NEWS & VIEWS FEATURE

DINOSAUR LOCOMOTION

Beyond the bones

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How did dinosaurs stand and move? Computer simulation and other methods have told us much about how dinosaurs did and did not move, but they have not yet reached their full potential.

Ray Harryhausen, famous animator of creatures in such films as *Jason and the Argonauts* and *The Valley of Gwangi*, has written that "I found dinosaurs to be the ideal subject for stop-motion animation... The fact that nobody knew how those huge reptiles had moved or, for that matter, exactly how they looked meant that I could bring them alive without any fear of criticism"[1]. Harryhausen indeed showed that nothing brings an extinct animal to life more than seeing it move. But can walking and running dinosaurs be animated with scientific rigour rather than just artistic flair? Dinosaurs are excellent study organisms for researchers interested in such aspects of biomechanics as the repeated evolution of large size, shifts to and from bipedalism and quadrupedalism[2,3], and changes in joint structure, musculature and behaviour[4–10].

Unlike investigators working exclusively on living animals, palaeobiologists can't directly record the motion, measure the forces or dissect the soft-tissue anatomy of their study organisms. Rather than consigning this problem to the unknowable, we can make general inferences about individual species[11–15], as well as about large-scale patterns of locomotor evolution[3,5,10,16]. But specific hypotheses about dinosaur motion, mechanics and performance (such as speed, acceleration and agility) remain controversial[7,11,13,15,17,18]. Several approaches to the generation and testing of such hypotheses are described in Box 1. Here we focus on a recent trend in the field: the increased use of computer animation and simulation to recreate dinosaur locomotion, taking *Tyrannosaurus rex* as our example.

Uncertainties

Uncertainty about movement stems directly from the framework of the animal's leg. Bony articulations (Fig. 1a) provide crucial evidence, but deciding which subset of potential joint positions a dinosaur habitually used to stand or move is by no means straightforward. Redundancy in the limb skeleton (what engineers call excess degrees of freedom) precludes a unique solution. For example, how high was the hip joint above the ground (Fig. 1b)? The bones alone do not establish this seemingly
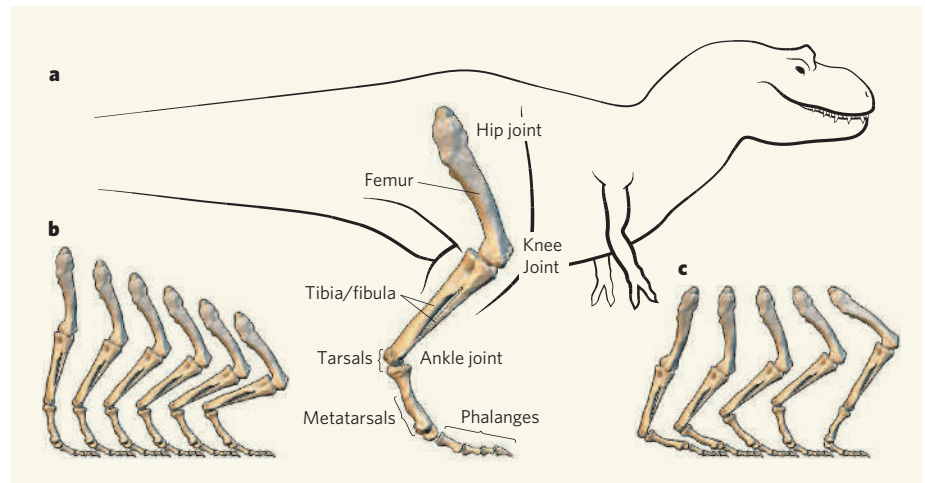

Figure 1 | *Tyrannosaurus rex* as an example of dinosaur anatomy and locomotion. **a,** The basic skeletal components and joints of the hindlimb. Only the third toe is shown for clarity. **b,** Redundancy allows the limb to assume a range of potential hip heights. **c,** For each position of the hip with respect to the foot, a spectrum of internal configurations is possible.

simple metric, because the joints are flexible enough to allow the tyrannosaur to lie down. Even after a hip position is chosen, a spectrum of poses still remains, because three segments, rather than one or two, span from hip to toes (Fig. 1c). If a dinosaur's hip, knee, ankle and main toe joints can flex and extend through an arc of 90°, variation of each by 1° increments would yield more than 67 million possible poses. Most of these can be excluded as geometrically or biologically implausible. Yet even in this two-dimensional example, thousands of possible configurations remain.

