

Evolution

The evolution of locomotion in archosaurs

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Abstract

Archosaurian reptiles evolved a more erect posture and parasagittal gait early on. Early dinosaurs were the first habitual striding bipeds, a trait retained by living birds. Yet there is much more to archosaur locomotor evolution than these two transitions. I review our understanding of the pattern of locomotor evolution from the first archosaurs to Crocodylia and Neornithes, outlining where transitions of locomotor function evolved. I evaluate current research approaches, advocating more experimental work on extant animals to establish rigorous form–function relationships, and more biomechanical research that is bolstered by validation and sensitivity analysis of its assumptions, methods, and results. **To cite this article:** *J.R. Hutchinson, C. R. Palevol 5 (2006)*. © 2006 Académie des sciences. Published by Elsevier SAS. All rights reserved.

Résumé

L'évolution de la locomotion chez les archosaures. Les reptiles archosauriens ont évolué tôt vers une posture plus dressée et une démarche parasagittale. Les premiers dinosaures ont été les premiers bipèdes à marcher à grandes enjambées, caractéristique retenue par les oiseaux vivants. Cependant, il y a beaucoup plus lors de l'évolution locomotrice des archosaures que ces deux transitions. Je réexamine notre compréhension du modèle de l'évolution locomotrice à partir des premiers archosaures jusqu'aux Crocodyliens et Néornithes, en soulignant où les transitions de la fonction ont évolué. J'évalue les approches de la recherche en cours en me faisant l'avocat de davantage d'études expérimentales sur les animaux pour établir des relations rigoureuses fonction–forme et de davantage d'études biomécaniques pour étayer l'analyse et la validation des suppositions, méthodes et résultats. **Pour citer cet article :** *J.R. Hutchinson, C. R. Palevol 5 (2006)*.

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1. Introduction

Extant crocodylians move in widely-varying ways, from very sprawling to somewhat erect postures [37,

81]. In contrast, neornithine birds stand and move in more erect postures and stereotyped motions, albeit with variation between species [1,40,43]. Yet how this difference evolved is equivocal from a neontological standpoint, because of 250 Myr of extinctions between the Triassic and the present – there are no extant non-avian bipedal archosaurs available for study. Current acceptance that birds evolved from theropod dinosaurs

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[48,70,97] has transformed this difficult question into a soluble one: birds now have dozens of fossil outgroup taxa among non-avian archosaurs for calibrating how avian locomotion evolved (Fig. 1). Hence data from fossils are vital for reconstructing the evolution of archosaur locomotion. The disparate anatomies of the fossil relatives of crocodiles and birds support the inference that their locomotor repertoires often were qualitatively somewhere between those of extant archosaurs, with marked specialization within side-branch clades (e.g.,

Pterosauria, Sauropodomorpha). This provides hope for reconstructing how living crocodiles and birds came to locomote so differently from each other and from more basal reptiles. The focus of this review is on how this reconstruction can be done and how the modern consensus on this topic became established. What have we learned in over a century of research on archosaur locomotor evolution since Marey, Muybridge, and others helped initiate the scientific study of locomotion?

