RESEARCH ARTICLE

The Tyrant Lizard King, Queen and Emperor: Multiple Lines of Morphological and Stratigraphic Evidence Support Subtle Evolution and Probable Speciation Within the North American Genus *Tyrannosaurus*

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Abstract

All skeletal specimens of the North American dinosaur *Tyrannosaurus* and a number of trace fossils have been attributed to the single species: *T. rex*. Although an unusual degree of variation in skeletal robustness among specimens and variability in anterior dentary tooth form have been noted, the possibility of sibling species within the genus *Tyrannosaurus* has never been tested in depth in both anatomical and stratigraphic terms. New analysis, based on a dataset of over three dozen specimens, finds that *Tyrannosaurus* specimens exhibit such a remarkable degree of proportional variations, distributed at different stratigraphic levels, that the pattern favors multiple species at least partly separated by time; ontogenetic and sexual causes being less consistent with the data. Variation in dentary incisiform counts correlate with skeletal robusticity and also appear to change over time. Based on the current evidence, three morphotypes are demonstrated, and two additional species of *Tyrannosaurus* are diagnosed and named. One robust species with two small incisors in each dentary appears to have been present initially, followed by two contemporaneous species (one robust and another gracile) both of which had one small incisor in each dentary, suggesting both anagenesis and cladogenesis occurred. The geological/geographic forces underlying the evolution of multiple *Tyrannosaurus* species are examined. A discussion of the issues involving the recognition and designation of multiple morphotypes/species within dinosaur genera is included.

Keywords *Tyrannosaurus* · Theropod · Dinosaur · Paleospecies · Biostratigraphy · Cretaceous · Maastrichtian

Introduction

Because of its exceptional size, perceived predatory prowess, and curiously reduced forelimbs with just two fingers (Fig. 1), the charismatic *Tyrannosaurus* (Osborn, 1905) has ruled as the world's most popular Mesozoic dinosaur since its discovery, over a century ago (Hone, 2016). That the genus was apparently the only gigantic predator extant in the latest Maastrichtian of western North America at the catastrophic End Mesozoic Extinction has added to the mystique and importance of *Tyrannosaurus*. This fascination extends to many professional paleontologists. The great beast has been the focus of an outsized number of modern studies on its size, growth, locomotor performance, population dynamics, soft tissue preservation, and predatory capabilities (Paul, 1988, 2008; Carpenter, 1990; Molnar, 1991, 2008; Horner, 1994; Chin et al., 1998; Carpenter & Smith, 2001; Carrano & Hutchinson, 2002; Brochu, 2003; Carr & Williamson, 2004; Erickson et al., 2004; Sampson & Loewen, 2005; Schweitzer et al., 2007; Schweitzer et al., 2016; Happ, 2008; Holtz, 2008; Hutchinson et al., 2011; Persons and Currie 2011, 2016; DePalma et al., 2013; Myhrvold, 2013; Wick, 2014; Gignac & Erickson, 2017; Cost et al., 2019; Persons et al., 2019; Snively et al., 2019; Carr, 2020; Woodward et al., 2020; Bijiert et al., 2021; Marshall et al., 2021; Ullmann et al., 2021). In 2008, an entire multi-author technical book (Larson and Carpenter 2008) was dedicated to the one paleospecies *T. rex*, a rare event in the dinosaur literature.

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Fig. 1 *Tyrannosaurus* known bone profile-skeletals to same scale, bar equals 2 m. **A** *Tyrannosaurus rex* holotype (morphotype II) CM 9380 (6.5 tonnes). **B** *Tyrannosaurus rex*? RSM 2523.8 (7.8). **C** *Tyrannosaurus regina* (morphotype III) exBHI 3033 (7.5). **D** *Tyrannosaurus regina* holotype (morphotype III) USNM 555000 (6.1). **E** *Tyrannosaurus imperator* holotype (morphotype II) FMNH PR2081 (7.8). **F** *Tyrannosaurus* incertae sedis AMNH 5027 (6.8)

Despite the abundance of research directed towards this one genus, the assumption that all adult *Tyrannosaurus* specimens from the plains of Canada to the southwestern United States belong to the single species *T. rex* (Carpenter, 1990; Brochu, 2003; Carr & Williamson, 2004; Sampson & Loewen, 2005; Wick, 2014; Brusatte and Carr 2016; Persons et al., 2019; Carr, 2020; Woodward et al., 2020) has never been quantitatively and stratigraphically tested with a large sample. This includes studies on the status of small tyrannosaurid specimens as potential juvenile members of the genus *Tyrannosaurus* (Carr, 2020; Woodward et al., 2020) and studies that have sought to diagnose the distinction between *Tyrannosaurus* from other tyrannosaurid taxa at the generic level (Brochu, 2003; Carr & Williamson, 2004; Osborn, 1905; Paul, 1988; Sampson & Loewen, 2005; Wick, 2014). So widespread and ingrained is this assumption that footprints attributable to a Late Maastrichtian giant theropod have been assigned specifically to *T. rex* (Caneer et al., 2021), despite their location 1000 km from the nearest skeletal material adequate to be assigned to the genus. The presumption that *T. rex* is the sole member of its genus is well illustrated by how frequently it is both professionally and popularly referred to by both its generic and specific titles in the above references. Normally, just the genus name is used for Mesozoic dinosaurs, as per the cohabitants of *Tyrannosaurus*: *Ankylosaurus*, *Edmontosaurus* and *Triceratops*; sometimes the divergence of using just a genus title for one animal, and both the genus and species for another is seen in the same title (Happ, 2008).

For over a century, the species *T. rex* potentially being a de facto taxonomic waste basket was to a fair extent a consequence of available sample size, the number of reasonably complete *Tyrannosaurus* skeletons being much too small to sufficiently examine the issue. However, that situation of taxonomic stagnation due to specimen deprivation has dramatically improved since the late 1900s. An in-depth examination is now possible.

Variability Within *Tyrannosaurus "rex"*

It has long been recognized that there is considerable variation in the stoutness of adult *Tyrannosaurus* specimens (Carpenter, 1990; Larson, 1994; Larson & Frey, 1992; Molnar, 1991; Paul, 1988). Most notably, femora of similarly sized individuals range in robusticity to a degree that it is visually obvious (Larson, 2008a, b; Paul, 2016) (Figs. 1A–E, 2A–C, E). This femoral robustness usually correlates with the robustness of other skeletal elements (Fig. 2D, F; Larson, 2008a, b), and it has been suggested that these proportional divergences reflect sexual dimorphism (Paul, 1988 implicitly, explicitly Carpenter, 1990; Molnar, 1991; Carpenter & Smith, 2001; Larson & Frey, 1992; Larson, 1994, Larson, 2008a, b). Based in part on the report of soft female reproductive tissues found in a stout femur (Schweitzer et al., 2005, 2007), robust morphs have sometimes been interpreted as the females of the single species (Carpenter, 1990; Carpenter & Smith, 2001; Larson, 1994, 2008a, b). Two alternative possibilities attribute this difference in robustness to different ontogenetic stages (Brochu, 2003; Carr, 2020) or to simple individual variation (Carr, 2020; Mallon, 2017). A fourth option is that the variability of skeletal robusticity records the presence of distinct paleospecies (Larson, 2008a, b; Molnar, 1991; Paul, 1988, 2016).

Robustness is not the only variable trait that has been considered a possible indicator of multiple *Tyrannosaurus* species. Some specimens possess a single incisiform, most
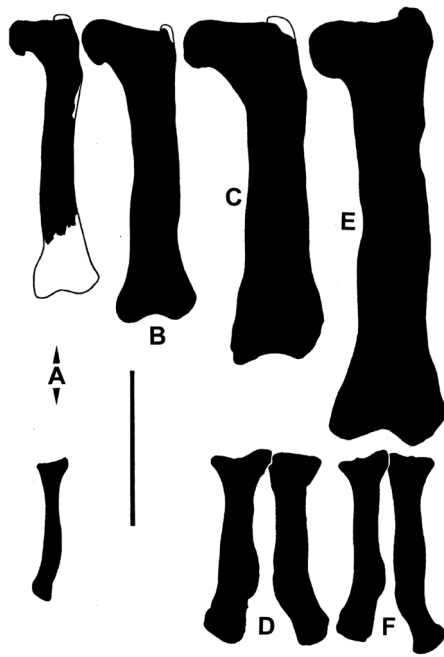
Fig. 2 *Tyrannosaurus* femora (top row) and metatarsals II (bottom row on left sides) and IV (on right sides) to same scale, bar equals 500 mm. **C** and **E** after Fig. 8.14 in Larson (2008a, b). **A** Gracile large juvenile *T. regina* (morphotype III) LACM 23845 (~1.5 tonnes). **B** Robust large juvenile *T.* incertae sedis USNM 6183 (~2.5). **C** Robust adult *T. rex* (morphotype II) BHI 6233 (~4). **D** Robust adult *T. rex* holotype CM 9380 (6.4). **E** Gracile adult *T. regina* exBHI 3033 (7.4). **F** Gracile subadult *T. regina* BHI 6230 (~3.7). Solid black is preserved bone, masses with an ~ indicator are scaled from volumetric estimates of more complete specimens
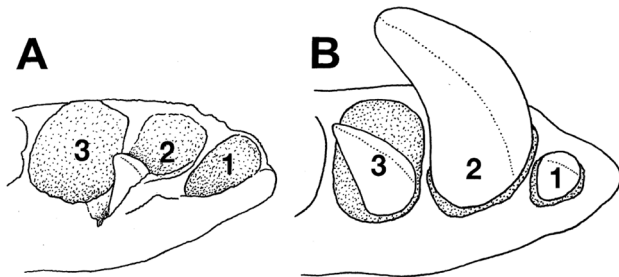

Fig. 3 *Tyrannosaurus* anterior left dentaries in dorsomedial view showing differing proportions of the first three tooth sockets. **A** *Tyrannosaurus imperator* (morphotype I) "Samson" with two small anterior-most incisors (after Fig. 8.5 in Larson, 2008a, b). **B** *Tyrannosaurus rex* (morphotype II) holotype CM 9380 with one small anterior-most incisor (after Fig. 8.4 in Larson, 2008a, b)

anterior dentary tooth with a D-shaped cross-section that is substantially smaller than the next dentary tooth in the series (Fig. 3B; Larson, 2008a, b incl. Bakker therein). Others possess two such incisiform dentary teeth (Fig. 3A).

