STRENGTH INDICATOR VALUES OF THEROPOD LONG BONES, WITH COMMENTS ON LIMB PROPORTIONS AND CURSORIAL POTENTIAL

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ABSTRACT: **Body mass and strength indicator values of the three hindlimb long bones have been calculated for a large number of theropod dinosaurs and compared to extant mammals of varying size and locomotory capability. Small to medium sized theropods have strength indicator values comparable to fast-moving ungulates and carnivorans, whereas all large genera have considerably lower strength indicator values, roughly comparable to elephants and hippopotamuses. This suggests that their locomotory potential was reduced compared to the smaller forms. Limb bone ratios of a large number of extant mammals clearly differentiate fast-moving forms, classified from their anatomy as subcursorial or cursorial, from forms capable of less rapid locomotion, classified as graviportal and mediportal. Limb bone ratios for theropods, however, somewhat contradict the above, as all theropods group among subcursorial mammals. Calculations on estimated peak locomotory performance indicates that even large theropods could have been fast moving without having to include a suspended phase in the stride, thus not subjecting their appendicular anatomy to large amounts of stress, due to their very long limbs.**

INTRODUCTION

Theropod dinosaurs were the only undoubtedly carnivorous terrestrial tetrapods for most of the Mesozoic that, at least theoretically, were large and powerful enough to succesfully hunt the great variety of herbivorous dinosaurs. As such their ability to move fast and hunt succesfully would appear self-evident. Most large extant tetrapod hunters are either fast-moving, such as the Carnivora, or use cryptic tactics and ambush hunting for catching prey, such as crocodiles and large snakes. Theropod dinosaurs anatomically resembled the former to a much greater extent and thus it would appear likely that they also displayed a similar capability for running and hunting. The gracile nature of small theropods has never generated much controversy as to their running ability. Substantial controversy has arisen, however, as to the locomotory potential of large theropods. Although some authors have credited the largest theropods with top speeds of around 20 m.s^{-1} (BAKKER, 1986; PAUL, 1988), they have most often been considered too large to have been fast-moving and have usually been credited with a walking gait only (e.g. LAMBE, 1917; NEWMAN, 1970; COLINVAUX, 1978; HALSTEAD & HALSTEAD, 1981; THULBORN, 1982; BARSBOLD, 1983).

However, COOMBS (1978) analyzed a long list of anatomical characters in various tetrapods and found that a number of these had probably developed convergently and were found in all forms capable of fast locomotion. Thus, he concluded that they were a prerequisite for fast locomotion, as displayed by extant subcursorial and cursorial animals, and could be used to identify good running capability in extinct animals. By far most of these characters were present in theropods, even large forms, including hinge-like joints, long limbs, long and slender distal limb elements, greatly reduced fibula, metatarsals interlocking into a single functional unit, pes with median symmetry, loss of outer pedal digits, digitigrade stance and reduced forelimb (bipeds only). Forelimb reduction is most pronounced among large non-avian theropod taxa, whereas dromaeosaurids, oviraptorosaurs, troodontids, and in part, ornithomimids, have quite long forelimbs. The hindlimb is still the largest and strongest, however. Non-avian theropods retained just one non-cursorial trait, a long femur. Unlike birds femoral retraction was a very important part of forwards propulsion in most forms (PAUL, 1988; GATESY, 1990, 1991).

HOLTZ (1994) found that ornithomimids, troodontids, elmisaurids, avimimids and, most importantly,

the large to gigantic tyrannosaurids, possessed an unusual metatarsal structure, which he termed the arctometatarsus, where the third metatarsal is greatly reduced proximally and the three metatarsals interlock tightly. In certain arctometatarsalian forms such as *Elmisaurus* OSMÓLSKA (OSMÓLSKA, 1981) and *Avimimus* KURZANOV (KURZANOV, 1987) the distal tarsals and proximal parts of metatarsals II-IV co-ossify into a tarsometatarsus, a condition reminiscent of certain "alvarezsaurid theropods" (BONAPARTE, 1996), although not *Mononykus* PERLE, NORELL, CHIAPPE & CLARK (PERLE *et al.*, 1994).

The arctometatarsalian genera have a longer metatarsus at any given limb length, a trait best interpreted as an adaptation to increased cursoriality, and HOLTZ (1994) showed that it was not biomechanically weaker despite its increased length. Furthermore, virtually all non-avian theropods possessed a very similar appendicular anatomy (BAKKER, 1986; PAUL, 1987, 1988, 1991; GATESY & MIDDLETON, 1997), and according to the Principle of Uniformitarianism, this would imply that the large theropods should have retained the ability to move fast, albeit probably slower relative to body size (COOMBS, 1978). If an animal is capable of fast locomotion its limbs must be stronger, at any given size, than animals which move more slowly. Thus the strength of the limb bones constitutes an additional parameter for evaluation of theropod locomotor capability. Previously this has only been investigated for very few species, probably due to difficulty of obtaining the necessary parameters, such as bone dimensions and body mass.

Most extant animals tend to move in a roughly dynamical fashion when their Froude numbers (v^2/gl) are alike, even when comparing animals of such different physical appearance as ostriches, humans and mammalian quadrupeds varying four orders of magnitude in mass (ALEXANDER, 1976, 1989, 1991; ALEXANDER & JAYES, 1983), although very small mammals do not appear to conform to this principle (ALEXANDER, 1991). The Froude number is a dimensionless number relating absolute speed (v) to a linear dimension (l), in this case limb length, and gravitation (g). Dynamic similarity implies that any differences between moving animals could be cancelled out by a constant multiple of the linear dimensions, time intervals or forces involved (ALEXANDER & JAYES, 1983).

However, extant animals are not strictly geometric in their physical proportions, but scale with increasing allometry as linear dimensions increase (e.g. PROTHERO & SERENO, 1982; ECONOMOS, 1983; BIEWENER, 1989a, 1989b; BERTRAM & BIEWENER, 1990, CHRISTIANSEN, 1999a, 1999b):theropod dinosaur limb bones apparently showed similiar al-

lometric trends to extant mammals (CHRISTIANSEN, 1999c). It is difficult to assess how this would further be affected once extinct animals, which lack extant anatomical analogs, such as non-avian theropods, were included. Still the approximation towards locomotory dynamic similarity displayed by extant animals of widely different sizes and morphology, suggests that it is reasonable to suppose that this would have been the case for dinosaurs also.

When an animal moves, forces act on the limbs which are proportional to mg, where m is body mass and g is the gravitational constant. Peak stress in the long bones occur in the middle of a stride, where the greatest fraction of body mass is supported (ALEXANDER, 1977a; BIEWENER, 1983), and it is convenient to divide the stress into two major components, an axial component, setting up compressive stress in the diaphysis, and a transverse component, acting to distort the diaphysis about its long axis in the parasagittal plane (ALEXANDER, 1977a; 1985; 1989; 1991).

The compressive stress is proportional to cross sectional area but is usually much less important than the transverse stress (ALEXANDER, 1989). As the forces acting on the limbs are proportional to mg, the peak transverse stress in the diaphysis is proportional to amgx/Z (ALEXANDER, 1977a, 1983a, 1985, 1989 1991; ALEXANDER & POND, 1992), where Z is the section modulus of a cross section of bone for bending in a parasagittal plane, and x is the distance from this cross section to the epiphysis. The value a is the fraction of body mass supported by fore and hindlimbs respectively, and applies only to quadrupedal animals. A higher value of Z thus reduces peak stress at any given body mass and similar bone length. As such ALEXANDER (1983a; 1985; 1989) argued that the reciprocal value Z/amgx would be a useful indicator of the ability of the bones to resist mechanical failure, and a high value of Z/amgx indicates a potential for enhanced physical activity. Bone from a variety of extant animals appears not to have different mechanical properties (BIEWENER, 1982; 1990) so the dimensions of a bone section appears to constitute a good measure for assessing its strength.

