Caudipteryx as a non-avialan theropod rather than a flightless bird

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Caudipteryx zoui is a small enigmatic theropod known from the Early Cretaceous Yixian Formation of the People's Republic of China. From the time of its initial description, this taxon has stimulated a great deal of ongoing debate regarding the phylogenetic relationship between non-avialan theropods and birds (Avialae) because it preserves structures that have been uncontroversially accepted as feathers (albeit aerodynamically unsuitable for flight). However, it has also been proposed that both the relative proportions of the hind limb bones (when compared with overall leg length), and the position of the center of mass in Caudipteryx are more similar to those seen in extant cursorial birds than they are to other non-avialan theropod dinosaurs. This conclusion has been used to imply that Caudipteryx may not have been correctly interpreted as a feathered non-avialan theropod, but instead that this taxon represents some kind of flightless bird. We review the evidence for this claim at the level of both the included fossil specimen data, and in terms of the validity of the results presented. There is no reason—phylogenetic, morphometric or otherwise—to conclude that Caudipteryx is anything other than a small non-avialan theropod dinosaur.

Key words: Dinosauria, Theropoda, Avialae, birds, feathers, Yixian Formation, Cretaceous, China.

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Introduction

The non-avialan theropod dinosaur Caudipteryx zoui (Fig. 1) was described by Ji et al. (1998) from the Early Cretaceous Yixian Formation of Liaoning Province, People's Republic of China (Ji et al. 1998; Zhou and Wang 2000; Zhou et al. 2000). Along with another taxon from the same deposits, Protarchopteryx robusta Ji and Ji, 1997, both fossils added significantly to our understanding of the relationship between birds (Avialae) and non-avialan theropods, because both preserve integumentary structures uncontroversially interpreted as feathers (Ji et al. 1998; Padian 2001; Padian et al. 2001; Prum and Williamson 2001; Xu et al. 2001). Although the feathers preserved in these taxa were certainly not aerodynamically suitable for active flight (Rayner 2001), they have been interpreted as providing clear evidence that the origination of these complex integumentary structures evolved prior to the phylogenetic divergence of Avialae (Archaeopteryx and later forms). Subsequent cladistic analyses have also supported the contention that Caudipteryx is a member of Maniraptora, close to (but not within) the phylogenetic divergence of birds (Avialae) (Currie et al. 1998; Ji et al. 1998; Holtz 1998; Sereno 1999; Norell et al. 2001), closely related to Oviraptor and its kin (Oviraptoridae; Fig. 2).

Despite some dissent regarding a relationship between birds and theropods (reviewed by Chatterjee 1997, and Feduccia 1999; see also Prum 2002, 2003), no quantitative analyses (phylogenetic or otherwise) have been published to date in support of the hypothesis that the evident similarities between the two groups can be explained as a result of convergence. Hence, the only currently available alternative hypothesis states that birds (Avialae) did not diverge from within non-avialan theropods, but from another, as yet unspecified taxon (Feduccia 1999).

As a result of this ongoing debate regarding the origination of Avialae, Jones et al. (2000) presented the results of a quantitative analysis of hind limb and body proportions, concluding that both the hind limbs and position of the centre of mass of Caudipteryx are more similar to extant “cursorial” (or “ground living”; including flightless) Neornithes (i.e., modern birds sensu Cracraft 1988) than they are to non-avialan theropods. On the basis of their analysis, Jones et al. (2000; see also Ruben and Jones 2001) suggested that previous interpretations of Caudipteryx as a feathered non-avialan theropod could be incorrect.

Because of the evident discrepancy between reported morphological trends and the conclusions of phylogenetic analyses, we revisit in this paper the analysis of Jones et al. (2000). In addition to highlighting a number of significant problems with their measurement data (Appendix 1), we demonstrate by use of a separate, and more complete, set of limb measurements (Appendix 2) that the hind limbs of Caudipteryx are not significantly different from those of other known non-avialan theropods.
Fig. 1. A. Photograph of the holotype specimen of *Caudipteryx zoui* (NGMC 97–4–A) described by Ji et al. (1998). B. Sketch of NGMC 97–4–A in left lateral view. Not to scale. Measurement of trunk length in this specimen is impossible (but was given to an accuracy of 1 mm by Jones et al. 2000). Fig. A is reproduced with permission from *Nature* (Ji et al. 1998), copyright (1998), Macmillan Magazines Ltd.

*Institutional abbreviations.*—AMNH, American Museum of Natural History, New York, USA; BPM, Beipiao Museum, Beipiao, China; CM, Carnegie Museum of Natural History, Pittsburgh, USA; CV, Municipal Museum of Chunking, Chunking, China; GI, Geological Institute, Ulaanbaatar, Mongolia; HN, Humboldt Museum für Naturkunde, Berlin, Germany; IVPP, Insitute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; MACN, Museo Argentinas...
Ciencias Naturales, Buenos Aires, Argentina; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MNHN, Muséum national d’Histoire naturelle, Paris, France; NGMC, National Geological Museum of People’s Republic of China, Beijing, China; NIGP, Nanjing Institute for Geology and Paleontology, Nanjing, China; NMC, National Museum of Canada, Ottawa, Canada; OUM, Oxford University Museum, Oxford, UK; PVL, Paleontologia de Vertebrados de la Fundación Miguel Lillo, Tucuman, Argentina; PVSJ, Museo de Ciencias Naturales de San Juan, San Juan, Argentina; USNM, United States National Museum, Washington D.C., USA; UC, University of Chicago, Chicago, USA; UCMP, University of California Museum of Paleontology, Berkeley, USA; QVM, Queen Victoria Museum, Salisbury, Zimbabwe.

Limb proportions revisited

Assumptions of function and phylogeny.—Jones et al. (2000) presented the results of a morphometric analysis of non-avian theropod and avian hind limb proportions on the basis of a data set comprising 24 “cursorial” (their use of the term) extant birds (Neornithes) and 40 non-avian theropod and ornithopod dinosaurs. They presented statistical regressions between limb and trunk lengths (Fig. 3) and concluded that the hind limb structure of Caudipteryx provides evidence that this taxon had a locomotor strategy similar to secondarily flightless Neornithes. The implication of this study being that because non-avian theropods and Neornithes had different locomotor strategies (reflected in their body shapes and limb proportions), the two groups are likely not related, and hence Caudipteryx cannot be considered simply as a non-avian theropod with feathers. This conclusion was subsequently cited in both technical (Ruben and Jones 2001) and popular literature (Gould 2000) because it appears to provide a direct empirical challenge to the hypothesis of a “bird–dinosaur” relationship. From the outset, we would argue that simply because two groups have different locomotor strategies, they are not necessarily unrelated. Many groups of modern birds hop when on the ground, for example, while some others prefer to run; all passerine birds, however, are still considered closely related to one another (Barker et al. 2004).

In addition to problematic assumptions of function and its relevance to phylogeny, we also highlight four further significant problems with the analysis (and hence conclusions) of Jones et al. (2000). These are: (1) assumptions of non-comparable hind limb function between non-avian theropods and Neornithes; (2) accuracy of included specimen data used as a basis of conclusions; (3) calculation and use of trunk lengths as approximations for overall body size; and (4) calculation of regression statistics and the subsequent significance of results. Furthermore, Jones et al.’s (2000) calculations of centre of mass in Neornithes and non-avian theropods are biased by assumptions concerning the position and extent of soft part anatomy in taxa that are closely related to avialans—the authors admit these were based on the skeletal reconstructions presented in G. Paul’s (1988) Predatory Dinosaurs of the World.

Hind limb and tail: centre of mass and total leg length.—Jones et al. (2000) presented two linear regression analyses (that we discuss below) on the basis of their original morphometric data (supplementary information to their publication that can either be downloaded from www.nature.com or provided electronically by GJD [gareth.dyke@ucd.ie]). In the second of two graphs (Jones et al. 2000: fig. b), effective hind limb lengths of terrestrial birds (Neornithes), non-avian theropods and ornithopod dinosaurs are plotted against total trunk length (i.e., in their analysis this was defined as the length from the first dorsal vertebra to the midpoint of the ischium). Effective hind limb length was used by Jones et al. (2000) because of a supposed difference in the contribution of the segments of the hind limb to terrestrial locomotion between non-avian theropods and Neornithes. As pointed out, for example by Gatesy (1990, 1991, 1995), reduction of the tail and the development of the caudofemoral musculature along the transition between non-avian theropods and avialans led to a forward shifting of the relative centre of mass in the latter group (Christiansen 1999; Farlow et al. 2000; Christiansen and Bond 2002). As a consequence, the more acutely angled femur seen in Neornithes contributes less to the total effective length of the hind limb (Gatesy 1990) than is the case in non-avian dinosaurs. In correspondence, the femora of Neornithes are shorter and stouter to preserve bending and torsional strength (Gatesy 1991; Carrano 1998). Recognizing this difference, Jones et al. (2000) did divide their measurement data set accordingly but for the regression calculations presented (their fig. 1b, reproduced herein as Fig. 3B), they
Measuring trunk length in dinosaurs.—The additional comparisons made by Jones et al. (2000) between hind limb proportions and estimated trunk length are extremely problematic. Total trunk length has not been considered seriously as a proxy for overall body size since the work of Böker (1935). The measurement, and significance, of this quantity is difficult to assess because not only do the numbers of dorsal vertebrae vary within both non-avian theropods and extant Neornithes (e.g., Mayr and Clarke 2003; Dyke et al. 2003), but there are serious problems with measurement of this quantity in many of the museum specimens cited by Jones et al. (2000). Differential preservation of fossils makes estimation of exact parameters such as trunk length problematic; separation of vertebral discs during fossilization, for example, will add significant error to a measurement of dorsal vertebrae. Jones et al. (2000) are unclear as to whether such factors were taken into account in their measurements of total trunk lengths.

