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Theropod Guild Structure and the Tyrannosaurid Niche Assimilation Hypothesis: Implications for Predatory Dinosaur Macroecology and Ontogeny in later Late Cretaceous Asiamerica

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ABSTRACT

Well-sampled dinosaur communities from the Jurassic through the early Late Cretaceous show greater taxonomic diversity among larger (>50kg) theropod taxa than communities of the Campano-Maastrichtian, particularly to those of eastern/central Asia and Laramidia. The large carnivore guilds in Asiamerican assemblages are monopolized by tyrannosaurids, with adult medium-sized (50-500 kg) predators rare or absent. In contrast, various clades of theropods are found to occupy these body sizes in earlier faunas, including early tyrannosauroids. Assemblages with "missing middle sized" predators are not found to have correspondingly sparser diversity of potential prey species recorded in these same faunas. The "missing middle sized" niches in the theropod guilds of Late Cretaceous Laramidia and Asia may have been assimilated by juvenile and subadults of tyrannosaurid species, functionally distinct from their adult ecomorphologies. It is speculated that if tyrannosaurids assimilated the niches previously occupied by mid-sized theropod predators that we would expect the evolution of distinct transitions in morphology and possibly the delay of the achievement of somatic maturity in species of this taxon.

Keywords: dinosaurs, ontogeny, theropod, paleoecology, Mesozoic, Tyrannosauridae

INTRODUCTION

Dale Russell's (1970) review of the Tyrannosauridae of the Late Cretaceous Western Canada represents one of the most significant contributions to the study of the tyrant dinosaur in the mid-20th Century. As well as introducing the species *Daspletosaurus torosus* and summarizing what was then the most extensive collections of North American tyrannosaurids, Russell also speculated on the anatomy and proportions of a hypothetical hatchling albertosaurine (Fig. 1), extrapolated from observed allometric changes in subadult and adult specimens. This hypothetical reconstruction emphasized that the early ontogenetic stages of an animal which undergoes very large increases in size might have strikingly different functional morphology and ecological roles than the adult of the same species.

The scale of ontogenetic morphological transformation in Tyrannosauridae was first explored by Rozhdestvesnky (1965). He observed that several specimens initially regarded as separate species (*Gorgosaurus novojilovi*, *Gorgosaurus lancinator*, *Tarbosaurus efremovi*, and *Tyrannosaurus bataar*) represented a single taxon, for which the proper name was *Tarbosaurus bataar*. Morphological distinctions beyond body size, such as changes in hindlimb proportion and a shift from relatively ziphodont (blade-like) maxillary and dentary teeth in the smaller "species" versus incrassate (inflated) teeth in the adult, had led previous authors to consider as separate taxa what were in fact a continuous growth series. Subsequently similar changes were observed in other Asian and North American tyrannosaurids, with recognition that some previously proposed species were parts of ontogenetic sequences (Carr 1999, 2020; Currie 2003; Carr and Williamson 2004).

Given these anatomical transitions at different age classes, the question of the possibility of substantial shifts in functional anatomy and ecology through ontogeny in tyrannosaurids has been speculated upon by a number of authors (Holtz 2004a, 2004b; Snively et al. 2006; Bates and Falkingham 2012; Woodward et al. 2020; Carr 2020). Indeed, an ontogenetic niche shift would be unavoidable in an animal that underwent a multiple order of magnitude increase in size from hatching to adulthood (Taylor 1979; Auffenberg 1981; Tucker et al. 1996; Purwanda et al. 2016), barring provisioning by an adult throughout the entire growth series or membership in a gregarious social group responsible for all food acquisition (but see Currie and Eberth (2010) for the possibility for gregariousness in the Early Maastrichtian tyrannosaurid *Albertosaurus sarcophagus*.)

How might these ontogenetic niche shifts be reflected in the structure of the communities of carnivorous dinosaurs, and do communities in which tyrannosaurids are the largest (presumably apex) predators differ from those in which the largest members are other theropod clades? Theropod dinosaurs first appeared in the Late Triassic (Sereno 1999; Holtz and Osmólska 2004) but were not the dominant predators until the loss of their competitors (primarily loricatan pseudosuchians: Zanno et al. 2015) in the Triassic-Jurassic extinction event (Olsen et al. 2002). During the subsequent 135 million years, theropods were the primary large-bodied flesh-eaters in terrestrial ecosystems.

As such, the assemblage of theropods in a given faunal community can be considered an ecological guild. As originally described by Root (1967), a guild comprises “a group of species that exploit the same class of environmental resources in a similar way." Therefore, members of a guild are expected to be in principle each other's most likely competitors, resulting in character displacement (Brown and Wilson 1956; Van Valkenburgh 1988, 1994; Henderson 2000): the selection for anatomical and behavioral adaptations that reduce the overlap of specific ecological parameters for each taxon.

Aspects of theropod guild structure has been the subject of several previous studies. For example, Henderson (2000) examined the functional differences in cranial form of sympatric large theropods of the Morrison Formation. Van Valkenburgh and Molnar (2002) compared the assemblages of theropods of the Morrison, Dinosaur Park, and Nemegt Formations with communities of carnivorous mammals from various Cenozoic communities. Farlow and Pianka (2003) observed the overlap in body size and form among the tyrannosaurids of the Dinosaur Park Formation. Carbone et al. (2011) utilized theoretical ecology and the observed size distribution of Hell Creek Formation dinosaurs to test the possibility of obligate scavenging in *Tyrannosaurus rex*. More recently Torices et al. (2018) examined the functional differences in tooth morphology for sympatric theropod species of western Canada. Frederickson et al. (2018) studied niche partitioning in theropod dinosaurs in terms of diet and habitat preference in the Mussentuchit Member of the Cedar Mountain Formation.

One significant observation about Mesozoic theropod guilds is the qualitative difference between Jurassic and Early Cretaceous assemblages relative to the later Late Cretaceous assemblages of western North America and eastern and central Asia (Foster et al. 2001; Farlow and Holtz 2002; Holtz 2004a, 2004b). While the former communities show a diversity of theropod lineages represented among the larger carnivores, the latter contain only members of Tyrannosauridae. This transition occurred sometime after the Turonian (Zanno and Makovicky 2013; Zanno et al. 2019; Nesbitt et al. 2019) and before the middle Campanian (Loewen et al. 2013) in North America. A similar pattern is observed in Asia, where the tyrannosauroid *Timurlengia* of the Turonian Bissekty Formation is a mid-sized predator (Brusatte et al. 2016), while a larger carcharodontosaurid has recently been reported from the same unit (Tanaka et al. 2020). The slightly stratigraphically younger Turonian-Santonian Upper Bayan Shireh Formation of Mongolia and Santonian Iren Dabasu Formation of Inner Mongolia (Averianov and Sues 2012) lack evidence at present of carcharodontosaurids, although in the former the large dromaeosaurid *Achillobator* rivals the sympatric tyrannosauroid cf. *Alectrosaurus* in size (Perle et al. 1999). In the post-Santonian no large carnivorous theropods other than tyrannosaurids are observed in this region.

The cause of the transition from carcharodontosaurid- to tyrannosaurid-dominated theropod guilds in Asiamerica is still not understood. The disappearance of previous apex theropod clades such as Spinosauridae and Allosauroidea between the Turonian and the Campanian may be due to out-competition by the newly evolved Tyrannosauridae, loss of the primary prey of these older taxa, or other environmental changes, but poor sampling of the interval involved leaves the cause of this transformation (and the similar event in Gondwana) unresolved at present.

The present study seeks to compare tyrant-dominated and non-tyrant-dominated theropod guilds through a number of different parameters. “Tyrant” in this context refers to Tyrannosauridae proper as well as other large-bodied immediate outgroups (such as *Teratophoneus* and

Appalachiosaurus: Brusatte and Carr 2016): taxa typically of 1000 kg or more with powerful jaws and laterally expanded (incrassate) teeth, reduced forelimbs ending in a didactyl manus, and elongate hindlimbs terminating in an arctometatarsus (Holtz 2004a). The more inclusive clade Tyrannosauroidea contains Jurassic and Early-to-early Late Cretaceous groups of smaller-bodied taxa including Coeluridae, Proceratosauridae (although at least two genera of this group achieved tyrannosaurid sizes, *Sinotyrannus* and *Yutyrannus*: Ji et al. 2009; Xu et al. 2012), and Stokesosauridae. These early tyrannosauroids were more typically middle-sized predators in their respective guilds. Some Early-to-early Late Cretaceous tyrannosauroids of North America and Asia such as *Xiongguanlong, Moros*, and *Suskityrannus* demonstrate that some of the anatomical traits characteristic of Tyrannosauridae evolved in the context of smaller body size (Li et al. 2010; Zanno et al. 2019; Nesbitt et al. 2019).

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York City, New York, USA; BMRP, Burpee Museum of Natural History, Rockford, Illinois, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ROM, Royal Ontario Museum, Toronto, Canada.a

METHODS AND MATERIALS

Statistics for this study were calculated using the PAST 4.03 software package (Hammer et al. 2001; 2020).

Theropods range in size from *Mellisuga hellenae* (the bee hummingbird) to 14 m long, 8 tonne or more giants including *Tyrannosaurus rex, Giganotosaurus carolinii,* and *Spinosaurus aegyptiacus* (Mazzetta et al. 2004; Holtz and Osmólska 2004; Persons et al. 2020; Campione and Evans 2020). Even removing the avialian (bird) component of this clade, the known lower end of Mesozoic theropod range includes 50-cm long taxa such as *Mei long* and *Microraptor zhaoianus*. Consequently, size represents a parameter in which the guild of carnivorous dinosaurs might easily partition the niche of flesh-eaters, especially as predator body size is positively associated with maximum prey body size and total range of prey sizes (Van Valkenburgh and Hertel 1998; Meers 2002; Radloff and Du Toit 2004).

Size estimates for individual theropod specimens are derived primarily from the supplementary data of Benson et al. (2018) and Campione and Evans (2020); for taxa not included in those previous analyses, size class was assigned based on those of other theropod species with the most similar femoral, tibial, or skull length. The size classes used in this study are: size class 1, 10 kg or less; size class 2, 11-50 kg; size class 3, 51-100 kg; size class 4, 101-500 kg; size class 5, 501-1000 kg; size class 6, 1001-5000 kg; and size class 7, greater than 5000 kg. These broad categories, rather than particular estimated masses, are employed to reduce the uncertainties resulting from differences in mass estimation techniques, inaccurate models, incomplete preservation of the specimens, and variability within the taxon (Campione and Evans 2020). Where possible, the size of the largest known individual of that species was used as the best approximation of adult body size, with the recognition that our limited data set for most dinosaur species might not currently include fully adult individuals (Hone et al. 2016). Carbone et al. (1999) found a transition in extant mammalian predators between those which fed on small prey (less than ½ predator mass) to large prey (near predator mass) at 21.5-25 kg. This inflection point is within size class 2 in this study. At present it is uncertain where the equivalent inflection point would be in Mesozoic theropods (or indeed if there is such an inflection rather than a gradual transition). Thus, the scheme used here is admittedly a simplification.

