Forelimb muscle and joint actions in Archosauria: insights from *Crocodylus johnstoni* (Pseudosuchia) and *Mussaurus patagonicus* (Sauropodomorpha) (#17707)

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Forelimb muscle and joint actions in Archosauria: insights from *Crocodylus johnstoni* (Pseudosuchia) and *Mussaurus patagonicus* (Sauropodomorpha)

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One of the major transitions during the evolution of 'ruling reptiles' (Archosauria), the lineage including crocodiles and birds as well as extinct Dinosauria, was a shift from quadrupedalism to bipedalism (and *vice versa*). Those occurred within a continuum between more sprawling and parasagittal modes of locomotion and involved drastic changes of limb anatomy and function in several lineages, including sauropodomorph dinosaurs. Transformations of hindlimb form and function have long been emphasized in studies of archosaurian evolution as part of these transitions. Yet the anatomical changes and biomechanical consequences of major transitions in archosaurian forelimbs remain less well explored, especially for non-flying taxa. We present biomechanical computer models of two locomotor extremes within Archosauria in an analysis of joint ranges of motion and the moment arms of the major forelimb muscles in order to quantify biomechanical differences between more sprawling, pseudosuchian (represented by a crocodile *Crocodylus johnstoni*) and more parasagittally oriented, dinosaurian (represented by the sauropodomorph *Mussaurus patagonicus*) modes of forelimb function. We compare these two locomotor extremes in terms of the reconstructed musculoskeletal anatomy, ranges of motion of the forelimb joints and the moment arm patterns of muscles across those ranges of joint motion. We reconstructed the three-dimensional paths of 31 muscles acting around the shoulder, elbow and wrist joints. We explicitly evaluate how forelimb joint mobility and muscle actions may have changed with postural and anatomical alterations from basal archosaurs to early sauropodomorphs. We thus evaluate in which ways forelimb posture was correlated with muscle leverage, and how such differences fit into a broader evolutionary context (i.e. transition from sprawling quadrupedalism to parasagittal bipedalism and then shifting to graviportal quadrupedalism). Our analysis reveals major differences of muscle actions between the more sprawling and parasagittal models at the shoulder joint. These differences are related not only to the articular surfaces but also to the orientation of the scapula, in which flexion/extension movements in *Crocodylus* correspond to elevation/depression in *Mussaurus*. Muscle action is highly influenced by limb posture, more so than morphology. Habitual quadrupedalism in *Mussaurus* is not supported by our analysis of joint range of motion, which indicates that glenohumeral protraction was severely restricted. Additionally, some active pronation of the manus may have been possible in *Mussaurus*, allowing semi-pronation by a rearranging of the whole antebrachium (not the radius against the ulna, as previously thought). The origin of quadrupedalism in Sauropoda is not only linked to manus pronation but also to multiple shifts of forelimb morphology, allowing greater flexion movements of the glenohumeral joint and a more columnar forelimb posture.

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ABSTRACT:

One of the major transitions during the evolution of ‘ruling reptiles’ (Archosauria), the lineage including crocodiles and birds as well as extinct Dinosauria, was a shift from quadrupedalism to bipedalism (and vice versa). Those occurred within a continuum between more sprawling and parasagittal modes of locomotion and involved drastic changes of limb anatomy and function in several lineages, including sauropodomorph dinosaurs. Transformations of hindlimb form and function have long been emphasized in studies of archosaurian evolution as part of these transitions. Yet the anatomical changes and biomechanical consequences of major transitions in archosaurian forelimbs remain less well explored, especially for non-flying taxa. We present biomechanical computer models of two locomotor extremes within Archosauria in an analysis of joint ranges of motion and the moment arms of the major forelimb muscles in order to quantify biomechanical differences between more sprawling, pseudosuchian (represented by a crocodile Crocodylus johnstoni) and more parasagittally oriented, dinosaurian (represented by the sauropodomorph Mussaurus patagonicus) modes of forelimb function. We compare these two locomotor extremes in terms of the reconstructed musculoskeletal anatomy, ranges of motion of the forelimb joints and the moment arm patterns of muscles across those ranges of joint motion. We reconstructed the three-dimensional paths of 31 muscles acting around the shoulder, elbow and wrist joints. We explicitly evaluate how forelimb joint mobility and muscle actions may have changed with postural and anatomical alterations from basal archosaurs to early sauropodomorphs. We thus evaluate in which ways forelimb posture was correlated with muscle leverage, and how such differences fit into a broader evolutionary context (i.e. transition from sprawling quadrupedalism to parasagittal bipedalism and then shifting to graviportal quadrupedalism). Our analysis reveals major differences of muscle actions between the more sprawling and parasagittal models at the shoulder joint. These differences are related not only to the articular surfaces but also to the orientation of the scapula, in which flexion/extension movements in Crocodylus correspond to elevation/depression in Mussaurus. Muscle action is highly influenced by limb posture, more so than morphology. Habitual quadrupedalism in Mussaurus is not supported by our analysis of joint range of motion, which indicates that glenohumeral protraction was severely restricted. Additionally, some active pronation of the manus may have been possible in Mussaurus, allowing semi-pronation by a rearranging of the whole antebrachium (not the radius against the ulna, as previously thought). The origin of quadrupedalism in Sauropoda is not only linked to manus pronation but also to multiple shifts of forelimb morphology, allowing greater flexion movements of the glenohumeral joint and a more columnar forelimb posture.

Keywords: Crocodylia, Dinosauria, biomechanics, musculoskeletal model, quadrupedalism, bipedalism, posture, pronation, range of motion, moment arm.

INTRODUCTION

Archosauria (all descendants of the most recent common ancestor of Crocodylia and Aves) has been a highly diverse and disparate clade since the Triassic period (<250 Ma), both morphologically and ecologically. This diversity and disparity is reflected not only in the great abundance and taxonomic richness that Archosauria achieved in the past, but also in its living representatives. Terrestrial locomotion in extant archosaurs (crocodiles and birds) is split between two extremes – ‘sprawling’ quadrupeds and parasagitally erect bipeds (not to mention amphibious habits vs. flight). The evolutionary patterns that preceded and gave rise to these disparities have long been an attractive research subject (e.g. Romer, 1956; Jenkins, 1993; Gatesy & Middleton, 1997; Hutchinson & Allen, 2009; Gauthier et al., 2011; Bates & Schachner, 2012), including the study of topics such as the transition from bipedalism to quadrupedalism (e.g. Bonnan & Yates, 2007; Maidment & Barrett, 2011), and the origin of avian flight (e.g. Jenkins, 1993; Dial, 2003), among others.

The functional anatomy of these locomotor transitions has also attracted considerable research effort (Romer, 1956; Jenkins, 1993; Gatesy & Middleton, 1997; Hutchinson & Allen, 2009; Gauthier et al., 2011; Bates & Schachner, 2012). Much of the attention has focused on the evolution of the hindlimb in Dinosauriformes as it adapted to the demands of bipedal locomotion (Romer, 1923; Carrano, 2000; Hutchinson & Gatesy, 2000; Hutchinson et al., 2005; Bates & Schachner, 2012), particularly in the theropod lineage (e.g. Gatesy, 1990). However, archosaur forelimbs have also undergone major functional transformations in Archosauria. Fewer studies have dealt with changes in forelimb function during the quadruped (e.g., basal archosaurs) to biped (e.g., basal sauropodomorphs) transition (but see Hutson & Hutson, 2013, 2014; Hutson, 2015). The lineage of Triassic archosaurs leading to sauropods began as quadrupeds, transitioned to bipedality close to the base of Dinosauria, and then shifted back to quadrupedality close to or at the base of Sauropoda (Wilson & Sereno, 1998; Carrano, 2005). The evolution of bipedalism itself has been a rare event, and such reversion to quadrupedalism from bipedalism is extremely rare, with known examples confined exclusively to the Dinosauria: sauropods themselves, and independently in three branches of ornithischian dinosaurs (ceratopsians, ornithopods and thyreophorans [Carrano, 1998; Brusatte et al., 2010; Maidment et al., 2012, 2014; VanBuren & Bonnan, 2013; Hutson, 2015]).

Along the archosaur lineage leading to sauropods, forelimbs thus evolved from a role as weight-bearing locomotor modules to a variety of grasping and manipulating functions, before re-evolving weight-bearing and locomotor capacity with the transition back to quadrupedalism (e.g., Cooper, 1981; Bonnan & Senter, 2007, Bonnan & Yates, 2007; Yates et al., 2010; VanBuren & Bonnan, 2013). The biped-quadruped transition occurred between basal sauropodomorphs and basal sauropods, near the boundary or the Triassic and Jurassic periods (ca. 200 Ma). Consequently, the forelimbs of basal sauropodomorphs have captured the attention of palaeontologists because their functional morphology was likely pivotal to the acquisition of quadrupedalism (Bonnan & Yates, 2007). Previous studies of the anatomical and functional evolution of archosaur forelimbs have focused on reconstructing their general role in locomotion (e.g. Ostrom, 1974; Cooper, 1981; Johnson & Ostrom, 1995; Dodson & Farlow, 1997; Paul & Christiansen, 2000; Schwarz, Frey & Meyer, 2007; Bonnan & Senter, 2007; Bonnan & Yates, 2007; Maidment & Barrett, 2012; Fujiwara & Hutchinson, 2012; Baier & Gatesy, 2013). Recently, studies have begun to focus on the evolution of manual pronation across the biped-quadruped transition (Bonnan & Yates, 2007; VanBuren & Bonnan, 2013; Hutson, 2015). A pronated manus was hypothesised to be necessary to effectively produce braking or propulsive forces at the manus-ground interface (e.g., Bonnan & Yates, 2007).

Considering that the ancestral condition of the manus in bipedal dinosaurs appears to have been more supinated, with palms that faced medially rather than caudally, the evolution of a pronated manus is thought to be crucial to the origin of quadrupedalism in both sauropods and ornithischians (see references above). In particular, the degree to which the the morphology of the ulna and radius (antebrachium; i.e. forearm) would have permitted pronation in basal sauropodomorphs, and if so how widespread this ability was across the group, remain crucial questions in understanding the evolution of sauropod locomotion. However, the timing and sequence of changes in the functional anatomy of the forelimbs that were involved in the evolution of sauropod locomotion remain unclear, partly because to date the biomechanical factors involved have largely been analysed using only qualitative, two-dimensional methods (but see Reiss & Mallison, 2014).

Here, we use three-dimensional biomechanical computer models to rigorously analyse the evolution of forelimb anatomy and function from early archosaurs to later sauropodomorphs. We model an adult *Mussaurus patagonicus* Bonaparte & Vince 1979, a well-preserved representative basal sauropodiform (*sensu* Sereno, 2007), close to the origin of Sauropoda (Otero & Pol, 2013; Otero et al., 2015), and the extant Australian freshwater crocodile, *Crocodylus johnstoni* Krefft, 1873, a long-tailed quadruped reasonably representative of the ancestral archosaurian condition (Parrish, 1986; Gatesy, 1990). The phylogenetic relationship between *Crocodylus* and *Mussaurus* is presented in Figure 1.

As in prior studies of archosaurian hindlimbs (e.g. Hutchinson et al., 2005; Hutchinson et al., 2008; Bates, Benson & Falkingham, 2012; Bates & Schachner, 2012; Maidment & Barrett, 2012), we use these musculoskeletal models to analyse the relationship between joint angles and moment arms for the muscles of the limb, as well as possible joint ranges of motion (e.g. Reiss & Mallison, 2014). By quantifying similarities and differences in estimated limb biomechanical properties from our *Crocodylus* and *Mussaurus* models, we can explicitly evaluate how forelimb muscle actions and joint mobility may have changed with posture from basal archosaurs to early sauropodomorphs. 'Action' here is used as a shorthand term for moment arms about particular joints; distinguished from 'function' which would ideally involve broader data such as muscle force output, length change, etc. (e.g. Zajac, 1989; Allen et al., 2014). Our analysis considers these key questions: (1) How did forelimb musculoskeletal anatomy evolve between early, quadrupedal archosaurs (approximated by *Crocodylus*) and early sauropodomorphs such as *Mussaurus*? (2) How did this alter muscle action and joint ranges of motion? Particularly, was forelimb pronation possible in early sauropodomorphs like *Mussaurus?* (3) What were the consequences of 1) and 2) for forelimb posture and function? Particularly, how may any observed functional changes have helped or hindered the use of the forelimbs in terrestrial locomotion? (i.e. may they relate to the transitions from sprawling quadrupedalism to parasagittal bipedalism in dinosaurs, and/or to the subequently evolution of graviportal quadrupedalism in sauropods?).

Our study represents the first attempt at comparative analysis of three-dimensional forelimb joint ranges of motion and muscle moment arms between a quadrupedal and a (at least facultatively) bipedal archosaur. We synthesize our findings with a review and meta-analysis of research on the biped-quadruped transition in sauropodomorphs.

MATERIALS AND METHODS

Digitization and Musculoskeletal Modelling

Our model-building procedure for *Mussaurus* and *Crocodylus* comprised five steps: (1) bone geometry acquisition, (2) joint axis estimation, (3) muscle reconstruction (*Mussaurus* only), (4) muscle path specification (using the results from the prior three steps), (5) joint range of motion analysis, and (6) analysis of muscle moment arms (automatically calculated from the muscle paths by the modelling software [see Delp & Loan, 2000]).

Bone geometry acquisition

The remains of the basal sauropodomorph *Mussaurus patagonicus* comprise several specimens of different ontogenetic stages, from post-hatchlings to adults (Bonaparte & Vince, 1979; Otero, Pol & Powell, 2012; Otero & Pol, 2013). Our study here focused on the best-preserved and complete right forelimb of the adult specimen number MLP 68-II-27-1 (Museo de la Plata, La Plata, Argentina), which comprises the scapula, partial coracoid, humerus, ulna, radius, three distal carpal elements, five metacarpals, first and ungual phalanges of digit one, and first phalanx of digit two (Otero & Pol, 2013). A three-dimensional portable surface scanner (NextEngine®, Santa Monica, California, USA) was used to digitize each bone of *Mussaurus*, obtaining a 3D bone file (.obj format); similar files were output from the CT scan data (see below) for *Crocodylus*. Meshlab software (Visual Computing Lab – ISTI – CNR, Pisa, Italy) was used to reduce the resolution of the original .obj files as needed. Each individual bone file was then imported to 3D Studio Max® software (Autodesk®, San Rafael, California, USA) in order to articulate the shoulder girdle and forelimb and to define the degrees of freedom (DOF; i.e. the possible axes of mobility) of each joint. We obtained our *Crocodylus johnstoni* specimen from the St. Augustine Alligator Farm and Zoological Park (St. Augustine, Florida, USA), where it had died of natural causes in captivity. This specimen was also used in studies by Allen, Paxton & Hutchinson (2009), Fujiwara & Hutchinson (2012) and Allen et al. (2014), and was approximately adult, with a total body mass of 20.19 kg. It was scanned using a Picker PQ 5000 CT scanner (axial 512 x 512 pixel slices at 2.5mm thickness; 100mA, 120 kVp, resolution 1.024 pixels mm^{-1}) and segmented in Mimics software (Materialise, Inc.; Leeuwen, Belgium) after CT scanning for simple 3D modelling in the aforementioned studies, especially Fujiwara & Hutchinson (2012), who reconstructed the major forelimb muscles in a computational model that we adapted here.

Joint axis estimation, reference pose and terminology

We first used the osteology of each bony joint to estimate the orientations of the 3D axes of that joint (Fig. 2). Those axes also set up the translations required to place the bones in relation to one another, from proximal to distal.

Considering that some extinct archosaurs have rather simply shaped appendicular condylar areas, implying the presence of large amounts of epiphyseal cartilage (Fujiwara, Taru & Suzuki, 2010; Holliday et al., 2010; Bonnan et al., 2013), thickness of soft tissues between the joints needed to be accounted for. Consequently, we left 10% of the total forelimb length as free space for epiphyseal cartilage in *Mussaurus*, distributed between the three main limb joints (i.e. glenohumeral, elbow, wrist), following the estimates of Holliday et al. (2010).

Geometric objects were used to link adjacent segments, using spheres (gimbal/ball-and-socket) for the glenohumeral joints and cylinders (hinges) for the other joints. These objects established the centres of rotation of each joint, through which the axes of joint rotation were positioned. Next, we defined the rotational degrees of freedom (DOFs) that were allowed around each joint axis. Although translation is known to occur in extant archosaur forelimb joints (namely the glenohumeral joint [Baier & Gatesy, 2013]), we judged the potential effects on moment arms to be relatively minor. For the glenohumeral and elbow joints, we inferred from the morphology that these joints might have three DOFs (flexion/extension, abduction/adduction, and supination/pronation) in both *Crocodylus* and *Mussaurus*. For *Crocodylus*, we also allowed three DOFs for the wrist joint, although only two DOFs for the wrist of *Mussaurus*. Finally, for the metacarpal-phalangeal, and interphalangeal joints (only for *Mussaurus*), we only allowed one DOF (flexion/extension), because the bony anatomy indicated that these joints acted almost exclusively as hinges. Our range of motion analysis (below) then considered how large the potential angular excursions of these DOFs might have been.

In order to set the initial position of the models, a reference pose at which all joint angles were set at 0° was chosen (e.g. Hutchinson et al., 2005; Hutchinson et al., 2015; Baier & Gatesy, 2013; Baier, Gatesy & Dial, 2013). Thus the reference pose constituted a starting point from which comparisons could be made, facilitating understanding of what any value for a joint angle represents (vs. this reference angle, a fully straightened limb orientation, with the forelimb extended laterally, perpendicular to the vertebral column and body's craniocaudal axis) (Fig. 2A–F).

The segments of the forelimb were positioned following Baier & Gatesy (2013), in which the humerus was laterally oriented, perpendicular to the vertebral column (0° flexion) and its long axis was parallel to the ground (0° abduction), whereas the axis connecting the medial and lateral distal condyles was parallel to the vertebral column and the deltopectoral crest pointed downwards (0° pronation). The major (longitudinal) axis of the ulna and radius (antebrachium) was parallel to that of the humerus (0° extension/abduction), and again the mediolateral axes of the distal condyles were parallel to the vertebral column's longitudinal axis. Unlike the model of Baier & Gatesy (2013), the curvature of the ulna was in a plane perpendicular to the long axis of the humerus (0° pronation/supination). Finally, the manus was oriented with the long axis of the metacarpus parallel to the long axis of the antebrachium (0° flexion and abduction), whereas the curvature of the ungual of the first manual digit was in the same plane as the long axis of the antebrachium (0° pronation) (Fig. 2).

Rotations away from 0° for each joint were defined as three successive rotations of the segment relative to the axis proximal to it (i.e. its reference position), in the order x (pronation/supination), y (adduction/abduction) and z (flexion/extension). Our models had right-handed coordinate systems, so pronation (around x), abduction (around y) and extension (around z) were negative values (i.e. of joint angle rotations), whereas supination, adduction and flexion were positive values.

Finally, the articulated forelimb model in the reference pose was exported to musculoskeletal modelling software (Software for Interactive Musculoskeletal Modeling;

Musculographics, Inc., Chicago, Illinois, USA) (Delp & Loan 1995, 2000), using custom MATLAB code (The Mathworks, Inc., Natick, Massachusetts, USA).

