

RESEARCH ARTICLE

Using the American alligator and a repeated-measures design to place constraints on *in vivo* shoulder joint range of motion in dinosaurs and other fossil archosaurs

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SUMMARY

Using the extant phylogenetic bracket of dinosaurs (crocodylians and birds), recent work has reported that elbow joint range of motion (ROM) studies of fossil dinosaur forearms may be providing conservative underestimates of fully fleshed *in vivo* ROM. As humeral ROM occupies a more central role in forelimb movements, the placement of quantitative constraints on shoulder joint ROM could improve fossil reconstructions. Here, we investigated whether soft tissues affect the more mobile shoulder joint in the same manner in which they affect elbow joint ROM in an extant archosaur. This test involved separately and repeatedly measuring humeral ROM in *Alligator mississippiensis* as soft tissues were dissected away in stages to bare bone. Our data show that the ROMs of humeral flexion and extension, as well as abduction and adduction, both show a statistically significant increase as flesh is removed, but then decrease when the bones must be physically articulated and moved until they separate from one another and/or visible joint surfaces. A similar ROM pattern is inferred for humeral pronation and supination. All final skeletonized ROMs were less than initial fully fleshed ROMs. These results are consistent with previously reported elbow joint ROM patterns from the extant phylogenetic bracket of dinosaurs. Thus, studies that avoid separation of complementary articular surfaces may be providing fossil shoulder joint ROMs that underestimate *in vivo* ROM in dinosaurs, as well as other fossil archosaurs.

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INTRODUCTION

Reliable estimates of forelimb range of motion (ROM) in fossilized dinosaurs, as well as other fossil archosaurs, are of great importance to researchers attempting to reconstruct different aspects of how they lived. Humeral ROM at the shoulder joint is particularly useful to forelimb reconstructions because this area provides the bony connection between the forelimb and the body wall (Fig. 1). Therefore, assessments of humeral ROM are crucial for providing information on the movements undertaken when non-avian and avian dinosaurs used their forelimbs for terrestrial or aerial locomotion, which has been a major focus of recent research in a diverse array of clades (Paul, 1988; Jenkins, 1993; Johnson and Ostrom, 1995; Bonnan, 2001; Gishlick, 2001; Bonnan, 2003; Wilhite, 2003; Senter, 2006a; Bonnan and Senter, 2007; Langer et al., 2007; Remes, 2007; Senter, 2007; Thompson and Holmes, 2007; Carpenter and Wilson, 2008). There has also been a recent surge of scientific and public interest on how humeral ROM affected idiomotion [i.e. non-locomotor limb movements (Fischer, 1998)] in bipedal dinosaurs, such as during prey capture, displays, grooming, etc. (Welles, 1984; Nicholls and Russell, 1985; Gishlick, 2001; Carpenter, 2002; Carpenter and Smith, 2001; Senter, 2005; Senter, 2006a; Senter, 2006b; Senter, 2006c; Senter, 2007; Senter and Robins, 2005; Senter and Parrish, 2006; Bonnan and Senter, 2007; Carpenter and Wilson, 2008; Lipkin and Carpenter, 2008). Unlike early, mostly qualitative reports of humeral ROM (e.g. von Huene, 1928), of late there has been a much-needed trend towards

rigorous, repeatable experimentation that utilizes comparisons with extant archosaurs and lacertilians (e.g. Nicholls and Russell, 1985; Bonnan, 2001; Carpenter, 2002; Wilhite, 2003; Bonnan and Senter, 2007; Carpenter and Wilson, 2008; Lipkin and Carpenter, 2008). However, despite the increasing importance of obtaining reliable empirical estimates of humeral ROM in dinosaurs, there is disagreement on whether the shoulder and hip joints of various fossil archosaurs would have allowed the extensive *in vivo* ROMs that some researchers report their fossilized, bony articular surfaces can allow (Bennett, 1991; Bennett, 1997), as well as descriptive and quantitative evidence that the articular cartilage lost in fossil archosaurs may markedly affect skeletonized ROM measurements (Schwarz et al., 2007; Holliday et al., 2010). Thus, there is a need to investigate whether quantitative constraints on *in vivo* shoulder joint ROM can be determined from the skeletonized shoulder joint ROMs being reported in fossil archosaurs. The use of the extant phylogenetic bracket (EPB) of dinosaurs (Witmer, 1995), provided by crocodylians and birds, gives us a tool with which we may be able to provide constraints for *in vivo* humeral ROM in extinct archosaurs.

Here, the effects that soft tissues have on humeral ROM in archosaurs were examined using an extant archosaur, the American alligator *Alligator mississippiensis* (Daudin 1802). *Alligator mississippiensis* was chosen over the flightless ratite, the ostrich *Struthio camelus*, because crocodylians possess a shoulder joint morphology more typical of that found in the vast majority of fossil