Specimen data.—Jones et al. (2000) presented measurements for segments of the hind limb and trunk length in a variety of dinosaur taxa. However, these measurements are extremely hard to reconcile with the actual specimens from which they were taken (Appendix 1). There are a number of aspects to this problem. First, as discussed above, to accurately measure trunk length a number of assumptions would have to be made with regard to the length of the vertebral discs. Second, there is a clear problem in identifying the number of dorsal vertebrae (relative to thoracics) that are preserved in many fossil specimens, especially when they are smashed. This point is illustrated by Currie and Zhao (1993:2057) who stated that “the 10th presacral vertebra of IVPP 10600 [Sinraptor] is identified as a cervical, although it is morphologically identical to the 10th presacral of Allosaurus which is a dorsal. The identification is based on the anatomy associated with the rib”. Hence, the simple evaluation of isolated vertebral elements in dinosaurs without identifying corresponding ribs will not give an realistic impression of trunk length. Third, and most problematically, we have identified a number of cases where Jones et al. (2000) provide measurements (to a resolution, in some cases, of 1 mm) for bones that do not exist—they are not preserved with the specimen numbers indicated.

A second issue is sampling. The measurement sample presented by Jones et al. (2000) cannot be considered to be an unbiased tabulation of non-avian theropod taxa. Notable by their absence, for example, are Archaeopteryx and Sinornithoides. The type, and only known specimen, of Sinornithoides was deleted (Jones et al. 2000) because it is purported to be a juvenile; however, Russell and Dong (1993:2164) indicate that “the animal was immature but approaching maturity upon death”. Interestingly, Sinornithoides, has been placed phylogenetically within Troodontidae and is therefore purportedly more closely related to avialans (e.g., Holtz 1994a; Gauthier 1986; Sereno 1997, 1999; Norell et al. 2001) than the majority of the taxa sampled by Jones et al. (2000). In addition, this taxon was reported to fall out on the “bird line” before removal by Jones et al. (2000), yet no other troodontids appeared in their study. Conversely, another taxon, Eustrepspondylus, which is known to be a subadult (Molnar et al. 1990) was included in the final analysis. Reasons for the exclusion of Archaeopteryx from the analysis remain unclear; presumably because this taxon has been shown to have been volant (Rayner 1991, 2001). However, since at the time, before the discovery of Jeholornis (Zhou and Zhang 2002), it was the only well-preserved avialan with a long tail, clear definition of its locomotor capabilities seem crucial to the Jones et al. (2000) analysis.
Finally, we note severe difficulties with measurements of trunk lengths reported by Jones et al. (2000) for three specimens of *Caudipteryx* (Appendix 1) as one of us (MAN) has spent significant time studying these specimens. We feel that the measurement of trunk length are at best imprecise, and at worst (e.g., in the case of NGMC 97-9a which preserves only a few fragments of the dorsal vertebrae and no ilia) hypothetical.

Phylogenetic control.—Despite the number of phylogenetic studies that have supported the placement of *Caudipteryx* within Oviraptoridae (e.g., Currie et al. 1998; Holtz 1998; Clark et al. 1999; Sereno 1999; Norell et al. 2001), only one other example (*Ingenia*) of these taxa was considered by Jones et al. (2000); no analyses were presented comparing either the hind limbs or trunk length of *Caudipteryx* to existing (and largely well-preserved) specimens such as *Oviraptor* (e.g., IGM 100/42). Further, and as discussed above, specimen IGM 100/30 of *Ingenia* lacks almost all of its dorsal vertebrae. Using specimens on loan to the AMNH from the IGM, we took measurements of hind limbs and estimated trunk lengths for two exceptionally well-preserved oviraptorids, IGM 100/1002 and IGM 100/973 (*Khaan*; Clark et al. 2001). Although both of these specimens are preserved in almost complete articulation, we noted differences in up to 20 percent when trunk length was measured based on the total extent of the dorsal vertebral series compared to taking individual measurements from each vertebral centrum. Given this percentage uncertainty when working even with well-preserved fossil material, the accuracy of the measurements presented by Jones et al. (2000) remains unclear.

Reanalysis of Jones et al. (2000)

Ignoring all the assumptions we have highlighted above, we reproduced the results presented by Jones et al. (2000) by use of their data. Following their methods, we calculated linear regressions for each data subsample to the exclusion of *Caudipteryx*. This taxon was then overlain onto the resultant regression lines.

Having replotted both total and effective hind limb lengths against trunk length, we then used a standard f-test (as done by Jones et al. 2000) to test for significant differences between the slopes and intercepts of the regression lines. Results show that for both “total” and “effective” hind limb length, there is significant difference between the slopes of regression lines, although their intercepts are different (Table 1).

Jones et al. (2000) recombined their “theropod” and “bird” subsets for further analysis. To test the significance of this further assumption, we conducted another standard t-test in order to make pairwise comparisons between the intercepts of the three regression lines and did find significant differences between the lines for ornithopod dinosaurs and those for theropods and birds (Table 1). Separation of the measurement data for ornithopods may be supportable, this is likely not the case for theropods or birds.

Although the question of the relative limb proportions of *Caudipteryx* is interesting (Christiansen and Bonde 2002), any consideration of this problem must incorporate rigorous phylogenetic control, especially with regard to included data for Neornithes. Although terrestriality has evolved at least six times within extant bird clades (Gatesy 1991) these events are not directly comparable because they are disparate phylogenetically.
Hind limb proportions of Caudipteryx

In order to further test the hypothesis of Jones et al. (2000) —the hind limbs of Caudipteryx are significantly different from those of non-avian theropod dinosaurs, more similar to those of terrestrial birds—we assembled a data-set of osteological measurements (Appendix 2). Because of the numerous measurement problems discussed above, we did not consider further the parameter of total trunk length. Our data set of measurements for both birds and theropods consists of the component segments of the hind limb against total leg length. On this basis, and considering the length of the femur against total leg length, a very well-defined linear correlation is recovered (Fig. 4). Significant differences in this parameter of total trunk length are ascertained between the principal divisions of the phylogenetic rationale outlined above and plotted the three component segments of the hind limb against total leg length. On this basis, and considering the length of the femur against total leg length, a very well-defined linear correlation is recovered (Fig. 4). Significant differences in this plot can be ascertained between the principal divisions of the data as defined, theropods \((r^2 = 0.90)\), birds (including Archaeopteryx; \(r^2 = 0.81\)) and oviraptorosaurs (including Caudipteryx; \(r^2 = 0.98\)). Both non-avian theropods and avialans exhibit a wide range of femur lengths (Gatesy and Middleton 1997), but in general the length of this element is well-correlated with the total length of the leg. Non-avian theropods are distributed across the trend line in a manner which does approximate recent phylogenetic hypotheses for the group (Fig. 2). The ornithomimids (e.g., Archaeornithniformes, Gallimimus) with long overall leg length and femur length cluster on the right-hand side of the trend line; oviraptorosaurs (with the exception of the much larger specimen IGM 100/973), including the three specimens of Caudipteryx, cluster at the base of the trend in the left hand side of the diagram (Fig. 4). In these taxa, the femur contributes about one-third of the total leg length, as is seen in many Neornithes as well as the basal avialan Archaeopteryx and the maniraptoran Protarchaeopteryx robusta (Ji et al. 1998).

Our plots of tibia length against total leg length also reveal two distinct trends within the bird and theropod data (Table 2; Fig. 4). Much of this variation, however, is contained within the ratites and non-avian theropods other than oviraptors (including Caudipteryx). The non-avian theropod included in our data with the shortest tibia to total leg length ratio is Protarchaeopteryx; Caudipteryx clusters with other small oviraptorosaurs (again with the exception of IGM 100/973) at the base of the trend lines along with some of the smaller ornithomimid specimens (e.g., Gallimimus), Saurornithoides and Archaeopteryx (Fig. 4). Regression coefficients for the two principal subsets of the data are significant (Table 2), but given the position of Caudipteryx within the basal convergence of the two trend lines (dividing our measurement data into non-avian theropods and Avialae), this taxon cannot be definitively grouped within either sub-sample.

Our data for metatarsal lengths (i.e., either the tarsometatarsus in Avialae or metatarsal III in non-avian theropods) vary widely both within, and between, taxa (Fig. 4).  Non-avian theropods are distributed all across this graph; the three Caudipteryx specimens group with one specimen of Gallimimus and Saurornithoides (Fig. 4).  Again, the non-avian theropod with the shortest metatarsal III compared to total leg length is Protarchaeopteryx.

