



LIMB DESIGN, FUNCTION AND RUNNING PERFORMANCE IN OSTRICH-MIMICS AND TYRANNOSAURS

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ABSTRACT: Examination of the limb morphology of small ornithomimids and large tyrannosaurids shows that they remained remarkably constant in design regardless of size. The changes that were present were consistent with maintaining limb strength and function constant with size. It is concluded that ornithomimid and tyrannosaurid legs functioned in a similar manner, and always exhibit the features normally associated with a fast running gait. This is in contrast to modern animals, in which elephants as gigantic as large tyrannosaurids have limbs that are modified for a slow walking gait.

INTRODUCTION

Because they had long, gracile, bird-like legs, it has long been accepted that the smaller predatory dinosaurs were swift runners (OSBORN [& GREGORY], 1916; COLBERT, 1961; RUSSELL, 1972; COOMBS, 1978; THULBORN, 1982; PAUL, 1988; HOLTZ, 1994). Much more controversial has been the locomotory abilities of their giant relatives, which have been restored as no faster than elephants (LAMBE, 1917; HALSTEAD & HALSTEAD, 1981; THULBORN, 1982; BARSBOLD, 1983), able to run at only modest speeds (COOMBS, 1978; MOLNAR & FARLOW, 1990; HORNER & LESSEM, 1993; FARLOW, SMITH & ROBINSON, 1995), or about as swift as their smaller relatives (BAKKER, 1986; PAUL, 1987, 1988; HOLTZ, 1994). The first two conclusions are based in part upon arguments that scaling effects force giant animals to have straighter jointed limbs ill suited for fast running (BIEWENER, 1989a, 1989b, 1990; BERTRAM & BIEWENER, 1990; HORNER & LESSEM, 1993; FARLOW, SMITH & ROBINSON, 1995). The ostrich-mimic ornithomimids and giant tyrannosaurids offer an unusual opportunity to study how closely related animals of similar form adjusted leg design over a size range from a few hundred kilograms to many tonnes (Fig. 1).

It is presumed in this study that animals are machines in which function and performance follows form, so that animals designed in a similar manner function and perform in a similar manner. The hypothesis that great size inhibits or prevents running can be supported if it can be shown that extinct adult giants consistently also show the same kind of dramatic skeletal changes associated with the inability

to run observed in elephants. The hypothesis can be challenged if it can be shown that at least some extinct giants retained the skeletal adaptations for running observed in smaller species, and in their own offspring. In turn, the hypothesis that giants can run fast if they retain limbs similar to smaller runners can be challenged if it is shown that the skeleton is too vulnerable to structural failure.

BODY MASSES

Sources for mass data for extinct and extant animals include PAUL (1988, 1997), NOWAK (1991) and MATTHEWS (1994). In birds the specific gravity is ~0.8 (DORST, 1971). The specific gravity of avetheropods is assumed to be 0.85 (PAUL, 1988), due to the probable presence of preavian air-sacs. The latter are indicated by the presence of certain ribcage features and pneumatic vertebrae and ribs (PAUL, 1988; REID, 1996; BRITT, 1997). In addition, the low, anterior position of the preserved liver of *Scipionyx* (just above the anterior most gastralia; SASSO & SIGNORE, 1998) suggests that the lungs were shallow and dorsally placed in the avian manner. Because the same space is empty in the type *Sinosauropteryx* the liver is probably not preserved. The dark material in the posterior half of the thorax probably represents remnants of the digestive tract. Direct examination of the specimen reveals that the hepatic septum indicated by RUBEN *et al.* (1997) is entirely an illusion created by breakage and repair work. There is no soft tissue evidence that theropods had a crocodylian-like pulmonary liver pump that would contradict the presence of large air-sacs.



Fig. 1 - Same scale comparison of body and hindleg skeleton form in a small to gigantic series of modern herbivores and extinct ornithomimids and tyrannosaurids. Black bones on white profile from top down: antelope, 75 kg; horse, 500 kg; rhino, 1400 kg; elephant, 2500 kg; Ostrich, 100 kg. Horse and elephants after MUYBRIDGE (1957). White bones on black profile from bottom up: juvenile *Gallimimus* ZPAL MgD-1/94, 27 kg; *Struthiomimus* AMNH 5339, 153 kg; juvenile *Albertosaurus* AMNH 5664, 700 kg; *Albertosaurus* AMNH 5458, 2500 kg; *Tyrannosaurus* CM 9380, 5700 kg. Scale bar equals 1 m. Note the consistency versus the lessening of limb joint flexion with increasing size in theropods versus mammals respectively, and the decreasing excursion arcs associated with increasing size in both groups.

THE CORRELATION BETWEEN LIMB DESIGN, FUNCTION AND STRENGTH, RISK FACTORS, AND SPEED IN LIVING AMNIOTES

In tetrapods, a run is a fast gait achieved via a ballistic suspended phase in which all limbs lose contact with the ground. Among amniotes the ability to run is common, and represents a primitive condition observed in lizards and crocodylians (especially galloping juveniles) which move as fast as 35 to perhaps 42 km.h⁻¹ (SUKHANOV, 1974; WEBB & GANS, 1982; GARLAND, 1984; GRECARD, 1991; SUZUKI & HAMADA, 1992). Among modern land animals top running speed is observed to be highest in animals of a few to few hundred kilograms. There is little firm data on the top speeds of gracile limbed mammals

and giant birds (Fig. 2). A comprehensive survey of African ungulates timed in the field observed speeds of 50 km/h (ALEXANDER, LANGMAN & JAYES, 1977), and ratites (ALEXANDER *et al.*, 1979c), canids (ESTES & GODDARD, 1967) and kangaroos appear capable of similar speeds. Accurately timed riderless horses and greyhounds can sprint over 70 km.h⁻¹, and cheetahs reach 105 km.h⁻¹ (MATTHEWS, 1994; SHARP, 1997). However, some animals in this size range are not fast. The best human sprinters approach only 37 km.h⁻¹ (MATTHEWS, 1994), tortoises cannot walk faster than 3.2 km.h⁻¹ (SUKHANOV, 1974).

Rhinos can gallop (PAUL, 1987; ALEXANDER & POND, 1992; contra THULBORN, 1982). Timing of a

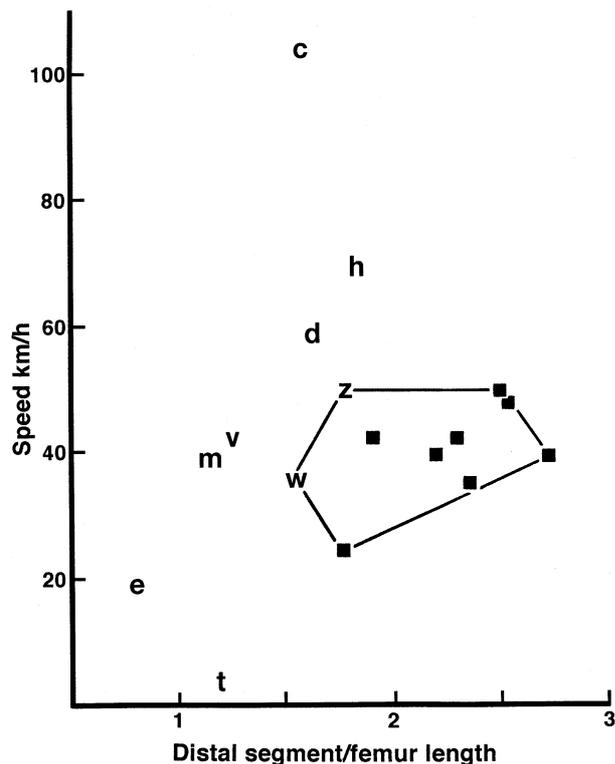


Fig. 2 - Accurately measured running speeds as a function of the relative length of the femur and distal segments (femur, tibia, tarsals, longest metatarsal) in medium sized to gigantic reptiles: t, tortoise; v, ora; and mammals: c, cheetah; d, greyhound; e, Asian elephant; h, race horse; m, human; w, warthog; z, zebra; squares, African artiodactyls. Data sources: SUKHANOV (1974), ALEXANDER, LANGMAN & JAYES (1977, data enclosed by least area polygon), SUZUKI & HAMADA (1992), MATTHEWS (1994), SHARP (1997), main text.