In order for this to apply to extinct animals one important, and often overlooked, factor must be addressed. All structures, whether biological or man made, are constructed with a given factor of safety, which is the relationship between the yeld stress of the structure and peak stress experimented. Fortunately, among extant biological structures of support the safety factors appear to vary remarkably litte and are in the order of 2-4 (ALEXANDER, 1981; BIEWENER, 1989a, 1989b, 1990). It is not possible to assess if this was also the case in non-avian theropods, but the constancy displayed in this respect by

most extant animals suggests that it is likely. However, if theropod dinosaurs frequently operated closer to the limit of mechanical failure, the results based on bone strength presented in this paper are open to alternative interpretation. ALEXANDER (1981) argued that the safety factor of a biological structure should be influenced by the decrease in fitness experienced by the organism upon failure of the structure, and as such it seems unlikely that non-avian theropods should have compromised their long bones to any greater extent than extant animals, given their probable importance for survival.

MATERIALS AND METHODS

Previously, strength indicator values have only been given for a few theropods, such as *Tyrannosaurus rex* OSBORN (ALEXANDER, 1985, 1989, 1991; FARLOW, 1990; FARLOW, SMITH & ROBINSON, 1995), *Allosaurus* MARSH and *Struthiomimus* OSBORN (FARLOW, 1990). However, as body mass has a profound influence on the final value, several of these are questionable. The scale model used by ALEXANDER (1985, 1989, 1991) for estimating body mass was clearly erroneously proportioned, and PAUL (1997) concluded that even the model of *Tyrannosaurus rex* MOR 555, used by FARLOW, SMITH & ROBINSON (1995), was incorrect in certain respects, a conclusion supported by this author based on detailed measurements of AMNH 5027 and TMP 81.12.1.

It seems that no commercially manufactured model of non-avian theropod dinosaurs is reliable enough to be included in these kind of experiments. As such, measurements were taken directly from mounted skeletons (TABLE I) and these formed the basis for constructing scale models. Initially, a frame of metal wires was constructed, and bent to fit the linear dimensions of the mounted skeleton. Then the muscles were added in the form of clay, and finally the model was covered in a thin coat of plastic, to make it water impermeable. The relative volume of muscles and the abdominal width follows PAUL (1987, 1988).

Most theropod finds are only partially complete and hence most mounted skeletons are composites. This implies that the proportions of certain of the included animals could be slightly incorrect, but compared to the potential variability of reconstructing soft tissue volume this should be a minor inaccuracy. For this investigation, it was required that the specimens included were fairly complete and that missing parts could be reconstructed with a reasonable degree of certainty, either by comparison with other specimens of the same species or by comparison with closely related species. The relative conservative nature of theropod anatomy suggests that the

latter method would not greatly influence the morphology of the model.

Some specimens were so incomplete that models could not be made, e.g. *Dryptosaurus aquilunguis* COPE. In these cases the linear dimensions of the limb bones, particularly femoral length, was used to assess the size of the animal, and this was compared to another taxon of presumably comparable morphology for which a model had been made. *Dryptosaurus* MARSH, for example, was compared to *Allosaurus*. The calculated mass of 1170 kg (TABLE I) is somewhat higher than suggested by CARPENTER *et al.* (1997). In mammals femoral length is highly correlated with body mass (BIEWENER, 1983; DAMUTH & MACFADDEN, 1990; CHRISTIANSEN, 1999b), displaying a correlation coefficient of around 0.98. Although femoral diaphysial least circumference shows an even better correlation, with r approaching or even exceeding 0.99 (BIEWENER, 1983; CHRISTIANSEN, 1999b), this measurement was not used, due to the bipedal nature of theropods.

The volume of the models were determined by weighing in air and water (as per ALEXANDER, 1985, 1989) using a balance scale that had been tested for accuracy to the level of ± 0.1 g. The method is based on the Principle of Archimedes, which states that an object immersed in a fluid will be boyed upwards by the weight of the displaced fluid. FARLOW, SMITH & ROBINSON (1995) found this method to be superior to the normal displacement method. The density of theropods was set at 950 kg.m^{-3}, which is higher than suggested by PAUL (1988), and also slightly higher than suggested for sauropods by CHRISTIANSEN (1997), due to their highly pneumatic presacrals.

Limb bones of the specimens were measured using a normal sized caliper in the case of smaller forms and a 61 cm caliper in the case of large forms. In the largest forms, e.g. *Gorgosaurus* LAMBE and *Tyrannosaurus*, the length of the limb bones were measured using a measuring tape and other measurements were taken with calipers. As the astragalus is usually firmly attached to, or co-ossified with, the distal part of the tibia, thus being included in the functional length of the epipodium, it was included in tibial length. In certain specimens, such as *Dryptosaurus*, where the astragalus was detached, its dorsoventral dimensions were measured in three places, the values averaged, and added to tibial length. Values from literature were not used in any cases. Some interesting species were discarded prior to analysis as the diaphyses showed clear signs of post-mortem distortion, e.g. *Chirostenotes pergracilis* GILMORE TMP 79.30.1, which would make calculations of section moduli unreliable. Especially anteroposterior crushing of the diaphysis

TABLE I
Strength indicator values and distribution of mass in theropod dinosaurs and mammals above 100 kg. The values of Z/amgx are in GPa^{-1} (continued next page).

TAXON	BODY MASS(kg)	a_f	a_h	Z/AMGX			
				HUMERUS	FEMUR	TIBIA	FIBULA
THEROPODA							
Allosaurus fragilis [1]	1620	-	1.00	-	12.3	9.1	0.8
Anserimimus planinychus [2]	170	-	1.00	-	24.7	15.0	0.3
Dilophosaurus wetherilli [1]	325	-	1.00	-	19.7	8.9	0.8
Dromiceiomimus brevitertius [1]	160	-	1.00	-	22.9	13.1	0.3
Dryptosaurus aquilunguis [3]	1170	-	1.00	-	13.6	10.3	-
Elaphrosaurus bambergi [1]	245	-	1.00	-	20.5	10.4	-
Gallimimus bullatus [1]	220	-	1.00	-	20.8	17.5	0.4
Gallimimus bullatus [1]	490	-	1.00	-	19.1	11.4	0.5
Gorgosaurus libratus [1]	750	-	1.00	-	9.6	8.2	0.5
Gorgosaurus libratus [1]	1610	-	1.00	-	7.6	7.0	0.7
Gorgosaurus libratus [4]	1685	-	1.00	-	8.4	8.5	0.4
Gorgosaurus libratus [4]	1170	-	1.00	-	12.2	6.4	1.0
Microvenator celer [5]	4.5	-	1.00	-	45.9	34.5	-
Ornitholestes hermanni [6]	16,5	-	1.00	-	35.5	16.3	2.9
Ornithomimus edmontonensis [1]	155	-	1.00	-	16.7	-	0.3
Oviraptor philoceratops [1]	58	-	1.00	-	31.9	12.8	-
Saurornithoides sp. [5]	2.7	-	1.00	-	33.9	16.7	-
Saurornitholestes langstoni [5]	22.5	-	1.00	-	27.4	19.5	-
Sinraptor dongi [1]	1700	-	1.00	-	10.0	4.6	0.4
Sinraptor heipingensis [1]	1895	-	1.00	-	14.2	7.9	2.0
Struthiomimus altus [1]	175	-	1.00	-	18.0	-	0.5
Tyrannosaurus bataar [1]	1210	-	1.00	-	14.4	10.2	0.6
Tyrannosaurus bataar [1]	1650	-	1.00	-	13.5	9.9	0.7
Tyrannosaurus rex [7]	6300	-	1.00	-	8.2	4.9	0.5
Tyrannosaurus rex [7]	6250	-	1.00	-	12.3	7.5	0.5
AVES							
Struthio camelus	78	-	1.00	-	53.3	22.6	-

