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Disparity and convergence in bipedal archosaur locomotion

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This study aims to investigate functional disparity in the locomotor apparatus of bipedal archosaurs. We use reconstructions of hindlimb myology of extant and extinct archosaurs to generate musculoskeletal biomechanical models to test hypothesized convergence between bipedal crocodile-line archosaurs and dinosaurs. Quantitative comparison of muscle leverage supports the inference that bipedal crocodile-line archosaurs and non-avian theropods had highly convergent hindlimb myology, suggesting similar muscular mechanics and neuromuscular control of locomotion. While these groups independently evolved similar musculoskeletal solutions to the challenges of parasagittally erect bipedalism, differences also clearly exist, particularly the distinct hip and crurotarsal ankle morphology characteristic of many pseudosuchian archosaurs. Furthermore, comparative analyses of muscle design in extant archosaurs reveal that muscular parameters such as size and architecture are more highly adapted or optimized for habitual locomotion than moment arms. The importance of these aspects of muscle design, which are not directly retrievable from fossils, warns against over-extrapolating the functional significance of anatomical convergences. Nevertheless, links identified between posture, muscle moments and neural control in archosaur locomotion suggest that functional interpretations of osteological changes in limb anatomy traditionally linked to postural evolution in Late Triassic archosaurs could be constrained through musculoskeletal modelling.

Keywords: archosaur; locomotion; bipedalism; *Poposaurus*; convergence; modelling

1. INTRODUCTION

The clade Archosauria contains a staggering level of morphological, functional and ecological diversity that includes living birds and crocodilians, in addition to an array of enigmatic extinct forms such as dinosaurs and pterosaurs [1,2]. Since Romer's seminal work on limb anatomy and myology [3,4], archosaur locomotion in particular has stood as a perpetual subject of interest and debate in vertebrate palaeontology and comparative biomechanics. Romer's work on extant and extinct archosaurs was built upon in a series of influential and widely cited studies examining the relationship between osteological anatomy and limb posture in lepidosaurs, crocodilians and dinosaurs [5–7]. However, it was not until formal recognition of living birds as the direct descendants of Mesozoic theropod dinosaurs that the true magnitude of variation in archosaur limb morphology and function was fully appreciated within an evolutionary framework [8–11].

Understanding this disparity requires a unified biomechanical and evolutionary perspective and, in recent years, fossils have played a fundamental role in elucidating aspects of avian biological and functional evolution [9]. Indeed, the study of form–function evolution in the musculoskeletal system of 'avian-line' (ornithodiran) archosaurs has reached real maturity, with the marrying of traditional anatomical studies with sophisticated mathematical–computational approaches [9–13]. By providing an insight into the musculoskeletal mechanisms used to achieve locomotion in extinct archosaurs, these functional analyses potentially offer a means to more directly test hypotheses about the evolution of archosaur locomotion, selective pressures behind disparate and convergent morphologies, and their relationship to shifts in ecology and biodiversity through the Mesozoic [1,2,5–7,14–17].

Work in this area has to date focused largely on form–function evolution along the theropod-bird lineage [9–11] and on the engineering challenges of large multi-ton body size in animals such as *Tyrannosaurus* [12,13]. In contrast, extinct crocodile-line (pseudosuchian) archosaurs have received considerably less attention, particularly from serious biomechanical analysis. This is highly surprising, given that the fossil record documents significant
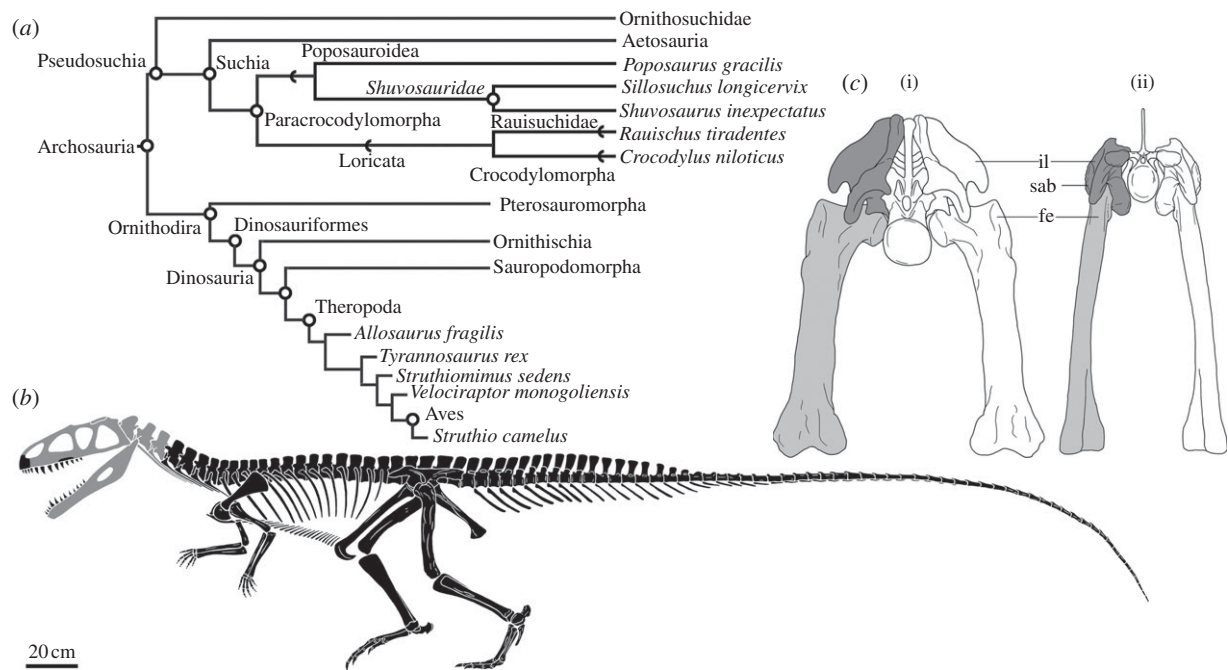
Figure 1. (*a*) Simplified phylogeny for Archosauria modified from Nesbitt [16]. (*b*) Idealized diagrammatic illustration of the articulated skeleton of *Poposaurus gracilis* (YPM 57100) in left lateral view, redrawn and modified from Gauthier *et al.* [8]. (*c*) Diagram of the ornithodiran 'buttress erect' hip in *Tyrannosaurus rex* (i), and the suchian 'pillar erect' hip in *Poposaurus* (ii) in caudal view with the pubes and ischia removed; modified from Schachner *et al.* [18]. Fe, femur; il, ilium; sab, supra-acetabular buttress.

anatomical (and by inference functional) disparity in their locomotor apparatus, particularly during the Late Triassic, a time of major shifts in biodiversity in terrestrial vertebrate communities [1,2,14]. During this period, pseudosuchian archosaurs underwent evolutionary shifts in locomotor posture, between both quadrupedalism and bipedalism and sprawling to more erect forms, and evolved body plans strikingly similar or convergent to dinosaurs [1,2,14–17]. As a result, locomotion has featured prominently in the heated debate surrounding diversification and extinction during the Late Triassic, and the rise of the dinosaurs [1,2,5–7,14]. However, the hypotheses of functional convergence and mechanical performance between pseudosuchians and dinosaurs (related to concepts of competition and superiority [1,2,5–7,14]) that underpin this controversy remain untested.

Herein, we aim to investigate the evolution of functional disparity in the locomotor apparatus of bipedal archosaurs. In particular, we provide a detailed biomechanical investigation of pelvic and hindlimb muscle mechanics in a bipedal poposauroid (a sub-clade of extinct pseudosuchian archosaurs that includes many bipedal taxa), with the aim of understanding the similarities and differences between the evolution of upright bipedal posture and locomotion in non-dinosaurian archosaurs and the theropod lineage that gave rise to extant birds (figure 1). Our analysis is facilitated by the discovery of a new, largely complete and articulated specimen of *Poposaurus gracilis* (YPM 57100; figure 1*b*), which represents the most complete poposauroid skeleton known to date, and is probably the most complete bipedal basal (non-ornithodiran) archosaur yet discovered [8,18]. The exceptional preservation of this specimen has conserved the majority of the muscle attachment sites on the pelvic and hindlimb skeletal elements,

enabling a phylogenetically based reconstruction of hindlimb myology [18] (figure 2*a*).

Investigating functional disparity in bipedal archosaur locomotion will be addressed through a number of more specific questions. Reconstruction of the musculotendinous system of a number of archosaurs in three-dimensional biomechanical models (figure 2) enables us to address our first two research questions: (i) how disparate are hindlimb muscle moment arms in bipedal archosaurs and (ii) how different are their muscle activation patterns? This is performed by comparing three-dimensional muscle moment arms in a number of exemplar living and extinct archosaurs (figure 2*b*–*e*) using our modelling approach. By providing estimates of muscle moment arms, this methodology provides valid mechanical comparisons between extinct and extant taxa, and as such, is particularly attractive in the study of fossil species for which other aspects of muscle design (e.g. muscle masses and architecture) are not available [9]. However, just how important is this unfossilized information on muscle design, and what similarities and differences between bipedal archosaurs might be missed by simply restricting analyses of fossil taxa to basic mechanical parameters such as moment arms? To address this important issue, we therefore also tackle two further questions in this study: (iii) to what extent are moment arms diagnostic of specific aspects of locomotion in archosaurs (such as habitual posture and limb kinematics)? or alternatively (iv) are other aspects of muscle design (e.g. mass, architecture, length, etc.) more diagnostic or 'optimized' for habitual gait?