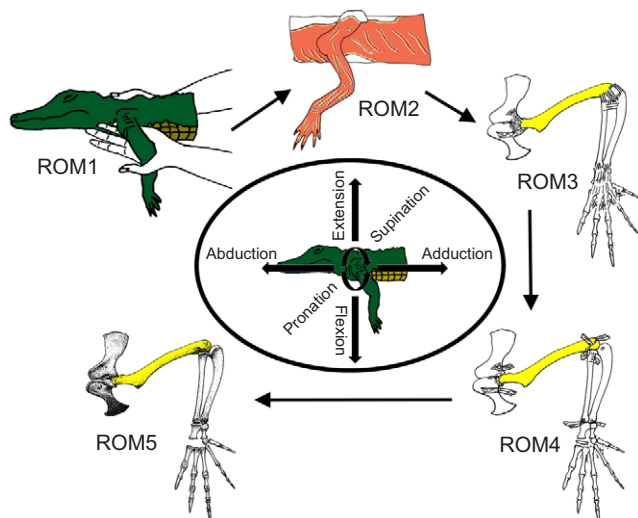


Fig. 1. *Alligator mississippiensis* forelimbs in lateral view. In the center, the three types of shoulder joint range of motion (ROM) investigated in this study are highlighted: flexion/extension, abduction/adduction and pronation/supination. The outer edge depicts five sequential levels of dissection performed between repeated measures of shoulder joint ROM. ROM1, fully fleshed; ROM2, minus integument; ROM3, minus muscles/tendons; ROM4, minus ligaments and joint capsules; ROM5, minus articular cartilage.

archosaurs (Jenkins, 1993; Meers, 1999; Carpenter, 2002; Bonnan and Senter, 2007). It has also been reported that the soft tissues surrounding the shoulder joint of *A. mississippiensis* may have been more similar to those of non-avian dinosaurs than to those of their avian descendants (Carpenter and Wilson, 2008; Lipkin and Carpenter, 2008) (cf. Dilkes, 2000). By contrast, *S. camelus* has a vestigial wing with a shoulder joint morphology substantially modified from that of other archosaurs and even flight-capable birds (Alix, 1874; Nicholls and Russell, 1985; Bonnan and Senter, 2007). Therefore, in this study, the dependent variable of interest was humeral ROM in degrees at the shoulder joint of *A. mississippiensis* (Fig. 1).

A test of the methodology used here was undertaken previously (Hutson and Hutson, 2012) in a quantitative investigation of the effects of soft tissues on elbow joint ROM in the EPB of dinosaurs from a fully fleshed to a skeletonized state. It was concluded that despite the large number of variables that need to be controlled for in a limb ROM experiment to reduce variance and observer bias, ROM studies of dinosaurian elbow joints may be obtaining meaningful data on the lower limits of *in vivo* ROM, provided that they use a conservative methodology (Hutson and Hutson, 2012). The term 'conservative' means that visible separation of complementary articular surfaces is assumed to have been harmful *in vivo*, while impaction between bones was not, because of the presence of fossae that form as a result of habitual contact. The study (Hutson and Hutson, 2012) lent support for this methodology, by finding that the elbow joints in the EPB of dinosaurs do not separate beyond the limits of their visible complementary articular surfaces without causing permanent damage to soft tissues. A major assumption of this methodology was that the application of force in a fully fleshed joint, until firm resistance is encountered, will replicate the extreme end point of active ROM that an animal could possibly perform *in vivo*. This assumption was based partially on Hultkrantz's observation that ROM researchers can force extremes of ROM on a joint that an animal could not replicate *in vivo*

(Hultkrantz, 1897). Based on this assumption, that a forced, fully fleshed ROM can be used as a proxy for the upper limits of *in vivo* ROM, the data from our previous study (Hutson and Hutson, 2012) indicated that *in vivo* elbow joint ROM is higher than skeletonized ROM. This conclusion ran counter to previous reasoning that fleshed ROMs should be less than skeletonized ROMs (Carpenter and Smith, 2001; Bonnan, 2003; Carpenter and Wilson, 2008); reasoning that was based on solid observations that integument and muscles/tendons (as well as muscle tonus *in vivo*) (Hultkrantz, 1897) act to restrict joint ROM. However, our (Hutson and Hutson, 2012) data revealed that soft tissues, intrinsic and extrinsic to a joint, have different effects on physically applied ROM. Specifically, extrinsic soft tissues do appear to decrease and reinforce the ROM dictated by articular surfaces, but intrinsic soft tissues, such as articular cartilage, may increase and reinforce ROM. These results call for further tests of whether the effects of soft tissues on elbow joint ROM are applicable to other types of joints besides the hinge-like elbow, such as the more mobile shoulder joint.

In this ROM study, we sought to rigorously test whether the results of our elbow joint ROM study (Hutson and Hutson, 2012) also apply to shoulder joint ROM (Fig. 2), which has important implications for determining whether ROM studies of fossilized limb joints are obtaining ROM values that can be used to extrapolate back to ROM *in vivo*. For example, the question of whether the humerus and femur have ROMs that allow them to move beyond the limits of their contacts with the shoulder and hip sockets is crucial to studies of the origins of flapping flight in basal avians (Jenkins, 1993; Gishlick, 2001; Carpenter, 2002; Senter, 2006a), whether the other lineage of aerial archosaurs, pterosaurs, were bipedal or quadrupedal on the ground (Bennett, 1997), and the ROM allowed in the shoulder joints of pterosaurs (Wellnhofer, 1985; Bennett, 1991). The limits of ROM at the shoulder joint have also been important to recurring debates on whether quadrupedal non-avian dinosaurs, such as ceratopsians (Johnson and Ostrom, 1995; Thompson and Holmes, 2007), and sauropodomorph dinosaurs (Holland, 1910; Bonnan, 2001; Bonnan, 2003; Wilhite, 2003; Remes, 2007), were capable of moving their forelimbs in a manner analogous to that of large mammals.

