Limb proportions and avian terrestrial locomotion

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Summary

Phylogenetic systematics unanimously concludes that birds (*Archaeopteryx* + crownclade Aves) are a subgroup of the theropod dinosaurs. The discovery of non-avian theropods from China with large pennaceous feathers offers additional support to this relationship and implies further that feathers cannot be used to define birds, as is traditionally advocated. A recent paper proposed that the feathered oviraptorosaur *Caudipteryx* was in fact a secondarily flightless bird. This was indicated by the anteriorly placed centre of gravity and the subsequent horizontal femoral posture and associated elongation of the lower leg compared to the trunk. A horizontal femoral posture was not present in non-avian theropods and is associated with profound proportional changes, particularly a thicker diameter to resist the increases in bending and torsional moments about the diaphysis. However, double graphic integration analysis of a more accurate model shows that the centre of gravity in *Caudipteryx* is situated no further anteriorly than in other non-avian theropods. The long limbs of *Caudipteryx* are not surprising as limb length is related to phylogeny and body size. Primitive non-avian theropods have proportionally shorter limbs at any given size than more advanced forms, and small species have proportionally longer limbs than large species, as in extant mammals. Other theropods are known with proportionally very long limbs. The femoral morphology of *Caudipteryx* is identical to those of other non-avian theropods, strongly arguing against avian limb kinematics. It is methodologically flawed to substitute functionally inferred characters for phylogenetic analyses.

Keywords: *Caudipteryx*, limb proportions, centre of gravity, femur proportions, phylogeny.

Zusammenfassung

Gliedmaßenproportionen und terrestrische Lokomotion der Vögel

Die fortgeschritteneren Raubdinosaurier haben eine große Menge apomorfer Merkmale mit den Vögeln (*Archaeopteryx* und crown-clade Aves) gemeinsam, und die meisten Analysen sind zu dem Schluss gekommen, dass die Vögel das Schwestertaxon der Dromaeosaurier sind. Vögel sind deshalb als eine Untergruppe der Dinosaurier, genauer der Raubdinosaurier, zu betrachten. Studien über die Biomechanik der Dinosaurier zeigten, dass alle Dinosaurier ihre Beine parasagittal bewegten, ähnlich wie es größere Säugetiere tun. Wie die rezenten Vögel liefen auch alle Raubdinosaurier nur auf den Hinterbeinen, aber neuere Studien haben gezeigt, dass es erhebliche Unterschiede zwischen primitiven

und avancierten Formen gegeben hat, und dass die letzteren viele Eigenschaften des loko-
motorischen Systems besaßen, die bisher als charakteristisch für die Vögel angesehen wur-
den. Deshalb ist es auch nicht überraschend, dass die avancierten Raubdinosaurier im
Vergleich zu primitiveren Formen biometrisch erheblich größere Ähnlichkeit mit Vögeln
zeigen.

Seit Mitte der 1990er Jahre sind im nordöstlichen China mehr und mehr Raubdinosaurier-
formen gefunden worden, von denen Weichstrukturen erhalten sind, unter anderem die
ersten Hautreste eines kleinen Raubdinosauriers. Die sieben bisher beschriebenen Arten
zeigen eindeutig, dass die landläufige Annahme, Raubdinosaurier besäßen eine be-
schuppte Haut, mindestens für die kleineren Formen ganz falsch ist. Diese Formen
besaßen eine Federtracht aus primitiven, haarähnlichen Filamenten, der die Körperbefie-
derung vieler kleiner fossiler Vögel (*Confuciusornis, Changchengornis*) ähnlich sieht, und
sowohl phylogenetische als morphologische Studien zeigen deutlich, dass es richtige
Federn sind. Das bedeutet, dass die Feder, die historisch als ausschließliches Merkmal der
Vögel angesehen wurde, für eine viel größere Gruppe charakteristisch ist und nicht nur
den Vögeln zukommt. Einige Wissenschaftler bezweifeln jedoch, dass es sich um richtige
Federn handelt und glauben nicht, dass Raubdinosaurier und Vögel eng miteinander ver-
wandt sind.

Einige Raubdinosaurier haben jedoch große, bis zu 18 cm lange „richtige" Konturfedern
an Armen und Schwanz. Phylogenetische Analysen haben eindeutig gezeigt, dass diese
Formen, *Protarchaeopteryx* und *Caudipteryx*, nicht echte Vögel sind, d. h. dass sie primi-
tiver als *Archaeopteryx*, weltweit anerkannt als der älteste und ursprünglichste Vogel, sind.
Trotzdem hat ein Artikel (Jones et al. 2000) neulich behauptet, dass bei *Caudipteryx* der
Schwerpunkt des Körpers weit vorn liege und dass die sehr langen Hintergliedmaßen die-
ses Tieres charakteristisch für Laufvögel seien. Alle rezenten Vögel, besonders die großen
Laufvögel, unterscheiden sich von allen bisher bekannten Raubdinosauriern nicht nur in
der Lage des Schwerpunktes, sondern auch in der subhorizontalen Haltung des Ober-
schenkelknochens (Femur). Wegen der viel größeren Torsions- und Biegungsmomente bei
horizontaler Stellung ist dieser Knochen bei Vögeln erheblich massiver als bei den übrigen
Raubdinosauriern. Obwohl Verwandtschaft nicht an ein paar funktionell interpretierten
Merkmalen erkannt werden kann, haben Jones et al. (2000) angedeutet, dass *Caudipteryx*
ein sekundär flugunfähiger Vogel sei, der fortgeschrittener ist als *Archaeopteryx*. Diese
Vermutung haben andere Autoren inzwischen ernst genommen, obwohl sie auf einer fal-
schen Methode basiert.

