**Supplementary**

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

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**Introduction**

In order to keep the contents of the main text to a reasonable length, and needing to address a myriad of taxonomic issues regarding the subjects under investigation—a substantial number stemming from Carr *et al*. (2022)—a large portion of the analysis is contained below (as per Engelman, 2024). The matters discussed largely concern those have been raised in opposition to the MTTH (also see Materials and methods), as well as other items relevant to the competing hypotheses.

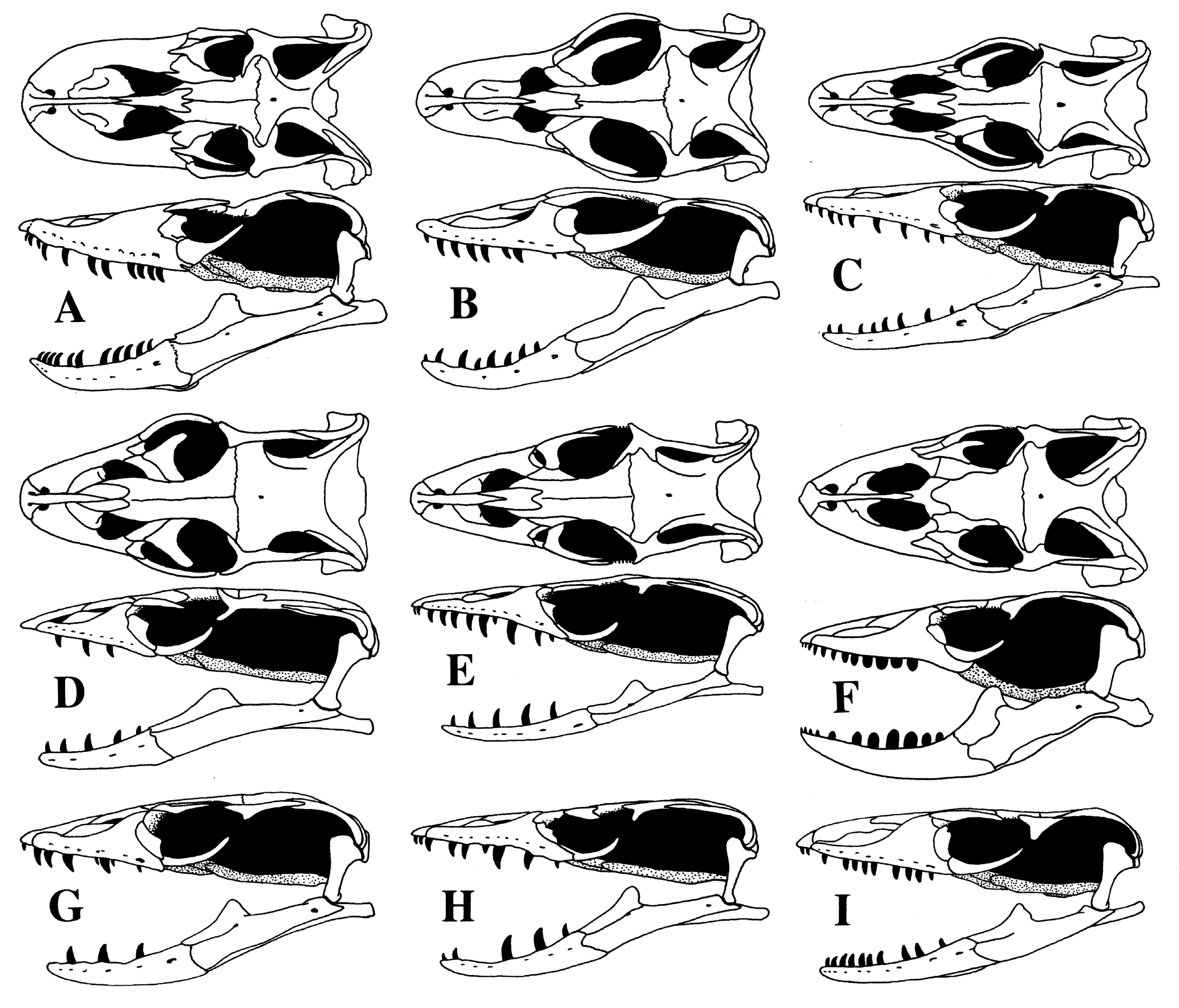
**Current standard general principles and practices for sorting and diagnosing paleospecies**

Being an expansion on Paul *et al*. (2022, including its Supplementary Information; Paul (2022b) discusses some items not herein), the following discussion on determining and diagnosing vertebrate intragenus sibling species examines and cites a large variety of recent examples in the technical literature that have not been considered controversial in the methods utilized. The soundness of the theoretical foundations behind work on paleospecies is examined and assessed from a practical perspective, and are used to test the validity of the assertions and conclusions regarding the subject in Carr *et al*. (2022, proceeding media comments made by the authors of that paper and others considered are addressed in Paul (2022b)).

The standards and practices assessment is used to ascertain the practical boundaries of what is and is not valid in defining sibling species in dinosaurs, in preparation for applying them to the species level taxonomy of TT-zone tyrannosaurs. The applicable results and methods are summarized at the end of the general paleospecies discussion.

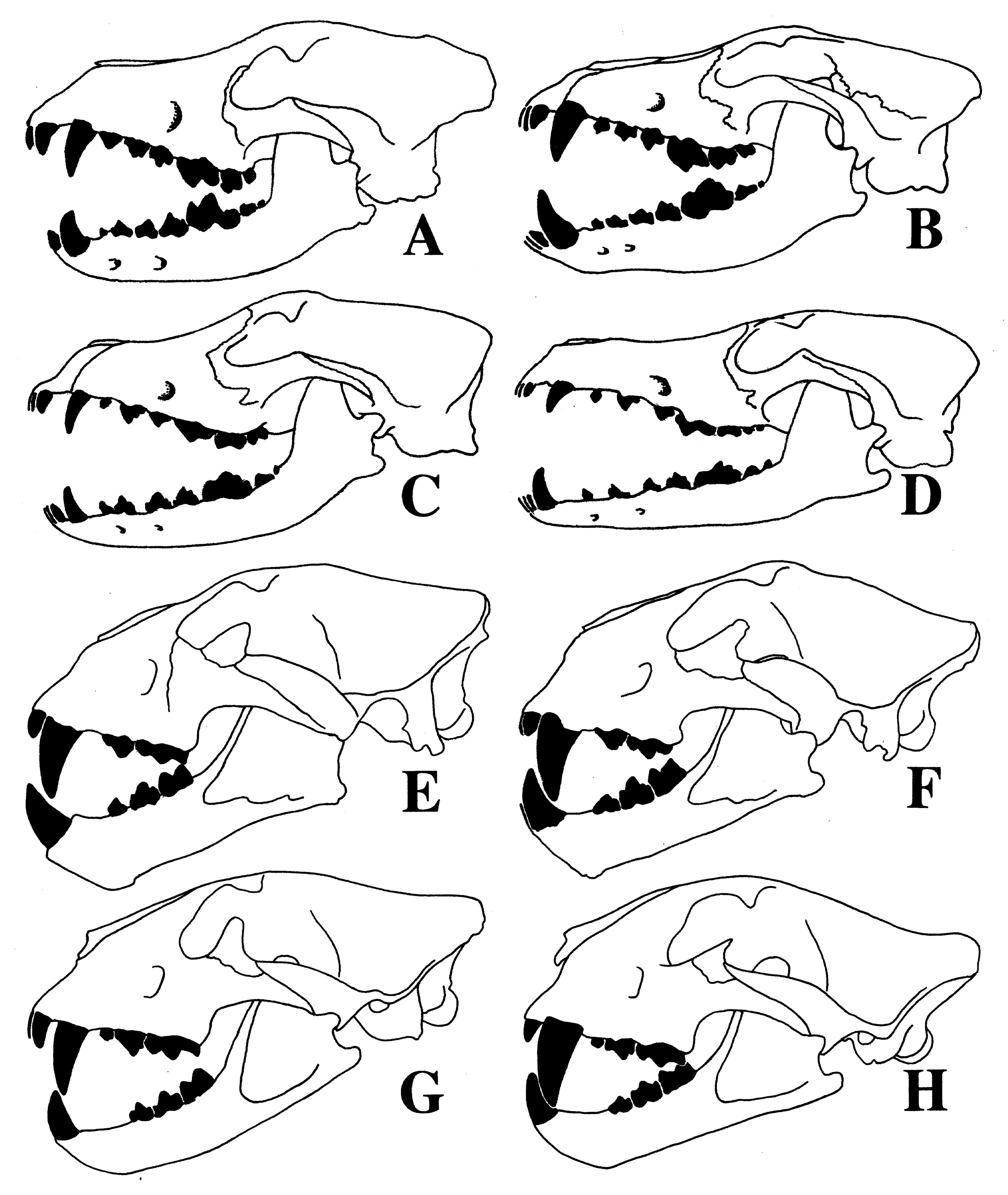
*Monospecificity in a genus is not the automatic null hypothesis*

Carr *et al*. (2022) contend that a single paleospecies is the null hypothesis for tetrapod fossil genera*.* The theory being that the simplest explanation should be presumed unless sufficient evidence indicates otherwise. This is simplistic and problematic for a number of reasons. Biology is normally complex, not simple. Specific to paleotaxa, a genus is always complicated in that it is inherently a collection of a number of species that express varying degrees of gradistic and phylogenetic evolution within the genus (Supplfigs. 1–3), until gradistic differentiation via speciation and phylogenetic divergence add up and result in one or more new genera. In paleozoological taxonomy, the longer a genus is preserved in the known geological record and/or the laterally wider its distribution, the higher the probability that more than one species has been recorded over that time. That is all the more true if other genera preserved in the same sediments show substantial evidence of having undergone speciation. Also a factor is that more than one species of a predatory genus is often found in the same habitat, as per *Canis lupus* and *C*. *latrans* and *Ursus horribilis* and *U*. *americanus* in North America, *Panthera leo* and *P*. *pardus* in much of Africa, and *Panthera tigris, P*. *pardus* and occasionally *P*. *leo* in India. Of course if just one specimen is known from a genus that is just one species, but the more specimens known the higher the likelihood more than one species are on hand. The larger the number of collected specimens contained within a paleogenus both vertically and at a given time, the greater is the probability multiple species have been preserved in the sample.

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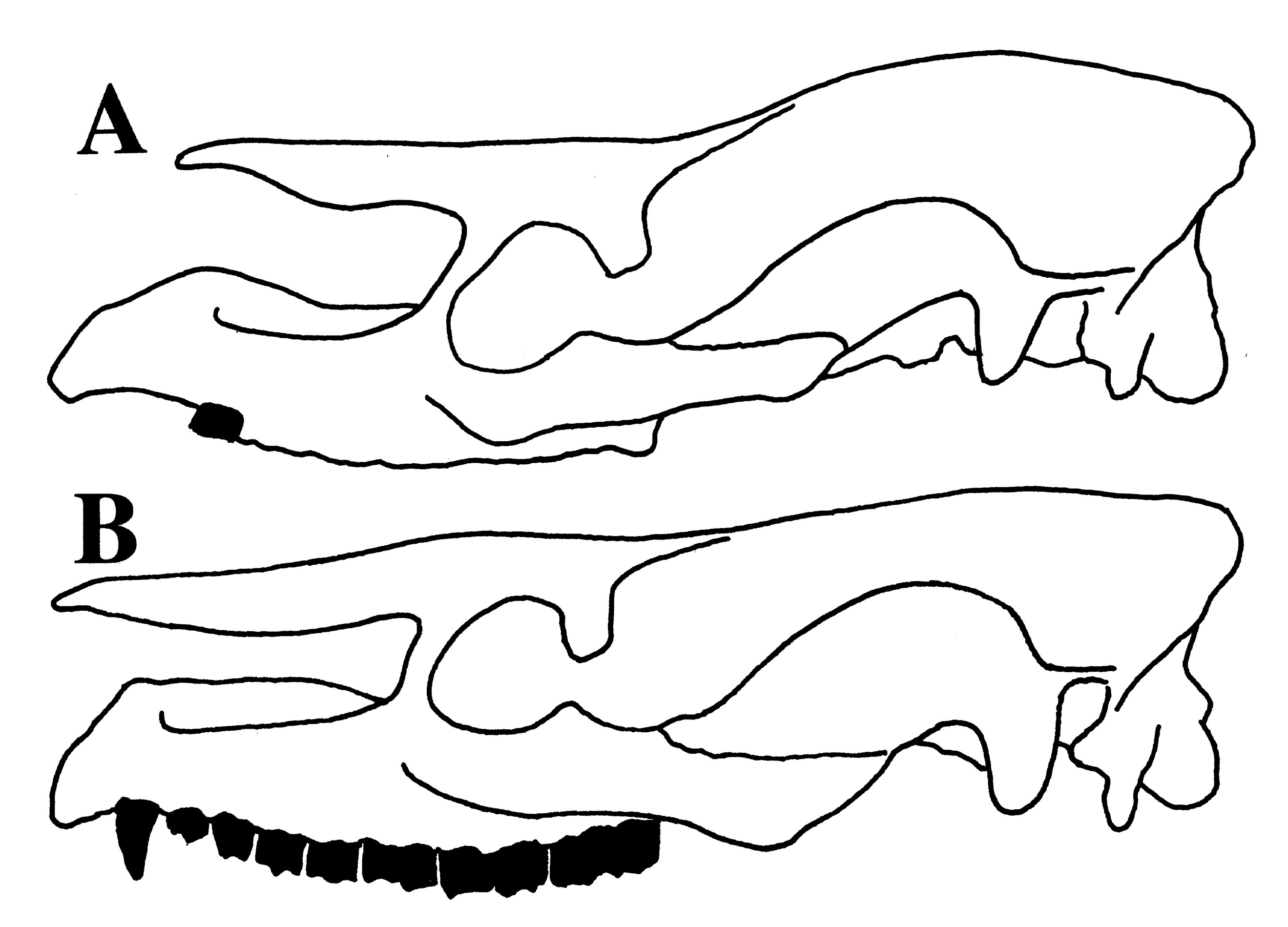
**SUPPLMENTRARY FIGURE 1.** Same length comparisons of predatory reptile *Varanus* skulls in dorsal and/or lateral views. **A**,*V*. *komodoensis*. **B**,*V*. *griseus*. **C**, *V*. *salvator*. **D**, *V*. *gilleni*. **E**, *V*. *prasinus*. **F**, *V*. *niloticus*. **G**, *V*. *semiremex*. **H**, *V*. *beccarii*. **I**, *V*. *bengalensis*. Image source Mertens (1942).

In order to establish that a genus known from a substantial sample collected from sediments that were deposited over a span of hundreds of thousands of years or more, is monospecific, it needs to be shown that there is very little or no pattern of variation in anatomy compared to other species, or within the remains over time, and the basal condition is largely or entirely retained throughout the sample. If instead the observed variation is atypically high, and/or than the variation shows a significant pattern when stratigraphically correlated, then the multispecies hypothesis which is the normal condition of genera is superior to the monospecific alternative. All the more so if the shifts tend to be away from the ancestral state.



**SUPPLMENTRARY FIGURE 2.** Same length comparisons of predatory mammal skulls. *Canis*: **A**, *C*. *dirus*. **B**, *C*. *lupus*. **C**, *C*. *anthus*. **D**, *C*. *simensis*. *Panthera*: **E**, *P*. *spelaea*. **F**, *P*. *atrox*. **G**,*P*. *leo*. **H**, *P*. *tigris*.

Taxonomic implications. The monospecific hypothesis is not automatically presumed superior over the multispecific alternative, if anything the opposite is more likely, especially if a considerable span in time and/or geography is on hand in terms of sediments bearing the fossils of the genus under taxonomic examination. Rather than loading the scientific dice with one or another presumption that can cryptically bias the results, the preponderance of cumulative evidence for whatever results best explain the best current data needs to be the predominant means for arriving at systematic conclusions.



**SUPPLMENTRARY FIGURE 3.** Same length comparisons of brontothere *Metarhinus* skulls. **A**, *M*. *abbotti*. **B**, *M*. *fluviatilis* (posterior skull somewhat dorso-ventrally crushed).

*The varying amount of variation between species within genera*

The amount of morphological skeletal variation between species contained in closely related paleogenera can be very substantial. For example, although the giant, early Maastrichtian Asian tyrannosaurid *T. bataar* was initially considered a species of the markedly later Maastrichtian North American *Tyrannosauru*s (Maleev, 1955; as some have continued to consider plausible (Paul, 1988, 2010, 2016, 2024a but not 2024b; Carr *et al*., 2005)), it is usually considered to be the one known species of *Tarbosaurus* (Brochu, 2003; Hurum & Sabath, 2003; Loewen *et al*., 2013). It is often thought that *Tarbosaurus* and *Tyrannosaurus* are close relatives relative to other tyrannosaurids contained in the Tyrannosaurini (Olshevsky & Ford, 1995; Carr *et al*., 2005; Paul, 1988, 2016, 2024a; Loewen *et al*., 2013; Carr, 2020; Carr *et al*., 2022), although it is possible that their gigantism caused them to parallel one another (Hurum & Sabath, 2003; Paul *et al*., 2022: Supplementary Information; Longrich & Saitta, 2024; this is highly plausible in view of the extensive amount of convergence and parallelism in vertebrates between geographical areas (Oyston *et al*., 2022)). As documented in the main text systematic paleontology section *Tarbosaurus bataar* is readily distinguished from the collection of *Tyrannosaurus* species by a number of features including relatively less massive and more bladed teeth, less extremely broad temporal region of the skull, lacrimals that do not nearly contact one another along the midline of the skull roof, a smaller pubic boot, longer lower hindlimb elements, a typical tyrannosaurid semi-lunate postorbital boss, and other details. That the two taxa are so distinct is not surprising because, well separated in time, geography, and to a certain extent in phylogeny, they are not very close sibling species in an unambiguous single genus. Much closer in form to one another are *Gorgosaurus libratus* and *Albertosaurus sarcophagus* which differ only in some barely noticeable skull features (Paul, 1988, 2008, 2016, 2024a, b; Currie, 2003a).

Within a genus the relationship between species ranges from very close to more distant, so interspecific skeletal variation tends to conversely range from substantial to very minimal at best. *Varanus* contains a large number of extant and recently extinct species (Supplfig. 1). Size ranges from small to gigantic (with *Megalania priscus* subsumed into *Varanus* (Molnar, 2004; Head *et al*. 2009)), teeth from serrated cutting blades to bulbous crushing teeth, skulls from fairly narrow to quite broad, skull roof suture patterns differing markedly, as can the robustness of postcrania. On the other hand, some *Varanus* species skeletal details are barely distinguishable (Supplfig. 1C, E, H). *Panthera* contains a number of extant and recently extinct species (Supplfig. 2E–H). Their skulls and skeletons range from significantly divergent, the snow leopard *P*. *uncia* sports an extra-long tail, to too difficult to osteologically segregate (Sotnikova & Nikolskiy, 2006; Christiansen & Harris, 2009; Supplfig. 2I, J). One of the few features that distinguishes the skulls of lions *P*. *leo* and tigers *P*. *tigris* is the convex ventral rim of the mandible of the former compared to the flatter configurations found in the tiger and other *Panthera*. Sotnikova & Nikolskiy (2006) observe that the cave lion *P*. *spelaea* and its probable descendent the American lion *P*. *atrox* are barely distinguishable from one another, including flat bottomed mandibles (Supplfig. 2E, F). While the robust timber wolf *Canis lupus* (Supplfig. 2B) is not difficult to tell apart from the Ethiopian *C*. *simensis* and African *C*. *anthus* wolves (Supplfig. 2C, D), the latter two and other gracile *Canis* are not easy to tell apart. The overall species situation with the genus and its close relatives is often problematic (Koepfli *et al*., 2015; Alvares *et al*., 2019; Perri *et al*., 2021), with taxa that are morphologically not distinguishable in their skeleton and even soft tissues appear to be different species genetically. It is interesting that while the skeletons of the Eurasian origin timber *C*. *lupus* and dire wolves *C*. *dirus* are so alike that they were long considered sibling species (Supplfig. 2A, B), molecular work indicates that the latter is of quite separate American origin (Perri *et al*., 2021) and is its own genus *Aenocyon.*

Taxonomic implications. The degree of differentiation between species is to a great extent a function of the degree of phylogenetic and therefore gradistic divergence between species. Because sibling species that have just diverged from one another are barely anatomically distinct from one another, it may be just one reasonably consistent character that distinguishes them. Large character sets are only expected when two species are evolutionarily spaced out and divergently evolved by a substantial number of intervening species.

*How many hard bone and tooth characters major and minor are needed to diagnose sibling paleospecies*

It follows that as detailed in Paul *et al*. (2022; Supplementary Information) in modern peer reviewed literature as few as one skeletal character, often minor, has been used to separate species extant and fossil known from well documented remains often including complete skulls and skeletons, with many cases involving just two, three or a few features, among continental and marine tetrapods, with proposed species sometimes being contemporary, or at least partly separated stratigraphically (tyrannosaurids, Currie (2003a); ornithopod *H*. *multidens*, Barrett *et al*. (2005); *Panthera spelaea*, *P*. *atrox*, Sotnikova & Nikolskiy (2006); hadrosaurs *Corythosaurus*, *Lambeosaurus*, Evans & Reisz (2007); stegosaurs *Stegosaurus*, *Hesperosaurus*, Carpenter (2010); ornithopods *Dryosaurus*, *Dysalotosaurus*, Hubner & Rauhut (2010); ichthyosaur *Stenopterygius*, Maisch (2008); Maxwell (2012); plesiosaur *Pliosaurus*, Knutsen (2012); brontotheres *Eotitanops*, *Palaeosyops*, *Metarhinus*, *Rhinotitan*, Mihlbacher (2008), Mader (2010); *Psittacosaurus*, Sereno (2010), Son *et al*. (2024); diplodocids *Apatosaurus*, *Brontosaurus*, *Diplodocus*, Tschopp *et al*. (2015); chasmosaurines *Chasmosaurus*, *Navajoceratops*, *Terminocavus*, Campbell *et al*. (2016); Fowler & Freedman (2020); ornithomimids *Ornithomimus*, *Dromiceiomimus*, MacDonald & Currie (2018); allosaurids *Allosaurus*, Chure & Loewen (2020), Danison *et al*. (2024); proboscideans *Mammut*, *Palaeoloxodon*, Dooley *et al*. (2019), Larramendi *et al*. (2020)).

In a reversal of the proposition that species best documented by fossil remains should be distinguished by lots of characters, the *Psittacosaurus* known by the largest number of specimens, *P*. *mongoliensis*, has been distinguished from sister species by the least number of attributes, two, in Sereno (2010). Both characters are minor, consisting of a raised lip on the orbital margin of the prefrontal, and the transverse distal expansion of the ischial blade being about twice the width of the midshaft. For *Mammut pacificus* the diagnostic characters are a molar being unusually narrow, six rather than five fused sacrals, an exceptionally robust femur, no mandibular tusks, and smaller primary tusks (Dooley *et al*., 2019). The characters diagnosing the species of *Stenopterygius* are variations in the degree of tooth reduction, subtle proportions of the body and fins, skull/body length ratios, and size of a distal tarsal relative to other ankle elements (Maxwell, 2012). For *Pliosaurus* the differences are tooth counts, the configuration of the retroarticular process, ventral anatomy of cervicals, and differing limb proportions (Knutsen, 2012). None of these examples has excited strong negative reaction including in the news media of the sort towards the splitting of the tyrant lizard king in their immediate wake.

Ironically, the use of very large skeletal character data sets to discern paleospecies involves its own set of issues. For a number of practical reasons including logistical assembling character lists involving many hundreds of cranial and postcranial attributes in a large number of sufficiently complete fossil specimens within a genus is rarely if ever tried much less achieved. One discouragement is that the utility of so much data is problematic. Because sibling species are so similar in most regards, large character sets risk producing a large amount of useless and potentially misleading background noise—just because 99.9….% of the anatomy of a set of intragenus skeletons is indistinguishable does not mean they are all in the same fossil based species. That is a reason why sibling paleospecies research tends to focus on discerning the limited number of characters that do vary between specimens, a far greater number of details are not tallied they being irrelevant. If a very large number of characters are assessed it becomes difficult to clearly illustrate what was examined and how, making verification and reproducibility increasingly difficult as the character and specimen list piles up. All the more so because the time and effort needed to verify all the character assessments may be very difficult at best to replicate. Godoy *et al*. (2024) note problems in the reproducibility of phylogenetic analyses. Using a very large character set to assess species within the only genus that such is available for is provisional, in that the method as not yet been tested in terms of practicality, utility and reliability on a wide basis. To demonstrate the efficacy of the method it would be necessary to employ it on genera the species of which are well established, including their stratigraphy. Examples would be *Panthera* that includes a number of well documented recent and extant species. *Mammuthus* would also be well suited. For dinosaurs *Triceratops* features a large number of specimens whose geology is established or will be, but the genus lacks a large sample of necessary postcrania. Lancian edmontosaurs have the latter, but not yet the stratigraphy (Paul *et al*., 2022). The dinosaur genus sporting the most species, *Psittacosaurus*, lacks postcrania in some examples, and tight stratigraphy. The number of characters discerning species within small samples of *Allosaurus* (Chure & Loewen, 2020; Danison *et al*., 2024) and *Daspletosaurus* (Carr *et al*., 2017) are not very large and somewhat problematic. Tschopp *et al*. (2015) examined 455 characters in a modest number of usually skullless diplodocid fossils, but in the end the numbers actually distinguishing the widely accepted species came down to just a handful each. Testing the mass character method in dinosaurs may not be possible at this time.

Carr *et al*. (2022) do not agree with earlier media suggestions that intragenus paleospecies require large character sets.

Taxonomic implications. Just one minor character can diagnose a sibling intragenus species, and the use of hundreds of characters to assay such may not be as efficacious as may be thought.

*Strong consistent bimodal character separation is not universal among species within a genus*

Carr *et al*. (2022) indicate character bimodality is important if not critical to species designation and diagnosis. However, as noted in Paul *et al*. (2022), characters used to differentiate and diagnose species are often not bimodal and nonoverlapping in distribution (Maisch, 2008; Maxwell, 2012; Scannella *et al*., 2014; MacDonald & Currie, 2018; Harvati & Ackermann, 2022), and statistical, measurements based bimodality is often not even presented in defense of paleospecies (Mihlbacher, 2008; Mader, 2010; Sereno, 2010; Knutsen, 2012; Tschopp *et al*., 2015; Chure & Loewen, 2020; Fowler & Freedman, 2020; Johnson *et al*., 2020; Danison, 2024). Carr *et al*. (2022) ignore these numerous examples that contradict their view. Bimodality is less likely to occur when more than two species are under examination—while two of the species may exhibit considerable bimodality, a transitional or sibling species may muddy those clear-cut taxonomic waters as exampled below. So can hybridization between closely related species (Barnosky & Bell, 2004; Lister & Sher, 2015; Harvati & Ackermann, 2022).

The promotion by Carr *et al*. (2022) of intrataxa consistency and intertaxa nonoverlap of characters used to diagnose taxa is any case inconsistent on their part, because they use maxillary tooth counts to distinguish *Tyrannosaurus* from *T*. *bataar* even though the numbers vary in the adults of both taxa and sometimes overlap (Osborn, 1905, 1916; Maleev, 1955, 1974; Rozhdestvensky, 1965; Brochu, 2003, Hurum & Sabath, 2003; Carr, 2020).

Taxonomic implications. Strong interspecific bimodality and intraspecific consistency in statistical character results is a paleospecies ideal by no means always achieved. Strong trends are often used.

*Reptile teeth can have diagnostic value at the species level*

The typically simple teeth of reptiles do not contain the intricate taxonomic information common to the complex dentitions of most mammals. But if the tooth characteristics within adults of a reptile genus exhibit of reasonably consistent pattern of differentiation between potential species, then they can be used to help diagnose intragenus paleospecies. Such is common in *Varanus i*n which a number of species have blunt crushing teeth (Supplfig. 1F) that distinguish them from species with more or entirely flesh slicing serrated blades (Supplfig. 1A–E, G–I). For that matter teeth help distinguish tyrannosaurid genera, with the more conical teeth of *Tyrannosaurus* marking it from the rest of the more blade toothed members of the family (Russell, 1970; Paul, 1988; Hurum & Sabbath, 2003; Carr, 2020; Longrich & Saitta, 2024). *Stenopterygius* species are diagnosed in part on differing degrees of tooth reduction (Maxwell, 2012), those of *Pliosaurus* by tooth counts (Knutsen, 2012).

Taxonomic implications. Although not as systematically valuable as is often true of intricate mammal teeth, reptile teeth can help determine the number of species within a genus. This utilization is often limited to large individuals, in order to minimize ontogenetic alterations in tooth forms and counts with ontogeny. Carr *et al*. (2022) do not object to use of reptilian teeth in the process of assaying theropod species.

*Variations in skeletal strength and other proportions can have diagnostic value at the species level*

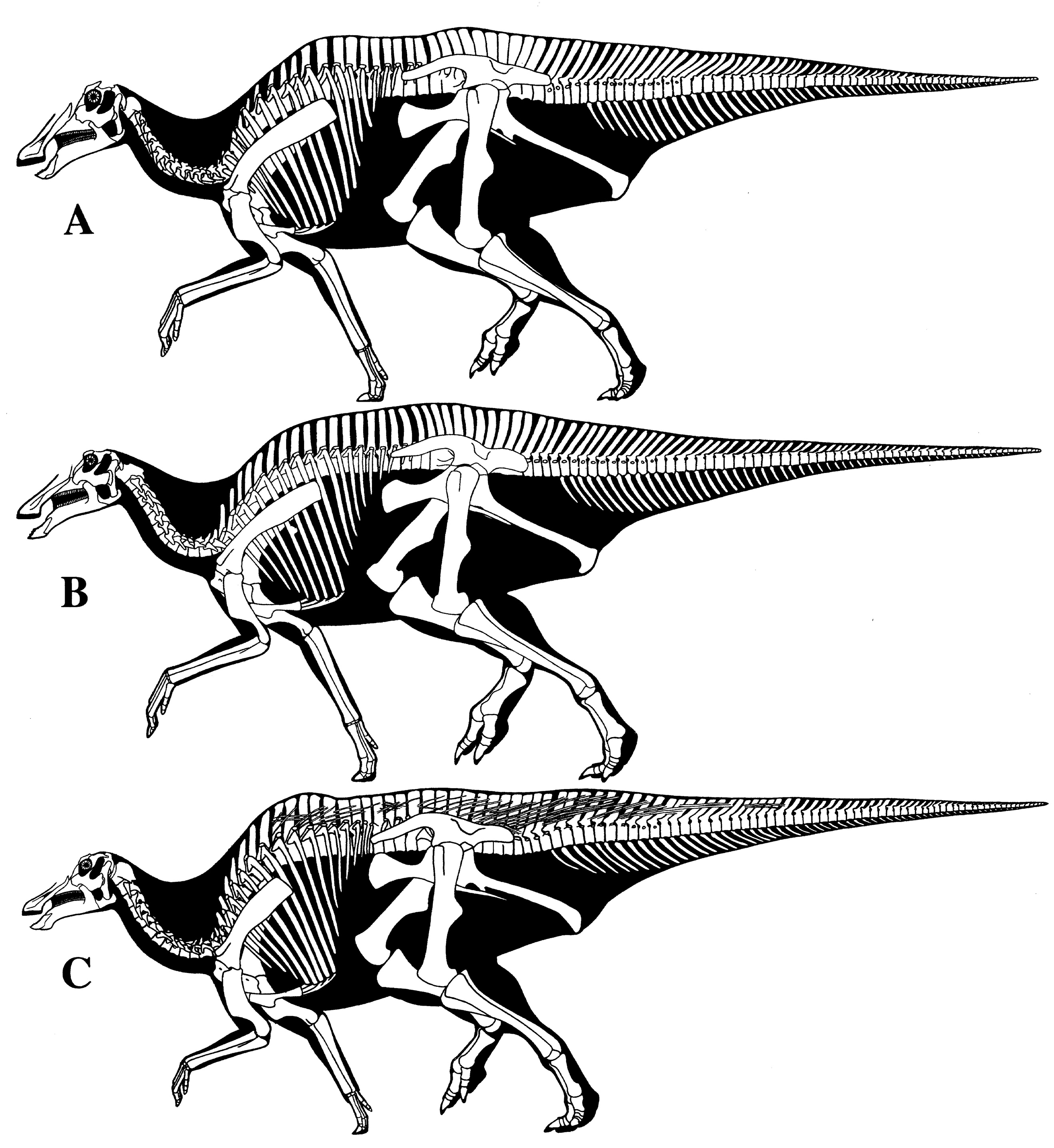
Robustness of the skull and skeleton has important functional implications, and may have additional reproduction associated identification and competition attributes. The latter may be especially true in predators that are less able to use prominent bone based display features. Differences in build that evolve for functional purposes can be secondarily exploited as visual species identification cues and reproductive competition without the development of elaborate display devices. The brontotheres species *Metarhinus abbotti* and *M*. *fluviatilis* are diagnosed only the robustness of their anterior nasals (Mihlbacher, 2008; Supplfig. 3). *Homo sapiens* and *H. neanderthalensis* are distinguished in part on the greater skeletal strength of the latter. Differing robustness is used to help diagnose mastodon and mammoth species (Dooley *et al*., 2019; Larramendi *et al*., 2020). Skeletal robusticity, especially that of the femur, has been used to help distinguish the tyrannosaurids *Daspletosaurus torosus* from *Gorgosaurus libratus* that share the same habitat (Russell, 1970; Paul, 1988; Currie, 2003b; Snively *et al*., 2006). Currently *Ornithomimus edmontonicus* and *Dromiceiomimus brevitertius* are morphologically differentiated by their different femur tibia ratios (MacDonald & Currie, 2018).

