Hind Limb Scaling in Birds and Other Theropods: Implications for Terrestrial Locomotion

STEPHEN M. GATESY
Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138

ABSTRACT   An analysis of hind limb skeletal elements of non-avian theropods and ground-dwelling birds was performed to reveal patterns of change in shape and proportion with size. When femora of equal length are compared, birds exhibit a significantly larger midshaft diameter than non-avian theropods. As total limb length increases, avian femora become relatively shorter (negative allometry), while those of non-avian theropods become relatively longer (positive allometry). Avian femoral/tibiotarsal ratios are all below 0.8 and decrease with limb size, whereas ratios of non-avian theropods are well above 0.8 and tend to increase with limb size. In addition, avian femora exhibit a unique diameter/length relationship not seen in other theropod hind limb bones.

Several studies have shown that within the avian limb, the short, robust femur resists bending to a far greater degree than the relatively longer, slimmer tibiotarsus. This is to be expected, as analyses of running birds show that the femur is oriented relatively perpendicular to the ground reaction force throughout the stride, which would subject it to high bending moments. When compared to birds, non-avian theropods have relatively long, slender femora that do not seem to be built to withstand the forces associated with such an orientation. Reconstructing all non-avian theropods in avian-like poses (subhorizontal femur, knee well flexed) with avian locomotor kinematics (relatively little hip extension at most speeds) ignores major differences in scaling between these groups of organisms.

Recent cladistic analyses of archosaur phylogeny (Gauthier, '84, '86; Gauthier and Padian, '85) strongly support a theropod ancestry for birds, an assertion espoused earlier by Ostrom and others (see Ostrom, '76a, for a review). This relationship between avian and non-avian theropods has led some paleontologists to reconstruct all members of the clade Theropoda as very bird-like. Several workers have considered the bipedal locomotion of modern birds to have been inherited relatively unchanged from non-avian theropod ancestors. It has been hypothesized that 1) the hind limb of all theropods was essentially like that of modern birds, and 2) the orientation of the skeletal elements and their changing positions through time (kinematics) during locomotion are not substantially different (Padian, '86; Paul, '88; Padian and Olsen, '89).

The inference of avian orientation and kinematics in non-avian theropods has met some opposition. Tarsitano ('83) stipulated that birds were not ideal analogues for reconstructing theropod locomotor systems. Based on a functional analysis of locomotion in crocodilians and birds, Gatesy ('90) found that many phylogenetically and functionally significant similarities exist between avian and non-avian theropods, but that certain derived states of birds (particularly the tail, pelvis, and main mechanism of limb retraction) make the direct use of their locomotor system as an analogue for all theropods unjustifiable. Gatesy ('90) concluded that all theropods utilize fully erect posture and essen-

tially sagittal limb movements, but that details of limb orientation, kinematics, and muscular mechanisms of movement appear to differ between the most primitive theropods and birds.

An alternative method of approaching this question is to study aspects of hind limb skeleton morphometrics. If all theropods (both avian and non-avian) are standing and moving in similar ways, their limb bones should be structured to withstand similar loading patterns. If bone scaling patterns differ, very specific alterations of muscle induced stresses must be invoked in order to conserve a primitive theropod limb segment orientation in the avian subclade. Differences in limb usage may be reflected in divergent patterns of bone scaling between birds and the remainder of the clade Theropoda. However, it has been asserted that modern ratites and Mesozoic theropods "are essentially identical in bone morphology" (Padian and Olsen, '89). This study examines one aspect of this hypothesis by determining the change in proportion of hind limb elements with size in non-avian theropods and ground-dwelling birds. Avian hind limb scaling is then related to external forces encountered during walking and running. These data are used to assess locomotor behavior in non-avian theropods and evaluate the changes that occurred during the origin of birds.

MATERIALS AND METHODS

In an effort to make comparisons with non-avian theropods most meaningful, only data from ground-dwelling birds were used in this study. Birds clearly specialized for locomotor modes other than walking and running (such as wading, diving, and prolonged flight) were not used. Among living birds these included tinamous, ratites, and gallinaceous birds. Extinct (presumably) flightless forms such as moas, *Aepyornis* (elephantbirds), *Dromornis,* and *Genyornis* were used to increase the data base for medium-sized and large birds. Most avian dimensions were measured from specimens in the Museum of Comparative Zoology collections. Other data were taken from the literature. Non-avian theropod genera were included if the hind limb skeleton of presumed individuals was adequately known. All measurements were taken from published data, photographs, or scale drawings of skeletal elements.

The morphometric data collected for each genus included femoral length, femoral anteroposterior (A-P) diameter at midshaft, tibiotarsal (tibia + astragalus) length, tibiotarsal anteroposterior diameter at midshaft, and tarsometatarsal (metatarsal III) length. In some non-avian theropods the tibiotarsal length did not include the astragalus. In other theropods a circumference measurement of the essentially cylindrical femoral shaft was used to calculate A-P diameter.

To study the scaling of bone shape, a measure of body size was needed. Body mass was not used due to the inherent problems of estimating mass in extinct and often incomplete animals. Additionally, a multivariate estimate of size would require the preservation of other skeletal elements in fossil taxa that would severely limit the data set. Instead, hind limb length (femur + tibiotarsus + tarsometatarsus) was used for some analyses. Clearly, relative limb length may change with body size, but it is assumed that there is a strong tendency for larger theropods to have longer limbs. While not ideal, this dimension was chosen because so little work on theropod scaling has been done that a more appropriate metric was unavailable.

Data were log transformed or used to calculate ratios before plotting. Least square linear regressions for log transformed data were performed to calculate exponents (slopes and 95% confidence intervals), which were compared by analyses of covariation. All correlation coefficients were greater than 0.979, so that exponents obtained by reduced major axis regression (RMA) do not differ substantially from those presented here.

Limb orientation and kinematics were taken from film analysis of birds walking and running over a wide speed range. Bobwhite quail and guineafowl were studied cineradiographically to document bone movement (Gatesy, '89, '90). Light film of chickens, turkeys, rheas, emus, and ostriches were analyzed to describe limb movements in birds over a wide range of sizes (Gatesy and Biewener, '91). Other kinematic descriptions, force plate measurements, and bone strength data were taken from the literature.

RESULTS

The measurements of theropod hind limb bones are listed in Table 1. Data for 44 avian species, 25 non-avian theropod genera, and *Archaeopteryx* were used in this study.