Das Modell des *Caudipteryx* von Jones et al. (2000) war falsch proportioniert, besonders
wegen des viel zu dicken Vorderkörpers, der den Fossilien nicht ähnlich sieht. Ein neues
dreidimensionales Modell nach einem fast kompletten Skelett von *Caudipteryx* und die
Proportionen von sieben anderen *Caudipteryx*-Exemplaren zeigen, dass der Schwerpunkt
nicht weiter vorn im Körper liegt als bei anderen Raubdinosauriern. Die Hintergliedmaßen
von *Caudipteryx* sind sehr lang im Vergleich zum Körper, ein oberflächlich vogelähnli-
ches Merkmal, aber Hintergliedmaßenproportionen sind mit der allgemeinen Körpergröße
und der phylogenetischen Position korreliert. Kleinere Raubdinosaurier haben erheblich
längere Hintergliedmaßen im Verhältnis zur Körperlänge als große Formen, und avancier-
tere Formen haben bei jeder Körpergröße längere Hintergliedmaßen als primitive Formen
vergleichbarer Größe. *Caudipteryx* ist klein und avanciert und hat deshalb sehr lange Hin-
tergliedmaßen, was auch bei anderen Formen der Fall ist, sogar bei einigen Ornithischiern.
Auch die Gliedmaßenproportionen (Femur/Tibia und Tibia/Metatarsus) sind nicht ver-

schieden von anderen kleinen avancierten Raubdinosauriern, aber statistisch signifikant verschieden von denen der Laufvögel. Das Femur von *Caudipteryx* hat nicht die Proportionen eines Laufvogels, was sehr darauf hindeutet, dass *Caudipteryx* wie andere Raubdinosaurier gelaufen ist, nämlich mit stark vertikal gehaltenem Femur; die apomorfe horizontale Orientierung des Femur der Vögel lag nicht vor.

Introduction

John Ostrom's now classic works (e. g. Ostrom 1973, 1975a, 1975b, 1976) demonstrated the presence of a plethora of advanced characters common to the urvogel *Archaeopteryx* and advanced theropod dinosaurs, most notably the dromaeosaurids. Subsequently, with the advance of cladistic methods, all phylogenetic analyses have unanimously concluded that extant birds are a subgroup of the theropod dinosaurs, most often the sister taxon to the Dromaeosauridae (e. g. Gauthier 1986, Chiappe 1995, Dingus & Rowe 1998, Holtz 1994a, 1998, 2000, Makovicky & Sues 1998, Padian & Chiappe 1998, Sereno 1999). A minority of scientists, however, continue to advocate that birds are unrelated to theropod dinosaurs (e. g. Tarsitano & Hecht 1980, Feduccia 1985, 1996, Martin 1991, Feduccia & Wild 1993, Feduccia & Martin 1996, Geist & Feduccia 2000, Ruben & Jones 2000, Martin & Czerkas 2000; see also Gibbons (1998)).

Among the most exciting forms found in recent years are the feathered, non-avian coelurosaurs from Liaoning, north-eastern China, in Early Cretaceous beds (Smith et al. 1998, Swisher et al. 1999). Forms so far described include primitive coelurosaurs such as the compsognathid *Sinosauropteryx* (Chen et al. 1998), and advanced forms such as *Protarchaeopteryx* and *Caudipteryx* (Ji et al. 1998), the therizinosaurid *Beipiaosaurus* (Xu et al. 1999a), the dromaeosaurids *Sinornithosaurus* (Xu et al. 1999b) and *Microraptor* (Xu et al. 2000), and an, as yet, unnamed dromaeosaurid, which may in fact be a *Sinornithosaurus* (Ji et al. 2001). Some have contested the feathery nature of the filamentous structures found on the bodies of these theropods, but the advanced

forms *Protarchaeopteryx* and *Caudipteryx* do, however, indisputably display pennaceous and very large (up to 18 cm) feathers on the arms and tails, which implies that feathers do not define birds, as is traditionally advocated (e. g. van Tyne & Berger 1961, Romer 1966, Ostrom 1985, Spearman & Hardy 1985, Juana 1992, Brush 1996, Feduccia 1985, 1996, Feduccia & Martin 1996, Carroll 1997). With the exception of *Microraptor* and the most recently described, unnamed dromaeosaurid, the other advanced forms are fragmentary, and display only parts of the plumage, and no large, pennaceous feathers.

Phylogenetic systematics unanimously conclude that *Caudipteryx* was a primarily flightless, pre-*Archaeopteryx* (i. e. non-avian) theropod (Currie et al. 1998, Ji et al. 1998; see also Maderson et al. 2000, p. 697), and all recent studies show it to be an oviraptorosaur (Sereno 1999, Currie 2000, Holtz 2000, Sumida & Brochu 2000), i. e. a side-branch to true birds, as exemplified by *Archaeopteryx* and Neornithes. Placing it above *Archaeopteryx* in the phylogenetic tree would necessitate a great number of character reversals (Holtz 1998). Biomechanical studies have demonstrated that the limbs of all dinosaurs operated in a near parasagittal manner, as in extant birds and most larger mammals (e. g. Gatesy 1991, 1995, Carrano 1998, Christiansen 1997, 1998, 1999a). Many characters in the anatomy of non-avian theropods suggest that they were cursorial animals capable of rapid locomotion, but with substantial movement of the much more vertically oriented femur, with femoral kinematics and thus a loading pattern more similar to that of fast running mammals than to avian theropods (Gatesy 1991, 1995, Carrano 1998, 1999, Christiansen 1998, 1999a, Carra-

no & Biewener 1999, Hutchinson & Gatesy 2000).

Unlike non-avian theropods and parasagittal mammals, avian theropods are, however, characteristic in having an anteriorly placed centre of gravity, primarily owing to the near absence of a tail, a more anteroposteriorly constricted torso and proportionally more mass in the anterior chest area, and a subsequent near horizontal femur that is necessary to position the feet under the centre of gravity. Slower forms of terrestrial locomotion consist primarily of rotation about the knee, whereas the femur is increasingly retracted during faster forms of locomotion (Clark & Alexander 1976, Alexander et al. 1979, Jacobson & Holiday 1982, Gatesy 1990, 1991, 1999, Gatesy & Biewener 1991, Carrano 1998, Carrano & Biewener 1999).

Such a limb posture has not been verified in any non-avian theropod (but see Carrano & Biewener 1999), and is associated with proportional changes of the limbs, most notably a considerably shorter, thicker femur compared to the tibia, to resist the great increase in bending and torsional moments about the diaphysis (Alexander et al. 1979, Alexander 1983, Gatesy 1991, Carrano 1998, Christiansen 1998, 1999a, 1999b, Carrano & Biewener 1999). The femur thus contributes less to effective limb length than in parasagittal mammals and non-avian theropods and, thus, non-flying cursorial ground birds also have proportionally longer lower legs to maintain their capacity for rapid locomotion (Alexander et al. 1979, Farlow et al. 2000, Jones et al. 2000). It appears, however, that ground birds take shorter strides for any given foot length than did non-avian theropods (Farlow et al. 2000).