Over geological time, non-speciation-related variation within a species can be close to static (Gould, 2002; Hunt

et al., 2015; Long et al., 2020). So, if significant morphological change is tracked within a genus over geologic time (i.e., across a stratigraphic sequence), that is potential evidence for evolution at the species level. The crucial role that stratigraphy plays in species-level dinosaur taxonomy has been demonstrated by a number of recent studies, which have shown perceived sexual dimorphs actually represent distinct species separated by stratigraphic level and time (Gates et al., 2012; Mallon, 2017, 2019; Paul, 2016; Ryan & Evans, 2005; Scannella et al., 2014). In particular, it had been widely speculated that two morphs of *Triceratops*, which lived over the same time span as *Tyrannosaurus* and were initially distinguished in part by the robustness of the snout, denoted sexual dimorphism (Forster, 1996). However, stratigraphic research has helped show that these two morphs record the evolution of *Triceratops horridus* into *Triceratops prorsus* perhaps via an intermediate species (Fowler, 2017, 2020; Paul, 2016; Scannella et al., 2014).

Dating issues have prevented determination of the exact geological time span within which specimens attributed to *T. rex* are preserved. Time spans of the deeper Lancian sediments that contain *Tyrannosaurus* have ranged from 0.7 to significantly over 1.5 million years, with no firm resolution on hand (Difley, 2007; Johnson, 2008; LeCain, 2010; Wilson et al., 2010; Scannella et al., 2014; Fowler, 2017, Fowler, 2020). A fragmentary specimen from the Texas–Mexican border sometimes attributed to the genus/species appears to add another 0.5 to 1 million years to the taxon (Wick, 2014), for a potential total span of 2–2.5 million years, Marshall et al. (2021) suggest the species was extant for 1.2 to 3.6 million years. The contemporaneous elephant-sized dinosaur *Triceratops* appears to have produced at least two and probably more sequential chronospecies, sporting skull morphologies disparate enough to be visually distinguishable, over the same temporal span (Fowler, 2017, 2020; Scannella et al., 2014). This suggests it is at least reasonable to contemplate the possibility that the *Tyrannosaurus* lineage was similarly diverse over the same time span. For a modern comparison, DNA analysis indicates that the split between the lion (*Panthera leo*) and leopard (*Panthera pardus*) clade occurred only 1–1.5 million years ago (Burger et al., 2004). Of course, speciation rates are highly variable across groups (Gould, 2002; Hunt et al., 2015; Long et al., 2020). A span of 0.7–2.5 million years does not firmly mandate the presumption of speciation within *Tyrannosaurus*. However, it is a reasonably long period over which a genus of large bodied terrestrial carnivore can be hypothesized to have experienced species-level evolution, especially at a grade more subtle than that recorded in *Triceratops*.

Similarly, the possibility of two concurrent *Tyrannosaurus* species cannot be dismissed on ecological grounds. Other well-sampled Mesozoic ecosystems contain multiple genera of large theropods. The Upper Jurassic Morrison

Formation had contemporaneous allosaurs, megalosaurs, and ceratosaurs; the Lower Cretaceous Bahariya Formation had abelisaurs, carcharodontosaurids, megaraptorans and spinosaurs; and the Upper Cretaceous Dinosaur Park Formation had the similarly large tyrannosaur genera *Daspletosaurus* and *Gorgosaurus* (Carr & Williamson, 2004; Currie, 2003; Paul, 1988, 2008, 2016; Russell, 1970; Salem et al., 2021).

Competing Explanations and Predictions

The four hypotheses for the variation seen within the genus *Tyrannosaurus* each postulate differing assumptions regarding the degree of this variation, the relative abundance of each morphotype, and each morphotype's temporal and geographic ranges. This permits the postulation of a corresponding set of predictions.

The individual variation hypothesis predicts that the extent of variability in *Tyrannosaurus* femoral robustness should not exceed that observed in other large-bodied theropod species, while the multiple-species hypothesis predicts that this variability can be greater. Failure to demonstrate exceptional variation would imply that the differential observed in *Tyrannosaurus* is consistent with that expected within a single species. In that case, variations in robustness of *Tyrannosaurus* specimens provides no support for the multiple species hypothesis, although that form of variation might still relate to ontogenetic changes or to sexual dimorphism, because a similar pattern may have been present among other theropods (although dimorphism has not been firmly demonstrated in the group Carr, 2020; Mallon, 2017; Saitta et al., 2020). Although it is possible that the extent of individual variation could (for whatever reason) be unusually great in *T. rex*, favoring such an interpretation requires arguing for exceptionalism, all the more so if the degree of *Tyrannosaurus* variability is found to exceed that of other tyrannosaurs, so the individuality hypothesis would be inferior. Because exceptional variation, if established to have existed, is not particularly predicted by either the sexual dimorphism or ontogenetic hypotheses, then its presence favors speciation as the most likely explanation, although sexual dimorphism can be variable even within closely related groups. The appearance of extensive proportional differences early in ontogeny can be compatible with sexual dimorphism if sexual reproduction began shortly after the divergence in proportions began.

The ontogenetic explanation for exceptional robustness predicts that the maximum extent of stoutness appears late in ontogeny, as individuals emphasize skeletal strength as an aspect of maturity. If ontogeny is the driving factor, robust specimens should be predicted to be primarily or entirely limited to the very large end of the size range, and the largest specimens should rarely, if ever, be gracile. If instead there is considerable variation in robustness starting well before adult size is reached, then robusticity cannot simply be considered a result of maturity—all the more so if gracility is found to be frequently present among large specimens.

The presence/absence of one or two D-shaped most anterior incisiform dentary teeth is a discrete trait that offers a possible independent validation of the hypothesis that skeletal robusticity denotes compound species. The multiple-species hypothesis predicts that the presence of the extra incisiform dentary tooth corresponds with either the robust/gracile morphs and that absence of the extra incisiform dentary tooth corresponds with the opposite morph. While it is conceivable that the extra incisor-like dentary tooth is a sexually dimorphic trait, its sex-specific role is not intrinsically obvious. As such, the sexual dimorphism hypothesis makes no prediction regarding any correlation (or lack thereof) between the extra D-shaped incisiform tooth and skeletal robusticity.

If two or more similar species were present in a manner that represents subtle evolutionary change over time, the fossil record should show some level of temporal/spatial nonuniformity. This could include the robust/gracile and/or the D-shaped incisiform dentary tooth morphs not overlapping in time and/or place. This could also be manifest if a large disparity exists in numbers, in which one form strongly outnumbers the other at given stratigraphic levels and/or in specific geographic regions. If two forms do overlap across a wide temporal/stratigraphic range, evidence of a progressive shift in the predominance of one form over the other would also favor species-level evolution. The sexual dimorphism hypothesis predicts temporal/spatial uniformity, with the number of each form being roughly equivalent overall (perhaps with the female form somewhat more numerous) and both forms consistently found together over the entire span of their existence. The ontogenetic and individual variation hypotheses also predicts that the forms will be found together over the entire stratigraphic span, but not necessarily in equal numbers.

Materials and Methods

To verify that a degree of robusticity or gracility is consistent throughout individual specimens, (rather than variable across different skeletal elements of the same individuals), a suite of anatomical measurements was taken from a sample of *Tyrannosaurus* specimens (n = 38), concerning the maxillae, dentaries, humeri, ilia, femora, and metatarsals 2 and 4. Robustness measurements are by Persons and Currie (in part in Persons & Currie, 2016; Persons et al., 2019; Currie pers. comm.), Paul, P. Larson (2008a, b in which the mode of measurements is illustrated in Fig. 8.9; pers. comm.), Brusatte et al. (2009), Sereno et al. (2009), Brochu

(2003), Russell (1970), Osborn (1905), and Loewen (pers. comm. for *Allosaurus*). When metatarsal circumferences could not be measured medio-lateral diameters were substituted. Bone measurements and resulting ratios are listed in Tables 1 and 2.

There are two large juvenile tyrannosaurid postcranial specimens (USNM 6183 and LACM 23845) that can be confidently assigned to *Tyrannosaurus*. The smaller BMRP 2002.4.1 may be a juvenile of the genus (Carr, 2020; Carr & Williamson, 2004; Woodward et al., 2020) or a distinct taxon (Larson, 2008a, b), but this study does not directly address that question (although the results of this work may have implications for future work on the issue). Because juveniles are less likely to exhibit sexual dimorphism and because allometry with growth significantly alters theropod element proportions (Currie, 2003; Persons & Currie, 2016), only near adult and adult specimens whose femoral length is at least 80% of the maximum observed in the sample are statistically assessed herein (Table 1).

Most applications of statistics in the field of dinosaur paleontology necessarily encounter the issue of small sample size. Although *Tyrannosaurus* has a comparatively large number of specimens available for consideration in the context of large Mesozoic vertebrates, the sample size is still on the small side in the context of general statistics. For this reason, the tests used in this paper were specifically chosen to be applicable to small sample sizes, are generally nonparametric (requiring no assumption of normal distribution), and are as robust as possible. Still, some uncertainty exists when working with such small samples.

Femoral proportions are used as the primary assessment of specimen robusticity, because the femur's critical role in supporting a biped's entire body mass makes its proportions a key indicator of body robustness. Further discussion of why femoral proportions are a suitable proxy for overall robusticity can be found later in the paper. In order to convincingly divide the array of femoral ratios into distinctive morphotypes, clustering algorithms were used. Clustering algorithms were chosen precisely because they make few assumptions about the data. They simply take the values and group them based on the rules of the algorithm, which reduces the chance of researcher bias and places no requirements on sample size or distribution.

The length/circumference ratio of each measurable femur was calculated manually, then input as a dataset into MATLAB (R2020b). Both a fuzzy C-means clustering algorithm and a K-means clustering algorithm were applied to the data (n = 20). The K-means clusters were generated using first a Cityblock distance metric and then a squared Euclidean metric.

Two different measures of femoral gracility were used in subsequent tests. The basic femoral ratio was calculated by dividing the measured length of a given femur by its measured circumference. This provided a simple, unitless number ranging from 2.063 to 2.673 that allowed easy comparison of femoral robusticity, with smaller values indicating higher robusticity. The other measure was a form of residual score, intended to indicate the degree of variation from an expected ratio while excepting the effects of size. This was generated by first graphing the femur length vs. circumference of all measurable specimens (n = 24, Fig. 4E). Then, a line of best fit was generated using Excel, and this was used to calculate a "predicted circumference" for each femur length. This was done by plugging each length value into the regression equation and solving to obtain a circumference value. The predicted circumference was then subtracted from the femur's actual circumference. That value was divided by the predicted circumference and then multiplied by 100. This generated a range of values between −11.904 and 14.342; negative values indicate a smaller actual circumference than predicted, and the femur is considered gracile. Positive values likewise indicate a robust femur. In mathematical notation, the residual score was calculated as follows: [(measured circumference − predicted circumference)/predicted circumference] × 100.