### Table 2. Statistics for reported hind limb analyses (left-right corresponding with A–C in Fig. 4).

|                      | slopes (P-values) | intercept (P-values) |
|----------------------|-------------------|----------------------|
| Total hind limb:     |                   |                      |
| birds                | 1.00, 0.98, 0.95  | 0.00, 0.00, 0.02     |
| Total hind limb:     |                   |                      |
| non-avian theropods  | 1.00, 0.95, 1.00  | 0.00, 0.02, 0.01     |
| Total hind limb:     |                   |                      |
| Oviraptoridae        | 1.00, 0.53, 0.95  | 0.00, 0.05, 0.05     |

### Conclusions

By use of proportional comparisons between hind limb and trunk lengths, Jones et al. (2000) purported to demonstrate that Caudipteryx zoui had both a locomotor strategy and limb proportions similar to extant “cursorial” birds. Jones et al. (2000) claimed that interpretations of specimens of Caudipteryx (based on phylogenetic analyses) as a small feathered non-avian theropod should be reevaluated in light of these results—in other words, the overwhelming number of osteological similarities evident between Caudipteryx and non-avian theropods are not the result of evolutionary relationship.

We have shown that the majority of the conclusions presented by Jones et al. (2000) are based on the a priori assumption that Caudipteryx is an avialan and that Avialae is unrelated to non-avian theropod dinosaurs. The most important conclusion made by Jones et al. (2000), that Caudipteryx had a locomotor strategy similar to that of extant “cursorial” birds, is dependant on the fact that the limbs of this taxon are treated as if it were a bird prior to inclusion in the analysis. Although Jones et al. (2000) did not directly claim that Caudipteryx is actually related to one of the diverse extant clades of Neornithes that are “cursorial”, they did imply that this taxon demonstrates some sort of “trend” or parallelism with extant birds in its “bauplan” (Ruben and Jones 2001).

We have cast significant doubt upon both the primary specimen data and conclusions presented by Jones et al. (2000). The majority of the non-avian theropod specimens measured by these workers are shown to be either too incomplete to allow for replication of their measurements, or sim-
ply do not exist. Furthermore, our own analysis, using much additional measurement data and incorporating phylogenetic control, supports the view that the locomotor capabilities of neornithines are similar to their closest non-avianian theropod relatives, including taxa such as *Caudipteryx*.

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**References**

Barker, F.K., Cibois, A., Shickler, P., Feinstein, J., and Cracraft, J. 2004. Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences* 101: 11040–11045.

Barsbold, R. and Osmólska, H. 1990. Ornithomimosauria. In: D.B. Weishampel, P. Dodson and H. Osmólska (eds.), *The Dinosauria*, 225–244. University of California Press, Berkeley.

Bidar, A., Demay, L., and Thomel, D. 1972. *Compsoptamus corallus*, nouvelle espèce de dinosaure théropode du Portlandian de Canjuers. *Extrême d’Annuaire Musée d’Histoire Naturelle de Nice* 1: 1972.

Böker, H. 1935. *Einführung in die Vergleichende Biologische Anatomie der Wirbeltiere*. Vol. I. 228 pp. G. Fischer, Jena.

Bonaparte, J.F., Novas, F.E., and Coria, R.A. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Contributions in Science, Natural History Museum of Los Angeles County* 416: 1–41.

Carrano, M.T. 1998. Locomotion in non-avian dinosaurs: integrating data from hind limb kinematics, in vivo strains, and bone morphology. *Paleobiology* 24: 450–469.

Chatterjee, S. 1997. *The Rise of Birds*: 225 Million Years of Evolution. 312 pp. Johns Hopkins University Press, Baltimore.

Chen, P.-J., Dong, Z.-M., and Zhen, S.-N. 1998. An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. *Nature* 391: 147–152.

Christiansen, P. 1999. Long bone scaling and limb posture in non-avianian theropods: evidence for differential allometry. *Journal of Vertebrate Paleontology* 19: 666–680.

Christiansen, P. and Bonde, N. 2002. Limb proportions and avian terrestrial locomotion. *Journal für Ornithologie* 143: 356–371.

Clark, J.M., Norell, M.A., and Chiappe, L.M. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avianlike brooding position over an ovipositorid nest. *American Museum Novitates* 3265: 1–36.

Clark, J.M., Norell, M.A., and Barsbold, R. 2001. Two new oviraptorids (Theropoda: Oviraptorosauria) from the Late Cretaceous Djadokhta Formation, Ukhaa Tolgod, Mongolia. *Journal of Vertebrate Paleontology* 21: 209–213.

Colbert, E.H. 1970. A saurischian dinosaur from the Triassic of Brazil. *American Museum Novitates* 2405: 1–39.

Cracraft, J. 1988. The major clades of birds. In: M.J. Benton (ed.), *Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds*, 339–361. Systematics Association, Oxford.

Cracraft, J. and Clarke, J.A. 2001. The basal clades of modern birds. In: J.A. Gauthier and L.F. Gall (eds.), *New Perspectives on the Origin and Evolution of Birds: Proceedings of the Ostrom Symposium*, 143–156. Yale University Press, New Haven.

Currie, P.J. and Zhao, X. 1993. A new carnosaur (Dinosauria. Theropoda) from the Jurassic of Xinjiang, People’s Republic of China. *Canadian Journal of Earth Sciences* 30: 2037–2081.

Currie, P.J., M.A. Norell, Q. Ji., and S. Ji. 1998. The anatomy of two feathered dinosaurs from Liaoning, China. *Journal of Vertebrate Paleontology* 18 (3): 36A.

Dyke, G.J., and J.M.V. Rayner. 2001. Forelimb shape and the evolution of basal birds. In: J.A. Gauthier and L.F. Gall (eds.), *New Perspectives on the Origin and Evolution of Birds: Proceedings of the Ostrom Symposium*, 275–282. Yale University Press, New Haven.

Dyke, G.J., Gulas, B.E., and Crowe, T.M. 2003. The suprageneric relationships of galliform birds (Aves, Galliformes): a cladistic analysis of morphological characters. *Zoological Journal of the Linnean Society* 137: 227–244.

Farlow, J.O., Gatesy, S.M., Holtz, T.R., Hutchinson, J.R., and Robinson, J.M. 2000. Theropod locomotion. *American Zoologist* 40: 640–663.

Feduccia, A. 1999. *The Origin and Evolution of Birds*. 420 pp. Yale University Press, New Haven.

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

Gatesy, S.M. 1991. Hind limb scaling in birds and other theropods: implications for terrestrial locomotion. *Journal of Morphology* 209: 83–96.

Gatesy, S.M. 1995. Functional evolution of the hind limb and tail from basal theropods to birds. In: J.J. Thomason (ed.), *Functional Morphology in Vertebrate Paleontology*, 219–234. Cambridge University Press, New York.

Gatesy, S.M. and Middleton, K.M. 1997. Bipedalism, flight, and the evolution of theropod locomotor diversity. *Journal of Vertebrate Paleontology* 17: 308–329.

Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. In: K. Padian (ed.), *The Origin of Birds and the Evolution of Flight*, 1–55. Memoirs of the California Academy of Sciences, Berkeley.

Gilmore, C.W. 1920. *Osteology of the carnivorous Dinosauria*. The Origin of Birds and the Evolution of Flight. 18 (3): 36A.

Glot, D.F. 1997. *Encyclopedia of Dinosaurs*. 1076 pp. McFarland, Jefferson.

Groth, J.G. and Barrowclough, G.F. 1999. Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. *Molecular Phylogenetics and Evolution* 12: 115–123.

Hazlehurst, G.R. 1992. *The Morphometrics of Pterosaurs*. 450 pp. PhD thesis, University of Bristol, Bristol.

Holtz, T.R., Jr. 1994a. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *Journal of Paleontology* 68: 1100–1117.

Holtz, T.R., Jr. 1994b. The arctometatarsalian pes, an unusual structure of the metatarsus of Cretaceous Theropoda (Dinosauria: Saurischia). *Journal of Vertebrate Paleontology* 14: 480–519.

Holtz, T.R., Jr. 2000. A new phylogeny of the carnivorous dinosaurs. *Gaia* 15: 5–61.

Huene, F. von. 1934. Ein neuerer Coelurosaurier in der thüringischen Trias. *Paläontologische Zeitschrift* 1935: 145–170.

Janesch, W. 1920. Über *Elaphrosaurus bambergi* and the Megalosaurus aus den Tendaguru-Schichten Deutsche-Ostafrikas. *Sitzungsberichte der Gesellschaft Naturforschernden Freunde zu Berlin* 1920: 225–235.

Ji, Q. and Ji, S.-A. 1997. Protarchaeopterygird bird (*Protarchaeopteryx* gen. nov.)—fossil remains of archaephyterygids from China. *Chinese Geology* 238: 38–41.

Ji, Q., Currie, P.J., Norell, M.A., and Ji, S.-A. 1998. Two feathered dinosaurs from northeastern China. *Nature* 393: 753–761.

Ji, Q., Norell, M.A., Gao, K.-Q., Ji, S.-A., and Ren, D. 2001. The distribution of integumentary structures in a feathered dinosaur. *Nature* 410: 1084–1088.
Lambe, L. 1917. The Cretaceous theropodus dinosaur Gorgosaurus. Canada Department of Mines, Geologic Survey, Memoir 100: 1–85.

Lauder, G.V., Jr. 1995. On the inference of function from structure. In: J.J. Thompson (ed.), Functional Morphology in Vertebrate Paleontology, 1–18. Cambridge University Press, New York.