TABLE 1. *Skeletal dimensions of avian and non-avian theropods in centimeters*

	Femur		Tibiotarsus		Hind limb	
	F_1	F_d	T_1	T_d	$Hind_1$	Source
Primitive dinosaurs						
Staurikosaurus	22.9	2.0	24.6	1.7		Colbert ('70)
Herrerasaurus	47.3	4.4	41.1	4.8	111.0	Reig ('63)
Undetermined Theropods						
Procompsognathus	9.3		11.3		27.5	Ostrom ('81)
Compsognathus	7.5		8.8		21.9	Ostrom ('78)
	11.0		13.6		32.7	Ostrom ('78)
Podokesaurus	8.6		10.4		25.5	Colbert ('64)
Coelurus	22.0	1.7	25.5	1.7		Ostrom ('70)
Ornitholestes	20.7		15.9		48.3	Camp ('36)
Ceratosaurs						
Ceratosaurus	62.0	5.2	55.5		143.0	Gilmore ('20)
Segisaurus	14.5		16.0		40.4	Camp ('36)
Dilophosaurus	55.7	5.0	55.5	4.5	141.0	Welles ('84)
Coelophysis	24.5		27.0		66.5	Padian ('86)
	20.9		22.4		55.9	Colbert ('64)
	20.3		22.1		54.9	Colbert ('64)
	16.4		18.8		46.0	Colbert ('64)
	13.5		15.4		37.4	Colbert ('64)
	14.1		15.7		39.3	Colbert ('64)
	12.6		14.0		34.7	Colbert ('64)
	11.8		13.5		33.7	Colbert ('64)
	12.6		14.7		36.0	Colbert ('64)
	17.2		19.9		48.5	Colbert ('64)
	17.3		19.5		48.8	Colbert ('64)
	12.2		13.6		33.7	Colbert ('64)
	12.5		13.8		34.7	Colbert ('64)
	19.6		20.7		51.3	Colbert ('64)
Syntarsus	20.8	1.6	22.3	1.1	56.3	Raath ('69)
Carnosaurs						
Allosaurus	85.0	9.5	69.0		187.0	Gilmore ('20)
	80.5	7.5				Gilmore ('20)
	64.5	7.2				Gilmore ('20)
	88.0	10.2	73.0	8.9	199.0	Madsen ('76)
	24.5	2.4				Madsen ('76)
	35.0	3.3				Madsen ('76)
	38.5	3.7				Madsen ('76)
	43.5	4.4				Madsen ('76)
	43.7	5.1				Madsen ('76)
	45.0	4.5				Madsen ('76)
	46.5	4.7				Madsen ('76)
	48.0	5.2				Madsen ('76)
	50.5	5.4				Madsen ('76)
	52.5	5.3				Madsen ('76)
	53.5	5.7				Madsen ('76)
	53.5	5.6				Madsen ('76)
	53.5	5.7				Madsen ('76)
	53.5	5.5				Madsen ('76)
	55.5	5.9				Madsen ('76)
	60.5	6.6				Madsen ('76)
	69.5	8.0				Madsen ('76)
	70.0	8.1				Madsen ('76)
	73.0	8.8				Madsen ('76)
	80.0	9.2				Madsen ('76)
	85.0	10.7				Madsen ('76)
	86.5	9.4				Madsen ('76)
	88.0	10.0				Madsen ('76)
	88.0	10.4				Madsen ('76)
	90.5	9.8				Madsen ('76)
	90.5	11.1				Madsen ('76)
	91.0	10.7				Madsen ('76)
Xenotarsosaurus	58.7	7.0	58.2	5.1		Martinez et al. ('86)
Megalosaurus	81.2	10.0				Owen (1856)

TABLE 1. *(continued)*

	Femur		Tibiotarsus		Hind limb	
	F_l	F_d	T_l	T_d	$Hind_l$	Source
Albertosaurus	104.0	13.6	100.0		263.0	Russell ('70)
	59.5	6.1	62.0		164.0	Russell ('70)
	103.0	11.4	99.0		264.0	Russell ('70)
	70.0		74.8		193.0	Russell ('70)
	86.0		81.0		220.0	Russell ('70)
	94.0		90.0		242.0	Russell ('70)
Daspletosaurus	100.0	12.4	87.0			Russell ('70)
	65.5	7.2	73.6			Russell ('70)
	100.0	13.2				Russell ('70)
Tarbosaurus	97.0	11.0	85.0		236.0	Maleev ('74)
Tyrannosaurus	130.0	18.0	114.0		312.0	Osborn ('16)
Ornithomimids						
Elaphrosaurus	52.9		60.8	4.5	153.0	Janensch ('25)
Ornithomimus	43.5		47.5		122.0	Russell ('72)
	50.0		55.2			Russell ('72)
Struthiomimus	48.0	4.4	53.5		138.0	Russell ('72)
	51.3	4.5	56.0		146.0	Russell ('72)
	43.0	4.5	56.0		133.0	Osborn ('16)
Gallimimus	27.0	2.2	30.6	1.8	79.6	Osmolska et al. ('72)
	36.0	3.0	39.0	2.5	103.0	Osmolska et al. ('72)
	66.5	6.2	74.0	4.3	194.0	Osmolska et al. ('72)
	19.2		23.0		57.9	Osmolska et al. ('72)
Dromiceiomimus	46.8		57.8		144.0	Russell ('72)
	43.2		53.7		134.0	Russell ('72)
	37.8		44.8			Russell ('72)
Deinonychosaurs						
Deinonychus	33.6	3.2	38.2	2.9	88.2	Ostrom ('76b)
Archaeopteryx						
Eichstätt	3.70	0.33	5.25	0.25	11.97	Wellnhofer ('74)
London	6.05	0.38	8.05	0.35	18.50	Wellnhofer ('74)
Berlin	5.26	0.35	6.85	0.30	15.81	Wellnhofer ('74)
Maxberg	5.80		8.00		18.00	Wellnhofer ('74)
Haarlem	5.40		8.00		18.20	Wellnhofer ('74)
Solenhofen	7.00		8.95		19.45	Wellnohofer ('88)
Living ratites						
Struthio camelus	23.0	3.07	41.0	1.98	103.8	MCZ 828
	32.0	5.07				MCZ 2686
	31.7	4.75				MCZ 2686
	28.5	4.09	49.5	2.60	121.0	MCZ 3701
	29.5	5.44				Prange et al. ('79)
	28.6	4.61				Prange et al. ('79)
	24.9		44.4		111.1	Alexander et al ('79b)
	31.4		55.0		133.8	Archey ('41)
	30.8		52.7		129.0	Archey ('41)
	30.5		51.1		126.3	Archey ('41)
	29.3		48.0		123.4	Archey ('41)
	27.3		49.7		118.0	Archey ('41)
	27.7		49.0		118.7	Archey ('41)
	27.8		49.0		120.0	Archey ('41)
Rhea americana	21.0	2.36	31.8	1.87	85.3	MCZ 2083
	19.0	2.23				Prange et al. ('79)
Casuarius casuarius	20.5	2.40				MCZ 121
	20.5	2.76				Prange et al. ('79)
Dromecius novae-hollan-diae						
	22.7	3.10	41.5	2.95	102.7	MCZ 198
	22.5	2.95	40.0	2.77	100.0	MCZ 1627
	18.7	2.78				Prange et al ('79)
	24.3		46.5		111.2	Archey ('41)
	22.8		45.1		105.9	Archey ('41)
	24.1		45.1		109.9	Archey ('41)
	23.4		43.6		107.1	Archey ('41)
	22.8		40.3		100.6	Archey ('41)
	21.8		39.0		99.7	Archey ('41)
	22.5		37.4		95.3	Archey ('41)
Apteryx australis	8.9		13.0		28.4	Alexander ('83a)
Moas						
Anomalopteryx didi-formis	27.5	3.6	42.7	3.9	91.4	Archey ('41)

TABLE 1. (continued)