To test whether the degree of variation observed in *Tyrannosaurus* exceeds that expected of a single large bodied theropod species, data was collected from a sample of *Allosaurus* specimens from the Cleveland-Lloyd Quarry (n = 13) and from specimens of the tyrannosaurids *Albertosaurus* (n = 9), *Daspletosaurus* (n = 6), *Gorgosaurus* (n = 9), and *Tarbosaurus* (n = 10) (Table 2; Fig. 4A–D). The cumulative tyrannosaurid sample spans approximately 10 million years and two continents. For the purposes of this study, it is assumed that these other theropod taxa each represent a single species; however, *Daspletosaurus* likely consists of at least a Canadian and an American pair of species (Carr et al., 2017), and the robust Canadian examples may in turn contain more than one species (Carabajal et al., 2021). The *Allosaurus*, *Tyrannosaurus*, and tyrannosaurid (*Albertosaurus*, *Daspletosaurus*, *Gorgosaurus* and *Tarbosaurus*) samples were plotted, and a best fit logarithmic equation was derived for each dataset. Residuals were calculated and expressed as a variation percentage.

For a specimen to be classified as possessing two slender anterior incisiform dentary teeth, there needs to be sufficient disparity between the diameter of the second and third dentary teeth. This value is set at a ratio of the third tooth being 1.2+ times larger across the base than the second. To test for a correlation between femoral robusticity and the number of incisiform dentary teeth, a Mann–Whitney U Test (n = 22) was run using MATLAB (R2020b).

For the purposes of this analysis, the northerly Lancian upper Maastrichtian formations that contain both *Tyrannosaurus* and *Triceratops* specimens are collectively termed the TT-zone, which straddles the Canadian/United States border region east of the Rockies (Fig. 5). The lack of datable volcanic

Table 1 Femur lengths and circumferences in mm, and resulting ratio, for entire theropod sample, plus known stratigraphic levels within TT-zone, and status as robust, gracile or borderline as determined by overall skeletal analysis for entire *Tyrannosaurus* sample, with additional calculations (variation percentage, ratio ranges, ratio averages and medians) for the large specimens of each taxon at the bottom of each taxon's dataset

		Level	Gracile or robust	Femur length	Femur circ	Femur ratio
Tyrannosaurus	exBHI 3033 Stan	h	g	1350	505	2.67
	Z-rex/Samson	l	r	1343	560	2.4
	RSM P2523.8 Scotty	h	r?	1333	590	2.26
	FMNH PR2081 Sue *T. imperator* type	l or m	r	1321	580	2.28
	BHI 6248 Cope	l	r	1300	630	2.06
	TMT v222 Lee	l	b	1295	545	2.38
	MOR 1128 G-rex	l	r	1280	580	2.21
	USNM 555000 Wankel *T. regina* type	h	g	1280	520	2.46
	CM 9380 *T. rex* type	h	r	1269	534	2.38
	MOR 980 Peck's Rex/Rigby	h	g	1232	483	2.55
	RMDRC 2002.MT-001	na	r	1220	580	2.1
	HMN MB.R.91216 Tristan	l	b	1220	520	2.35
	TMP 81.6.1 Black Beauty	h	g	1210	460	2.63
	LL 12823	m	g	1200	467	2.57
	BHI 6242 Henry	na	r	1189	512	2.3
	LACM 150167 Thomas	h	g	1181	470	2.51
	BHI 6232	m	r	1180	527	2.24
	BHI 6435	h	r	1180	512	2.3
	BHI 6436	h	r	1170	530	2.21
	RGM 792.000 Trix	l	r	1170	529	2.21
	MOR 1125 B-rex	l or m	r	1150	515	2.23
	BHI 6233	h	r	1110	515	2.16
	BHI 6230 Wy-rex	h	r	1100	494	2.23
	MOR 009 Hager	h	b	1100	469	2.34
	USNM 6183	na	r juv	990	430	2.32
	LACM 23845	h	g juv	~900	305	~2.95
	LACM 23844	h	b			
	BHI 4100 Duffy	h	r?			
	BHI 4182	l	?			
	BHI 6231	m	R?			
	MOR 008	na	?			
	AMNH 5027	?	?			
	NHMUK R7994 *D. imperiosus* type	m	r?			
	SDSM 12047	l	?			
	TCM 2001.90.1 Bucky	l or m	R			
	UCMP 118742	na	g?			
	NMMNH P-3698	l	r?			
	n 24 femora 1100+ mm all levels					Variation 30%
						Range 2.06–2.67
						Median 2.37
						Average 2.27
	n 12 femora 1100+ mm h level					Variation 24%
						Range 2.16–2..67
						Median 2.42
						Average 2.39
	n 8 femora 1100+ mm					Variation 17%
						Range 2.06–2.4

Table 1 (continued)

		Level	Gracile or robust	Femur length	Femur circ	Femur ratio
						Median 2.23
						Average 2.27
Nanotyrannus?	BMRP 2002.4.1			720	245	2.34
	BHI-6437			657		
Tarbosaurus	MPC-D107/02			1120	480	2.33
	MPC-D PJC2012.48			1050	417	2.52
	PIN 551-2			965	390	2.47
	MPC-D100/63			960	410	2.34
	ZPAL MgD-1/109			800	300	2.67
	CMMD 1			785	273	2.88
	MPC-D100/61			780	290	2.69
	Pohl			599	215	2.79
	MPC 970716KmT			564	203	2.78
	MPC D107/07a			303	90	3.37
	n 4 femora 900+ mm					Variation 8%
						Median 2.43
						Average 2.42
Raptorex?	LH PVi8			338	85	3.98
Alioramus	MPC-D 100/1844			560	170	3.29
Alectrosaurus	MPC-D 100/51			616	216	2.85
Daspletosaurus	AMNH 5438			1005	395	2.5
	UALVP 11			1000	415	2.41
	UALVP 52981			980	330	2.97
	TMP 2001.36.1			960	382	2.51
	FM PR308 (AMNH 5434)			940	370	2.54
	MOR 590			865	335	2.58
	n 6 femora 800+ mm					Variation 23%
						Median 2.69
						Average 2.59
Albertosaurus	ROM 807			1020	355	2.87
	TMP 1982.13.30			1008	380	2.65
	AMNH 5218			954	310	3.08
	TMP 1981.10.1			940	305	3.08
	MOR 553			912	339	2.69
	AMNH 5235			870	314	2.77
	TMP 1999.50.52			780	280	2.79
	CMN 11315			680	214	3.18
	TMP 1999.50.19			490	200	2.45
	n 6 femora 800+ mm					Variation 16%
						Median 2.87
						Average 2.85
Gorgosaurus	CMN 2120			1040	378	2.75
	USNM 16754			1015	364	2.79
	CMN 350			965	385	2.51
	CMN 11593			940	320	2.94
	TMP 94.12.602			920	330	2.79
	TCM 2001.89.1			830	296	2.8
	ROM 1247			765	266	2.88
	TMP 91.36.500			645	191	3.38
	AMNH 5423			605	194	3.12

Table 1 (continued)

		Level	Gracile or robust	Femur length	Femur circ	Femur ratio
	n 6 femora 800+ mm					Variation 17%
						Median 2.71
						Average 2.76
Dasp+Alber+Gorg						Variation 23%
Allosaurus	UMNH 7889			836	320	2.61
	UMNH 7912			785	302	2.6
	UMNH 7890			755	290	2.6
	UMNH 7882			750	295	2.54
	UMNH 7911			660	239	2.76
	UMNH 7884			656	253	2.6
	UMNH 7883			637	242	2.63
	UMNH 7891			608	221	2.75
	UMNH 7885			593	226	2.62
	UMNH 6453			585	217	2.7
	UMNH C-52			565	195	2.9
	UMNH 7899			558	189	2.95
	UMNH 12231			551	209	2.64
	n 5 femora 660+ mm					Variation 9%
	n 10 femora 585+ mm					Variation 9%
	n 14 femora all					Variation 16%

Each specimen listed in order of declining femur length within a given taxon, except for those *Tyrannosaurus* lacking the element. All the *Tyrannosaurus* specimens available for analysis are included in this table for a quick look at their stratigraphic level and assessed robusticity or gracility

horizons makes temporal correlation of TT-zone sediments imprecise, as does the sloping time-transgressive nature of the bases of the Hell Creek and Lance formations, which is associated with the progressive regression of the interior seaway to the east (Johnson, 2008). However, confident placement of 29 *Tyrannosaurus* specimens into the categorical stratigraphic positions of "lower", "middle", and "upper" sections of the TT-zone is possible based on archival and published field notes (Table 1, Supplementary Information; information sources on the stratigraphic level of the specimens is led by Larson, 2008a, b; amended by Stein, 2019a, b, supplemented and in a few cases corrected by Larson pers. comm., and Kaskes et al., 2016, Carr, 2020). No scale finer than these three broad stratigraphic divisions is herein considered. The Late Cretaceous stratigraphic correlations in Fowler (2017) and Dean et al. (2020) were too limited in geography and too coarse temporally to be of use for this analysis. The laterally modest portion of the Montana Hell Creek meticulously detailed in Scannella et al. (2014) and Fowler (2020) are of limited utility for assessing *Tyrannosaurus*, because they geographically span only a small portion of the TT-zone and incorporate only a small number of the total specimens. The Canadian TT-zone formations did not begin forming as early as the Hell Creek and Lance and are broadly equivalent to the upper of those two formations in the case of the Frenchman, and the upper and perhaps at least part of the middle in the case of the Scollard

(Catuneanu et al., 2000; Brown et al., 2011; Fowler, 2020; Roloson et al., 2021; see further discussion in Supplementary Information). To test for increasing gracility over time, two Mann–Whitney U Tests were run between specimens found in the lower TT-zone and the upper TT-zone (n=19).

Most *Tyrannosaurus* specimens that are sufficient to be confidently assessed as robust or gracile are from a relatively small area of eastern Montana, eastern Wyoming, the western Dakotas, southern Alberta and southern Saskatchewan (Fig. 5). There is insufficient data from the poorly preserved specimens further to the southwest and from other regions of North America. As such, no hypothesis regarding long-range geographic distributions of potential *Tyrannosaurus* species can be tested at this time.