Regardless of the phylogenetic analyses, a recent paper (Jones et al. 2000) proposed that *Caudipteryx* had an anteriorly placed centre of gravity, and the very long limbs in relation to trunk length allegedly characteristic of fast running birds. The paper proposed that the systematic position of *Caudipteryx* should be

re-evaluated in light of these results, and that *Caudipteryx* could be a secondarily flightless bird more closely related to crowngroup Aves than is *Archaeopteryx*. Previously, Elzanowski (1999) had made the suggestion that on the basis of four cranial characters all oviraptorosaur are closer to birds, although his phylogenetic analysis failed to confirm this. This is, however, a different suggestion from the one made by Jones et al. (2000) as they do not address the issue of whether or not *Caudipteryx* is an oviraptorosaur, but only its position relative to *Archaeopteryx*. This issue is seemingly trivial since phylogeny is simply not reconstructed on the basis of a few functionally inferred characters but on that of phylogenetic analyses, and these unanimously conclude that *Caudipteryx* was not a bird, as traditionally defined (see Padian et al. 1999). We decided, however, to expand on the arguments pu forward by Jones et al. (2000), as following traditional methods for phylogenetic reconstruction would simply dismiss the allegedly avian characters in *Caudipteryx* as convergences.

Advances in our understanding of dinosaur locomotion in recent years have made it clear that most of the advanced characters of the hind limbs and pelvis formerly regarded as characteristic of birds probably evolved in a gradual fashion. In more advanced coelurosaurs the number of caudal vertebrae become reduced, the transition point in the tail moves forward and the fourth trochanter on the femur decreases dramatically in size (Gatesy 1990, 1991, 1995, Gatesy & Dial 1996, Hutchinson & Gatesy 1999). This indicates a size reduction of the tail-based caudifemoralis longus muscles. It is not true, as claimed by Jones et al. (2000), that absence of the fourth trochanter is characteristic of birds (another of the supposedly avian characteristics of *Caudipteryx*), as it is greatly reduced or even absent in many advanced non-avian theropods (Gatesy 1990, 1991, Holtz, 1998), among others dromaeosaurids, troodontids and oviraptorosaurs. Several features of theropod limb function appear to have differed in plesiomor-
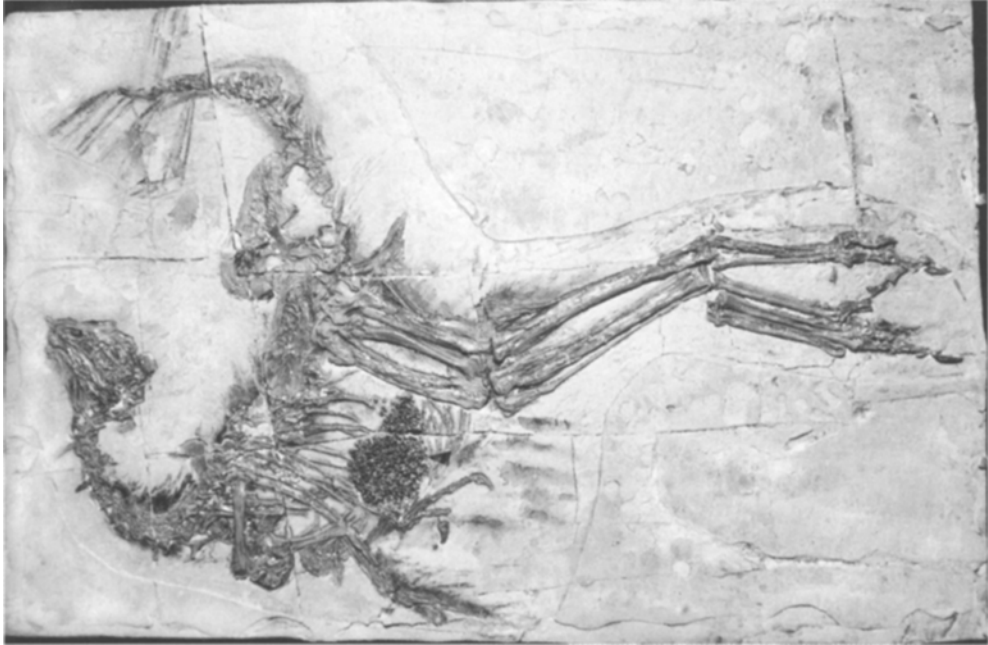
Fig. 1. Cast of *Caudipteryx* specimen BPM 0001 used for construction of the model. The cast is housed at the Jura Museum in Eichstätt.
Abb. 1. Abguss von *Caudipteryx* BPM 0001, der zur Herstellung des Modells benutzt wurde. Der Abguss befindet sich im Jura Museum in Eichstätt.

phic versus advanced taxa, for instance the function of several of the muscles of the pelvis and thigh, the marked reduction of the tail-based femoral retractors and more reliance on rotation about the knee in advanced taxa, as indicated by the morphology of the pelvis, tail and fourth trochanter of the femur (e. g. Gatesy 1990, 1991, 1995, Hutchinson & Gatesy 2000, Hutchinson 2001a, 2001b).