Taxonomic implications. Carr *et al*. (2022) do not a-priori object to the use of bone robustness to help examine and diagnose paleospecies.

*How critical a role do or do not differences in prominent display characters play in distinguishing species, particularly in predators*

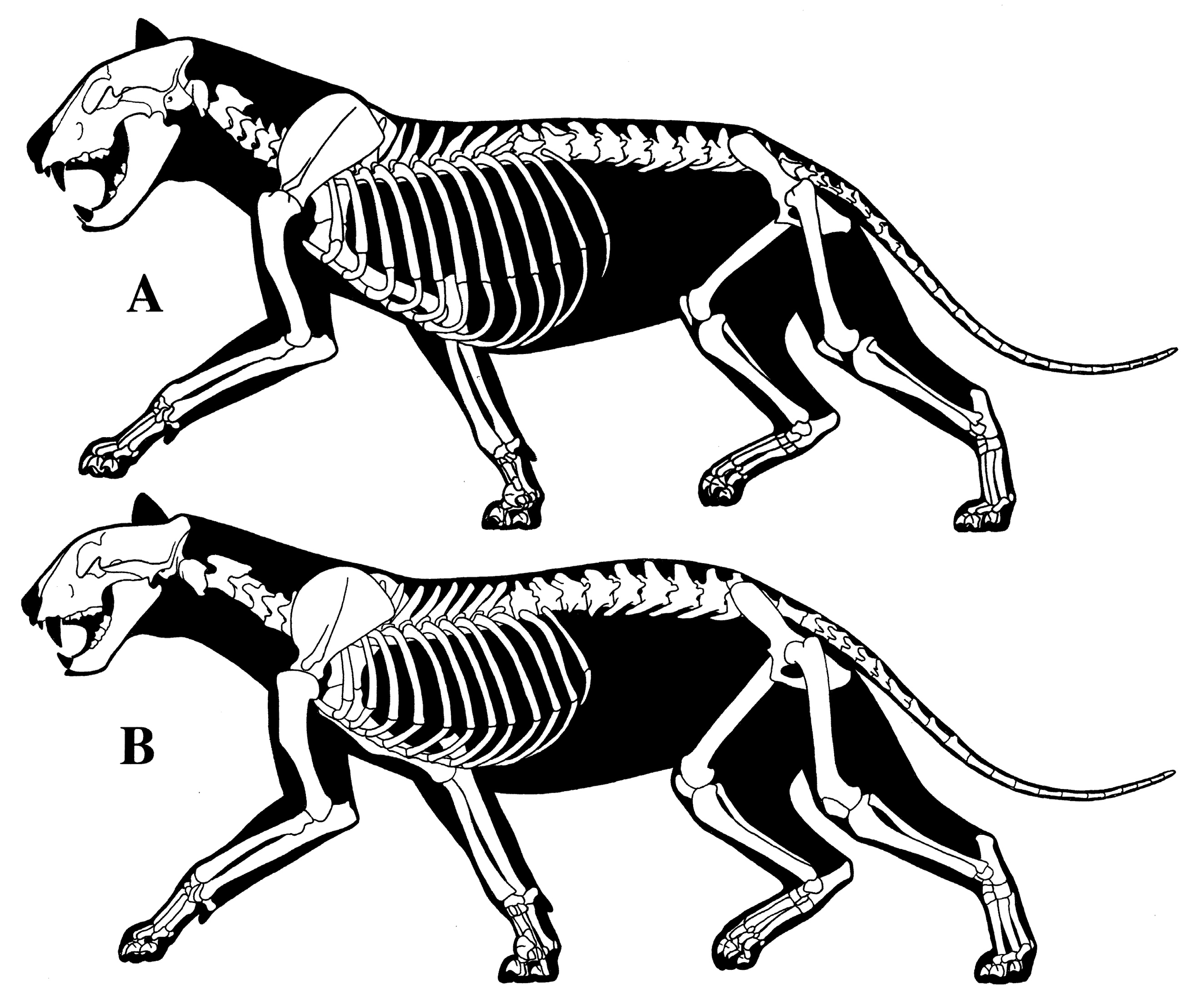
An important feature of species is a reproductively isolated population, although this is not an absolute (Mayr, 1982; Zeinio, 2012). It has therefore been argued that visual display structures commonly evolve for purposes of species identification in order to achieve reproductive isolation, including among dinosaurs (Padian & Horner, 2011, 2014). Others disagree (Hone & Naish, 2013; Knapp *et al*., 2018), and it is notable that African white and black rhinos living in the same habitats share broadly similar horn arrangements, and are otherwise not strongly divergent in appearance aside from their lip morphologies. At the same time, it is true that species are not prone to sport strongly divergent display features regarding their basic shape, particularly between males of a given species, although their degree of development may vary due to dimorphism, maturity, and individual variation. Reasonably consistent differences in bone based cranial displays are therefore widely used to help sort out paleospecies including dinosaurs whether they share a habitat or not (Evans & Reisz, 2007; Mihlbacher, 2008; Scannella *et al*., 2014; Campbell *et al*., 2016; Paul, 2016; Fowler & Freedman, 2020; Mallon *et al*., 2025).

Continental herbivores often evolve elaborate display devices, frequently formed from horns, antlers and tusks that may have evolved at least in part as anti-predator weapons (Nowak, 1991). As well as crests that may have no other important function than display, such as the those of the modest set of birds that have evolved bony cranial displays (Hoyo *et al*., 1992, 1994, 1996, 1997, 2001; Mayr, 2018). Some dinosaur taxa, such as the lambeosaurin species in *Corythosaurus, Lambeosaurus* and others (which ae candidates for being in the same genus (Paul, 2020, 2016, 2024), are not significantly distinguishable cranially outside their display structures or postcranially (Supplfig. 4), it’s all in the crests. Because herbivores commonly evolve large cranial structures in part for defense, these display features can then be modified into very distinctive shapes, even between sibling species. This is true in the primary prey of *Tyrannosaurus*, *Triceratops*, in which the differences in the nasal horns of *T*. *horridus* and its probable descendent *T*. *prorsus* are readily visible—however the differentials between those two species and the intermediate taxon, and between the postorbital horns, are less so as discussed below.

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**SUPPLMENTRARY FIGURE 4.** Same length and approximate same scale comparisons of Campanian North American lambeosaurin dinosaur skeletons sans cranial species specific display structures. **A**,ROM1218. **B**, ROM845. **C**,AMNH5240; testing ability of viewers to tell which are *Corythosaurus casuarius*, *C*. *intermedius* and *Lambeosaurus lambei* without their crests. Full skeletals in Paul (2010, 2016, 2024).

Predators are often another matter. Not bearing large defensive weapons that can be readily utilized and differentiated for display purposes, while using other skeletal elements such as cranial crests solely for display risks being a hindrance to predatory combat, bone based display features are often minimal or absent in land predators. There are no notable sexual display characters decorating the crania and postcrania of *Varanus, Panthera, Canis* and a host of other predaceous tetrapods (Supplfigs 1, 2). Living lions and tigers are easy to visually distinguish because of major differences in fur and coloration, but their skeletons are difficult to tell apart (Supplfig. 5). In many examples skeletal features used to help distinguish species are not sexual display adornments. Among the few predatory groups to have exhibited a fairly frequent propensity towards evolving major cranial display features in the form of ridges, crests, bosses, hornlets and short horns are nonmaniraptor avepods including some basal tyrannosauroids, but tyrannosaurids were limited to very modest structures. Because predators do not need cranial weapons that can also be used for intraspecific display for defense the females are especially free to lack ornamentation as well developed as the males if they have any at all. If male and female skeletons are say robust and graciles respectively, then the configuration of the display structures should not dramatically change in either sex over time. If instead there is a major alteration in either sex, then this is substantial evidence for speciation occurring as time progresses.



**SUPPLMENTRARY FIGURE 5.** Same length and approximate same scale comparisons of *Panthera* species skeletons. **A**, *P*. *leo*. **B**, *P*. *tigris*.

Reducing the sexual selective requirement for significant alterations in display organs can be the evolution of chronospecies. Because the two species do not meet at the same place and time, there is not a need for reformation of display structures even when they are present. This appears to have been true of *Gorgosaurus libratus* and its possible direct descendent *Albertosaurus sarcophagus*, the dorsal display features adorning the nasals, lacrimals and postorbital are not diagnostically distinguishable between the two closely related tyrannosaurid taxa (Fig. 4T–U). The skeletal adaptations used to diagnose the taxa are largely limited to characteristics of the basal braincase (Currie, 2003a).

All the above said, the presence of distinctively divergent optically obvious display characters is strong evidence for the existence of two or more species in a genus. Such is characterized in sibling paleospecies by easily seeable difference in the shape and perhaps the size of readily visible bone display structures, usually cranial. The presence of a single distinctive difference in a display feature is sufficient to distinguish and define sibling species from one another even if there are no other differences in the morphology of the specimens.

Complicating matters is how variation dimorphic, individual and ontogenetic can produce background noise (Hone & Naish, 2013; Knapp *et al*., 2018) that the requires appropriate analysis to sort out species specific display ornaments. In dimorphic species, when females possess species exclusive displays in the form of cranial projections, they tend to be at least basically similar to those of the males in form (as per Nowak, 1991, Hoyo *et al*., 1992, 1994, 1996, 1997, 2001; Mayr, 2018) in order to facilitate species identification—having grossly different cranial displays on the two sexes in one species risks species ID confusion. In the great majority of cases the more elaborate and/or larger display organs adorn the males, so that is the general null hypothesis. The difference is size and shape between the intraspecific sexes range from minimal to substantial. Cassowaries are an exception in that female crests are similar sized to those of males at least relative to body size (Green *et al*., 2022), which may be related to how males provide most of the parental care (Hoyo *et al*., 1992). Differentiation of display structures may be dependent on complex qualitative shape variations that are not amenable to quantitative analysis such as simple orientation or size dimensions, but this does not preclude their critical importance.

Also complicating the situation in fossils is that bony cranial ornaments were covered by keratin sheaths that at least have the potential to alter their appearance relative to their skinless appearance. Among lizards cranial prominences are ensheathed in rather thin, shape conforming keratin (Vickaryous *et al*., 2015; Marghoub *et al*., 2022). Bird crests small and large are usually covered by thin keratin sheaths according to what data is available (Richardson, 1991; Gamble, 2007; Naish & Perron, 2016). An exception is the crest of the helmeted hornbill *Rhinoplax vigil* in which the anterior portion of the casque is extended by an ivory like keratin about two centimeters thick that can be carved (pixels.com/featured/helmeted-hornbill-skull-natural-history-museum-londonscience-photo-library.html; Mayr pers. comm. pointed this out to me), but the gross form of the crest is still not radically altered. The best preserved direct example of nonavian dinosaur cranial display soft tissues, those on the modest sized hornlets of an ankylosaur, indicate that the keratin significantly but not greatly enlarged the ornamentation, by about a fifth to perhaps a third, and retained the basic shape of the underlying bone (Brown *et al*., 2017). It is presumed the same was true of the similarly modest sized cranial structures of tyrannosaurids. The soft tissues that sometimes greatly enlarge the transversely flattened midline crests of pterosaurs (Paul, 2022) do not appear applicable to the lower lying, lateral projections of tyrannosaurid crania. Same regarding the entirely soft tissue midline crests atop edmontosaur hadrosaur crania (Paul, 2016).

Taxonomic implications. It is common, especially among terrestrial predators, for sibling species to not exhibit differences in bony sexual display structures, either because they are not present, or are not different. Establishing consistent variation in such display organs is not necessary to distinguish and diagnose paleospecies. But if the latter are present, then the species based nature of the divergences is solidly established.

*Individual variation has very limited explanatory power for evolutionary trends*

Random individual variation is not a selective force that drives evolution in a direction that is well off the norm for an anatomically uniform group. Ergo, individual variation is a primary causal explanation for variation within a paleogenus only when the observed variation exhibits little or no pattern over time. If a documented pattern of change in one direction or another does exist, then citing individual differences as a cause is at best an idle fallback position of non-scientific opinion that lacks supporting evidence or any cogent evolutionary explanatory power. That is all the more true if the observed variation in a genus exceeds that previously observed in its close relations, including the entire family outside the genus. Also working against individuality is when the pattern over time moves the contents of the fossil genus away from the basal/ancestral condition in one or especially more ways. Nor is genetic drift within a species an optimal causal explanation when the fossils are located in the same core region because there is not a coherent causal case of geographic isolation involved and if the changes occur over a wide geography then the drift is likely to result in classic drift speciation (Mayr, 1982).

Taxonomic implications. Genetic evolution via speciation is the superior, positive, go-to hypothesis when the fossil record reveals a distinct pattern of directional change, especially when it is away from the ancestral condition.

*Sample sizes do not need to be large, nor is deep statistical analysis necessary, to designate regularly used intragenus paleospecies*

*Psittacosaurus i*s widely accepted to contain a large number of species with some consisting of a few or just one specimen (Sereno, 2010; Son *et al*., 2024). The number of specimens placed within two species of *Apatosaurus* is four, within three species of *Brontosaurus* is three, in two species of *Diplodocus* it is five; most of these specimens lack skulls (Tschopp *et al*., 2015). MacDonald & Currie (2018) used about two dozen ornithomimid specimens to statistically parse out species of *Ornithomimus* and *Dromiceiomimus*, with nine actually pertaining to the two genera. The species of *Lambeosaurus* have been determined by about a dozen large specimens (Dodson, 1975; Evans & Riesz, 2007). Scannella *et al*. (2014) state that over 50 specimens were examined, but the number of specimens that are both stratigraphically correlated and the measurements of which are statistically analyzed is about three dozen, some of which are juveniles. The adult specimens needed to determine a second *Daspletosaurus s*pecies was less than half a dozen according to Carr *et al*., (2017).

Papers dealing with paleospecies that have not deployed extensive number crunching statistical analysis if any include Barrett *et al*. (2005) Sotnikova & Nikolski (2006), Evans & Reisz (2007), Mihlbacher (2008), Mader (2010), Maxwell (2012), Sereno (2010), Knutsen (2012), Tschopp *et al*. (2015), Carr *et al*. (2017); Dooley *et al*. (2019), Chure & Loewen (2020), Fowler & Freedman (2020), Larramendi *et al*. (2020) and Danison (2024).

Taxonomic Implications. While more is better when it comes to science, a large array of tetrapod sibling paleospecies are named without statistical analysis, and/or based on just one or a few specimens, such being a normal practice. Although in principle such paleospecies are provisional until large samples become available, in practical terms many low specimen based intragenus paleospecies are widely accepted and utilized. Paleozoology regularly works with the data on hand, not what is wished for.

*Stratigraphic correlations do not need to be precise*

Carr *et al*. (2022) assert that stratigraphic positioning needs to be “accurate” and “precise” for the purposes of intragenera paleospecies assignment. The first is correct, the latter is not because the first is not dependent on the other in the context of paleospecies determination, as causally occurs regarding *Daspletosaurus* in Carr *et al*. (2017). And shortly then after Carr *et al*. (2022) note that taxa can indeed be sorted into broad stratigraphic bins that are taxonomically informative. That is true because unlike many areas of science biology is almost always sloppy and fuzzy. In particular, fine stratigraphic resolution within formations such as that utilized by Scannella *et al*. (2014) are not required for paleospecies determination because fossil species are prone to last for hundreds of thousands of years (Gould, 2002; Burger *et al*., 2004; Maisch, 2008; Scannella *et al*., 2014; Hunt *et al*., 2015; Long *et al*., 2020; Mallon *et al*., 2025). Therefore, all that needs to be known with confidence is at what gross level—lower, upper, middle—a given specimen is from. With formation sublevels usually being many tens to hundreds of meters thick, precisely how many meters a specimen is from the top or bottom of the geological unit is usually not vital. Knowing the sublevel of specimens only generally and not necessarily precisely is commonly followed in intragenus paleospecies studies, Maisch (2008) being an example.

Taxonomic implications. Although the more precision the better is true in science, perfection is the enemy of good enough for what is on hand, when that gets the basic job done. As per the course stratigraphic data that is the best that is available from the sprawling Morrison Formation (Tschopp *et al*., 2015; Chure & Loewen, 2020; Danison, 2024). Because tetrapod species are prone to exist over significant geological time, the stratigraphic measures of that time do not need to be more precise than overall sublevels.

*Stratigraphic correlations do have great utility*

Stratigraphic correlations are not always necessary to designate sibling species, sometimes it is not available (as is often the case regarding specious *Psittacosaurus*, note imprecision of stage levels cited in Paul, 2016, 2024a), but they are likely to be very useful when the data is present. Works that center on stratigraphic correlations include ichthyosaurs (Maisch, 2008; Maxwell, 2012; Brontotheres (Mihlbacher, 2008; Mader, 2010), ceratopsids (Scannella *et al*., 2014; Campbell *et al*., 2016; Fowler & Freedman, 2020).

That the probably permanent inability to determine the basic stratigraphic position in the Hell Creek Formation, much less its precise vertical level to within a few meters, of *Tyrannosaurus* AMNH5027 is an important reason its species status cannot be assigned, is a sterling example of how stratigraphy is very important, but precision not so much.

Taxonomic implications. Paleospecies studies need to incorporate as much geological information as is possible but no need to go overboard on it.

*Taxonomic floaters*

Carr *et al*. (2022) emphasize that for a paleospecies diagnosis to have practical value, it must produce consistent results in identifying incomplete, but not necessarily fragmentary, remains. No references in support of this position are cited. The premise is problematic in view of how it is difficult in respect to some extant genera, such as *Canis*, to assign some members of the genus to specific species (Grubb *et al*., 2000). A substantial number of articulated dinosaur specimens, including some tyrannosaurids, from the Dinosaur Park Formation, have not been assigned down to the species level as per Currie & Russell (2005). Forcing the species of a stratigraphic zone to be one has the advantage of allowing all specimens of that genus to that species, but that may be a false convenience if in doing so results in the evidence for more than one species being played down when more than one was actually present.

Conversely, as long as confidence that only one species is present in a particular level of a formation is well founded, then assigning partial specimens assignable to the parent genus to the known species when the remains lack diagnostic features, but do not possess contrary characters, is the acceptable norm. Galton (1981) being an example.

Taxonomic implications. The goal should not be to diagnose paleospecies in a manner designed to maximize the ability to assign specimens to a species. Diagnoses should be a best effort to characterize the paleospecies that did exist and let the specimens fall where the data on each favors including indeterminate. The more closely species in the sediments are related to one another to more likely it will be difficult to place specimens that are either so incomplete they lack diagnostic structures, and/or have characters that do not sufficiently match diagnosed species.

*Popular prehistoric taxa do not require and must not receive special scientific treatment*

Statements that fossil taxa that enjoy exceptional levels of popularity deserve and require special levels of scientific analysis at the species level are entirely nonscientific. Note that such has not been said regarding extant taxa. Widely liked *Loxodonta* has been split into two species (Grubb *et al*., 2000) with no attention paid to popular thinking on the matter, and the probability that extant *Giraffa* are multispecific (Coimbra *et al*., 2021) has not aroused ardent dispute in popular venues. The quality of scientific research should obviously be the same regardless of public opinion regarding the taxon.

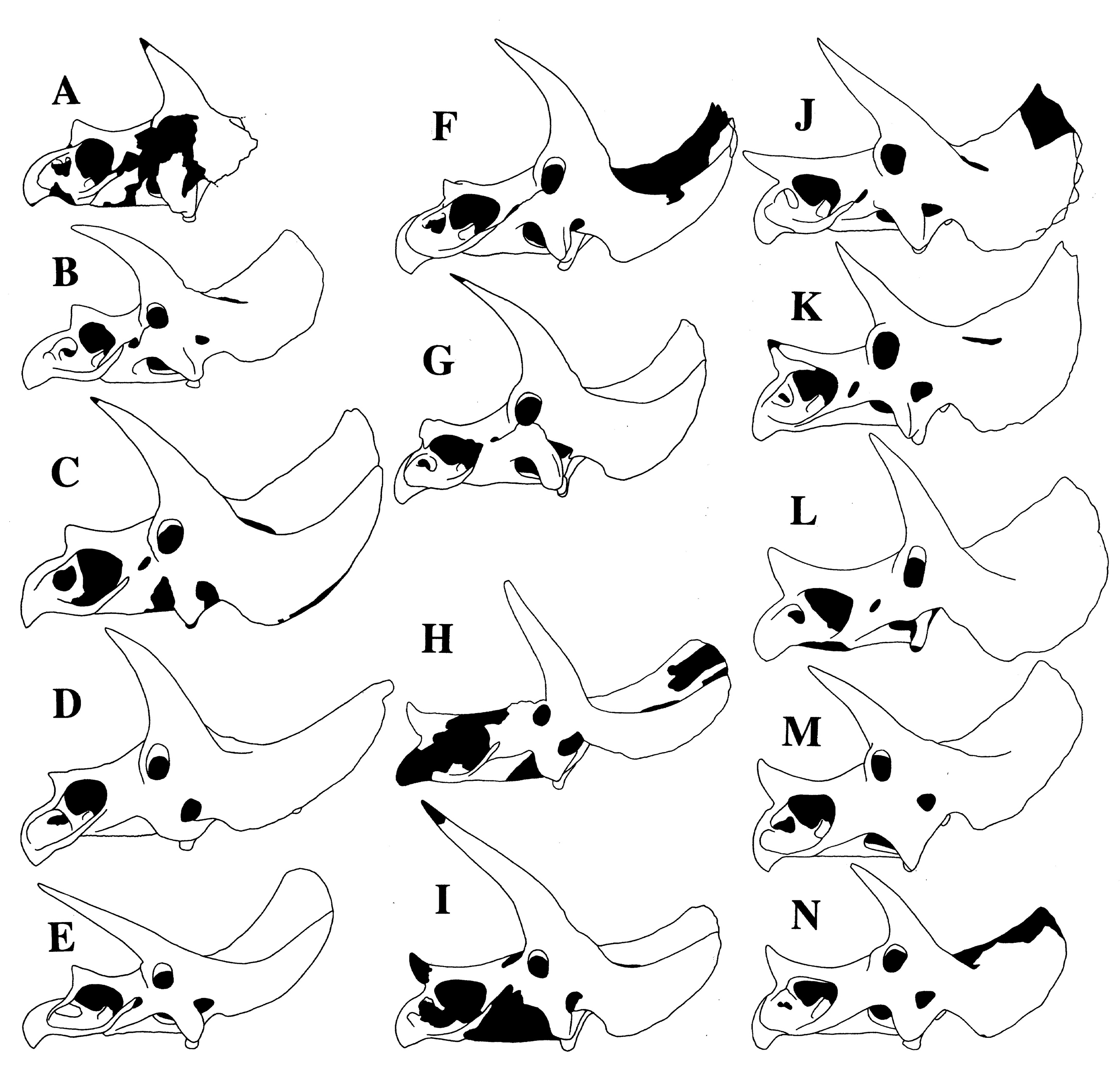
Taxonomic implications. Popular feelings must not play any role in scientific procedures.

*The Scannella et al. intragenera paleospecies assessment standard*

The determination of multispecies of *Triceratops* by Scannella *et al*. (2014) has been considered as setting a new and high standard for the procedure among dinosaurs that other works should aspire to (as per Paul *et al*., (2022), Carr *et al*. (2022) also cite the study as a favorable example). The conclusions of the study are widely accepted and have not been challenged. A detailed examination of the *Triceratops* study shows that while its conclusions are sound, its data and analytical methods contents should not be overstated.

The stratigraphic data is more detailed than usual for Mesozoic dinosaurs, yet in the end it still comes down to basically three levels of the Lancian mid latitude Laramidia TT-zone (as per Paul *et al*., 2022), lower, middle, upper—in their Figure 2 the intricate original data illustrated in Fig. 1 is condensed down to 6 levels, and further contracting them to 3 as they effectively do does not make a difference in the final results. The sample from the lower level is relatively small compared to those from higher in the column. The entire sample is from a limited geographic area, so a large portion of *Triceratops* remains are not considered (skulls illustrated in Supplfig. 6A–G, J–M for example are not in their study). When *Triceratops* specimens from abroad were examined in the 2025 follow up study by Mallon et al. they did not employ precise stratigraphic placement data because such does not exist. Scannella *et al*. incorporates an unusually large sample for dinosaurs, about two and a half dozen specimens of large subadults and adults of varying completeness being stratigraphically correlated (Fig. 1 in Scannella *et al*. (2014)). All are skulls of which the mandible is not examined, nor are postcrania. In a number of cases dimensional values used to calculate ratios are estimates. 6 character ratios or angles relative to stratigraphic level are plotted, all cranial. A few other nondimensional characters are examined. Many hundreds of characters are not assessed. Of the 6 ratios and degrees it is 5 that exhibit significant trends with time, all having to do with the anatomy of the rostrum. Although there is not overlap in the ratios between the extremes of early *T*. *horridus* and much later *T*. *prorsus i*n 5 examples, there is always some degree of overlap one way or another with the unnamed intermediate species, in 5 cases considerable. There are some ratio outliers within species, particularly *T*. *horridus*. Ergo, clear character separation between the proposed species and bimodality is affirmed as not being the norm. This is all the more true because inclusion of specimens from outside the geographic study zone is certain to further increase the overlaps.

An example is the length of the brow horns relative to that of the main body of the skull. There are no particularly short or long examples in *T*. *prorsus*, so this is an attribute that can be used to help diagnose the species unless future discoveries indicate otherwise. *T*. sp. have postorbital horns that range from moderate to very long, so the later can be used to help diagnose the taxon at least relative to *T*. *prorsus*. Overlap with both other species is extensive. *T*. *horridus* brow horns can be almost as long as those of *T*. sp., the difference not being statistically significant. Within the sample utilized in Scannella *et al*. (2014) *T*. *horridus* lacks short postorbital horns. But those of the large *T*. *horridus* holotype (Supplfig. 6A) are shorter than any other *Triceratops* including those in the Scannella *et al*. (2014) sample, so brow horns cannot be used to diagnose that species. How much of the brow horn variation is due to dimorphic, individual or ontogenetic factors has not been fully explored. That the small nasal horn clearly distinguishes *T*. *horridus* from big nose horned *T*. *prorsus* makes this and especially clear cut species specific feature between the two taxa, but this factor is highly variable in the intermediate level skulls that extensively overlaps the other two species while not reaching the extremes of either, so *T*. sp. nasal horns at most can be used to define that taxon by not being either especially small nor large. While the size of the nasal horn is very different between *T*. *horridus* and *T*. *prorsus*, the orientation is not, that factor ranging from nearly horizontal to much more vertical in both due to unknown levels of dimorphism, individuality, or ontogeny. In Scannella *et al*. the one plotted rostrum of a *T*. *horridus* is longer than those of any other *Triceratops*, and such appears true of other members of the species relative to the higher placed species (Supplfig. 6B, D–F), but the beaks of other specimens of that taxon including the holotype do not appear to be especially long Supplfig. 6A, C, G). All *T*. *horridus* specimens in Scannella *et al*. sport an acute angle between the nasal process and the narial strut of the premaxilla in contrast to the shallow angle common to *T*. *prorsus*, but in USNM2412, 4928, and SDSM2760 the angle is very shallow, perhaps more so than yet observed in *T*. *prorsus*. Future expansion of measurements of the narrowness of the nasal process of the premaxilla is likely to increase the degree of overlap between the species, indeed this high probability applies to all the characters.

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**SUPPLMENTRARY FIGURE 6.** Same main length comparisons of *Triceratops* skulls. *T*. *horridus* from lower TT-zone: **A**, holotype YPM1820. **B**, TCM2001.93.1. **C**, SDSM2760. **D**, MNHN1912.20. **E**, AMNH5116. **F**, USNM4928. **G**, USNM1201. *T*. sp. from middle TT-zone: **H**, UCMP113697. **I**,MOR3027. *T*. *prorsus* from high TT-zone: **J**,holotype YPM1822; **K**, YPM1834. **L**, SMNHP1163.4. **M**, LACM7207. **N**,MOR1604.

While the combined anatomy of *T*. *prorsus* skulls is fairly consistent (Supplfig. 6J–N), that of *T*. *horridus* is highly variable (Supplfig. 6A–G; Fig. 2 in Scannella *et al*. (2014)), all the more so when *N*. *hatcheri* and *T*. *latus* are considered to be in that species (Scannella *et al*., 2014; Paul, 2016), so *T*. *horridus* is harder to define, and the possibility that multiple species are involved is a real possibility. The relative scarcity of *T*.sp. specimens, and that none are highly complete (Supplfig. 6H, I), hinders assessing and diagnosing that species.

No autapomorphies were noted by Scannella *et al*. (2014), collective differences being used to sort out the morphotypes as is the frequent practice (contra Carr *et al*. (2022) stating unique features being a necessity for taxa). Interestingly Scannella *et al*. (2014) did not offer a formal systematics diagnoses of the species with assigned specimens even regarding those that they sampled. For purposes of comparative results draft diagnoses are done here, using their characters in the *Triceratops* systematic paleontology section at the end of this Supplement. Some specimens included are from outside their sample. The results show that the three species are not separated from one another by clear, nonbimodal boundaries with consistent character separations. There is considerable overlapping and some ambiguity, with the occasional character exceptions. This is as explained in Paul *et al*. (2022) and herein normal in biology, being the result of mosaic evolution—the potential of hybridization is low for this genus because the species are sequential rather than contemporary. The large expansion of the sample will inevitably further blur the boundaries between the species. Ergo, the diagnoses are inherently somewhat unstable, and will always be so because of the constant expansion of the fossil sample over time. Because the three morphotypes do not overlap in time sexual dimorphism cannot be used to explain the observed pattern. Nor do individual variation or ontogeny offer explanation for what is an apparent selection driven evolutionary pattern. All lower TT-zone *Triceratops* are currently assignable to *T*. *horridus,* and all high placed fossils are *T*. *prorsus*, in part because there is not solid current evidence for contemporary species at those levels the higher especially, in part because specimens appear to sufficiently fit into one or the other taxon. But the much greater variability present in *T*. *horridus* leaves open the possibility of more than one species in the lower TT-zone. Also possible and more probable is sexual dimorphism, with *T*. *latus* perhaps being the adult males of *T*. *horridus* (Paul, 2016) —the consistency of *T*. *prorsus* skulls interestingly leaves no compelling evidence of dimorphism in the species. The situation in the middle level is more ambiguous regarding the number of species and assignments of specimens. Further work may be required to assign some specimens, and it may not be possible to place all examples in the future.

