Femoral dimensions and mid-thigh circumference in *Alligator mississippiensis*
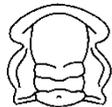
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LETHAIA

The mid-thigh circumference of the intact hindlimb in *Alligator mississippiensis* is tightly correlated with transverse dimensions of the proximal and distal articular surfaces of the femur, and with minimum midshaft femoral circumference. Maximum diameter of the proximal articular end, width across the distal articular end, and midshaft circumference are the best femoral predictors of circumference of the intact thigh. Regression equations of mid-thigh circumference against these femoral dimensions can be used to estimate the transverse dimensions of the intact hindlimb in extinct crocodylian-like archosaurs. □ *Alligators, femur, soft-tissue reconstruction.*

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Reconstructing the soft anatomy of extinct archosaurs is a challenging enterprise (cf. Brown 1916; Romer 1923; Lull & Wright 1942; Galton 1969; Russell 1972; Borsuk-Białynicka 1977; Coombs 1979; Norman 1986; Rowe 1986; Paul 1987; Gatesy 1990; Dodson 1996; Dilkes 2000; Carrano & Hutchinson 2002). Critical to the task are comparisons with extant forms, guided by the extant phylogenetic bracket (Bryant & Seymour 1990; Bryant & Russell 1992; Witmer 1995, 1997). The hindlimb plays a key role in archosaurian locomotion (Gatesy 1990; Hutchinson & Gatesy 2000; Hutchinson 2001), and so many workers have attempted to reconstruct its musculature in extinct forms. Such reconstructions are usually qualitative, showing only hypothetical muscle origins and insertions, with little indication of how the muscles and other hindlimb soft tissues would have affected the transverse dimensions of the hindlimb. In the present study we quantitatively compare the circumference of the intact upper leg with dimensions of the femur in the American alligator (*Alligator mississippiensis*).

Materials and methods

We measured the hindlimbs of wild and captive alligators sacrificed in 1999 at the Rockefeller Wildlife Refuge, Grand Chenier, Louisiana (Farlow & Britton 2000). Captive individuals had been caged outdoors in large pens under natural conditions, but received supplemental food rations in addition to wild prey taken in their enclosures. Our sample comprised 3 wild females (total length ranging 1.7–2.2 meters), 7 wild males (total length 1.6–3.1 m), 14 captive females (total length 2.5–2.8 m), and 4 captive males (total length 3.6–3.9 m).

We measured the mid-thigh circumference (MTC) about half-way between the knee and the body trunk of the alligator by wrapping string around it, taking care not to compress the surface of the thigh. One femur was removed from each animal and cleaned, from which the following measurements were made (Fig. 1):

(1) Maximum proximal diameter (Fpmx): greatest dimension across the proximal articular surface of the bone (Fig. 1A, B).
(2) Minimum proximal diameter (Fpmn): greatest dimension across the proximal articular surface perpendicular to the maximum proximal diameter (Fig. 1B).
(3) Minimum midshaft circumference (Fc): measured with string distal to the fourth trochanter, and proximal to where the bone flares outward toward the distal condyles (not illustrated).
(4) Distal width (Fdw): greatest transverse width of the distal articular surface of the bone (Fig. 1C).
(5) Distal height (Fdh): greatest dimension across the distal articular surface perpendicular to distal width, across the lateral condyle (Fig. 1C).

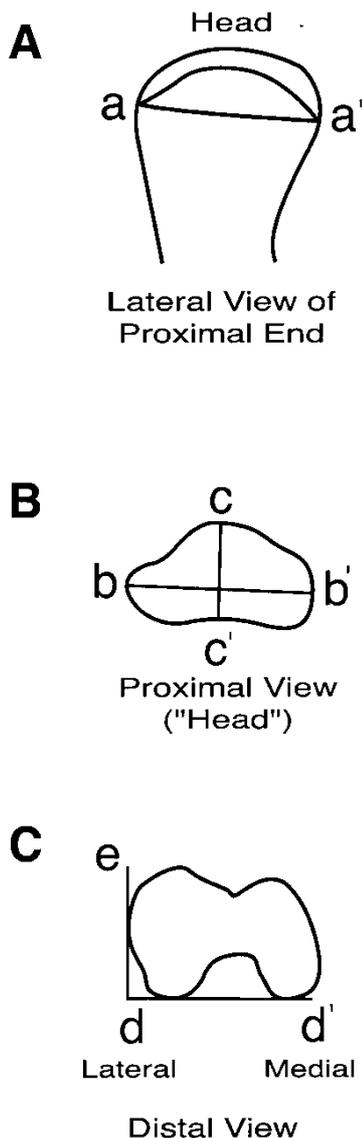All measurements were made in millimeters.