	Femur		Tibiotarsus		Hind limb	
	F_1	F_d	T_1	T_d	Hind$_1$	Source
Megalapteryx didinus	26.5	3.1	40.5	3.0	86.0	Archey ('41)
Megalapteryx benhami	29.3	3.9	45.4	3.9		Archey ('41)
Pachyornis elephantopus	32.9	6.1	57.4	6.0	114.5	Archey ('41)
Pachyornis mappini	20.3	3.3	33.6	3.1	69.5	Archey ('41)
Pachyornis oweni	14.3	2.2	24.3	1.9	49.9	Archey ('41)
Emeus huttonii	24.4	3.3	39.7	3.3	82.8	Archey ('41)
Emeus crassus	28.7	4.5	49.3	4.3	100.0	Archey ('41)
Eurapteryx gravis	31.5	4.9	52.0	4.8	105.2	Archey ('41)
Eurapteryx geranoides	23.1	4.1	41.1	3.8	81.7	Archey ('41)
Eurapteryx exilis	20.5	3.4	34.7	3.0	70.4	Archey ('41)
Eurapteryx curtus	17.9	2.7	28.6	2.4	60.1	Archey ('41)
Dinornis novae-zealan-						
diae	27.8	3.9	56.0	3.8	115.1	Archey ('41)
Dinornis ingens	34.0	4.5	73.7	4.8	149.4	Archey ('41)
Dinornis giganteus	37.5	6.6	75.9	5.9	160.4	Archey ('41)
Dinornis torosus	33.0	5.1	65.0	4.5	131.4	Archey ('41)
Dinornis robustus	35.5	5.5	73.2	5.6	147.7	Archey ('41)
Elephantbirds						
Aepyornis maximus	46.5	9.1	81.0	6.5	175.5	Monnier ('13)
	41.0	8.6	73.0	5.7	156.0	Monnier ('13)
Aepyornis medius	36.8	7.6	68.0	5.4	142.8	Monnier ('13)
	33.0	6.7	57.2	4.9	123.2	Monnier ('13)
Aepyornis hildebrandti	32.0	6.2	58.0	4.5	120.3	Monnier ('13)
	24.0	5.0	48.5	3.5	100.0	Monnier ('13)
Aepyornis gracilis	32.2	5.4				Monnier ('13)
Dromornithids						
Dromornis australis	29.1	5.4				Stirling and Zietz ('13)
Genyornis newtoni	33.9	7.5	60.2	5.4	131.5	Stirling and Zietz ('13)
	34.5	7.5				Stirling and Zietz ('13)
	32.2	6.9				Stirling and Zietz ('13)
Tinamidae						
Tinamous tao	7.00	0.67	10.80	0.58	24.88	MCZ 3705
Tinamous major	6.50	0.56	9.82	0.50	23.22	MCZ 2774
Crypturellus boucardi	5.07	0.38	7.59	0.36	17.86	MCZ 2750
Crypturellus noctivagus	5.80	0.41	8.64	0.36	20.39	MCZ 276
Rhyncotus rufescens	7.26	0.55	9.85	0.46	23.61	MCZ 1633
Eudromia elegans	5.60	0.45	7.71	0.40	17.97	MCZ 3064
Tetraonidae						
Tetrao urogallus	8.39	0.72	10.71	0.53	24.70	MCZ 315
Lagopus muxtus	6.00	0.47	7.97	0.38	18.03	MCZ 1469
Bonasa umbellus	5.62	0.49	7.50	0.38	17.26	MCZ 3999
Tympanuchus cupido	6.61	0.57	8.95	0.45	20.13	MCZ 2196
Centrocerus urophe-						
sianus	7.40	0.60	9.28	0.48	21.58	MCZ 1441
Phesianidae						
Lophura ignita	9.43	0.83	14.20	0.54	35.43	MCZ 3144
Pavo cristatus	10.90	1.27	20.20	0.95	44.80	MCZ 7161
Numida meleagris	7.90	0.70	11.40	0.69	26.80	MCZ 1648
Meleagris ocellata	11.10	1.02	19.30	0.88	44.50	MCZ 2878
Gallus gallus	9.10	0.75	12.80	0.62	31.30	MCZ 1388
	2.20	0.20	3.11	0.17	7.70	Manion ('84)
	2.15	0.20	3.02	0.15	7.51	Manion ('84)
	2.22	0.20	3.12	0.16	7.66	Manion ('84)
	2.22	0.19	3.05	0.16	7.57	Manion ('84)
	2.57	0.23	3.51	0.17	8.73	Manion ('84)
	2.57	0.24	3.66	0.19	8.95	Manion ('84)
	2.48	0.22	3.41	0.19	8.45	Manion ('84)
	3.02	0.27	4.26	0.20	10.41	Manion ('84)
	3.13	0.28	4.31	0.22	10.56	Manion ('84)
	3.06	0.27	4.28	0.21	10.60	Manion ('84)
	3.01	0.27	4.13	0.20	10.25	Manion ('84)
	3.45	0.30	4.76	0.25	11.76	Manion ('84)
	3.62	0.33	5.10	0.25	12.49	Manion ('84)
	3.50	0.33	4.77	0.27	11.76	Manion ('84)
	4.77	0.45	6.84	0.37	16.86	Manion ('84)
	4.59	0.43	6.23	0.31	15.38	Manion ('84)
	4.59	0.43	6.23	0.31	15.38	Manion ('84)
	4.44	0.42	6.11	0.34	15.26	Manion ('84)
	4.40	0.40	6.49	0.30	15.60	Manion ('84)
	4.42	0.38	6.37	0.30	15.65	Manion ('84)

TABLE 1. (continued)

	Femur		Tibiotarsus		Hind limb	
	F_1	F_d	T_1	T_d	$Hind_1$	Source
	4.25	0.40	5.98	0.30	14.69	Manion ('84)
	4.53	0.41	6.38	0.30	15.86	Manion ('84)
	5.40	0.50	7.65	0.38	19.12	Manion ('84)
	5.68	0.50	8.20	0.38	20.31	Manion ('84)
	5.26	0.47	7.38	0.39	18.36	Manion ('84)
	5.69	0.51	8.02	0.38	19.84	Manion ('84)
	6.87	0.58	10.18	0.48	24.89	Manion ('84)
	7.07	0.61	10.67	0.49	26.15	Manion ('84)
	7.03	0.64	10.27	0.49	25.34	Manion ('84)
	8.54	0.70	12.75	0.60	31.18	Manion ('84)
	8.90	0.78	13.60	0.64	32.93	Manion ('84)
	7.71	0.68	11.41	0.52	27.57	Manion ('84)
	8.35	0.69	12.38	0.56	29.69	Manion ('84)
	8.66	0.71	13.41	0.59	32.00	Manion ('84)
	7.78	0.68	11.80	0.55	28.20	Manion ('84)
	7.65	0.67	11.40	0.54	27.39	Manion ('84)
	8.86	0.79	13.92	0.63	33.01	Manion ('84)
	8.87	0.82	13.63	0.63	32.79	Manion ('84)
	7.53	0.71	11.63	0.61	27.52	Manion ('84)
	7.66	0.69	11.46	0.56	27.40	Manion ('84)
	8.74	0.86	13.44	0.68	32.17	Manion ('84)
	8.17	0.75	12.49	0.57	29.89	Manion ('84)
	8.30	0.84	12.51	0.61	29.89	Manion ('84)

Femoral shape

A logarithmic plot of femoral antero-posterior diameter versus femoral length (Fig. 1) shows that these data form two distinct groups, each with relatively linear distributions. The equations for the two data sets are

Avian (n = 57):

$$\log F_d = -1.459 + 1.458 (\log F_1) \quad r = 0.989$$

Non-avian (n = 54):

$$\log F_d = -1.419 + 1.249 (\log F_1) \quad r = 0.988$$

The slopes of these regressions (1.458 ± 0.060 and 1.249 ± 0.053) are significantly different ($P < 0.001$). From Figure 1 it is immediately clear that most birds can be distinguished from almost all other theropods by these two femoral dimensions alone. For femora of comparable length, those of ground-dwelling birds always have a larger midshaft diameter than those of non-avian theropods. This is particularly true of the larger genera, where the disparity in femoral proportion between birds and other theropods is greatest (Fig. 2). An elephantbird (Aepyornis) represents the longest avian femur measured; it has a length of 46.5 cm and a diameter of 9.1 cm. Non-avian theropods with comparable femoral lengths have diameters about half (4.4–4.7 cm) that of Aepyornis. Similarly, non-avian theropods with femoral diameters near 9 cm have femoral lengths of 73–80 cm, over 50% longer than that of the elephantbird.