There is not a general consensus regarding anatomical terminology among tetrapods because of their great morphological disparity (Harris, 2004; Wilson, 2006). Caution is thus warranted when attempting to compare animals with sprawling (ancestral, at some level for Archosauria) versus parasagittal (derived) locomotor modes because each one can imply a different typical orientation for homologous or corresponding bones. To partly circumvent this problem, Jasinoski, Russell & Currie (2006) used two terms for bone orientation: ‘developmental’ and ‘functional’ orientations. The term ‘developmental orientation’refers to the ancestral (sprawling) state, which is equivalent to that often present in tetrapod embryos, especially forms with relatively plesiomorphic limbs (e.g. *Crocodylus*). The term ‘functional orientation’ corresponds to the typical, approximate standing positions present in adults, which vary in different groups of tetrapods according to their locomotor mode(s) used. Our model oriented the forelimb segments from the most proximal to distal ones, starting with the scapula. We thus chose a developmental position of the scapula, which means that the scapular blade was initially oriented vertically and the glenohumeral joint was caudolaterally oriented, as retained by extant crocodiles. Positioning *Mussaurus*’s scapula the same way as in *Crocodylus* ensured the same kind of movements (flexion/extension, abduction/adduction, pronation/supination) around the same axes in both models, in the starting configuration (i.e. reference pose).

As our reference (‘developmental’) pose did not necessarily reflect a biologically plausible pose (i.e. a pose that is mechanically allowed by their joints without risk of dislocation, or ‘functional’ orientation), a standardized, biologically plausible pose was also chosen in order to make realistic comparisons between taxa in terms of joint ranges of motion and moment arm analysis. Hence we used a ‘resting’ pose for both taxa, which was modified from the reference pose and represented an approximate *in vivo* plausible pose that was feasible for *Crocodylus* and (in our judgement based on the anatomy) *Mussaurus*. In our analysis, starting from the reference pose (all 0° values), the resting pose for *Mussaurus* was set at 5° of supination, 25° of adduction and -40° of extension for the glenohumeral joint; while 70° of flexion was chosen for the elbow. In *Crocodylus* (also starting from the reference pose), the same values were chosen as in *Mussaurus*, except for long-axis rotation (pronation/supination) at the glenohumeral joint, which remained at 0° (Fig. 3). These admittedly were subjective judgements based on the joint morphology and function, but were deemed far more plausible than the reference pose and thus more suitable for biological comparisons.

Regarding the terminology for naming the DOFs in this study (e.g. Gatesy & Baier, 2005; Hutchinson et al., 2005; Baier & Gatesy, 2013), we used pronation and supination for long axis rotation, the former alluding to internal (medial) and the later to external (lateral) rotation. We expressed those DOFs relative to the axes of the reptilian saddle-shaped glenoid on which they were acting, no matter if the limb would be elevating, depressing, protracting or retracting (see also Baier & Gatesy, 2013; Baier et al., 2013). Hence the abduction/adduction axis lay parallel to the long axis of the glenoid and the flexion/extension axis was perpendicular to the long axis of the glenoid (Fig. 4A–C).

Whilst the reference pose was used as a common point of comparison in terms of the DOFs, caution is warranted when one of the studied taxa (in this case *Mussaurus*) is shifted from the reference pose (with a vertically oriented scapular blade and caudally-oriented glenoid) to the resting pose (with a caudodorsally oriented scapular blade and a caudoventral glenoid). Such reorientation of the glenoid (Jenkins, 1993; Gatesy & Baier, 2005) entails drastic modifications of the anatomical and functional implications of the joints' DOFs (except for long axis rotation). This means that homologous movements in both poses are expressed as different functions in each of them. Consequently, an abduction and adduction movement (i.e. action) is expressed as elevation and depression (i.e. function) in the reference pose but becomes retraction and protraction in the resting pose, respectively (Fig. 4D–G). This shifting of joint functions must be kept in mind when comparing our results with those of previous work (see Discussion). To minimize confusion and to keep consistency with the *Crocodylus* model, we conserved the same terms for motions in the reference and the resting poses for *Mussaurus*, rather than converting the resting pose's joint motions into different terms. That is, the movement that describes abduction in the reference pose (i.e. the movement parallel to the long axis of the glenoid), was also called abduction in the resting pose, with no reference to the movement relative to the ground that the limb would be performing, unless otherwise stated.

Muscle reconstruction

Soft tissue inferences for the myology of *Mussaurus patagonicus* were established via reference to the literature, by comparisons and homology hypotheses from previous studies of the anatomy of living archosaurs as well as extinct forms (Cooper, 1981; Meers, 2003; Jasinoski, Russell & Currie, 2006; Langer, Franca & Gabriel, 2007; Remes, 2008; Maidment & Barrett, 2011; Burch, 2014; Allen et al., 2014) and via additional reference dissections of two specimens of *Caiman latirostris* (Crocodylia, Alligatoriidae) and *Gallus gallus* (Aves, Galliformes). The Extant Phylogenetic Bracket (EPB, Witmer, 1995) was used to formulate hypotheses about the soft tissue relations in extinct taxa that could be tested by reference to the known osteological correlates of the soft tissues in fossil taxa enclosed by the bracket, constraining speculation to a minimum (Witmer, 1995). We inferred the forelimb muscles' origin and insertion sites for *Mussaurus* using this EPB method. Muscle nomenclature used herein is based on Meers (2003) and Burch (2014). A total of 31 muscles were reconstructed in *Mussaurus* (although some were summed into functional groups for some actions). Muscle abbreviations and EPB levels of inferences are given in Table 1. Our placements of the origin and insertion of each muscle qualitatively approximated the centroids of the estimated areas of attachment inferred from crocodiles and birds (following Hutchinson et al., 2005; Hutchinson et al., 2015). These centroid approximations were used in the next step.

Muscle path specification

Once muscles were positioned at their respective origins and insertions, the next step was to model plausible paths over which each muscle would move during motion of the joints. Otherwise a uniformly straight line of action of muscles would create unnatural paths, crossing over (or through) the bones or other muscles in implausible ways, resulting in dubious moment arms as outputs. We used 'via points' and 'wrapping surfaces' to create anatomically realistic paths. Via points are fixed points attached to a body segment that can be used to implement simple constraints on a muscle's path relative to a bone or other structure (Fig. S1). For example, the triceps muscle group, originating on the scapula/coracoid and the humeral shaft, needed via points to avoid the assumed shape that the more internally located muscles might have had, as exemplified by M. triceps brachii caput mediale 1 (TBM1) (internally placed) and M. triceps brachii caput scapulare (TBS) (externally placed).

A wrapping object (or surface) is a geometric form, also associated with a body segment, which is assigned to one or more muscle(s) and creates a deflection of their path when crossed, preventing any associated muscle from penetrating it (Delp et al., 1990; see also Hutchinson et al., 2005; Hutchinson et al., 2015). Wrapping objects' attributes are listed in Table S1.

Most wrapping objects were represented as cylinders, used to represent physical bone surfaces, to constrain muscle paths, and to imitate unpreserved attributes (e.g. cartilage). This latter point is very important because a large amount of articular cartilage is missing in extinct reptiles, affecting the paths of muscles involved (Hutchinson et al., 2005). The elbow joint is critical because our inferences of its morphology would be affected by missing articular cartilage (Fujiwara, 2010; Holliday et al., 2010) and the main elbow (and other distal) extensor and flexor musculature would pass closely around this joint, with their paths influenced by this cartilage. A set of cylinders, serving as wrapping surfaces for one or more muscles, was placed parallel to the humeral condylar axis at varied distances from the condyles (see sensitivity analysis of moment arms below and in Discussion), taking the role of the articular cartilage on constraining muscle paths around the elbow.

Considering that our *Mussaurus* model exhibited differences in joint orientations between the reference and the resting pose, and the former was actually an implausible pose for a basal sauropodomorph, some muscle paths required additional constraints to fit the reference pose. For example, M. biceps brachii (BB) and the supracoracoideus complex (SC) were the most affected muscles, which needed extra wrapping surfaces constraining their paths when crossing the glenohumeral joint (Fig. S3; Table S1).

Our complete models for the forelimbs of *Crocodylus* and *Mussaurus* are available online upon request.

Joint range of motion analysis

Analyses of the forelimb joints' ranges of motion (ROM) were conducted for both the reference and resting poses, for each DOF allowed for each joint in the model. Estimation of ROM was done with the musculoskeletal software, by manipulating each DOF manually and visualizing in 3D at which joint angles the bones came into close proximity and thus would pass through each other (or their presumed cartilage) if moved further (e.g. Pierce et al., 2012; Reiss & Mallison, 2014). ROM estimation was not performed directly from bone to bone surfaces, but rather left 10% space of total bone length distributed among the glenohumeral, elbow and wrist joints for emulation of the cartilage volume that might have existed in life (following Holliday et al., 2010). Thus our ROM analysis was roughly equivalent to 'ROM4' of Hutson & Hutson (2012) in which all soft tissues but cartilage was removed. Considering that the reference pose is not a realistic posture, we expected that ROM values estimated from a resting pose would be smaller.

Analysis of muscle moment arms

We calculated muscle moment arms about the glenohumeral, elbow, and wrist joints for the *Mussaurus* and *Crocodylus* models. Additionally, we explored muscle actions in flexion/extension for manual digit I in *Mussaurus* because this digit in early sauropodomorphs has a medially deflected claw that has been hypothesized as having played a key role in manus functions other than locomotion, such as grasping and browsing (Galton & Upchurch, 2004; Yates et al., 2010).

For the glenohumeral joint, moment arms were calculated for all three rotational DOFs, considering that movements of the humerus allowed for appreciable amounts of flexion/extension, abduction/adduction, and supination/pronation in both *Mussaurus* and *Crocodylus* (see ranges of motion below). For the remaining joints (i.e. elbow, wrist, metacarpo-phalangeal and interphalangeal), only flexion and extension moment arms were calculated because this DOF corresponded to the main axis around which those joints predominantly would act, and this simplied our analysis (but see Discussion for the elbow joint).

Moment arms were first calculated in the *Mussaurus* and *Crocodylus* models for the reference pose. If a muscle had a certain action for more than 75% of a given DOF’s range of motion, it was plotted as a ‘pure’ action muscle (e.g., ‘pure’ flexor), otherwise it was plotted as ‘mixed’. If there was a mismatch between the taxa (e.g. a muscle being a flexor in *Crocodylus* but an extensor in *Mussaurus*), then we also plotted that muscle in the ‘mixed’ action category. We also calculated the moment arms for the *Mussaurus* model in the resting pose for comparison with the reference pose.

Moment arm values vary depending on the paths of muscles (Delp et al., 1990; Hutchinson et al., 2005), so alteration of either origin or insertion sites (as well as paths influenced by wrapping or via points) may affect moment arm estimations, and possible muscle actions. Here we focused our sensitivity analysis on the elbow of *Mussaurus*, for which the articular cartilage volume is unknown and likely was considerable. We started with a minimum amount of cartilage, increased the elbow cap to a maximum, and then evaluated how extensor muscle moment arms were affected by these assumptions (see Discussion).

Our presentation of moment arm values required some normalization to facilitate comparisons between *Crocodylus* and *Mussaurus*, because these taxa differ so greatly in body size and forelimb morphology. Following typical practice (e.g. Hutchinson et al., 2008; Bates & Schachner, 2012), we normalized the moment arms by their corresponding segment lengths (humerus, antebrachium and manus for shoulder, elbow and distal joints; data in Table S2). However, as forelimb proportions clearly changed between Archosauria and these two taxa, segment lengths are not the ideal metrics for normalization, and we consider this problem in the Discussion.

RESULTS

Muscle reconstruction

Non-avian archosaurs represent a particular challenge when reconstructing forelimb musculature based on an extant phylogenetic bracketing framework because of deep functional disparities, related to the different modes of locomotion existing between extinct and the living forms (e.g., sprawling vs parasagittal; biped vs quadruped; non-flying vs flying). Although the inferences of presence/absence of the forelimb musculature reconstructed herein for *Mussaurus* (Fig. 3) were based on the Extant Phylogenetic Bracket approach (Witmer, 1995), our final decisions of muscle position and extent (e.g. in equivocal cases; Level II' inferences) were based mainly on extant Crocodylia because of the greater morphological similarities that this group shares with non-avian dinosaurs than with birds (Jasinoski, Russell & Currie, 2006; Remes, 2008; Burch, 2014; Maidment et al., 2012).

Within the shoulder musculature, one important difference from previous contributions is the reconstruction of the M. teres major (TM) in *Mussaurus*. This muscle is absent in most sauropsids (Remes, 2008) and was reconstructed neither in theropods (Nicholls & Russell, 1985; Jasinoski, Russell & Currie, 2006; Burch, 2014) nor in basal ornithischians (Maidment & Barrett, 2011). However, the TM is present in extant Crocodylia (e.g., Meers, 2003; Allen et al., 2014), thus representing a level II inference for an insertion on the humerus, just medial to the deltopectoral crest, on a proximodistally elongated crest. The TM muscle was also inferred to have been present in the basal sauropodomorphs *Saturnalia* and *Efraasia* (Remes, 2008).

The origin and insertion of M. deltoides clavicularis (DC) are rather congruent among different studies, taking origin from the acromial area of the scapula and inserting on the lateral aspect of the deltopectoral crest of the humerus in both Crocodylia and non-avian Dinosauria (Meers, 2003; Jasinoski, Russell & Currie, 2006; Suzuki & Hayashi, 2010; Maidment & Barrett 2011; Burch, 2014). However, an origin from the clavicle was reported in lepidosaurs (Russell & Bauer, 2008) and birds (Burch, 2014), but clavicles are only known for the basal sauropodomorphs *Massospondylus*, *Plateosaurus* (Yates & Vasconcelos, 2005) and *Adeopapposaurus* (Martínez, 2009). Considering that there is no evidence of clavicles in *Mussaurus*, such an origin site was not reconstructed here. Remes (2008), on the other hand, proposed the presence of clavicles throughout sauropodomorph evolution, and that these were the osteological correlate for the DC. Regardless, the origin site and the line of action of this muscle would not be drastically affected by the presence of clavicles as reconstructed by Yates & Vasconcelos (2005) or Remes (2008).

The coracobrachialis (CB) muscle was reconstructed in *Mussaurus* with a single head (M. coracobrachialis brevis), and two divisions of that (*pars* ventralis and dorsalis; CBV and CBD) as in living crocodiles (Meers, 2003; Suzuki & Hayashi, 2010; Allen et al., 2014). There are two heads for this muscle (*pars* cranialis and caudalis) in extant birds, both originating from the craniolateral aspect of the coracoid (Vanden Berge & Zweers, 1993). Based on its anatomical position, the M. coracobrachialis cranialis of birds should be equivalent to the CBV of Crocodylia, and it would insert on the base of the deltopectoral crest of the humerus (Vanden Berge, 1982). An additional head, M. coracobrachialis longus, was reported as absent in Crocodylia (Jasinoski, Russell & Currie, 2006; Remes, 2008; but see Nicholls & Russell, 1985) and present in some birds (Jasinoski, Russell & Currie, 2006). Langer, Franca & Gabriel (2007), however, inferred the presence of this muscle in *Saturnalia*, taking into account that most neognaths have it, although we do not agree with such an inference considering the drastic modifications of avian forelimbs (i.e. a level II inference for *Mussaurus*) so we did not reconstruct the M. coracobrachialis longus in *Mussaurus*.

The supracoracoideus (SC) muscle has two heads in *Alligator mississippiensis* (Meers, 2003). In extant birds there is a single head, but with multiple origins (e.g. keel, mesosternum, manubrium, Vanden Berge & Zweers, 1993; Jasinoski, Russell & Currie, 2006). Homologies with Crocodylia are controversial, with no consensus on whether the scapular (Remes, 2008) or coracoid (Maidment & Barrett, 2011) head was lost in birds. The origin site (either single or multiple) of the supracoracoideus complex is consistently located around the scapula-coracoid boundary in Crocodylia, and always inserts on the deltopectoral crest. Thus for the biomechanical purposes of this study, we reconstructed the SC in *Mussaurus* as a single head originating from the centroid of the area where any head(s) should have originated. In addition, that area is not preserved in any of the Patagonian specimens, precluding the identification of osteological correlates for the origin of this muscle.

The scapulohumeralis was reconstructed in *Mussaurus* as a single head (M. scapulohumeralis posterior, SHP), corresponding to the M. scapulohumeralis caudalis of Crocodylia (Meers, 2003; Remes, 2008; Suzuki & Hayashi, 2010; Allen et al., 2014). Scapulohumeralis anterior was not reconstructed in *Mussaurus* because it is absent in Crocodylia (Meers, 2003; Jasinoski, Russell & Currie, 2006; Suzuki & Hayashi, 2010; Burch, 2014), although it is reported in birds. The medial side of the scapula of *Mussaurus* has a long ridge running parallel to both margins (ventromedial ridge, Otero & Pol, 2013), which has been hypothesized as the boundary of SHP (ventrally) and SBS (dorsally) (Langer, Franca & Gabriel, 2007; Burch, 2014).

The inferred number of heads of the Mm. triceps brachii (TB) for archosaurs are four (Jasinoski, Russell & Currie, 2006; Burch, 2014) or five (Meers, 2003; Remes, 2008). In *Mussaurus*, as in extant Crocodylia we infer that there were two origin sites from the scapulocoracoid (i.e. TBS, TBC) and two from the humeral shaft (i.e. TBL, TBM). Regardless of all controversies surrounding the precise number of humeral heads in living archosaurs, for our purposes of muscle moment arm analysis and considering the lines of action of this large muscle group, the reconstruction of the humeral head in *Mussaurus* (TBM) was split into four portions, which corresponded to the different areas on the humeral shaft from which the TBM should have originated. Previous reconstructions of M. triceps in dinosaurs vary. It was reconstructed with two scapulocoracoid heads and one humeral head in *Saturnalia* (Langer, Franca & Gabriel, 2007) and only two heads in early ornithischian dinosaurs (one from the scapulocoracoid and one from the humerus; Maidment & Barrett, 2011). Within later ornithischians, five heads were inferred in *Euoplocephalus*, corresponding to those described for extant crocodiles (Coombs, 1978).

The origin of the biceps brachii (BB) mucle in extinct forms is equivocal: some studies place it just cranially to the glenoid lip of the coracoid (Langer, Franca & Gabriel, 2007; Remes, 2008; Burch, 2014), whereas the origin in Crocodylia is even more cranially placed, close to the scapulocoracoid boundary (Meers, 2003; Suzuki & Hayashi, 2010), a hypothesis followed here (see also Maidment & Barrett, 2011). A second head of this muscle on the humerus (as present in some birds, Remes, 2008) is too speculative (Level II') because it is absent in Crocodylia (e.g. Meers, 2003) and no corresponding scars are evident in *Mussaurus*.

The brachialis (BR) and humeroradialis (HR) muscle attachments seem to retain their ancestral origins and insertions in most sauropsids, with some secondary changes in birds. In *Mussaurus* we infer that they originated from the humeral shaft, close to the deltopectoral crest, and inserted on the proximomedial surface of the radius (Jasinoski, Russell & Currie, 2006; Remes, 2008; Burch, 2014). However, Cooper (1981), Langer, Franca & Gabriel (2007) and Maidment et al. (2011) placed the BR origin more distally, as in birds; a conclusion that we deem to be less convincing (Level II' inference).

Most of the muscles originating from the humeral condyles and inserting either on the radius or ulna, such as the supinator (SU), flexor ulnaris (FU) (anconeus *sensu* Burch, 2014), and pronator teres (PT) do not exhibit major differences between extant Archosauria. Therefore, qualitative reconstructions in extinct forms remain unequivocal (Remes, 2008; Burch, 2014; but see Langer, Franca & Gabriel, 2007), with the exception of the abductor radialis (AR), which is not present in birds.