For purposes of comparison, this study seeks to examine sympatric communities of organisms: that is, those which actually inhabited the same geographical region at the same time. Almost assuredly most carnivorous theropod species had ranges that extended beyond a single depositional basin (Farlow 1993), but most species of dinosaur are currently known from only a single stratigraphic unit. The question as to the degree of intracontinental endemism and provincialization in dinosaurian faunas remains a matter of debate (Sampson et al. 2010; Vavrek and Larsson 2010; Lucas et al. 2016; Whitlock et al. 2018). While there may be some interaction between faunal assemblages in different neighboring regions that are currently unrecognized due to low levels of sampling (Vavrek and Larsson 2010), the present study takes the conservative approach in using only taxa presently observed in the same stratigraphic units as being sympatric. In at least the case of one individual of hadrosaurid from the Dinosaur Park Formation it was found that the total geographic range based on strontium isotopic data was only on the scale of a few 100 kms (Terrill et al. 2020), potentially justifying the restriction of faunas to single depositional basins.

For some very well-sampled dinosaur-bearing strata, recent work has provided detailed biozonation of the individual species, reducing the chance of including taxa that did not actually exist at the same time. Fowler (2017) provides a comprehensive overview of this for dinosaurs of the Santonian through Maastrichtian of the Western Interior of North America. Examples of specific Western North American formations for which such data are available include the Kimmeridgian-Tithonian Morrison Formation (Foster 2003), the middle-to-upper Campanian Dinosaur Park Formation (Mallon 2019), and the Horseshoe Canyon Formation of the late Campanian-early Maastrichtian (Eberth and Kamo 2019). These works additionally show that individual dinosaur species were often present for relatively short geologic durations, shorter that the deposition of the formations in which they were present. Thus, including all the species recovered in a single formation as being part of the same faunal community may be exaggerating the diversity, transforming successions of taxa into one fauna. However, detailed biostratigraphic work has not been conducted or published for many dinosaur bearing strata. Consequently, the study here may be combining taxa which did not actually interact in life for these formations.

The focus of this analysis is theropods as hypercarnivorous specialists feeding on other dinosaurs. As such, regarding “carnivorous theropods” as a guild (a group of species that exploit the same class of environmental resources in a similar way) rather than a clade (an ancestor and all of its descendants), the highly derived pygostylians (*Confusciusornis*, enantiornithine, and more derived birds: Cau 2018) are excluded from this particular study. None of the currently known Mesozoic members of this clade are likely to have competed over the primary resource of significance here, namely dead dinosaurs. The skull, and consequently the feeding ecology, of the large probable ornithurine bird *Gargantuavis* remains unrecovered (Buffetaut and Angst 2020); however, barring discovery that this was a Maastrichtian phorusrhacid-mimic it will be omitted as a dinosaur-eating theropod.

Similarly, the size class 1 theropods are excluded from the calculations in this study, as taxa of such body size are more likely feeding on invertebrates and microvertebrates and again would not be competing for comparable resources (Hirt et al. 2020). Additionally, several theropod clades (including elaphrosaurine noasaurids, ornithomimosaurs, therizinosaurs, and oviraptorosaurs) evolved away from the ancestral hypercarnivorous diet, instead incorporating foods such as insects and plants (Zanno and Makovicky 2011); these non-predaceous theropods are excluded from the histogram analysis but are included in the total dinosaurian diversity portion of the study. While some of them may have consumed vertebrates, these were likely restricted to small fish, amphibians, mammals, and lizards; it is unlikely that any of these taxa routinely killed and ate other dinosaurs, except for eggs and hatchlings.

The skulls of the peculiar bahariasaurid (Motta et al. 2016; Porfiri et al. 2018; Lamana et al. 2020) theropods *Deltadromeus agilis* and *Bahariasaurus ingens* of early Late Cretaceous northern Africa and *Gualicho shinyae* and *Aoniraptor liberatem* of comparable age in Argentina lack cranial material, and it is possible that these represent large-bodied elaphrosaurine-like noasaurids similar to the much-smaller non-carnivorous *Limusaurus* (Ibrahim et al. 2020). If so, they should not be included among the predatory forms. However, they are here conservatively assumed to have retained the ancestral carnivorous diet.

Other contemporaneous carnivorous taxa, including mammals (Hu et al. 2005), squamates (Wick et al. 2015), and crocodyliforms (Boyd et al. 2013; Sellés et al. 2020) competed with theropods, especially in the smaller size classes. However, the limited size and/or mobility of these taxa compared to predatory dinosaurs meant they were likely only a minor portion of the terrestrial predator guild where larger-bodied dinosaurs were concerned (but see Dal Sasso et al. 2017 for a case of a substantial-sized terrestrial crocodyliform which may have served as the apex predator of its Middle Jurassic community.) These non-dinosaurian carnivores are not included here either as members of the predatory guild nor in the count of prey items.

Adult body size distribution histograms of each community (or potential community) of carnivorous dinosaurs were assembled. Previous work (for example, Travouillon and Legendre 2009) has used this technique in comparing mammalian faunas. Longrich and Currie (2009) and Carbone et al. (2011) have used this method in a limited fashion for a single theropod fauna each, while Mallon (2019) used it to compare the Dinosaur Park Formation dinosaurian assemblage to a series of Cenozoic mammalian communities.

This study only examines faunal assemblages of the Jurassic and Cretaceous. While theropods (Zahner and Brinkmann 2019; Marsh and Parker 2020; Müller 2020) and non-theropod herrerasaurids (Pacheco et al. 2019) were part of the guild of medium-sized terrestrial carnivores in the Late Triassic, the largest predators (as well as the most abundant and morphologically disparate) in these faunal assemblages were pseudosuchian archosaurs (Brusatte et al. 2008; Zanno et al. 2015). Future research to compare the carnivorous guilds of the Triassic with those of the Jurassic and Cretaceous is planned but is not part of the present set of analyses.

The following parameters were used to evaluate whether a particular faunal assemblage was included. At least three distinguishable carnivorous theropod taxa in size classes 2 upwards had to have been confirmed. Additionally, a total of at least six distinguishable dinosaurian taxa (in this case, including size class 1 carnivorous theropods, non-carnivorous theropods of any size, and ornithischian and sauropodomorph dinosaurs) must be documented from this assemblage. In determining total faunal diversity, instantaneous diversity counts were used rather than time-binning: for instance, stratigraphically successive species within subclades of Centrosaurinae in the same faunal zone in the Dinosaur Park Formation (Mallon 2019) would be considered as a single species present at a given time, rather than two species for that fauna. (Whether these are actually chronospecies or represent the termination of a lineage and a replacement from outside this depositional basin is not considered in this analysis.) Woodruff (2019) highlighted some of the difficulties in determining horizon-based species diversity in large dinosaurian taxa.

As a consequence, some particular faunas in a sequence may be excluded even if those stratigraphically above or below were part of the analysis. For instance, the uppermost biozone of the Horseshoe Canyon Formation, containing the triceratopsin *Eotriceratops xerinsularis*, was not included as total dinosaurian diversity was too low (Eberth and Kamo 2019). Similarly, Morrison Zone 1 (the lowermost biozone of that unit) was excluded as lacking sufficient number of diagnosable theropod taxa (Foster 2003). The Middle-to-Late Jurassic Yanliao biota of the Daohugou Formation (Xu et al. 2013) and the Early Cretaceous Jehol biota of the Yixian and Jiufotang Formations (Zhao 2014) were excluded as well: although exceptionally diverse in terms of smaller-bodied (size classes 1 and 2) dinosaurian taxa, the depositional setting of these *Lagerstätten* preferentially excludes common preservation of larger-bodied organisms and hence these assemblages are not broadly comparable samples to more typical fluviolacustrine and deltaic dinosaur-bearing formations. In the case of the Jiufotang Formation among hypercarnivorous dinosaurs there is none currently described between the various (all size class

1) species of *Microraptor* and the proceratosaurid tyrannosauroid (size class 6) *Sinotyrannus kazuoensis*: consequently, there is only that latter carnivorous theropod in the study range and this assemblage fails to meet the “three or more diagnosable size 2 or larger carnivorous theropod” criterion. A few of the Yixian hypercarnivorous coelurosaurs (the primitive tyrannosauroid *Dilong paradoxus* and the compsognathids *Huaxiangnathus orientalis* and *Sinocalliopteryx gigas*) reach size class 2. The first two of these are from the Liujiatun Bed, while *Sinocalliopteryx* is from the older Jianshangou Bed and consequently nearly 1 Myr older. Unfortunately, the stratigraphic level (and indeed most of the relevant geologic context) of the one known giant theropod within the 8 Myr duration of the Yixian Formation (Chang et al. 2009), namely *Yutyrannus huali* (size class 6), is not presently described (Xu et al. 2012). This hinders our ability to put this proceratosaurid in its proper faunal assemblage with regards to the stratigraphically better constrained smaller bodied taxa.

It is recognized that the parameters chosen for the criteria are ultimately arbitrary and not necessarily informed by some biological or sampling reality. They represent an intentional compromise between restricting the study only to the small number of faunal assemblages that have been subjected to substantial multi-decadal research on the one hand and the desire to include as extensive a geographic and stratigraphic range of dinosaurian communities as possible. Potentially future iterations of this or similar work might refine the methodology from its initial version here.

A total of 60 faunal assemblages were recognized, from the Toarcian Cañadon Asfalto Formation of Argentina (Pol et al. 2020) and the Bajocian-Callovian Xiashaximiao Formation

(Lower Shaximiao Formation, or *Shunosaurus-Omeisaurus* assemblage), of Sichuan and Yunnan Basins, China (Li et al. 2011) through latest Maastrichtian upper Hell Creek Formation fauna of the North American Western Interior (Fowler 2017). Twenty-nine of these (mostly from the later Late Cretaceous of Asia and western North America: the Asiamerican landmass of that interval) represent assemblages in which tyrannosaurids and their immediate outgroups were the apex predators; the remaining 31 (representing the Jurassic through early Late Cretaceous, as well as the Gondwanan landmasses of the late Late Cretaceous) had other taxa as their largest predators. These faunal assemblages are described in Tables 1, S1, and S2.

Tyrannosauridae is not presently represented in any fauna in which that clade is not the apex predator; however, earlier tyrannosauroids such as coelurids, proceratosaurids, and stokesosaurids are present in communities with other theropods as the largest forms. These earlier tyrannosauroids are so indicated on their respective histograms. In the present study megaraptorids are not listed as being members of Tyrannosauroidea. However, some recent analyses, such as Delcourt and Grillo (2018), Cau (2018), and Lamanna et al. (2020), find this clade to represent a lineage within Tyrannosauroidea phylogenetically close to Tyrannosauridae. Regardless of their phylogenetic affinity, the long slender snouts, ziphodont dentition, and large grasping forelimbs with exceedingly large unguals of megaraptorids (Lamanna et al. 2020) indicates a different style of prey acquisition in Megaraptoridae relative to Tyrannosauridae. The presence or absence of members of Tyrannosauroidea other than Tyrannosauridae in the non-tyrant faunas is not a factor of the analysis, but the position of these taxa as smaller predators in earlier dinosaurian communities is shown of the histograms.

After histogram construction, the number of size classes in which adult predaceous theropods are not currently discovered was assessed. Size class 1 (<10 kg) was excluded, as was size class 7 (>5000 kg) as only a few theropod lineages achieved this size. In some assemblages no size classes were missing; in others all size classes between 2 and 7 were unoccupied (and thus 4 classes were missing.)

