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ORIGINAL RESEARCH

Testing Utility: Developing an Assessment to Evaluate *Tyrannosaurus rex* Forelimb Use Cases

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ABSTRACT

Tyrannosaurus rex is infamous for its large body size and seemingly mismatched forelimbs, which are extremely small relative to body size. Since its first description by Osborn in 1905, the diminutive size of this attribute has fueled an arms race of sorts wherein specialists have advanced numerous theories seeking to prove a seemingly single-track use or non-use for the arms. While the overall debate on the evolutionary processes behind the small limb size is not addressed here, previous functional theories are reviewed within a functionalist perspective. This paper contends that *Tyrannosaurus rex* would have used its limbs for whatever purposes possible and that selecting one function to the exclusion of others is not a realistic approach to understanding the lifeways of the Tyrant King. Rather, a functionality assessment is suggested and tested using existing theories with the aim of providing a tool to assess future use case theories.

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Introduction

The forelimb of *Tyrannosaurus rex* is a captivating riddle of biology that has fueled numerous theories ranging from roles in reproduction, active hunting and slashing, and being useless. What makes pondering the function of the forearms so captivating, besides their ridiculously small size, is that dinosaur paleobiologists must account for evolutionary forces pushing to minimize arm size while still acknowledging significant residual function. Benton and Harper (2013) note parts of the body, whether an appendage, organ, or bone, are adapted to do something, presumably as efficiently as possible. In this frame, the forelimbs of *Tyrannosaurus rex* were on their way out. Studies like Fastovsky and Weishampel (2005), and Lockley *et al*. (2008) make cases for the mechanism behind the dwindling arm size. That said, studies such as Carpenter and Smith (2001), Carpenter (2002), and Lipkin and Carpenter (2008) show that the arms, while small and with a limited range of motion, were powerful and thus capable of serving some active role in life activities. With *T. rex*, we have a glimpse at a forelimb doomed by natural selection yet not reduced to a stage wherein it lacks any function. The arms were capable of some level of functionality that could potentially support a certain spectrum of activity. While still useful in everyday life, this utility was not probably enough to preserve them via natural selection considering the other selective forces in play.

Exploring potential uses is a challenging effort. While most dinosaur paleobiologists no doubt hold that the forelimbs could serve more than one purpose as they had the potential to manipulate something, use studies still exhibit what Lockley et al (2008) noted as “trying to find one that is compelling” (2008, p. 156). Further, no study has clearly stated that the theory it proposed is but one possible function and this covers the work of Osborn and Brown (1906), Newman (1970), Mattison and Griffin 1989, Carpenter and Smith (2001), Holtz (2007), Lipkin and Carpenter (2008), Krauss and Robinson (2013), and Stanley (2017). Theories should be assessed against what is known of *T. rex* forelimb biomechanics and lifeways and seen not as an exclusive use, but as part of a plausible suite of functions that without further evidence cannot be proven or disproven. This assessment is not intended to be used for theories involving the evolutionary progression toward smaller arms, but rather only to explore the range of remaining functionality as natural selection reduced the forelimbs.

Review of Morphological Analyses

Functionality

The *Tyrannosaurus* forelimb consists of thirteen bones in total and terminates in two clawed digits; a small metacarpal is also present but not visible in the flesh (Brochu, 2003). Based on its proportions relative to the overall size of the animal, the forelimbs appear rather puny. For example, the *Tyrannosaurus* specimen known as Sue measures 12.3 meters long (Hutchinson et al., 2011). That said, the *Tyrannosaurus* forelimb measures about 1 meter in length. The average height of a human male is 1.6764 meters. Using the same ratio (1 to 12.3), a human with similarly proportioned forelimbs would have limbs measuring 136.3 mm, shorter than the average human hand (177.9 mm according to Wang & Cai, 2016). *Tyrannosaurus*'s arms were smaller in length than its head and could not reach its mouth.