It is notable that the basal *T*. *horridus* retained some basic characteristics of the earlier relative *Eutriceratops xerinsularis* (Scannella *et al*., 2014, Paul, 2016, 2024a) of a small nasal horn, a long anterior rostrum, and the often large brow horns (indeed the strong similarity between *E*. *xerinsularis* and *T*. *horridus* suggests they are congeneric, as per Paul (2016, 2024a), all the more so because *T*. *xerinsular*is is in many regards more similar to *T*. *horridus* than the latter is to *T*. *prorsus*). The later derivation of *Triceratops* away from the old morphotype over the span of the hundreds of thousands of years of the TT-zone is additional and strong evidence that it was undergoing selection driven speciation. Scannella *et al*. could not quantitatively compare the degree of variation in *Triceratops* to still earlier triceratopsines, the data sample for the latter does not exist.

While it incorporates a half of a percent of the characters scored in Carr (2020), Scannella *et al*. (2014) is a far superior examination of intragenus species because the latter was designed to test the question rather than assuming monospecifity, and stratigraphically correlated over five times as many specimens.

Taxonomic implications. Having helped set the modern standard for assessing dinosaur species within a genus, Scannella *et al*. (2014) establishes the following. Necessary for best results is a substantial sample size in the dozens but not necessarily many dozens of specimens—if that is considered insufficient then the conclusion that *Triceratops* or any other dinosaur genus encompasses more than one species is to date not substantiated because larger samples of measureable specimens are either not available or have not yet been analyzed in terms of species determination. A point that applies to an enormous number of tetrapods extinct and extant. All or nearly so of the specimens need to be stratigraphically correlated if a large geological time span is involved. The latter ultimately can be assessed at gross levels of lower, middle and upper within a formation. The sample does not necessarily need to incorporate all known major specimens although doing so produces the most complete possible results (contrary to the insistence that all significant remains be placeable into paleospecies by Carr *et al*. (2022)), and can be limited to just cranial features. Species diagnoses are not set in stone, being subject to significant alterations as new specimens and analysis comes on line. Quantitative dimensional values need not be precise when such are not fully preserved for exact measurement. Unnecessary are large numbers of characters that show strong trends with time, nor clear, consistent, nonoverlapping and explicit character separation and bimodality between species, autapomorphies, or the ready ability to assign all well preserved skulls to a species (contra such claims in Carr *et al*. (2022)). If the basal species retain ancestral conditions that reinforces the reality of that species relative to latter, more derived taxa. The exercise of formally diagnosing the *Triceratops* species demonstrated the utility of the practice, and indicates it should be the required, systematic norm when assaying and determining paleospecies (this is in line with Paul *et al*., 2022 and Carr *et al*., 2022).

*The* Allosaurus *sibling species standard*

Morrison Formation *Allosaurus* has been split into multiple species, *A*. *fragilis* and *A*. *jimmadseni* (Chure & Loewen, 2020; Danison, 2024; skeletals in Paul (2024a, b)), with little or no dissent much less the intense reaction to the species division of TT-zone *Tyrannosaurus*. The type species lived temporally later than the new species, the stratigraphic data is not at all precise with the exceptionally laterally large paleogeography of the Morrison Formation hindering vertical correlations, but is adequate. The characters distinguishing the two species is just 7, all shape morphological, none proportional there being little such variation in the genus (Paul *et al*., 2022), all minor to the degree that the two taxa’s skeletal material is not readily visibly distinguished as is true of large *Panthera* and the like. The one cited display feature is the size of the lacrimal hornlet, that of *A*. *jimmadseni* being seemingly larger. This is problematic in that the quite prominent hornlet of the *A*. *fragilis* lectotype appears to be relatively about as large as that of the *A*. *jimmadseni* holotype and larger than that of MOR693. So at the least there is overlap if the distinction is real, the sample size being too small to be determinative—in that case the diagnostic characters drops to 6, none of a species display nature. The Chure & Loewen (2020) species designation is based on qualitative systematic diagnoses, there are no statistical or phylogenetic analyses, such not be necessary regarding intragenus sibling species which are predominantly a matter of grade, species identification and stratigraphy. The subtle visual variability between *Allosaurus s*pecies is not greater than present in *Tyrannosaurus* (compare Fig. 16 in Chure & Loewen (2020) to Fig. 2A–I herein).

Taxonomic implications. There is no more need to apply statistical or phylogenetic procedures to the *Tyrannosaurus* sibling species problem than there is to the *Allosaurus* species which has not elicited significant opposition. Just a handful or two of characters are required as presented in species diagnoses based on a modest number of specimens, character overlap between the species being allowed. Those who oppose the MTSH subset of the MTTH need to either directly show how the evidence and analysis presented in favor of MTSH is inferior to that for multispecific *Allosaurus*, or that the latter is poorly founded as well (same regarding species within *Daspletosaurus* as per Carr *et al*. (2017), see main text).

*Paleospecies Non/Necessities*—*Results and Summary*

Monospecificity is not the automatic null hypothesis relative to multispecificity within genera, if anything the opposite is true. A given situation is resolved by the preponderance of the currently available collective evidence.

The longer the time over which a genus exists, the more probable it will be the fossils it contains include multiple species, specifically if the existence span exceeds a few hundred thousand years. In that case the null hypothesis shifts somewhat in favor of multiple species.

Between two and three dozen adequate specimens have been used for modern statistical sibling paleospecies work. Far less at the upper end have been used to designate sibling paleospecies, which not do automatically require statistical analysis to be widely accepted.

A study reexamining a prior establishment of paleospecies should not utilize a smaller sample of specimens to do so. All diagnostic type specimens need to be utilized.

Sibling paleospecies are normally diagnosed by a small number of skeletal attributes, as few as one. This is true even if the specimen sample is large.

Degrees of variation observed in one genera need to be compared to those present in other genera, and on up the systematic ladder if necessary, within the clade to help determine the species norms.

Characters used to diagnose sibling paleospecies do not need to include sexual display structures, especially in predators, but because visual species IDs are part and parcel of what a species is, such visually obvious differentiation display features alone are sufficient to determine, diagnose, and name sibling species even when the crania and postcrania are otherwise identical.

Character distribution between sibling species often is not nonoverlapping, bimodal or consistent.

Autapomorphies need not be present to define sibling species.

Reptilian teeth can and are used to help diagnose paleospecies.

Element robustness can and is used to help diagnose paleospecies.

Because the available data is often improving over time, the diagnoses of paleospecies are often adjusted over time.

When the time span covered by a genus is sufficient for speciation to be a serious possibility or probability, over a few hundred thousand years, it is critical that as many specimens as possible be stratigraphically correlated, in order to try to discern if patterns that indicate the evolutionary trends indicative of speciation exist or not.

Stratigraphic correlations to not need to be very tightly constrained, basic time separations are sufficient to geotemporally sort out paleospecies.

To produce compelling results a follow up reexamination of prior works on a set of intragenus paleospecies intended to test the earlier results, the reexamination needs to be a thorough analysis that addresses all critical aspects of the preceding studies.

Not applying the same high scientific standards to unpopular extinct taxa is unscientific, and popular fossils do not require and should not receive elevated standards.

If a substantial sample of fossils from a genus that existed over a sufficient period of time for speciation to have occurred that also exhibit notable variation between specimens is on hand, then defending and establishing monospecifity is not achieved by preferential opinion. A single species must be shown to provide a more coherent and cogent explanation for the variation in the context of the logic of evolutionary adaptation than the multispecies alternative. This is all the truer when the variation exhibits reasonably consistent shifts over geotime.

The methods and procedures for determining paleospecies are not highly rigorous and exacting, biology being inherently irregular and sloppy, not precise and consistent.

Neither complex statistical nor phylogenetic analyses are required for discerning and naming intragenus sibling species, gradistic divergence as presented in diagnoses being fully sufficient and current practice.

All analyses of paleospecies do need to incorporate and consider the alternative possible explanations for the observed pattern, including dimorphism, individual variation, and ontogeny, and a systematic species diagnosis.

**The TT-Zone tyrannosaur taxa problem**

Having taken a look at the general matter of taxonomy in extinct vertebrates, they are applied to the specific issues concerning the Lancian tyrannosaurs.

*Prior work did not show that there is just the one species at any of the size classes*

From the naming of *Tyrannosaurus* (Osborn, 1905) until the 1980s the paucity of specimens precluded analysis of the species the contains. Paul *et al*. (2022) noted that even as the sample began to grow, no prior study had investigated the question of *Tyrannosaurus* species in close to sufficient depth. Carpenter (1990), Larson (1994), Carpenter & Smith (2001) and Brochu (2003) were working with the very limited sample of specimens available at those times, and did not directly test the species question it being de facto assumed there was one species. Larson (2008) was the first analysis that had taken a serious look at the topic, including the first to examine the varying robustness versus gracility of a number of elements in a substantial sample. But that sample was still inadequate. A stratigraphic correlation—which at the time would have observed the critical absence of graciles and one incisiform dentary toothed specimens low in the TT-zone—was not conducted. The degree of femoral variation in *Tyrannosaurus* was not compared to other species and groups. Statistical analyses were not executed. Larson (2008, 2013a, b) and Schmerge & Rothschild (2016a, b) presented extensive evidence that while not necessarily challenging giant *Tyrannosaurus* fossils belonging to *T*. *rex*, did argue that *Nanotyrannus* is a distinct taxon that contains a number of small TT-zone remains. This is turn was countered by Brusatte & Carr (2016), Brusatte *et al*. (2016), Woodward *et al*. (2020), and especially Carr (2020). Who were in turn countered by Longrich & Saitta (2024).

In the wake of the Paul *et al*. (2020) study, Carr (2020) which utilized 1850 characters was suddenly, insistently and remarkably proclaimed as a definitive prerebuttal of the later work that Paul et al. had errantly failed to take into necessary account. This occurred in a wide array of popular venues, as well as Carr *et al*. (2022). This claim was off base in the 2020 study never was intended to be a major test of the question. The titles and contents of the Carr (2020) refute the claims. Carr (2020) is titled “A high-resolution growth series of *Tyrannosaurus rex* obtained from multiple lines of evidence”, there is no mention of the species issue at the adult level. Or in the introductory sections of the paper. Nor in the conclusions except for a brief mention that the *Tyrannosaurus* “x” hypothesis is not viable which Paul *et al*. (2022) agreed with (but see main text). The titles for the supplements include “Character list used to resolve the ontogeny of *Tyrannosaurus rex*, sources cited, and list of ordered characters” and “Character states for each specimen included in the character matrix for recovering the growth series of *Tyrannosaurus rex*”, none of the additional materials were claimed to be pertinent to the species problem. All that makes sense in that the paper focused on the status of the small tyrannosaurid specimens from the TT-zone vis-à-vis the adults, and barely addressed the systematic status of the large specimens that Paul *et al*. (2022) focuses on.

The first mention of intra *Tyrannosaurus* species in Carr (2020) was in a section titled “Assumptions” in which the following is stated—“For the purposes of this study, it was *assumed* (italics added) that the assemblage of *T*. *rex*, which spans Laramidia for a duration of less than 1.0 Ma (Fowler, 2017 note: was more likely 1.5 Ma or even more (Mallon *et al*., 2022; Paul *et al*., 2022 and refs. therein)) was a single nonanagenetic population”. Carr basically presumed that there was only *T*. *rex* from the start, so the paper did not conduct a serious test of the issue in a study mainly looking at the proposed growth of small specimens into the one monospecies. Therefore, because Carr did not take an in-depth look at the species question, that prevented him from finding the evidence for more than one species, so he assumed one species. In contrast, Paul *et al*. (2022) did not make a-priori assumptions about the number of species in the genus of interest, it being part of a long term exploratory effort to see what would turn up one way or the other, and based any whatever conclusions arose out of the preponderance of evidence.

There was a small effort to look at the stratigraphic issue in Carr (2020), but it included only 7 adult specimens (Table 18), just a quarter of the number geologically correlated in Paul *et al*. (2022: Table 1 and Fig. 6 therein). That the stratigraphy was limited to simple lower, middle and upper was entirely acceptable, but even had the paper been designed to detect speciation patterns, so few correlations were far from sufficient to begin to properly test the competing species hypotheses. Carr did not examine the robustness, as is critical to the later Paul *et al*. (2022) study, of the maxilla, dentary, ilium, and humerus. This is difficult to understand because these parameters had been examined in Larson (2008) some of whose other characters were reexamined in Carr (2020), and have obvious potentially critical importance in multiple regards. Without this data species analysis is simply not practical. Femur stoutness was considered for only 4 large specimens, of which just 2 were geoplaced. Paul *et al*. (2022) has a dozen times more stratigraphically placed femurs) which is statistically useless. Same for just two tibias (problematic to use because the strength of the parallel fibula that bore part of the stress load of the middle limb is not taken into account), and there are no adult metatarsals. Nor did Carr look at the fine gradation of robustness as per Paul *et al*. (2022), it was only scored whether the femur ratio is above or below 2.27 (a value that is too low because BHI specimens are excluded, as result of the inclusion of those specimens the more correct dividing value is 2.4 in Paul *et al*. (2022)). What data is in Carr (2020) did not find is low lying graciles. In Carr (2020) the anterior dentary teeth were processed in a nonquantitative manner that is statistically inferior, and with a smaller sample both in total numbers and those that can be stratigraphically assessed than in Paul *et al*. (2022). While the Carr stratigraphic sample is much too small (in part because it excludes all private specimens) to be definitive, it does show all sampled graciles were high in the TT-zone. Not considered in Carr (2020) was the amount of variation in *Tyrannosaurus* compared to other dinosaurs, tyrannosaurids especially. That was entirely logical because Carr’s paper was not devised to examine the species question.

Repeatedly emphasized in Carr *et al*. (2022), as well as many popular commentaries (see Paul, 2022b), were the “1850 variable characters from throughout the skull and skeleton for over 40 (44) specimens” supposedly contained in Carr (2020). The implication, whether intended or not, was that characters were scored 81,400 times, which is not feasible for a single researcher to achieve in a practical time frame. Of the 44 specimens 26 were large known *Tyrannosaurus* specimens critical to species determination. Because the smaller specimens include fossils that do not qualify as tyrannosaurids their inclusion is very problematic at best. Nor were 81,400 characters actually assayed that not being practical. Hundreds of attributes were examined in only two, three or a few specimens. A very large portion were recorded in only one juvenile and one adult, with many being minor attributes of vertebrae caudals especially, and manal and pedal elements, apparently in order to produce an accounting of basic differences between a small individual and an adult in tune with the actual primary subject of the paper. Only a modest fraction of the attributes were scored for up to a dozen to a dozen and a half large specimens and not many more small TT-zone tyrannosaurid fossils they being scarce. So while the Carr character list was laterally broad, its sample depth was too shallow to be statistically highly useful for the species problem. In a large number of cases it is not entirely clear exactly what was being assessed, it not being feasible to clearly illustrate the item being examined and how. An example is character 601 which concerns a groove on the postorbital of ambiguous nature. As a result, verification and replication are often difficult at best and may not be practical—there is irony in this in that Carr has strongly criticized the problems of data replication of privately held specimens as further discussed below. Some features were assessed in a simplistic manner. For example, the postorbital bosses were described as prominent in all large individuals even though there is considerable variation in their development as detailed below, the irregularity of the nasal ridge was treated in a similarly either or manner; presumably again because the only purpose was to contrast the juvenile and adult conditions. A quite large number of the characters that were observed in a substantial number of specimens appear minor in nature and their taxonomic value is correspondingly problematic, risking being the potentially misleading background noise issue cautioned about above. Longrich & Saitta (2024) noted some issues with the Carr (2020) character list.

Carr (2020) was nowhere close to using 1850 characters to examine cryptic species in *Tyrannosaurus*, an issue the paper barely touched upon. It is correspondingly notable that while Carr *et al*. (2022) promotes the value of the 1850 character tabulation in Carr (2020), the former also does not actually attempt to use the over vaunted data base to examine the species question, doing so being highly likely to fail.

While it incorporates over a third of a percent of the features scored in Carr (2020), Paul *et al*. (2022) is a far superior examination of intragenus species because the latter was designed to test the question rather than presuming monospecifity by zeroing in on those few characters that have species identification potential, and geologically correlating over five times as many specimens.

The Carr (2020) work abjectly lacked the ability to discern a species level taxonomic signal with just 7 (albeit adequately) stratigraphically correlated large specimens, only 2 femora tied to the geology, and robustness measured for just a few elements of a few specimens, in a work that largely assumed one species from the start. That 1850 characters were examined was not decisive because they are off a limited set of specimens too limited in number to be statistically assessed, and they are missing key measures of robustness. Carr (2020) paper did not scientifically test the number of species recorded by large *Tyrannosaurus* remains which it was not designed to do. Paul *et al*. (2022) correspondingly did not even think to utilize the Carr data set because that was neither set up for the purpose that Paul and company were investigating. Had such been attempted it would have been a waste of effort because the data set is not up to the task at hand. *E*.*g*. of the large specimens in Carr (2020) just 11 can be assessed using the Paul *et al*. (2022) stratigraphic data, compared to the much more quantitatively significant 31 in the later study. The only data specific citation on Paul *et al*. of Carr (2020) is a note that what stratigraphic data in the latter is present is in line with that in the former, and the femoral ratios for the same specimens are also in good accord. The claim of the Carr (2020) title that the study is high resolution is exaggerated to the point of being perplexing, Paul *et al*. (2022) is more refined and sophisticated in critical aspects, especially regarding assaying paleospecies. Rather than having demonstrated *Tyrannosaurus* monospecificity, the 2020 study confirms that (as observed by Paul *et al*. (2022)) little effort had been conducted to directly challenge the *T*. *rex* issue due to the long casual assumption there was only one species. That leaves Paul *et al*. (2022) as the first and until this work the only one to directly take on the issue seriously with a sufficient data set.

That Carr (2020) fails to properly address the question of *Tyrannosaurus* intragenus species at the level of the big fossils is not especially surprising because the paper was not intended to do so. It was designed to test whether any or all lesser sized TT-zone tyrannosaur fossils are or are not juveniles of *T*. *rex*—a distinct question that is tested in the main text. The united growth curve that appears to unify all examined TT-zone fossils into one species or at last genus did not include a single actual curve for a small specimen, and is therefore invalid and potentially misleading. Carr (2020) continues, as per Carr (1999; Carr *et al*., 2017, 2022), to propose that changes in tooth counts with ontogeny are normal when no such shifts have been observed in any other predaceous avepod species starting with basal Triassic examples in studies over many decades, including other tyrannosaurs (Rozhdestvensky, 1965; Maleev, 1974; Madsen, 1976; Colbert, 1989; Currie, 2003a,b; Hurum & Sabath, 2003; Rinehart et al., 2009; Larson, 2013a, b; Tsuihiji *et al*., 2011; Burnham *et al*., 2018), none of these studies regarding nondeclining tooth counts was cited by Carr (2020) or Carr *et al*. (2017, 2022). Carr (2020) proposes that maxillary tooth count initially increases from 15 to 16 which considering the small sample size is likely to represent individual variation, and later makes a much more statistically real and significant drop from 16 to 12. A peculiar pattern not documented among other amniotes not undergoing radical changes in trophic roles involving replacement of teeth with beaks, in the most extensive study on the issue to date it was observed that aside from the premaxilla there was “no correlation of tooth count with any element of any species examined here” (Brown *et al*. (2015) which Carr (2022) cites but does not mention that primary conclusion of the first directly refutes his substantial tooth loss in growing *Tyrannosaurus* hypothesis). Later, Carr (2020) places emphasis on the small if not illusory initial increase of tooth count citing it as in line with the far more dramatic increase observed in a basal archosauriform with far more numerous and smaller teeth (Ezcurra & Butler, 2015; also see Brown *et al*. (2015) on tooth increases with maturity). Not explained in Carr (2020) is why small tyrannosaurs with overly high tooth counts should be considered juvenile *Tyrannosaurus*, when there are actual juvenile *Tyrannosaurus* with the same tooth count as the adults. The discussion on the lateral dentary groove by Carr (2020) follows Brusatte *et al*. (2016) in overemphasizing their presence in large *Tyrannosaurus*, while not discussing their absence in juveniles of the genus relative to the structures prominence in similar sized TT-zone tyrannosaur fossils. Nor have the other character and proportional disparities between *Tyrannosaurus* and comparable sized non*Tyrannosaurus* specimens been addressed (Longrich & Saitta, 2024). Astonishingly, the possession of forelimbs the manus especially of which exceed that the actual dimensions of adult *Tyrannosaurus* by small bodied TT-zone tyrannosaur remains first noted in the literature in 2013 (Larson, a), which renders the latter being the young of the prior biologically impossible, has been apparently carefully ignored by Brusatte & Carr (2016), Brusatte *et al*. (2016), Carr (2020) and Woodward *et al*. (2020).

Taxonomic implications. Claims in the media (Paul, 2022b) and then Carr *et al*. (2022) that Carr’s (2020) analysis was a resounding pre-refutation of the Paul *et al*. (2022) paper that had not yet been published, and that contains a many times larger sample of stratigraphically placed specimens whose robustness is much more extensively examined, as well as cross comparisons of variation in *Tyrannosaurus* relative to other theropods, should not have occurred, and it cannot be scientifically cited as such in the future. Carr (2020) barely addressed the subject and lacked the data to do so. No work prior to Paul *et al*. (2022) has had significant impact on the species issue, so *T*. *rex* increasingly was a taxonomic wastebasket as specimens accumulated without rigorous testing of the contents of the genus, further testing the subject will require ongoing and future work. As for future application of the Carr data set on *Tyrannosaurus*, which Carr *et al*. (2022) did not attempt, that may not prove as productive as hoped, for the reasons discussed earlier in this analysis. That the nearly all the 1850 characters may prove randomly distributed is not of importance that being normal between species, it is the few differences that count. Until the efficacy of the mass character set method is properly tested with a number of other suitable genera, its utility regarding *Tyrannosaurus* is open to challenge—if Carr in any future work claims to demonstrate one species based on his 2020 data base, then how will that be verified if the same procedure has not been used to affirm or deny the species in *Triceratops*, and *Panthera*? Regarding the question of the non/juvenile status of small TT-zone tyrannosaur specimens, Carr *et al*. (2020) also falls short of producing sound results, even though that was the primary intent of the paper. In proposing that *Tyrannosaurus* grew up like a fish Carr did not practice scientific due diligence by limiting hypotheses to what is biologically normal and plausible—or present compelling evidence it occurred in any case—and offered an ontogenetically impractical ad-hoc scenario that was needed to try to discount how certain small TT-zone tyrannosaurs clearly do not fit into the *Tyrannosaurus* growth lines (Suppltable 1). Carr *et al*. (2020) therefore lacks significant scientific value. Nor are Brusatte and Carr (2016), Brusatte *et al*. (2016), and Woodward *et al*. (2020) effective refutations of multiple tyrannosauroid taxa at all size classes in the TT-zone. By staying in good accord with what is known about amniote ontogenetic biology, Larson (2008, 2013a, b) and Longrich and Saitta (2024) produced plausible, parsimonious, scientifically solid results that verify the MTTH at the level of the lesser remains.

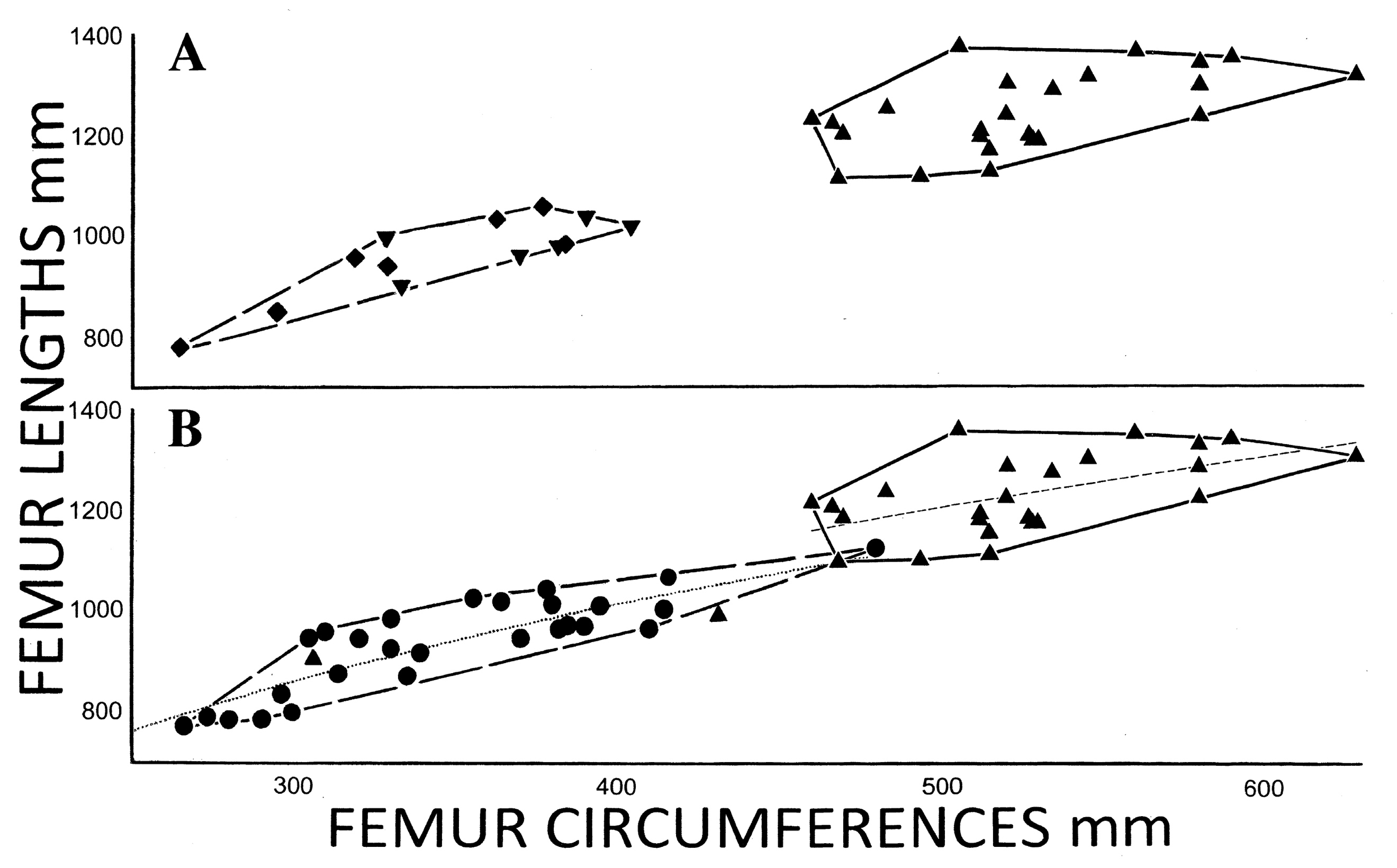
*The comparative cases of Tyrannosaurus and Triceratops multiple species studies*

Paul *et al*. (2022) cited Scannella *et al*. (2014) as setting a standard that could not be approached by the former study. Conducting this analysis found that was an over statement in that the studies are actually more comparable to one another. The following considers both the Paul *et al*. (2022) study, plus that combined with this work’s new data and analysis.

Both projects center on about two and a half dozen large subadult and adult specimens of varying completeness that are stratigraphically correlated. The last factor is somewhat superior in Scannella et al., but the difference that that creates in the results is not critical. Paul *et al*. (2022) includes nearly all major large *Tyrannosaurus* specimens from the entire geographic TT-zone, the *Triceratops* study is much more limited in that regard, and as a result does not capture as much of the full available variation in the known fossils of the ceratopsid as does the work on the tyrannosaurid which is close to complete as it can be at this time in that regard. In both analyses the number of specimens on hand is higher in upper TT-zone levels than in the lower level. Scannella *et al*. include estimated dimensions to a greater extent. Paul *et al*. examine 8 character dimensions to the 6 in Scannella *et al*., both expressed as fine gradations rather than simplistic over or under the median value rankings. The former analysis is more whole body in that it incorporates cranial including mandibular features, as well as postcranial parameters that tend to produce similar results, not just the upper cranial features of the ceratopsid in which only rostral features have proven determinative. A visual comparison of Fig. 6 in Paul *et al*. versus Fig. 2 in Scannella *et al*. shows that of the 8 *Tyrannosaurus* ratios 7 show trends over time, compared to 5 in 6 ratios and angles for *Triceratops*—but that declines to 4 in 6 when the premaxilla angle data from additional specimens is factored. In this paper’s Figure 3, 12 in 14 ratios have trends. In both genera there are sometimes considerable variations in the ratios for a given character in a given species, occasionally involving statistical outliers within a species, resulting in considerable ratio overlaps between the proposed taxa, with bimodality correspondingly not being present in those cases. As a result, clear cut character separation between the proposed species and bimodality is not the norm, although it does sometimes occur in both genera, albeit not usually between all three species regarding a given individual character. Cranial display structures suitable for species designation are present in both genera. In *Tyrannosaurus* one of the species, the atypically gracile *T*. *regina*, exhibits a persistence without exceptions in proportional extremes not seen in the *Triceratops* sample. The exceptional gracility of the femora of *T*. *regina* is an apparent autapomorphy relative to other *Tyrannosaurus*, and to the Tyrannosauridae as a whole. This is further revealed by how the two juveniles that can confidently be assigned to *Tyrannosaurus*, robust USNM6193 and even the apparently gracile LACM23845, both plot in or near the general tyrannosaurid pattern, and are well below the adult *Tyrannosaurus* graciles (Supplfig. 7B). The same is true of the absence of two small anteriormost dentary teeth in in the last *Tyrannosaurus* vis-à-vis the *T*. *imperator* norm and more basal tyrannosaurids. Species diagnoses for predator and prey are correspondingly often qualified and characterized by trends rather than absolutes, as can be seen when comparing the diagnoses for the species of the two genera in their systematic paleontology sections. While *Triceratops* species do not show autapomorphies, *Tyrannosaurus* species do regarding the atypical gracility and the distinctive forms of the postorbital bosses. The two studies agree that stratigraphic separation of key characters precludes sexual dimorphism as an explanation for the observed circumstances in certain cases.

With a large sample of more basal tyrannosaurids available, the *Tyrannosauru*s studies can do what Scannella *et al*. could not, quantitatively compare the variation in earlier species to the TT-zone taxa that exposes the very unusual variability of the last *Tyrannosaurus* during the last few hundred thousand years of the Cretaceous.

That in Paul *et al*. and Scannella *et al*. the basal TT-zone taxon retains ancestral features from recent earlier clade members, and then evolves new, derived anatomies, is powerful evidence for classic Darwinian speciation—involving three species according the data on hand in both analyses. The early outlier observed in *Tyrannosaurus*, a sole specimen lacking the two incisiform teeth widely present in earlier tyrannosaurids and *T*. *imperator* in favor of the only one common to upper TT-zone *Tyrannosaurus*, is not serious evidence against intragenus speciation because it is paralleled in *Triceratops* species evolution in its wide variation in the angle measurement of the upper posterior medial border of the premaxilla in the basal early *T*. *horridus*. Interestingly the two genera then evolve in opposite manners—in *Triceratops* variability *declines* progressing towards the end of the Mesozoic, in *Tyrannosaurus* it *rises* dramatically. In the herbivore, the mode of speciation appears to have been anagenetic with only one species extant at a given time—although the possibility of more than one contemporary intragenus species cannot be ruled out in the low and middle TT-zone. In its hunter the situation looks more complicated, with the anagenetic versus cladogenetic evolution of two contemporary species from one earlier taxon being less clear in its pathways.



