LETTER

Linking the evolution of body shape and locomotor biomechanics in bird–line archosaurs

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Locomotion in living birds (Neornithes) has two remarkable features: feather-assisted flight, and the use of unusually crouched hindlimbs for bipedal support and movement. When and how these defining functional traits evolved remains controversial[1–8]. However, the advent of computer modelling approaches and the discoveries of exceptionally preserved key specimens now make it possible to use quantitative data on whole-body morphology to address the biomechanics underlying this issue. Here we use digital body reconstructions to quantify evolutionary trends in locomotor biomechanics (whole-body proportions and centre-of-mass position) across the clade Archosauria. We use three-dimensional digital reconstruction to estimate body shape from skeletal dimensions for 17 archosaurs along the ancestral bird line, including the exceptionally preserved, feathered taxa *Microraptor, Archaeopteryx, Pengornis* and *Yixianornis,* which represent key stages in the evolution of the avian body plan. Rather than a discrete transition from more-upright postures in the basal-most birds (Avialae) and their immediate outgroup deinonychosauria[5,6], our results support hypotheses of a gradual, stepwise acquisition of more-crouched limb postures across much of theropod evolution[1–4], although we find evidence of an accelerated change within the clade Maniraptora (birds and their closest relatives, such as deinonychosaurs). In addition, whereas reduction of the tail is widely accepted to be the primary morphological factor correlated with centre-of-mass position and, hence, evolution of hindlimb posture[1–8], we instead find that enlargement of the pectoral limb and several associated trends have a much stronger influence. Intriguingly, our support for the onset of accelerated morpho-functional trends within Maniraptora is closely correlated with the evolution of flight. Because we find that the evolution of enlarged forelimbs is strongly linked, via whole-body centre of mass, to hindlimb function during terrestrial locomotion, we suggest that the evolution of avian flight is linked to anatomical novelties in the pelvic limb as well as the pectoral.

Terrestrial animals exert a force against the ground to support and move their body. The vector of the incurred ground reaction force (GRF) generally points at or close to the centre of mass (CoM) to stabilize the body[9,10]. The GRF is mainly vertical during the middle of the supportive (stance) phase of locomotion (see, for example, refs 11, 12). Bipedal animals such as birds and many extinct non-avian dinosaurs use a single supporting limb for most of the stance phase. Therefore, the foot of this limb must be placed directly underneath the CoM around mid-stance to exert a vertical GRF, and the joints of the limb must be suitably positioned to allow the antigravity muscles to push against the ground (the GRF passes on the flexor side of the ankle, knee and hip[11,13–16]). The location of the CoM is therefore a major determinant of the limb orientation at mid-stance. Hence, the 'crouched' mid-stance postures of Neornithes, in which the hip is highly flexed, placing the feet well cranial to the hip and the knee cranial to the GRF, are correlated with a strongly cranial (for a biped) CoM[8,17]. In contrast, the ancestral archosaur is likely to have had a more caudal CoM[18] and, by inference, a different limb orientation.

Reconstruction of evolutionary trends in CoM position along the bird line therefore represents an important and under-used source of data on the origin and evolution of aspects of pelvic limb function that were inherited by extant birds. Analysis has previously been limited to qualitative inferences of mass distribution from theropod skeletal proportions, which have led to conflicting interpretations of CoM evolution. On the basis of a trend towards reduced tail size along the bird line, it has been suggested that the CoM steadily moved cranially from coelurosaurian theropods to extant birds[1,2]. The inference of a gradual change in pelvic limb posture is supported by contemporaneous trends in hip anatomy indicating increasingly flexed hip joints[3]. Alternatively, it has been suggested that a trend towards a more triangular chest (concentrating chest mass caudally) in theropods closely related to birds counteracted tail reduction to some extent, and that a more concentrated cranial shift in CoM occurred subsequently within the avian stem clade Avialae[6]. Some support for a later, more discrete shift in limb posture and function is intimated by studies finding distinct differences between the pelvic limb proportions[19] and stride parameters[20] of non-avian theropods and extant Avialae. Thus, when and how critical functional traits of living birds evolved remains controversial, and this limited understanding prohibits tests of the interplay between the evolution of terrestrial locomotion and flight, in addition to other physiological and ecological aspects of the origin of birds.