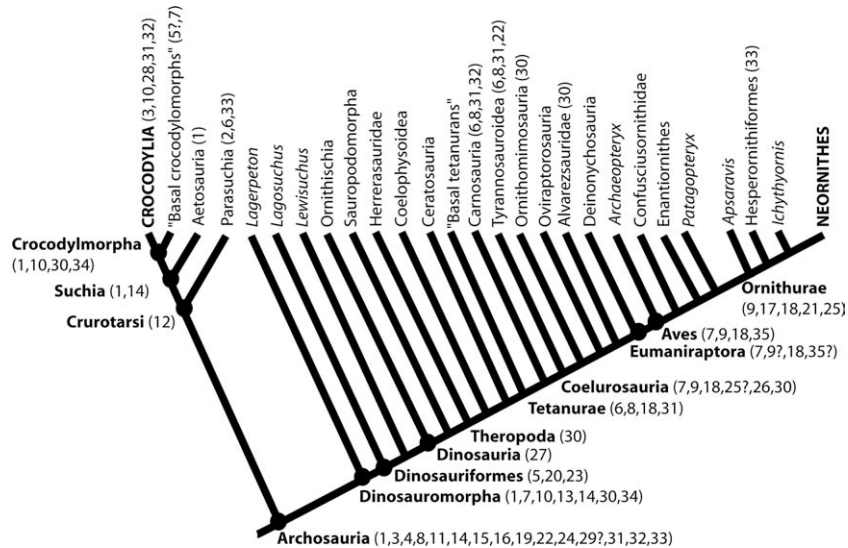


Fig. 1. 'Consensus' phylogenetic framework for Archosauria, modified from references listed in [55–57], showing major transformations of locomotor function in Archosauria. Numbers indicate the latest likely timing of locomotor shifts within clade indicated: 1, more erect posture; 2, less erect posture; 3, variable posture from sprawling to erect; 4, quadrupedalism; 5, Striding bipedalism; 6, body-size increase; 7, body-size decrease; 8, more upright pose; 9, more crouched pose; 10, shift to digitigrady/plantigrady; 11, primitive mesotarsal ankle; 12, crocodile-normal ankle; 13, advanced mesotarsal ankle; 14, more parasagittal gait; 15, large tail and fourth trochanter, predominant hip-based propulsion during stance; 16, metatarsus held low to ground; 17, near-vertical metatarsus; 18, reduced tail and fourth trochanter, increased knee-based propulsion during stance; 19, adductor-based postural support; 20, abductor-based postural support; 21, medial rotator-based postural support; 22, poor bipedal running ability; 23, good bipedal running ability; 24, poor turning ability; 25, improved turning ability; 26, medially-offset femoral head; 27, open acetabulum; 28, bounding and galloping locomotor modes; 29, near-isometric bone scaling; 30, more cursorial limb proportions; 31, less cursorial limb proportions; 32, near-horizontal vertebral column; 33, semi-aquatic habits; 34, more terrestrial habits; 35, flight. Question marks indicate extremely ambiguous evidence for the timing of origin of certain traits. Not all taxa (e.g., pterosaurs, ornithosuchids) are included; some taxa may lie in slightly different positions than indicated but this would not affect the conclusions.

Fig.1. Diagramme phylogénétique de « consensus » pour les archosauriens, modifié à partir des références listées [55–57], montrant les transformations majeures de la fonction locomotrice chez les archosauriens. Les nombres indiquent le moment vraisemblablement le plus récent des changements de locomotion dans le clade : 1, posture plus dressée ; 2, posture moins dressée ; 3, posture variable entre à terre et dressée ; 4, quadrupédie ; 5, bipédie à grands pas ; 6, augmentation de la taille du corps ; 7, diminution de la taille du corps ; 8, attitude plus verticale ; 9, attitude plus accroupie ; 10, changement vers le mode digitigrade/plantigrade ; 11, cheville mésotarsale primitive ; 12, cheville normale de crocodile ; 13, cheville mésotarsale avancée ; 14, démarche plus parasagittale ; 15, grande queue et quatrième trochanter, propulsion basée de façon prédominante sur la hanche pendant la posture ; 16, métatarse maintenu bas par rapport au sol ; 17, métatarse presque verticale ; 18, queue réduite et quatrième trochanter, propulsion basée sur le genou, augmentée pendant la posture ; 19, support postural basé sur l'adducteur ; 20, support postural basé sur l'abducteur ; 21, support postural basé sur le rotateur médian ; 22, faible aptitude à la course bipède ; 23, bonne aptitude à la course bipède ; 24, faible aptitude à tourner ; 25, aptitude à tourner améliorée ; 26 tête du fémur débutant médialement ; 27, acetabulum ouvert ; 28, modes locomoteurs par bond et galop ; 29, recouvrement à peu près isométrique d'écailles d'os ; 30, proportions des membres plus adaptées à la course ; 31, proportions des membres moins adaptées à la course ; 32, colonne vertébrale presque horizontale ; 33, habitudes semi-aquatiques ; 34, habitudes plus terrestres ; 35, vol ; les points d'interrogation indiquent une évidence extrêmement ambiguë sur le « timing » d'origine de certaines caractéristiques. Tous les taxons (par exemple, Ptérosaures, Ornithosuchides) ne sont pas inclus ; certains taxons peuvent se trouver dans des positions légèrement différentes de celles qui sont indiquées, mais ceci n'affecte pas les conclusions.

First, I survey the methods and evidence used to reconstruct archosaur locomotor function and evolution (focusing on functional morphology and scaling/biomechanics approaches), outlining what I consider to be the modern consensus. Second, I highlight the major unresolved questions and evaluate the promise of, or challenges for, particular methods that might resolve them. I conclude by explaining a simple biomechanical approach for understanding what limb orientations different archosaurs may have used, as an example of how we can better understand archosaur locomotor mechanics and evolution. My chief concern is detailing the ancestral mechanisms by which archosaurian clades positioned and moved their hindlimbs, and tracing the evolution of these mechanisms along the crocodile and bird lines (*sensu* [41]). I summarize this information in Fig. 1. Events within crocodylomorph or theropod side-branches, and within ornithischians or sauropodomorphs, are exciting topics but are less crucial for resolving how the terrestrial locomotor modes of extant crocodiles and birds came to be the way they are today. The latter question in my opinion is the most profound one in the evolution of terrestrial locomotion in archosaurs. Arboreality in any taxa, or the origins of flight in pterosaurs [72] and birds [21,31,70,73] are reviewed elsewhere. Some basal archosaurs may have been semi-aquatic (it is well accepted that non-avian dinosaurs were habitually terrestrial), and many lineages within Archosauria independently returned to the water, but this too cannot be covered here in detail. Following Gatesy [37,39], I try to emphasize a continuum of limb positions, and use ‘posture’ only to refer to more/less abducted poses (more sprawling to more erect), and ‘limb orientation’ or simply ‘pose’ to refer to the degree of limb joint extension (*i.e.*, straightening; more crouched to more upright).