1 - Mass based on scale model made from measurements taken on mounted skeletons, a total of 26 measurements per mount. 2 - Mass found by comparison of linear dimensions to model of *Gallimimus* holo type G.I. DPS 100/11. 3 - Mass found by comparison of linear dimensions to *Allosaurus*. 4 - Mass found by comparison of linear dimensions to TMP 91.36.500 and TMP 81.10.1, for which models were made. 5 - Model was made of *Saurornitholestes langstoni* TMP 88.121.39, with *Deinonychus antirrhopus* as reference for missing parts. Mass of *Microvenator* and juvenile *Saurornithoides* were found by comparison of linear dimensions to TMP 88.121.9. 6 - Mass of *Ornitholestes* found by comparison of linear dimensions to model of *Struthiomimus altus* AMNH 5339 and *Saurornitholestes langstoni* TMP 88.121.39. 7 - Model was made from measurements on composite TMP 81.12.1 and mass of composite AMNH 5027 was found by comparison of linear dimensions. The diaphyses of TMP 81.12.1 appear slightly distorted which could be part of the explanation of the low strength indicator values compared to AMNH 5027. The long bones of TMP 81.12.1 were slightly thinner than in AMNH 5027 though.

would make it appear weaker than was really the case.

All section moduli calculated in this analysis are based on external measurements of the bones. In order to calculate the section modulus, it is required that the cortical thickness of the diaphysis is known in the case of animals with hollow long bones, such as most mammals and theropod dinosaurs. How-ever, this would require either breakage or CT-scanning to expose the cross sections, which is not possible in most cases. In calculating the strength indicator value for the femur of *Tyrannosaurus rex*, FARLOW, SMITH & ROBINSON (1995) subtracted the section modulus for the marrow cavity from the value obtained from external measurements. How-ever, the final strength indicator value based on ex-

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TAXON	BODY MASS (kg)	a_f	a_h	Z/AMGX			
				HUMERUS	FEMUR	TIBIA	FIBULA
MAMMALIA							
Bison bonasus	225	0.56	0.44	29.5	26.8	16.4	-
Bubalus bubalis	382	0.56	0.44	23.1	18.0	15.3	-
Ceratotherium simum	1900	0.52	0.48	24.4	12.4	15.0	0.3
Choeropsis liberiensis	250	0.54	0.46	21.5	16.7	19.3	0.2
Diceros bicornis	875	0.52	0.48	34.8	29.6	29.7	-
Elephas maximus	850	0.58	0.42	10.0	9.7	-	-
Elephas maximus	3534	0.58	0.42	12.0	12.7	9.0	0.7
Elaphurus davidianus	194	0.55	0.45	22.5	18.7	14.6	-
Equus caballus	675	0.55	0.45	20.7	30.3	11.6	-
Hippopotamus amphibius	680	0.54	0.46	18.5	17.0	19.5	-
Hippopotamus amphibius	2400	0.54	0.46	8.9	6.6	6.1	-
Loxodonta africana	6250	0.58	0.42	12.6	10.0	7.0	0.9
Okapia johnstoni	260	0.55	0.45	34.8	34.0	22.0	-
Okapia johnstoni	310	0.55	0.45	29.1	28.5	24.9	-
Oreamnos americanus	120	0.55	0.45	21.4	24.3	12.9	-
Panthera leo	170	0.52	0.48	32.8	21.8	19.6	0.3
Panthera tigris	145	0.52	0.48	24.1	17.5	23.3	0.4
Panthera tigris	230	0.52	0.48	24.6	15.2	19.6	0.4
Rhinoceros sondaicus	1435	0.52	0.48	24.7	19.8	16.4	-
Syncerus caffer	440	0.56	0.44	30.9	26.0	14.5	-
Tapirus terrestris	173	0.54	0.46	23.6	30.9	16.3	1.6
Tapirus indicus	317	0.54	0.46	27.6	20.6	14.0	-
Tragelaphus strepsiceros	190	0.55	0.45	36.4	37.9	21.1	-
Ursus middendorffi	496	0.54	0.46	23.4	12.4	13.5	-

ternal dimensions alone would be only about 5% higher than the value obtained when subtracting the marrow cavity. In an *Allosaurus* tibia this was 9% (Christiansen, pers. obs.) and both of the above two bones had large medullary cavities. Thus, unless the medullary cavity is very large, relatively little error should be introduced in the final value by using external bone dimensions only, especially compared to using a badly proportioned model for predicting body mass. Section moduli were calculated using formulae for elliptical and circular cross sections, as appropriate.

For comparison, a number of large mammals were chosen (TABLE I), spanning a wide phylogenetic and locomotory spectrum, from graviportal elephants to cursorial bovids and cervids. An adult, but only medium-sized Ostrich was also included. All mammals are housed at the Zoological Museum in Copenhagen, and both captive and wild caught specimens were included. Body mass is quite rarely recorded for museum specimens, but fortunately a number of specimens in the collections at the Zoological Museum in Copenhagen had their body

mass recorded, either prior to or just after death. Even the gigantic *Loxodonta africana* BLUMENBACH CN 3684 was weighed just after death at the Zoological Garden in Copenhagen in August 1970, by suspending it from a mobile crane.

As the mammals are quadrupedal the centre of gravity, and hence distribution of mass, was found by suspension of models (as per ALEXANDER, 1983b) in the case of *Rhinoceros* LINNAEUS, *Hippopotamus* LINNAEUS and *Elaphurus davidianus* MILNE-EDWARDS. In the other cases literature values were used, primarily from ROLLINSON & MARTIN (1981), and ALEXANDER (1985, 1989). It was assumed that phylogenetically and anatomically closely related species displayed similar mass distributions, e.g. the big cats were assumed to be similar to *Acinonyx* BROOKES, for which mass distribution is known (ROLLINSON & MARTIN, 1981), and *Tapirus* BRÜNNICH, *Diceros* GRAY and *Ceratotherium* GRAY were assumed to be similar to *Rhinoceros*.

Uncertainties could be introduced by this comparative method, however, as the two extant species of *Camelus* LINNAEUS are phylogenetically and anatomically closely related, but appear to display different distributions of mass (ROLLINSON & MARTIN, 1981). Furthermore, different experiments with *Elephas maximus* LINNAEUS yielded slightly different results, 0.55 and 0.45 for fore and hindlimbs, respectively, in one case, (ROLLINSON & MARTIN, 1981), and 0.58 and 0.42, respectively, in another (ALEXANDER, 1985, 1989). Since the actual body mass of the specimens was known in this investigation, the strength indicator values for the elephants and rhinoceroses could be more reliable than previously reported values, based on calculated body masses (ALEXANDER *et al*., 1979a; ALEXANDER, 1985, 1989; ALEXANDER & POND, 1992).

Stength indicator values for femora only were calculated for an additional 24 mammal specimens, and along with the mammals from TABLE I, these were assigned to one of the four major locomotory categories described by GREGORY (1912) and followed by COOMBS (1978), based on their anatomy. These are graviportal animals, which have an appendicular anatomy adapted for support of mass and almost devoid of adaptations for enhanced locomotory activity; mediportal animals, with an appendicular anatomy primarily adapted for support of mass but with some adaptations for increased locomotory potential; subcursorial animals, with extensive adaptations for increased locomotory potential; and cursorial animals, in which these characters are taken to even greater extremes than in the subcursorial animals.