RESULTS

Some representative histograms from the better sampled tyrant faunas are shown in Fig. 2, and from non-tyrant faunas in Fig. 3.

Box-and-whisker plots of the representative classes of fauna are shown as Fig. 4. For the tyrant assemblages the mean number of missing cells was found to be 2.9±0.8 and a median of 3, while for the non-tyrant assemblages this mean was 1.8±1.2 and a median of 2 (full statistics for this and other analyses available in Table S3). To test to see if these represent statistically significant distributions, Student *t*-tests testing for equal means and Mann-Whitney *U*-tests for distributions around equal medians were conducted. These two classes were found to have statistically distinct means ($p = 0.000077$) and medians ($p = 0.00024$). Thus, there is a quantitative difference in the size distribution of theropods in communities in which tyrannosaurids are present versus those in which tyrants are absent.

It is recognized that not all formations have been equally well surveyed. Some have only been explored for a few field seasons, while others have had multiple teams engaged in field work every field season for multiple decades. Nevertheless, this difference in fieldwork does not seem to be the sole or even primary reason for missing medium-sized theropods in the tyrant-dominated assemblages. While it is true that some of the Campano-Maastrichtian Asiamerican strata have only been explored for a few field seasons, other tyrant-bearing formations such as the Hell Creek, Horseshoe Canyon, Dinosaur Park, Nemegt, and Kaiparowits are among the most intensely surveyed dinosaur-bearing units known, rivaled by very few others (e.g., the Morrison). Thus, we would expect on average a better knowledge of theropods of all sizes within these formations compared to more poorly sampled ones, and yet intermediate-sized taxa are rare or absent in these well-studied units. In contrast, less well-studied units such as the Cañadón Asfalto and Huincul Formations of Argentina have already yielded a high diversity of medium-to-large carnivorous theropods (in the first case, the allosauroid *Asfaltovenator vialidadi*, the megalosauroids *Piatnitzkysaurus floresi* and *Condorraptor currumili*, and the abelisauroid *Eoabelisaurus mefi*, and in the second the carcharodontosaurids *Mapusaurus rosea* and *Taurovenator violantei*, the abelisaurids *Skorpiovenator bustingorryi*, *Ilokelesia aguadagrandensis*, and *Tralkasaurus cuyi*, and the ?bahariasaurids *Gualicho shinyae* and *Aoniraptor liberatem*.)

One possibility that might explain this difference would be if the potential prey diversity were lower in the tyrant-dominated assemblages, so that there was less opportunity for niche partitioning among the carnivores and thus lower overall spread of theropod sizes. Recognizing that not all theropods would have eaten dinosaurs of all size classes (Hone and Rauhut 2010), in principle we might expect a more diverse food resource base to support a broader variety of carnivores and thus more extensive niche partitioning. Additionally, all the prey taxa had to pass through the smaller size classes on their way to adulthood, and thus were potentially prey for smaller theropods while they were hatchlings and juveniles (e.g., even *Brachiosaurus* and *Brontosaurus* were potential food for *Ornitholestes*).

Fig. 5A shows the plot of carnivorous theropod diversity against total faunal size; no clear distinction between the two classes is apparent. Box-and-whisker plots of these data are shown in Fig. 5B. The mean number of dinosaurian taxa in the tyrant-dominated assemblages is 13.9±5.8 and a median of 14. In contrast the non-tyrant mean is in fact slightly lower, with a mean of 12.4±4.3 and a median of 12. This slight difference is statistically insignificant, however, as analysis fails to reject the null hypothesis for either the mean (p = 0.28) or the median (p = 0.47).

A related issue to consider is the effect of the presence or absence of sauropod dinosaurs within the community. Such exceedingly large-bodied prey, often greatly exceeding the predator mass in the same faunal assemblage (Sander et al. 2010), could conceivably serve as food items for the entire predatory theropod guild between their eggs to adulthood. The same tyrant dominated Asiamerican communities, or more specifically most of the western North American (Laramidian) component of these, are noteworthy in being among the very few Jurassic and Cretaceous dinosaurian faunal assemblages in which sauropods were absent (D'Emic et al. 2010). Among the faunas in this study, only the Bissekty Formation (Turonian of Uzbekistan) among the non-tyrant assemblages lacks a known sauropod presence, while among the tyrant assemblages sauropods are known at present only from the Iren Dabasu, Bayan Shireh, and Nemegt Formations of Mongolia and the Javelina Formation and Naashoibito Member of the Ojo Alamo Formation of the late Maastrichtian of the American Southwest (D'Emic et al. 2010).

In order to see if the presence of sauropods is reflected in the number of missing size classes, another iteration of comparisons was conducted (Fig. 6). The mean number of missing sizes in sauropod faunas was a mean of 1.9±0.2 and a median value of 2, while those lacking sauropods had a mean of 2.9±0.2 and a median value of 3. Similar to the comparison of tyrant vs. non-tyrant faunas, it was found that these classes were found to have statistically distinct means (p = 0.0021) and medians (p = 0.0059). Thus, this reinforces the observation that the dinosaurian faunas of Campano-Maastrichtian Laramidia (at least) show a different observed guild structure than typical Jurassic-Cretaceous theropod communities.

DISCUSSION

Might the apparent lack of middle-sized (50-1000 kg) predatory dinosaurs in many communities of the Campanian and Maastrichtian of Asiamerica be the product of undersampling? This seems unlikely, as these include some of the best studied dinosaurian assemblages in the world (e.g., Lyson and Longrich 2011; Horner et al. 2011; Larson and Currie 2013; Fowler 2017; Mallon 2019; Eberth and Kamo 2019).

That is not to say that middle-sized predatory dinosaurs are entirely absent in these assemblages. DePalma et al. (2015) document the existence of *Dakotaraptor steini*, a size class 4 (101-500 kg) dromaeosaurid in the upper Hell Creek community. However, its remains are apparently rare enough that its presence was not recovered at all in major census studies of the Hell Creek Formation (Lyson and Longrich 2011; Horner et al. 2011). The troodontid *Latenivenatrix mcmasterae* is a size class 3 (50-100 kg) theropod distributed in both Megaherbivore Zones 1 and 2 within the Dinosaur Park Formation (van der Reest and Currie 2017). Holtz et al. (1998)

proposed that at least some of the troodontids were omnivorous rather than strictly herbivorous, and it might be that they fed on smaller-bodied dinosaurs than comparable-sized eudromaeosaurs; this would be consistent with Torices et al.'s (2018) estimation that troodontids favored softer, smaller, or immobile prey. Potentially *Latenivenatrix* may have effectively been a "smaller" predator than its body size would suggest. Similarly, in the Nemegt Formation the enigmatic theropod *Bagaraatan ostromi* is a size class 3 carnivore (Osmólska 1996). However, the latter is known from a single incomplete skeleton at present. Additionally, there is a size class 4 tyrannosaurid (*Alioramus altai*) in that community, as well as the apex predator *Tarbosaurus bataar* (at size class 5).

However, as the histogram studies show, this situation is in contrast to that seen in typical Jurassic and Early Cretaceous dinosaurian communities, where middle sized taxa (including ceratosaurids, piatnitzkysaurids, metriacanthosaurids, neovenatorids, megaraptorids, and early tyrannosauroids such proceratosaurids and stokesosaurids) occupied these intermediate sizes below the apex predators.

If the distinction of the missing middle-sized portion of the theropod communities is indeed an actual attribute of these assemblages and not simply a taphonomic sampling issue, what might this imply about dinosaurian ecosystems of the Campanian and Maastrichtian of Asiamerica? One possibility briefly suggested previously by Holtz (2004a, 2004b) is that the younger individuals of tyrannosaurids might have occupied these middle-sized niches. That is while the earlier growth stages of (for example *Tarbosaurus bataar*) were not actually distinct taxa such as "*Gorgosaurus novojilovi*' and "*Gorgosaurus lancinator*", but that they were ecologically functioning as distinct predators in their communities. Ontogenetic niche shifts have recently been proposed on isotopic evidence in the Early Cretaceous dromaeosaurid *Deinonychus antirrhopus* (Frederickson 2020).

Consider small-bodied tyrannosaurid individuals such as juvenile *Tyrannosaurus rex* BMRP 2002.4.1 or the juvenile *Gorgosaurus libratus* AMNH 5664 or ROM 1247 (size class 5 individuals). At this size their bite forces are an order of magnitude smaller than the adult individuals (Bates and Falkingham 2012; Gignac and Erickson 2017; Therrien et al. this issue), while their agility as measured by the ability to turn quickly was considerably higher (Snively et al. 2019). At less than 1000 kg these individuals would still be in a size range in which their elongate distal limb proportions would provide a net benefit in maximal speed relative to shorter limbed animals (Dececchi et al. 2020). Such an individual would be functionally distinct from adults of the same species. It might be easier for these partially grown individuals to acquire and dispatch smaller and more agile prey such as ornithomimids, thescelosaurids, and pachycephalosaurids than it would be for the more massive adult relatives. Indeed, Codron et al. (2013) argued that very large theropods may have found such small prey insufficient to supply their meat requirements. In contrast, young tyrannosaurid individuals would likely lack sufficient force to take down the large prey animals such as adult hadrosaurids and ceratopsids known to have been fed upon by fully grown tyrannosaurids (Gignac and Erickson 2017; Therrien et al. this issue). At least some subadult tyrannosaurids were feeding on large-sized food sources (Peterson and Daus 2019), but whether they were scavenging or took down this large prey cannot be determined. Even the mode of prey acquisition and manipulation would be expected to be different in juvenile and sub-adult tyrannosaurids relative to adults. For instance, in some tyrannosaurid taxa the smaller individuals have proportionately longer arms (compare 660 kg *Tyrannosaurus rex* BMRP 2002.4.1 with a humerus 0.39 times the estimated length of the femur, to 0.29 for the same ratio in the ten-times larger specimen FMNH PR2081); the proportionately longer forelimb of younger and weaker-jawed *Tyrannosaurus* might have served in a form of prey capture or manipulation which was lost or greatly reduced in later growth stages.

While some workers consider certain tyrannosaurid specimens (including BMRP 2002.4.1) of the Hell Creek Formation as representing a distinct taxon *Nanotyrannus lancensis* (Bakker et al. 1988; Larson 2013; Persons and Currie 2018), the observation would still remain that younger individuals of *Tyrannosaurus rex* would necessarily pass through these intermediate size ranges. Furthermore, the published specimens of this proposed taxon demonstrate juvenile histological (Woodward et al. 2020) and morphological (Carr 2020) traits, so that even if it is its own species the adult form would presumably be a larger animal.

Brett-Surman (1989, 1997) proposed the concept of "niche assimilation": the observation that large dinosaurs, as terrestrial animals which went through multiple orders of magnitude size growth during ontogeny, were functionally equivalent to what would be in large mammals several successive niches occupied by separate species. For instance, an individual of *Edmontosaurus annectens* was hatched as a dik-dik (*Madoqua* spp.) sized small browser but as an adult equaled or exceeded the size of *Loxodonta africana*, and thus throughout its life cycle operates as the functional ornithischian equivalent of the Serengeti's entire size range of hoofed mammals.