herd of white rhinos (in a video) showed them sustaining a speed of $\sim 30 \text{ km.h}^{-1}$ for a few kilometers (similar to the 27 km.h^{-1} speed observed by ALEXANDER & POND, 1992). The animals were not sprinting at top speed, and burst speed may be $40\text{--}45 \text{ km.h}^{-1}$. Modern rhinos reach 2.5 tonnes; extinct examples with similar running limbs such as *Elasmotherium* weighed perhaps 5 tonnes. The biggest living land animals, elephants, reach 2.5 to 11 tonnes. Limitations of stride length - created by restrictions of excursion arcs combined with limitations of stride frequency - prevent giant animals from walking faster than $\sim 20 \text{ km.h}^{-1}$ (THULBORN, 1982; MCMAHON & BONNER, 1983). Because elephants are unable to run, and must always walk with at least one foot contacting the ground, they should not be able to exceed $\sim 20 \text{ km.h}^{-1}$. A racing large Asian elephant bull (in a video) won with a peak speed of 19 km.h^{-1} (close to the 16 km.h^{-1} speed for *Loxodonta* observed by ALEXANDER *et al.*, 1979b). Higher speeds cited for elephants (GARLAND, 1983; FARLOW,

SMITH & ROBINSON, 1995) were not rigorously measured, and should be considered implausible.

The relationship between leg skeletal adaptations and running performance is in some respects strong, in other regards is inconsistent. Many of the limb features that change with in concert with speed in mammals have been detailed by GREGORY (1912), OSBORN (1936/42), GAMBARYAN (1974) and COOMBS (1978). PAUL (1987, 1988) observed that amniotes that cannot run at all, such as tortoises and elephants, have immobile ankles and short feet that cannot help propel the body into a suspended phase. If you try to run on just the heels of your feet you cannot do so; at most a fast walk is possible with ankle immobility. All animals that can run have flexible ankles that allow the foot propulsion needed to produce a completely ballistic phase.

Nonrunning elephants have straight elbows and knees (Fig. 1, 3B), but the same is true of humans and bears (GAMBARYAN, 1974; ALEXANDER *et al.*, 1979b). Athletes can sprint as fast as 40 km.h^{-1} (MATTHEWS, 1994), and brown bears appear to be even faster (a video showed a grizzly chasing down an elk over an open field). Most running mammals and all birds that can move terrestrially, however, have flexed elbows and/or knees that act as active springs to increase the propulsive effect of the legs (Fig. 1, 3B; CRACRAFT, 1971; GAMBARYAN, 1974; COOMBS, 1978; ALEXANDER *et al.*, 1979a, b, c; MCMAHON & BONNER, 1983; PAUL, 1987, 1988; BIEWENER, 1989a, 1989b, 1990; BERTRAM & BIEWENER, 1990); this includes rhinos (ALEXANDER & POND, 1992). Knee flexure is not correlated with femur curvature because elephants have straight femora, humans curved femora, and flexed kneed birds, ungulates and carnivores all have both straight and curved femora. In general, the greater maximum knee extension is, the more distally rotated are the articular surfaces of the femoral condyles (Fig. 3B). In birds, the knee is fully articulated only as long as the narrow, wedge-like, semirectangular lateral condyle sits in the depression between the tibia and fibula heads (Fig. 3D). Straightening the knee until the lateral condyle is disarticulated from its groove frees the knee to rotate along the long axis of the limb, which leads to catastrophic dislocation of the knee. Ligaments prevent the knee from fully straightening in birds (CRACRAFT, 1971; PAUL, 1987, 1988). PAUL (1987, 1988) noted that the femoral excursion arc in fast running birds is more extensive than sometimes thought (CRACRAFT, 1971), but because avian femora are more anteriorly directed than in ungulates and carnivores bird knees are more flexed.

HOTTON (1980) and FARLOW, SMITH & ROBINSON (1995) suggested that cylindrical hip joints are ill suited for running. The limb joints of fast ground