Unlike the generalized archosaurian forearm, which is mostly restricted to flexion and extension in one plane at the elbow joint, the humeri of archosaurs can have substantial mobility at the shoulder joint in all three anatomical planes, including the capacity

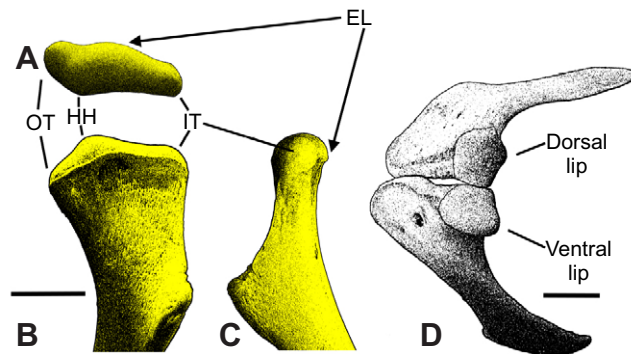


Fig. 2. Morphological landmarks of the shoulder joint in *A. mississippiensis*. Proximal humeral epiphysis of *A. mississippiensis* in (A) proximal, (B) flexor/ventral and (C) preaxial/lateral views. (D) The glenoid cavity of an *A. mississippiensis* scapulocoracoid in an oblique, posterolateral view. OT, outer tuberosity; HH, humeral head; IT, inner tuberosity; EL, extensor lip. Scale bars, 1 cm.

for long-axis rotation (Carpenter and Wilson, 2008). Thus, the increased mobility at the shoulder joint in *A. mississippiensis*, compared with that at its elbow joint, necessitated assessment not only of humeral flexion/extension but also of abduction/adduction and pronation/supination (see Fig. 1). To keep ROMs as simple and repeatable as possible, we treated each of the three types of shoulder joint mobility as three separate experiments, each with its own set of repeated measures data, and its own statistical analysis. The results were then compared with each other, with the primary objective of quantitatively investigating whether soft tissues affect humeral ROM in a manner similar to that of the elbow joint ROM. Secondary objectives important to this study included determining whether fossilized humeral ROM studies of fossil archosaurs are providing accurate estimates of *in vivo* humeral ROM, and assessing the empirical validity and repeatability of ROM studies on the more mobile shoulder joint of fossil archosaurs.

MATERIALS AND METHODS

Experimental animals and figures

The dead *A. mississippiensis* specimens obtained for this study were described previously (Hutson and Hutson, 2012). All figured forelimb elements are from the left forelimb of a 127 cm female (NIU biology department collections). The camera used was a 6.0 megapixel digital Canon PowerShot SD600. To highlight surface detail, digital photographs of articulated bones were opened in Adobe Photoshop Elements 5.0 and the background erased. Each photograph was then modified with the 'stamp' function under the 'sketch' and 'filter' toolbars. The smoothness setting was adjusted accordingly and the humerus was shaded yellow to help separate it visually from the scapulocoracoid. To obtain stylized ROM figures, the humerus was photographed in extremes of ROM against the immobile scapulocoracoid, and these extremes were digitally superimposed.

Collection of repeated-measures data

The five sequential levels of dissection treatment that separated each round of three repeated measures by observers one (J.D.H.) and two (K.N.H.) of *A. mississippiensis* humeral ROM, and the steps that were taken to reduce variance and observer bias, were described previously (Hutson and Hutson, 2012). In ROM1, repeated measures of shoulder mobility were performed on fully fleshed specimens. In ROM2, the integument was removed, while for ROM3 repeated measures, muscles and tendons were dissected away. In ROM4, ligaments and joint capsules were cut, and for ROM5, articular cartilage was removed until only bare bones were left (see Fig. 1).

During the first three levels of dissection treatment (ROM1–ROM3) for repeated measures of humeral flexion/extension, the *A. mississippiensis* specimens were positioned horizontally so that the forelimb hung freely over the edge of a table. The forelimb was rotated on its long axis at the shoulder so that the forearm pointed downwards. This orientation positioned the upper arm so that only extremes of humeral flexion/extension were measured. By this, we mean that the humerus was held and moved in an orientation in which the flattened plane of the proximal humeral epiphysis was perpendicular to the ROM of flexion and extension being measured. This orientation was established in ROM1–ROM3 using forelimb elements from two extra specimens that we dissected for practice and reference throughout the study. One hand was used to press down on the body (see ROM1 of Fig. 1) to help restrict independent movements of the scapulocoracoid against the body wall (Meers, 2003). The inclinometer used to record degree measurements was pressed or positioned parallel to the long axis

of the humerus on its extensor edge, for repeated measures of the extreme end points of forced flexion and extension. The difference in degrees between these two measurements was calculated and recorded. For ROM4 and ROM5, the scapulocoracoid of each forelimb was immobilized in clay in the same orientation as ROM1–ROM3. The bulbous humeral head (Fig. 2B) was then pressed firmly into the center of the glenoid cavity and flexed and extended until the flattened extensor and flexor surfaces of the proximal humeral epiphysis impacted upon the dorsal and ventral lips (Carpenter, 2002) of the glenoid cavity (Fig. 2D). This procedure was halted before the humeral head separated from the glenoid cavity (Fig. 3). The right coracoid of the 137 cm specimen had been broken and healed. This injury did not overlap with the glenoid cavity, and did not appear to affect humeral ROM.