In addition to modelling, we therefore also assemble quantitative muscle data from studies of extant archosaurs to investigate correlations between muscle properties
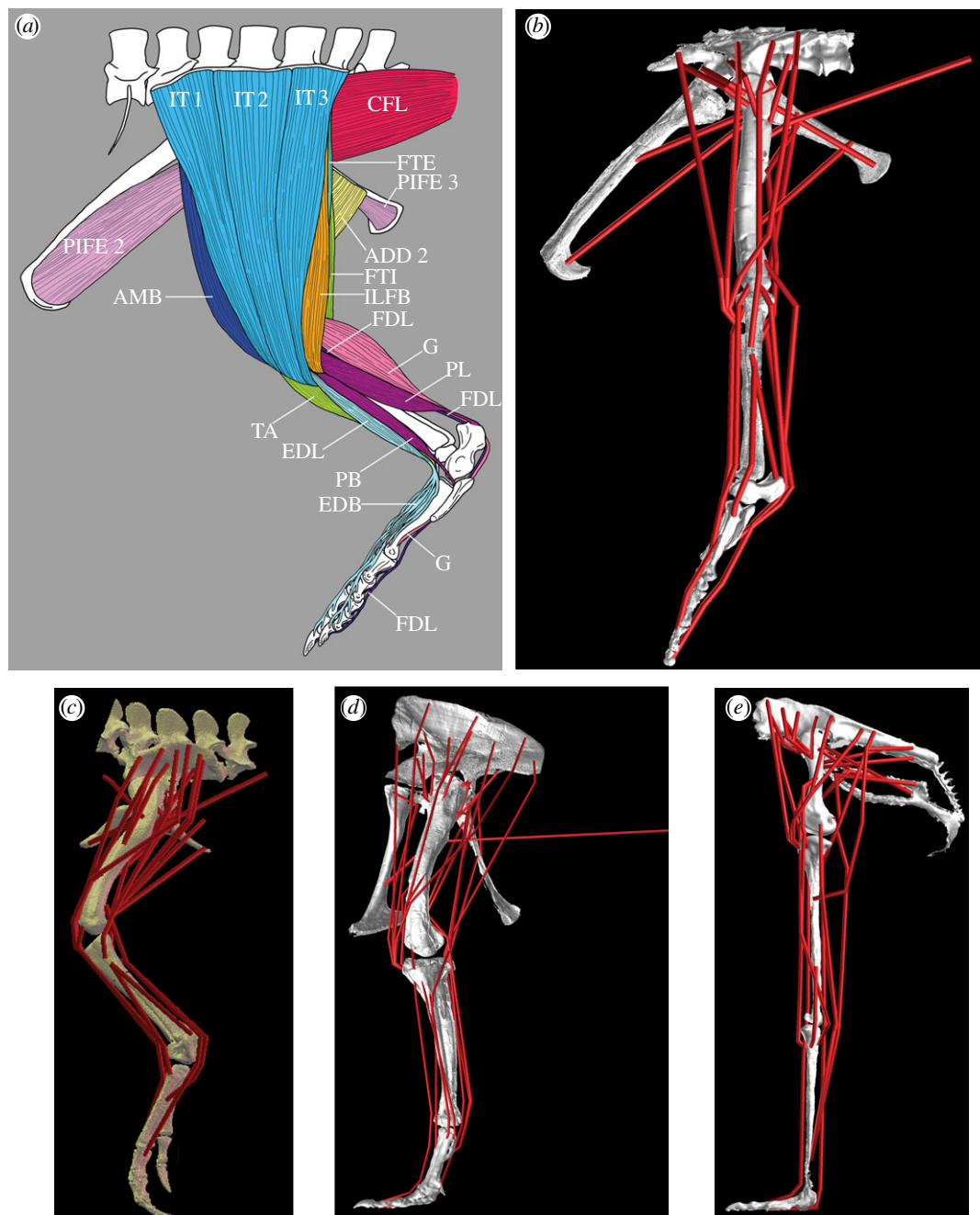
Figure 2. (*a*) Hindlimb myology of *Poposaurus gracilis* YPM 57100 (modified from Schachner *et al.* [18]) and the three-dimensional musculoskeletal models of (*b*) *Poposaurus*, (*c*) *Alligator*, (*d*) *Allosaurus* and (*e*) the ostrich in left lateral view (see table 1 for abbreviations). (Online version in colour.)

(e.g. size and architecture) and overall locomotor style. Specifically, we compare living taxa with diverse locomotor strategies in terms of how muscle mass is functionally distributed within their hindlimbs [19–23], and use the concept of muscle 'function space' [21] to explore structure–function links in muscle design. Combining knowledge of these parameters in extant taxa with data from our modelling analysis addresses two fundamental questions in evolutionary biomechanics: how are animals adapted to the functions they perform and is this discernable from fossil evidence? In the current context, this study provides a preliminary dataset to begin disentangling the evolutionary sequence of musculoskeletal changes associated with the various postural shifts that occurred in extinct archosaurs.

2. MATERIAL AND METHODS

2.1. Three-dimensional muscle moment arms

The moment arm, or leverage, of a muscle–tendon unit can be defined as the shortest perpendicular distance from the joint centre of rotation to the muscle's line of action. Moment arms provide qualitative definition of muscle function in terms of the direction of torque they impart at joints, and are fundamental to quantifying how forces generated by muscles are converted to torques at joints. Three-dimensional musculoskeletal models of *Poposaurus* (YPM57100; figure 2*b*), *Alligator mississippiensis* and three ornithodiran bipeds (*Allosaurus fragilis*, MOR693; *Struthiomimus sedens*, BHI1266; and an extant paleognath bird, the ostrich,

Struthio camelus) were constructed in order to quantitatively compare locomotor anatomy by predicting pelvic and hindlimb muscle moment arms (figure 2). These taxa were chosen specifically because they belong to theropod sub-groups ('carnosaurs' (large-bodied tetanurans) and Ornithomimosauria) to which bipedal pseudosuchians have been directly compared by previous researchers [1,2,14–17]. The ostrich and *Alligator* specimens were chosen because limb segment lengths closely matched those of specimens for which muscle architecture and moment arms have been published [19–21]. Information on digitization and model construction can be found in the electronic supplementary material.

Pelvic limb muscle attachments in *Poposaurus* were based on Schachner *et al.* [18] (figure 2a), and the myologies of the non-avian theropod models were derived from previous reconstructions [10,12,13] (see electronic supplementary material). In the absence of extensive soft tissue preservation in fossils, the definition of muscle paths was guided by information from homologous muscles in extant taxa and osteological correlates of muscle origin and insertion sites [10,12,13]. Muscle homologies and abbreviations are listed in table 1. Biomechanical analyses of the models were carried out in GAITSYM [13]. Effective moment arms of each muscle for joint flexion–extension at all major hindlimb joints, along with the abduction/adduction and long-axis rotation moment arms of muscles crossing the hip joint, were estimated. The flexion–extension muscle moment arms in the ostrich model closely match experimentally measured values [18] (see electronic supplementary material), and we therefore infer that predicted abduction/adduction and long-axis rotation moments are good estimates of values for this taxon. Additional data on flexion–extension moment arms in *Tyrannosaurus* and *Velociraptor* were extracted from the literature [12,24] to provide more complete phylogenetic coverage of bipedal ornithodirans. Rather than discuss the relationship between posture and three-dimensional moments arms on a muscle-by-muscle basis (which would require comparison of over 200 individual muscles), we concentrate on muscle groups cited as key to three-dimensional control of the hip joint in archosaurs [9,10,12,24–27] and gross comparisons of muscle–joint mechanics by summing muscle moments for a given function (e.g. flexion, extension, etc.) at each joint angle measured. Moment arms are normalized by the relevant segment length to account for size differences.