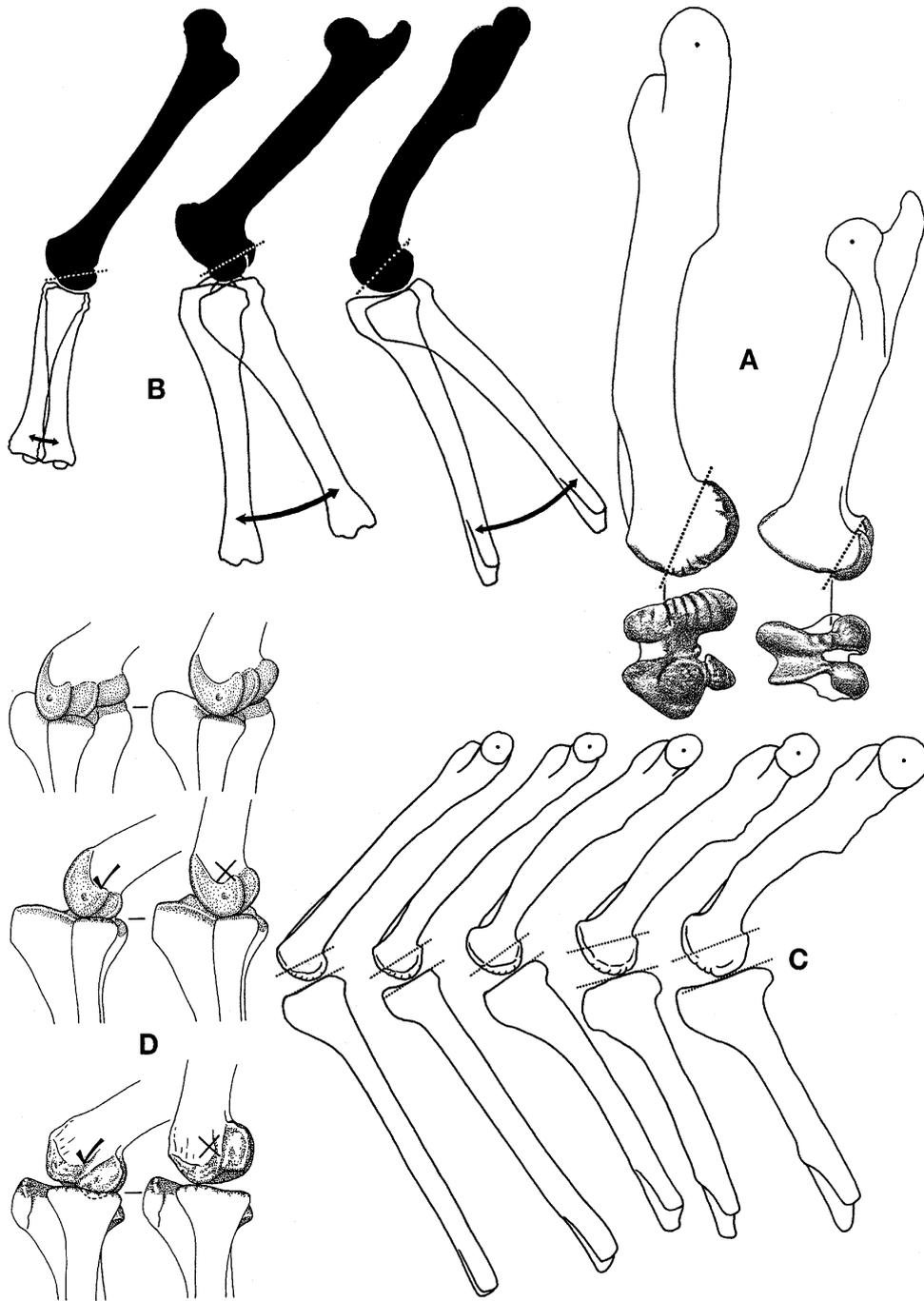


Fig. 3 - Knee flexion in living and extinct tetrapods. All elements are rights, usually in medial view. **A** - Demonstration of how the relative orientation of the femoral condyles can be estimated by drawing a line through the proximal most and distal most extent of the medial condyle for the tibia; the tibial surface is more rugose than the patellar surface in theropods; tyrannosaurid USNM 16745 on left, horse on right. **B** - Series showing how the observed (horse and elephant in MUYBRIDGE, 1957) and restored (PAUL, 1988) orientation of the femoral condyles correlates with maximum and minimum knee flexion during the fastest gait hindlimb propulsion stroke with the foot on the ground; note that the femoral condyles are directed more distally in the straight kneed elephant on the left than in the flexed kneed horse, and that in the flexed kneed forms the long axis of the retracted tibia is almost perpendicular to the line of femoral orientation. **C** - Comparative restored knee flexion in ornithomimids and tyrannosaurids, drawn to same femur length to facilitate comparison, size increases from left to right; *Gallimimus* ZPAL MgD-1/94, 27 kg; *Gallimimus* ZPAL MgD-1/8, 400 kg; juvenile *Tarbosaurus* ZPAL MgD-1/3, 760 kg; large juvenile *Tyrannosaurus* USNM 6183, 2800 kg; *Tyrannosaurus* CM 9380, 5700 kg. **D** - Knee articulation in pigeon in upper four figures, and *Tyrannosaurus* CM 9380 in lower two; in the left row the knees are fully articulated with lateral femoral condyle set in space between fibula and tibia heads; in the right row the knee is straight, so the lateral femoral condyle is no longer properly articulated and the knee is vulnerable to long axial rotational dislocation.

