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 cusorial 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, *Protarchaeopteryx 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 dissention 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 similarites 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 as 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.

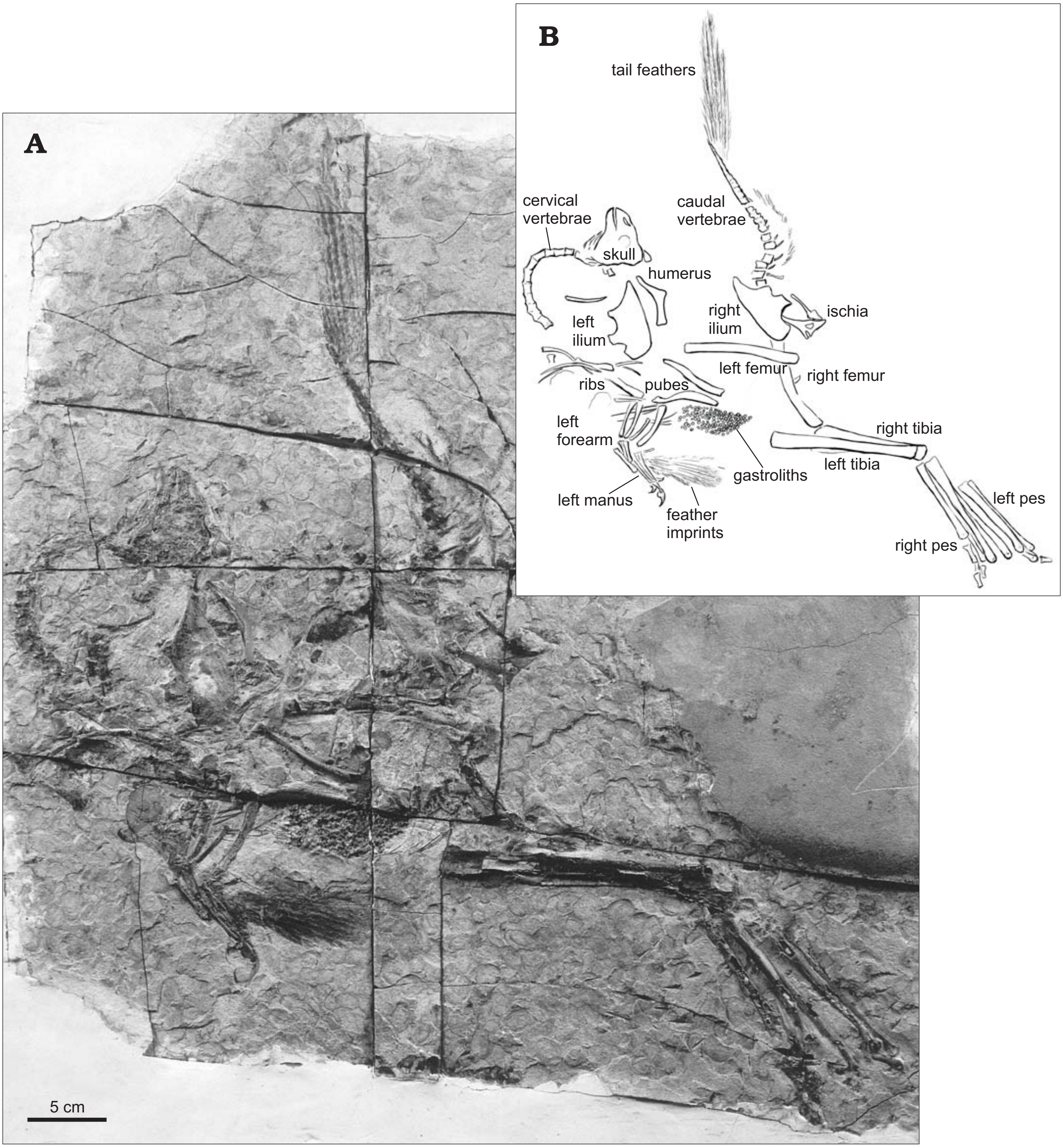

Fig. 1. **A**. Photograph of the holotype specimen of *Caudipteryx zoui* (NGMC 97-4-A) described by Ji et al. (1998). **B**. Sketch of NGMC 97-4-A in left lateral view. Not to scale. Measurement of trunk length in this specimen is impossible (but was given to an accuracy of 1 mm by Jones et al. 2000). 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; HMN, 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 nationale 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 Llilo, 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.