Thus, advanced non-avian theropods had evolved a set of advanced (i. e. bird-like) characters relating to locomotion that were not present in plesiomorphic forms, and in advanced forms such as oviraptorosaurs, troodonts or dromaeosaurs many of the modifications towards an avian style of walking had already taken place (Hutchinson & Gatesy 2000, Hutchinson 2001a, 2001b). The more avian-style functional morphology is also reflected in their limb proportions as compared to those of more plesiomorphic theropods (Fig. 2, below; see also Gatesy & Middleton 1997, p. 311–312; Christiansen 1998, p 248). This of course implies that the locomotory system of advanced non-avian theropods will in many respects bear substantial resemblance to those of birds, but differences are evident, particularly the near absence of the tail in birds, a more barrel-shaped chest, proportionally more anterior chest mass, a cranially situated centre of gravity and a horizontally oriented femur. These characters appear not to have been present in any non-avian theropod. However, whereas this is characteristic of all extant birds, it may not have been true of the earliest birds (Gatesy 1990, 1991, Carrano 1998; but see below). But since Jones et al. (2000) claim that *Caudipteryx* was built like a ground bird these characters would certainly have to be present in this taxon.
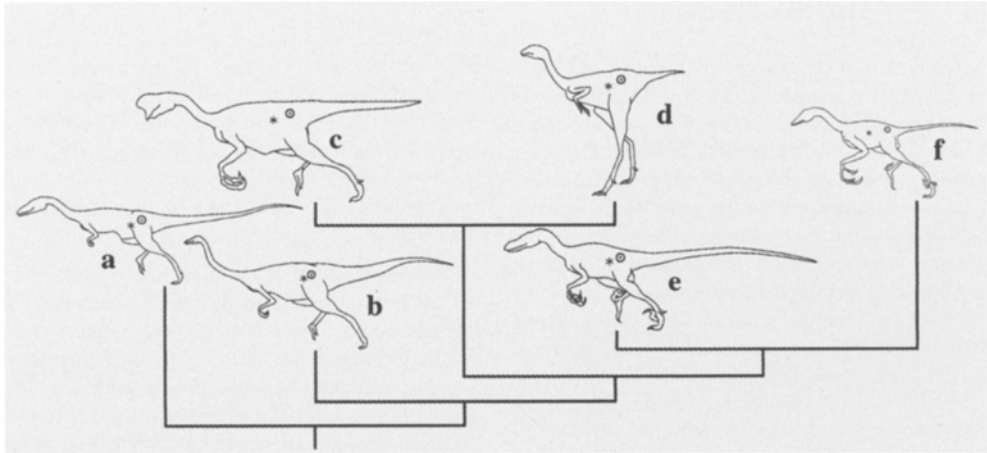
Fig. 2. The centre of rotation of the hind limb (circle) and the centre of gravity (star) in six theropod species, spanning a wide phylogenetic spectrum. a, *Coelophysis*; b, *Gallimimus*; c, *Oviraptor*; d, *Caudipteryx*; e, *Deinonychus*; f, *Archaeopteryx*. The centre of gravity in *Archaeopteryx* is virtually as far forwards as in modern birds, but its exact position depends on the position of the very long arms which are held rather far forwards in this reconstruction. If the wing was folded along the back, which was probably a more natural posture, the centre of gravity would move posteriorly. The specimen used of *Caudipteryx* is one of the large specimens and it measures 841 mm in total length with a total volume of 7583.4 cm³ and a surface area of 2175.8 cm².

Abb. 2. Rotationszentrum der Hinterextremität (Kreis) und Schwerpunkt (Stern) in sechs Theropoden aus einem weiten phylogenetischen Spektrum: a, *Coelophysis*; b, *Gallimimus*; c, *Oviraptor*; d, *Caudipteryx*; e, *Deinonychus*; f, *Archaeopteryx*. Der Schwerpunkt bei *Archaeopteryx* liegt sehr weit vorn wie bei modernen Vögeln, doch ist seine Position stark von der Position der sehr langen Arme bestimmt, die im Modell weit nach vorn gehalten sind. Wird der Flügel entlang des Rückens gefaltet, was eher der natürlichen Haltung entsprechen dürfte, so bewegt sich der Schwerpunkt nach hinten. Das verwendete *Caudipteryx* Exemplar ist eines der größten mit 841 mm Körperlänge, einem Volumen von 7583,4 cm³ und einer Oberfläche von 2175.8 cm².

Gatesy (1990, 1991, 1995), Carrano (1998) and Hutchinson (2001a, 2001b), among others, advocated analysing locomotor patterns in a phylogenetic context, which is undoubtedly the correct methodology. However, these observations are irrelevant to the present problem, as several of the authors of the Jones et al. (2000) paper also continue to advocate that birds are unrelated to theropods (Ruben & Jones 2000, Ruben 2001; see also Stokstad 2000), and that the protofeathers found with theropods dinosaurs have nothing to do with feathers (Geist et al. 1997, Ruben & Jones 2000), despite their striking resemblance to feathers (Xu et al. 2001). By this token all similarity of characters between theropods and birds must be due to convergence. Accordingly, what needs to be established is whether or not *Caudipteryx* was built like an undisputed ground bird, since this is what was advocated by Jones et al. (2000) and Ruben & Jones (2000). Despite being based on a flawed methodology, the suggestion that *Caudipteryx* might be a flightless bird, and the implications this may have for feather origins, has been taken seriously and is included in a number of recent papers (e. g. Geist & Feduccia 2000, Martin & Czerkas 2000, Ruben & Jones 2000, Zhang & Zhou 2000). In this paper we re-evaluate the position of the centre of gravity in *Caudipteryx*, and show that its limb proportions argue convincingly against avian limb kinematics.

Materials and methods

Jones et al. (2000) argued that *Caudipteryx* had a centre of gravity markedly further forwards than in other non-avian theropods, and that it walked like a bird, which could indicate that it was in fact a secondarily flightless bird, closer to crownclade Aves than is *Archaeopteryx*. In the paper by Jones et al. (2000) it was not mentioned how the model of *Caudipteryx* was constructed. The model was, however, not based on measurements of the fossils but rather on published colour reconstructions of the animal and a too portly and inaccurate three-dimensional model (Henderson, pers. comm 2001), which was then tested using computer software for computation of mass and centre of mass (see Henderson 1999).

For this paper, volumes, centres of gravity (and surface areas) were computed using graphic double integration (see Henderson 1999, Hulburt 1999). We used the illustrations in Paul (1988) as a basis, and checked all illustrations for accuracy against morphometric data collected directly on mounted skeletons by the senior author (see Christiansen 1998, 1999a). Slight alterations were necessary in five cases. Lung volume was set as 10 % of body volume, and placed anteriorly in the body. This is a conservative estimate, since it is now well established that most non-avian theropods had avian-like lungs with air diverticulae inside the bones, and presumably inside the body cavity as well (for review see Christiansen & Bonde 2000). Detailed three-dimensional skeletal restorations (Paul 1988) demonstrate that more plesiomorphic theropods with long tails had streamlined and narrow bodies in dorsal and lateral profile. This is consistent with measurements taken by the senior author (e. g. Christiansen 1998).

The fossils of *Caudipteryx* are generally well preserved and the bones are often three-dimensional (P. J. Currie, pers. comm. 2000), but the fossils have not been prepared out, so that they are in effect more two-dimensional than three-dimensional. Thus, in contrast to the other included non-avian theropods, a profile in dorsal view cannot be reconstructed directly from the fossils. We based the illustration in lateral profile on morphometric data collected from a cast of specimen BPM (Beipiao Province Museum, China) 0001, housed at the Jura-Museum in Eichstätt, Southern Germany (Fig 1). This specimen is nearly complete and articulated, and appears to be one of the largest specimens of *Caudipteryx*. We checked these data against morphometric data taken from all available *Caudipteryx* specimens, kindly made available to us by Dr. Philip J. Currie of the Royal Tyrrell Museum in Canada, to verify that specimen BPM 0001 was not an outlier. For comparative purposes we also examined a cast of *Sinosauropteryx*, also housed in the Jura-Museum in Eichstätt.

