

Locomotion in terrestrial mammals: the influence of body mass, limb length and bone proportions on speed

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Traditionally a few limb proportions or total limb lengths have been regarded as indicative of peak running velocity. This is due to physical principles (inferred in- and out-velocities around the joints, stride lengths) and also the observation that fast-moving animals tend to share a number of purported key features which are either absent or not developed to near the same extent in slower moving forms. Previous studies have shown hind limb length and metatarsus/femur ratio to be correlated significantly, albeit modestly with running speed. These studies have nearly all been bivariate analyses. Based on the physical principles, there is reason to suppose that more variables than just m/f ratio could be important as adaptations for fast locomotion, and also that bivariate analyses are too simple. In this study a sample of 76 running mammals was used, with running speeds taken from literature. A number of osteological parameters were discovered to covary significantly with peak running speed, albeit only modestly. Using the information from phylogeny reduced all correlations, often significantly so. Multivariate analyses resulted in markedly higher correlation coefficients. Animals probably do not optimize their anatomy for the purpose of running very fast, which occurs only on rare occasions, but for reducing costs of locomotion. © 2002 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2002, 136, 685–714.

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INTRODUCTION

Despite suggestions to the contrary (e.g. Gambaryan, 1974; Coombs, 1978; Halstead & Halstead, 1981; Thulborn, 1982; Garland, 1983), there is no *a priori* reason to assume that extant mammals fill the maximum speed potential possible at any given body size. Several species of extinct proboscideans significantly exceeded extant elephants in size (Garrutt & Nikolskaja, 1988; Shoshani *et al.*, 1991; Mol & van Essen, 1992; Paul, 1997), although being morphologically very similar to the latter, and thus there would be little reason to suppose that they had a radically different locomotor capability. Significantly, several extinct mammals, such as certain rhinos (e.g. *Megacerops*, *Elasmotherium*), brontotheres and ceratopsian dinosaurs (Paul & Christiansen, 2000) morphologically appeared to have been able to perform true running with body masses approaching those of extant elephants. Certain extinct carnivorans also appear to have greatly exceeded their extant counterparts in

size, while probably retaining the ability to run (e.g. Osborn, 1910; Kurtén, 1967; Anyonge, 1993; Turner, 1997; Christiansen, 1999a). In fact, the largest terrestrial mammal (Alexander, 1989a; Fortelius & Kappelman, 1993; Paul, 1997), the primitive rhinoceros *Indricotherium* from the Oligocene of Asia, has a number of anatomical features indicative of it having had a greater ability for fast locomotion than extant elephants (Paul & Christiansen, 2000).

Adaptations for speed apparently have been an important factor in mammalian evolution (for review, see Howell, 1944). Simple observation of most larger mammals demonstrates that some are a lot faster than others (i.e. speed is not a simple linear reflection of body size, as also found by Garland, 1983) and that fast-moving species tend to share a substantial number of morphological traits either absent or not developed to nearly the same extent among slower moving forms. Accordingly, several anatomical variables have been identified that are traditionally considered as indicative of fast locomotion. These include epipodials and metapodials reduced to a single functional unit, hinge-like joints, mobile scapula, a high metatarsus/femur ratio and long limbs relative to body size (e.g.

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Gregory, 1912; Howell, 1944; Maynard Smith & Savage, 1956; Gambaryan, 1974; Savage, 1977; Coombs, 1978; Bakker, 1983; Hildebrand & Hurley, 1985; Van Valkenburgh, 1987; Hildebrand, 1988).

These variables have often been used to infer locomotory capabilities of extinct mammals (Howell, 1944; Maynard Smith & Savage, 1956; Bakker, 1983; Van Valkenburgh, 1987; Janis & Wilhelm, 1993; Paul & Christiansen, 2000) and also in non-avian dinosaurs (Coombs, 1978; Thulborn, 1982; Holtz, 1994; Christiansen, 1997, 1998; Paul & Christiansen, 2000), which in many ways bear substantial resemblance to larger, parasagittal mammals (Carrano, 1998). Thus, in many aspects of neontological and palaeobiological research it is desirable to have some reliable parameters for inference of adaptations for fast locomotion. Identifying such variables across a phylogenetically wide range of species is important, as more vague, intuitive inferences based on overall similarity and close phylogenetic affinity are often not possible. Horses such as *Hipparion* or *Hippidion* are sufficiently closely related and morphologically similar to extant *Equus* that it may be defensible to infer similar locomotory capability to *Equus* in these forms. But how about *Arsinoitherium*, or even unguligrade, one-toed litopterns such as *Thoatherium* or *Diadiaphorus* (Protheroheriinae), which, although resembling small horses are not even perissodactyls (Osborn, 1910; Simpson, 1945; McKenna & Bell, 1998), invalidating the arguments of phylogenetic affinity? This is further compromised when attempting to infer the locomotory capabilities of dinosaurs.

Although empirical verification of the above variables was lacking for many years, recent analyses have demonstrated a significant relationship between running speed and metatarsus/femur ratio and hind limb length (Garland & Janis, 1993), although the correlations were not impressive. Likewise, a relationship between hind limb length and feeding ecology has been demonstrated in carnivorans (Harris & Steudel, 1997) as previously suggested by Gonyea (1976). There are strictly mechanical reasons for assuming a close relationship of limb ratios, not just the m/f ratio, and overall limb length to running speed. Longer limbs of course facilitate longer strides. This would be particularly important during true running with a suspended phase in the stride. During slower forms of locomotion, such as walking and trotting, speed increases as a function of increases in stride length and stride frequency, but during the gallop, speed increases mainly from increases in stride length (Heglund *et al.*, 1974; Pennycuik, 1975; Biewener, 1983; Alexander, 1989b; Biewener & Baudinette, 1995).

However, for efficient locomotion, limbs should not merely become longer. Most fast running mammals

have proximally placed limb muscles in the legs, proximally placed limb muscle insertions on the bones, elongate distal parts of the limbs, and are either digitigrade or unguligrade, thus incorporating the metapodium into effective limb length. Additionally, the limb joint morphology effectively restricts motion to a predominantly parasagittal plane (e.g. Howell, 1944; Coombs, 1978; Hildebrand & Hurley, 1985; Hildebrand, 1988). The physical principles behind this are well founded.

A limb can be regarded as a system of levers which pivot around each other at the joints (for a thorough review see, e.g. Alexander, 1983, or Hildebrand, 1988). Although the detailed functional morphology of a moving limb is highly complex, a simple example may be given of the elbow joint. The olecranon process can be regarded as the inlever (L_i) for the *m. triceps*, which extends the joint by contracting and exerting a force (the inforce, F_i) on the olecranon process. This results in motion of the distal part of the limb and an outforce (F_o) at the tip of the outlever (L_o), which is the distal part of the radius, or rather, the third metacarpal, as this bone touches the ground. At equilibrium, $F_i L_i = F_o L_o$ (Hildebrand, 1988). Motion around the elbow is termed the invelocity (V_i) and at the distal part of the limb it is termed the outvelocity (V_o). As $V_i L_o = V_o L_i$ (Hildebrand, 1988), it follows that $V_o = V_i L_o / L_i$, implying that increases in outlever length will increase out-speed by increasing the angular velocity, but will decrease the outforce, due to the well known inverse relationship between muscle shortening velocity and resistance.

From the above it follows that muscles should be proximally placed in the limbs, to reduce the angular momentum (angular velocity multiplied by the moment of inertia, which is related to mass). This would also imply relatively less energy consumption from oscillation of the limbs. Fast-moving mammals also tend to reduce the number of metapodials, reduce the ulnar diaphysis and have a reduced (e.g. felids, canids) or nearly absent (many bovids and cervids) fibula. This also reduces distal limb mass, and thus angular momentum. Additionally, proximally placed limb muscles allow the muscles to operate the bones by means of long tendons, suitable for the storage of large amounts of elastic potential energy, to be released during the propulsive phase of the stride (e.g. Taylor *et al.*, 1980; Alexander, 1984a; Dimery *et al.*, 1986; Hildebrand, 1988; Roberts *et al.*, 1997). This implies that muscles produce force during locomotion but do little work, as most of the shortening occurs in the tendons (Taylor *et al.*, 1980; Dimery *et al.*, 1986; Roberts *et al.*, 1997).

Hinge-like joints would ensure proper summation of the independent angular velocities around the joints, as several joints arranged in a series makes the angu-

lar velocities of individual segments roughly additive (Hildebrand, 1988). Muscles appear not to shorten appreciably during the stance phase, however (e.g. Roberts *et al.*, 1997; Biewener *et al.*, 1998), implying that adaptations for increasing the angular velocity, if any, should be important during the swing phase, or, more likely, to facilitate a more rapid down stroke, increasing ground forces (Weyand *et al.*, 2000). Hinge-like joints probably also prevent easy dislocation of joints during rapid locomotion, which would be important as this activity places a tremendous stress on the skeleton (e.g. Alexander, 1977, 1984b; Rubin & Lanyon, 1982; Biewener *et al.*, 1983; Biewener, 1983; Thomason, 1985; Biewener & Taylor, 1986).

It follows from the above that the metatarsus/femur ratio is but one of several limb bone ratios that could potentially influence adaptations for speed. It would seem equally important to study the relationship of other long bone ratios to speed, such as the radius/humerus ratio, metacarpus/humerus ratio and tibia/femur ratio. Also, the relationship of the in- and out-levers could be important, in this case the olecranon process and calcaneal tuber, due to their prominence. The empirical relationship of these variables to running speed has hitherto not been well studied.

Additionally, previous analyses of this nature (e.g. Garland, 1983; Garland & Janis, 1993) or analyses of anatomy to ecology (Harris & Steudel, 1997) or physiology (Strang & Steudel, 1990; Steudel & Beattie, 1995) have all analysed single traits separately (but see Bonine & Garland, 1999, for a multivariate study on lizard locomotion). If, for instance, hind limb length is found to correlate with running speed, it may be expected that a significantly better correlation could be obtained by including the 'other half' of the locomotory system, the fore limb.

Accordingly, in this paper a large number of anatomical parameters are analysed for their relationship to running speed, both separately and in multivariate analyses. Provisional results were presented in Christiansen (2000). Identifying variables that correlate significantly with, and thus may be considered as adaptations or even prerequisites for, fast locomotion would be important in studies of not only extant, but extinct mammals as well. Additionally, because much of the rationale behind this correlation is founded not just on the presence of these features in fast-moving forms, but on physical and mechanical principles, one may argue that variables that correlate well with speed across a wide phylogenetic spectrum and size range in extant mammals could be indicative of the ability for fast locomotion *per se*. Thus, they may be used in inferences of speed in extinct animals not closely related to extant mammal species, such as nimravids, brontotheres, litopterns or non-avian dinosaurs.

MATERIALS AND METHODS

DATA SAMPLE

A data sample of 76 mammals was used (Table 1). In order to make the species in the data sample more comparable, all included species are flexed-limbed and capable of true running with a suspended phase in the stride, with the possible exception of the hippo, which appears to be restricted to fast trotting. Restricting the sample to running mammals only ensures a reasonable uniformity of locomotor mechanics (see Alexander & Jayes, 1983, for a thorough review). All specimens are housed in the Zoological Museum in Copenhagen. No saltatorial species are included and elephants are not included either, owing to their apomorphic appendicular anatomy and mode of locomotion (Gambaryan, 1974; Alexander *et al.*, 1979; Christiansen, 1997). Body masses were known for some individuals but in other cases the body masses were taken from literature (Table 1), mainly Nowak (1991) and Silva & Downing (1995). Frequently, body masses from these two and other literature sources were checked against the values reported in the series Mammalian Species.

Maximum articular lengths of the major limb bones of the included 76 species (humerus, radius, femur, tibia, longest metacarpal and longest metatarsal) were measured using digital callipers for lengths up to 155 mm, and normal callipers for lengths over 155 mm (see Table 1). The length of the olecranon process was determined as the maximal linear distance from the centre of rotation at the articular surface for the humerus to the tip of the process. Calcaneal tuber length was determined as the linear distance from the centre of rotation of the joint to the tip of the tuber. Total limb length was the sum of pro, epi, metapodium, disregarding carpals and tarsals.

Maximal running velocity was taken from a variety of literature sources, as noted in Table 1. Many are not timed distances, but have been collected with a number of different methods. A frequently used method is chasing the animal by car and noting its speed from a speedometer reading (e.g. many values from Howell, 1944). Peak velocity could thus constitute a problem because of its potential inaccuracy. How reliable are the commonly reported values? One could reasonably expect that the most severe inaccuracies were to be found among the very fast-moving species, both owing to the greater difficulty of observing a very fast-moving animal over longer distances, and also owing to common exaggerations.

Alexander *et al.* (1977) conducted vehicle chases of African ungulates while filming them to facilitate computation of speed. All analyses showed animals running 'reasonably fast' (p. 293), and most of the reported values were considerably lower than previ-

Table 1. Body masses and estimated maximal running speeds of mammals. Running speed (km h^{-1}), body mass (kg) and fore and hind limb lengths (mm) are all log. Length measurements in ratios are all raw values (mm), e.g. fore limb length to cube root of mass ($\text{Fl}/\sqrt[3]{\text{M}}$) or tibia/femur (T/F) ratio. Abbreviations: Fl, fore limb; R, radius; H, humerus; Mc, metacarpus; Op, olecranon process; HI, hind limb; T, tibia; F, femur; Cc, cnemial crest; Mt, metatarsus; C, calcaneal tuber