The M. extensor digitorum longus (EDL; extensor carpi ulnaris longus *sensu* Meers, 2003) of sauropsids has an insertion that varies between the dorsal proximal portions of the metacarpals, depending on the group (Remes, 2008; Burch, 2014). Insertions onto the bases of metacarpals I and II are phylogenetically unequivocal for *Mussaurus*. Considering that reconstructions of the insertion onto MCI, MCII or both would not appreciably affect the EDL's line of action as it crosses the wrist joint, we reconstructed this muscle as inserting only onto MCII.

The archosaurian ECR (extensor carpi radialis longus *sensu* Meers, 2003) muscle inserts onto the radiale. Considering that *Mussaurus* lacks a radiale, we reconstructed its ECR as inserting onto the carpus (as in Aves). Similarly, the origin site of the abductor pollucis longus (APL; extensor carpi radialis brevis *sensu* Meers, 2003) was placed on the lateral side of the radius in *Mussaurus*. The osteological correlate of this origin was assessed to be a small tubercle on the lateral and distal area of the radius, also reported in *Saturnalia* (Langer, Franca & Gabriel, 2007). An additional origin from the lateral ulna (Remes, 2008; Burch, 2014) was omitted because it would have had the same general line of action and hence would not affect the action of this muscle in *Mussaurus*.

The flexor digitorum longus (FDL) muscle ancestrally had humeral, ulnar, and carpal heads, all of them joining into a single tendon that then diverged to insert on the manual digits

(Meers, 2003). As one single common tendon passes across the wrist, we reconstructed only the humeral head for *Mussaurus*, inserting on the flexor surfaces of the manual phalanges (i.e. proximoventral aspect).

Nomenclature for the extensor and flexor musculature of the digits remains controversial among living sauropsids, especially considering the extensive modifications of the avian forelimb. Thus we withheld from reconstructing these muscles in detail for *Mussaurus*. We simply followed the scheme from Meers (2003). Muscles extensores digitorum superficiales (EDS) and profundus (EDP) in *Mussaurus* both originated from the distal aspect of metacarpal I, and also from the proximal side of the radiale in the case of the superficial head (for a similar myology, see Burch, 2014: extensores digitores breves, EDB), although leaving no muscle scars. In extant birds, the EDP's putative equivalent by position would be the M. extensor brevis alulae, but originating from the extensor apophysis of the metacarpus and the alula (Vanden Berge, 1982). Hence a Level II inference resulted for this muscle in *Mussaurus*, and we assumed the state in Crocodylia to apply.

The flexores digitorum superficialis (FDS) and profundus (FDP) muscles originate proximally from the distal carpals and distally insert onto the flexor process of the first phalanx of the digits in Crocodylia (Meers, 2003; Burch, 2014). As with the extensor musculature of the digits, avian homologues are difficult to establish, but judging from its position the M. flexor alulae is a plausible candidate (Vanden Berge, 1982; Burch, 2014). We applied crocodylian myology to *Mussaurus*.

Joint range of motion analysis

Here we consider the results of the range of motion (ROM) analysis for *Mussaurus patagonicus* in the resting pose, whereas for *Crocodylus johnstoni*, ROMs for the reference pose were the same as those for the resting pose (Tables 2, S3).

Pronation and supination values around the glenohumeral joint had similar values for *Mussaurus* (-25°/25°) and *Crocodylus* (-20°/20°), for a total maximal ROM of 50° and 40°, respectively. The glenohumeral joint of *Mussaurus* allowed -25° of abduction and 40° of adduction for a total ROM of 65°. On the contrary, the *Crocodylus* model showed a reduced capacity for abduction from the reference pose (-5°) and allowed 45° of adduction, for a total glenohumeral ROM of 50°. The flexion and extension axis of the glenohumeral joint in *Mussaurus* allowed -35° of flexion and -70° of extension from the 0° pose, for a total ROM of 35°. *Crocodylus* showed the opposite pattern for the flexor/extensor axis, allowing greater flexion mobility (60°) and limited extension 5°) ROM.

Long axis rotation at the elbow showed interesting values in the *Mussaurus* model, allowing -30° of pronation and 5° of supination, for a total ROM of 35°. In *Crocodylus*, less pronation than in *Mussaurus* was allowed (-20°) starting from the reference pose, but more supination as well (8°), for a total of 28° of long axis rotation. Abduction and adduction, on the other hand, showed no differences between both *Mussaurus* and *Crocodylus*, allowing a total ROM of 10° (5° in each direction). Finally, flexion and extension at the elbow showed similar ROM values in *Mussaurus* and *Crocodylus*, allowing flexion to 130° in *Mussaurus* and 110° in *Crocodylus*. Extension values reached 20° in *Mussaurus* and 0° in *Crocodylus*.

Pronation and supination at the wrist were precluded in *Mussaurus*. Abduction and adduction showed the same values for *Mussaurus* (-10°/10°), whereas *Crocodylus* had more abduction capacity (-30°) in contrast to adduction (5°). Flexion and extension of the wrist joint was 70° and -30°, respectively for *Mussaurus*, whereas in *Crocodylus* flexion showed smaller ROM values (40°) and extension ROM was greater (-60°) than in *Mussaurus*. The metacarpo-phalangeal joint of digit I in *Mussaurus* had 50° of flexion and -40° of extension ROM, whereas the interphalangeal joint allowed the angle of flexion to increase to 70° and extension could decrease to -25°.

Muscle moment arm analysis

Here we compare the moment arm values obtained for *Crocodylus* and *Mussaurus* in the resting pose. For the glenohumeral joint, we analysed three DOFs (pronation/supination, abduction/adduction, and flexion/extension), whereas only flexion/extension for the remaining joints. Then we focus on inferences about broad trends in muscle actions (and, where feasible, general functions) inferred from the resting pose.

Glenohumeral joint (Fig. 5; Tables 3, S5)

Some muscles showed similar actions for long axis rotation around the glenohumeral joint in *Crocodylus* and *Mussaurus*, whereas others displayed changes in muscle action (Fig. 5A). Muscles originating from the scapular blade and inserting well lateral or well medial on the proximal humerus had the same action for both taxa; e.g. some humeral supinators such as DC, DS, TM, and CBD. Similarly, TBC also consistently was a supinator, although it inserted on the olecranon process of the ulna rather than on the humerus in both taxa, and originated on the proximal scapula and coracoid and not on the scapular blade. The SBS and CBV remained as humeral pronators for both taxa.

In contrast, BB, SHP and TBS fell into the category of ‘mixed’ muscles, because their actions differed between *Mussaurus* and *Crocodylus*. SHP acted as a supinator in *Crocodylus*, but was a pronator in *Mussaurus*; BB was fully a supinator in *Crocodylus*, but had a mixed action in *Mussaurus*; and finally TBS acted as mixed in both taxa.

Within the category of long axis rotator actions, muscles showed contrasting patterns in *Crocodylus* and *Mussaurus* for moment arm magnitudes around the glenohumeral joint, especially as joint orientation was varied between supination and pronation (Fig. 5A). For example, most supinator muscles in *Crocodylus* (DC, SHP, TM, SC, TBS, TBC and BB) experienced an increase of their moment arms with pronation. In contrast, in *Mussaurus*, only three (CBD, SC and TBC) of the six supinator muscles increased their supinator moment arms with pronation. The remaining glenohumeral rotators in *Mussaurus* (DS, DC, TM, CBV and SBS) displayed patterns of increasing supinator moment arms with glenohumeral supination, not pronation. Pronator muscles, however, displayed similar patterns in both taxa, showing an increase of pronator moment arms with supination; with the exception of the SBS muscle in *Mussaurus*, which exhibited almost constant large moment arms (more than -0.10 unit).

The BB, CBD, SC, DS and DC muscles, which originated from the cranial surface of the scapulocoracoid, were shoulder flexors in both taxa. The CBV was also a shoulder flexor in *Mussaurus* but had a mixed action in *Crocodylus*, shifting from extension to flexion at about -30° (Fig. 5B). On the other hand, SBS, SHP, TBC and TM were extensors in both taxa, as well as TBS in *Crocodylus* (but TBS was mixed in *Mussaurus*, shifting from extensor to flexor at -60°).

In *Crocodylus*, all flexor muscles increased their moment arm about the glenohumeral joint with flexion, except for the CBD, which displayed the opposite pattern. In *Mussaurus*, DS, DC and CBV also increased their flexor moment arms with joint flexion, whereas SC and BB showed an increase of flexor moment arms with joint extension. The only muscle that increased its extensor moment arm with glenohumeral joint flexion in both taxa was SBS. The remaining extensor muscles exhibited different patterns (Fig. 5B).

We found that muscles acting about the glenohumeral ab/adductor axis displayed similar patterns in both *Crocodylus* and *Mussaurus*. The BB, CBV, SBS and SC muscles had adduction actions for both taxa, whereas CBD acted as an abductor in *Crocodylus* and as an adductor in *Mussaurus*. The remaining muscles (DC, DS, SHP, TBC, TBS and TM) were glenohumeral abductors in both *Crocodylus* and *Mussaurus* (Fig. 5C).

In *Crocodylus*, most adductor muscles (CBV, BB and SC) increased their moment arms with glenohumeral joint adduction, except for SBS and CBD, which had the opposite pattern. In *Mussaurus*, BB and SC increased their adduction moment arms with humeral abduction, whereas SBS and CBV remained rather constant and only CBD increased its adduction moment arm with joint adduction. Regarding glenohumeral abductor muscles, DC, DS and TBS increased their moment arm with joint abduction in *Crocodylus*, whereas all abductor muscles except for CBD (DC, DS, SHP, TBC, TBS and TM) in *Mussaurus* showed the same pattern.

Elbow joint (Fig. 6; Tables 3, S6)

Although elbow adduction and abduction occur during ‘sprawling’ locomotion in *Alligator* (Fujiwara & Hutchinson, 2012; Baier & Gatesy, 2013) and we allowed three DOFs at this joint in both models, here we only consider flexion and extension (but see below), because we expect elbow flexion/extension to have predominated in *Mussaurus*. Generally, muscle actions around the elbow showed fewer differences between *Crocodylus* and *Mussaurus* compared to the glenohumeral joint. In addition, the major elbow extensors and flexors had similar patterns in both taxa, although varying in their relative moment arm magnitudes.

Elbow flexor muscles revealed similar patterns in *Crocodylus* and *Mussaurus*, generally increasing their flexor moment arm with increasing joint flexion. The BB, BR and HR all reached peak flexor moment arms (two times the minimal values) at moderate elbow flexion angles (~90°). In contrast, the PT and FDL acted as elbow flexors in *Mussaurus*, with minimal changes of their moment arms (less than 0.05 units).

The remaining muscles acting around the elbow joint corresponded to those originating on the distal humeral condyles. We found that, in *Mussaurus*, most of these antebrachial muscles (AR, SU, ECR, EDL and FU) shifted from flexor to extensor moment arms as the elbow became more flexed (between 55°– 65°). One interesting difference observed between *Crocodylus* and *Mussaurus* was that, apart from the triceps group, different muscles acted as elbow extensors in the crocodile (AR, SU, ECR, EDL, PT and FU); FDL being the only mixed-action muscle.

The triceps group includes the main elbow extensor muscles. In *Crocodylus* and *Mussaurus*, these muscles maintained a similar pattern of action (Fig. 6), with smaller values at full extension, mostly increasing their extensor moment arms as the elbow was flexed. Regardless, the most noteworthy difference between the action of M. triceps in both taxa is that the moment arm value in *Mussaurus* was substantially increased (almost twice as large) between full extension to full flexion, whereas in *Crocodylus* the values between maximal flexion and extension were fairly constant. In both taxa, the peak values of moment arms did not occur in full extension or full flexion, but at moderate elbow joint angles.

Wrist and manus joints (Fig. 7; Tables 4, S6, S7)

Except for the crocodile's EDL, which was purely a wrist extensor, the remaining muscles acting around the wrist joint of both taxa displayed a mixed flexor/extensor action. In both taxa, APL and ECR were found to be mostly extensors (except at low angles of flexion), as was EDL for *Mussaurus*. The FDL was estimated as predominantly a carpal flexor in both taxa, although at extreme flexion it switched to an extensor.

Moment arms for manus digit I were analyzed only for *Mussaurus*. Regarding muscles crossing the metacarpo-phalangeal joint ('MCP' in Fig. 7), the FDL showed a peak (flexor) moment arm at a moderate joint angle, whereas the EDP and EDS exhibited similar patterns (due to their common paths) of reduced flexor moment arms with MCP joint flexion. For the interphalangeal joint ('INP' in Fig. 7), FDL (and FDP, FDS) acted fully as a flexor (showing a pattern very similar to that for the metacarpo-phalangeal joint), whereas EDP and EDS switched from flexor to extensor moment arms at about -35° of extension, increasing their moment arms to a rough plateau near 0°.

DISCUSSION

Here, first we compare the results of our forelimb joint ROM analysis in *Mussaurus* and *Crocodylus* considering these in light of conclusions from previous studies of this topic in other sauropodomorphs and theropods. Second, we compare the patterns of muscle moment arms in our two study taxa in the context of the evolution of muscle function across Archosauria, comparing with previous qualitative studies dealing with archosaur forelimb myology in which muscle function has been inferred (e.g. Meers, 2003; Jasinoski, Russell & Currie, 2006; Langer, Franca & Gabriel, 2007; Allen et al., 2014; Burch, 2014). As an important component of this comparison of muscle moment arms, we discuss the effects of altering: (1) joint posture (e.g. reference vs. resting pose); and (2) articular cartilage extent around the elbow in *Mussaurus*. Finally, we review the evolution of manus pronation in Sauropodomorpha in the light of our results for joint ROM and, where potentially relevant, muscle moment arms.

Joint ROM analysis: Implications for the evolution of forelimb posture in sauropodomorphs

Our analysis considered how forelimb joint ROM in *Mussaurus* differed between the reference and resting poses as well as how the estimated ROM compared with *Crocodylus* and various saurischian dinosaurs (as previous studies estimated). Here we also evaluate how our findings might reflect potential evolutionary trajectories of maximal forelimb joint ROM in Archosauria, as well as the limitations of these ROM assessments and comparisons. Where relevant, in tandem we also consider our results for muscle moment arms.

The most conservative DOF around the glenohumeral joint in *Crocodylus* and *Mussaurus* was long axis rotation (Tables 2, S3), showing the same ROM value in the reference and resting poses of *Mussaurus* and grossly similar values in *Crocodylus*. This similarity can partly be attributed to the relatively conserved morphology of the glenohumeral joint surfaces in both taxa, in which the scapular and coracoid lips form an inverted ‘V’ surface. Additionally, the potential ROMs in long axis rotation were relatively independent to the orientation of the glenoid (or pectoral girdle and forelimb) and hence, the same values were estimated for the reference and resting poses of *Mussaurus* (-25°/25° in pronation/supination), with almost the same values found for *Crocodylus johnstoni* (-20°/20°). It is perhaps reassuring that the latter values were crudely similar to the actual ROM used *in vivo* during walking in *Alligator mississippiensis* (-17.9°/27.2° pronation/supination, Baier & Gatesy, 2013). However, our ROM results are smaller than those obtained by Pierce, Clark & Hutchinson (2012; -75°/70°, pronation/supination) for fleshed specimens of *C. niloticus* as well as results (approximated as 3D) for *A. mississippiensis* (Hutson & Hutson, 2013). However, skeletonized specimens (e.g. the crocodile used in the present study) might underestimate ROMs vs. fleshed ones (Hutson & Hutson, 2012, 2013), although this is controversial (Pierce, Clark & Hutchinson, 2012), probably depending strongly on methods and investigators as well as definitions of 3D joint axes and DOFs. Thus any corroboration of our ROM results for pronation/supination in *Crocodylus* remains tentative.

In contrast, the remaining DOFs (abduction/adduction, flexion/extension) exhibited different ROM values in both taxa but also in the reference and the resting poses for *Mussaurus*, which are linked directly to the orientation of the glenohumeral joint. Interestingly, in both the reference and resting poses, *Mussaurus* displayed unambiguously larger ROMs for glenohumeral add/abduction than *Crocodylus* (Tables 2, S3). This difference was probably because of the smooth, broader glenohumeral surface in *Mussaurus*. It remains problematic that the extent and shape of glenohumeral articular cartilage in *Mussaurus* is unknown, and we used admittedly simple models of the joint, but our models are provided with this study so that others might build upon our efforts.

A major focus in studies of basal sauropodomorph locomotion is the likelihood of habitual quadrupedalism (Jaekel, 1910; Fraas, 1913; Galton, 1990; Bonnan & Senter, 2007, Bonnan & Yates 2007; Mallison, 2010b; Yates et al., 2010; VanBuren & Bonnan, 2012; Hutson, 2015). However, the ROMs of the forelimb joints depend on the morphology of the articular surfaces (e.g. a wider glenoid surface should allow larger ROMs), and the orientation of such articular surfaces will ultimately determine the way in which ROMs will influence forelimb function (e.g. Jenkins, 1993; Gatesy & Baier, 2005). Our ROM analysis of *Mussaurus* indicated that if the scapula were oriented in an anatomical position of about 55°– 60° from the horizontal (i.e. caudodorsally), the maximal humeral protraction (i.e. glenohumeral joint abduction) allowed would not pass vertical, which concurs with previous reports for other basal sauropodomorphs (Bonnan & Senter 2007; Mallison, 2010a; Mallison, 2010b) and theropods (Senter & Robins, 2005). This inference partially contradicts the possibility of quadrupedalism as a habitual mode of locomotion in early sauropodomorphs such as *Mussaurus*. Our finding contrasts with the condition inferred in sauropods, in which the glenoid was more ventrally oriented but a caudodorsal scapular blade orientation was maintained (Schwarz, Frey & Meyer, 2007). A ventrally oriented glenoid seems to have allowed sauropods to protract their humerus forward from vertical, facilitating glenohumeral abduction (i.e. joint movement parallel to the long axis of the glenoid) during quadrupedal locomotion.

Additionally, for the glenohumeral flexion/extension axis, *Mussaurus* exhibited a combination of peak moment arms at full extension (BB, SC, TBC, TM and SHP) but also at full flexion (DC, DS, SBS, CBV and TBS), although *Crocodylus* displayed mostly peak moment arms at full flexion (Fig. 5B). In the case of the glenohumeral abduction/adduction axis, *Mussaurus* had peak moment arms with a more abducted humerus than in *Crocodylus* (Fig. 5C). These results indicated that *Mussaurus* had greater leverage with a more abducted glenohumeral joint than in *Crocodylus*, but the consequences of this leverage, and of glenohumeral posture in flexion/extension, are ambiguous. Furthermore, the lowest leverage for elbow extensor muscles in both *Crocodylus* and *Mussaurus* were at full extension (i.e. a fully columnar forelimb). Nonetheless, it is interesting to note that peak moment arms were reached at different elbow joint angles in both taxa. In *Crocodylus*, peak moment arms were at joint angles of ~45°–55° (Fig. 6), which implies that leverage could be maximized at a moderately flexed elbow joint. In *Mussaurus*, elbow extensor moment arms at full extension in the reference pose (close to 0°) fell drastically to minimal values. Nonetheless, peak moment arms around the elbow were present at about 85°–95° (Fig. 6), meaning that maximal muscle leverage was achieved at an even more flexed pose than in *Crocodylus*, which could be speculated to argue against a forelimb with strong specialization for supportive or locomotor functions, and thus inconsistent with habitual quadrupedalism in *Mussaurus*. Overall, *Crocodylus* and *Mussaurus* show interesting postural dependencies of their muscles' moment arms, but their consequences for quadrupedalism in either taxon are unclear. Similarly, results for moment arm analyses in the hindlimbs of *Tyrannosaurus* (peak extensor moment arms near full joint extension; Hutchinson et al., 2005) and ostriches (extensor moment arms seeming to be suboptimal for antigravity support in walking and running; Hutchinson et al., 2015) show divergent results that make it difficult, at present, to use these data to test inferences about habitual joint posture. Regardless, all of these studies' findings reveal how sensitive the moment arms of muscles are to joint orientation. Hence, assuming a constant moment arm is far more risky than checking for this sensitivity.

