Why tyrannosaurid forelimbs were so short: An integrative hypothesis

KEVIN PADIAN

Padian, K. 2022. Why tyrannosaurid forelimbs were so short: An integrative hypothesis. *Acta Palaeontologica Polonica* 67 (1): 63–76.

The unusually shortened limbs of giant theropods, including abelisaurids, carcharodontosaurids, and derived tyrannosauroids such as *Tyrannosaurus rex* have long been an object of wonder, speculation, and even derision on the part of both paleontologists and the public. Two questions commonly asked are "Why did the forelimbs become so short?" and "What did the animals use such short forelimbs for, if for anything?" Because basal tyrannosauroids and their outgroups, as well as the outgroups of other giant theropods, had longer forelimbs, the foreshortening of these elements in derived taxa was secondary, and it ostensibly involved a shift in developmental timing of the forelimb elements. Factors proposed to have influenced the evolutionary foreshortening include natural selection, sexual selection, energetic compensation, ontogenetic vagaries, and rudimentation due to disuse. Hypotheses of use have varied from a supporting anchor that allows the hindlimbs a purchase to stand from a reclining position to a pectoral version of pelvic claspers during intercourse to a sort of waving display during sexual or social selection. None of these hypotheses explain selective regimes for reduction; at best, they might argue for maintenance of the limb, but in all cases a larger limb would have suited the function better. It is likely that we have been looking the wrong way through the telescope, and that no specific function of the forelimbs was being selected; instead, another crucial adaptation of the animal profited from forelimb reduction. Here I propose, in the context of phylogenetic, ontogenetic, taphonomic, and social lines of evidence, that the forelimbs became shorter in the context of behavioral ecology: the great skull and jaws provided all the necessary predatory mechanisms, and during group-feeding on carcasses, limb reduction was selected to keep the forelimbs out of the way of the jaws of large conspecific predators, avoiding injury, loss of blood, amputation, infection, and death. A variety of lines of evidence can test this hypothesis.

Key words: Dinosauria, Theropoda, *Tyrannosaurus*, *Abelisaurus*, *Carcharodontosaurus*, predation, limb proportions.

Kevin Padian [kpadian@berkeley.edu], Museum of Paleontology and Department of Integrative Biology, University of California, Berkeley 94720, USA.

Received 25 June 2021, accepted 9 August 2021, available online 30 March 2022.

Introduction

The oldest known tyrannosauroids, such as *Dilong*, were relatively small, the size of average coelurosaurians, only a meter or two long; *Guanlong* was somewhat larger, at about 3 m, and some such as *Yutyrannus* and *Sinotyrannus* were larger still, a size increase likely independent from those of later tyrannosaurids (Delcourt and Grillo 2018). Their forelimb lengths, as far as known, were generally commensurate with those of other small coelurosaurians, that is to say, more than 50% the length of the hindlimbs (Xu et al. 2006); and they retained the full coelurosaurian complement of three fingers (I–III, as in birds, which are coelurosaurs). In these and other respects they differed little from other coelurosaurian lineages.

However, phyletically some lineages of tyrannosauroids increased in adult size, and the more derived tyrannosaurids (tyrannosaurids and albertosaurids) greatly reduced their forelimbs. This must be empirically a consequence of differential developmental arrest (progenesis, Alberch et al. 1979) because we can observe the pattern: the forelimb becomes comparatively shorter than in more basal tyrannosaur**oids** and outgroups, and the more distal elements are proportionally even shorter; some manual elements may be lost (see below), not necessarily according to a single pattern, such as that of birds (Padian and Chiappe 1997). Other factors are involved and will be discussed later.

Abelisaurids (Coria et al. 2002; Pol and Rauhut 2012) and carcharodontosaurids (Rauhut 2011; Novas 2013) are two other groups of theropods with giant members in which the forelimbs are highly reduced; they are not closely related to tyrannosauroids or to each other, even though both carcharo-

https://doi.org/10.4202/app.00921.2021

dontosaurids and abelisaurids are mostly Gondwanan in distribution. Carcharodontosaurids are related to allosaurids, outside coelurosaurians, and abelisaurids are close to ceratosaurids (Tykoski and Rowe 2004). Carcharodontosaurids comprise medium to very large forms; basal taxa such as *Neovenator* have forelimbs of relatively average proportional length, but most larger forms have highly reduced forelimbs. Ceratosauria are also of medium to large size and many of the larger forms have reduced forelimbs; some basal forms such as *Limusaurus* have shortened forelimbs with unusual digital configurations, but nothing approaching *Tyrannosaurus*.

The purpose of this essay is to address two perennial questions that have been posed about large tyrannosauroids and, ceteris paribus, abelisaurids and carcharodontosaurids: "why did the forelimbs become so short?" and "what, if anything, were they used for?". Because far more attention has been devoted to tyrannosaurids on this subject, I will confine most remarks to this lineage, although it does not follow that these remarks necessarily apply to the others. I propose a hypothesis that is at least indirectly testable that may explain the reduction of the forelimbs.

Institutional abbreviations.—MOR, Museum of the Rockies, Bozeman, USA; UCMP, University of California Museum of Paleontology, Berkeley, USA.

Previously proposed hypotheses to explain the brevity of large theropod forelimbs

This subject has been reviewed extensively (see Arp 2020 for a recent summary) and although some retrospective is inevitable here, readers are referred to these excellent sources for details. Following the pioneering lead of Weishampel (1981) on the possible function of the cranial crest in the hadrosaurid *Parasaurolophus*, here I will treat proposed hypotheses as testable and even falsifiable, and will discuss possible ways of examining them further.

Functional hypotheses.—These are myriad and variably accepted by paleobiologists; many have been tested and rejected or weakened. Almost none is convincing to most other authors, although Arp (2020) showed in a useful table how he thought some could be compatible with each other. The inferred limited mobility of the arms is a big problem.

Many authors have agreed that the forelimbs were too small to have been of any functional use. They could not reach the mouth, they could not reach each other, and they could not reach anything in front of the head, let alone the head (Carpenter and Smith 2001; Lipkin and Carpenter 2008; Senter and Parrish 2006).

To put functional hypotheses in anatomical context, I took some relevant measurements from the mounted skeleton of *Tyrannosaurus rex* outside the University of California Museum of Paleontology, within the Valley Life Sciences Building (Fig. 1). It is based mainly on the relatively complete skeleton in the Museum of the Rockies (MOR 555), collected from the latest Cretaceous Hell Creek Formation of Montana, restored by Matt Smith of Livingston, USA, and mounted by Mark Goodwin of the UCMP in the early 1990s. Whereas reconstructions must be used with caution, the relative completeness of this specimen is reassuring. However, a furcula was not recovered, and as a consequence the coracoids may be slightly closer to each other than they were in life. A mounted skeleton in the Los Angeles County Museum of Natural History has a furcula, but the shoulder girdles appear to be placed too far from each other, too "low-slung" below the neck on the rib cage, and angled too horizontally. Here I base estimates (approximate) on the UCMP reconstruction.

The skull of the MOR 555 mount is 120 cm long and 60 cm wide at the jaw joints. The neck is S-shaped: the anterior (horizontal) vertebral section is 45 cm long, the middle (diagonal) section is 75 cm long, and the posterior (horizontal) one is 60 cm long. The scapulocoracoid is 127 cm long, the humerus is 37 cm long, the ulna 20 cm long, digit I 22 cm long, and digit II 25 cm long. The horizontal distance between the glenoid fossae is 68 cm, and the femur is 130 cm long.

The following estimates are not based on reconstructions of functional morphology, but on "best case" scenarios of joint mobility. With the neck in this S-shaped position, the tip of the skull is 135 cm in front of the glenoid socket. If the skull and jaws are extended forward of this position, the distance between skull and glenoid would be horizontally longer but vertically shorter (because the head would be lowered with extension of the neck). If the forelimb is fully extended forward (which Carpenter and Smith [2001] determined was not possible), the second digit reaches just in front of the orbits, but the skull is still 75 cm above the forelimb. If the humerus is maximally extended forward, and if the glenoid and elbow joints could be manipulated so that the forearm and hand reached toward the skull, there is still a 30-cm gap to the jaw joint. If the humeri are extended forward and the elbows are flexed so that the forearms reach toward the midline, the bases of the fingers would be able to touch each other and the hands would overlap; however, this is considered unlikely for several reasons: (i) the morphology of the shoulder joint would cast doubt on the ability of the humerus to be rotated and extended directly forward (Carpenter and Smith 2001), (ii) the humerus is not long enough to extend in front of the body wall at the midline, so the elbow would not have been able to form a 90° angle, and as a result (iii) the hands likely would not have been able to extend to touch each other. These inferences support the conclusions of the authors cited above that the forelimbs could not reach the mouth, they could not reach each other, and they could not reach anything in front of the head, let alone the head.