The three specimens of Archaeopteryx (Berlin, London, and Eichstätt) were not used in calculating either regression (Fig. 1). These points fall at the extreme low end of the avian distribution in a region where the regression line for non-avian theropods is highly uncertain. Unfortunately, reliable data for femoral diameter are not available for several genera of small non-avian theropods.

The ontogenetic stages of individual non-avian theropod genera show a pattern similar to the distribution of all genera (Fig. 3). However, a sample of 31 Allosaurus femora varying 3.7-fold in length (Madsen, '76) has a slope (1.160 ± 0.066) that is significantly different ($P < 0.05$) from that of the largest specimens of each non-avian genus (1.280 ± 0.107, N = 15). However, because of the large overlap in the data between growth stages (such as Allosaurus, Albertosaurus, and Gallimimus) and the largest individuals, the inclusion of immature specimens does not significantly affect the scaling exponent (1.280 vs. 1.249, $P < 0.6$). Therefore, the similarity between non-avian theropods of all ontogenetic ages indicates that the selection of specimens is not creating the difference between birds and other theropods seen in Figure 1.
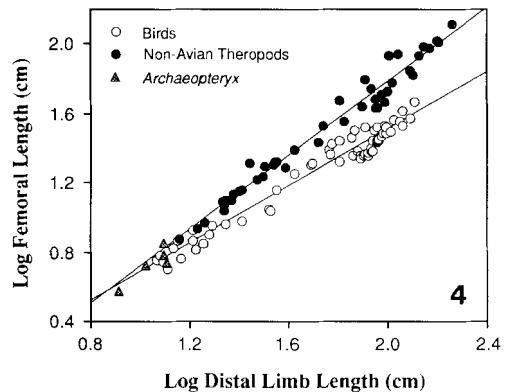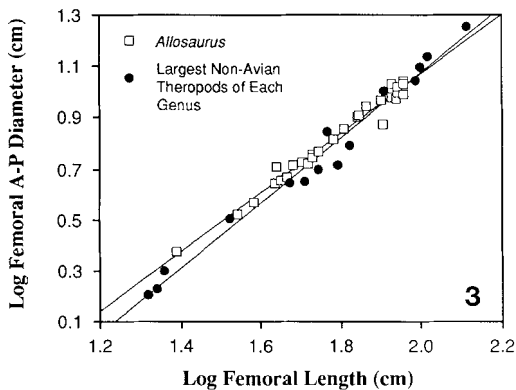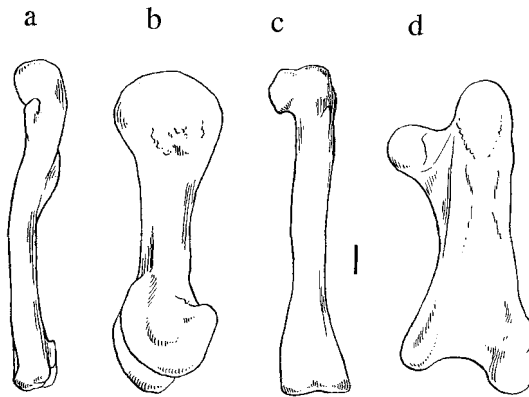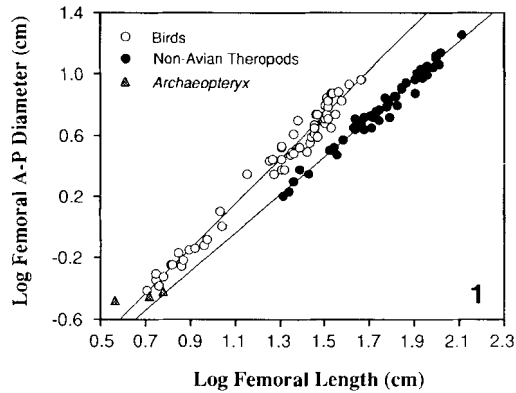
Fig. 1. Femoral scaling in ground-dwelling theropods. Plot of antero-posterior femoral diameter against femoral length of birds (open circles), non-avian theropods (filled circles) and *Archaeopteryx* (gray triangles) on logarithmic axes.

Fig. 2. Femora of the non-avian theropod *Dilophosaurus* (**a,c**) and the elephantbird (*Aepyornis*) (**b,d**) in lateral and anterior views. Note the disparity in diameter between femora of comparable length. Bars equal 5 cm.

Fig. 3. Ontogenetic femoral scaling in 31 specimens of *Allosaurus* (open squares) and the largest members of other non-avian theropod genera (filled circles). Axes are the same as in Figure 1.

Fig. 4. Relative femoral length in ground-dwelling theropods. Plot of femoral length versus tibiotarsus + tarsometatarsus length of birds (open circles), non-avian theropods (filled circles), and *Archaeopteryx* (gray triangles) on logarithmic axes.

Relative length of the femur

Although avian femora are of larger diameter than non-avian theropod femora of comparable size, relative femoral length may differ between these groups. By graphing the femoral length against the remainder of the hind limb (tibiotarsus + tarsometatarsus), it is possible to justify this claim (Fig. 4). Birds tend to have shorter femora at each limb length. There is some overlap, however, among small members of the clade Theropoda, including *Archaeopteryx*.

What is most striking, however, is the pattern of change in femoral proportion with an increase in limb size. This is apparent from the regression equations for each group:

Avian (n = 60):

$$\log F_d = -0.136 + 0.820 \,(\log (T_1 + M_1)) \; r = 0.979$$

Non-avian (n = 46):

$$\log F_1 = -0.348 + 1.066 \,(\log (T_1 + M_1)) \; r = 0.987$$

These slopes are significantly different ($P < 0.001$). Birds exhibit negative allometry; as limb length increases the femur becomes relatively shorter (slope of 0.820 ± 0.044 less than 1; $P < 0.001$). In contrast, non-avian theropod femora show positive allometry, becoming relatively longer as limb length increases (slope of 1.066 ± 0.052 greater than 1; $P < 0.01$). Avian and non-avian exponents are also significantly different when femoral length is related to tarsometatarsal length (0.727 ± 0.076 vs 1.035 ± 0.074; $P < 0.001$). This pattern appears to hold ontogenetically as well (Callison and Quimby, '84). For regressions of femoral length against the length of the remainder of the limb, six specimens of *Albertosaurus* (F_1 range 59.5–104 cm) have an exponent of 1.332, in contrast to a value of 0.934 in 44 chickens (F_1 range 2.15–9.10 cm).