Additionally, the limb proportions of theropods were compared to 193 specimens of mammals, representing 104 extant species and four extinct species and spanning a body mass range from 1.4 kg *Tragulus javanicus* BRISSON to 6250 kg *Loxodonta africana* for the extant species. The extinct species were all graviportal (*Mammuthus primigenius* LINNAEUS, *M. meridionalis* NESTI, *Gomphotherium* sp. BURMEISTER and *Amebelodon angustidens* CURVIER. All specimens of extant species are housed at the Zoological Museum in Copenhagen, and the extinct species were from the Natural History Museum in Paris, The Natural History Museum in Bruxelles, The Field Museum of Natural History in Chicago, and the Royal Tyrrell Museum of Paleontology in Alberta, Canada.

As with the above data set, the mammals were assigned to one of the four major locomotory categories, based on their morphology. In addition, 28 adult ratite specimens were included, representing *Struthio* LINNAEUS, *Rhea* BRISSON, *Dromaius* VIEILOTT and three species of *Casuarius* BRISSON. These were housed at the Zoological Museum in

Copenhagen and the Museum für Naturkunde in Berlin. In addition to personal measurements on the theropod specimens from TABLE I data were taken from OSBORN (1916) on *Struthiomimus*, GILMORE (1920) on *Ceratosaurus* MARSH, PARKS (1926) and RUSSELL (1972) on *Dromiceiomimus* RUSSELL, STOVALL & LANGSTON (1950) on *Acrocanthosaurus* STOVALL & LANGSTON, RUSSELL (1970) on *Gorgosaurus* OSBORN and *Daspletosaurus* RUSSELL, OSMÓLSKA, RONIEWICZ & BARSBOLD (1972) on *Gallimimus* OSMÓLSKA, RONIEWICZ & BARSBOLD, RUSSELL (1972) on *Ornithomimus* MARSH, MADSEN (1976) on *Allosaurus*, OSTROM (1978) on *Compsognathus* WAGNER, NOVAS (1993) on *Herrerasaurus* REIG, RAATH (1969) on *Syntarsus* RAATH, RUSSELL & DONG (1993) on *Sinornithoides* RUSSELL & DONG, SERENO *et al*. (1996) on *Deltadromeus* SERENO, DUTHEIL, LAROCHENE, LARSSON, LYON, MAGWENE, SIDOR, VARRICCHIO & WILSON, and HOLTZ (1994) on *Tyrannosaurus bataar* MALEEV, *Archaeornithomimus* RUSSELL, *Coelophysis* COPE, *Eustreptospondylus* WALKER, *Chuandongocoerus* HE, *Megalosaurus* BUCKLAND, *Maleevosaurus* CARPENTER and *Procompsognathus* FRAAS.

It is worth pointing out, however, that *Acinonyx* in each of the above two cases was assigned to the cursorial category, despite grouping anatomically with the subcursors (COOMBS, 1978). This was done primarily due to the enormous velocity attained by this species, well in excess of 100 km.h^{-1}. This is an often quoted figure previously based only on dubious measurements, but which has finally been verified scientifically (SHARP, 1997). Conversely, the ursids were considered mediportal, despite the ability of most species to attain reasonably high absolute speeds (NOWAK, 1991), due to their numerous mediportal morphological characters, such as both epipodial bones well developed and largely separate (only united by syndesmoses proximally and distally), plantigrade metatarsus with all five metapodials separate and largely unreduced in size, and their short epipodia and long propodia.

RESULTS AND DISCUSSION

Among extant mammals the strength indicator values appear to correlate fairly well with peak locomotory performance (TABLE I). In mammals capable of fast locomotion the strength indicator values of humerus and femur are usually between 20 and 30 GPa^{-1}, whereas mediportal animals have slightly lower values. The graviportal elephants have strength indicator values around 10 GPa^{-1}, which is similar to previously published values (ALEXANDER, 1981, 1991; ALEXANDER & POND, 1992). It is also evident that for both mammals and theropods, including the Ostrich, the long bones that are more
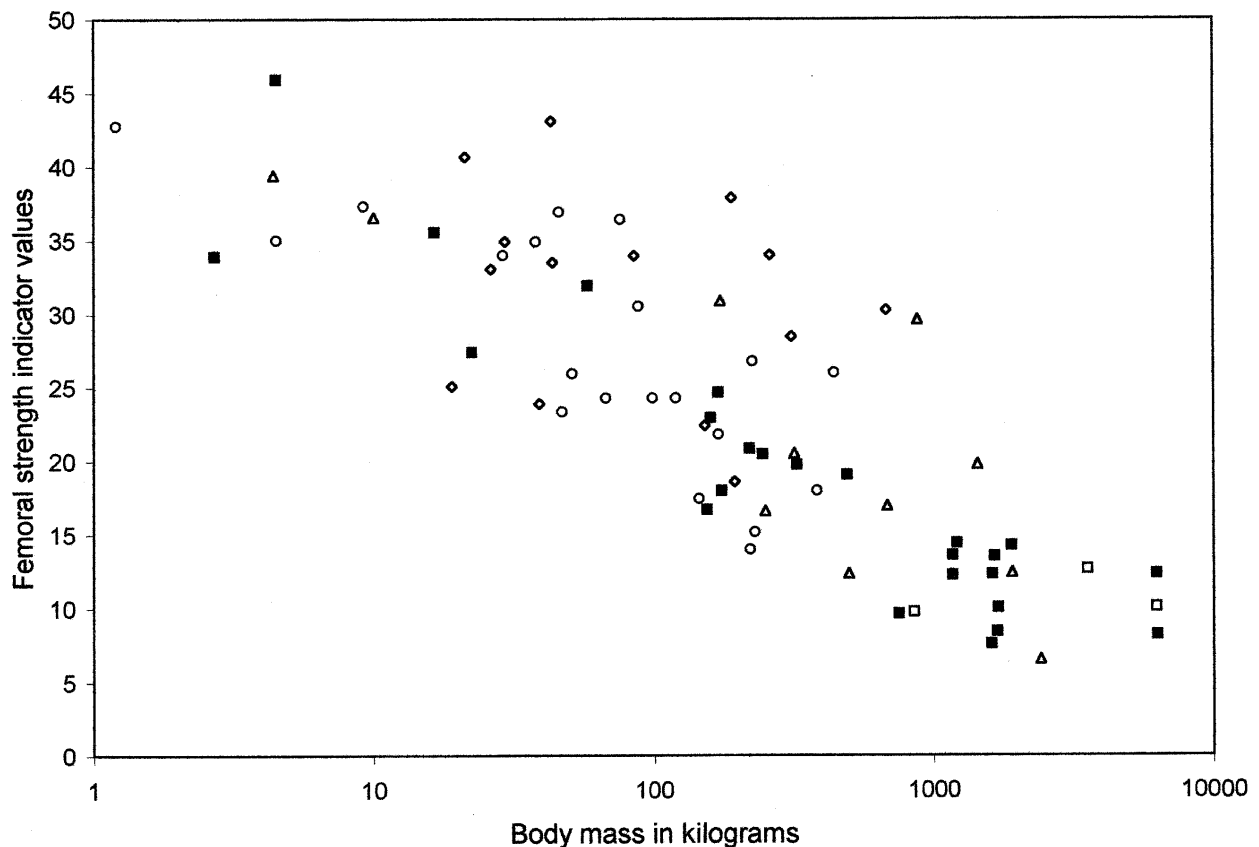
Fig. 1 - Strength indicator values of femur compared to body size and locomotory potential. Black squares, theropods (species from TABLE I); Open squares, graviportal mammals (*Elephas* and *Loxodonta*); Open triangles, mediportal mammals (*Ailurus, Ceratotherium, Choeropsis, Diceros, Hippopotamus, Meles, Rhinoceros, Tapirus, Ursus*); Open circles, subcursorial mammals (*Alopex, Bison, Bubalus, Canis, Fennecus, Hydrochaeris, Oreamnos, Ovis, Panthera, Phacochoerus, Potamochoerus, Syncerus*); Open diamonds, cursorial mammals (*Acinonyx, Antidorcas, Cervus, Damaliscus, Elaphurus, Equus, Gazella, Hemitragus, Okapia, Saiga, Tragelaphus*).

steeply angled to vertical, in this case tibia, are mechanically weaker than are humerus and femur.

