femur among larger juveniles, and a tibia only a little longer than the femur. If all the TT-zone smaller tyrannosaur fossil shared these features, then there would be no choice but to conclude that *Tyrannosaurus* was for reasons unclear the only large predatory dinosaur taxon present in the TT-zone.

But that is far from the actual situation. While *Tyrannosaurus* juveniles as are to be expected not missing from the TT-zone, most of the fauna's medium sized tyrannosaur fossils are not close to having the characteristics expected of, and actually present in, growing *Tyrannosaurus*. Starting with having forelimbs actually larger than those of their proposed parents, which is abjectly not ontogenetically possible. Growth curves show individuals' growth beginning to plateau at a small fraction of the elephantine size of the great tyrant lizard, while bone textures and fusions indicate the same. Teeth are blades and more numerous, and dentaries are clearly groovy, even at the same dimensions of the juvenile *Tyrannosaurus* fossils. These disconnects from *Tyrannosaurus*, the big arms most of all, indicate a disconnect even from western tyrannosaurids, and origins in eastern dryptosaur type non-tyrannosaurids. The anatomical and ontogenetic uniformity required to sustain the ETRH in the face of the North American Interchange is absent.

The ETRH is not a conservative hypothesis because it demands that one known amniote species, *T. rex*, for reasons unexplained experienced dramatic metamorphosis as it matured, something not seen even in its close relatives. That while the eastern baso-eutyrannosaurs did not move into the TT-zone. The ETRH is therefore an extremely radical postulate that lacks any evidentiary support, the actual *Tyrannosaurus* juveniles showing entirely normal amniote patterns of growth. It is the MTTH that is the conservative, parsimonious theory that needs to be accepted unless extraordinary evidence otherwise is produced.

The anatomical, ontogenetic and paleogeographic evidence for *Nanotyrannus* and *Stygivenator* is so significant that the strong opposition to the hypothesis raises more scientific procedural questions. The great, dryptosaur style size of the arms of some specimens that abort the just one species thesis have long been knowledge in the field, being discussed in the technical literature in Larson (2013a) at a palaeontological convention that many of the pertinent researchers attended, and has since been widely discussed online. Yet this critical fact has been ignored in all the ETRH defences of only *T. rex* juveniles included ever since (Brusatte & Carr, 2016; Brusatte *et al*., 2016; Carr, 2020; Woodward *et al*., 2020). That tooth loss does not occur in growing predatory dinosaurs including tyrannosaurids as demonstrated by a long line of studies cited previously has either been ignored or misrepresented by Carr (1999, 2020) and Carr *et al*. 2017, 2022). Lateral dentary grooves have been claimed to be present when they are not and absent when they are present, while dismissing that they are consistently well developed or not in the ontogenies of species, in order to force all TT-zone tyrannosaur fossils of all dimensions into *T. rex* (Brusatte *et al*., 2016; Carr, 2020). Carr's (2020) united "growth curve" is paleo fiction. Part of the opposition seems to be taxonomic inertia mistaken for scientific prudence, combined with an ardent defence of the most iconic dinosaur species. Also a complication are serious concerns regarding private ownership of some specimens, but ignoring the fossils while coming to published conclusions that those specimens contradict is not practical palaeozoological science.

With it not being biologically practical for the big armed small bodied TT-zone baso-eutyrannosaurs to be juvenile *Tyrannosaurus*, the next issues are what kind of tyrannosauroids are they, how many taxa do they represent, and what if anything they should be labeled? Even within non-*Tyrannosaurus* TT-zone BMRP2006.4.4 and 2002.4.1, CMNH7541, HRS15001, HRS08i, Jodi, LACM28471 and NCMNSBM distinct differences suggest they are not as often presumed just *Nanotyrannus lancensis* which has been in danger of becoming a wastebasket taxon itself, but three or even four types are represented, probably spread among more than one genus. This is in full accord with the large predator generic diversity predicted in a given tyrannosaur dominated habitat over time sitting between recently reunited landmasses. That large arms appear to be common to the collection automatically places them outside of the small forelimbed Tyrannosauridae unless future data and analysis indicates otherwise. Because they apparently share large, two fingered forelimbs with Maastrichtian and more easterly *Dryptosaurus*, the possibility that these fossils form a clade is high. That said, the very fragmentary condition of the New Egypt Formation specimen, and the limited information for the above specimens, severely hinders in-depth analysis.