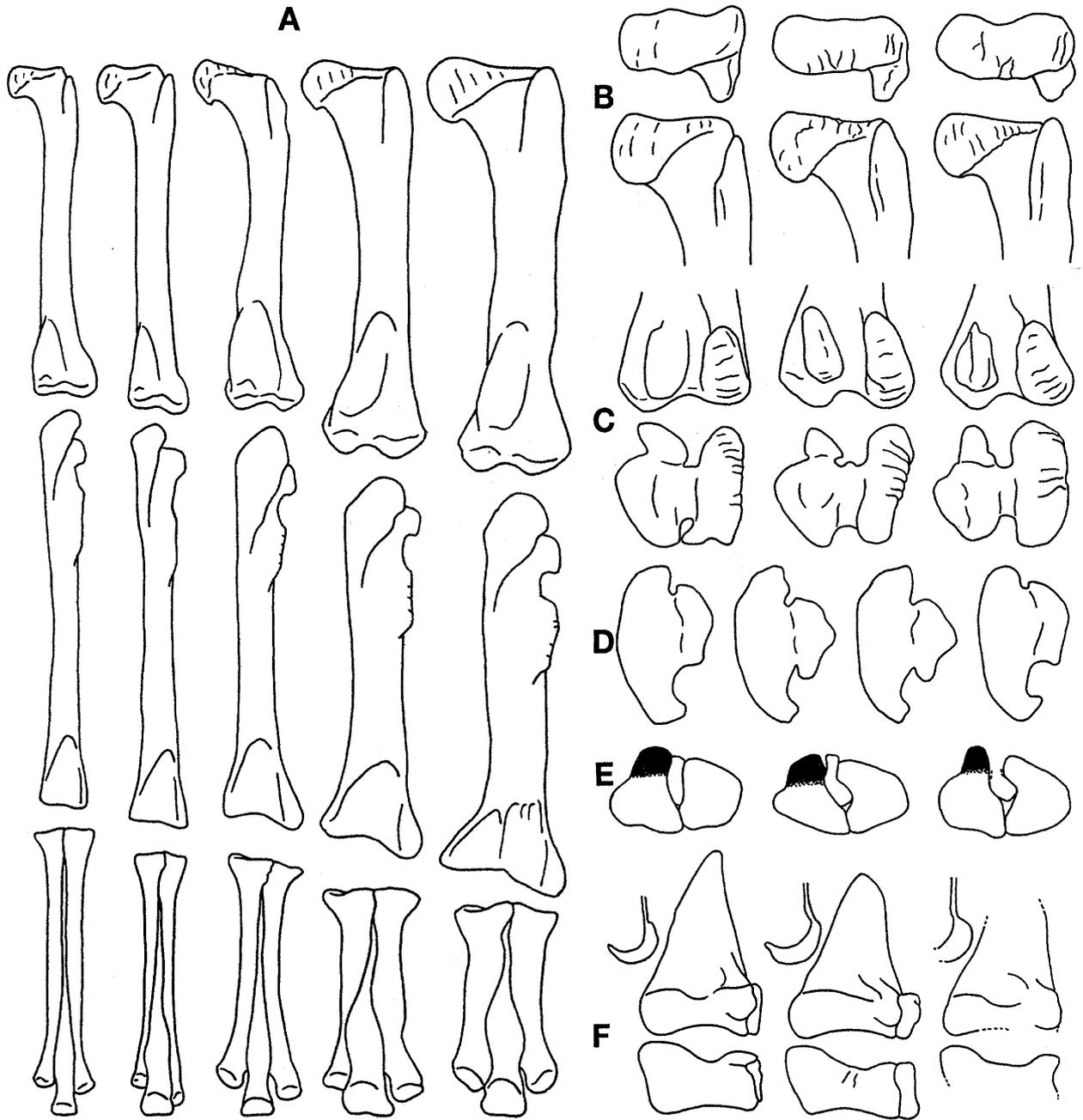


Fig. 4 - **A** - Left ornithomimid and tyrannosaurid femora, tibiae, and primary metatarsi in anterior aspect, drawn to same total length to facilitate comparison of changes in proportions and robustness. Size increases from left to right; juvenile *Gallimimus* GI 100/10, femur length 192 mm, 13 kg; *Struthiomimus* primarily AMNH 5339, 480 mm, 153 kg; juvenile *Tarbosaurus* PIN 552-2, 640 mm; 575 kg; subadult *Tarbosaurus* PIN 551-3, 970 mm, 2100 kg; *Tyrannosaurus* CM 9380 with central metatarsal LACM 23844, 1300 mm, 5700 kg. **B-F** - Left hindlimb joint surfaces of ornithomimids and tyrannosaurids, drawn to constant dimensions to facilitate comparison, size increases from left to right. **B** - Femoral head in anterior and proximal views and **C** - femoral condyles in posterior and distal views; juvenile *Gallimimus* ZPAL MgD-1/94, 27 kg; *Albertosaurus* USNM 16745, 2400 kg; *Tyrannosaurus* CM 9380. **D** - Tibia head in proximal view; juvenile *Gallimimus* ZPAL MgD-1/94; juvenile *Tarbosaurus* PIN 552-2; *Tarbosaurus* PIN 555-1, 2100 kg; *Tyrannosaurus* CM 9380. **E** - Metatarsus in proximal view; juvenile *Gallimimus* ZPAL MgD-1/8, 380 kg; *Tarbosaurus* PIN 552-1, 2200 kg; *Tyrannosaurus* CM 9380 with central metatarsal LACM 23844, hypotarsus indicated by black. **F** - Astragalus and calcaneum in anterior, medial and distal views; juvenile *Gallimimus* ZPAL MgD-1/94; *Albertosaurus* NMC 2120, 2500 kg; *Tyrannosaurus* CM 9380. Data sources include OSBORN (1906, 1916), OSMÓLSKA, RONIEWICZ & BARSBOLD (1972), MALEEV (1974).

birds are cylindrical. HOTTON (1980) cited highly cartilagenous limb joints as a barrier to high speeds. The hip joints of birds, including large ratites, are poorly ossified, yet they are able to withstand high speeds when the bird is fully grown but not yet fully mature.

There is a correlation between muscle attachment area and speed among birds and mammals. Fast running cheetah, canids, gazelles and horses have more limb muscle mass relative to total body mass than slower cattle and goats (TAYLOR *et al.*, 1974; HOPPLER *et al.*, 1987). In slow elephants and humans the ilium is not long, and anchors a narrow thigh musculature. Faster running mammals and birds have longer ilia that anchor a broader, more powerful thigh musculature. Birds have large cnemial crests and hypotarsi that anchor a powerful "drumstick" shank musculature (PAUL, 1988).

Figure 2 shows that tetrapods with distal element/femur length (D/F) ratios below 1.0 are slow, but otherwise the correlation between speed and limb proportions is inconsistent (GATSEY, 1991; GARLAND & JANIS, 1993). Speed can be estimated from trackways, using a formula derived by ALEXANDER (1989). However, animals take only a small fraction of their steps at high speeds, so top speeds are rarely recorded.

ALEXANDER's (1989) method for estimating speed potential by calculating limb bone strength appears to be only partly reliable. For example, the strength of the similarly long human femur and tibia are calculated as being equally modest, suggesting a correspondingly modest speed potential in both bones. However, the long tibia of the fast running ostrich is calculated to be only a little stronger than the human tibia, the bird's short femur is estimated to be three times stronger. Taken at face value this would mean that ostrich tibia should easily break at the high speeds that the femur easily withstands; of course this is not true. It appears that the ALEXANDER (1989) formula is overly sensitive to bone length, in that longer bones appear artificially weak compared to otherwise equally strong short bones. There may, therefore, be problems in comparing bipeds to quadrupeds, because the hindlegs of the former are longer than those of quadrupeds of similar mass and locomotory performance (PAUL, 1988). Bone pneumaticity also seems to affect the results, in that thin walled cylinders are larger in overall diameter than thicker walled cylinders of similar strength (GORDON, 1978). Also, the unusually horizontal femoral posture of birds (CRACRAFT, 1971; PAUL, 1987, 1988) probably increases stress loads, and forces the femur to be stronger than expected in similarly athletic animals with more vertical femora (CAMPBELL & MARCUS, 1992). The cross-sectional dimensions of a long bone must not be too damaged

for analysis. The ALEXANDER (1989) method is also dependent upon body mass, in that any percentage difference in body mass applied to the same bone results in the same percentage change in calculated bone strength (FARLOW, 1990). When analyzing fossils, it is best to restore the mass of a series of reasonably complete skeletons of varying size. The bone strength of the larger individuals can then be compared to the smaller examples, and any relative changes with size revealed.

A number of researchers have concluded that modern animals fill the maximum speed potential possible at any given body size, that the fastest animals weigh from a few to a few hundred kilograms, and that animals as big or bigger than elephants must be slow (GAMBARYAN, 1974; COOMBS, 1978; THULBORN, 1982; GARLAND, 1983; BIEWENER, 1989a, 1989b; 1990; FARLOW, SMITH & ROBINSON, 1995). The hypothesis that giant animals must be slow because they are gigantic is potentially circular, and assumes that living giants have evolved to be as fast as they can be. Contrary to the general belief, there are reasons that speed can be expected to remain high in properly built giant runners. The mass specific cost of locomotion decreases with increasing size (FEDAK & SEEHERMAN, 1979; LANGMAN *et al.*, 1995). Scaling theories such as elastic similarity predict, and observation shows, that as size increases stride length increases more rapidly than stride frequency decreases (MCMAHON & BONNER, 1983). This is true even though limb excursion arcs decline with increasing size. As a result the length of the suspended phase needed to run at a given speed decreases, and the gait needed to achieve a certain speed becomes less extreme, with increasing size. Therefore a mouse must gallop to achieve the same speed as a small trotting dog or a fast walking human (but this effect only goes so far, an elephant sized animal can move faster than an elephant only if it uses a suspended phase). In these regards the relative running performance needed to move at a given speed decreases with increasing size. Conversely, if locomotory abilities are kept constant as size increases, then limb robustness and shortness should increase in order to maintain a constant ability to resist stress induced limb failure. This effect is observed in the large ungulates, in which speed remains the same or increases with maturity as the distal limbs become shorter and more robust, and limb excursion arcs decline. Juvenile elephants are no faster than the biggest bulls (video showed that even fast moving juveniles cannot lift all feet off the ground). Significant loss of speed with growth is rare among amniotes, especially the fully terrestrial examples (crocodilian top speeds decrease from galloping juveniles to the more aquatic adults which have much smaller limbs; WEBB & GANS, 1982).

As size increases, there are two ways to keep stress loads on limb elements from rising to intolerable levels as speed stays the same. One is structural, the other is postural. The former centers around making the legs stronger by increasing their diameter/length ratio and/or cortex/bone length ratios, and shortening the legs relative to body mass, as mass increases (MCMAHON, 1975; MCMAHON & BONNER, 1983; PAUL, 1988; GATSEY, 1991). Note that if the cortex/bone length ratios increase with size then relative shaft diameter should not increase as rapidly as predicted by simpler versions of Elastic Similarity in which the cortex/bone length ratio is assumed to remain constant. Femoral shaft diameters scale more in accord with Elastic Similarity in birds (to length^{1.5}; GATSEY, 1991) than in mammals (to length^{2.5}; MCMAHON, 1975). This may be because the walls of highly pneumatic bird femora must remain thin, while those of ungulates are free to thicken in order to help resist bending; neither possibility has been closely examined. Postural changes include decreasing limb flexion and excursion arcs as mass rises (GAMBARYAN, 1974; MCMAHON & BONNER, 1983; BIEWENER, 1989a, 1989b; 1990; BERTRAM & BIEWENER, 1990). BIEWENER (1990) concluded that in mammals under ~300 kg postural changes were primarily responsible for keeping stress levels from increasing, but in large examples allometry was the primary factor. However, the legs of slow elephants are considerably straighter than those of less massive, faster ungulates. In mammals overall, knee flexion goes from very high in shrews to nearly none in elephants, and leg bones are semi-isometric (ALEXANDER *et al.*, 1979a; BIEWENER, 1989a, 1989b; 1990; BERTRAM & BIEWENER, 1990), so it appears that postural changes predominate over structural in this diverse assemblage. Among the more phylogenetically and structurally uniform ungulates limb flexion decreases with size but never disappears, and elastically similar allometry of leg bone dimensions is more important (MCMAHON, 1975).