The strength indicator values of the large theropods are in the order of, or slightly above, the few results previously published for large theropods, mainly *Tyrannosaurus rex*. The two included *Tyrannosaurus rex* specimens display rather different strength indicator values, despite being nearly identical in size. The specimen TMP 81.12.1 appears considerably weaker than AMNH 5027, but the long bones of the former appeared to have suffered slight anteroposterior crushing, which would make the section modulus lower. In AMNH 5027 they are more circular, and this probably reflects the natural morphology. Additionally, the femoral diaphysis in AMNH 5027 is thicker. The hindlimbs from AMNH 5027 unfortunately were not recovered, however, but casts of the type CM 9780 are used on the mounted skeleton. They seem appropriate in size for this animal, but apparantly are from a more robust individual (Thomas Holtz Jr., *pers. comm.*,

1998). Also the metatarsals are restored incorrectly non-arctometatarsalian.

All the large theropod species have strength indicator values for the femora that are roughly equivalent to hippopotamuses and elephants, and their limbs apparently were not as resistent to mechanical failure as those of smaller forms, such as the ornithomimids, which have strength indicator values roughly twice as high. This suggests that large species were less fleet relative to body size than the smaller species, although potentially just as fast in absolute terms.

This is not unexpected, as extant mammals do not significantly vary in maximal running speed across a size spectrum of three orders of magnitude (GARLAND, 1983; GARLAND & JANIS, 1993). However, it does imply that smaller species move faster relative to body size and have lower duty factors than large species. This implies that peak locomotion forces during fast locomotion will be lower multi-
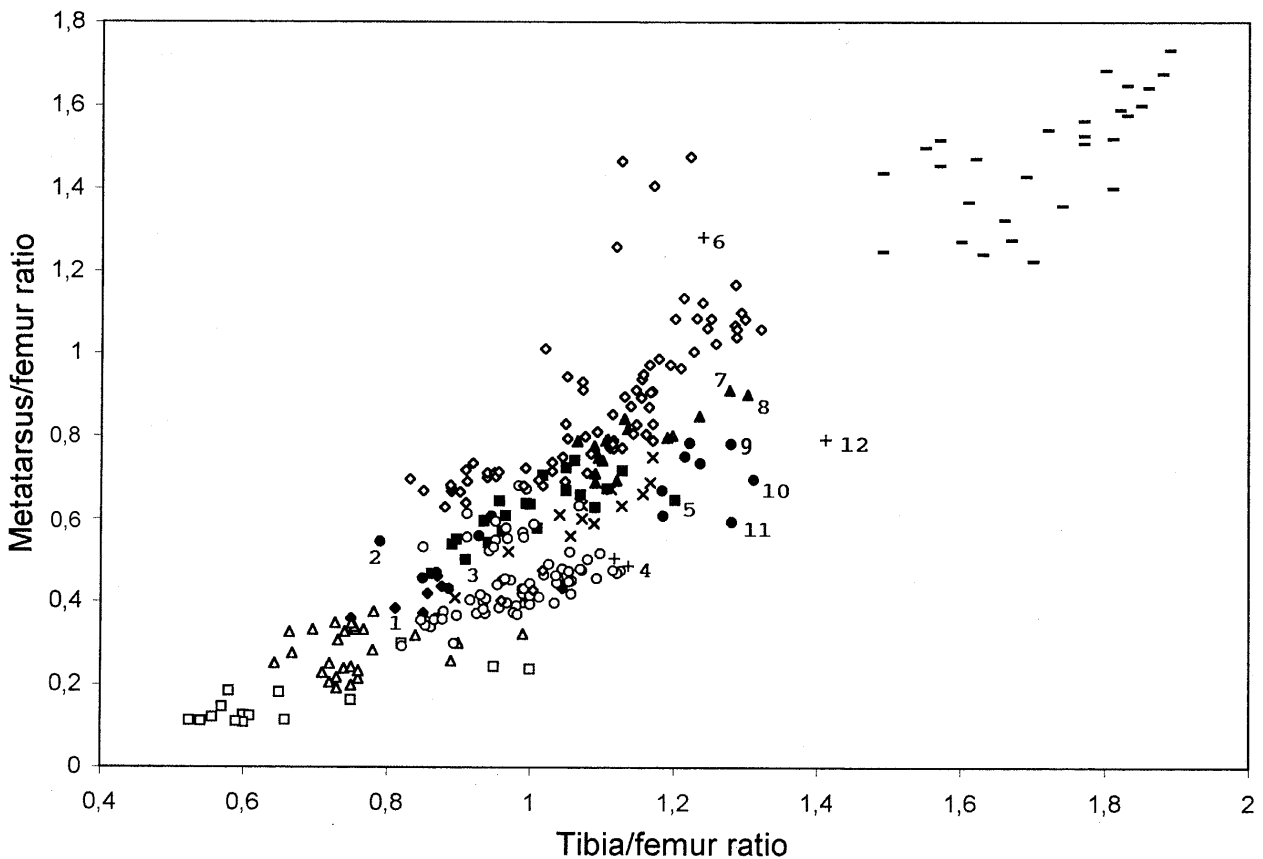
Fig. 2 - Limb proportions in mammals (187 specimens, 98 species), ratites (28 specimens, five species), and non-avian theropods (76 specimens, 38 species). Black symbols are theropods and ratites and open symbols are mammals. Black X's ceratosauroids (*Ceratosaurus, Coelophysis, Dilophosaurus, Elaphosaurus, Syntarsus*); Black diamonds, allo-sauroids (*Allosaurus, Acrocanthosaurus, Sinraptor* ;including "*Yangchuanosaurus*" *heipingensis*); Black squares,tyran-nosaurids (*Albertosaurus, Alectrosaurus, Aublysodon,Gorgosaurus, Maleevosaurus, Tyrannosaurus* [*T. bataar, T. rex, T. torosus*]); Black triangles, ornithomimosaurus (*Anserimimus, Archaeornithomimus, Dromiceiomimus, Gallimimus, Or-nithomimus, Struthiomimus*); Balck crosses, dromaeosaurids and troodontids (*Deinonychus, Saurornithoides, Sinorni-thoides*); Black circles, other theropods (*Caudipteryx, Chirostenotes, Chuandongocoelurus, Compsognathus, Deltadromeus, Dryptosaurus, Eustreptospondylus, Gasosaurus, Herrerasaurus, Megalosaurus, Ornitholestes, Ovirap-tor, Procompsognathus, Protarchaeopteryx*); Black dashes, ratites (*Casuarius, Dromaius, Rhea, Struthio*); Open squares, graviportal mammals (*Amebelodon, Gomphotherium, Elephas, Loxodonta, Mammuthus, Manis, Myrmeco-phaga, Priodontes, Tamandua*); Open triangles, mediportal mammals (*Ceratotherium, Choeropsis, Diceros, Gulo, Hip-popotamus, Meles, Mellivora, Rhinoceros, Tapirus, Ursus*); Open circles, subcursorial mammals (*Alopex, Bison, Bubalus, Canis, Cerdocyon, Chrysocyon, Felis, Lycalopex, Lycaon, Neofelis, Ovibos, Panthera, Phacochoerus, Pota-mochoerus, Sus, Syncerus, Tayassu, Urocyon, Vulpes*); Open diamonds, cursorial mammals (*Acinonyx, Aepyceros, Al-celaphus, Antidorcas, Antilope, Boselaphus, Camelus, Cephalophus, Connochaetes, Equus, Gazella, Giraffa, Hippotragus, Kobus, Lama, Litocranius, Okapia, Oryx, Redunca, Saiga, Sylvicapra*). Numbers: 1 - *Allosaurus*; 2 - *Orni-tholestes*; 3 - *Tyrannosaurus* (*rex*); 4 - *Deinonychus*; 5 - *Mallevosaurus*; 6 - *Saurornithoides*; 7 - *Dromiceiomimus*; 8 - *Stuthiomimus*; 9 - *Caudipteryx*; 10 - *Protartchaeopteryx*; 11 - *Oviraptor*; 12 - *Sinornithoides*.