The lateral width of the chest has to be assessed by comparison with other theropods, which was not pointed out by Jones et al. (2000). Relative chest width (to body size) is, however, rather conservative in most theropods (Christiansen unpubl.; see also Paul 1988), so this should introduce little error in the final estimate. Hip width could, however, be reconstructed from the width between the pubic rami, and the hip region appears to have been narrower than in the closely related *Oviraptor*. Data for the hind limb length vs. trunk length ratios in non-avian theropods were all based on measurements taken by the senior author, except the additional ratios for *Caudipteryx*, which were based on data made available by Dr. Philip J. Currie.

Hind limb element (femur, tibiotarsus, tarsometatarsus) lengths were measured in 341 specimens, representing 178 species from 12 orders and 36 families of extant birds. All are housed at the Zoological Museum in Copenhagen. Additionally, 15 specimens (9 species) of moas, 3 specimens (3 species) of phorusrhacoids and the gastornithid *Diatryma* were included. The non-avian theropod sample consisted of 41 specimens, representing 24 species. All had been measured by the senior author (Christiansen 1998, 1999a). For femoral lengths/circumferences a total of 184 species were used for the total sample of birds, whereas the subsample of large, flightless ground birds (extant ratites, moas, phorusrhacoids and *Diatryma*) consisted of 19 species. Additionally, a sample of hind limb elements from non-avian theropods was used, which was taken from Christiansen (1999a), and consisted of 34 species, spanning almost the entire size range of known adults. Femoral circumferences of *Caudipteryx* and *Protarchaeopteryx* are not directly available, because the fossils are still partially encased in rock. Instead we used femoral shaft diameter, and assumed that the shaft was circular. This is reasonable as many smaller theropods have near circular femoral shafts. Assuming circular femoral shafts in *Caudipteryx* and *Protarchaeopteryx* should slightly

overestimate the actual circumference. *Protarchaeopteryx* and *Caudipteryx* were not included in computation of regression equations, but were used as individual comparisons to equations for non-avian and avian theropods, respectively.

Results and discussion

The centre of gravity in *Caudipteryx* was probably not as anteriorly placed as concluded by Jones et al. (2000). The short tail of *Caudipteryx* (Fig. 1, Fig. 2) could indicate that the centre of gravity should have moved far anteriorly compared to more plesiomorphic taxa, but in certain advanced theropod groups, for instance some of the other oviraptorosaurs (in this case *Oviraptor*), the hips are proportionally very wide. Hip width in *Caudipteryx* appears to have been less than in the closely related *Oviraptor* (width between pubic rami is 58.9 mm). The bodies of most primitive theropods are usually more elongate, slender and rectangular than in advanced forms (Fig 2, or see Paul 1988). Characteristic of many advanced non-avian theropods with proportionally reduced tails, the body becomes triangular in lateral view, thus shifting trunk mass posteriorly, and maintaining the centre of gravity in approximately the same location as in more plesiomorphic taxa with proportionally longer tails (Fig. 2). This "triangular" body was clearly present in *Caudipteryx* also, and in this respect it appears more similar to ornithomimids than to *Oviraptor*. The reconstruction of *Caudipteryx* by Martin & Czerkas (2000) is clearly erroneous. Apart from a near vertically oriented dorsal vertebral column and a too shallow ribcage, particularly posteriorly, *Caudipteryx* is restored with an opisthopubic pelvis, which it did not have. Additionally, the pubis is much too short, only a little in excess of 50 % of femur length. In the present specimen the pubis measures 117.6 mm and the femur 146.1 mm (se Fig. 1). Other specimens of *Caudipteryx* are also proportioned like this (data courtesy of Dr. Philip J. Currie).

The present reconstruction differs quite a lot from that of Jones et al. (2000), as they used a more barrel-shaped or rectangular lateral profile, which our data suggest is incorrect. The rather long pubes of *Caudipteryx* would imply a very deep anterior chest region if the lateral body profile were to have been more rectangular, as it is in many extant birds. There is no evidence of this and the fossils actually display a markedly tapered anterior chest region in lateral view, which is particularly easy to verify in the present, nearly complete and articulated specimen (see also Ji et al. [1998] p. 759), as in most other advanced non-avian theropods. Unlike the result proposed in Jones et al. (2000) this implies that the centre of gravity does not move very far anteriorly and it is nearly identical to the position in most other non-avian theropods (Fig. 2).

It has recently been confirmed that another oviraptorid, *Nomingia*, had a pygostyle, and thus also a short tail (Barsbold et al. 2000a, 2000b), but that is not in itself indicative of an anteriorly placed centre of gravity. *Oviraptor* (Fig. 2) has no pygostyle, but its tail is rather short. All non-avian theropods have centres of gravity located just anteriorly to the hips (Fig. 2), and in more plesiomorphic taxa the pelvis is narrow, and the long tail counterbalances the body. In more advanced taxa the body is usually more triangular, which shifts the trunk mass posteriorly. Regardless of the size of the tail, non-avian theropods from a wide phylogenetic spectrum all appear to have had centres of gravity close to the hips. The position of the centre of gravity in *Caudipteryx* is very similar to that of *Oviraptor* and the other non-avian theropods (Fig. 2). Proportional reduction in tail volume, thus, does not appear to be accompanied by a forward migration of the centre of gravity in non-avian theropods (contra Farlow et al. 2000), owing to proportional changes in body outline. And even advanced theropods still had a much larger tail than neornithine birds.

In the present reconstruction of *Archaeopteryx* (Fig. 2) the centre of gravity is located considerably further anteriorly in the body

than in the non-avian theropods, mainly owing to the long forelimbs being extended. A centre of gravity in this position would imply a more horizontal femoral posture, but it is not certain if this was present in the most basal birds (Gatesy 1990, 1991, Carrano 1998). The normal position of the forelimb would, however, be very different, and with the wing folded up the centre of gravity would move considerably posteriorly, although probably not to a position similar to that in the non-avian theropods.

