

Per CHRISTIANSEN

Zoological Museum, Department of Vertebrates. Universitetsparken 15, 2100 COPENHAGEN Ø. DENMARK E-mail: p2christiansen@zmuc.ku.dk

Gregory S. PAUL

3109 North Calvert St., Side Apt. BALTIMORE MD 21218. USA E-mail: GSP1954@aol.com

ABSTRACT: Ceratopsid dinosaurs have traditionally been restored with sprawling forelimbs and were considered unable to run at high speeds. However, recent analyses on forelimb functional anatomy strongly suggest that their limbs operated in a near parasagittal manner, with elbows only moderately averted. As such, the allometric trends of their appendicular anatomy may be compared to those of mammals. The long bones usually scale with similar regression slopes to those of mammals, but in some instances (e.g. forelimb length) the intercept is slightly lower in ceratopsians. Ceratopsians have rather long limbs compared to extant large mammals, such as rhinos, especially hindlimbs, and their forelimbs are not proportionally as short as is usually assumed. Limb proportions indicate that the locomotory potential of ceratopsids could have been comparable to extant tapirs and rhinoceroses. Protoceratopsids appear to have been relatively more agile, which is to be expected from their smaller size alone. Analyses of bone strength confirm the similarity to extant large mediportal to subcursorial mammals, such as large bovids and rhinoceroses, indicating that even large forms were adapted to locomotor performances exceeding those of extant elephants. The running performance of even the largest ceratopsids is restored as significantly exceeding that of elephants, and being broadly similar to that of rhinos.

INTRODUCTION

The Neoceratopsia was a fairly numerous dinosaurian clade in terms of species, that ranged from Aptian-Albian to Late Maastrichtian (DODSON & CURRIE, 1990; Dodson, pers. comm., 1998), and appear to have been extremely abundant in the case of certain taxa, as suggested by the enormity of some bonebeds. Their sister group, the Psittacosauridae, appear to have been restricted to Asia, whereas the Neoceratopsia had spread to North America also. The ceratopsids were strictly North American animals and have often been considered the dinosaurian equivalent to the Rhinocerotidae, due to convergent resemblances in overall morphology (e.g. ALEXANDER, 1985, 1989, 1991; BAKKER, 1986, 1987).

Substantial controversy has been generated as to the forelimb posture and mode of locomotion in these animals (e.g. BAKKER, 1986; CZERKAS & CZERKAS, 1990; DODSON, 1996; DODSON & FAR-

LOW, 1997; JOHNSON & OSTROM, 1995; PAUL & CHRISTIANSEN, 2000). Recent detailed analyses of forelimb functional morphology have shown that both the forelimbs and hindlimbs clearly operated in a near parasagittal plane, as in large mammals (FORD, 1997; PAUL & CHRISTIANSEN, 2000). This is been confirmed by studies of trackways (LOCKLEY & HUNT, 1995; FORD, 1997). Several aspects of the functional anatomy and morphology of the limbs also resemble features found in large mammals (COOMBS, 1978), and the bone strength of the large form *Triceratops* has been used to assess locomotory potential in large ceratopsids (ALEXANDER, 1985, 1989, 1991).

Most ceratopsid genera were large, although no larger than extant rhinos, but *Triceratops*, *Torosaurus* and *Pentaceratops* were elephant-sized (PAUL, 1997; PAUL & CHRISTIANSEN, 2000). It has been controversial whether protoceratopsids sometimes employed bipedality during fast locómotion (BAK-

KER, 1968; COOMBS, 1978) or remained quadrupedal (THULBORN, 1982; TERESHCHENKO, 1994). The size and overall morphology of ceratopsids makes it unlikely that they employed bipedality, despite the fact that their forelimbs are often considered to have been proportionally short (e.g. THULBORN, 1982; BAKKER, 1986; DODSON & CURRIE, 1990).

Ceratopsians, especially large ceratopsids, appear to have had powerful limbs, and a superficial glance at a mounted skeleton invokes the impression of a massive appendicular anatomy. Apart from more generalized comparisons with extant mammals (COOMBS, 1978; BAKKER, 1980, 1986, 1987) long bone allometry has not previously been investigated. Although BAKKER (1980), in his analysis of bone proportions in dinosaurs, did not calculate regression equations, he did note that femoral length scaled approximately to circumference^{0.67}, as predicted by the theory of elastic similarity (MCMAHON, 1973, 1975a, b). However, ALEXANDER et al. (1979a), BIEWENER (1983) and CHRISTIANSEN (1999a, b) found that analysing a larger sample of extant mammals usually yields values closer to geometric similarity, predicting lengths proportional to circumference.

Rather than increased positive bone allometry mammals evolve increasingly more vertical limb postures as a means of decreasing the bending and torsional stresses set up in their diaphyses during locomotion, which tend to distort the bones about their long axes. More upright limb postures favour increased axial stresses, acting along the long axes of the bones and setting up compressive stresses only. More upright limbs decrease the amount of muscular force required for locomotion by increasing the effective mechanical advantage of the muscles (see BIEWENER, 1989b for details), which reduces the mass specific amount of force the muscles must exert to counteract moments about the joints. This accounts for most of the reduction in bone stress among small to rather large extant mammals (BIEWENER, 1989a, b, 1990).

However, largely geometric scaling and subsequent postural changes in mammals appear only to apply up to a body mass of about 300 kilograms (BIEWENER, 1989b, 1990), after which either decreases in locomotory performance and/or increased skeletal allometry maintains peak stresses at similar levels. This is probably so, because at this body size the limbs have become nearly straight and pillar-like limbs are unfit for fast locomotion. BERTRAM & BIEWENER (1990) and CHRISTIANSEN

(1999a, b) found that limb bones in mammals become increasingly positively allometric as species size increases. The former authors suggested that mammals only scale geometrically at body sizes below 100 kg, after which skeletal allometry increases, apparently reaching its maximum among 300 kg animals, e.g. large ceratomorphs (PROTHERO & SERENO, 1982).

The allometric trends of ceratopsian appendicular anatomy has not previously been investigated, nor compared to those of extant mammals. Also, the limb proportion analysis done by COOMBS (1978), to assess locomotory potentials in dinosaurs, used a reference set of mammals of which many were extinct. Although there is little reason to suppose that COOMBS (1978) did not assess the locomotory capabilities of the extinct mammals fairly accurately, a reference data set should be as free of assumptions as possible in order to be reliable. In this paper we present analyses of long bone allometry and limb proportions in ceratopsians, and compare them to extant mammals. Additionally, we have calculated the body masses, centres of gravity and strength indicator values for the long bones of several ceratopsian taxa, and these may also give indication of the locomotory capabilities of the animals (e.g. ALEXAN-DER, 1985, 1989, 1991).

MATERIALS AND METHODS

LIMB SCALING ANALYSES

For comparison of bone proportions to body mass in ceratopsians and mammals a reference set of 66 species of extant mammals was used, spanning a large size range from 1,2 kg Fennecus zerda to 6250 kg Loxodonta africana (see Fig. 1). All mammals are housed at the Zoological Museum in Copenhagen, and all had been weighed prior to, or most frequently, just after death. Thus, for mammals the masses employed are the actual masses of the skeletal specimens, not averages from literature. We calculated the masses of 11 neoceratopsian dinosaurs representing 7 species (APPENDIX I), by constructing plasticine models based on detailed measurements taken directly on the skeletons and assuming a density of 950 kg.m⁻³. Most modern animals have densities close to that of water (e.g. ALEX-ANDER, 1985, 1989), although some authors have used lower estimates of density for dinosaurs (COL-BERT, 1962; BAKKER, 1980).