**SUPPLMENTRARY FIGURE 7.** Femoral proportions of all large *Tyrannosaurus* (triangles) compared to **A**, *Gorgosaurus libratus* (diamonds) and *Daspletosaurus torosus* (inverted triangles), note that two immature *Tyrannosaurus* specimens are not contained in the least area polygon that incorporates only large specimens of the genus. **B**, All tyrannosaurids (circles) aside from those from the TT-zone, modified from Fig. 4C in Paul *et al*. (2022) including regression lines for two groups. All femora over 700 mm long.

The two sets of work share a level of data availability and sophistication above the norm for dinosaurs. This is logical because both focus on popular and correspondingly extensively searched for dinosaurs from perhaps the most heavily researched dinosaur fossil beds set in two prosperous and peaceful nations. That in part because the TT-zone is the last before the great extinction and therefore of special importance in evolutionary and palaeobiological sciences. Being so alike in so many regards, both are similarly greatly superior as intragenus species assessments to the Carr (2020) paper that was not about that particular subject in the first place.

Taxonomic implications. The data content and analytical quality of Scannella *et al*. (2014) that Carr *et al*. (2022) correctly cite as a positive example, and Paul *et al*. (2022) and herein, are relatively close, with both enjoying advantages and disadvantages vis-à-vis one another. The ceratopsid study may have a noncritical edge over the tyrannosaurid because of its more detailed stratigraphy. And an inherent advantage enjoyed by research of *Triceratops* species is that the genus sported the garish display enhancing horns that often facilitate identification of species, that these are subtler in the predator that fed upon it results in a somewhat finer level of speciation that is well marked by the postorbital bosses. In addition, *Triceratops* appears to have been evolving a little more rapidly than its predator, and because the species were not contemporary hybridization would not have muddled differences between taxa as is likely to have occurred between *T*. *rex* and *T*. *regina*. Advantages for Paul *et al*. (2022) include the inclusion of postcranial as well as cranial anatomy from all accessible major specimens, the consistent extremities of the proportions of one of the latter species and its strong divergence from the basal species of the genus, and possibly some autapomorphies. The many parallels between the two works means that evidence presented in both that the two genera evolved away from their ancestral states into new species over the span of the TT-zone is compelling for both. And that the results of Paul *et al*. need to be taken with more serious equanimity than they have been. As the lateral geographic stratigraphic correlations of the TT-zone improve and the percentage of *Triceratops* specimens being stratigraphically correlated rises to all specimens with adequate quarry data, then the horned dinosaur will begin to enjoy a permanent larger sample size lead over its apex predator.

*There were and are enough characters in Paul et al. (2022) and herein to diagnose* *Tyrannosaurus species*

A comparison of the diagnoses for the species of *Tyrannosaurus* and *Triceratops* presented in the main text systematic paleontology section and the end of the Supplement demonstrates how the number of characters is somewhat higher than that for the latter examination, which is widely accepted as valid. The same is shown comparing Fig. 2 in Scannella *et al*. (2014) to Figure 3 herein. The dozen characters utilized herein is well above that used by Chure & Loewen (2020) and Danison *et al*. (2024) regarding *Allosaurus* species, and may be comparable to that for *Daspletosaurus* although the Carr *et al*. (2017) character count is ambiguous as noted in the maintext. It is not clear if a larger set of characters will be markedly more informative, such not being the norm when sorting out sibling species.

Taxonomic implications. The number of characters utilized in this examination and Paul *et al*. (2022) is typical for studies on dinosaur species, and well within the range of those used to diagnose many fossil tetrapods.

*The characters are not all minor*

The differentiation in femoral robustness in the single genus *Tyrannosaurus* from the last few hundred thousand years of the Mesozoic being half again as great as all other Tyrannosauridae taxa spanning a dozen or more times longer span of time put together (when smaller juveniles are excluded as per Paul *et al*., 2022) is a distinctive evolutionary development that is far from taxonomically minor. All the more so because it is a major divergence from the ancestral tyrannosaurid condition both in the sudden unprecedented onset, and in being driven by an atypical autapomorphic burst of gracility (Supplfig. 7B; see Fig. 6C in Paul *et al*. (2022) for full set of curves). And that when the shift to slenderer proportions is expressed in much of the skull and skeleton in features minor and major, and represents a reduction of bone strength in a genus known for the opposite. To that can be added the very major issue of the visual species level display organs provided by the highly distinctive autapomorphic orbital bosses.

Taxonomic implications. The characters range from minor to major—the latter including two features of the strength of the maxilla and the robustness of the femur, and the orbital bosses—as they do for *Triceratops* and many other intragenus sibling paleospecies. It is when combined that they consist major evidence of significant evolutionary species level developments.

*The sample size is better than normal for dinosaur species, and data replication problems have been exaggerated*

The sample of large specimens in this examination and Paul *et al*. (2022) is larger than normal for multispecific dinosaur genera, and matches or exceeds that for many fossil tetrapods—this is even truer with the inclusion of additional proportional data (Supplfig. 8, Fig. 3). The size of the sample is dependent upon inclusion of all specimens for which data is available. Omitting a large set of remains as per Carr (2020) advocates and does, and Carr *et al*. (2022) advocate and do not do—after criticizing Paul *et al*. (2022) for not practicing due scientific and ethical diligence for using BHI specimens and X-rex they then used our entire femoral data set—is a major evidence exclusion. A game of pretend that when actually practiced, severely reduces the ability to test the monospecies versus multispecies hypothesis. To the degree that the results will be too impaired to overturn the multispecies *Tyrannosaurus* hypothesis that is not the automatic inferior alternative—for example the most robust and gracile known femora are/were both BHI specimens, 6248 and NHMADS. Data replication can if necessary usually be achieved via casts and photographs. That Carr *et al*. (2022) used those and other private specimens because they had to maximize their *Tyrannosaurus* data set indicates that they do not actually consider the replication issue to be seriously critical (despite Carr (2025), which fails to logically show how the TT-zone eutyrannosaur sample would be doubled if not for commercial collecting). That some of the data in Carr (2020) has replication difficulties as described above further indicates that criticism of use of private specimens on that basis has been inconsistent and exaggerated. Further note that a number of technical papers have utilized private *Tyrannosaurus* specimens (Bates *et al*., 2009; Hutchinson *et al*., 2011; Sellers *et al*., 2017). That said private possession of major fossils does create problems. NHMADS is the most optimal holotype for *T*. *regina*, but its private status during the process of producing Paul *et al*. (2022; future status uncertain) precluded that possibility. It is important that the total *Tyrannosaurus* sample includes very large specimens from the lower and upper TT-zone, and from all three proposed species, doing so effectively precludes differences in ontogeny and size providing explanations for the variations in proportions and teeth.

Whether a dramatically larger data set will produce a major alteration in taxonomic conclusions is possible but by no means certain. Consider whether a much larger sample is likely to overturn the basic results of Scannella *et al*. (2014), or tweak them? A dinosaur genus that does have a far larger sample of fossils is *Coelophysis* via the Ghost Ranch Whitaker quarry that contains many hundreds of usually articulated skeletons (Rinehart *et al*., 2009). But the thin walled bones including the femora are often too crushed to provide diameter or circumference data, and are still imbedded in the matrix in any case.

Taxonomic implications. Critics of multiple tyrant lizard species as per Carr *et al*. (2022) cannot have it both ways—assert the hypothesis lacks a sufficient sample size, and then try to test the hypothesis with a smaller sample. Either incorporate the full sample, or get out of the taxonomic research that depends upon it. The results of a sub sample will not be valid. Also taxonomically inconsistent to is to criticize the *Tyrannosaurus* sample when Carr *et al*. (2017) split *Daspletosaurus* into more than one species on a much smaller set of fossils.

*The stratigraphic data base is adequate*

In tune with prior media commentaries, Carr *et al*. (2022) take Paul *et al*. (2022) to lengthy task for the latter’s simple stratigraphic positioning of *Tyrannosaurus* specimens into low, middle and high bins in the geographically laterally expansive TT-zone, in comparison to the tighter metric specific placements for *Triceratop*s specimens in the geographically limited section of the Hell Creek in Scannella *et al*. (2014), The extensive criticism is perplexing in a number of regards. Including how Carr (2020) has been widely praised as superior to Paul *et al*. (2022), even though it too only uses generalized low, middle and high stratigraphic categories for cross data analysis for far fewer specimens. Carr *et al*. (2022) accept broad stratigraphic bins for the actual correlative taxonomic work. That Paul *et al*. (2022) cite and use the data in Carr (2020), and as a result the data sources he utilized, was not noted in Carr *et al*. (2022).

To be specific. The Paul *et al*. (2022) multispecific *Tyrannosaurus* hypothesis makes the gross level proposition that the species of the genus in the lower portion of the TT-zone that lasted a very substantial geological time did not survive into the upper zone where there were new species, with a probable but uncertain mix in between—this is illustrated in Fig. 1b in Carr *et al*. (2022) in which each species spans about two thirds of the TT-zone/ Paul *et al*. (2022) do not offer a more time precise theory in which there was one species in the lowest fifth of the formation, a new sequential one in the next fifth, yet another in the fifth after that, and two more anagenetic species in the final two fifths. It terms of geotime it is a very simple either/or stratigraphic issue of lower and upper, with an apparent—but concerning the validity of the hypothesis not critical—species overlap. As per perfection being the enemy of sufficient to get the core paleotaxonomic job done, placing specimens in such time broad zones simply does not require metric precision.

Regarding the Canadian sample, there is no significant vertical placement issue relative to the Paul *et al*. (2022) lower and upper species hypothesis since all the formations north of the border are upper TT-zone (see main text). It follows that, no *Tyrannosaurus* found in Canada is from the early portions of the TT-zone, so all Canadian *Tyrannosaurus* have to be generally assigned to the upper sections (as done in Mallon *et al*. (2025) who also did not try to directly apply the three zones earlier utilized for Montana *Triceratops* stratigraphy to the Canadian specimens, that not being possible at this time if ever). This widely accepted reality is not directly mentioned by Carr *et al*. (2022), although it is in accord with the data cited by Carr (2020) and references cited by the latter and in Carr *et al*. (2022).

Whatever geostrata issues if any may pertain to the subjects under consideration apply to the United States sample, that extending from the bottom to the top of the TT-zone. While Carr *et al*. (2022) negatively critique without positive evidence the stratigraphy of Paul *et al*. (2022), they do not actually challenge the placement of a specimen American or otherwise in the latter with hard data. That is not surprising because the Paul *et al*. (2022) data set is, despite the imprecise complaints, actually well founded as to the basic positioning of the specimens, although future modifications in a few cases cannot be ruled out. The probability of any known adult gracile proving to come from the lower TT-zone is low. Same for a known spindle boss turning out to be from the upper layers, or a knob boss from low in the zone.

The situation with the spindle bossed, two small incisor toothed, robust *T*. *imperator* holotype well illustrates the American TT-zone situation. Carr *et al*. (2020) sharply criticize Paul *et al*. (2022) for relying on Larson (2008) and pers. communications for much of their stratigraphy. FMNHPR2081 is stated as coming from just 5 meters above the base of the Hell Creek in Larson (2008). This is in basic accord with the stratigraphy that Carr (2020) and Carr *et al*. (2022) cite, as do Paul *et al*. (2022) because that cites Carr (2020). However, Larson personally informed Paul that being from the shallow eastern portion of the Hell Creek Formation probably precludes the specimen from being from being very low in the TT-zone, upper lower or lower middle being more plausible. So Paul *et al*. (2022) discussed the issue and took care to provisionally position FMNHPR2081 between the two levels as is done in this analysis. In contrast Carr (2020: Table 18) simply assigned the specimen to the lower TT-zone with no discussion of the geological complexities, perhaps being unaware of them because of a lack of pers. comm. with the person who excavated the specimen—this helps show why pers. communications are a frequently useful and oft cited norm in science, expert personal knowledge sometimes not being in the literature. That aside is not of critical importance exactly how many meters above the bottom of the TT-zone FMNHPR2081 was preserved. It is whether the fossil is from the lower portion or the upper, and that the possibility that the holotype of *T*. *imperator* dwelled in the upper third of the TT-zone is so improbable that it does not warrant consideration. The paleozoological problem is not that Carr (2020) did what he did in vertically positioning FMNHPR2081, it being sufficient for paleospecies determination. The problem is that Carr *et al*. (2022) then criticize Paul *et al*. (2022) for their geological methods when Carr (2020) was not superior and was if anything inferior, and the results in Paul *et al*. (2022) are sufficient for the task at hand. It follows that while raising some concerns is legitimate, the excessive criticism contained in Carr *et al*. (2022) was not fair and objective as well as perplexing, especially because it did not actually discredit any of the vertical placements.

Carr (2020) observed that resolving the time transgression issue for the TT-zone resulting from the eastwardly regressing interior seaway was “beyond the scope of this work, the results of which are offered here as a hypothesis for further, more rigorous testing of stratigraphic correlation” exactly. So why were sufficient but not exacting time correlations issues acceptable in the study that some claim shows there was only *T*. *rex* in the TT-zone, while doing the same was not in an analysis that stated it was based on the best available preponderance of evidence—including a much larger geological anatomical correlating data set—that discovered more than one species? A major methodological inconsistency that Carr *et al*. (2022) do not acknowledge or address?

Only about one out of nine of the large specimens being examined in Paul *et al*. (2022) and herein cannot be reasonably confidently grossly stratigraphically placed at this time; that compares to how only about one in four large specimens were stratigraphically correlated in Carr (2020). To seriously contradict the stratigraphy of Paul *et al*. (2022) it is necessary to actively refute an acute set of the geological positions that that study presented for specific specimens. Which Carr *et al*. (2022) do not do because such is apparently not possible at this time if ever. If specimens seriously contradicting the Paul *et al*. (2022) hypothesis from the stratigraphic end of things do exist, it is likely that they have yet to be excavated. If such happens then that will be time for a major reconsideration of the species numbers.

The critical stratigraphic items regarding the tyrant king are that graciles and knob postorbital bosses so far have not been documented to be preserved in the lower TT-zone, and going into the future are likely to prove to be at best rare compared to robusts that retain the tyrannosaurid basal stout femur condition in the lower TT-zone. Where the tyrannosaurid basal condition of two incisiform dentary teeth is nearly exclusive, and spindles bosses are the norm, while such are so far absent in younger sediments, where variation on robustness by the sampled elements is usually much higher.

Limited to members of the Morrison, the course stratigraphic data used by Chure & Loewen (2020) and Danison *et al*. (2024) to determine *Allosaurus* species is not superior to that in Paul *et al*. (2022) and herein.

Taxonomic implications. As Paul *et al*. (2022) explain and Carr *et al*. (2022) note, improving the *Tyrannosaurus* stratigraphic correlations to the Scannella *et al*. (2014) precision will require a large scale organizational effort over many decades. If such is possible across the TT-zone in view of the scarcity of radiometrically datable lateral deposits, and the possibility that laterally varying habitat conditions may complicate other means of lateral cross dating. Even if markedly finer stratigraphic placement of nearly all specimens becomes possible, unless in the improbable event that the results dramatically differ from the basic information in Paul *et al*. (2022) and herein, the multiple species hypothesis is likely to survive. Finer stratigraphic data is detail work that may help parse out intricacies of how and why *Tyrannosaurus* species evolved, but is not necessary to establish the initial outlines as being constructed with the currently available information. Because it has not been possible to actually refute or even cast critical doubt on the geodata in Paul *et al*. (2022) relative to the stratigraphic accuracy needs of the not exact time critical hypothesis it contains, the criticism of it has been very excessive and not refutative.

*Tyrannosaur teeth have diagnostic value at the paleospecies level*

Paul *et al*. (2022) measured the base dimensions of the anteroposterior anterior dentary teeth on a given side from either the teeth themselves, or the alveoli which are usually barely larger. Measurements were not combined from different sides (contra Carr *et al*. (2022)). Paul *et al*. (2022) set the boundary between one and two incisiforms at a ratio of 1.2. Because a specimen with one incisiform has a ratio of 1.19, the ratio divide is reset at 1.25 herein (Fig. 3H), with the proviso that specimens close to this value on both sides are intermediates. Note the criticism by Carr *et al*. (2022) that the assignment of a ratio boundary regarding these teeth is arbitrary and therefore lacking utility because of the lack of a bimodal gap is as valid as how Carr (2020) used a femur ratio boundary despite the absence of a bimodal separation in the sample in that study.

Carr *et al*. (2022) disputed a few of the measurements of Paul *et al*. (2022) on varying grounds. Their results for *T*. *rex* RSM2523.8 differ very little from ours (Fig. 3H)—it is noted that as the upper TT-zone with the highest ratio this specimen is too marginal in to be considered to have two small incisors, and has a much lower ratio than most lower TT-zone specimens. Both 2nd dentary teeth of marginally robust, possible *T*. *rex*, or *T*. *imperator*, NHMUKR7994 are about the same base diameter at about 40 mm. That is about 15–20% less than that of the right 3rd tooth based on large format, high resolution photographs on both sides of that dentary (opposite tooth absent), and the 2nd teeth are also somewhat shorter than the next few more posterior dentary teeth. So the Paul *et al*. (2022) ratio for the specimen stands, and as per that study the taxonomically marginal NHMUKR7994 has the intermediate condition in accord with a specimen from the middle TT-zone. The Paul *et al*. (2022) measurement for *T*. *regina* MOR980 is from Larson (2008), the left 2nd tooth is about the same height as the left 3rd so it is not a smaller incisiform tooth, and even the Carr *et al*. (2022) results do not put the specimen into the ratio range of specimens with two properly small incisors. The right second tooth of probable *T*. *regina* LACM23844 has a base about as large as is the diameter of both the alveoli behind it and the left 3rd tooth, so this is another high TT-zone specimen without two small anterior dentary teeth.

Carr *et al*. (2022) make what is a cryptic radical suggestion concerning a possible ontogenetic factor behind the configuration of the anterior dentary teeth, contending that the first tooth position is essentially lost with growth in some adults. In that case some of the measurements in Paul *et al*. (2022) seemingly of positions 2 and 3 are actually of 3 and 4. The Carr *et al*. (2022) hypothesis is critically flawed because it rests on the premise that growing *Tyrannosaurus* lost teeth with maturity, which is incorrect for multiple reasons discussed at length elsewhere. But, even if the Carr *et al*, (2022) ontogenetic tooth thesis were correct, then their results do not show that there are high TT-zone *Tyrannosaurus* with two functional small incisiform teeth, there to date not being a single documented case of a specimen with such near the K/Pg boundary, the *T*. *rex* holotype included. The basic Paul *et al*. (2022) results therefore stand with only minor modification. Nor does the Carr *et al*. (2022) ontogenetic hypothesis explain why the supposed reduction—which in practical terms would be a functional adaptation, tooth count homology is not the critical issue (contra Carr *et al*. (2022))—occurs almost exclusively in the last *Tyrannosaurus,* almost all earlier *T*. *imperator,* as well as early Maastrichtian and earlier Campanian tyrannosaurids dating back 10 Ma and on two continents, having the two small incisors (including *T*.? *mcraeensis*, see main text). Whether few if any of the last *Tyrannosaurus* came to possess two small anterior lower teeth because tooth 2 became large (perhaps during ontogeny), or tooth 1 largely disappeared (during ontogeny), what is evolutionarily and therefore taxonomically important is that one way or another a significant shift occurred in this expressed, functional feature on a highly consistent basis, and that was probably a DNA driven bioevolutionary event that can be used to help track speciation patterns and diagnose species like any other such characters regardless of the ontogeny factor. This conclusion is not impacted by related ontogenetic factors because only similarly large specimens from differing levels of the TT-zone are compared. The Carr *et al*. (2022) remeasurements have not significantly altered the basic statistical results of Paul *et al*. (2022), there still being a very strong skew from nearly always two small incisiform dentary teeth in basal *Tyrannosauru*s, towards one functioning incisiform on the derived species. Some data tweaking may be required as more information becomes available.

Taxonomic implications. The apparent sudden and very late evolution of *Tyrannosaurus* frontmost lower teeth from the longstanding tyrannosaurid ancestral to a new derived functional condition is fully and most compatible with the speciation expected over the long evolutionary time span of the genus in the TT-zone.

*Individual and ontogenetic causes do not explain the variations in the “super predator” taxon Tyrannosaurus rex*

A version of the individuality hypothesis for *Tyrannosaurus* variability proposes that the long lifespan of the dinosaur combined with its exceptional final size is responsible for inconsistent anatomy in a genus that underwent lots of transformation as it matured (Witton, 2022). The result being a super predator species that dominated the TT-zone at all body sizes above that of dromaeosaurs. The three decades that *Tyrannosaurus* could achieve (Erickson *et al*., 2004; Hutchinson *et al*., 2011; Carr, 2020; Cullen *et al*., 2020; Longrich & Saitta, 2024) is short by the standards of mammals of similar size (Nowak, 1991). Other giant theropods including tyrannosaurids had similarly long lives (Erickson, *et al.* 2004; Cullen *et al*., 2020). Growing from a few kilograms to elephantine mass in a taxon that may have exhibited little or no parental care may have potential to explain tremendous variation in form with ontogeny. But this did not happen in *Tyrannosaurus* as shown by the actual juvenile specimens whose body forms were those of protoadults in the pattern observed in other tyrannosaurids; the rest of the baso-eutyrannosaurs being so divergent from adult *Tyrannosaurus* because they are too radically different to be their juveniles by amniote norms, which is way their bone histology records very different growth arcs. Nor is it clear how the super predator scenario offers a compelling evolutionary explanation for the variation observed in the nearly and entirely mature members of a species known from a limited geographic area over which the variations are laterally uniform, the changes having occurred over a considerable span of time in a pattern that smells of Darwinian speciation. As per the remarkable postorbital display boss diversity pattern present in *Tyrannosaurus.*

Taxonomic implications. *Tyrannosaurus rex* was not a super predator that filled all predation roles at all sizes, if anything its juveniles were having trouble coping with the more specialized baso-eutyrannosaurs.

*Variations in tyrannosaur proportional skeletal strength has diagnostic value at the paleospecies level*

Carr *et al*. (2022) compare femoral lengths to circumferences in extant birds with those of extinct tyrannosaurids. They do not cite prior examples of such being done in paleotaxonomy. This procedure was not followed by Paul *et al*. (2022) because it risks the possibility of comparing statistical fossil archaic apples to extant modern oranges, in that the samples ancient and modern may not be comparable. It not clear whether the avian sample includes or excludes birds raised in captivity that are at significant risk of exhibiting variations well away from those that grew up under natural conditions. Bird femora are highly pneumatic and thin walled, the birds are much smaller, having varying lifestyles, and are fliers in which the hindlimbs provide secondary locomotion, sometimes semiaquatic. Paul *et al*. (2022) follow the more common paleontological practice of comparing fossil elements dimensions to those of other fossils among animals of similar form and function as discussed in the section on standards for determining paleospecies. It was of course not intended in Paul *et al*. (2022) nor herein to try capture and compare the full range of element variations in the actual populations of the taxa, that not being possible or necessary in paleozoology. The crucial taxonomic need is to compare the relative differences between tax and changes over time in the theropod proportions, which having tried to dismiss by the problematic comparisons to modern taxa Carr *et al*. (2022) do not attempt. That is best done by limiting sample comparisons to once wild living fossils of comparably arch predatory megatheropods that shared thick walled femora in hindlimbs that were the only locomotary organs and were used almost solely on land. Comparing element ratios to stratigraphic positions is a normal paleotaxonomic practice as per Scannella *et al*. (2014).

Carr *et al*. (2022) note that because Paul *et al*.’s (2022) *Allosaurus* femoral sample does not include many adults it may be missing the variation that the population actually had. That paper neglects to note that the small sample of *Tyrannosaurus* large juveniles detailed by Paul *et al*. (2022) shows that substantial variability was present in the genus well before maturity was reached, so the absence of the same in the subadult allosaurs gives some support to lesser variability in that species vis-a-via the genus *Tyrannosauru*s.

The available fossil data finds that the distribution of the strength proportions as measured by the intraelement comparative dimensions of a number of major elements is not random in tyrannosaurids and *Tyrannosaurus* specifically (Paul *et al*., 2022). The normal basal condition of Asian and American Campanian and early Maastrichtian tyrannosaurids, retained in nearly all early *T*. *imperator*, is robust femora. Late Maastrichtian *T*. *rex* and *T*. *regina* fossils show a much wider variation of robustness in the femur and a number of other cranial and postcranial elements, driven by the sudden appearance—after 10 million years of tyrannosaurid evolution—of the much more gracile condition in *T*. *regina*, in opposition to the expectation of enhanced robustness in the dinosaurian giant. The latest was a major and evolutionarily systematically telling finding of Paul *et al*. (2022) that Carr *et al*. (2022) did not directly address. Concerning the Carr *et al*. (2022) criticism of comparing *Tyrannosaurus* femurs to those of other family species of lesser numbers, combined, observe that femoral variation in TT-zone *Tyrannosaurus* (n = 24) is about twice that present in the Dinosaur Park Formation’s *D*. *torosus* (n = 6) and *G*. *libratus* (n = 7) femora over 700 mm, whether the latter two are considered independently or combined (n = 13) (Supplfig. 7A)—that doubling the sample size via the combination barely changes the results suggests that the difference between the latest Maastrichtian dinosaur and its late Campanian precedents is not just the result more specimens producing more variation. The same results persist when the data for the two albertosaurins *A*. *sarcophagus* (n = 7) and *G*. *libratus* are compared individually or combined (n = 14) (Fig. 6B in Paul *et al*., 2022), and when the femoral proportions of all albertosaurins and daspletosaurins are united (n = 20) which is approaching the *Tyrannosaurus* sample. That proposition is confirmed by how the divergence remains so much larger in the single genus *Tyrannosaurus* than all tyrannosaurids from two continents over 10 million years combined, being three quarters greater when all the latter with femora at least 700 mm (n = 27 for non-TT-zone, non-*Tyrannosaurus*) are compared (Paul *et al*., 2022: Supplfig. 7B). Ergo, expansion of the sample size of non-*Tyrannosaurus* to equal to that of the one genus does not come close to eliminating the gap. While Carr *et al*. (2022) dubiously compared *Tyrannosaurus* ancient bones to those of today’s birds some possibly raised in captivity, they dismissed the more taxonomically informative fossil patterns. That such extreme variations in skeletal strength have not been documented in any one dinosaur species is the opposite of supportive with the single species hypothesis. The last is true whether the single species is applied to the TT-zone as a whole, or the upper section specifically.

Taxonomic implications. Divergences in fossil tyrannosaurid skeletal proportions within the clade and other megatheropods, including those of the femur—they not being overturned by less taxonomically pertinent comparisons of femoral robustness variability in ancient tyrannosaurids to today’s birds—constitute standard osteological differences and changes that can be used to help discern evolutionary patterns and diagnose paleotaxa. The apparent evolution of *Tyrannosaurus* bone proportions from the ancestral to a derived condition is fully and most compatible with the speciation expected over the long evolutionary time span of the TT-zone.

*More on adult* Tyrannosaurus *sexes*

Differences in tyrannosaurid robustness may have visual species specific attributes. The depth of the maxilla and dentary relative to their lengths can result in a deeper or shallower head that can have species identification and competitive implications for the living animals. Same can be true for a heftier versus a lither body supported by a corresponding difference in the robustness of the skeletal framework. The latter could parallel the difference between the body build of the African black rhino and the somewhat heftier white rhino. These effects may be subtle, which is appropriate for predators than could not repurpose major developments in weaponry evolved for in combat performance for objectives related to sexual selection. The status of the anteriormost dentary teeth was not likely a reproductive indicator because it was probably not especially visible, all the more so if the teeth were normally covered by lips and gums (Fig. 6; as per Paul, 2018; Cullen *et al*., 2023).

Taxonomic implications. The amount of species ID divergence within *Tyrannosaurus* appears to have ranged from visually readily apparent via the supraorbital bosses to subtle differences in head and body proportions. This point leads to another species identification factor.

*Neural pattern recognition as applied to* Tyrannosaurus *head shape*

Science is often quantitative. But the human brain-mind system has well developed pattern recognition abilities that in combination with data based artistic imaging are employed in sophisticated scientific research (Imara *et al*., 2021; Imara, 2024). In particular, having evolved in environments that demand rapid identification of the local fauna, the human visual complex is an excellent species recognition system that works about as well as scientific identification procedures (Berlin, 2014; Deikumah *et al*., 2015). If one set of animals is readily visually distinctive from another set, they are different species, only strong sexual dimorphism can alter this situation. Bird watching is based on the principle that one or a few key features can be used to distinguish closely related species. It is more common for species to be visually cryptic, being genetically distinct while visually too similar to easily recognize as not being the same species (Koepfli *et al*., 2015; Alvares *et al*., 2019; Perri *et al*., 2021). Therefore, as an adjunct to the technical processes, visual identification has been utilized in this study. If two specimens look like the same species taking size and possible sexual differences into consideration they probably are, if they don’t they probably are not. In either case the visual intuitive possibility needs to be more deeply examined with comparative data.

Deploying the human visual-neural pattern recognition complex on *Tyrannosaurus* the following observations ensue. As a living kob (*Kobus kob*) can be readily visually distinguished from a waterbuck (*Kobus ellipsiprymnus*), and a *T*. *horridus* skull easily from that of a *T*. sp. and both from *T*. *prorsus*, the big skull of the *T*. *imperator* holotype with its long, low massive boss by no means looks like the same species as the equal sized *T*. *rex* RSMP2523.8 with its short, high set display discs, and neither looks the same as also huge *T*. *regina* NHMADS with its more subtle boss. At the same time, smaller MOR1125 does look compatible with being an immature version of the contemporary *T*. *imperator* holotype, while it looks distinctive from similarly immature UWBM99000 which with its high set discs is just what a young *T*. *rex* shouldlook like, while the immature *T*. *regina* holotype looks like neither of the other species.

If anything, the visual variability between *Tyrannosaurus* skulls (Fig. 2A–I) is greater than that between *Allosaurus fragilis* and *A*. *jimmadseni* and between the intragenera species of *Daspletosaurus* (Fig. 16 in Chure & Loewen, 2020; Fig. 13 in Warshaw & Fowler, 2022; Fig. 4 in Warshaw *et al*., 2024; Paul, 2024a, b).

Taxonomic implications. That adult *Tyrannosaurus* skulls are very visually identifiable at the species level indicates they were such. As per the patent implausibility of RSM2523.8 and FMNHPR2081 being members of a united species when viewing their dramatically different appearances (Figs 2B, G, 6A, B) in combination with their long geotemporal separation.

Tyrannosaurus *nasal and lacrimal display structures are not diagnostic at the species level*

Unlike most other sub/adult eutyrannosaurs whose lacrimals bear a modest subtriangular hornlet (Figs 2 P–R, 4P, Q), like its fellow tyrannosaurin *Tarbosaurus* the *Tyrannosaurus* lacrimal is consistently little adorned and correspondingly so consistent in form that little if any taxonomic information can be obtained (Figs 2A–J, 6). The size of the lacrimal foramen is often difficult to measure and compare – it is drawn too small for AMNH5027 in Figure 8.6 in Larson (2008)—and does not appear to show a consistent pattern in the genus (Persons pers. comm.).

The following rankings are cited in Table 1. The varying degree of rugosity of the nasal ridges, especially the midline profile, is assessed in a manner broadly similar to that of the postorbital bosses as discussed in the main text with similar methodological and outcome caveats as fairly smooth (FS), fairly rugose (FR), rugose (R), very rugose (VR), extra rugose (ER). Many tyrannosaurids *Tyrannosaurus* included share broadly similar, irregularly rugose nasal displays. Nor is there much difference in the shape of the nasal ridges in the sample of large *Tyrannosaurus* specimens. While no nasal is truly smooth, roughness is highly variable ranging from low to quite high, with MOR008 alone earning a rating of ER—which is about as maximally rugose as seen in most other tyrannosaurids, but does not match that seen in *Alioramus* (Brusatte *et al*., 2012; Paul, 2010, 2016, 2024a, b). In the great majority of examples there is very close to good correlation between the roughness of the nasal with the prominence of the postorbital bosses. But in four cases there is a large disparity with the nasals being seriously rugose while the postorbital protuberances are not especially prominent, or the reverse, FMNHPR2081 being especially notable in having VP bosses and a FS nasal. There is some tendency for smaller specimens to have smoother nasals than larger examples and big MOR008 is exceptionally heavily textured, but there are a number of exceptions such as RGM792.000 and FMNHPR2081. While VP and EP nasals decorate skulls assigned to robust *T*. *rex* and *T*. *imperator*, known gracile *T*. *regina* appear to lack such, whether that constitutes a taxonomic feature is not clear.