Lee, K., Felsenstein, J., and Cracraft, J. 1997. The phylogeny of ratite birds: resolving conflicts between molecular and morphological data sets. In: D.P. Mindell (ed.), Avian Molecular Systematics and Evolution, 173–211. Academic Press, New York.

Livezey, B.C. 1993. Morphology of flightlessness in Chendytes; fossil seaducks (Anatidae: Mergini) of coastal California. Journal of Vertebrate Paleontology 13: 185–199.

Livezey, B.C. 1997. A phylogenetic analysis of basilan Asseriforines, the fossil Presbyornis and the interordinal relationships of waterfowl. Zoological Journal of the Linnean Society 121: 361–428.

Livezey, B.C. and Zusi, R.L. 2001. Higher-order phylogenetics of modern Aves based on comparative anatomy. Netherlands Journal of Zoology 51: 179–205.

Magnan, A. 1922. Les caractéristiques des oiseaux suivant le mode de vol. Annales des Sciences naturelles, Zoologie 5: 125–334.

Matthew, W.D. and Brown, B. 1923. Preliminary notices of skeletons and the origin of bird flight. In: D.H. Tanke, K. Carpenter, and M.W. Strepnick (eds.), Mesozioc Vertebrate Life: New Research Inspired by the Paleontology of Philip J. Currie, 117–135. Indiana University Press, Bloomington.

Paul, G.S. 1988. Predatory Dinosaurs of the World: A Complete Illustrated Guide. 464 pp. Simon and Schuster, New York.

Prum, R.O. and Williamson, S. 2001. Theory of the growth and evolution of feather shape. Journal of Experimental Zoology 291: 30–57.

Prum, R. O. 2002. Why ornithologists should care about the theropod origin of birds. Ask 119: 1–17.

Prum, R.O. 2003. Are current critiques of the theropod origin of birds science? Rebuttal to Feduccia(2002). Auk 120: 550–561.

Psiloyas, L. 1994. Hunting Dinosaurs. 267 pp. Random House, New York.

Rayner, J.M.V. 1991. Avian flight evolution and the problem of Archaeopteryx. In: J.M.V. Rayner and R.J. Wootton (eds.), Biomechanics in Evolution, 183–212. Cambridge University Press, Cambridge.

Rayner, J.M.V. 2001. On the origin and evolution of flapping flight aerodynamics in birds. In: J.A. Gauthier and L.F. Gall (eds.), New Perspectives on the Origin and Evolution of Birds: Proceedings of the Ostrom Symposium, 363–385. Yale University Press, New Haven.

Reig, O. 1963. La presencia de dinosaurios sauriosuicios en los “Estatros del Ischigualasto” (Mesotriasico superior) de las Provincias de San Juan y La Rioja (Republica Argentina). Ameghiniana 3: 3–20.

Rowe, T., and J.A. Gauthier. 1990. Ceratosaurus. In: D.B. Weishampel, P. Dodson, and H. Osmolska (eds.), The Dinosauria, 151–168. University of California Press, Berkeley.

Ruben, J. and Jones, T. 2001. Feathered dinosaurs and other myths: a cold, hard look at reality. Journal of Morphology 248 (3): 278.

Russell, D.A. 1970. Tyrannosaurs from the Late Cretaceous of Western Canada. National Museum of Science Publications in Paleontology 1: 1–34.

Russell, D.A. and Dong, Z.-M. 1993. A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous of the Ordos Basin, Inner Mongolia, People’s Republic of China. Canadian Journal of Earth Sciences 30: 2163–2173.

Seroen, P.C. 1997. The origin and evolution of dinosaurs. Annual Reviews of Earth and Planetary Sciences 25: 435–489.

Seroen, P.C. 1999. The evolution of dinosaurs. Science 284: 2137–2147.

Seroen, P.C., Wilson, J.A., Larsson, H.C.E., Duthiel, D.B., and Saes, H.-D. 1994. Early Cretaceous Dinosaurs from the Sahara. Science 265: 267–271.

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

Xu, X., Zhou, Z.-H., and Prum, R.O. 2001. Branched integumentary structures in Sinornithosaurus and the origin of feathers. Nature 410: 290–294.

Zhou, Z.-H. and Wang, X.-L. 2000. A new species of Caudipteryx from the Yixian Formation of Liaoning, northeast China. Vertebrata Palasiatica 38: 111–127.

Zhou, Z.-H. and Zhang, F.-C. 2002. A long-tailed, seed-eating bird from the Early Cretaceous of China. Nature 418: 405–409.

Zhou, Z.-H., Wang, X.-L., Zhang, F.-C., and Xu, X. 2000. Important features of Caudipteryx – Evidence from two nearly complete new specimens. Vertebrata Palasiatica 38: 241–254.
Appendix 1

List of taxa

As discussed in the text, because recent phylogenetic studies have demonstrated that non-avian theropods are relevant to the issue of avialan origins and body plan evolution, we review here the specimens of non-avian theropods cited by Jones et al. (2000). Measurements taken from these specimens were used in our attempts to reproduce the graphs and conclusions of Jones et al. (2000). Please note that throughout this section specimens numbers are listed as cited by Jones et al. (2000).

Afrovenator UC OBA 1.—The original figure published by Sereno et al. (1994) indicates that the thoracic column of Afrovenator is extremely fragmentary. Indeed, as few as four vertebral elements may be preserved (Sereno et al. 1994) making measurement of trunk length impossible for this taxon.

Albertosaurus AMNH 5458.—This is an excellent specimen preserving all of the relevant bones for the study of Jones et al. (2000). However, the femur length reported (1025 mm) is identical to that given by Russell (1970: table 1) where only an estimate is provided. It is further unclear how a measurement for trunk length for this taxon was derived, as this quantity was not reported by Matthew and Brown (1923). AMNH 5458 has been on display and behind glass at the AMNH for more than 40 years thus rendering any measurement of this specimen impossible.

Ceratosaurus USNM 4735.—According to Gilmore (1920), the actual number of vertebrae in the dorsal column is unknown. Gilmore (1920) notes that in the mounted reconstruction of this specimen at least one additional vertebra is included.

Carnotaurus.—No museum number was reported by Jones et al. (2000) for this taxon. Presumably, reference is made to MACN CH 894 since this is the only described specimen of Carnotaurus. Although the vertebral column is complete in this taxon, Bonaparte et al. (1990: 31) state that the tibiae are “represented only by their proximal parts”, and that no metatarsal bones were found with the specimen. Yet Jones et al. (2000) provide lengths for both metatarsal III and tibia for Carnotaurus.

Coelophysis AMNH 7224.—The metatarsals of this specimen are reconstructed (MAN, personal observations), and as a result of flattening it is hard to estimate the total number of dorsal vertebrae. Hence measurements of these quantities are problematic.

Compsognathus MNHN MCHJ 79.—Several of the vertebrae are not preserved. For instance, Bidar et al. (1972: 9) remark that in dorsal 2 “les dimensions ne peuvent être appréciées”. Dorsal vertebra 3 is considered “hypothétique” and “non visible (cassure du squelette)”, and a number of others are so poorly preserved that they can not be accurately measured (Bidar et al. 1972).

Daspletosaurus AMNH 5438.—Inclusion of this taxon in this morphometric analysis (as well as that of Jones et al. 2000) is impossible because AMNH 5438 consists of only a sacrum, a right femur and a single metatarsal.

Deinonychus MCZ 4371.—This specimen includes a very well-preserved hind limb and pelvis. However, as noted by Ostrom (1976: 2) and Peter Makovicky (personal communication 2002), the dorsal vertebrae are not well enough preserved to allow accurate measurement. Even by use of the Deinonychus reconstruction given in Ostrom (1976: 3) we were unable to reconcile the measurement of 601 mm given by Jones et al. (2000) for trunk length. We estimate that this length was approximately 503 mm.

Dilophosaurus UCMP 37302.—According to Welles (1984), many of the vertebrae in this specimen are extremely crushed thus making any measurement of trunk length problematic. For instance, Welles (1984: 113) states in the description of dorsal 2 that: “in lateral view, the centrum is 78 mm long above and 70 below”. Similar distortions as a result of preservation are also reported for dorsals 5 and 6 (Welles 1984: 116), and in dorsal six: “this and the next three were rotated 180 degrees to the right so that their spines pointed ventrally. The centrum is crushed just below the center, the arch is pushed forward. The centrum is similar to the preceding but its length has been increased from an estimated 88 mm to 113 mm by the crushing” (Welles 1984: 116). Most of the preserved vertebrae of Dilophosaurus show clear variance between dorsal and ventral centrum lengths (Welles 1984).

Eoraptor PVSJ 512.—This specimen is reasonably complete and includes both hind limbs and a presacral series (MAN, personal observations). However, since a detailed osteological treatment of this taxon has not yet been published, it is difficult to verify the measurements reported by Jones et al. (2000).

Eustreptospondylus OUM J13558.—This is a reasonably well-preserved specimen that includes the hind limbs (including the feet) and pelvis. However, a number of the vertebrae are reconstructed, and hence the entire vertebral series may not be complete. In addition, this specimen is a juvenile (Molnar et al. 1990).