As proposed here, the "tyrannosaurid niche assimilation hypothesis" is the concept that juvenile and subadult members of Tyrannosauridae were the functional equivalent of earlier middle-sized theropod carnivores. Of course, all theropods of size classes 6 and 7 would have occupied these smaller size classes during their growth from hatching to maturity, and thus broadly speaking went through the same general niche shifts as tyrannosaurids. However, species in communities with closer packing of niches might be suspected as being under a different set of selective pressures than those experienced by a species which was the only member of the guild occupying those sizes. Thus, from this hypothesis several predictions can be made.

1) Transitions from one phase of niche occupation to the next might involve rapid transitions or transformations rather than simple gradual allometric trends. Imansyah et al. (2008) and Purwanda et al. (2016) have demonstrated such transformations in anatomy and life habits in *Varanus komodoensis*. Ecological thresholds concerning (for instance) size of prey and style of prey acquisition may be relatively abrupt with increasing size, as described by Carbone et al. (1999), Randolff and Du Toit (2004), and Hirt et al. (2020) (although these authors were concerned with predatory taxa of different sizes rather than different sized individuals of the same species.) Carr (2020), in the most thorough analysis of Mesozoic theropod ontogeny so far, has demonstrated that in *Tyrannosaurus rex* in particular a "secondary metamorphosis" from juvenile to subadult forms, evidenced in nearly every portion of the skeletal anatomy he studied. Additional comparable work on the ontogeny of other large theropods species may demonstrate to what degree this was unique to *Tyrannosaurus rex*, or if were more widespread among tyrannosaurids, or if it were present in theropods in more closely packed guilds. Cullen et al. (2020) demonstrated in a single individual of large bodied carcharodontosaurid from the Huincul

Formation that it showed a much more gradual growth pattern rather than the accelerated growth phase as seen in tyrannosaurids; whether this attribute is present in other non-tyrannosaurids remains to be discovered.

2) In faunas with multiple middle-to-large bodied predatory theropod species, niche partitioning would favor the rapid achievement of adult body size to reduce competition with other sized sympatric theropod species. In contrast, under the tyrannosaurid niche assimilation hypothesis such a pressure might be relaxed for tyrant dinosaurs, such that the energy available from small-to-middle sized prey might be more effectively exploited by the predatory species before it grew too large to acquire such food resources.

The study of ontogeny has been greatly enhanced by histologically based within-species growth curve analysis (Erickson et al. 2001; Erickson 2014; Woodward et al. 2015). Tyrannosaurids have been among the first and most extensively dinosaurian taxa so studied (Erickson et al. 2004, 2006, 2010). While the best or preferred specific methodology for growth curve fitting remains debated (Lee and Werning 2008; Erickson 2014; Myhrvold 2016), age of somatic maturity can generally be assessed by the onset of the external fundamental system (EFS). Previous work has found that tyrannosaurids have among the latest such onset among non-sauropod dinosaurs. For instance, Erickson et al. (2004) found the EFS appeared in tyrannosaurids around ages 14-16 for *Albertosaurus*, *Gorgosaurus*, and *Daspletosaurus* and 18.5 for *Tyrannosaurus*; in contrast, full somatic maturity was found to be achieved at 9 years in the hadrosaurid *Maiasaura* (Woodward et al. 2015) and estimated at 10-15 years in the larger hadrosaurid *Edmontosaurus* (Vanderven et al. 2014).

However, at present while the data for tyrannosaurids can compared to small-bodied theropods and to herbivorous dinosaur species, there are few published studies of other large-bodied theropods for comparison. Despite a large sample size examined no specimen of the Jurassic allosauroid *Allosaurus fragilis* has been found with an EFS (Bybee et al. 2006; Lee and Werning 2008), suggesting we may not have a fully-grown specimen of this commonly recovered theropod species or alternatively that this species did not have determinate growth. (The large sympatric allosaurid *Saurophaganax maximus* may in fact be the fully adult form of *Allosaurus*, but this has yet to be assessed histologically.) Thus, we are not currently in a situation to compare growth history patterns of tyrannosaurids to most other large theropods. Such data would be extremely useful in determining if theropods in closely packed ecosystems had growth patterns similar to tyrannosaurids (perhaps achieving full body size earlier) or not. Indeed, Cullen et al. (2020) found the opposite of the prediction here, and instead that the growth of an unnamed Huincul Formation carcharodontosaurid was more gradual and extended than in tyrannosaurids. Future studies will help to see if this is a typical pattern among non-tyrannosaurid giant theropods.

3) Similar patterns of niche assimilation may be present in later Late Cretaceous Gondwanan theropod guilds. While earlier Late Cretaceous southern continent theropod guilds typically included members of both the ceratosaurian group Abelisauridae and the enigmatic coelurosaur clade Megaraptoridae, the latter clade is not known to extend beyond the Santonian or early Campanian in northern South America, while giant megaraptorids are present and abelisaurids apparently absent in Campano-Maastrichtian southern South America (Porfiri et al. 2018;

Lamanna et al. 2020). Thus, just as the Tyrannosauridae would have been the sole large-bodied theropods of late Campanian and Maastrichtian, the Abelisauridae and Megaraptoridae may have been in the same situation for their respective regions of Gondwana in the same time interval. Thus, they would have had a similar release from the selective pressure of niche partitioning and might have assimilated the niches once occupied by middle-sized theropods in a comparable fashion. If so, we might similarly predict comparable rapid transformations in morphology during ontogeny and/or delays in achievement of somatic maturity as hypothesized for Tyrannosauridae.

As is typical for dinosaurian studies, however, we are hindered by the small sample size of individuals and a dearth of relevant specimens. Future discoveries of growth series of abelisaurids, allosauroids, and other large-bodied theropods, including documentation of their anatomical transformations and histologically assessed chronological ages, will bring our understanding of these other groups of carnivorous dinosaurs to a comparable state as that achieved for tyrannosaurids.

CONCLUSIONS

All large-bodied carnivorous theropod dinosaurs necessarily passed through a wide range of body sizes from hatching to adulthood. Consequently, unless they were provisioned throughout growth, the ecological niche of any given individual shifted throughout its lifetime. For Jurassic through early Late Cretaceous this transition occurred in the context of ecosystems in which the juveniles and subadults potentially competed with other theropod species with medium adult body sizes. As shown here, however, there is an observed quantitative distinction between the theropod guilds of Campano-Maastrichtian Asiamerica and most of the rest of theropod-dominated communities. In the former, tyrannosaurid juveniles and subadults represent most or all of the intermediate-sized carnivorous forms, as medium-sized predatory taxa of other clades are rare or absent. This distinction is independent of the total diversity of potential dinosaurian prey. The cause of this ecological isolation of Tyrannosauridae in Campano-Maastrichtian Asiamerica compared to the rather more ecologically densely packed guilds of other dinosaurian communities remains unresolved. It is noteworthy that in Campanian and early Maastrichtian Laramidia at least these same tyrant-dominated communities are also absent any confirmed sauropod dinosaurs, which might serve throughout their own ontogeny to serve as prey for theropods of all size classes; that said, sauropods are present in at least some Asian tyrant-dominated communities and in the American southwest during the late Maastrichtian.

The absence of potential mid-sized competitors in Campano-Maastrichtian Asiamerica may be a factor in some evolutionary transformations in Tyrannosauridae not yet documented in other large-bodied theropod clades. In particular, tyrannosaurids show profound transitions in potential prey acquisition and dispatch adaptations such as bite force and agility, and recent work on the ontogeny of tyrant dinosaurs demonstrates that in at least some of these species these ontogenetic transformations occurred quite rapidly and dramatically. This might reflect selection in tyrannosaurid evolution favoring distinctly different ecomorphologies and prey selection at different ontogenetic phases as this lineage assimilated the otherwise missing niches of the theropod predatory guilds.

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TABLES

TABLE 1. List of theropod guilds

Faunas within each category listed in stratigraphic order. Tyrannosauroid taxa denoted by asterisk (*). Size classes: 1 = <10 kg; 2 = 11-50 kg; 3 = 51-100 kg; 4 = 101-500 kg; 5 = 501-1000 kg; 6 = 1001-5000 kg; 7 = >5000 kg. Correlations for Western Interior Formations from Fowler (2017).

Tyrant-dominated communities

Hell Creek Formation, Upper (latest Maastrichtian; Montana, South Dakota, North Dakota, USA)

Carnivorous Theropods:

Size class 7	*Tyrannosaurus rex**
Size class 6	--
Size class 5	--
Size class 4	*Dakotaraptor steini*
Size class 3	--
Size class 2	*Acheroraptor temertyorum,* cf. *Richardoestesia gilmorei*, *Pectinodon bakkeri*

Size class 1	--

Non-carnivorous Dinosaurs: 10 spp.

Hell Creek Formation, Middle (late Maastrichtian; Montana, South Dakota, North Dakota, USA)

Carnivorous Theropods:

Size class 7	*Tyrannosaurus rex**
Size class 6	--
Size class 5	--
Size class 4	--
Size class 3	--
Size class 2	*Acheroraptor temertyorum*, cf. *Richardoestesia gilmorei*, *Pectinodon bakkeri*
Size class 1	--

Non-carnivorous Dinosaurs: 11 spp.

Hell Creek Formation, Lower (late Maastrichtian; Montana, South Dakota, North Dakota, USA)

Carnivorous Theropods:

Size class 7	*Tyrannosaurus rex**
Size class 6	--
Size class 5	--
Size class 4	--

Size class 3	--
Size class 2	*Acheroraptor temertyorum,* cf. *Richardoestesia gilmorei*, *Pectinodon bakkeri*
Size class 1	--

Non-carnivorous Dinosaurs: 11 spp.

Scollard Formation (late Maastrichtian; Alberta, Canada)

Carnivorous Theropods:

Size class 7	*Tyrannosaurus rex**
Size class 6	--
Size class 5	--
Size class 4	--
Size class 3	--
Size class 2	Dromaeosauridae indet.*,* cf. *Richardoestesia gilmorei*, Troodontidae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 7 spp.

Frenchman Formation (late Maastrichtian; Saskatchewan, Canada)

Carnivorous Theropods:

Size class 7	*Tyrannosaurus rex**
Size class 6	--
Size class 5	--
Size class 4	--

Size class 3	--
Size class 2	*Acheroraptor* sp., Troodontidae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 4 spp.

Lance Formation (late Maastrichtian; Wyoming, USA)

Carnivorous Theropods:

Size class 7	*Tyrannosaurus rex**
Size class 6	--
Size class 5	--
Size class 4	--
Size class 3	--
Size class 2	*Acheroraptor* sp.., *Richardoestesia* sp., *Pectinodon bakkeri*
Size class 1	--

Non-carnivorous Dinosaurs: 11 spp.

Naashoibito Member, Ojo Alamo Formation (late Maastrichtian; New Mexico, USA)

Carnivorous Theropods:

Size class 7	*Tyrannosaurus* sp.*
Size class 6	--
Size class 5	--
Size class 4	--
Size class 3	--

Size class 2	*Dineobellator notohesperus*, *Richardoestesia* sp., Troodontidae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 8 spp.

Javelina Formation (late Maastrichtian; Texas, USA)

Carnivorous Theropods:

Size class 7	*Tyrannosaurus* sp.*
Size class 6	--
Size class 5	--
Size class 4	--
Size class 3	--
Size class 2	Saurornitholestinae indet., Troodontidae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 4 spp.