Intralimb disparity of segment size

Comparison of bone proportion within the limb of individual animals offers other information. In all the ground-dwelling birds studied, the femur is less than 80% of tibiotarsal length (Fig. 5). Birds show a decrease in F/T ratio (femoral length/tibiotarsal length) as limb length increases. In sharp contrast, non-avian theropods tend to increase F/T with limb size. Most non-avian theropods show little similarity to birds in this relationship. Only the smallest genera and several ostrich mimics (*Struthiomimus* and *Dromiceiomimus*) obtain avian values. Several large thero-
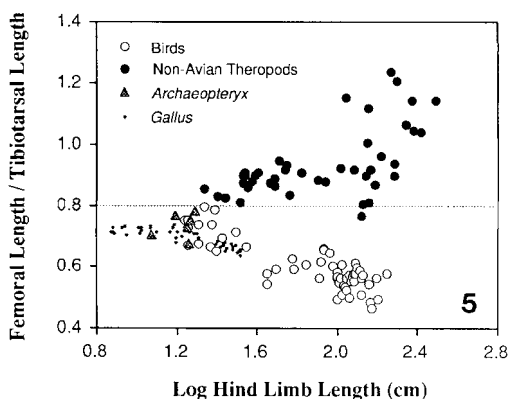

Fig. 5. Plot of femoral length/tibia length (F/T ratio) versus log hind limb length in birds (open circles), non-avian theropods (filled circles), *Archaeopteryx* (gray triangles), and *Gallus* (small circles). The dashed line signifies the largest avian value of 0.8.

pods have a F/T greater than 1, indicating a femur that is longer than the tibia.

Data points for chicken ontogeny (Manion, '84) show an decrease in F/T with limb size that follows the drop in F/T seen using individuals from different avian genera. F/T values for the five specimens of *Archaeopteryx* range from 0.675 to 0.782. This puts *Archaeopteryx* well within the avian values, but in the region where data for small theropods (both avian and non-avian) might converge (Fig. 5).

Of the birds sampled, 41 of 44 have femora that are equal (2) or larger (39) in diameter than the tibiotarsus from the same limb. When the disparities in bone length and diameter are taken together, the characteristic nature of the avian femur becomes apparent. Figure 6 shows the ratio of midshaft A-P diameter to bone length (D/L ratio) for theropod femora and tibiotarsi plotted against the hind limb length. D/L ratios for bird femora form a distinct set of points exhibiting a markedly steeper slope. Non-avian femora, non-avian tibiotarsi, and avian tibiotarsi increase their D/L ratio much more slowly as limb length increases. Non-avian femora and tibiotarsi are similar to bird tibiotarsi, but clearly differ from avian femora.

DISCUSSION

From the data presented, several characterizations of hind limb scaling in ground-dwelling theropods can be made: 1) For femora over about 10 cm long, the A-P midshaft diameter of avian femora is always substan-
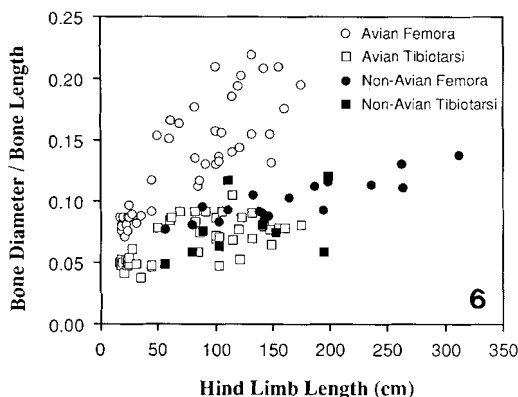
Fig. 6. Plot of diameter/length (D/T ratio) versus hind limb length for bird femora (open circles), bird tibiotarsi (open squares), non-avian femora (filled circles), and non-avian tibiae (filled squares). Avian femora scale differently from all other theropod long bones.

tially larger than that of non-avian theropods. This feature alone is enough to distinguish birds from other theropods in this size range. 2) When compared at equal distal limb lengths, most birds have a shorter femur than non-avian theropods. Avian femora become relatively shorter (negative allometry), while non-avian femora become relatively longer (positive allometry) as limb length increases. 3) Birds exhibit a very different scaling of femoral and tibiotarsal length. Avian F/T values are all under 0.8 and decrease in longer limbed birds, while non-avian F/T values are larger (except for four genera) and tend to increase with limb size. 4) D/L ratios show that avian femora scale unlike any other long bone in this study. These are fundamental distinctions between the hind limbs of birds and other theropods that have not been quantified previously. Do these differences in proportion and scaling have functional significance?

Cantilever strength

The unique shape of the avian femur suggests that this element might be particularly resistant to bending. The ability to resist bending (cantilever strength) is dependent on a bone's length and the moment of inertia of its cross section at midshaft. Therefore, long narrow bones are more easily bent than short thick ones. It is well known that bone can withstand higher forces of compression (as in axial loading) than tension (as in bending) before failure. Studies of bird bones have shown a disparity in cantilever strength be-

tween the femur and tibiotarsus. If a load is applied perpendicular to the bone's long axis, the femur can withstand a significantly greater absolute load than the tibiotarsus before breaking. This is particularly true in large birds, although the femora of small quail are about 10% stronger than their tibiotarsi (A.A. Biewener, pers. comm.). Alexander et al. ('79b) calculated the cantilever strength of an ostrich femur to be 2.5 times greater than the value for the tibiotarsus. Similar calculations on the moa *Pachyornis elephantopus* yielded a femoral cantilever strength over 5.5 times as great as tibiotarsal strength (Alexander, '83b). In an allometric study of eight running birds, femoral cantilever strength scaled as $8.3 \, Mb^{-0.08}$, while tibiotarsal strength scaled as $4.3 \, Mb^{-0.19}$ (Maloiy et al., '79). These relationships show that femoral cantilever strength is greater and decreases with size more slowly than tibiotarsal cantilever strength.

The scaling pattern of medium-large non-avian theropod femora indicates that they are markedly less robust than those of birds. Unlike the situation in birds, the D/L ratios of non-avian femora and tibiae are very similar. These relationships suggest that the disparity in bending resistance seen within the avian limb was not present in non-avian theropods. From these data, the cantilever strength of a non-avian theropod's femur would not be expected to be substantially greater than that of its tibia. The tibia's ability to resist bending would also be augmented by a substantial fibula in non-avian theropods. The avian fibula does not reach the ankle and does not contribute to tibiotarsal cantilever strength.

Functional implications for theropod locomotion

Limb bone stresses are produced by gravity and by muscular forces used to support and move the body. In walking and running, the foot exerts a force on the ground during the propulsive phase. The ground exerts an equal but opposite force on the foot, the ground reaction force (GRF). The orientation of each limb element to the GRF indicates the relative contribution of axial and bending forces to external bone loading. A bone perpendicular to the GRF will be subjected to a greater external bending force than if it were oriented more parallel to the GRF.