The method of weighing in air and water was employed (ALEXANDER, 1985, 1989), which is based on the Principle of Archimedes, stating that an object

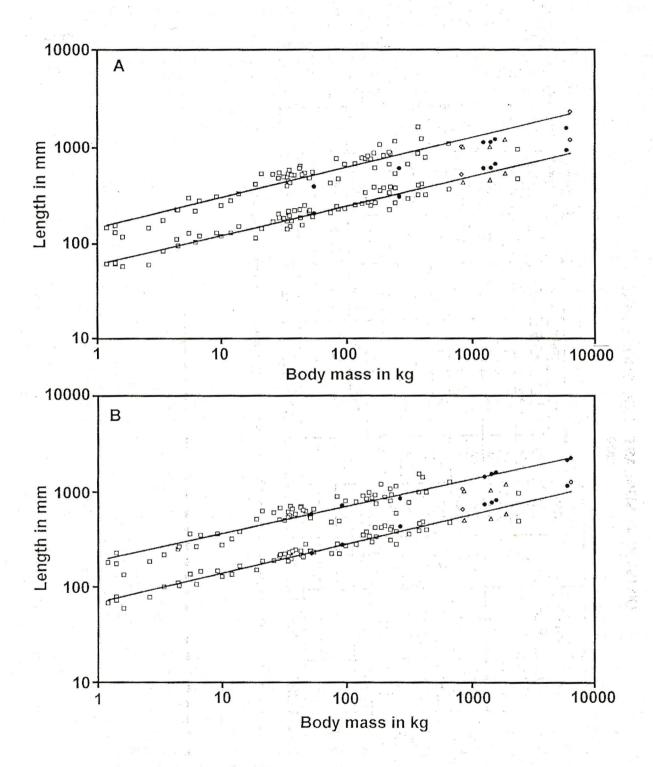


Fig. 1 - Body mass and limb lengths and propodial lengths, respectively, in mammals and ceratopsian dinosaurs. A - Body mass to forelimb length (upper regression line) in mammals (n = 66; Y = $148.16 \, \text{X}^{0.296}$; r = 0.936), and body mass to humeral length (lower regression line) in mammals (n = 67; Y = $60.61 \, \text{X}^{0.289}$; r = 0.962). B - Body mass to hindlimb length (upper regression line) in mammals (n = 66; Y = $192.36 \, \text{X}^{0.274}$; r = 0.925), and body mass to femoral length (lower regression line) in mammals (n = 67; Y = $70.19 \, \text{X}^{0.296}$; r = 0.971). Symbols: •: ceratopsians (n = 66 [humerus] and 7 [femur]); \triangle : rhinoceroces (n = 3); \lozenge : elephants (n = 2); \square : other mammals (n = 61).

immersed in a fluid will be buoyed upwards by a force equivalent to the amount of fluid it displaces. Unfortunately, most mounted skeletons are composites, although not the three *Protoceratops* specimens from APPENDIX I. It is nevertheless assumed that the proportions of the included specimens are accurate. Even the well-known *Triceratops* is not known from a single complete skeleton (DODSON & CURRIE, 1990; DODSON, 1996; GARSTKA & BURNHAM, 1997).

The many *Pachyrhinosaurus* bones included in APPENDIX I, including the mounted skeletons, are not from the Scabby Butte locality of the holotype (STERNBERG, 1950; LANGSTON, 1967, 1968, 1975) but were collected in the Wapiti Formation at Pipestone Creek (TANKE, 1988) and are significantly smaller than the first specimens recognized of this species. DODSON (1996) suggested that it may represent a different species, which appears entirely likely, but until this has been properly analysed we prefer the conservative approach, and keep it in *Pachyrhinosaurus canadensis*.

Intrabone allometry of the 3 major long bones (humerus, femur and tibia) was also compared in ceratopsians and mammals, using a large reference data set on extant mammals, including over 200 species and spanning in excess of four orders of magnitude in mass (see Fig. 2). Most mammals are housed at the Zoological Museum in Copenhagen, although additional data were collected from museums across Europe and USA.

Regression lines were fitted to the data by means of least squares regression after transformation to logarithms and confidence limits were calculated for the exponents. We also tested the calculated regression exponents for ceratopsians for significance against the corresponding values calculated for mammals, and for significant departure from geometric and elastic similarity (sensu MCMAHON, 1973). In mammals only one specimen per species was used for calculation of the regression equations, and for ceratopsians the values for species with multiple specimens were averaged prior to analysis in order not to bias the samples. However, in the analyses of intra-bone allometry, the ceratopsian specimens with an uncertain identity (APPEN-DIX I, Ceratopsidae sp.) were not averaged prior to analysis. This of course introduces an amount of uncertainty as some are probably from species already included. This could especially be the case in the humerus sample where the unidentified category makes up half of the sample.

LIMB PROPORTIONS ANALYSES

Inter-limb proportions have previously been used to assess locomotory potential in dinosaurs, as fast moving animals usually have long gracile limbs with hinge-like joints, large and proximally placed limb muscles, long epi - and particularly metapodia and rather short propodia (COOMBS, 1978). Fastmoving quadrupeds usually also have mobile scapulae, and this was probably the case in ceratopsians as well (FORD, 1997; PAUL, 1991; PAUL & CHRISTIANSEN, 2000).

Attempting to assess the locomotory potential of dinosaurs COOMBS (1978), following GREGORY (1912), subdivided a reference set of mammals into four rather arbitrary locomotory categories based on appendicular morphology, unfortunately relying heavily on extinct taxa, for which locomotion cannot be observed. Graviportal animals have short and broad metapodia that are generally unreduced in number and plantigrade, often columnar limbs, short epipodia, long propodia, and in general lack any adaptations for fast locomotion. Proboscideans, ground sloths, glyptodonts and the giant marsupial Diprotodon are examples of graviportal animals. Graviportal animals are capable of only fast walking or ambling. However, due to the size of especially elephants this does not necessarily imply that they are slow in absolute measure (km.h⁻¹).

Mediportal animals have moderate adaptations for fast locomotion, notably often relatively longer metapodia, a semidigitigrade stance and flexed joints, potentially allowing a true running gait, but the appendicular anatomy appears primarily adapted for support of mass. Extant mediportal animals range from forms capable of a fast trot, as in hippos, to forms capable of a moderately fast run with a suspended phase, such as rhinos, tapirs and ursids. Subcursorial animals have limbs extensively modified for fast locomotion and in cursorial forms this is taken to extremes.

Note that *Acinonyx* in this analysis is included in the cursorial category, despite grouping anatomically at the upper range of subcursors (Coombs, 1978). This was decided due to the extreme velocity reached by this animal, verified to be well in excess of 100 km.h⁻¹ (Sharp, 1997). In *Acinonyx* dorsoventral mobility of the dorsal vertebral column as a means of increasing stride length is an important contributing factor for attaining this remarkable velocity (GAMBARYAN, 1974; NOWAK, 1991).