Being congruent in some but not necessarily all attributes (Longrich & Saitta, 2024), CMNH7541, BMRP2002.4.1 and 2006.4.4, and HRS08 can be provisionally diagnosed as possible but not certain members of the genus *Nanotyrannus*. Of these none is sufficiently complete to allow those that are not CMNH7541 to be assessable at the species level, a situation made worse by the current lack of certain basic stratigraphic placement outside the holotype. The different growth arcs of BMRP2002.4.1 and 2006.4.4 may be due to their being different taxa at at least the species level. It is therefore not possible to refer any other remains to *N. lancensis* specifically. If other specimens prove to not be as yet narrow snouted and broad aft as CMNH7541, that may be evidence of specific and even generic differentiation. As Longrich & Saitta (2024) observe, being similar to one another in their distinctive attributes LACM28471 and NCMNSBM appear to form another distinct group that does not include *Nanotyrannus* and can be tentatively diagnosed, but at what systematic level is not clear. The very fragmentary condition of the *Stygivenator molnari* holotype does not help matters. The short anterior rostrum of the latter relative to the extraordinary length of that of NCMNSBM, the differential presence or absence of the lateral dentary groove, and the very large snaggly teeth of LACM28471, indicate they are not the same species, and even same genus looks problematic. Assigning any of these specimens or types to *Dryptosaurus aquilunguis*, or more likely the genus, is possible if that is also from the late Maastrichtian. But whether fragmentary *Dryptosaurus* can be diagnosed well enough to tell if it is more like nanotyrannos or stygivenators is questionable. With dozens of large *Tyrannosaurus* specimens on hand most of whose basic stratigraphy is known are markedly more assessable at the subfamily-genus-species level than are the far fewer and less well documented smaller TT-zone tyrannosaurs.

Discussion

The cumulative taxonomy-stratigraphy picture for all TT-zone eutyrannosaurs

If all TT-zone tyrannosaur adult fossils shared a consistent display, proportional, dental and other anatomy similar to that observed in other dinosaur species including other tyrannosaurids *Tarbosaurus* included, and all small remains represented a reasonably progressive growth continuum up to maturity that did not involve extreme metamorphic transformations seen in invertebrates and nonamniote vertebrates, then the simple, non-Darwinian ETRH would be at least plausible despite the resulting long stratigraphic span of the species *T. rex*. The ETRH would remain plausible if the anatomical divergences among adults are as substantial as they actually are, but do not correlate with stratigraphy, although the MTTH would also be viable in that case. Also compatible with the ETRH as well as the inherently problematic teleost inspired FMTRGH is the lesser specimens being consistently similar to one another at all size stages including as they undergo an extreme metamorphosis at sexual maturity. All the adults being *T. rex* would remain the optimal hypothesis if they did not exhibit anatomical divergences that correlated with stratigraphy, even if the small fossils possess features they indicate they are not all juvenile tyrant lizards. If a set of the small TT-zone tyrannosaurs that are not *Tyrannosaurus* exhibited a strong anatomical commonality, then those could all be assigned to *Nanotyrannus*, perhaps to *N. lancensis* even if they span the full depth of the formations.