Osborn's first analysis showed the forelimb, despite its proportional oddity, had significant muscular attachments (Osborn & Brown, 1906). Carpenter and Smith (2001) did the first biomechanical analysis of *Tyrannosaurus*' forelimb. This initial work evidenced that the forelimb was strongly muscled, had a well-structured and stout humerus, and thick cortical bone. The forelimbs, it was suggested, could lift upwards of 199 kgs, with most of the power involving flexion and not an extension. Carpenter (2002), in comparing three nonavian theropod forelimbs, found ample evidence that *T. rex*'s puny arms were strong enough to find utility in hunting.

Lipkin and Carpenter (2008) addressed some analytic issues with Carpenter and Smith (2001) but note that the forelimbs were "capable of resisting large forces" while flexed and could move at "high accelerations" (p. 186). Further, the arms exhibited a limited yet somewhat effective range of motion. The study showed that the forelimbs had a range of motion of 40-45 degrees.

Another structural limitation for the forelimb were the claws. While Rothschild (2013), and Stanley (2017) provide evidence that the claws could have inflicted damage, Hone (2016) notes that the claws are less curved than previously seen in tyrannosaurids and probably had less gripping power and/or function because of this. Despite the small size and limited reach, the arms exhibit a robust structure and the potential for usable motion and strength.

Selected against

Given the small relative size of the Tyrannosaur forelimb, it is easy to dismiss it as non-functional and call it a vestigial appendage that is slowly being removed via evolution. First, clearly, we have to accept that the forelimbs were on a path to the disappearance. The reason for this is still debatable.

The function does not appear to be playing a role in any discernable type of selective shriveling of the forelimbs. Fastovsky and Weishampel (2005) advance a theory that the forelimbs were small to make up for increases in head size, thus providing for a weight balance of the *Tyrannosaurus*. While dismissing Fastovsky and Weishampel (2005), Lockley *et al*. (2008) note, "Functionalist arguments can only take us so far because they ignore inherent, intrinsic, or formal growth and development." (2008, p. 132). That research team makes a compelling case that "such developmental exaggeration or emphasis in one organ or region of the body inevitably results in underdevelopment in adjacent organs, as required by the principle of compensation, also known as heterochronic trade-offs" (Lockley, 2008, p. 131) and that:

> 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. Thus, anterior growth bypassed other anterior organs and concentrated in the head (Lockley 2008, p. 132).

Lacovara (2017) takes a more simplified approach, noting a return-on-investment structure and that the arms were reduced to conserve energy as they were no longer needed with the development of the head. Lacovara bases this approach on a study of blind versus nonblind cavefish that found sighted fish used more oxygen for a sense that was useless.

Although the forelimbs were on the way out, they were not useless, as can be attested by the biomechanical research (Carpenter & Smith, 2001) and evidence of use (Rothschild, 2013). Finding those use cases is the issue at hand here and is a stance that counters those like Paul, who dismisses the forelimb entirely: "much speculation has been directed towards the use of these forelimbs" and "this obsession is misplaced. They were not important to their owners, so they should not be important to us" (Paul, 1988, 320).

Tyrannosaurus was clearly capable of useful function. Look at an Abelisaurid like *Carnotaurus*, which provides an excellent example of forelimbs that, via natural selection, had ceased to be able to grasp or manipulate anything. *Carnotaurus*' forelimbs, when compared to body size, are even smaller than *Tyrannosaurus*' (Ruiz et al., 2001, p. 1276). The hand itself is a mess, lacking carpalia (Ruiz et al., 2011), with its four fingers (Bonaparte et al., 1990) not capable of motion (Agnolin & Chiarelli, 2010). Further, Senter (2010) found nerve fiber size so greatly reduced that there was almost no transmission ability. However, according to the work of Burch and Carrano (2012), abelisaurids like *Carnotaurus* had a shoulder structure that could have allowed the forelimb a wide range of motion. It is difficult to know, given the nerve and other limitations, if the forelimb could move and utilize this range of motion. If it could move, perhaps the arms flapped or swatted as a visual or even auditory signaling function.