Fig. 1. Measurement of alligator femoral dimensions. □A. Proximal articular end of femur in lateral view, showing maximum (a-a') diameter. □B. Proximal articular end of femur in proximal view, again showing maximum (b-b') and also minimum (c-c') diameters. □C. Distal articular end of femur in distal view, showing distal width (d-d') and distal height (d-e).

Table 1. Summary comparison of the ratio of mid-thigh circumference (MTC) of the intact alligator hindlimb to various femoral dimensions.

Ratio	Minimum	Maximum	Mean	N
MTC/Maximum proximal diameter	7.5	9.7	8.4	23
MTC/Minimum proximal diameter	13.3	17.4	14.8	22
MTC/Minimum midshaft circumference	5.0	6.7	5.8	23
MTC/Distal articular width	7.3	9.7	8.0	23
MTC/Distal articular height	10.9	13.6	12.0	23

Results

MTC averages from 6–15 times the magnitude of the femoral dimensions we measured (Table 1). Despite the fact that captive alligators were heavier than wild individuals, plots of MTC against femoral dimensions show captive and wild alligators following the same trend (Fig. 2). MTC is highly correlated with all femoral dimensions (Table 2); the highest correlations are with Fpmx and Fc.

However, Fdw is the only femoral dimension that consistently maintains a significant relationship with MTC when partial correlation analysis controls for each of the other femoral dimensions in turn (Table 3, top), and stepwise multiple regression of MTC against the femoral parameters first selects Fdw, and then adds – oddly enough – Fpmn, albeit with a negative correlation with MTC: (MTC = [15.11 * Fdw] − [11.33 * Fpmn] − 45.00; $r = 0.984$, $p < 0.001$).

Note, though, that Fpmn was measured on one fewer than the number of alligators for the other femoral dimensions (Table 1). Given the relatively small number of alligators for which data were available, results of partial correlation and stepwise regression analysis may be sensitive to the sample size. This can be checked by doing partial correlation and

Table 2. Regression and reduced major axis (RMA) relationships between mid-thigh circumference and femoral dimensions in *Alligator mississippiensis*; all measurements in millimeters. Statistical abbreviations: r = correlation coefficient; SEE = regression standard error of estimate; P = probability associated with F test.

Independent variable	Treatment	Slope	Intercept	r	SEE	P	N
Maximum proximal diameter	Regression	9.09	−28.87	0.981	24.40	<0.001	23
	RMA	9.27	−36.98				
Minimum proximal diameter	Regression	14.30	12.73	0.963	30.00	<0.001	22
	RMA	14.84	−0.96				
Minimum midshaft circumference	Regression	6.46	−38.25	0.980	25.16	<0.001	23
	RMA	6.59	−47.12				
Distal articular width	Regression	9.09	−46.06	0.970	30.20	<0.001	23
	RMA	9.36	−59.19				
Distal articular height	Regression	12.59	−16.79	0.974	28.47	<0.001	23
	RMA	12.93	−27.62				23