2. Functional morphology

As Archosauria came to be recognized as a major group within Reptilia that gave rise to crocodiles, birds, and many extinct taxa, it was clear they had evolved novel ways of standing and moving, atypical of more basal reptiles [13,20,27,29,30,74,76,77,85–87]. Initially, the main source of information about archosaur locomotion was trackway evidence but this was not well-integrated with the anatomical record, as the track-makers typically were ambiguous [74,94]. Likewise, much anatomical/functional information was not yet synthesized into a widely-accepted phylogenetic perspective [43,70] – even dinosaurs were not accepted as monophyletic for many years, at least to the exclu-

sion of basal archosaurs such as ornithosuchids and rauisuchians [27]. Huene’s [54] early functional work was not well received [86].

Romer’s [85–87] studies are a classic and influential work on archosaur locomotor evolution that set the standard for over 50 years, revealing how pelvic muscles had fragmented and shifted dorsocaudally in Archosauria, corresponding to a generally more erect posture and parasagittal gait. However, his studies emphasized the limb myology of alligators and specialized dinosaurs (*e.g.*, sauropods and coelurosaurs), as birds were not yet accepted as dinosaur descendants, and fewer basal archosaurs were well known. Myological reconstructions and functional studies have nonetheless been tightly linked ever since Romer’s work – osteological descriptions of archosaurs are replete with inferences about what soft tissues adhered to particular bony structures, and these inferences are often used to support higher-level inferences about function [101].

A few important anatomical and functional analyses such as Schaeffer [88] on ankle function and Colbert [27] on saurischian evolution followed Romer’s work, but Charig’s [20] classic work on the transition between sprawling and erect postural grades had the broadest impact. Some of Charig’s ideas were heavily criticized – for example, he made many errors and oversimplifications in his inferences about muscle reconstructions, function, and mechanics. His ‘femur-knocking-on-the-pubis’ problem (*i.e.*, that the femur would be overly adducted by femoral protractors arising from the pubis during hip flexion) over-emphasized the role of pubic muscles in femoral protraction [62,91,96]. Yet Charig’s basic conclusions remain generally accepted: (1) archosauromorphs transitioned from more to less-sprawling (more erect) postures, reflected in osteological and myological features detailed by Charig and many others (*e.g.*, inturned femoral head and fenestrated acetabulum), (2) quadrupedalism was ancestral for Archosauria, not bipedalism as some previous authors had argued, and (3) digitigrady is correlated with an erect posture, although with exceptions [76,77].

Later studies elucidated that archosauromorphs plesiomorphically had a ‘primitive mesotarsal’ ankle, which was elaborated into functional complexes such as the complex ‘crocodile-normal’ (on the crocodile line), bizarre ‘crocodile-reversed’ (ornithosuchids), and hingelike ‘advanced mesotarsal’ (on the bird line) ankles [29,30,43,89,90]. An excellent experimental study of crocodylian limb function [13] determined that crocodiles differed from the ancestral diapsid condition in maintaining a cranially-oriented tarsus and metatarsus

(i.e., a more parasagittal gait) during the first half of stance phase, then rotated this unit laterally during plantarflexion later in stance. Dinosaurs presumably lost the calcaneal tuber intrinsic to the ‘crocodile-normal’ ankle as they adopted a more erect posture and parasagittal gait, reducing distal limb rotation. Parrish [76,77] complemented this work with a detailed analysis of inferred form-function relationships in archosaur ankles and overall limb structure. He inferred that the evolution of a more erect posture occurred at least twice in archosaurs: once on the crocodile line (most importantly, that crocodiles were secondarily less erect and more aquatic than their crocodylomorph forebears), and once on the bird line. Additionally he emphasized that there was much parallelism between archosaur lineages, especially in secondarily more sprawling aquatic forms. Since then, studies have emphasized a continuum of postures [37,81,90], admitting that it is difficult to pigeon-hole taxa into Charig’s grades of sprawling, semi-erect, and erect.

Walker [96] provided some well-considered refinements of Romer’s studies [see,18,55,56]. Tarsitano [91] also came to some different conclusions from Romer, but many of these later were contradicted by stronger arguments [68,75,78] (but see [39]). The multitude of dinosaur myological studies was nicely reviewed elsewhere [32]. A chief problem with most of these is the choice of extant animals for soft tissue data – too often single taxa (alligators, birds, or lizards) were used as models rather than all of these animals (and fossil outgroups) in an explicit phylogenetic context as is now favoured [18,32,101]. Furthermore, many studies used myological data to infer ranges of joint motion and limb orientation, but these usually had inaccurate assumptions about how muscles control or produce movement in living animals. For example, a priori assumptions about how long hip flexor/extensor muscle fibres were, or how much they could shorten, were employed to infer how extinct archosaurs moved [20,79,91], but generally ignored the complex architecture of muscle-tendon units [35,102], treating muscles as simple lines.