Taxonomic implications. Unlike the postorbital cornuals, there does not appear to be significant taxonomic diagnostic information contained in large *Tyrannosaurus* nasals and lacrimals.

Tyrannosaurus *species floaters*

Carr *et al*. (2022) are highly and problematically critical of the inability of the *Tyrannosaurus* species diagnoses of Paul *et al*. (2022) to place a substantial number of specimens in a specific species. That the species of the tyrannosaurid genus of concern are siblings very similar in most attributes heightens the probability that diagnostically insufficient specimens will exist. The placement herein of all but one major specimen is a named species undermines the Carr *et al*. (2022) criticisms. The remaining unidentified specimens lack critical diagnostic features, and those in the upper layers are further conflicted by the apparent existence of two species. Lack of ability to vertically position a number of specimens is a hindrance that future stratigraphic work can be expected to alleviate but probably not eliminate.

Taxonomic implications. This and the proceeding Paul *et al*. (2022) are best efforts to determine and diagnose the *Tyrannosaurus* species that the evidence on hand indicates existed, not to make one taxon so broadly defined that it conveniently but probably inaccurately accommodates all specimens on hand.

*Only one major skull and skeleton still systematically adrift*

As noted by Paul (1988) and Paul *et al*. (2022: Supplementary), the one complete *Tyrannosaurus* skull that cannot be readily taxonomically placed, AMNH5027, is significantly distorted, being crushed so the top of the skull is pushed subtly but substantially ventroposteriorly and to the right relative to the lower sections (contra Carr *et al*. (2022) who indicate this skull is nearly perfect). As a result, the left and right sides do not match in configuration, with the right more altered, the right orbit being slanted too posteriorly progressing dorsally, and the right squamosal and quadratojugal are disarticulated. The upper teeth are more procumbent than normal in the genus because the maxillae are dorsoventrally crushed in tune with the rest of the skull, leaving it probably shallower than it was in life, making it appear more gracile than it actually was. What bones can be reliably measured scores as borderline to gracile, but the limb material most critical to the proportional portion of species determination is missing. Photos of the anterior dentary teeth find that the ratio between third and second is 1.25–1.3, another borderline value that while not one incisor, does not firmly place the specimen in the two small incisor category either (not in full accord with the nonquantitative claim by Bakker in Larson, 2008). As just discussed the postorbital bosses are not in accord with those of other species. The quarry has been flooded by the New Deal project Lake Peck reservoir, very probably permanently precluding determination of its stratigraphic placement, and any hope of finding the rest of the skeleton. It is possible that the intermediate 5027 is a distinct species, as per the *T*. “x” hypothesis (Bakker in Larson, 2008), albeit when applied only to the one specimen (all the other specimens considered potential *T*. “x” in Larson are robusts assignable to *T*. *imperator*). It cannot be overemphasized that in the tyrannosaurid fossil rich TT-zone no *Tyrannosaurus* specimen that is as anatomically and stratigraphically deficient as AMNH5027 should be used as a holotype—all current holotypes include an intact femur for instance and that needs to hold for future species holotypes in TT-zone examples of the genus—so testing *T*. “x” requires verification by additional specimens. In any case 5027 may be a transitional form between the other species, perhaps between *T*. *imperator* and *T*. *regina* in that its bosses have features of both, especially if 5027 is from the mid-levels of the TT-zone. Longrich & Saitta (2024) tentatively listed 5027 as a *T*. *imperator*. Another possibility is that it is a hybrid, perhaps of the just mentioned two species if they overlapped in time (Paul *et al*., 2022; Harvati & Ackermann, 2022). It may prove impossible to ever taxonomically place this specimen.

Taxonomic implications. The *Tyrannosaurus* data base for assessing species is now sufficiently well-developed to assign nearly all major skeleton and/or skull specimens with varying degrees of confidence to one of the three proposed species, as well as a large number of highly incomplete remains. *T*. “x” if it exists consists of only one specimen to date, the stratigraphically and systematically ambiguous AMNH5027.

*Tyrannosaurini diagnoses*

The statement by Carr *et al*. (2022) that “*Tyrannosaurus rex* can be distinguished from its *sister* (italics added) species *T*. *bataar*” is incorrect in that they are not that closely related. Being substantially separated by time, geographic distance, and anatomy, there had to have been a number of anatomically gradistic intervening species between them even if the two genera shared a common direct ancestor distinct from earlier large western hemisphere tyrannosaurids. And yet more interceding species if the American *Tyrannosaurus* descended from earlier tyrannosaurids on that continent rather than from Asian examples as is being indicated by recent analyses (as per Dalman *et al*., 2024; also Stein & Triebold, 2013; Wick, 2014). Because they do not consider the situation at the genuine species level Carr *et al*. (2022) are actually diagnosing genera, or at least subgenera. In the process of doing so they fail to capture the complexities of the taxonomic data. In particular, the greater anatomical diversity contained exhibited by *Tyrannosaurus* vis-à-vis its more uniform Asian relation. The Carr *et al*. (2022) effort is also obsolete in lacking any consideration of the postorbital bosses, which their forcing of all *Tyrannosaurus* specimens into one species renders it impossible to define the visually catching divergences in the species display structures. Also out dated is their failure to take the stratigraphy into account.

The diagnoses herein are for the two most derived tyrannosaurine genera—although it remains possible that *Tarbosaurus* is a subgenus—and all the named species of both. Doing so better reflects the complexities of the anatomy and taxonomy. The characterizations are based on large specimens, and are collected from Paul *et al*. (2022), Carr *et al*. (2022), and those produced in this work. All of the dozen pertinent characters are detailed, rather than some being diagnosed collectively as in Paul *et al*. (2022), partly in order to more explicitly describe the differences while avoiding the character undercount alleged by Carr *et al*. (2022). Some of the characters are tweaked vis-à-vis Paul *et al*. (2022), but there are not major alterations from those used in that study. These diagnoses include the postorbital bosses, Paul *et al*. (2022) being obsolete in that regard. Not utilized at the genus level are size differences because the contents of genera often vary greatly in dimensions, as per *Varanus, Canis, Panthera, Homo, Balaenoptera*. There is no observed size difference in the species of *Tyrannosaurus* (Paul *et al*., 2022). Character overlaps and caveats are allowed as per *Triceratops* species diagnoses based on the Scannella *et al*. (2014) results, and for that matter in Carr *et al*. (2022) when it comes to tooth counts, as well as studies cited in the paleospecies determinations section. The stratigraphic factor is fully utilized.

Being exemplars of species determination, the postorbital bosses play in major role in this first broad diagnosis of the greatest tyrannosaurid genera and species. As discussed in the main text, large *Tarbosaurus* possess a rather subtle subcircular knob that is most similar to those of all other tyrannosaurids except for *Tyrannosaurus*. The lack of diversity in these structures is a reason all *Tarbosaurus* specimens can be accommodated in one species at least concerning this basis. The bosses of *Tyrannosaurus* are so radically divergent that it is not possible to produce a single, short description that accommodates all the variants, they range from horizontally elongated, low spindles to short but tall knob discs to less vertically prominent hat shapes. A situation entirely different to the uniformity in *Daspletosaurus* with its at least two species and *Tarbosaurus* with its current one, the only way to generate species pertinent diagnostic descriptions for the *Tyrannosaurus* variants in display devices is to place them in distinct species diagnoses, specifically three. Those who disagree with the multispecies diagnoses for *Tyrannosaurus* are challenged to produce a monospecific diagnosis for *T*. *rex* that incorporates all the differences in supraorbital bosses, as well as those in element robustness versus gracility.

Also a diagnoses based determination of intragenus sibling species, the distinguishing characters for *Allosaurus fragilis* and *A*. *jimmadseni* (Chure & Loewen, 2020) are no more extensive than for *Tyrannosaurus*, and lack comparable species identification display divergence which may not exist between the allosaurid taxa.

Taxonomic implications. Carr *et al*. (2022) are correct that diagnoses are an important part of determining and defining paleospecies, but doing so for *Tyrannosaurus* using the full anatomical and stratigraphic data set produces different results from their much more limited comparison of what are genera.

*Multiple species is the null hypothesis for the tyrant lizard genus*

If *Tyrannosaurus* was known only from a shallow set of sediments spanning just a couple hundred thousand years, with little in the way of evidence of speciation of other dinosaurs in the same deposits, and if multiple taxa of large predators dinosaurian and otherwise dwelling in the same ecospace were rare or absent, then monospecificity would be the null hypothesis. As it is, the titanic predator is known from sediments that span at least half a million and more likely up to or over 1.5 million years (refs. in Paul *et al*., 2022; Mallon *et al*., 2022), with strong evidence for speciation in contemporary ceratopsids, some evidence for in pachycephalosaurs, and perhaps in hadrosaurs (Scannella *et al*., 2014; Fowler, 2017; Paul *et al*., 2022; Carr *et al*., 2022). And two or a host of big theropods living in the same habitat is frequent in the Mesozoic. In this situation convincingly demonstrating monospecificity would require showing that the amount of cranial and postcranial variation in the giant TT-zone tyrannosaurid genus is low and randomly distributed. Instead, the scale of the variation and its distribution in a pattern that indicates evolution away from the ancestral condition refutes individual or dimorphic variation within a species, and is in much better accord with speciation toward more derived conditions that recap the contemporary robust and gracile species observed in earlier tyrannosaurids.

Carr *et al*. (2022) argue that the geological longevity of more basal tyrannosaurid species indicates the same could have been true of *T*. *rex*. This postulate is weak because it is not certain those species really were just one taxon each (as noted by Paul *et al*., 2022; Carr *et al*., 2022) in part because of limited sample sizes. Particularly pertinent is the possibility that *D. torosus* contains a cryptic sympatric species (Paulina-Carabajal *et al*., 2021), a pertinent item Carr *et al*. (2022) do not mention (also see Napoli *et al*., 2023 regarding similar possibilities in other tyrannosaur genera). And *Tarbosaurus* may contain intragenus species as noted below. *Daspletosaurus* evolved multiple species (Carr *et al*., 2017) within a similar ~1.5 Ma span (Warshaw & Fowler, 2022; Scherer & Voiculescu-Holvad, 2024; Warshaw *et al*., 2024; Scherer, 2025). It seems *Albertosaurus* was specious over similar geotime (Stock *et al*., 2024). Sibling intragenera paleospecies is becoming the big tyrannosaurid norm.

Taxonomic implications. Multiple species is the null hypothesis unless the fundamental data concerning *Tyrannosaurus* is seriously challenged by examination of the status of the specimens utilized in Paul *et al*. (2022) and this analysis. The simplistic argument by Carr *et al*. (2022) that a monospecific *Tyrannosaurus* is the null hypothesis is correspondingly biased towards that theory.

*Famed* Tyrannosaurus rex *does not deserve nor reuire special scientific deference, protection and research effort*

In the submitted version of Paul *et al*. (2022) it was repeatedly noted that *Tyrannosaurus* is just another dinosaur and it should be treated like such, and our results not be subjected to greater or lesser critical analysis. Reviewers required that those comments be cut back, which proved to be a mistake. So was inattentively not pointing to that the recent designation of *Allosaurus* species by Chure & Loewen (2020) was properly accepted with little criticism despite lacking statistics, tight stratigraphy, numerous nonoverlapping characters, and so forth—had that been done that criticism of Paul *et al*. (2022) would have been technically undercut and perhaps tamped down.

Taxonomic implications. It bears repeating, *Tyrannosaurus* is just another dinosaur, and the status of the species it contains must be dealt with like those of other extinct tetrapods with no special consideration. The notion that any fossils deserve special scientific attention should never have been proposed.

*Carr et al*. *(2022) criticized*, *but failed to actually refute the existence of* *T*. *imperator* *and* *T*. *regina*

Putting it all together, Carr *et al*. (2022) does not overturn the MTTH for the following reasons.

It sets higher standards for determining, diagnosing, and naming sibling paleospecies than is the norm in vertebrate paleozoology—the uncontested results of Chure and Loewen just a couple of years prior that ignored statistics, phylogeny and lacked stratigraphic precision while including overlap between a small number of diagnosed characters in a modest sample of *Allosaurus* was ignored. Not did Carr *et al*. (2022) cite as they needed to the particularly pertinent example of Carr *et al*. (2017) which did not incorporate statistics, exacting stratigraphy, or a large well documented set of characters resting on a large fossil sample for a new species of *Daspletosaurus*.

The assumption that monospecifity of *Tyrannosaurus* is null hypothesis problematic because genus existed over a sufficient time span for speciation to have occurred. As a result, the quickly produced Carr et al. (2022) is a narrow and technically negative examination of Paul et al. (2022), rather than a positive expansive examination that takes a deep data and analysis dive into testing the number of species in genus (this being the only study to do so since the latter paper).

Does not cite evidence that other tyrannosaurid species that appear to be long lasting may be taxonomic chimeras.

Claims that Carr (2020) demonstrated one species when that work assumed such, was not designed to test the specie question, and used inferior anatomical and stratigraphic data bases for determination of paleospecies.

Does not document that any stratigraphic data in Paul *et al*. (2022) is errant, or note that some of it is in accord with Carr (2020).

Does not demonstrate that the quality of the stratigraphic data in Paul *et al*. (2022) is not adequate for determination of paleospecies over a span of many hundreds of thousands of years.

Criticism of the Paul *et al*. (2022) sample size is excessive because it is larger than for most other noncontroversial dinosaur paleospecies including intragenera, is markedly larger than used by Carr (2020), and approaches that of Scannella *et al*. (2014) *Triceratops* sample that Carr *et al*. (2022) cite favorably.

Strong criticism of Paul *et al*. (2022) for using private specimens on practical grounds including data replication, as well as ethical issues, is itself ethically and scientifically problematic. Excluding the data severely hinders testing the species problem by seriously reducing the sample size and eliminating some of the extreme data ends. And Carr *et al*. (2022) themselves use the Paul *et al*.’s data without alteration or deletion of the privately held remains to test Paul *et al*.’s results.

Does not consider how dramatic geographic changes underway in late Maastrichtian North America accelerated evolutionary rates in the dinosaurs of that time and place.

Does not refute any Paul *et al*. (2022) robustness measurements, utilizes some of them as per immediate above.

Comparison of proportions of ground striding, free living, fossil megapredators’ thick walled femora to small, flying, sometimes semiaquatic extant archosaur’s thin walled femurs is problematic. In part because Paul *et al*. (2022) conduct the paleozoological research norm of comparing and tracking differences and changes among fossils in variations and directions in robustness, especially between last *Tyrannosaurus* to more basal examples of genus, and to all earlier tyrannosaurids combined, which Carr *et al*. (2022) do not consider.

Does not consider the sudden exceptional increase in proportional variation and the sudden trend towards gracility in the last *Tyrannosaurus* vis-a-via early members of the fossil genus and earlier tyrannosaurids, including the variation if femoral proportions being much greater than all tyrannosaurids combined.

Does not consider that *Tyrannosaurus* robusts are about twice as common as graciles.

Does not refute major shift from two small incisiform anterior dentary teeth in nearly all lower TT-zone specimens to no examples in later specimens. Their attempt to reject the meaning of the differentiation fails on multiple grounds, including that the claim intrinsic to their effort that tooth count decreased in maturing *Tyrannosaurus* has itself been firmly refuted.

Criticism of lack of nonoverlapping bimodality in data sets is excessive because such is not critically necessary is assaying sibling paleospecies, and because not all the data used by Carr *et al*. (2022) to diagnose *T. rex* is intraspecies consistent and interspecies entirely distinctive.

Diagnosis of *T*. *rex* is simplistic actually being of genus *Tyrannosaurus* vis-à-vis *T*. *bataar*, does not attempt to address complexities of stratigraphy or directly text species diagnoses.

Taxonomic implications – In addition to its flaws when published, Carr et al. (2022) in now obsolete in view of later pertinent publications. If they are to be effective refutations of the MTTH future attempts to defend the ETRH need to provide actual, positive evidence that *T. rex* was the sole large to gigantic predator of the TT-zone. And do so not in taxonomic isolation, but using standards normally applied to other intragenus sibling paleospecies.

To wit, in any future effort to contradict a specious *Tyrannosaurus* compelling positive evidence has to be presented to show that the tremendous variations in the orbital bosses and skeletal proportions, which correlate well with one another and over time, and the dental differences, are normal fossil intraspecies variations that are substantially less than the character diagnoses and stratigraphy used of late to separate and distinguish other sibling species, *A. fragilis* and *A. jimmadseni* being an example. If that cannot be done, then acknowledge multiple *Tyrannosaurus* species. Or if not the latter, then be sufficiently scientifically uniform to challenge ongoing paleotaxonomic norms by denying that the evidence for *A. jimmadseni* and other pertinent paleospecies is adequate, as part of the major reform of the system.

*Anagenesis or cladogenesis in TT-zone* Tyrannosaurus*?*

If the only upper TT-zone species is *T*. *rex*, then it is a candidate for direct descent from *T*. *imperator*, but anagenesis is not certain, all the more so because the postorbital display bosses of the two species were so divergent. If there are two upper TT-zone species, then at least some degree of cladogenesis must have occurred. That neither *T*. *rex* nor *T*. *regina* bore the distinctive spindle postorbital bosses of *T*. *imperator* further complicates the difficulty of determining which if either of the first two species directly descended from the latter (Paul *et al*., 2022), and again increases the possibility that anagenesis was not involved. So does how while the orbital boss of *T*. *regina* was somewhat more similar to that of *T*. *imperator* than was that of *T*. *rex*, the latter better retained the robust construction of the tyrant lizard emperor. Yet another complication is that none of the TT-zone species retains cornual bosses like those of *Tarbosaurus* and *Daspletosauru*s. That increases the possibility of cladogenesis of the later species relative to *T*. *imperator*. Figure 1b in Carr *et al*. (2022) is therefore simplistic in that is represents only the anagenesis from *T*. *imperator* to *T*. *rex* with cladogenesis for *T*. *imperator* hypothesis, the alternatives are not included. And *T*. *imperator* probably evolved before the advent of the zone, while substantial populations of *T*. *rex* and *T*. *regina* were probably liquidated by the K/Pg crisis. Also possible are intermediate populations, perhaps in the mid TT-zone, of which AMNH5027 may be a representative.

Demonstrating anagenesis in limited fossil samples is inherently problematic (Scherer & Volculescu, 2024; Scherer, 2025). The hypothesis of anagenesis occurring over ~1.5 Ma in the other multispecific tyrannosaurid (Carr *et al*., 2017; Warshaw & Fowler, 2022; Warshaw *et al*., 2024) is complicated by the presence of a middle Campanian gigantic tyrannosaurid that cannot be *Tyrannosaurus* because of a prominent lacrimal hornlet may be a contemporary super *Daspletosaurus* (Stein & Triebold, 2013; Paul, 2024a, b).

Taxonomic implications. Determining the mode of evolution within TT-zone *Tyrannosaurus* is not workable with the current data, and this impediment may never change.

Is *T. mcraeensis* *a* Tyrannosaurus? And what about the Javelina *Tyrannosaurus*? Because *T*. *mcraeensis* (Dalman *et al*., 2024) is many millions of years younger than the first TT-zone *Tyrannosaurus*, *T*. *imperator*, lacks a deep posterior dentary retaining the more basal tyrannosaurid condition, and the lacrimal critical to identifying tyrannosaurins is absent, hence its placement in the genus is problematic. The issue awaits additional remains from the lower Hall Lake Formation for resolution.

Fragmentary, large tyrannosaur specimens from the late Maastrichtian, Edmontonian middle Javelina Formation may be compatible with being *Tyrannosaurus,* but not necessarily a named species (Lawson, 1976; Wick, 2014; Dalman *et al*., 2022; Paul *et al*., 2022, Supplementary Information; Longrich & Saitta, 2024). The low maxillary tooth count of the subadult of about 3 tonnes is appropriate for the genus as far as is known. The thin interfenestral pillar is outside the *T*. *imperator* zone, it suggests the *T*. *rex* or even more the *T*. *regina* condition. But being considerably older than the TT-zone fossils, and the maxilla having a short anterior section (Ford pers. comm.), indicates that these remains are not assignable to a named species.

For discussion of other fragmentary remains see Supplementary Information for Paul *et al*. (2022).

*Evidence for multiple north American large Tyrannosaurus sibling species—a summary*

**For at least two species**

Studies prior to Paul *et al*. (2022) had not thoroughly tested much less strongly verified the monospecific status of the wastebasket taxon *T*. *rex*.

Multiple species are the norm within a genus.

Sufficient geotime was available for sibling level speciation and may favor such, in parallel to speciation observed in *Triceratops* over exactly the same stratigraphic span.

Paleospecies can be and are regularly designated based on the sample that is available, it does not require an ideal large statistical data set which if it becomes available can then be used to test the hypothesis—perfection is rare at best in biology.

The cumulative data in support of multiple species of *Tyrannosaurus* is broadly comparable for *Triceratops*, in some regards better (the tyrannosaurid work is more holistic in that significant patterns are observed in both the crania and postcrania, not just the rostrum as in the ceratopsid), and superior to other intrageneric dinosaur species in terms of sample size, stratigraphic changes over time, and other factors. *Allosaurus* is a contemporary example of a well-founded and widely accepted multispecific genus that does not meet the extreme and unnecessary standards set for *Tyrannosaurus,* including by critics of Paul *et al*. (2022).

Specimen sample size analysis is based upon is larger than usual for nonavian dinosaur genera which can be as few as two, and is comparable to that for *Triceratop*s and *Allosaurus*.

Number of characters utilized to diagnose species, 13, is well within norms for identifying fossil sibling species which can be as few as one.

Stratigraphic data is adequate for purposes, and comparable or superior to that for most paleospecies level taxonomic work including *Allosaurus*.

There is stratigraphic separation between distinctive postorbital boss visual displays—horizontally elongated spindles only low in the TT-zone, anteriorly placed, elevated knobs only high in the formations—that are in full accord with, and a leading identifier of species. The monospecies hypothesis lacks a viable explanation via ontogenetic, individual or dimorphic inconsistency for the variable and sometimes time separated bosses, which alone firmly establish that the genus was multispecific.

The variation in bone based species grade features as represented by the postorbital bosses is higher in *Tyrannosaurus* than is usual for predators, including other tyrannosaurid species, and is comparable to that present in some herbivores; cranial ornamentation. Other intrageneric avepod species such as those of *Allosaurus* do not show nearly as much orbital display variation.

The general consistency between right and left bosses—there are no specimens with a spindle on one side and the disc knob on the other—confirms that they were genetically programmed, adaptative emergent structures that evolved among differing species.

Much more variation in fossil 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 including two that dwelled in the same formation, and statistically well above that yet observed 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.

That growth and maturation curves do not match up with robustness contradicts dimorphism as a cause.

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

Proportional variation being low in the lower TT-zone and remarkably 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 doubling of 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 recognition of species differentiation.

The visually dramatic shift in supraorbital display structures in parallel to the great increase in proportional variation combines to produce overwhelming evidence of the shift in reproductive behavior indicative of species differentiation.

In 7 characters there is in increase in variation within a given element from modest to many fold. In none is there a decrease in variation.

The persistently 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 when allometry is accounted for, and represent a highly atypical shift over a short period of time, directly contradicts ontogeny while strongly favoring subtle adaptative evolution via speciation.

10 other measurements of robustness in crania and postcrania favor actuality of robust and gracile morphs in generally good accord with femoral robustness.

In 7.5 items the most robust or two incisor tooth condition is observed in basal *T*. *imperator*.

*T*. *imperator* is never the most gracile in any element or ratio—such proportional extremity has not been observed in *Triceratops*.

In only 2 ratios is a *T*. *regina* the most robust overall, in two cases the sample is on the small side, especially for *T*. *imperator*.

In 9 ratios the most gracile condition is observed in derived *T*. *regina*.

In 5 elements all *T*. *regina* are more gracile than any *T*. *imperator*.

In all 11 elements and 12 ratios there is an overall trend, form minor to strong, toward greater gracility progressing geologically upwards. Trends towards increasing robusticity have not been discovered.

There are 10 cases of nonoverlapping bimodal separation between the species—the extent of non/bimodality is broadly similar to that observed in many other tetrapod intragenera paleospecies including *Triceratops*.

General shift from the probable ancestral condition of 2 small functional anteriormost dentary incisiform teeth to just one progressing or less upwards in TT-zone, is an adaptative trend not actively explained by dimorphism, individual variation, or ontogeny.

“Long” life span and related issues do not provide strong explanation for the observed patterns.

Progressive change in functional dentary incisor number over time correlates with changing robustness femoral and otherwise, plus the dramatic alteration in supraorbital boss shapes, all occurring in synch, strongly accords with evolutionary speciation rather than dimorphism, ontogeny, or mere individual variation.

The unique shapes of *Tyrannosaurus* postorbital bosses, and the exceptional gracility of *T*. *regina*, are species level autapomorphies.

The preponderance of the cumulative evidence including sample size and other parameters that is the norm in modern paleospecies work now overwhelmingly favors speciation over all alternatives, and is stronger than average for other multiple sibling species in dinosaur genera, being close to that documented for contemporary *Triceratops*, including the species definitive diversity in species category display features. Multiple species of *Tyrannosaurus* is at this time easily the best documented hypothesis over the alternatives.

**For three *Tyrannosaurus* species rather than only two chronospecies**

Three species are readily diagnosable with each being about as distinguishable from the other two as are the others, diagnosing just two chronospecies greatly reduces the number of characters distinguishing the remaining taxa without justification, fails to take into account the tremendous level of variation within and between the upper TT-zone specimens, and that is the opposite of taxonomic logic.

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

No prior tyrannosaurid or dinosaur species has been shown to have been sexually dimorphic to the degree seen in late TT-zone *Tyrannosaurus.*

Two taxa of earlier western North American giant tyrannosaurids, with one more robust than the other, are present in the same levels of the same formation.

Strong divergence in postorbital boss visual displays, including the apparently male knob versus hat shapes, in upper TT-zone is a leading indicator of species. The chronospecies hypothesis lacks a similarly viable explanation for the very different bosses of *T*. *rex* and *T****.*** *regina*.

The number of upper TT-zone skulls with a prominent knob shaped postorbital boss is half that expected if they represent one sex of one species.

Two high TT-zone species 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.

In 5 elements all *T*. *regina* are more gracile than any *T*. *rex* among high level specimens.

In all 6 cranial robusticity plots the most gracile ratio is that of a *T*. *regina*—such proportional cranial extremity has not been observed in *Triceratops*.

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

That *T*. *regina* cranial elements always include the most gracile or all gracile examples as well as the femur, indicates it underwent an extensive evolutionary overhaul involving *reducing* the strength of major and minor skull and skeletal bones in a genus known for its immense size and massive construction, a species level development that was highly divergent from more basal and traditionally robust *T*. *imperator*, rather than just a side variant of *T*. *rex*.

The three sibling species hypothesis offers the ability to provisionally determine the sexual dimorphism patterns in the species, while adding to the cumulative evidence that *T*. *rex* and *T*. *regina* are not conspecific.

*What needs to be done to firmly refute the MTTH - A Summary*

**For gigantic *Tyrannosaurus* sibling species**

Do not cite papers prior to Paul *et al*. (2022) as having had established the monospecificity of *T*. *rex*, unless it can be shown that any of them included a large sample of dozens of stratigraphically correlated specimens that did not show a pattern of change over time.

Because monospecificity is not the null hypothesis either in general, or for *Tyrannosaurus* because the evidence for multispecies meets current paleozoological standards, and the popular status of *T*. *rex* must be ignored in scientific analysis, it needs to be convincingly shown that the preponderance of evidence favors one species over more than one sibling species.

That requires a large sample of dozens of stratigraphically correlated specimens that do not show a notable pattern of change over time.

It follows that the maximum available data sample must be used as per Paul *et al*. (2022). If the sample is smaller, then any results are automatically less or none definitive, and may be misleading.

The second need also requires showing that there is not an exceptional level of variation in *Tyrannosaurus* compared to other tyrannosaurids.

The above in turn further requires at least in part demonstrating that there are significant errors in the proportional measurements in Paul *et al*. (2022) and herein that when altered favor monospecificity.

And/or positively demonstrate that there are significant errors in the stratigraphic placement in a number of specimens in Paul *et al*. (2022).

In particular, firmly establish that a number of gracile large specimens were located in the lower TT-zone. If that is not possible then the multispecies hypothesis is strongly supported over the alternatives. Firmly establish that a number of specimens with two small incisiform dentary teeth are present high in the TT-zone. If that is not possible then the multispecies hypothesis is strongly supported over the alternatives.

If the above cannot be done, present a plausible, natural selection based hypothesis that logically explains the selection of visually distinctive display organs of the type well suited for species determination and diagnosis, without the evolution of new species.

In more general terms show that the amount of variation over time within the genus is less than observed in other species, especially fossil examples of a similar sample size over a similar time span in order to maximize the cross comparability of the situations. Showing examples of large variation within species from one shallow stratigraphic horizon may be a statistical apples and oranges comparison that cannot be definitive.

In the case that the variation over time patterns observed by Paul *et al*. largely hold, then if dimorphism, ontogeny or individual variation are proposed to explain the observed pattern it must be explained in detail how any or all are positively superior to the speciation hypothesis in the context of adaptative natural selection as per evolutionary theory; the “long” lifespan of gigantic *Tyrannosaurus* is a weak ad-hoc opinion for the reasons noted above. Studies that show that such patterns of variation within paleospecies need to be specifically cited and discussed.

In other words, actually show that there was just one species, not merely try to negate the evidence for more species, the latter hypothesis being at least as plausible as the former if not more so. For example, the current evidence currently favors the existence of only one species in the early TT-zone because of the overall low variability of the characters. It is the late TT-zone that contradicts one species both because of significant changes in characters from the basal tyrannosaurid and *Tyrannosaurus* conditions, and the uniquely wide variations both among between the latest specimens of the genus, away from the basal condition of the genus and its family. So show why the condition of the upper TT-zone *Tyrannosaurus i*s not indicative of speciation, when the circumstances are so radically different form the earlier *Tyrannosaurus* that more clearly fit into one species at that level. How for instance is the extreme variability in femoral proportions in large *Tyrannosaurus* compared to the rest of the genera and species in Tyrannosauridae clearly explainable without speciation in the one former genus?

A mass data base in number of characters has not been tested for efficacy, may not be replicable by other researchers, and a resulting small number of distinguishing characters meets norms for designating sibling paleospecies.

Do not treat Paul *et al*. (2022) and the *Tyrannosaurus* situation in isolation from that seen in other modern works of dinosaur and other tetrapod paleospecies. Such taxonomic compartmentalization leaves open the possibility of claiming the data does not support multiple species when it has not been shown that is true relative to the prevailing norms, and it fact the standards have been met. It is therefore necessary to directly demonstrate that Paul *et al*. (2022) and herein do not meet and been consistent with the methodological and procedural criteria widely used to establish and diagnose fossil sibling species of dinosaurs and other tetrapods based on skeletal remains (such as Carr *et al*., 2017; Chure & Loewen, 2020; Chure & Danison *et al*., 2024), with citations and comparative analysis of a variety of studies herein and in Paul *et al*. (see the 2022 paper’s supplement). That includes citing studies that found similar patterns of variation over time while explicitly rejecting speciation as the cause. Or, demonstrate that the current standards are insufficient, need extensive reform, and detail how such should be done in the context of the current literature on the subject—and in view of the inability to even rigorously define what a species is whether living much less extinct—while noting what other paleogeneric multispecies do not stand up to the elevated standards. Do not fail to do one or the other; treating *Tyrannosaurus* species determination outside the context of current norms is inconsistent and not scientific as it evades critical comparative analysis—*i*.*e*. it is giving the genus the special status that no genus should receive. Explicitly explain in detail why Paul *et al*. (2022) and this analysis are markedly inferior to Chure and Loewen (2020) and Danison *et al*. (2024), or show that the latter also fails to demonstrate more than one species of *Allosaurus*.