Here we present a quantitative analysis of bird-line CoM evolution, using empirically validated[18] three-dimensional computational models of mass distribution (Methods Summary and Supplementary Video 1) based on digitized fossil specimens of the range of bird-line taxa shown in Fig. 1 (for full specimen data, see Supplementary Table 1; for animated visualizations of all models, see Supplementary Video 2). Representative modelled body volumes are shown in Fig. 2. To address trends along the bird line itself, rather than at terminal taxa, estimates of CoM and other mass properties were mapped onto the evolutionary splitting events, or nodes (Fig. 1; 1–16), using a squared-change parsimony method based on temporal branch length (see Methods Summary). Our results corroborate a significant ($P < 0.05$, $R = 0.44$, Pearson's correlation of phylogenetic node date and CoM estimates) cranial shift in CoM position over the entire bird line. Visualization of the results indicates that this cranial shift was not evenly distributed or monotonic, but started sometime during the diversification of the clade Maniraptora (Fig. 3, between nodes 11 and 12) in the Jurassic period. We also discern a marked cranial shift in CoM position (approximately twofold) that reaches a maximum in basal Ornithurae (birds closely related to Neornithes; Fig. 3, node 15) before shifting somewhat caudally again in Neornithes. Our sensitivity analysis (Fig. 3 error bars; see Methods Summary) indicates that these trends are still evident when allowing for considerable variation in the morphological assumptions underlying our reconstruction methodology.

Figure 4 (black dashed line) shows evolutionary trends in the (size-normalized) first mass moment of individual segments about the mediolateral axis (that is, segment mass multiplied by segment CoM

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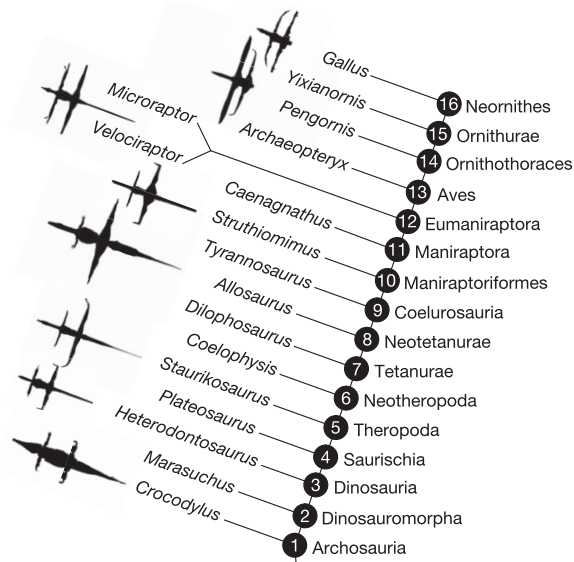
Figure 1 | Dorsal views of models of study taxa, arranged along a phylogenetic tree of Archosauria. Limbs are splayed laterally to show relative dimensions. See Supplementary Tables 1 and 2 for specimen numbers and references used to construct the phylogeny, divergence times and branch lengths.