ples of body mass in large animals, as in extant ungulates and megaherbivores (ALEXANDER, LANG-MAN & JAYES, 1977; ALEXANDER *et al.*, 1979a; ALEX-ANDER& POND, 1992), although the evidence is equivocal when analyzing phylogenetically wider samples (BIEWENER, 1983). This would reduce the stress in the diaphyses of large species but would not necessesarily imply lower maximal speeds, due to their great limb length. However, the strength indi-cator values of all the large species do not support

the great speed suggested for giant theropods by some authors (BAKKER, 1986, 1987; PAUL, 1988), providing that large theropods operated with factors of safety comparable to those of extant mammals.

The smaller theropod species have strength indi-cator values suggestive of a higher locomotory po-tential. In addition to their long and gracile limbs with well developed muscle scars, the presence of the arctometatarsus in ornithomimids, the dolichoiliac pelvis and elongation of the preacetabular and es-

pecially postacetabular processes in advanced forms, implyng massive epipodial extensors, this supports earlier conclusions that these animals were probably capable of relatively fast locomotion (e.g. RUSSELL, 1972; COOMBS, 1978; THULBORN, 1982, NORMAN, 1985; PAUL, 1988; HOLTZ, 1994).

As expected the strength indicator values for the femur and tibiotarsus of the Ostrich differed markedly from each other. Being held subhorizontally and largely immobile, unless when running at high velocities (PAUL, 1991), the Ostrich femur is subjected to large amounts of bending stress. GATESY (1991) found that avian theropod femora had significantly greater diameters at any given length compared to those of non-avian theropods or mammals, in which the femur is oriented more vertically. Thus, the tibiotarsal value of 23 GPa^{-1} is probably more comparable with the non-avian theropod values, and quite similar to the femoral strength indicator values of small to medium sized theropods. The Ostrich is a fast moving biped, capable of at least 50 km.h^{-1} (ALEXANDER *et al.*, 1979b)

However, in TABLE I there are several important exceptions among recent mammals that must be addressed. It is evident that *Diceros*, and to a lesser extent the large *Rhinoceros*, possess a powerfully built appendicular anatomy, in accordance with their increased locomotory potential compared to elephants and hippopotamuses. However, the large *Ceratotherium* has a strength indicator value for the femur comparable to those of elephants and large theropod dinosaurs. CHRISTIANSEN (1997) tentatively suggested that because this animal, which was a captive specimen, was known to have been ill for some time prior to death, the femoral diaphysis could have been reduced in girth. However, he found little evidence for this when comparing femoral length and least diaphysial circumference in this animal to seven other White Rhinoceroses.

This result is clearly at odds with the conclusions of ALEXANDER & POND (1992), but these authors performed their analysis on a juvenile specimen, with an estimated mass of 750 kg. In all mammals femoral length exceeds humeral length and the metaphysial expansion also take up more space of overall length in the humerus. It is possible that really large mammals have rather low strength indicator values, usually interpreted as elephantine, in limb bones where the diaphysis is long, thus providing a larger lever for the secondary moments about the diaphysis.

This could also explain the great difference in the strength indicator values for the humerus and femur of *Ceratotherium*. Conversely, as is evident from TABLE I, all mammals have larger strength indicator values for the humeri, despite supporting the majority of body mass on the forelimbs. Non-avian theropods retained long femora, probably because femoral retraction remained very important in forwards propulsion in all taxa, with the possible exception of advanced dromaeosaurids, unlike their avian decendants (GATESY, 1990, 1991; GATESY & MIDDLETON, 1997).

CHRISTIANSEN (1997) pointed out that in large animals strength indicator values appear to decrease ontogenetically, and juveniles of large species have stouter long bones than comparably sized adults of smaller, more cursorial species, even if the animal in question is a mediportal species. This can be illustrated by using body mass and osteological data for four hippopotamuses, of which one was juvenile, one a subadult, one an adult female and one a huge adult male. Strength indicator values for the humerus and femur declined with mass and were 33.05 GPa^{-1} and 34.64 GPa^{-1}, respectively, for the juvenile (150 kg), 18.45 GPa^{-1} and 16.99 GPa^{-1}, respectively, for the subadult (TABLE I, 680 kg), 19.23 GPa^{-1} and 17.83 GPa^{-1}, respectively, for the adult female (1210 kg), and only 8.87 GPa^{-1} and 6.55 GPa^{-1}, respectively, for the huge bull (TABLE I, 2400 kg). The large bull, however, had been kept at Copenhagen Zoo for many years, with little opportunity for physical activity, and was probably somewhat overweight.

The large male Kodiak Bear has a strength indicator value for the humerus almost twice as high as for the femur, the latter comparable to elephants, despite being able to attain a full gallop. Thus, as pointed out by ALEXANDER (1985, 1989, 1991) despite having rather low strength indicator values for the long bones, the very different morphology of large theropods from recent elephants urges for caution in subscribing an elephantine locomotory potential to them. The evidence suggests that large extant mediportal animals sometimes have long bone strength indicator values only slightly higher than in elephants.

When comparing femoral strength indicator values of theropod dinosaurs to mammals assigned to the four locomotory categories noted above (Fig. 1), the small to medium-sized taxa group with mediportal and subcursorial mammals, whereas the large taxa group with the elephants, the White Rhinoceros bull and the large Hippopotamus bull. Due to the horizontal nature of the Ostrich femur this animal was not included in the figure. Interestingly, when comparing strength indicator values to body mass in the four locomotory groups of extant mammals, the results are markedly different.

In mediportal mammals the strength indicator values are fairly correlated with mass, decreasing as linear dimensions increase to M$^{-0.1978}$ (n = 11, r =

0.7494), and in subcursorial mammals strength indicator values scale to $M^{-0.1546}$ (n = 20, r = 0.7233).

In cursorial mammals, however, strength indicator values appear independent of body size, scaling to $M^{-0.0434}$ (n = 14, r = 0.236). This supports the conclusions of ALEXANDER (1977a) that peak bone stress during fast locomotion of cursorial African ungulates is largely independent of body mass. In theropod dinosaurs they are well correlated with mass (r = 0.8974) and scale to $M^{-0.2130}$. Thus for animals with extreme anatomical adaptations for cursoriality, the strength indicator values appear to remain largely constant across a size spectrum of nearly two orders of magnitude. However, there appear to be size dependent decreases in limb strength among other groups. It should be noted, however, that the above values are tentative as species with multiple specimens, e.g. the Tiger, Hippopotamus or *Gorgosaurus*, which are both represented by two specimens, have not been averaged.

The limb bone ratios (Fig. 2) are much at odds with the suggestion that large theropods should have been relatively slow moving. Theropods group with subcursorial mammals, as found by COOMBS (1978) and HOLTZ (1994), and do not approach the limb proportions of graviportal or even mediportal mammals. Even the large tyrannosaurids display tibiofemoral and metatarsofemoral ratios nested within, and somewhat above, respectively, the ranges of subcursorial mammals.

