Bipedal Hopping and the Origin of Dinosaurs

by
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ABSTRACT

Recent theories of dinosaur endothermy purport to explain the dinosaurs' fully erect gait by analogy to modern cursorial mammals and ground birds. However, these theories fail to take into account the constraints imposed by dinosaur hip structure on the possible gaits employed by dinosaurs. Moreover, these theories provide no insight whatsoever into the origin of obligatory bipedality, a primitive condition in dinosaurs and one that persisted in many lineages to the very end of the Mesozoic. Both of these deficiencies can be remedied if it is assumed that dinosaurs were originally adapted for bipedal hopping. The adoption of such a gait would explain in functional terms the dinosaurs' peculiar hip structure and the shift to obligatory bipedality. Moreover, since hopping relies on elastic storage and rebound, dinosaurs would have been capable of high speed locomotion without any increase in physiological grade.

INTRODUCTION

In advancing his "heretical" ideas about dinosaur endothermy, Robert T. Bakker (1968, 1971, 1980, 1986) argues that the dinosaurs' upright limb architecture indicates a capacity for high speed running, on a par with modern mammals and ground birds. Although this analogy between dinosaurs and modern cursorial animals is quite compelling, it suffers from two very serious shortcomings. First, any comparison in the limb architecture of dinosaurs and mammals is belied by their very dissimilar hip structures. Mammals have a ball-and-socket hip structure which permits lateral adjustments of footfalls to compensate for the inherent instabilities associated with high speed running. By contrast, dinosaur hip structure rigidly constrained leg motion to the parasagittal plane which would have impaired the ability of dinosaurs to maintain stability at high running speeds (Hotton, 1980). Second, mammals were primitively quadrupedal; dinosaurs were not. All dinosaurs, with the possible exception of the giant sauropods, descended from bipedal ancestors (Stahl, 1985). Many dinosaurs were bipedal, and dinosaur bipeds flourished to the very end of the Mesozoic. Bakker's theory offers no insight whatsoever into the origin of obligatory bipedality. Indeed, when asked why bipedality evolved, Bakker replies (1987, oral comm.), with uncharacteristic humility, "I have no idea." Gregory Paul (1988), a Bakker disciple, is equally agnostic: "The reason predatory dinosaurs became bipedal is not at all clear." "The only thing that can be said in the end, is that bipedalism was a serendipitously crucial adaptation...."

In this paper, we will critique Bakker's theory of dinosaur cursoriality and offer an alternate explanation for dinosaur limb mechanics and locomotion. It will be argued that both the fully erect gait *and* obligatory bipedality were concomitant adaptations to a bipedal hopping gait. This alternate theory is superior to Bakker's on at least two counts: first, it is consistent with, and indeed explains, the peculiar dinosaur hip structure; second, it explains how and why obligatory bipedality evolved. Bipedal hopping would also explain how dinosaurs were able to achieve high speeds without any significant increase in physiological grade. Bipedal hopping is powered by elastic storage and rebound; the metabolic input is relatively low. Therefore, dinosaurs need not have been endothermic.

BIPEDALITY AND THE FULLY ERECT GAIT

By most accounts, there were three phases in the evolution of archosaur locomotion: (1) the primitive Sprawling Gait; (2) the intermediate Semierect Gait; and (3) the advanced Fully Erect Gait (Bakker, 1971; Charig, 1979). Proterosuchican thecodonts were sprawlers; ornithosuchian thecodonts and crocodiles were semierect; and the dinosaurs, which descended from the ornithosuchians, were fully erect.

The primitive sprawling gait "probably was already standardized in the very first tetrapods at the end of the Devonian or beginning of the Carboniferous, long before the first reptile appeared." (Bakker, 1971). In the sprawling gait, the upper limbs extended horizontally from the pelvis and shoulder and were joined at the knees and elbows to the vertical lower limbs. Leg motion described a wide sweeping arc of the upper limbs with complex long axis rotations of the lower limbs. The proterosuchian thecodonts from the Upper Permian, were, like most of their contemporaries, low-slung sprawling quadrupeds showing "little if any trend towards bipedalism that was so marked in archosaur evolution." (Colbert, 1967)

Beginning with *Euparkeria*, an ornithosuchian thecodont from the Early Triassic, all thecodonts above the proterosuchian grade were equipped with a variable semierect gait. When it moved slowly or stood still, *Euparkeria* held its hind limbs in a horizontal sprawling position; but when it ran, the legs were brought beneath its body into a more upright stance. The semierect gait effectively raised the body higher off the ground, narrowed the trackway, increased stride length, and permitted faster locomotion. Deflecting the hind legs down and inward greatly simplified leg motion by bringing it closer to the ideal of a freely swinging pendulum (Thompson, 1961), a condition ultimately achieved in the dinosaurs.