Fig. 1. The mounted skeleton of *Tyrannosaurus rex* Osborn, 1905, in the atrium of the Valley Life Sciences Building at the University of California, Berkeley based mainly on the relatively complete skeleton in the Museum of the Rockies (MOR 555), collected from the latest Cretaceous Hell Creek Formation of Montana, USA. Courtesy University of California Museum of Paleontology and the Regents of the University of California. For details see text.

Carpenter and Smith (2001) reconstructed the forelimbs as being able to "bench press" (elevate) some 400 lbs (nearly 200 kg), but how would they get close enough to anything to be able to do this, and what sorts of things would have been lifted? Other authors have suggested that the forelimbs could have helped to hold down prey (Carpenter and Smith 2001), or anchor the animal to the ground as it tried to rise from a prone position (Newman 1970), or to hold on to the female during copulation; but a limited mobility to bench-press nearly 200 kg with such tiny forelimbs has not convinced most authors about any of these hypotheses. Here I briefly discuss their testability, arguing that none is plausible, testable, or possible, and none accounts for reduction: at best they suggest why even a miniscule functionality could have been maintained.

(i, ii) *Sexual or social display*: Arp (2020) attributes this idea to Holtz (2007: 125), although many authors have previously mentioned the idea of a display structure in one form or another, without analyzing it in detail. Unless it could be shown reliably that the phylogenetic antecedents of *T. rex* had clearly performed this behavior and *T. rex* had simply inherited it, there would be no way to test the hypothesis. However, it is problematic for another reason, besides being untestable. First, the shoulder and elbow joints together, as functionally reconstructed, appear to have had a very limited range of less than 90° and that in only one plane (Carpenter and Smith 2001; somewhat different reductions in mobility occurred in other large theropods). Second, usually social signaling structures become larger, not smaller, in evolution and ontogeny (Darwin 1871), so there is no obvious rationale for this hypothesis. Besides, like most other "functional" hypotheses, it tries to explain maintenance of size, not reduction of size.

(iii) *Hold down prey*: This hypothesis is due to Carpenter and Smith (2001). However, the same question applies: why would a reduced forelimb be selected for, and of what use would a 200-kg force be to restrain a struggling prey that weighed possibly as much as the predator? The measurement estimates provided above indicate that the jaws would have been buried in the prey before the forelimbs could reach it, if at all. This proposal appears to be inviable and untestable, and also does not account for reduction.

(iv) *Pectoral claspers during sex*: This hypothesis was simply mentioned by Osborn (1906: 291): "while absurdly reduced as compared with the femur [the humerus] nevertheless is provided with very stout muscular attachments, a powerful deltoid ridge, which proves that it served some function, possibly that of a grasping organ in copulation". Osborn was apparently making an analogy to the pelvic claspers of some chondrichthyans, which hold the female in place during copulation. The main problems are that this is an analogy, which epistemologically provides no evidence for anything; the copulatory organs in vertebrates are pelvic, not pectoral, so it is not clear how this organ would have helped (a correlative hypothesis for the hindlimb was not provided); and it is not clear how a tiny forelimb even capable of flexing and extending about 200 kg could have assisted in copulation with a partner of 3000 kg or greater, even if we knew in the first place how copulation occurred in tyrannosaurids (recall that the bases of the two lever arms of the forelimbs are only about 68 cm apart, whereas the ribcage is well over a meter wide). This idea appears to be untestable and impossible.

(v) *Anchors for standing up*: Newman (1970) proposed this without any mechanical analysis. Again, animals with larger forelimbs would have been able to provide a better anchor, so why would smaller forelimbs be selected for in this context? This explanation appears to be the opposite of logical expectations. Lipkin and Carpenter (2008) pointed to the thick cortex of the humerus as possible evidence for strength, but there may be a simpler histological explanation: thicker cortices with greater secondary tissue remodeling are correlated with the smallest long bone elements in rapidly growing ornithodirans (Padian et al. 2016). The reason for the excess deposition and remodeling could be that the larger long bones (tibia, femur) are growing quickly and are being fed by nutrient-bearing blood vessels that course through all bones in the body. The smaller bones do not "want" to grow larger but they cannot simply shunt off the supply of nutrients, so instead they build thicker (but functionally useless) cortices and secondarily rework and replace the primary bone (Padian et al. 2016). Furthermore, the preponderance of fractures observed in humeri (Molnar 2000; Rothschild and Molnar 2008) suggests that the element was not strong enough to support quotidian functions of an animal of that size. If these observations can be said to test Newman's (1970) hypothesis, it does not appear to be supported. And again, this is not a hypothesis of reduction, but a (failed) hypothesis of maintenance.

(vi) *Stabbing*: Stanley (2017) proposed this in a Geological Society of America Meeting abstract, and it received a lot of media attention, but as the measurements above show, the idea is impossible because the estimates of anatomical length and functional range of motion were inaccurate. The arms were simply too short and weakly powered to be of such use. And again, the jaws would have been lodged in the other animal before the arms could reach it (if they could reach it at all, which appears unlikely).

(vii) *Feeding utility as a juvenile*: If the arms were relatively larger in juveniles than in adults, could they have been of use in feeding for younger individuals? Mattison and Giffin (1989) suggested this in an abstract for an annual meeting of the Society of Vertebrate Paleontology, but there is no sufficient evidence of juvenile forelimb proportions to test the idea. However, in basal tyrannosauroids such as *Guanlong*, the arms were already reduced enough that the head and neck would have been far anterior to them during capturing and feeding, even though the hands may have theoretically been able to reach part of the mouth in some forms; so the idea may be moot (Carpenter and Smith 2001; Lipkin and Carpenter 2008; Senter and Parrish 2006). Again, this does not address reduction in the limbs, only their maintenance in juveniles (in which derived features of a clade, such as shortened arms, may not be as evident in juveniles as in adults). See Carr (2020, notably fig. 2) for a summary of proportional ontogenetic changes in *Tyrannosaurus*.

Non-functional hypotheses.—Because "ever since Darwin", as the phrase goes, natural selection has been almost synonymized with evolutionary theory, morphological structures are often assumed to be part of a structural-functional complex shaped by processes associated with natural selection (e.g., Gould and Lewontin 1979; Lockley et al. 2008). But not all treatments of the questions I examine here (i.e., why are the forelimbs so short and what could they have been used for) accept that a functional explanation is the most logical approach.

(i) Paul (1988: 320) is frequently quoted on the subject of the greatly reduced forelimbs of tyrannosauroids that it is essentially a non-hypothesis: "They were not important to their owners, so they should not be important to us". There is likely wisdom in this view, because it represents the classic "null hypothesis"; which is important, because hypotheses of function have to provide evidence in order to be considered seriously. But it could also be seen as a "science-stopper" in the sense that no further inquiry is considered fruitful. And it overlooks the important question of how the forelimbs became so small in the first place.

(ii) Lockley et al. (2008), following the lead of Gould and Lewontin (1979), Gould (1977), McKinney and McNamara (1991), McNamara (1997), and others, abjured the "adaptationist paradigm" that in the tradition of the Modern Synthesis of evolution supports the hegemony of Natural Selection to the point that every structure must have a function that has been selected. To these authors, such explanations are merely "adaptationist just-so stories" (alluding to Rudyard Kipling's "Just So Stories" about how the elephant got its trunk, and so on).

Lockley et al. (2008: 132) stated succinctly: "We argue that *T. rex* and other tyrannosaurids had small forelimbs because they had such large heads—or more accurately, we stress the morphodynamic compensation between head and forelimbs". In other words, the forelimbs were so small because the skull and jaws were so large. Like other authors, they cited examples from very different organisms and very different organ systems to show reduction of one system apparently at the expense of the other (ironically, often in selectionist terms); but they failed to show that these analogical examples have any direct evidentiary relevance to the case at hand. In short, their argument fails on homological, phylogenetic, and developmental grounds (which does not necessarily mean that they are wrong). In a sense, they are substituting a developmental just-so story for an adaptationist one. As to their analysis, their morphological comparisons among forelimbs and hindlimbs of various saurischians have no phylogenetic context and do not take into account body size, which is a major determinant of allometry in limb proportions. It is difficult to see what in their discussions is testable.

(iii) I am indebted to John R. Horner (personal communication 2021) for his excellent articulation of a neo-classic "disuse" hypothesis: the arms were not needed in predation for various ecological reasons, and so they were reduced phyletically, but the specific developmental-genetic mechanism (the "how" in contrast to the selective "why") varied among taxa, thus producing different vestigial limb patterns among large theropods, much as in their living relatives the ratites (e.g., Phillips et al. 2009; Huynen et al. 2014). I agree with all these insights, but I will argue that there may have been a positive (or negative?) selective pressure to reduce the limbs, as opposed to simple disuse. But disuse is one critical part of the hypothesis I present.