Especially the lengths of the metatarsals in theropods greatly exceed the corresponding values in graviportal and mediportal mammals of similar body mass. In the 1435 kg *Rhinoceros* and 875 kg *Diceros* (TABLE I) the longest metatarsal is 161 and 159 mm, respectively, whereas the 750 kg juvenile *Gorgosaurus* has a third metatarsal fully three times as long (474 mm), and the adults have third metatarsals that are 569-589 mm. The cursorial mammals in Figure 2, most of which are small to medium-sized bovids, have metatarsals that are relatively as long as to somewhat longer than, those of the theropod dinosaurs, due to their greatly elongated, fused cannon bones. At the upper extreme are the giraffes, which have metatarsofemoral ratios approaching 1.5. As with the ratites this does not imply an extraordinarily cursorial anatomy in this species, as giraffid limbs are greatly elongated as an adaptation for high browsing. The Giraffe attains speeds of 40 km.h^{-1} (ALEXANDER, LANGMAN & JAYES, 1977).

No other animal approaches the ratite tibiofemoral values, but this is due to the very short propodia of birds at any given body size compared to mammals and non-avian dinosaurs. In birds the femur is held subhorizontally in order to bring the feet anteriorly, to position them below the centre of gravity (e.g. TARSITANO, 1983; GATESY, 1990). This subjects the femur to a great deal of torsional stress, which probably accounts for the thick and short diaphyses at any given body mass (CRACRAFT, 1976; GATESY, 1991). The very high tibiofemoral ratios of birds should not be taken to imply an extreme cursorial potential of large ground birds compared to other animals, especially since the most extreme avian ratios are not from fast-moving ground birds, but from animals such as flamingos (GATESY, 1991; GATESY & MIDDLETON, 1997).

The limb bone ratios, size and morphology of the ilium, and the overall hindlimb morphology and size of the muscle scars of even large theropods, appear to strongly contradict a slow-moving, bipedal amble as their fastest gait. The author agrees with BAKKER (1975, 1986, 1987), COOMBS (1978), NORMAN (1985) and PAUL (1987, 1988, 1991), among others, that large theropods were probably quite fast in absolute terms (km.h^{-1}), due to the great size of the animals and length of their limbs, but in relative terms (strides/second or speed/body mass) they may well have been fairly slow.

Limb bone ratios appear fairly correlated to the maximum running speed of subcursorial and cursorial mammals, although substantial variation exists (ALEXANDER, LANGMAN & JAYES, 1977; GARLAND & JANIS, 1993), but overall leg length appears to be a better predictor of maximal speed (GARLAND & JANIS, 1993, HARRIS & STEUDEL, 1997). As such, even large theropods should have been fairly fast moving. The two specimens of *Tyrannosaurus rex* included in this analysis, TMP 81.12.1 and AMNH 5027, were equal in mass to the large *Loxodonta africana* CN 3684 bull, but the length of their hindlimbs differed markedly. In the elephant total hindlimb length, defined as the combined length of femur, tibia and longest metatarsal, is 2078 mm, but in the two *Tyrannosaurus* specimens it is fully 50 % greater, 3109 mm and 3165 mm, respectively, even though the elephant is considerably more long-limbed compared to body mass than other large, extant mammals (ALEXANDER *et al.*, 1979c; ALEXANDER & POND, 1992; CHRISTIANSEN, 1999a, 1999b).

Among extant mammals the largest species capable of fast locomotion with a suspended phase are the rhinoceroses. Extant mammals appear to adapt to increases in body size while maintaining the ability to gallop not by evolving very thick long bone diaphyses as is usually assumed (e.g. ALEXANDER & POND, 1992). Instead the long bones become progressively shorter, thus reducing the lever arm of the secondary moments about the diaphysis, preserving bone strength (CHRISTIANSEN, 1999b). The seemingly thick long bone diaphyses of large bovids and rhinoceroses are in fact only as thick as could be

expected from their body mass, and no thicker than the diaphyses of elephants (CHRISTIANSEN, 1999b). Elephants are unusual in preserving the long limbs usually characteristic of smaller animals, and thus their long bones are mechanically markedly weaker (TABLE I). This matters little as they are unable to perform true running with a suspended phase.

Theropod dinosaurs did become gradually more stout as they increased in size and at rates very similar to extant mammals (CHRISTIANSEN, 1999c), but the limbs of even the largest species were remarkably long, thus apparently compromizing bending resistance. Yet their morphology seems to rule out a bipedal, elephantine amble as their fastest gait. It is difficult to interpret exactly how large theropods moved at their fastest gait, but it seems unlikely that they included long suspended phases in the strides. Possibly the preservation of very long limbs in large non-avian theropods was an adaptation for moving rapidly, employing rather fast cadences, long strides and brief, if any, suspended phases. A columnar, elephantine limb morphology implies that stride length will only increase proportionally to the square root of limb length, but the long limbs of theropods would certainly have allowed long strides to be taken, as the limbs displayed joint flexure, even in the largest animals.

Curiously, this matches quite well the gait and speed suggested for *Tyrannosaurus rex* in the movies Jurassic Park and, most recently, The Lost World, although the grossly exaggerated trampling performed by the animal during normal walking is ridiculous for an animal weighing a mere 6 tonnes. Despite suggestions to the contrary (ALEXANDER, 1996) *Tyrannosaurus* was far from running in the above movies, but simply enhanced its speed by substantially lengthening its stride length with duty factors above 0.5, a gait which appears quite realistic and in accordance with the above.

Predicting the maximal running speed of extinct organisms is a questionable undertaking, particularly in animals with no extant parallels. GATESY (1990, 1991) pointed out, that although most theropod tracways may appear largely indistinguishable from those of large extant ground birds, there are important underlying differences in appendicular functional anatomy that makes it likely that avian and non-avian theropod locomotion different in certain respects, primarily in the orientation and mobility of the femur, and hence its contribution to forwards propulsion.

In many ways extant ungulates, with their long gracile limbs, hinge-like joints, and long and mobile propodia could potentially be better analogs for theropod locomotion, as also concluded by CAR-RANO (1997). Thus, the above limb bone ratios of mammals should constitute a superior analog for evaluating cursorial potential in theropod dinosaurs than the values for the ratites. Below I have attempted to give an approximate estimate of the possible maximal running speed for the theropods included in TABLE I, using two different, but closely related approaches.

ALEXANDER, LANGMAN & JAYES (1977) calculated the equation

$$l/h \quad 1.8(v^2/gh)^{0.39} \qquad (1)$$

where l is stride length, h is hip height, v is velocity and g is the gravitational constant. This equation relates speed to limb kinematics in galloping ungulates. THULBORN (1982) estimated the hip height of dinosaurs as the combined length of femur, tibia and longest metatarsal and multiplied this value by 1.09 to account for the tarsals and cartilage in the joints. Here, h is defined simply as leg length, as the large tarsals are included in tibial length, and there does not appear to have been large menisci in theropod limbs as was probably the case for some quadrupedal dinosaurs, e.g. sauropods (CHRISTIANSEN, 1997), but just a thin layer of hyaline cartilage, as in extant tetrapods.

In order for the above equation to apply to extinct animals it is required that l/h be defined. ALEXANDER (1976) found that quadrupedal animals change gait from walking to trotting at l/h of around 2.0, and THULBORN (1982) recalculated data from ALEXANDER (1977b), and found that animals change gait from a trot to a slow run at l/h of around 2.9. Bipeds cannot trot and thus change gait directly from fast walking with long strides to running, i.e. including a suspended phase. Contrary to the suggestions of THULBORN (1982) that large theropods were unable to exceed a l/h value of 2.0, the results presented above suggest that they were able to move faster. This does not necessarily imply a long unsuspended flight phase as THULBORN (1982) suggested, but simply that they were able to move relatively fast, and probably reach the bipedal walk-run transition with a l/h of around 2.9.