For repeated measures of humeral abduction and adduction in ROM1–ROM3, the *A. mississippiensis* specimens were held so that the long axis of their body was vertical. The upper arm was oriented sideways with the forearm flexed at 90 deg and pointing forwards and upwards. Manipulations of skeletonized and partially dissected practice *A. mississippiensis* specimens were used to establish that this orientation only measured abduction and adduction of the humerus along the flattened plane of the proximal humeral epiphysis (Fig. 2C) between the dorsal and ventral lips of the glenoid cavity (Fig. 2D). This methodology allowed the extreme ROM of humeral

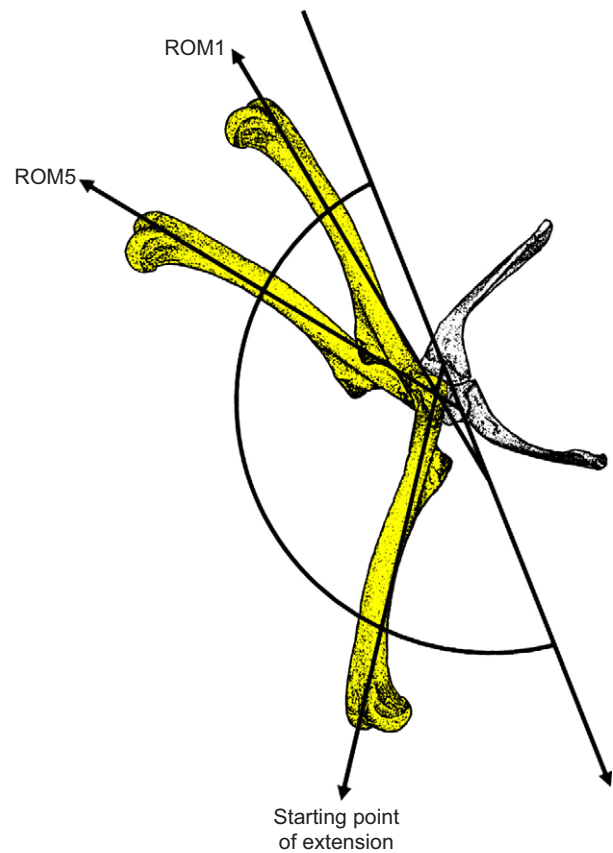


Fig. 3. The shoulder joint of *A. mississippiensis* in posterior view, showing a stylized comparison between ROM1 (139.4 deg) and ROM5 (112.5 deg) means of humeral flexion and extension. Note that this and the following two ROM figures have arbitrary starting points, and are depicted primarily to illustrate the comparative difference in degrees between fully fleshed and bone-on-bone ROMs, the latter being comparable to those used in fossil ROM studies.

abduction to be measured, but we observed that the extreme ROM of adduction could not be measured using our technique because the upper arm impacted the body wall when the forelimb was allowed to drop freely. Thus, we pressed the upper arm firmly against the body wall for a degree measurement of extreme adduction. The specimens were small enough that the observer's hand holding the body wall could be used to hold the scapulocoracoid, in an attempt to restrict protraction and retraction of the scapulocoracoid against the body wall (Meers, 2003). The inclinometer was held in an orientation analogous to that used for flexion and extension above. For ROM4 and ROM5, the scapulocoracoid of each forelimb was immobilized in clay in the same orientation as ROM1–ROM3. The humeral head was pressed into the center of the glenoid cavity. The humerus was abducted and adducted until the inner and outer tuberosities, which border the main articular surface of the humeral head (Fig. 2A–C) impacted against the recessed, saddle-shaped areas immediately in front of and behind the glenoid cavity (Fig. 4, Fig. 1) (see also Jenkins, 1993). Any further movement would have caused separation of the articular surfaces. We made the decision initially not to attempt to slide or glide the humeral head onto the very end of the articular extension of the outer tuberosity as a means of ascertaining the extreme of abduction as per Meers (Meers, 1999), because extensions of the articular surface of the humerus have not been demonstrated to cause gliding in lacertilians, but only hinge-like abduction using the humeral head as the pivot point (Peterson, 1973; Jenkins, 1993).

For repeated measures of humeral pronation/supination, each forelimb was positioned by an identical procedure to that described above for flexion/extension. Initially, the forelimb was grasped firmly at the elbow and supinated post-axially on its long axis at the shoulder until firm resistance was met. This end point was measured with the inclinometer pressed against the upper surface

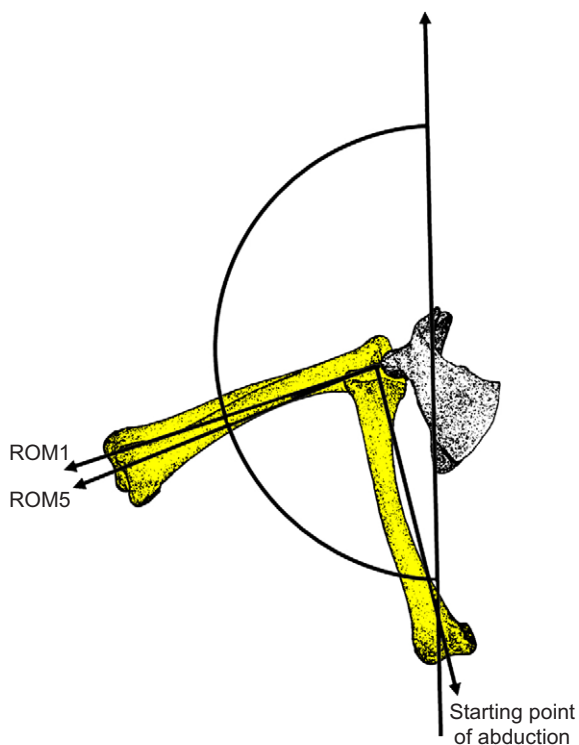


Fig. 4. The shoulder joint of *A. mississippiensis* in dorsal view, showing a stylized comparison between ROM1 (84.9 deg) and ROM5 (82.7 deg) means of humeral abduction and adduction.