Euparkeria is also noteworthy for being the first tetrapod capable of bipedal locomotion. Unlike the dinosaurs, however, *Euparkeria* was merely a habitual biped: it ran on two legs but reverted to all fours when not in a hurry (Ewer, 1965).

During the Middle Triassic, when the mammal-like reptiles were being challenged by a "bewildering variety" of thecodonts (Bakker, 1980), bipedality and an increasingly upright stance continued to develop in tandem in several thecodont lineages. In ornithosuchian thecodonts, such as *Lagosuchus*, an animal very close to the common ancestry of the dinosaurs, the limbs were almost fully erect as indicated by a sharply inturned femoral head approaching the dinosaurian condition. The rauisuchids, largest of all the Middle and Upper Triassic thecodonts, "evidently attained a vertical posture independently of the lineage that led to the dinosaurs." (Carroll, 1988) Both ornithosuchians and rauisuchians showed a strong tendency toward bipedal locomotion, evident in the increasing disproportion between the long hind limbs and short forelimbs.

The final stage of archosaur limb development -- the fully erect bipedal gait-- was achieved by the dinosaurs and is clearly evident in *Staurikosaurus*, the earliest known dinosaur (Carroll, 1988). In the fully erect gait, also known as the fully improved gait, the legs were held rigidly in the vertical plane; leg motion was restricted to the parasaggital plane with no long axis rotation (Charig, 1972). The fully erect gait was maintained by a sharply inturned and cylindrical femoral head which fit snugly into a perforated hip socket (acetabulum). In addition, the tibia and tarsals tended to be dorsoventrally flattened and bowed.

Associated with the development of the fully erect bipedal gait were important modifications in the lower limb elements -- the metatarsals and feet. In the sprawling reptiles, the pose was *plantigrade*: the metatarsals served as proximal foot elements -- the 'heel' -- which helped distribute body weight over the substrate. But in shifting to an upright gait, the thecodonts and dinosaurs adopted a *digitigrade* pose: the metatarsals were raised off the ground and converted into distal leg elements and the foot was essentially reduced to the digits alone. In thecodonts, the foot was pentadactyl; in dinosaurs, tridactyl.

It is generally agreed that the fully erect gait is the absolute diagnostic feature which sets dinosaurs apart from all other reptiles, including thecodonts (Charig, 1972). And though obligatory bipedality and the digitigrade pose were inherited from the thecodonts, they nevertheless developed in tandem with the fully erect gait. From a functional point-of-view, if not a cladistic one, bipedality, the digitigrade pose, and the fully erect were interrelated and coequal adaptations.

DINOSAUR LOCOMOTION

According to Bakker (1971, 1986), dinosaurs ran in a bird-like, or mammal-like, fashion, with alternating leg swings and footfalls. Because such a gait presumably requires a high aerobic exercise metabolism, Bakker (1971) has argued that dinosaurs must have possessed an advanced endothermic physiology, comparable to that of modern birds and mammals. This link between a high speed running gait, on the one hand, and physiology, on the other, is central to Bakker's thesis that dinosaurs were "warm-blooded." But the more fundamental question remains: did dinosaurs run? The dinosaurs' long limbs certainly indicate a capacity for high speed locomotion which, at the very least, undermines traditional ideas about dinosaur sluggishness. But they do not necessarily imply high *running* speeds.

Speed is the product of stride length times stride rate. For a running animal, stride length is a direct function of leg length. Hence, in order to increase its speed, a running animal must increase its stride rate, *i.e.* the rate at which it swings it's legs fore-and-aft (Alexander, 1982). Running, however, is inherently unstable. Each step taken by a running animal causes a lateral shift in the center-of-mass and torques the body, causing it to rotate slightly with each step (McMahon, 1984). Accordingly, a high speed running animal not only requires rapid fore-and-aft leg motion, it must also be able to shift its feet laterally -- to the left and right -- in order maintain stability, especially when moving over irregular terrain (Hotton 1980; McMahon, 1984).