But none of the above is actually true, the opposite being the case. According to all the parameters listed in Methods and Materials, the MTTH alone is operative. The overwhelming combined evidence and points of proof therefore leave little if any doubt that the MTTH is correct, specifically in its broadest expression via the large and small species MTASH, which is consequently superior to the more size selective MTSH and MSTH. That many of the smaller tyrannosaurs have lower arms and hands larger than those of the adult *Tyrannosaurus* scientifically bars them from being juveniles of the genus, and indicates they are not even tyrannosaurids. That means the question is how many taxa were on the hunt in the TT-zone. The non-tyrannosaurids are themselves so different from one another that they cannot be one species, and probably incorporate different genera. The variability within gigantic *Tyrannosaurus*, especially its orbital displays, well exceeds that present in any other tyrannosaurid species, while its proportional divergence exceeds that of the entire Tyrannosauridae, so the preponderance of evidence strongly favours the MTTH as applied to the big fossils. The TT-zone contains a plethora of tyrannosauroid taxa, both among the giants, and within the smaller non-tyrannosaurids. The differences between the three species in respect to proportions and dentition detailed in Paul *et al*. (2022) were subtle, but the highly divergent display bosses where not at all subtle, they would have made it easy to visually tell them apart on that feature alone.

The origin and evolution of TT-zone tyrannosauroids great and small, an integrated geohistorical and paleogeographic scenario

With the basics of TT-zone tyrannosauroid systematics on hand, it is now possible to examine their ancestry and evolution, and propose a cogent, parsimonious hypothesis that readily combines their paleogeography, stratigraphy, anatomy and ontogeny in a coherent whole.

Paul *et al*. (2022) presented a provisional hypothesis for the evolutionary events that led to, and then occurred within, the specious genus *Tyrannosaurus* focused on the giants of the TT-zone. It suggested that the reconnection of eastern and western North America led to an expansion of the resource base for super predators preying on increasingly titanic ornithischians, boosting both prey and predator from rhino to elephantine dimensions. Whether the ancestry of *Tyrannosaurus* was predominantly or entirely Asian or American in origin was left unresolved. After its appearance at some stage before the TT-zone, *Tyrannosaurus* was at first in that region limited to *T. imperator*, which retained the robust build basic to large tyrannosaurids. And the two small dentary incisors normal for tyrannosaurids (Brusatte *et al*., 2009; Paul *et al*., 2022) including the giant Judith River taxon (Stein & Triebold, 2013), and *T.*? *mcraeensis* as noted above. Late in the TT-zone *T. imperator* was replaced by evolutionary means uncertain by *T. rex* which retained a condition almost as robust, and the atypically gracile *T. regina*, as the genus via sibling species began to parallel the earlier sharing of robust and gracile tyrannosaurids of the same Laramidia habitats (daspletosaurins and albertosaurins). The possession of only one incisor in both *T. regina* and *T. rex* suggests but does not establish that they were a clade onto themselves. That scenario did not consider the evolution of the cornual display bosses. Due to recent developments (especially Dalman *et al*., 2024; Longrich & Saitta, 2024), and consideration of Stein & Triebold (2013) and Wick (2014), and the analysis herein, the Paul *et al*. (2022) model is out of date, and heavily revised as follows.

The Paul *et al*. (2022) evolutionary scheme rested on the presumption that the big Laramidian tyrannosaurids were rhino sized predators feeding on generally similar sized ornithischian prey, the 5 tonne plus tyrannosaurids not appearing until well into the Maastrichtian. However, an elephant sized tyrannosaurid, perhaps a daspletosaur with a lacrimal hornlet not present in tyrannosaurins was present in Montana in the middle Campanian (Stein & Triebold, 2013). Perhaps a little later still larger *T.*? *mcraeensis* was extant in the late Campanian/early Maastrichtian of New Mexico, where it could prey on titanic titanosaurs (Dalman *et al*., 2024). The TT-zone *Tyrannosaurus* were therefore not recent innovations in predaceous gigantism just before the K/Pg events, it was a continuation of events extending back well into the Campanian of Laramidia. The presence over 10 million years of massive tyrannosaurids in western North America, including one that either is a basal *Tyrannosaurus*, or close to the genus, favors the evolution of the giant tyrant lizard on the continent, over it being an Asian import via the Bering land bridge—which may have been hindered by polar climate issues that suppressed size as discussed in Paul *et al*. (2022 Supplementary Information and references therein), there being no 4+ tonne tyrannosaurs known from the Alaskan early Maastrichtian when such were present in Asia and Laramidia. Cross Bering interchange was significant it seems, the tyrannosaurids of both continents sporting very reduced forelimbs in favor of cranial killing power. It is possible that the Asian tyrannosaurins were in part or whole American imports, or the exchanges went both ways.