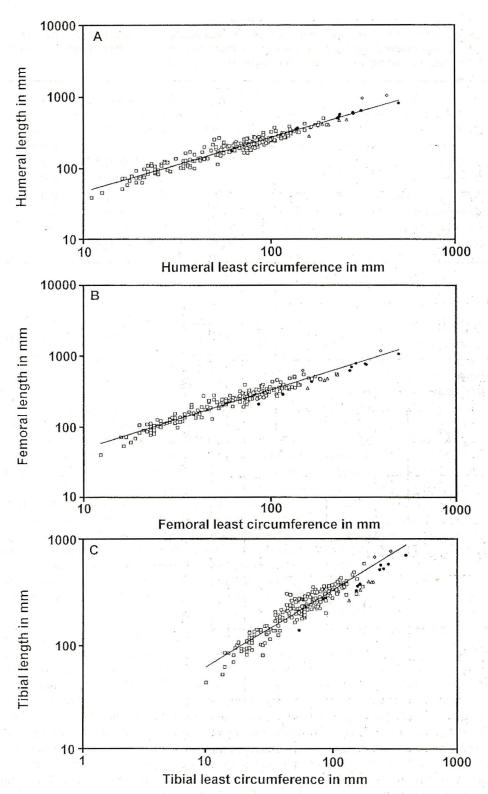


Fig. 2 - Long bone allometry in mammals and ceratopsian dinosaurs. A - Least circumference of humeral diaphysis against length of humerus in mammals and ceratopsian dinosaurs. Regression line for mammals (n = 201; Y = 8.19 \times 1.762; r = 0.962). B - Least circumference of femoral diaphysis against length of femur in mammals and ceratopsian dinosaurs. Regression line for mammals (n = 201; Y = 7.252 \times 1.829; r = 0.962). C - Least circumference of tibial diaphysis against length of tibia in mammals and ceratopsian dinosaurs. Regression line for mammals (n = 203; Y = 11.84 \times 1.84 \times 1.85 \times 1.85

TABLE I
Regression equations and correlation coefficients for limb allometry in neoceratopsian dinosaurs. n is number of species. All linear dimensions are in millimeters and body mass is in kilograms. An asterisk after the regression slope indicates significance from the corresponding value calculated for mammals (Fig. 1-2).

X	Υ	n	а	B + 95 5 CI	r 0.992	
Body mass	Forelimb length	6	109.05	0.304±0.052		
Body mass	Humeral length	6	51.21	0.326±0.055	0.993	
Body mass	Hindlimb length	7	194.87	0.274±0.033	0.995	
Body mass	Femoral length	7	58.52	0.343±0.013*	0.997	
Body mass	Hum. + fem. least circ.	5	34.91	0.385±0.029	0.999	
Humeral least circ.	Humeral length	14	7.17	0.762±0.065	0.992	
Femoral least circ.	Femoral length	9	3.03	0.960±0.105*	0.993	
Tibial least circ.	Tibial length	11	8.00	0.726±0.138	0.973	

BONE STRENGTH ANALYSES

When animals move the forces acting on their limbs are proportional to mg (ALEXANDER, 1985, 1989), where m is body mass and g is the gravitational constant. When two animals move in a dynamically similar fashion, which means that differences in the cadences of the limbs or absolute speed may be cancelled out by multiplying the motions of one animal by a constant factor of the linear dimensions, time intervals or forces involved (ALEX-ANDER & JAYES, 1983), the peak stress in their diaphyses will be proportional to mgx/Z (ALEXANDER, 1983a, 1985, 1989, 1991; ALEXANDER & POND, 1992). Z is the section modulus, a geometric property describing the proportions of the cross section of the diaphysis for bending in a parasagittal plane, and x is the distance from the cross section to the epiphysis. For quadrupedal animals, such as most mammals or neoceratopsian dinosaurs, mgx is multiplied by a_f or a_h, which is the fraction of total body mass supported by the fore and hindlimbs, respectively.

As such, ALEXANDER (1983a, 1985, 1989, 1991) argued that the reciprocal value Z/amgx would be a useful indicator of the strength of the bones, and thus their ability to withstand rigorous physical activity. The safety factors of limb bones, *i.e.* the relationship between yield strength of the bone and peak stress during fast locomotion or strenuous jumping, is usually 2-4 in recent mammals as diverse as dogs and elephants (BIEWENER, 1989a, 1989b, 1990), and even locusts (ALEXANDER, 1981). This indicates that safety factors are probably heavily constrained and implies that it is reasonable to suppose that this was also the case for extinct animals. Recently, how-

ever, BLOB & BIEWENER (1997) found greater safety factors for hind limb bones of sprawling reptiles, suggesting that the above may hold primarily for animals with an upright limb posture, such as larger mammals and dinosaurs.

Fossil bones have been geochemically altered and thus the mechanical properties of the bone tissue cannot be measured directly. However, bone structure in extinct and extant animals is basically identical and the tissue properties in extant tetrapods, and hence strength per cross sectional area, is largely the same over a wide phylogenetic spectrum (BIEWENER, 1982, 1990). The above indicates that the strength indicator value should apply to dinosaurs also. A higher value of Z/amgx implies greater resistance to mechanical failure and hence greater potential for rigorous physical activity, although it does not prove superior athletic abilities for the animals in question.

In addition to ceratopsian dinosaurs, we calculated strength indicator values for a number of large mammals, spanning all of the above mentioned four locomotor categories. The included mammals were mainly from zoological gardens and safari parks, and all had been weighed just after death. All values were calculated using external bone dimensions. In order to calculate the section modulus of a bone with a hollow medullary cavity the cortical thickness will have to be known. Many mammals have hollow long bones. Fractured long bones of large ceratopsids, however, usually display only a small medullary cavity (pers. obs.). Thus, ignoring the influence of the medullary cavity should introduce little error in the final estimate. The body mass of ceratopsians (AP-PENDIX I) was calculated using the water

TABLE II
Strength indicator values of mammalian and ceratopsian limb bones. The values of Z/amgx are in Gpa⁻¹.