Gallimimus GI 100/11.—This specimen is a well-preserved, but incomplete skeleton (Osmólska et al. 1972). The dorsal column is very incomplete including only fragments of the centra of dorsal vertebrae 11—213 and 17–23 (Osmólska et al. 1972: 107). Only the lengths of 6 of these vertebrae are reported by Osmólska et al. (1972). Fortunately (but not used
by Jones et al. 2000), a number of specimens of Gallimimus are known that do preserve the dorsal series (Osmólska et al. 1972).

Gorgosaurus NMC 2120.—This is an excellent and nearly complete specimen (Lambe 1917; Russell 1970). However, the poor preservation of the femur and metatarsal III led Lambe (1917: 76) and later Russell (1970: table 1) to report only approximate measurements for these elements. The trunk region of this specimen is also incompletely preserved. Russell (1970: table 1) did not provide a measurement for this part of the skeleton (yet he does for other tyrannosaur specimens in the same table). Lambe (1917: 24) indicated that the centra of dorsals 6–9 are not well enough preserved to measure.

Herrerasaurus PVL 2566.—Reig (1963) noted that the vertebral column of this specimen is incomplete. A measurement of total trunk length for this specimen is impossible.

Ingenia IGM 100/30.—The type specimen of this taxon is a well-preserved skeleton but including only a few fragments of the dorsal vertebrae. As is visible in the figure provided by Psiloyas (1994: 211; MAN, personal observations), it is impossible to reconstruct an accurate trunk length for this specimen (as measured by Jones et al. 2001).

Lilliensternus HMN R1291.—This taxon consists of two partial skeletons. Reconstructions of Lilliensternus (derived from Huene 1934) are based on a composite of the two differently sized specimens (Glut 1997). Although the limbs are complete, both lack a complete sacrum. The only dorsals that are preserved are numbered 1–3 and 12–14 (Huene 1934), although some other isolated bone fragments may also form different sized specimens (Glut 1997). Although the limbs are complete, both lack a complete sacrum. The only dorsals that are preserved are numbered 1–3 and 12–14 (Huene 1934), although some other isolated bone fragments may also form part of this series. Rowe and Gauthier (1990) suggested that Lilliensternus may be a subadult (on the basis of the lack of fusion between the tarsus and the tibia).

Sinosauropteryx NIGP 127587.—This specimen is well preserved for all of the measurements reported by Jones et al. (2001).

Sinraptor IVPP10600.—This specimen is complete in all areas measured by Jones et al. (2000) (Currie and Zhao 1993). Yet, see our comments above about distinguishing dorsal vertebrae.

Staurikosaurus MCZ 1669.—Although the skeleton of this taxon is relatively complete, Colbert (1970) and personal observation (MAN) indicate that there are no metatarsals preserved. This measurement was nevertheless included by Jones et al. (2000).

Struthiomimus AMNH 5339.—This is a nearly complete specimen (Osborn 1917) from which all of the relevant measurements can be taken.

Syntarsus QVM QG/1.—Raath (1969) notes that at least the anterior three dorsal vertebrae of this specimen are not preserved: “the first vertebra preserved in the present specimen is dorsal 4” (Raath 1969: 2). The remainder of the hind limb and pelvic elements are complete and can be measured.

Tyrranosaurus CM 9380.—According to Osborn (1906: 282), this specimen lacks a number of dorsal vertebrae. Although Osborn (1906) does indicate that metatarsal III is complete, examination of his figure (and accompanying table; Osborn 1906: 282) shows that only the distal end of this element is preserved.

Velociraptor GI 100/25.—This is a nearly complete specimen that has never been adequately described. All of the elements that are measured by Jones et al. (2000), are preserved on this specimen. However, their measurements do not correspond with the actual specimen. For instance they list the femur length as 200 mm, when in fact it is 185 mm in length. The tibia is listed by Jones et al. (2000) as 210 mm in length when in fact it is 225 mm (231 with the astragalus), metatarsal III is 108, not the 95 mm reported. Similarly the twisted nature of the specimen makes accurate (to 1 mm resolution) measurement of the dorsal series impossible.

Yanglehuaunosaurus CV 00215.—This specimen is reasonably complete, having a good vertebral series, but incomplete hind limbs (Molnar et al. 1990). Both the metatarsals and feet are unknown for CV 00215 (Molnar et al. 1990; Philip Currie, personal communication 2002), hence hind limb length cannot be calculated for this taxa. Glut (1997) further indicated that this specimen may be a subadult.

Caudipteryx IVP (uncatalogued).—The correct museum number for this specimen is BPM 001 (Zhou et al. 2000). While this specimen is very well-preserved, the actual number of dorsal vertebrae is uncertain: “there appear to be only 9 thoracic vertebrae” (Zhou et al. 2000: 246). As is the case in other specimens of Caudipteryx (see below), the ilia are disarticulated from the sacral vertebrae which are crushed beneath them. It is therefore impossible to have an accurate impression of the relationship between the acetabulum and the dorsal vertebral column. Although the limb bones are well-preserved, a number of the measurements given by Jones et al. (2000) differ from those provided in the original specimen description (Zhou et al. 2000).

Caudipteryx NGMC 97-9A.—This specimen, figured by Ji et al. (1998: fig. 5), is the worst preserved of any of the yet published Caudipteryx specimens. Whereas the hind limbs are mostly complete, the ilia and sacrum are not preserved. Only a few crushed and smeared fragments of dorsal vertebrae are preserved.

Caudipteryx V 12344.—The correct museum number for this specimen is IVPP 1240. The same problem in identifying the number of thoracic vertebrae in BPM 001 also applies to this specimen. In addition, the sacrum is crushed and obscured by the displaced blade of the ilia thus making accurate measurement of sacral length impossible. As a consequence, it is not possible to measure the trunk length in this specimen (the relationship between the acetabulum and the dorsal series cannot be ascertained). Although the hind limbs are well-preserved, again the measurements for this elements given by Jones et al. (2000) differ from those presented in the original specimen description (Zhou et al. 2000).
Appendix 2

Measurement data (in mm) used as the basis for new analyses.