Left unanswered is why if elephantine size tyrannosaurids were extant on parts of Laramidia, did lesser taxa remain dominant in other regions into the early Maastrichtian, such as *Albertosaurus sarcophagus*? It appears, after all, that the Judith River Formation sported both rhino and elephant sized (Stein & Triebold, 2013) tyrannosaurids in the same place and time, both predators subsisting on a fauna of largely rhino sized ornithischians. Further south *T.*? *mcraeensis* (Dalman *et al*., 2024) and other giant tyrannosaurins (Wick, 2014) had more logically been taking on the whale sized titanosaurs.

The early Maastrichtian if not earlier *T.*? *mcraeensis* sported a low, long and subtle postorbital boss quite different from either the subtle discs extant in most other American and Asian tyrannosaurids including big albertosaurins, daspletosaurins and tarbosaurs, and the gracile alioramins, and very unlike the exceptionally prominent display discs of terminal TT-zone *T. rex*. While *T.*? *mcraeensis* may not have been directly ancestral to TT-zone tyrannosaurins (Longrich & Saitta, 2024), the condition of its display boss was an antecedent to the also low and long but much more garish spindle of early TT-zone *T. imperator*, followed by the complex evolution of the bosses proceeding upwards through the TT-zone. A driving factor in the evolution of the unusually high diversity of postorbital display bosses in *Tyrannosaurus* is likely to have been the dramatic broadening of the temporal box in the genus. Expanded in order to greatly boost the closing power of the jaw musculature by enlarging the volume of the portion of the skull containing the muscles, the lateral expansion of the aft skull had the side effect of laterally elongating the postorbital so that it was transversally much broader than the lacrimal to a degree not seen in other tyrannosaurids. That incidentally rendered the postorbital boss much more visible when the head was viewed from the front that in other tyrannosaurids. That in turn placed exceptional visual emphasis on the now uniquely prominent *Tyrannosaurus* boss, subjecting it to more sexual selective pressure that previously seen in the family, resulting in a greater variety of shapes. These intricate Darwinian evolutionary events are made apparent only in the context of the complex MTTH, the much more evolutionarily static ETRH is too simplistic to capture them. By the latest Maastrichtian TT-zone tyrannosaurids were limited to ~7 tonnes plus, dealing with triceratopsines, edmontosaurs, ankylosaurs in some cases exceeding a dozen tonnes (Paul, 2024a). At first they were apparently limited to *T. imperator* retaining the ancestral robust femur, a broad interfenestral pillar, two lower incisors, and long and low postorbital boss identification systems. This species disappeared in the middle of the TT-zone, at a time the rest of the fauna was also experiencing significant overturn (Scannella *et al*., 2014; Fowler, 2017; Paul *et al*., 2022; Paul, 2024a: similar to events in the Horseshoe Canyon Formation as *Albertosaurus* speciated (Stock *et al*., 2024)). The rapid anagenetic speciation of *Triceratops* being especially pertinent, changes in edmontosaurs and ankylosaurs may have also been operative. Whether via anagenesis from *T. imperator*, or cladogenesis, or both, also robust *T. rex* with one incisor and unique postorbital displays appeared, at about the same time as did *T. regina* also with one incisor suggesting but not establishing it formed a miniclade with *T. rex*, while exhibiting, a narrow interfenstral pillar, and a degree of postcranial gracility not before seen in giant tyrannosaurids relative to its size—note that there was no change in tonnage, the largest specimens of all three species being about 7. 5 tonnes (see Supplementary). The advent of two otherwise similar sympatric species of the same genus at the same time forced the evolution of yet new, divergent display bosses. This represented a splitting of the TT-zone inhabiting members of the genus into two body morphs, a robust and a gracile, that mimicked the similar disparity in form between earlier habitat sharing albertosaurins and daspletosaurins in which the former concentrated on fleet hadrosaurs and the latter on horned ceratopsids (Russell, 1970). Possibly *T. rex* with its more reinforced skull and skeleton remained most suited to hunt *Triceratops*, while *T. regina* was more adapted to engage with *Edmontosaurus* (Paul, 2016, 2024a, b; Paul *et al*., 2022). The coexistence of two elephant sized tyrannosaurids in the same habitat was made possible by the greatly expanded prey base—compared to the constricted Laramidia faunas—resulting from the reunification of the re-expanded great continent. Alternatively, the presence of two *Tyrannosaurus* species in the higher TT-zone was coincidental to that place and time, the normally distinct ranges of the two taxa happening to overlap in what are now the upper plains and associated Rockies, with one species dominating one portion of the continent, the other another portion of the united landmass, and not normally interacting. That the TT-zone was set between the western and eastern section of the continent suggests that any geographic segregation was east–west rather than north–south. If not for the sudden extinction of *T. rex* and *T. regina* due to dire K/Pg events, the two taxa may have continued to diverge, eventually evolving into a robust and a gracile genus. The simple ETRH cannot discern these intra *Tyrannosaurus* evolutionary probabilities and possibilities.