Another of the characters of *Caudipteryx* advocated by Jones et al. (2000) as bird-like was that it possessed very long hind limbs in realetion to body length (length of hind limb/length first dorsal to anterior rim of acetabulum: 2.13–2.26). Birds apparently have higher hind limb/trunk ratios (1.78–2.95) than non-avian theropods (0.79–1.55; values taken from their data set), owing mainly to their more compact bodies. Our data from five specimens indicate that *Caudipteryx* has limb/trunk ratios of 2–2.13, slightly lower than suggested by Jones et al. (2000). Whereas these are among the highest ratios so far verified from a non-avian dinosaur, they are, however, not as unusual as Jones et al. (2000) propose. A number of other smaller, long-limbed bipedal dinosaurs have hind leg/trunk ratios that fall very close to or within the avian range. Limb/trunk ratios are clearly influenced by both size and phylogeny position, in the sense that smaller theropods on average have proportionally longer limbs than large forms, which is also evident from the allometry patterns of their long bones (Christiansen 1999a). Evolving proportionally shorter limbs with size seems to be a way of mechanically adapting to faster locomotion at large body sizes, and it is also found in parasagittal, terrestrial mammals (Christiansen 1998, 1999b, 2002). Additionally, more plesiomorphic theropod taxa have proportionally shorter limbs than more advanced taxa of comparable size. This is to be expected if enhanced locomotor performance was a driving force in theropod evolution, as appears to have been the case (Christiansen 1998, Holtz 1994b).

A large plesiomorphic taxon such as *Allosaurus* has a hind limb/trunk ratio of 1.18, whereas the values in the advanced, comparably sized *Gorgosaurus* are 1.35–1.44. Small plesiomorphic theropods have lower limb/trunk ratios (e. g. *Coelophysis* 1.05; *Herrerasaurus* 1.30; *Compsognathus* 1.35; *Sinosauropteryx* 1.38, not 1.72 as indicated in the data from Jones et al. [2000]) than comparably sized advanced taxa (e. g. *Deinonychus* 1.54; *Oviraptor* 1.50; *Ornithomimus* 1.82; *Dromiceiomimus* (1.83–1.86); the latter are within the avian range). However, with the exception of the plesiomorphic *Compsognathus* and *Sinosauropteryx* these advanced forms are all considerably larger than *Caudipteryx*, a fact which in itself would indicate that its limb/trunk ratio should be higher. Unfortunately most smaller theropods are not complete enough to allow computation of a reliable leg/trunk ratio, particularly many of the advanced, Late Cretaceous taxa, which appear to have been very long-limbed (e. g. caenagnathids, troodontids, some dromaeosaurids). Some bipedal ornithischians also have very long limbs in relation to the trunk, e. g. the iguanodont *Gasparinisaura* (1.73), which is much higher than in larger forms.

The troodontid *Sinornithoides* is one of the few small, advanced taxa which are complete enough for a full reconstruction (Russell & Dong 1993). It has an estimated hind limb/trunk ratio of nearly 2.2, as high as that of *Caudipteryx*. Jones et al. (2000) dismissed this taxon as immature, as it was "very small and possessed a cartilaginous sternum". In fact they are nearly the same size, but *Sinornithoides* is longer than *Caudipteryx*, owing in part to the longer tail. Although it is possible, it cannot be verified that the sternum was cartilaginous, as it simply was not recovered (Russell & Dong 1993). Skeletal ossification suggests that it was a subadult, approaching maturity (Russell & Dong 1993), and the absence of the sternum is merely missing data, as with the clavicles from many theropods. Troodontids appear to have been very gracile,
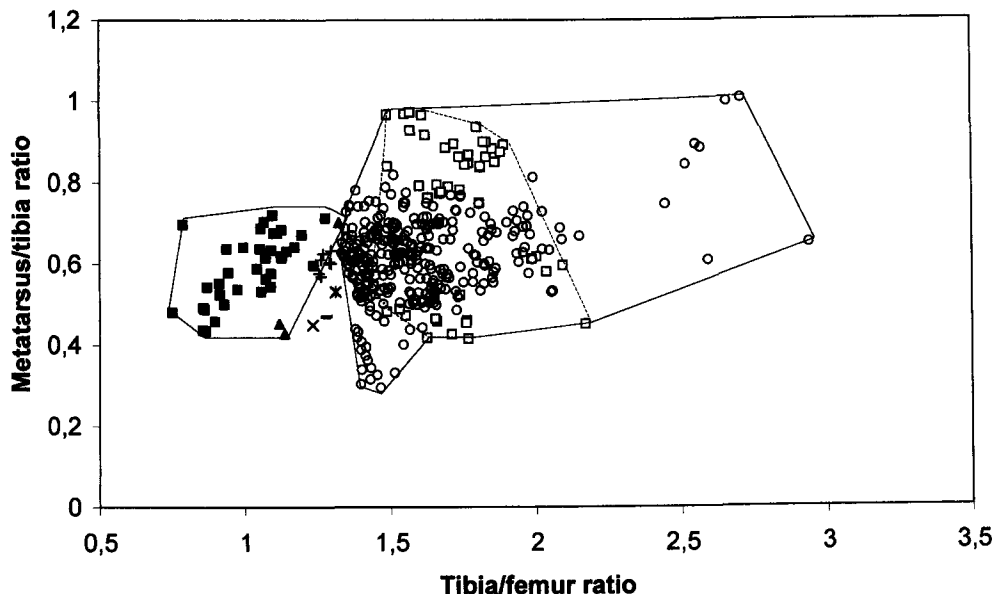
Fig. 3. Hind limb proportions in avian and non-avian theropods. The tibia/femur ratio of non-avian theropods (n = 41; x̄ = 1.044; S = 0.140) is highly significantly lower than in all birds (n = 362; x̄ = 1.621; S = 0.240; $t_{0.05[401]}$ = 22.842; p << 0.001) and ground birds (n = 54; x̄ = 1.714; S = 0.164; $t_{0.05[93]}$ = 21.423; p << 0.001). Symbols: ■, non-avian theropods; ▲, dromaeosaurids; +, *Caudipteryx*; x, *Ingenia*; —, *Oviraptor;* *, *Protarchaeopteryx*; ○, volant birds; □, flightless ground birds. The birds at the extreme right are mainly water dwellers (e. g. *Arctophilornis, Jacana*). Dashed area includes extant and extinct, secondarily flightless ground birds.