Summary.—The functional hypotheses proposed to date are neither testable nor supported by specific lines of evidence. But they also appear implausible or impossible, based on measurements of a reconstruction of a fairly complete specimen. The non-functional hypotheses are either not testable or very poorly supported.

In the first instance, most functional hypotheses have the same ontological problem (as well as the problem that the forelimbs are too short): for each function, despite how implausible or impossible each is physically, it is difficult to explain how it would benefit the lineage to evolve smaller arms rather than retain larger ones: these are at best hypotheses of the maintenance of the structure, not of its reduction. To aid the hindlimbs in pushing up from the ground, larger forelimbs would be more useful. To clasp the female during copulation, larger forelimbs would be more useful. To rake and slash competitors or prey, larger forelimbs would be more useful. To hold struggling prey for the jaws to dispatch, larger forelimbs would be more useful. To advertise one's attractiveness to females, or to warn off potential rivals and malefactors, larger forelimbs would be more useful. The question, therefore, is: What environmental influences would provide an advantage for the forelimbs to become phyletically reduced, and how can their anatomical features be explained? I regard the non-functional hypotheses as non-explanatory because they do not provide specific mechanisms for the forelimb reduction.

Phylogeny and ontogeny in the interpretation of the evolution of tyrannosaurid forelimb reduction

Phylogeny.—No one doubts that the reduction of forelimbs in large tyrannosaurids, abelisaurids, and carcharodontosaurids is secondary, because the relative sizes of the forelimbs in smaller and more basal theropods in all of these groups (and outgroups), as far as known, are larger than in these giant derived forms (e.g., Coria et al. 2002; Senter and

Parrish 2006). Although we have no records of the forelimbs of some basal tyrannosauroids such as *Dilong*, we know that tyrannosauroid outgroups among coelurosaurs (e.g., *Guanlong*: Xu et al. 2006) had relatively longer arms than derived tyrannosaurids did, although still relatively reduced. So there was clearly a reduction among the latter group, and this can be seen as a phylogenetic trend in abelisaurids and carcharodontosaurids as well (ceteris paribus). Specifically, Lipkin and Carpenter (2008: fig. 10.18) produced a graph that shows that *Guanlong* generally retained the limb proportions of other basal theropods, but in all the later, larger tyrannosaurids the forelimb elements were proportionally reduced and very similar to each other in proportions.

We also know that forelimb reduction is not a necessary consequence of phyletic size increase. This is demonstrated by the case of *Deinocheirus mirificus*, a giant (ca. 11 m long) Cretaceous ornithomimosauroid with forelimbs some 2.4 m long (Lee et al. 2014). A *Tyrannosaurus rex* 12 m long, in contrast, had a forelimb only one meter long, so that of *Deinocheirus* was about 240% its length. It is presumed that these animals were very different ecologically. In contrast to tyrannosaurids, *Deinocheirus* had a duckbill-shaped beak with a deep, downturned and U-shaped lower jaw that was toothless; it is considered to have been generally omnivorous (Lee et al. 2014). Thus, *Deinocheirus mirificus* had a relatively smaller skull with smaller teeth than tyrannosaurids had, which meets the expectations of the Lockley et al. (2008) model, as did *Gigantoraptor* (Xu et al. 2007). These facts imply that large size in theropods could have evolved in the context of different selective regimes and was not strictly related to a single dimension of diet, skull size, forelimb size, or locomotion. They also suggest that skull size and forelimb size are developmentally decoupled, thus weakening if not falsifying the "developmental trade-off" hypothesis similar to the "loi de balancement" proposed by Geoffroy St.-Hilaire (see Lockley et al. 2008).

To summarize a pattern in theropods: reduced limbs evolved in both large and small taxa. Large taxa had skulls that were both enlarged and not. Enlargement itself may not necessarily indicate a shift in feeding ecology (*Deinocheirus mirificus* may have simply eaten what smaller relatives ate, only more of it or larger examples of it). Change in size does not necessarily entail a change in forelimb function. Enlarged skulls may reflect an ability to prey on larger taxa, but the unique banana-shaped teeth of tyrannosaurids definitely reflect a change in feeding strategy. Limbs were reduced in lineages of gigantic macropredaceous theropods before giant size and dental enlargement (in the case of tyrannosaurids) evolved. The bottom line is that the reduction of forelimbs requires explanation in functional terms; their reduction cannot simply be dismissed.

Ontogeny.—It is commonplace to note that the feeding ecologies of many tetrapods change through life, whether frogs, lizards, birds, or mammals. Much of this depends on the size of the individual animal and the kinds of prey that it can trap, kill, and eat, from insects to small vertebrates to larger ones. There are unusual cases especially in altricial birds and mammals where the parents feed the young a different diet than the young pursue when they become independent.

In extinct vertebrates much of this reconstruction is guesswork. Developmental series in large theropod taxa are poorly known (but see Carr 2020). The section below, "Life-history growth dynamics...", explores some of what is speculatively known for tyrannosaurid feeding ecology in ontogenetic terms. I argue here that the ontogeny of feeding ecology itself is not driving the reduction of the forelimbs, but the feeding ecology of the adults is.

Life history strategies of tyrannosaurids

Horner and Padian (2004) established on the basis of histological thin-sections taken from the long hindlimb bones of *Tyrannosaurus rex*, from the Hell Creek Formation (Maastrichtian) of Montana, USA, that the taxon reached skeletal adult size by its late teens to early twenties. This high rate of growth is commensurate with those of other dinosaurs such as the hadrosaurid *Maiasaura peeblesorum* (Horner et al. 2000; Woodward et al. 2015). To put this in perspective, consider that humans and *T. rex* reach skeletal adult size in a comparable number of years; yet we could conservatively estimate an adult *T. rex* body mass at three metric tonnes (6600 lbs; the exact number is not important, although twice that mass has been estimated), whereas an average adult feral human would weigh about 75–80 kg (counting both sexes; again, the exact number is not important). This suggests that the net growth rate of *T. rex* was about 40 times that of humans, whose growth rate (as for other hominins) is unusually low for their body size among mammals (traditionally considered a byproduct of extended parental care and large brain size).

Because herbivorous non-avian dinosaurs, as far as they have been assessed, appear to have grown at least as rapidly as their predators (Padian and Woodward 2021), it has been presumed that rapid growth was a kind of escape strategy for the prey species: in the Mesozoic Era predators of small to large size abounded (and even the young of large species could dispatch smaller prey), so in a sense, no matter what size you were, there was someone ready to kill you. This situation conferred an advantage on growing quickly to adulthood, but it did not solve the problem of escape from predation, partly because other factors such as alertness and ability to run would have been important, and also because the predators were growing nearly as fast as the prey. This is not the case for today's large mammal communities: young felids and canids are nurtured for weeks by their parents and take many months before they can trap prey on their own, so they take to hunting gradually; whereas a newborn wildebeest or horse must be on its feet within minutes to an hour if it is not to be left behind by the herd and abandoned to predators (Estes 2012; KP personal observation).

The predator-scavenger problem.—Whether large macrocephalic theropods were primarily predators or scavengers is difficult to resolve (e.g., Horner and Lessem 1993; Holtz 2008), and likely it is fruitless to examine the question on a taxon-by-taxon basis, as I suggest below. However, it has figured strongly in discussions of the function of tyrannosaurid forelimbs (Horner and Lessem 1993). Analogies are of limited use, and cannot constitute evidence, but it may be worth noting that today's African large mammal predators follow a general law: why risk injury trying to kill a prey when you can simply chase off smaller predators who have already done so? Hyenas kill more prey than lions do, and leopards and cheetahs hide their prey from larger predators who will scavenge it (Estes 1991). Why then do we think it unusual that *T. rex* would have chased away smaller predators from their kill, and on the other hand, why do we think that *T. rex* could not have killed its prey?

Preying and scavenging should be viewed not as binary choices but as opportunistic life history strategies of behaviorally flexible animals.

DePalma et al. (2013), in a review of alleged predatory behavior by *T. rex*, described a tyrannosaurid tooth embedded in a hadrosaurid tail centrum, and rightly saw this as evidence of predatory behavior. They also noted several instances in which injuries from bites had at least partly healed, suggesting escape from predation. However, a handful or two of cases provides no evidence of the prevailing strategy of procuring food by any predator. Other cases of damage without healing, even to conspecifics (many examples provided in Molnar 2001 and Rothschild and Molnar 2008), cannot resolve the question of the strategic dominance of predation vs. scavenging in any large theropod taxon. Furthermore, the fact that today we have no analogous "large bodied obligate scavenger" (DePalma et al. 2013: 12560) similar to *T. rex* means nothing in considering the paleobiology of Mesozoic dinosaurs.