Similar to long axis rotation around the glenohumeral joint, we found the ROM of flexion and extension around the elbow to be rather conservative between *Crocodylus* and *Mussaurus*, even though epiphyseal cartilage in the early sauropodomorph cannot be assessed with great confidence. Full elbow extension (0°) was only allowed (indeed, required) in the reference pose (Table S3), whereas full extension in the resting pose was 20° for both taxa, avoiding full extension of the elbow, as previously reported for the basal tetrapod *Ichthyostega* (Pierce, Clark & Hutchinson, 2012), the crocodile *Alligator* (Hutson & Hutson, 2012; Baier & Gatesy, 2013), basal saurischians (Sereno, 1993), basal sauropodomorphs (Bonnan & Senter, 2007; Mallison, 2010b; Vargas-Peixoto, Da Rosa & Franca, 2015) non-avian theropods (Senter & Robins, 2005; White et al., 2015) and birds (Baier, Gatesy & Dial, 20[illegible]). Thus our models reject the inference that *Mussaurus* would have routinely used a columnar forelimb pose. This inference also supports the conclusion that no matter if manipulation is being done with fleshed (Hutson & Hutson, 2012) or skeletonized material (Sereno, 1993; Senter & Robins, 2005; Bonnan & Senter, 2007; Mallison, 2010b; Pierce, Clark & Hutchinson, 2012; Vargas-Peixoto, Da Rosa & Franca, 2015; White et al., 2015), elbow hyperextension close to 180° leads to a high risk of disarticulation.

Although we focused on flexion/extension as the major DOF considered for our analysis of wrist biomechanics, it may be that *Mussaurus* (like *Crocodylus*) was capable of other motions (e.g. abduction/adduction), to some smaller degree. However, wrist osteology in *Mussaurus* makes reconstruction of ad/abduction and pronation/supination ROM difficult to do with confidence. Indeed, understanding of the mobility of the wrist joints among early sauropodomorphs is limited because there is a lack of information regarding the osteology of the proximal carpus, and the distal carpus is represented by two or three elements with a 'block' configuration (Senter & Robins, 2005; Bonnan & Senter, 2007; Mallison, 2010a; Mallison, 2010b). The only DOF inferred with confidence in *Mussaurus* is flexion and extension, although even this is speculative. In the case of *Crocodylus*, the presence of proximal carpal elements allows more confident interpretations regarding pronation/supination and adduction/abduction (e.g. Hutson & Hutson, 2014), exhibiting greater ROMs than *Mussaurus* (Table 2). Nonetheless, in addition to the issues of cartilage non-preservation noted above, considerable long-axis rotation has been reported for the hindlimb bones of *Alligator mississippiensis* during walking (Gatesy, 1991; Blob & Biewener, 2001).

Within digit I in *Mussaurus*, both the metacarpo-phalangeal and the interphalangeal joints present in early sauropodomorphs (and in dinosaurs in general) displayed ginglymoid, well-defined articular surfaces, contrasting with the flatter (and sometimes pitted) ends of their proximal long bones, for which thick articular cartilage has been inferred (Schwarz, Frey & Meyer, 2007; Holliday et al., 2010; Bonnan et al., 2013). In *Mussaurus*, we inferred that minimal hyperextension ROM was possible for both joints, with flexion predominating, which would be similar to the condition reported for the ungual of digit I of *Massospondylus* (Cooper, 1981), the digits of *Plateosaurus* (Reiss & Mallison, 2014; see also White et al., 2015 for the theropod *Australovenator*). Despite that basal sauropodomorphs share similar manus morphology, more work is needed to test if there are any detectable differences in ROM within this lineage. A limited amount of phalangeal hyperextension has been proposed to be evidence against quadrupedalism because it might also limit the stride length of the forelimb, particularly for the short forelimbs of early sauropodomorphs (Reiss & Mallison, 2014). However, to the degree that any such limitation imposed on stride length existed, it would have been modest relative to the influences of the ROMs of more proximal joints, considering their associated segments' greater lengths and thus the arcs swept for a given amount of joint ROM. Furthermore, ROMs of the same joints in quadrupedal sauropod(omorph)s still deserve careful study for comparison, as it is questionable whether phalangeal joint motion was important early in the evolution of their quadrupedalism, given the rapid appearance of a columnar, bundled manus in sauropods (Bonnan, 2003; Bonnan & Yates, 2007). Regardless, the mobility of digit I in the manus would be important for other non-locomotor behaviours such as grasping and thus deserves study in more taxa and ultimately in a phylogenetic context.

Archosaur forelimb muscle actions: Major differences between sprawling quadrupedalism and parasagittal bipedalism

Although the hindlimbs are/were a terrestrial locomotor module in essentially all archosaurs (living and extinct), the biological role of the forelimbs varies, depending on the locomotor pattern of the organism. Facultative bipedal vertebrates tend to devote the forelimbs to biological roles other than solely body support or locomotion; e.g. manipulation, digging, display and combat. Consequently, among our most interesting findings are estimates of how the mechanical actions of some (but not all) muscles appear to differ between the more sprawling forelimb posture of *Crocodylus*; presumably at least somewhat similar to the ancestral locomotor pattern of basal archosaurs; to the more derived, parasagittal, at least facultatively bipedal pattern in *Mussaurus*. More studies are certainly needed to test how much our assumption that *Crocodylus*'s joint ROM and moment arm patterns are similar to those of ancestral archosaurs (but see Parrish, 1986) and if *Mussaurus*'s patterns are typical for Sauropodomorpha, especially close to the origin of Sauropoda, but our estimates are important first steps in this direction. Although quantitative functional shifts have been proposed previously for hindlimb muscles in various archosaurs (e.g. Hutchinson et al., 2008; Hutchinson et al., 2015; Bates & Schachner, 2012; Maidment & Barrett, 2012), quantitative data for such shifts in the forelimbs of extinct archosaurs have not been reported before.

It is important to note that our study considers muscle actions around the three main DOFs (i.e. long axis rotation, adduction/abduction, flexion/extension) for the glenohumeral joint, which had substantial mobility in both taxa modelled. Past studies, however, have tended to focus on major muscle actions around a single axis, sometimes implicitly assuming that actions around other axes were negligible or unimportant, but more often simplifying muscles to only have one major action (see also Hutchinson et al., 2015; Rankin, Rubenson & Hutchinson, 2016 for similar points regarding 3D actions and broader biomechanical functions – e.g. strut, motor, spring, brake, damper – in the pelvic limb muscles of ostriches). An advantage of our musculoskeletal modelling approach is that, once constructed, actions in any directions can be quantified, and these models could be used in the future to test broader issues about biomechanical functions, biological roles and (with the addition of more musculoskeletal models) comparative evolutionary patterns.

In the above context, the first part of the following section focuses on the influence of the reference versus resting pose on muscle function, exploring how muscles respond to the shifting from ancestral to derived limb postures in our studied taxa. We then examine how moment arms in the resting pose differ between *Crocodylus* and *Mussaurus*, in all cases trying to identify the muscles with actions most influenced by morphology and/or posture. Finally, we reflect on our findings in light of the challenge presented in finding an 'ideal' metric by which to normalize moment arm values for comparisons between taxa.

Influence of the reference versus resting pose on muscle action

When we compared the actions estimated for the reference and resting poses for our two study taxa, noteworthy differences appeared, with the most drastic changes evident at the glenohumeral joint. Most muscle groups crossing the glenohumeral joint that we analysed in the reference pose had evidence for differences of action between *Crocodylus* and *Mussaurus* (12 out of 14 of the muscles in at least one DOF), whereas only 2 out of 17 muscles acting around the elbow had differences of flexor/extensor action, and no muscle crossing the wrist displayed differences of action (Table S4). In the case of the resting pose, differences in muscle action between *Crocodylus* and *Mussaurus* were less marked, with 4 out of 14 of the muscles analysed having differences of action in at least one degree of freedom for the shoulder and 5 out of 17 of the muscles displaying some differences around the elbow. Muscles acting around the wrist again lacked marked differences between *Crocodylus* and *Mussaurus* in the resting pose (Table 3).

Most of the abovementioned differences in muscle action are a consequence of both limb posture and morphology. For example, BB seems the most variable muscle for analysis of muscle actions across the glenohumeral joint in our study, differing in two of the three DOFs analysed in the reference pose. These differences were influenced not only by our findings for joint ROM, but also by morphological disparity and postural configurations between both taxa. Indeed, the orientation of the glenoid is the main factor influencing differences in the action of BB. In *Crocodylus*, the glenoid is laterally oriented, forcing the humerus to be transversely oriented with respect to the scapulocoracoid plane. Conversely, in *Mussaurus*, the glenoid is caudally oriented in the reference pose, resulting in the humerus lying in essentially the same plane as the scapulocoracoid. With this configuration, the path of the BB in *Mussaurus* required the use of a wrapping surface (Table S1; Fig. S3) to prevent the BB muscle from intersecting with the pectoral limb bones in an unrealistic way. The placement of a torus onto the proximal humerus, just below the glenoid, restricted the path described by the BB, permitting only a glenohumeral flexor action for this muscle, but with mixed adduction/abduction as well. In *Crocodylus*, however, the lateral orientation of the humerus allowed the BB muscle to move more freely around the glenohumeral joint, obviating the need for wrapping surfaces, and thus allowing a mixed flexion/extension action for this taxon, but restricting it to only adduction. On the contrary, in the resting pose, the total potential joint ROM of *Mussaurus* was changed to an anatomically more realistic trajectory around the glenoid, similar to that of *Crocodylus*, resulting in the same BB muscle actions for flexion/extension and adduction/abduction in both taxa (Table 3).

Considering that both musculoskeletal models were set in the same reference pose, in equally sprawled limb orientations, it might seem that the most relevant factor influencing disparity of muscle moment arms is skeletal morphology. While, perhaps unsurprisingly, this appears to generally be correct, limb posture (i.e. behavioural choice of joint orientations) also influences muscle action (e.g. Hutchinson et al., 2005; Hutchinson et al., 2015). In particular, we found notable differences in muscle moment arms for glenohumeral flexion/extensión between the reference pose and resting pose for our *Mussaurus* model, with the SHP, SCI, SCB and SCP switching from mixed actions in the former to exclusively flexor (SCI, SCB, SCL) or extensors (SHP) in the latter (Table 3). These differences in moment arm values between the reference and the resting pose in a single taxon can be explained in terms of posture and ROM. For example, the SHP displayed a mixed action in the reference pose of *Mussaurus*, remaining an extensor across some of the glenohumeral joint's ROM, but switching to a flexor at about -53° of flexion from the reference pose. However, the resting pose of *Mussaurus* had a more restricted ROM (35° vs. 80° in the reference pose) that prevented the SHP from changing into a shoulder flexor action. The above examples show how deep the influence of the reference pose could be on the action of a single muscle, particularly for an organism in which such pose is not anatomically likely emphasising the need for comparisons made in a context of biologically plausible ('resting') posture, as analysed below.

Functional differences in the resting pose

We focus here on muscles whose actions differed between *Crocodylus* and *Mussaurus* in the resting pose. That pose represents a more realistic limb configuration for *Mussaurus*, allowing us to speculate on underlying causes of such functional changes (e.g. morphology, posture).

It is important to distinguish muscles that change their action owing to a shift in their paths (in any posture) because of anatomical changes; and muscles that change their actions because of reorientation of the joints and its effects on muscle paths. Muscles DC and DS provide a good example of this distinction. These two muscles did not change their paths appreciably from the reference to the resting pose in each taxon, and thus maintained their moment arm patterns. However, the line to dinosaurs involved a counterclockwise (as seen from a right lateral view) rotation of the glenohumeral articular face, as previously noted (Jenkins, 1993; Gatesy & Baier, 2005). This reorientation of the glenoid transformed the functions (i.e. elevation vs. depression; protraction vs. retraction) of muscles such as the DC and DS (Figs. 4D–G, 8A).

For example, in *Crocodylus*, a flexor action could be incurred by muscles to move the humerus perpendicular to the long axis of the glenoid surface (in the same plane as the vertebral column; in a craniocaudal arc), whereas an adductor action would move the humerus parallel to the glenoid surface (and perpendicular to the vertebral column; in a dorsoventral arc). In a dinosaur such as *Mussaurus*, the long axis of the glenohumeral joint is not perpendicular to the vertebral column (as in *Crocodylus*), but caudoventrally (or obliquely) oriented. In birds such glenohumeral reorientation is taken to an extreme, with the long axis more parallel to the vertebral column (Fig. 8B). This reorientation of the shoulder joint along the dinosaurian lineage means that a flexor movement in a crocodile (or other non-dinosaurian archosaur) would protract the humerus. In a typical dinosaur, conversely, a homologous movement (i.e. a movement perpendicular to the long axis of the glenohumeral joint) would elevate the humerus, and this transformation of flexion (for example) would apply to *Mussaurus* (Fig. 8).

In the resting pose, SHP was identified as a humeral supinator in *Crocodylus* but a pronator in *Mussaurus*, although its origin and insertion sites in both taxa are placed in topologically similar areas on the scapula and humerus, respectively. A role in glenohumeral long axis rotation has not been previously reported for this muscle, to our knowledge. The cause of this divergence in muscle actions would thus be the morphological disparity of the humerus between the crocodile and *Mussaurus*. The humerus of *Crocodylus* has a narrow proximal shape in comparison with its shaft, whereas *Mussaurus* presents an expanded humeral proximal end, as is typical for all early sauropodomorphs (Galton & Upchurch, 2004). Hence the more laterally positioned insertion of the SHP in *Mussaurus* resulted in a sustained pronator action. Conversely, in *Crocodylus*, SHP’s insertion slightly medial from the humeral midline (Meers, 2003) resulted in a supinator action.

Other morphology-based differences between our study taxa are clearly caused by osteological correlates indicating soft tissue attachments, rather than by general bony geometry. The insertion site of CBD was just above the deltopectoral crest of the humerus, in an area positioned proximally on the humerus of *Mussaurus*, but more distally in *Crocodylus*. Consequently, CBD would pull further away (laterally) from the glenohumeral joint in *Crocodylus*, performing an abductor action because of the more distal and lateral position of the deltopectoral crest, and closer (medially) to the that joint in *Mussaurus*, adducting the humerus. For both taxa, CBD also would aid in flexing glenohumeral joint, an action also inferred for extant crocodiles (Meers, 2003) and various theropod dinosaurs (Jasinoski, Russell & Currie, 2006; Burch, 2012).

Some muscles had different action(s) in at least one degree of freedom in the resting pose for *Crocodylus* and *Mussaurus*. CBV retained the same pronator and adductor actions in both taxa (see also Meers, 2003; Jasinoski, Russell & Currie, 2006), but differed around the flexion/extension axis, being a mixed muscle in *Crocodylus* and solely a flexor in *Mussaurus*. This is because the switch from flexor to extensor action in *Crocodylus* occurred at about -30°, but the glenohumeral joint's maximal angle for this axis in *Crocodylus* was -60°; hence, the remaining 30° involved an extensor action, resulting in a mixed muscle action but only for half portion of the joint's presumed ROM in our model. The protractor and adductor actions of CBV seem to be ancestral for Crocodylia (Meers, 2003; Jasinoski, Russell & Currie, 2006; Burch, 2014). As is ancestral for archosaurs in general (Meers, 2003; Jasinoski, Russell & Currie, 2006; Burch, 2014), TBS was a glenohumeral extensor in *Crocodylus*. However, the TBS had a flexor action in *Mussaurus* when the joint was moved beyond -60° of flexion. As the ROM for glenohumeral flexion/extension was limited to -60° in *Crocodylus* vs -70° in *Mussaurus*, this 10° difference in ROM was sufficient to alter the TBS from being a pure extensor to having a mixed action (Fig. 5).

Not all forelimb muscles in our analysis, however, showed different actions in *Crocodylus* and *Mussaurus*. Such muscles are interesting, too, because they might have had a conservative function across (at least non-avian) Archosauria. For example, DC and DS were the only muscles acting around the glenohumeral joint that preserved the same action in the three

DOFs for both *Crocodylus* and *Mussaurus* (Table 3), combining glenohumeral supination, abduction and flexion. These qualitatively identical muscle actions (regardless of their functions in the resting pose) are reflected by the conservative attachment sites of both DS and DC on the lateral scapular blade and proximal humerus in these two taxa and, more generally, in Archosauria (Meers, 2003; Jasinoski, Russell & Currie, 2006; Langer, Franca & Gabriel, 2007; Remes, 2008; Suzuki & Hayashi, 2010; Burch, 2014). The conservative action of the deltoid muscle heads is partially congruent with previous studies that qualitatively inferred crocodile forelimb functions (Meers, 2003; Jasinoski, Russell & Currie, 2006; Allen et al., 2014).

Muscles crossing well cranial (i.e. BB, HR and BR) or caudal (i.e. triceps group) to the elbow joint also showed unambiguous actions in *Crocodylus* and *Mussaurus*, and more generally in Archosauria (Meers, 2003; Jasinoski, Russell & Currie, 2006; Burch, 2014). However, less straightforward actions were evident for muscles that originated at either side of the distal condyles, which could experience posture-dependent switches of their actions. We found complex actions like these for FU, PT, EDL, EDL, and ECR, which were elbow extensors in *Crocodylus* but had mixed actions in *Mussaurus* (see Meers, 2003; Burch, 2014 for different interpretations), or FDL, which had a mixed action in *Crocodylus* but was purely a flexor in *Mussaurus*. The differences in ROM values between both taxa seemingly did not affect the actions of these muscles (see Tables 3, S4, S6, S9). Instead, the actions of these muscles were extremely sensitive to placements of their origin sites. The main problem resulting from this sensitivity is the uncertainty about the location of the origin sites in *Mussaurus*, which are obscured by pitting and other artefacts left by the articular cartilage. Below, we consider the effects of missing cartilage on our general conclusions about forelimb biomechanics in *Mussaurus*.

Implications of normalization metrics used for moment arm comparisons

The general patterns that we present here for moment arm postural changes and muscle actions (e.g. flexor/extensor/mixed) in *Crocodylus* and *Mussaurus* are not influenced by our choice of segment length as a normalizing metric. However, comparisons of the absolute and normalized values of moment arms are influenced by the vast differences in morphology and posture (and phylogenetic divergence times) between our two study taxa. Considering that relative rather than absolute values were most needed here, and the latter problems of moment arm comparisons across disparate taxa, we have generally not emphasized those values of moment arms. As Table S2 shows, the ratios of corresponding segment lengths from our two models vary between ~1.2-2 (*Mussaurus* has relatively longer proximal segments, especially scapula). These ratios complicate proximodistal comparisons across the limbs, which were not a focus of our study. More problematically, the ideal normalization metric would be body mass (to remove size influences), but this is unknown for *Mussaurus*. Using the minimal humeral and femoral circumferences of our *Mussaurus* specimen and equation 2 from Campione & Evans (2012), we obtained an estimate of 1486 kg body mass, 73.6 times that of our *Crocodylus* specimen, or 4.19 times if the cube root of body mass were desired as an approximately linear normalizer (reducing moment arms in meters to dimensionless units as in this study's main results). If more taxa were included in our analysis, this issue would become more important to consider, so we raised it here but did not elaborate further. An alternative approach would be to present ratios of moment arms (e.g. flexor/extensor vs. abductor/adductor) but for simplicity we did not add this analysis here.