FARLOW, SMITH & ROBINSON (1995) argued that the risk of falling may be so high that gigantic, long limbed bipeds do not run fast. Farlow and company focused on a rhino as a modern model for a large running animal, but this low slung, stout limbed form's risk of impact damage to body and limb is relatively low. Potentially more informative is the other modern running giant, the bull giraffe. Its ultra-long legs are in danger of interfering with one another and tripping the animal. The legs may be easily broken because they are spindly, yet support a body weighing one to nearly two tonnes carried 2 m above ground level. Even so, adult giraffes regularly gallop ~50 km.h⁻¹. Animals with bodies and heads as heavy and carried as high as those of elephants are at higher risk of crippling or lethal injury if they fall at any

speed than smaller animals (MCMAHON & BONNER, 1983; FARLOW, SMITH & ROBINSON 1995). On the other hand, researchers opinions of what is too dangerous may be overly pessimistic. The risk of death from falling increases sharply with increasing body size, so it may appear overly risky for animals weighing over 50 kg to spend much time in trees. Yet leopards, chimpanzees and orangutans up to 90 kg regularly climb high (NOWAK, 1991).

It is particularly difficult to assess the risk factors associated with the inherently dangerous lifestyle of chasing and attacking large herbivores. In order to thrive a large predator must repeatedly attack and kill similarly large and often well armed animals without experiencing a single injury that is serious enough to kill the hunter either directly, or indirectly via disabling damage that prevents further hunting before starvation ensues. High speed increases the safety from counterattack. The faster a predator is, the more easily it can surprise and confuse its victim, reducing the possibility of counterattack. High speed also minimizes the time spent within the range of the prey's weaponry, and improves its ability to evade counterattacks. The advantages of the fast surprise attack apply even if the prey is slow, the latter can better employ whatever defense they have the more time they have to do it. The requirements to be able to chase down and safely dispatch prey explains why all large land predators are fast runners.

Does the need for speed apply to giant predators? They are especially vulnerable to injury during combat, because the risk of being seriously injured if they are pushed over during close combat is high. The risk of falling while fighting can be minimized by the same high speed hit-and-run tactics that surprise and minimize contact with prey. At the same time, high speed increases a giant's risk of a gravity induced impact injury. On the other hand, the chase is brief in duration, and takes up only a small portion of the many steps taken by a giant that is always at risk of an accidental fall. So the risk of falling while running may be worth the reduction in the severe risks of falling or being wounded during combat. Minimizing risk involves a balance between that incurred during the chase versus contact with the prey, and it is this balance that must be assessed when examining extinct predators. This is difficult to do because a scarcity of data on how frequently large running mammals and birds fall and injure themselves, plus an absence of data on the combat injury rate of slow predators, inhibits assessing the balance in a rigorous quantitative manner. So much so that the utility of this method of estimating locomotory performance is at best limited. Because there are no slow predators extant, it may never be possible to rectify this problem.

Running performance, especially endurance, is determined not only by limb anatomy, but by respirocirculatory capacity. Reptile heart-lung capacity is too low to sustain high speeds, which are powered almost entirely anaerobically (BENNETT, 1991; PAUL & LEAHY, 1994). The higher respirocirculatory capacity needed for oxygen based endurance running can be indicated by the presence of air-sac lung ventilation, very large limb muscle volume, and high cruising speeds (PAUL & LEAHY, 1994). However, ground birds and mammals include both sprinters and endurance runners, and there is no reliable way to distinguish between these types via the skeletal anatomy of the thorax.

LIMB DESIGN, FUNCTION AND STRENGTH, AND RISK FACTORS IN ORNITHOMIMIDS AND TYRANNOSAURIDS

This study focuses on the classic advanced ornithomimids and advanced tyrannosaurids for which complete skeletons are known. Ornithomimids for which complete skeletons are known weighed from about 100 kg to about half a tonne (PAUL, 1988). Small tyrannosaurid specimens probably represent juveniles, known adult specimens weighed from about 2 to 8 tonnes, larger individuals are probable (PAUL, 1988, 1997; HOLTZ, 1991). The two groups are sophisticated, bird-like avetheropods that lived in the Late Cretaceous. Their heads, necks and arms are very dissimilar. The close similarity of their compact trunks, moderately long tails, large pelvises, and elongated, laterally compressed legs with the distinctive arctometatarsalian pes has long been recognized (OSBORN, 1916; PAUL, 1988; HOLTZ, 1994). The degree to which the similarities represent shared genetic heritage versus parallelism due to similarity in locomotory abilities remains uncertain due to a current absence of transitional forms.

Because tyrannosaurids cover a size range that at one end is associated with high speeds, and at the other with slow speeds, they pose an interesting challenge to the size-speed patterns observed in modern tetrapods. On one hand, if running speed remained persistently high with increasing size, then these dinosaurs did not conform to the speed limitations supposedly associated with great bulk. On the other hand, if speed did decline with size in tyrannosaurids, then it did so in violation of the seeming ontogenetic constancy of speed in animals. We can begin to tell which principle was violated by examining how limb structure did or did not change with size in tyrannosaurids and their smaller ornithomimids relatives.

Ornithomimid and tyrannosaurid pelvic and limb elements were so similar that it is sometimes somewhat difficult to distinguish isolated or partial bones

when they are from individuals under half a tonne; a detailed character analysis may be required to segregate them. It is equally important that aside from the increase in over all size and robustness, leg bone and joint morphology remained remarkably constant all the way up the mass scale to the largest *Tyrannosaurus* (Fig. 1, 3C, 4). The uniformity applies to shape of the ilium, the design of the hip, knee and ankle joints (Fig. 4B-F), the structure of the metatarsus, and to the central three digits. The most significant differences were the more reduced distal fibula and calcaneum, and absence of the hallux in ornithomimids compared to tyrannosaurids (Fig. 1).

Ornithomimids and tyrannosaurids had typical theropodian, cylindrical, hinge action hip, knee and ankle joints. These were not identical to those of birds, but were very similar and should have offered similar speed potential. Hindlimb joints were larger in theropods than in birds even when the subjects weigh about the same. This may have been an adaptation for retaining cartilagenous joints through life, and into gigantic dimensions.

The astragular condyles were large rollers (probably enlarged by cartilage surfaces as in non-mature birds) that allowed the tarsometatarsus to rotate through an arc of about 150°, from nearly straight to nearly collapsed relative to the tibia-fibula (Fig. 4F). The foot was long in these theropods. Therefore the foot had the excursion arc and length needed to propel the body into a suspended phase in ornithomimids and tyrannosaurids small and gigantic.