The orientation of the femur and tibiotarsus in birds during locomotion is consistent
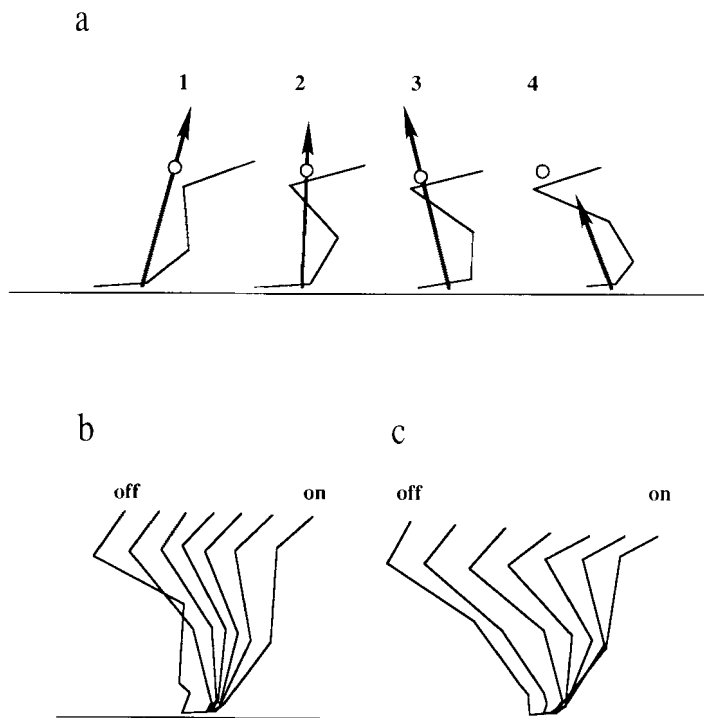
a

b   c

Fig. 7. **a:** Ground reaction forces and limb segment orientation in a running quail at four times during the propulsive phase (modified from Clark and Alexander, '75). The GRF (arrow) tends to be directed at the bird's center of mass (open circle), which is located well anterior to the hip joint. Note that the femur is always at a larger angle to the GRF than the tibiotarsus. **b:** Limb position of an ostrich during the propulsive phase of a slow walk and (c) a moderate run (modified from Gatesy and Biewener, '91). On and off designate the limb position at initial and final contact with the substrate.

with the difference in cantilever strength between these two elements. It is well known that the avian femur is oriented sub-horizontally, putting it in a position to experience the GRF at close to a right angle. In contrast, the tibiotarsus is more aligned with the GRF, especially in large birds, so that it would be subjected to loading at more obtuse angles and thus experience a smaller component of this force in bending. The femur does undergo considerable excursion during the stance phase of locomotion at higher speeds (Gatesy, '89, '90; Gatesy and Biewener, '91), but the direction of the GRF changes as the body is first decelerated and then reaccelerated during each footfall, so that the femur remains at a large angle with respect to the GRF.

Evidence for this disparity in design led Maloiy et al. ('79: p. 165) to calculate separate allometric exponents for avian limb elements that were "roughly horizontal" (femur and toe) and those that were "roughly vertical" (tibiotarsus and tarsometatarsus) because they were so different. Data from running quail show that the femur is at an angle of 70° from the GRF at mid-stance, whereas the tibiotarsus is at 41° (Clark and Alexander, '75). This difference is seen in femoral/tibiotarsal values throughout the stance phase (Fig. 7a), where the angles for the four positions shown are 54°/19°, 70°/41°, 84°/42°, and 88°/45°. Larger birds, such as guineafowl, turkeys, emus, rheas, and ostriches, show that this pattern of limb movement (Fig. 7b,c; Gatesy and Biewener, '91) and applied forces (Cavagna et al., '77) is consistent for ground-dwelling birds across a broad range of size and speed. Thus, although orientation is only one factor contributing to bone stress, birds use their long bones in a manner consistent with their construction.

The scaling pattern of non-avian theropod femora does not indicate that they are constructed to be subjected to the same loading

regime as the femora of birds. In comparison to avian femora, those of medium-large non-avian theropods are markedly less robust. Because the femur becomes relatively longer rather than shorter as non-avian theropods increase size, its ability to withstand tensile stresses would be highly reduced if it were oriented in a sub-horizontal position equivalent to that seen in modern birds. D/L ratios of non-avian femora are most similar to tibiotarsi; this implies that femoral orientation was more parallel to the GRF. These differences in skeletal scaling data support the hypothesis that the femoral orientation of most non-avian theropods is likely to have been more parallel to the GRF than in modern ground-dwelling birds.

Muscular forces within the limb are also major contributors to bone stress, particularly in small animals. These have been found to decrease with size, such that in large ungulates forces about a joint from muscles and the GRF are about equal (Biewener, '89a,b). It is assumed that skeletal design is influenced by the need to withstand these internal and external forces imposed during locomotion. If so, the differences in limb bone morphology found in this study indicate that the hind limbs of birds and other theropods experience dissimilar loading patterns. Dissimilar loading patterns could result from differences in orientation, muscular forces, or both. To reconstruct non-avian theropods with the limb orientation of modern birds, we must invoke very specific muscular forces to yield such different skeletal proportions. While modification of the musculature during the evolution of birds clearly occurred (e.g., Romer, '23; Gatesy, '90), it seems highly unlikely that it could completely compensate for skeletal differences and permit hind limb orientation to be inherited unchanged from other theropods.

Conflicting evidence

Since few birds have been analyzed, an obvious limitation of this study is the assumption that external diameter is indicative of a bone's resistance to bending. Clearly, such features as cross-sectional shape, cortical thickness, and ossification are important in determining a bone's cantilever strength. It would be ideal to know the internal diameters of all theropod bones. However, in birds that have been studied the femur is more resistant than the tibiotarsus to bending as a cantilever, as would be predicted by external dimensions alone. Even if large diameter, thin-walled bones are a unique characteristic of birds, this does not explain the difference in cantilever strength between elements within the avian limb.

Additionally, almost all previous studies of skeletal scaling in tetrapods have used external dimensions (McMahon, '75; Cracraft, '76; Alexander, '77; Alexander et al., '79a; Maloiy et al., '79; Prange et al., '79; Prothero and Sereno, '82; Alexander, '83a,b; Bertram and Biewener, '90). External dimensions have been used to arrive at conclusions about theropod locomotion and behavior (Paul, '88). Paul's data for non-avian theropods has been said to fit McMahon's elastic similarity model quite well (McMahon and Bonner, '83). The elastic similarity hypothesis (McMahon, '73, '75) predicts that skeletal elements will scale in a manner that preserves equivalent distortion in bending. Elastic similarity predicts a relationship where diameter is proportional to length$^{1.5}$, while different exponents would result from geometric similarity (length$^{1.0}$) or static stress similarity (length$^{2.0}$). Femoral diameters of ostrich-mimic and tyrannosaurid theropods were found to scale as length$^{1.28}$ (Paul, '88). This is very similar to the value of length$^{1.249}$ of medium-large non-avian theropods found in this study. It is different, however, from the avian results presented here (length$^{1.458}$) and elsewhere (length$^{1.563}$, Cracraft, '76), which are much closer to the relationship predicted by elastic similarity.