2.2. Archosaur muscle data

Moment arms allow quantitative comparison of muscle function, but gait is also determined by the size, architectural geometry and contractile properties of muscle–tendon units (data not available for fossil taxa). Rather than ignore these crucial aspects of locomotor biology, we explore the disparity in hindlimb muscle parameters available in the literature for living archosaurs and lepidosaurs [19–23]. First, we focus on how muscle mass is functionally distributed within the limbs of a number of taxa from these groups by calculating the percentage of hindlimb muscle capable of inducing specific directional torque at each joint (e.g. hip extension versus flexion, hip adduction versus abduction, etc.). Second, we sought to investigate how gross size and architectural properties of proximal hindlimb musculature varied between an exemplar semi-erect, quadrupedal archosaur and an obligate bipedal archosaur. For comparison, hip muscle fibre lengths (FLs) from *Alligator* [21] and ostriches [19] were normalized to body mass$^{0.33}$ and muscle physiological cross-sectional areas (PCAs) to body mass$^{0.67}$. Plotting FLs against PCAs produces a muscle 'function space', providing a basic insight into the relative working range and force-generating capacity of muscles within and between taxa (see Allen *et al.* [21] for discussion). For example, muscles with both relatively large PCAs and FLs are expected to be designed for exerting comparatively high forces over long contraction distances. Relatively smaller PCAs are considered indicative of lower force capability and shorter FLs of reduced contraction working range or distance [21]. In a study of *Alligator* muscle function, Allen *et al.* [21] conceptualized the distribution of locomotor muscles in this function space into a number of categories, which are subsequently followed here. Specifically, muscles with relatively large PCAs and FLs are considered 'high-power specialists', muscles with high PCAs but shorter fibres are considered 'force specialists' and muscles with low PCAs and relatively long fibres are considered 'displacement specialists'. Other factors, such as contraction velocity and moment arm, may exaggerate or mediate differences between muscles in this function space. Where appropriate we integrate moment arm data from our three-dimensional musculoskeletal models to further inform our comparison of muscle function but, for the purpose of this preliminary study, we make the simplification of assuming constant contraction velocity across muscles [21].

3. RESULTS

3.1. Muscle moment arms

Muscle moment arm polarities and joint angle relationships in key hip muscle groups [10] are generally conservative despite the shifts in skeletal architecture, posture, body size and locomotor behaviour covered by our sample taxa (figure 3; see electronic supplementary material for full data). This suggests that muscle origins and insertions remained relatively stable with respect to the hip joint across Archosauria. However, a number of interesting differences and trends are present in the data. CFB abducts the femur in *Poposaurus*, but is an adductor in all other taxa (figure 3b). The cranial portion of the IF group has a much larger medial rotation moment arm in the ostrich (figure 3d). PIFE1 (figure 3e) and 2 extend the hip and rotate the femur laterally in the ostrich, but are hip flexors and medial rotators in all other taxa. Abduction–adduction and long-axis rotation moment arms are consistently low in *Poposaurus*, whereas adduction moment arms are generally low in the ostrich but high in *Alligator* (figures 3 and 4).

Much of the above is reflected in the summed moment arm data (figure 4). The sum of hip extensor moment

Table 1. Homologies and abbreviations of the pelvic and hindlimb muscles in select extant diapsids. There is some variation within the different groups with respect to muscle presence and morphology, so the condition listed is representative of the inferred plesiomorphic state for the group. Not all pedal muscles are included (based on earlier studies [8,15]).

squamata	crocodylia	aves
muscles from the pelvis		
M. iliotibialis (IT)	M. iliotibialis 1 (IT 1)	M. iliotibialis cranialis (IC)
—	M. iliotibialis 2 (IT 2)	M. iliotibialis lateralis (IL)
—	M. iliotibialis 3 (IT 3)	M. iliotibialis lateralis (IL)
M. ambiens (AMB)	M. ambiens 1 (AMB 1)	M. ambiens (AMB)
—	M. ambiens 2 (AMB 2)	—
M. femorotibialis (FT)	M. femorotibialis externus (FMTE)	M. femorotibialis lateralis (FMTL)
—	M. femorotibialis internus (FMTI)	M. femorotibialis intermedius (FMT)
—	—	M. femorotibialis medialis (FMT)
M. iliofibularis (ILFB)	M. iliofibularis (ILFB)	M. iliofibularis (ILFB)
M. iliofemoralis (IFM)	M. iliofemoralis (IFM)	M. iliofemoralis externus (IFM)
—	—	M. iliotrochantericus caudalis (ITC)
M. puboischiofemoralis internus 1 (PIFI)	M. puboischiofemoralis internus 1 (PIFI 1)	M. iliofemoralis internus (IFI)
M. puboischiofemoralis internus 2 (PIFI)	—	M. iliotrochantericus medialis (ITM)
M. puboischiofemoralis internus 3 (PIFI)	M. puboischiofemoralis internus 2 (PIFI 2)	M. iliotrochantericus cranialis (ITCR)
M. pubotibialis (PT)	—	—
M. puboischiotibialis (PIT)	M. puboischiotibialis (PIT)	—
M. flexor tibialis internus 1 (FTI)	M. flexor tibialis internus 1 (FTI)	—
—	M. flexor tibialis internus 2 (FTI)	—
M. flexor tibialis internus 2 (FTI)	M. flexor tibialis internus 3 (FTI)	M. flexor cruris medius (FCM)
—	M. flexor tibialis internus 4 (FTI)	—
M. flexor tibialis externus (FTE)	M. flexor tibialis externus (FTE)	M. flexor cruris lateralis pars pelvica (FCL)
M. adductor (ADD)	M. adductor 1 (ADD 1)	M. puboischiofemoralis pars medialis (PIFM)
—	M. adductor 2 (ADD 1)	M. puboischiofemoralis pars lateralis (PIFL)
M. puboischiofemoralis externus (PIFE)	M. puboischiofemoralis externus 1 (PIFE 1)	M. obturatorius lateralis (OL)
—	M. puboischiofemoralis externus 2 (PIFE 2)	M. obturatorius medialis (OM)
—	M. puboischiofemoralis externus 3 (PIFE 3)	—
M. ischiotrochantericus (ISTR)	M. ischiotrochantericus (ISTR)	M. ischiofemoralis (ISF)
M. caudofemoralis brevis (CFB)	M. caudofemoralis brevis (CFB)	M. caudofemoralis pars pelvica (CFP)
M. caudofemoralis longus (CFL)	M. caudofemoralis longus (CFL)	M. caudofemoralis pars caudalis (CFC)
muscles to the pes		
M. gastrocnemius lateralis (G)	M. gastrocnemius externus (G)	M. gastrocnemius pars lateralis (G)
—	—	M. gastrocnemius pars intermedia
M. gastrocnemius medialis (G)	M. gastrocnemius internus (G)	M. gastrocnemius pars medialis (G)
M. tibialis anterior (TA)	M. tibialis anterior (TA)	M. tibialis cranialis (TA)
M. popliteus	M. popliteus	M. popliteus
M. peroneus longus (PL)	M. peroneus longus (PL)	M. fibularis longus (FL)
M. peroneus brevis (PB)	M. peroneus brevis (PB)	M. fibularis brevis (FB)
M. extensor digitorum longus (EDL)	M. extensor digitorum longus (EDL)	M. extensor digitorum longus (EDL)
M. extensor digitorum brevis (EDB)	M. extensor digitorum brevis (EDB)	—
M. flexor digitorum longus (FDL)	M. flexor digitorum longus (FDL)	M. flexor digitorum longus (FDL)
M. flexor digitorum brevis (FDB)	M. flexor digitorum brevis (FDB)	—
M. extensor hallucis longus (EHL)	M. extensor hallucis longus (EHL)	M. extensor hallucis longus (EHL)
M. flexor hallucis longus (FHL)	M. flexor hallucis longus (FHL)	M. flexor hallucis longus (FHL)

arms in all taxa vary considerably with joint angle, but all peak at similar moderately flexed joint angles, and decrease with hip flexion and extension (figure 4*a*). *Alligator* and *Poposaurus* have summed flexor moment arms lower than ornithodiran taxa (figure 4*b*). Both hip abduction (figure 4*c*) and adduction (figure 4*d*) moment arms