GATSEY (1991) claimed that PAUL (1988) restored theropods with subhorizontal femora and believed "that non-avian theropods moved with their knees highly flexed, comparable to modern birds", but this is not fully correct. PAUL (1987; 1988) explained that the theropod femur could not retract much past vertical in theropods because doing so would misarticulate the articular surfaces, and over shorten the ischium based retractors. This means that the knee should have been flexed. However, Paul also restored theropods with a less anteriorly oriented femoral excursion arc than observed in birds (see fig. 4-16 in PAUL, 1988), so the theropod knee should have been correspondingly less flexed than in birds, although the exact amount of difference cannot be determined. Further evidence for knee flexion starts with the observation that the small, wedge shaped lateral femoral condyle was not a load bearing process, but was an articulation guide that had to remain in articulation with the depression between the heads of the fibula and tibia (Fig. 3D). This was possible only when the knee was flexed. Straightening the knee would have resulted in dislocation (PAUL, 1987, 1988), so ligaments should have prevented the knee from straightening.

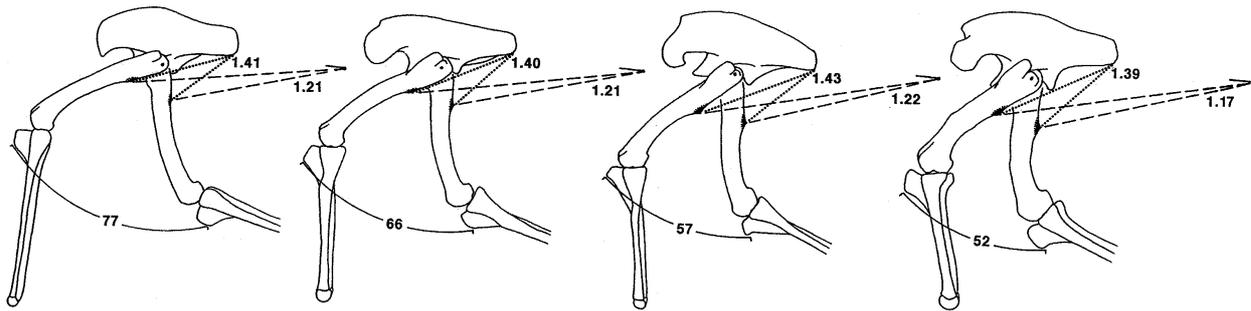


Fig. 5 - A demonstration of how the distal migration of the 4th trochanter (indicated by black) kept the stretch factor (as quantitatively indicated on the figures) of the caudofemoralis brevis (dotted line) and c. longus (dashed line, posteriorly anchored on the 7th caudal) nearly constant as limb excursion arcs (as quantitatively indicated on the figures) declined with increasing size (as per MCMAHON & BONNER, 1983) in ornithomimids and tyrannosaurids. If the trochanter did not migrate distally, then the muscles would be less stretched as dimensions increased. This chart compares relative estimated, not absolute, limb excursion arcs. From left to right; *Struthiomimus* AMNH 5339, 153 kg; juvenile *Albertosaurus* AMNH 5664, 700 kg; *Albertosaurus* AMNH 5458, 2500 kg; *Tyrannosaurus* CM 9380, 5700 kg.

This was as true of adult *Tyrannosaurus* as of small ornithomimids. Because ornithomimid and tyrannosaurid knees were better ossified than other theropods' the approximate orientation of the articular surfaces of the medial femoral condyle can be determined (Fig. 3A-C). Its strong posterior orientation was most compatible with a flexed knee. Orientation of this condyle did not show a consistent change with size in ornithomimids and tyrannosaurids (Fig. 3C), so a decrease in knee flexion was absent or at most modest even at the largest sizes. This is contrary to those that restore giant tyrannosaurids with femora that retract well past vertical, and straight or slightly flexed knees (OSBORN, 1916; NEWMAN, 1970; TARSITANO, 1983; GATSEY, 1991). Note that the shaft of the femur was *more* curved in tyrannosaurids than in ornithomimids, within each group shaft curvature appears to have been constant as size changed (Fig. 1, 4C).

The primary change with size in ornithomimids and tyrannosaurids was in the proportions and ratios of the limb elements. As expected in a set of animals with such consistent limb form and flexion, limb allometry was pronounced. Bone shaft diameter, joint breadth, and cortex thickness all tended to increase relative to bone length as size rises (Fig. 1, 3C, 4A; PAUL, 1988). GATSEY (1991) suggested that the failure of ornithomimid and tyrannosaurid femoral shaft diameters to scale as predicted by Elastic Similarity suggests that limb flexion decreased with size, but this neglects the compensating increase in cortex thickness. The scaling of shaft dimensions in ornithomimids and tyrannosaurids to length²⁸ was ungulate-like. This may reflect the absence of pneumatic femoral cavities that prevented changes in wall thickness, rather than a change of limb posture. A more extensive analysis of external and internal

long bone dimensions is needed. Distal segment lengths tended to decrease relative to the femur; the changes were modest (Fig. 1, 3C, 4A). In juvenile and adult ornithomimids D/F ratios ranged from 1.8 to 2.18. Among tyrannosaurids the ratio was 1.72-1.8 in 400 kg juveniles to 1.45-1.53 at over 2 tonnes in albertosaurs and tarbosaurids, and was 1.4-1.5 in adult *Tyrannosaurus* (the latter values are about 80% higher than observed in elephants). No complete juvenile *Tyrannosaurus* limb is yet known, but fragmentary elements (MOLNAR, 1980) are gracile.

Because ornithomimids were gracile limbed cursors, and because the limb form of increasingly gigantic tyrannosaurids were an allometric continuation of the former, adult tyrannosaurids were effectively as "gracile" limbed and potentially as cursorial as ornithomimids and juvenile tyrannosaurids, and about as gracile and as cursorial as such enormous animals could have been.

Another progressive size related change was the distal migration of the 4th trochanter as mass rose. This distal shift served to keep the stretch ratios of the caudofemoralis muscles constant as over all limb excursion arcs declined with increasing size (Fig. 3C, 5). This decrease should have hindered speed no more than it does in large ungulates.

The ilial plate that the thigh muscles anchored upon was similarly large - and larger than in most other theropods - in ornithomimids and tyrannosaurids of all sizes. The shank musculature also appears to have been powerful. Proximally, the cnemial crest was well developed over the entire size range. Distally, it has not been widely recognized that there was a true hypotarsus on metatarsal II in theropods; it was well developed in or-

nithomimids and tyrannosaurids regardless of size (Fig. 4E).

Very long stride/foot length trackways prove that theropods up to 700 kg could run (FARLOW, 1981; THULBORN & WADE, 1984). The highest speed estimated so far from trackways is $\sim 40 \text{ km}\cdot\text{h}^{-1}$, this does not necessarily reflect the maximum performance. The large limb musculature, extremely long, gracile legs, and strongly laterally compressed shank (in which the distal fibula is very slender) and foot (in which the central metatarsal is very slender distally) of ornithomimids suggest they were among the fastest dinosaurs (OSBORN, 1916; RUSSELL, 1972; COOMBS, 1978; THULBORN, 1982; PAUL, 1988; HOLTZ, 1994). Ornithomimids appear to have broadly matched cursorial birds and mammals, and were better designed for running than humans. HOTTON's (1980) suggestion that their long limbs were primarily adapted for walking long distances is a minority opinion. Ostrich-mimic top speeds may have been in the range of modern ratites. Juvenile tyrannosaurids of similar size appear to be almost as well adapted for fast running. Did adult tyrannosaurids retain a similar or lesser locomotory capacity? A partial trackway (LOCKLEY & HUNT, 1995) suggests that an adult *Tyrannosaurus* moved at least at a fast walk of $16 \text{ km}\cdot\text{h}^{-1}$. It is improbable that this one example recorded the dinosaur's longest stride and highest speed.