Analogies with extant animals (or optimal design criteria; [76]) are often a mainstay of this functional morphology approach [53]. Form-function relationships are typically inferred from an intuitive consideration of these links in extant animals, rather than demonstrated, and then transferred to similar anatomies in extinct animals. This approach will always be a useful foundation for locomotor research, but is severely limited, often raising or obscuring more questions than it conclusively answers. For example, analogies between bipedal lizards and ther-

opods [19,70], rhinoceroses and ceratopsians [3,4,80], or elephants and large theropods [3,4] were deficient because in many cases form-function relationships were poorly demonstrated for extant animals ([14] is a good exception), and anatomical/functional differences tended to be de-emphasized in favour of similarities. One can find many similarities between extinct theropods and extant taxa (some homologous), but one can also find many differences – that is the problem. If extinct and extant archosaurs were not so different in some aspects, there would be fewer problems in reconstructing their locomotor function and evolution, and the questions involved might even be less exciting.

The integrative work of Gatesy [36,39] was a paradigm shift for studies of archosaur locomotor evolution, because it combined methods that previously were not well-integrated: osteology and myology, form-function relationships based on rigorous experimental studies of extant animals, and an explicit phylogenetic context. This exemplifies the benefits of avoiding vague analogical comparisons, instead focusing on homologous form-function complexes. In doing so, old approaches emphasizing crocodylian [85–87,91] or avian [75,78] were shown to be misleading; both ancestral and derived mechanisms could be inferred in non-avian theropods [39]. Gatesy [36] showed that the hip extensor *M. caudofemoralis longus* is crucial for retracting the femur during the stance phase of locomotion in extant saurian reptiles. In contrast, he also demonstrated that extant birds have de-emphasized femoral retraction during walking and correspondingly reduced their homologue of *M. caudofemoralis longus*. Flexion/extension of the knee joint concurrently became a more crucial component of avian locomotion. Gatesy then reconstructed how the tail and the fourth trochanter on the femur, which are osteological correlates of caudofemoral muscle attachments, gradually reduced in size from basal archosaurs to crown-group birds. This supported the inference that as these structures were reduced in theropod dinosaurs, tetanurans (especially coelurosaurs) transitioned from the ancestral saurian mechanism of ‘hip-driven’ locomotion toward the more ‘knee-driven’ one typical of walking birds. Furthermore, Gatesy inferred that as the tail shortened, the centre of gravity of theropod bodies [3] was shifted further cranially, requiring a more crouched limb orientation. Hence basal dinosaurs probably stood and moved with more upright limbs than later non-avian theropods or birds did, and this transition was probably gradual across the bird line. These conclusions contradicted some earlier studies [75,78] that emphasized extremely ‘bird-like’ stance

and gait even in basal theropods. Gatesy's [36] conclusions have become the consensus, supported and elaborated on by additional studies [14–17,25,38–46].

Importantly, this consensus is consistent with the fossil trackway record, which shows little change in foot placement along the bird line [75] – an erect posture and parasagittal gait were maintained. Until recently, archosaur trackways suffered from the problem that they did not reveal much about how proximal limb joints moved during locomotion, beyond general postural clues [39]. Previous trackway studies had difficulty integrating track data into whole-limb and phylogenetic perspectives because of the latter problem and because the identities of trackmakers were unknown beyond a general taxonomic level. In another major advance for the field, Gatesy et al. [47] integrated fossil trackway data, functional anatomy, computer animation, and experimental studies of track-making by birds, illustrating how deep footprints of basal theropods revealed that, early in the stance phase of locomotion, the metatarsus was held closer to the ground (compared with its more vertical position in birds). Because limb joint angulations are interdependent (see below), this supported the contention that basal theropods moved with more vertical femora and less bent knees than extant birds of similar size [36,43]. This and similar integrative studies [100] demonstrate how trackway data can yield specific information about how archosaur locomotion evolved.

Hutchinson and Gatesy [61] synthesized anatomical [20,55–57,85–87], functional, and phylogenetic data to reconstruct how archosaur locomotion evolved (see also [41]). We considered four major hindlimb muscle groups with methods similar to [36], and inferred that locomotor evolution on the line to birds was stepwise, involving a plesiomorphic adductor-based postural support mechanism that transformed into an abductor-based one in bipedal dinosauriforms, followed by a long-axis rotational mechanism in neornithine birds and some extinct relatives. These transformations ultimately reduced the adductor/abductor motions and muscles associated with the more sprawling posture of basal archosaurs. We concluded that these modifications involved alterations not only of anatomy but also motor control, although in some cases limb function evolved without changes of motor control.

3. Scaling and biomechanical studies

Alexander [2] was the first study to convincingly transfer knowledge from biomechanics to dinosaur lo-

comotor biology, by estimating speeds for fossil footprints (also [92–94]) using the assumption of dynamic similarity. Coombs [28] applied a different quantitative approach to dinosaur locomotion, categorizing dinosaur limb proportions and structure into 'graviportal', 'cursorial', and other functional groups. These classic studies have had a major impact on the study of archosaur locomotion, inspiring more detailed biomechanical studies. Yet it is important to be wary of speed estimates from trackways as these can often be very inaccurate [5], and simple categories of locomotor function can be misleading [15,37]. Furthermore, the importance of limb dimensions for locomotor performance is complex and not necessarily related mainly to running speed, so there is no simple test – even with direct data from tracks or bones – for how fast an extinct archosaur could move.