	Speed	Mass	$\sqrt[3]{\text{Mass}}$	Fl	$\text{Fl}/\sqrt[3]{\text{M}}$	R/H	Mc/H	Op/R	Op/ $\sqrt[3]{\text{M}}$	HI	$\text{HI}/\sqrt[3]{\text{M}}$	T/F	Cc/T	Cc/ $\sqrt[3]{\text{M}}$	Mt/F	C/ $\sqrt[3]{\text{M}}$	C/Mt	
ARTIODACTYLA																		
Antilocapridae																		
<i>Antilocapra americana</i>	1.940	1.663	3.583	2.799	175.5	1.080	1.065	0.245	14.79	2.871	207.4	1.123	13.50	16.47	0.963	5.582	0.254	
Bovidae																		
<i>Aepyceos melampus</i>	1.875	1.699	3.684	2.824	181.1	1.192	1.177	0.246	15.74	2.906	218.8	1.209	12.79	6.515	0.965	14.12	0.212	
<i>Alcelaphus buselaphus</i>	1.845	2.176	5.312	2.931	160.7	1.306	1.083	0.254	15.71	2.980	179.9	1.165	13.59	5.082	0.870	13.74	0.266	
<i>Antidorcas marsupialis</i> *	1.944	1.326	2.768	2.703	182.5	1.254	1.406	0.251	15.72	2.787	221.5	1.211	15.86	5.058	1.137	15.54	0.207	
<i>Antilope cervicapra</i>	1.977	1.544	3.271	2.730	164.2	1.219	1.245	0.238	13.76	2.806	195.7	1.227	16.20	4.586	1.005	13.91	0.229	
<i>Bison bison</i>	1.716	2.845	8.879	2.984	108.6	0.874	0.512	0.382	15.20	3.059	129.1	0.911	9.196	5.181	0.558	11.49	0.394	
<i>Bison bonasus</i> *	1.748	2.352	6.082	2.914	135.0	0.952	0.679	0.323	15.78	3.011	168.5	0.995	10.32	6.083	0.674	14.63	0.344	
<i>Boselaphus tragocamelus</i>	1.681	2.301	5.848	2.903	136.8	1.111	0.943	0.268	13.34	2.968	159.0	1.030	10.48	5.643	0.738	14.53	0.343	
<i>Capra aegaeus</i>	1.653	1.663	3.583	2.651	125.0	1.025	0.724	0.234	10.88	2.728	149.0	1.191	14.53	4.186	0.727	10.33	0.278	
<i>Capra caucasica</i>	1.653	1.740	3.803	2.671	123.3	0.914	0.608	0.329	14.73	2.747	146.7	1.143	17.85	3.418	0.606	10.26	0.317	
<i>Connochaetes gnou</i>	1.903	2.196	5.395	2.850	131.2	1.248	0.885	0.284	14.83	2.908	150.1	1.170	16.63	3.522	0.830	11.40	0.275	
<i>Connochaetes taurinus</i>	1.903	2.255	5.646	2.884	135.5	1.251	0.897	0.280	15.05	2.942	155.0	1.127	13.00	4.605	0.790	12.04	0.287	
<i>Damaliscus dorcas</i> *	1.845	1.638	3.517	2.777	170.3	1.232	1.153	0.257	15.92	2.831	192.8	1.205	14.88	4.834	1.024	15.21	0.249	
<i>Damaliscus hunteri</i>	1.845	2.201	5.418	2.876	138.8	1.290	1.113	0.225	11.81	2.934	158.7	1.160	15.19	3.876	0.967	12.18	0.248	
<i>Damaliscus lunatus</i>	1.845	2.100	5.000	2.895	157.0	1.329	1.114	0.244	14.80	2.938	172.4	1.215	14.13	4.800	0.892	13.80	0.277	
<i>Gazella dorcas</i> *	1.903	1.279	2.668	2.586	144.5	1.221	1.399	0.231	11.24	2.681	179.9	1.298	14.08	4.872	1.106	11.80	0.202	
<i>Gazella granti</i>	1.908	1.699	3.684	2.800	171.3	1.236	1.309	0.243	14.52	2.904	217.7	1.201	14.65	5.429	1.086	15.20	0.211	
<i>Gazella subgutturosa</i>	1.987	1.380	2.885	2.685	167.8	1.210	1.297	0.243	14.04	2.766	263.1	1.251	14.60	5.200	1.086	13.52	0.205	
<i>Gazella thomsoni</i>	1.903	1.279	2.668	2.659	170.9	1.209	1.326	0.247	14.43	2.755	213.2	1.287	13.75	5.996	0.961	14.62	0.219	
<i>Hippotragus equinus</i>	1.748	2.352	6.082	2.945	144.8	1.190	0.968	0.256	13.98	3.001	164.7	1.093	12.16	5.097	0.811	13.15	0.286	
<i>Hippotragus niger</i>	1.756	2.258	5.657	2.918	146.4	1.171	0.907	0.263	14.67	2.974	166.4	1.072	12.38	5.127	0.737	13.97	0.320	
<i>Madoqua kirki</i>	1.623	0.708	1.721	2.410	149.3	1.158	1.224	0.182	9.295	2.535	199.0	1.364	15.00	5.229	1.096	12.20	0.194	
<i>Oreamnos americanus</i> *	1.519	2.079	4.932	2.777	121.2	0.915	0.619	0.271	11.86	2.848	142.7	1.067	15.94	3.649	0.550	10.64	0.355	
<i>Ourebia ourebi</i>	1.699	1.161	2.438	2.625	173.1	1.177	1.370	0.239	13.74	2.712	211.2	1.307	14.29	5.741	1.059	15.17	0.228	
<i>Ouibus moschatus</i>	1.602	2.322	5.944	2.820	111.0	0.966	0.553	0.320	13.63	2.854	120.1	0.968	10.15	4.542	0.555	11.10	0.420	
<i>Ovis ammon</i>	1.778	2.057	4.849	2.869	152.6	1.102	0.907	0.269	15.06	2.954	185.6	1.207	12.93	5.775	0.793	12.99	0.265	
<i>Ovis canadensis</i>	1.681	1.978	4.563	2.793	136.1	1.009	0.839	0.280	13.48	2.888	169.2	1.180	12.83	5.260	0.778	11.83	0.266	
<i>Rupicapra pyrenaica</i> *	1.699	1.531	3.240	2.713	159.3	1.006	0.814	0.228	12.96	2.807	197.9	1.298	16.63	4.939	0.829	12.50	0.238	
<i>Rupicapra rupicapra</i>	1.699	1.580	3.362	2.721	156.5	0.894	0.799	0.223	12.34	2.804	189.5	1.296	14.83	5.354	0.796	12.79	0.262	
<i>Saiga tartarica</i> *	1.875	1.418	2.970	2.698	168.0	1.123	0.957	0.250	15.32	2.768	197.3	1.195	13.00	5.724	0.973	13.47	0.222	
<i>Syncerus caffer</i> *	1.756	2.643	7.606	2.914	107.8	0.868	0.529	0.364	14.20	2.996	130.3	0.952	10.47	4.733	0.551	11.70	0.408	
<i>Taurotragus derbianus</i>	1.845	2.833	8.794	3.041	125.1	0.912	0.930	0.295	11.83	3.123	151.0	1.008	12.76	4.321	0.753	12.28	0.298	
<i>Taurotragus oryx</i>	1.845	2.748	8.243	2.946	107.3	1.047	0.939	0.310	11.65	3.083	136.0	1.021	11.71	4.125	0.854	11.77	0.291	

Camelidae	1.778	2.740	8.193	3.085	148.5	1.274	0.839	0.199	12.08	3.102	154.4	1.089	12.49	4.272	0.683	10.62	0.259
<i>Camelus bactrianus</i>	1.716	2.618	7.459	3.078	160.6	1.306	0.914	0.202	13.14	3.092	165.8	0.912	12.03	4.826	0.693	9.787	0.222
<i>Camelus dromedarius</i>	1.748	1.954	4.481	2.886	171.8	1.112	0.850	0.215	13.84	2.943	195.9	0.982	11.14	6.471	0.687	12.05	0.239
<i>Lama guanicoe</i>	1.672	1.653	3.557	2.766	164.2	1.204	0.935	0.219	13.78	2.825	187.8	0.956	9.958	6.747	0.716	12.37	0.246
<i>Vicugna vicugna</i>																	
Cervidae	1.748	2.613	7.429	3.069	157.9	1.065	0.889	0.241	13.73	3.138	184.8	1.132	13.34	5.115	0.933	14.27	0.254
<i>Alces alces</i> *	1.778	1.398	2.924	2.681	164.2	1.057	1.000	0.232	13.17	2.782	207.2	1.241	15.47	5.130	1.000	13.85	0.217
<i>Capreolus capreolus</i>	1.857	1.929	4.397	2.855	162.8	1.079	1.061	0.260	14.56	2.934	195.4	1.175	11.93	6.141	0.960	15.01	0.251
<i>Cervus elaphus</i> *	1.813	1.653	3.557	2.716	146.2	1.023	1.018	0.271	13.35	2.818	185.0	1.111	12.05	5.904	0.922	13.34	0.212
<i>Dama dama</i> *	1.806	1.748	3.826	2.719	136.7	1.017	0.889	0.251	12.02	2.823	174.1	1.117	11.81	5.489	0.883	13.33	0.260
<i>Odocoileus hemionus</i>	1.806	1.792	3.958	2.727	134.7	0.984	0.821	0.238	11.24	2.831	171.3	1.121	11.82	5.556	0.802	13.26	0.282
<i>Odocoileus virginianus</i>	1.845	2.204	5.429	2.866	135.4	1.061	0.744	0.263	13.45	2.958	167.1	1.159	13.72	4.605	0.905	13.63	0.276
<i>Rangifer tarandus</i> *																	
Giraffidae	1.748	2.778	8.434	3.242	206.8	1.550	1.378	0.138	11.26	3.219	196.2	1.185	17.22	3.794	1.374	12.45	0.164
<i>Giraffa camelopardalis</i> *																	
Hippopotamidae	1.398	3.083	10.65	2.875	70.38	0.665	0.396	0.471	10.70	2.977	89.15	0.657	9.235	3.191	0.257	10.23	0.886
<i>Hippopotamus amphibius</i> *																	
Suidae	1.740	1.944	4.448	2.641	98.47	0.734	0.313	0.439	15.51	2.675	106.3	0.894	9.650	4.496	0.296	11.24	0.781
<i>Phacochoerus aethiopicus</i> *	1.544	1.519	3.208	2.456	89.17	0.683	0.374	0.379	11.22	2.535	106.8	0.938	9.786	4.365	0.408	9.821	0.529
<i>Tayassu pecari</i>	1.544	1.342	2.802	2.446	99.57	0.636	0.357	0.427	13.56	2.540	123.8	0.916	13.70	3.569	0.405	11.78	0.545
<i>Tayassu tajacu</i>																	
CARNIVORA																	
Canidae	1.748	0.964	2.095	2.471	141.3	0.976	0.392	0.164	9.545	2.550	169.4	1.034	21.57	3.341	0.397	9.783	0.353
<i>Canis aureus</i> *	1.740	1.462	3.072	2.656	147.5	0.933	0.390	0.203	12.04	2.694	160.8	0.990	12.69	5.208	0.420	11.07	0.395
<i>Canis familiaris</i> *	1.748	1.090	2.308	2.494	135.2	0.985	0.397	0.167	9.314	2.575	162.9	1.032	19.88	3.466	0.409	9.531	0.349
<i>Canis latrans</i>	1.806	1.544	3.271	2.704	154.7	0.995	0.426	0.211	13.45	2.747	170.6	1.027	12.16	5.809	0.453	12.23	0.392
<i>Canis lupus</i> *	1.778	0.881	1.966	2.449	142.9	0.992	0.370	0.169	10.17	2.530	172.4	1.021	20.57	3.560	0.383	9.918	0.361
<i>Canis mesomelas</i>	1.820	1.342	2.802	2.626	151.0	1.053	0.435	0.204	13.03	2.663	164.2	0.989	12.53	5.353	0.432	11.96	0.409
<i>Lycan pictus</i>	1.623	0.580	1.560	2.342	141.0	0.904	0.436	0.182	9.933	2.441	176.9	0.965	18.33	3.845	0.456	9.612	0.288
<i>Urocyon cinereoargenteus</i>	1.681	0.740	1.765	2.455	161.5	0.955	0.371	0.171	11.33	2.517	209.0	1.070	17.25	4.532	0.481	10.76	0.306
<i>Vulpes vulpes</i> *																	

Table 1. Continued.

	Speed	Mass	$^3\sqrt{\text{Mass}}$	FI	FI/ $^3\sqrt{\text{M}}$	R/H	Mc/H	Op/R	Op/ $^3\sqrt{\text{M}}$	HI	HI/ $^3\sqrt{\text{M}}$	T/F	Cc/T	Cc/ $^3\sqrt{\text{M}}$	Mt/F	C/ $^3\sqrt{\text{M}}$	C/Mt
Felidae																	
<i>Acinonyx jubatus</i> *	2.021	1.591	3.391	2.741	162.5	0.949	0.386	0.185	12.24	2.784	179.4	1.004	12.55	5.898	0.430	13.27	0.419
<i>Panthera leo</i> *	1.740	2.230	5.540	2.906	145.4	0.910	0.353	0.216	12.63	2.946	159.6	0.848	11.72	5.235	0.357	12.27	0.476
<i>Panthera pardus</i> *	1.778	1.708	3.708	2.654	121.6	0.866	0.366	0.277	13.08	2.737	147.2	0.957	13.94	4.314	0.386	10.25	0.422
<i>Panthera tigris</i> *	1.748	2.161	5.253	2.845	133.2	0.860	0.362	0.262	13.51	2.906	153.2	0.846	11.41	5.139	0.365	12.09	0.477
Hyaenidae																	
<i>Crocuta crocuta</i>	1.778	1.813	4.021	2.706	126.3	1.014	0.382	0.228	12.19	2.712	128.2	0.836	10.21	4.726	0.386	9.202	0.413
<i>Hyaena hyaena</i> *	1.699	1.505	3.175	2.722	166.0	1.095	0.403	0.169	12.28	2.703	159.1	0.914	13.47	4.725	0.371	9.449	0.366
Procyonidae																	
<i>Nasua nasua</i> *	1.431	0.531	1.504	2.290	129.7	0.870	0.250	0.213	11.31	2.398	166.3	0.946	21.20	3.325	0.286	9.643	0.453
<i>Procyon lotor</i>	1.038	0.875	1.957	2.326	108.3	0.928	0.258	0.167	7.663	2.412	132.1	1.013	22.90	2.554	0.274	6.897	0.435
Ursidae																	
<i>Ursus americanus</i> *	1.681	2.021	4.718	2.771	125.1	0.909	0.228	0.167	8.903	2.806	135.4	0.762	10.70	4.875	0.217	9.433	0.636
<i>Ursus arctos horribilis</i>	1.681	2.190	5.372	2.828	125.3	0.921	0.285	0.203	10.61	2.851	132.2	0.800	10.61	4.840	0.258	8.750	0.528
<i>Ursus maritimus</i> *	1.699	2.243	5.593	2.850	126.6	0.884	0.274	0.248	12.87	2.895	140.3	0.769	9.967	5.363	0.249	13.05	0.753
PERISSODACTYLA																	
Equidae																	
<i>Equus asinus</i>	1.740	2.218	5.485	2.797	114.3	1.140	0.777	0.261	11.67	2.874	136.4	0.940	12.05	4.011	0.713	9.937	0.271
<i>Equus burchelli</i> *	1.845	2.134	5.143	2.858	140.4	1.136	0.835	0.241	12.93	2.940	169.4	0.908	11.33	5.250	0.677	12.45	0.281
<i>Equus caballus</i>	1.806	2.724	8.093	2.985	119.2	1.122	0.750	0.239	11.12	3.050	138.5	0.877	11.88	4.078	0.631	10.87	0.312
<i>Equus hemionus</i>	1.806	2.344	6.046	2.842	115.0	1.209	0.813	0.234	10.75	2.916	136.5	0.942	10.14	4.797	0.702	10.17	0.281
<i>Equus zebra</i>	1.806	2.441	6.511	2.946	135.6	1.134	0.829	0.216	11.21	3.018	160.2	0.895	9.154	5.990	0.719	10.90	0.247
Rhinocerotidae																	
<i>Ceratotherium simum</i> *	1.602	3.279	12.39	3.038	88.17	0.847	0.414	0.399	13.16	3.053	91.32	0.728	8.313	3.876	0.336	8.397	0.565
<i>Diceros bicornis</i> *	1.653	2.942	9.565	2.992	102.7	0.914	0.430	0.339	13.59	2.989	102.0	0.756	7.674	4.809	0.334	8.260	0.506
Tapiridae																	
<i>Tapirus terrestris</i> *	1.602	2.238	5.572	2.751	101.2	0.846	0.447	0.322	12.02	2.845	125.6	0.804	10.36	4.487	0.370	10.77	0.504

*Body mass known as skeletal specimen had been weighed either prior to, or, most frequently, just after death.