of the forearm. The forelimb was then pronated pre-axially until firm resistance was met, and the inclinometer was used to measure this end point as before. The difference between these two extremes of long-axis rotation was then calculated and used as a total ROM measurement for humeral long-axis rotation. For ROM4 and ROM5, the scapulocoracoid was immobilized in clay in the same orientation as it occupied in ROM1–ROM3. Here, however, because of the extreme difficulty of holding the forearm bones against the elbow with only one hand, the inclinometer was placed instead along the extensor edge of the distal humeral epiphysis. The humerus was then pressed firmly into the center of the glenoid cavity and rotated on its long axis into supination until the inner tuberosity was observed to impact on the laterally projecting, anteroposteriorly expanded, ventral lip of the glenoid cavity (Fig. 2D). This end point was measured and then the humerus was rotated on its long axis into pronation until the outer tuberosity impacted on the ventral lip of the glenoid cavity; the difference between this end point and the end point of supination was recorded (Fig. 5).

Statistical analyses

The repeated-measures data from the six *A. mississippiensis* forelimbs were statistically analyzed using previous methodology (Hutson and Hutson, 2012). Species (i.e. *A. mississippiensis* versus *S. camelus*) was not used as a between-subjects factor. Handedness (two levels) was added as a within-subject factor. Statistical significance was set at $P < 0.05$.

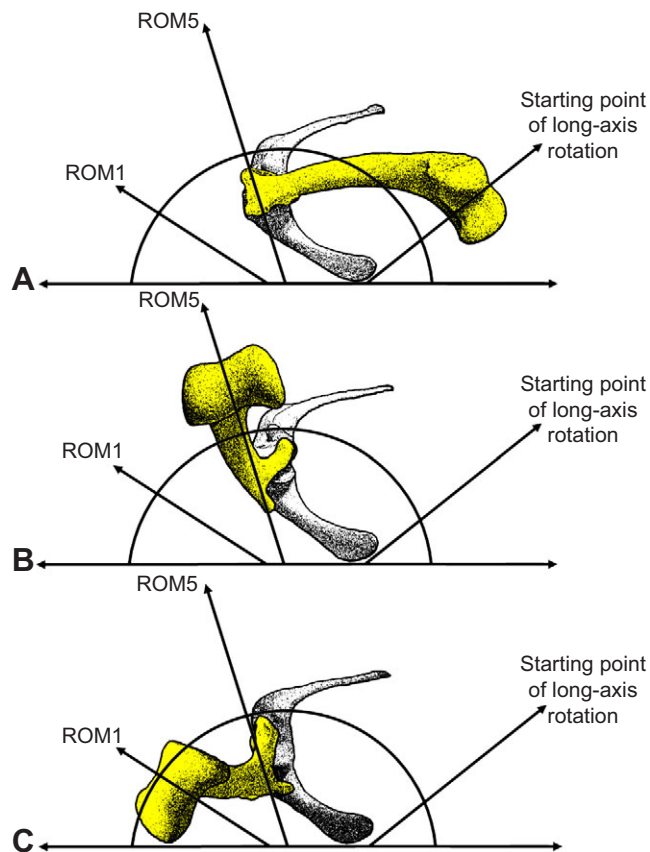


Fig. 5. The shoulder joint of *A. mississippiensis* in lateral view, showing a stylized comparison between ROMs of humeral pronation and supination. (A) Starting point. (B) ROM1 mean (95.2 deg). (C) ROM5 mean (56.2 deg). ROMs have been separated here for clarity, and the humerus was positioned obliquely to the camera in order to better portray long-axis rotation.

RESULTS

Our data show that each of the three separate humeral ROMs had higher ROM1 than ROM5 repeated-measures means (Figs 3–5; see also supplementary material Tables S1–S3). The five levels of dissection treatment had a statistically significant effect on the three humeral ROMs (Figs 5–8). By contrast, the separate effects of observer, handedness, repeated measures, or any combination of interactions between all four factors, were not found to be statistically significant (see supplementary material Tables S4–S6). These data show that the methods used previously to test the validity of elbow joint ROM studies in fossil archosaurs are repeatable on shoulder joints. Humeral flexion/extension ROMs followed a pattern similar to that previously reported for elbow joint flexion/extension ROM in *A. mississippiensis*, whereby passively forced ROM increased significantly as soft tissues extrinsic to the joint were removed, but ROM decreased significantly as soft tissues intrinsic to the joint were removed. The abduction/adduction ROMs also exhibited a peaked response curve, but with a slight increase from ROM4 to ROM5 that was likely due to an error in methodology. The pattern generated for pronation/supination ROMs exhibited a continual negative slope as soft tissues extrinsic to the shoulder joint were dissected away, likely due to an unplanned variation in force application. When errors in methodology are accounted for, ROM patterns comparable to that of flexion/extension are inferred for abduction/adduction and pronation/supination. For each of the three humeral ROM experiments, the articular (ROM4) and bony (ROM5) morphologies of the humerus and glenoid cavity were found to give approximate guides to fleshed ROM1–ROM3 humeral mobility. Our data indicate that physical separation of complementary articular surfaces does not occur *in vivo*, but that the humerus moves until it impacts against the borders of the glenoid cavity, while soft tissues act to guide ROM. ROM1–ROM3 represent progressively increasing levels of forced joint separation, in contrast to ROM4 and ROM5, which avoid separation of articular surfaces and therefore represent more conservative estimates of *in vivo* ROM. These data indicate that *in vivo* humeral ROM lies between ROM1 and ROM5, and support the pre-existing hypothesis that articular cartilage in ROM4