stepwise multiple regression excluding Fpmn, increasing the sample size of alligators by one. After controlling for Fpmx, Fc, Fdw, and Fdh do not have significant correlations with MTC, and Fpmx is the only femoral parameter that consistently maintains a significant relationship with MTC after controlling for the effects of the other parameters (Table 3, bottom); stepwise multiple regression analysis now selects only Fpmx as a significant predictor of MTC. However, Fc does retain significant correlations with MTC after
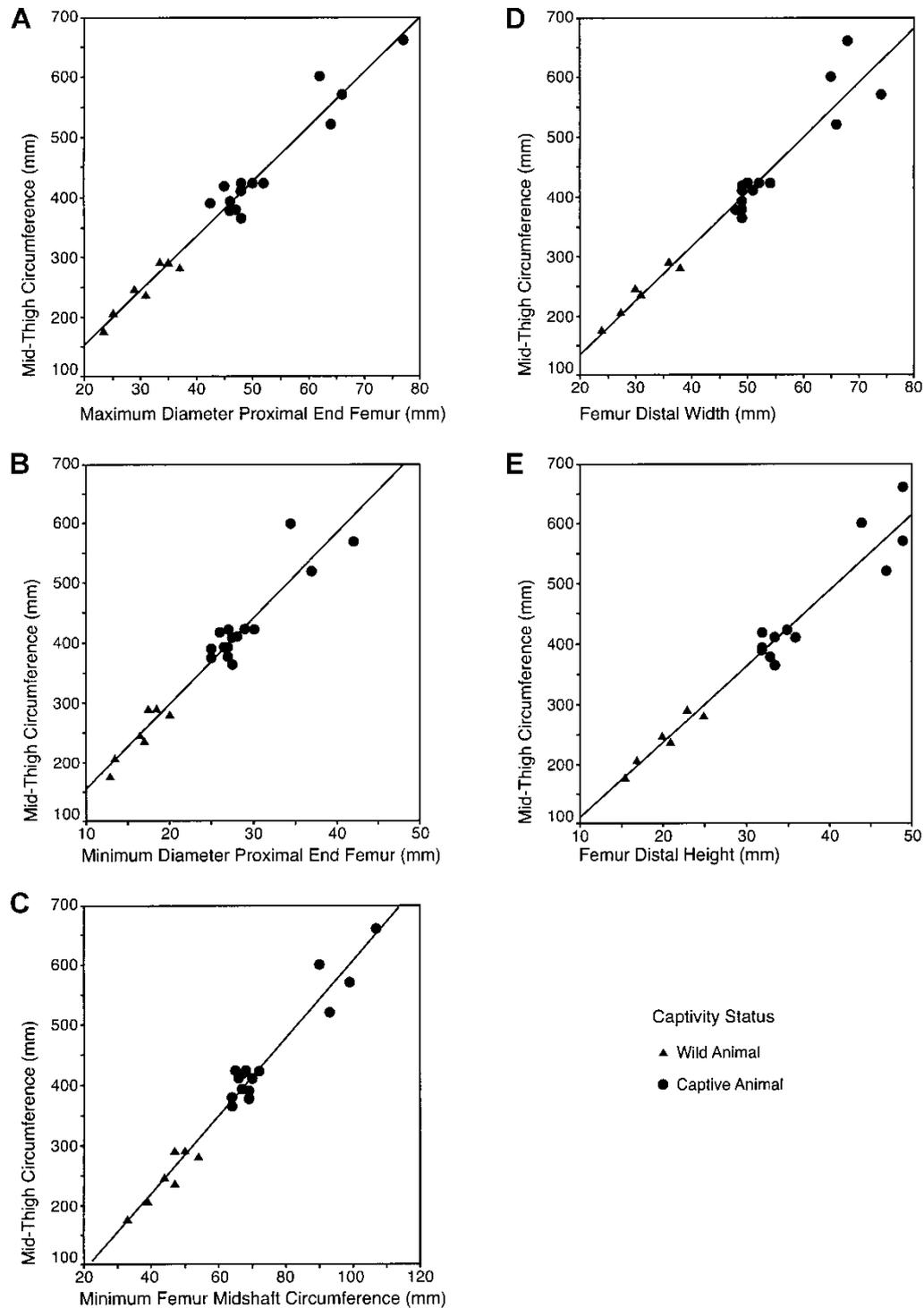

Fig. 2. Mid-thigh circumference of the intact alligator hindlimb as a function of various femoral dimensions; regression lines are fitted to all data plots.

Table 3. Partial correlations of mid-thigh circumference (MTC) with femoral dimensions after controlling for each of the femoral dimensions in turn. Cell contents = partial correlation coefficient (2-tailed significance). Fc = femoral minimum midshaft circumference, Fdh = femoral distal height, Fdw = femoral distal width, Fpmn = minimum diameter of proximal end of femur, Fpmx = maximum diameter of proximal end of femur.

Controlling variable	Correlation with MTC after removing effects of controlling variable:				
	Fpmx	Fpmn	Fc	Fdw	Fdh
Fpmx	—	−0.060 (0.798)	0.383 (0.086)	0.455 (0.038)	0.219 (0.340)
Fpmn	0.563 (0.008)	—	0.542 (0.011)	0.745 (<0.001)	0.548 (0.010)
Fc	0.452 (0.040)	0.194 (0.399)	—	0.511 (0.018)	0.362 (0.107)
Fdw	0.127 (0.584)	−0.440 (0.046)	0.133 (0.564)	—	0.107 (0.643)
Fdh	0.263 (0.250)	−0.033 (0.885)	0.299 (0.188)	0.470 (0.032)	—

	Fpmx	Fc	Fdw	Fdh
Fpmx	—	0.395 (0.069)	0.340 (0.122)	0.223 (0.319)
Fc	0.454 (0.034)	—	0.285 (0.198)	0.253 (0.255)
Fdw	0.650 (0.001)	0.602 (0.003)	—	0.371 (0.089)
Fdh	0.550 (0.008)	0.519 (0.013)	0.173 (0.442)	—

controlling for two of the other three femoral parameters.

Fdw, Fc, and especially Fpmx therefore seem to be the best predictors of MTC.