| Taxon                  | Museum No. | Source                        | femur | tibia | tarsus | total leg |
|------------------------|------------|-------------------------------|-------|-------|--------|-----------|
| Struthio camelus       | –          | Holtz (1994b)                 | 385   | 327   | 176    | 888       |
| Struthio camelus       | –          | Gatesy (1991)                 | 287   | 493   | 220    | 1000      |
| Struthio camelus       | –          | Holtz (1994b)                 | 390   | 483   | 288    | 1161      |
| Struthio camelus       | –          | Holtz (1994b)                 | 293   | 480   | 461    | 1234      |
| Struthio camelus       | –          | Holtz (1994b)                 | 285   | 450   | 225    | 960       |
| Struthio camelus       | –          | Holtz (1994b)                 | 286   | 280   | 134    | 700       |
| Struthio camelus       | –          | Hazlehurst (1992)             | 340   | 320   | 230    | 890       |
| Struthio camelus       | MCZ 2686-1| Holtz (1994b)                 | 305   | 511   | 447    | 1263      |
| Struthio camelus       | MCZ 2686-2| Holtz (1994b)                 | 520   | 500   | 235    | 1255      |
| Struthio camelus       | MCZ 6502  | Gatesy (1991)                 | 83    | 134   | 119    | 336       |
| Rhea americana         | MCZ 1631  | Gatesy (1991)                 | 210   | 318   | 325    | 853       |
| Rhea americana         | MCZ 2083  | Gatesy (1991)                 | 210   | 318   | 325    | 853       |
| Rhea americana         | MCZ 689   | Gatesy (1991)                 | 159   | 278   | 284    | 721       |
| Rhea americana         | YPM 11524 | Gatesy (1991)                 | 195   | 329   | 306    | 830       |
| Rhea americana         | YPM 14047 | Gatesy (1991)                 | 206   | 346   | 322    | 844       |
| Rhea americana         | YPM 6503  | Gatesy (1991)                 | 187   | 278   | 285    | 750       |
| Rhea americana         | YPM ost. 2234| Holtz (1994b)             | 210   | 330   | 320    | 860       |
| Rhea americana         | YPM ost. 564| Holtz (1994b)              | 110   | 163   | 147    | 420       |
| Anomalopteryx didiformis| –         | Gatesy (1991)                 | 265   | 405   | 190    | 860       |
| Anomalopteryx didiformis| YPM 9883 | Holtz (1994b)                 | 235   | 360   | 190    | 785       |
| Dinornis sp.           | YPM-PU acc. W.8095| Holtz (1994b)            | 225   | 390   | 168    | 783       |
| Dinornis giganteus     | –          | Gatesy (1991)                 | 320   | 580   | 303    | 1203      |
| Dinornis giganteus     | –          | Gatesy (1991)                 | 317   | 567   | 493    | 1377      |
| Dinornis maximusus     | –          | Holtz (1994b)                 | 285   | 585   | 295    | 1165      |
| Dinornis maximusus     | –          | Holtz (1994b)                 | 330   | 650   | 334    | 1314      |
| Dinornis novaezealandiae| –         | Gatesy (1991)                 | 320   | 545   | 483    | 1348      |
| Dinornis novaezealandiae| YPM 9207 | Holtz (1994b)                 | 310   | 367   | 208    | 885       |
| Dinornis novaezealandiae| YPM 9892 | Holtz (1994b)                 | 364   | 360   | 200    | 924       |
| Dinornis robustus      | –          | Holtz (1994b)                 | 502   | 556   | 398    | 1456      |
| Dinornis struthoides   | –          | Hazlehurst (1992)             | 265   | 521   | 282    | 1068      |
| Dinornis struthoides   | YPM 9891  | Hazlehurst (1992)             | 280   | 475   | 210    | 965       |
| Dinornis terosus       | –          | Hazlehurst (1992)             | 435   | 475   | 310    | 1220      |
| Dinornis terosus       | –          | Hazlehurst (1992)             | 313   | 525   | 470    | 1308      |
| Emeus crassus          | –          | Hazlehurst (1992)             | 273   | 464   | 214    | 951       |
| Emeus crassus          | –          | Holtz (1994b)                 | 245   | 435   | 200    | 880       |
| Emeus crassus          | –          | Holtz (1994b)                 | 255   | 422   | 190    | 867       |
| Emeus crassus          | –          | Holtz (1994b)                 | 260   | 460   | 215    | 935       |
| Emeus crassus          | –          | Holtz (1994b)                 | 260   | 450   | 188    | 898       |
| Emeus crassus          | –          | Holtz (1994b)                 | 473   | 411   | 223    | 1107      |
| Emeus crassus          | –          | Holtz (1994b)                 | 397   | 430   | 297    | 1124      |
| Emeus huttonii         | –          | Holtz (1994b)                 | 238   | 387   | 184    | 809       |
| Taxon                  | Museum No. | Source                  | femur | tibia | tarsus | total leg |
|-----------------------|------------|-------------------------|-------|-------|--------|-----------|
| Emeus huttonii         | VIII A     | Gatesy (1991)           | 244   | 397   | 187    | 828       |
| Euryapteryx curtus     | –          | Hazlehurst (1992)       | 168   | 269   | 125    | 561       |
| Euryapteryx curtus     | AM4        | Hazlehurst (1992)       | 179   | 286   | 136    | 601       |
| Euryapteryx exilis     | –          | Hazlehurst (1992)       | 198   | 332   | 148    | 678       |
| Euryapteryx exilis     | AM6        | Hazlehurst (1992)       | 205   | 347   | 152    | 704       |
| Euryapteryx geranoides | –          | Hazlehurst (1992)       | 237   | 388   | 175    | 799       |
| Euryapteryx geranoides | AM37       | Gatesy (1991)           | 231   | 411   | 175    | 817       |
| Euryapteryx geranoides | YPM 9830   | Gatesy (1991)           | 331   | 370   | 168    | 869       |
| Euryapteryx geranoides | YPM 9886   | Holtz (1994b)           | 268   | 455   | 205    | 928       |
| Euryapteryx gravis     | –          | Gatesy (1991)           | 336   | 382   | 164    | 882       |
| Euryapteryx gravis     |            | Holtz (1994b)           | 273   | 497   | 410    | 1180      |
| Euryapteryx tane       | –          | Hazlehurst (1992)       | 191   | 328   | 149    | 668       |
| Megalapteryx didinus   | –          | Hazlehurst (1992)       | 246   | 385   | 179    | 810       |
| Megalapteryx didinus   | –          | Holtz (1994b)           | 265   | 405   | 190    | 860       |
| Pachyornis elefantopus| –          | Holtz (1994b)           | 295   | 485   | 210    | 900       |
| Pachyornis elefantopus| MCZ 9.1.14 | Holtz (1994b)           | 440   | 520   | 370    | 1330      |
| Pachyornis elefantopus| YPM 9884   | Holtz (1994b)           | 376   | 511   | 308    | 1195      |
| Pachyornis elefantopus| YPM 9888   | Holtz (1994b)           | 280   | 472   | 210    | 962       |
| Pachyornis mappini     | –          | Hazlehurst (1992)       | 206   | 366   | 156    | 728       |
| Pachyornis mappini     | YPM 384    | Gatesy (1991)           | 203   | 336   | 156    | 695       |
| Pachyornis oweni       | MCZ 384    | Gatesy (1991)           | 143   | 243   | 113    | 499       |
| Pachyornis septentrionalis| –        | Hazlehurst (1992)       | 174   | 292   | 133    | 599       |
| Aepyornis hildebrandi  | –          | Gatesy (1991)           | 315   | 520   | 217    | 1052      |
| Aepyornis hildebrandi  | –          | Gatesy (1991)           | 240   | 485   | 275    | 1000      |
| Aepyornis maximus      | –          | Holtz (1994b)           | 529   | 608   | 391    | 1528      |
| Aepyornis maximus      | –          | Hazlehurst (1992)       | 295   | 588   | 303    | 1187      |
| Aepyornis medius       | –          | Holtz (1994b)           | 513   | 560   | 385    | 1458      |
| Aepyornis medius       | –          | Holtz (1994b)           | 320   | 525   | 225    | 1070      |
| Genyornis newtoni      | –          | Holtz (1994b)           | 280   | 540   | 296    | 1116      |
| Casuarius sp.          | YPM 4351   | Gatesy (1991)           | 218   | 350   | 295    | 863       |
| Casuarius sp.          | YPM 2123   | Gatesy (1991)           | 198   | 323   | 264    | 785       |
| Casuarius bennetti     | MCZ display | Gatesy (1991)           | 203   | 320   | 250    | 773       |
| Casuarius casuarius    | –          | Hazlehurst (1992)       | 232   | 365   | 305    | 902       |
| Casuarius casuarius    | –          | Gatesy (1991)           | 47    | 82    | 65     | 194       |
| Dromaeus novaehollandiae| –         | Holtz (1994b)           | 243   | 465   | 404    | 1112      |
| Dromaeus novaehollandiae| –         | Holtz (1994b)           | 228   | 451   | 380    | 1059      |
| Dromaeus novaehollandiae| –         | Holtz (1994b)           | 241   | 451   | 407    | 1099      |
| Dromaeus novaehollandiae| –         | Holtz (1994b)           | 234   | 436   | 401    | 1071      |
| Dromaeus novaehollandiae| –         | Holtz (1994b)           | 228   | 403   | 375    | 1006      |
| Dromaeus novaehollandiae| –         | Holtz (1994b)           | 218   | 390   | 389    | 997       |
| Dromaeus novaehollandiae| –         | Holtz (1994b)           | 225   | 374   | 354    | 953       |
| Dromaeus novaehollandiae| –         | Hazlehurst (1992)       | 211   | 364   | 369    | 945       |
| Dromaeus novaehollandiae| MCZ 1627  | Gatesy (1991)           | 225   | 400   | 375    | 1000      |
| Dromaeus novaehollandiae| MCZ 198  | Gatesy (1991)           | 227   | 415   | 385    | 1027      |
| Apteryx australis      | –          | Hazlehurst (1992)       | 87    | 121   | 66     | 274       |
| Apteryx australis      | –          | Cracraft (1976)         | 90    | 130   | 65     | 284       |
| Apteryx australis      | YPM 13486  | Gatesy (1991)           | 99    | 145   | 78     | 322       |
| Apteryx australis      | YPM 4384   | Gatesy (1991)           | 87    | 128   | 69     | 284       |
| Apteryx oweni          | MCZ 308    | Gatesy (1991)           | 80    | 114   | 63     | 257       |