It is assumed that the large species in TABLE I, i.e. those exceeding 500 kg, were capable of reaching the bipedal walk-run transition, and thus a l/h of 3.0. Given their anatomy, it would appear that this is a rather conservative estimate of their locomotory potential. In contrast it is assumed that species between 100-500 kg were capable of a l/h of 4.5, but 5.0 in the case or ornithomimids, which is similar to extant *Connochaetes* LICHTENSTEIN (ALEXANDER, LANGMAN & JAYES, 1977). This is in full accord with their limb strength and limb bone proportions, and still considerably below the value of 8.0 reached by highly cursorial ungulates, such as *Gazella* DE

TABLE II
Velocities (km.h⁻¹) calculated for theropod dinosaurs and extant mammals, and the actual measured speed of the mammal species. The value h is hindlimb length.

TAXON	BODY MASS (kg)	h (m)	SPEAD PREDICTED BY EQUATION		ACTUAL SPEED
			(2) - (4)	(5)	
THEROPODA					
Allosaurus fragilis	1620	1.947	30	55	-
Anserimimus planinychus	170	1.204	46	76	-
Dilophosaurus wetherilli	325	1.376	43	69	-
Dromiceiomimus brevitertius	160	1.348	48	89	-
Elaphrosaurus bambergi	245	1.517	45	86	-
Gallimimus bullatus	220	1.419	50	83	-
Gallimimus bullatus	490	1.941	51	88	-
Gorgosaurus libratus	750	1.817	29	69	-
Gorgosaurus libratus	1610	2.439	34	72	-
Gorgosaurus libratus	1685	2.461	34	71	-
Gorgotosaurus libratus	1170	2.125	32	69	-
Ornithomimus edmontonensis	155	1.249	47	82	-
Oviraptor philoceratops	58	0.871	39	79	-
Sinraptor dongi	1700	2.114	32	59	-
Sinraptor heipingensis	1895	2.155	32	58	-
Struthiomimus altus	175	1.381	49	88	-
Tyrannosaurus bataar	1210	2.030	31	65	-
Tyrannosaurus bataar	1650	2.162	32	62	-
Tyrannosaurus rex	6300	3.109	38	56	-
Tyrannosaurus rex	6250	3.165	39	57	-
MAMMALIA					
Ceratotherium simum	1900	1.132	-	24	25[1]
Connochaetes taurinus	-	0.875	36	-	40[2]
Elephas maximus	3534	1.727	-	33	18[3]
Equus burchelli	136	0.871	-	56	50[2]
Gazella dorcas	19	0.504	54	64	50[2]
Phacochoerus aethiopicus	88	0.473	-	30	36[2]
Syncerus caffer	440	0.935	28	37	25[2]

Actual speeds of mammals from: 1 - ALEXANDER & POND (1992); 2 - ALEXANDER, LANGMAN & JAYES (1977); 3 - ALEXANDER (1991).

BLAINVILLE (ALEXANDER, LANGMAN & JAYES, 1977). Due to the size of the holotype of *Gallimimus* G.I.DPS 100/11, which has an estimated mass of 490 kg (TABLE I), this animal was credited with a l/h of 4.5 only. *Oviraptor* OSBORN was credited with a l/h of 5.0 as the ornithomimids.

Thus in order to apply equation (1) to the three categories of l/h, l was in each case substituted for h times the chosen number for the category.

For large species v is calculated using the equation

$$v \quad gh(3.0h/1.8h)^{2.5641} \qquad (2)$$

- for non-ornithomimid, medium-sized species v is calculated using the equation

$$v \quad gh(4.5h/1.8h)^{2.5641} \qquad (3)$$

- for ornithomimids and *Oviraptor* v is calculated from the equation

$$v \quad gh(5.0h/1.8h)^{2.5641} \qquad (4)$$

BAKKER (1975) found that peak running speed and the relative length of the hindlimb (RHL) correlated quite well (r = 0.924) for larger mammals (>10 kg), and calculated the following equation

$$v_{(max)} = 4.132(RHL) - 14 \qquad (5)$$

where $v_{(max)}$ is maximal running speed and RHL is leg length divided by the cube root of body mass. BAKKER (1975) cautioned that this equation applied only for animals of comparable anatomical design, and as such the equation would overestimate the speed of animals with greatly elongated limbs for high browsing, such as *Giraffa* BRÜNNICH, and underestimate it for animals which use extenive spinal flexion-extension for attaining long stride lengths, such as *Acinonyx*.

COOMBS (1978) applied this equation to several kinds of dinosaurs, and calculated some quite spectacular speeds for the long-limbed sauropods, for which the morphology of the limbs strongly contradicts fast locomotion (CHRISTIANSEN, 1997), and COOMBS himself did consider the results unreliable. In contrast, theropods have limbs that are indicative of fast locomotion, and that were probably not elongated for other ecological purposes. As bipeds they could not have used spinal flexion as a means of extending stride length. Thus, the equation should apply fairly well to them.

The results of the equations are shown in TABLE II and for convenience all results are given as km.h^{-1}. In addition to the dinosaurs, a number of extant mammals have also been included. Their speeds were predicted using the above equations. For some of the mammals the value of l/h was known (ALEXANDER, LANGMAN & JAYES, 1977) and equation (1) was used to calculate their speed. It appears that both equations (1) and (5) predict the speed of the mammals quite satisfactorily. In the case of the elephant the long limbs makes the speed calculated from equation (5) considerably higher than the actual speed. Elephants have columnar limbs, very different limb proportions from subcursorial and cursorial mammals, and also from theropod dinosaurs (Fig. 2), and rather small limb muscles for their mass (GAMBARYAN, 1974; ALEXANDER *et al.*, 1981), unlike subcursorial and cursorial mammals and most likely also theropod dinosaurs.

It would appear that large theropods could have moved at rather impressive speeds before reaching the walk-run transition due to their very long limbs. It would appear that large theropods would have had no trouble catching extant megaherbivores, even if they were capable of only a fast walk. Smaller species, especially ornithomimids, appear to have been as fast as extant subcursorial and cursorial ungulates. The speeds predicted for the smaller theropods species from equation (5) appear excessive and are probably also slightly too high for the large species. It is by no means certain that animals such as ornithomimids were incapable of l/h above 5.0 as assumed above, and if they were able to attain values of l/h of 6.0, which is still below that of extant cur-

sorial mammals, they would be almost as fast as racehorses.

Conversely, if *Tyrannosaurus* was capable of reaching a l/h of just 3.5, which would still be a rather slow running gait with a quite high duty factor, it would have moved at 47 km.h^{-1} and would thus be as fast as a zebra. Higher values of l/h are probably not realistic due to the rather low strength indicator values of all the large theropod species. It is evident, however, that giant theropods could have been fast in absolute measure despite a low locomotory potential relative to body size. It would appear that they could easily have been fast enough to catch large ceratopsians and ornithopods, even if these were as fast as, or even faster than extant megaherbivore mammals.

Trackways usually document only walking speeds, which is to be expected, but a few cases have been found of apparently sprinting animals with values of l/h around 5.0 (FARLOW, 1981; THULBORN, 1984; PAUL, 1988). These were small to medium-sized species and as it is not possible to assess whether or not they were running at maximal speed, a l/h value of around 5.0 for theropod dinosaurs up to several hundred kilograms, as suggested above, appears reasonable, if not conservative. The fact that trackways do not get preserved unless the substrate is moist, which is an unlikely surface on which to attain maximum running velocity, suggests that the l/h value of 5.0 was not the highest value possible for these animals.

Furthermore, the conservative nature of theropod appendicular anatomy suggests that if small to medium-sized species were capable of l/h values in excess of 5.0 the value of 3.0 used in this paper for large species is probably reasonable, if not also on the conservative side. Thus it would appear that ALEXANDER's (1991, 1996) suggestions of trying to outrun *Tyrannosaurus* would be an unfortunate strategy, unless it was attempted from horseback.

cript. The author, however, is the only one responsible for the conclusions and suggestions presented in the paper.

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