That is the American tyrannosaurid giants. The known fossils of the long armed two fingered baso-eutyrannosaurs of Appalachia do not exceed rhino masses. Perhaps surprising in view of the much greater extent of the region compared to Laramidia, but the sample size is very small. A lack of interchange with Laramidia and Asia is indicated by the apparent retention of less derived long arms that exceeded the length of the femur—although the condition of alioramin forelimbs is not yet known. If gracile alioramins were absent from Laramidia in the Campanian and early Maastrichtian suggests they did not migrate east across the Bering land bridge. Upon the reconnection of east and west lands with the recession of the interior seaway the relatively small but big armed eastern gracile tyrannosauroids were free to head west and intermingle and compete with the massive but tiny armed tyrannosaurins as some of those migrated east. The mid latitudes intermixing was aided by a benign subtropical climate over and around the TT-zone. It is possible that some or all the TT-zone non-tyrannosaurid species, especially those in the lower Hell Creek/Lance, had origins in Appalachia. Significantly different niche adaptations between the disparate forms from east on the one hand and west on the other allowed habitat coexistence, with the large armed tyrannosauroids competing most directly against the small armed juvenile *Tyrannosaurus*. That there seems to be a mix of nanotyrannos and stygivenators in the TT-zone implies competitive coexistence between those two gracile types as well. It was the extraordinary, recent, geographical/evolutionary event of the North American Interchange that resulted in a TT-zone packed with an extraordinary number of tyrannosaurid genera and species some titans and other graciles. TT-zone dinosaur diversity stemming from the east–west cross mixing appears to have been limited to the predators, the herbivore diversity being low compared to earlier in the Late Cretaceous (Paul, 2010, 2016, 2024a; Fowler, 2017; Condamine *et al*., 2021); there is no current evidence of non-tyrannosauroid dinosaurs making the journey west, but the Maastrichtian dinosaur fauna of Appalachia is very poorly known. The timing of the ability of dinosaurs to easily move east and west relative to the beginning of the deposition of the Hell Creek/Lance is not certain, so it is possible that baso-eutyrannosaurs had invaded the west and undergone evolution there significantly before deposition of the TT-zone. That the large arms outnumbered the juvenile small arms two to one in the TT-zone indicates that far from being archaic inferiors, the former were highly competitive vis-a-vis the growing *Tyrannosaurus*; although a higher death rate among maturing baso-eutyrannosaurs versus young juveniles may be a factor in the fossil disparity. This is logical. Juvenile *Tyrannosaurus* were compromise organisms whose characteristics—sans a fish like metamorphosis—were constrained by being in important respects miniature tyrant lizards stuck with the small hands of tyrannosaurids, and the stouter teeth, and less elongated lower hindlimbs of the *Tyrannosaurus* adult condition they were growing towards. Having evolved as specialized medium sized predators in Appalachia, the baso-eutyrannosaurs were likely better adapted for their body size, including their long hands, bladed teeth, and very long distal legs. They are likely to have provided competition never before seen by the juveniles of the Laramidia tyrannosaurids. On the other hand, the latter had the advantage of being better suited for gigantism after a long history of doing so in Asia and Laramidia, and the tyrant lizard reigned as the only and extreme megapredator of the TT-zone. Its juveniles proving able to survive the nontyrannosaurid tyrannosaurid invasion in sufficient numbers to allow the genus to speciate. Whether the baso-tyrannosaurs remained dominant over juvenile *Tyrannosaurus* is not clear because of the poor stratigraphic documentation of the specimens to date. Also experiencing competition from baso-eutyrannosaurs combined with the juvenile *Tyrannosaurus*—not just the latter as the ETRH posits—were the deinonychosaur predators. And medium and small sized prey were under the many tyrannosaur taxa assault. Tyrannosaur diversity in the region may have declined over time as competition winnowed down the competitors. Or, and again, the TT-zone may record overlapping portions of otherwise differing geographic ranges of taxa. Whether if not for the great extinction the basal tyrannosauroids or tyrannosaurins would have dominated the other perhaps to the exclusion of one is unknowable, although the tremendous power of the latter should have put them in a good position at least at the higher end of the size range. The less Darwinian ETRH does not provide a compelling, coherent account for these complex evolutionary patterns, and leaves the peculiar absence of immigrant eutyrannosaurs from the east without a compelling explanation. Nor does the fossil data support the concept of *T. rex* being a super predator that dominated the entire TT-zone at all sizes alone among eutyrannosaurs (as per Witton, 2022), it was undergoing competitive pressures within and from outside the genus as is the evolutionary norm.