In modern cursorial mammals, the femoral head articulates with the pelvis in a flexible ball-and-socket configuration. This allows considerable freedom of leg movement and permits lateral adjustments of footfalls. According to Nicholas Hotton (1980) "Mammals have capitalized on the capability of the ball-joint for quick adjustments of footfall, to evolve the fast cursorial locomotion of horses and camels, not to mention the acrobatics of dik-diks and mountain goats." But dinosaurs did not possess a ball-and-socket hip structure. In dinosaurs, the femoral head was cylindrical and fit snugly into a deep hip socket (acetabulum) with the legs held rigidly in a parasaggital plane of travel. Such a hip configuration would have prevented lateral adjustments of footfalls; and *"[w]ithout comparable flexibility of the hip articulation, dinosaurs could not have attained comparable cursoriality.* Small dinosaurs may have been disproportionately more agile than large ones, if instability of the hip imposed less rigid constraints on animals of lighter weight, but *the structure of the dinosaur hip joint would have precluded the speed and flexibility of mammals.* [Emphasis added.]"

Hotton's analysis contradicts Bakker's contention that dinosaurs were high speed *runners* and thus undermines one of Bakker's principal arguments in favor of dinosaur endothermy. But Hotton's alternative -- that dinosaurs were limited to a leisurely walking gait -- is also difficult to accept given the dinosaurs' highly specialized lower limb elements. Why would a walking animal need the flexibility provided by the mesotarsal joint? Why would a walking animal require clawed tridactyl feet? Claws provide traction, but traction is superfluous to a walking animal. And why would walking animals need dorsoventrally bowed limbs, structures "designed" to withstand the stresses generated by high speed locomotion. As Bakker has argued, all of these features are suggestive of high speed running. But as Hotton has demonstrated, dinosaur hip structure rendered high speed running impossible. We are thus left with a paradox: dinosaurs had the lower limb elements of a runner but the upper limb elements of a walker. Their long flexible limbs should have enabled them to run with great speed; yet their rigid hip joint precluded them from doing so. Clearly, dinosaurs were 'designed' for some other form of locomotion-- a gait faster than a walk, but more stable than a run. And in bipeds, the only plausible alternative to walking and running is hopping.

At first glance, hopping would seem even less stable than running. But, in fact, the opposite is true: hopping is *more* stable. A running biped pushes off the ground with one foot (power phase), is momentarily propelled forward inertially when both feet are off the ground (suspended phase), and lands on the opposite foot (recovery phase). As discussed above, the alternating footfalls of a running gait causes lateral displacements of the center-of-mass and generates a destabilizing torque; these disparate forces require compensatory adaptations (e.g. ball-and-socket hip, flexible pelvis, etc.) to ensure dynamic stability. By contrast, a hopping biped pushes off the ground with *both* feet simultaneously, and lands on both feet upon completion of the suspended phase. The force vector generated by the two legs of a hopping biped is directed downward and to the rear (launching the animal upward and forward) with little if any lateral deviation. No torque is generated. Hence, a bipedal hopping gait does not suffer from the dynamic instability inherent in an alternating running gait

With this in mind, let us take a second look at dinosaur limb architecture. The long, multijointed, dorsoventrally bowed hind limbs were well suited for both running and hopping: they assured a long stride length and were strong enough to withstand the stresses generated by high speed locomotion. Stride *rate*, however, would have been inhibited by the dinosaur's large clawed feet. Clawed feet enhance traction, but they also increase a limb's moment of inertia and thus dampen stride rate. This impairs a running animal, for whom a high stride rate is critical, but not an animal that hops. Despite its large feet (and correspondingly slow stride rate), a hopping animal has plenty of time to swing its legs forward during the prolonged suspended phase when both feet are off the ground (Emerson, 1985).

The inherent instability of an alternating (running) gait requires a capacity for lateral adjustment of footfalls, a capacity which dinosaurs lacked. For a hopping animal, however, a capacity for lateral adjustments is not only is unnecessary, it is downright undesirable. Any deviation in leg motion from a purely fore-and-aft direction will create a destabilizing torque and impair a hopping animal's ability to land squarely on both feet upon completion of the suspended phase (McMahon, 1984). Hence, for a well-adapted hopping biped, leg motion should ideally be constrained to the parasagittal plane. And this is precisely the way dinosaur hips and limbs were designed.