position along the craniocaudal axis), representing the total influence of each segment on whole-body craniocaudal CoM position (see equation (1) in Methods Summary). Positive shifts concurrent, and therefore potentially correlated, with the Maniraptora-to-Ornithurae cranial CoM shift are evident in the first mass moments of most segments. However, the closest matches of whole-body CoM and these moments (large deviation starting around Maniraptora (nodes 11 and
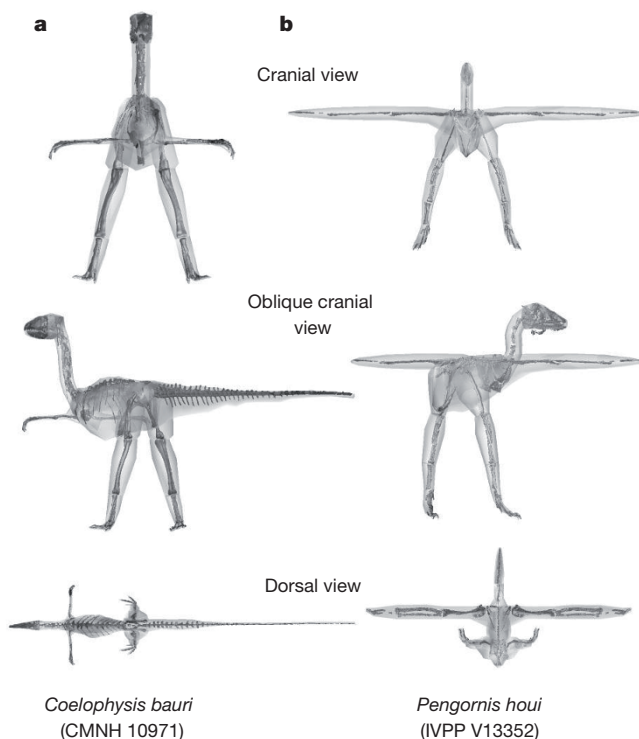

Figure 2 | Reconstructed body volumes. Based on digitized fossil skeletons and computed tomography scan data from modern relatives, for a basal dinosaur (**a**) and a basal bird (**b**); in cranial (top), oblique cranial (middle) and dorsal (bottom) views. These exemplify the major changes in body proportions that evolved on the bird line. Specimen numbers are shown under taxon names. For more details, see Supplementary Videos 1 and 2.
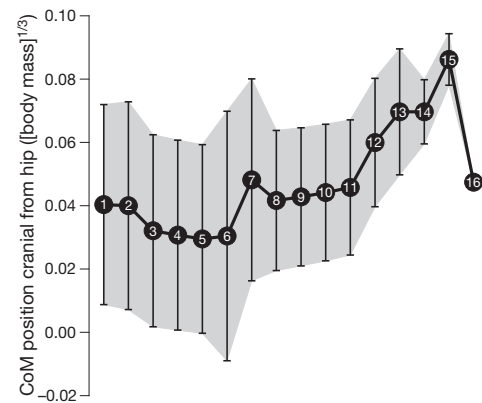

Figure 3 | Estimated evolutionary trends in whole-body CoM position along the craniocaudal axis. Whisker plot bars represent the range of values indicated by our sensitivity analysis. Numbers 1–16 correspond to the nodes in Fig. 1. Values towards the extreme ends of the whisker plots are less plausible, maximal/minimal models with extreme proportions, whereas values towards the middle are more plausible, conservatively proportioned models. Although biomechanically implausible, whisker plot ranges showing negative craniocaudal CoM positions (behind the hip) are included for completeness.

12), reaching a maximum in basal Ornithurae (node 15)), are evident only for the head, tail, pectoral and pelvic limbs (Fig. 4). Yet, correlation analysis (Spearman's rank; see Methods Summary and Supplementary Tables 9–12 for details and results) supports a significant ($P < 0.05$) positive relationship between first mass moments and whole-body CoM position only for the pectoral ($P < 0.01$, $R = 0.67$) and pelvic ($P = 0.02$, $R = 0.58$) limbs. Furthermore, separate analysis of segment mass (Fig. 4, red) and segment CoM (Fig. 4, blue) indicates that, morphologically, the influence of the pelvic limb on whole-body CoM is largely a result of cranial evolutionary shifts of the segment CoM ($P = 0.06$, $R = 0.50$, same method) associated with expansion of the preacetabular ilium and the cnemial crest of the tibia, both of which add mass cranially to the thigh. In contrast, the influence of the pectoral limb on whole-body CoM is mainly due to increases in its mass ($P = 0.05$, $R = 0.51$).