| Apteryx oweni          | YPM 2118   | Gatesy (1991)           | 72    | 104   | 57     | 233       |
| Taxon                          | Museum No. | Source         | femur | tibia | tarsus | total leg |
|-------------------------------|------------|----------------|-------|-------|--------|-----------|
| Tinamus major                 | MCZ 2774   | Gatesy (1991)  | 65    | 98    | 69     | 232       |
| Tinamus tao                   | MCZ 3705   | Gatesy (1991)  | 70    | 108   | 71     | 249       |
| Crypturellus boucardi         | MCZ 2750   | Gatesy (1991)  | 51    | 76    | 52     | 179       |
| Crypturellus noctivagus       | MCZ 276    | Gatesy (1991)  | 58    | 86    | 60     | 204       |
| Rhynchosator rufescens        | –          | Hazlehurst (1992)| 70   | 99    | 66     | 235       |
| Rhynchosator rufescens        | MCZ 1633   | Gatesy (1991)  | 73    | 99    | 65     | 236       |
| Rhynchosator rufescens        | YPM acc. 2041 | Holtz (1994b)| 70   | 95    | 59     | 224       |
| Nothura maculosa              | MCZ 1653   | Gatesy (1991)  | 42    | 62    | 39     | 144       |
| Nothura maculosa              | –          | Hazlehurst (1992)| 46   | 62    | 38     | 146       |
| Anhima cornuta                | MCZ 307    | Gatesy (1991)  | 92    | 166   | 113    | 371       |
| Anhima cornuta                | MCZ 6993   | Gatesy (1991)  | 91    | 177   | 126    | 398       |
| Chauna chavaria               | –          | Hazlehurst (1992)| 96   | 177   | 123    | 396       |
| Chauna torquata               | –          | Hazlehurst (1992)| 78   | 138   | 93     | 309       |
| Anseranas semipalmata         | –          | Hazlehurst (1992)| 53   | 99    | 60     | 212       |
| Dendrocygna autumnalis        | MCZ 273    | Gatesy (1991)  | 50    | 87    | 56     | 193       |
| Dendrocygna autumnalis        | MCZ 7071   | Gatesy (1991)  | 49    | 84    | 52     | 185       |
| Cygnus atratus                | MCZ 6936   | Gatesy (1991)  | 84    | 141   | 93     | 318       |
| Cygnus columbianus            | MCZ 3544   | Gatesy (1991)  | 114   | 212   | 113    | 439       |
| Cygnus cygnus                 | –          | Hazlehurst (1992)| 260  | 240   | 200    | 700       |
| Cygnus cygnus                 | MCZ 335    | Gatesy (1991)  | 107   | 188   | 110    | 405       |
| Cygnus olor                   | –          | Hazlehurst (1992)| 309  | 543   | 231    | 1082      |
| Anser albifrons               | –          | Hazlehurst (1992)| 71   | 121   | 72     | 263       |
| Anser caerulescens            | MCZ 1883   | Gatesy (1991)  | 69    | 124   | 74     | 267       |
| Anser erythrophus             | MCZ 330    | Gatesy (1991)  | 87    | 148   | 85     | 320       |
| Anser fabalis                 | –          | Hazlehurst (1992)| 76   | 124   | 73     | 273       |
| Anser fabalis                 | MCZ 262    | Gatesy (1991)  | 75    | 127   | 74     | 276       |
| Branta bernicla               | –          | Hazlehurst (1992)| 60   | 104   | 61     | 226       |
| Branta canadensis             | –          | Hazlehurst (1992)| 85   | 156   | 92     | 334       |
| Branta canadensis             | MCZ 6738   | Gatesy (1991)  | 89    | 148   | 94     | 331       |
| Branta canadensis             | MCZ 7645   | Gatesy (1991)  | 78    | 140   | 85     | 303       |
| Branta leucopsis              | –          | Hazlehurst (1992)| 65   | 115   | 72     | 253       |
| Branta leucopsis              | MCZ 6931   | Gatesy (1991)  | 71    | 123   | 74     | 268       |
| Cereopsis novaehollandiae     | MCZ 7095   | Gatesy (1991)  | 81    | 146   | 95     | 322       |
| Chloephaga picta              | MCZ 3031   | Gatesy (1991)  | 88    | 159   | 97     | 344       |
| Alopenchus aegyptiacus        | MCZ 260    | Gatesy (1991)  | 75    | 140   | 87     | 302       |
| Tadorna ferruginea            | –          | Hazlehurst (1992)| 56   | 99    | 60     | 215       |
| Tadorna tadorna               | MCZ 7538   | Gatesy (1991)  | 57    | 102   | 68     | 227       |
| Tachyeres brachypterus        | MCZ 2204   | Gatesy (1991)  | 76    | 120   | 61     | 257       |
| Anas clypeata                 | –          | Hazlehurst (1992)| 39   | 66    | 36     | 141       |
| Anas clypeata                 | MCZ 7105   | Gatesy (1991)  | 49    | 65    | 34     | 148       |
| Anas crecca                   | –          | Hazlehurst (1992)| 32   | 54    | 29     | 115       |
| Callonetta leucophrys         | MCZ 7445   | Gatesy (1991)  | 33    | 53    | 32     | 118       |
| Anas penelope                 | –          | Hazlehurst (1992)| 43   | 74    | 41     | 158       |
| Anas platyrhynchos            | –          | Hazlehurst (1992)| 49   | 78    | 43     | 170       |
| Anas platyrhynchos            | MCZ 1898   | Gatesy (1991)  | 48    | 78    | 43     | 169       |
| Anas platyrhynchos            | MCZ 1914   | Gatesy (1991)  | 41    | 67    | 37     | 145       |
| Anas rubripes                 | –          | Hazlehurst (1992)| 51   | 79    | 44     | 173       |
| Anas rubripes                 | MCZ 2850   | Gatesy (1991)  | 48    | 75    | 42     | 165       |
| Taxon                  | Museum No. | Source       | femur | tibia | tarsus | total leg |
|-----------------------|------------|--------------|-------|-------|--------|-----------|
| Anas specularoides    | MCZ 3053   | Gatesy (1991)| 56    | 87    | 49     | 192       |
| Anas strepera         | –          | Hazlehurst (1992)| 45    | 71    | 38     | 154       |
| Merganetta armata     | MCZ 5094   | Gatesy (1991)| 35    | 65    | 38     | 138       |
| Somateria mollissima  | –          | Hazlehurst (1992)| 61    | 100   | 51     | 213       |
| Somateria mollissima  | –          | Livezey (1993)| 66    | 109   | 53     | 228       |
| Somateria mollissima  | –          | Hazlehurst (1992)| 67    | 113   | 56     | 236       |
| Somateria mollissima  | MCZ 7453   | Gatesy (1991)| 67    | 110   | 50     | 227       |
| Aythya ferina         | –          | Hazlehurst (1992)| 45    | 74    | 38     | 157       |
| Aythya marila         | MCZ 1471   | Gatesy (1991)| 44    | 70    | 35     | 149       |
| Netta peposaca        | MCZ 2988   | Gatesy (1991)| 51    | 82    | 40     | 173       |
| Aix galericulata      | –          | Hazlehurst (1992)| 42    | 66    | 39     | 147       |
| Aix sponsa            | MCZ 7372   | Gatesy (1991)| 40    | 62    | 35     | 137       |
| Cairina moschata      | MCZ 1901   | Gatesy (1991)| 58    | 90    | 49     | 197       |
| Plecopterus gambensis | MCZ 196    | Gatesy (1991)| 97    | 173   | 113    | 382       |
| Melanitta fusca       | –          | Livezey (1993)| 56    | 99    | 48     | 202       |
| Melanitta fusca       | –          | Hazlehurst (1992)| 57    | 93    | 48     | 198       |
| Melanitta fusca       | –          | Livezey (1993)| 59    | 105   | 51     | 215       |
| Melanitta fusca       | MCZ 6956   | Gatesy (1991)| 55    | 90    | 47     | 192       |
| Melanitta nigra       | –          | Hazlehurst (1992)| 49    | 80    | 43     | 172       |
| Histrionicus histrionicus | MCZ 2957  | Gatesy (1991)| 44    | 70    | 38     | 152       |
| Clangula hyemalis     | –          | Hazlehurst (1992)| 42    | 67    | 35     | 144       |
| Clangula hyemalis     | MCZ 6497   | Gatesy (1991)| 40    | 64    | 32     | 136       |
| Bucephala albeola     | MCZ 1915   | Gatesy (1991)| 40    | 59    | 33     | 132       |
| Bucephala clangula    | –          | Hazlehurst (1992)| 42    | 63    | 33     | 138       |
| Mergus albellus       | –          | Hazlehurst (1992)| 40    | 62    | 32     | 134       |
| Mergus merganser      | MCZ 1436   | Gatesy (1991)| 51    | 84    | 45     | 181       |
| Mergus merganser      | MCZ 1436   | Gatesy (1991)| 51    | 84    | 45     | 181       |
| Mergus merganser      | MCZ 318    | Gatesy (1991)| 52    | 86    | 48     | 185       |
| Mergus serrator       | –          | Hazlehurst (1992)| 47    | 82    | 46     | 175       |
| Mergus serrator       | MCZ 2835   | Gatesy (1991)| 49    | 83    | 47     | 179       |
| Oxyura australis      | MCZ 1437   | Gatesy (1991)| 46    | 73    | 37     | 156       |
| Bizura lobata         | MCZ 2067   | Gatesy (1991)| 62    | 108   | 50     | 220       |
| Chendytes lawi        | –          | Livezey (1993)| 71    | 149   | 67     | 287       |
| Macrocephalon maleo   | MCZ 355    | Gatesy (1991)| 85    | 127   | 91     | 304       |
| Ortalis motmot        | –          | Hazlehurst (1992)| 60    | 94    | 61     | 215       |
| Ortalis vetula        | MCZ 3099   | Gatesy (1991)| 66    | 95    | 62     | 223       |
| Penelope purpurascens | MCZ 293    | Gatesy (1991)| 95    | 137   | 83     | 315       |
| Penelopeina nigra     | MCZ 2084   | Gatesy (1991)| 108   | 163   | 107    | 378       |
| Crax alberti          | MCZ 209    | Gatesy (1991)| 107   | 155   | 103    | 365       |
| Crax mitu             | MCZ 3575   | Gatesy (1991)| 106   | 157   | 110    | 373       |
| Crax pauxi            | MCZ 2121   | Gatesy (1991)| 110   | 169   | 113    | 392       |
| Tetrao urogallus      | MCZ 315    | Gatesy (1991)| 81    | 107   | 55     | 243       |
| Tetrao urogallus      | MCZ 315    | Gatesy (1991)| 81    | 107   | 55     | 243       |
| Lyurus tetrix         | –          | Hazlehurst (1992)| 74    | 95    | 48     | 217       |
| Lagopus lagopus scoticus | –           | Hazlehurst (1992)| 61    | 78    | 41     | 180       |
| Lagopus lagopus       | MCZ 1469   | Gatesy (1991)| 59    | 80    | 41     | 179       |
| Lagopus mutus         | –          | Hazlehurst (1992)| 52    | 70    | 37     | 159       |
| Lagopus mutus         | MCZ 1469   | Gatesy (1991)| 59    | 80    | 41     | 179       |
## Dyke and Norell—Non-Avian Theropod Caupipteryx