INCIPIENT BIPEDALITY

The ornithosuchian thecodonts were the first incipient bipeds. In all likelihood, the initial shift to a bipedal gait may have had nothing to do with hopping. Rather, it may have begun innocuously as a transient biomechanical consequence of acceleration in a *quadrupedal* gait. When a quadruped accelerates, the turning couple generated by the limbs against the body tends to rotate the body about the hip and momentarily lift the anterior limbs off the ground (Gray, 1968). This transient effect is quite natural and commonly occurs in many otherwise quadrupedal animals, such as the quarterhorse rearing up as it bolts from the starting block, the small crocodile lunging after prey on its two hind limbs, or the lizard *Basiliscus basiliscus* scurrying across the Outback. It is the biological analogue of the motorcyclist performing a "wheelie" as his bike accelerates.

The tendency of an animal to rear up on its hind legs is magnified if the center-of-mass is located near the hips (Gray, 1968), as is the case in crocodiles, lizards, and thecodonts. All thecodonts above the proterosuchian grade possessed long, massive tails and disproportionately long hind limbs. The thecodonts' long tail and hind limbs are typically cited as primitive adaptations for swimming associated with the presumed aquatic lifestyle of their riparian ancestors (Romer, 1966). Whether this is true or not, the thecodonts' long hind limbs and tail were certainly well-suited for bipedal locomotion.

Finally, incipient bipedality, and hopping in particular, may have been facilitated by a prior shift from a quadrupedal *trotting* gait to a quadrupedal *gallop*. In a quadrupedal gallop, the leg swings and footfalls are slightly out-of-phase (Hildebrand, 1985); there is no bipedal equivalent, except perhaps "skipping". Nevertheless, leg motion in a gallop is much more closely synchronized than it is in the alternating trotting gait.

Perhaps, then, the early ornithosuchians began as bounding or galloping quadrupeds. How and why this change in gait may have occurred is obscure. It is generally assumed that energetic factors (*i.e.* minimal energy expenditure) determines gait selection (Alexander, 1982). The essential point, however, is that such a shift is not unreasonable: and, indeed, crocodiles are known to gallop, but only under the most unusual (or contrived) circumstances (Paul, 1988).

These three factors -- incipient bipedality resulting from the transient biomechanical forces generated during acceleration, long hind limbs and tail, and the synchronized leg movements of a bounding or galloping quadrupedal gait -- may have been the necessary prerequisites for the shift to obligatory bipedality. But were they sufficient? Modern crocodiles also have long hind limbs and tails; they occasionally break into a bipedal gait when accelerating; and they are capable of galloping. Yet crocodiles are not bipeds.

Therefore, we must conclude that these various factors alone were not sufficient to cause the shift to obligatory bipedal hopping. Perhaps, then, the final, and most crucial, step toward the acquisition a fully bipedal gait involved a shift in locomotive behavior. Ideally, this change in behavior would not only have enabled thecodonts to move about on two legs, it would have *required* them to do so.

SELECTION OF THE BIPEDAL HOPPING GAIT

Gait selection in tetrapods is based in large measure on economical factors, *i.e.* the highest possible speed at the lowest possible energetic cost (Alexander, 1982). Walking, for example, is a ballistic gait in which the potential energy of height (acquired as the animal's body is raised during the first half of each step) is converted into the kinetic energy of velocity (as the animal "falls" forward during the second half). Walking is very economical because the metabolic cost of walking is practically nil: walking is powered almost exclusively by gravitational potential energy (McMahon, 1984).

The shift from walking to a running or trotting gait occurs at that speed at which ballistic walking gait is no longer efficient. In a running gait, gravitational potential energy is effectively lost; energy is drawn from metabolic sources (anaerobic for short sprints, aerobic for sustained running), augmented by elastic energy stored in the muscles and tendons (Hildebrand, 1985). Quadrupeds shift from a walk to a trot at medium speeds and, at high speeds (*i.e.* above a critical speed threshold) break into a gallop. Galloping is marginally more efficient than trotting at high speeds, but it nevertheless is very expensive because it, too, relies on metabolic input.