Maximal running speeds and body masses for species in which this was not known were taken from: Howell (1944), Schaller (1968), Dagg (1971), Groves (1972), Hildebrand (1988), von Richter (1974), Sokolov (1974), Bekoff (1977), Elliott *et al.* (1977), Haltenroth & Diller (1977), Fritzell & Haroldson (1982), Kingdon (1982), Garland (1983), Anderson & Wallmo (1984), Shackleton (1985), Meagher (1986), Mayer & Wetzel (1987), Feldhamer *et al.* (1988), Penzhorn (1988), Nowak (1991), Smith (1991), Garland & Janis (1993), Whitehead (1993), Gompper (1995), Silva & Downing (1995), Yom-Tov *et al.* (1995), Kingswood & Blank (1996), Sempéré *et al.* (1996), Skinner & Louw (1996), Kingswood & Kumamoto (1997).

ously reported, e.g. 47 km h⁻¹ for impala (*Aepyceros melampus*) and 50 km h⁻¹ for Thomson's gazelle (*Gazella thomsoni*). It is universally agreed that the impala is very fleet and capable of performing astounding leaps of up to 3 m in height and 9–11 m in length (e.g. Schenkel, 1966; Haltenroth & Diller, 1977; Kingdon, 1982; Hildebrand, 1988; Nowak, 1991). Nowak (1991: 1462) called its running speed 'considerable'. Clearly, this does not correlate well with a peak velocity of just 47 km h⁻¹. Haltenroth & Diller (1977) ascribed a velocity of 60 km h⁻¹ to impalas. There is reason to suppose that the values reported by Alexander *et al.* (1977) may not represent peak velocities, and the authors themselves indicate that the included species could have been faster (p. 298).

A common problem is whether the species in question is running at, or considerably below, its peak velocity. Peak velocity is probably only reached when the animal is highly motivated, for instance a herbivore attempting to evade a predator. Cheetahs (*Acinonyx jubatus*) are traditionally considered capable of achieving peak velocities of around 100 km h⁻¹ (e.g. Howell, 1944; Hildebrand, 1959, 1961; Nowak, 1991), a seemingly astounding figure. The peak velocity of this species has traditionally been assessed using the same methods that have been used for assessing peak velocities of other fast-moving species (references in Table 1). As a predator, the cheetah probably only reaches peak velocity during a high-speed chase, where rapid swerving and dodging by the prey commonly makes the chase very hard to follow visually over longer distances. Additionally, as the cheetah is evidently extremely fast, regardless of its true peak velocity, it would seem a prime candidate for exaggerations. However, experiments conducted under strict scientific control verified this, seemingly incredible, velocity (Sharp, 1997), reporting an average speed of 104 km h⁻¹ timed across a 200 m track.

The cheetah mainly kills smaller prey, such as gazelles and impalas (Schaller, 1968; Nowak, 1991; Bailey, 1993; Caro, 1994). Clearly, if the cheetah is capable of running in excess of 100 km h⁻¹, it cannot be true that the impala and Thomson's gazelle are only capable of half this value. Gazelles are frequently credited with top speeds of around 80 km h⁻¹ (e.g. Howell, 1944; Nowak, 1991; Yom-Tov *et al.*, 1995). Previous analyses, not just estimates, are also strongly at odds with these low values. The value of 50 km h⁻¹ for Thomson's gazelle from Alexander *et al.* (1977) is much lower than the value of 104 km h⁻¹ reported by Elliott *et al.* (1977), based on film analysis during attacks by lion (*Panthera leo*), corroborating the suggestion that only highly motivated animals achieve peak running velocities, most commonly during attacks or predator evasion. Howell (1944) reported that a Goitered gazelle (*Gazella subgutturosa*) chased

by a car reached 97 km h⁻¹, a figure endorsed by other specialists (e.g. Kingswood & Blank, 1996). In this analysis these values were used for these two species, but the widely cited lower values of 80–81 km h⁻¹ were used for the other gazelles (Table 1); however, they may well be equally fast.

In fact, many alleged traditional velocity estimates are not just qualified guesses but are often speedometer readings, and some are the result of timed distances. Thus, it is likely that most traditional peak velocity values may be somewhat inaccurate, but there seems to be little reason to suppose that they are consistently exaggerated to the level of dozens of km h⁻¹ greater than the actual values. The traditional values reported for gazelles and other fast-moving forms are thus also generally accepted.

In other cases, lower values for some species are used than traditionally cited. Garland & Janis (1993) used a value of 64 km h⁻¹ for grey fox (*Urocyon cinereoargenteus*), but here the lower value of 42 km h⁻¹ (chased by car; Howell, 1944) is used. Garland (1983) used 67 km h⁻¹ for domestic dog (*Canis familiaris*), but in this analysis 55 km h⁻¹ (recorded on racetrack; Howell, 1944) is used. Garland (1983) and Garland & Janis (1993) used 70 km h⁻¹ for the kulan (*Equus hemionus*), whereas Howell's (1944) lower value of 64 km h⁻¹ (method not stated) is used here. The latter value, comparable to those of racehorses, still seems slightly exaggerated. Groves (1974) credits the wild ass (*Equus asinus*) with a top speed of 50 km h⁻¹, but Hildebrand (1988) reports on a wild ass supposedly running for 26 km at 48 km h⁻¹. This cannot be true if the peak velocity is only 50 km h⁻¹, and accordingly it was arbitrarily set at 55 km h⁻¹. This is in accord with the value of 63 km h⁻¹ reported by Elliott *et al.* (1977) for Burchell's zebra (*Equus burchelli*).

The wildebeests are most often credited with speed of around 80 km h⁻¹ (e.g. Howell, 1944; Schaller, 1968; Garland, 1983; Nowak, 1991). However, based on film analyses, Elliott *et al.* (1977) found a considerably lower value of 57 km h⁻¹ for blue wildebeest (*Connochaetes taurinus*). Accordingly, a value of 60 km h⁻¹ is accepted here for both species (Table 1). Garland (1983) and Garland & Janis (1993) used 105 km h⁻¹ for the blackbuck (*Antelope cervicapra*), an animal widely held to be among the fastest of all ungulates. In this analysis the lower value of 95 km h⁻¹ (Seshadri, 1969), apparently a timed value, was used. Nowak (1991) stated that the American bison (*Bison bison*) is capable of 60 km h⁻¹, and Garland (1983) and Garland & Janis (1993) used 56 km h⁻¹. The lower value of 52 km h⁻¹ (chased by car; Howell, 1944) is used in this analysis. Some species are problematic. Howell (1944) considers the eland antelopes (*Taurotragus*) among the slowest antelopes, but reported literature speeds are all around, or slightly above 70 km h⁻¹. This value

seems exaggerated, but seems to be the only figure available.

STATISTICAL ANALYSES

Running velocity was considered the dependent variable in all regression analysis. Besides log body mass and the cube root of body mass (to normalize for size), 14 additional parameters were used, either as measurement variables (log limb lengths) or as various ratios (Table 2). A few of these variables have previously been found to correlate with running speed, for instance total hind limb length and the traditional 'indicator of cursoriality', the metatarsus/femur ratio (e.g. Howell, 1944; Garland & Janis, 1993). Other long bone ratios were also included (Table 2).

To normalize for the discrepancy between increase in body mass (a three-dimensional parameter) and increases of bone lengths (one-dimensional parameters) the cube root of mass was used in cases of ratios of anatomical parameters to body mass. The size of the olecranon process and calcaneal tuber (inlever moment arms) relative to epipodial and metapodial lengths (outlever moment arms), respectively, and cube root of body mass were also included, as this could affect the development of force and outvelocity of the pedes during locomotion.

All 16 independent variables were regressed against running velocity (km h^{-1}) using Model I (Least Squares) regression. Although error must clearly be assumed on both variables, thus requiring a model II regression analysis (Labarbera, 1989; Sokal & Rohlf, 1995), the least squares method was preferred as

Table 2. Anatomical parameters used as 'independent' variables in the regression analyses. All lengths are in mm

Parameter	Number
Log body mass (kg)	1
$\sqrt[3]{\text{body mass}}$	2
Log forelimb length	3
Forelimb length/ $\sqrt[3]{\text{body mass}}$	4
Radius length/humerus length	5
Metacarpus length/humerus length	6
Olecranon length/radius length	7
Olecranon length/ $\sqrt[3]{\text{body mass}}$	8
Log hindlimb length	9
Hindlimb length/ $\sqrt[3]{\text{body mass}}$	10
Tibia length/femur length	11
Metatarsus length/femur length	12
Cnemial crest height/tibia length	13
Cnemial crest height/ $\sqrt[3]{\text{body mass}}$	14
Calcaneal tuber length/metatarsus length	15
Calcaneal tuber length/ $\sqrt[3]{\text{body mass}}$	16

dependence is, perhaps somewhat arbitrarily, assigned to running speed in analyses such as the present one.

Additionally, multivariate regression analyses were performed. Regressing more than one 'independent' variable against a 'dependent' variable often results in a higher correlation, thus explaining more of the variation in the 'dependent' variable. Multivariate analyses were performed on velocity to fore limb and hind limb parameters, respectively, and also on fore limb and hind limb parameters combined. For both bivariate and multivariate analyses the correlation coefficient (R), standard error of the estimate (SEE) and significance of the regression (F-statistic) was computed. Confidence limits (95% CI) were computed for intercept (a) and slopes (b). Plots of residuals against predicted values were generated for all analyses, to evaluate the presence and significance of outliers and examine for systematic departure, if any, from the applied model.

Besides correlation between the 'dependent variable' and the various 'independent' variables, multivariate regression introduces possible intercorrelation of the 'independent' variables as well. The latter are thus not truly independent. This intercorrelation was evaluated by computing the tolerance values of the 'independent' variables (one minus the multiple correlation between a given predictor and the other predictors in the model). By default, the tolerance value in a bivariate regression analysis is one. Low tolerance values indicate substantial intercorrelation of the 'independent' variables, which can inflate standard errors and attenuate the F-statistic. Such regression equations could be less reliable, due to potential computational inaccuracy. The eigenvalues of the regressions were also computed. Low eigenvalues, approaching zero, indicate redundancy of the predictor variables. Additionally, the condition index was computed, which is the square root of the ratios of the largest eigenvalue to each successive eigenvalue (Belsley *et al.*, 1980). A condition index greater than 15 indicates a possible problem with intercorrelation, whereas a value exceeding 30 would normally be considered problematic (Belsley *et al.*, 1980).

However, in a biological sample, such as the present, intercorrelation of the 'independent' variables is probably unavoidable, as this would imply that, for instance, fore limb length was uncorrelated with hind limb length. However, to reduce possible intercorrelation, variables in which the same parameter occurred were not used together in a multiple regression analysis. For instance, radius/humerus and metacarpus/humerus ratios (Table 2) both include the humerus. Accordingly, a combination of the two was avoided, and so on for the other variables. Total limb lengths were, however, used with the ratio variables.

Combining both fore and hind limb variables in multiple regression would theoretically facilitate a

huge number of different equations, even with the above-mentioned constraints in variable combination. However, most regression equations display little increase in correlation with the addition of variables beyond certain point. Addition of further variables only leads to redundancy of some variables. Thus, a total of 500 variable combinations was used for the combined fore and hind limb data set. All multiple equations with redundant slope (b) variables were discarded. The significance level for redundancy of the variables (two-tailed P) was set at 0.1.

Bivariate and multivariate regression analyses were performed in the traditional fashion, i.e. without addressing the possible influence of the phylogeny of the included species, and also using the method of independent contrasts. A traditional regression equation may be written as:

$$y = \alpha + \beta x_1 + \beta x_2 + \dots \beta x_i + \varepsilon$$

where α is the intercept, β are the slope coefficients and ε is the error term, which is assumed to be normally distributed with a mean of zero. In biological samples the error terms are, however, inevitably correlated through the hierarchical nature of evolution, as exemplified by phylogeny reconstruction. Individual data points are thus not independent, violating one of the assumptions of regression analyses. Thus, the independent contrasts method (Felsenstein, 1985) may be employed, using the program PDTREE (Garland *et al.*, 1992, 1999; Garland & Ives, 2000). The structure of the phylogenetic tree for the included species was assembled from a variety of literature sources (Fig. 1). The total height of the tree (the basal split between Carnivora and Artiodactyla + Perissodactyla) was set at 85 million years, predating the known fossil record of these extant orders by at least a dozen million years.

A basal split age of 85 mya was chosen, as many authors place the ordinal splits within Eutheria well into the Cretaceous, even Lower Cretaceous (e.g. Novacek, 1992a; Archibald, 1996; Hedges *et al.*, 1996; Madsen *et al.*, 2001; Murphy *et al.*, 2001) and because of the age of the Proboscidea (not included in the analysis). The earliest known fossil remains of the Proboscidea are Late Paleocene (Gheerbrant *et al.*, 1996), thus providing a minimum age for the Proboscidea and its sister group. The true split age could well be higher. Traditionally, Proboscideans are either considered the sister taxon of Artiodactyla + Perissodactyla (Shoshani, 1986) or, most frequently, of the Perissodactyla (e.g. Novacek, 1992a; Archibald, 1996; Rowe, 1999), suggesting that the basal split between Carnivora and the ungulates occurred some time into the Cretaceous. A value of 85 mya (also used in Christiansen, 2002) is very close to the average value

of 84 mya suggested by Murphy *et al.* (2001) for the supraordinal divergence of the placentals.

Contrasts for each trait are computed by subtracting the values of the traits in two sister taxa or from a node, as appropriate (Garland *et al.*, 1992; Garland & Janis, 1993). To standardize the contrasts, i.e. bring them to a common variance, each contrast is divided by the square root of the sum of all branch lengths that make up the contrast. Proper standardization implies that the common variance of the contrasts is virtually independent of the branch lengths. Evaluation of the standardization is performed by generating plots of the standard deviations of the contrasts to the absolute values of the contrasts (Garland *et al.*, 1992, 1999; Garland & Janis, 1993; Garland & Ives, 2000). Such a plot should show as little correlation between the variables as possible, and if a significant linear relationship is detected one may transform the branch lengths by various methods (Garland *et al.*, 1992).

In this analysis the correlation of the contrasts and their standard deviations were evaluated for raw (unmodified) branch lengths, log-transformed branch lengths, square root of the branch lengths, cube root of the branch lengths and transformations of Grafen's (1989) rho. Rho values were set at 0.1–0.9, with an interval of 0.1. It was assumed that all r values below 0.05 indicated non-significant correlation. Whichever transformation resulted in the lowest correlation was chosen for independent contrasts analysis. Independent contrasts analysis produces regressions through the origin, which can be used to test for correlation of traits and linear relationships (Garland *et al.*, 1992, 1999; Garland & Janis, 1993; Garland & Ives, 2000). In this analysis the correlation between running speed, body mass and the anatomical parameters was of course the prime concern. Regression slopes are thus of less relevance.

Finally, multivariate regression analyses were also performed on the generated contrasts, and in this case the combination of variables followed the combinations found with normal regression analyses, as noted above. As for the standard multivariate least squares regression analyses, redundancy of the slope variables was evaluated (two-tailed P , significance level 0.1). Multivariate regressions on independent contrasts were computed using the same combinations that resulted in a significant correlation between the 'dependent' and 'independent' variables in the standard least squares analyses and in non-redundant slope variables. This implies, however, that some of the variables in the independent contrasts multivariate analyses potentially could be redundant, but it was decided to give each multivariate regression analysis both as standard and independent contrasts equation.