This paper follows the examples of determining and diagnosing dinosaur paleomorphospecies presented in recent decades. As further detailed in Supplementary Information, standards are not consistent and do not require overwhelming evidence over the alternatives. This is because of a number of practical reasons involving the indefinite nature of species and even more so paleospecies, and because the data and analytical circumstances differ tremendously from one paleogenus to another. For example, there are recently published large dinosaur and other vertebrate paleospecies sharing the same paleohabitat distinguished by a single character. In view of those factors, and that a number of
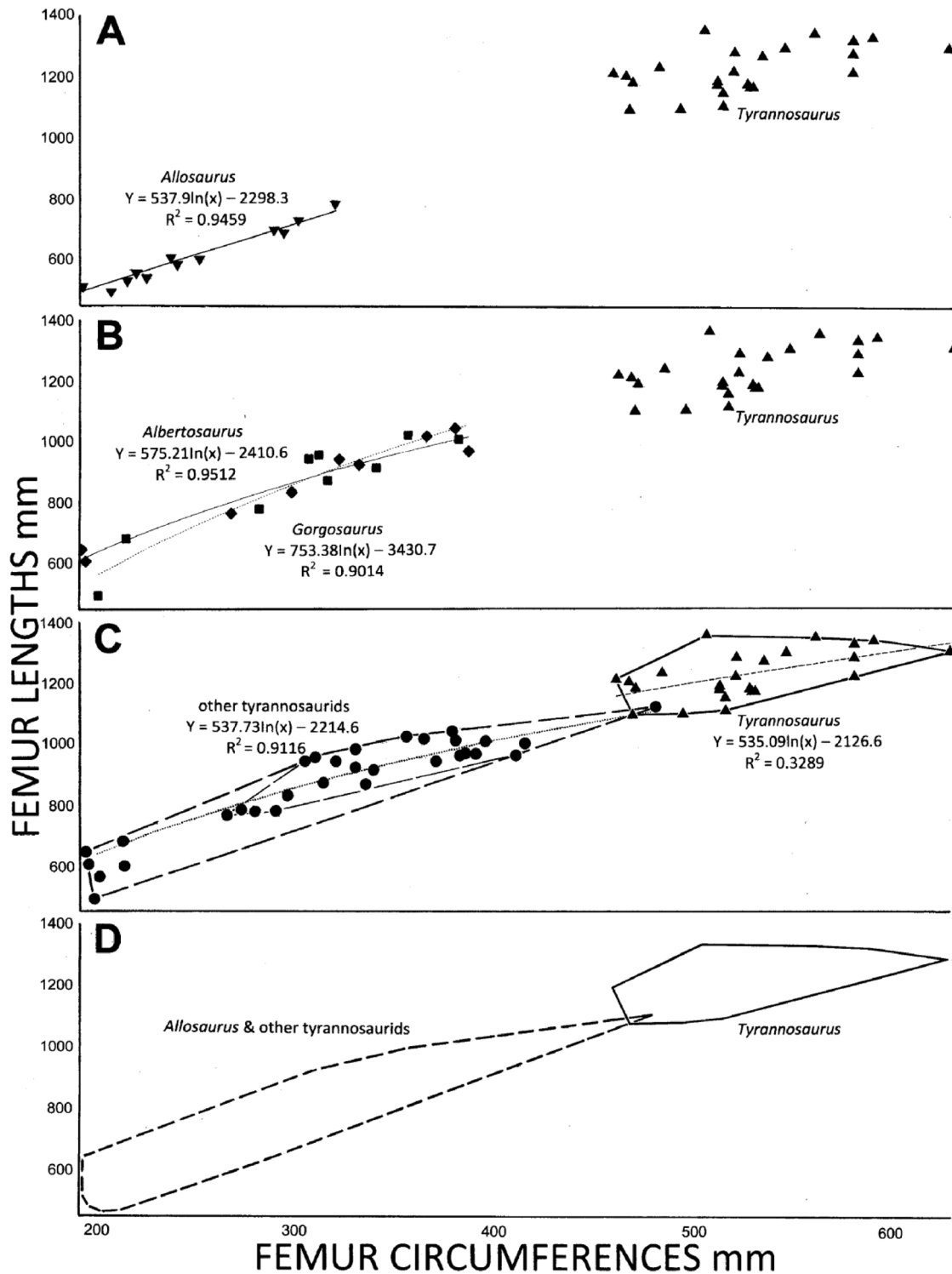
Fig. 4 Femoral proportions and ratios with statistical results. **A–D** Circumferences versus lengths with best fit curves and/or least area polygons, the large *Tyrannosaurus* data is included in all these plots, higher placement on plots indicates higher gracility. **A** *Allosaurus*. **B** *Gorgosaurus* (squares), *Albertosaurus* (diamonds). **C** All large *Tyrannosaurus* and all tyrannosaurids aside from those from the TT-zone, the smaller of the two polygons for the latter excludes specimens with femora below 250 mm long. **D** All large *Tyrannosaurus* and all other sampled theropods. **E–H** Lengths versus circumferences with best fit curves for all large *Tyrannosaurus* and the three species, higher placement on plots indicates more robusticity. **I** and **J** Femur proportional ratios and C-means and K-means analyses: note that these plots represent one-dimensional data on a two-dimensional coordinate plane, which is why the x and y axes are the same and the data follows a perfect y = x line; not an error in application of the clustering algorithms, it is the way the graphics software defaults to a two-dimensional plot in all cases
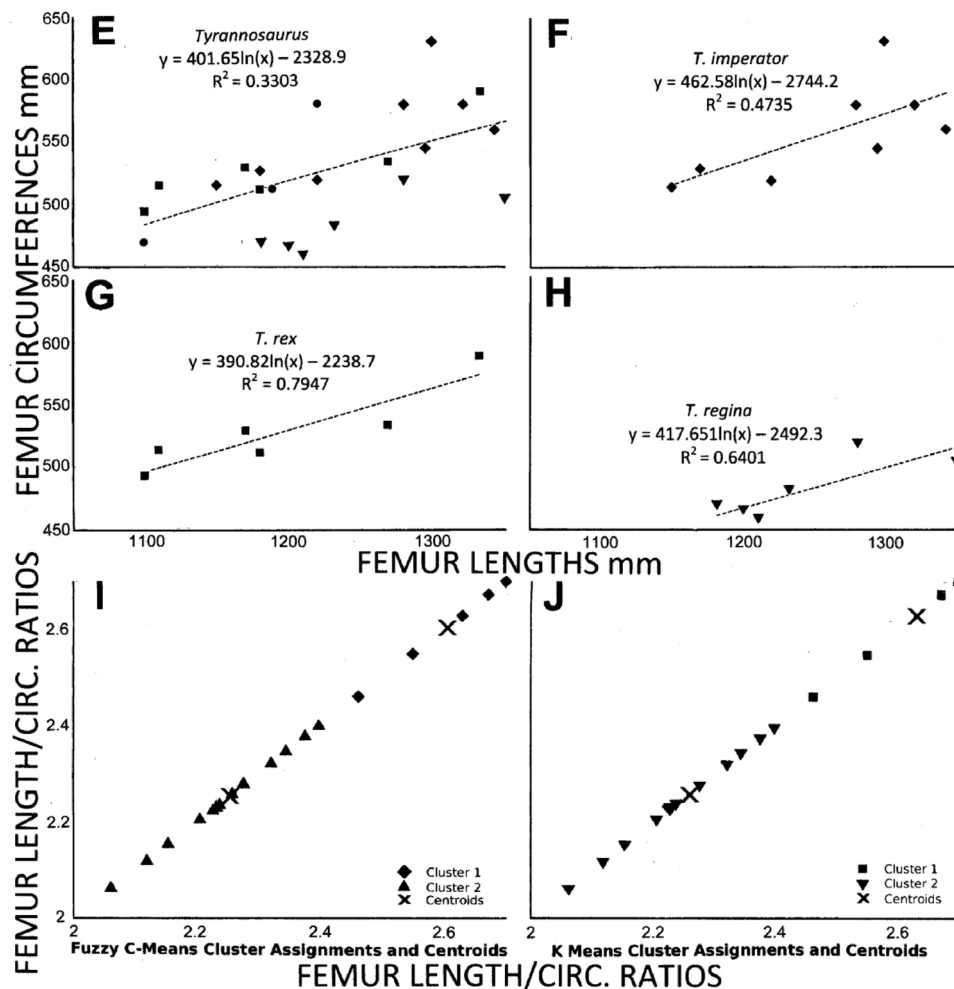
Fig. 4 (continued)

Mesozoic ecosystems contain multiple taxa of large theropods as listed previously, neither the single or multiple species hypotheses should be presumed correct unless one is shown to be superior, based upon the preponderance of the available evidence. The factors for and against multiple TT-zone *Tyrannosaurus* species are tabulated in Table 3.

All data generated or analyzed during this study are included in this published article (Tables 1 and 2) and its Supplementary Material Files.

Results

Skeletal Robusticity is Consistent Within Specimens But is Not Correlated with Absolute Size and Presumed Maturation

In the analysis of the bimodality of femoral proportions, the fuzzy C-means clustering algorithm and the K-means

clustering algorithms (both those utilizing a first Cityblock distance and then a squared Euclidean metric) generated identical groups (Fig. 4I, J). In all cases, the largest member of the first cluster is 2.398 and the smallest member of the second cluster is 2.462. This supports the designation of those specimens with femur ratios greater than 2.4 as gracile, and those with ratios less than that as robust.