Abb. 3. Proportionen der Hinterextremität bei Vögeln und Raubdinosauriern. Das Tibia/Femur-Verhältnis der Raubdinosaurier (n = 41; x̄ = 1.044; S = 0.140) ist gesichert kleiner als das aller Vögel (n = 362; x̄ = 1.621; S = 0.240; $t_{0.05[401]}$ = 22.842; p << 0.001) oder von Bodenvögeln (n = 54; x̄ = 1.714; S = 0.164; $t_{0.05[93]}$ = 21.423; p << 0.001). Symbole: ■, Raubdinosaurier; ▲, Dromaeosaurier; +, *Caudipteryx*; x, *Ingenia*; —, *Oviraptor;* *, *Protarchaeopteryx*; ○, flugfähige Vögel; □, flugunfähige Laufvögel. Die Arten ganz rechts sind vornehmlich Wasservögel (z. B. *Arctophilornis, Jacana*). Die gepunktete Fläche beinhaltet rezente und ausgestorbene Arten von sekundär flugunfähigen Laufvögeln.

and the high limb/trunk ratio of *Sinornithoides* is to be expected from its smaller adult size compared to the larger North American *Troodon*, as reconstructions of this more fragmentary animal indicate a limb/trunk ratio of 1.8, perhaps more (pers. obs.). The effects of size are best seen in the recently described, very small but nonetheless adult dromaeosaur *Microraptor* (Xu et al. 2000), which appears to have had a limb/trunk ratio of nearly 3, which is at the upper extreme of the range of avian theropods. Thus, Jones et al. (2000) have basicly shown that *Caudipteryx* has very long

limbs, as could be expected from a small, advanced, cursorial non-avian theropod. Rather than indicating avian ancestry, this is probably better explained as indicative of the capability for fast running (e. g. Carrano 1998, Christiansen 1998, 1999a). In order for it mechanically to have been able to walk like a bird, it would have to have had the thick and apomorphically short (compared to the tibia) femur characteristic of birds, particularly larger ground birds.

Birds have proportionally longer tibiotarsi and tarsometatarsi compared to femora than non-avian theropods, in order to achieve long
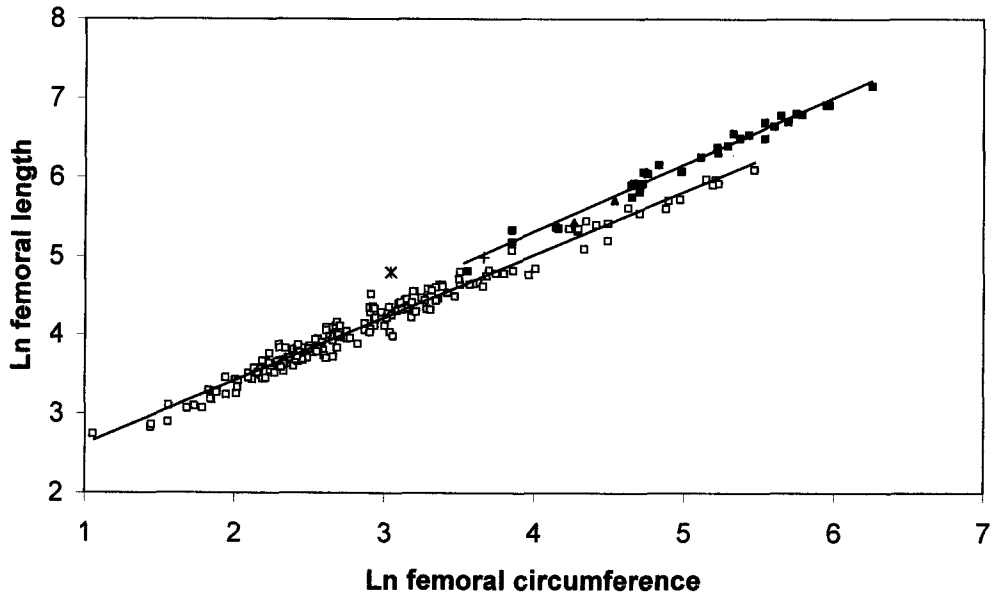
Fig. 4. Femur length and least circumference of shaft in non-avian and avian theropods. Regression lines were fitted to the data by means of Model II (RMA) analysis. Y is femur least circumference and X is femur length, both in mm. Regression line for non-avian theropods (n = 34; $\ln Y = 1.801 \pm 0.195 + 0.870 \pm 0.039 \ln X$; r = 0.992) is statistically different ($t_{214} = 2.526$; $0.02 > p > 0.01$) from regression line for all birds (n = 184; $\ln Y = 1.765 \pm 0.056 + 0.816 \pm 0.019 \ln X$; r = 0.988), and also ($t_{49} = 3.112$; p <0.001) from regression line for ground birds (not shown) (n = 19; $\ln Y = 2.241 \pm 0.534 + 0.709 \pm 0.113 \ln X$; r = 0.950). Symbols: ■, non-avian theropods; ▲, *Oviraptor* and *Ingenia*; +, *Caudipteryx;* *, *Protarchaeopteryx*; □, birds.

Abb. 4. Zusammenhang zwischen Länge und Minimalumfang des Femurs bei verschiedenen Therapoden (RMA, Modell II, mit Y = Femurlänge und X = Femurumfang). Die Regression für Raubdinosaurier (n = 34; $\ln Y = 1.801 \pm 0.195 + 0.870 \pm 0.039 \ln X$; r = 0.992) ist signifikant verschieden von der für alle Vögel zusammen (n = 184; $\ln Y = 1.765 \pm 0.056 + 0.816 \pm 0.019 \ln X$; r = 0.988; $t_{214} = 2.526$; $0.02 > p > 0.01$) und auch von der für die flugunfähigen Laufvögel (Regressionslinie nicht gezeigt: n = 19; $\ln Y = 2.241 \pm 0.534 + 0.709 \pm 0.113 \ln X$; r = 0.950; $t_{49} = 3.112$; p <0.001). Symbole: ■, Raubdinosaurier; ▲, *Oviraptor* and *Ingenia*; +, *Caudipteryx;* *, *Protarchaeopteryx*; □, Vögel.

stride lengths during terrestrial locomotion with more horizontal femora, and correspondingly shorter and stouter femora to preserve bending strength (Alexander 1983, Gatesy 1991, Gatesy & Middleton 1997, Carrano 1998, Christiansen 1998, 1999a, Farlow et al. 2000). In this respect they differ significantly from non-avian theropods (Gatesy 1991, Carrano 1998, Christiansen 1998, 1999a). Within birds the ratios do, however, vary greatly. This is due to the fact that the hind limbs of many extant birds are clearly specialised for many other purposes than terrestrial locomotion and modifications for arboreal-

ity, wading, paddling and so on, are numerous (e. g. Gatesy & Middleton 1997, Farlow et al. 2000). All these adaptations are conspicuously absent in non-avian theropods, which appear to have been a much more homogenous assemblage of small to gigantic, bipedal, striding, terrestrial cursers (Carrano 1998, Gatesy & Middleton 1997, Christiansen 1998, Farlow et al 2000). They are, thus, clearly comparable to ground birds only, as also advocated by Jones et al. (2000).