Review of use theories

Gould so simply framed a somewhat complex question: "what, if anything, did Tyrannosaurus do with its puny front legs anyway?" (Gould, 2010, p. 12). Despite the claim of Paul (1988) that no one should care about *T. rex*'s arms, many have, but each was hampered by a self-imposed limitation. Lockley *et al*. (2008) note that most efforts seek to find one single use. While many dinosaur paleobiologists believe in more than one use for the forelimbs, none have clearly couched their theory into a suite of other theories. The arguments look, on their faces, to be somewhat exclusive, although this may have not been the intention.

Feeding utility as a juvenile (Mattison & Griffin, 1989)

Based on the premise that the adult forelimb lacked usable strength, Mattison and Griffin (1989) suggest that *Tyrannosaurus*' arm had feeding functionality during youth. They argue that as the Tyrannosaur grew, the forelimbs fell to disuse as the animal moved food with its mouth and not its forelimbs as it progressed from predator to scavenger. While interesting, this use case disregards any real usage in adulthood, which conflicts with studies such as Carpenter and Smith (2001), Carpenter (2002), and Lipkin and Carpenter (2008).

Raising the body (Newman, 1970)

In examining the posture and mobility of Tyrannosaurs, Newman (1970) suggested that the forelimbs could be used to help the dinosaur rise from a prone position. While interesting, the work of Carpenter and Smith (2001), and later employed by Krauss and Robinson (2013), shows that the power of the forelimbs rested in flexing and not an extension.

Reproduction (Osborn & Brown, 1906)

Osborn and Brown (1906) noted the small size of the forelimbs compared to the evidence that each limb had signs of potential strength and suggested the arms played a role in reproduction. This seems possible, but the forces needed to grip during copulation are as of yet unexplored.

Signaling (Holtz, 2007)

In line with reproduction-focused theories, Holtz (2007) suggested that *Tyrannosaurus*, possibly having some form of feathers, may have had plumage on its forearms that could serve as either part of reproduction or social interactions.

> The arms may have had another function, though. In modern flightless birds, the wings are still useful in signaling to other members of the species. It might be that tyrannosauirds also used these little arms to signal. (In fact, I wonder if the largest tyrannosauirds may have retained some protofeathers on their arms to make them more 'showy') (Holtz 2007, p. 125).

Holding prey (Carpenter & Smith, 2001)

As noted above, Carpenter and Smith (2001) did the first biomechanical analysis of *Tyrannosaurus*' forelimbs, using the analysis to suggest the arms would be useful for holding prey. The further work of Lipkin and Carpenter (2008) supports this theory.

Ceratopsian-Tipping (Krauss & Robinson, 2013)

Krauss and Robinson (2013) took the findings of Carpenter and Smith (2001) and applied them, with some additional analysis, to develop a theory for a *Tyrannosaurus* hunting method. Based on the concept of 'cow-tipping', an activity wherein people, usually teenagers, tip oversleeping cows, Krauss and Robinson argue that *Tyrannosaurus rex* could have rammed the side of a ceratopsian and held on with its forelimbs as it pushed the animal over. Once toppled, the ceratopsian was rendered somewhat helpless and vulnerable as its largely unprotected abdominal areas were exposed to attack. While more reliant on hind-limb power, the grasping or clinging action of the forelimbs falls in line with the accepted structural analysis of Carpenter and Smith (2001) and Lipkin and Carpenter (2008).

Slashing (Stanley, 2017)

Stanley argues that the forelimb exhibits six attributes that make it ideally suited for slashing actions. Stanley argues that: the forelimb's shortness provided leverage; possessed strong musculature; bones were stout; reduction in digits increased pressure per claw by 50%, and the main shoulder joint provided useful mobility; and the claws, averaging 8-10 cm in length, would have caused grievous wounds. Stanley concludes that such attributes allowed *Tyrannosaurus rex* to slash its prey while holding it in its large jaws. He notes that the *Tyrannosaurus* could have made 1-meter long slashes with each of its claws, with each slash being somewhat less deep than the 8-10 cm average claw length (unless force compressed allowing for a deeper slash). Stanley goes so far as to say that “natural selection kicked in opportunistically and put them to good use for slashing at close quarters.”