It is surprising, then, that non-avian theropod femora have been considered to scale elastically and that this is used as evidence to invoke similar locomotor abilities in ostrich-mimics and tyrannosaurs, despite the dramatic differences in body size (Paul, '88). Additionally, Paul ('88) repeatedly asserts that all theropods, avian and non-avian alike, walked and ran in very similar ways. One such suggestion is that non-avian theropods moved with their knees highly flexed, comparable to modern birds. Results from this study clearly show that bird femora scale differently than those of other theropods. Femoral shape in large non-avian theropods is significantly less robust than in birds, suggesting that these animals must have employed more columnar limbs with the knee less flexed. When combined with other differences (Gatesy, '90), the hind limb scaling pattern in these two groups do not support Paul's conclusions.

Small theropods

An interesting result of this analysis is the strong similarity between small theropods, whether avian or non-avian. However, despite similar proportions, differences in body plan still make it unlikely that all small theropods were standing and locomoting in an identical manner. Primitive theropods are noted for their long tails with large numbers of caudal vertebrae (Gauthier, '86; Gatesy, '90). A long tail functioning as a cantilever is the primitive condition found in these small theropods and is quite unlike the avian system. Therefore, the distinctive hind limb orientation and kinematics of modern birds must be considered a novelty of a subset of theropods, rather than the primitive state of the clade Theropoda.

Hind limb dimensions of *Archaeopteryx* are comparable to those of other small theropods. Although the hind limb proportions of *Archaeopteryx* may be used to show either its avian or dinosaurian affinities, it is not clear from this study that either of these conclusions is more favored. Indeed, because all small theropods are so similarly proportioned, it would be very unusual if *Archaeopteryx* was significantly different.

Femoral scaling in large theropods

Several theropod clades evolved large size independently. Large mammalian and dinosaurian quadrupeds show adaptations to reduce bending by transmitting forces axially through relatively vertically oriented femora (Coombs, '78). The femur in these animals is relatively long and the F/T ratio is high (e.g., Gregory, '12). In the same way, the femora of large non-avian theropods (carnosaurs and some ceratosaurs) are relatively longer than in smaller forms and have F/T ratios near or above 1.0. I propose that in these theropods the femur could act as an axially loaded column. Clearly, this would have important consequences for facilitating the evolution of gigantism within non-avian theropods.

Birds, however, do not show these "typical" changes towards more columnar femora with large size. Rather than becoming relatively longer, bird femora exhibit negative allometry with respect to limb length. These data agree with previously reported findings showing negative femoral allometry with body size in moas (Cracraft, '76). This relative shortening may occur because birds are constrained to a sub-horizontal femoral orientation by their reduced tail (Gatesy, '90). Unlike other theropods, birds have a relatively small postacetabular body mass, which locates the body's center of mass (CM) far anterior to the hip joint. Birds (and perhaps some non-avian coelurosaurs with reduced tails) maintain balance by orienting the femur close to horizontal. The adoption of this femoral orientation places the foot beneath the CM, and appears to have been accompanied by a shift in the primary limb retraction mechanism during theropod evolution (Gatesy, '90).

A shift to a more horizontal femoral orientation raises the possibility that femoral scaling has become a constraint on avian body size. If large birds are forced to maintain a relatively horizontal femur to compensate for low postacetabular body mass, femoral bending could limit the forces that can be transmitted by the hind limb, and thus body size. By being limited to a more horizontal femoral orientation, birds may be restricted from using the femur as a column as in large mammals and non-avian dinosaurs. This constraint may explain the distinctly different scaling pattern in avian and non-avian theropods, which is particularly striking considering the relatively conservative scaling of mammalian femora (Bertram and Biewener, '90).

Limb ratios

Limb proportions appear to be strongly influenced by femoral orientation in birds and other theropods. Therefore, the traditional use of ratios (such as F/T) as indicators of cursoriality is very misleading. From a phylogenetic perspective, the avian femur is relatively short for at least two reasons: 1) to maintain balance without failing in bending and 2) for cursoriality. For example, it has been noted that "even so obvious a runner as *Dromiceiomimus*," an ostrich mimic dinosaur, "falls far short of modern *Struthio*" in the "cursorial" nature of its limb proportions (Coombs, '78: p. 410). While *Struthio* is an extreme example, it is important to note that *all* medium-large birds in this study have F/T ratios lower than any non-avian theropod measured. This does not indicate that all medium-large birds are more cursorial than non-avian theropods. In conjunction with the extremely low F/T ratios in long-limbed birds (such as waders) this finding supports the hypothesis of a strong constraint on femoral length imposed by the avian body plan. In comparison to other theropods, the low avian F/T ratios merely reflect the limited degree to which the femur

can lengthen in comparison to the tibiotarsus and metatarsus.

SUMMARY

Results from this study support the hypothesis that most non-avian theropods did not stand or move like birds in several important details. Avian femora, which are oriented sub-horizontally, scale differently and appear to be far better designed to resist bending than those of other theropods. Primitive theropods had a large, balancing tail that would allow the feet to be located below the acetabulum with the knee slightly flexed. This would keep the femoral axis well in line with the GRF and help reduce bending moments. More extended, columnar limbs would have been preadaptive for gigantism, but do not necessitate slow, lethargic theropods. Rather, it is proposed that while many theropod characteristics are retained, some aspects of hind limb orientation and movement changed during avian evolution. Tail reduction, and the ensuing anterior shift in the center of mass, appear to have been accompanied by modifications of the hind limb, giving rise to the condition seen in modern ground-dwelling birds.

ACKNOWLEDGMENTS

LITERATURE CITED

Alexander, R.M. (1977) Allometry of the legs of antelopes (Bovidae). J. Zool. *183:*125–146.

Alexander, R.M. (1983a) Allometry of the leg bones of moas (Dinornithes) and other birds. J. Zool. *200:*215–231.

Alexander, R.M. (1983b) On the massive legs of a Moa (*Pachyornis elephantopus,* Dinornithes). J. Zool. *201:*363–376.

Alexander, R.M., A.S. Jayes, G.M.O. Maloiy, and E.M. Wathuta (1979a) Allometry of the limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). J. Zool. *189:*305–314.

Alexander, R.M., G.M.O. Maloiy, R. Njau, and A.S. Jayes (1979b) Mechanics of running of the ostrich (*Struthio camelus*). J. Zool. *187:*169–178.

Archey, G. (1941) The moa. A study of the Dinornithiformes. Bull. Auck. Inst. Mus. *1:*1–145.

Bertram, J.E.A., and A.A. Biewener (1990) Differential scaling of the long bones in the terrestrial Carnivora and other mammals. J. Morphol. *204:*157–169.

Biewener, A.A. (1989a) Scaling body support in mammals: limb posture and muscle mechanics. Science *245:* 45–48.

Biewener, A.A. (1989b) Mammalian terrestrial locomotion and size. BioScience *39*(11):776–783.

Callison, G., and H.M. Quimby (1984) Tiny dinosaurs: are they fully grown? J. Vert. Paleontol. *3:*200–209.

Camp, C.L. (1936) A new type of small bipedal dinosaur from the Navajo Sandstone of Arizona. Univ. Calif. Publ. Geol. Sci. *24:*39–56.

Cavagna, G.A., N.C. Heglund, and C.R. Taylor (1977) Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. Am. J. Physiol. *233*(5):R243–R261.

Clark, J., and R.M. Alexander (1975) Mechanics of running in quail (*Coturnix*). J. Zool. *176:*87–113.

Colbert, E.H. (1964) The Triassic dinosaur genera *Podokesaurus* and *Coelophysis*. Am. Mus. Novitates *2168:*1–12.