Sensitivity analysis: Influence of cartilage volume on moment arms at the elbow joint

One of the major challenges inherent to soft tissue reconstructions in extinct archosaurs is the reliable inference of sites of origin and insertion of muscles, as well as 3D paths between them. However, some muscles leave notable scars and protuberances on the bone surfaces, and thus inferences about their existence and locations become less speculative than those muscles for which no osteological correlates exist (Bryant & Seymour, 1990; Witmer, 1995). This is relevant not only for the correct interpretation of the anatomy of the animal, but also has a profound impact on biomechanical inferences based on the musculoskeletal anatomy (e.g. Hutchinson et al., 2005). The moment arms of some limb muscles are very sensitive to the inferences made about muscle attachments and paths, especially insertions. Fortunately, in many cases the concentrated nature of insertions (vs. more diffuse nature of proximal origins of muscles, which tend to taper toward their insertions) means that the insertions have clearer scars and thus locations, thereby sometimes reducing concerns about that sensitivity. Yet as noted above for the elbow (e.g. distal humerus), missing articular/epiphyseal cartilages is one clear case where there is cause for special concern and thus attention to potential sensitivity of the moment arms of muscles that cross the elbow joint.

The inference of epiphyseal cartilage in extinct archosaur limbs has been the subject of debate and speculation since the late 1800s (e.g. Owen, 1875; Cope, 1878; Osborn, 1898), w main focus of discussions centred on the estimated volume occupied by the original cartilage cap (Holliday et al., 2010; Bonnan et al., 2013; Reiss & Mallison, 2014; White et al., 2015). However, inferences about the impact of cartilage volume in functional studies have received less attention (but see Gatesy, Bäker & Hutchinson, 2009; Fujiwara, Taru & Suzuki, 2010; Tsai & Holliday, 2014; Taylor & Wedel, 2013). The lost cartilage during the process of fossilization in dinosaurs is evident in the simplified epiphyseal surfaces of the long bones. These missing surfaces also complicate interpretations of musculoskeletal biomechanics because they affect the assumed length of the segment(s) analyzed and the shape of the articular facet(s) as well (Holliday et al., 2010; Bonnan et al., 2013). Similarly, functional analyses dealing with joint articulations of limb bones in archosaurs have mostly focused on how the absence (or presence) of cartilage can influence the ranges of motion (ROM) of joints (Mallison, 2010b; Hutson & Hutson, 2012, 2013, 2014; Reiss & Mallison, 2014), although some studies opted for a bone-on-bone analysis, arguing that speculation about cartilage extent was simply excessive (White et al., 2015). Overall, there is virtually no information on how unpreserved cartilage volumes may affect muscle function in archosaur limbs. To address this matter in our musculoskeletal model by testing estimated moment arms are influenced by articular cartilage morphology, we varied the effective cartilage volume of the epiphyses by altering the wrapping surfaces of muscles crossing the elbow joint.

Increasing or decreasing the radius of the cylinder that muscles traversing the distal humeral condyles must wrap around when they contacted it represented an increase/decrease of the epiphyseal cartilage assumed for the elbow joint. Originally, the radius of the cylinder that was used for moment arm estimations was 3.12 cm (Table S1), which corresponded to 7.5% of the total length of the humerus. Added to the 5% of inferred cartilage space at the glenohumeral joint, this summed to 12.5% of the total length of the humeral segment being devoted to cartilage space, comparing well with the 10% inferred by Holliday et al., (2010) and Fujiwara, Taru & Suzuki (2010). Subsequently, the radius of this wrapping cylinder was then increased or decreased by 25% of its original value, and in each case we recalculated all of the affected muscles' moment arms (Fig. 9; Tables S10, S11).

Our results from this sensitivity analysis showed that altering the effective cartilage volume at the elbow did not affect the qualitative pattern of moment arms for extensor musculature (Fig. 10). There was an increase of extensor moment arm with increasing elbow flexion in all cases. In spite of the similar trajectories of the moment arm curves, altering the volume of the hypothetical cartilage cap did effectively alter moment arm values at the elbow. Reduction of this wrapping surface at the elbow by 25% of its radius considerably decreased the overall moment arms of extensor muscles. At full elbow extension, moment arms with 25% reduction of the wrapping surface (i.e. 'cartilage') were smaller by almost half of the original values, and about four times smaller than the model with enlarged (+25%) wrapping surfaces. On the other hand, when the virtual cartilage cap at the elbow was increased by 25%, the moment arms showed less difference in magnitudes at full extension compared to the unaltered cartilage cap, displaying almost identical values. At full flexion, however, leverage differences increased, involving larger values for the model with increased cap volume, as expected (Fig. 10; Table S10). These results were expected because muscle moment arms can be defined as the minimal distance between the line of action of a muscle-tendon complex and the centre of rotation of a joint (e.g. Pandy, 1999). On average, moment arms calculated for the 25% reduced 'cartilage cap' experienced a decrease of 19% of moment arms relative to the non-altered model, whereas an increase of 25% to the ‘cartilage cap’ resulted in a 14% increase of moment arm values. Hence, reduction of the cartilage cap (as a wrapping surface) around a given joint should lead to a reduction (although non-proportional) of the moment arms for that joint. Thus, although consideration of cartilage volume and estimated shape in ROM analysis deserves scrutiny because of potential for subjectivity (White et al., 2015), our results demonstrate that missing articular cartilage could strongly influence muscle moment arm variations, highlighting the importance of epiphyseal caps for inferences about muscle functions and evolution.

Manus pronation in *Mussaurus* and the evolution of quadrupedalism in Sauropodomorpha

The biped-quadruped transition in Sauropodomorpha was linked with the dramatic postural changes that evolved from the smaller sauropodomorph ancestors to the gigantic sauropods (Upchurch, Barrett & Galton, 2004). Such changes also involved a series of anatomical transformations, including increased body mass and a forward shift of the body’s centre of mass (Bates et al., 2016), modification of limb proportions (Wilson, 2002), and successive addition of sacral vertebrae (Wilson & Sereno, 1998; Pol, Garrido & Cerda, 2011), among others. However, over the past 15 years, pronation of the manus has been proposed as a critical anatomical feature associated with the acquisition of quadrupedal locomotion in different lineages of Dinosauria (Bonnan, 2003; Bonnan & Senter, 2007; Bonnan & Yates, 2007; Maidment & Barrett, 2012; VanBuren & Bonnan, 2013; Hutson, 2015). The growing consensus is that manus pronation originated during the early evolution of large-bodied, quadrupedal and graviportal sauropodomorphs. This consensus exists in contrast to the evolution of pronation capabilities in extant taxa, including some lizards and mammals, in which pronation seems to have been correlated with increased arboreality at small body sizes (Matthew, 1904; Haines, 1958; VanBuren & Bonnan, 2013; Hutson, 2015).

It has broadly been accepted that a permanently pronated manus in sauropodomorph dinosaurs was facilitated by the evolution of the craniolateral process of the proximal ulna that accommodated the radius in a cranial (not medial) position relative to the ulna. This pronation of the manus should have aided the forelimbs to generate craniocaudally directed propulsive or braking forces that roughly paralleled the actions of the pes in a parasagittal plane (Bonnan, 2003). Excluding (putatively ancestrally) bipedal forms such as *Panphagia* and *Saturnalia*, most non-sauropod sauropodomorphs are hypothesized to have been either facultative quadrupeds or bipeds, although few studies have delved deeply into this topic.

Moreover, although widely cited in the literature, the terms ‘active’ and ‘passive’ pronation have not been formally defined, existing only in an implicit fashion (see Bonnan & Senter, 2007; Bonnan & Yates, 2007; VanBuren & Bonnan, 2013). Here we define active pronation as the muscle-driven ability to rotate the manus around its longitudinal axis, from pronation to supination, by virtue of any kind of rearrangements of the antebrachial bones. Active pronation may facilitate facultative quadrupedalism. Passive pronation implies a manus permanently fixed into pronation, with no clear ability to supinate, leading to obligate quadrupedalism.

Bonnan & Senter (2007) suggested that the early Jurassic massopodans *Plateosaurus* and *Massospondyus* had poor abilities for quadrupedal locomotion (thus favouring bipedalism) based on the restricted ROMs of their limb joints and the morphology of their radius and ulna (i.e. straight radius, not crossing the ulna), which may have precluded active or passive pronation. Additionally, ROM analysis performed on a 3D skeleton of *Plateosaurus* showed that radius rotation around the ulna was impossible, mainly because of its oval-shaped proximal end, precluding pronational capabilities and thus quadrupedal locomotion (Mallison, 2010a; Mallison, 2010b). Nonetheless, a permanently semi-pronated manus was not ruled out for *Plateosaurus* (Mallison, 2010b). It is important to keep in mind that pronation and supination of the manus is not a simple dichotomy but rather a spectrum from a semi-pronated manus (palms facing medially; sometimes confusingly called semi-supinated) that probably precluded quadrupedalism to a fully pronated manus that could be planted firmly on the ground and was ideally positioned to produce craniocaudally directed forces.

In contrast, a permanently semi-pronated manus is inferred to have been present in *Melanorosaurus* (Bonnan & Yates, 2007), a sauropodomorph closely related to Sauropoda (Yates, 2007; Pol et al., 2011; Otero et al., 2015). In the latter studies, a semi-pronated manus was concluded to have evolved at least in sauropodomorphs close to Sauropoda, at the base of the 'quadrupedal clade'. This clade retained other clearly 'prosauropod-like' forelimb features (e.g. an arched metacarpus, three manus claws, and a medially divergent pollex), indicating a potential decoupling of manus shape and quadrupedalism. Other features hint at a functional connection between forelimb morphology (e.g. presence of a craniolateral process on the ulna) and manus shape (i.e. presence of an arched, rather than bundled, metacarpus) (Bonnan & Yates, 2007).

Nonetheless, the question remains: how much manus pronation is needed to facilitate a switch from bipedalism or facultative quadrupedalism to obligate quadrupedalism? Fully quadrupedal dinosaurs (sauropods, thyreophorans and ceratopsids) had a permanently pronated manus, and sauropodiforms such as *Melanorosaurus* had a semi-pronated manus, so the latter condition might have facilitated at least facultative quadrupedalism (Bonnan & Yates, 2007). Regardless, how the forelimbs of early sauropodomorphs were used for functions other than purely locomotion has hitherto not been convincingly addressed, and the functional steps that ultimately produced the derived locomotor mechanisms present in Sauropoda remain obscure, deserving testing with a wider sample of taxa.

The forelimb of *Mussaurus patagonicus* is particularly interesting because it displays a combination of plesiomorphic and derived features. For example, it has sauropodomorph plesiomorphies such as expanded humeral epiphyses, a metacarpus that is arranged into a gentle arch, and a robust metacarpal I with a medially divergent pollex (Otero & Pol, 2013). Contrastingly, the evolution of an incipient craniolateral process of the proximal ulna (indicating potential pronation capacity of the radius and manus; Bonnan & Yates, 2007) is a derived feature in *Mussaurus*, shared with other sauropodiforms (e.g. *Aardonyx*, *Sefapanosaurus*, *Melanorosaurus*) and sauropods. Moreover, *Mussaurus* is phylogenetically placed at the base of the sauropodiform clade (Otero & Pol, 2013; McPhee et al., 2015; Otero et al., 2015), constituting an intermediate taxon to test pronation capabilities between the plesiomorphic pattern present in non-sauropodiforms sauropodomorphs (i.e. *Massospondylus*, *Plateosaurus*) and the derived pattern inferred for the closest relatives of Sauropoda (i.e. *Melanorosaurus*).

To estimate the potential for manus pronation in *Mussaurus*, we used our 3D musculoskeletal model to evaluate how the radius might have been accommodated against the ulna and which antebrachial configurations *Mussaurus* could have adopted in order to achieve some amounts of manus pronation. Recent studies demonstrated that the morphology of the radius is an important determinant of pronation capabilities, such as the presence of radial shaft curvature (allowing the radius to cross the ulna) and a rounded proximal articular face (permitting the radius to rotate around the proximal end of the ulna during active pronation); a condition typical of extant mammals (VanBuren & Bonnan, 2013). Nonetheless, the presence of a mediolaterally expanded radial head and the absence of radial shaft curvature may have precluded active manus pronation in most dinosaurs (VanBuren & Bonnan, 2013) (and perhaps other archosaurs; e.g. Hutson, 2015). Moreover, another feature would have prevented active manus pronation specifically in sauropodomorph dinosaurs. The distal end of the radius of several sauropodomorphs across the transition to Sauropoda had a prominent tubercle on the caudodistal surface of the radius, which was suggested to be an osteological correlate of the radioulnar ligament's attachment (Remes, 2008, Yates et al., 2010, Otero & Pol, 2013, McPhee et al., 2014; Otero et al., 2015). This caudodistal tubercle of the radius is a feature characteristic of basal sauropodiforms such as *Mussaurus*, *Aardonyx*, *Sefapanosaurus*, *Melanorosaurus* and *Antetonitrus* (Fig. 11; McPhee et al., 2014; Otero et al., 2015), and it is also present in the basal sauropod *Tazoudasaurus* (Allain & Aquesbi, 2008: Fig. 22).

Digital manipulation of our 3D model of *Mussaurus* in our ROM analyses showed that there was limited possibility of radial movement against the ulna both proximally and distally. The elliptical proximal surface of the radius precluded long axis rotation and the distal tubercle would have locked the distal radius and ulna, placing the former cranial to the latter. Furthermore, the radius of *Mussaurus* is rather straight, making radial crossing around the ulna impossible. Considering these constraints, the most plausible way to articulate the radius and ulna in an anatomically plausible way was with the radius cranial to the ulna proximally, and slightly medially distally, as previously suggested by Bonnan (2003). Nonetheless, with this antebrachial configuration, we infer that appreciable manus pronation (via radioulnar rotation) was not possible in *Mussaurus*, unlike the condition postulated for *Melanorosaurus*, in which at least partial pronation was previously inferred. Thus, the only way to achieve some degree of pronation in *Mussaurus* was through internal (medial) rotation of the whole antebrachium as a single unit (i.e. around the elbow joint) by up to about 30° (Table 2). With this configuration, some degree of manus pronation might have been achievable, although far from the full pronation of the manus that might be consistent with permanently quadrupedal locomotion (Fig. 12).

All of the above features in our ROM and morphological analysis of *Mussaurus* support the inference that mobility of the radius against the ulna was severely restricted in most non-sauropodiform sauropodomorph dinosaurs, making active pronation of the manus through antebrachial rotation highly unlikely. Nonetheless, our ROM analysis showed that active semi-pronation might have been possible in *Mussaurus* through internal rotation of the whole antebrachium (30°). This rotation constitutes a novel finding for basal sauropodomorphs, consistent with the inference that facultative quadrupedalism should not be ruled out for this taxon (and perhaps close relatives), although obligate quadrupedalism was unlikely. Our moment arm analysis for long axis rotation around the elbow shows that most muscles acting around the joint (i.e. BB, BR, SU, AR, Triceps group) had larger moments at full supination, indicating a potentially overall greater leverage of the forelimb in supination (Fig. S6), favouring the hypothesis of more than one biological role for the forelimbs of *Mussaurus*. As we cautioned above, however, these inferences are strongly contingent on our assumptions and conclusions about elbow joint morphology and articular cartilage in *Mussaurus*.

The evolution of a pronated manus has been postulated to have begun at least prior to the rise of sauropods, at the origin of the quadrupedal sauropodiform clade (i.e. *Melanorosaurus*, Bonnan & Yates, 2007; Yates et al., 2010). *Aardonyx*, a basal member relative to *Melanorosaurus* outside the quadrupedal clade, was proposed to have had some features that preceded quadrupedal locomotion in sauropodomorphs, such as an incipient craniolateral process of the ulna and a rather straight femoral shaft (Yates et al., 2010), but the question of how much earlier this evolution began has remained unresolved. We conclude, considering past studies as well as our new data for *Mussaurus*, that full, passive manus pronation was not present at the base of Sauropodiformes (*sensu* Sereno, 2007), but instead much closer to the origin of Sauropoda than previously thought (see also Yates et al., 2010). However, we cannot exclude some capacity for active pronation in *Mussaurus* and presumably some other sauropodiforms, as a potential intermediate state in this transformational series of forelimb function. Ultimately, reconstruction of the origin, and perhaps stepwise acquisition, of manus pronation in Sauropodomorpha will depend upon further analyses using not only qualitative, descriptive approaches but also quantitative, explicitly three-dimensional methods such as the one adopted here.

CONCLUSIONS

We have presented the first quantitative evaluation of forelimb muscle actions in a sauropodomorph dinosaur, and combined this with assessments of joint mobility and phylogenetic inferences. Comparisons made with *Crocodylus*, which represents a mode of locomotion that is closer to the presumed ancestral state for Archosauria, frame our study in a broader context to better understand major locomotor shifts in the sauropodomorph line within Archosauria, including a review of the major literature.

Analysis of moment arms revealed that, first: major differences of muscle actions between *Crocodylus* and *Mussaurus* are evident at the glenohumeral joint, and such changes are correlated with the morphology of the scapula and the orientation of the glenohumeral articulation in both taxa (supporting the inference that many of these changes occurred from Archosauria to Dinosauria/Sauropodomorpha). Second, forelimb posture has great impact on moment arm values, more so in many cases than morphology. Third, our analysis of reference versus resting pose in the studied taxa demonstrated how extensive the influence of such poses could be on the action of a single muscle, particularly for an organism in which that pose is not anatomically likely (such as *Mussaurus*), requiring the need for comparisons made in a context of biologically plausible posture (i.e. resting pose). Fourth, caution is warranted when comparing organisms with shifted joint coordinate systems, like *Crocodylus* (sprawled limb/vertical scapula) and *Mussaurus* (erect limb/caudoventrally inclined scapula), in which the same homologous movement, like flexion/extension, actually corresponds to protraction/retraction in the former and elevation/depression in the latter. Fifth, sensitivity analysis conducted on *Mussaurus'* elbow joint reveals that more extensive cartilage volume would increase the moment arms of elbow extensor muscles, in particular.

Finally, habitual quadrupedalism in *Mussaurus* is not supported by our joint ROM analysis, in which glenohumeral protraction was found to be severely restricted. Additionally, some small amount of active pronation of the manus might have been possible in *Mussaurus*, and perhaps in other earlier sauropodomorphs, via long-axis rotation at the elbow to achieve semi-pronation of the whole antebrachium (not rotation of the radius around the ulna, as previously thought). In summary, then, the rise of quadrupedalism in Sauropoda would be linked not only to manus pronation, which should have occurred very close to the node Sauropoda. This quadrupedalism was also enabled by shifting forelimb morphology as a whole, allowing larger flexor excursions of the glenohumeral joint and a more columnar forelimb posture. Our open modelling methods allow others to inspect and build upon these findings.

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Figure 1

Simplified cladogram of crown group Archosauria depicting the relationship between *Crocodylus johnstoni* and *Mussaurus patagonicus*.