As can be seen from Fig. 3 the limb proportions of the advanced non-avian theropods ap-

proach the lower range of extant (and extinct) avian theropods. The seven used specimens of *Caudipteryx* cluster at the upper extreme of the non-avian theropod range, but if one wants to advocate this as being indicative of *Caudipteryx* being a bird, then by that token the other oviraptorosaurids (*Ingenia, Oviraptor*) would also be birds, as would some of the dromaeosaurids (Fig. 3; see also Christiansen 1998, p. 248). This of course is nonsense. Evidently the oviraptorosaurs had long, gracile limbs and could have been very fast-moving (Christiansen 1998). *Caudipteryx*, being smaller than *Ingenia* and *Oviraptor*, simply follows this trend. *Protarchaeopteryx* most closely approaches the values for extant birds, in accordance with its phylogenetic position (Ji et al. 1998). All non-avian theropods, even the most long-limbed forms, are, however, distinctly different from the ground birds (Fig. 3, dashed area), particularly the more fast-moving forms (*Struthio, Rhea, Dromaius*, phorusrhacoids) at the upper right of the dashed area. In this respect *Caudipteryx* bears little resemblance to a ground bird. The distinct values of the ground birds are particularly due to their having short, stout femora.

The tibia/femur ratios of *Caudipteryx* (Fig. 3) and *Protarchaeopteryx* (Ji et al. 1998) are not significantly different from those of all birds (t_{361} = 1.421 and 1.283, respectively; $0.20 > p > 0.10$), but neither are those of other gracile, small to medium-sized theropods (e. g. *Compsognathus, Elaphrosaurus, Ingenia*, ornithomimids, *Oviraptor*). This is due to the more stubby-legged birds at the lower left of the avian range, for instance parrots and raptors. Conversely, all non-avian theropods have significantly longer femora compared to tibiae than ground birds, including *Caudipteryx* (t_{53} = 2.971; $0.01 > p > 0.001$) and *Protarchaeopteryx* (t_{53} = 2.428; $0.02 > p > 0.01$). This corroborates previous conclusions (Gatesy 1990, 1991, Carrano 1998, Christiansen 1998) that no non-avian theropod had limb kinematics and loading patterns like those of avian theropods.

Birds have proportionally short and thick femora compared to those of non-avian theropods and mammals (Alexander 1983, Gatesy 1991, Carrano 1998, Christiansen 1998, 1999a, Hutchinson 2001b). It is evident that the femora of *Caudipteryx* and *Protarchaeopteryx* did not share these proportions, and they group with other non-avian theropods (Fig. 4). The regression line for femur length/least circumference in non-avian theropods is significantly different from that of all birds ($0.02 > p > 0.01$) and the large ground birds ($p < 0.001$), corroborating previous analyses of this nature (Gatesy 1991, Carrano 1998, Christiansen 1999a). Femoral circumference to length in *Caudipteryx* is significantly less than in ground birds (t_{18} = 2.151; $0.05 < p < 0.01$) but not compared to those of other theropods (t_{33} = 1.029; $0.30 < 0.20$). The avian tibiotarsus has a loading pattern more comparable to both femora and tibiae of non-avian theropods and parasagittal mammals, and is proportionally much weaker than the avian femur (Alexander et al. 1979, Alexander 1983, Gatesy 1991, Carrano 1998, Christiansen 1998, 1999a). The femora and tibiae of non-avian theropods and parasagittal mammals do not display this great difference in bone strength (Christiansen 1998). Correspondingly, the regression lines of tibia length to circumference in 23 non-avian theropods (Christiansen 1999a) and 19 species of large ground birds (see materials and methods) are not statistically different ($0.40 > p > 0.30$). The above clearly indicates that the loading pattern of the femora of *Caudipteryx* and *Protarchaeopteryx* was similar to those of other non-avian theropods and differed from those of birds. Biomechanically this strongly argues against their having been able to walk like birds, with sub-horizontal femora.

One could argue that the above are all based on external bone dimensions, and, thus, that long bones with a medullary cavity, as in theropods (avian and non-avian) could show a different strength indicator pattern than is revealed by external dimensions. This is, however, not so. Analyses of this nature have re-

vealed that external bone dimensions account for more than 99 % of the variation in strength indicator patterns (Fariña et al., ms). The only differences are the absolute bone strength values, not the relative values (relative to other bones from the same skeleton or bones from other individuals or species). Thus, for evaluation of ratios, as in this case the ratio between the strength of the femora and tibia of non-avian and avian theropods, ignoring the medullary cavity should have no effect.

Finally, we would like to emphasise that the approach of Jones et al. (2000) is incorrect. In arguing for a systematic position of *Caudipteryx* as a bird more advanced than *Archaeopteryx*, they cite several functionally anatomical characters (hind limb/trunk proportions and position of the centre of gravity). Even if these were in fact correct, those three purported bird synapomorphies are contradicted by a plethora of other anatomical characters (Gauthier 1986, Holtz 1998, Makovicky & Sues 1998, Sereno 1999), which indicates that they are convergences, unless assigned a much higher weight. Cladists have repeatedly emphasised that the function of anatomical features is irrelevant to characters in phylogenetic analyses (e. g. Cracraft 1981, Bonde 1984). An emphasis on function inevitably leads to confusion of analogy (= convergence) and homology (= synapomorphy). Additionally, Jones et al. (2000) note several convergent traits common to secondarily flightless birds, and, thus, the purported similarities between *Caudipteryx* and these ground birds cannot be taken as indicative of it being a bird more advanced than *Archaeopteryx*, unless those similarities can be shown to be restricted to *Caudipteryx* and some specific group of ground birds. As this is not the case it is really invalid to cite these characters as being indicative that *Caudipteryx* was a secondarily flightless bird. Ironically, according to the more traditional, functional and adaptational models of avian origins (Geist & Feduccia 2000, Tarsitano et al. 2000), an approach also favoured by Ruben & Jones (2000), the body proportions of *Caudipteryx*

would effectively rule out its avian status! This apparent contradiction further underlines the need for a rigorous cladistic framework for phylogeny reconstruction.

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