Nemegt Formation (early Maastrichtian; Bayankhongor, Ömnögovi, Övörkhangai, Mongolia)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Tarbosaurus bataar*
Size class 5	--
Size class 4	*Alioramus altai*
Size class 3	*Bagaraatan ostromi*

Size class 2	*Adasaurus mongoliensis, Tochisaurus nemegtensis, Borogovia gracilicrus, Zanabazar junior*
Size class 1	--

Non-carnivorous Dinosaurs: 22 spp.

Horseshoe Canyon Formation, Middle (early Maastrichtian; Alberta, Canada)[1]

Carnivorous Theropods:

Size class 7	--
Size class 6	*Albertosaurus sarcophagus**
Size class 5	--
Size class 4	--
Size class 3	--
Size class 2	Dromaeosauridae indet., *Richardoestesia* sp., Troodontidae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 12 spp.

Horseshoe Canyon Formation, Lower (late Campanian; Alberta, Canada)[2]

Carnivorous Theropods:

Size class 7	--
Size class 6	*Albertosaurus sarcophagus**
Size class 5	--
Size class 4	--
Size class 3	--

Size class 2	*Atrociraptor marshalli*, *Richardoestesia* sp., *Albertavenator curriei*
Size class 1	--

Non-carnivorous Dinosaurs: 10 spp.

De-na-zin Member, Kirtland Formation (late Campanian; New Mexico, USA)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Bistahieversor sealeyi**
Size class 5	--
Size class 4	--
Size class 3	--
Size class 2	*Saurornitholestes sullivani,* Troodontidae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 8 spp.

Kaiparowits Formation, Middle (late Campanian; Utah, USA)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Teratophoneus curriei**
Size class 5	--
Size class 4	--
Size class 3	*Talos sampsoni*
Size class 2	*Paronychodon* indet., *Richardoestesia* sp.

Size class 1	--

Non-carnivorous Dinosaurs: 7 spp.

Dinosaur Park Formation, Megaherbivore Assemblage Zone 2b (late Campanian; Alberta, Canada)[3]

Carnivorous Theropods:

Size class 7	--
Size class 6	*Daspletosaurus* sp.*
Size class 5	--
Size class 4	--
Size class 3	*Latenivenatrix mcmasterae*
Size class 2	*Dromaeosaurus albertensis*, *Richardoestesia* sp.
Size class 1	*Hesperonychus elizabethae*

Non-carnivorous Dinosaurs: 9 spp.

Dinosaur Park Formation, Megaherbivore Assemblage Zone 2a (late Campanian; Alberta, Canada)[3]

Carnivorous Theropods:

Size class 7	--
Size class 6	*Gorgosaurus libratus**, *Daspletosaurus* sp.*
Size class 5	--
Size class 4	--
Size class 3	*Latenivenatrix mcmasterae*

Size class 2	*Dromaeosaurus albertensis*, *Richardoestesia gilmorei*
Size class 1	*Hesperonychus elizabethae*

Non-carnivorous Dinosaurs: 12 spp.

Kaiparowits Formation, Lower (late Campanian; Utah, USA)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Teratophoneus curriei**
Size class 5	--
Size class 4	--
Size class 3	*Talos sampsoni*
Size class 2	*Paronychodon* indet., *Richardoestesia* sp.
Size class 1	--

Non-carnivorous Dinosaurs: 3 spp.

Dinosaur Park Formation, Megaherbivore Assemblage Zone 1b (late Campanian; Alberta, Canada)[3]

Carnivorous Theropods:

Size class 7	--
Size class 6	*Gorgosaurus libratus*, Daspletosaurus* sp.*
Size class 5	--
Size class 4	--
Size class 3	*Latenivenatrix mcmasterae*

Size class 2	*Dromaeosaurus albertensis*, *Saurornitholestes langstoni, Richardoestesia gilmorei*, *Stenonychosaurus inequalis*
Size class 1	*Hesperonychus elizabethae*

Non-carnivorous Dinosaurs: 17 spp.

Dinosaur Park Formation, Megaherbivore Assemblage Zone 1a (late Campanian; Alberta, Canada)[3]

Carnivorous Theropods:

Size class 7	--
Size class 6	*Gorgosaurus libratus**
Size class 5	--
Size class 4	--
Size class 3	*Latenivenatrix mcmasterae*
Size class 2	*Dromaeosaurus albertensis*, *Saurornitholestes langstoni, Richardoestesia gilmorei*, *Stenonychosaurus inequalis*
Size class 1	*Hesperonychus elizabethae*

Non-carnivorous Dinosaurs: 16 spp.

Two Medicine Formation, Upper (middle Campanian; Montana, USA)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Daspletosaurus horneri**, *Gorgosaurus* sp.*
Size class 5	--

Size class 4	--
Size class 3	--
Size class 2	*Saurornitholestes* sp., *Richardoestesia* sp., *Troodon* sp.
Size class 1	*Bambiraptor feinbergorum*

Non-carnivorous Dinosaurs: 10 spp.

Judith River Formation (middle Campanian; Montana, USA)

Carnivorous Theropods:

Size class 7	--
Size class 6	Tyrannosauridae indet.*.
Size class 5	--
Size class 4	--
Size class 3	--
Size class 2	*Dromaeosaurus albertensis, Saurornitholestes* sp., *Troodon formosus*
Size class 1	--

Non-carnivorous Dinosaurs: 6 spp.

Oldman Formation, Upper (middle Campanian; Alberta, Canada)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Daspletosaurus torosus**
Size class 5	--
Size class 4	--

Size class 3	--
Size class 2	*Dromaeosaurus albertensis*, *Saurornitholestes langstoni, Richardoestesia* sp., Troodontidae indet.
Size class 1	*Hesperonychus elizabethae*

Non-carnivorous Dinosaurs: 13 spp.

Oldman Formation, Lower (middle Campanian; Alberta, Canada)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Daspletosaurus torosus**
Size class 5	--
Size class 4	--
Size class 3	--
Size class 2	*Dromaeosaurus albertensis*, *Saurornitholestes langstoni, Richardoestesia* sp., Troodontidae indet.
Size class 1	*Hesperonychus elizabethae*

Non-carnivorous Dinosaurs: 2 spp.

Two Medicine Formation, Lower (middle Campanian; Montana, USA)

Carnivorous Theropods:

Size class 7	--
Size class 6	Tyrannosauridae indet.*
Size class 5	--

Size class 4	--
Size class 3	--
Size class 2	*Dromaeosaurus* sp., *Saurornitholestes* sp.
Size class 1	--

Non-carnivorous Dinosaurs: 4 spp.

Hunter Wash Member, Kirtland Formation (middle Campanian; New Mexico, USA)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Bistahieversor sealeyi**
Size class 5	--
Size class 4	--
Size class 3	--
Size class 2	Dromaeosauridae indet., Troodontidae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 5 spp.

Fruitland Formation (middle Campanian; New Mexico, USA)

Carnivorous Theropods:

Size class 7	--
Size class 6	Tyrannosauridae indet*
Size class 5	--
Size class 4	--

Size class 3	--
Size class 2	Dromaeosauridae indet., Troodontidae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 4 spp.

Aguja Formation (middle Campanian; Texas, USA)

Carnivorous Theropods:

Size class 7	--
Size class 6	Tyrannosauridae indet*
Size class 5	--
Size class 4	--
Size class 3	--
Size class 2	cf. *Dromaeosaurus* sp., *Richardoestesia* sp., Troodontidae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 8 spp.

Djadochta Formation (early Campanian; Ömnögovi, Mongolia)

Carnivorous Theropods:

Size class 7	--
Size class 6	--
Size class 5	Tyrannosauridae indet.*
Size class 4	--
Size class 3	--

Size class 2	*Velociraptor mongoliensis*, *Tsaagan mangas*, *Gobivenator mongoliensis*, *Saurornitholestes mongoliensis*, *Byronosaurus jaffei*
Size class 1	*Archaeornithoides deinosauriscus, Mahakala omnogovae, Almas ukhaa*

Non-carnivorous Dinosaurs: 15 spp.

Iren Dabasu Formation (Santonian; Nei Mongol, China)

Carnivorous Theropods:

Size class 7	--
Size class 6	--
Size class 5	*Alectrosaurus olseni**
Size class 4	--
Size class 3	--
Size class 2	Velociraptorinae indet., Troodontidae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 12 spp.

Bayan Shireh Formation, Upper (late Turonian-late Santonian; Dornogovi, Ömnögovi, Mongolia)

Carnivorous Theropods:

Size class 7	--
Size class 6	--
Size class 5	cf. *Alectrosaurus**, *Achillobator giganticus*
Size class 4	--

Size class 3	--
Size class 2	Velociraptorinae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 12 spp.

<u>Non-tyrant-dominated communities</u>

Lameta Formation (late Maastrichtian; Madhya Pradesh, Gujarat, Maharashtra, India)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Indosaurus matleyi, Rajasaurus narmadensis, Rahiolisaurus gujaratensis*
Size class 5	--
Size class 4	--
Size class 3	--
Size class 2	*Laevisuchus indicus*
Size class 1	--

Non-carnivorous Dinosaurs: 5 spp.

Maevarano Formation (Maastrichtian; Mahajanga, Madagascar)

Carnivorous Theropods:

Size class 7	--
Size class 6	--
Size class 5	*Majungasaurus crenatissimus*
Size class 4	--

Size class 3	--
Size class 2	*Masiakasaurus knopfleri*
Size class 1	*Rahonavis ostromi*

Non-carnivorous Dinosaurs: 3 spp.

Allen Formation (middle Campanian-early Maastrichtian; Rio Negro, Neuquèn, La Pampa, Argentina)

Carnivorous Theropods:

Size class 7	--
Size class 6	--
Size class 5	--
Size class 4	*Quilmesaurus curriei, Austroraptor cabazai*
Size class 3	*Niebla antiqua*
Size class 2	--
Size class 1	--

Non-carnivorous Dinosaurs: 11 spp.

Anacleto Formation (late Santonian-early Campanian; Mendoza, Rio Negro, Neuquèn, Argentina)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Abelisaurus comahuensis, Aerosteon riocoloradensis*
Size class 5	*Aucasaurus garriodi*

Size class 4	--
Size class 3	--
Size class 2	--
Size class 1	--

Non-carnivorous Dinosaurs: 5 spp.

Bajo de la Carpa Formation (middle-late Santonian; Rio Negro, Neuquèn, Argentina)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Tratayenia rosalesi*
Size class 5	*Viavenator exxoni*
Size class 4	--
Size class 3	--
Size class 2	*Velocisaurus unicus*
Size class 1	--

Non-carnivorous Dinosaurs: 7 spp.

Portezuelo Formation (late Turonian-early Coniacian; Mendoza, Rio Negro, Neuquèn, Argentina)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Megaraptor namunhuaiquii*
Size class 5	--

Size class 4	--
Size class 3	*Unenlagia comahuensis*
Size class 2	*Neuquenraptor argentinus*
Size class 1	*Pamparaptor micros*

Non-carnivorous Dinosaurs: 6 spp.