Within about three quarters of the 16 *Tyrannosaurus* specimens with more than one element that can be proportionally assessed, most or all skeletal elements consistently exhibit robust, or borderline, or gracile dimensions, affirming that the proportional divergences represent a reasonably consistent morphological reality. This does not constitute justification for dividing the specimens into two categories (that was supported by the clustering algorithms), but rather is an indication that femur size is a reliable proxy for overall skeletal robusticity. Notably, this holds true for all 11 mature specimens that include a femur and at least one other assessable element. All five specimens with at least six measurable

Table 2 Measurements in mm and ratios for *Tyrannosaurus* humeri, ilia, metatarsals 2 and 4, maxillae, dentaries, and dentary teeth 2 and 3, with additional calculations

Tyrannosaurus	Hum Leng	Hum Circ	Hum Ratio	Ilium Leng	Ilium Depth	Ilium Ratio	Meta2 Leng	Meta2 Circ	Meta2 L/C Ratio	Meta2 Diam	Meta2 L/D Ratio
BHI 3033				1540	585	2.63	595	280	2.13	69	8.6
Z-rex					515	3	610	305	2		
RSM P2523.8				1545							
FMNH PR2081	390	185	2.11	1525	608	2.51	584			78	7.49
BHI 6248											
TMT v222											
MOR 1128											
USNM 555000	375	162	2.31	1470	513	2.86	585	295	1.98		
CM 9380	330	145	2.28	1515	~530	~2.85	615				
MOR 980	362	165	2.19	1397	483	2.89	597	232	2.57	89	6.91
RMDRC 2002											
HMN MB.R.91216											
TMP 81.6.1	302	150	2.01								
LL 12823											
BHI 6242											
LACM 150167											
BHI 6232											
BHI 6435											
BHI 6436											
RGM 792.000											
MOR 1125											
BHI 6233											
BHI 6230	330	145	2.28				600	272	2.21	64	9.38
MOR 009				1180	407	2.9	540			70	7.71
USNM 6183											
LACM 23845							465			48	9.69
LACM 23844							575			75	7.67
BHI 4100											
BHI 4182											
BHI 6231	360	172	2.09								
MOR 008											
AMNH 5027				1448	470	3.08					
NHMUK R7994											
SDSM 12047											

Table 2 (continued)

Tyrannosaurus	Hum Leng	Hum Circ	Hum Ratio	Ilium Leng	Ilium Depth	Ilium Ratio	Meta2 Leng	Meta2 Circ	Meta2 L/C Ratio	Meta2 Diam	Meta2 L/D Ratio
TCM 2001.90.1				1275	490	2.6	550	267	2.06	74	7.43
UCMP 118742											
NMMNH P-3698											
Range			2.01–2.31			2.51–3.08			1.98–2.57		6.91–9.69
Median			2.16			2.8			2.28		8.3
Average			2.18			2.81			2.16		8.11

Tyrannosaurus	Meta4 Leng	Meta4 Circ	Meta4 L/C Ratio	Meta4 Diam	Meta L/D Ratio	Max Leng	Max Depth	Max L/D Ratio	Dent Leng	Dent Depth	Dent L/D Ratio
BHI 3033	600	247	2.43			740	378	1.96	880	151	5.83
Z-rex	635	280	2.27			811	434	1.87	901	176	5.12
RSM P2523.8											
FMNH PR2081	621			83	7.48				954	189	5.05
BHI 6248											
TMT v222											
MOR 1128											
MOR 555	605	253	2.39			824	408	2.02	879	151	5.82
CM 9380	600			87	6.9	690	378	1.83	850	178	4.78
MOR 980						627	277	2.26	843	164	5.14
MT 2002											
HMN MB.R.91216											
TMP 81.6.1						667	304	2.19	705	131	5.38
LL 12823											
BHI 6242											
LACM 150167											
BHI 6232											
BHI 6435											
BHI 6436											
RGM 792.000											
MOR 1125						610	324	1.88	699	129	5.42
BHI 6233											
BHI 6230	625	238	2.63	87	7.18						

Table 2 (continued)

Tyrannosaurus	Meta4 Leng	Meta4 Circ	Meta4 L/C Ratio	Meta4 Diam	Meta L/D Ratio	Max Leng	Max Depth	Max L/D Ratio	Dent Leng	Dent Depth	Dent L/D Ratio
MOR 009	560			67	8.36						
USNM 6183											
LACM 23845											
LACM 23844						658	303	2.17	883	168	5.26
BHI 4100									789	164	4.81
BHI 4182											
BHI 6231											
MOR 008						664	322	2.06	836	171	4.89
AMNH 5027						680	345	1.97	850	135	6.3
NHMUK R7994									941	182	5.17
SDSM 12047											
TCM 2001.90.1	565	263	2.15								
UCMP 118742						754	363	2.08			
NMMNH P-3698											
Range			2.15–2.63		6.9–8.36			1.83–2.26			4.81–5.83
Median			2.39		7.63			2.05			5.54
Average			2.43		7.48			2.02			5.31

Tyrannosaurus	2nd Dentary tooth base diameter	3rd Dentary tooth base diameter	Hum Ratio	Number of incisors
BHI 3033	60	56	1.07	1
Z-rex	54	33	1.64	2
RSM P2523.8	48	38	1.26	b
FMNH PR2081	50	35	1.43	2
BHI 6248				
TMT v222				
MOR 1128				
USNM 555000	56	52	1.08	1
CM 9380	54	55	0.98	1
MOR 980	51	52	0.98	1
MT 2002				
HMN MB.R.91216	68	46	1.48	2
TMP 81.6.1	50	44	1.14	1
LL 12823				

Table 2 (continued)

Tyrannosaurus	2nd Dentary tooth base diameter	3rd Dentary tooth base diameter	Hum Ratio	Number of incisors
BHI 6242				
LACM 150167				
BHI 6232				
BHI 6435				
BHI 6436				
RGM 792.000				
MOR 1125	39	31	1.26	b
BHI 6233				
BHI 6230				
MOR 009				
USNM 6183				
LACM 23845				
LACM 23844	49	45	1.09	1
BHI 4100				
BHI 4182	34	33	1.03	1
BHI 6231				
MOR 008	64	48	1.33	2
AMNH 5027				
NHMUK R7994	50	42	1.19	1
SDSM 12047	55	35	1.57	2
TCM 2001.90.1				
UCMP 118742				
NMMNH P-3698	54	36	1.5	2
Range			0.98–1.64	
Median			1.31	
Average			1.25	

elements reasonably fit into one of the possible categories. A few specimens are borderline in their overall degree of robustness versus gracility, and a number are difficult to assess, both because there are few elements available and/or because the femur is absent (such as AMNH 5027).

Tyrannosaurus Femoral Proportions Do Show Unusual Variation

The numerous *Allosaurus* sp. specimens from the Cleveland-Lloyd Quarry record a population of a species that lived at the same time and place, and likely represent a single species of large avepod. The variation in femoral-length/circumference of these *Allosaurus* sp. specimens is only 9% in the five most mature specimens; this value remains the same even when including the 10 femora that are at least 70% maximum length, and is still only 16% when the 14 specimens that are 66% the maximum are included (Fig. 4A). The two dozen mature *Tyrannosaurus* specimens exhibit much greater variation in femoral length/circumference ratios (2.06–2.67), a variation of 30% (Figs. 2A–C, E, 4A). A nonparametric Tukey Fence test for outliers confirms none are likely present (k = 1.5). A Shapiro–Wilk Test suggests that both the *Allosaurus* and *Tyrannosaurus* residual percentage datasets have approximately normal distributions (p-values are 0.141 and 0.417, respectively). As both p-values are larger than 0.05, the test does not support a non-normal distribution. The result of the F Test for Variances, which requires a normal distribution, finds that the difference between the standard deviation of the *Allosaurus* and *Tyrannosaurus* data is significant (p = 0.000245362 < 0.05).

The variation in the mature specimens assigned to the tyrannosaurids *Albertosaurus* and *Gorgosaurus* is 17% and 16%, respectively, with a sample of a half dozen for each (Fig. 4B). Because both taxa are known from multiple locations in formations that span considerable time and contain rapid turnover of other dinosaur species (Fowler, 2017; Gates et al., 2012; Mallon, 2019; Paul, 2016; Ryan & Evans, 2005), the possibility that one or both of these taxa contain more than one species is higher than for the Cleveland-Lloyd *Allosaurus*. Although there is overlap between the proportions of these two tyrannosaurids, the femora of the earlier *Gorgosaurus* are, overall, more robust than are those of *Albertosaurus*, which appears in the fossil record after a substantial time gap (Fig. 5; Paul, 1988, 2008, 2016; Russell, 1970). Interestingly the femora of *Daspletosaurus* are not found to be overall more robust than those of contemporary *Gorgosaurus*, but this is because one particularly gracile specimen of the former (UALVP 52981) skews the total sample. The variation in femoral proportions in the half a dozen *Daspletosaurus* is 23%. When the dozen and a half similar-sized mature *Albertosaurus*, *Daspletosaurus* and *Gorgosaurus* femora are combined into one sample, the total

variation, from 2.51 to 3.08, is still just 23%. For four mature *Tarbosaurus* the variation is just 8%. Thus, the variation seen in the femoral proportions of *Tyrannosaurus* is atypically large. The smaller sample size of some other tyrannosaurid genera is too small to permit similar comparisons.

Even when comparing the *Tyrannosaurus* dataset to the combined sample of all other tyrannosaurids (*Albertosaurus*, *Daspletosaurus*, *Gorgosaurus*, *Tarbosaurus*, *Alioramus*, *Alectrosaurus*, "Raptorex"; Fig. 4C) of all ontogenetic stages and using residual scores to take allometry into account, the variation in femoral robustness in the smaller *Tyrannosaurus* data set is still greater, by ~14%. Although this difference is markedly less than in comparisons with other individual genera, and its significance cannot be statistically proven (an F Test for Variances yield a p-value of 0.529907 > 0.05), this is a notable—and unexpected—result considering that the general tyrannosaurid sample consists of a variety of genera and species of differing structural characteristics that span ~10 million years. The disparity becomes even more significant when the few very small tyrannosaurid specimens with femora below 250 mm length are removed (see smaller non *Tyrannosaurus* tyrannosaurid polygon in Fig. 4C), then the robustness variation is a quite substantial ~55% greater in *Tyrannosaurus* than in other tyrannosaurids. Even adding *Allosaurus* to the total non-*Tyrannosaurus* sample still does not result in a variation equal to the one genus (Fig. 4D).

Also notable is how the great variation observed in the *Tyrannosaurus* dataset is unidirectional, being skewed towards *greater* femoral gracility (Fig. 4C).