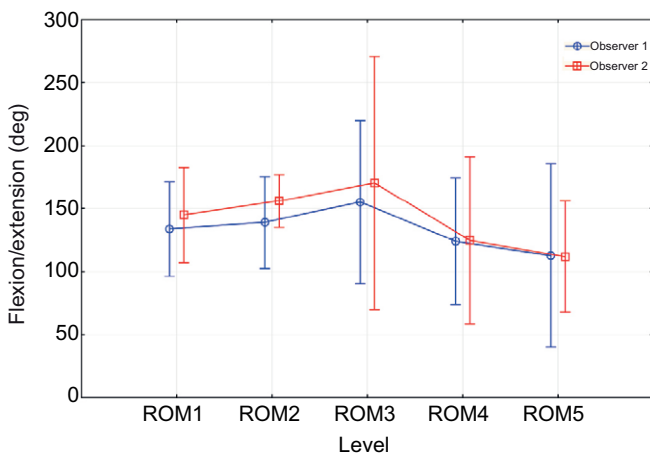


Fig. 6. Effect of five sequential levels of dissection treatment on humeral flexion/extension ROM. The data from the two observers are depicted separately here and in Figs 7 and 8, using graphs of the statistically insignificant treatment×observer interactions, in order to illustrate individual differences in force application and variability in repeated measures that helped us interpret ROM patterns. Error bars indicate ±2 s.d. (95% confidence intervals) of degree measurements here and in Figs 7 and 8.

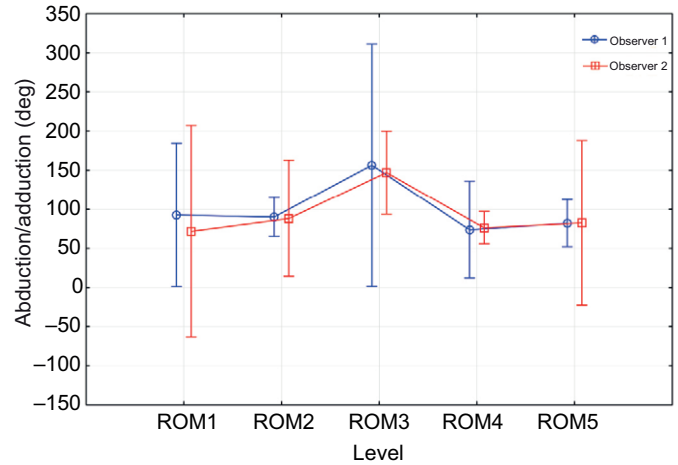


Fig. 7. Effect of five sequential levels of dissection treatment on humeral abduction/adduction ROM.

increases ROM, as compared with ROM5. Thus, ROM5 reports of fossil archosaur shoulder joints, which avoid joint separation, may provide ROM estimates that are less than or equivalent to *in vivo* humeral ROM.

DISCUSSION

Significant effects and interactions among the four factors analyzed in the three humeral ROM experiments

The five levels of dissection treatment had a statistically significant effect upon ROM for each of the three humeral experiments. The adjusted Greenhouse–Geisser treatment *P*-values were similar for each experiment, and were slightly significant at *P*=0.0119 for humeral flexion/extension (supplementary material Table S4), *P*=0.0360 for humeral abduction/adduction (supplementary material Table S5) and *P*=0.0367 for humeral pronation/supination (supplementary material Table S6). The basis for treatment significance in humeral flexion/extension (Fig. 6) and humeral abduction/adduction (Fig. 7) is an increase in ROM from ROM1 to ROM3, followed by a decrease in slope to ROM4. These peaked

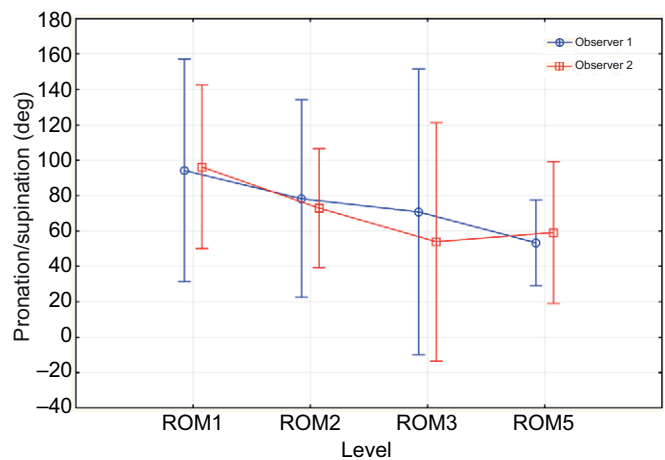


Fig. 8. Effect of four levels of dissection treatment on humeral pronation/supination ROM. Note that the observers did not collect repeated-measures data for ROM4, and that the slope of the line is persistently negative. See Discussion for explanations.