also show a clear taxonomic signal in their relative magnitudes. *Poposaurus* has the lowest summed moment arms for abduction and adduction, followed by non-avian theropods. The ostrich has extremely high values for hip abduction but values equally as low as *Poposaurus* for hip adduction (figure 4*c,d*). *Alligator* has similar
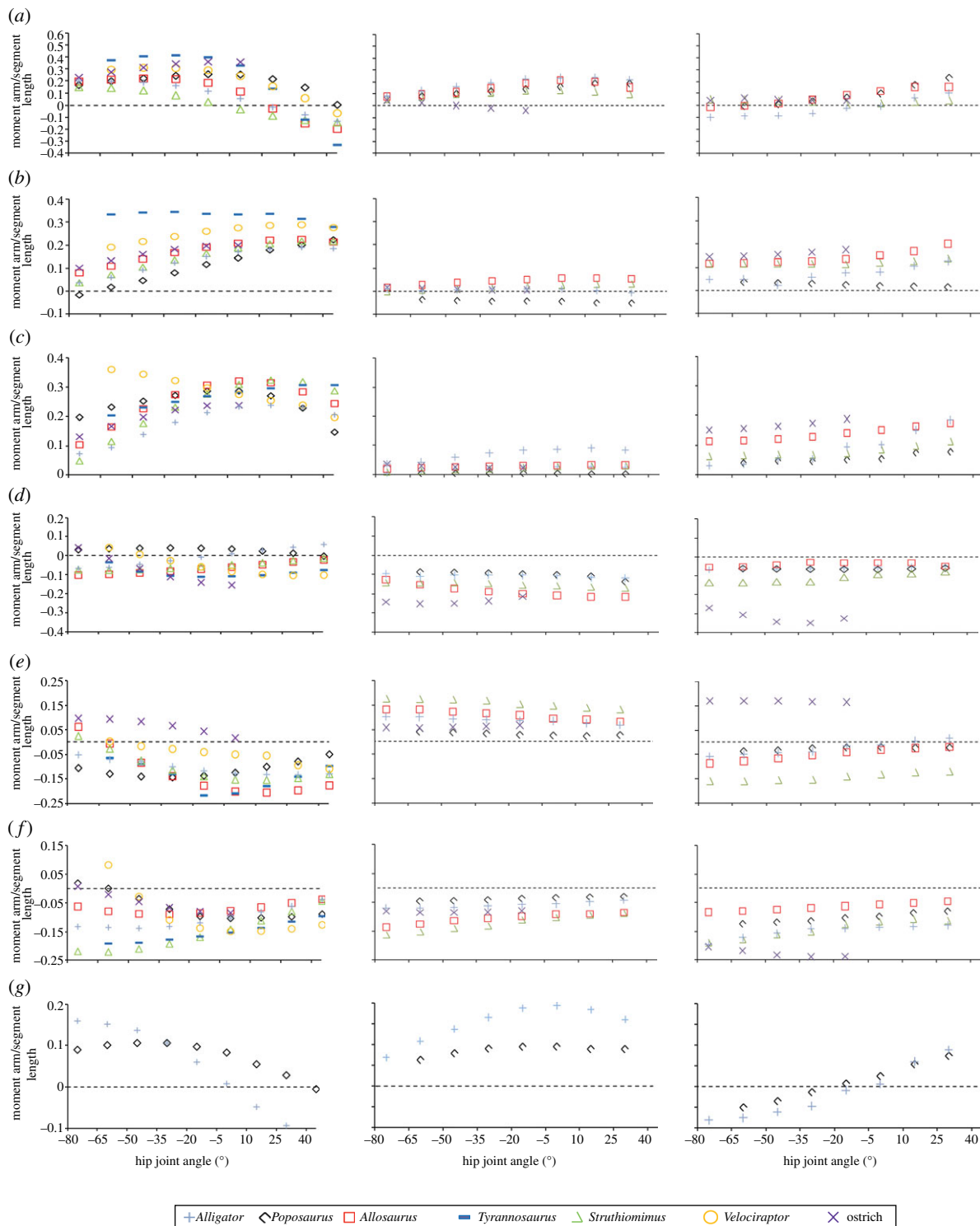
Figure 3. Predicted pelvic muscle moment arms for hip flexion–extension (left), abduction–adduction (centre) and long-axis rotation (right) in key muscle groups (*a*) ADD1, (*b*) CFB, (*c*) CFL, (*d*) IF, (*e*) PIFE1, (*f*) PIFI2 and (*g*) PIT over a range of hip joint flexion–extension angles. See table 1 for abbreviations. All data normalized by femoral length. Only flexion–extension data are available for *Tyrannosaurus* and *Velociraptor* from previous studies [12,24], while PIT is present only in *Poposaurus* and *Alligator*, having been lost in ornithodirans (see text for discussion). (Online version in colour.)

overall leverage for abduction as non-avian theropods (figure 4*c*), but has by far the highest summed adduction moment arms (figure 4*d*). Predictions for both medial and lateral femoral long-axis rotation produce a similar pattern; *Poposaurus* has the lowest moment arms, with moderately higher magnitudes for non-avian theropods and *Alligator*, and significantly higher magnitudes for the ostrich.

In the rotary crurotarsal ankle joint, the astragalus is fixed to the distal end of the tibia and fibula. The calcaneum rotates about a peg-like, laterally directed process on the astragalus, bringing about flexion and extension of the ankle. Without preservation of any soft tissues around the ankle, the range of motion possible at the joint between the calcaneum and metatarsals in *Poposaurus* is unclear, and so we present moment arm data
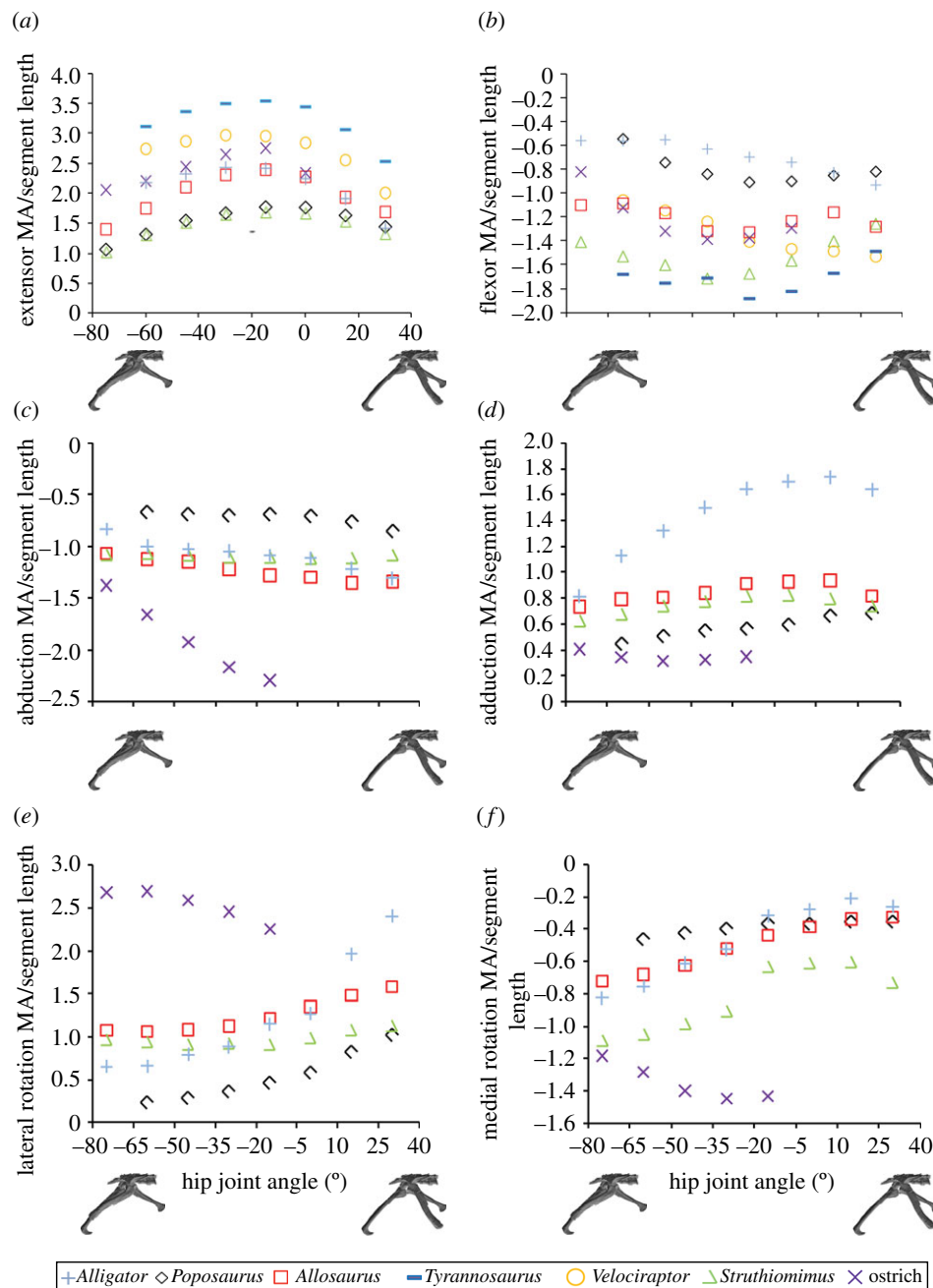
Figure 4. Sum of (*a*) hip extensor, (*b*) hip flexor, (*c*) hip abduction, (*d*) adduction, (*e*) lateral femoral rotation and (*f*) medial femoral rotation muscle moment arms normalized by segment length for *Poposaurus*, *Alligator* and ornithodiran bipeds (for further comparisons, see electronic supplementary material). All data normalized by femoral length. Only flexion–extension data are available for *Tyrannosaurus* and *Velociraptor* from previous studies [12,24]. (Online version in colour.)

for both the astragalo-calcaneal and calcaneo-metatarsal joints separately, and in the former case over a wide range of joint angles that likely exceeds maximum flexion possible at this joint. At both joints, significantly higher ankle extensor leverage is predicted for *Poposaurus* relative to ornithodiran bipeds and *Alligator* (figure 5) as a direct result of the enlarged calcaneal tuber, which displaces the gastrocnemius and digital flexor muscles caudally with respect to the ankle joints (figure 2*a*). If ankle extensors are allowed to pass through the tuber in the *Poposaurus* digital model to artificially mimic the passage of the ankle extensor tendons along the caudal surface of the astragalus as in ornithodiran taxa, then

ankle extensor moment arms are reduced to broadly similar magnitudes (figure 5).