The question of whether large tyrannosaurids were predators or scavengers is not directly relevant to the hypothesis proposed here, in the sense that it is concerned with feeding behavior on carcasses, regardless of how they became carcasses. However, in concert with the next section, I hope that its relevance to the hypothesis presented here becomes clearer.

Life-history growth dynamics of *Tyrannosaurus rex*, and implications for ecology.—Because most organisms change shape as they grow through life, for reasons related to ecological factors or physical mechanics, it is naïve to assume that juveniles of a species necessarily would deal with their environments (evading death, procuring food, etc.) just as adults would. Ontogenetic allometric trajectories (Gould 1977; Alberch et al. 1979) affect not only skeletal proportions but ecological strategies. There are extreme examples among invertebrates, but tyrannosaurids present a striking case that is pertinent to the present thesis.

In the early 1900s the great dinosaur hunter Barnum Brown was exploring the Campanian (Late Cretaceous) outcrops along the Red Deer River in Alberta, Canada, and came upon a trove of dinosaur bones that he collected for the American Museum of Natural History (AMNH) in New York (USA). Brown identified the large theropod bones as tyrannosaurid (that is, albertosaurid), and the smaller, more gracile bones as ornithomimid. He never published his work, but his notes resided in the AMNH, where Phil Currie, then of the Royal Tyrrell Museum in Drumheller, Alberta, found the notes in the late 1990s and examined the specimens that Brown had collected. Currie (1998) realized that the "ornithomimids" that Brown identified were actually juvenile albertosaurids, and that the assemblage that Brown collected was a thanatocoenosis of what was plausibly a conspecific group of predators (Currie 2000). He inferred on the basis of skeletal forms and proportions that the juvenile albertosaurids were agile and fleet-footed, at least comparable to the prey species, and unlike the adult albertosaurids.

In the next field season, under strenuous conditions, Currie relocated Brown's quarry and collected additional specimens of both albertosaurids and other species. There was no evidence that at the time of death the albertosaurids had been preying on any of the individuals of other taxa represented in the quarry (Currie and Eberth 2010), of which there turned out to be several. The deaths of the various taxa seemed to be unrelated, but the albertosaurids evidently died together. The idea that albertosaurids may have associated (perhaps hunted) in (possibly family) groups, in which the smaller, younger, more gracile and speedy individuals may have flushed out prey to be dispatched by the larger and more powerful adults (as only one possible scenario) is both circumstantially supported and terrifying. It brings to mind the speculative hunting cooperation of the "velociraptors" (actually *Deinonychus*) in the first "Jurassic Park" movie. Similar assemblages have come to light more recently (Currie et al. 2005; Woodward et al. 2020; Titus et al. 2021), and they add credibility to Currie's (1998) original scenario: tyrannosaurids may have hunted in packs cooperatively (though perhaps not exclusively), with different roles for the adults and juveniles. This may at least partly explain the lack of "medium-sized" theropod species in Cretaceous ecosystems (Schroeder et al. 2021; Holtz 2021): the adaptive zone may have been largely occupied by juveniles of larger species.

So far we lack extensive skeletal evidence of juveniles of tyrannosaurids, abelisaurids, and carcharodontosaurids (but see Carr 2020). At least on the basis of phylogenetic proximity it appears plausible that large Late Cretaceous tyrannosaurids such as *T. rex* could have hunted much as did albertosaurids (which had even relatively smaller forelimbs than those of *T. rex*). I argue below that this puts a different perspective on the feeding ecology of large tyrannosaurids (although the interpretation cannot be automatically extended to abelisaurids and carcharodontosaurids, but see Heredia et al. 2020).

The hunting behavior of tyrannosaurids is not directly material to the hypothesis I propose here for the phyletic reduction of the forelimbs, because the hypothesis concerns feeding behavior on a carcass, not hunting behavior. However, if tyrannosaurids were hunters, and if they hunted in packs of individuals of various sizes or ages (or even if adults hunted alone but their kills attracted other adults and juveniles, or simply scavenged as groups the kills of others), the presence of several individuals feeding on a carcass is relevant to the central hypothesis proposed here.

A hypothesis to account for the reduction of the forelimbs in large derived tyrannosaurids

This problem needs to be explained in phylogenetic (where in tyrannosauroid history did reduction begin and how did it proceed), ontogenetic (how do skull and limb proportions change through growth), and functional (what if anything were they used for) terms. A complex of features may allow us to test the hypothesis.

Hypothesis.—The forearms of large, derived tyrannosaurids were reduced to essentially non-functional structures for a specific selective reason: they were a liability to adults and larger sub-adults during competitive feeding on carcasses. They could have been bitten, amputated, and infected, leading to weakness, disease, and sometimes death. This derived complex of reduced features would have been less evident (or not at all expressed) in more basal members of the clade because the selective regimes would not have been as strong (the skulls and jaws would not have been so formidable). Reduction may already have evolved in the early ontogenetic stages of derived tyrannosauroids because forelimb function may have already been reduced in the hunting and feeding ecology of younger individuals (and the reduction in forelimbs required for adults may have been hard-wired through progenesis even in juveniles).

Testing.—If it can be tested, on the basis of available fossil evidence, that in adult large theropods with massive skulls, aggressive damage to body parts is differentially greater in elements that would have been closer to the depredation of a carcass than to more distal parts, it could be inferred (not exclusively) that there was danger in having excess body parts too close to a carcass.

Expectations.—These apply to adult and near-adult individuals. (i) Skeletal features closest to the carcass, apart from skull and jaws, would experience reduction in structure and function of elements, increasingly with a position distal to the body wall and closer to the carcass. (ii) Intraspecific damage to elements closer to the body wall, with allowance for relative size, would be less frequent than damage to elements closer to the prey item. (iii) The functionality of the reduced arms could be less than in theropods with unreduced arms, but ranges of motion in joints that tended to retract the limbs out of harm's way would be expected. (iv) Younger individuals would not show the same pattern of intra-specific damage because they would not be as aggressive (especially in feeding) as their elders. (v) Smaller, more basal members of the clade would not show the same pattern of intra-specific damage, because their skulls and jaws were smaller. (vi) The extreme predatory syndrome of large theropods would correlate with the maximum size of the prey being taken, including the consideration of ontogenetic changes in prey selection by predators.

In this context, "intra-specific damage" specifically means wounds, usually bite wounds, that are inflicted on an individual by another member of its species but that do not prove immediately fatal. As a result, there should be evidence of some healing at the wound, except if the individual died shortly thereafter from that or another cause. "Essential locomotory elements" are those necessary for normal locomotion because they are major weight-bearing bones and are needed to both propel and steady the animal, including in maneuvering. The femur and tibia, the ankle bones, and likely most elements of the third (middle) and fourth toes might fit this description. The fibula and some peripheral bones of the foot (including those of digits II, which is lost in the ostrich) would fit less well. This is related to the erect stance and parasagittal gaits of ornithodirans in general.

Results

(i) Skeletal features closest to the carcass, apart from skull and jaws, would experience reduction in structure and function of elements, increasingly with a position distal to the body wall and closer to the carcass.—This pattern appears to hold in tyrannosauroids: the scapulocoracoid is relatively smaller than in other theropods, but still disproportionately larger than the forelimbs, which is to say that the forelimbs are proportionally reduced compared to the already reduced scapulocoracoid. In some tyrannosauroids the third digit persists but in *T. rex* it may be reduced to a loss of its phalanges, and perhaps sometimes the loss of the digit altogether (so a phalangeal formula of 2-3-0-x-x or 2-3-x-x-x, Padian 1992). As to functions of the forelimb elements, given that the fingers cannot reach the mouth, cannot reach each other, and did not hypothetically have the strength to manipulate more than 200 kg in a limited range of movement (relative to the thousands of pounds that their prey species weighed), reduction of function from the basal coelurosaurian or tyrannosauroid condition is difficult to argue against.

(ii) Intraspecific damage to these elements closer to the body wall, with allowance for relative size, would be less frequent than damage to those elements closer to the prey item.—Reports of damage to forelimb elements are limited, and this may be a function of their small size (ironically) and relatively infrequent preservation. But forelimb elements are not prominent in lists of wounded bones (Molnar 2001; Rothschild and Molnar 2008). In fact, Molnar (2001: table 24.1) listed ten presumed bite marks in a variety of large theropods, of which seven were on cranial elements, and the rest on a metacarpal, a pedal phalanx, and an ilium. Fractures of the humerus are reported, which may imply that the element was poorly suited to bear the effects of forces of mass, as from the weight of the body. If so, then several "functional" hypotheses would be correspondingly weakened. If intra-specific aggression, resulting in biting wounds that were healed, were random across skeletal elements, we would expect a significant proportion of such wounds in the forelimbs; but this pattern has not been sustained so far.