Conclusion

The everything in the TT-zone is *Tyrannosaurus rex* hypothesis is permanently refuted, the large hands of small TT-zone tyrannosauroids leaving no practical scientific doubt regarding that basic matter. The follow up issue of how many tyrannosaur taxa were extant in the wake of the land bridging between the once isolated Laramidia and Appalachia starts with titanic *Tyrannosaurus* very probably consisted of several species. Based on current data they can be diagnosed as *T. rex*, *T. regina*, and *T. imperator*. The last being the earliest and retaining features present in more basal tyrannosaurids including earlier tyrannosaurin *T.*? *mcraeensi*s, and the first two late appearing contemporaries with *T. rex* sporting exceptionally vertical display bosses, and *T. regina* being remarkably gracile for a gigantic avepod. Paul *et al.* (2022) proposed that the evolution of sibling species within *Tyrannosaurus* was an example of a level of evolution subtler than seen in other dinosaurs including contemporary *Triceratops*. With the addition of the data of the visually vivid differences in the supraorbital bosses, the evolution of *Tyrannosaurus* species was not so understated after all—the data and analysis supporting multiple *Tyrannosaurus* species at least matches that for *Allosaurus*, and unless critics of the first are able to show otherwise, or show that the latter work is defective (same for species of *Daspletosaurus*), then opposition to multispecific *Tyrannosaurus* needs to cease. To illustrate the issue, the ETRH requires that researchers consider Scotty and Sue (Figs 2B, G, 6A, B) with the radically different display structures—much more divergent than in any other tyrannosaurid genus and in the rest of the family as a whole—be in the same species and that despite being from near opposite layers of the TT-zone. More scientifically productive will be investigation of the evolutionary and functional implications of the evolution of these species, including the remarkable reduction of skull and skeletal strength of gracile *T. regina*—did the weakening of the vertical cranial bars reduce biting power, and if so why? The small graciles were even more dramatically divergent, representing based on the limited information two currently observed genera—*Nanotyrannus* and *Stygivenator*—and numerous species. This fascinating mix, apparently representing the highest known tyrannosauroid diversity in a paleohabitat, appears to record the unusual circumstances of the mixing of once isolated faunas from east and west in a benign paleoclimate. Because all actual *Tyrannosaurus* juveniles are fragmentary, it is not currently possible to restore the ontogenetic, functional, and anatomical development of the genus.