ROM patterns are similar to the ROM pattern previously reported for elbow joint ROM in the same three *A. mississippiensis* specimens (Hutson and Hutson, 2012), particularly for the humeral flexion/extension levels of ROM, which continue to decrease from ROM4 to ROM5 (Fig. 6). By contrast, the repeated-measures mean for humeral abduction/adduction increased slightly from ROM4 to ROM5 for both observers (Fig. 7). For repeated measures of humeral pronation/supination ROM, a marked negative slope caused the effect of dissection treatment to be significant (Fig. 8).

A lack of significance for the effect of observer was previously reported for the elbow joint ROMs in these *A. mississippiensis* specimens (Hutson and Hutson, 2012). We predicted at the onset of this study that there would be a statistically significant effect of observer on ROM because we expected there to be a large amount of variance between the repeated measures gathered by the two observers, as a result of the increased mobility of the shoulder joint. Despite the presence of variance in each of the three humeral experiments (Figs 6–8; supplementary material Tables S4–S6) this prediction was not borne out for this factor, which offers support for the empirical validity and repeatability of ROM studies on fossil limb joints. However, it should be noted that the effect of observer upon ROM approached the threshold of significance in all three experiments (Greenhouse–Geisser $P=0.0604, 0.0682, 0.0624$), likely due to a greater application of force by observer 2 throughout all treatment levels except ROM5 for humeral flexion/extension (Figs 3, 6), higher repeated-measures means for observer 1 in ROM1 and ROM3 for humeral abduction/adduction (Figs 4, 7), and a nearly 20 deg disparity in repeated-measures means for ROM3 in humeral pronation/supination (Fig. 8). Using the statistically insignificant treatment×observer interactions, Fig. 6–8 display the separate plotted repeated-measures means of observers 1 and 2 to illustrate the overall similarity (i.e. lack of statistical significance) in ROM patterns throughout treatment levels, despite these reported differences in observer repeated-measure means.

We did not report the effect of handedness (i.e. right *versus* left forelimbs) in our previous study on elbow joint ROM (Hutson and Hutson, 2012) because this effect was found to be insignificant in a preliminary analysis. However, we decided to test for the significance of the effect of handedness on ROM in the present study because of: (1) the expectation that the greater mobility of the shoulder joint might exacerbate differences in soft tissue flexibility due to left or right arm dominance; (2) the low power of our *A. mississippiensis* sample ($N=3$); and (3) observations that revealed that the 137 cm *A. mississippiensis* specimen sustained injuries to its right scapulocoracoid sometime during its lifetime. However, the effect of handedness upon ROM was not found to be significant using a Greenhouse–Geisser adjustment for any of the three humeral ROM experiments (supplementary material Tables S4–S6). This result is noteworthy because it indicates that, as with the more restricted hinge-like elbow joint ROM, differences between left/right humeral joint ROM did not vary significantly within the same specimens.

Our repeated-measures ANOVA did not find statistical significance for the effect of three repeated measures (i.e. time) upon ROM in any of the three humeral ROM experiments (supplementary material Tables S4–S6). As was reported above for the effect of observer upon our repeated-measures data, this result was unexpected in view of the increased variance expected in the more mobile shoulder joint of *A. mississippiensis*, as compared with the more restricted mobility of their elbow joints. In other words, we expected each of our three separate repeated measures at each of the five levels to vary more widely from one another, and from the

other observer's data, because of the effects of increased mobility in all three anatomical planes. Practice, and our methodological attempts to eliminate extraneous movements of the humerus and scapulocoracoid during repeated measures, by splitting humeral movement into three separate ROMs, may be responsible for the lack of significance.

The empirical validity and repeatability of shoulder joint ROM studies

We (Hutson and Hutson, 2012) recently argued that some of the empirical problems and soft tissue concerns associated with ROM studies of dinosaur forelimbs can be addressed with statistical analyses of a repeated-measures design. Greenhouse–Geisser adjusted P -values from repeated-measures ANOVA were used in this and our previous study (Hutson and Hutson, 2012) because taking ROM measurements at different times throughout sequential dissections of the same joints fits the requirements of a repeated-measures analysis. That is, a repeated-measures design takes into account the expected correlation between measurements on the same subject by the same observer (Myers, 1997), which cannot be assumed to be independent of one another, as is assumed during a factorial ANOVA (Von Ende, 2001). To account for the resulting correlation in repeated measures, which could cause erroneously significant P -values, adjustments are performed to alter the degrees of freedom to make it more difficult to find significance (Zar, 1999). We used two common adjustments to our P -values during the statistical analysis of our repeated-measures data: a liberal Huynh–Feldt adjustment and a more conservative Greenhouse–Geisser adjustment. As it is more difficult to find significance with the Greenhouse–Geisser adjustment, this estimate generally provides the best indication of significance in analyses of repeated-measures data that may be correlated (Von Ende, 2001). This distinction is important to reiterate in this discussion because, here, unlike with the elbow joint ROM values found previously (Hutson and Hutson, 2012), our univariate repeated-measures ANOVAs could be used to generate different conclusions based upon adjusted and unadjusted P -values. For example, in our humeral pronation/supination ROM experiment (Fig. 8; supplementary material Table S6), our repeated-measures ANOVA generated significant unadjusted P -values for the treatment×observer interaction ($P=0.0352$), as well as the treatment×arm×observer interaction ($P=0.0229$). Although the Greenhouse–Geisser adjustments for these values were not close to the threshold of significance ($P=0.126$ and 0.101 ; supplementary material Table S6), the more liberal Huynh–Feldt adjustments were closer to the threshold of significance ($P=0.0837$ and 0.0538 ; supplementary material Table S6). This situation demonstrates the necessity of using these two adjustments, particularly the conservative Greenhouse–Geisser adjustment, to account for correlation between replicate measurements on the same subjects over time, by the same observer. The unadjusted treatment×observer interaction during humeral pronation/supination was likely significant because of the 20 deg disparity in repeated-measures means in ROM3 (Fig. 8), while the unadjusted treatment×arm×observer interaction was likely due to larger repeated measures on the left shoulder joints in ROM2 and ROM3 by observer 1 (supplementary material Table S3).