Modified from Brusatte et al., 2010; Otero et al., 2015.

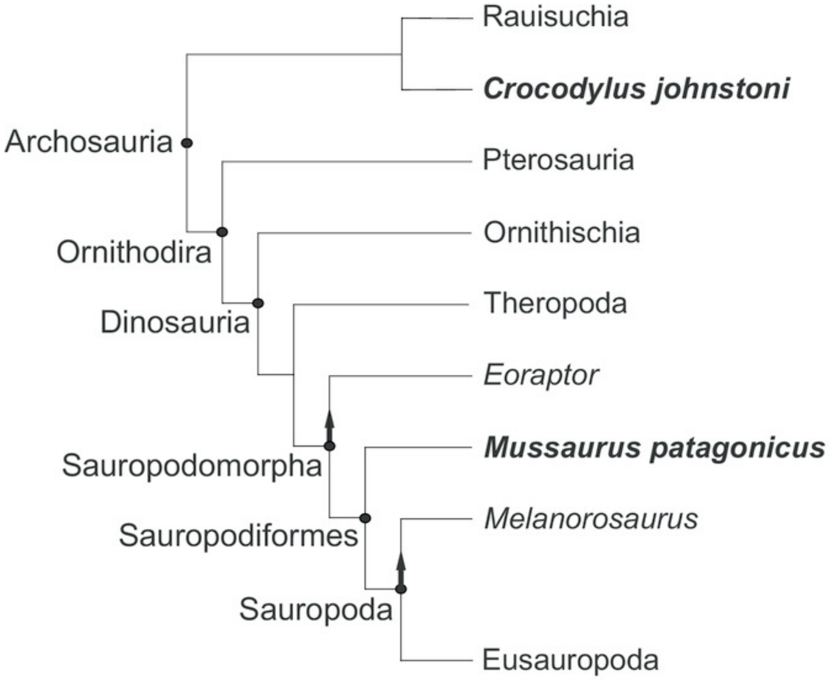
Rauisuchia
Crocodylus johnstoni
Archosauria
Pterosauria
Ornithodira
Ornithischia
Dinosauria
Theropoda
Eoraptor
Sauropodomorpha
Mussaurus patagonicus
Sauropodiformes
Melanorosaurus
Sauropoda
Eusauropoda

Figure 2

Crocodylus and *Mussaurus* models

Joint axes for rotation (x, y, z) in the reference pose showing the whole forelimb (A–F) and manus (G–I) in cranial (A, B), dorsal (C, D, G), craniolateral (E, F), medial (H) and ventromedial (I) views. Joint axis ‘x’ (red) corresponds to pronation/supination; ‘y’ (green) corresponds to adduction/abduction; and ‘z’ (blue) corresponds to flexion/extension, based on the coordinate system described by Baier & Gatesy (2013).

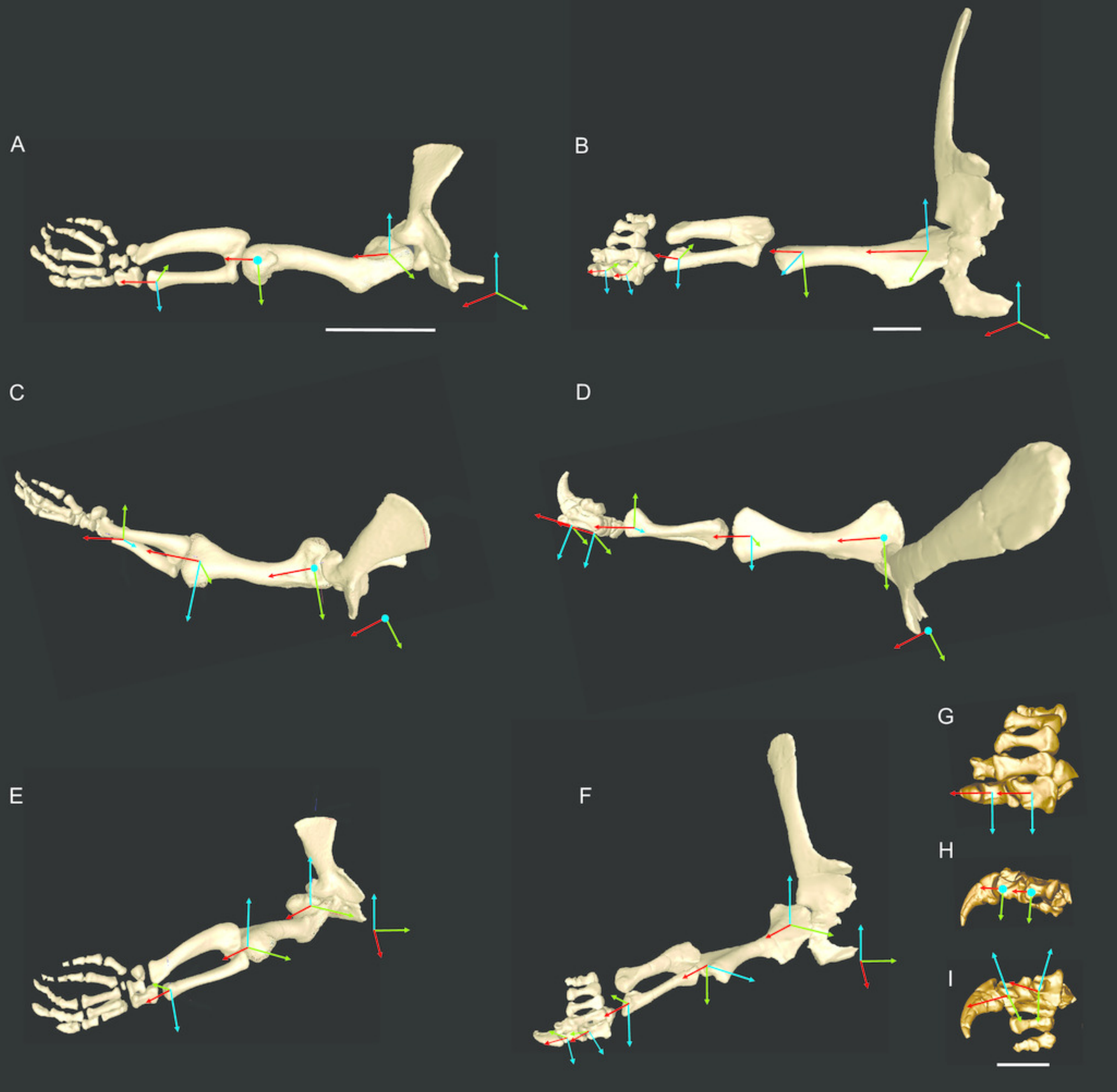
A
B
C
D
E
F
G
H
I

Figure 3

Muscle reconstruction

Right forelimb muscle reconstruction for *Crocodylus* and *Mussaurus* models in the resting pose in lateral (A–D), medial (B–E), and dorsomedial (C, F) views

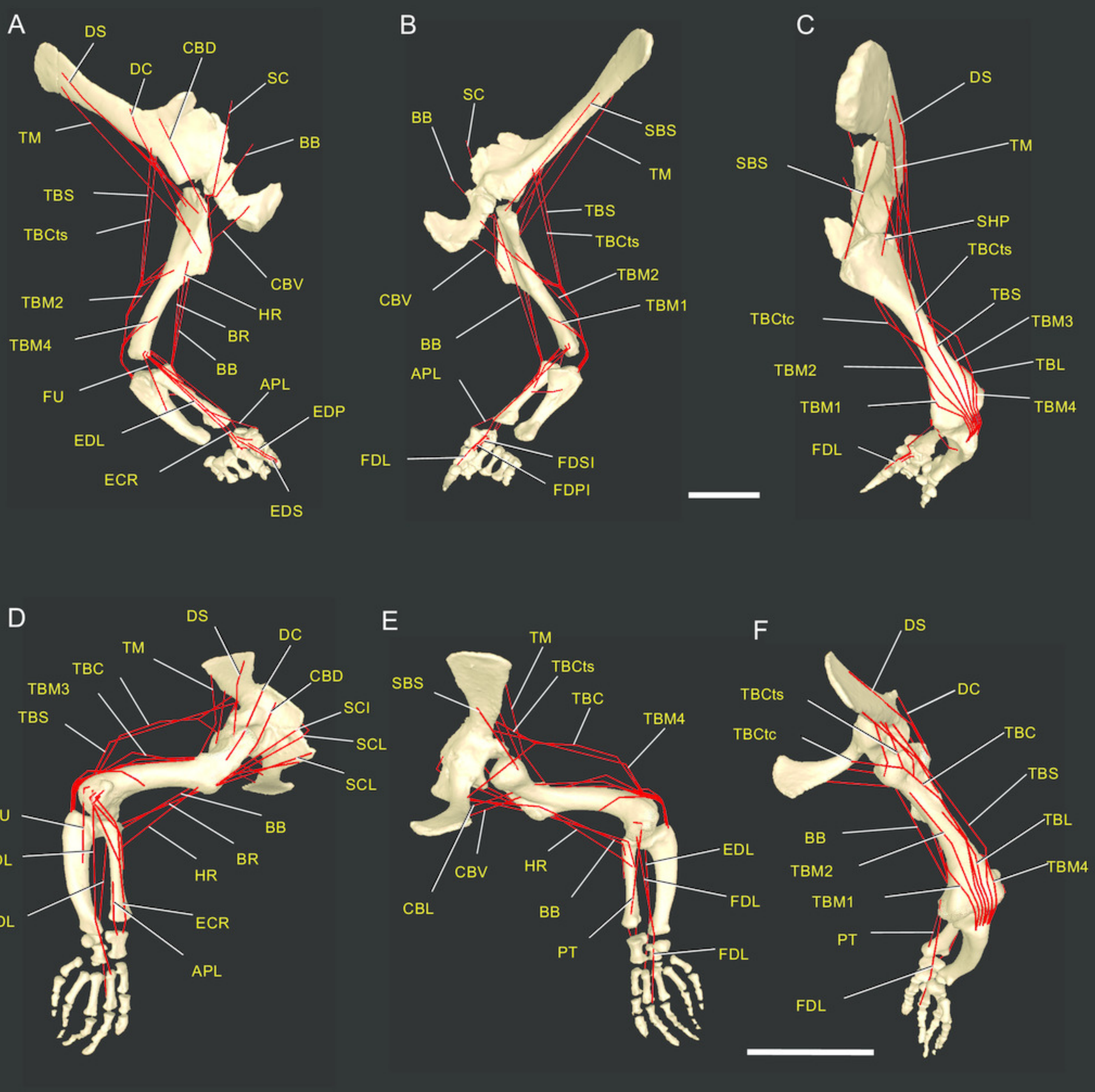
A
DS
CBD
DC
SC
TM
BB
TBS
TBCts
CBV
TBM2
HR
BR
TBM4
BB
APL
FU
EDP
EDL
ECR
EDS
B
SC
BB
SBS
TM
TBS
TBCts
TBM2
CBV
TBM1
BB
APL
FDL
FDSI
FDPI
C
DS
TM
SBS
SHP
TBCts
TBS
TBCtc
TBM3
TBL
TBM2
TBM1
TBM4
FDL
D
DS
DC
TM
CBD
TBC
TBM3
SCI
TBS
SCL
SCL
FU
BB
BR
EDL
HR
ECR
FDL
APL
E
TM
TBCts
SBS
TBC
TBM4
EDL
HR
CBV
FDL
CBL
BB
PT
FDL
F
DS
DC
TBCts
TBCtc
TBC
TBS
BB
TBL
TBM2
TBM4
TBM1
PT
FDL

Figure 4

Joint axis nomenclature for the glenohumeral joint used in this study

Reference pose in *Mussaurus patagonicus* showing ‘x’ (A), ‘y’ (B) and ‘z’ (C) axes. Reference pose in *Mussaurus* showing the vertical scapular blade, with a caudal orientation of the glenohumeral joint, depicting abduction/adduction joint motion (D), and the elevation action of the M. deltoideus scapularis (DS) (E). Resting pose of *Mussaurus* showing the caudoventrally inclined scapular blade, with a caudoventral orientation of the glenohumeral joint, depicting abduction/adduction joint motion (F), and the retraction action of the M. deltoideus scapularis (DS) (G). Note that the movements/actions depicted in both the reference and resting poses are the same (i.e. they are homologous), but differ in the resulting functions performed, because of the reorientation of the glenohumeral joint.

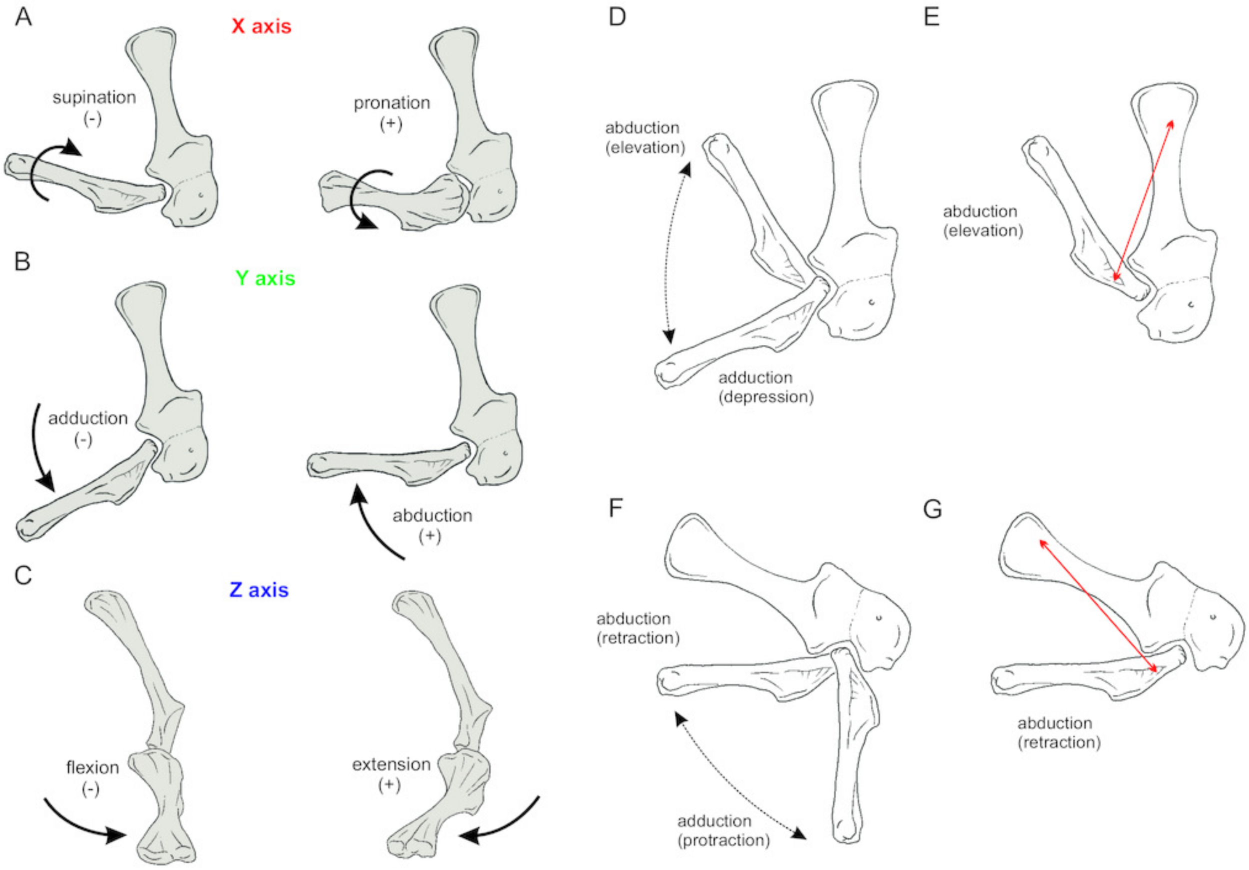
A
X axis
supination
(-)
pronation
(+)
B
Y axis
adduction
(-)
abduction
(+)
C
Z axis
flexion
(-)
extension
(+)
D
abduction
(elevation)
adduction
(depression)
E
abduction
(elevation)
F
abduction
(retraction)
adduction
(protraction)
G
abduction
(retraction)

Figure 5

Moment arms at the glenohumeral joint, normalized to humerus segment length, plotted against joint degrees of freedom for *Crocodylus* and *Mussaurus* in the resting pose

(A) pronation/supination; (B) flexion/extension; (C) abduction/adduction. Positive moment arms correspond to supination, flexion and adduction, while negative values correspond to pronation, extension and abduction. Negative glenohumeral angles correspond to pronation, extension and abduction, while positive angles correspond to supination, flexion and adduction.

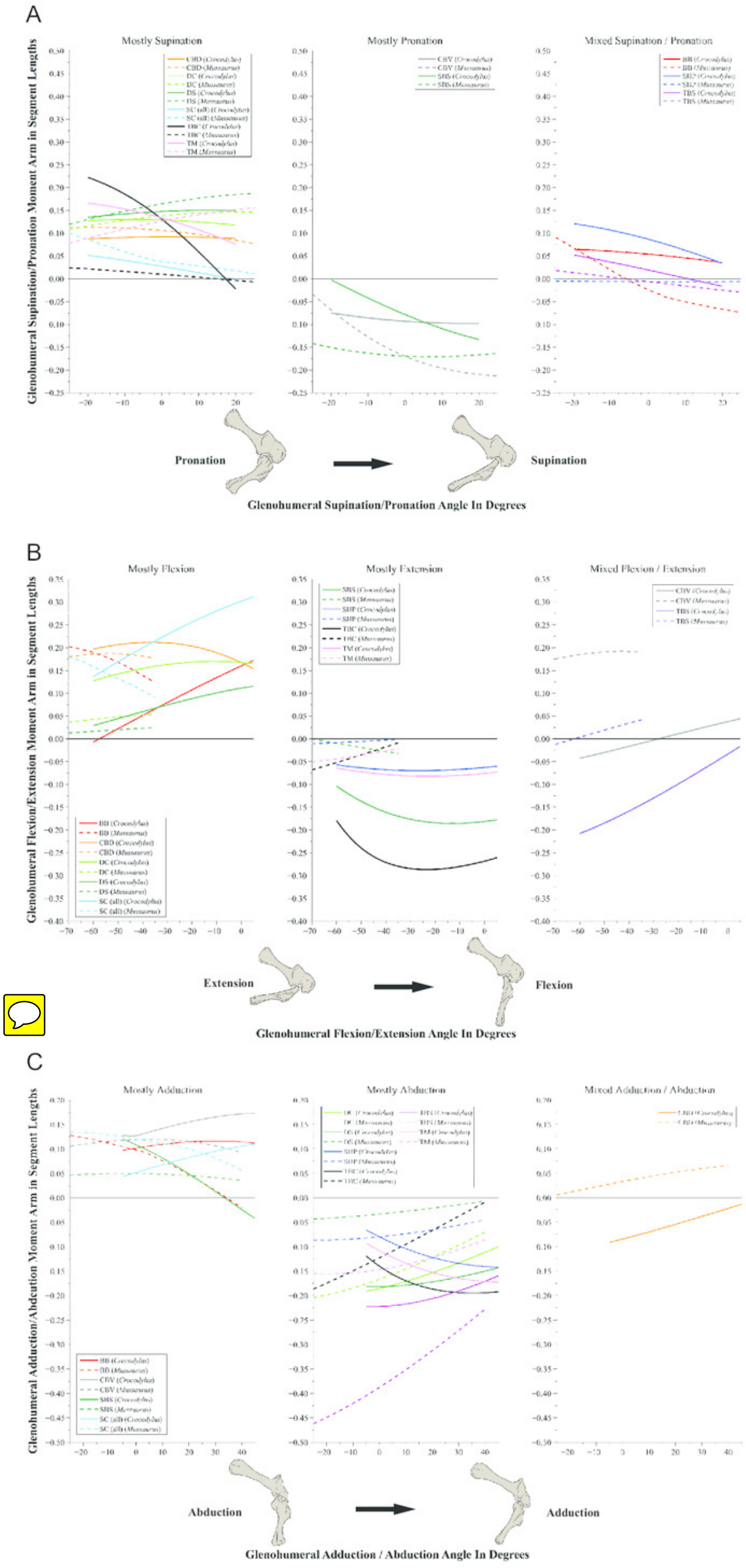
A
Mostly Supination
Mostly Pronation
Mixed Supination / Pronation
Glenohumeral Supination/Pronation Moment Arm in Segment Lengths
CBD (Crocodylus)
CBD (Mussaurus)
DC (Crocodylus)
DC (Mussaurus)
DS (Crocodylus)
DS (Mussaurus)
SC (all) (Crocodylus)
SC (all) (Mussaurus)
TBC (Crocodylus)
TBC (Mussaurus)
TM (Crocodylus)
TM (Mussaurus)
CBV (Crocodylus)
CBV (Mussaurus)
SBS (Crocodylus)
SBS (Mussaurus)
BB (Crocodylus)
BB (Mussaurus)
SHP (Crocodylus)
SHP (Mussaurus)
TBS (Crocodylus)
TBS (Mussaurus)
Pronation
Supination
Glenohumeral Supination/Pronation Angle In Degrees
B
Mostly Flexion
Mostly Extension
Mixed Flexion / Extension
Glenohumeral Flexion/Extension Moment Arm in Segment Lengths
Extension
Flexion
Glenohumeral Flexion/Extension Angle In Degrees
C
Mostly Adduction
Mostly Abduction
Mixed Adduction / Abduction
Glenohumeral Adduction/Abdcution Moment Arm in Segment Lengths
Abduction
Adduction
Glenohumeral Adduction / Abduction Angle In Degrees

Figure 6

Moment arms at the elbow joint, normalized to antebrachium segment length, plotted against joint degrees of freedom for *Crocodylus* and *Mussaurus* in the resting pose

Positive moment arms correspond to flexion, while negative values correspond to extension.