The situation, however, is quite different with respect to bipeds. In order to achieve maximum speed, bipeds shift from a running gait to a hopping gait (Emerson, 1985). But in contrast to galloping, with its high metabolic cost, the metabolic cost of bipedal hopping actually *declines* with increasing speed. Hopping is not only more efficient than galloping, it is less expensive as well. This fact is amply demonstrated in studies of kangaroo locomotion (Dawson, 1977; Alexander, 1988).

A hopping kangaroo relies almost exclusively on elastic energy stored in large tendons anchored in the tail. The gravitational potential energy acquired at the height of each jump is converted upon impact into elastic energy stored in tendons and is then converted back into kinetic energy to propel the animal upward and forward in its next hop. In other words, a kangaroo essentially bounces, a gait McMahon (1984) likens to a spring-torsion system. Because of its reliance on elastic storage and rebound, the metabolic cost of hopping is relatively small.

If the analogy with kangaroos is valid, then thecodonts may have shifted to a bipedal hopping gait because it proved to be the most economical high speed gait available. To the extent that such a gait was beneficial (and if it conserved energy, it *was* beneficial), bipedal hopping behavior would have been reinforced and perfected by natural selection. Henceforth, the evolutionary path to an obligatory bipedal hopping gait became practically inevitable, as were all of the related anatomical changes, including the acquisition of the fully erect gait.

The notion that a behavior shift engendered structural modifications may, at first glance, smack of the discredited Lamarckian view that the use of an organ contributes to its improvement. But in fact, it is not Lamarckianism, but orthodox Darwinism, and it is well described by Erwin Schrodinger (1969): "A new character may easily arouse the organism in relation to its environment to an activity that tends to increase the usefulness of the character and hence the 'grip' of selection on it. By possessing a new or changed character, the individual... *may be caused to change its behavior* toward its environment, all this in a fashion so as to strongly reinforce the usefulness of the new character and thus speed up its further selective improvement in the same direction." [Emphasis added.]

Having been 'preadapted' for incipient bipedality, the thecodonts 'discovered' hopping to be a very successful form of locomotion. Their long hind limbs and tail, originally adapted perhaps for swimming, were *exapted* (Gould and Vrba, 1982) in the service of bipedal hopping. The evolutionary success of hopping would have created selection pressures leading to structural modifications in the feet, legs and hip which reinforced and fixed bipedal hopping behavior in the thecodont-dinosaur lineage. The ornithosuchid thecodonts may have begun as habitual bipedal runners, but obligatory bipedality became fixed in their descendants only *after* they had already shifted to a hopping gait.

In lineages that adopted a bipedal hopping gait, natural selection would have induced structural changes that optimized dynamic stability. A well-adapted hopping biped will 'bounce' up and down, not unlike a pogo stick rider, with no lateral deviations. Moving forward requires simply that the hopping animal (or pogo stick rider) lean forward, with the force vector directed to the rear per Newton's Second Law. Whereas a running animal can adjust its footfalls to accommodate lateral shifts in the center-of-mass, a hopping animal (like a pogo-stick rider) cannot: it must be *perfectly* balanced at all times, and *especially* during take-offs and landings. Body mass must be centered directly above the hind legs with little if any margin for error. This need for exquisite balance would exert selection pressures that would tend to align the center-of-mass directly above the hips. Footfalls must be precisely synchronized, ensuring that the animal applies equal force through both legs at the beginning of the powered phase, and also that the animal land squarely on both feet upon completion of the suspended phase, all in accordance with Newtonian mechanics.

Successful bipedal hopping requires exquisite balance during *all* phases of locomotion, from takeoff to landing. Once this problem is solved, a well-adapted hopping biped would have no trouble at all maintaining a stable bipedal pose even when it was not moving at all! Put another way, by fulfilling the needs of *dynamic* stability, Natural Selection would, as a matter of course, also solve the problem of *static* stability.

Thus, bipedal hopping offers a simple and straightforward solution to the mystery of obligatory bipedality. Obligatory bipedality was the logical consequence of a bipedal hopping gait. Hopping also explains why dinosaur limb motion was restricted to the parasaggital plane and why dinosaurs were equipped with a rigid cylindrical hip structure. The dinosaurs' long flexible limbs provided maximum power; their hingelike hip-socket ensured that the leg thrust was directed vertically downward and to the rear with no lateral deviations. Such a gait would also dispense with the purported need for stepped-up metabolic rates. Bipedal hopping would have enabled dinosaurs to move quickly and effortlessly; to cover great distances with a minimal expenditure of energy.

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