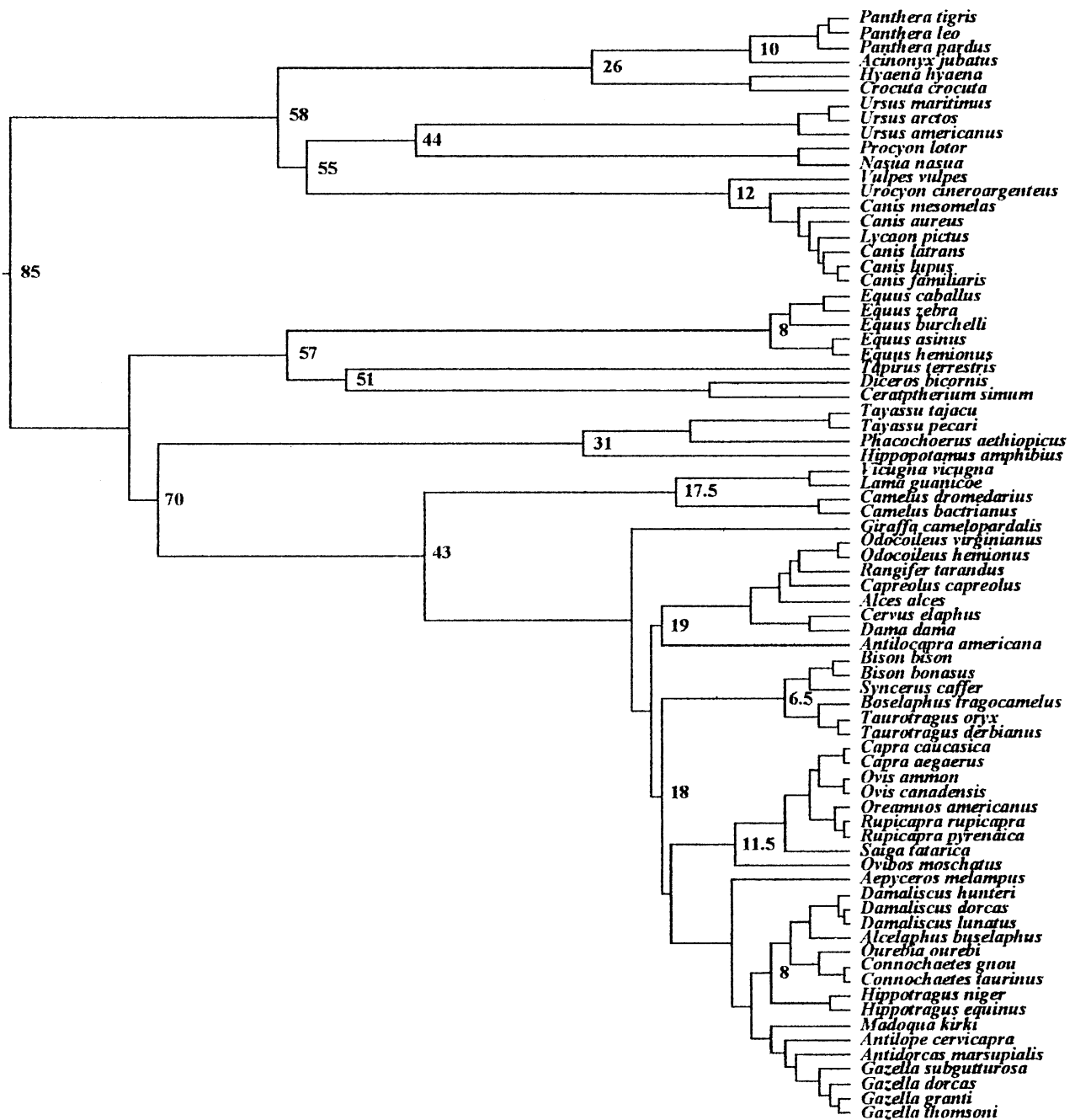


Figure 1. Phylogenetic relationships between the 76 species of mammals used in the study. Numbers adjacent to the nodes refer to split ages in units of millions of years. Total height of tree is 85 million years. Literature sources used in constructing the tree are Kielan-Jaworowska *et al.* (1979), Bennett (1980), Janis (1982), Savage & Russel (1983), Lanave *et al.* (1985), Shoshani (1986), Janis & Scott (1987), Wayne & O'Brien (1987), Gentry & Hooker (1988), Flynn *et al.* (1988), Novacek *et al.* (1988), Padmadisastra (1988), Prothero *et al.* (1988), Tassy & Shoshani (1988), Georgiadis *et al.* (1990), Marshall (1990), Miyamoto *et al.* (1990), Nowak (1991), Geffen *et al.* (1992), Novacek (1992a,b), Garland & Janis (1993), Wyss & Flynn (1993), Flynn (1996), Hunt (1996), Foote *et al.* (1999) and Penny *et al.* (1999).

RESULTS

The two inlever moment arms about the elbow and ankle, the olecranon process and calcaneal tuber, respectively, were included in the analysis (Table 2). The long hind limb metapodials of especially ungulate ungulates, and their rather short, more horizontally orientated humeri, make the ankle joint near functionally equivalent to the elbow. As such, it is curious, but perhaps not surprising, that the length of the olecranon process is strongly correlated with and near isometrically related to the length of the calcaneal tuber (Model II [RMA] analysis: olecranon = (calcaneal tuber) $^{0.937 \pm 0.056}$; $n = 76$; $r = 0.967$; $P \ll 0.001$). The two species of rhino constitute outliers, as their calcaneal tubers are markedly shorter compared to their olecranon processes than is the case among the other species (olecranon process is 163 mm and calcaneal tuber is 104 mm in *Ceratotherium*, and 130 mm and 79 mm, respectively, in *Diceros*).

Of the 16 independent variables analysed (Table 2), 13 showed significant correlations (R) with speed, as noted below. In eight out of these 13 cases (12 of the total of 16 cases), branch length transformations using Grafen's (1989) rho method resulted in the lowest correlations (r) between the contrasts and their standard deviations (Table 3). The ratio-variable olecranon process length/radius length showed the lowest correlation with a square root transformation of the branch lengths, and the ratio-variable calcaneal tuber/metatarsus length displayed the lowest correlation with unmodified branch lengths (Table 3, variables 7 and 15, respectively). The ratio-variable calcaneal tuber length/cube root of body mass (Table 3, variable 16) displayed the lowest correlation with a log transformation of the branch lengths. However, the correlation value of 0.055 still indicated a slight correlation between the contrasts and their standard deviations. As the other methods of transformation resulted in even higher correlations, the log transformation was used for further analysis despite the slight correlation. Otherwise, the correlations obtained were very low, indicating that the samples had been properly standardized (Table 3, Fig. 2).

In Table 4 the parameters that covary significantly with running speed are shown (full regression equations in the Appendix). In accordance with some (Garland & Janis, 1993) and in contrast to other previous analyses (Garland, 1983), no bivariate regression of log body mass or cube root of body mass to speed was statistically significant. This is probably because of the more homogeneous data sample used in this study (and in the study of Garland & Janis, 1993), having excluded extremely large animals not capable of running (elephants) and very small mammals which move in a different manner to most

Table 3. Branch length transformations of the independent variables from Table 2. The lowest correlation (R) values (bold) were used for independent contrasts analysis. In all cases the dependent variable is log running speed. A number after the correlation value in transformations using Grafen's rho method indicates the value of rho.

Var	Correlation				
	Raw	Log	$\sqrt{\quad}$	$\sqrt[3]{\quad}$	Grafen
1	0.2156	0.2689	0.0738	0.1802	0.0064 (0.7)
2	0.1447	0.2285	0.1299	0.2101	0.0021 (0.8)
3	0.2361	0.2703	0.0421	0.1491	0.0298 (0.7)
4	0.3181	0.2091	0.0509	0.0697	0.0216 (0.4)
5	0.2698	0.2035	0.0212	0.0867	0.0044 (0.5)
6	0.1602	0.4014	0.1019	0.2144	0.0055 (0.6)
7	0.2169	0.1972	0.0087	0.1046	0.0208 (0.6)
8	0.4266	0.1690	0.3686	0.3100	0.0166 (0.1)
9	0.2406	0.2876	0.0436	0.1569	0.0385 (0.7)
10	0.3046	0.2152	0.0646	0.0514	0.0006 (0.3)
11	0.1516	0.3818	0.1452	0.2644	0.0388 (0.8)
12	0.2311	0.3551	0.0527	0.1750	0.0221 (0.5)
13	0.4563	0.0652	0.3197	0.2345	0.0034 (0.2)
14	0.2834	0.1316	0.0960	0.0002	0.0097 (0.3)
15	0.0085	0.3252	0.2702	0.3381	0.0143 (0.1)
16	0.3936	0.0546	0.2571	0.1836	0.0704 (0.7)

larger running mammals (Alexander & Jayes, 1983; Alexander, 1991). Curiously, when regressing raw body mass (in kg) to log running speed, a slight, but significant correlation exists (log speed: 9.44×10^{-5} (Mass) + 1.7702; $R = 0.2233$). The ratio-variable cne-mial crest height/tibia length also resulted in non-significant correlation.

It is evident from Table 4 that the correlation coefficients unanimously decrease when taking phylogeny into account. In eight of the 13 cases that showed significant correlations with log running speed, the correlations obtained by independent contrasts analyses (ICLS) were significantly lower than the corresponding values obtained from standard least squares analyses (SLS), as indicated by the 95% confidence limits for the correlation coefficients (Table 4). This strongly corroborates the conclusions of Grafen (1989) and Martins & Garland (1991), among others, that there is an inherent danger of high type I error rates when doing correlation analyses and disregarding the information from phylogeny. In fact, in one case, olecranon process/radius length (Table 4, variable 7), the correlation was modest but significant using SLS, but the effect of phylogeny accounted for most of this alleged correlation, and the ICLS analysis resulted in non-significant correlation ($r = 0.07$). Limb length is clearly a better predictor of running speed when tak-

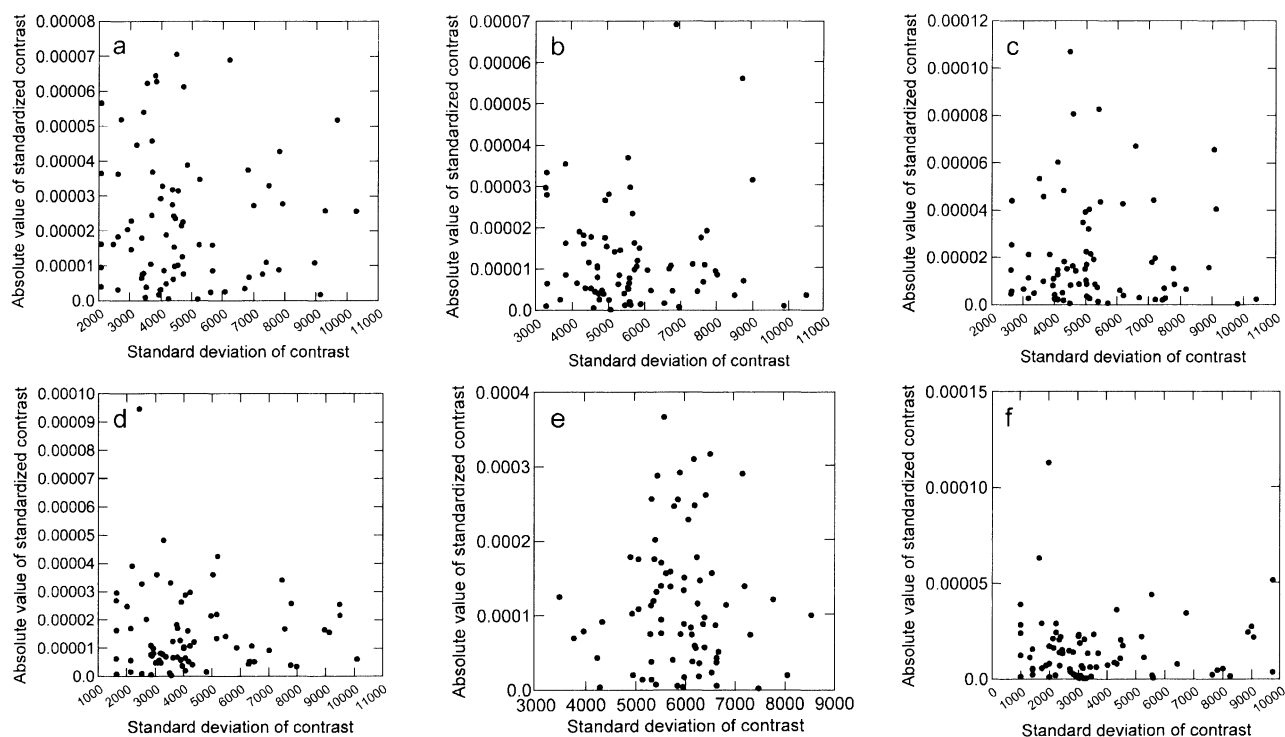


Figure 2. Plots of standardized contrasts to their standard deviations. a, log forelimb length in mm; b, radius/humerus ratio; c, metacarpus/humerus ratio; d, tibia/femur ratio; e, cnemial crest height in $\text{mm}^3/\text{body mass}$ in kilograms; f, calcaneal tuber/metatarsus ratio.

Table 4. Correlation coefficients of the standard least squares (SLS) and independent contrasts least squares (ICLS) bivariate analyses. 95% confidence intervals (Fischer's z method) are shown for the SLS correlation coefficients. The variable numbers in parentheses correspond to the numbers in Table 2. A SLS correlation coefficient in bold have confidence limits that exclude the corresponding ICLS value. Full regression equations are displayed in Appendix 1

Variable	SLS	ICLS	Variable	SLS	ICLS
	$R \pm 95\% \text{ CI}$			R	
Forelimb			Hindlimb		
3	0.289 \pm 0.211	0.252	9	0.307 \pm 0.209	0.259
4	0.560 \pm 0.160	0.376	10	0.550 \pm 0.162	0.366
5	0.575 \pm 0.156	0.355	11	0.436 \pm 0.188	0.235
6	0.562 \pm 0.159	0.250	12	0.566 \pm 0.158	0.327
7	0.236 \pm 0.217	0.066	14	0.462 \pm 0.182	0.340
8	0.444 \pm 0.186	0.377	15	0.527 \pm 0.166	0.172
			16	0.597 \pm 0.150	0.383

ing the mass of the animal into account (Table 4, variables 3 vs. 4 and 9 vs. 10; Figs 3a and 4a). This is not unexpected, as animals show size-related differences in bone allometry in order to maintain mechanical strength (e.g. Bou *et al.*, 1987; Biewener, 1989a,b,

1990; Bertram & Biewener, 1990; Christiansen, 1999b,c), which would be of particular importance during fast locomotion.