Colbert, E.H. (1970) A saurischian dinosaur from the Triassic of Brazil. Am. Mus. Novitates *2405:*1–39.

Coombs, W.P., Jr. (1978) Theoretical aspects of cursorial adaptations in dinosaurs. Q. Rev. Biol. *53:*393–418.

Cracraft, J. (1976) The hindlimb elements of the moas (Aves, Dinornithidae): a multivariate assessment of size and shape. J. Morphol. *150:*495–526.

Gatesy, S.M. (1989) Archosaur neuromuscular and locomotor evolution. Ph.D. thesis, Harvard University.

Gatesy, S.M. (1990) Caudofemoral musculature and the evolution of theropod locomotion. Paleobiology *16(2):* 170–186.

Gatesy, S.M., and A.A. Biewener (1991) Bipedal locomotion: effects of size, speed and limb posture in birds and humans. J. Zool. (in press).

Gauthier, J. (1984) A cladistic analysis of the higher systematic categories of the Diapsida. Ph.D. thesis, University of California, Berkeley.

Gauthier, J. (1986) Saurischian monophyly and the origin of birds. Mem. Calif. Acad. Sci. *8:*1–55.

Gauthier, J., and K. Padian (1985) Phylogenetic, functional, and aerodynamic analyses of the origin of birds. In M.K. Hecht, J.H. Ostrom, G. Viohl, and P. Wellnhofer (eds): The Beginnings of Birds: Proceedings of the International *Archaeopteryx* Conference, Eichstätt 1984. Eichstätt: Freunde des Jura-Museums Eichstätt, pp. 185–198.

Gilmore, C.W. (1920) Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus (Allosaurus)* and *Ceratosaurus*. Bull. U.S. Natl. Mus. *110:*1–154.

Gregory, W.K. (1912) Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. Ann. N.Y. Acad. Sci. *22:*267–294.

Janensch, W. (1925) Die Coelurosaurier und Theropoden der Tendaguru-Schichten Deutsch-Ostafrikas. Palaeontographica *1(Suppl. 7):*257–276.

Madsen, J.H. (1976) *Allosaurus fragilis:* a revised osteology. Bull. Utah Geol. Min. Surv. *109:*1–163.

Maleev, E.A. (1974) Gigantic carnosaurs of the family Tyrannosauridae. Sovm. Sov.-Mong. Paleontol. Eksped. Trudy *1:*132–191.

Maloiy, G.M.O., R.M. Alexander, R. Njau, and A.S. Jayes (1979) Allometry of the legs of running birds. J. Zool. *187:*161–167.

Manion, B.L. (1984) The effects of size and growth on the hindlimb locomotion in the chicken. Ph.D. thesis, University of Illinois at Chicago.

Martinez, R., O. Gimenez, J. Rodriguez, and G. Bochatey (1986) *Xenotarsosaurus bonapartei* nov. gen. et sp. (Carnosauria, Abelisauridae), un nuevo Theropoda de la Formacion Bajo Barreal, Chubut, Argentina. Actas IV Congr. Argent. Paleontol. Bioestrat. *2:*23–31.

McMahon, T.A. (1973) Size and shape in biology. Science *179:*1201–1204.

McMahon, T.A. (1975) Allometry and biomechanics: limb bones of adult ungulates. Am. Nat. *109(969):*547–563.

McMahon, T.A., and J.T. Bonner (1983) On Size and Life. New York: Scientific American Books, Inc.

Monnier, L. (1913) Paleontologie de Madagascar VII.-Les Aepyornis. Ann. Paleontol. *8:*125–172.

Osborn, H.F. (1916) Skeletal adaptations of *Ornitholestes, Struthiomimus, Tyrannosaurus.* Bull. Am. Mus. Nat. Hist. *35:*733–771.

Osmolska, H., E. Roniewicz, and R. Barsbold (1972) A new dinosaur, *Gallimimus bullatus* n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. Palaeontol. Polonica *27:*103–143.

Ostrom, J.H. (1970) Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana. Bull. Yale Peabody Mus. Nat. Hist. *35:*1–234.

Ostrom, J.H. (1976a) *Archaeopteryx* and the origin of birds. Biol. J. Linn. Soc. *8:*91–182.

Ostrom, J.H. (1976b) On a new specimen of the Lower Cretaceous theropod dinosaur *Deinonychus antirrhopus.* Breviora *439:*1–21.

Ostrom, J.H. (1978) The osteology of *Compsognathus longipes* Wagner. Zitteliana *4:*73–118.

Ostrom, J.H. (1981) *Procompsognathus*-theropod or thecodont? Palaeontographica A *175:*179–195.

Owen, R. (1856) Monograph on the fossil reptilia of the Wealden Formations. Part III. *Megalosaurus bucklandi.* Palaeontogr. Soc. Monogr. 1–26.

Padian, K. (1986) On the type material of *Coelophysis* Cope (Saurischia: Theropoda), and a new specimen from the Petrified Forest of Arizona (late Triassic: Chinle Formation). In K. Padian (ed): The Beginning of the Age of Dinosaurs. Cambridge: Cambridge University Press, pp. 45–60.

Padian, K., and Olsen, P.E. (1989) Ratite footprints and the stance and gait of Mesozoic theropods. In D.D. Gillette, and M.G. Lockley (eds): Dinosaur Tracks and Traces. Cambridge: Cambridge University Press, pp. 231–241.

Paul, G.S. (1988) Predatory Dinosaurs of the World. New York: Simon and Schuster.

Prange, H.D., J.F. Anderson, and H. Rahn (1979) Scaling of skeletal mass to body mass in birds and mammals. Am. Nat. *113(1):*103–122.

Prothero, D.R., and P.C. Sereno (1982) Allometry and paleoecology of medial Miocene dwarf rhinoceroses from the Texas Gulf Coastal Plain. Paleobiology *8(1):*16–30.

Raath, M.A. (1969) A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. Arnoldia *4(28):*1–25.

Reig, O.A. (1963) La presencia de dinosaurios saurisquios en los "Estratos de Ischigualasto" (Mesotriásico superior) de las Procincias de San Juan y La Rioja (República Argentina). Ameghiniana *3:*3–20.

Romer, A.S. (1923) The pelvic musculature of saurischian dinosaurs. Bull. Am. Mus. Nat. Hist. *48:*605–617.

Russell, D.A. (1970) Tyrannosaurs from the Late Cretaceous of western Canada. Natl. Mus. Nat. Sci. Publ. Palaeontol. *1:*1–34.

Russell, D.A. (1972) Ostrich dinosaurs from the Late Cretaceous of western Canada. Can. J. Earth Sci. *9:*375–402.

Stirling, E.C., and A.H.C. Zietz (1913) Fossil remains of lake Callabonna Part II. I. Genyornis newtoni. A new genus and species of fossil struthious bird. Mem. R. Soc. S. Austr. *I(II):*41–80.

Tarsitano, S. (1983) Stance and gait in theropod dinosaurs. Acta Pal. Pol. *28(1–2):*251–264.

Welles, S.P. (1984) *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. Palaeontographica A *185:*85–180.

Wellnhofer, P. (1974) Das fünfte Skelettexemplar von *Archaeopteryx.* Palaeontographica A *147:*169–216.

Wellnhofer, P. (1988) A new specimen of *Archaeopteryx.* Science *240:*1790–1792.