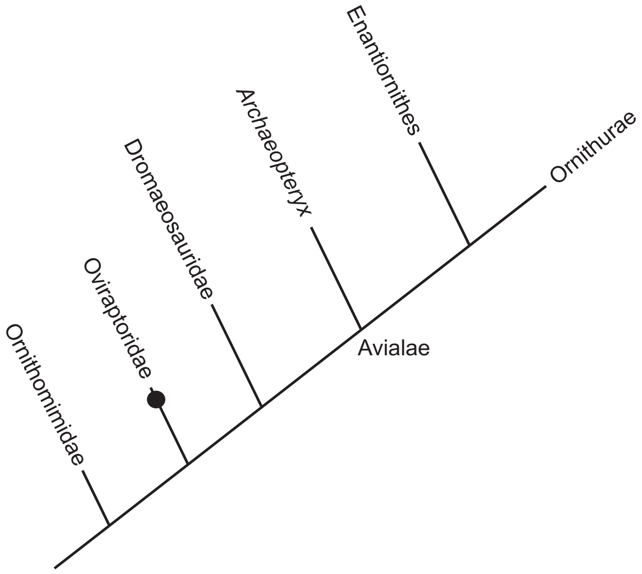

Fig. 2. Cladogram showing hypothesised placement of *Caudipteryx* (solid circle) and other oviraptorosaurs within Maniraptoriformes (compiled from many authors).

Limb proportions revisited

Assumptions of function and phylogeny.—Jones et al. (2000) presented the results of a morphometric analysis of non-avialan theropod and avialan hind limb proportions on the basis of a data set comprising 24 "cursorial" (their use of the term) extant birds (Neornithes) and 40 non-avialan 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-avialan 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-avialan 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-avialan 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-avialan 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-avialan 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-avialan 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-avialan 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 Bonde 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-avialan 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

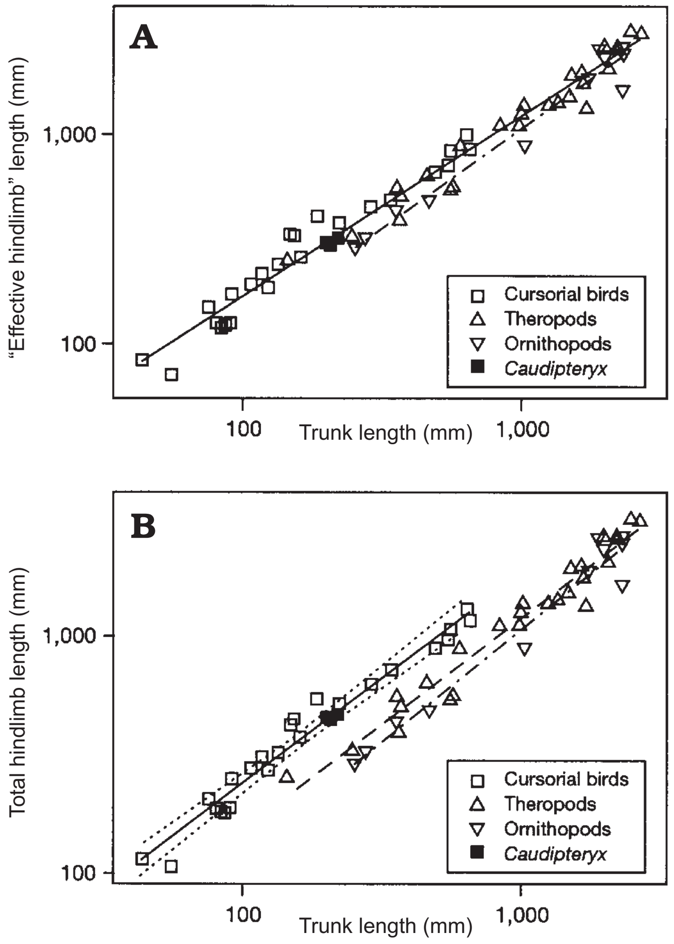

Fig. 3. The graphs presented by Jones et al. (2000). **A**. Total hind limb length against trunk length. **B**. Effective hind limb length against trunk length. Regression statistics based on our re-analysis are given in Table 1 (see Jones et al. 2000 for original statistics). This figure redrawn with permission from *Nature* (Jones et al. 2000), copyright (2000), Macmillan Magazines Ltd.

made the *a priori* assumption, contradictory to the available skeletal evidence uniting *Caudipteryx* with Oviraptoridae (see above), that this taxon is a member of Avialae (i.e., a bird). As a result, in their second graph for *Caudipteryx,* they included only measurements for the distal segments of the hind limb (Fig. 3). *Caudipteryx* plots out with the birds because only data from these taxa were included in the analysis.

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-avialan 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 have been 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-avialan 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 puportedly 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, *Eustreptospondylus*, 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.