Apart from relative limb lengths, the best predictors of running speed are olecranon process and calcaneal

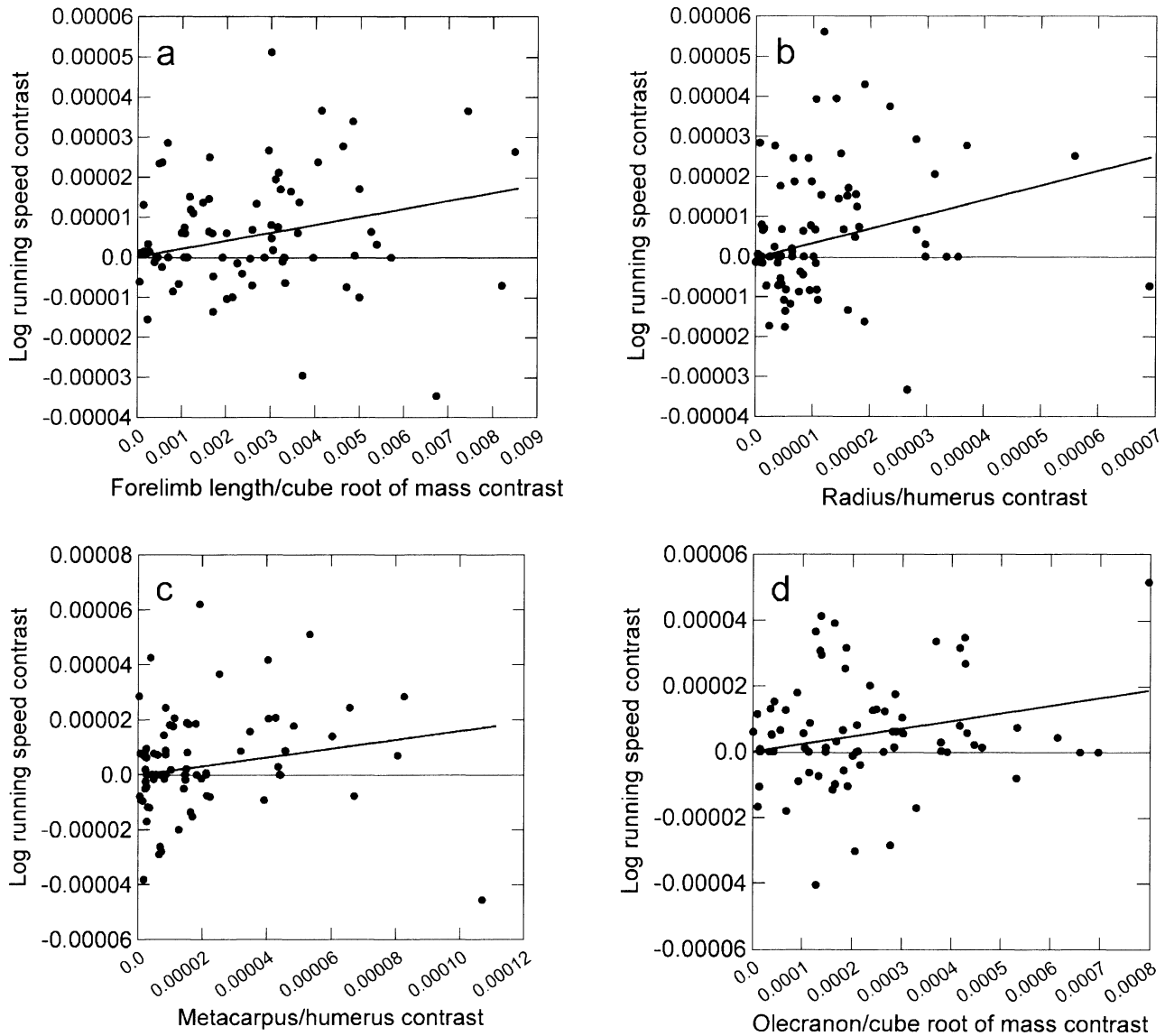


Figure 3. Regression plots of independent contrasts for fore limb parameters. Log running speed is in km h^{-1} . a, Fore limb length in $\text{mm}/\sqrt[3]{\text{body mass}}$ in kg; b, radius/humerus ratio; c, metacarpus/humerus ratio; d, olecranon process length in $\text{mm}/\sqrt[3]{\text{body mass}}$ in kg. Regression lines fitted to the contrasts by means of least squares (model I) analysis.

tuber, both normalized for body mass (Table 4, variables 8 and 16; Figs 3d and 4d). Thus, running speed apparently is more influenced by the mass that has to be accelerated about the joints than the relative in- and outforces and velocities, described in the Introduction. Even better correlations might be obtained if differences in limb postures with size, and thus in the effective mechanical advantage of the muscles, as described by Biewener (1989a; 1989b, 1990) were taken into account, but this is not possible with the present data sample. The metatarsus/femur ratio (Table 4, variable 12; Fig. 4b) is among the good predictors of speed, but the suggestion made in the Intro-

duction, that hitherto overlooked limb ratios might also have a significant influence, is corroborated (Table 4, variables 5, 6 and 11; Figs 3b,c). In fact, the radius/humerus ratio (variable 5) correlates better with log running speed than the metatarsus/femur ratio, although the difference is non-significant.

Garland (1983) and Garland & Janis (1993) found that log body mass displayed a more complex, curvilinear relationship with log running speed. To examine for possible effects of curvilinearity a polynomial regression model was also fitted to the data. In five cases this resulted in a significantly improved correlation with log running speed (Table 5, Fig. 5); among

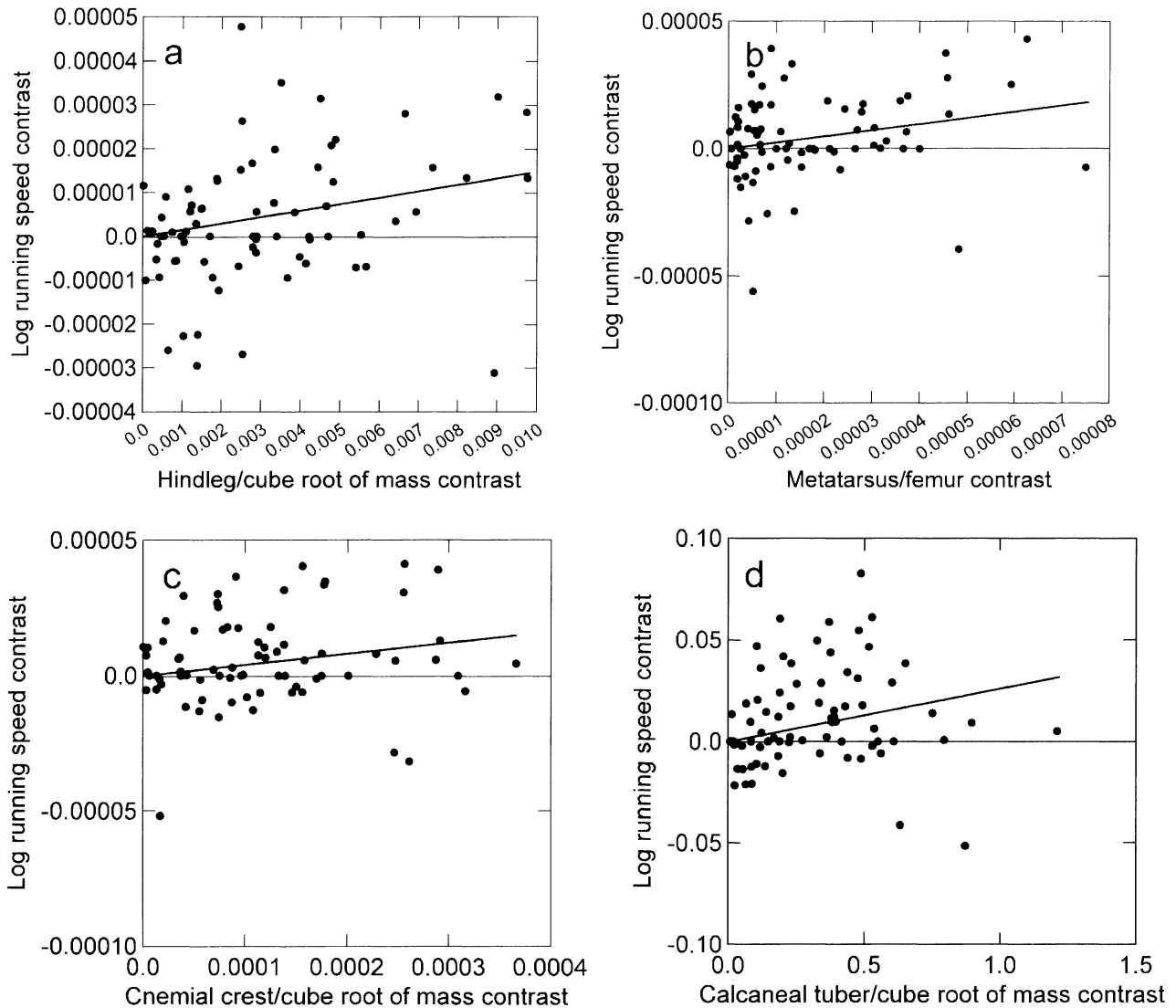


Figure 4. Regression plots of independent contrasts for hind limb parameters. Log running speed is in km h^{-1} . a, Hind limb length in $\text{mm}^3/\sqrt{\text{body mass in kg}}$; b, metatarsus/femur ratio; c, cnemial crest height in $\text{mm}^3/\sqrt{\text{body mass in kg}}$; d, calcaneal tuber length in $\text{mm}^3/\sqrt{\text{body mass in kg}}$. Regression lines fitted to the contrasts by means of least squares (model I) analysis.

others the three cases which showed no significant correlation with log running speed under a linear statistical model (log body mass, cube root of body mass and cnemial crest/tibia ratio). However, none of the variables that correlated well with log running speed showed significant signs of curvilinearity (Tables 4 and 5).

The two remaining variables which show distinct signs of curvilinearity (log forelimb length, olecranon process/radius length) did show significant correlations under a linear model with log running speed, but the correlations were low (Tables 4 and 5). This curvilinear trend (and also log hind limb length, only barely non-significant) is to be expected from the negative

allometry of the proportions of the long bones of large mammals (e.g. Bertram & Biewener, 1990; Christiansen, 1999b,c). Accordingly, when these variables are normalized for size (Table 5, variables 4, 8 and 10), the tendency for curvilinearity disappears altogether and the correlation markedly improves, as noted above. This should be taken into account when assessing running speeds in fossil species based solely on their limb length.

As might be expected, the addition of more variables into the linear models resulted in markedly improved correlations with log running speed (Tables 6 and 7 and Appendix). As with the bivariate analyses, the incorporation of phylogenetic information resulted in

Table 5. Polynomial regression equations on all variables. In all cases *Y* equals log running speed. Regression coefficients where the 95% CI for the polynomial analysis excludes the correlation coefficients for the standard least squares analysis are indicated in bold. One, two, or three asterisks after a SLS correlation coefficient indicates significance at the level of 0.05, 0.01 and 0.001, respectively, and ns indicates *P* > 0.05. Symbols as in Table 4

Variable	<i>R</i> (SLS)	Polynomial regression	<i>R</i> ± 95% CI
1	0.001 ns	$Y = -0.117X^2 + 0.435X + 1.388$	0.431 ± 0.185
2	0.114 ns	$Y = -0.057X^2 + 0.060X + 1.620$	0.330 ± 0.202
3	0.289*	$Y = -0.971X^2 + 5.480X - 5.945$	0.470 ± 0.178
4	0.560***	$Y = -2 \times 10^{-5}X^2 + 0.009X + 0.941$	0.605 ± 0.146
5	0.575***	$Y = -0.720X^2 + 1.927X + 0.542$	0.603 ± 0.146
6	0.562***	$Y = 0.012X^2 + 0.194X + 1.596$	0.573 ± 0.154
7	0.236*	$Y = -8.132X^2 + 4.267X + 1.226$	0.480 ± 0.176
8	0.444***	$Y = -0.002X^2 + 0.082X + 1.052$	0.434 ± 0.185
9	0.307**	$Y = -1.177X^2 + 0.778X - 7.971$	0.474 ± 0.177
10	0.550***	$Y = -4 \times 10^{-6}X^2 + 0.004X + 1.279$	0.583 ± 0.152
11	0.436***	$Y = -0.639X^2 + 1.666X + 0.724$	0.466 ± 0.179
12	0.566***	$Y = -0.181X^2 + 0.513X + 1.499$	0.578 ± 0.153
13	0.071 ns	$Y = -0.005X^2 + 0.143X + 0.772$	0.538 ± 0.163
14	0.462***	$Y = -0.034X^2 + 0.393X + 0.664$	0.565 ± 0.156
15	0.527***	$Y = 0.490X^2 - 0.925X + 1.999$	0.538 ± 0.163
16	0.597***	$Y = -0.002X^2 + 0.088X + 1.000$	0.622 ± 0.141

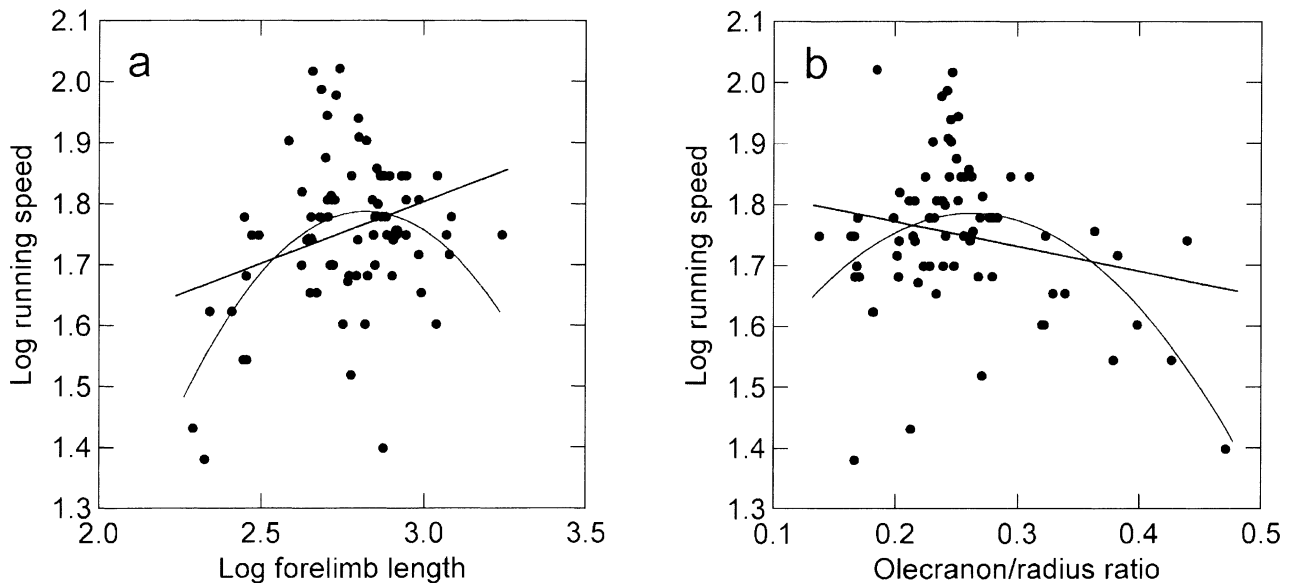


Figure 5. Regression plots of anatomical variables to log running speed in km h⁻¹, showing the distinct curvilinearity of some of the samples, in this case, log forelimb length in mm (a) and olecranon process/radius ratio (b). The polynomial regression model yielded a significantly better fit to the data than ordinary least squares regression lines. For equation see Table 5.

uniformly lower correlation coefficients than obtained by the standard linear model, in several cases much lower correlation coefficients. In these cases the data sets were examined for possible outliers. Removal of

these outliers often markedly improved the correlations (see Appendix for details).

For simplicity, only the improved results, based on the restricted data sets are shown in Tables 6 and 7.