From the above findings, we infer that the Maniraptora-to-Ornithurae cranial CoM shift resulted from increased relative pectoral limb mass (Fig. 4d, red) and increasingly cranial segment CoMs for the pelvic limb (Fig. 4e, blue). Less significant ($P < 0.1$), but possibly important, positive correlations with a more cranial whole-body CoM are first mass moments for the head ($P = 0.08$, $R = 0.47$) and neck ($P = 0.08$, $R = 0.44$). On the basis of trends for these segments (Fig. 4a, b), we therefore suggest that, secondary to changes in limb morphology, a cranial shift in CoM may also have been associated with increased relative mass of the head and neck.

As predicted from gross anatomy[1,2], relative tail mass is estimated to have declined within Theropoda and tail CoM to have moved cranially (Fig. 4f, node 5), particularly within Maniraptora (node 11), to a minimum in basal Ornithurae (node 15). That the suggested[1,2] correlation between these trends and a more cranial whole-body CoM was not found to be significant (Supplementary Table 12) is notable. Considering that the tail represents the majority of body mass caudal to the hip, reduction or cranial concentration of tail mass, or both, would be expected to bias the whole-body CoM position strongly cranially. However, our results indicate that the effects of tail reduction were not significant in comparison to concurrent changes to the limbs (especially pectoral) and, to a lesser extent, the head and neck. Therefore we infer that adding mass to the front of theropod bodies was more influential for CoM evolution than was removing it from the back.

In addition to overall tail mass, we used volumetric reconstruction[21,22] to estimate evolutionary trends in the relative mass of the M. caudofemoralis longus (CFL) muscle (Fig. 5). The CFL is a principal locomotor muscle in most non-avian Reptilia, and was probably so in
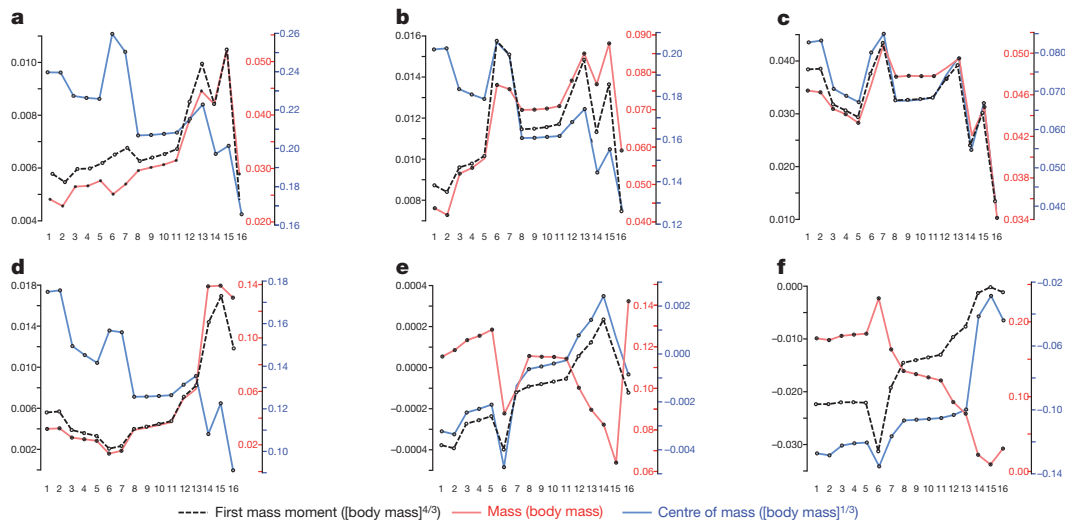
Figure 4 | Estimated evolutionary trends. Shown are trends in individual segment first mass moments (black dashed lines), individual segment masses (red lines) and individual segment craniocaudal CoM positions (blue lines) for ancestral archosaurs and dinosaurs as well[1,23]. It extends from the tail to the proximal femur and knee, and retracts the femur powerfully through a large arc during the stance phase. In Neornithes, the CFL has atrophied, and femoral retraction during walking is mostly replaced by knee flexion powered by enlarged 'hamstring' muscles[24,25]. Because the CFL's mass would have been a major locomotor power source in ancestral archosaurs, its mass is a reasonable proxy for its relative importance in hip extension or femoral retraction. Previously, tail reduction and the evolution of a suite of anatomical hip features associated with novel, long-axis control of the femur have been used to infer that the transition between tail-based to knee-based locomotion (and crouched limbs) began in earlier theropods[1–4]. Specifically, it was inferred that this trend began within basal Tetanurae, and that a derived system had already evolved in the clade Eumaniraptora[3].