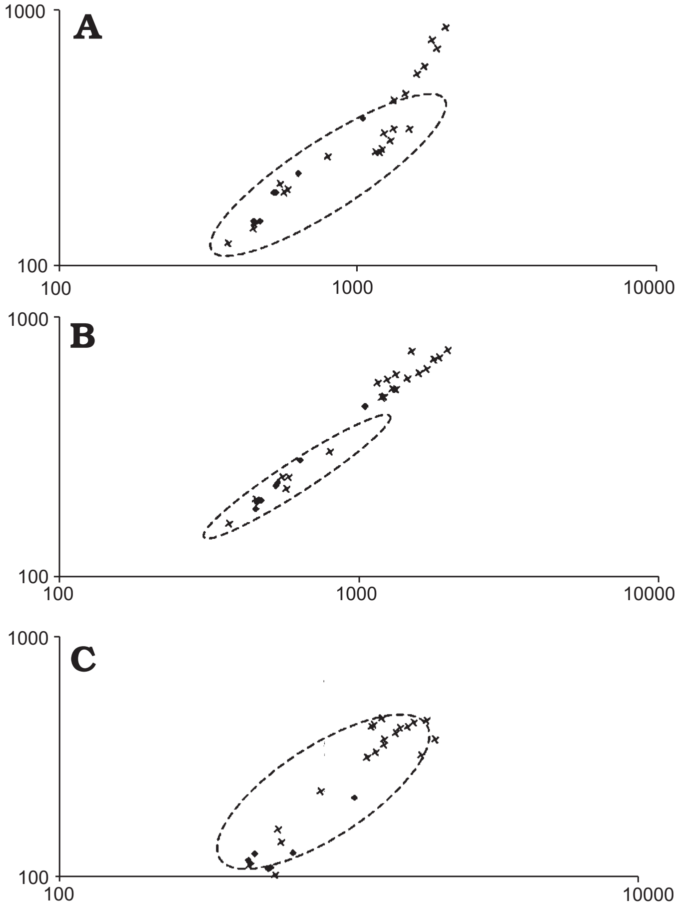

Fig. 4. Logarithmic plots of hind limb measurements (in mm). **A**. Femur length against total leg length. **B**. Tibia length (against total leg length. **C**. Tarsal length (mt. III) against total leg length. Regression statistics for principal data subdivisions are given in Table 2. Symbols: dotted lines, extent of neornithean bird distributions; crosses, non-avialan theropods; circles/diamonds, oviraptorosaurs (including *Caudipteryx*).

Table 1. Statistics from re-analysis of Jones et al. (2000).

	slope (P-value)	intercept (P-value)
Total hind limb: birds	0.99	0.00
Total hind limb: theropods	1.00	0.00
Total hind limb: ornithopods	1.00	0.67
Effective hind limb: birds	0.55	0.02
Effective hind limb: theropods	1.00	0.01
Effective hind limb: ornithopods	1.00	0.67

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-avialan 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, obtained either by direct measurement of specimens or from the relevant literature (e.g., Magnan 1922; Böker 1935; Gatesy 1991; Hazlehurst 1992; Holtz 1994b; Gatesy and Middleton, 1997; Dyke 2000; Dyke and Rayner 2002; Nudds et al. 2004).

The measurement data were subdivided according to 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-avialan 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-avialan 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., *Archaeornithomimus*, *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-avialan theropods other than oviraptors (including *Caudipteryx*). The non-avialan 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-avialan theropods and Avialae), this taxon cannot be definitively grouped within either subsample.

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

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

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-avialan theropod should be reevaluated in light of these results—in other words, the overwhelming number of osteological similarities evident between *Caudipteryx* and non-avialan 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-avialan 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-avialan theropod specimens measured by these workers are shown to be either too incomplete to allow for replication of their measurements, or simply 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-avialan theropod relatives, including taxa such as *Caudipteryx*.

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Appendix 1

List of taxa

As discussed in the text, because recent phylogenetic studies have demonstrated that non-avialan 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 preceeding 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).

Elaphrosaurus HMN Gr S 38-44.—Janensch (1920: 225) described only 10 dorsal and 7 cervical vertebrae for this specimen. In addition, a number of the vertebrae in this specimen have been substantially reconstructed (Peter Makovicky, personal communication 2002). Hence measurement of trunk length in this taxon is impossible.

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–?13 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 Psihoyas (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 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 enough preserved for all of the measurements reported by Jones et al. (2000) to be replicated.

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 from cervical 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.

Tyrannosaurus 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.