In particular, treat *Tyrannosaurus* as just another fossil predator that as usual for the trophic type possesses little in the way of species specific display structures, do not primarily compare the variation the genus contains to herbivores with prominent horns, antlers, crests and the like.

Assess whether the *Tyrannosaurus* data supports sibling species that have minimally diverged from one another, not species in large genera that have widely diverged from one another over many millions of years, or are in different genera.

If multiple species are accepted, but just two chronospecies (*T. rex* and *T. imperator*), then it needs to be directly explained how this hypothesis is superior to two high TT-zone species when such a large variation in robustness is not observed in other tyrannosaurid species or the rest of the family as a whole, while two taxa one robust and the other gracile are observed in other tyrannosaurids from the same paleohabitat, and the graciles are so extreme in their proportions.

To repeat, remember that *Tyrannosaurus,* and *T. rex*, are just another tetrapod, and that the nondivisibility of the taxon requires no more or less defense than does *Allosaurus fragilis, Triceratops horridus, Stenopterygius quadriscissus, Psittacosaurus mongoliensis, Metarhinus abbotti*, etc.

The above list is not necessarily all that is required.

**For small TT-zone tyrannosaurs**

For reasons already detailed it is not practical to refute the portion of the MTTH hypothesis concerning TT-zone tyrannosaurs with hands larger than adult *Tyrannosaurus*, and far longer than the manus of juvenile *Tyrannosaurus* (Fig. 9). In the essentially impossible situation that a refutation can be achieved, it needs to be shown that it is possible for amniote appendages to dramatically morph via atrophy with maturity, by citing an example of such having occurred in the great clade. Even in such can be produced, it needs to be demonstrated why *Tyrannosaurus* is so radically different other dinosaurs including its close relations which are entirely normal in this regard. Also requiring plausible solution resulting in parsimony is the general issue of fish like nonamniote grade metamorphosis occurring in *Tyrannosaurus*, but among other items that requires the nonexistence of the normal juvenile *Tyrannosaurus* fossils that do exist.

Taxonomic implications. The effort to maintain the ETRH is scientifically inherently futile.

**Holotypes and synonymies**

*Adequacy and not of holotypes*

The original holotype assignable to *Tyrannosaurus*, that of *Manospondylus* *gigas* (Cope, 1892) has fortunately long been suppressed in on the basis of its fragmentary, insufficiently diagnostic nature in favor of CMNH9380 *Tyrannosaurus rex* (Osborn, 1916). Although not ideal, including the absence of the potentially diagnostic postorbital and its display boss, the specimen’s skull and skeleton are sufficiently complete to constitute a useful type by paleozoological measures, and its basic stratigraphic level is known. The same is true for the *T*. *regina* and *T*. *imperator* holotypes that were chosen as the best quality, accessioned fossils for their species (Paul *et al*., 2022). The very incomplete *Dinotyrannus megagracilis* holotype is inadequate, all the more so because it is a juvenile *Tyrannosaurus* rather than a near adult as presumed by Paul (1988; see Paul *et al*., 2022 for additional discussion).

The *T*.? *mcraeensis* holotype is poor it being a minority of a skull. In particular, it lacks the lacrimal recording the presence or absence of an adorning hornlet, that being definitive regarding its being a tyrannosaurin much less *Tyrannosaurus*. On the positive side it is an adult, and even better includes the taxonomically informative at the species level postorbital boss, and the relative size of the anterior dentary teeth is preserved, plus its basic stratigraphic level is known. Because it is many millions of years older than *T*. *imperator*, and the posterior dentary is shallower than that of adult *Tyrannosaurus* and resembles other tyrannosaurids in the gentle postero-dorsal curvature, the status of *T*.? *mcraeensis* as a member of *Tyrannosaurus* is significantly problematic. But giving the taxon a new generic title if it becomes necessary should await the discovery of additional Hall Lake Formation remains that better elucidates its generic status.

The *Nanotyrannus lancensis* holotype is problematic because it is a significantly damaged and distorted skull sans any postcrania. The latter deficit especially promises to seriously hinder comparative assessments of similar sized tyrannosauroid fossils as potential members of the genus and species, which it is warned threatens to render this taxon into yet another TT-zone tyrannosaur wastebasket. Even if CMNH7541 were a juvenile of a much larger adult, then its holotype utility would be further reduced. Fortunately, the *N*. *lancensis* holotype stratigraphic level is known. Even worse in anatomical regards is the *Stygivenator molnari* holotype, it consisting of just the anterior ends of the rostrum and dentary with some in place teeth. This fragmentary juvenile may be a numen dubium. On the other hand, its, unusual for non*Tyrannosaurus* fossils, absence of dentary grooves increase its differential diagnostic potential, all the more so if its stratigraphy is determined. Potentially an excellent type at the species if not the genus level is NCMNSBM, it showing divergences in rostral, dentary and tooth form from LACM28471 that indicate that the two may not be the same taxon, which is all the more likely if they are not stratigraphic contemporaries. Less suitable is BMRP2002.4.1 because it lacks the systematically valuable distal forelimbs.

It is possible that all or some TT-zone baso-eutyrannosaurs belong to the same subclade as *Dryptosaurus*, which may be the same age as the TT-zone (Gallagher, 2023). The one specimen of which is so fragmentary that its utility for determining the parameters of the group are severely constrained. The earlier *Appalachiosaurus* holotype is somewhat superior, but its lack of the forelimb limits its systematic utility.

*T. imperator and T*. *regina are not junior synonyms of juveniles of the species T*. *lancensis and T*. *megagracilis*

Paul *et al*. (2022) notes that the *Nanotyrannus lancensis* (Bakker *et al*., 1988) holotype from the lower TT-zone is not a potential holotype for the *Tyrannosaurus* species of that time, taking precedence over *T*. *imperator*. For that purpose it is close to being if not a nomen dubium—only a distorted skull too immature to possess the diagnostic supraorbital boss or robust/gracile skull proportions, and lacking the diagnostic appendicular material, or that or other postcrania to examine and compare its growth pattern, and too juvenile to assess whether it would grow up to be a robust or gracile in any case. Even if CMNH7541 is considered a juvenile *Tyrannosaurus* it cannot be used to name a low TT-zone species. In any case discussion of this being a species holotype for *T*. *imperator* is moot if the specimen is an adult as found by Griffin *et al*. (2024).

The holotype of *A*. *megagracilis* (Paul, 1988) is from high in the TT-zone, very probably is a *Tyrannosaurus*, and may belong to *T*. *regina* as suggested in Paul *et al*. (2022). But this fossil also is too juvenile and incomplete to be used as the holotype of the gracile species. The individual is too small to apply to it the critical 2.4 femur dimensional ratio. Although the incomplete femur looks like it was gracile by juvenile standards, that is an estimate not a measurement, so the actual ratio is not known, and it is possible that some contemporary *T*. *rex* juveniles of this size had the same femur ratio. Not available for assessment is a mature postorbital boss. Placement of this holotype in *T*. *regina* is therefore automatically tentative—to the point is a *T*. incertae sedis—too much so to be taxonomically significant. *A*. *megagracilis* is another nomen dubium.

A cautionary taxonomic tale. The first described remains that unambiguously belong to *Tyrannosaurus* and—if the genus is considered monospecific—to *T*. *rex*, is the very fragmentary AMNH3982 that is the holotype of *Manospondylus gigas* as per above discussion. The fossil may be from the lower TT-zone, possibly being part of BHI6248 (Larson, 2008) which scores as a robust *T*. *imperator* (Paul *et al*., 2022). The specimen was logically dismissed as a nomen dubium by Osborn (2016). Because it can be referred to *Tyrannosaurus,* *Manospondylus* would be the proper name for the genus if being referable to a taxon alone means the name of the holotype of the earlier named genus takes precedence regardless of its diagnostic nonvalue. Also overturned is *T*. *rex* if the genus is monospecific, or *T*. *imperator*/*T*. *lancensis* if the later low placed species is valid. Ergo, if *T*. *lancensis* must be the name that takes precedence over *T*. *imperator*, and *T*. *megagracilis* over *T*. *regina*, then the same taxonomic il/logic forces *Tyrannosaurus* to be subsumed into *Manospondylus*—note that *M*. *rex* and *M*. *regina/megagracilis* survive if the multispecies hypothesis holds. The moral of this systematic tale is that a paleogenus and its species need to be founded on sufficiently diagnostic types.

Taxonomic implications. Had Paul *et al*. (2022) used the *N. lancensis* skull as the foundation for the species of the lower TT-zone *Tyrannosaurus* (*T*. *imperator*) instead of big and highly complete FMNHPR2081, doing so would have been severely and correctly criticized. Same if Paul *et al*. (2022) had it tried to use the immature and fragmentary *A*. *megagracilis* holotype in place of the far better adult USNM555000 for the higher gracile TT-zone *Tyrannosaurus* (*T*. *regina*). Opposition would have approached that had Paul *et al*. (2022) tried to sink *Tyrannosaurus* and *T*. *rex* into *Manospondylus* (*M*. *gigas*), or *Dynamosaurus* (*D*. *imperiosus*).

**TT-Zone tyrannosaur taxonomy wrap up**

Paul *et al*. (2022) and this examination are the first studies that found the following. That—as demanded by some multispecies skeptics—the three named species bore the diversity of cranial display features that are hallmarks of species determination, while in the process allowing provisional assignment of specimens to sexes. That basal *Tyrannosaurus* retained some of the general ancestral tyrannosaurid conditions that had previously been in force for ~10 million years. Starting with limited proportional variation, in particular with femoral proportions continuing to be persistently robust when allometry is accounted for. The anterior lower incisiforms numbering two. The interfenestral pillar being robust. The postorbital boss being most similar to an earlier tyrannosaurin. That with exceptional evolutionary rapidity—apparently in association of the elevation of dinosaur evolution driven by the reunification of North America—the proportional differentiation suddenly expanded in major elements of the crania and postcrania for the first time, many fold in most cases, exceeding all previous tyrannosaurids combined in femoral variation. Dentary incisiforms dropped to an unprecedented just one as the new norm. Those very nonrandom events left the latest portion of the TT-zone inhabited by robust and gracile examples of giant tyrannosaurids, replicating the presence of a similar situation in earlier habitats in the same region. The sudden gracility of half of the most recent specimens was the opposite of the massiveness expected in the most gigantic tyrannosaurid, and included strength reduction of the most important tooth bearing elements and the vertical struts in a skull otherwise notable for its exceptional biting power, unmatched in any other terrestrial predators. The remarkable changes in robustness regarding both variation and more gracility, in anterior dentary tooth counts, and in display boss shapes all occurred in evolutionary synch with one another. Because these developments fly in the face of longstanding tyrannosaurid patterns, and/or are the opposite of the attributes predicted to characterize the most titanic genus of the clade, and are the changes expected between divergent species, they are dramatic evolutionary shifts that cannot without convincing warrant be dismissed as minor and intraspecific. Ergo *Tyrannosaurus* was multispecific, thrice so, based on current evidence.

Instead of noting that ground breaking nature of Paul *et al*. (2022) and its utility for study of the genus and its species, the general reaction by researchers most especially Carr *et al*. (2022; popular media commentaries listed in Paul, 2022b) was to make a series of sometimes severe criticisms of the paper not seen before in paleozoology regarding other dinosaur intragenera species. This examination documents that the criticisms were often factually problematic at best both in regards to the issue of *Tyrannosaurus* taxonomy, and the determination of tetrapod paleospecies in general.

If the basic data supporting the evolutionary patterns observed by Paul *et al*. (2022) and herein bear out over time, is it viable to attribute such a notable set of nonrandom events to individual variability which is inherently random, or to ontogenetic or dimorphic factors that do not fit the nature of the changes? The answer is a solid negative. Attempts to dismiss such a complex of internally logical events by attributing them to either random individuality or ontogeny or dimorphic factors that do not fit the nature of the changes, are likely to prove uncompelling and arbitrary because they do not meet the basic criteria of a constructive cogent scientific hypothesis. Such intraspecific risk being ad-hoc, casual opinion that do not via a positive explanatory hypothesis actually explain the outstanding pattern, and consequently have a low possibility of being correct and informative. Such is not rigorous, evolution based coherent explanations for a pattern that is readily and fully explained by genetics driven speciation in response to selective factors. To synonymize *T*. *regina* and even more so *T*. *imperator* with *T*. *rex* will require a major set of positively affirming data, incorporating all the specimens.

In addition to future examinations of possible sibling paleospecies being required to examine all potential causal explanations for variation including dimorphism, ontogeny and individuality as proposed by Paul *et al*. (2022: suppl.), another necessity should be a diagnoses of the species at that basic taxonomic level.

**Other items**

*Supposed studies of the ontogenetic developmental changes of Tyrannosaurus have not been actual studies of the ontogenetic developmental changes of Tyrannosaurus*

The removal of the best small TT-zone tyrannosauroid fossil skeletons from the genus *Tyrannosaurus* means that the former cannot be utilized to reconstruct the changing functional ontogeny of the genus with growth regarding assorted factors such as locomotary performance and agility, head power and tooth form, muscle power and action, over all proportional differences, neural and sensory capabilities, and forelimb function (contra Henderson & Snively, 2004; Hutchinson *et al*., 2011; Snively, 2019; Carr, 2020). Those are ontogenetic-taxonomic chimeras, with BMRP2002.4.1 being the go-to specimen for such spurious efforts. Also excluded from such analyses is NCMNSBM—efforts to use its big lower arms to model the ontogeny of *Tyrannosaurus* forelimb proportions and function would be biononsense. Using TT-zone baso-eutyrannosaurs to restore *Tyrannosaurus* growth is the equivalent of applying *Lynx rufus* to the ontogeny of *Puma concolor*, or *Panthera pardus* to that of *P. leo* and *P. tigris*. Because the baso-eutyrannosaurs may be even more lithe than juvenile *Tyrannosaurus*, using the former as proxies for the latter has somewhat exaggerate the estimated functional differences between immature and mature *Tyrannosaurus*. Restoring the actual ontogeny related functional anatomy and so forth of the most powerful known land predator will require the discovery of much more complete juvenile remains that truly belong to the genus. But even then there can be significant differences between the species, especially the robusts versus graciles.

Using nontyrannosaurid fossils such as BMRP2002.4.1 and 2006.4.4 to restore the growth curve of *Tyrannosaurus* and other aspects of its ontogeny is comparable to doing the same with *Alioramus* concerning *Tarbosaurus* from the same paleohabitat. As touched upon in Paul *et al*. (2022: Supplementary Information) the multispecific status of *Tyrannosaurus* specimens complicates restoring the growth curves of the taxon even when using specimens assignable to the genus. Different species within a genus may diverge in their growth. Robust FMNHPR2081 is the holotype of *T. imperator*, robust MOR1128 can be referred to that species, and gracile USNM555000 is the markedly later living holotype of *T*. *regina* (Fig. 12). Even if these are one species they may represent different sexes with divergent growth. To restore the growth curve of the genus *Tyrannosaurus* below the ~150 kg minimum of MOR1128 requires examination of the hindlimb elements of LACM12845 that are on display, and the very small Baby Bob is in private hands. At the species level restoring growth curves of *Tyrannosaurus* should be based on juvenile-adult specimens that can be confidently assigned to the same species. Such is more viable concerning low TT-zone fossils that can be assigned to *T*. *imperator*. Higher in the formations matters become more complicated because of the presence of two *Tyrannosaurus* species.

Examining the actual ontogenetic developments of *Tyrannosaurus* species awaits the discovery of well-preserved juveniles of the taxon. Also needed are comparative examination of the course of growth recorded in the bones of tyrannosaurid taxa with much better sets of juvenile specimens, such as *Gorgosaurus* and *Tarbosaurus*.

*Lumping all TT-zone* Tyrannosaurus *in* rex *obscures functional studies of the differing morphotypes within the highly variable genus*

Rowe & Rayfield (2024) use the *T*. *imperator* holotype alone to typify the cranial bite stress patterns of *T*. *rex* in accord with the ETRH which they assume remains operative without consideration of the alternatives. Aside from the skull being very damaged, it is a very robust, two incisor cranium from the lower TT-zone that does not diagnose as a later appearing *T*. *rex*, and is even more different from the markedly less strongly constructed *T*. *regina* crania. The Rowe & Rayfield (2024) study actually delineates the functionality of the skull of a specific form of *Tyrannosaurus* that does not apply to the genus as a whole, and should be compared to that of more gracile members of the genus. That is one example of future paleoresearch possibilities.

*Research opportunities that ensue from the MTTH*

With the rigid, simplistic ETRH overturned in favor of a much more complex evolutionary and functional situation with TT-zone tyrannosaurs, more realistic possibilities for innovative investigation are now available. Extensive work has been conducted on the diminutive forelimbs of tyrannosaurids, *Tyrannosaurus* especially (Carpenter & Smith, 2001; Lipkin & Carpenter, 2008; Stanley, 2017; Padian, 2022). With TT-zone baso-eutyrannosaurs no longer mere juveniles of giant, what are the functional and evolutionary aspects of their relatively and absolutely longer two digit hands vis-à-vis tyrannosaurids? Are more capable forelimbs a reason why stygivenators and nanotyrannos appear to outnumber juvenile *Tyrannosaurus*? What role did the configuration of the *nonTyrannosaurus* tyrannosauroid skulls and bladed teeth play in their success as they intermixed and competed with the western tyrannosaurids, and how did this impact their niche selection and competition? Chemical analysis of trace hormones may allow sex determination of *Tyrannosaurus* specimens (Saitta *et al*., 2023). Many TT-zone specimens await histological examination of their growth patterns, including the small fossils that qualify as growing *Tyrannosaurus*. A particularly interesting item for future analysis is the unexpected weakening of elements in the atypically gracile *T*. *regina*, including the hindlimb with potential locomotary implications, and even more oddly the skull the biting power of which may have been reduced.

Nanotyrannus *not a juvenile*

[Voris](https://doi.org/10.1038/s41586-025-08964Voris) *et al.* (2025) suggest that tooth reduction by one socket in an adult *Tyrannosaurus* shows that tooth loss was the norm in growing juveniles, among them *Nanotyrannus.* This is contradicted by the numerous lines of evidence against significant tooth reduction in reptile ontogeny, tyrannosaurids included, cited in the main text that are not addressed by [Voris](https://doi.org/10.1038/s41586-025-08964Voris) *et al.* (2025). Among those issues being that *Nanotyrannus* has far too many teeth to be a juvenile *Tyrannosaurus* compared to the actual dental pattern in the fossil growth series in the latter genus. The absence of the prefrontal process of the frontal in the small tyrannosaur is probably causally associated with the narrowing of the rostrum, apparently in parallel with narrow nosed *Tyrannosaurus*. As detailed in the main text too many attributes discount *Nanotyrannus* as growing over less than a tonne. Because it was not a juvenile, scoring its characters does not falsely result in it appearing more baaal than it actually was due to immaturity. Whether *Nanotyrannus* qualifies as a baso-eutyrannosaur or a tyrannosaurid has yet to be fully resolved.

*How big were the three* Tyrannosaurus *species*?

In the wake of Paul *et al*. (2022) apparent misunderstandings led a few journalists to state that gracile *T*. *regina* was lower tonnage than robust *T*. *rex* and *T*. *imperator*. The largest specimens of the three species are actually all very similar in dimensions and mass, they being in the area of 7.5 tonnes (Fig. 1B, C, E; Paul *et al*., 2022; Paul, 2024a, b). The consistency in the size of the largest specimens suggests that the calculation that the genus on occasion reached 15 tonnes (Paul, 1988, 1997; Mallon & Hone, 2024) is significantly excessive, variations in adult mass typically being less (Paul, 2019, 2024; Larramendi *et al*., 2021).

*Restoring the differing life appearances of* Tyrannosaurus *species*

Until now there has been little effort to use scientific techniques to restore *Tyrannosaurus* in the context of multiple species, it in particular being assumed that the widely differing postorbital bosses were merely intraspecies variants including in Paul *et al*. (2022). That the exceptional bosses of *T*. *rex* as exemplified by UWBM99000 and RSM2523.8 (Figs 1B, 2A, B, 4I, J, 5, 6B, D) were not available until recently has contributed to this failure to pay closer paleobiological and paleoartistic attention to the bosses. With the data and improved analysis now on hand, restorations of *Tyrannosaurus* need to be executed bearing the appropriate species specific structures (as per Fig. 6A–C). Whether the illustration is new, or revised in accord with the new data. If an illustration is intended to represent *T*. *imperator*, then the supraorbital bosses should be spindles at least if they are intended to represent mature males, and *T*. *rex* and *T*. *regina* should never be shown with such (nor should *T*. *imperator* ever be shown with *Triceratops prorsus*), there are a few restorations of *Tyrannosaurus* that show the spindle (but such should never be used to represent the genus near or at the K/Pg boundary). If *T*. *rex* mature males are being illustrated, then supraorbital bosses need to be the vertically prominent knob discs limited to the anterior section of the postorbital, which should never be shown adorning *T*. *regina* or *T*. *imperator* (and neither *T*. *rex* nor *T*. *regina* should never be shown in the same scene with *T*. *horridus*), I have not seen these newly realized knob structures correctly illustrated.

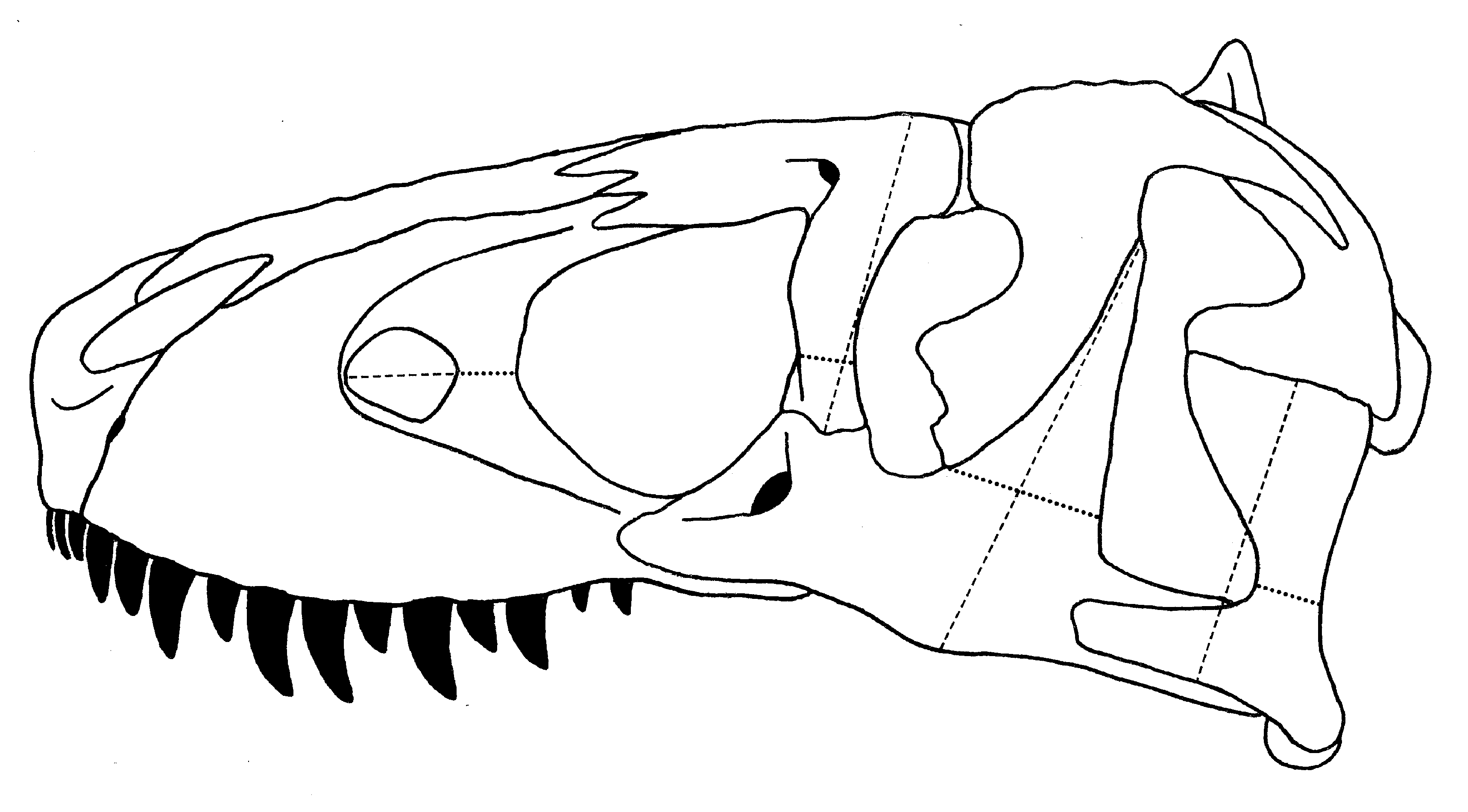
*Is* Tarbosaurus *one taxon, or more*?

After the conclusion by to that effect by Rozhdestvensky (1965) it has been widely assumed that *Tarbosaurus* constitutes the one species *T*. *bataar* (exceptions being Maleev, 1955; Carpenter, 1992; Olshevsky & Ford, 1995; Paul, 2024a, b) However, the deep Nemegt Formation probably formed over an extended period compatible with speciation. And the long, low *T*. *bataar* holotype originally assigned to the *Tyrannosaurus* (Maleev, 1955) that it resembles, looks distinctive from the almost as long ZPALMgD-1/4. The latter is markedly deeper in absolute measure (Fig. 2J, K). Also possessing s similarly high depth/length ration is the immature *T*. *efremovi* holotype (Fig. 2L). Not distinctive at the species level between the specimens are their consistently conventional tyrannosaurid postorbital bosses. If the two morphs were at least partly temporally separated, then they probably were species. If contemporary, then intraspecific dimorphism is favorable, although gracile/robust species remains viable. At this time the stratigraphic data needed to test these possibilities is not available. The possibility that there were more than one taxon may complicate future efforts to generate growth curves and examine ontogenetic functional changes.

*The status of* T. mcraeensis

Morrison *et al.* (2025) and Voris et al. (2025) question whether *T. mcraeensis* was significantly earlier than and/or different from *T. rex*. If it was not as geologically early as proposed by Dalman *et al.* (2023) then this impinges on the possibility of early evolution of proboscidean sized tyrannosaurids in Laramidia, but does not eliminate the phenomenon as per the giant Judith river fossil (Stein & Triebold, 2013). And as detailed by Dalman *et al.* (2023), the *T. macreensis* remains do not fit within the osteological variation observed in TT-zone *Tyrannosaurus*, the retention of a basal tyrannosaurid nonconcave lower margin of the dentary being one such feature, as well its distinctive orbital boss. The basal condition of the holotype is itself evidence that it was not a late Maastrichtian dinosaur, nor in one of the named TT-zone *Tyrannosaurus* species, as well as potentially not being in the genus.

Tyrannosaurus *skull measurements illustration*



**SUPPLMENTRARY FIGURE 8.** Generalized *Tyrannosaurus* skull showing measurements of skull dimensions presented in Table 1 and Fig. 3K–N.

**Corrections to Paul *et al*. (2022)**

The number of specimens examined was 37.

In the systematics section, AMNH9340 should be 9380.

In Table 1, USNM555000 in referred to by its MOR number 555 in one location.

In Table 1, in the section containing tooth dimension data the column heading Hum Ratio should be Inc Ratio.

**Provisional systematic paleontology for** ***Triceratops***

Informal draft species diagnoses for large specimens of TT-zone *Triceratops* for evaluation of data quality and consistency within and between species within this genus compared to the diagnoses in the main text for *Tyrannosaurus*, see further discussion in main text. Based on characters utilized in Scannella *et al*. (2014), sample expanded to include some of the specimens outside the limited geographic area of the Hell Creek examined by Scannella *et al*. (2014; Supplfig. 6) and including Mallon *et al*. (2025), stratigraphic data in part from Hatcher *et al*. (1907; Lull, 1933). It is expected that the diagnoses will be further modified with the inclusion of additional specimens beyond those considered in Scannella *et al*. (2014) plus herein as well as new finds, and revisions and expansions to the data base.

***T. horridus***

**Material.** Holotype: YPM1820

Referred specimens: AMNH5116, MNHN1912.20, MOR981, 1120, 1122, 2985, 3081, SDSM2760, TCM2001.93.1, YPM1823?, USNM1201, 2100, 2412, 4720, 4842, 4928.

**Diagnosis.** Rostrum sometimes exceptionally elongated, length of nasal short to moderate, all shorter than *T*. sp. and *T. prorsus*, snout usually but not always shallow, angle between nasal process and narial strut of premaxilla usually shallow to sometimes acute, nasal process of premaxilla narrow, all narrower than *T. prorsus* but not *T*. sp., large anteromedial process on nasal; small dorsal boss on nasal, nasal horns very small to moderate size, all smaller than *T. prorsus,* postorbital horns short to very long; front parietal fontanelle constricted and closed in late subadults and young adults; variability within species high, and may in part represent dimorphism.

***T*. sp.**

**Material.** Potential specimens:MOR2569, 2570, 2982, 3004, 3005, 3006, 3010, 3011, 3027, 3045, 3055, 3058, 3064, UCMP128561, 113697.

**Diagnosis.** Rostrum short. Length of nasal moderate, all longer than *T*. *horridus* but not all *T*. sp. Snout shallow or deep. Angle between nasal process and narial strut of premaxilla shallow to acute. Nasal process of premaxilla width moderate, always broader than *T*. *prorsus* but not all *T*. *horridus*. Large anteromedial process on nasal. Small dorsal boss on nasal. Nasal horns small to fairly large. Postorbital horn length moderate to very long. Frontoparietal fontanelle open in late subadults and young adults.

***T*. *prorsus***

**Material.** Holotype: YPM1822

Referred specimens:CM1221, EMp15.1, LACM7207, MOR004, 2574, 2576, 2702, 2923, 2924, 2936, 2938, 2950, 2951, 2958, 2971, 2972, 2979, 2999, 3000, 3008, 3029, 3047, 3056, 3057, MWC7584, SMNHP1163.4, SVMPP60/2/1, 62/1/1, YPM1821, 1834, UCMP136092, 137263.

**Diagnosis.** Rostrum length short to moderate. Length of nasal moderate to long, all longer than *T*. *horridus* but not all *T*. sp. Snout deep. Angle between nasal process and narial strut of premaxilla moderate to acute, all more acute than *T*. sp. but not all *T*. *horridus*. Nasal process of premaxilla broad, all broader than *T*. sp. and especially *T*. *horridus*. Small anteromedial process on nasal. No dorsal boss on nasal. Nasal horns fairly large to large, all larger than *T*. *horridus* but not all *T*. sp. Postorbital horn length moderate. Frontoparietal fontanelle constricted and closed in late subadults and young adults. Variability within species low, evidence for dimorphism lacking.

**Supplementary references**

Alvares, F., Bogdanowicz, W., Campbell, L.A., Hatlauf, J., Godinho, R., Jhala, Y.V. & Werhahn, G. (2019) Old World *Canis* spp. with taxonomic ambiguity: Workshop conclusions and recommendations. *Biodiversity and Evolutionary Biology*, 1-8.

Bakker, R.T. & Williams, M. (1988) *Nanotyrannus*, and new genus of pygmy tyrannosaur, from the Latest Cretaceous of Montana. *Hunteria*, 1, 1-30.