Discussion

Hip and hindlimb function in *Alligator* retains features that likely were present in plesiomorphic archosaurs, and that were considerably but gradually altered in the lineage that led through non-avian theropods to birds (Gatesy 1990, 2002; Hutchinson & Gatesy 2000; Hutchinson 2001). Although it would obviously be desirable to have data for additional crocodylian species, our *Alligator* regression equations could be helpful in constraining reconstructions of the size of the soft tissues enveloping the femur not just of crocodylians, but possibly also of other archosaurs more closely related to crocodylians than to birds, and even basal archosaurs. Combining crocodylian data with comparable data for ground birds, it might even be possible to make quantitative estimates of the transverse dimensions of thigh soft tissues in non-avian dinosaurs. This in turn might be helpful in constraining femoral muscle mass estimates for making interpretations of the capacity of extinct forms to engage in vigorous locomotor activity (cf. Hutchinson & Garcia 2002 for *Tyrannosaurus)*.

References

Borsuk-Białynicka, M. 1977: A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii* gen. n., sp. n. from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica 37*, 5–64.

Brown, B. 1916: *Corythosaurus casuarius*: skeleton, musculature and epidermis. *Bulletin American Museum of Natural History 35*, 709–716.

Bryant, H.N. & Russell, A.P. 1992: The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philosophical Transactions of the Royal Society of London, Series B 337*, 405–418.

Bryant, H.N. & Seymour, K.L. 1990: Observations and comments on the reliability of muscle reconstruction in fossil vertebrates. *Journal of Morphology 206*, 109–117.

Carrano, M.T. & Hutchinson, J.R. 2002: Pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria: Theropoda). *Journal of Morphology 253*, 207–228.

Coombs, W.P., Jr 1979: Osteology and myology of the hindlimb in the Ankylosauria (Reptilia, Ornithischia). *Journal of Paleontology 53*, 666–684.

Dilkes, D.W. 2000: Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. *Transactions Royal Society of Edinburgh, Earth Sciences 90*, 87–125.

Dodson, P. 1996: *The Horned Dinosaurs: A Natural History*. 346 pp. Princeton University Press, Princeton, N.J.

Farlow, J.O. & Britton, A. 2000: Size and body proportions in *Alligator mississippiensis*: implications for archosaurian ichnology. *Paleontological Society of Korea Special Publication 4*, 189–206.

Galton, P.M. 1969: The pelvic musculature of the dinosaur *Hypsilophodon* (Reptilia: Ornithischia). *Postilla 131*, 1–64.

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

Gatesy, S.M. 2002: Locomotor evolution on the line to modern birds. *In* Chiappe, L.M. & Witmer, L.M. (eds): *Mesozoic Birds: Above the Heads of Dinosaurs*, 432–447. University of California Press, Berkeley.

Hutchinson, J.R. 2001: The evolution of femoral osteology and soft tissues on the line to extant birds (Neornithes). *Zoological Journal of the Linnean Society 131*, 169–197.

Hutchinson, J.R. & Garcia, M. 2002: *Tyrannosaurus* was not a fast runner. *Nature 415*, 1018–1021.

Hutchinson, J.R. & Gatesy, S.M. 2000: Adductors, abductors, and the evolution of archosaur locomotion. *Paleobiology 26*, 734–751.

Lull, R.S. & Wright, N.E. 1942: Hadrosaurian dinosaurs of North America. *Geological Society of America Special Paper 40*, 1–242.

Norman, D.B. 1986: On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 56*, 281–372.

Paul, G.S. 1987: The science and art of restoring the life appearance of dinosaurs and their relatives: a rigorous how-to guide. *In*

Czerkas, S.J. & Olson, E.C. (eds): *Dinosaurs Past and Present*, 5–49. Natural History Museum of Los Angeles County and University of Washington Press, Seattle.

Romer, A.S. 1923: The pelvic musculature of saurischian dinosaurs. *Bulletin American Museum of Natural History 48*, 605–617.

Rowe, T. 1986: Homology and evolution of the deep dorsal thigh musculature in birds and other Reptilia. *Journal of Morphology 189*, 327–346.

Russell, D.A. 1972: Ostrich dinosaurs from the Late Cretaceous of western Canada. *Canadian Journal of Earth Sciences 9*, 375–402.

Witmer, L.M. 1995: The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. *In* Thomason, J.J. (ed.): *Functional Morphology in Vertebrate Paleontology*, 19–33. Cambridge University Press, Cambridge, UK.

Witmer, L.M. 1997: The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Journal of Vertebrate Paleontology 17 Supplement to No. 1*, 73 pp.