Animation

The availability of sophisticated animation and simulation software allows palaeobiologists to tackle fundamental questions about dinosaur locomotion in a new way. However, digital dinosaurs are most commonly seen in the popular media, and more often than not little scientific substance underlies such films and documentaries. Yet making virtual dinosaurs move can be done scientifically. This is an excellent opportunity to let the public see science in action.

We had first-hand experience of the complexities of animating a walking *Tyranno-saurus* as consultants for the 'Dinosaurs: Ancient Fossils, New Discoveries' exhibit at the American Museum of Natural History[19]. Having previously avoided complete reconstructions in our own research, we wondered whether we could legitimately present our 'result' as a scientific hypothesis rather than just a pretty moving picture. We found the process humbling — not because creating a walking stride for the model was difficult, but because (with the aid of the museum's animator, Scott Harris) inventing motion was all too easy. How would we know which limb poses were off the mark and which were closer to reality? We reluctantly settled on one animation that captured the basic principles of animal locomotion (see Movie 1 in Supplementary Information). Yet we could have produced thousands of animations that were no better or worse. Computational tools offer tremendous power to generate motion, but we now face the new problem of how to choose among countless hypotheses.

Palaeontologists have two main options when confronting redundancy in an articulated chain of bones (Fig. 1). The first is to set arbitrary constraints on the system to reduce the number of possibilities. A dinosaur's

limb orientation is often taken for granted by duplicating a mammalian, avian or some other intuitively pleasing pose[7,20]. Other studies invoke simple geometric rules: for example, the knee and ankle can be restricted to identical angles, or the hips fixed midway between the planted feet[21]. Such constraints simplify the redundancy enough to calculate a narrow range of solutions, but one risks answering a question that no longer has relevance to reality[18]. Assuming a pose *a priori* is untenable.

Beyond the bones

The second, alternative option is to use demonstrably realistic constraints to exclude, rather than include, possible limb motions. Only by admitting that a single solution is unachievable can we begin to search for a set of movements that cannot be ruled out. A rigorous dynamic simulation[22,23] of a moving dinosaur, one encompassing all motions and forces, cannot yet plausibly be done. But a major goal is to move towards an integrative analysis based on solid evidence and an adequate consideration of unknown factors. Because the limb skeleton is so redundant, this can be done by moving beyond the bones to include the forces (muscular, external, gravitational) that actually create limb motion.

A complete locomotor cycle, or stride, consists of a stance phase and a swing phase (Fig. 2a). In the stance phase, the limb pushes down on the ground to incur an equal but opposite force (the ground reaction force or GRF; Fig. 2b). In early stance, the GRF points up and back, decelerating the body as the limb shortens. At mid-stance, the GRF is vertical and is at its peak value for a stride. Its relative magnitude is a function of the fraction of a stride that each foot is on the ground. In late stance, the GRF points up and forward, reaccelerating the body[24,25]. Throughout the stance phase, forces from muscles act at a distance from a joint axis (the moment arm[26]) to produce moments (rotational forces) that prevent the limb from collapsing. Figure 2c–e shows three possible stance phases for a running *Tyrannosaurus*, none of which can be excluded based on the articulations between bones or other common criteria. The first is a very upright 'columnar' limb[21]. The second represents a more crouched 'bird-like' limb[7]. The third uses poses between these two extremes. How could we know which of these is more or less likely?

Rather than tackle the intricacies of a complete stance phase, a single time point can define the problem better — linking multiple instants of locomotion might allow reconstruction of a full stance phase, then a full stride. We begin with a simple example: a *Tyrannosaurus* frozen at mid-stance (Fig. 3). This can act as a 'filter' for excluding improbable poses, as it is a time when high stresses

are placed on the musculoskeletal system. The GRF increases with speed, and so at top speed the maximum GRF can be used to estimate the size of the muscles needed to support the limb[13–15].