The 1970s also saw a burgeoning of studies applying scaling principles of biomechanical relevance to animal locomotion [7,66,67]. These methods were later applied to dinosaur bones [3,14,17,22,23,25,38], convincingly showing from direct osteological evidence that dinosaurs generally changed bone shape with size in ways similar to most mammals [14,17,23,24]. So far, no clades of non-avian dinosaurs demonstrate limb bone scaling that is stunningly different from isometry or slight positive allometry – few scaling patterns match the most extreme scaling in large mammals [8], bovid artiodactyls [7,67], or even running birds [66]; dinosaurian limb design is rather conservative [14,17]. It is my impression that bone scaling studies have largely mined the data to near-exhaustion, for extinct dinosaurs at least, so additional such studies will offer quickly-diminishing revelations. I do not argue that archosaur locomotor scaling studies have covered all important areas though — osteological data have been emphasized but little is well known about soft tissue scaling in many extant taxa, a line of evidence which generally needs more integration with bone scaling [58,59].

Alexander [3,4] provided another advancement by applying static mechanics to interpret dinosaur locomotion. He found that body centres of mass tended to lie closer to the hindlimbs (i.e., the hindlimbs may have supported more weight, perhaps assisting in attaining bipedalism). Also, 'strength indicators' for the long bones of large dinosaurs were generally comparable to large mammals; for some taxa this supported the inference that they were not very fast runners. Blob [11; also 12] conducted similar bone geometry studies with basal reptiles and synapsids, consistent with the hypotheses that: (1) many intermediate taxa used a wide variety

of postures from sprawling to erect (as crocodylians do today; [37,81]), and (2) bone bending stresses increased in more erect taxa, although a decreased body size or parasagittal gait would keep stresses lower. Unlike in the origin of mammals and their closest relatives, few archosaurs experienced a size decrease with a more erect posture, except in dinosaurian ancestors.

Recently, an inverse dynamics approach, in which the forces and moments incurred in a particular limb orientation are estimated and related to the function of muscle-tendon units in locomotion [10,26,84], was applied to a variety of bipedal taxa, including birds and other theropods [58–60,62]. We have shown that the size of ankle extensor muscles is an important limiting factor for bipedal running ability, and that this limitation (along with hip extensor muscle size) reinforces why larger theropods probably did not run very fast. Conversely, smaller bipedal archosaurs probably had a relatively broader range of running abilities, which constricted as they evolved larger body size. Lineages that evolved very large body size probably reduced or even lost running ability [28,15,59], although this is controversial for large theropods [33,68,78,79]. Fossil footprints have revealed that some dinosaurs of small to medium size ran quickly, whereas so far large dinosaurs (5,000+ kg) lack known running trackways [33,79,92–94]. The locomotor abilities of early archosaurs are uncertain, but early dinosaurs probably were adept runners. Tetanuran dinosaurs evolved a moderately large body size, which was secondarily reduced in coelurosaurs, including birds, so running ability probably changed repeatedly on the bird line. Likewise, as size increased/decreased, limb orientation likely became more/less upright [38,23,59,62].

Modern biomechanical approaches have adopted sophisticated computer technologies to analyze complex aspects of dinosaur locomotor biomechanics. 3D computer renderings of various archosaur bodies have been used to estimate body masses, centres of mass, and mass moments of inertia [49–51]. Such models were used to estimate turning biomechanics [52], supporting the hypothesis that turning ability (about a vertical axis) in many bipedal archosaurs was limited by high rotational inertia [19]. Yet scaling of rotational inertia in theropods improved turning capacity relative to other archosaurs [52], and features such as smaller body size and shortened tails further improved rotational inertia along the bird line [19]. Important unaddressed non-inertial components of turning ability include muscular capacity to rotate the trunk about the hip and the capacity to deflect the velocity vector of the centre of mass

in order to turn [63], which relates more to mass, velocity, and ground-reaction force production than inertia. The medially-offset femoral head that evolved at least three times in dinosaurs [16] increased long-axis rotational muscle moment arms [61], so it may have improved turning ability over the ancestral condition in these lineages. Yet size changes also probably played a major role in the evolution of turning capacity, much like straight-line running ability.

Biomechanical research may seem to be a departure from classical anatomically-based work in palaeontology, but it can also be seen as a distillation of anatomical information into its most pertinent components, described in quantitative, physical terms using biomechanical methods. Where anatomy is important, it can be considered in as much detail as needed – within the bounds of technological capacity, which has caught up to the level of scientific questioning. Indeed, biomechanics often reveals that the complexity of morphology cannot be adequately captured in some traditional functional morphology approaches, as multiple levels of interaction (e.g., body segment dynamics, muscle physiology, and motor control) lie between anatomical structure and animal movement [64,65]. This is my rationale for advocating biomechanical approaches in current archosaur locomotor research. However such methods are no faultless panacea – there are two important caveats, as follows.