The retention of a long mobile foot in the biggest tyrannosaurs means they retained the critical adaptation for a ballistic running gait unattainable by elephants. Because the area available for leg muscle attachment is comparable to that of large ground birds (Fig. 1), the dinosaurs' limb musculature should have been large enough to power a fast gait. The extreme anatomical changes associated with the inability to run that are present in elephants are entirely absent in giant tyrannosaurs (the many adaptations expected in a slow *Tyrannosaurus* are illustrated in fig. 6-5 in PAUL [1988]), so their adaptations for limb strength are not of the kind associated with slow speed gigantism (contra MOLNAR & FARLOW, 1990). Instead, they are of the type associated with powering high speeds. The assertion by HORNER & LESSEM (1993) that the distal limb segments of giant tyrannosaurids were too short for fast running is false. The 0.84-0.97 tibia/femur ratios of 2 to 8 tonnes tyrannosaurids are comparable to the 0.88 value of much smaller race horses, are well above the 0.65 ratio of galloping rhinos, and far exceed the 0.55 ratio of slow elephants. Distal segment/femur length ratios are lower in ornithomimids and tyrannosaurids than in fast birds and kangaroos, but this is probably a represents differences in limb function (PAUL, 1988; GATSEY, 1991) rather

than speed in bipeds as suggested by COOMBS (1978).

Further, ornithomimids and tyrannosaurids exhibit a remarkable uniformity of leg form over a broad size range from little larger than humans to elephantine. The uniformity of form exceeds that observed in fast ungulates over their broadly similar size multiplication, and occurs into a much larger size zone. Nor is there any evidence for a decrease in limb flexion as size increases in giant tyrannosaurids, indeed the evidence favors a consistently high degree of knee flexion. The changes in limb robustness, proportions and excursion arcs observed in growing tyrannosaurids are very similar to the modest changes observed in growing ungulates that retain a constant speed performance. Therefore, there is no evidence of the speed decline with maturity postulated for tyrannosaurids by HORNER & LESSEM (1993) and FARLOW, SMITH & ROBINSON (1995). It is concluded that the limb configuration and posture of giant tyrannosaurids in no way indicates they could not run, and that there is no evidence that speed declined with increasing size in ornithomimids and tyrannosaurids. To put it another way, large tyrannosaurid limbs were constructed and proportioned in the manner expected if they retained high speeds.

If the last conclusion is correct, then tyrannosaurids violated the principle of slow speeds in land giants. If speed declined with size in tyrannosaurids, then it occurred without major changes in limb morphology and function, and did so in violation of the ontogenetic constancy of speed in animals whose limbs undergo similarly modest proportional changes with growth. In order to show that the latter happened requires enough positive evidence to counter the morphological evidence that *Tyrannosaurus* was fast.

Were the giant tyrannosaur's legs strong enough or too weak to run on? ALEXANDER (1989) and FARLOW, SMITH & ROBINSON (1995) calculated that the femur of *Tyrannosaurus* was too slender and weak to allow a fast gait, although a slow run that was faster than an elephantine amble was not ruled out. However, theropods had longer, more solid walled, vertical femora than ratites of equal size, and this may explain why ornithomimid femora are apparently incorrectly calculated to be much weaker than those of ratites according to the ALEXANDER (1989) formula (FARLOW, 1990). The specimen examined by FARLOW, SMITH & ROBINSON (1995), MOR 555 appears to have been a little smaller than the type and 5027, and the lower 5400 kg mass estimate used by FARLOW, SMITH & ROBINSON is probably close to correct. However, the femur of MOR 555 is fractured and imploded to the point that bone shards partly fill the originally hollow center (Fig. 6). The bone's original cross-sectional dimensions cannot



Fig. 6 - Same scale comparison of femoral shaft cross-sections of *Tyrannosaurus*. Left, uncrushed CM 9380 (after OSBORN, 1906), 5700 kg. Right, crushed MOR 555 (traced from fig. 2 in FARLOW, SMITH & ROBINSON, 1995), 5400 kg. Scale bar equals 50 mm.

be reliably restored, nor its strength. ALEXANDER (1989) estimated that the type *Tyrannosaurus* femur was too weak for a fast gait. Estimated body mass was 8000 kg, but this was based on an inaccurate toy model. A technical restoration of the type specimen cannot distinguish its mass from the similar sized and more complete AMNH 5207, which is estimated via a careful skeletal restoration and model to mass 5700 kg (PAUL, 1988, 1997). The type femur is preserved intact, and is therefore more robust than that of MOR 555 (Fig. 6). At 5700 kg, femur strength of the type is similar to that of an ornithomimid (FARLOW, 1990). This suggests that giant tyrannosaur limb bones were as well able to withstand running forces as those of their smaller relatives. At this time a complete *Tyrannosaurus* skeleton with an intact femur is not available. To better challenge or confirm the strength factor evidence for fast tyrannosaurs will require analysis of series of complete ornithomimid and tyrannosaurid skeletons with uncrushed femora.

FARLOW, SMITH & ROBINSON (1995) calculated that the effects of a high speed impact would kill a fast running *Tyrannosaurus*, and that the predator should have avoided the risk of falling by not running at speeds higher than 36 to perhaps 54 km.h⁻¹. However, gigantic bipedal theropods such as *Tyrannosaurus* probably put their life at a unique level of risk of death from tripping with every step they took. Never running at high speeds may not have reduced the overall risk profile. If *Tyrannosaurus* could only walk or run slowly, it would be less able to surprise and overwhelm its prey with a sudden, swift charge. Reduced would have been its ability to avoid the horns of *Triceratops*, a club wielding *Ankylosaurus*, or the kick of an *Edmontosaurus*. A *Tyrannosaurus* able to move no faster than an elephant or even a human would have been a rather poor hunter, even if it ambushed prey over a short distance (pure scavenging is not a viable lifestyle for these large predators: PAUL, 1988; MOLNAR & FARLOW, 1990;

FARLOW, 1990). It may have been to the advantage of *Tyrannosaurus* to risk injury during a high speed chase and reduce possibly greater combat related risks by delivering a high speed hit-and-run attack that surprised and minimized contact with the prey (PAUL, 1988). In this view giant tyrannosaurs were similar to leopards, which accept the risk of accident associated with dragging a heavy carcass into to tree because it eliminates the dangers associated with carcass stealing lions and hyenas. In tyrannosaurs, frequent losses due to accidents and wounds may have been made up for via a combination of rapid reproduction and growth (PAUL, 1994).

The risk factor hypothesis that *Tyrannosaurus* was slow can be falsified (by the discovery of a high speed trackway), but it may not be verifiable because it may never be possible to determine with sufficient accuracy the various risk factors involved in slow versus high speed predation in giant hunters. Indeed, the opposing conclusions that it was too risky for *Tyrannosaurus* to run fast, and that it was too risky for it not to run fast, are both more in the way of opinions than rigorous quantitative assessments of risk factors. The method appears too weak and untestable to overturn the morphological evidence for higher speeds.