Table 6. Correlation coefficients of the multivariate analyses, two 'independent' variables. Symbols as in Table 4. Correlation coefficients in bold indicate that the ICLS correlation coefficient is significantly lower than the corresponding SLS coefficient. The symbol # in front of a correlation coefficient refers to ICLS analysis on a restricted data set

SLS		ICLS	SLS		ICLS	SLS		ICLS
Variable	$R \pm 95\% \text{ CI}$	R	Variable	$R \pm 95\% \text{ CI}$	R	Variable	$R \pm 95\% \text{ CI}$	R
Forelimb			Hindlimb			Fore + hindlimb		
(1,3)	0.638 ± 0.139	#0.466	1,9	0.655 ± 0.134	#0.492	3,10	0.659 ± 0.133	0.475
(2,3)	0.668 ± 0.130	0.493	1,11	0.496 ± 0.176	#0.493	3,16	0.618 ± 0.145	#0.476
(3,7)	0.414 ± 0.192	0.271	2,9	0.681 ± 0.126	0.510	4,12	0.621 ± 0.144	#0.517
(4,5)	0.614 ± 0.146	#0.477	9,11	0.564 ± 0.159	#0.560	4,13	0.617 ± 0.145	#0.481
(4,6)	0.623 ± 0.144	#0.497	9,15	0.576 ± 0.156	0.373	5,10	0.632 ± 0.141	#0.504
(4,7)	0.584 ± 0.154	#0.462	10,12	0.605 ± 0.149	#0.422	5,12	0.608 ± 0.148	#0.483
(5,8)	0.655 ± 0.134	0.540	10,13	0.630 ± 0.142	#0.502	5,13	0.597 ± 0.151	#0.427
(6,7)	0.584 ± 0.154	#0.422	11,14	0.571 ± 0.158	#0.534	5,14	0.660 ± 0.133	#0.517
			12,14	0.632 ± 0.141	#0.590	5,16	0.696 ± 0.122	#0.544
			12,16	0.629 ± 0.142	#0.567	6,10	0.608 ± 0.148	#0.507
						6,14	0.623 ± 0.144	#0.529
						6,16	0.631 ± 0.141	#0.539
						7,16	0.644 ± 0.138	#0.486
						8,12	0.617 ± 0.145	0.536
						8,15	0.630 ± 0.142	0.489

Table 7. Correlation coefficients of the multivariate analyses, three and four 'independent' variables. Symbols as in Table 4. Correlation coefficients in bold indicate that the ICLS correlation coefficient is significantly lower than the corresponding SLS coefficient. The symbol # in front of a correlation coefficient refers to independent contrast analysis on a restricted data set

SLS		ICLS	SLS		ICLS	SLS		ICLS
Variable	$R \pm 95\% \text{ CI}$	R	Variable	$R \pm 95\% \text{ CI}$	R	Variable	$R \pm 95\% \text{ CI}$	R
Three variables			Fore + hindlimb			Fore + hindlimb		
Forelimb			Hindlimb			Fore + hindlimb		
1,3,6	0.666 ± 0.131	0.510	10,12,13	0.658 ± 0.133	#0.559	1,3,12	0.666 ± 0.131	#0.564
1,3,7	0.657 ± 0.134	#0.466				2,3,12	0.700 ± 0.120	#0.582
1,6,7	0.482 ± 0.179	#0.414				2,3,15	0.687 ± 0.125	#0.527
2,3,6	0.701 ± 0.120	0.504				2,5,13	0.636 ± 0.140	#0.509
						2,6,9	0.696 ± 0.122	#0.562
						3,7,16	0.677 ± 0.128	#0.573
						3,11,14	0.632 ± 0.141	#0.655
						4,5,13	0.658 ± 0.133	#0.565
						6,7,13	0.620 ± 0.145	#0.467
						6,7,16	0.663 ± 0.132	#0.601
Four variables			Fore + hindlimb			Fore + hindlimb		
						1,3,5,13	0.675 ± 0.128	#0.532
						1,3,6,13	0.683 ± 0.126	#0.520

All correlations and associated regressions are, however, shown in the Appendix. Several ICLS correlations, even on restricted data sets were significantly lower (three for fore limb, four for hind limb and five for fore + hind limb combined) than the corresponding

SLS values. However, had the correlation coefficients of the SLS model been compared to the ICLS coefficients obtained from unrestricted data sets, they would all have been significantly lower, for both forelimbs, hind limbs and fore + hind limbs. The only

exceptions are three data sets in which outliers could not be identified (Table 6, variables 3 + 7 and 5 + 8). In these cases there was no significant difference in correlation coefficients between SLS and ICLS models.

With two 'independent' variables, the highest ICLS correlation of 0.590 was obtained on a restricted data set (collapsing two nodes in the phylogeny, see Appendix), with the variables metatarsus/femur ratio and cnemial crest/cube root of mass. The highest correlation in the forelimb was 0.540 (unrestricted data set) and for the fore and hind limb combined it was 0.544. The eigenvalues usually did not indicate significant problems of autocorrelation and the condition indices were low, usually below 20, but on two occasions (body mass and forelimb length and body mass and hind limb length) they indicated severe autocorrelation (condition indices of 80 and 84, respectively). This is probably unavoidable in a biological sample, as noted above, particularly as limb lengths are highly correlated with body mass (e.g. Garland & Janis, 1993; Steudel & Beattie, 1993; Christiansen, 1999b).

Adding progressively more variables led only to redundancy of some of them. However, with three 'independent' variables from fore and hind limbs, a correlation coefficient of 0.655 (Table 7, variables 3, 11 and 14) could be obtained, the highest of all the ICLS analyses. In some cases the eigenvalues and condition indices indicated only moderate problems of autocorrelation, but in some cases the highest condition indices exceeded 100. For hind limb parameters only one analysis did not lead to redundancy of one or more variables (Table 7, variables 10, 12, 13), but compared to the analyses on just two 'independent' variables (Table 6, variables 10 + 12 or 10 + 13) the correlation coefficient did not improve markedly. For a fossil species it would be desirable to use variables 12 and 13 only (see Table 2) to avoid body mass. Unfortunately, these two did not correlate significantly better with running speed than metatarsus/femur ratio (variable 12) alone (Table 4).

With four 'independent' variables, only two equations did not result in redundancy of one or more variables (Table 7). The eigenvalues and condition indices indicated severe problems of autocorrelation (values up to 159) but as noted previously this is probably unavoidable in a biological sample. Assembling four parameters from a species, particularly a fossil species, is sometimes not feasible. Additionally, the gain in correlation with four vs. two 'independent' variables is, at best, negligible (compare correlation coefficients in Tables 6 and 7). Thus, the best and most widespread correlations are found with two 'independent' variables, after which addition of variables only leads to redundancy. This should also be kept in mind when assessing the potential speed of fossil species. One

variable, such as the m/f ratio, is not as reliable as two.

DISCUSSION

For prediction of speed in fossil animals it would of course be desirable not to include inferences of body mass (most equations in the tables have body mass included as a parameter) and several equations indicate that a reliable result may be obtained without it. Thus, the best single variables to use are the radius/humerus and metatarsus/femur ratios (Table 4). Using two variables yields considerably more reliable results, and good predictions can be made on the basis of the metacarpus/humerus ratio + olecranon/radius ratio, log hind limb length + calcaneal tuber/metatarsus ratio, radius/humerus ratio + metatarsus/femur ratio, and radius/humerus ratio + cnemial crest height/tibia length. The best combination to use is, however, log hind limb length + tibia/femur ratio (Table 6). Little, if any, additional reliability may be gained from adding more variables to the above.

The bivariate correlations with top running speed found in this paper, although significant, are not impressive. There are several possible reasons for this. It is superfluous to cite the possible inaccuracy of some the speed data used, as these are not, and probably cannot be, accurate to the letter. If timed distances were known for all included species this could improve resolution, but 10 specimens of the same species are unlikely to run equally fast and it is probably impossible to determine if an animal runs at its highest possible speed. But there is little reason to suppose that speed values, as suggested by Garland & Janis (1993) are the chief agents of residual scatter. There is reason to suppose that the appendicular anatomy of terrestrial mammals may not be optimized for speed as suggested by Howell (1944) but rather to minimize energy consumption during all forms of locomotion. Thus, top running speed possibly is not tightly correlated with appendicular anatomy.

It seems more sensible to optimize the appendicular skeleton for minimizing costs of locomotion at all gaits than simply for running faster. Evolution supposedly acts to maximize fitness and most of the time animals do not run, but walk. Reduced costs of locomotion might imply that a relatively greater percentage of energy consumption can be directed towards reproduction or, alternatively, less energy is needed overall and so forage times can be reduced (Stephens & Krebs, 1986). It will also allow animals to travel a greater distance on any given amount of energy. Longer legs imply longer stride lengths, and thus potentially higher speed, but may also imply that stride frequency decreases at any given speed. Long outlevers and proximally placed muscles imply faster angular veloc-

ities at any given speed, not just at peak running velocity.

Empirical verification for this is, among others, that animals, including man, have been found to change gaits and adopt stride frequencies at various speeds so as to minimize costs of locomotion (e.g. Zarrugh *et al.*, 1974; Hoyt & Taylor, 1981; Heglund & Cavagna, 1985; Taylor, 1985; Heglund & Taylor, 1988; Alexander, 1989b). The inferred in and out velocities around the joints depend not only on the relationship of the in and outlevers (as used in this paper), but also on the muscle fibre composition. Some muscles contract fast and generate a greater amount of force than others, but also use more energy (Goldspink *et al.*, 1970; Taylor *et al.*, 1980; Johnston, 1985; Heglund & Cavagna, 1987; Alexander, 1989b). Ignorance of the muscle fibre composition of the individual inlevers (as in analyses such as the present) of the various species could also contribute to residual scatter in analyses of speed to in and outlever ratios.

In fast-moving animals the limb muscles are usually located proximally in the limb (supposedly to reduce angular momentum) and insert proximally on the bones (to produce a greater angular velocity). However, during the stance phase muscles appear to shorten relatively little (e.g. Roberts *et al.*, 1997; Biewener *et al.*, 1998), casting doubt on these assumptions. More significantly, proximally placed muscles can operate the limbs by means of long tendons that can store great amounts of elastic energy, which can then be used in the succeeding step. Taylor *et al.* (1980) and Heglund & Cavagna (1985) found that small animals are less energy-efficient during locomotion than larger animals. Similarly, Alexander & Jayes (1983) found that smaller animals use longer relative stride lengths, and, thus, that the dynamic similarity of locomotion is somewhat different in smaller mammals, but of course they use very high stride frequencies during fast locomotion.

The mass-specific cost of locomotion is related to stride frequency, and thus, force generation by the muscles (Taylor *et al.*, 1980; Heglund & Taylor, 1988). It is well known that energy cost of locomotion increases with running speed and decreases with body mass (e.g. Tucker, 1970; Taylor *et al.*, 1982; Heglund & Cavagna, 1985; Heglund & Taylor, 1988; Strang & Steudel, 1990). Additionally, energy efficiency is highest during running gaits (Cavagna & Kaneko, 1977; Alexander *et al.*, 1985; Heglund & Cavagna, 1985). This implies that, during fast locomotion, tendons are heavily involved in the generation of positive work from passive recoil, at the expense of muscular work (Cavagna & Kaneko, 1977; Alexander, 1984a; Taylor, 1985; Dimery *et al.*, 1986; Heglund & Taylor, 1988; Roberts *et al.*, 1997). As this system will be enhanced with rather long legs (to allow room for both muscle

and large tendons), and limbs which are not heavily crouched (as in small mammals) and work primarily in the parasagittal plane, this implies that it should be most efficient in large animals, in accordance with the above. This problem, however, is not addressed in analyses such as the present one.

Limb lengths are, however, directly related to stride lengths and thus to speed. Alexander & Jayes (1983) showed that larger animals (above 10 kg or so in mass) move in a dynamically similar fashion, which, again, probably is related to minimization of energy costs of locomotion (Alexander, 1989b). When animals run with equal Froude numbers (v^2/gL ; see Alexander, 1976, 1983, 1989a, b), speed is proportional to (limb length)^{0.5}. If their motions are dynamically similar, stride frequencies (speed/limb length) are proportional to (limb length)^{-0.5}. This has been verified by empirical studies of running animals (Pennycuik, 1975). Accordingly, limb lengths could be expected to show a high correlation with speed. As shown in this paper, this is not the case. When normalized for body mass, limb lengths show a higher correlation with speed, although still not as impressive as might be expected. There are several reasons for this.

Limb lengths in the above analyses implies hip (or shoulder) height. Limb length in this analysis, and others like it (e.g. Garland & Janis, 1993; Steudel & Beattie, 1993, 1995) is the sum of the lengths of the individual limb bones, disregarding the carpals and tarsals. However, as species size increases, limb postures become progressively more upright, in order to reduce the mass-specific amount of force required to counteract moments about the joints (Biewener, 1983, 1989a, 1989b, 1990). Functional limb length is thus not linearly related to the sum of the individual limb bones across a large size range. Additionally, some equally large forms do (ungulates, most carnivorans) or do not (ursids) incorporate the metapodium into effective limb length. The above is of course most evident when comparing a small, stockily built, 'non-cursorial' insectivore, rodent or xenarthran to an antelope. As all animals in this analysis move their limbs in a roughly parasagittal plane, are capable of true running (with the exception of the hippo) and most are fairly large, the influence of this should not be too severe. Despite being plantigrade, the ursids in this sample did not, however, constitute outliers in any of the analyses (see Appendix).

Additionally, the epaxial and hypaxial muscles are also involved in stride lengths, although to varying extents in different species (e.g. Hildebrand, 1959, 1961, 1988; Alexander *et al.*, 1985; Alexander, 1989b; Pridmore, 1992). Other parameters also potentially influence running speed and endurance, such as details of the pulmonary and cardiovascular system (Harrison & Denny, 1985; Young *et al.*, 1992; Simons,

1996) but all these factors are of course not addressed in studies such as the present one. Undoubtedly, these unknown parameters also contribute to 'residual' scatter (residual in quotation, as some of it may well be explicable).

Finally, limbs are optimized for more than 'just' running velocity or minimization of energy consumption. Support of mass is very important and becomes progressively severe at increasing body sizes. In this analysis it was attempted to circumvent this problem by normalizing for body size (limb lengths) or compare the inlever moment arms about the joints to both their respective outlevers and cube root of body mass. In all cases the incorporation of body mass improved correlation (see Table 4). This consideration is not usually included in more traditional views of how limb ratios correlate with speed (e.g. Howell, 1944; Maynard Smith & Savage, 1956; Gambaryan, 1974; Van Valkenburgh, 1987; Garland & Janis, 1993; Janis & Wilhelm, 1993). It is oversimplified to assume that the humerus and femur are shorter and stouter than the lower limb bones solely due to the energetics of moving the limb segments (Maynard Smith & Savage, 1956). These bones are held at a less steep incline to vertical than are the epi- and metapodials. Accordingly, they need to be stronger to resist the increases in bending moments about the diaphyses compared to the distal limb bones (e.g. Carrano, 1998; Christiansen, 1998; Christiansen & Paul, 2001; Christiansen & Bonde, 2002).

Higher correlations of anatomical variables to speed could be obtained by restricting the data samples even further, to encompass, e.g. carnivores or felids only (see, e.g. Garland & Janis, 1993: Table 1). In felids the forelimbs are very important in subduction of prey (e.g. Gonyea, 1976; Turner, 1997), and this is therefore also an important parameter in limb morphology in these forms, which is certainly not present in any herbivore or even any canid. Additionally, some mammals are anatomical 'outliers' compared to each other (e.g. a rhinoceros and a giraffe, which have nearly equal body masses; Nowak, 1991; Silva & Downing, 1995). However, such restriction of the data sample would render the analysis useless for many fossil species of mammals, and all species of non-avian dinosaurs.