Gracile Subadults and Adults are Stratigraphically Limited

Robust *Tyrannosaurus* were found to outnumber gracile *Tyrannosaurus* more than two to one. Such a large disparity indicates that the discrepancy is not an artifact of the current sample size. There is not complete vertical/temporal separation between the robust and gracile morphs, but neither is there complete overlap (Fig. 6A). Robust morphs are known from all levels of the TT-zone. Of six femora from the lower level, all are stout with length/circumference ratios within a narrow zone of just 2.06 to 2.4, a variation of only 17%, which is similar to the low variation present in both *Albertosaurus* and *Gorgosaurus*. Three femora from the middle of the TT-zone also fall within that range, as do the seven from high in the TT-zone. None of the higher placed robust femora are as stout as the most robust femur from the lowest level. Of all 13 specimens from the lower or middle TT-zone, only a single middle level specimen is definitely gracile. The other five definite gracile femora are from the upper TT-zone. As such, gracile *Tyrannosaurus* appear limited to the upper half of the TT-zone, which helps explain why they are less common overall. High in the TT-zone, the number

Fig. 5 Stratigraphic-temporal separation of adults of western North American Campanian–Maastrichtian tyrannosaurid species, to same scale, bar equals 2 m, showing sudden size increase in Late Maastrichtian in association with retreating interior seaway resulting in reconnection of North America into a contiguous continent. From bottom to top; *Gorgosaurus libratus* (2.6 tonnes), *Albertosaurus sarcophagus* (2.8), *Tyrannosaurus imperator* (7.2), *T. regina* (7.4). Stippled areas are the formations that preserve the illustrated tyrannosaurids, from bottom to top Dinosaur Park, Horseshoe Canyon, TT-zone
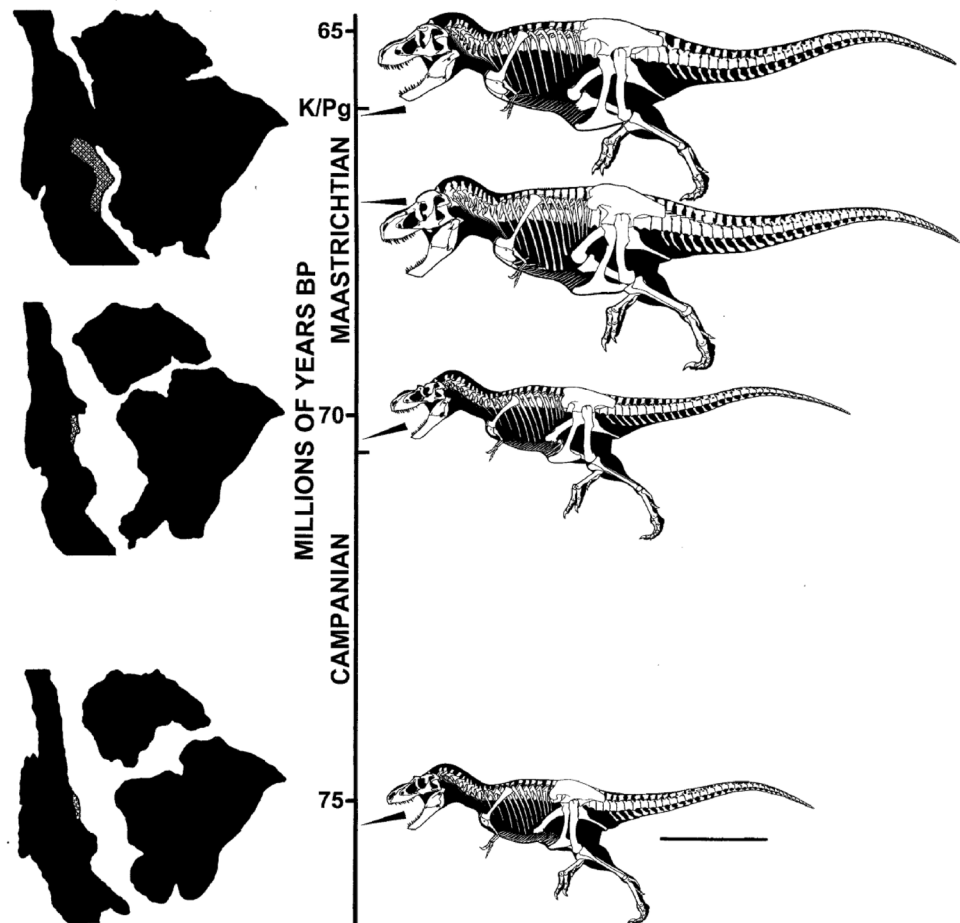
of gracile specimens roughly matches the number of robust specimens. The difference between the median robustness ratios of femora from the lower versus the upper TT-zone is 8% more gracile.

This same basic pattern is also observable in the robustness ratios of the other half dozen skull, pelvic and limb elements utilized herein (Fig. 6B–I). In no case are gracile morphs, in terms of either individual elements or specimens, documented from low in the TT-zone. Whereas the smaller, low positioned sample can be expected to result in somewhat less proportional variation than the larger data set from higher in the TT-zone, there is not an expectation that the difference in sample sizes should result in a strong skew one way or the other. So the time related differential very probably reflects lower TT-zone *Tyrannosaurus* being overall more robust than those higher up. The current sample suggests that if graciles do begin to appear low in the TT-zone in the future, the graciles/robusts ratio will probably remain lower at that level than high in the zone as a reflection of differing robustness ratios in the populations at those times. In the tests for correlation between gracility and stratigraphic position, the test utilizing continuous values of femur ratios failed to find significance (using the

basic femoral ratio: $p = 0.1734$, $U = 25.5 > 18$; using residual femoral scores: $p = 0.0836$, $U = 21 > 18$). However, using discrete values based on overall morphotype did establish a correlation ($p = 0.0207$, $U = 14 < 16$). This success should be qualified, as using discrete values tends to exaggerate the differences between the two groups, whereas the continuous values tend to minimize differences. That said, discrete values are consistent with the taxonomic conceit of any given specimen existing strictly as one species or another.

Incisiform Dentary Tooth Arrangement Correlates with Femoral Robusticity and Also Appears to Change with Time

The available sample size of specimens with both assessable femoral proportions and dentary tooth counts is low. Even so, the results of the Mann–Whitney U Test found the condition of just one anterior incisiform dentary tooth to correlate significantly with higher femoral gracility (using the basic femoral ratio: $p = 0.0054$, $U = 6.5 \leq 17$; using residual femoral scores: $p = 0.0048$, $U = 6 < 17$). Note: both U- and p-values are here provided for convenience, as most readers are likely more familiar with p-values; the actual decision of
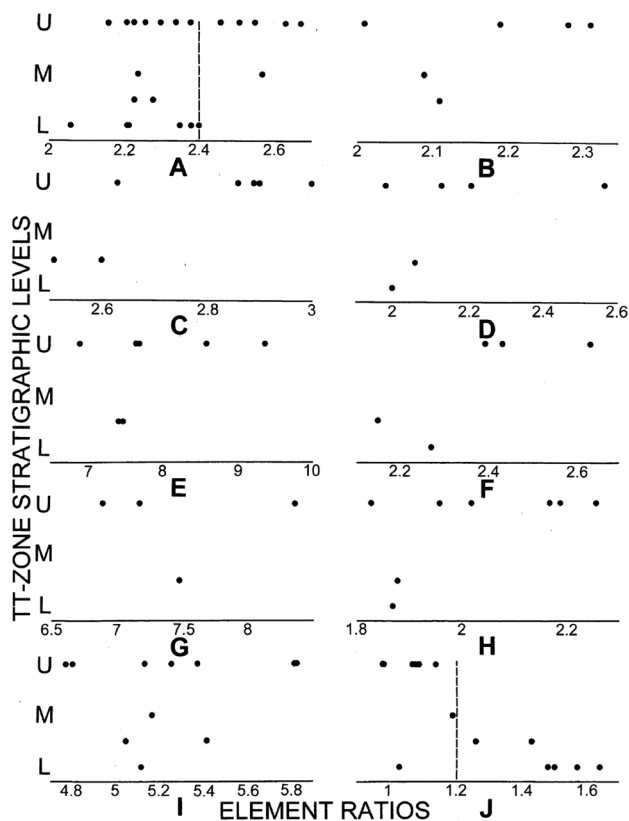
Fig. 6 Element ratios for large *Tyrannosaurus* specimens at differing stratigraphic levels (lower L, middle M, upper U) in the TT-zone (vertical axis); specimens that may be from either the upper lower or lower middle T-zone are plotted between the lower and middle levels. For **A** to **I** increasingly bone gracility is to the right, for **J** increasing 2nd incisor robustness is the left. **A** Femur length/circumference, division between robusts and graciles indicated by dashed line. **B** Humerus length/circ. **C** Ilium length/depth. **D** Metatarsal 2 length/circ. **E** Metatarsal 2 length/diameter. **F** Metatarsal 4 length/circ. **G** Metatarsal 4 length/diameter. **H** Maxilla length/depth. **I** Dentary length/depth. **J** Dentary teeth 2/3 base diameters, division between one and two incisors indicated by dashed line

whether to reject the null hypothesis is based on the U-value, with the p-value as an approximation generated from the U-value; this approximation becomes less robust at smaller sample sizes.

It would be desirable to establish a similar correlation between incisiform dentary tooth count and stratigraphic level. Unfortunately, the current number of specimens with assessable tooth counts is too small to run a Mann–Whitney U Test. In the absence of such a direct test, it is reasonable to conclude that some form of transitivity may apply: femur type correlates to stratigraphic level and tooth counts correlate to femur type, thus incisiform dentary tooth counts likely do correlate with stratigraphic level (Fig. 6J). The available data is at least consistent with this interpretation. Two slender anterior incisiform dentary teeth are normal in the more basal and earlier North American *Albertosaurus* and

Daspletosaurus (Brusatte et al., 2009), and this is true of the most anterior preserved dentary teeth of several of the largest *Tarbosaurus* (including MPC-D107/5 and PIN 551-1). Six *Tyrannosaurus* specimens with two slender anterior incisiform dentary teeth are known from the lower and middle TT-zone, including one from the U.S. southwest that may be the stratigraphically lowest known *Tyrannosaurus* specimen. No specimen known from high in the TT-zone has the two small incisiform condition well developed, although one possesses a borderline condition (RSM 2523.8). The highest disparities in tooth base diameter between positions 2 and 3 is low in the Hell Creek and Lance. Three intermediate specimens are from intermediate levels of the TT-zone. Six specimens— each with one slender anterior incisiform dentary tooth—are from the upper TT-zone, one is from the lower.

Discussion

The data do not meet the ideal proof of any of the four hypotheses, but they do significantly favor one over the other three. In selecting which of the four competing hypothesis is most compatible with the current dataset, the critical features of *Tyrannosaurus* variability in robustness are as follows: the total variation is much more extensive than observed in other large avepod dinosaur species, including all other tyrannosaurid species and even all other tyrannosaurids combined; this unique degree of variation in robusticity is entirely due to a skew towards greater gracility; robustness appears to have no relationship with absolute size (with some large specimens possessing gracile proportions and some small specimens robust proportions) or apparently maturity (other than, presumably, very small juveniles); robust *Tyrannosaurus* individuals are more numerous than gracile forms (roughly 2:1); no gracile forms are currently known from the lower TT-zone but are contemporaneous with robust forms in the upper TT-zone; and variation is notably not exceptional in *Tyrannosaurus* from low in the TT-zone. To this, add the correlation of one incisiform dentary tooth with gracility and the absence of single-incisiform dentaries from the lower TT-zone.