If ornithomimids and tyrannosaurids were as swift as they appear, did they only sprint, or run long distances? The probable presence of air-sacs suggests that the lungs were better ventilated than those of reptiles (PAUL, 1988). The very large ilia suggest that limb muscles were larger than expected in reptiles, and trackways indicate that theropods normally walked at speeds higher than can be sustained by reptiles (PAUL & LEAHY, 1994). These respiratory and locomotory features suggest that the aerobic exercise capacity of ornithomimids and tyrannosaurids exceeded that of reptiles. In this case theropods may have been able to oxygenate extended high speed runs as in large ratites, canids, ungulates. It is also possible that the respiratory systems were more oriented towards cat-like sprints. The long, gracile legs appear to be more similar to those of long distance bird, carnivore and ungulate runners, than to the shorter, heavier limbs characteristic of ambush predators. If so then ornithomimids may have used a combination of speed and endurance to outrun predators, and tyrannosaurids the same combination to catch prey (PAUL, 1988; HOLTZ, 1994). However, the stockier daspletosaurs and giant tyrannosaurs may have been more prone to sprint tactics than the more gracile albertosaurs and ornithomimids.

CONCLUSIONS

Taken together, ornithomimids and tyrannosaurids appear to have done something that no liv-

ing tetrapods do. They maintained remarkably uniform, flexed jointed limbs that appear to have been suited for running at high speeds at sizes up into the elephantine range. The hypothesis that animals must strongly modify limb form in order to become gigantic is falsified. Strongly challenged if not also falsified are the hypotheses that limb flexion and running speed must decrease with gigantic size. Tyrannosaurids appear to have paralleled and exceeded ungulates in emphasized increasing limb strength over changing limb posture as they became gigantic. If so, then maximum speeds of ornithomimids and tyrannosaurids were probably not below 50 km.h^{-1} , may have reached 60 km.h^{-1} , and higher speeds cannot be ruled out.

$50\text{-}60 \text{ km.h}^{-1}$ is similar to the highest *Tyrannosaurus* speed predicted by FARLOW, SMITH & ROBINSON (1995). The 36 km.h^{-1} value they preferred is no higher than that of plantigrade, straight kneed, modestly muscled humans with legs only one quarter as long. Such modest performance would be logical if adult *Tyrannosaurus* had extremely short feet, flexed knees and/or relatively less impressive muscles than smaller tyrannosaurids. Conversely, if the giant dinosaur was as slow as humans it should be expected to exhibit anatomical adaptations appropriate for such speeds. As it is, flexed kneed and digitigrade *Tyrannosaurus* adults were much better designed for running than humans or elephants. It is particularly difficult to explain why the supertheropod retained the very large ilium and cnemial crest suitable for supporting the enormous limb muscles needed to run fast if it was only matching a human pace. Was the tyrant king as slow as Olympians despite its long, cursorial legs? Possibly, but the positive, testable evidence needed to show that adult *Tyrannosaurus* moved more slowly than when young, or compared to smaller relatives, is so far lacking. The results of risk analysis are ambiguous, and may always be so. Bone strength analysis is also ambiguous at this time, and it is not clear that a more comprehensive study would contradict high speeds. A comprehensive scaling study has not been performed, and it too may support high speeds. Better trackway data can only falsify arguments that *Tyrannosaurus* could not catch Carl Lewis.

Are tyrannosaurids the only examples of extinct gigantic runners? The shoulder glenoid of ceratopsid dinosaurs faced more posteriorly, and the distal humeral condyles more anteriorly, than in sauropods, so the humerus should have been more horizontal and the elbow more flexed in the former than in the latter (PAUL, 1987). In ceratopsids, iguanodontids and hadrosaurids a bird-like acetabular antitrochantor suggests the femur was not vertical, and the knee joint had the same configuration indicative

of flexion seen in theropods-birds (PAUL, 1987). The mesotarsal ankle could rotate through a wide arc, and the feet are longer and more laterally compressed than in elephants. Ceratopsid limb elements were strong enough to withstand a running gait (ALEXANDER, 1989). Ceratopsids of 1.5 to 10 plus tonnes were probably able to trot, and may have been able to gallop at rhino-like speeds. Iguanodontids and hadrosaurids of 2 to 20 plus tonnes were probably able to run bipedally, and trot quadrupedally.

The Late Cretaceous appears to have been an era in which an unusually high degree of running capability was present in a number of giants, specifically tyrannosaurids, hadrosaurids and ceratopsids (in comparison, the Late Jurassic sauropod, stegosaur, allosaur fauna was a slower one). The focus of this combination of size and speed may have been western North America, in which all these forms co-existed. This situation suggests that the Late Cretaceous saw a predator-prey race involving size, speed, and in the case of ceratopsids and tyrannosaurids weaponry as well. This is contrary to opinions that the giant herbivores of the time were too slow to require fast predators (HALSTEAD & HALSTEAD, 1981; THULBORN, 1982; HORNER & LESSEM, 1993). The extreme size of the predatory tyrannosaurids may have been made possible by a combination of rapid growth and high rates of reproduction (PAUL, 1994), a combination not present in either living reptiles or mammals. Faced by such large, fast moving and powerful enemies, the ceratopsids and hadrosaurs responded by becoming well armed and/or fast. The high speed of juvenile tyrannosaurids may have influenced the development of high speeds in ornithomimids, which were also under predation pressure from fast aublysodonts, troodonts and dromaeosaurs.

In the Cenozoic titanotheres reached 3 to 5 tonnes. Flexed, rhino-like limbs, and a long mobile foot suggest they were able to trot and gallop (OSBORN, 1929). Larger still were indricotheres of 15 to 20 tonnes (PAUL, 1997). Their legs were very different from those of elephants, and were similar to those of running ungulates. The short humerus allowed the elbow to be flexed and held behind the shoulder joint as in ungulates, rather than the long vertical humerus characteristic of proboscideans. GRANGER & GREGORY (1936) noted that the knee was flexed. The foot was long, and a roller type astragalus allowed the ankle to rotate. These features suggest indricotheres could trot and perhaps gallop in the manner of large work horses. The apparent retention of a running capability in indricotheres does not appear to have been induced by a predator threat, and may reflect retention of a running ancestral condition.

NOTES ADDED IN PROOF

RUBEN *et al.* (1998) noted that the preserved liver of *Scipionyx* is probably as deep as in crocodylians, but a similarly deep liver is present in some birds (DUNCKER, 1979).

HAZLEHURST & RAYNER (1992) observed an average specific gravity of 0.73 in a sample of birds. The average density of the birds was underestimated in that air-sacs are not always fully inflated in a breathing animal, and a 0.85 value remains viable for ornithomimids and tyrannosaurids.

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MUSEUM ABBREVIATIONS

AMNH - American Museum of Natural History, USA; CM - Carnegie Museum of Natural History, USA; LACM - Los Angeles County Museum, USA; MOR - Museum of the Rockies, USA; NMC - National Museums of Canada, Canada; PIN - Palaeontological Institute, Moscow, Russia; USNM - United States National Museum, USA; ZPAL - Palaeozoological Institute, Warsaw, Poland.

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