	MASS	a_{f}	a _h _				
Taxon	(kg)	, , ,		Humerus	FEMUR	Тівіа	
CERATOPSIA							
Protoceratops ¹	44	0.40	0.60	44.87	62.47	49.94	
Protoceratops ¹	45	0.40	0.60	49.20	47.77	38.96	
Centrosaurus ¹	1280	0.44	0.56	36.53	25.36	21.74	
Pachyrhinosaurus ²	1450	0.45	0.55	24.65	22.61	13.97	
Pachyrhinosaurus ²	1475	0.45	0.55	26.87	24.05	28.86	
Chasmosaurus ²	1495	0.45	0.55	36.10	29.55	26.25	
Chasmosaurus ²	1685	0.45	0.55	22.28	25.72	11.51	
Triceratops ¹	5850		0.52	26.01	13.65	13.67	
PROBOSCIDEA					,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,		
Elephas maximus ³	850	0.58	0.42	9.95	9.74	-	
Elephas maximus ³	3534	0.58	0.42	12.00	12.66	8.97	
Loxodonta africana ³	6250	0.58	0.42	12.62	10.04	7.04	
PERISSODACTYLA							
Equus caballus ¹	675	0.55	0.45	20.70	30.29	11.64	
Equus burchelli ¹	136	0.55	0.45	45.84	63.02	38.09	
Tapirus indicus ⁴	317	0.54	0.46	27.61	20.55	14.03	
Rhinoceros sondaicus ⁵	1475	0.52	0.48	24.74	19.80	16.39	
Ceratotherium simum ⁵	1900	0.52	0.48	24.42	12.44	14.97	
Diceros bicornis ⁵	875	0.52	0.48	34.78	29.64	29.70	
ARTIODACTYLA		0.02		0 0	20.0	20.70	
Hippopotamus amphibius ⁴	680	0.54	0.46	18.45	16.99	19.47	
Hippopotamus amphibius ⁴	2400	0.54	0.46	8.87	6.55	6.13	
Choeropsis liberiensis ⁴	250	0.54	0.46	21.52	16.65	19.27	
Synserus caffer ⁶	440	0.56	0.44	30.90	26.02	14.48	
Bison bonasus ⁶	225	0.56	0.44	29.50	26.79	16.38	
Bubalus bubalis ⁶	382	0.56	0.44	23.08	18.01	15.28	
Tragelaphus strepsiceros ⁷	190:	0.55	0.45	36.41	37.91	21.09	
Okapia johnstoni ⁷	310	0.55	0.45	29.14	28.50	24.85	

^{1 -} Distribution of mass found by suspension of model. For the horses a model of Equus caballus was used and Equus burchelli was assumed be similar. 2 - Distribution of mass found by suspension of model of Chasmosaurus and Pachyrhinosaurus was assumed to be similar. 3 - Mass distribution of Elephas from ALEXANDER (1989) and Loxodonta was assumed to be similar. 4 - Mass distribution of Hippopotamus found by suspension of model and Choeropsis and Tapirus were assumed to be similar. 5 - Mass distribution of Rhinoceros found by suspension of model and Diceros and Ceratotherium were assumed to be similar. 6 - Mass distribution of Bos taurus from ROLLINSON & MARTIN (1981) and Syncerus, Bison and Bubalus were assumed to be similar. 7 - Mass distribution of Lama from ROLLINSON & MARTIN (1981) and Tragelaphus and Okapia were assumed to be similar.

displacement method described above. The values of a_f and a_h were found by suspension of scale models (ALEXANDER, 1983b) or taken from literature, as appropriate (see TABLE II).

RESULTS

LIMB SCALING ANALYSES

All the regression equations are shown in TABLE I, and as can be seen all correlation coefficients in ceratopsian dinosaurs are extremely high, often ex-

ceeding 0.99. The corresponding regression equations and correlation coefficients for mammals are shown with the various figures.

Figure 1A is a comparison of humeral length and total forelimb length to body mass in mammals and ceratopsian dinosaurs, the latter given as the combined lengths of humerus, radius and the longest metacarpal. Total forelimb length in mammals shows negative allometry with size. Additionally, large species have even shorter limbs than predicted, presumably as a means of preserving limb

bone strength by reducing the size of the lever arm of the bending and torsional moments about the diaphyses (CHRISTIANSEN, 1999a). However, the African elephant is long-limbed and has a total forelimb length close to the predicted value, probably due to the markedly decreased locomotory performance of elephants compared to rhinos (ALEXANDER et al., 1979b; ALEXANDER & POND, 1992). Having long limbs and rather slender diaphyses (ALEXANDER et al., 1979a; CHRISTIANSEN, 1997, 1999a, b) at a large body mass makes running impossible, as the limb bones are not strong enough to allow running, as pointed out by ALEXANDER et al. (1979b).

Ceratopsid forelimb lengths are rhinoceros-like as they are 79-89% of the predicted values for mammals of similar body masses, compared to 72-84% for extant rhinos. Compared to body mass the ceratopsid forelimb does not appear as short as it is usually considered. The average value for the three *Protoceratops* specimens and *Avaceratops*, however, are considerably shorter, being 76% and 72%, respectively, of the predicted values for comparably sized mammals.

The humeri of ceratopsids are proportionally long (Fig. 1A), and considerably exceed the corresponding values for rhinos, and the hippo in the case of the large ceratopsids, with *Protoceratops* and *Avaceratops* falling close to the regression line. In large mammals the humeri are shorter than predicted, being 73% of the predicted value in *Hippopotamus*, 83-92% in the rhinos, and among the megaherbivore mammals only the elephants have humeri of comparable length to the large ceratopsids, which is in accordance with the results of ALEXANDER *et al.* (1979a) and CHRISTIANSEN (1999a).

Total forelimb length and humeral length in mammals scale somewhat intermediately between the predicted values for elastic similarity, as per MCMA-HON (1973, 1975a, b) (Fig. 1A), which predicts bone length proportional to M^{0.25}, and isometry, which predicts bone length proportional to M^{0.33}. The corresponding values for ceratopsians are slightly higher (TABLE I), and both the forelimb exponent and the humeral exponent are in fact geometrically similar $(t_4 = 1.3784; 0.30 > p > 0.20 \text{ and } t_4 = 0.5946;$ 0.60>p>0.50 for forelimb and humerus, respectively). The exponent for humerus length is significantly different from elastic similarity ($t_4 = 2.9290$; 0.05>p>0.02), but the exponent for forelimb length is not ($t_4 = 2.6908$; 0.10>p>0.05), due to the low sample size making a rejection of the null hypothesis more difficult.

In contrast to the forelimb, total hindlimb lengths compared to body mass in ceratopsians fall close to the predicted values for similarly sized mammals, as in elephants, but are much longer than in rhinos (Fig. 1B). As with the forelimb, the length of the hindlimb appears primarily to be due to the long propodium. In contrast to the proportions of the forelimb, the ceratopsian hindlimb propodia (femora) are so long that they make total hindlimb lengths fall close to the predicted values. Total limb length and femoral length, respectively, compared to body mass in ceratopsids are comparable to elephants only, and clearly longer than in rhinos or hippos.

Total hindlimb length in mammals and ceratopsians scale close to the theory of elastic similarity, with very similar exponents (TABLE I; Fig. 1B; for ceratopsians $t_5 = 0.9496$; 0.40>p>0.30), whereas femoral length in ceratopsians scales isometrically (TABLE II; $t_5 = 0.8640$; 0.50>p>0.40). Most length exponents for mammals are intermediate between isometry and elastic similarity and thus at odds with the results of both ALEXANDER et al. (1979a) who found the former to be the case, and McMahon (1973, 1975b) who found the latter, which formed the basis for mathematically introducing the theory of elastic similarity (MCMAHON, 1975a). When analyzing a large data set of mammals neither elastic not geometric similarity is able to explain long bone scaling (CHRISTIANSEN, 1999a, b). Thus, if extant animals fail to conform to the above across a large size spectrum, it is perhaps less surprising that ceratopsians should fail to do as well. In all cases the correlation coefficients for the mammal samples are high, and for the ceratopsians samples they exceed 0.99.