Zero elbow angle corresponds to full extension, while larger angles correspond to flexion.

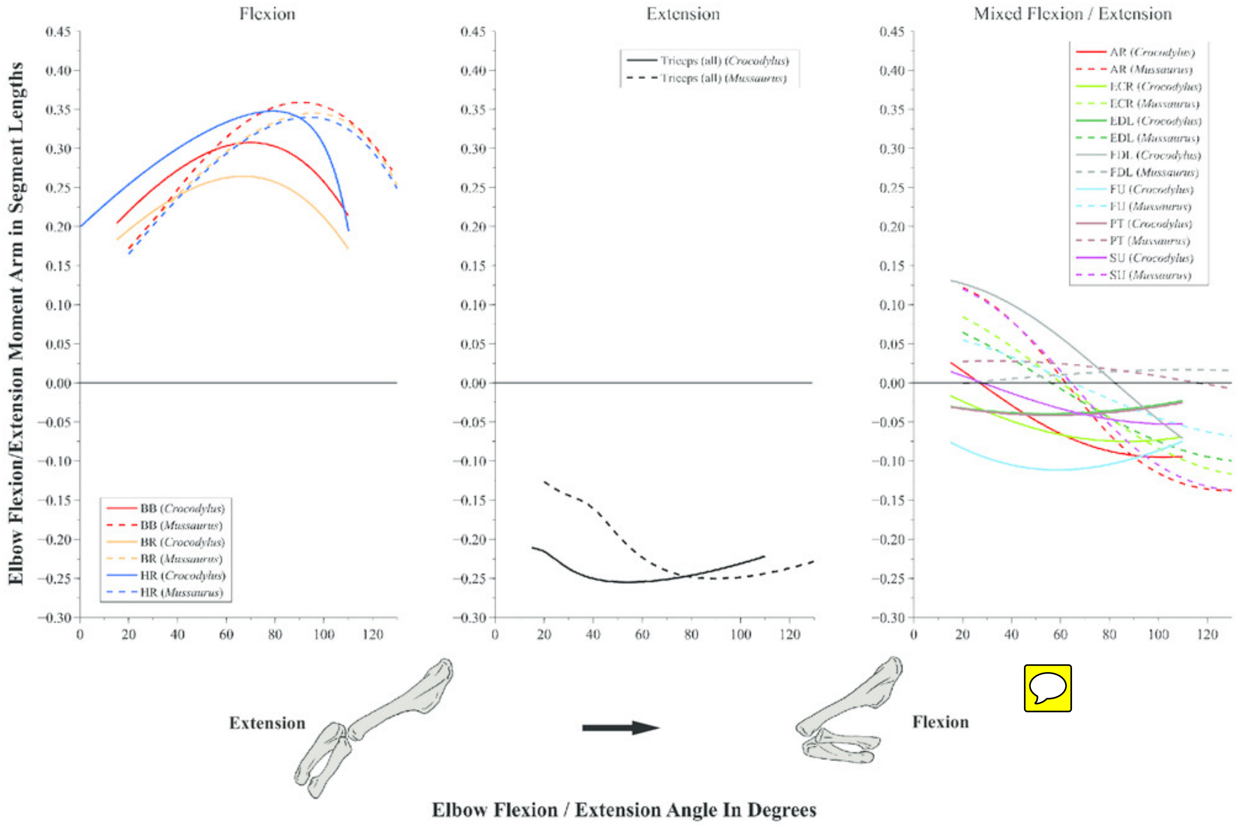
Flexion
Extension
Mixed Flexion / Extension
Elbow Flexion/Extension Moment Arm in Segment Lengths
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
−0.05
−0.10
−0.15
−0.20
−0.25
−0.30
0
20
40
60
80
100
120
BB (Crocodylus)
BB (Mussaurus)
BR (Crocodylus)
BR (Mussaurus)
HR (Crocodylus)
HR (Mussaurus)
Triceps (all) (Crocodylus)
Triceps (all) (Mussaurus)
AR (Crocodylus)
AR (Mussaurus)
ECR (Crocodylus)
ECR (Mussaurus)
EDL (Crocodylus)
EDL (Mussaurus)
FDL (Crocodylus)
FDL (Mussaurus)
FU (Crocodylus)
FU (Mussaurus)
PT (Crocodylus)
PT (Mussaurus)
SU (Crocodylus)
SU (Mussaurus)
Extension
Flexion
Elbow Flexion / Extension Angle In Degrees

Figure 7

Moment arms at the wrist, metacarpo-phalangeal and interphalangeal joints, normalized to manus segment length, plotted against joint degrees of freedom for *Crocodylus* and *Mussaurus*

Wrist (A), metacarpo-phalangeal-MCP (B), and interphalangeal-INP (C) joints. Positive moment arms correspond to flexion, while negative values correspond to extension. Negative joint angle corresponds to extension, while positive angles correspond to flexion.

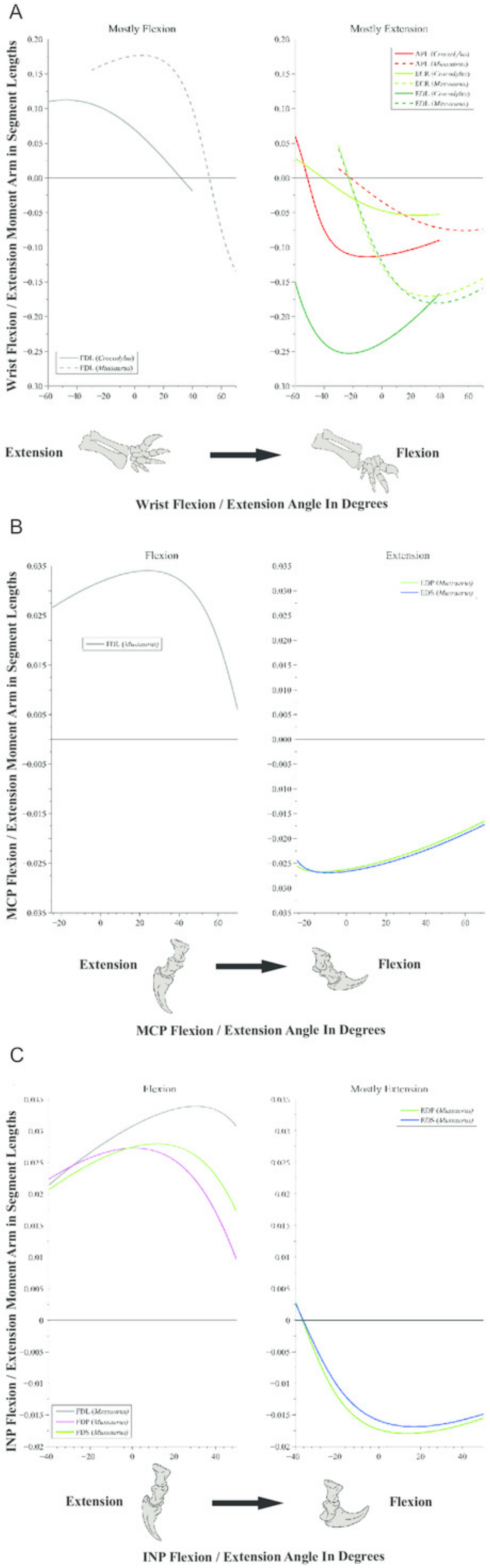
A
Mostly Flexion
Mostly Extension
Wrist Flexion / Extension Moment Arm in Segment Lengths
0.20
0.15
0.10
0.05
0.00
−0.05
−0.10
−0.15
−0.20
−0.25
0.30
−60
−40
−20
0
20
40
60
FDL (Crocodylus)
FDL (Mussaurus)
APL (Crocodylus)
APL (Mussaurus)
ECR (Crocodylus)
ECR (Mussaurus)
EDL (Crocodylus)
EDL (Mussaurus)
Extension
Flexion
Wrist Flexion / Extension Angle In Degrees
B
Flexion
Extension
MCP Flexion / Extension Moment Arm in Segment Lengths
0.035
0.030
0.025
0.020
0.015
0.010
0.005
0.000
−0.005
−0.010
−0.015
−0.020
−0.025
0.030
0.035
−20
0
20
40
60
FDL (Mussaurus)
EDP (Mussaurus)
EDS (Mussaurus)
Extension
Flexion
MCP Flexion / Extension Angle In Degrees
C
Flexion
Mostly Extension
INP Flexion / Extension Moment Arm in Segment Lengths
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
−0.005
−0.01
−0.015
−0.02
−40
−20
0
20
40
FDL (Mussaurus)
FDP (Mussaurus)
FDS (Mussaurus)
EDP (Mussaurus)
EDS (Mussaurus)
Extension
Flexion
INP Flexion / Extension Angle In Degrees

Figure 8

Terminology for homologous joint movements as the glenohumeral articular surface transformed across Archosauria

A) *Crocodylus* and a generalized bird showing homologous joint movement (in this case perpendicular to the long axis of the glenoid) along the extremes of locomotor patterns within Archosauria. (B) Evolution of muscle action around the flexion/extension axis along the ornithodiran line from the ancestral archosaurian pattern for a homologous movement. Same colour/tone indicates the same glenohumeral joint orientation. Line drawings modified from: *Crocodylus* and generalized bird (Gatesy & Baier, 2005); Pterosauria (Witton, 2015); Ornithischia (Maidment & Barrett, 2011); *Camarasaurus* (Wilson & Sereno, 1998) and *Tawa* (Burch, 2014).

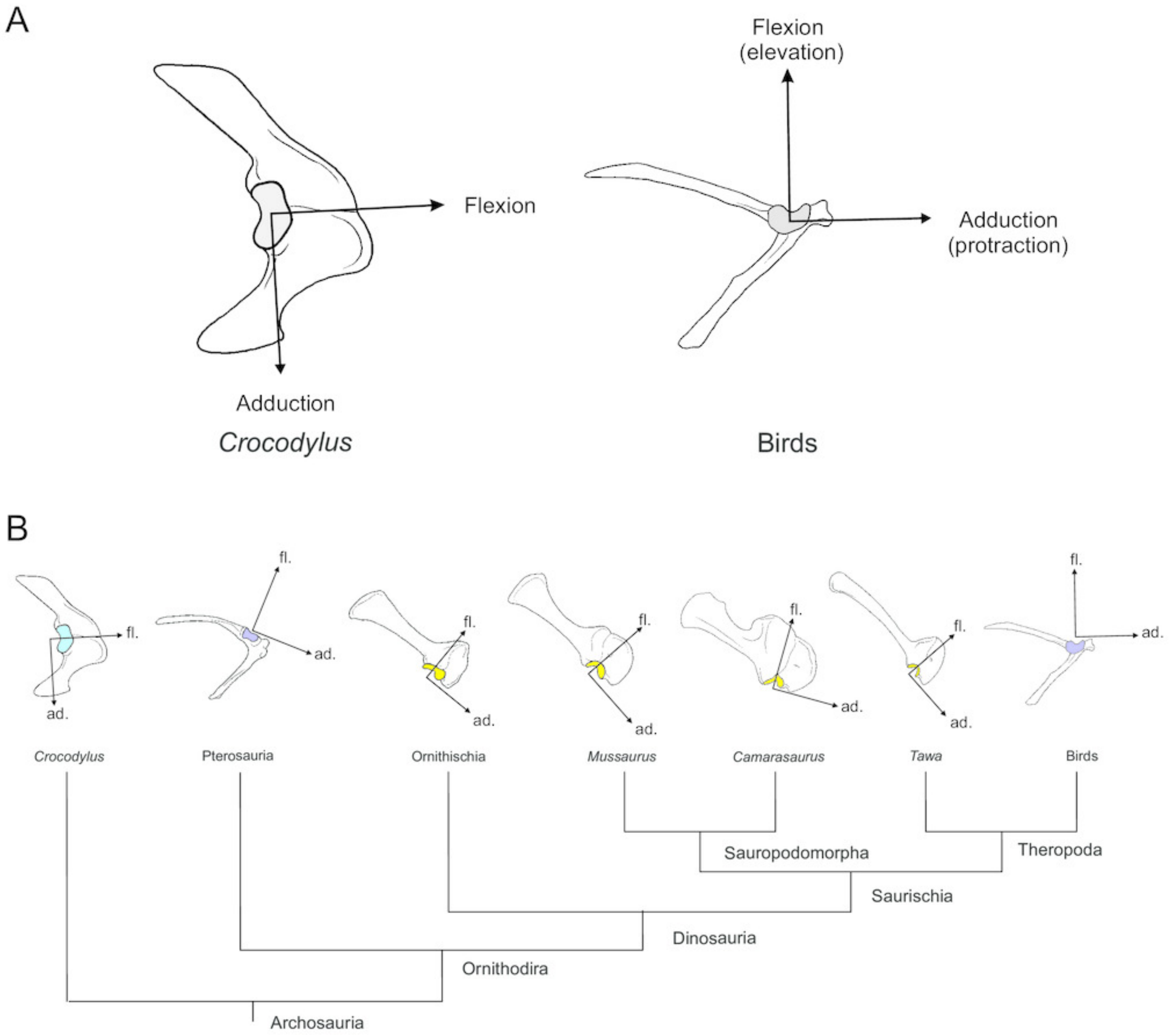
A
Flexion
Adduction
Crocodylus
Flexion
(elevation)
Adduction
(protraction)
Birds
B
fl.
ad.
Crocodylus
Pterosauria
Ornithischia
Mussaurus
Camarasaurus
Tawa
Birds
Sauropodomorpha
Theropoda
Saurischia
Dinosauria
Ornithodira
Archosauria

Figure 9

Sensitivity analysis of elbow extensor muscles of *Mussaurus patagonicus*

Cartilage diameter is shown for reduced by 25% from original (A), original (B) and enlarged by 25% from original (C).

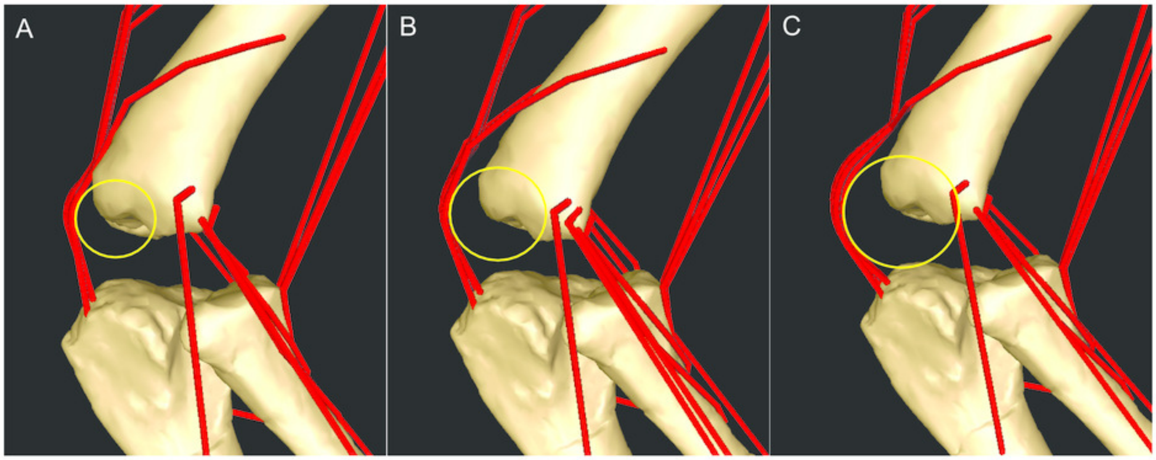
A
B
C

Figure 10

Sensitivity analysis of elbow extensor muscles of *Mussaurus patagonicus*

Moment arms at the elbow joint, normalized to antebrachium segment length, plotted against joint degrees of freedom for *Mussaurus* in the resting pose. Positive moment arms correspond to flexion, while negative values correspond to extension. An elbow angle of 0° corresponds to full extension, while larger angles correspond to flexion.