Mallon (2017), Carr (2020) and Saitta et al. (2020) did not discover definitive evidence for sexual dimorphism in *Tyrannosaurus*, although the hindrance of not having a larger sample was noted. That the atypically large variation in *Tyrannosaurus* robustness appears to be continuous rather than strongly bimodal is not strongly consistent with the sexual dimorphism hypothesis, but is more compatible with ontogeny, individual differences, and speciation (Supplementary Information). However, that the variability is higher than that observed in all other presumed monospecific theropod samples and all other tyrannosaurids combined, contradicts the expectations of the individual-variation hypothesis.

Amongst the longest *Tyrannosaurus* femora, some are gracile and others are robust. The single longest femur (exBHI 3033) is easily the most gracile known among the mature specimens, and it is even substantially more gracile than that of the large juvenile USNM 6183, despite being 36% longer. Conversely, USNM 6183 is markedly more robust than that of similar sized adult *Albertosaurus*, and even exceeds that of all *Daspletosaurus* (Figs. 2B, 3D). Yet, an incomplete femur from a large juvenile two thirds maximum size is the slenderest in the *Tyrannosaurus* sample, as is its complete metatarsal IV (Fig. 2A). The divergence in *Tyrannosaurus* proportional robusticity appears, therefore, to have been present early in ontogeny, but the absence of smaller femora confidently attributable to the same taxon as the adults presently prevents observing how far down in growth the disparity extends. That a large disparity in robustness was already present when juveniles were two-thirds adult dimensions, and that some of the largest specimens were gracile is not at all the pattern predicted if robustness were simply the product of maturation. The pattern is compatible with sexual dimorphism if reproduction began early in ontogeny in *Tyrannosaurus*. But while reproduction does appear to have been underway in a female of ~85% observed maximum size of the genus (Schweitzer et al., 2016), that is well above the juvenile size at which major divergence in skeletal proportions was occurring. Therefore, sexual dimorphism does not currently offer a compelling explanation for the ontogenetically early and geologically late surge in proportional divergence in the genus (Carr, 2020 came to the same conclusion regarding the ontogenetic pattern). That may change if it can be shown that reproduction began earlier in growth.

That robust forms are overall more than twice as numerous as graciles is additionally problematic for the ontogeny hypothesis in view of the expectation that robust forms should be the relatively rare product of the few individuals that reached old age. The overall two to one ratio is compatible with sexual dimorphism only in that, assuming the robust forms were females, it is possible that females outnumber males in a reproductively viable population, but the ratio appears rather high for that scenario. That the robust and gracile morphs are similar in numbers at high stratigraphic levels is compatible with the expectation of sexual dimorphism approaching the K/Pg boundary, but the apparent absence of the gracile form from the lower TT-zone appears to seriously contradict the sexual dimorphism hypothesis.

A striking result of the femoral comparisons across tyrannosaurs is how the extreme variation unique to *Tyrannosaurus* is skewed towards greater relative gracility. Not predicted by any of the competing hypotheses (or the expectations of participants in this study), this result is interesting regardless of the status of species within the genus. It would be expected that the very large and correspondingly allometrically stoutly constructed *Tyrannosaurus* would maintain at least the scaling level of robustness observed in the rest of the Tyrannosauridae, with any divergence from the general trendline to be in the direction of *more* robusticity for further strength. Instead, the genus developed a divergent major subpopulation that was actually substantially *more gracile* than the norm predicted for tyrannosaurids in the 5+ tonnes mass range—note that the largest known *Tarbosaurus* (MPC-D107/02) has the stout femoral proportions of a robust *Tyrannosaurus* (Fig. 4C).

The available stratigraphic data indicate that the greater proportional variation via greater gracility in *Tyrannosaurus* did not appear at the beginning of the genus, but instead occurred during the latter half of the taxon's evolution. This belated appearance of more slender proportions is expected in the context of the now realized evolution of *Tyrannosaurus* away from the general tyrannosaurid trendline, with early *Tyrannosaurus* having the same robust femoral proportions as the slightly earlier and nearly as large relative *Tarbosaurus.* This supports both the premise that the consistently robust femora of early *Tyrannosaurus* reflect the reality of the time, rather than the size of the sample, and further affirms that *Tyrannosaurus* gracility was probably not integral to the genus, being instead a late appearing feature.

The same appears generally true for the character of incisiform dentary tooth number: the basal characteristic (two incisiform dentary teeth) appears to be a retention of the ancestral condition, and an apparently more derived condition (one incisiform dentary tooth) becomes increasingly abundant at higher stratigraphic levels. As predicted by the multiple morphotype or species hypothesis, the derived trait of one incisiform dentary tooth does correlate with femoral proportion (gracility). However, this correlation is not completely clear cut, and some robust forms from high in the TT-zone have a borderline condition.

Conclusion and Systematic Paleontology

The results of this study indicate that three morphotypes are recognizable within the genus *Tyrannosaurus* in the TT-zone: Morphotype I, a stratigraphically low and evolutionarily basal form that retains the robust proportions and usually the two incisiform dentary teeth of more basal tyrannosaurids; Morphotype II (holotype *T. rex*), a stratigraphically high robust form that has reduced the incisiform dentary tooth number to one; and Morphotype III, a stratigraphically high gracile form (contemporaneous with Morphotype II) that also has only one incisiform dentary tooth. If the early and later robust forms had retained the same incisiform configuration, then it would seem reasonable to postulate that they constitute a single morph extant from the bottom of the TT-zone to the top and that the late appearing gracile form

with a reduced number of incisiform teeth was a second morph that split off during the mid TT-zone. Bioevolution is often a complex affair, and the lack of simplicity should, perhaps, not be at all surprising.

The amount of observed variation between these morphotypes is too modest to justify consideration of distinct genera, and subspecies are not traditionally applied to Mesozoic vertebrates. The question is, therefore, whether the three morphotypes should be merely noted and otherwise not formally recognized, or if separation at the species level is advisable. During extensive discussions amongst authors of this paper all agreed there is sufficient evidence to show that there were morphological changes over time, and that the degree is sufficient to at least justify and perhaps compel taxonomic recognition.

If the results of this study had found that the great majority of *Tyrannosaurus* specimens shared the same proportional traits as the holotype of *T. rex*, then the need for taxonomic action would be minimal. As it is, the results find that the only specimen that can with high confidence be placed in *T. rex* is the holotype, and a few other specimens are probable members of the species. As a consequence, the great majority of *Tyrannosaurus* specimens, including the most complete examples, would be left taxonomically hanging if not assigned to new named taxa. As detailed at length in Supplementary Information, although the evidence for more than one *Tyrannosaurus* paleospecies does not meet the highest standards yet achieved for a dinosaur (that being Scannella et al., 2014, which is based on a uniquely high-quality data set), the available taxonomic evidence is greater and has more statistical support than most cases of species level distinctions within the recent dinosaur literature, and matches or exceeds that seen in a number of nondinosaur tetrapods. There are also notable scientific reasons for naming the species discussed in Supplementary Material. In accord with the preponderance of data (Table 3), the following diagnoses for two additional *Tyrannosaurus* species are offered. The full expectation is that these new taxa will be tested and, if necessary, accordingly revised as additional specimens and analysis come to light. It is similarly expected that colleagues across the splitter/lumper continuum will opt to use or reject the proposed species in accordance with their own standards and evidentiary perspectives; however, it is our hope that the three *Tyrannosaurus* morphotypes recognized by this study (I, II, and III) will be of universal value, as a means for framing and focusing future inquiry into the multiple species question. For further discussion of the specimen assignments and related information including recommendations for testing these taxonomic hypothesis in future works see Supplementary Information. Note that the species diagnoses incorporate the cumulative proportions of six elements in addition to the femur.

Genus *Tyrannosaurus* Osborn, 1905

Type species: Tyrannosaurus rex Osborn, 1905
Tyrannosaurus rex Osborn, 1905 (Morphotype II)
Etymology: Tyrant lizard king
Holotype: CM 9340
Referred specimens: BHI 6230, BHI 6233, BHI 6435, BHI 6436, RSM 2523.8? BHI 4100? MNHUK R7994?
Age and stratigraphy: Latest Maastrichtian, upper and possibly middle Hell Creek and Lance, Ferris, Denver, Frenchman, Willow Creek, Scollard.
Geographic distribution: Montana, Colorado, Dakotas, Wyoming, Alberta, Saskatchewan.
Diagnosis: generally robust with an adult femur-length/circumference ratio of about 2.4 or less; usually one slender anterior incisiform dentary tooth.

Tyrannosaurus imperator sp. nov. (Morphotype 1)
Etymology: Tyrant lizard emperor
Holotype: FMNH PR2081
Referred specimens: BHI 4182, BHI 6231, 6248, HMN MB.R.91216, MOR 1125, MOR 1128, RGM 792.000, SDSM 12047, TCM2001.90.1, TMT v2222, NMNNH P-3698?
Age and Stratigraphy: Late Maastrichtian, lower, lower middle and possibly middle Hell Creek and Lance, Laramie, Arapahoe, McRae? North Horn? Javelina?
Geographic distribution: Montana, Dakotas, Wyoming, New Mexico? Texas? Utah?
Diagnosis: Generally robust with an adult femur-length/circumference ratio of 2.4 or less; usually two slender anterior incisiform dentary teeth.

Tyrannosaurus regina sp. nov. (Morphotype III)
Etymology: Tyrant lizard queen.
Holotype: USNM 555000
Referred specimens: exBHI 3033, MOR 980, LACM 23485, LL 12823, TMP 81.6.1, LACM 23845.
Age and stratigraphy: Latest Maastrichtian, upper and possibly middle Hell Creek and Lance, Ferris, Denver, Frenchman, Willow Creek, Scollard.
Diagnosis: Generally gracile with an adult femur-length/circumference ratio over 2.4, usually one slender anterior incisiform dentary tooth.
Geographic distribution: Montana, Colorado, Dakotas, Wyoming, Alberta, Saskatchewan.