Yangchuanosaurus 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 IVPP (uncatalogued).—The correct museum number for this specimen is BPM 001 (Zhou et al. 2000). While this specimen is very well-preserved, the acual 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	–	Holtz (1994b)	278	490	432	1200
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 3701	Holtz (1994b)	360	392	280	1032
Struthio camelus	MCZ 828	Gatesy (1991)	230	410	398	1038
Struthio camelus	YPM 4347	Gatesy (1991)	266	494	437	1197
Rhea americana	–	Hazlehurst (1992)	219	345	324	889
Rhea americana	MCZ 1631	Gatesy (1991)	215	325	320	860
Rhea americana	MCZ 2083	Gatesy (1991)	210	318	325	853
Rhea americana	MCZ 6552	Gatesy (1991)	83	134	119	336
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	332	884
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 maxiumus	–	Holtz (1994b)	285	585	295	1165
Dinornis maxiumus	–	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 torosus	–	Hazlehurst (1992)	435	475	310	1220
Dinornis torosus	–	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	VIIIA	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 riverton	–	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 elephantopus	–	Holtz (1994b)	295	485	210	990
Pachyornis elephantopus	MCZ 9.1.14	Holtz (1994b)	440	520	370	1330
Pachyornis elephantopus	YPM 9884	Holtz (1994b)	376	511	308	1195
Pachyornis elephantopus	YPM 9888	Holtz (1994b)	280	472	210	962
Pachyornis mappini	–	Hazlehurst (1992)	206	366	156	728
Pachyornis mappini mangao	–	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
Rhynchotus rufescens	–	Hazlehurst (1992)	70	99	66	235
Rhynchotus rufescens	MCZ 1633	Gatesy (1991)	73	99	65	236
Rhynchotus rufescens	YPM acc. 2041	Holtz (1994b)	70	95	59	224
Nothura maculosa	–	Hazlehurst (1992)	46	62	38	146
Nothura maculosa	MCZ 1653	Gatesy (1991)	42	62	39	144
Eudromia elegans	MCZ 3064	Gatesy (1991)	56	77	47	180
Anhima cornuta	MCZ 1387	Gatesy (1991)	99	184	126	409
Anhima cornuta	MCZ 6993	Gatesy (1991)	92	166	113	371
Chauna chavaria	MCZ 307	Gatesy (1991)	95	177	126	398
Chauna torquata	–	Hazlehurst (1992)	96	177	123	396
Anseranas semipalmata	–	Hazlehurst (1992)	78	138	93	309
Dendrocygna autumnalis	–	Hazlehurst (1992)	53	99	60	212
Dendrocygna autumnalis	MCZ 273	Gatesy (1991)	50	87	56	193
Dendrocygna bicolor	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 erythropus	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
Alopochen 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	–	Livezey (1993)	67	113	56	236
Somateria mollissima	MCZ 7453	Gatesy (1991)	67	110	50	227
Aythya ferina	–	Hazlehurst (1992)	45	74	38	157
Aythya marila	–	Hazlehurst (1992)	46	76	39	161
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	–	Hazlehurst (1992)	50	86	48	185
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
Biziura 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
Penelopina 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
Lyrurus 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

Taxon	Museum No.	Source	femur	tibia	tarsus	total leg
Bonasa bonasia	–	Hazlehurst (1992)	52	68	36	156
Bonasa umbellus	MCZ 3809	Gatesy (1991)	27	36	22	86
Bonasa umbellus	MCZ 3999	Gatesy (1991)	56	75	41	173
Bonasa umbellus	MCZ 6061	Gatesy (1991)	53	76	42	171
Bonasa umbellus	MCZ 7371	Gatesy (1991)	57	78	42	176
Bonasa umbellus	MCZ 7666	Gatesy (1991)	53	76	42	170
Bonasa umbellus	MCZ 7935	Gatesy (1991)	53	75	41	169
Tympanuchus cupido	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 nigrogularis	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 nigrogularis	MCZ 5030	Gatesy (1991)	35	47	28	109
Colinus virginianus	–	Hazlehurst (1992)	40	54	31	126
Colinus virginianus	MCZ 7337	Gatesy (1991)	40	54	32	126
Colinus virginianus	MCZ 7347	Gatesy (1991)	38	52	31	121
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 rufa	–	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
Perdicula asiatica	–	Hazlehurst (1992)	30	38	25	93
Excalfactoria chinensis	–	Hazlehurst (1992)	27	31	19	77
Excalfactoria 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 2098	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
Dromiceiomimus brevitertius	NMC 12068	Gatesy (1991)	340	602	374	1316
Dromiceiomimus brevitertius	NMC 12069	Gatesy (1991)	330	572	330	1232
Dromiceiomimus brevitertius	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
Saurornithoides mongoliensis	AMNH 6516	Holtz (1994b)	198	243	139	580
Sinornithoides youngi	IVPP V9612	Russell and Dong (1993)	140	198	111	449
Deinonychus antirrhopus	MCZ 4371	Holtz (1994b)	440	527	353	1320
Deinonychus antirrhopus	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