First, computerized biomechanical simulations of dinosaur locomotion in particular are (and should be) popular approaches, but these too depend on empirical knowledge – making a dinosaur move ‘convincingly’ is a trustworthy conclusion only if it is based on a valid method. I urge, and have tried to practice [59], that scientific reconstructions of dinosaur locomotion (whether simple or complex) should be produced using methods that are shown to work well on extant as well as extinct animals. This validation step not only builds confidence in the methods and illuminates where they might be weakest, but can also shed light on how extant animals work [58], increasing the value of such research.

Second, many quantitative studies of dinosaurs focus on obtaining a single number (or maybe two) as their result; e.g., speeds [2,28]. The great degree of potential error in all methods for reconstructing archosaur locomotion obliges us to emphasize a range of potential results, using sensitivity analysis to address how much what we do not know about extinct taxa (assumptions about missing data) or locomotor dynamics (simplifica-

tions of methods) matters for the conclusions drawn about them [58,59].

Approaches mindful of these two caveats can substantially advance biomechanical studies beyond the trailblazing work of Alexander [2–4], progress that I argue is an important goal for future studies.

4. Crucial questions and challenges

The inference of function from form is a challenging enterprise [64,65], but biomechanical and experimental studies offer great promise to tease apart this complex relationship and address fundamental questions about how archosaurs stood and moved. We cannot study the locomotion of extinct archosaurs with the experimental methods that Marey and others pioneered, yet palaeobiological ‘detective work’ and strong inferences can tell us much about this major transition. Such research not only depends on form-function principles learned from living animals, but also is a powerful test of the utility and validity of those principles, as their implicit goal is to have broad application and explanatory power [4,6,9]. If we are able to reconstruct in detail how archosaur locomotion evolved, this should by reciprocal illumination demonstrate how well we understand some locomotor biomechanical principles. Hence I see a fertile synergy where others might see a divisive dichotomy between neontology and palaeontology, or between functional morphology and biomechanics.

Individual extinct archosaurs such as *Edmontosaurus*, *Triceratops*, and *Tyrannosaurus* are fascinating creatures, but studies of locomotion in single extinct archosaur taxa typically provide few revelations unless they are shown to be important components of a broad question [41]. It is through integrating such studies into the broad framework of archosaur locomotor evolution that they can become quite informative, especially outgroup taxa on the bird line. Most large dinosaurs, such as *Tyrannosaurus*, have negligible importance for understanding avian locomotor evolution, but they help answer historical questions about how different large land animals support their weight [3,4,58–60,62,68,79,80]. Justification of such single-taxon studies however remains an important consideration – how useful would it be to reconstruct how each species of the clade Carnosauria moved, for example? This is particularly important in cases in which little evidence for appreciable functional disparity exists. The morphospace occupied by non-avian theropod hindlimbs is quite narrow [14,46]. If this anatomical disparity is correlated with functional disparity, then we should expect little difference

of limb function among many taxa, except between extreme edges of the morphospace, divergent body sizes, or anatomical novelties that have major biomechanical significance. Theropod locomotion evolved gradually [36] so there might only be slight differences among many taxa, especially across narrow phylogenetic and functional spectra. This should hold for other archosaurs as well.

Despite much progress in reconstructing archosaur locomotor evolution (Fig. 1), important details remain unresolved. How much the locomotion of the common ancestor of the crocodile and bird lines differed from that of extant crocodylians is ambiguous – anatomical and trackway data suggest few major differences [61,74]. Yet which aspects of crocodylian locomotion are apomorphic or parallel acquisitions – and at what level within Archosauria – remain vexing mysteries. Bounding and galloping locomotor modes are ancestral for Crocodylia [83,103], but did any archosaurs share this derived trait or convergently evolve it? [77,89]. Whether bipedalism was present in any members of the crocodile line, or if it had anything to do with the origin of crocodylian locomotion, is also uncertain. Moreover, how locomotion evolved from early saurians to Archosauria is largely ambiguous, but surely some important functional changes evolved on this line.

Many of these questions depend on the establishment of a stable phylogeny of Archosauromorpha, especially for basal archosaurs. Yet an improved biomechanical understanding of structure-function relationships in extant crocodylians is just as important as phylogenetic resolution. Following crucial earlier experiments [13,37], recent studies of alligators determined that tail-dragging may increase locomotor energetic costs [99], and that whereas hindlimb extensor muscles act as expected and increase activity in more erect postures, muscles other than the ‘adductor’ muscles of alligators concurrently increase femoral adduction [82]. These experimental findings illuminate what changes (reduced tail-dragging, increased hindlimb adductor and extensor muscle activation) might have accompanied more erect postures in archosaurs, lending empirical weight to evolutionary speculations. They also reveal how function sometimes does not easily follow from structure or meet a priori expectations – without such tests of form-function relationships, studies of archosaur locomotor evolution would have little ground to stand on [81].

Locomotor evolution on the bird line also has many open questions. Bipedalism among pterosaurs remains contentious [72,91,95,98] and depends somewhat on

the phylogenetic position of pterosaurs. This controversy also renders inconclusive how many times bipedalism evolved in archosaurs, and when habitual striding bipedalism first evolved on the bird line, although some bipedal ability was present in the first dinosauriforms. Our increasing understanding of the most basal dinosaurs and the phylogeny of basal ornithischians, sauropodomorphs, and theropods [97] is improving resolution of locomotor evolution in the Triassic, which sets the ancestral conditions for the dinosaur radiation. Dinosaurs evolved quadrupedalism several times [14–17]. What specific biomechanical and musculoskeletal factors were involved in these transformations are open questions, although outwardly little else might seem to have changed [14,17].