Constraints

A range of kinematic (motion-based or geometric) and kinetic (force-based) criteria help to exclude certain poses for *Tyrannosaurus* as unrealistic. The goal is to constrict the 'configuration space' of poses as narrowly as possible, by sequentially adding constraints that rule out poses as impossible or unlikely, depending on the strength of support from studies of the locomotion of extant animals. We add kinematic constraints first. For example, body segments cannot penetrate each other or the surface of the ground, and joints cannot exceed certain maximal and minimal joint angles — in particular, the ankle and knee cannot bend backwards. But a huge configuration space remains, and many plausible poses cannot be excluded (Fig. 3).

Next, kinetic constraints based on biomechanical studies are added. First, the GRF is oriented vertically through its point of application at the foot–ground interface[24,25]. Second, poses are excluded in which any joints have unreasonable joint moments incurred by the GRF — the hip, knee and ankle require the action of extensor muscles that straighten the limb and work against the force of gravity. Again, this constraint is congruent with living animals[16]. It excludes the first example pose (Fig. 3a), because the GRF is in front of the knee, requiring net knee flexor (bending) muscle activity to balance it, not knee extensors. The third kinetic constraint is that the moment arm of the GRF about any joint cannot exceed a maximal distance, This is determined by the maximal extensor muscle moment that could be generated by an animal with 5% of its body mass dedicated to muscles crossing that joint[14,15]. This maximal distance is inversely related to the magnitude of the GRF and excludes the second pose (Fig. 3b); the dinosaur would not have enough knee extensor muscles even to run slowly.

These realistic kinetic constraints involve more assumptions than the kinematic ones. They exclude many more poses than are shown here; yet many remain, such as Figure 3c. That pose allows running, although not very quickly (no more than 29 km h^{-1}), as the hip extensor muscles would not have been able to sustain higher speeds under the assumptions invoked.

The challenges don't end with identifying candidate mid-stance poses. The remainder of the stance phase and the swing phase expand the potential motion space of the limb enormously. Once such an analysis moves beyond a single pose, the issue of time must be dealt with (see Movie 2 in Supplementary Information). One can calculate the stride length for any motion (Fig. 2a). To estimate the velocity,
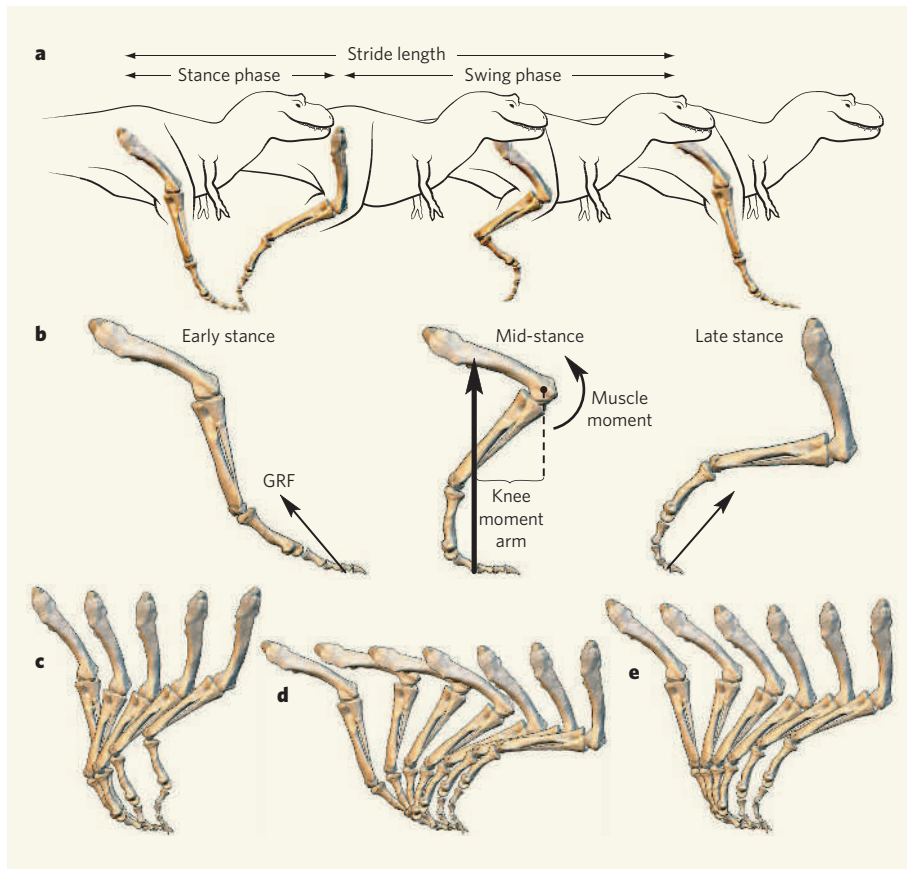
Figure 2 | Locomotor cycle (stride) for *Tyrannosaurus*.   a, The main components of a stride. **b,** A stance limb induces an equal and opposite ground reaction force (GRF), represented here as a vector. The GRF requires opposing muscle activity to balance it. The horizontal bracket indicates the moment arm of the GRF about the knee joint. **c–e,** Three possible stance-phase movements for a running *Tyrannosaurus*.