In the data sets for mammals (Fig. 1) some of the length exponents indicate a tendency towards elastic similarity, and hence negative allometry among mammals as a group, which appears to be at odds with the findings of ALEXANDER et al. (1979a). However, our data set is almost twice as large the one used by ALEXANDER et al. (1979a) and includes many more large species, obscuring the greater degree of isometry displayed by the smaller species, as also suggested by ECONOMOS (1983), BERTRAM & BIEWENER (1990) and CHRISTIANSEN (1999b). BAKKER's (1980) analysis on bone proportions in dinosaurs was mainly on large to very large forms, and thus could be expected to display positive allometric scaling.

Intra-bone allometry (Fig. 2A-C) displays high correlation coefficients for mammals, and particularly high for ceratopsians (TABLE I), which would make Model II regression equations virtually identi-

cal to the ones calculated by least squares regression. For geometrically similar animals length would be proportional to least circumference whereas elastic similarity predicts length proportional to circumference^{0.67}.

Ceratopsian humeri are robust, considerably more so than elephant humeri, although not with quite as massive diaphyses compared to length as in rhinoceroses (Fig. 2A). Humeral scaling in ceratopsians does not conform exactly to elastic similarity (TABLE I). The exponent for humerus is not significantly different from elastic similarity (0.10>p>0.05). The exponent for humerus is significantly different from geometric similarity (p<0.001). The humerus of *Triceratops*, despite visually appearing extraordinarily massive, actually falls close to the predicted value (Fig. 2A). Both the coefficient and exponent of the regression equation for humerus in ceratopsians are very similar to the corresponding constants for mammals (TABLE I; Fig. 2A).

In contrast, intraspecific humeral scaling in Pachyrhinosaurus displays a steeper regression slope than all ceratopsians (n = 20; Y = 5.330 $X^{0.858\pm0.092}$; r = 0.977). The limbs of very large mammals, which are precluded from using postural changes as compensation for further increases in body size, apparently scale with extreme allometry (PROTHERO & SERENO, 1982) conforming quite closely to the theory of static stress similarity (MCMAHON, 1975a), predicting length to circumference^{0.5}. This is clearly not the case in ceratopsian dinosaurs, despite the highly flexed elbows of all ceratopsians, even the huge chasmosaurines (BAK-KER, 1986; DODSON, 1996; FORD, 1997; PAUL, 1991; PAUL & CHRISTIANSEN, 2000). The humeri apparently are so massive among smaller individuals that even when scaling isometrically the humeri of large specimens remain proportionally sturdy.

Femoral circumference to length (Fig. 2B) in ceratopsians scales isometrically (TABLE I; t_4 = 2.5299; 0.10>p>0.05), but it is significantly different from elastic similarity (t_4 = 7.5897; p<0.001). The intercept is only about half of the corresponding value for mammals (TABLE I; Fig. 2B), and the slope of the latter is lower. An intraspecific regression equation for *Pachyrhinosaurus* has a slightly higher coefficient and lower exponent (n = 20; Y = 4.740 $X^{0.886\pm0.097}$; r = 0.982). The exponent for tibiae in ceratopsians is significantly different from geometric similarity (t_6 = 3.2324; 0.02>p>0.01) but not from elastic similarity (t_6 = 1.7221; 0.20>p>0.10). The exponent is closer to the value of mammals, but the coefficient is lower (TABLE I; Fig. 2C).

The femora and especially tibiae of ceratopsians are consistently more massive than in mammals as a group, and much more so than in elephants (Fig. 2A-C). *Centrosaurus* and especially *Pachyrhinosaurus* have considerably higher exponents for the tibiae than either mammals or ceratopsians as a group (*Centrosaurus*: n = 5; $Y = 4.218 \, X^{0.866\pm0.160}$; r = 0.995; *Pachyrhinosaurus*: n = 14; $Y = 3.322 \, X^{0.930\pm0.127}$; r = 0.976). In none of the above cases do mammals scale according to geometric similarity.

LIMB PROPORTION ANALYSES

A reference data set consisting of a large number of extant mammals divided into the above four locomotory categories was used for comparison with ceratopsians (Fig. 3). A few mammals were extinct forms, but they were all graviportal proboscideans. The forelimb proportions of the ceratopsians cluster at the lower range of both the metacarpus/humerus ratio and the radius/humerus ratio. Although there is clear separation of the cursorial mammals from the other groups (Fig. 3A), mainly in their considerably greater metacarpus/humerus ratios, the separation among the really large forms in the graviportal and mediportal categories is not pronounced, as also found by COOMBS (1978). Elephants have metacarpus/humerus ratios of around 0.17-0.22, which is lower than in rhinos or hippos (around 0.40), but not very different from those of ceratopsids (0.22-0.28). However, the similarity of this ratio in hippos and rhinos indicates that it is not a particularly reliable indicator of locomotor performance, as rhinos are capable of substantially faster running than hippos (e.g. ALEXANDER & POND, 1992; NOWAK, 1991).

When comparing similar sized ceratopsids to rhinos, e.g. a Chasmosaurus belli with a predicted body mass of 1685 kg (APPENDIX I) to a 1900 kg Ceratotherium, the longest metacarpal in the former (142 mm) is considerably shorter than in the latter (192 mm). The metacarpals of Triceratops are 20% longer than in the African elephant. The moderately long metacarpals, limbs with permanent joint flexure, large limb bone muscle attachment sites and digitigrade stance of ceratopsians tend to group them with mediportal mammals.

The hindlimb proportions are less equivocal (Fig. 3B), and the four categories show much less overlap than was the case for the forelimb. The lowest tibiofemoral values in ceratopsids are still within the graviportal range but overall they tend to group more closely with the mediportals. The metatarsus/femur ratios of ceratopsids clearly fall within the range of the mediportal mammals and are considerably

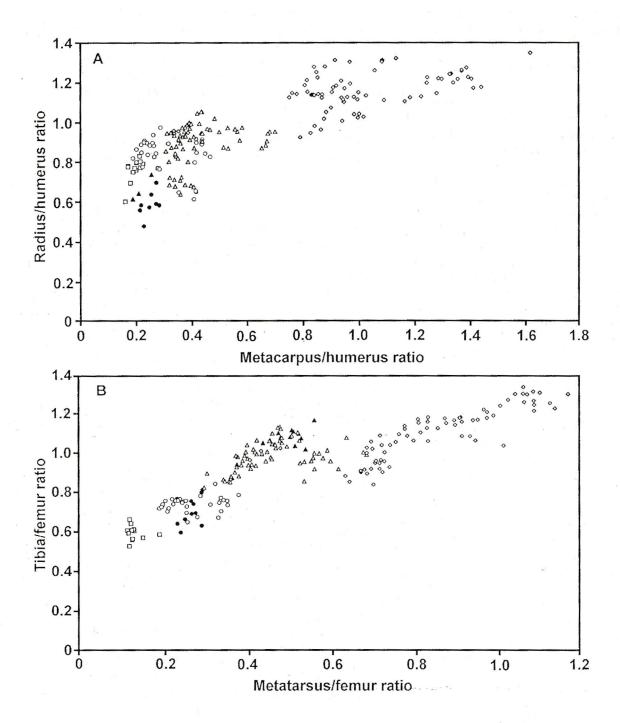


Fig. 3 - Limb proportions in mammals and ceratopsian dinosaurs. In addition to extant mammals, a few extinct taxa were included, but they were all graviportal proboscideans. A - Forelimb porportions. B - Hindlimb proportions. Symbols:

▲: protoceratopsids (*Leptoceratops*, *Microceratops* [hindlimb only], *Protoceratops*); ●: ceratopsids (*Avaceratops*, *Centrosaurus*, *Chasmosaurus*, *Pachyrhinosaurus*, *Triceratops*); □: graviportal mammals (*Amebelodon*, *Cuvieronius*, *Gomphotherium*, *Elephas*, *Loxodonta*, *Mammuthus*); ①: mediportal mammals (*Ceratotherium*, *Choeropsis*, *Diceros*, *Hippopotamus*, *Rhinoceros*, *Tapirus*, *Ursus*); △: subcursorial mammals (*Alopex*, *Bison*, *Bos*, *Bubalus*, *Canis*, *Cerdocyon*, *Chrysocyon*, *Felis*, *Lycalopex*, *Lycaon*, *Neofelis*, *Ovibos*, *Panthera*, *Phacochoerus*, *Potamochoerus*, *Sus*, *Syncerus*, *Tayassu*, *Urocyon*, *Vulpes*); ◊: cursorial mammals (*Acinonyx*, *Aepyceros*, *Alcelaphus*, *Antidorcas*, *Antilope*, *Boselaphus*, *Camelus*, *Cephalophus*, *Connochaetes*, *Equus*, *Gazella*, *Hippotragus*, *Kobus*, *Lama*, *Litocranius*, *Okapia*, *Oryx*, *Redunca*, *Saiga*, *Sylvicapra*).

higher than in graviportal animals. This measure apparently is a superior predictor of locomotor performance to the tibia/femur ratio (GARLAND & JANIS, 1993). Protoceratopsids cluster within the upper range of subcursorial mammals. Thus, the conclusions of COOMBS (1978) and THULBORN (1982), that protoceratopsids were probably swift and agile are supported by our data. As with the forelimb, no ceratopsian approaches the range of the cursorial mammals. The discrepancy between the gracility of the forelimbs and hindlimbs of protoceratopsids indicate the possibility of bipedalism during fast locomotion, although forms with proportionally large heads, such as Leptoceratops (PAUL, 1997; PAUL & CHRIS-TIANSEN, 2000) would probably have encountered problems of balance if running bipedally.

Evidently ceratopsian dinosaurs were rather long-limbed animals (Fig. 1, 3), even in the case of the forelimb, and among large ceratopsids the relative lengths of the hindlimbs are comparable to elephants only. The limb bone ratios of ceratopsids usually fall within the mediportal range, with protoceratopsids being somewhat more gracile, as could be expected from their smaller size. The results from limb proportions support the suggestions of COOMBS (1978) that ceratopsids could have been low to intermediate grade mediportal animals, roughly equivalent in locomotory potential to extant rhinos.

However, although limb length is correlated to locomotor behaviour in extant animals such as the Carnivora (HARRIS & STEUDEL, 1997), peak locomotor performance has been found to be rather similar in African ungulates with varying limb lengths to body mass and different limb bone ratios, e.g. warthog and topi (ALEXANDER, LANGMAN & JAYES, 1977). Among fully cursorial mammals of roughly similar osteoanatomy, GARLAND & JANIS (1993) found that limb length is a better predictor of peak locomotor performance than limb bone ratios. Hyaenids and felids have shorter and stockier limbs than comparably sized ungulates. Particularly their metapodials are much shorter than the fused cannon bones of artiodactyls and third metapodial of extant equids. However, the top speed appears not to vary considerably between the carnivores and their prey (e.g. ESTES & GODDARD, 1967; GAMBARYAN, 1974; NOWAK, 1991; GARLAND & JANIS, 1993). Unlike COOMBS (1978) we do not feel that limb proportions alone should be used to differentiate locomotor performance in Triceratops from the smaller ceratopsid species given the constancy of their appendicular morphology.

BONE STRENGTH

Ceratopsians, and indeed most dinosaurs, were hindlimb dominant (TABLE II; see also ALEXANDER, 1985, 1989; CHRISTIANSEN, 1997), despite the fact that the enormous heads of many ceratopsians made up one eighth to one quarter of total body mass (FORD, 1997; PAUL, 1997). The capacious belly, the retroverted pubes shifting the abdominal mass further aft than in sauropods, and presence of the large tail (by mammalian standards) are responsible for the posterior placement of the centre of gravity compared to large mammals.

Among extant mammals, the graviportal and lowgrade mediportal taxa such as elephants and Hippopotamus have strength indicator values that are considerably below the values for equally large rhinos, which can run faster (TABLE II). Subcursorial and cursorial mammals have strength indicator values of 25 GPa⁻¹ or more for the humerus whereas the corresponding values for femora and tibiae are slightly lower. This is to be expected as the latter two bones are usually held at a less acute angle to vertical than the former, and thus subjected to less bending and torsional stress during locomotion (CARRANO, 1998). Humeri are also always shorter than femora, and thus the lever arm of the bending moments is also shorter, increasing the strength indicator value.

The strength indicator values of the large white rhinoceros bull are rather lower than expected, but this animal was quite old and had been ill prior to succumbing (CHRISTIANSEN, 1997), which could have affected the girth of the bones. CHRISTIANSEN (1997), however, failed to demonstrate that its long bones were significantly thinner than those of other rhinos. It is thus likely that this low value in fact reflects the true strength indicator value for the femur in large adults. This is at odds with the findings of AL-EXANDER & POND (1992), who suggested that rhinoceroses may be unusually sturdily built. However, the animal used in the analysis of ALEXANDER & POND (1992) was a juvenile, and CHRISTIANSEN (1997, 1998) found that juvenile specimens of large species usually have relatively much stronger long bones than adults. The huge Hippopotamus bull has surprisingly low strength indicator values (TABLE II), but had lived in Copenhagen Zoo for decades and could have been overweight, which is also indicated by the rather impressive body mass of 2400 kg.

The ceratopsian taxa have strength indicator values comparable to those of rhinos and large bovids, and distinctly higher than in elephants or hippos. The tibial values are even considerably higher than

in extant rhinos. The rather short humeri compared to femora and the relatively low percentage of mass supported by the forelimbs, provide the humeri with high strength indicator values. This is to be expected as the humeri were held considerably more horizontally than the femora, and thus would have been subjected to greater bending and torsional forces. Evidently ceratopsid humeri, despite the highly flexed nature of the forelimb and their great length compared to body size (Fig. 1A), were built to withstand this increased stress.

Apart from the humerus, Triceratops has considerably lower strength indicator values than the other large ceratopsids, but higher than the elephant values. However, just as in the large white rhinoceros bull the rather low femoral value could simply reflect the more vertical orientation of this bone compared to the humerus. Along with the morphology and proportions of the limbs it could also indicate, however, that Triceratops was slightly less athletic compared to body size than the smaller ceratopsids, which would not be unexpected from its great size. Still the Triceratops femur is 36% stronger than in the comparably sized African elephant, and the other strength indicator values are similar to those calculated for the white rhinoceros bull. The values for the protoceratopsids are uniformly high, comparable to and even exceeding the corresponding values of small to medium-sized, cursorial ungulates (CHRIS-TIANSEN, 1998).