There has been much discussion on the orientation of the vertebral column in dinosaurs [19,20,34,59,69,70,75,91] but little resolution. The modern consensus seems to be that, like other archosaurs, dinosaur trunks were oriented near-horizontally, but likely with much phylogenetic/behavioural variation [40,78]. Trackway evidence supports this conclusion; the early notion that dinosaurs routinely dragged their tails has long been dismissed by these data and tail functional anatomy [3,34]. Similarly, various studies have interpreted the relationship between limb joint anatomy and orientation in archosaurs, particularly dinosaurs, quite differently – some contended that similar femoral condyle morphology indicates very flexed knees in small and large theropods alike [75,78,79] (but see [23]), whereas others inferred that these flexed articulations were only used in extreme joint positions, favouring a more straightened limb in large theropods [69]. I have argued elsewhere [59] that this qualitative evidence is inconclusive, as possible limb orientations in most non-avian theropods span a wide range from fairly vertical to strongly flexed [33].

The controversies about vertebral column and limb orientation benefit much from a biomechanical perspective, as this elucidates the relative benefits and tradeoffs of specific poses [59,62]. Although the consensus (reviewed above; Fig. 1) is that the femur was held in a more vertical position (during standing and slow movement at least) in non-avian theropods compared with birds, this neither means that it was completely vertical nor only trivially less flexed than the poses used by extant birds – it likely was positioned somewhere between these extremes. This ambiguity is not trivial either – slight differences in limb orientation could have massive effects on limb mechanics (see below; also [58–60,62]). Hence this mystery is an important one

for understanding the evolution of stance and gait in dinosaurs and other archosaurs, and below I provide a simple example of how it could be clarified.

Available evidence supports the hypothesis that some coelurosaurs stood and moved in more crouched ‘bird-like’ poses, but still not in the same way as extant birds do, and it is expected that this would even apply to basal birds like *Archaeopteryx*. Yet the timing, tempo, and sequence of these changes during theropod evolution are ambiguous. It is widely agreed (reviewed above) that the ancestor of crown-group birds and a few outgroups (Ornithurae) stood and moved much like living birds do, but how much locomotion changed before this clade is an interesting question. As heavy, muscular theropod tails turned into ‘dynamic stabilizers’ and thence into the fronds and finally fans of feathered flyers [42,44], with the grasping arms following suit as they transformed into wings, what happened to hindlimb function, the third ‘locomotor module’ [45]? Did the hindlimbs have much to do with the origin of flight [31,71,73] or were they mainly ‘along for the ride’? The quickening pace of fossil discoveries, the validation and application of biomechanical tools, and better insight into how living archosaurs work are together refining phylogenetic inferences about archosaur locomotor evolution. Therefore we can expect robust answers to many of these questions.

5. Principles of limb orientation: one way forward

I provide here a simple example of how a biomechanical perspective could reveal details about how archosaurs stood and moved. A concept implicit in most previous studies of archosaur locomotion is that, particularly in bipeds, for a given orientation of one limb joint, there is a fairly narrow range of orientations of the other limb joints that would be functional for standing and moving. Hence if the hip joint of a bipedal archosaur was fairly flexed, the knee joint must have been so as well, and this ‘zigzag’ arrangement should have continued down the limb. Conversely, a more extended hip joint (i.e. near-vertical femur) would require a straighter knee.

In Fig. 2, I use a simple 2D model of a representative bipedal archosaur [59,60] to examine how narrowly limb joint angles can be proscribed in certain conditions, with the assumption that (as during standing or moving in a striding biped) the centre of mass (CM) must be positioned over the foot to maintain stability. The hip angle is arbitrarily fixed at 50° (quite flexed), the metatarsophalangeal joint varies its angle accord-

ingly to keep the vertebral column horizontal at all joint angles of the distal limb, and the pes remains flat on the ground. A ‘static stability space’ exists for those combinations of joint angles that satisfy the conditions. The result is that if the orientation of some joints can be established (or bounded) for an extinct archosaur, the overall limb orientation could be inferred within about a 15–20° envelope for each joint.

This would still not be ideal, as for a given hip joint angle, a range of potential knee and ankle angles exists (Fig. 2). A refinement of this simple approach could narrow the envelope of static stability space. For example, extant bipeds normally keep their CM just behind the knee joint during standing or at mid-stance of locomotion [10,26,58,84], maintaining a flexor joint moment about the knee that requires a knee extensor muscle moment to balance it statically (Fig. 3A).