Stanley over estimates wound length by not factoring in a range of motion issues and other traits of *Tyrannosaurus.* In Pickrell (2017), Thomas Holtz is quoted on the issue, noting: “Tyrannosaurus would have to push its chest up against the side of the victim. In such a position the tyrannosaur wouldn't be able to use its far more powerful armament: its massively powerful jaws.” Interestingly, while slashing may not have been advantageous with prey, *Tyrannosaurus* did possess enough range of motion to make use of the claws for slashing others of its species. Rothschild (2013) provides evidence of bone-scarring slashes inflicted on one *Tyrannosaurus* by another.

Materials and methods

Developing a functionality test of use cases

Based on the structure and functionality of the *Tyrannosaurus* forelimb, coupled with key attributes of its lifestyle (such as being a carnivore), a simple test can be developed to assess possible use cases for the forelimbs, seeking to understand what is possible over finding the less plausible and illogical single-use theory. This test consists of the following questions and model answers, along with the citation evidencing that attribute’s answer.

Does the use case conform to *Tyrannosaurus* being a carnivore (hunter and/or scavenger)?

> *Yes*—from the earliest work of Osborn and Brown (1906) to that of Horner and Lessem (1993) and Carpenter (1998), it is clear *Tyrannosaurus rex* was a carnivore. This paper chooses not to cloud its purpose by delving into the debate of whether *T. rex* was a predator, scavenger, or both as the debate makes little difference in assessing use cases as of yet.

Does the use case recognize functionality in adulthood although the theory advances a use as a juvenile?

> *Yes*—While interesting, the work of Mattison and Griffin (1989) tries to establish that the forelimbs were functional during youth and became much less so as the *T. rex* reached adult size. The problem with this use case is that based on studies like Carpenter and Smith (2001), Carpenter (2002), and Lipkin and Carpenter (2008), we know the adult *T. rex* forelimb was strong enough to perform some function or functions. Theories focused on juvenile uses must acknowledge the adult functionality or at the very least not dismiss the possibility.

Does the use case require the arms to touch?

> *No*—Clearly stated by Hanna (2003) and others, the forelimbs of *T. rex* are too short to reach one another, thus any use case requiring such action is dismissed.

Does the use case require arms to reach the mouth?

> *No*—As noted by many, including Horner and Lessem (1993) and Lockley *et al*. (2008), *T. rex* could not reach its mouth with its forelimbs, thus any use case requiring such action is dismissed.

Does the use case rely on flexion and not extension?

> *Yes*—Studies such as Carpenter and Smith (2001) and Lipkin and Carpenter (2008) establish that *T. rex*’s forelimb was based on flexion and not an extension. Therefore, theories relying on extension are dismissed as they are not supported by the biomechanical evidence.

Does the use case require a grasping motion of the hand?

> *No*—Hone (2016) suggests reduced claw curvature, which adversely effected grip function and power. Further, gripping is challenging with only two fingers.

Does the use case require more than two fingers?

> *No*—While *Tyrannosaurus* had three metacarpals, only two terminated in digits; the third metacarpal remained hidden on the flesh of the hand (Brochu, 2003). For a theory to be plausible, it must account for *T. rex* having only two fingers.

Does the use case require lifting more than 199 kgs?

No—Per the work of Carpenter and Smith (2001), the maximum working range (MWR) for the adult *Tyrannosaurus* forelimb was around 199 kgs. Plausible theories cannot expect more weight to be lifted unless new evidence of the biomechanics of the forelimbs is presented to redefine the MWR upward.