<https://doi.org/10.1075/z.31.02int>

Barnosky, A.D. & Bell, C. (2004) Evolution, climatic change and species boundaries: Perspectives from tracing *Lemmiscus curtatus* populations through time and space. *Proceedings of the Royal Society B*: *Biological Sciences*, 270, 2585–2590.

<https://doi.org/10.1098/rspb.2003.2543>

Barrett, P.M., Butler, R.J. & Knoll, F. (2005) Small-bodied ornithischian dinosaurs from the Middle Jurassic of

Sichuan, China. *Journal of Vertebrate Paleontology*, 25, 823-834.

https://doi.org/10.1671/0272-4634(2005)025[0823:SODFTM]2.0.CO;2

Bates, K.T., Manning, P.L., Hodgetts, D. & Sellers, W.I. (2009) Estimating mass properties of dinosaurs using laser imaging and 3D computer modeling. PLOS one, 4, e4532.

<https://doi.org/10.1371/journal.pone.0004532>

Berlin, B. (2014) *Ethnobiological Classification, Principles of Categorization of Plants and Animals in Traditional Societies*. Princeton University Press, 1-354.

Brochu, C.A. (2003) Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology*, 22, 1-138.

<https://doi.org/10.1080/02724634.2003.10010947>

Brown, C.M., VanBuren, C.S., Larson, D.W., Brink, K.S., Campione, N.E., Vavrek, M.J. & Evans, D.C. (2015) Tooth counts through growth in diapsid reptiles: implications for interpreting individual and size-related variation in the fossil record. *Journal of Anatomy*, 226, 322-333.

Brown, C.M., Henderson, D.M., Vinther, J., Fletcher, I., Sistiaga, A., Herrera, J. & Summons, R.E. (2017) An exceptionally preserved three-dimensional armored dinosaur reveals insights into colorations and Cretaceous predator-prey dynamics. *Current Biology*, 27, 1-8.

  https://doi.org/[10.1016/j.cub.2017.06.071](https://doi.org/10.1016/j.cub.2017.06.071#_blank)

Brusatte, S.L. & Carr, T.D. (2016) The phylogeny and evolutionary history of tyrannosauroid dinosaurs. Scientific Reports, 6, 20252.

https://doi.org/10.1038/srep20252

Brusatte, S.L., Carr, T.D. & Norell, M.A. (2012) The osteology of Alioramus, a gracile and long-snouted tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. Bulletin of the American Museum of Natural History, 366, 1–197.

<https://doi.org/10.1206/770.1>Brusatte, S.L., Carr, T.D., Williamson, T.E., Holtz, T.R., Hone, W.E. & Williams, S.A. (2016) Dentary groov morphology does not distinguish “Nanotyrannus” as a valid taxon of tyrannosauroid dinosaur. Comment on: “Distribution of the dentary groove of theropod dinosaurs: Implications for theropod phylogeny and the validity of the genus *Nanotyrannus* Bakker et al., 1988”. *Cretaceous Research*, 65, 232-237.

[https://doi.org/10.1016/j.cretres.2016.02.007](https://doi.org/10.1016/j.cretres.2016.02.007#_blank)

Burger, J., Rosendahl, W., Loreille, O., Hemmer, H., Ericksson, T., Gotherstrom, A., Hiller, J., Collins, M.J.,

Wess, T., & Alt, K.W. (2004). Molecular phylogeny of the extinct cave lion *Panthera leo spelaea.*

*Molecular Phylogentics and Evolution*, 30, 841-849.

https://doi.org/10.1016/j.ympev.2003.07.02

Burnham, D.A., Atkins-Weltman, K.L. & Jevnikar, E.M. (2018) A new juvenile *Tyrannosaurus rex* from the Hell Creek Formation of eastern Montana provides insights into cranial and dental ontogeny. *Society of Vertebrate Paleontology 78th Annual Meeting Abstracts*, 99.

Campbell, J.A., Ryan, M.J, Holme, R.B. & Schroder-Adams, C.J. (2016) A re-evaluation of the chasmosaurine ceratopsid genus *Chasmosaurus* from the upper Cretaceous Dinosaur Park Formation of western Canada. *PLOS one*, 11, e0145805.

Carpenter, K. (1990) Variation in *Tyrannosaurus rex*. *In*: Carpenter, K. & Currie, P.J.

(Eds), *Dinosaur Systematics: Perspectives and Approaches*. Cambridge University Press, pp. 141-145.

Carpenter, K. (1992) Tyrannosaurids of Asia and North America. *In*: Mateer, N.J. & Peiji, C. (Eds), *Aspects of Nonmarine Cretaceous Geology*. China Ocean Press, pp. 250-268.

Carpenter, K. (2010) Species concept in North American stegosaurs. *Swiss Journal of Geosciences*, 103, 155-162.

https://doi.org/10.1007/s00015-010-0020-6

Carpenter, K. & Smith, M. (2001) Forelimb osteology and biomechanics of *Tyrannosaurus rex*. *In*: Tanke, D. & Carpenter, K. (Eds), *Mesozoic Vertebrate Life*. Indiana University Press, pp. 90-116.

Carr, T.D. (1999) Craniofacial ontogeny in tyrannosaurid dinosaurs. *Journal of Vertebrate Paleontology*, 19, 497-523.

Carr, T.D. (2020) A high-resolution growth series of *Tyrannosaurus rex* obtained frommultiple lines of evidence. *PeerJ*, 8, e9192.

<https://doi.org/10.7717/peerj.9192>

Carr, T.D. (2025) *Tyrannosaurus rex*: An endangered species. *Palaeontologica Electronica*, 28, a16.

[https://doi.org/10.26879/1337](https://doi.org/10.26879/1337#_blank)

Carr, T.D., Williamson, T.E. & Schwimmer, D.R. (2005) A new genus and species of tyrannosauroid from the Late Cretaceous (Middle Campanian) Demopolic Formation of Alabama. *Journal of Vertebrate Paleontology*, 25, 119-143.

[https://doi.org/10.1671/0272-4634(2005)025[0119:ANGASO]2.0.CO;2](https://doi.org/10.1671/0272-4634(2005)025%5B0119:ANGASO%5D2.0.CO;2)

Carr, T.D., Varricchio, D.J., Sedlmayr, J.C., Roberts, E.M. & Moore, J.R. (2017) A new tyrannosaur with evidence for anagenesis and crocodile-like facial sensory system. Scientific Reports, 7,44942.

Carr, T.D., Napoli, J.G., Brusatte, S.L., Holtz, T.R., Hone, D.W., Williamson, T.E. & Zanno, L.E. (2022) Insufficient evidence for multiple species of *Tyrannosaurus* in the latest Cretaceous of North America: A comment on “The tyrant lizard king, queen and emperor: Multiple lines of evidence support subtle evolution and probable speciation within the North American genus *Tyrannosaurus*”. Evolutionary Biology, 49, 327-341.

https://doi.org/10.1007/s11692-022-09573-1

Christiansen, P. & Harris, J.M. (2009) Craniomandibular morphology and phylogenetic affinities of *Panthera atrox*: Implications for the evolution and paleobiology of the lion lineage. *Journal of Vertebrate Paleontology*, 29, 934-945.

<https://doi.org/10.1671/039.029.0314>

Chure, D.J. & Loewen, M.A. (2020) Cranial anatomy of *Allosaurus jimmadseni*, a new species from the lower Morrison Formation (Upper Jurassic) of Western North America. *PeerJ*, 8, e7803.

Coimbra, R.T.F., Winer, S., Kumar, V., Koepfli, K.P., Gooley, R.M., Dobrynin, P., Fennessy, J. & Janke, A. (2021) Whole-genome analysis of giraffe supports four distinct species. *Current Biology*, 32, 2929-2938.

Colbert, E.H. 1989. The Triassic dinosaur *Coelophysis*. Museum of Northern Arizona Bulletin, 57, 1-160.

Cope, E.D. (1892) *Fourth note on the dinosaurs of the Laramie.* American Naturalist, 26, 756-758.

Cullen, T.M., Canale, J.I., Apesteguía, S., Smith, N.D., Hu, D.Y. & Makovicky, P.J. (2020) Osteohistological analyses reveal diverse strategies of theropod body-size evolution. *Proceedings of the Royal Society B*, 287, 2020-2258.

<https://doi.org/10.1098/rspb.2020.2258>

Cullen, T.M., Larson, D.W., Witton, M.P., Scott, D., & Reisz, R. (2023). Theropod dinosaur facial

reconstruction and the importance of soft tissues in paleobiology. *Science*, 379, 1348-1352.

Currie, P.J. (2003a) Cranial anatomy of tyrannosaurids from the Late Cretaceous of Alberta, Canada. *Acta Palaeontologica Polonica*, 48, 191-226.

Currie, P.J. (2003b) Allometric growth in tyrannosaurids from the Upper Cretaceous of North

America and Asia. *Canadian Journal of Earth Sciences*, 40, 651-665.

Currie, P.J. & Russell, D.A. (2005) The geographic and stratigraphic distribution of

articulated and associated dinosaur remains. *In*: Currie, P.J. & Koppelhus, E.B. (Eds), *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed*. Indiana University Press, pp. 537-569.

Dalman, S.G., Lucas, S.G., Jasinski, S.E. & Longrich, N.R. (2022) *Sierraceratops turneri*, a new chasmosaurine ceratopsid from the Hall Lake Formation of south-central New Mexico. Cretaceous Research, 130, 105034.

Dalman, S.G., Loewen, M.A., Pyron, R.A., Jasinski, S.E., Malinzak, D.E., Lucas, S.G., Fiorillo, A.R., Currie, P.J. & Longrich, N.R. (2024) A giant tyrannosaur from the Campanian-Maastrichtian of southern North America and the evolution of tyrannosaurid gigantism. Scientific Reports, 13, 22124.

<https://doi.org/10.1038/s41598-023-47011-0>

Danison, A., Wedel, M., Barta, D., Woodward, H., Flora, H., Lee, A. & Snively, E. (2024). Chimerism in specimens referred to *Saurophaganax maximus* reveals of new species of Allosaurus. Vertebrate Anatomy Morphology Palaeontology, 12, 81-114.

<https://doi.org/10.18435/vamp29404>

Deikumah, J.P., Konadu, V.A. & Kwafo, R. (2015) Bird naming systems by Akan people in Ghana follow scientific nomenclature with potentials for conversation monitoring. *Journal of Ethnobiology and Ethnomedicine*, 11, 75.

https://doi.org/10.1186/s13002-015-0062-y

Dodson, P. (1975) Taxonomic implications of relative growth in lambeosaurine hadrosaurs. *Systematic Zoology*,

24, 37–54. <https://doi.org/10.1093/sysbio/24.1.37>

Dooley, A.C., Scott, E., Green, J., Springer, K.B., Dooley, B.S. & Smith, G.J. (2019) *Mammut pacificus* sp. nov., a newly recognized species of mastodon from the Pleistocene of western North America. *PeerJ*, 7, e6614.

Engelman, R.K. (2024) Reconstructing *Dunkleosteus terrelli* (Placodermi: Arthrodira): A new look for an iconic Devonian predator. *Palaeontologica Electronica*, 27.3.a45.

[https://doi.org/10.26879/1343](https://doi.org/10.26879/1343#_blank)

Erickson, G.M., Makovicky, P.J., Currie, P.J., Norell, M.A., Yerby, S.A. & Brochu, C.A. (2004) Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature*, 430, 772-775.

<https://doi.org/10.1038/nature16487>

Evans, D.C. & Reisz, R.R. (2007) Anatomy and relationships of *Lambeosaurus magnicristatus*, a crested hadrosaurid dinosaur (Ornithischia) from the Dinosaur Park Formation, Alberta. *Journal of Vertebrate Paleontology*, 27, 373-393.

[https://doi.org/10.1671/0272-4634(2007)27[373:AAROLM]2.0.CO;2](https://doi.org/10.1671/0272-4634(2007)27%5B373:AAROLM%5D2.0.CO;2)

Ezcurra, M.D. & Butler, R.J. (2015) Post-hatchling cranial ontogeny in the Early Triassic diapsid reptile *Proterosuchus fergusi*. *Journal of Anatomy*, 226, 387-402.

<https://doi.org/10.1111/joa.12300>

Fowler, D.W. (2017) Revised geochronology, correlation, and dinosaur stratigraphic

ranges, correlation, and dinosaur stratigraphic ranges of the Santonian-Maastrichtian formations of the Western Interior of North America. PLOS one, 12, e0188426.

https://doi.org/10.1371/journal.pone.0188426

Fowler, D.W. & Freedman, E.A.F. (2020) Transitional evolutionary forms in chasmosaurine ceratopsid dinosaurs: evidence from the Campanian of New Mexico. *PeerJ*, 8, e9251.

Gallagher, W.B. (2023) An unusual theropod specimen from the late Maastrichtian of New Jersey. The Anatomical Record, 306, 1757-1761.

https://doi.org/10.1002/ar.25114

Galton, P.M. (1981) *Dryosaurus*, a hypsilophodontid dinosaur from the Upper Jurassic of North America and Africa postcranial skeleton. *Palaontologische Zeitschrift*, 55, 271-312.

https://doi.org/10.1007/BF02988144

Gamble, K.C. (2007) Internal anatomy of the hornbill casque described by radiography, contrast radiography, and computed tomography. *Journal of Avian Medicine and Surgery*, 21, 38-49.

[https://doi.org/10.1647/1082-6742(2007)21[38:IAOTHC]2.0.CO;2](https://doi.org/10.1647/1082-6742(2007)21%5B38:IAOTHC%5D2.0.CO;2)

Godoy, P.L., Meachen, J., Lopez-Abarello, A., & D’Emic, M.D. (2024) The reproducibility crisis in phylogenetic analysis. *The Society of Vertebrate Paleontology 84th Meeting Abstracts*, 222-223.

Gould, S.J. (2002) *The Structure of Evolutionary Theory*. Cambridge, Harvard University

Press, 1-1433.

Green, T.L., Kay, D.I. & Gignac, P.M. (2022) Intraspecific variation and directional casque asymmetry in adult southern cassowaries (*Casuarius casuarius*). *Journal of Anatomy*, 241, 951-965.

<https://doi.org/10.1111/joa.13733>

Griffin, C., Poust, A.W., Bugos, J.E, Morris, Z.S., Petermann, H., Fabbri, M. & Colleary, C. (2024) Assessing the ontogenetic maturity of the ‘*Nanotyrannus lancensis*’ holotype with hyoid osteohistology. The Society of Vertebrate Paleontology 84th Meeting Abstracts, 232–233.

Grubb, P., Groves, C.P., Dudley, J.P. & Shoshani, J. (2000) Living African elephants belong to two species: *Loxodonta africana* (Blumenbach, 1797) and Loxodonta cyclotis (Matschie, 1900). *Elephant*, 2, 1-4.

Hatcher, J.B., Marsh, O.C. & Lull, R.S. (1907) *The Ceratopsia.* Monographs of the United States Geological Survey, 49, 1-300.

Harvati, K. & Ackermann, R.R. (2022) Merging morphological and genetic evidence to assess hybridization in western Eurasian late Pleistocene hominins. *Nature Ecology & Evolution*, 6, 1573-1585.

https://doi.org/10.1038/s41559-022-01875-z

Head, J.J., Barrett, P.M. & Rayfield, E.J. (2009) Neurocranial osteology and systematic relationships of *Varanus* (*Megalania*) *prisca* Owen, 1859 (Squamata: Varanidae). *Zoological Journal of the Linnean Society*, 155, 445-457.

<https://doi.org/10.1111/j.1096-3642.2008.00448.x>

Henderson, D.M. & Snively, E. (2004) *Tyrannosaurus* en pointe: allometry minimized rotational inertia of large carnivorous dinosaurs. *Proceedings of the Royal Society B*, 271, S57-S60.

<https://doi.org/10.1098/rsbl.2003.0097>

Hone, D.W.E. & Naish, D. (2013) The ‘species recognition hypothesis’ does not explain the presence and evolution of exaggerated structures in non-avialan dinosaurs. *Journal of Zoology*, 290, 172-180.

<https://doi.org/10.1111/jzo.12035>

Horner, J.R. & Padian, K. (2004) Age and growth dynamics of *Tyrannosaurus rex*. Proceedings of the Royal Society, B 271, 1875-1880.

<https://doi.org/10.1098/rspb.2004.2829>

Hoyo, J.D., Elliott, A. & Sargatal, J. (1992) *Handbook of the Birds of the World, V 1*. Lynx Edicions, Barcelona, 1-696.

Hoyo, J.D., Elliott, A. & Sargatal, J. (1994) *Handbook of the Birds of the World, V 2*. Lynx Edicions, Barcelona, 1-638.

Hoyo, J.D., Elliott, A. & Sargatal, J. (1996) *Handbook of the Birds of the World, V 3*. Lynx Edicions, Barcelona, 1-182.

Hoyo, J.D., Elliott, A. & Sargatal, J. (1997) *Handbook of the Birds of the World, V 4*. Lynx Edicions, Barcelona, 1-679.

Hoyo, J.D., Elliott, A. & Sargatal, J. (2001) *Handbook of the Birds of the World, V 6*. Lynx Edicions, Barcelona, 1-759.

Hubner, T.R. & Rauhut, O.W.M. (2010) A juvenile skull of *Dysalotosaurus* *lettowvorbecki* (Ornithischia: Iguanodontia) and implications for the cranial ontogeny, phylogeny and axonomy in ornithopod dinosaurs. *Zoological Journal of the Linnean Society*, 160, 366-396.

<https://doi.org/10.1111/j.1096-3642.2010.00620.x>

Hunt, G., Hopkins, M.J. & Lidguard, S. (2015) Simple versus complex models of trait evolution and stasis as a response to environmental change. *Proceedings of the National Academy of Sciences*, 112, 4885-4890.

<https://doi.org/10.1073/pnas.1403662111>

Hurum, J.H. & Sabath, K. (2003) Giant theropod dinosaurs from Asia and North America: Skulls of *Tarbosaurus bataar* and *Tyrannosaurus rex* compared. *Acta Paleontologica Polonica*, 48, 161-190.

Hutchinson, J.R., Bates, K.T., Molnar, J., Allen, V. & Makovicky, P.J. (2011) A computational analysis of limb and body dimensions in *Tyrannosaurus rex* with implications for locomotion, ontegeny, and growth. *PLOS one*, 6, e26037.

<https://doi.org/10.1371/journal.pone.0026037>

Imara, N. (2024) Touching the stars. *Scientific American*, 330(3), 30-35.

Imara, N., Forbes, J.C. & Weaver, J.C. (2021) Touching the stars: Using high-resolution 3D printing to visualize stellar nurseries. *The Astrophysical Journal Letters*, 918, id.L3.

https://doi.org/10.3847/2041-8213/ac194e

Johnson, M.M., Young, M.T. & Brusatte, S.L. (2020) The phylogenetics of Teleosauridea (Crocodylomorpha, Thalattosuchia) and implications for the ecology and evolution. *PeerJ*, 8, e9808.

Knapp, A., Knell, R.J., Farke, A.A., Loewen, M.A. & Hone, D.W.E. (2018) Patterns of divergence in the morphology of ceratopsian dinosaurs, sympatry is not a driver of ornament evolution. *Proceedings of the Royal Society B*, 285, 20180312.

<https://doi.org/10.1098/rspb.2018.0312>

Knutsen, E.M. (2012) A taxonomic revision of the genus *Pliosaurus*. *Norwegian Journal of Geology*, 92, 259-276.

Koepfli, K.P., Pollinger, J., Godinho, R., Lea, A., Hendricks, S. & Schweizer, R.M., Thalmann, O., Silva, P., Fan, Z.X., Yurchenko, A.A., Dobrynin, P., Makunin, A., Cahill, J.A., Shapiro, B., Álvares, F., Brito, J.C., Geffen, E., Leonard, J.A., Helgen, K.M., Johnson, W.E., O’Brien, S.J., Van Valkenburgh, B. & Wayne, R.K. (2015) Genome-wide evidence reveals that African and Eurasian golden jackals are distinct species. *Current Biology*, 25, 2185-2165.

Larramendi, A., Zhang, H., Palombo, M.R. & Ferretti, M.P. (2020) The evolution of *Palaeoloxodon* skull structure: Disentangling phylogenetic, sexually dimorphic, ontogenetic, and allometric morphological signals. *Quaternary Science Reviews*, 229, 106090.

[https://doi.org/10.1016/j.quascirev.2019.106090](https://doi.org/10.1016/j.quascirev.2019.106090#_blank)[Get rights and content](https://s100.copyright.com/AppDispatchServlet?publisherName=ELS&contentID=S0277379119302690&orderBeanReset=true#_blank)

Larramendi, A., Paul, G.S. & Hsu, S.Y. (2021) A review and reappraisal of the specific gravities of present and past multicellular organisms, with an emphasis on tetrapods. *Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology*, 304, 1833-1888.

https://doi.org/10.1002/ar.24574

Larson, N. (2008) One hundred years of *Tyrannosaurus rex*: The skeletons. *In*: Larson, P. & Carpenter, K. (Eds) *Tyrannosaurus rex: The Tyrant King*. Indiana University Press, pp. 1-55.

Larson, P. (1994) *Tyrannosaurus sex*. *Paleontological Society Special Publication*, 7, 139-155.

[https://doi.org/10.1017/S2475262200009485](https://doi.org/10.1017/S2475262200009485#_blank)

Larson, P. (2008) Variation and sexual dimorphism in *Tyrannosaurus rex*. *In*: Larson P. & Carpenter, K. (Eds), *Tyrannosaurus rex: The Tyrant King*. Indiana University Press, pp. 103–130.

Larson, P. (2013a) The validity of *Nanotyrannus lancensis*. *Society of Vertebrate Paleontology 73rd Annual Meeting*, 159.

Larson, P. (2013b) The case for *Nanotyrannus*. *In*: Parrish, J.M., Molnar, R.E., Currie, P.J. & Koppelhus, E.B. (Eds), *Tyrannosaurid Paleobiology*. Indiana University Press, Bloomington, 15-53.

Lawson, D.A. (1976) *Tyrannosaurus* and *Torosaurus*, Maastrichtian dinosaurs from TransPecos Texas. *Journal of Paleontology*, 50, 158-164.

Lipkin, C. & Carpenter, K. (2008) Looking again at the forelimb of *Tyrannosaurus rex*. *In*: Larson, P. & Carpenter, K. (Eds), *Tyrannosaurus rex, the Tyrant King*. Indiana University Press, pp. 166–190.

Lister, A.M. & Sher, A.V. (2015) Evolution and dispersal of mammoths across the

northern hemisphere. *Science*, 350, 80-–809.

https://doi.org/[10.1126/science.aac5660](https://doi.org/10.1126/science.aac5660)

Loewen, M.A., Irmis, R.B., Sertich, J.J.W., Currie, P.J. & Sampson, S.D. (2013) Tyrant dinosaur evolution tracks the rise and fall of Late Cretaceous oceans. PLoS One, 8, e79420.

<https://doi.org/10.1371/journal.pone.0079420>

Long, K.L., Prothero, D.L. & Syverson, V.J.P. (2020) How do small birds evolve in response to climate change? Data from the long-term record at La Brea tar pits. *Integrated Zoolology*, 15, 249-261.

<https://doi.org/10.1111/1749-4877.12426>

Longrich, N.R. & Saitta, E.T. (2024) Taxonomic status of *Nanotyrannus lancensis*—a distinct taxon of small-bodied tyrannosaur. *Fossil Studies*, 2, 1-25.

<https://doi.org/10.3390/fossils2010001>

Lull, R.S. (1933) A revision of the Ceratopsia or horned dinosaurs. Memoirs of the Peabody Museum of Natural History, 3(3), 1-175.

Macdonald, I. & Currie, P.J. (2018) Description of a partial *Dromiceiomimus* (Dinosauria: Theropoda) skeleton with comments on the validity of the genus. *Canadian Journal of Earth Sciences*, 56, 129-157.

<https://doi.org/10.1139/cjes-2018-0162>

Mader, B.J. (2010) A species-level revision of the North American brontotheres *Eotitanops* and *Palaeosyops* (Mammalia, Perissodactyla). *Zootaxa*, 2339, 1-43.

Madsen, J.H. (1976) *Allosaurus fragilis*: A revised osteology. *Utah Geological and Mineral Survey Bulletin*,

109, 1-163.

Maisch, M.W. (2008) [Revision der Gattung *Stenopterygius* Jaekel, 1904 emend. VON HUENE, 1922 (Reptilia: Ichthyosauria) aus dem unteren Jura Westeuropas](http://www.palaeodiversity.org/pdf/01/Palaeodiversity_1_14_227-272.pdf). *Palaeodiversity*, 1, 227–271.

Maleev, E.A. (1955) Giant carnivorous dinosaurs of Mongolia. *Doklady*, *Academy of Sciences USSR*, 104, 634–637.

Maleev, E.A. (1974) Giant carnosaurs of the family Tyrannosauridae. *Joint Soviet-Mongolian Paleontological Expedition*, 1, 132-191.

Mallon, J.C. & Hone, D.W. (2024) Estimation of maximum body size in fossil speces: A case study using *Tyrannosaurus rex*. *Ecology and Evolution*, 14, e11658.

<https://doi.org/10.1002/ece3.11658>

Mallon, J.C., Holmes, R.B., Bamforth, E.L. & Schumann, D. (2022) The record of *Torosaurus* (Ornithischia: Ceratopsidae) in Canada and its taxonomic implications. *Zoological Journal of the Linnean Society*, 195, 157-171.

<https://doi.org/10.1093/zoolinnean/zlab120>

Mallon, J.C., Roloson, M., Bamforth, E., Scannella, J.B. & Ryan, M.J. (2025) The Canadian fossil record supports anagenesis in *Triceratops* (Ornithischia, Ceratopsia). Canadian Journal of Earth Sciences, 1-15.

<https://doi.org/10.1139/cjes-2024-0170>

Marghoub, A., Williams, C.J.A., Leite, J.V., Kirby, A.C., Kéver, L., Porro, L.B., Bertazzo, S., Abzhanov, A., Vickaryous, M., Herrel., A., Evans, S.E. & Moazen, M. (2022) Unraveling the structural variation of lizard osteoderms. *Acta Biomaterialia*, 146, 306-316.

[https://doi.org/10.1016/j.actbio.2022.05.004](https://doi.org/10.1016/j.actbio.2022.05.004#_blank)

Maxwell, E.E. (2012) New metrics to differentiate species of *Stenopterygius* (Reptilia: Ichthyosauria) from the Lower Jurassic of southwestern Germany. *Journal of Paleontology*, 86, 105-115.

[https://doi.org/10.1666/11-038.1](https://doi.org/10.1666/11-038.1#_blank)

Mayr, E. (1982) *The Growth of Biological Thought, Diversity, Evolution and*

*Inheritance*. Harvard University Press, Cambridge, 1-974.

Mayr, G. (2018) A survey of casques, frontal humps, and other extravagant bony cranial protuberances in birds. *Zoomorphology*, 137, 457-472.

https://doi.org/10.1007/s00435-018-0410-2

Mertens, R. (1942) *Die familie der Warane (Varanidae)*. Abhandlungen der Senckenbergischen Naturforschenden

Gesellschaft, Abhandlung, 462.

Mihlbachler, M.C. (2008) Species taxonomy, phylogeny, and biogeography of the Brontotheriidae. *Bulletin of the American Museum of Natural History*, 311, 1-475.

[https://doi.org/10.1206/0003-0090(2008)501[1:STPABO]2.0.CO;2](https://doi.org/10.1206/0003-0090(2008)501%5B1:STPABO%5D2.0.CO;2)

Molnar, R.E. (2004) The long and honorable history of monitors and their kin. *In*: King, R.A., Pianka, E.R. & King, D. (Eds), *Varanoid Lizards of the World*. Indians University Press, Bloomington, pp. 10-67.

Morrison, C., Scherer, C.R., O’Callaghan, Layton, C., Boisvert, C. Rolando M.A., Durrant, L., Salas, P. Allain, S.J.R. & Gascoigne, S.J.L. (2025). Rise of the king. Gondwanan origins and evolution of megaraptorans dinosaurs. *Royal Society Open Science*, 12, 242238.

http://doi.org/10.1098/rsos.242238

Naish, D. & Perron, R. (2016) Structure and function of the cassowary’s casque and its implications for cassowary history, biology and evolution. *Historical Biology*, 28, 507-518.

<https://doi.org/10.1080/08912963.2014.985669>Napoli, J. G., Powers, M.J., Ruebenstahl, A.A., Voris, J.T., Green, T.L., Turner, A.H., Flynn, J.J., Currie, P.J., & Norell, M.A. (2023) Cryptic species in the theropod fossil record. *Society of Vertebrate Paleontology 83rd Annual Meeting*, 319.

Nowak, R.M. (1991) *Walker’s Mammals of the World*. Johns Hopkins University Press, 1-1629.

Olshevsky, G. & Ford, T.L. (1995) The origin and evolution of the Tyrannosauridae, part 2.

*Dino Frontline,*6, 75–99.

Osborn, H.F. (1905) *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bulletin of*

*the American Museum of Natural History*, 21, 259-265.

Osborn, H.F. (1916) Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. *Bulletin of the American Museum of Natural History*, 35, 733-771.

Oyston, J.W., Wilkinson, M., Ruta, M. & Wills, M.A. (2022) Molecular phylogenies map to biogeography better than morphological ones. *Communications Biology*, 5, 521.

https://doi.org/10.1038/s42003-022-03482-x

Padian, K. (2022) Why tyrannosaurid forelimbs were so short: An integrative hypothesis. *Acta Palaeontologica Polonica*, 67, 63-76.

Padian, K. & Horner, J. (2011) The evolution of ‘bizarre structures’ in dinosaurs: biomechanics, sexual selection, social selection, or species recognition? *Journal of Zoology*, 283, 3-17.

<https://doi.org/10.1111/j.1469-7998.2010.00719.x>

Padian, K. & Horner, J.R. (2014) The species recognition hypothesis explains exaggerated structures in non-avialan dinosaurs better than sexual selection does. Comptes Rendus Palevol, 13, 97-107.

[https://doi.org/10.1016/j.crpv.2013.10.004](https://doi.org/10.1016/j.crpv.2013.10.004#_blank)

Paul, G.S. (1988) *Predatory Dinosaurs of the World*. Simon & Schuster, 1-464.

Paul, G.S. (2008) The extreme lifestyles and habits of the gigantic tyrannosaurid superpredators of the Late Cretaceous of North America and Asia. *In*: Larson, P. & Carpenter, K. (Eds), *Tyrannosaurus rex: The Tyrant King*. Indiana University Press, pp. 307-352.

Paul, G.S. (2016) *The Princeton Field Guide to Dinosaurs 2nd ed*. Princeton University Press, 1-360.

Paul, G.S. (2018).Nonornithschian dinosaurs did too have lips. probably big lips, here’s why. *Prehistoric Times*, 127, 44-49.

Paul, G.S. (2019) Determing the largest known land animal: A critical comparison of

differing methods for restoring the volume and mass of extinct animals. *Annals of Carnegie Museum*, 85, 335-358.

<https://doi.org/10.2992/007.085.0403>

Paul, G.S. (2022) *The Princeton Field Guide to Pterosaurs*. Princeton University Press, 1-184.

Paul, G.S. (2022b) Observations on paleospecies determination, with additional data on *Tyrannosaurus* including its highly divergent species specific supraorbital display ornaments that give *T. rex* a new and unique life appearance. *BioRxiv*.

https://doi.org/10.1101/2022.08.02.502517

Paul, G.S. (2024a) *The Princeton Field Guide to Dinosaurs 3rd ed*. Princeton University

Press, 1-384.

Paul, G.S. (2024b) *The Princeton Field Guide to Predatory Dinosaurs*. Princeton

University Press, 1-256.