Our estimates of CFL mass support some elements of this hypothesis, in that the CFL and tail mass are strongly reduced from Eumaniraptora onwards (Fig. 5). However, we estimate that the CFL muscle remained relatively large in basal Tetanurae despite overall tail mass reduction (Fig. 5, nodes 7–9, dotted line), indicating that locomotion remained plesiomorphically more hip driven than knee driven. In addition, our CoM and other body proportion estimates do not unambiguously support alterations of posture at these more basal nodes (Figs 3 and 4). Therefore, the origin of novel hip control features in basal Tetanurae may not have been directly associated with or driven by a postural shift, but

the head (**a**), neck (**b**), trunk (**c**), pectoral limb (**d**), pelvic limb (**e**) and tail (**f**). Numbers 1–16 correspond to the nodes in Fig. 1. For reference, node 5 is Theropoda and node 13 is Aves.

instead may have been co-opted for later usage in supporting a more crouched posture.

Our results have clear implications for the evolution of bipedal locomotion along the bird line. The pattern of cranial CoM migration, proportional evolution and CFL reduction reconstructed here supports a gradual, stepwise acquisition of more-crouched limb postures across much of theropod evolution[1–4], rather than a rapid transition from more-upright postures occurring around the base of Avialae[5,6,8]. Our models explicitly yield the strongest support for a locomotor transition within the clade Maniraptora, and, perhaps more conservatively, Eumaniraptora (by which time the trend is well under way (Fig. 3, node 12)), in which considerable cranial CoM migration and concomitant strong reduction in CFL mass (Fig. 5, node 11 onwards) occurred. The fully derived modern condition probably did not evolve until well within Aves (for example Ornithurae (Figs 3 and 4, node 15)), when CoM position reached its cranial maximum and the CFL was most reduced[1–4]. Rather than being a phenomenon associated with or driven by tail reduction, we instead find that enlargement of the pectoral limb into the 'raptorial' forelimbs (and, ultimately, wings) of many eumaniraptorans is the strongest associated morphological trend. However, a more cranially biased pelvic limb CoM and perhaps increased head and neck mass were also involved. Note that this is also without considering the added mass of pectoral plumage (the geometry of which is too uncertain to model rigorously), particularly the large primary or primary-like feathers of Maniraptoriformes and later bird-line taxa (see, for example, ref. 26), which would only strengthen the relationship of cranially shifted body CoM and pectoral mass. Additional support for a locomotor transition within Eumaniraptora comes from the evolution of highly retroverted pubes, which, as previous studies have proposed, is likely to have fundamentally altered the moment arms (and, by inference, functions) of several major locomotor muscles[3,27,28].

Detailed phylogenetic and temporal aspects of the evolution of flight in the bird line remain controversial[4]. However, our finding that accelerated morpho-functional trends commenced around the node Eumaniraptora is closely correlated with the origin and diversification of animals with some degree of flight capability. Until more robust phylogenetic and aerodynamic assessments for early maniraptoriforms are made, it is impossible to assess conclusively whether our predictions of CoM and body shape change preceded, coincided with or followed the origin of flight. Our openly available data set (Methods Summary) and novel whole-body evolutionary approach mean that future studies can use our data to address these and other controversies. For example,
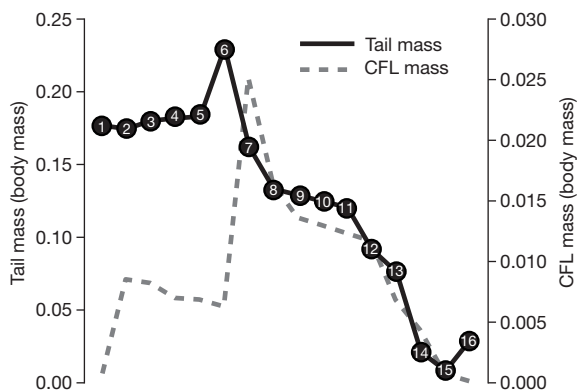