Thus, the majority of available evidence indicates that the appendicular anatomy of terrestrial mammals is probably not optimized to facilitate top running speeds but to minimize energy consumption during all forms of locomotion. Muscle fibre composition, the influence of axial muscles, modifications of the pulmonary and cardiovascular system, ecological variables and support of mass are also of major influence. If speed was of primary importance, animals could simply evolve very long and strong limbs with size, powered by over-enlarged muscles. Most of the

time, however, this would be equivalent to 'energetic overkill', and thus, economically highly inefficient.

One problem of traditional analyses of anatomical variables to speed which was addressed in this study, incorporation of more than just variable in the correlation analyses, led to markedly increased correlation coefficients, which demonstrates that bivariate analyses simply use too little of the available osteological information. Accordingly, the rather poor correlations of single anatomical variables to speed, reported both in this and previous studies, are not necessarily due to poor speed data (as suggested by Garland & Janis, 1993) but might to a certain extent reflect the true nature of the correlations of one osteological variable and top running speed.

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APPENDIX 1

Regression coefficients, 95% confidence intervals for the regression coefficients, significance of the variables (two-tailed P ; significance level set at $P \leq 0.10$), correlation coefficients, standard errors of the estimate (SEE) and F statistics for significance of the regression ($DF = t_{n-i+1}$, where i is number of variables) for all regression equations. A number in parentheses in front of a regression slope coefficient indicates the 'independent' variable in question and the numbers correspond to the numbers listed in Table 2. In all cases the 'dependent' variable is log running speed (km h^{-1}). Standard and independent contrasts regression equations within the various categories are ordered according to the size of the correlation coefficient, going from the lowest to the highest value. Some multivariate independent contrasts regression equations are in italic. They were based on re-analysis on a restricted data set, where some contrasts were removed as the initial analysis on the full data set had indicated that they were either outliers or possessed a large leverage.

BIVARIATE ANALYSIS

Forelimb

Standard least squares regression

A \pm 95% CI	P	B \pm 95% CI	P	R	SEE	F	P
1.868 \pm 0.114	0.000	(7) -0.454 \pm 0.433	0.040	0.236	0.123	4.366	0.040
1.271 \pm 0.412	0.000	(3) 0.193 \pm 0.148	0.011	0.289	0.122	36.624	0.011
1.361 \pm 0.184	0.000	(8) 0.031 \pm 0.015	0.000	0.444	0.114	18.165	0.000
1.362 \pm 0.135	0.000	(4) 0.003 \pm 0.001	0.000	0.560	0.105	33.818	0.000
1.596 \pm 0.059	0.000	(6) 0.208 \pm 0.071	0.000	0.562	0.105	34.127	0.000
1.301 \pm 0.151	0.000	(5) 0.432 \pm 0.142	0.000	0.575	0.104	36.624	0.000

Independent contrasts least squares regression

B \pm 95% CI	P	R	F	P
(7) -0.146 \pm 0.514	0.574	0.066	0.321	0.574
(6) 0.158 \pm 0.142	0.029	0.250	4.916	0.029
(3) 0.178 \pm 0.158	0.028	0.252	5.005	0.028
(5) 0.346 \pm 0.211	0.002	0.355	10.684	0.002
(4) 0.002 \pm 0.001	0.001	0.376	12.209	0.001
(8) 0.023 \pm 0.013	0.001	0.377	12.252	0.001

Hindlimb

Standard least squares regression

A \pm 95% CI	P	B \pm 95% CI	P	R	SEE	F	P
1.132 \pm 0.446	0.000	(9) 0.219 \pm 0.157	0.007	0.307	0.121	7.718	0.007
1.394 \pm 0.174	0.000	(11) 0.344 \pm 0.165	0.000	0.436	0.114	17.320	0.000
1.427 \pm 0.147	0.000	(14) 0.067 \pm 0.030	0.000	0.462	0.113	20.124	0.000
1.914 \pm 0.065	0.000	(15) -0.474 \pm 0.177	0.000	0.527	0.108	28.396	0.000
1.402 \pm 0.125	0.000	(10) 0.001 \pm 0.001	0.000	0.550	0.106	32.108	0.000
1.576 \pm 0.064	0.000	(12) 0.261 \pm 0.088	0.000	0.566	0.105	34.850	0.000
1.298 \pm 0.144	0.000	(16) 0.038 \pm 0.012	0.000	0.597	0.102	41.038	0.000

Independent contrasts least squares regression

B ± 95% CI	P	R	F	P
(15) -0.240 ± 0.319	0.140	0.172	2.245	0.140
(11) 0.269 ± 0.257	0.041	0.235	4.331	0.041
(9) 0.203 ± 0.175	0.024	0.259	5.317	0.024
(12) 0.237 ± 0.159	0.004	0.327	8.855	0.004
(14) 0.041 ± 0.026	0.003	0.340	9.654	0.003
(10) 0.002 ± 0.001	0.001	0.366	11.469	0.001
(16) 0.025 ± 0.014	0.001	0.383	12.717	0.001

MULTIVARIATE ANALYSIS, TWO 'INDEPENDENT' VARIABLES

Forelimb

Standard least squares regression

A ± 95% CI	P	B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	R	SEE	F	P
1.257 ± 0.396	0.000	(3) 0.232 ± 0.145	0.002	(7) -0.582 ± 0.416	0.007	0.414	0.116	7.562	0.001
1.157 ± 0.270	0.000	(4) 0.003 ± 0.001	0.000	(7) 0.422 ± 0.479	0.083	0.584	0.104	18.929	0.000
1.681 ± 0.116	0.000	(6) 0.200 ± 0.071	0.000	(7) -0.310 ± 0.368	0.097	0.584	0.104	18.896	0.000
1.258 ± 0.151	0.000	(4) 0.002 ± 0.001	0.022	(5) 0.269 ± 0.196	0.008	0.614	0.101	22.127	0.000
1.416 ± 0.134	0.000	(4) 0.002 ± 0.001	0.004	(6) 0.129 ± 0.086	0.004	0.623	0.100	23.139	0.000
-0.566 ± 0.654	0.089	(1) -0.285 ± 0.080	0.000	(3) 1.032 ± 0.291	0.000	0.638	0.098	25.059	0.000
1.078 ± 0.188	0.000	(5) 0.373 ± 0.137	0.000	(8) 0.022 ± 0.010	0.001	0.655	0.097	27.459	0.000
-0.175 ± 0.515	0.499	(2) -0.062 ± 0.017	0.000	(3) 0.802 ± 0.211	0.000	0.668	0.095	29.410	0.000

Independent contrasts least squares regression

B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	R	F	P
(6) 0.179 ± 0.166	0.035	(7) 0.002 ± 0.008	0.622	0.256	2.564	0.084
(6) 0.269 ± 0.156	0.001	(7) 0.001 ± 0.007	0.809	0.422	7.704	0.001*
(3) 0.185 ± 0.159	0.024	(7) -0.003 ± 0.008	0.383	0.271	2.882	0.062
(4) 0.002 ± 0.001	0.020	(6) 0.023 ± 0.153	0.762	0.378	6.084	0.004
(4) 0.001 ± 0.001	0.024	(6) 0.124 ± 0.139	0.079	0.497	11.650	0.000*
(4) 0.002 ± 0.001	0.001	(7) 0.003 ± 0.006	0.418	0.387	6.417	0.003
(4) 0.002 ± 0.001	0.000	(7) 0.001 ± 0.005	0.952	0.462	9.639	0.000*
(1) -0.173 ± 0.106	0.002	(3) 0.683 ± 0.345	0.000	0.426	8.076	0.001
(1) -0.208 ± 0.096	0.000	(3) 0.668 ± 0.308	0.000	0.466	9.846	0.000*
(4) 0.001 ± 0.001	0.037	(5) 0.207 ± 0.219	0.064	0.426	8.098	0.001
(4) 0.002 ± 0.001	0.003	(5) 0.113 ± 0.199	0.261	0.477	10.454	0.000*
(2) -0.037 ± 0.017	0.000	(3) 0.558 ± 0.232	0.000	0.493	11.704	0.000
(5) 0.385 ± 0.196	0.000	(8) 0.023 ± 0.012	0.000	0.540	15.012	0.000

*Excluding contrasts 67 (collapsing node between *Ourebia* and *Connochaetes*) and 70 (collapsing node between *Madoqua* and *Antilope* + *Antidorcas* + *Gazella*)

Hindlimb

Standard least squares regression

A ± 95% CI	P	B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	R	SEE	F	P
1.197 ± 0.237	0.000	(1) 0.055 ± 0.047	0.022	(11) 0.434 ± 0.177	0.000	0.496	0.111	11.937	0.000
0.631 ± 0.440	0.006	(9) 0.257 ± 0.138	0.000	(11) 0.376 ± 0.153	0.000	0.564	0.106	17.053	0.000
1.201 ± 0.189	0.000	(11) 0.273 ± 0.156	0.001	(14) 0.055 ± 0.028	0.000	0.571	0.105	17.667	0.000
1.426 ± 0.403	0.000	(9) 0.168 ± 0.137	0.017	(15) -0.444 ± 0.173	0.000	0.576	0.104	18.147	0.000
1.450 ± 0.126	0.000	(10) 0.001 ± 0.001	0.024	(12) 0.163 ± 0.120	0.008	0.605	0.102	21.099	0.000
1.364 ± 0.153	0.000	(12) 0.131 ± 0.120	0.032	(16) 0.025 ± 0.016	0.003	0.629	0.099	23.942	0.000
1.497 ± 0.130	0.000	(10) 0.003 ± 0.001	0.000	(13) -0.013 ± 0.008	0.001	0.630	0.099	23.999	0.000
1.397 ± 0.130	0.000	(12) 0.212 ± 0.089	0.000	(14) 0.044 ± 0.028	0.003	0.632	0.099	24.248	0.000
-0.786 ± 0.685	0.025	(1) -0.278 ± 0.084	0.000	(9) 1.080 ± 0.291	0.000	0.655	0.097	27.398	0.000
-0.361 ± 0.544	0.190	(2) -0.061 ± 0.017	0.000	(9) 0.847 ± 0.215	0.000	0.681	0.094	31.549	0.000

Independent contrasts least squares regression

B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	R	F	P
(11) 0.131 ± 0.184	0.164	(14) 0.036 ± 0.026	0.009	0.370	5.872	0.004
(11) 0.256 ± 0.163	0.003	(14) 0.042 ± 0.023	0.001	0.534	14.191	0.000*
(9) 0.267 ± 0.177	0.004	(15) -0.260 ± 0.209	0.016	0.373	5.889	0.004
(1) 0.097 ± 0.069	0.006	(11) 0.557 ± 0.321	0.001	0.384	6.297	0.003
(1) 0.060 ± 0.060	0.050	(11) 0.635 ± 0.271	0.000	0.493	11.408	0.000*
(10) 0.002 ± 0.001	0.001	(13) -0.001 ± 0.001	0.219	0.390	6.536	0.002
(10) 0.002 ± 0.001	0.000	(13) -0.001 ± 0.001	0.076	0.502	11.930	0.000*
(10) 0.001 ± 0.001	0.090	(12) 0.122 ± 0.179	0.178	0.394	6.717	0.002
(10) 0.001 ± 0.001	0.036	(12) 0.177 ± 0.153	0.024	0.422	13.280	0.000*
(12) 0.168 ± 0.162	0.042	(16) 0.001 ± 0.001	0.012	0.426	8.073	0.001
(12) 0.241 ± 0.135	0.001	(16) 0.001 ± 0.001	0.001	0.567	16.800	0.000*
(1) -0.175 ± 0.104	0.001	(9) 0.771 ± 0.316	0.000	0.438	8.653	0.000
(1) -0.216 ± 0.094	0.000	(9) 0.773 ± 0.331	0.000	0.492	11.331	0.000*
(12) 0.226 ± 0.159	0.006	(14) 0.032 ± 0.026	0.017	0.451	9.297	0.000
(12) 0.286 ± 0.136	0.000	(14) 0.039 ± 0.022	0.001	0.590	18.981	0.000*
(9) 0.416 ± 0.205	0.000	(11) 0.511 ± 0.263	0.000	0.478	10.807	0.000
(9) 0.303 ± 0.177	0.001	(11) 0.627 ± 0.226	0.000	0.560	16.209	0.000*
(2) -0.039 ± 0.017	0.000	(9) 0.649 ± 0.257	0.000	0.510	12.850	0.000

*Excluding contrasts 67 (collapsing node between *Ourebia* and *Connochaetes*) and 70 (collapsing node between *Madoqua* and *Antilope* + *Antidorcas* + *Gazella*)

Fore and hindlimbs

Standard least squares regression

A ± 95% CI	P	B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	R	SEE	F	P
1.367 ± 0.168	0.000	(5) 0.452 ± 0.142	0.000	(13) -0.007 ± 0.006	0.091	0.597	0.103	20.261	0.000
1.387 ± 0.168	0.000	(5) 0.258 ± 0.214	0.019	(12) 0.140 ± 0.131	0.037	0.608	0.101	21.445	0.000
1.455 ± 0.126	0.000	(6) 0.130 ± 0.093	0.007	(10) 0.001 ± 0.001	0.015	0.608	0.102	21.399	0.000
1.447 ± 0.143	0.000	(4) 0.003 ± 0.001	0.000	(13) -0.011 ± 0.008	0.006	0.617	0.101	22.413	0.000
1.372 ± 0.163	0.000	(8) 0.018 ± 0.013	0.009	(12) 0.214 ± 0.092	0.000	0.617	0.101	22.484	0.000
1.026 ± 0.347	0.000	(3) 0.108 ± 0.126	0.091	(16) 0.036 ± 0.012	0.000	0.618	0.101	22.521	0.000
1.410 ± 0.133	0.000	(4) 0.002 ± 0.001	0.007	(12) 0.161 ± 0.110	0.005	0.621	0.100	22.884	0.000
1.422 ± 0.130	0.000	(6) 0.167 ± 0.073	0.000	(14) 0.042 ± 0.028	0.005	0.623	0.100	23.111	0.000
1.581 ± 0.184	0.000	(8) 0.024 ± 0.012	0.000	(15) -0.411 ± 0.166	0.000	0.630	0.099	24.063	0.000
1.369 ± 0.154	0.000	(6) 0.105 ± 0.094	0.029	(16) 0.025 ± 0.016	0.002	0.631	0.099	24.101	0.000
1.244 ± 0.149	0.000	(5) 0.289 ± 0.168	0.001	(10) 0.001 ± 0.001	0.005	0.632	0.099	24.257	0.000
1.414 ± 0.163	0.000	(7) -0.463 ± 0.343	0.009	(16) 0.038 ± 0.011	0.000	0.644	0.098	25.856	0.000
0.694 ± 0.361	0.000	(3) 0.245 ± 0.119	0.000	(10) 0.002 ± 0.001	0.000	0.659	0.096	28.011	0.000
1.134 ± 0.166	0.000	(5) 0.366 ± 0.136	0.000	(14) 0.049 ± 0.027	0.000	0.660	0.096	28.146	0.000
1.114 ± 0.156	0.000	(5) 0.296 ± 0.138	0.000	(16) 0.028 ± 0.012	0.000	0.696	0.092	34.380	0.000