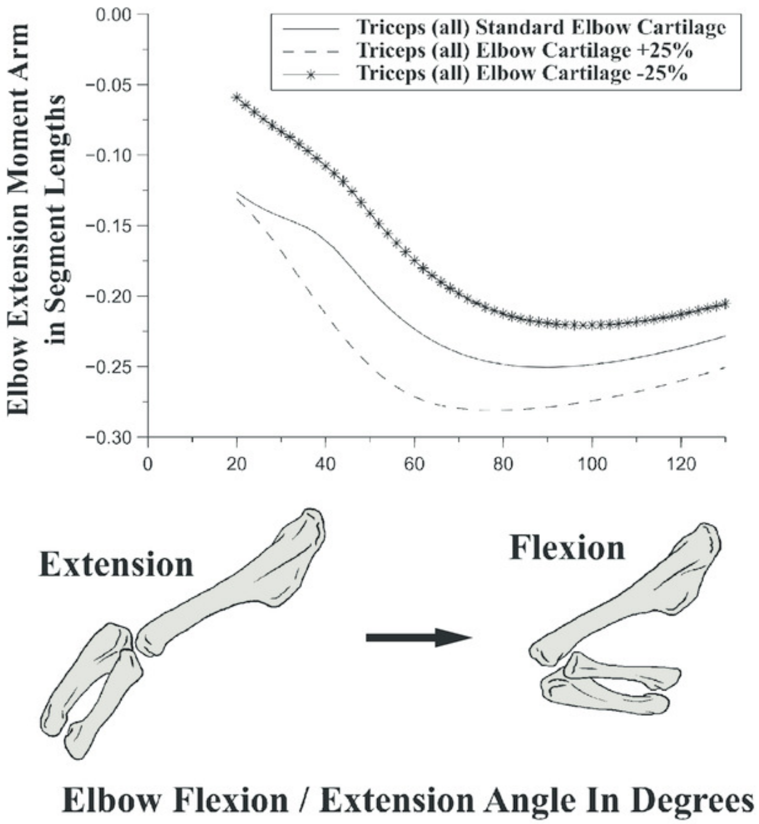
Elbow Extension Moment Arm
in Segment Lengths
0.00
−0.05
−0.10
−0.15
−0.20
−0.25
−0.30
0
20
40
60
80
100
120
Triceps (all) Standard Elbow Cartilage
Triceps (all) Elbow Cartilage +25%
Triceps (all) Elbow Cartilage -25%
Extension
Flexion
Elbow Flexion / Extension Angle In Degrees

Figure 11

Antebrachial bones of *Mussaurus patagonicus*

Radius and ulna (A) showing the articulation of the distal ends in medial (B), distomedial (C), dorsolateral (D) and lateral (E) views. Not to scale.

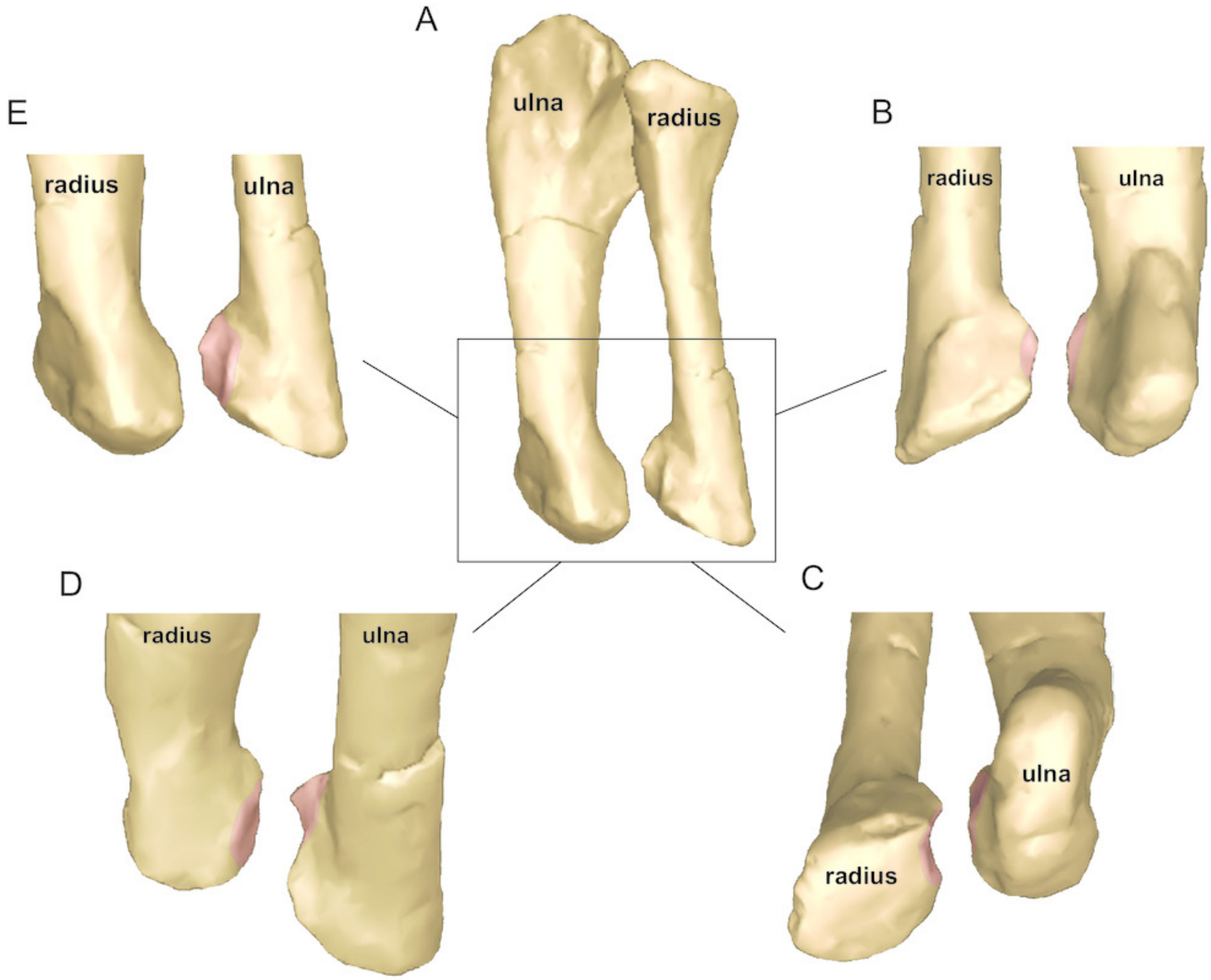
A
ulna
radius
E
radius
ulna
B
radius
ulna
D
radius
ulna
C
ulna
radius

Figure 12

Antebrachial movements of *Mussaurus patagonicus*

Non-pronated (A, C, E) and pronated (B, D, F) poses depicting the relationships among antebrachial bones. Radius and ulna in proximal (A, B) views, forelimb in cranial (C, D) views, and manus in proximal (E, F) views.

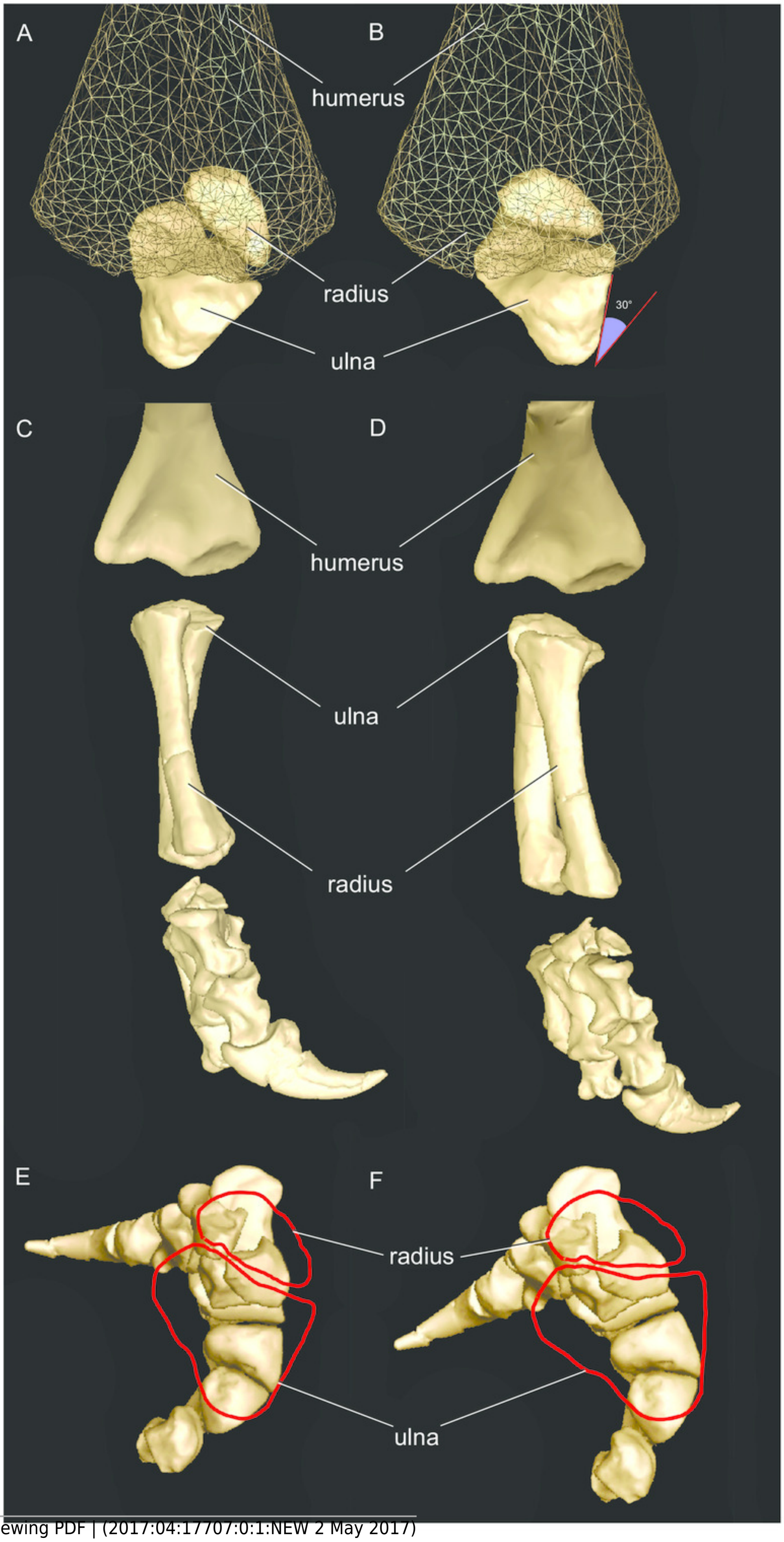
A
B
humerus
radius
ulna
30°
C
D
humerus
ulna
radius
E
F
radius
ulna

Table 1(on next page)

Shoulder and forelimb muscles inferred to be present in *Mussaurus patagonicus*, and their approximate locations

Levels of inference correspond to those that are conservative in extant archosaurs (I) or varied and thus ambiguous for Archosauria (II); level III inferences (parsimoniously absent in ancestral Archosauria) were not used. Prime (I’, II’) annotations indicate attachments lacking clear osteological correlates, which can still be reconstructed but only have approximate, relative rather than more specific, direct locations (I,II).

Table 1. Shoulder and forelimb muscles inferred to be present in *Mussaurus patagonicus*, and their approximate locations.

Muscle	Abbreviation	Origin	Level of Inference	Insertion	Level of Inference
Deltoideus scapularis	DS	Lateral surface of the scapular blade	II’	Dorsocranial side of the humerus, close to the humeral head	II
Deltoideus clavicularis	DC	Acromial region along the craniodorsal surface of the scapula	I’	Caudal surface of the deltopectoral crest	I’
Teres major	TM	Caudoateral surface of the scapular blade, on the distal half of the blade	II’	Caudal surface of the humerus, medial to the deltopectoral crest	II
Subscapularis	SBS	Medial surface of the scapular blade, just above the ventromedial ridge	I’	Proximal end of the humerus, medial to the humeral head	I
Scapulohumeralis posterior	SHP	Caudal margin of the scapular blade, above the scapular glenoid lip	I’	Proximocaudal surface of the humerus, below the humeral head	I’
Supracoracoideus complex	SC				
S. longus	SCL	Medial scapula-coracoid boundary	I’	Distal portion of the deltopectoral crest	I’
S. intermedius	SCI	Lateral scapula-coracoid boundary	I’ or II’	Distal portion of the deltopectoral crest	I’ or II’
S. brevis	SCB	Lateral coracoid, above the SCL	I’ or II’	Distal portion of the deltopectoral crest	I’ or II’
Coracobrachialis brevis dorsalis	CBD	Lateral surface of the scapula, close to the acromion	II’	Proximolateral margin of humerus, above the deltopectoral crest	II’
Coracobrachialis brevis ventralis	CBV	Lateral coracoid	I’	Internal surface of the deltopectoral crest	I’
Triceps brachii					
T. caput scapulare	TBS	Caudolateral surface of the glenoid rim	I	Ulnar olecranon process	I
T. caput coracoideus	TBC	Ramii on the caudal margin of scapula and coracoid	II	Ulnar olecranon process	II
T. lateralis	TBL	Caudolateral surface of humeral shaft	I’	Ulnar olecranon process	I
T. caput mediale 1	TBM1	Medial and distal portion of the humeral shaft	I’	Ulnar olecranon process	I
T. caput mediale 2	TBM2	Caudomedial surface of proximal humerus	I’	Ulnar olecranon process	I

T. caput mediale 3	TBM3	Caudal surface of the humeral shaft	II’	Ulnar olecranon process	II
T. caput mediale 4	TBM4	Lateral and distal portion of the humeral shaft	II’	Ulnar olecranon process	II
Biceps brachii	BB	Craniodorsal surface of the coracoid	I	Proximomedial surface of the radius	I
Humeroradialis	HR	Craniodorsal surface of humerus, caudal to the deltopectoral crest	II	Humeroradialis tubercle of the proximal radius, on craniolateral side	II
Brachialis	BR	Craniomedial surface of the humerus, distal to the deltopectoral crest	I	Proximomedial surface of the radius	I
Supinator	SU	Ectepicondyle of the humerus	I	Cranial radial shaft	I
Extensor carpi radialis	ECR	Ectepicondyle of the humerus	I	Craniodorsal surface of radiale	I
Flexor ulnaris	FU	Ectepicondyle of the humerus	I	Craniolateral surface of ulna	I
Abductor radialis	AR	Ectepicondyle of the humerus	II	Cranial surface of the radius	II
Pronator teres	PT	Entepicondyle of the humerus	I	Proximomedial surface of radius	I
Abductor pollicis longus	APL	Lateral shaft of the radius and ulna	I	Proximomedial margin of metacarpal I	I
Extensor digitorum longus	EDL	Ectepicondyle of the humerus	I	Proximodorsal margin of metacarpal II	II
Extensor digiti I superficialis	EDS	Proximal side of radiale and dorsodistal portion of metacarpal I	II’	Extensor process of ungual phalanx	II
Extensor digiti I profundus	EDP	Dorsolateral and dorsodistal surface of metacarpal I	II’	Extensor process of ungual phalanx	II
Flexor digitorum brevis superficialis digiti I	FDSI	Distal carpals	II	Flexor processes of phalanx I	II
Flexor digitorum profundus digiti I	FDPI	Distal carpals	I	Flexor process of phalanx I	I
Flexor digitorum longus	FDL	Entepicondyle of the humerus, caudal surface of the ulna, and ulnar surface of distal carpals	I	Flexor surface of ungual phalanges	I

Levels of inference correspond to those that are conservative in extant archosaurs (I) or varied and thus ambiguous for Archosauria (II); level III inferences (parsimoniously absent in ancestral Archosauria) were not used. Prime (I’, II’) annotations indicate attachments lacking clear osteological correlates, which can still be reconstructed but only have approximate, relative rather than more specific, direct locations (I,II).

Table 2(on next page)

Ranges of motion (ROMs) of each degree of freedom for *Mussaurus* and *Crocodylus* in the resting pose

Table 2. Ranges of motion (ROMs) of each degree of freedom for *Mussaurus* and *Crocodylus* in the resting pose.

	Joint	Pronation (°)	Supination (°)	**Total long-axis rotation (°)**	Abduction (°)	Adduction (°)	**Total ab/ adduction (°)**	Flexion (°)	Extension (°)	**Total flexion/ extension (°)**
Mussaurus patagonicus	Glenohumeral	-25	25	**50**	-25	40	**65**	-35	-70	**35**
	Elbow	30	0	**30**	-5	5	**10**	130	20	**110**
	Wrist	-	-	**-**	-10	10	**20**	70	-30	**100**
	Metacarpo-phalangeal	-	-	**-**	-	-	**-**	50	-40	**90**
	Interphalangeal	-	-	**-**	-	-	**-**	70	-25	**95**
Crocodylus johnstoni	Glenohumeral	-20	20	**40**	-5	45	**50**	-60	5	**65**
	Elbow	-20	8	**28**	5	-5	**10**	110	0	**110**
	Wrist	-10	30	**40**	-30	5	**35**	40	-60	**100**

Table 3(on next page)

Muscle actions for the glenoid and elbow joints for *Crocodylus* and *Mussaurus* in the resting pose

Bold font highlights a difference between the two taxa. '—' indicates that the muscle was inferred not to act around that axis in the model.

Table 3. Muscle actions for the glenoid and elbow joints for *Crocodylus* and *Mussaurus* in the resting pose.

	Glenoid						**Elbow**	
	Long axis rotation		Flexion/extension		Abduction/adduction		Flexion/extension	
Muscle	*Crocodylus*	*Mussaurus*	*Crocodylus*	*Mussaurus*	*Crocodylus*	*Mussaurus*	*Crocodylus*	*Mussaurus*
DS	supination	supination	flexion	flexion	abduction	abduction	—	—
DC	supination	supination	flexion	flexion	abduction	abduction	—	—
TM	supination	supination	extension	extension	abduction	abduction	—	—
SBS	pronation	pronation	extension	extension	adduction	adduction	—	—
SHP	**supination**	**pronation**	extension	extension	abduction	abduction	—	—
SCI	supination	supination	flexion	flexion	adduction	adduction	—	—
SCB	supination	supination	flexion	flexion	adduction	adduction	—	—
SCL	supination	supination	flexion	flexion	adduction	adduction	—	—
CBV	pronation	pronation	**mixed**	**flexion**	adduction	adduction	—	—
CBD	supination	supination	flexion	flexion	**abduction**	**adduction**	—	—
CBL	pronation	—	mixed	—	adduction	—	—	—
TBS	mixed	mixed	**extension**	**mixed**	abduction	abduction	extension	extension
TBC	supination	supination	extension	extension	abduction	abduction	extension	extension
TBM4	—	—	—	—	—	—	extension	extension
TBM1	—	—	—	—	—	—	extension	extension
TBM3	—	—	—	—	—	—	extension	extension
TBL	—	—	—	—	—	—	extension	extension
TBM2	—	—	—	—	—	—	extension	extension
BB	**supination**	**mixed**	flexion	flexion	adduction	adduction	flexion	flexion
HR	—	—	—	—	—	—	flexion	flexion
BR	—	—	—	—	—	—	flexion	flexion
SU	—	—	—	—	—	—	mixed	mixed
FU	—	—	—	—	—	—	**extension**	**mixed**
AR	—	—	—	—	—	—	mixed	mixed
PT			—	—	—	—	**extension**	**mixed**
FDL	—	—	—	—	—	—	**mixed**	**flexion**
EDL	—	—	—	—	—	—	**extension**	**mixed**
ECR	—	—	—	—	—	—	**extension**	**mixed**

Bold font highlights a difference between the two taxa. '—' indicates that the muscle was inferred not to act around that axis in the model.

Table 4(on next page)

Muscle actions for the wrist and manus for *Crocodylus* and *Mussaurus* in the resting pose

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Table 4. Muscle actions for the wrist and manus for *Crocodylus* and *Mussaurus* in the resting pose.

	Wrist		**Metacarpo-phalangeal**	**Interphalangeal**
	Flexion/extension		Flexion/extension	Flexion/extension
Muscle	*Crocodylus*	*Mussaurus*	*Mussaurus*	*Mussaurus*
ECR	Mixed	Mixed	–	–
APL	Mixed	Mixed	–	–
EDL	**Extension**	**Mixed**	–	–
EDS	–	–	Extension	Mixed
EDP	–	–	Extension	Mixed
FDL	Mixed	Mixed	Flexion	Flexion
FDSI	–	–	–	Flexion
FDPI	–	–	–	Flexion

Bold font highlights a difference between the two taxa. '—' indicates that the muscle was inferred not to act around that axis in the model.