(iii) The functionality of the reduced arms could be less than in theropods with unreduced arms.—This appears to be the case generally. *Tyrannosaurus rex* has an odd shoulder joint that confers limited mobility compared to more basal theropods, but more in some directions than in others (Carpenter and Smith 2001; Lipkin and Carpenter 2008). This has also been noted in albertosaurids, which have arms that are even proportionally smaller (Currie 2003). It is not clear what possible functions this altered mobility could serve; no plausible hypotheses have been advanced and tested. Senter and Parrish (2006) noted that in *Carnotaurus* the mobility of joints distal to the shoulder was essentially nil, and that the humerus could do little more than wave up and down a bit; they also noted that this derived limitation in mobility first occurred in more basal abelisaurids, in which forelimbs were already reduced, so the reduction in functionality occurred well before the evolution of *Carnotaurus* (Coria et al. 2002). The reasons are so far not clear. Thomas D. Carr (peronal communication 2021) found that the range of motion at the shoulder and elbow in *Tetraphoneus curriei* was so limited that their arms were held posteroventrally and of less use than in basal members of the clade.

This expectation may be a weaker test of the overall hypothesis (avoidance of damage and disease to forelimbs during feeding) than some other expectations. However, it is not unimportant. A loss of functionality would mean that the limbs are not being used for anything (or for very little), but it does not necessarily follow that they would be reduced phyletically (pace arguments from Lockley et al. 2008, inter alii). Phyletic reduction of limbs has occurred many times for many reasons (e.g., Wiens et al. 2006). The question that remains to be answered is: in what phylogenetic context, and in what selective/functional context, were these elements reduced? It is possible that in a phyletic lineage when range of motion is significantly reduced and (or) limb length is significantly reduced, functionality is reduced or lost before the expression of the terminal taxa of the lineage.

(iv) Younger individuals would not show the same pattern of intra-specific damage.—Several recent studies (Currie 1998; Currie and Eberth 2010; Woodward et al. 2021; Titus et al. 2021) have opened our eyes to the distinct possibility that tyrannosaurids may have hunted in packs, and that juveniles may have had a different role than adults in hunting (see above). The similarity of juvenile tyrannosaurids to agile, gracile ornithomimids has been noted (Currie 1998; Currie and Eberth 2010; Woodward et al. 2020; Titus et al. 2021), and so have differences between these juveniles and the adult tyrannosaurids. Currie (1998) estimated that the young would have been faster and more agile than the adults, which is quite probable; likely they served a different role in predation, such as flushing out prey and herding it toward the adults to dispatch it, but this entails speculation. However, it is difficult to conceive of quite different scenarios when the age classes are preserved together (Currie 1998; Currie and Eberth 2010; Woodward et al. 2020; Titus et al. 2021), suggesting that they hunted and fed together. This would appear to be supported by an analysis that suggested that juveniles of larger theropod species filled the ecological predatory niches of adults of smaller species. Smaller (mid-sized) theropod predator species are unusually absent in Cretaceous ecosystems in which tyrannosauroids dominated (Schroeder et al. 2021), although individual tyrannosauroids may have been abundant (Marshall et al. 2021).

Here we enter the realm of analogy, which is epistemologically not evidence of anything. However, potential similarities in demographic age structure of populations may be suggestive and even diagnostic. In the living Komodo dragon (*Varanus komodoensis*), a killed prey is set upon by an aggregate of individuals of various sizes, ages, and sexes (Auffenberg 1981). The larger, more aggressive individuals first ravage the carcass, ripping and tearing flesh and organs and spilling the leavings farther afield, and these can be consumed by the smaller individuals. When the larger and more aggressive individuals are sated, the others move in. If a similar pattern held in tyrannosaurids—and Komodo dragons are not evidence of this one way or the other—the larger individuals may have shoved out the smaller ones to feed first, so the latter did not compete with the former and suffered less skeletal damage, whereas the larger ones remained to gouge each other competitively at times.

Remaining in the realm of analogy temporarily, it is well known that crocodylians will not only cannibalize their young but will attack and dismember adult conspecifics when they get the chance (one only has to search for "crocs biting each other during feeding" on the internet). The bite force of crocodylians is far more formidable than that of *V. komodoensis*).

Longrich et al. (2010) catalogued four *T. rex* specimens that were plausibly gouged by the teeth of other *T. rex*: two pedal phalanges, a metatarsal, and a humerus. The longitudinal furrows, distinct from bite punctures, suggest feeding, although there must not have been much meat on these elements compared to other parts of the body. Large *T. rex* are known to have bitten off large chunks of flesh and bone and swallowed them whole (osteophagy, Gignac and Erickson 2017), and one would have thought that a large individual would simply have severed the whole foot and swallowed it, if it had enough meat to be worthwhile. Longrich et al. (2010) did not attempt to determine the size or age of the individual who made the bite marks. Could we be looking at marks of juveniles not yet able to get access to the meatier parts? If young tyrannosaurids avoided the jaws of adults when feeding, we would not expect them to show extensive wounds, especially on elements that would have been close to the carcass.

As far as I can determine there has been no systematic analysis of bite wounds on the skeletal elements of *V. komodoensis*, nor an actualistic behavioral study of wounds observed to be inflicted during the feeding of groups on carcasses. As interesting as more information on this topic might be, insofar as it concerns tyrannosaurids and other large theropods the comparison is merely analogical. The question is whether any kind of vastly different scenario to explain the observed evidence of tyrannosaurids is plausible.

(v) Smaller, more basal members of the clade would not show the same pattern of intra-specific damage.—The evidence to test this hypothesis at present is insufficient. However, in smaller and more basal theropods, there is no clear evidence, although statistical significance may be lacking, that the skulls and forelimbs of these animals were disproportionally wounded by intra-specific biting (e.g., Molnar 2001; Rothschild and Molnar 2008).

(vi) The extreme predatory syndrome of large theropods would correlate with the size of the prey being taken, including the consideration of ontogenetic changes in prey selection by predators.—This hypothesis is complex, and there will be exceptions for various reasons, but it is not as simple as a two-variable correlation, so readers will be asked to bear with the argument.

Various authors have observed that in taxa such as coelophysoids and allosaurids, in which the limbs appear to be of general basal proportions for theropods, the size of the prey was likely not larger than the size of the predator. It is difficult to know exactly which animals killed and ate which other animals, and how, without direct evidence (such as the "Mongolian fighting dinosaurs" [Kielan-Jaworowska and Barsbold 1972] or the remarkable footprint series recorded by Barnum Brown of an *Acrocanthosaurus*-like theropod chasing down and jumping on the back of a much larger sauropod, possibly *Pleurocoelus*, Thomas and Farlow [1997]).

These trophic relationships evolved through the Mesozoic Era. During the Triassic Period, dinosaurs were almost unexceptionally small (up to 3 or 4 meters in total length), compared to their later relatives; the largest known Triassic dinosaur was likely the basal sauropodomorph *Plateosaurus* and similar taxa, which were possibly up to 10 m long but usually closer to 6–7 m). The Early Jurassic changed this mainly by raising the size limit of prey species, notably sauropods such as *Ohmdenosaurus* and *Vulcanodon*. Ornithischians evolved at least by the Early Jurassic but they were relatively small (3 m length or less). The largest known predators were basal theropods such as *Dilophosaurus* (6–7 m long), the first theropods known so far to exceed the "*Coelophysis*"-level size.

The Middle Jurassic is too poorly represented to enable generalizations about relative body sizes of predators and prey without considerable assumptions. However, this changes in the Late Jurassic, with the first known very large predators (*Allosaurus*, *Saurophaganax*, Foster 2007), up to 9–10 m long. Sauropods by this time had become large to gigantic, and the first large ornithopods evolved (iguanodontians, etc.). Stegosaurians had also become quite large, but we have little direct evidence of predation on them or other ornithischian lineages (e.g., ankylosauroids, other ornithopods).

We know little about the prey species that inhabited Gondwana in the Early Cretaceous, but the predator species evidently had not evolved the "tyrannosaurid" bauplan of huge skulls and banana-shaped teeth. (Tyrannosaurid teeth do not retain the laterally compressed, dagger-like morphologies of more basal theropods, although this may not have been true for juveniles [Carr 2020]; and consider *Nanotyrannus*, which is widely considered a juvenile of a larger tyrannosaurid, and which has compressed, dagger-like teeth. In large adult tyrannosaurids the entire tooth is banana-shaped, tapering both toward the tip that encounters prey and the tip that originates in the skull.)