3.2. Extant archosaur muscle distribution and function

The relative contribution to total hindlimb muscle mass of muscles with predominantly hip extension and medial rotation moment arms varies considerably between sampled taxa (figure 6*a*). Lateral rotators are also somewhat varied, though they have a noticeably higher contribution in *Alligator* than in other taxa (figure 6*a*). However, most other categories show at least moderate
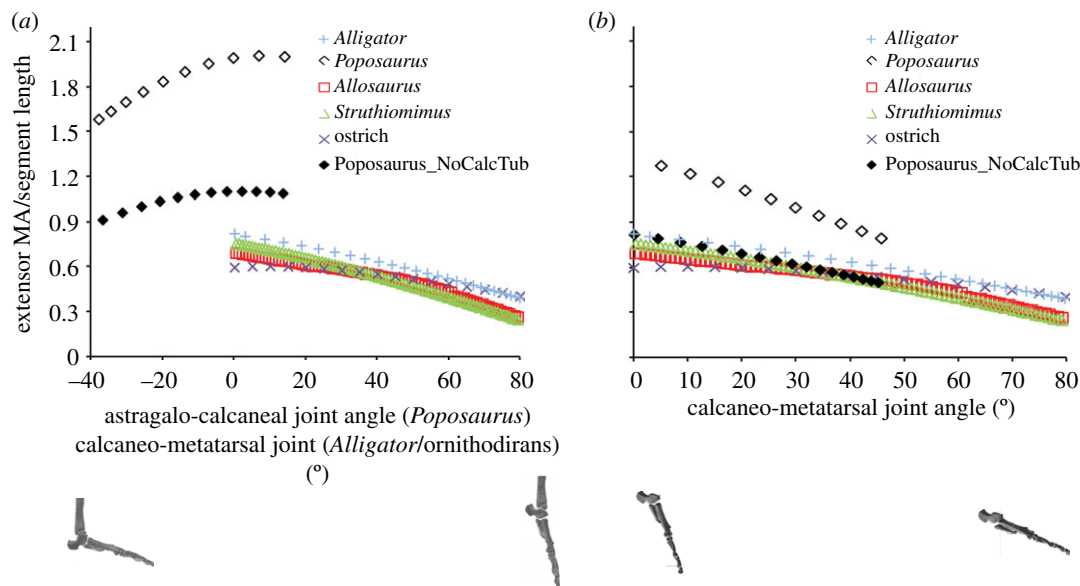
Figure 5. The sum of ankle extensor moment arms normalized by segment length across a range of ankle flexion–extension joint angles in our sample of taxa. (*a*) Extensor moment arms of *Poposaurus* about the crus–calcaneum joint versus the calcaneum–metatarsal joint in other taxa and (*b*) extensor moment arms across the calcaneum–metatarsal joint in all taxa. The enlarged calcaneal tuber of *Poposaurus* gives its ankle extensor muscles significantly greater moment arms, particularly at extended joint postures. If ankle extensors are allowed to pass through the calcaneal tuber in the model, then moment arms are more similar to *Alligator* and the ornithodiran bipeds. All data normalized by length of the metatarsal segment. (Online version in colour.)

distinction between more basal, quadrupedal crocodilians and lepidosaurs and derived avian bipeds in our sample. Hip flexors and adductors show the greatest disparity, with crocodilians and lepidosaurs having much higher proportion of muscle mass dedicated to these muscles than birds (figure 6*a*). Conversely, abductors tend to be relatively larger in *Gallus* and the ostrich than those of crocodilians and lepidosaurs. A clear distinction at distal joints is also evident (figure 6*b*). In more basal quadrupedal taxa, the ratio of flexor to extensor muscle mass is more equal, whereas bipedal birds invest a significantly higher proportion of distal limb muscle mass in extensors than flexors (figure 6*b*).

The normalized plot of muscle PCA against FL reveals that overall *Alligator* and the ostrich share closely aligned or overlapping total muscle function space, but vary somewhat in the relative distribution of muscles within this space (figure 6*c*). In *Alligator*, the most power-specialized hip muscles are large extrinsic muscles, namely CFL and PIFI2, and also FTE (figure 6*c*). By contrast, ILFB appears to be the only power-specialist hip muscle in the ostrich (figure 6*c*). Two muscles in the ostrich, IC and FCL, plot in the extreme displacement-specialist region of function space. Although with shorter fibres than IC and FCL in the ostrich, *Alligator* has a relatively greater number of hip muscles plotting in the displacement-specialist region (IT1, FTI4, ILFB, PIT, ADD1, ADD2, FTI2; figure 6*c*). Neither taxon appears to have highly force-specialized hip muscles, perhaps consistent with the observation that muscles operating across distal joints, rather than proximal joints, tend to have relatively large PCAs and short fibres [21]. The homologous muscles of the iliotibialis group (IT2 in *Alligator*, IL in the ostrich) are moderately force specialist (figure 6*c*). The remainder of muscles in

both taxa plot towards lower left extremity of function space and therefore range from weak displacement- to weak force-specialist (figure 6*c*).

4. DISCUSSION

In this discussion, we address our four research questions in two separate sections. First, we evaluate the moment arm estimates from our musculoskeletal models of extinct and extant archosaurs to address the questions of disparity and convergence in muscle moment arms and neuromuscular control of the hip in bipedal archosaurs (questions (i) and (ii) mentioned earlier). In the second section, we use model data, together with muscle data from the literature, to assess whether moment arms or other aspects of muscle design (specifically size and architecture) are more 'optimized' (hence predictive) of habitual gait in living archosaurs (questions (iii) and (iv) mentioned earlier).

4.1. Moment arms and neuromuscular control of locomotion in bipedal archosaurs

Predicting three-dimensional muscle moment arms in extinct taxa involves a degree of subjectivity. While many muscles have well-constrained origins and insertions in extinct taxa and conserved paths among living archosaurs, others are clearly poorly constrained by fossilized osteology (see Hutchinson *et al.* [12] for discussion). While these uncertainties must always be acknowledged when reconstructing soft tissues in extinct taxa, homologous muscles in this study were reconstructed with a consistent set of osteological correlates [10,12,13,18] (table 1) and identical geometrical constraints in each model (e.g. position and number of via points defining muscle paths), and each model was
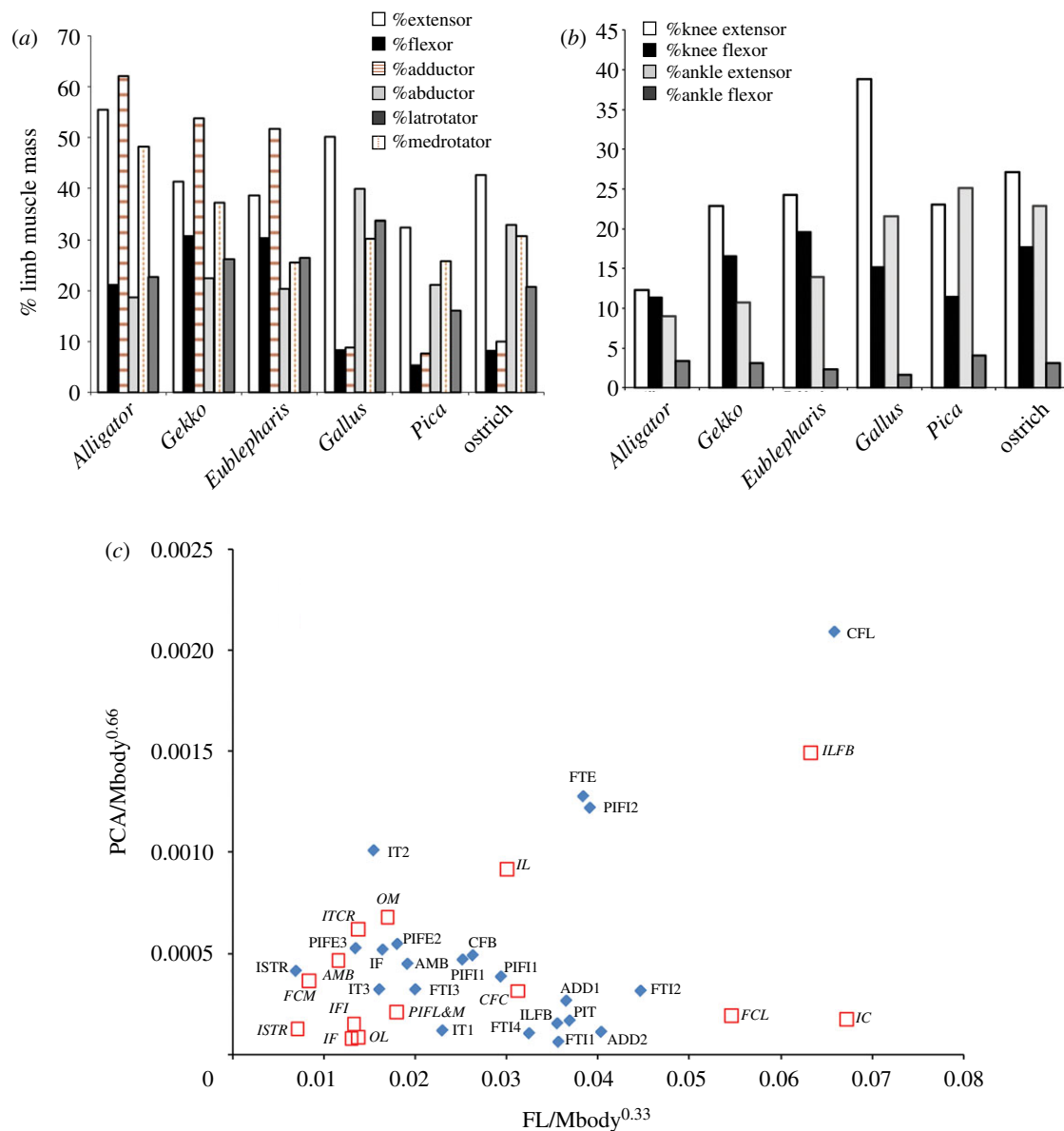
Figure 6. Muscle mass and architecture in extant lepidosaurs and archosaurs [19,21–23]. (*a*) Percentage of hindlimb muscle mass capable of exerting torque in specific directions at the hip, specifically flexion versus extension, abduction versus adduction and medial versus lateral long-axis rotation. (*b*) Percentage of hindlimb muscle mass capable of extension versus flexion at the knee and ankle joints. (*c*) Muscle function space plot (normalized PCA against normalized fascicle length) for hip muscles of *Alligator* (filled diamonds) and the ostrich (open squares). See table 1 for abbreviations. (Online version in colour.)