It cannot be overemphasized that there is not the slightest item that is extraordinary about the MTTH in principle or the evidence when applied to TT-zone tyrannosaurs of all sizes. The giant intragenus species are easily visually identified by their highly distinctive cranial displays in the manner than humans regularly use to tell apart and designate species, and animals decide whether or not to have sex with one another. These are backed by exceptional proportional differences that also correlate with stratigraphic placement. The juveniles that are attributed to the tyrant king are in full accord with the normal growth patterns typical of amniotes and tyrannosaurids, leaving nothing unusual about that situation. The MTTH rests on a large preponderance of positive evidence. In evolutionarily improbable contrast the ETRH is filled with implausible, extraordinary hypotheses such as just one species among a genus sporting a high diversity of cranial displays far beyond that seen in other tyrannosauroids that could sexually confuse members of one species, atypically high variations in skeletal proportions that change over time, in a region undergoing a mixing of continental scale faunas, with the youngsters undergoing abnormal fish style growth modifications limited to nonamniotes and entirely unlike albertosaurins and tarbosaurs, and showcasing skulls that don't look like one another. Rather than being driven by positive affirming data, the ETRH is largely a negative criticism of the MTTH. A theory in search of justification by means that are biologically problematic if not impossible and consequently the opposite of parsimonious. The MTTH fits smoothly and naturally into a large body of fossil data. That data goes on the demonstrate that *T. rex* is not the only TT-zone wastebasket taxon, the MTASH subset of the MTTH goes on to show that *N. lancensis* too has ironically in some cases been a wastebasket taxon for the TT-zone non*Tyrannosaurus* fossils, many if not most of those not belonging to that genus and species, some being candidates for being *Stygivenator* and perhaps other genera (Longrich & Saitta, 2024).

Those who reject the basic conclusions herein cannot just address this work's contents and Paul *et al.* (2022) in compartmentalized isolation. They must further establish that the methods, data and results do not match those of noncontroversial examinations of noniconic amniote paleospecies, Chure & Loewen (2020), Danison *et al.* (2024) and Carr *et al.* (2017) being particularly pertinent examples. Or—as part of a broad review of the intragenus palaeospecies issue—show that the latter and similar efforts as well as this are defective and why. In other words, apply consistent standards to intragenus sibling palaeospecies determinations, including for *Tyrannosaurus*. This not being done by many to date stems it appears from the overly renowned status of *T. rex*. That has led to its status as a species—when it one way or another was a one species in a genus—being overly defended to the point of the demanded level of supporting evidence being elevated well above that regularly employed with uncontested palaeospecies. TT-zone tyrannosaur research needs to be normalized to the procedures being no less and no more rigorous, and biologically plausible, as for other fossil species.

Future research on the taxonomy of TT-zone tyrannosauroids is highly unlikely to dramatically overturn the basic conclusions herein, and cannot save the basic ETRH because of the big hands present among lesser specimens. It will be a matter of filling in the details as to the number of *Tyrannosaurus* species, and especially better understanding what appears to be a complex systematic situation with the non-*Tyrannosaurus* fossils. A complexity that seems startling because of the long failure to consider the implications of the End Cretaceous North American Interchange. Needing to cease is the automatic tendency of dinosaurologists to refer to the general taxon *Tyrannosaurus* as *T. rex* in a manner not applied to other palaeogenera—best to be scientifically consistent by using the latter tag only when it is necessary to be so specific, and other dinosaur taxa in the publication are likewise being referred to at their species level. For example, if an article persistently refers to *Triceratops* or *Tarbosaurus* with just those generic tags, then do the same with *Tyrannosaurus*, it being just another dinosaur.

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All Supplementary materials are available at:
https://doi.org/10.11646/mesozoic.2.2.1

Supplementary materials:
Supplementary Text—A presentation of the current data on the exceptionally diverse nontyrannosaurid eutyrannosaur and tyrannosaurini genera and species of western North America during the End Cretaceous North American Interchange
Supplementary figures—STFig1–8