| Taxon                        | Museum No. | Source                  | femur | tibia | tarsus | total leg |
|------------------------------|------------|-------------------------|-------|-------|--------|-----------|
| Bonasa bonasia               | –          | Hazlehurst (1992)       | 52    | 68    | 36     | 156       |
| Bonasa umbellas              | MCZ 3809   | Gatesy (1991)           | 27    | 36    | 22     | 86        |
| Bonasa umbellas              | MCZ 3999   | Gatesy (1991)           | 56    | 75    | 41     | 173       |
| Bonasa umbellas              | MCZ 6061   | Gatesy (1991)           | 53    | 76    | 42     | 171       |
| Bonasa umbellas              | MCZ 7371   | Gatesy (1991)           | 57    | 78    | 42     | 176       |
| Bonasa umbellas              | MCZ 7666   | Gatesy (1991)           | 53    | 76    | 42     | 170       |
| Bonasa umbellas              | MCZ 7935   | Gatesy (1991)           | 53    | 75    | 41     | 169       |
| Tymanuchus capido            | MCZ 2193   | Gatesy (1991)           | 62    | 82    | 46     | 190       |
| Centrocercus urophasianus    | MCZ 110    | Gatesy (1991)           | 71    | 91    | 45     | 206       |
| Centrocercus urophasianus    | MCZ 1441   | Gatesy (1991)           | 71    | 91    | 49     | 212       |
| Lophura sp.                  | MCZ 3144   | Gatesy (1991)           | 94    | 142   | 118    | 354       |
| Colinus nigrocularis         | MCZ 5029   | Gatesy (1991)           | 37    | 50    | 30     | 117       |
| Callipepla squamata          | MCZ 1254   | Gatesy (1991)           | 37    | 56    | 31     | 124       |
| Lophortyx gambelli           | MCZ 7254   | Gatesy (1991)           | 38    | 55    | 33     | 126       |
| Colinus nigrocularis         | MCZ 5029   | Gatesy (1991)           | 35    | 47    | 28     | 109       |
| Colinus virginianus          | MCZ 7337   | Gatesy (1991)           | 40    | 54    | 31     | 126       |
| Colinus virginianus          | MCZ 7347   | Gatesy (1991)           | 40    | 54    | 32     | 126       |
| Odontophorus guttatus        | MCZ 2727   | Gatesy (1991)           | 50    | 70    | 45     | 166       |
| Odontophorus guttatus        | MCZ 2770   | Gatesy (1991)           | 47    | 67    | 43     | 157       |
| Alectoris graeca             | –          | Hazlehurst (1992)       | 57    | 75    | 42     | 174       |
| Alectoris rafa               | –          | Hazlehurst (1992)       | 55    | 73    | 41     | 169       |
| Coturnix coturnix            | –          | Hazlehurst (1992)       | 38    | 50    | 30     | 118       |
| Coturnix coturnix            | MCZ 3164   | Gatesy (1991)           | 35    | 42    | 26     | 102       |
| Coturnix coturnix            | MCZ 3298   | Gatesy (1991)           | 34    | 44    | 27     | 105       |
| Coturnix delegorguei         | MCZ 3037   | Gatesy (1991)           | 32    | 40    | 24     | 96        |
| Perdica asiatica             | –          | Hazlehurst (1992)       | 30    | 38    | 25     | 93        |
| Exaulfactoria chinensis      | –          | Hazlehurst (1992)       | 27    | 31    | 19     | 77        |
| Exaulfactoria chinensis      | MCZ 7497   | Gatesy (1991)           | 27    | 34    | 21     | 82        |
| Tragopan satyra              | –          | Hazlehurst (1992)       | 89    | 123   | 77     | 289       |
| Gallus gallus                | –          | Fisher (1946)           | 85    | 121   | 82     | 287       |
| Gallus gallus                | MCZ 1388   | Gatesy (1991)           | 91    | 128   | 94     | 313       |
| Phasianus colchicus          | –          | Hazlehurst (1992)       | 76    | 102   | 68     | 247       |
| Pavo cristatus               | –          | Hazlehurst (1992)       | 106   | 182   | 126    | 414       |
| Pavo cristatus               | MCZ 2651   | Gatesy (1991)           | 105   | 175   | 116    | 396       |
| Pavo cristatus               | MCZ 311    | Gatesy (1991)           | 107   | 193   | 139    | 439       |
| Pavo cristatus               | MCZ 7161   | Gatesy (1991)           | 109   | 202   | 137    | 448       |
| Numida meleagris             | MCZ 1648   | Gatesy (1991)           | 79    | 113   | 74     | 266       |
| Guttera edouardii            | MCZ 2998   | Gatesy (1991)           | 78    | 112   | 77     | 267       |
| Meleagris gallopavo          | –          | Hazlehurst (1992)       | 103   | 172   | 119    | 394       |
| Meleagris gallopavo          | MCZ 1494   | Gatesy (1991)           | 139   | 230   | 168    | 537       |
| Meleagris gallopavo          | MCZ 7157   | Gatesy (1991)           | 127   | 200   | 144    | 471       |
| Meleagris gallopavo          | MCZ 819    | Gatesy (1991)           | 119   | 193   | 141    | 453       |
| Agriocharis ocellata         | MCZ 2878   | Gatesy (1991)           | 110   | 193   | 145    | 448       |
| Agriocharis ocellata         | MCZ 3046   | Gatesy (1991)           | 107   | 185   | 138    | 430       |
| Agriocharis ocellata         | MCZ 3049   | Gatesy (1991)           | 101   | 177   | 131    | 409       |
| Archaeopteryx lithographica  | –          | Dyke (pers. obs.)       | 37    | 53    | 30     | 120       |
| Archaeopteryx lithographica  | –          | Dyke (pers. obs.)       | 53    | 69    | 36     | 158       |
| Archaeopteryx lithographica  | –          | Dyke (pers. obs.)       | 61    | 81    | 40     | 182       |
| Archaeopteryx lithographica  | –          | Dyke (pers. obs.)       | 70    | 90    | 48     | 207       |
| Taxon                              | Museum No. | Source                        | femur | tibia | tarsus | total leg |
|-----------------------------------|------------|-------------------------------|-------|-------|--------|-----------|
| Archaeopteryx lithographica       | –          | Dyke (pers. obs.)             | 48    | 71    | 41     | 160       |
| Struthiomimus altus               | UCMZ 1980.1| Gatesy (1991)                 | 760   | 687   | 321    | 1768      |
| Gallimimus bullatus               | GI 100/10  | Osmolska et al. (1972)        | 192   | 218   | 157    | 567       |
| Gallimimus bullatus               | GI 100/11  | Holtz (1994b)                 | 850   | 745   | 372    | 1967      |
| Gallimimus bullatus               | ZPAL MgD-I/1| Holtz (1994b)                | 278   | 560   | 313    | 1151      |
| Gallimimus bullatus               | ZPAL MgD-I/8| Holtz (1994b)                | 340   | 737   | 417    | 1494      |
| Dromiceiomiinus brevittus         | NMC 12068  | Gatesy (1991)                 | 340   | 602   | 374    | 1316      |
| Dromiceiomiinus brevittus         | NMC 12069  | Gatesy (1991)                 | 330   | 572   | 330    | 1232      |
| Dromiceiomiinus brevittus         | NMC 12228  | Holtz (1994b)                 | 600   | 630   | 440    | 1670      |
| Archaeornithomimus asiaticus      | AMNH 6565  | Gatesy (1991)                 | 285   | 495   | 430    | 1210      |
| Elaphrosaurus bambergi            | HMN Gr.S 38-44| Holtz (1994b)            | 700   | 700   | 445    | 1845      |
| Chirostenotes pergracilis         | TMP 79.30.1| Holtz (1994b)                 | 277   | 490   | 420    | 1187      |
| Saurothoides mongoliensis         | AMNH 6516  | Holtz (1994b)                 | 198   | 243   | 139    | 580       |
| Sinornithoides youngi             | IVPP V9612 | Russell and Dong (1993)      | 140   | 198   | 111    | 449       |
| Deinonychus antirrhopsus          | MCZ 4371   | Holtz (1994b)                 | 440   | 527   | 353    | 1320      |
| Deinonychus antirrhopsus          | YPM        | Holtz (1994b)                 | 308   | 527   | 455    | 1290      |
| Protarchaeopteryx robusta         | NGMC 2125  | Ji et al. (1998)              | 122   | 160   | 85     | 367       |
| Khaan mckennai                    |            | Norell (pers. obs.)           | 193   | 231   | 108    | 532       |
| Khaan mckennai                    |            | Norell (pers. obs.)           | 374   | 453   | 212    | 1039      |
| Ingenia yanshini                 | GI 100/30  | Norell (pers. obs.)           | 228   | 281   | 125    | 634       |
| Caudipteryx zoui                  | NGMC 97-9-A| Ji et al. (1998)              | 149   | 182   | 117    | 448       |
| Caudipteryx zoui                  | IVPP (uncatalogued) | Ji et al. (1998)     | 146   | 193   | 113    | 452       |
| Caudipteryx zoui                  | V 12344    | Ji et al. (1998)              | 149   | 196   | 124    | 469       |