generated with the same methodology. When differences in osteology support clear differences in muscle moment arms, then genuine functional differences in muscular joint control can be safely inferred [10,12,13]. Given these caveats, what are the implications for (i) disparity in hindlimb muscle moments and (ii) neuromuscular control of the hip in bipedal archosaurs?

Many Late Triassic pseudosuchians, such as *Poposaurus* and *Postosuchus kirkpatricki*, were previously erroneously identified as ancestral dinosaurs or even as basal members of the Dinosauria [14]. This has led to categorization of these basal archosaurs as 'carnosaur-like' (e.g. *Postosuchus*) [17] and 'ornithomimid-like' (e.g. *Effigia*) [15,16] and the suggestion that these forms were exploiting similar ecological niches [1,14]. Whether erect posture evolved once at the base of Archosauria or independently in dinosaurs and

basal pseuoduchians is currently unclear. However, bipedal pseudosuchians developed a ventrally projecting acetabulum, or 'pillar erect' hip, in contrast to the laterally projecting acetabulum, or 'buttress erect' hip morphology of ornithodiran bipeds (figure 1).

The three-dimensional model quantitatively demonstrates that the acetabular osteology of *Poposaurus*, and by inference that of other pillar-erect pseudosuchians, is clearly synchronized with a configuration of muscle leverage significantly geared towards limb protraction–retraction rather than either abduction–adduction or long-axis rotation (figures 3 and 4). This contrasts sharply with *Alligator* (and by inference other sprawling to semi-erect quadrupedal archosauromorphs) in which high adduction and rotational moment arms aid in producing large arcs of non-parasagittal motion in abducted, rotary gaits (see later text). Bipedal poposauroids possess a

deep, perforate ventrally facing acetabulum as well as vertically orientated ilia, and lacks an offset femoral head (figures 1 and 2). Furthermore, in poposauroids the femoral head forms a rounded bulge with only slight deviation from the proximal shaft and lacks the significant medial offset achieved by the distinct neck present in dinosaurs [25,28]. The femoral head inserts tightly and ventrally into the acetabulum, and abduction–adduction and long-axis rotation are tightly constrained by the prominent supra-acetabular crest in this 'pillar erect' configuration (figure 1c). As a result, muscle insertions on the femora are situated close to both their pelvic origins and the hip joint in the mediolateral plane, producing relatively low moment arms for hip abduction–adduction and long-axis rotation (figures 3c–f and 4c–f). This configuration has a slightly lesser effect on hip adduction moment arms in *Poposaurus* (figures 3d and 4d) owing to the more distal insertions of adductor muscles (distal femoral and tibial insertions) and the fact that the femoral shaft is somewhat laterally inclined when articulated properly with the acetabulum. In tetanuran theropods, the enlarged barrel-like femoral head and neck laterally offset the proximal femur (figure 1c) and its associated muscle insertions from the mediolateral plane of the hip joint and pelvic muscle origins, thereby relatively enhancing their abduction and long-axis rotation moment arms (figures 3c,e,f and 4c,e,f). The dorsoventrally taller ilia and enlarged and laterally situated femoral trochanters of tetanuran theropods further increase the moment arms of proximal muscles for abduction and long-axis rotation [25] relative to poposauroids.

When three-dimensional hip moments are considered, *Poposaurus* differs from both *Alligator* and non-avian theropods. Indeed, in most aspects of muscle leverage (particularly abduction–adduction and long-axis rotation moment arms), large-bodied tetanurans ('carnosaurs' [17]) and ornithomimids are shown to be more similar to each other than either is to *Poposaurus* (figures 3 and 4). Furthermore, differences in specific muscles are also evident in *Poposaurus*, notably the adductor group (ADD1 and 2) and CFB. A raised process midway down the caudal aspect of the femoral shaft and a vertically oriented ridge that extends distally from this process are reconstructed as the insertion sites of ADD1 and 2 in *Poposaurus* [18]. These insertion sites of the adductor complex in *Poposaurus* are significantly larger than those in any other archosaur, extinct or extant (see electronic supplementary material). Also, Nesbitt [2] and Brusatte *et al.* [1] note that the large ventrally directed fossa present on the posteroventral surface of the ilium of poposauroids (e.g. *Poposaurus*, *Effigia* and *Shuvosaurus*) is likely analogous to the brevis fossa present in dinosaurs and subsequently reconstruct CFB origins on this surface, as we do in our models [18]. However, this example of convergent osteology is not matched in functional predictions for the associated CFB. In non-avian theropods, this muscle passes posteroventrally to the hip joint centre, producing a weak adduction moment arm, while in *Poposaurus* CFB originates and passes dorsolateral to the joint centre, yielding a weak abduction moment arm (figure 3b). *Poposaurus* also retains PIT, a muscle hypothesized to have been lost in

ornithodiran archosaurs [12], which would likely have been a major contributor to hip extension and limb retraction during stance, as in living *Alligator* [26] (see later text). Understanding the functional significance of lower leverage for non-sagittal rotation and differences in individual muscles is not straightforward (see below), but clearly these differences suggest some limit to the functional convergence of basal tetanuran theropods and bipedal pseudosuchians.

Nevertheless, obligate pseudosuchian bipeds still faced the same fundamental constraints on stability as ornithodirans, namely the need to balance a net adduction moment at the hip during limb support. During the support phase, bipedal animals typically place the foot beneath the body medial to the hip, incurring an adduction moment at the hip joint. In basal theropods, Hutchinson & Gatesy [10] proposed that stance phase hip stability was achieved through a counteractive abduction moment created by activation of the IF muscles placed dorsal to the hip joint (figure 2). In extant birds, the IF group has shifted its origin cranially, increasing its moment arm for medial rotation (figure 3d). Stance phase activation of the IF group is retained, but medial rotation of the femora is employed to counter the adduction moment of the ground reaction force (GRF). Pubic retroversion in birds also shifts the origins of the PIFE group caudal to the hip joint, switching its function from hip flexion and medial rotation to extension and lateral rotation (figure 3e).

Hutchinson & Gatesy [10] inferred a stepwise evolution from the abductor-based mode of limb support in basal bipedal Dinosauriformes to the long-axis rotational mechanism in crown-group birds. Although our phylogenetic coverage across Theropoda is not sufficient to detail the timing and specific nature of this transition, it is clear that muscle leverage for both medial and lateral femoral long-axis rotation is much higher in the ostrich relative to basal tetanurans, *Poposaurus* and *Alligator* (figures 3e,f and 4e,f). Our models, therefore, support Hutchinson & Gatesy's [10] hypothesis that rotational moment arms increased along the line to birds, and further suggest that this occurred in groups more derived than basal tetanurans (e.g. Maniraptora). Adduction moment arms are also greatly reduced in the ostrich (figure 4d), resulting largely from pubic and ischial retroversion and caudolateral expansion of the pelvis, which moved muscle origins close, and in some postures lateral, to the hip joint (switching their function to hip abduction and lateral rotation). Together with the cranial expansion of the preacetabular ilium, this explains the maintenance of relatively high abduction moment arms in the ostrich (figure 4c).