Bissekty Formation (middle-late Turonian; Uzbekistan)

Carnivorous Theropods:

Size class 7	--
Size class 6	Unnamed carcharodontosaurid[4]
Size class 5	*Timurlengia euotica**
Size class 4	--
Size class 3	--
Size class 2	*Itemirus medullarius, Euronychodon asiaticus, Urbacodon* sp.
Size class 1	--

Non-carnivorous Dinosaurs: 7 spp.

Bajo Barreal Formation (middle Cenomanian-Turonian; Chubut, Santa Cruz, Argentina)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Xenotarsosaurus bonapartei*, Carcharodontosauridae indet., Megaraptoridae indet.
Size class 5	--

Size class 4	--
Size class 3	--
Size class 2	*Aniksosaurus darwini,* Dromaeosauridae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 6 spp.

Huincul Formation (late Cenomanian; Mendoza, Rio Negro, Neuquèn, Argentina)

Carnivorous Theropods:

Size class 7	*Mapusaurus rosae*
Size class 6	*Skorpiovenator bustingorryi, Taurovenator violantei*
Size class 5	*Ilokelesia aguadagrandensis, Gualicho shinyae, Aoniraptor liberatem*
Size class 4	*Tralkasaurus cuyi*
Size class 3	--
Size class 2	--
Size class 1	*Overoraptor chimentoi*

Non-carnivorous Dinosaurs: 7 spp.

Candeleros Formation (early Cenomanian; Mendoza, Rio Negro, Neuquèn, Argentina)

Carnivorous Theropods:

Size class 7	*Giganotosaurus carolinii*
Size class 6	*Ekrixinatosaurus novasi*
Size class 5	--
Size class 4	--

Size class 3	--
Size class 2	*Bicentenaria argentina, Buitreraptor gonzalezorum*
Size class 1	--

Non-carnivorous Dinosaurs: 5 spp.

Bahariya Formation (early Cenomanian; Western Desert, Egypt)

Carnivorous Theropods:

Size class 7	*Spinosaurus aegyptiacus*, *Carcharodontosaurus saharicus, Bahariasaurus saharicus*
Size class 6	*Deltadromeus agilis*
Size class 5	*Rugops* sp.
Size class 4	--
Size class 3	--
Size class 2	Dromaeosauridae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 3 spp.

Aoufous Formation (early Cenomanian; Errachidia, Morocco)

Carnivorous Theropods:

Size class 7	*Spinosaurus* cf. *S. aegyptiacus*, *Sigilmassasasaurus brevicollis* (?= *Spinosaurus*), *Carcharodontosaurus saharicus*
Size class 6	*Sauroniops pachytholus, Deltadromeus agilis*
Size class 5	*Rugops* sp.

Size class 4	--
Size class 3	--
Size class 2	Noasauridae indet., Dromaeosauridae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 3 spp.

Echkar Formation (late Albian-early Cenomanian; Agadez, Niger)

Carnivorous Theropods:

Size class 7	*Spinosaurus* sp., *Carcharodontosaurus iguidiensis*, *Bahariasaurus* sp.
Size class 6	--
Size class 5	*Rugops primus*
Size class 4	--
Size class 3	--
Size class 2	--
Size class 1	--

Non-carnivorous Dinosaurs: 2 spp.

Mussentuchit Member, Cedar Mountain Formation (early Cenomanian; Utah, USA)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Siats meekerorum*
Size class 5	--
Size class 4	--

Size class 3	*Moros intrepidus**, Dromaeosauridae indet.
Size class 2	cf. *Richardoestesia*, Troodontidae indet.
Size class 1	--

Non-carnivorous Dinosaurs: 7 spp.

Elrhaz Formation (late Aptian-early Albian; Niger)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Suchomimus tenerensis, Eocarcharia dinops*
Size class 5	*Kryptops palaios*
Size class 4	--
Size class 3	--
Size class 2	*Afromimus tenerensis*
Size class 1	--

Non-carnivorous Dinosaurs: 5 spp.

Cloverly Formation (Aptian-Albian; Wyoming, Montana, USA)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Acrocanthosaurus* sp.
Size class 5	--
Size class 4	Tyrannosauroidea indet.*
Size class 3	*Deinonychus antirrhopus*

Size class 2	--
Size class 1	--

Non-carnivorous Dinosaurs: 8 spp.

Yellow Cat & Poison Strip Members, Cedar Formation (Barremian-early Aptian; Utah, USA)

Carnivorous Theropods:

Size class 7	--
Size class 6	--
Size class 5	*Utahraptor ostrommaysi*
Size class 4	--
Size class 3	--
Size class 2	*Yurgovuchia doellingi, Geminiraptor suarezorum*
Size class 1	--

Non-carnivorous Dinosaurs: 12 spp.

Sao Khua Formation (Barremian; Thailand)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Siamosaurus suteethorni*
Size class 5	*Siamotyrannus isanensis, Phuwiangovenator yaemniyomi*
Size class 4	*Vayuvenator nongbualamphuensis*
Size class 3	--

Size class 2	--
Size class 1	Compsognathid indet.

Non-carnivorous Dinosaurs: 2 spp.

Wessex Formation (late Berriasian-Barremian; Dorset, Isle of Wight, UK)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Baryonyx walkeri, Neovenator salierii*
Size class 5	Tyrannosauroidea indet.*[5], Basal tetanurine[5]
Size class 4	*Eotyrannus lengi**
Size class 3	*Thecocoelurus daviesi*
Size class 2	*Aristosuchus pussilis*, *Calamosaurus foxi*, Dromaeosauridae indet.
Size class 1	*Ornithodesmus cluniculus, Yaverlandia bitholus*

Non-carnivorous Dinosaurs: 10 spp.

Upper Dinosaur Member, Tendaguru Formation (Tithonian; Lindi, Tanzania)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Ostafrikasaurus crassiserratus*, Basal tetanurine[6]
Size class 5	Basal ceratosaur[6]
Size class 4	--
Size class 3	--
Size class 2	--

Size class 1	--

Non-carnivorous Dinosaurs: 8 spp.

Lourinhã Formation (Kimmeridgian-Tithonian; Lourinhã, Portugal)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Torvosaurus gurneyi, Allosaurus europaeus*
Size class 5	*Ceratosaurus* sp., Abelisauridae indet.
Size class 4	*Lourinhanosaurus antunesi*
Size class 3	*Lusovenator santosi*
Size class 2	*Aviatyrannis jurassica,* cf. *Richardoestesia*
Size class 1	--

Non-carnivorous Dinosaurs: 13 spp.

Morrison Formation, Zone 6 (early Tithonian; Western Interior, USA)[7]

Carnivorous Theropods:

Size class 7	--
Size class 6	*Allosaurus fragilis*
Size class 5	*Ceratosaurus nasicornis*
Size class 4	--
Size class 3	--
Size class 2	*Koparion douglassi*
Size class 1	--

Non-carnivorous Dinosaurs: 12 spp.

Morrison Formation, Zone 5 (late Kimmeridgian-early TIthonian; Western Interior, USA)[7]

Carnivorous Theropods:

Size class 7	*Saurophaganax maximus*
Size class 6	*Torvosaurus tanneri, Allosaurus fragilis*
Size class 5	*Ceratosaurus nasicornis*
Size class 4	*Marshosaurus bicentissimus*
Size class 3	*Stokesosaurus clevelandi**
Size class 2	*Coelurus fragilis**
Size class 1	--

Non-carnivorous Dinosaurs: 9 spp.

Middle Dinosaur Member, Tendaguru Formation (late Kimmeridgian; Lindi, Tanzania)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Veterupristatisaurus milneri*
Size class 5	Basal ceratosaur[6]
Size class 4	--
Size class 3	--
Size class 2	Abelisauroid[2], Basal tetanurine[2]
Size class 1	--

Non-carnivorous Dinosaurs: 8 spp.

Morrison Formation, Zone 4 (late Kimmeridgian; Western Interior, USA)[7]

Carnivorous Theropods:

Size class 7	--
Size class 6	*Torvosaurus tanneri, Allosaurus fragilis*
Size class 5	*Ceratosaurus nasicornis*
Size class 4	--
Size class 3	--
Size class 2	--
Size class 1	*Hesperornithoides miessleri*

Non-carnivorous Dinosaurs: 13 spp.

Morrison Formation, Zone 3 (middle Kimmeridgian; Western Interior, USA)[7]

Carnivorous Theropods:

Size class 7	--
Size class 6	*Torvosaurus tanneri, Allosaurus fragilis*
Size class 5	*Ceratosaurus nasicornis*
Size class 4	*Marshosaurus bicentissimus*
Size class 3	--
Size class 2	--
Size class 1	--

Non-carnivorous Dinosaurs: 11 spp.

Morrison Formation, Zone 2 (middle Kimmeridgian; Western Interior, USA)[7]

Carnivorous Theropods:

Size class 7	--
Size class 6	*Allosaurus fragilis*
Size class 5	*Ceratosaurus nasicornis*
Size class 4	--
Size class 3	*Stokesosaurus clevelandi**
Size class 2	*Coelurus fragilis**, *Tanycolagreus topwilsoni**, *Ornitholestes hermanni*
Size class 1	--

Non-carnivorous Dinosaurs: 14 spp.

Shangshaximiao Formation (?Oxfordian; Sichuan, China)

Carnivorous Theropods:

Size class 7	--
Size class 6	*Yangchuanosaurus shangyouensis*
Size class 5	*Szechuanosaurus campi, Yangchuanosaurus hepingensis*
Size class 4	--
Size class 3	--
Size class 2	--
Size class 1	--

Non-carnivorous Dinosaurs: 12 spp.

Shishugou Formation, Upper (Callovian-Oxfordian; Xinjiang, China)

Carnivorous Theropods:

Size class 7	--
Size class 6	--
Size class 5	*Sinraptor dongi*
Size class 4	*Guanlong wucaii**
Size class 3	--
Size class 2	*Zuolong salleei*
Size class 1	--

Non-carnivorous Dinosaurs: 12 spp.

Xiashaximiao Formation (Bajocian-Callovian; Xinjiang, China)

Carnivorous Theropods:

Size class 7	--
Size class 6	--
Size class 5	*Leshansaurus qianweiensis, Yangchuanosaurus zigongensis*
Size class 4	*Kiajiangosaurus lini, Xuanhanosaurus qilixiaensis*
Size class 3	*Gasosaurus constructus*
Size class 2	*Chuandongocoelurus primitivus*
Size class 1	--

Non-carnivorous Dinosaurs: 11 spp.

Cañadon Asfalto Formation (Toarcian[8]; Chubut, Argentina)

Carnivorous Theropods:

Size class 7	--
Size class 6	--
Size class 5	*Asfaltovenator vialidadi*
Size class 4	*Eoabelisaurus mefi, Piatnitzkysaurus floresi*
Size class 3	*Condorraptor currumili*
Size class 2	--
Size class 1	--

Non-carnivorous Dinosaurs: 3 spp.

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[1] The *Hypacrosaurus altispinus-Saurolophus osborni* Dinosaur Macrofossil Assemblage Zone of Eberth et al. (2013).

[2] The *Edmontosaurus regalis-Pachyrhinosaurus canadensis* Dinosaur Macrofossil Assemblage Zone of Ebert et al. (2013).

[3] Megaherbivore Assemblage Zones and subdivisions from Mallon et al. (2012) and Mallon (2019)

[4] Bissekty Formation carcharodontosaurid reported in Tanaka et al. (2020).