Two alternative strategies have problems that may explain why they are not typically observed in habitually-striding bipeds. Keeping the CM directly above the knee (Fig. 3B; i.e., a knee joint moment of zero)

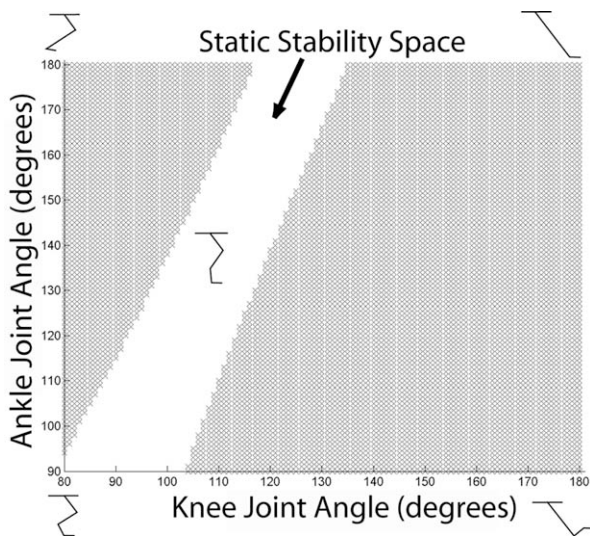


Fig. 2. Ranges of statically stable joint angles for a bipedal archosaur (*Tyrannosaurus*). See text for explanation. The hatched areas represent regions where the CM is not over the foot and hence static stability would be impossible. Stick figures in each corner and the near-centre of static stability space show the limb orientations for those regions. Taxon choice does not matter; the same qualitative conclusions would hold for any bipedal archosaur.

Fig. 2. Intervalles des angles d’articulation statiquement stables pour un archosaure bipède (*Tyrannosaurus*). Voir le texte pour les explications. Les zones hachurées représentent les régions où le CM n’est pas au-dessus du pied et où, par conséquent la stabilité statique serait impossible. Les repères, à chaque coin et proches du centre de l’espace de stabilité statique, montrent l’orientation des membres pour ces régions. Le choix du taxon n’importe pas ; les mêmes conclusions vaudraient pour tout archosaure bipède.

might be very unstable and difficult to control, as the joint moment would likely oscillate unpredictably between flexor and extensor moments. Alternatively, keeping the CM cranial to the knee (Fig. 3C) would require knee flexor muscle activity to stabilize the knee. At first this might seem useful, as many knee flexors also extend the hip and hence could balance moments about two joints at once. Yet a biped using such a strategy would need to rapidly switch from using its knee flexors to stabilize the knee to using its knee extensors in order to propel itself forward, which might be difficult to control or energetically expensive. More convincingly, extinct theropods had large knee extensor muscles with fairly high mechanical advantage about the knee joint [57,59,62,77,87], much as extant birds and humans do [10,58]. Presumably they habitually used these muscles to balance knee flexor moments during standing and moving, as extant bipeds do. In other words, the mechanism of using knee extensor muscles to balance a GRF (or CM) that is behind the knee is most reasonably assumed to be homologous for bipedal dinosaurs, including birds. Hence reconstructions of bipedal archosaurs standing or walking with their CM far in front of their knees at mid-stance are less plausible than the mechanism outlined here, and demand strong justification.

Certainly during running a more dynamic mechanism of stabilization might be important, and during phases of the stride before/after mid-stance the CM is often in front of the knee (e.g., [26]). Regardless, within

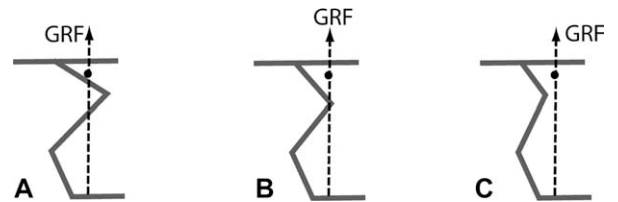


Fig. 3. Right hindlimbs of generalized bipeds in three different poses, showing three strategies for positioning the centre of mass (CM; dot) and ground reaction force (GRF; assumed to pass through the CM) relative to the knee joint during standing or mid-stance of locomotion (modified from [58]): A, CM behind the knee as in extant striding bipeds; B, CM in line with the knee joint centre, resulting in a negligible knee joint moment; C, CM in front of the knee, requiring active knee flexor muscles to balance.

Fig. 3. Membres arrière droits de tous les bipèdes dans trois différentes postures, montrant trois stratégies de positionnement du centre de gravité (CM: point) et force de pesanteur (GRF supposée passer au travers du centre de gravité) pour l’articulation du genou, pendant la locomotion en station debout ou à moitié (modifié d’après [58]) : A, centre de gravité en arrière du genou, comme les bipèdes actuels marchant à larges enjambées ; B, centre de gravité en ligne avec l’articulation du genou ; C, centre de gravité en avant du genou, requérant des muscles de flexion du genou actifs pour équilibrer.

the range of limb orientations that could keep the CM over the foot at mid-stance, only some of these orientations would satisfy other biomechanical criteria. Additional information about position of the GRF (probably close to midway along the foot), muscle fibre strain or force production, cost of muscle force generation, passive force contributions to balance, or inertial effects from body segment dynamics would likely narrow this range further. Explicit and quantitative approaches like this would augment specific reconstructions of how particular archosaurs stood and moved. By integrating such data from multiple taxa we could achieve detailed inferences about how their locomotion evolved.

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