While noting differences in the magnitude of muscle leverage (figures 3 and 4), we infer that stance phase lateral limb stability in bipedal suchians was achieved in the same manner as inferred for basal theropods, specifically a support phase abduction moment generated by the IF group (figure 7), represented by IFM in *Poposaurus* [18]. Given the triradiate arrangement of the pelvis, and the likely more upright posture and caudofemoralis-driven limb retraction, it is likely that femoral abduction predominantly countered the adduction GRF moment in *Poposaurus*, rather than medial rotation as in extant

Figure 7. Hindlimb muscles hypothesized to be active during the (*a*) swing and (*b*) stance phase of locomotion in *Poposaurus*. See table 1 for abbreviations. (Online version in colour.)

birds [10], which is greatly aided by enhanced muscle leverage for this action (figures 3 and 4). In *Poposaurus,* the IF group maintains higher moment arms for abduction and a position dorsal to the hip joint, consistent with the morphology and hip abduction mode of lateral limb support proposed for non-avian theropods [10] (figures 3*d* and 4). The long slender femur of bipedal suchians is poorly suited to resisting bending and torsional stresses incurred under a flexed 'avian-like' posture and a rotational-based system of muscular support [25]. Thus we infer the same shift in neural control of the IF group from swing phase abduction and protraction (in basal quadrupedal archosaurs and *Alligator*) to stance phase abduction as hypothesized by Hutchinson & Gatesy [10] for basal Dinosauriformes (figure 6). If these hypotheses of multiple independent shifts in motor control of the IF group are correct, then this functional and neurological adaptation may be ubiquitously associated with the evolution of bipedalism in archosaurs.

Gatesy [26] showed that femoral protraction was achieved through swing phase activation of the PIFI group and PIFE1 and 2 in *Alligator*, while the CFL retracts the femur during stance, helping in controlling abduction of the lower limb (figure 3*c*) [26]. ADD1 and 2 and PIT also activate during early stance to prevent collapse by resisting femoral abduction (figure 3*a*) [26]. Major femoral protractor (e.g. PIFI1 and 2, PIFE1 and 2) moment arms in *Poposaurus* are similar to *Alligator*, and it is likely that swing phase activation of the PIFI group and PIFE1 and 2 was present in *Poposaurus* (figure 7*a*), as in extant archosaurs [10]. Thus, the plesiomorphic archosaurian stance phase activation of these muscles was likely maintained in bipedal pseudosuchians, as in quadrupedal *Alligator*, despite their change in posture (figure 7*b*).

4.2. Muscle design and locomotion in living archosaurs: how redundant is fossil evidence?

By integrating moment arm predictions from three-dimensional musculoskeletal reconstructions with muscle activation patterns measured in living taxa, it is possible to constrain aspects of limb control and habitual locomotion in extinct bipeds such as *Poposaurus* and non-avian theropods. On the basis of this data, an abductor-based mode of stance phase limb support mediated by the IF group is supported for bipedal pseudosuchians, as previously suggested for non-avian theropods [10], and it is likely that both groups used a predominantly hip-based system of limb retraction, in contrast to flexed postures and predominantly knee-based limb retraction observed in extant birds [10,25,27]. Musculoskeletal models also produce trends that appear to reflect differences in limb control and habitual locomotion in living archosaurs, notably the high leverage for hip adduction in *Alligator* important for large arcs of femoral rotation and resisting lateral limb collapse during stance in abducted postures [26]. The ostrich also has relatively high values for femoral long-axis rotation but very low hip adduction moment arms, consistent with relatively adducted posture and a rotational-based system of lateral limb support [10] (figure 4*c*,*d*).

Our first three research questions asked how disparate are muscle moment arms in archosaurs and to what extent do they appear optimized for habitual locomotion? Qualitative and quantitative disparity in muscle moment arms estimates do appear to differentiate major functional categories in terms of locomotor mechanics, specifically animals with quadrupedal rotator gaits from parasagittal bipeds, and bipeds with abductor-based versus rotation-based mechanisms of lateral limb support. However, it is clear that beyond these broad functional dichotomies, muscle moment arms alone are unable to provide clear insight into aspects of locomotion such as habitual kinematics and maximal performance. For example, hip extensor moment arms in *Alligator* are extremely similar (quantitatively and qualitatively; figures 3 and 4*a*) to the ostrich despite significant differences in the habitual limb motion and locomotor ability (e.g. running ability) of these taxa (see below). Indeed, summed leverage for hip extension is both similar in magnitude and its angular dependency in extinct and extant taxa modelled here (figure 4). This has been observed despite numerous anatomical and functional changes, such as the retention of PIT and five flexor cruris muscles in pseudosuchians (FTI1–2 and 4 are lost in neornithine birds) [10], and pubic

retroversion in birds switching the function of PIFE1 and 2 from flexion to extension (figure 3 and also see electronic supplementary material). Furthermore, where disparity in moment arms exists, it is important to remember that this may be balanced by compensatory differences in muscle mass or architecture. For example, *Alligator* is predicted to have relatively low overall leverage for hip flexion, but muscle data suggest that this may be compensated for by the relatively high mass of hip flexor muscles (figure 6*a*).

Analyses of muscle size and architecture in living archosaurs (addressing our fourth research question) strongly suggest that these unfossilized traits are more indicative or 'optimized' for habitual gait (figure 6). Even in slow running gaits (approx. 3.3 m s^{-1}), ostriches have been shown to maintain a relatively flexed hip between $-48°$ and $-60°$ [29], whereas in fast walking (approx. 0.62 m s^{-1}), *Alligator* retracts the femur from around $-40°$ hip flexion to approximately $60°$ hip extension [30]. This is a considerable difference in joint excursion and one that cannot be diagnosed from moment arms alone (figures 3 and 4). Experimental studies have shown CFL and PIFI2 to be the prime retractors (CFL) and protractors (PIFI2) of the limb in *Alligator* [26,27]. Our results suggest that CFL and PIFI2 do not have the highest flexion–extension moment arms in *Alligator*, nor are their moment arms substantially larger in *Alligator* than the ostrich (figure 3*c,f*). CFL inserts on the proximal femur and tibia and is active during stance to retract the entire limb, generating much of the power required for acceleration and gravitational support [26,27,30]. PIFI2 originates in front of hip and is active during swing to protract the limb. As noted by Allen *et al.* [21], CFL and PIFI2 are the largest muscles in the *Alligator* hindlimb, both of these extrinsic muscles plotting in the power-specialized region of muscle function space (figure 6*c*). The long FLs and high PCAs (especially CFL) of these muscles make them ideally suited for generating high forces across the large working range habitually used by *Alligator* in terrestrial locomotion [26,30].

In the ostrich, the most powerful hip extensor is ILFB (figure 6*c*), a two-joint muscle that also exerts a flexor moment at the knee. The hip extension moment arm for ILFB is considerably higher in the ostrich than *Alligator* (electronic supplementary material, figure S4*i*), consistent with the idea that synchronous hip extensor and knee flexor moments may be important during late swing and early stance in birds while the GRF passes cranial to the knee joint (see Gatesy [31] and below for discussion). Thus, differences in both architectural design and the moment arm of ILFB appear consistent with the contrasting limb segment movements in *Alligator* and the ostrich. In the ostrich, a larger PCA and extensor moment arm enable significant contribution to early stance anti-gravity support at the hip, while relatively long fibres allow force to be generated for knee flexion over a wider working range (figure 6*c*). In *Alligator*, ILFB is active near the stance–swing transition, contributing to knee flexion and femoral abduction [26], which may require less force over a shorter range of joint angles relative to the ostrich.

Homologous single-joint hip extensors in *Alligator* and the ostrich are generally consistent with their relative locomotor styles and the magnitude of hip joint excursions. Muscles of the adductor femoris group (ADD1 and 2 in *Alligator* and PIFM and PIFL in the ostrich) are noticeably more displacement specialist in *Alligator*, while the caudofemoralis of the ostrich is significantly reduced in terms of both force (PCA) and working range (FL). Pubic retroversion means that OM and OL in the ostrich (homologues of PIFE1 and 2 in *Alligator*) are single-joint hip extensors, and OM plots in force-specialized function space, though OL is moderately displacement specialized (figure 6*c*). Single-joint hip flexors (IFI, ITCR) in the ostrich also show reduced FLs and PCA compared with *Alligator* (PIFI1–2) again reflecting lesser joint excursion at the hip in birds (figure 6*c*).

Consistent with conceptualization of their locomotion as 'hip-based' and 'knee-based', the relative magnitude of joint excursion at the hip is reversed at the knee; *Alligator* exhibits less than 20° flexion–extension at the knee [30] versus 50–55° in the ostrich [29]. Knee extensors in the ostrich are spread across a wide range of function space, including those capable of generating force over larger working ranges (notably IC and IL; figure 6*c*) and large PCA, short-fibred force-specialist muscles (e.g. femorotibial group muscles; figure 6*c*). By contrast, two-joint (figure 6*c*) and one-joint knee extensors [21] in *Alligator* are predominantly force-specialist (e.g. IT2) or weakly specialized for force or displacement (i.e. more generalist; IT3, IT1, AMB), and therefore less well suited to generating force over a large working range.