The test aligns with a functional hypothesis, allowing many items to be acted upon by the forelimbs, and does not exclude any theory unless it cannot pass the test. If all answers match the model answers, then the theory is termed ‘plausible’ meaning, based on what we know about arm biomechanics and *T. rex* lifeways, the theory is functionally possible. If the attribute is not relevant to the use case, it can be dismissed and does not affect theory plausibility. For example, one theory advanced is that the arms were used to signal another *T. rex*, so conformity with its status as a carnivore is not relevant. A single answer contrary to the model answer makes the theory Not Plausible. That said, the question might not be answerable, leading to a ‘Develop’ designation meaning it requires further research to test an aspect before the theory can be assessed. For example, while Osborn’s theory about the arms playing a role in reproduction passes several questions, we lack an estimate on how much strength would be needed, so the last question cannot be definitively answered.

Results and discussion

Applying the test to suggested use cases

The diminutive size of the forelimbs in comparison to the rest of the body has fueled speculation as to the functionality of the limbs. Applying the assessment to the theories discussed in this article tests the theory and sets it in a context with similarly scored theories. By assessing each use theory and comparing it to every other, we get a clearer picture of the potential function and proof that there could have been more than one function. Table 1 records the answers for the seven theories assessed and notes the conclusion on plausibility.

Table 1. Assessing the current arm use theories.

	Model Answer	**Feeding as a Juvenile**	**Raising the body**	**Reproduction**	**Signaling**	**Holding prey**	**Ceratopsian-Tipping**	**Slashing**
Does the use case conform to Tyrannosaurus being a carnivore (hunter and/or scavenger)?	Yes	Yes	N/A	N/A	N/A	Yes	Yes	N/A
Does the use case recognize functionality in adulthood although the theory advances a use as a juvenile?	Yes	No	N/A	N/A	N/A	N/A	N/A	N/A
Does the use case require the arms to touch?	No	No	No	No	No	No	No	No
Does the use case require arms to reach the mouth?	No	Maybe	No	No	No	No	No	No
Does the use case rely on flexion and not extension?	Yes	Yes	No	Yes	Yes	Yes	Yes	Yes
Does the use case require a grasping motion of the hand?	No	No	No	No	No	No	No	No
Does the use case require more than two fingers?	No	No	No	No	No	No	No	No
Does the use case require lifting more than 180 kgs?	No	?	Yes	?	No	No	?	No
Result	Plausible	Not Plausible	Not Plausible	Develop	Plausible	Plausible	Develop	Plausible

As can be seen from the table, two theories were determined not plausible, two needed additional research but passed many of the questions, and three were found plausible. A task like raising the body requires an extension of the arm and support for a great deal of weight that is not plausible as it is not compliant with the known biomechanical capabilities of the *T. rex* arm.

For theories deemed plausible, none are mutually exclusive of any other. For example, a feathered arm could be used for signaling, slashing at prey or enemies, and help latch on to a prey item. Without field observation and study of living animals, which clearly cannot occur, we will never know which theory is correct (Weishampel, 1995). Finding evidence in the fossil record for much of this is unlikely.

Conclusions

The forelimbs of *Tyrannosaurus rex* present dinosaur paleobiologists with the chance to observe evolutionary forces forcing the arms to reduce in size but find them at a stage wherein they have a significant residual function. Based on the extant biomechanical studies, the forelimbs have the potential for a limited yet possibly useful spectrum of activity, albeit a functionality not powerful enough to stop the evolutionary forces already underway. Efforts to explore forelimb function have not focused on a spectrum of activity but seemingly choose to seek to find a single use case that is better than all others, a practice that makes little sense given that most paleobiologists believe the forelimbs could serve more than one purpose. To date, no study has presented its theory as part of a functional suite. Using the biomechanical studies and a basic understanding of *T. rex* lifeways, it is possible to develop a simple assessment that determines the plausibility of each suggested use case. Of seven theories assessed, three were plausible and two needed additional research; two were found not plausible. Further theories should self-test using the assessment, not only to check the overall viability of the case presented but to place the theory into an operational spectrum for *T. rex*'s forelimbs.

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