[5] Wessex Formation theropods after Naish et al. (2001).

[6] Tendaguru Formation theropods after Rauhut (2005, 2011).

[7] Morrison Formation biozonation from Foster (2003).

[8] Toarcian age for the Cañadón Asfalto Formation from Pol et al. (2020).

FIGURE CAPTIONS

Fig. 1. Hypothetical hatchling albertosaurine tyrannosaurid, from Russell (1970). Reproduced by permission: Dale Russell © Canadian Museum of Nature. Femur length 100 mm. Although other researchers have estimated somewhat different proportions for these individuals (Currie 2003), this reconstruction emphasizes the different morphology, and consequently different ecological role, of young tyrant dinosaurs compared to the adult stages.

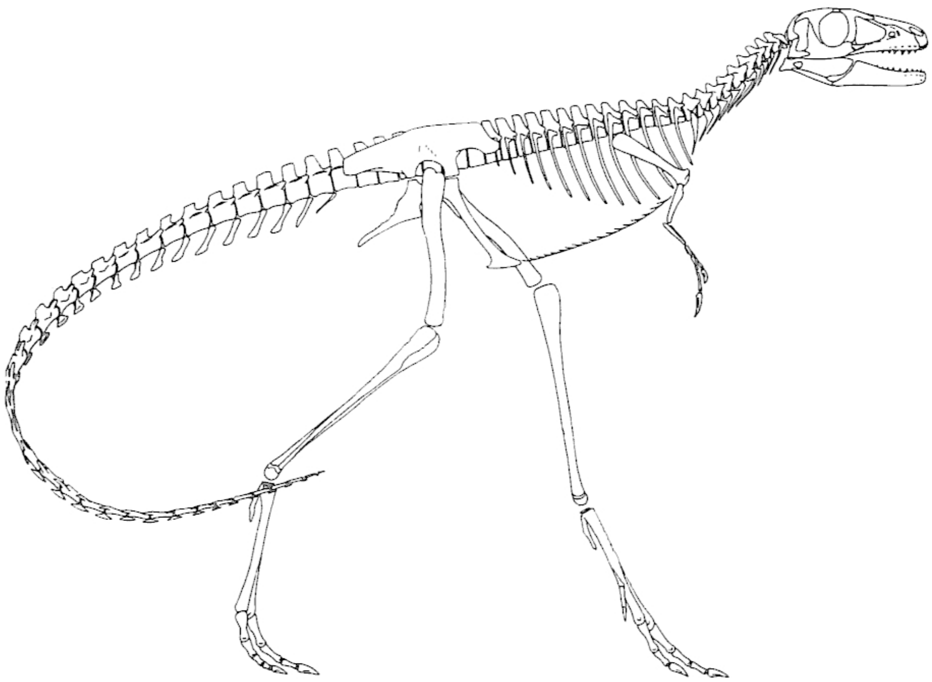
Fig. 2. Histogram of theropod size distribution in selected tyrant-dominated guilds. Solid bars represent non-tyrant taxa; bars with diagonal pattern represent tyrannosauroids. Data from Table 1.

Fig. 3. Histogram of theropod size distribution in selected non-tyrant-dominated guilds. Solid bars represent non-tyrant taxa; bars with diagonal pattern represent tyrannosauroids. Data from Table 1.

Fig. 4. Box-and-whisker plot of number of missing size classes for tyrant and non-tyrant guilds. Data from Table 1. Silhouettes of *Teratophoneus curriei* and *Allosaurus fragilis* from PhyloPic.org, by Scott Hartman and reproduced under CCA-NC-SA 3.0 Unported License: For *Teratophoneus curriei:* http://phylopic.org/image/ad05ef4a-3533-4b30-b1ff-3d1faf393337/ *Allosaurus fragilis:* http://phylopic.org/image/a3fe8af3-8bcf-469a-b3d8-08bc0f071c98/

Fig. 5. A, Scatter plot of number of carnivorous theropod taxa against total number of dinosaur species in faunal assemblages. Crosses, tyrant-dominated faunas; open circles, non-tyrant-dominated faunas. B, Box-and-whisker plot of total number of dinosaurian species in faunal assemblages for tyrant and non-tyrant-dominated faunas. Data from Table 1. Silhouettes of *Teratophoneus curriei* and *Allosaurus fragilis* from PhyloPic.org, by Scott Hartman and reproduced under CCA-NC-SA 3.0 Unported License: For *Teratophoneus curriei:* http://phylopic.org/image/ad05ef4a-3533-4b30-b1ff-3d1faf393337/ *Allosaurus fragilis:* http://phylopic.org/image/a3fe8af3-8bcf-469a-b3d8-08bc0f071c98/

Fig. 6. Box-and-whisker plot of number of missing size classes in theropod guilds for dinosaurian faunas in which sauropods were present and absent. Data from Table 1. Silhouette of *Camarasaurus supremus* from PhyloPic.org, by Mathew Wedel and reproduced under CCA-NC-SA 3.0 Unported License: http://phylopic.org/image/7a99b167-b719-4233-946c-addf3ef1c06c/



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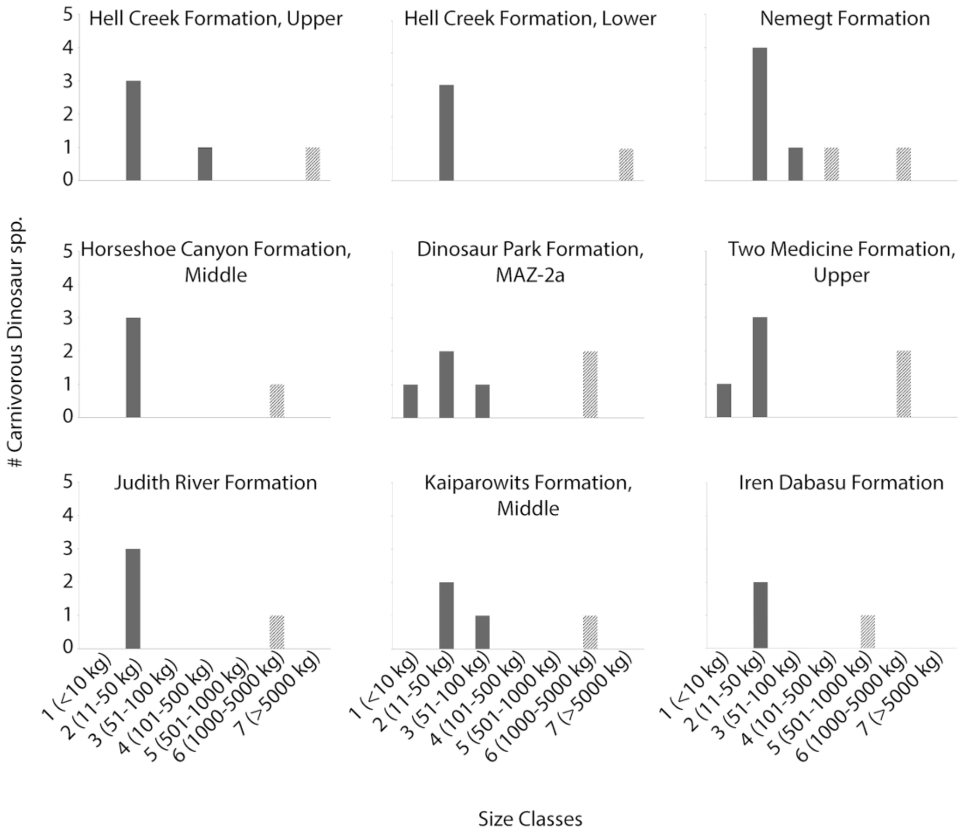

Fig. 2. Histogram of theropod size distribution in selected tyrant-dominated guilds. Solid bars represent non-tyrant taxa; bars with diagonal pattern represent tyrannosauroids. Data from Table 1.

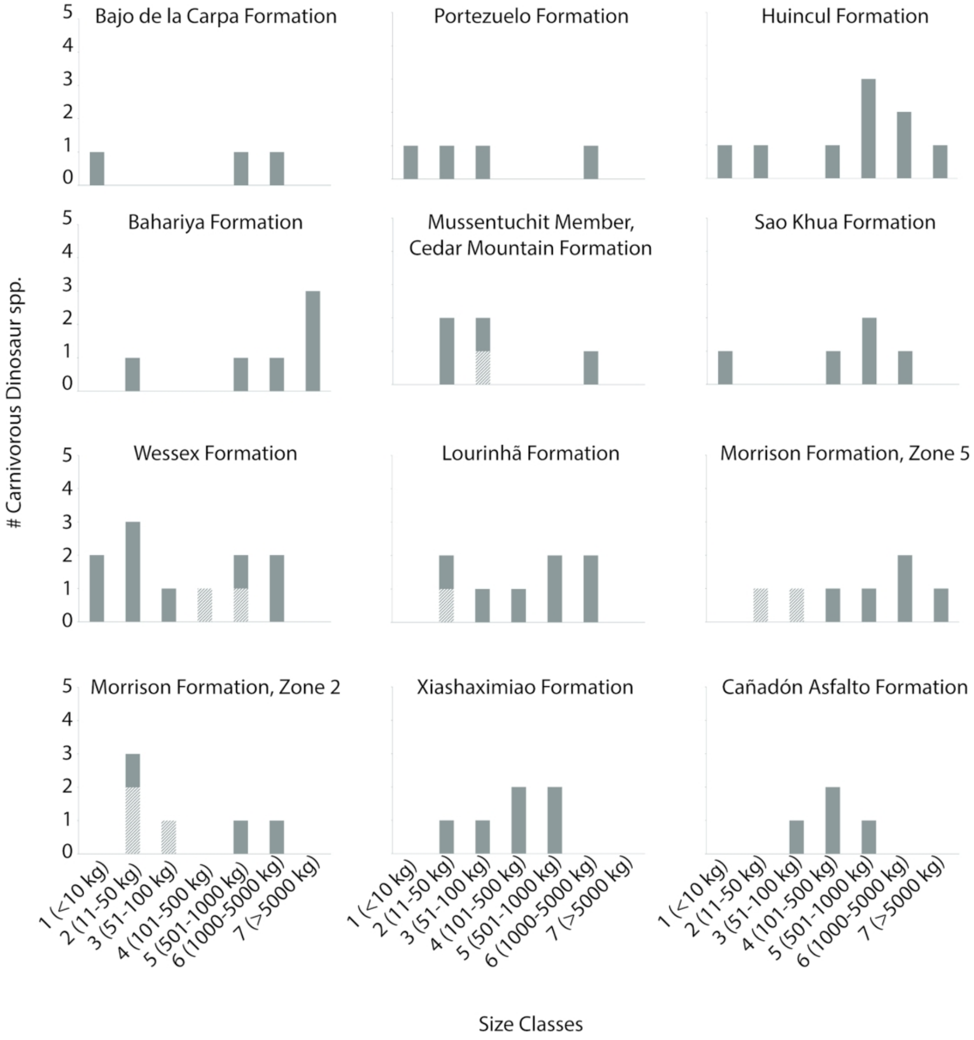

Fig. 3. Histogram of theropod size distribution in selected non-tyrant-dominated guilds. Solid bars represent non-tyrant taxa; bars with diagonal pattern represent tyrannosauroids. Data from Table 1.