Figure 5 | Estimated evolutionary trends for tail segment and M. caudofemoralis longus muscle masses. Numbers 1–16 correspond to the nodes in Fig. 1.

the addition of accurate feathering to our models of *Microraptor* and *Archaeopteryx* could result in a reassessment of the position of the centre of lift relative to that of the CoM (important for gliding and stable flight) or more complex flight aerodynamics[29]. However, our discovery that the evolution of CoM on the bird line was more influenced by body shape changes cranial to the hips than in the caudal region reverses the widely accepted view[1–8] and opens new questions about the degree of independence between fore- and hindlimb function[7] (that is, modularity) across this transition. The proposed relationship between novel hip control mechanisms and more-crouched pelvic limbs[3], and the linkage proposed here between pectoral limb size, CoM position and hindlimb posture, suggest that the evolution of both aerial and terrestrial locomotor anatomy were highly interconnected. Aerially adapted pectoral limbs and terrestrially adapted pelvic limbs belong to the same body, and the physical characteristics of one cannot logically be changed without affecting the mechanical functioning of the other. This reinforces the importance of whole-body biomechanical analysis in interpreting morpho-functional data from the fossil record.

METHODS SUMMARY

Body segment masses and CoM positions were estimated from computer reconstructions based on digitized skeletons. Fossil specimens were digitized (Supplementary Table 1; various scanners and settings; MIMICS 13 segmentation software, Materialise). Reconstructions of body shape were made in three-dimensional modelling software (BLENDER 2.49 (http://www.blender.org)); Autodesk MAYA 2012) using established methodology[18,22,28,30]. CoMs for individual body segments were analysed using custom code, and whole-body CoM was calculated using the equation

$$\mathrm{CoM}_{[x,y,z]} = \frac{1}{M}\sum_{i=1}^{n} m_i r_{i[x,y,z]} \qquad (1)$$

Here M is the total body mass, m_i is mass of segment i and r_i is the distance from system origin to the CoM of segment i (calculated separately for each set of x, y and z coordinates). The term $m_i r_i$ (first mass moment) represents the total influence of segment i on the overall system CoM.

Maximal and minimal iterations of body segments were made in steps of $\pm 20\%$ of the radial dimensions (adjusted for cross-sectional profile) away from our initial 'best estimate' models, on the basis of the minimum variation (about mean values) in the extra-skeletal dimensions of saurian tails[18]. This is probably too generous for less 'fleshy' segments; a more complete study of such dimensions is needed. Segment iterations were combined to represent the most cranial, caudal, dorsal and ventral distributions of mass and maximal and minimal overall mass (Supplementary Video 1). Mass properties were estimated using validated custom software[18,30]. Data and software code used are deposited in the Dryad repository at http://dx.doi.org/10.5061/dryad.hh74n.

CoM positions and segment masses were then normalized (divided by body mass or the cube root of body mass) and used to reconstruct ancestral node states with the 'trace characters' function (squared-change parsimony) in Mesquite 2.75 phylogenetic analysis software, using the phylogeny in Fig. 1 and estimated branch lengths in millions of years. See Supplementary Tables 3–12 for data sets and analysis results. Owing to non-normality, associations between normalized segment morphometrics (first mass moment, mass and CoM) were assessed using a non-parametric correlation test in R ('Hmisc' package, Spearman's rank).

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