By the Early Cretaceous, the Gondwanan ceratosaurian abelisauroid lineage had evolved to a size between 7 and 11 m length (Senter and Parrish 2006). Abelisaurids such as *Carnotaurus* evolved larger size and larger skulls. However, the phalanges were extremely reduced, there were no claws, and the arms past the shoulder joint were effectively immobile. More basal members of the lineage had greater mobility (Senter and Parrish 2006). However, their skulls were not enlarged as in tyrannosaurids, but foreshortened and deepened; their teeth were not enlarged or reduced in number. The articular possibilities of their forelimbs were different than those of tyrannosauroids. The Gondwanan carcharodontosaurids included some of the largest carnivorous dinosaurs known, beginning in the Late Jurassic and continuing to the Late Cretaceous; however, they also did not evolve the enlarged banana-shaped teeth of tyrannosaurids.

In the Late Cretaceous we find the greatest macro-predaceous theropods, the tyrannosaurids, distinguished by huge heads and jaws and enlarged teeth. We also find the largest overall prey species, including hadrosaurids such as *Edmontosaurus* that were comparable in size to *T. rex*, plus large ceratopsians, ankylosaurs, and pachycephalosaurs. It appears important that the large banana-shaped teeth of tyrannosaurids did not evolve until the prey species became comparably large, at least in some lineages (although it could be argued that Late Jurassic allosaurids and iguanodontids were comparable in size, if smaller than their Cretaceous relatives). The teeth of tyrannosaurids, however, suggest a new feeding syndrome including osteophagy. No other giant theropods with foreshortened limbs evolved the huge jaws and teeth of tyrannosaurids, but no other fauna outside North America (and parts of Asia) in the Late Cretaceous was populated by such large prey species.

Here, although it is a minor point, it should be noted that sauropods have been left out of this discussion. They are not important to the central hypothesis of this paper, which has to do with carcasses, however large. It may be important that although since the Early Jurassic very large sauropods have co-evolved with theropods of gradually increasing size, it is not clear that any hunting or feeding adaptations in large theropod lineages (let alone the reduction of the forelimbs) were related to large adult sauropods. One would think that a solitary predator would not try to bring down a sauropod too large to subdue, although see Thomas and Farlow (1997). It would be preferable to think that during the trajectory from hatchling to adult (with a significant inflection at breeding age), younger sauropods were grist for the mill. At present there seems to be no evidence for this scenario one way or another.

Discussion

Because these are extinct animals, we acknowledge that nearly all evidence of behavior advanced to test a hypothesis is indirect. That does not mean that a hypothesis cannot be strong, especially if it is supported by independent, converging lines of evidence (Whewell 1837; Wilson 1998).

The central hypothesis of this paper is that the forelimbs of large tyrannosaurids were reduced phyletically not for any reason connected functionally to the forelimbs themselves, but because they posed a hazard to the survival of individuals large enough to feed communally on a carcass. A hypothesis of reduction due to disuse would not conflict with this, but disuse by itself does not explain reduction, any more than (unsupported) hypotheses of maintenance would explain persistence. Longer arms, especially in their natural, somewhat anteriorly extended orientation, would have brought them into the ambit of the deadliest jaws ever recorded on land. The danger of wounds, amputations, infections, disease and ultimate death, it is argued here, would have been a selective force for reduction, irrespective of relict functionality of the limbs. A constellation of correlative expectations is provided by way of potential tests of the hypothesis.

The Results section (above) details the morphological patterns that we might expect to support or weaken this hypothesis. All things being equal, large predators that hunted larger prey would be expected to have large skulls with large, sharp teeth (although only tyrannosaurids evolved the "banana" form, reflecting their bone-crushing power and likely the great size of their prey species as adults). But among large theropods there are exceptions to this pattern.

It is important to explain exceptions (Darwin 1859). *Deinonychus* and its relatives (some quite large, such as *Utahraptor*) evolved longer, higher skulls with fewer, larger teeth; they also retained long arms with sharp recurved claws, and they evolved enlarged reverse-articulated second pedal digits that were ostensibly used in dispatching prey (Ostrom 1969). They also apparently hunted in packs, as inferred from an unusual collection of shed tooth crowns in association with a *Tenontosaurus* carcass (Maxwell and Ostrom 1995). In many ways, including the enlarged teeth and pack hunting, they converged with tyrannosaurids, but not with the foreshortened arms, which perhaps reflects the less lethal effect of congeneric bites; or, to put it another way, the potentially fatal effects of an adult tyrannosaurid bite were a deterrent not experienced in less derived, smaller theropods.

Deinocheirus, a gigantic Cretaceous ornithomimosaurid, and *Gigantoraptor*, a gigantic Cretaceous oviraptorosaurid, had relatively unreduced forelimbs. However, they were not macro-predators; they had none of the cranial and dental specializations of tyrannosaurids. They had skull sizes proprtionally commensurate with those of typical theropods and their diets are presumed to be omnivorous, including small game. Pack hunting has not been proposed.

Another extreme example is the small alvarezsaurid *Mononykus*, an animal about a meter or two long with a unique forelimb: the humerus has an oddly shaped and deflected deltopectoral crest, the ulna has an enormous olecranon process, and the manus is reduced to a very robust digit I, with a large unrecurved claw. Most paleontologists who have studied the animal have agreed that its forelimb was adapted to burrow into anthills (review in Senter 2005), but here we apply the same question we applied to the reduction of tyrannosaurid arms: why would such a hyper-reduced forelimb be selected for in the context of such a function? In *Mononykus*, the forelimbs could barely reach beyond the sternal midline. Instead, the question has to be asked: at what point in the evolution of this lineage was some kind of derived function, suggested by the highly derived morphology, selected for? This was presumably at a point when the forelimbs were relatively larger. However, even in more basal alvarezsaurids, the forelimbs were already greatly reduced (Xu et al. 2018) and it is difficult to posit or test any kind of function for them. Although the original alvarezsaurid function may have been lost in the known forms, the morphology was not further modified beyond further reduction of digits and phalanges (and reduction of the forelimb does not necessarily entail loss of digits and phalanges, as carcharodontosaurids show). Looking at the forelimb alone will likely not illuminate this problem: As Gans (1975) said (see below), the reduction itself may not be functionally important; rather, another function may be selected of which this one is simply a side effect.

This panoply of exceptions or anomalies in other theropods to the pattern predicted for tyrannosaurids cannot be used as evidence against the hypothesis as applied to tyrannosaurids; it merely indicates that the morphological features of interest to this hypothesis (body size, skull size, tooth form and size, arm size and mobility, etc.) varied among theropods for various reasons (predatory strategy, social structure, size of predator vs. size of prey, etc.). This hypothesis is meant to include mechanical, locomotory, prehensile, ontogenetic, ethological, and other factors that would be difficult to dismiss with a single counterfactual.

This brings us to the question of the function of such reduced arms in tyrannosaurids. Arp (2020) provided a useful dissection of various functional hypotheses as they matched ontological questions and other correlates. He determined that of seven hypotheses he considered, three (signaling, holding prey, and stabbing) were plausible, two (feeding as a juvenile and raising the body) were not, and two (reproduction, i.e., claspers, and ceratopsian-tipping) needed further development. However, he did not ask whether they were testable, and no one has considered in depth whether two or more hypotheses might be plausible together. For reasons developed above, however, none of them seems plausible because the arms are simply too small to be of use, and they do not explain why in the course of evolution selection would have favored reduction rather than maintenance of size or even enlargement. Whereas it is good to be pluralistic about hypotheses, if none of them is individually plausible their combined plausibility does not improve. Of the hypotheses that Arp (2020) considered at least not implausible, the uses as pectoral claspers during mating, as signaling devices, for holding prey, ceratopsian-tipping, and stabbing are actually implausible because the arms were too small to have been of any real use, as noted above.

Conclusions

Carl Gans, in an influential and classic paper (1975), examined the forces that reduced forelimb size phyletically and how they should be studied. He noted: "the search for a particular selective mechanism responsible for the atrophy or hypertrophy of a particular system in diverse organisms involves a basic fallacy, namely, the unwarranted assumption that the syndrome was driven by the same selective force in each case. It also incorporates the assumption that the aspect being studied was indeed the primary target of selection" (Gans 1975: 455).