The architecture of knee flexors is best understood in terms of their role in three-dimensional control of the hindlimb. In *Alligator,* members of the flexor cruris group are responsible for adducting the limb during late swing and into the stance phase [26], and indeed many knee flexors plot close to other limb adductors (e.g. ADD1 and 2) in moderately displacement-specialist function space (figure 6*c*). Hamstring muscles with moderately longer fibres may therefore reflect the use of relatively large adduction arcs in *Alligator* (approx. 35–40° at the hip [30]). FTE is active in stance in *Alligator* [26] and it is possible that this moderately power-specialist muscle (figure 6*c*) principally assists with hip extension and anti-gravity support. Ostriches habitually rotate their femora through much smaller arcs of abduction–adduction (approx. 10° [29]), and during stance they exert a medial rotation moment at the hip to resist limb collapse through adduction (rather abduction as in *Alligator*). PIT, FTI1–2 and FTI4 were lost during avian evolution [10] and it is noteworthy that birds retain flexor cruris muscles with the largest moment arms for hip extension (also important during stance) [31] and that the adduction leverage of these muscles (and others; figure 4) is reduced owing to lateral expansion of the pelvis, at least in our ostrich model, relative to *Alligator* (figures 3 and 4; electronic supplementary material).

This comparative analysis of *Alligator* and the ostrich emphasizes that muscular parameters such as size and architecture (figure 6) are highly adapted to

their usage and loading during habitual locomotion. This has a number of important implications for evolutionary biomechanics. In itself, it is an important form–function finding that muscles appear to be optimized more in terms of size and architecture rather than moment arms. These data suggest that locomotor adaptations in archosaurs have been largely achieved by selection of these traits rather than by alteration of moment arms. By emphasizing the importance of aspects of muscle design that are not directly retrievable from fossil animals, this analysis illustrates the difficulty of discerning detailed measures of gait and performance in extinct taxa.

Sophisticated computational simulations are now commonly used to study detailed muscle dynamics and locomotion in living animals, and recently some of these approaches have been used to explore aspects of gait and performance in fossil species [32–34]. The challenge facing palaeobiologists and biomechanicists attempting to construct these models for extinct archosaurs clearly lies in defining muscle properties (inputs into biomechanical models) in a meaningful and objective way. It is highly unlikely that either living crocodilians or birds provide good analogues for muscle properties in non-avian dinosaurs and bipedal pseudosuchians. It may therefore be more appropriate to employ a wider 'functional bracket' approach [33] to quantitative muscle reconstruction in extinct archosaurs. For example, muscle FLs in *Alligator* and the ostrich appear to correlate well with habitual joint excursions, perhaps suggesting FLs might be more precisely constrained or estimated as a proportion of length change over the likely range of joint motion in extinct taxa.

Where attempts have been made to simulate locomotion in extinct archosaurs, redundancies in muscle input values have been addressed using sensitivity analyses; plausible ranges for input values, rather than single values, are tested resulting in a spectrum of gait predictions [33,34]. Where fossilized osteology is similar, along with estimatable parameters such as muscle moment arms, as we have shown to be the case with bipedal pseudosuchians and non-avian theropods (figures 3 and 4), then more detailed tests of functional disparity and convergence may be extremely difficult owing to large (hence overlapping) error bars on predictions [9,34]. However, where gross anatomy differs more considerably, then functional disparity may be more robustly established. We illustrate this using a simple analysis of muscle moments at the ankle joint in our sample of archosaurs.

4.3. Archosaur ankle mechanics

Our analysis of muscle moment arms and mass distribution within the hindlimbs of extant lepidosaurs and archosaurs reveals a dichotomy in the ratio of muscle mass devoted to joint extensors versus flexors (figure 6a,b). Bipedality naturally requires greater limb joint extension capacity because only two limbs are supporting the body against gravity (versus four in quadupedality). This represents a greater constraint during locomotion, and particularly running with an aerial phase when a single limb must support the body, versus multiple limbs in a quadruped. In

archosaurs, functional disparity appears to be the greatest at the ankle joint, where skeletal morphology and moment arms also differ significantly. Pseudosuchians (and particularly *Poposaurus*; figure 5) have relatively higher ankle extensor moment arms, while crown-group birds have a much higher proportion of hindlimb muscle mass (and body mass) as ankle extensor musculature than more basal quadrupedal taxa (figure 6b). The latter is particularly true of extant ratites such as the ostrich, a trait that underpins its ability to generate high muscle torques at the ankle [19,20].

Unless basal taxa were very poor runners, these data strongly suggest that the evolution of bipedalism in ornithodirans was likely coupled with a notable increase in ankle extensor muscle mass relative to basal, quadrupedal archosaurs, possibly reaching masses proportionally similar to those in extant terrestrial birds. This phylogenetic and functional pattern clearly emphasizes the crucial role of the calcaneal tuber in bipedal pseudosuchian locomotion. By increasing ankle extensor moment arms, retention of the calcaneal tuber (plesiomorphic for Archosauria) may have eliminated the need for higher ankle extensor muscle masses hypothesized for ornithodiran bipeds. Ankle extensors in the ostrich are noticeably more power-specialized (i.e. higher PCA, longer FL) than those of *Alligator*, suggesting a higher capacity to contribute to limb acceleration and support [19–21]. These different strategies for ankle joint control may have had further consequences elsewhere in the hindlimb, particularly as most large ankle extensors also cross the knee joint in archosaurs (figure 2). Stance phase activation of ankle extensors would have synchronously imparted a flexor moment at the knee, which was probably undesirable given knee extension was likely required to contribute to straightening the limb during the second half of stance. By increasing ankle extensor moment arms in bipedal pseudosuchians, the enlarged calcaneal tuber may have produced larger muscle torques distally in the limb, without major impacts at the knee that might be incurred purely from an increased ankle extensor muscle mass. The potential for disparity in relative ankle extensor muscle masses, moment arms and lengths in pseudosuchians versus ornithodirans (figures 5 and 6) highlights this joint as a key area for future biomechanical studies of disparity in archosaur locomotor evolution.

5. CONCLUSIONS

This quantitative analysis supports inferences that bipedal suchians were generally similar to large-bodied basal tetanurans ('carnosaurs') [7,17] and ornithomimids [15,16] in their basic hindlimb muscular mechanics and neuromuscular control of locomotion. These groups independently evolved similar musculoskeletal solutions to the challenges of parasagittally erect bipedalism. Homologous muscles responsible for femoral protraction and retraction retained plesiomorphic activation patterns. However, the IF musculature, responsible for swing phase abduction in basal quadrupedal archosaurs and *Alligator*, retained its moment arm but switched to stance phase activation to provide lateral limb stability in an adducted bipedal

posture in both bipedal pseudosuchians and non-avian theropods.

Musculoskeletal models also produce moment arm estimates that appear to reflect some general differences in hindlimb control and habitual locomotion in living archosaurs. Notably, the high leverage for hip adduction in *Alligator* appears consistent with the need to adduct the limb and counteract abduction moments in rotary gaits, while high values for femoral long-axis rotation moment arms in the ostrich help facilitate the rotation-based mode of lateral stance phase support present in birds [10]. These findings support a link between posture, muscle moment arms and neural control in archosaur locomotion, and perhaps suggest that interpretations of osteological changes in pelvic and hindlimb morphology and links to postural evolution in Late Triassic pseudosuchians [1,2,5−7,14−17] could be appropriately constrained through the quantitative reconstruction of muscle moment arms, as we have carried out here.

While analyses such as these provide a quantitative measure of the convergence and disparity in musculoskeletal *bauplans* and their relationships to postural evolution, it is important to emphasize that they do not test directly for similarities or differences in gait. Muscles function to convert metabolic energy to mechanical work, and it is the rate of contraction and the amount of work performed in a single contraction–extension cycle that is the crucial muscular determinant of gait and performance. Muscle dynamics are dictated primarily by their mass, architecture and contractile properties [35], and a more sophisticated analysis is required to test for disparity and convergence beyond the resolution of the broadest functional categories (e.g. quadrupedal rotator gaits versus parasagittal gaits, bipeds with abductor-based versus rotation-based mechanisms of lateral limb support). This clearly limits our ability to even qualitatively assess how the walking and running gaits of bipedal pseudosuchians and ornithodirans may have differed dynamically in biomechanical terms. We therefore urge that our conclusions regarding comparative musculoskeletal anatomy are not over-extrapolated to make biomechanical speculations about similarities in locomotor performance in extinct taxa, and subsequently to support or reject macroevolutionary hypotheses regarding, for example, pseudosuchian and dinosaur diversity during the Late Triassic [1,2,5−7,14−17]. Analysing functional convergence and mechanical performance (related to concepts of competition and superiority [5−7,14]) from purely osteological characters—whether that be through structure–function analogies [5−7,17] or statistical measures of disparity [14] as previously attempted—ignores many important causative factors underlying form–function relationships and at best provides an abstract picture of animal locomotion. Musculoskeletal models, and their insights into functional anatomy, provide a firm foundation for further biomechanical studies to test notions of functional convergence and dominance more directly.

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