Previously, strength indicator values in ceratopsians have only been reported for one taxon, namely *Triceratops*, and only for humerus and femur (ALEXANDER, 1985, 1989, 1991). Our values for this animal are slightly higher, but unlike those of Alexander our results are all based on actual measures taken directly on the skeletons and the models used are based on detailed measurements taken from the same skeletal mounts. Thus, we feel that our results are probably more accurate. Our results indicate a quite uniform and powerfully built appendicular anatomy for all large ceratopsids.

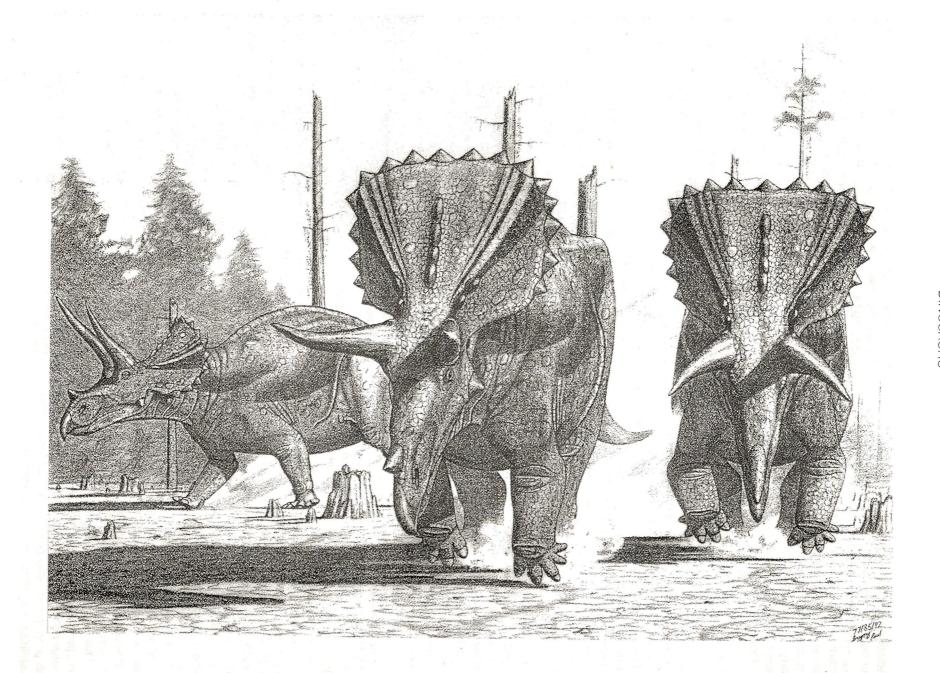
DISCUSSION

The results obtained from calculations of strength indicator values are consistent with our suggestions based on limb bone scaling and limb proportions that the medium-sized ceratopsid species were anatomically comparable to extant rhinos. Thus, it appears likely that their locomotory capabilities were also broadly similar. Triceratops may have been slightly less athletic than the smaller taxa, although evidently built to withstand long bone stresses exceeding those of extant elephants. Along with the functional morphology of the limbs (PAUL & CHRISTIANSEN, 2000), this indicates that the locomotory potential of Triceratops could have been intermediate between extant those of rhinos and hippos, although the great length of its limbs could potentially have provided it with considerably greater absolute speed. Suggestions that protoceratopsids could have been fast-moving, but large ceratopsids were forced to be slow-moving are not supported by the above data. It is also not supported by limb morphology (PAUL & CHRISTIANSEN, 2000).

Strength indicator values are obviously greatly influenced by the estimated mass of the animal, in the case of extinct forms. For example, the model of Triceratops used by COLBERT (1962) was distinctly portly and erroneously proportioned, thus resulting in a suspicously high body mass estimate (8480 kilograms). The method of sand displacement used by COLBERT (1962) also appears crude. Such a great mass would place the long bone strength indicator values for Triceratops squarely within the proboscidean values. In contrast, a recent study by HENDER-SON (1999), using sophisticated computer modelling, resulted in a body mass for *Triceratops* of only 3938 kg. This remarkably low value was the result of a scaling error, in which an adult Triceratops was assumed to be just 6,2 m in overall length. Most specimens are, however, about a meter larger. If scaled to this size Henderson's value would be very similar to the one calculated in this paper.

next page →

Fig. 4 - Restoration of galloping *Triceratops* group. Recent analyses (PAUL & CHRISTIANSEN, 2000) suggest a wider forelimb gauge for ceratopsians, as in this illustration, than has previously been thought (compare to fig. 21 in PAUL, 1987). We suggest that it may have been possible for *Triceratops* to reach the same froude number as the extant white rhinoceros. White rhinos can gallop at speeds of up to 27 km.h⁻¹ (ALEXANDER & POND, 1992). At a hip height of 1.2 m (ALEXANDER, 1991) this implies a froude number of 4.78. At this speed *Triceratops*, at a leg length of 1.98 m, would be travelling close to 35 km.h⁻¹. For *Triceratops* to have reached 27 km.h⁻¹, the proposed peak velocity of the white rhino, it would have needed to reach a froude number of just 2.9. This was almost certainly possible, as white rhinos, and indeed most mammals change from trotting to slow running at froude numbers around 2.55-2.57 (ALEXANDER, 1991).



Predicting the top speed of ceratopsians is a tentative undertaking as no track ways exist that display running. A number of researchers have suggested that extant animals fill the maximum speed potential possible at any given size and that fast animals have body masses ranging from a few to several hundred kilograms, which implies that elephant-sized animals are forced to be relatively slow (GAMBARYAN, 1974; COOMBS, 1978; HALSTEAD & HALSTEAD, 1981; THULBORN, 1982; GARLAND, 1983; BIEWENER, 1989a, b, 1990; FARLOW, SMITH & ROBINSON, 1995).

The suggestions that giant terrestrial animals are forced to be slow due to their size is potentially circular and assumes that extant giants have evolved to be as fast as is physically possible at any given size. In fact, there is reason to suppose that speed can remain fairly high in large terrestrial animals. The mass specific cost of locomotion decreases with increasing size (FEDAK & SEEHERMAN, 1979; LANG-MAN et al., 1995), and stride length increases more rapidly than the decrease in stride frequency (MCMAHON & BONNER, 1983). The columnar limbs of elephants work mainly as inverted pendulums, implying that speed will increase only to the square root of the increase in effective limb length. Equally long limbs with permanent joint flexure could attain longer strides even without a suspended phase. Hinge-like joints and longer metapodials with greater mobility also suggest that ceratopsids were not restricted to an elephantine amble.