Independent contrasts least squares regression

B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	R	F	P
(5) 0.347 ± 0.212	0.002	(13) -0.001 ± 0.001	0.484	0.363	5.555	0.006
(5) 0.427 ± 0.218	0.000	(13) -0.001 ± 0.001	0.658	0.427	7.924	0.001*
(7) -0.126 ± 0.482	0.604	(16) 0.001 ± 0.001	0.001	0.369	5.740	0.005
(7) -0.359 ± 0.413	0.087	(16) 0.001 ± 0.001	0.000	0.486	11.001	0.000**
(6) 0.045 ± 0.143	0.533	(10) 0.001 ± 0.001	0.035	0.372	5.875	0.004
(6) 0.126 ± 0.128	0.055	(10) 0.001 ± 0.001	0.019	0.507	12.300	0.000**
(6) 0.082 ± 0.149	0.277	(16) 0.001 ± 0.001	0.012	0.375	5.979	0.004
(6) 0.199 ± 0.139	0.006	(16) 0.001 ± 0.001	0.001	0.539	14.713	0.000***
(5) 0.243 ± 0.257	0.064	(12) 0.131 ± 0.191	0.176	0.385	6.339	0.003
(5) 0.294 ± 0.243	0.019	(12) 0.192 ± 0.173	0.030	0.483	10.783	0.000*
(4) 0.002 ± 0.001	0.001	(13) -0.001 ± 0.001	0.376	0.389	6.491	0.003
(4) 0.002 ± 0.001	0.000	(13) -0.001 ± 0.001	0.204	0.481	10.684	0.000**
(4) 0.001 ± 0.002	0.056	(12) 0.110 ± 0.186	0.244	0.397	6.835	0.002
(4) 0.001 ± 0.001	0.037	(12) 0.183 ± 0.159	0.025	0.517	12.974	0.000**
(6) 0.131 ± 0.135	0.057	(14) 0.031 ± 0.028	0.030	0.398	6.864	0.002
(6) 0.229 ± 0.132	0.001	(14) 0.034 ± 0.025	0.009	0.529	13.977	0.000***
(3) 0.162 ± 0.150	0.035	(16) 0.001 ± 0.001	0.002	0.419	7.751	0.001
(3) 0.095 ± 0.146	0.198	(16) 0.001 ± 0.001	0.000	0.476	10.573	0.000***
(5) 0.239 ± 0.187	0.013	(10) 0.001 ± 0.001	0.014	0.452	9.374	0.000
(5) 0.321 ± 0.193	0.001	(10) 0.001 ± 0.001	0.020	0.504	12.064	0.000*
(5) 0.334 ± 0.207	0.002	(14) 0.034 ± 0.025	0.008	0.474	10.579	0.000
(5) 0.404 ± 0.222	0.001	(14) 0.029 ± 0.024	0.019	0.517	12.940	0.000*
(3) 0.154 ± 0.104	0.004	(10) 0.002 ± 0.001	0.000	0.475	10.664	0.000
(5) 0.312 ± 0.200	0.003	(16) 0.001 ± 0.001	0.002	0.484	11.165	0.000
(5) 0.271 ± 0.188	0.005	(16) 0.001 ± 0.001	0.000	0.544	15.113	0.000***
(8) 0.028 ± 0.013	0.000	(15) -0.243 ± 0.160	0.003	0.487	11.377	0.000
(8) 0.024 ± 0.012	0.000	(12) 0.282 ± 0.146	0.000	0.536	14.693	0.000

*Excluding contrasts 36 (collapsing node between *Giraffa* and Cervidae + Bovidae) and 70 (collapsing node between *Madoqua* and *Antilope* + *Antidorcas* + *Gazella*)

**Excluding contrasts 67 (collapsing node between *Ourebia* and *Connochaetes*) and 70 (collapsing node between *Madoqua* and *Antilope* + *Antidorcas* + *Gazella*)

***Excluding contrast 67 (collapsing node between *Ourebia* and *Connochaetes*)

MULTIVARIATE ANALYSIS, THREE 'INDEPENDENT' VARIABLES

Forelimb

Standard least squares regression

A ± 95% CI	P	B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	B ₃ ± 95% CI	P	R	SEE	F	P
1.672 ± 0.142	0.000	(1) 0.309 ± 0.152	0.000	(6) -0.507 ± 0.450	0.028	(7) -0.079 ± 0.042	0.007	0.482	0.113	7.252	0.000
-1.103 ± 0.883	0.015	(1) -0.366 ± 0.127	0.000	(3) 1.240 ± 0.370	0.000	(7) 0.443 ± 0.497	0.080	0.657	0.097	18.250	0.000
-0.036 ± 0.800	0.929	(1) -0.211 ± 0.110	0.000	(3) 0.764 ± 0.374	0.000	(6) 0.094 ± 0.085	0.032	0.666	0.096	19.177	0.000
0.199 ± 0.576	0.493	(2) -0.048 ± 0.020	0.000	(3) 0.617 ± 0.250	0.000	(6) 0.098 ± 0.077	0.013	0.701	0.092	23.248	0.000

Independent contrasts least squares regression

B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	B ₃ ± 95% CI	P	R	F	P
(1) 0.043 ± 0.053	0.113	(6) 0.240 ± 0.194	0.016	(7) 0.002 ± 0.008	0.727	0.304	2.443	0.071
(1) 0.006 ± 0.048	0.808	(6) 0.302 ± 0.182	0.001	(7) 0.001 ± 0.008	0.794	0.414	4.831	0.004*
(1) -0.188 ± 0.120	0.002	(3) 0.724 ± 0.373	0.000	(7) 0.002 ± 0.008	0.560	0.430	5.450	0.002
(1) -0.210 ± 0.108	0.000	(3) 0.673 ± 0.339	0.000	(7) 0.001 ± 0.007	0.945	0.466	6.473	0.001*
(1) -0.143 ± 0.138	0.042	(3) 0.606 ± 0.416	0.005	(6) 0.065 ± 0.196	0.510	0.431	5.489	0.002
(2) -0.029 ± 0.018	0.001	(3) 0.469 ± 0.218	0.000	(6) 0.067 ± 0.147	0.366	0.504	8.188	0.000

*Excluding contrasts 67 (collapsing node between *Ourebia* and *Connochaetes*) and 70 (collapsing node between *Madoqua* and *Antilope* + *Antidorcas* + *Gazella*)*Hindlimb*

Standard least squares regression

A ± 95% CI	P	B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	B ₃ ± 95% CI	P	R	SEE	F	P
1.520 ± 0.129	0.000	(10) 0.002 ± 0.001	0.001	(12) 0.125 ± 0.117	0.037	(13) -0.012 ± 0.008	0.005	0.658	0.097	18.286	0.000

Independent contrasts least squares regression

B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	B ₃ ± 95% CI	P	R	F	P
(10) 0.001 ± 0.001	0.070	(12) 0.128 ± 0.178	0.156	(13) -0.001 ± 0.001	0.190	0.419	5.107	0.003
(10) 0.001 ± 0.001	0.021	(12) 0.186 ± 0.150	0.016	(13) -0.001 ± 0.001	0.048	0.559	10.578	0.000*

*Excluding contrasts 67 (collapsing node between *Ourebia* and *Connochaetes*) and 70 (collapsing node between *Madoqua* and *Antilope* + *Antidorcas* + *Gazella*)

Fore and hindlimbs

Standard least squares regression

A ± 95% CI	P	B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	B ₃ ± 95% CI	P	R	SEE	F	P
1.871 ± 0.202	0.000	(6) 0.200 ± 0.069	0.000	(7) -0.546 ± 0.414	0.010	(13) -0.010 ± 0.008	0.027	0.620	0.101	15.014	0.000
0.671 ± 0.400	0.001	(3) 0.193 ± 0.130	0.004	(11) 0.329 ± 0.153	0.000	(14) 0.042 ± 0.028	0.004	0.632	0.100	15.933	0.000
1.509 ± 0.201	0.000	(2) -0.015 ± 0.013	0.020	(5) 0.468 ± 0.139	0.000	(13) -0.013 ± 0.009	0.006	0.636	0.099	16.267	0.000
1.345 ± 0.159	0.000	(4) 0.002 ± 0.001	0.003	(5) 0.245 ± 0.189	0.012	(13) -0.010 ± 0.008	0.010	0.658	0.097	18.313	0.000
1.455 ± 0.167	0.000	(6) 0.083 ± 0.093	0.079	(7) -0.401 ± 0.345	0.024	(16) 0.028 ± 0.016	0.001	0.663	0.096	18.808	0.000
-0.032 ± 0.806	0.937	(1) -0.206 ± 0.114	0.001	(3) 0.757 ± 0.381	0.000	(12) 0.118 ± 0.109	0.034	0.666	0.096	19.117	0.000
1.067 ± 0.328	0.000	(3) 0.146 ± 0.121	0.019	(7) -0.543 ± 0.339	0.002	(16) 0.035 ± 0.011	0.000	0.677	0.095	20.288	0.000
0.220 ± 0.659	0.508	(2) -0.048 ± 0.023	0.000	(3) 0.659 ± 0.257	0.000	(15) -0.185 ± 0.198	0.066	0.687	0.094	21.436	0.000
-0.007 ± 0.680	0.984	(2) -0.049 ± 0.022	0.000	(6) 0.072 ± 0.085	0.094	(9) 0.684 ± 0.285	0.000	0.696	0.092	22.532	0.000
0.191 ± 0.579	0.514	(2) -0.047 ± 0.020	0.000	(3) 0.616 ± 0.253	0.000	(12) 0.119 ± 0.096	0.016	0.700	0.092	23.012	0.000

Independent contrasts least squares regression

B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	B ₃ ± 95% CI	P	R	F	P
(6) 0.177 ± 0.167	0.038	(7) 0.002 ± 0.008	0.696	(13) -0.001 ± 0.001	0.511	0.267	1.841	0.147
(6) 0.253 ± 0.144	0.001	(7) -0.001 ± 0.007	0.762	(13) -0.001 ± 0.001	0.138	0.467	6.430	0.001*
(6) 0.078 ± 0.180	0.391	(7) -0.001 ± 0.008	0.938	(16) 0.001 ± 0.001	0.014	0.375	3.934	0.012
(6) 0.135 ± 0.147	0.071	(7) -0.003 ± 0.006	0.302	(16) 0.001 ± 0.001	0.000	0.601	13.013	0.000*
(2) -0.004 ± 0.009	0.383	(5) 0.346 ± 0.212	0.002	(13) -0.001 ± 0.001	0.387	0.376	3.948	0.012
(2) -0.011 ± 0.008	0.010	(5) 0.356 ± 0.177	0.000	(13) -0.001 ± 0.001	0.052	0.509	8.048	0.000*
(3) 0.169 ± 0.151	0.029	(7) -0.003 ± 0.007	0.410	(16) 0.001 ± 0.001	0.003	0.428	5.374	0.002
(3) 0.018 ± 0.126	0.773	(7) -0.007 ± 0.006	0.019	(16) 0.001 ± 0.001	0.000	0.573	11.235	0.000*
(4) 0.001 ± 0.001	0.033	(5) 0.205 ± 0.220	0.067	(13) -0.001 ± 0.001	0.391	0.436	5.628	0.002
(4) 0.002 ± 0.001	0.000	(5) 0.148 ± 0.185	0.115	(13) -0.001 ± 0.001	0.099	0.565	10.810	0.000*
(1) -0.085 ± 0.104	0.106	(3) 0.405 ± 0.316	0.013	(12) 0.173 ± 0.187	0.069	0.467	6.676	0.000
(1) -0.135 ± 0.090	0.004	(3) 0.436 ± 0.269	0.002	(12) 0.164 ± 0.157	0.041	0.564	10.734	0.000*
(3) 0.340 ± 0.189	0.001	(11) 0.449 ± 0.276	0.002	(14) 0.026 ± 0.035	0.157	0.493	7.719	0.000
(3) 0.168 ± 0.147	0.027	(11) 0.508 ± 0.209	0.000	(14) 0.051 ± 0.028	0.000	0.655	17.323	0.000*
(2) -0.033 ± 0.018	0.001	(3) 0.549 ± 0.231	0.000	(15) -0.144 ± 0.207	0.171	0.512	8.539	0.000
(2) -0.042 ± 0.021	0.000	(3) 0.524 ± 0.235	0.000	(15) -0.071 ± 0.185	0.451	0.527	8.828	0.000*
(2) -0.031 ± 0.018	0.001	(6) 0.055 ± 0.146	0.458	(9) 0.547 ± 0.243	0.000	0.517	8.751	0.000
(2) -0.030 ± 0.018	0.001	(6) 0.149 ± 0.136	0.033	(9) 0.417 ± 0.244	0.001	0.562	10.614	0.000*
(2) -0.025 ± 0.015	0.002	(3) 0.408 ± 0.188	0.000	(12) 0.160 ± 0.157	0.046	0.540	9.885	0.000
(2) -0.027 ± 0.016	0.001	(3) 0.345 ± 0.196	0.001	(12) 0.186 ± 0.143	0.012	0.582	11.772	0.000*

*Excluding contrasts 49 (node between *Boselaphus* and *Taurotragus*), 67 (collapsing node between *Ourebia* and *Connochaetes*) and 70 (collapsing node between *Madoqua* and *Antelope* + *Antidorcas* + *Gazella*)

MULTIVARIATE ANALYSIS, FOUR 'INDEPENDENT' VARIABLES

Fore and hindlimbs

Standard least squares regression

A ± 95% CI	P	B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	B ₃ ± 95% CI	P	B ₄ ± 95% CI	P	R	SEE	F	P
0.120 ± 0.904	0.792	(1) -0.236 ± 0.133	0.001	(3) 0.722 ± 0.459	0.002	(5) 0.207 ± 0.219	0.064	(13) -0.010 ± 0.010	0.041	0.675	0.096	14.824	0.000
0.067 ± 0.798	0.868	(1) -0.246 ± 0.117	0.000	(3) 0.790 ± 0.370	0.000	(6) 0.096 ± 0.084	0.026	(13) -0.008 ± 0.010	0.088	0.683	0.095	15.525	0.000

Independent contrasts least squares regression

B ₁ ± 95% CI	P	B ₂ ± 95% CI	P	B ₃ ± 95% CI	P	B ₄ ± 95% CI	P	R	F	P
(1) -0.144 ± 0.139	0.043	(3) 0.605 ± 0.420	0.005	(6) 0.065 ± 0.198	0.515	(13) -0.001 ± 0.001	0.937	0.432	4.061	0.005
(1) -0.149 ± 0.127	0.022	(3) 0.552 ± 0.384	0.006	(6) 0.179 ± 0.190	0.064	(13) -0.001 ± 0.001	0.583	0.520	6.494	0.000*
(1) -0.109 ± 0.095	0.023	(3) 0.423 ± 0.320	0.010	(5) 0.192 ± 0.236	0.109	(13) -0.001 ± 0.001	0.774	0.458	4.721	0.002
(1) -0.116 ± 0.098	0.021	(3) 0.490 ± 0.344	0.006	(5) 0.298 ± 0.270	0.031	(13) 0.001 ± 0.001	0.651	0.532	6.812	0.000**

*Excluding contrast 67 (collapsing node between *Ourebia* and *Connochaetes*), 36 (collapsing node between *Giraffa* and Cervidae + Bovidae) and 50 (collapsing node between *Taurotragus oryx* and *T. derbianus*)