Tyrannosaurus incertae sedis

Robusts of uncertain stratigraphic position that are probably *T. imperator* or *T. rex*—BHI 6231 BHI 6232, BHI 6242, USNM 6183; of uncertain proportions and high stratigraphic placement that are probably *T. rex* or *T. regina*—BHI 6249, DMNS 2827, LACM 23844, MOR 009, TMP 81.12.1, UCMP 118742, UWBM 99000; insufficient proportional and/or stratigraphic information for a species assignment—AMNH 5027, AMNH 30564, CM 1400, MOR 008, RMDRC 2002.MT-001.

Tyrannosauridae incertae sedis

Table 3 Summaries of arguments and evidence for and against multiple species of *Tyrannosaurus* in the TT-zone

For multiple species

Multiple species are the norm within a genus

Multiple species have been documented in other dinosaur genera, especially contemporary *Triceratops*

Sufficient time available for subtle speciation and may favor such, in parallel to speciation observed in *Triceratops* over exactly the same stratigraphic span

Radical alterations in regional geography in Maastrichtian as North American continent reunited and dramatically expanded resource base, probably favored a burst of rapid evolution in tyrannosaurids that could favor rapid speciation both over time and laterally

Much more variation in femoral robustness than observed in any other theropod or dinosaur species—the variation being significantly statistically greater than a sample of femora of an allosaur species from a single quarry—including any tyrannosaurid species, and more than in all other tyrannosaurids combined consisting of up to 7 genera and 8+ species from two continents spanning 10 million years compared to 0.7–1.5+ million years for a smaller *Tyrannosaurus* sample from a small region, strongly favoring speciation over sexual dimorphism, ontogeny, or individual variation

That total number of robust femora are over twice that of all gracile femora strongly contradicts both sexual dimorphism and ontogeny as causes

Some femora that are only two thirds adult size are robust, in some cases more so than some of the longest femora, while the some of the largest and the largest are gracile with the longest known femur being the slender-most among adults, directly contradicting ontogeny as the cause of robustness

That reproduction has not been shown to have been occurring as early in ontogeny as the onset of large variations in the robustness of juveniles means that early reproduction does not currently offer an explanation for the observed pattern

That the solely robust femora of early *Tyrannosaurus* followed by the much greater variation in proportions higher up include substantial gracility is due to a relatively smaller earlier sample is not the most likely scenario, because while the variation in a smaller sample may be less than in a larger sample, is not likely to be skewed one way or the other relative to the latter

The most robust femora from the upper TT-zone not being as stout as the most robust examples from low in the zone further supports the pattern being real, and is in accord with a proportional shift in the genus, rather than the stasis most compatible with no speciation

Because low variability limited to robustness in early *Tyrannosaurus* appears to be a retention of the ancestral condition observed in other earlier tyrannosaurids (both individual species or in total) additionally supports the limitation to only robustness among basal *Tyrannosaurus* as probably being real

That gracile femora are found only in upper TT-zone, while robusts are present in all levels, contradicts the consistent strong proportional variation necessary for dimorphism to be persistently present

That proportional variation in low TT-zone *Tyrannosaurus* is not higher than observed in other tyrannosaurid species is compatible with and indicates that only one species was extant at that level

That proportional variation in high TT-zone *Tyrannosaurus* is higher than observed in other theropod species is compatible with and indicates that two species were extant at that level

Proportional variation being low in the lower TT-zone and high in the higher TT-zone strongly indicates speciation either because the sudden onset of major dimorphism indicates the kind of dramatic shift in reproductive behavior that is the epitome of species separation and designation, or two new contemporary species with each retaining the limited dimorphism apparently typical of dinosaurs

The same basics as immediately above apply if the new proportional variation in the upper TT-zone was primarily due to a new ontogenetic pattern or individual variation both of which are improbable, but in any case indicate a change radical enough to require species recognition

The solely robust *Tyrannosaurus* sample from the lower TT-zone is smaller than the more gracile set from higher levels, but the sample size difference should not result in the strong skew. So as the lower sample increases in abundance it is not likely that gracile specimens will prove to be as proportionally numerous as they are higher up if they appear at low levels at all

If the smaller sample of lower TT-zone femora greatly expands to include much more gracility than in other tyrannosaurids with future finds, then the great proportional variation compared to other theropods is most in accord with the presence of two species early in the evolution of the genus. If a future lower set shows that graciles are a present but rare compared robusts then the case for two species at that level will be at least as strong, or more so

That gracile *Tyrannosaurus* femora are unusually slender by normal tyrannosaurid standards, and represent a highly atypical shift over a short period of time, directly contradicts ontogeny while favoring subtle evolution via speciation

Other measurements of robustness in crania and postcrania favor actuality of robust and gracile morphs in good accord with femoral robustness

There are general progressive trends towards more gracility progressing stratigraphically upwards as recorded by most of the proportional measures in addition to femora

General shift from the probable ancestral condition of two small anterior-most dentary incisors to just one progressing upwards in TT-zone is not explained by dimorphism, individual variation, or ontogeny, instead suggests subtle chronospeciation in at least one lineage

Progressive change in dentary incisor number over time correlates statistically strongly with changing femoral robustness accords with evolutionary speciation rather than dimorphism, individual variation, or ontogeny

Table 3 (continued)

Specimen sample size analysis is based upon is larger than usual for nonavian dinosaur genera

No statistical analysis contradicts multiple species, and statistical support is often significant for variations in robustness and dentary incisors being indicative of species

The preponderance of evidence strongly favors speciation over all alternatives, and is stronger than average for other multiple species in dinosaur genera

For three species rather than just two chronospecies

Much more variation in femoral robustness than observed in any other theropod or dinosaur species high in the TT-zone, and in all other tyrannosaurids combined, strongly favors lateral speciation in addition to and over just vertical chronospeciation

Two and perhaps more species of earlier western North American giant tyrannosaurids, with one more robust than the other, are present in the same levels of the same formations

Is in best accord with the hypothesis that expansion of the resource base was a driving factor in the combination of both vertical and lateral speciation of elephant sized giant predators as the latest Maastrichtian progressed

Against multiple species

Time span of TT-zone is not sufficiently long to require speciation

Cannot be entirely ruled out that observed patterns are due to extreme individual variation

Statistical support not always strong because of small samples

Stratigraphy of some specimens is not precisely known

Cannot be entirely ruled out that similar variation in femoral and other proportions is present in other fossil dinosaur species

Evidence does not match the exceptional level documented for multiple species of *Triceratops*

One low TT-zone specimen has just one small incisor

Presence of one small incisor in all upper TT-zone specimens may indicate just one species at that level

BMRP 2002.4.1, BMRP 2006.4.4, CMNH 7541, DDM 344.1, LACM 28741, RSM 2990.1, RSM 2347.1, TMM 41436-1, TMM 46028-1, UMNH 11000.

Having devised these three species delineations, a final statistical test of how well they reflect the femoral proportion data is possible. Specimens with measurable femora were grouped according to their proposed species. Each group was graphed by femur length and circumference, just as the entire *Tyrannosaurus* group was previously. The resulting trendlines and R^2 values displayed significantly stronger correlation than that generated for the cumulative *Tyrannosaurus* group. R^2 values are essentially measures of how well the data matches the regression lines. More specifically, they indicate how much of the variation observed is explained by the linear model. Higher R^2 values indicate a close relationship between the data and the line of best fit. The *T. imperator* graph has an R^2 value of 0.4735, *T. rex* 0.7947, and *T. regina* 0.6401 (Fig. 4F–H). These results show that each proposed species has a statistically more consistent femur ratio than that of the *Tyrannosaurus* group overall. Because part of the motivation for considering the possibility of multi-speciation within the current "*T. rex*" umbrella was the extent of variation in femur robusticity, this suggests that the proposed species designations are more fitting in this regard. It must be stressed that these graphs are significant because they provide retroactive confirmation for morphotype or species designations that were generated first. Creating the groups based on what would make nice graphs would *not* be a powerful justification for doing so. However, generating groups on the combined basis of femoral ratios, incisiform dentary tooth numbers, and stratigraphic layers, and *then* graphing to reveal stronger linear conformity does provide support for the groups.

Assuming that the three proposed *Tyrannosaurus* species do reflect evolutionary reality, the question then emerges as to why the older and basal *T. imperator* split into two similarly gigantic species. Prior to the late Maastrichtian, the western interior seaway was intact and restricted the resource base of the geographically modest sized Laramidia Peninsula such that it was sufficient to support only rhinosized predators, albeit sometimes two contemporaneous tyrannosaurids (one robust and the other gracile) sharing the same ecospace (Fig. 5). It is possible that the earlier Asian tyrannosaur *Tarbosaurus* is the ancestor of *Tyrannosaurus* or close to it (Brusatte and Carr 2016, but see Supplementary Information), in which case *T. imperator* or its Asian ancestor arrived in North America via a founding event of a population crossing the Bering Land Bridge. That occurred concurrent with the partial retreat of the interior seaway, which greatly expanded the available resource base by reuniting North America into a single large continent. North America was now able to support numerous proboscideansized herbivores (including *Ankylosaurus*, *Edmontosaurus*, and *Triceratops* in the TT-zone, and even larger titanosaur sauropods elsewhere), which were preyed upon by predators of similarly scaled up, elephantine size (Fig. 5; Mallon, 2019). *Tyrannosaurus imperator* retained the robust proportions normal at that size for the clade, as well as the two small dentary incisors of earlier, more basal tyrannosaurids. The subsequent evolution of *T. rex* and *T. regina*

may be the result of ecological diversification, with robust *T. rex* perhaps being the anagenetic descendent of robust *T. imperator* with fewer dentary incisors, and the unusually gracile *T. regina* evolving via cladogenesis to hunt somewhat swifter and less heavily armed prey. The atypically slender proportions of *T. regina* could have been developmentally achieved by a paedomorphic partial retention into adulthood of slender juvenile proportions. The two end Cretaceous *Tyrannosaurus* taxa appear to have had broadly equivalent populations. If not for the general K/Pg extinction, the two species may have further evolved into distinct robust and gracile genera, similar to the earlier daspletosaur and albertosaur groups.

ZooBank Registration

Of new species contained in this study: urn:lsid:zoobank.org:pub:5D191E10-7361-48E6-BE9C-D9FDC98BA65F

T. imperator: urn:lsid:zoobank.org:act:403B3497-08ED-4B0F-9E01-A4A86E83E7FB

T. regina: urn:lsid:zoobank.org:act:718123A3-82BE-405A-AF43-2B43D9D59175

Data Availability Not applicable.

Code Availability Not applicable.

Declarations

Conflict of interest The authors declare they have no conflict of interest.

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