BENNETT & DALZELL (1973), RUSSELL (1977), HALSTEAD & HALSTEAD (1981), THULBORN (1982), CZERKAS & CZERKAS (1990), JOHNSON & OSTROM (1995) and DODSON (1996), among others, have credited large ceratopsids with locomotory potentials comparable to or, at best, slightly exceeding those of elephants, and capable of a slow trot at best. However, these authors are also of the opinion that ceratopsid forelimbs displayed a heavy sprawl in the natural pose. The recognition that ceratopsids probably had forelimbs that operated in the near parasagittal plane, albeit with the elbows slightly more averted than in most large mammals (FORD, 1997; PAUL & CHRISTIANSEN, 2000) corroborate the present analyses, demonstrating rather close similarities in bone strength with mediportal and lowintermediate grade subcursorial mammals (Ceratotherium, Diceros, Tapirus, Bison, Bubalus, Syncerus). This makes it likely that ceratopsids, even large forms, probably were capable of similar levels of locomotor activity as these large mammals (Fig. 4). Limb proportions also point to greater locomotory capabilities than those of proboscideans.

There is general agreement that protoceratopsids could have been fast-moving (BAKKER, 1968; COOMBS, 1978; THULBORN, 1982; PAUL, 1987), which is to be expected simply from their smaller size, and speed estimates range from 25-44 km.h⁻¹, but are usually ball-park estimates. More controversial is the speed of large ceratopsids. BAKKER (1968, 1986, 1987), PAUL (1987) and ALEXANDER (1985, 1989, 1991) have suggested that they were able to attain speeds comparable to or somewhat exceeding those of extant rhinos (Fig. 4). ALEXANDER (1991) pointed out that if Triceratops was able to attain the same froude number (v²/gl) as Ceratotherium, which our data suggest was possible, it would be moving about 7,2 km.h⁻¹ faster due to its greater size and limb length.

Thus, it appears possible that the large ceratopsids were in fact faster in absolute measure than extant white rhinos, which are capable of reaching 27 km.h⁻¹ (ALEXANDER, 1989; ALEXANDER & POND, 1992), perhaps more, simply by virtue of their longer limbs. Whether or not they were capable of equalling the top speed of the smaller black rhinoceros, which is usually credited with speeds approaching 50 km.h⁻¹ (e.g. BAKKER, 1986; NOWAK, 1991), is perhaps more doubtful. The bone strengths, however, appear to indicate that the rhinoceros-sized taxa might have been able to. A slow-moving elephantine amble or wide-gauge waddle appears a highly unlikely peak locomotor performance. Thus, ceratopsids may have been the dinosaurian equivalent to the Rhinocerotidae in other respects than just cranial ornamentation.

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APPENDIX I

TAXON	n	ESTIMATED — BODY MASS — (kg)	HUMERUS		Radius Lovæst	FEWUR		TIBIA		LONGEST	
			LENGTH (mm)	MIN. CIRC. (mm)	LENGTH (mm)	METACARPAL (mm)	LENGTH (mm)	MIN. CIRC. (mm)	LENGTH (mm)	MN. GRC. (mm)	METATARSAL (mm)
PROTOCERATOPSIDAE					276	V V V T		1			
Leptoceratops gracilis	1	_	299	25	192	62		_			
Leotoceratops gracilis	1	_	1-	· 2	-	_	230	-	240	_	100
Leatoceratops gracilis	1	_	-	_	_	_3	256	_	280	100	125
Leptoceratops gracilis	1	93	-	_	_	2.5	270	_	290		135
Maroceratops gobiensis	1	-	86	-	60		95	_	110	-	53
Protoceratops andrewsi	1	_	152	122	112	(<u></u>	189		208	Fire service	96
Protoceratops andrewsi	1		-		112		221	, - y	241	- Car	115
Protoceratops andrewsi	1				-	_	226	_	241	_	119
Protoceratops andrewsi	1	68	220		135	41	248	_	273		125
Protoceratops andrewsi	1	45	176	64	119	41	213			70	
	1		174					91	219	76	109
Protoceratops andrewsi		44		59	128	44	203	82	205	76	109
Protoceratops andrewsi	1		-	1-	-	en,	-	-	276	84	=
CERATOPSIDAE											
Avaceratops lammersi	1	270	285	-	198	77	414		285		113
Brachyceratops montanensis	1	- 7	-		-		337	-	268	_ 3	97
Centrosaurus apertus	1	1280	547	260	322	148	695	306	476	231	163
Centrosaurus apertus	1	-	239	95	-	-	-	_	-		-
Centrosaurus apertus	1	_	600	-	350	130	740	_	600		215
Centrosaurus apertus	1		-	·			800	-	500	-	230
Centrosaurus apertus	2	_	-	-	_		453-699	180-306	500		200
Centrosaurus apertus	4			-		A 1 (1)	-	-	247-373	105-177	40× 2.
Chasmosaurus belli	1	1495	543	268	316	153	747	310	491	249	185
Chasmosaurus belli	1	1685	668	285	373	142	788	351	592	245	207
Chasmosaurus belli	1	-	555	270	-	172	705	308	486	244	201
Chasmosaurus belli	2	-	-	210	-		700	300	491-532	211-225	3.1
Chasmosaurus mariscalensis	3		_	-	-		-			C-100 - 100	. J.
Chasmosaurus sp.	1		-			-	778		266-297	79-95	-
Manadarius arassus	1	-	573	232		-	12320	285	-	~4	-
Monodorius crassus	1	-		232	10 -		740	297	558	294	v =3
Manadarius crassus		-	-			. 19 Take	633	242	400.040	470.004	
	2	1450	541	~~	244	407	720	-	408-619	179-284	400
Pachyrhinosaurus canadensis				262 253	344	137	738	326	543	290	198
Pachyrhinosaurus canadensis	1	1475	561		321	138	712	305	544	236	163
Pachyrtinosaurus canadensis	18		198-577	76-215	5.55	, ·	050.000	-		-	-34
Pachyrtinosaurus canadansis	14	-			-	-	258-678	97-264	- t -	5	- 1 - 1 - 1 - 1 - 1 - 1 - 1 - 1 - 1 - 1
Pachyrhinosaurus canadensis	12	- 1		7-	-	-	-	-	191-558	84-227	
Styracosaurus albertensis	1	-			-			- 1	364	157	77
Triceratops homidus	1	5850	826	473	396	187	1068	473	668	359	245
Triceratops horridus	1	~	800	-	400	-	980	-	610		233
Triceratops horricus	2		823-834	481-488	-	-	-	-	17-		
Triceratops horridus	2	T=+ 101	-	-1		-	1026-1063	464-505	1 m2	- Y	
Triceratops horridus	1	(· · · · · · · · · · · · · · · · · · ·			-	-	-	-	742	396	1 3 5
Ceratopsidae sp.	7	-	206-645	78-302	-	-	-	_	-		
Ceratopsidae sp.	2		-		-		286-766	116-319			7
Ceratopsidae sp.	3	-	-		- 7	-	2.5	-	139-583	54-275	-

In addition to personal measures data were taken from BROWN (1914; 1917), WIMAN (1930), OSBORN (1933), BROWN & SCHLAIKJER (1940; 1942), MARYANSKA & OSMOLSKA (1975), OSTROM (1978), DODSON (1986) and LEHMAN (1993).

NOTE ADDED TO REPRINT (GSP)

The trot-gallop transition speed rises with increasing mass, and the estimated values for a quadrupedal animal of 6000 kg are 30-45 km.h⁻¹ (Heglund & Taylor, 1988). It therefore may have been unnecessary for ceratopsids approaching and in this size class to gallop in order to achieve such high running speeds, a fast trot may have been sufficient (also see Paul & Christiansen, 2000).

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