however, a time-dependent factor — the stride frequency — is also required, because velocity equals the distance travelled per cycle multiplied by the number of cycles per unit time. How fast do the limbs swing forward through the air, and what are their motions while unconstrained by the GRF? This is one of the most vexing problems for reconstructing

Figure 3 | Mid-stance poses for the three sequences shown in Figure 2. The horizontal bracket indicates the moment arm of the GRF about the knee joint. Kinetic constraints can rule out poses **a** and **b**, and many others, but not pose **c** and many others.

dinosaur locomotion. Potential solutions depend on invoking experimentally validated constraints from living animals, but these constraints are often not well enough understood to apply them to extinct animals. Yet now that researchers know what to look for, better constraints will probably be found.

Back to biology
The subject of dinosaur locomotion requires palaeontologists to become better functional biologists — experts in more than just skeletal morphology. The most appropriate approaches focus on the entire limb rather than just bones. With the tools now available, we can begin to study how fast certain dinosaurs could move, how their muscles functioned, and how they stood or moved. But the problems of missing data (such as muscle size or moment arms[15,26]) will always remain and cannot be overlooked.

We have provided a case study of how to embrace the uncertainty in reconstructions of the locomotion of extinct animals. The example of mid-stance poses shows that it is possible to move forward without being confounded by the vast reaches of this uncertainty or making arbitrary assumptions, by using a range of kinematic and kinetic constraints that depend on their applicability to living animals.
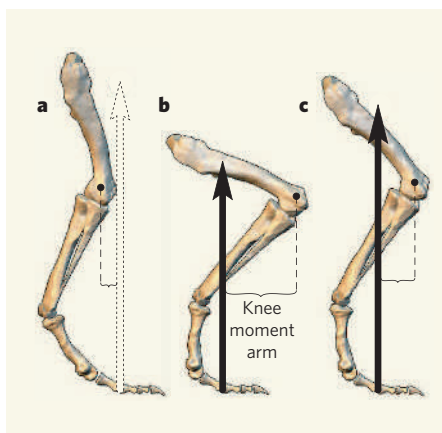
Such an approach to reconstructing behaviour in extinct animals can bolster confidence in the conclusions, and thereby move the field in a more progressive, sustainable direction. In publicly engaging and often fast-moving fields such as dinosaur palaeobiology, it is essential that the questions do not get too far ahead of the evidence, that tides of enthusiasm do not drown concerns about ambiguity, and that novel tools are not recklessly applied. The main principles of this approach apply not only to dinosaur locomotion, but also to all functional studies of extinct organisms — from breathing and feeding, to swimming and flight.

Ray Harryhausen preferred animated dinosaurs to retain "a look of pure fantasy because their movements are beyond anything we know"[1]. We may indeed never know for sure how dinosaurs moved. But if we can find out what their movements were not like, that will be real progress. ∎

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