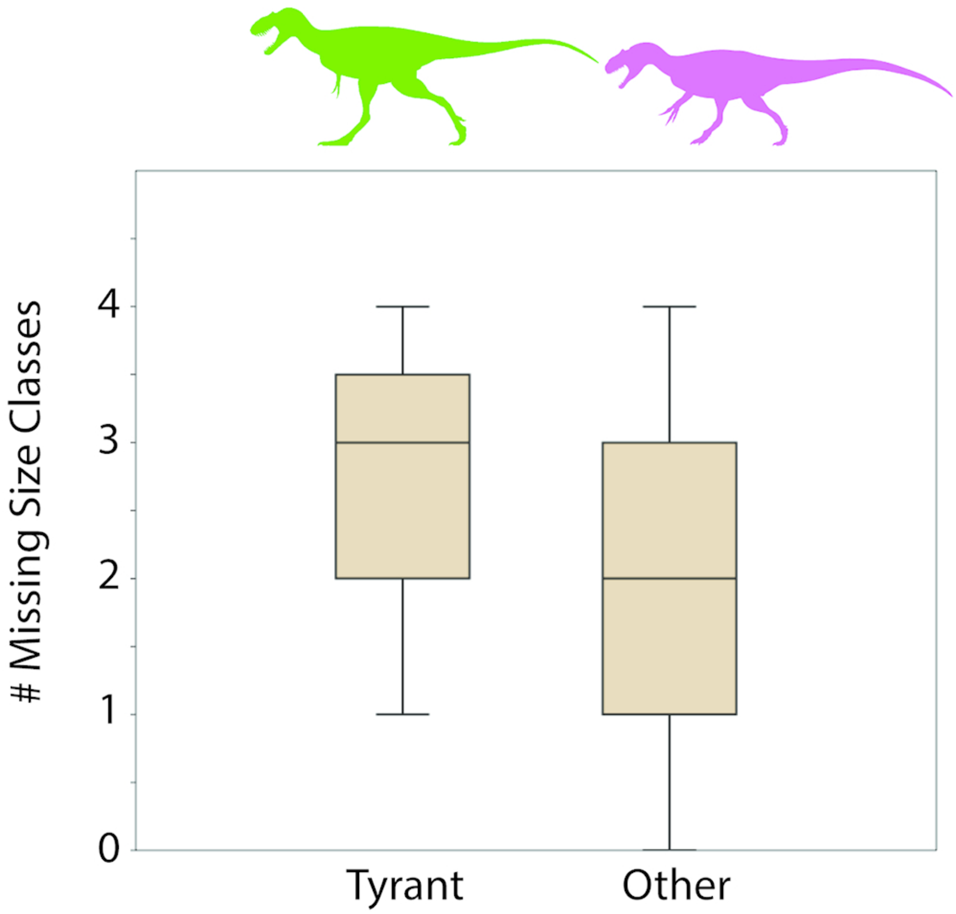

Fig. 4. Box-and-whisker plot of number of missing size classes for tyrant and non-tyrant guilds. Data from Table 1. Silhouettes of Teratophoneus curriei and Allosaurus fragilis from PhyloPic.org, by Scott Hartman Silhouettes of Teratophoneus curriei and Allosaurus fragilis from PhyloPic.org, by Scott Hartman and reproduced under CCA-NC-SA 3.0 Unported Licence: For Teratophoneus curriei: http://phylopic.org/image/ad05ef4a-3533-4b30-b1ff-3d1faf393337/ Allosaurus fragilis: http://phylopic.org/image/a3fe8af3-8bcf-469a-b3d8-08bc0f071c98/

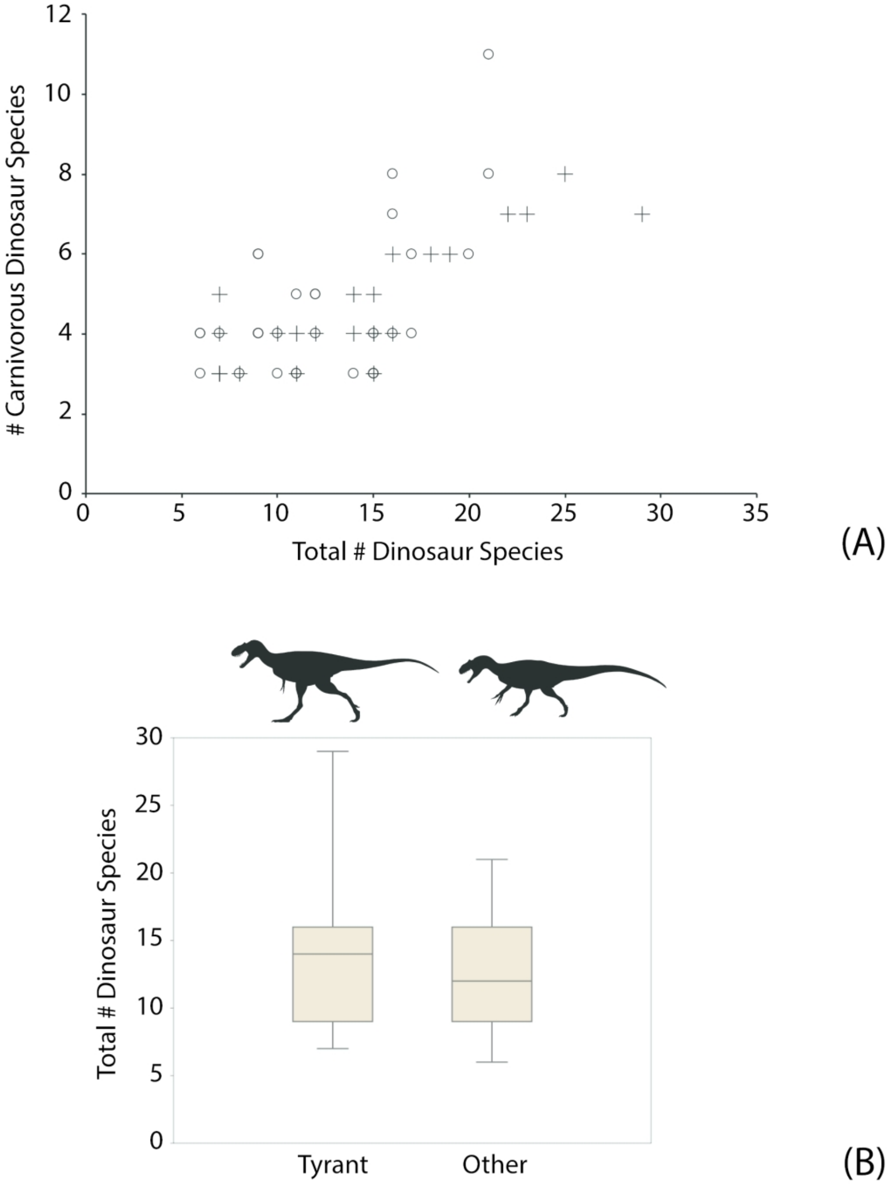

Fig. 5. A, Scatter plot of number of carnivorous theropod taxa against total number of dinosaur species in faunal assemblages. Crosses, tyrant-dominated faunas; open circles, non-tyrant-dominated faunas. B, Box-and-whisker plot of total number of dinosaurian species in faunal assemblages for tyrant and non-tyrant-dominated faunas. Data from Table 1. Silhouettes of Teratophoneus curriei and Allosaurus fragilis from PhyloPic.org, by Scott Hartman Silhouettes of Teratophoneus curriei and Allosaurus fragilis from PhyloPic.org, by Scott Hartman and reproduced under CCA-NC-SA 3.0 Unported Licence: For Teratophoneus curriei: http://phylopic.org/image/ad05ef4a-3533-4b30-b1ff-3d1faf393337/
Allosaurus fragilis: http://phylopic.org/image/a3fe8af3-8bcf-469a-b3d8-08bc0f071c98/

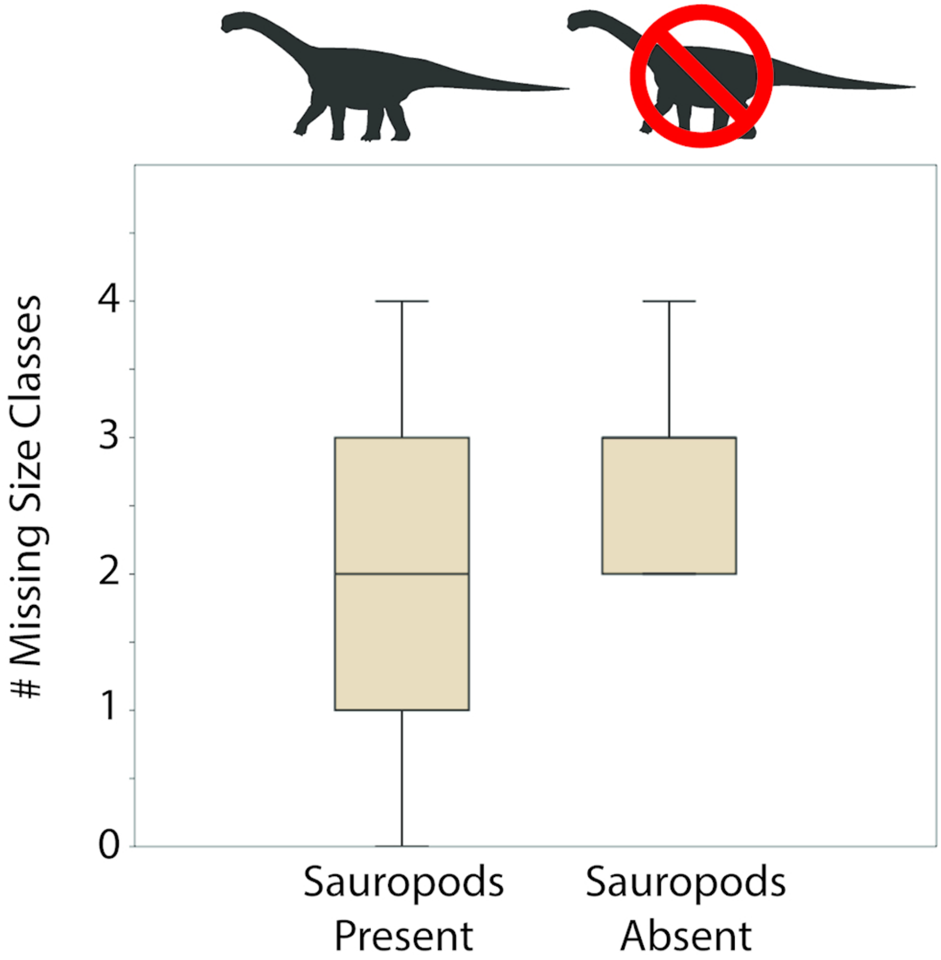

Fig. 6. Box-and-whisker plot of number of missing size classes in theropod guilds for dinosaurian faunas in which sauropods were present and absent. Data from Table 1. Silhouette of Camarasaurus supremus from PhyloPic.org, by Mathew Wedel and reproduced under CCA-NC-SA 3.0 Unported Licence: http://phylopic.org/image/7a99b167-b719-4233-946c-addf3ef1c06c/