It is possible that we have been looking through the wrong end of the telescope. Perhaps the question should not be "What function were the reduced arms selected to perform?" but "How was the reduction of the arms selected so as to provide another, over-riding benefit to the organism?" It does not seem that any functional hypothesis so far proposed addresses this question. The "morphodynamic compensation" hypothesis of Lockley et al. (2008) comes close convergently, but without evidence. It seems that no functional or non-functional argument proposed so far can explain anything about the reduction of the arms in tyrannosauroids, except perhaps simple disuse; but the disuse also has to be explained (for example, why the forelimbs are reduced in abelisaurids but not in allosaurids).

Let us hypothesize, therefore, that the reduction of forelimb size was a secondary function of selection for something else. As such, we should not look for functionality in these reduced limbs, but for how that reduction served a larger purpose. That purpose, we propose here, was to take out of the behavioral equation the forelimbs, which were vulnerable to injury, infection, and amputation that could lead to death during group feeding by conspecific individuals that bore huge heads and jaws with teeth capable of crushing the bones of nearly any large dinosaur. Peterson et al. (2021) review estimates of the bite force of adult *T. rex* (over 8000 to over 34 000 N, and possibly over 64 000 N; see also Gignac and Erickson 2017) and estimate that the bite force of juvenile *T. rex* was nearly twice previous estimates, to exceed 5600 N. How would any tyrannosaurid, regardless of ontogenetic stage, benefit from functionally useless arms long enough to get in the way?

If this hypothesis is workable, it can be tested by the expectations set out above. It will be valuable insofar as it explains evidence that other hypotheses cannot. Modifications of the expectations to make them better testable will improve the hypothesis, not destroy it. The testing will require many objective eyes and hands, working with specimens in collections, with field notes, and in quarries, because the animals in question are found widely around the world, and data will need to be compiled and tested against expectations. It will require a kind of paleontological crowd-sourcing, but the effort will be worth it. In the end, we have an opportunity to address a question that is perennially interesting both to scientists and the public; and moreover, an opportunity to show how we do our work, how we think we know what we know, and how things came to be in the evolution of this fascinating group of animals.

Acknowledgements

It is a pleasure to dedicate this essay, whatever its merits and deficits, to my colleague Rich Cifelli. Since the 1970s I have enjoyed and appreciated his scholarship, his wit, and his love of the history and philosophy of our discipline. We have had far too few evenings around the campfire to discuss mutual interests. He has been a wonderful colleague and friend. Inevitably, in an essay this wide-ranging, in Rich's spirit, I acknowledge the influence of others, including my old friend and mentor Carl Gans (University of Texas, Austin, USA, deceased), as well as David Wake (University of California, Berkeley, USA), who passed away as I was finishing this essay, and whose influence on me, like Carl's, was inestimable, whatever the eventual effect of the present effort. I thank Mathew Wedel (Western University of Health Sciences, Pomona, USA) for inviting me to contribute. This has been a difficult paper to write. Many of us have been constrained from investigating specimens in our museums, asking colleagues to investigate specimens in theirs, and even using our libraries, by one of the worst pandemics in human history. As I write I still do not have access to my own Museum and have not had for 18 months. I propose this essay as a starting point. If the hypothesis has merit, colleagues will be able to test and modify it. In the spirit of historical research that Rich and I have appreciated, I hope that the present small effort can advance this interesting and frustrating question. I thank Philip J. Currie (University of Alberta, Edmonton, Canada), David Evans (University of Toronto, Canada), Mark Goodwin, Ralph Molnar, and Jack Tseng (all University of California, Berkeley, USA), John R. Horner (Chapman University, Orange, USA), Armita Manafzadeh (Brown University, Providence, USA), and J. Michael Parrish (Southern Connecticut State University, New Haven, USA) for discussions, references, ideas, and collegiality. Thomas D. Carr (Carthage College, Kenosha, USA) and Thomas R. Holtz Jr. (University of Maryland, College Park, USA) provided very helpful reviews of the manuscript. Any errors or misinterpretations are of course my own. This work was supported by the Sakana Foundation and the Uplands Foundation.

References

Alberch, P., Gould, S.J., Oster, G.F., and Wake, D.B. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* 5: 296–317.

Arp, D. Jr. 2020. Testing utility: developing an assessment to evaluate *Tyrannosaurus rex* forelimb use cases. *Biosis: Biological Systems* 1: 102–108.

Auffenberg, W. 1981. *The Behavioral Ecology of the Komodo Monitor*. 406 pp. University of Florida Press, Gainesville.

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

Carr, T.D. 2020. A high-resolution growth series of *Tyrannosaurus rex* obtained from multiple lines of evidence. *Peer J* 8: e9192.

Coria, R.A. and Currie, P.J. 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas* 28: 71–118.

Coria, R.A., Chiappe, L.M. and Dingus, L. 2002. A new close relative of *Carnotaurus sastrei* Bonaparte 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology* 22: 460–465.

Currie, P.J. 1998. Possible evidence of gregarious behavior in tyrannosaurids. *Gaia* 15: 271–277.

Currie, P. J. 2000. Possible evidence of gregarious behavior in tyrannosaurids. *Gaia* 15: 271–277.

Currie, P.J. 2003. Allometric growth in tyrannosaurids (Dinosauria: Theropoda) from the Upper Cretaceous of North America and Asia. *Canadian Journal of Earth Sciences* 40: 651–665.

Currie, P.J. and Eberth, D.A. 2010. On gregarious behaviour in *Albertosaurus*. *Canadian Journal of Earth Sciences* 47: 1277–1289.

Currie, P.J., Trexler, D., Koppelhus, E.B., Wicks, K., and Murphy, N. 2005. An unusual multi-individual tyrannosaurid bonebed in the Two Medicine Formation (Late Cretaceous, Campanian) of Montana (USA). *In*: K. Carpenter (ed.), *The Carnivorous Dinosaurs*, 313–324. Indiana University Press, Bloomington.

Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection*. 502 pp. John Murray, London.

Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. 528 pp. John Murray, London.

Delcourt, R. and Grillo, O.N. 2018. Tyrannosauroids from the Southern Hemisphere: implications for biogeography, evolution, and taxonomy. *Palaeogeography, Palaeoclimatology, Palaeogeography* 511: 379–388.

DePalma, R.A. II, Burnham, D.A., Martin, L.D., Rothschild, B.M., and Larson, P.L. 2013. Physical evidence of predatory behavior in *Tyrannosaurus rex*. *Proceedings of National Academy of Sciences USA* 110: 12560–12564.

Estes, R.D. 2012. *The Behavior Guide to African Mammals*. 611 pp. University of California Press, Berkeley.

Foster, J. 2007. *Jurassic West: The Dinosaurs of the Morrison Formation and Their World*. 389 pp. Indiana University Press, Bloomington.

Gans, C. 1975. Limblessness: Evolution and functional corollaries. *American Zoologist* 15: 455–467.

Gould, S.J. 1977. *Ontogeny and Phylogeny*. 501 pp. Harvard University Press, Cambridge.

Gould, S.J. and Lewontin, R. C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of Royal Society of London B* 205: 581–598.

Gignac, P.M. and G.M. Erickson. 2017. The biomechanics behind extreme osteophagy in *Tyrannosaurus rex*. *Scientific Reports* 7: art. 2012.

Heredia, A.M., Diaz-Mrtinez, I., Pazos, P.J, Comerio, M. and Fernandez, D.E. 2020. Gregarious behaviour among non-avian theropods inferred from trackways: A case study from the Cretaceous (Cenomanian) Candeleros Formation of Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 538: 109480.

Holtz, T.R., Jr. 2007. *Dinosaurs: The Most Complete, Up-To-Date Encyclopedia for Dinosaur Lovers of All Ages.* 428 pp. Random House, New York.

Holtz, T.R., Jr. 2008. A critical re-appraisal of the obligate scavenger hypothesis for *Tyrannosaurus rex* and other tyrant dinosaurs. *In*: P. Larson and K. Carpenter (eds.), Tyrannosaurus rex, *the Tyrant King*, 371–398. Indiana University Press, Bloomington.

Holtz, T.R., Jr. 2021. Theropod guild structure and the Tyrannosaurid Niche Assimilation Hypothesis: Implications for predatory dinosaur macroecology and ontogeny in later Late Cretaceous Asiamerica. *Canadian Journal of Earth Sciences* [published online, https://doi.org/10.1139/cjes-2020-0174]

Horner, J.R. and Lessem, D. 1993. *The Complete* T. rex. 239 pp. Simon & Schuster, New York.

Horner, J.R. and Padian, K. 2004. Age and growth dynamics of *Tyrannosaurus rex*. *Royal Society of London, Proceedings B* 271: 1875–1880.

Horner, J.R., Ricqlès, A.J. de, and Padian, K. 2000. The bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. *Journal of Vertebrate Paleontology* 20:109–123.