Paul, G.S., Persons, W.S. & Van Raalte, J. (2022) The tyrant lizard king, queen and

emperor: Multiple lines of evidence support subtle evolution and probable speciation within the North American genus *Tyrannosaurus*. *Evolutionary Biology*, 49, 156-179.

https://doi.org/10.1007/s11692-022-09561-5

Paulina-Carabajal, A.P., Currie, P.J., Dudgeon, T.W., Larsson, H.C.E. & Miyashita, T. (2021) Two braincases of *Daspletosaurus* (Theropoda: Tyrannosauridae): anatomy and comparison. *Canadian Journal of Earth Sciences*, 58, 885-910.

<https://doi.org/10.1002/ar.24118>

Perri, A.R., Mitchell, K.J., Mouton, A., Álvarez-Carretero, S., Hulme-Beaman, A., Haile, J., Jamieson, A., Meachen, J., Lin, A.T., Schubert, B.W., Ameen, C., Antipina, E.E., Bover, P., Brace, S., Carmagnini, A., Carøe, C., Castruita, J.A.S., Chatters, J.C., Dobney, K., dos Reis, M., Evin, A., Gaubert, P., Gopalakrishnan, S., Gower, G., Heiniger, H., Helgen, K.M., Kapp, J., Kisintsev, P.A., Linderholm, A.,Ozga, A.T., Presslee, S., Salis, A.T., Saremi, N.F., Shew, C., Skerry, K., Taranenko, D.E., Thompson, M., Sablin, M.V., Kuzmin, Y.V., Collins, M.J., Sinding, M.H.S., Gilbert, M.T., Stone, A.C., Shapiro, B., Van Valkenburgh, B., Wavne, R.K., Larson, G., Cooper, A. & Franz, L.A.F. (2021) Dire wolves were the last of an ancient New World canid lineage. *Nature*, 591, 87-91.

https://doi.org/10.1038/s41586-020-03082-x

Richardson, K.C. (1991) The bony casque of the southern cassowary, *Casuarius casuarius*. *Emu*, 91, 56–58.

<https://doi.org/10.1071/MU9910056>

Rinehart, L.F., Lucas, S.G., Heckert, A.B., Spielmann, J.A. & Celeskey, M.D. (2009) The paleobiology of *Coelophysis bauri* from the Upper Triassic Whitaker quarry, New Mexico, with a detailed analysis of a single quarry block. *The New Mexico Museum of Natural History & Science*, 45, 1-260.

Rowe, A.J. & Rayfield, E.J. (2024) Morphological evolution and functional consequences of gigantism in tyrannosauroid dinosaurs. *iScience*, 27,110679.

https://doi.org/[10.1016/j.isci.2024.110679](https://doi.org/10.1016/j.isci.2024.110679#_blank)

Rozhdestvensky, A.K. (1965) Growth changes in Asian dinosaurs and some problems of their taxonomy. *Paleontologicheskii Zhurnal*, 1965, 95-109.

Russell, D.A. (1970) Tyrannosaurs from the Late Cretaceous of western Canada. *National*

*Museum of Natural Sciences Publications in Paleontology*, 1, 1-34.

Saitta, E.T., Latte, H., Vinther, J., Gnoske, T., Kaey, T.G., Brooker, R., Bull, I.D., & Sereno, P. (2023)

Sexing dinosaurs; Possible detection of trace sex hormones in fossils as old as the Jurassic and the thermal

stability of estrogen. *Society of Vertebrate Paleontology 83rd Annual Meeting Abstracts*, 376-377.

Scannella, J.B., Fowler, D.W., Goodwin, M.B. & Horner, J.R. (2014) Evolutionary trends

in *Triceratops* from the Hell Creek Formation, Montana. *PNAS*, 111, 10245–10250.

<https://doi.org/10.1073/pnas.1313334111>

Scherer, C.R. & Voiculescu-Holvad, C. (2024) Re-analysis of a dataset refutes claims of

anagenesis within *Tyrannosaurus*-line tyrannosaurines (Theropoda, Tyrannosauridae). *Cretaceous Research*,

155, 105780.

[https://doi.org/10.1016/j.cretres.2023.105780](https://doi.org/10.1016/j.cretres.2023.105780#_blank)

Scherer, C.R. (2025) Multiple lines of evidence support anagenesis in *Daspletosaurus* and cladogenesis in derived tyrannosaurines. *Cretaceous Research*, 155, 106080.

[https://doi.org/10.1016/j.cretres.2025.106080](https://doi.org/10.1016/j.cretres.2025.106080#_blank)

Schmerge, J.D. & Rothschild, B.R. (2016a) Distribution of the dentary groove of theropod dinosaurs: Implications for theropod phylogeny and the validity of the genus Nanotyrannus. *Cretaceous Research*, 61, 26-33.

[https://doi.org/10.1016/j.cretres.2015.12.016](https://doi.org/10.1016/j.cretres.2015.12.016#_blank)[Get rights and content](https://s100.copyright.com/AppDispatchServlet?publisherName=ELS&contentID=S0195667115301415&orderBeanReset=true#_blank)

Schmerge, J.D. & Rothschild, B.R. (2016b) When a groove is not a groove: Clarification of the appearance of the dentary groove in tyrannosauroid theropods and the distinction between *Nanotyrannus* and *Tyrannosaurus*: Reply to Comment on, Distribution of the dentary groove of theropod dinosaurs: Implications for theropod phylogeny and the validity of the genus *Nanotyrannus* Bakker et al., 1988”. *Cretaceous Research*, 65, 238-243.

[https://doi.org/10.1016/j.cretres.2016.04.015](https://doi.org/10.1016/j.cretres.2016.04.015#_blank)

Sellers, W.I., Pond, S.B., Brassey, C.A., Manning, P.L. & Bates, K.T. (2017) Investigating the running abilities of *Tyrannosaurus rex* using stress-constrained multibody dynamic analysis. *PeerJ*, 5, e3420.

Sereno, P.C. (2010) Taxonomy, cranial morphology, and relationships of parrot-beaked dinosaurs. In: Ryan, M.J., Chinnery-Allgeier, B., Brenda, J. & Eberth, D.A. (Eds), New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium. Indiana University Press, pp. 21–58.

Snively, E., O’Brien, H., Henderson, D.M., Mallison, H., Surring, L.A., Burns, M.E., Holtz Jr, T.R., Russell, A.P., Witmer, L.M., Currie, P.J., Hartman, S.A. & Cotton, KJ.R. (2019) Lower rotational inertia and larger leg muscles indicate more rapid turns in tyrannosaurids than in other large theropods. *PeerJ*, 7, e6432.

Snively, E., Henderson, D.M. & Philips, D.S. (2006) Fused and vaulted nasals of tyrannosaurid dinosaurs, Implications for cranial strength and feeding mechanics. Acta Palaeontologica Polonica, 51, 435-454.

Son, M., Erickson, G.M., Zhou, C.F., Yin, Y.L. & Makovicky, P. (2024). Intra- and inter-specific variation in Psittacosaurus. *The Society of Vertebrate Paleontology 84th Meeting Abstracts*, 512-513.

Sotnikova, M. & Nikolskiy, P. (2006) Systematic position of the cave lion *Panthera*

*spelaea* (Goldfuss) based on cranial and dental characters. *Quaternary International*, 142–3, 218-228.

[https://doi.org/10.1016/j.quaint.2005.03.019](https://doi.org/10.1016/j.quaint.2005.03.019#_blank)

Stanley, S.M. (2017) Evidence that the arms of *Tyrannosaurus rex* were not functionless but adapted for vicious slashing. Geological Society of America. *Abstracts with Program*, 131–138.

https://doi.org/[10.1130/abs/2017AM-297346](https://ui.adsabs.harvard.edu/link_gateway/2017GSAA...4997346S/doi:10.1130/abs/2017AM-297346#_blank)

Stein, W.W. & Triebold, M. (2013) Preliminary analysis of a sub-adult tyrannosaurid skeleton from the Judith River Formation of Petroleum County, Montana. *In*: Parrish, J.M., Molnar, R.E., Currie, P.J. & Koppelhus, E.B. (Eds), *Tyrannosaurid Paleobiology*. Indiana University Press, Bloomington, pp. 55–77.

Stock, J.C., Powers, M.J., Coppock, c. Raun, G.S., Sharpe, H.S., Henry, S., Jared, T., Napoli, J.G., & Currie, P.J. (2024) New species of *Albertosaurus* from a distinct stratigraphic unit of the Horseshoe Canyon Formation corresponding to faunal and climatic changes. *The Society of Vertebrate Paleontology 84th Meeting Abstracts*, 518–519.

Terrien, F., Zelenitsky, D.K., Tanaka, K., Voris, J.T., Erickson, G.M., Currie, P.J., Debuhr, C.L. & Kobayashi, Y. (2023) Exceptionally preserved stomach contents of a young tyrannosaurid reveal an ontogenetic dietary shift in an iconic extinct predator. *Science Advances*, 9, eadi0505.

https://doi.org/[10.1126/sciadv.adi0505](https://doi.org/10.1126/sciadv.adi0505)

Tschopp, E., Mateus, O.V. & Benson, R.B. (2015) A specimen-level phylogenetic analysis and taxonomic revision of Diplodocidae. *PeerJ*, 3, e857.

Tsuihiji, T. , Watabe, M., Tsogtbaatar, K., Tsubamoto, T., Barscold, R., Suzuki, S., Lee, A.H., Ridgely, R.C., Kawahara, Y. & Witmer, L.m. (2011) Cranial osteology of a juvenile specimen of *Tarbosaurus bataar* (Theropoda, Tyrannosauridae) from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia. Journal of Vertebrate Paleontology, 31, 497-517.

<https://doi.org/10.1080/02724634.2011.557116>

Vickaryous, M.K., Meldrum, G. & Russell, A.P. (2015) Armored geckos, a histological investigation of osteoderm development in *Tarantola* (Phyllodactylidae) and *Gekko* (Gekkonidae) with comments on their regeneration and inferred function. *Journal of Morphology*, 276, 1345-1357.

<https://doi.org/10.1002/jmor.20422>

Voris, J.T., Zelenitsky, D.K., Kobayashi, Y., Modesto, S.P., Therrien, F., Tsutsumi, H, Tsogtbaater, C. & Tsogtbatar, K. (2025) A new Mongolian tyrannosauroid and the evolution of Eutyrannosauria. *Nature,* 2025.

https://doi.org/10.1038/s41586-025-08964-6

Warshaw, E.A. & Fowler, D.W. (2022) A transitional species of *Daspletosaurus* Russell, 1970 from the Judith River Formation of eastern Montana. *PeerJ*, 10, e14461.

Warshaw, E.A., Barrera, G.D. & Fowler, D.W. (2024) Anagenesis and the tyrant pedigree, a response to “Re-analysis of a dataset refutes claims of anagenesis within *Tyrannosaurus*-line tyrannosaurines”. *Cretaceous Research*, 155, 105957.

[https://doi.org/10.1016/j.cretres.2024.105957](https://doi.org/10.1016/j.cretres.2024.105957#_blank)

Wick, S.L. (2014) New evidence for the possible occurrence of *Tyrannosaurus* in west Texas, and discussion of Maastrichtian tyrannosaurid dinosaurs from Big Bend National Park. *Cretaceous Research*, 50, 52–58.

[https://doi.org/10.1016/j.cretres.2014.03.010](https://doi.org/10.1016/j.cretres.2014.03.010#_blank)

Witton, M.P. (2022) Tyannouroboros: how everything old is new again in recent proposals of *Tyrannosaurus* taxonomy. Mark P. Witton’s blog, http://markwitton-com.blogspot.com/2022/03/tyrannouroboros-how-everything-old-is.html.Woodward, H.N., Tremaine, K., Williamson S.A., Zanno, L.E., Horner, J.R. & Myhrvold, N. (2020) Growing up *Tyrannosaurus rex*: Osteohistory refutes the pygmy “*Nanotyrannus*” and supports ontogenetic niche partitioning in juvenile *Tyrannosaurus*. *Science Advances*, 6, eaax6250.

<https://doi.org/10.1126/sciadv.aax625>

Zeinio, K. (2012) Species concepts. *Scientific American*.

<https://blogs.scientificamerican.com/evo-eco-lab/species-concepts>.

**SUPPLEMENTARY TABLE 1.** Femur and tibia shafts bone cross section data and growth calculations for Laramidia Late Cretaceous eutyrannosaurs, bone measurements in mm. Radii are from center of bone to lines of arrested growth and inner and outer cortex surfaces (Fig. 12A), the later records final adult size only in FMNHPR2081. Only final lengths and length/radius ratios are based on direct measurements. All other lengths are approximated while taking into account changing ontogenetic allometry, which based on the limited available data appears to have been least in extent early in growth, becoming most significant at over a tonne in total mass. So ratios are often constant at smaller dimensions because data is inadequate for greater precision and results would not be markedly different. Length/radius ratios are higher for tibiae than femora at a given body size. The k factor is femur or tibia length in decimeters[[1]](#endnote-1)3 xk = kg, k’s are lower due to ontogenetic allometry at smaller sizes where k’s are more constant in manner similar to length/radius ratios. Data sources Horner & Padian (2004), Cullen *et al*. (2020), Woodward *et al*. (2020) and Therrien *et al*. (2023). Results in Fig. 12.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Femur or tibia radius | length/  radius | length | k | Total mass kg | kg/year |
| FMNHPR2081 femur **S** | 289 | 4.57 | 1321 | 3.18 | 7340 | - |
| *T. imperator* | 287 | 4.57 | 1320 | 3.18 | 7129 | 210 |
|  | 282 | 4.6 | 1316 | 3.05 | 6852 | 277 |
|  | 273 | 4.72 | 1288 | 2.91 | 6205 | 647 |
|  | 265 | 4.75 | 1258 | 2.81 | 5574 | 631 |
|  | 258 | 4.78 | 1233 | 2.70 | 5064 | 510 |
|  | 246 | 4.82 | 1185 | 2.68 | 4334 | 730 |
|  | 234 | 4.85 | 1134 | 2.57 | 3800 | 534 |
|  | 224 | 4.88 | 1093 | 2.46 | 3134 | 666 |
|  | 214 | 4.93 | 1055 | 2.36 | 2818 | 316 |
|  | 201 | 4.97 | 999 | 2.25 | 2193 | 625 |
|  | 163 | 5 | 815 | 2.1 | 1137 | 1056 |
|  |  |  |  |  |  |  |
| USNM555000 tibia **U** | 188 | 6.1 | 1150 | 4 | 6081 | - |
| *T. regina* | 186 | 6.1 | 1135 | 4 | 5842 | 239+ |
|  | 183 | 6.1 | 1116 | 3.8 | 5282 | 560 |
|  | 180 | 6.1 | 1098 | 3.5 | 4633 | 649 |
|  | 174 | 6.2 | 1075 | 2.9 | 3643 | 990 |
|  | 167 | 6.3 | 1052 | 2.2 | 2561 | 1082 |
|  | 157 | 6.4 | 1004 | 1.6 | 1619 | 942 |
|  | 138 | 6.8 | 938 | 1.1 | 908 | 711 |
|  | 111 | 7 | 777 | 1 | 777 | 439 |
|  |  |  |  |  |  |  |
| MOR1128 tibia  **R** | 168 | 6.6 | 1120 | 4.6 | 6500 | - |
| *T. imperator* | no data | nd | nd | nd | nd | nd |
|  | 114 | 7 | 798 | 1 | 508 | - |
|  | 96 | 7 | 672 | 1 | 303 | 205 |
|  | 89 | 7 | 623 | 1 | 242 | 61 |
|  | 84 | 7 | 588 | 1 | 203 | 39 |
|  | 78 | 7 | 546 | 1 | 163 | 40 |
|  |  |  |  |  |  |  |
| BMRP 2002.4.1 femur **J** | 122 | 5.9 | 720 | 1.43 | 533 | - |
| *Nanotyrannus*? | 119 | 5.9 | 702 | 1.43 | 495 | 38+ |
|  | 114 | 5.9 | 673 | 1.43 | 435 | 60 |
|  | 109 | 5.9 | 643 | 1.43 | 380 | 55 |
|  | 102 | 5.9 | 601 | 1.43 | 312 | 68 |
|  | 95 | 5.9 | 561 | 1.43 | 252 | 60 |
|  | 85 | 5.9 | 507 | 1.43 | 180 | 72 |
|  |  |  |  |  |  |  |
| BMRP2006.4.4 femur **P** | 119 | 6.5 | 774 | 1.43 | 663 | - |
| *Nanotyrannus*? | 117 | 6.5 | 761 | 1.43 | 628 | 31+ |
|  | 115 | 6.5 | 748 | 1.43 | 597 | 31 |
|  | 112 | 6.5 | 728 | 1.43 | 552 | 45 |
|  | 108 | 6.5 | 702 | 1.43 | 495 | 57 |
|  | 98 | 6.5 | 637 | 1.43 | 370 | 125 |
|  | 79 | 6.5 | 514 | 1.43 | 194 | 175 |
|  |  |  |  |  |  |  |
| BMRP2006.4.4 tibia | 107 | 8.7 | 936 | 0.8 | 663 | - |
| *Nanotyrannus*? | 105 | 8.7 | 914 | 0.8 | 610 | 53+ |
|  | 102 | 8.7 | 887 | 0.8 | 559 | 51 |
|  | 99 | 8.7 | 861 | 0.8 | 511 | 48 |
|  | 94 | 8.7 | 818 | 0.8 | 438 | 73 |
|  | 91 | 8.7 | 792 | 0.8 | 397 | 41 |
|  | 84 | 8.7 | 731 | 0.8 | 312 | 85 |
|  | 78 | 8.7 | 679 | 0.8 | 250 | 62 |
|  |  |  |  |  |  |  |
| TMP 2009.12.14 tibia **G** | 77 | 8 | 614 | 1.31 | 304 | - |
| *G. libratus* | 71 | 8 | 568 | 1.31 | 240 | 64+ |
|  | 69 | 8 | 552 | 1.31 | 220 | 20 |
|  | 67 | 8 | 536 | 1.31 | 201 | 19 |
|  | 64 | 8 | 512 | 1.31 | 175 | 26 |
|  | 63 | 8 | 504 | 1.31 | 168 | 8 |
|  | 61.5 | 8 | 156 | 1.31 | 156 | 12 |
|  | 60 | 8 | 145 | 1,31 | 145 | 11 |

**SUPPLEMENTARY TABLE 2.** Measurements in mm and ratios for TT-zone *Tyrannosaurus* femora, humeri, ilia, metatarsals 2 and 4, maxillae, dentaries, and dentary teeth 2 and 3, with additional calculations (variation percentage, ratio ranges, ratio averages and medians), plus known stratigraphic levels within TT-zone, and status as robust, gracile or borderline as determined by overall skeletal analysis for entire *Tyrannosaurus* sample. 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. Dentary tooth base diameters always measured on same side. From Paul *et al*. (2022) with some minor updates and additions, for more details on the specimens see same reference (Supplementary Information), same for non*Tyrannosaurus* Mesozoic large avepod femora data.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | Level | Gracile or Robust | Femur  Length | Femur  Circ. | Femur  Ratio |
| NHMAD (exBHI3033) Stan | h | g | 1350 | 505 | 2.67 |
| Z-rex/Samson | l | r | 1343 | 560 | 2.4 |
| RSMP2523.8 Scotty | h | r? | 1333 | 590 | 2.26 |
| FMNHPR2081 Sue *T. imperator* type | l or m | r | 1321 | 580 | 2.28 |
| BHI6248 Cope | l | r | 1300 | 630 | 2.06 |
| TMTv222 Lee | l | b | 1295 | 545 | 2.38 |
| MOR1128 G-rex | l | r | 1280 | 580 | 2.21 |
| USNM555000 Wankel *T. regina* type | h | g | 1280 | 520 | 2.46 |
| CM9380 *T. rex* type Barnum | h | r | 1269 | 534 | 2.38 |
| MOR980 Peck’s Rex/Rigby | h | g | 1232 | 483 | 2.55 |
| RMDRC2002.MT-001 | na | r | 1220 | 580 | 2.1 |
| HMNMB.R.91216 Tristan | l | b | 1220 | 520 | 2.35 |
| TMP81.6.1 Black Beauty | h | g | 1210 | 460 | 2.63 |
| LL12823 | m | g | 1200 | 467 | 2.57 |
| BHI6242 Henry | na | r | 1189 | 512 | 2.3 |
| LACM150167 Thomas | h | g | 1181 | 470 | 2.51 |
| BHI6232 | m | r | 1180 | 527 | 2.24 |
| BHI6435 | h | r | 1180 | 512 | 2.3 |
| BHI6436 | h | r | 1170 | 530 | 2.21 |
| RGM792.000 Trix | l | r | 1170 | 529 | 2.21 |
| MOR1125 B-rex | l or m | r | 1150 | 515 | 2.23 |
| BHI6233 | h | r | 1110 | 515 | 2.16 |
| BHI6230 Wy-rex | h | r | 1100 | 494 | 2.23 |
| MOR009 Hager | h | b | 1100 | 469 | 2.34 |
| USNM6183 | na | r juv. | 990 | 430 | 2.32 |
| LACM23845 | h | g juv. | ~900 | 305 | ~2.95 |
| LACM23844 | h | b |  |  |  |
| BHI4100 Duffy | h | r? |  |  |  |
| BHI4182 | l | ? |  |  |  |
| BHI6231 | m | R? |  |  |  |
| MOR008 | na | ? |  |  |  |
| AMNH5027 Brown | na | ? |  |  |  |
| NHMUKR7994 *D. imperiosus* type | m | r? |  |  |  |
| SDSM12047 | l | ? |  |  |  |
| TCM2001.90.1 Bucky | l or m | R |  |  |  |
| UCMP118742 | na | g? |  |  |  |
| NMMNHP-3698 | l | r? |  |  |  |
| UWBM99000 Tufts-Love | h | g |  |  |  |
| n24 femora 1100+ mm all levels |  |  |  |  | Variation 30% |
|  |  |  |  |  | Range 2.06–2.67 |
|  |  |  |  |  | Median 2.37 |
|  |  |  |  |  | Average 2.27 |
| n12 femora 1100+ mm h level |  |  |  |  | Variation 24% |
|  |  |  |  |  | Range 2.16–2..67 |
|  |  |  |  |  | Median 2.42 |
|  |  |  |  |  | Average 2.39 |
| n8 femora 1100+ mm |  |  |  |  | Variation 17% |
|  |  |  |  |  | Range 2.06–2.4 |
|  |  |  |  |  | Median 2.23 |
|  |  |  |  |  | Average 2.27 |

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *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 |
| NHMAD |  |  |  | 1540 | 585 | 2.63 | 595 | 280 | 2.13 | 77 | 7.7 |
| Z-rex |  |  |  |  |  |  | 610 | 305 | 2 |  |  |
| RSMP2523.8 |  |  |  | 1545 | 515 | 3 |  |  |  |  |  |
| FMNHPR2081 | 390 | 185 | 2.11 | 1525 | 608 | 2.51 | 584 | 283e | 2.06e | 78 | 7.49 |
| BHI6248 |  |  |  |  |  |  |  |  |  |  |  |
| TMTv222 |  |  |  |  |  |  |  |  |  |  |  |
| MOR1128 |  |  |  |  |  |  |  |  |  |  |  |
| USNM555000 | 375 | 162 | 2.31 | 1470 | 513 | 2.86 | 585 | 295 | 1.98 |  |  |
| CM9380 | 330 | 145 | 2.28 | 1515 | ~530 | ~2.85 | 615 | 323e | 1.9e | 89 | 6.91 |
| MOR980 | 362 | 165 | 2.19 | 1397 | 483 | 2.89 | 597 | 232 | 2.57 |  |  |
| RMDRC2002 |  |  |  |  |  |  |  |  |  |  |  |
| HMNMB.R.91216 |  |  |  |  |  |  |  |  |  |  |  |
| TMP81.6.1 | 302 | 150 | 2.01 |  |  |  |  |  |  |  |  |
| LL12823 |  |  |  |  |  |  |  |  |  |  |  |
| BHI6242 |  |  |  |  |  |  |  |  |  |  |  |
| LACM150167 |  |  |  |  |  |  |  |  |  |  |  |
| BHI6232 |  |  |  |  |  |  |  |  |  |  |  |
| BHI6435 |  |  |  |  |  |  |  |  |  |  |  |
| BHI6436 |  |  |  |  |  |  |  |  |  |  |  |
| RGM792.000 |  |  |  |  |  |  |  |  |  |  |  |
| MOR1125 |  |  |  |  |  |  |  |  |  |  |  |
| BHI6233 |  |  |  |  |  |  |  |  |  |  |  |
| BHI6230 | 330 | 145 | 2.28 |  |  |  | 600 | 272 | 2.21 | 74 | 8.1 |
| MOR009 |  |  |  | 1180 | 407 | 2.9 | 540 | 254e | 2.13e | 70 | 7.71 |
| USNM6183 |  |  |  |  |  |  |  |  |  |  |  |
| LACM23845 |  |  |  |  |  |  | 465 | 174e | 2.67e | 48 | 9.69 |
| LACM23844 |  |  |  |  |  |  | 575 | 272e | 2.11e | 75 | 7.67 |
| BHI4100 |  |  |  |  |  |  |  |  |  |  |  |
| BHI4182 |  |  |  |  |  |  |  |  |  |  |  |
| BHI6231 | 360 | 172 | 2.09 |  |  |  |  |  |  |  |  |
| MOR008 |  |  |  |  |  |  |  |  |  |  |  |
| AMNH5027 |  |  |  | 1448 | 470 | 3.08 |  |  |  |  |  |
| NHMUKR7994 |  |  |  |  |  |  |  |  |  |  |  |
| SDSM12047 |  |  |  |  |  |  |  |  |  |  |  |
| TCM2001.90.1 |  |  |  | 1275 | 490 | 2.6 | 550 | 267 | 2.06 | 74 | 7.43 |
| UCMP118742 |  |  |  |  |  |  |  |  |  |  |  |
| NMMNHP-3698 |  |  |  |  |  |  |  |  |  |  |  |
| UWBM99000 |  |  |  |  |  |  |  |  |  |  |  |
| 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 |

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| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *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 |
| NHMAD | 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 |
| RSMP2523.8 |  |  |  |  |  |  |  |  |  |  |  |
| FMNHPR2081 | 621 | 228e | 2.72e | 83 | 7.48 |  |  |  | 954 | 189 | 5.05 |
| BHI6248 |  |  |  |  |  |  |  |  |  |  |  |
| TMTv222 |  |  |  |  |  |  |  |  |  |  |  |
| MOR1128 |  |  |  |  |  |  |  |  |  |  |  |
| USNM555000 | 605 | 253 | 2.39 |  |  | 824 | 408 | 2.02 | 879 | 151 | 5.82 |
| CM9380 | 600 | 316e | 1.9e | 87 | 6.9 | 690 | 378 | 1.83 | 850 | 178 | 4.78 |
| MOR980 |  |  |  |  |  | 627 | 277 | 2.26 | 843 | 164 | 5.14 |
| MT2002 |  |  |  |  |  |  |  |  |  |  |  |
| HMNMB.R.91216 |  |  |  |  |  |  |  |  |  |  |  |
| TMP81.6.1 |  |  |  |  |  | 667 | 304 | 2.19 | 705 | 131 | 5.38 |
| LL12823 |  |  |  |  |  |  |  |  |  |  |  |
| BHI6242 |  |  |  |  |  |  |  |  |  |  |  |
| LACM150167 |  |  |  |  |  | 631 | 298 | 2.11 | 423+? | 88 | 4.80+ |
| BHI6232 |  |  |  |  |  |  |  |  |  |  |  |
| BHI6435 |  |  |  |  |  |  |  |  |  |  |  |
| BHI6436 |  |  |  |  |  |  |  |  |  |  |  |
| RGM792.000 |  |  |  |  |  | 781 | 422 | 1.85 |  |  |  |
| MOR1125 |  |  |  |  |  | 610 | 324 | 1.88 | 699 | 129 | 5.42 |
| BHI6233 |  |  |  |  |  |  |  |  |  |  |  |
| BHI6230 | 625 | 238 | 2.63 | 87 | 7.18 |  |  |  |  |  |  |
| MOR009 | 560 | 184e | 3.04e | 67 | 8.36 |  |  |  |  |  |  |
| USNM6183 |  |  |  |  |  |  |  |  |  |  |  |
| LACM23845 |  |  |  |  |  |  |  |  |  |  |  |
| LACM23844 |  |  |  |  |  | 658 | 303 | 2.17 | 883 | 168 | 5.26 |
| BHI4100 |  |  |  |  |  |  |  |  | 789 | 164 | 4.81 |
| BHI4182 |  |  |  |  |  |  |  |  |  |  |  |
| BHI6231 |  |  |  |  |  |  |  |  |  |  |  |
| MOR008 |  |  |  |  |  | 664 | 322 | 2.06 | 836 | 171 | 4.89 |
| AMNH5027 |  |  |  |  |  | 680 | 345 | 1.97 | 850 | 135 | 6.3 |
| NHMUKR7994 |  |  |  |  |  |  |  |  | 941 | 182 | 5.17 |
| SDSM12047 |  |  |  |  |  |  |  |  |  |  |  |
| TCM2001.90.1 | 565 | 263 | 2.15 |  |  |  |  |  |  |  |  |
| UCMP118742 |  |  |  |  |  | 754 | 363 | 2.08 |  |  |  |
| NMMNHP-3698 |  |  |  |  |  |  |  |  |  |  |  |
| UWBM99000 |  |  |  |  |  | 740 | 394 | 1.87 |  |  |  |
| 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 |  |  | 2.00 |  |  | 5.31 |

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| --- | --- | --- | --- | --- |
| *Tyrannosaurus* | 3nd Dentary Tooth Base Diameter | 2rd Dentary Tooth Base Diameter | Dentary Teeth 2/3 Ratio | Number of Incisors |
| NHMAD | 60 | 56 | 1.07 | 1 |
| Z-rex | 54 | 33 | 1.64 | 2 |
| RSMP2523.8 | 48 | 38 | 1.26 | b |
| FMNHPR2081 | 50 | 35 | 1.43 | 2 |
| BHI6248 |  |  |  |  |
| TMTv222 |  |  |  |  |
| MOR1128 |  |  |  |  |
| USNM555000 | 56 | 52 | 1.08 | 1 |
| CM9380 | 54 | 55 | 0.98 | 1 |
| MOR980 | 51 | 52 | 0.98 | 1 |
| MT2002 |  |  |  |  |
| HMNMB.R.91216 | 68 | 46 | 1.48 | 2 |
| TMP81.6.1 | 50 | 44 | 1.14 | 1 |
| LL12823 |  |  |  |  |
| BHI6242 |  |  |  |  |
| LACM150167 |  |  |  |  |
| BHI6232 |  |  |  |  |
| BHI6435 |  |  |  |  |
| BHI6436 |  |  |  |  |
| RGM792.000 |  |  |  |  |
| MOR1125 | 39 | 31 | 1.26 | b |
| BHI6233 |  |  |  |  |
| BHI6230 |  |  |  |  |
| MOR009 |  |  |  |  |
| USNM6183 |  |  |  |  |
| LACM23845 |  |  |  |  |
| LACM23844 | 49 | 45 | 1.09 | 1 |
| BHI4100 |  |  |  |  |
| BHI4182 | 34 | 33 | 1.03 | 1 |
| BHI6231 |  |  |  |  |
| MOR008 | 64 | 48 | 1.33 | 2 |
| AMNH5027 | ~60 | ~47 | 1.28 |  |
| NHMUKR7994 | 50 | 42 | 1.19 | 1 |
| SDSM12047 | 55 | 35 | 1.57 | 2 |
| TCM2001.90.1 |  |  |  |  |
| UCMP118742 |  |  |  |  |
| NMMNHP-3698 | 54 | 36 | 1.5 | 2 |
| UWBM99000 | 43 | 45 | 0.95 | 1 |
| Range |  |  | 0.95–1.64 |  |
| Median |  |  | 1.30 |  |
| Average |  |  | 1.24 |  |

1. [↑](#endnote-ref-1)