Huynen, L., Suzuki, T., Ogura, T., Watanabe, Y., Millar, C.D., Hofreiter, M., Smith, C., Mirmoeini, S., and Lambert, D.M. 2014. Reconstruction and in vivo analysis of the extinct *tbx5* gene from ancient wingless moa (Aves: Dinornithiformes). *BMC Evolutionary Biology* 14: art. 75.

Kielan-Jaworowska, Z. and Barsbold, R. 1972. Narrative of the Polish-Mongolian Palaeontological Expeditions, 1967–1971. *Palaeontologia Polonica* 27: 1−12.

Kipling, R. 1902. *Just So Stories*. 184 pp. Macmillan, London.

Lee, S.A. and Thomas, J.D. 2014. Forelimbs of *Tyrannosaurus rex*: A pathetic vestigial organ or an integral part of a fearsome predator? *Physics Teacher* 52: 521–524.

Lipkin, C. and Carpenter, K. 2008. Looking again at the forelimb of *Tyrannosaurus rex*. *In*: P. Larson and K. Carpenter (eds.), Tyrannosaurus rex, *the Tyrant King*, 166–190. lndiana University Press, Bloomington.

Lockley, M., Kukihara, R., and Mitchell, L. 2008. Why *Tyrannosaurus rex* had puny arms: an integral morphodynamic solution to a simple puzzle in theropod paleobiology. *In*: P. Larson and K. Carpenter (eds.), Tyrannosaurus rex, *the Tyrant King*, 131–164. Indiana University Press, Bloomington.

Longrich, N.R., Horner, J.R., Erickson, G.M., and Currie, P.J. 2010. Cannibalism in *Tyrannosaurus rex*. *PLoS ONE* 5 (10): e13419.

Marshall, C.R., Latorre, D.V., Wilson, C.J., Frank, T.M., Magoulick, K.M., Zimmt, J.B., and Poust, A.W. 2021. Absolute abundance and preservation rate of *Tyrannosaurus rex*. *Science* 372: 284–287.

Mattison, R.G. and Giffin, E.G. 1989. Limb use and disuse in ratites and tyrannosaurids. *Journal of Vertebrate Paleontology* 9 (Supplement to 3): 32A.

Maxwell, W.D. and Ostrom, J.H. 1995. Taphonomy and paleobiological implications of *Tenontosaurus–Deinonychus* associations. *Journal of Vertebrate Paleontology* 15: 707–712.

McKinney, M.L. and McNamara, K. 1991. *Heterochrony: The Evolution of Ontogeny*. 437 pp. Plenum Press, New York.

McNamara, K. 1997. *Shapes of Time: The Evolution of Growth and Development*. 360 pp. Johns Hopkins Press, Baltimore.

Molnar, R.E. 2001. Theropod paleopathology: a literature survey. *In*: D.H. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life*, 337–363. Indiana University Press, Bloomington.

Newman, B.H. 1970. Stance and gait in the flesh-eating *Tyrannosaurus*. *Biological Journal of the Linnean Society* 2: 119–123.

Novas, F.E. 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. *Cretaceous Research* 45: 174–215.

Osborn, H.F. 1905. *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bulletin of American Museum of Natural History* 21: 259–265.

Osborn, H.F. 1906. *Tyrannosaurus*, Upper Cretaceous carnivorous dinosaur (second communication). *Bulletin of American Museum of Natural History* 22: 281–290.

Ostrom, J.H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Peabody Museum of Natural History Bulletin* 30: 1–165.

Padian, K. 1992. A proposal to standardize tetrapod phalangeal formula designations. *Journal of Vertebrate Paleontology* 12: 260–262.

Padian, K. and Chiappe, L.M. 1997. Bird Origins. *In*: P.J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*, 71–79. Academic Press, San Diego.

Padian, K. and Woodward, H.N. 2021. Diapsids: Avemetatarsalia. Dinosaurs and their relatives. *In*: V. de Buffrénil, A.J. de Ricqlès, L. Zylberberg, and K. Padian (eds.), *Vertebrate Skeletal Histology and Paleohistology*, 511–549. CRC Press, Boca Raton.

Padian, K., Werning, S., and Horner, J.R. 2016. A hypothesis of differential secondary bone formation in dinosaurs. *Comptes Rendus Palevol* 15: 41–49.

Paul, G. 1988. *Predatory Dinosaurs of the World*. 464 pp. Simon and Schuster, New York.

Peterson, J.E., Tseng, Z.J., and Brink, S. 2021. Bite force estimates in juvenile *Tyrannosaurus rex* based on simulated puncture marks. *PeerJ* 9: e11450.

Phillips, M.J., Gibb, G.C., Crimp, E.A., and Penny. D. 2009. Tinamous and moa flock together: mitochondrial genome sequence analysis reveals independent losses of flight among ratites. *Systematic Biology* 59: 90–107.

Pol, D. and Rauhut, O.W.M. 2012. A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. *Proceedings of the Royal Society B* 279 (1804): 3170–3175.

Rauhut, O.W.M. 2011. Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). *Special Papers in Palaeontology* 86: 195–239.

Rothschild, B.M. and Molnar, R.E. 2008. Tyrannosaurid pathologies as clues to nature and nurture in the Cretaceous. *In*: P. Larson and K. Carpenter (eds.), Tyrannosaurus rex, *the Tyrant King*, 287–304. Indiana University Press, Bloomington.

Schroeder, K., Lyons, S.K., and Smith, F.A. 2021. The influence of juvenile dinosaurs on community structure and diversity. *Science* 371: 941–944.

Senter, P. 2005. Function in the stunted forelimbs of *Mononykus olecranus* (Theropoda), a dinosaurian anteater. *Paleobiology* 31: 373–381.

Senter, P., and Parrish, J.M. 2006. Forelimb function in the theropod dinosaur *Carnotaurus sastrei*, and its behavioral implications. *PaleoBios* 26(3): 7–17.

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* 2017: 131–138.

Thomas, D.A. and Farlow, J.O. 1997. Tracking a dinosaur attack. *Scientific American* 1997 (12): 48–53.

Titus, A.L., Knoll, K., Sertich, J.J.W., Yamamura, D., Suarez, C.A., Glasspool, I.J., Ginouves, J.E., Lukacic, A.K., and Roberts, E.M. 2021. Geology and taphonomy of a unique tyrannosaurid bonebed from the upper Campanian Kaiparowits Formation of southern Utah: implications for tyrannosaurid gregariousness. *PeerJ* 9: e11013.

Tykoski, R.S. and Rowe, T. 2004. Ceratosauria. *In*: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria (2nd Editon)*, 47–70. University of California Press, Berkeley.

Weishampel, D.B. 1981. Acoustic analyses of potential vocalization in lambeosaurine dinosaurs (Reptilia: Ornithischia). *Paleobiology* 7: 252–261.

Whewell, W. 1837. *History of the Inductive Sciences, from the Earliest to the Present Times.* Vol. 1: 437 pp.; Vol. 2: 534 pp.; Vol. 3:624 pp. J.W. Parker, London.

Wiens, J.J., Brandley, M.C., and Reeder, T.W. 2006. Why does a trait evolve multiple times within a clade? Repeated evolution of snakelike body form in squamate reptiles. *Evolution* 60: 123–141.

Wilson, E.O. 1998. *Consilience: The Unity of Knowledge*. 332 pp. Alfred A. Knopf, New York.

Woodward, H.N., Freedman Fowler, E.A., Farlow, J.O., and Horner, J.R. 2015. *Maiasaura*, a model organism for extinct vertebrate population biology: a large sample statistical assessment of growth dynamics and survivorship. *Paleobiology* 41: 503–527.

Woodward, H.N., Tremaine, K., Williams, S.A., Zanno, L.E., Horner, J.R., and Myhrvold, N. 2020. Growing up *Tyrannosaurus rex*: Osteohistology refutes the pygmy "*Nanotyrannus*" and supports ontogenetic niche partitioning in juvenile *Tyrannosaurus*. *Scientific Advances* 6: eaax6250.

Xu, X., Choiniere, J., Tan, Q., Benson, R.B.J., Clark, J., Sullivan, C., Zhao, Q., Han, F., Ma, Q., He, Y., Wang, S., Xing H., and Tan, L. 2018. Two Early Cretaceous fossils document transitional stages in alvarezsaurian dinosaur evolution. *Current Biology* 28: P2853–2860.

Xu X., Clark, J.M., Forster, C.A., Norell, M.A., Erickson, G.M., Eberth, D.A., Jia C., and Zhao Q. 2006. A basal tyrannosaurid dinosaur from the Late Jurassic of China. *Nature* 439: 715–718.

Xu X., Tan Q., Wang J., Zhao X., and Tan L. 2007. A gigantic bird-like dinosaur from the Late Cretaceous of China. *Nature* 447: 844–847.