Interpreting the effects of osteology and soft tissues on humeral flexion/extension ROM

During the gathering of repeated-measures data for humeral flexion/extension, we followed the methodology used previously (Hutson and Hutson, 2012). In that methodology, it was assumed that

the extremes of ROM in skeletonized forelimb bones were represented by impaction of bones against one another and/or when bones began to separate from their complementary articular surfaces. This is an important assumption to reiterate because, in contrast, previous ROM studies of fossil archosaur forelimbs have often stated that the edges of articular surfaces are presumed to represent the limits of ROM [see pp. 1–2 of Senter (Senter, 2007)]. If this statement is taken literally, then the most conservative measurement of joint ROM would end when the edge of one articular surface meets the edge of the complementary articular surface, even if the bone could be moved until it eventually separated from the joint or impacted against another bone [see pp. 461 and 503 of Bennett (Bennett, 1991)].

Our means for humeral flexion/extension were higher than those for abduction/adduction (Figs 3, 4, 6, 7), unlike what has been reported previously for these movements in archosaurs (Bonnar, 2001; Carpenter, 2002). The response curves plotted for our repeated-measures means of the ROM of humeral flexion/extension in *A. mississippiensis* were very similar to those reported for the elbow joint ROMs in these specimens (Hutson and Hutson, 2012). This relationship indicates that as the humerus was moved until firm, passive resistance was met, the ROM of flexion and extension increased as soft tissues were dissected away in ROM1–ROM3. As explained previously (Hutson and Hutson, 2012), ROM1–ROM3 reveal the constraining (i.e. protective) effects of soft tissues extrinsic to a joint that combine to keep the joint in articulation and prevent dislocation; namely, integument and muscles/tendons [see also fig. 35 of Carpenter and Wilson (Carpenter and Wilson, 2008)]. Thus, dislocation during ROM1–ROM3 is inferred from the visible prevention of joint separation in lower ROM4 values. The integument of *A. mississippiensis* consists of skin and scales, but the bulk of soft tissue-dependent prevention of dislocation came from the musculature surrounding the shoulder joint (Meers, 2003), as revealed by the marginally larger increase in ROM from ROM2 to ROM3 (Fig. 6; supplementary material Table S1). The effect of ligaments and joint capsules is to restrain the bones from separating completely during extremes of humeral ROM *in vivo* (Haines, 1952; Peterson, 1973; Jenkins and Goslow, 1983), although we could infer that these tissues were loose enough that substantial dislocation of the humerus from the glenoid cavity was occurring at the extremes of flexion and extension that we forced. Haines (Haines, 1952) reported that *A. mississippiensis* does not possess the four cruciate ligaments found in many non-mammalian tetrapods (Jenkins, 1993), which dictate ROM during a sprawling step cycle by keeping the humeral head pressed firmly against the glenoid cavity. Haines thus implied that the reduced number of shoulder ligaments in crocodylians allows for more ROM than is typically found in most non-mammalian tetrapods (Haines, 1952). Jenkins described the two ligaments of the shoulder joint in *A. mississippiensis* (Jenkins, 1993), and it was clear from our ROM3 observations that the dorsal scapulothoracic ligament prevented the humerus from completely separating from the glenoid cavity during extreme flexion, and that the ventral coracohumeral ligament prevented the humerus from completely separating from the glenoid cavity during extreme extension (Fig. 1).

Similar to findings for other archosaurs (Bonnar and Senter, 2007), the ROM of humeral flexion/extension was greatest during extension throughout each level of dissection treatment. Peterson noted a similar ROM pattern for various lacertilians (Peterson, 1973), in that protraction (i.e. flexion) of the humerus is almost impossible if the humerus is brought to verticality *via* adduction towards the midline. This phenomenon is due in part to a posteroventrally directed, saddle-shaped glenoid cavity that restricts protraction of

the humerus in the anterior quadrant past verticality at the glenoid in many tetrapods (Jenkins and Weijts, 1979), particularly if the humerus is adducted inward to the midline as per Peterson's descriptions of this effect (Peterson, 1973). We concur with these observations, but also note that in ROM5 the increased ability of the humerus to extend upwards appears to be due in part to the more vertical inclination of the dorsal lip of the glenoid cavity, which allowed the humerus to extend considerably before impacting against it, as well as an extension of the articular surface of the humeral head that prolonged humeral extension (extensor lip of Fig. 2C) [see also fig. 4.5 of Meers (Meers, 1999)]. By contrast, in ROM5 the ventral lip of the glenoid cavity projected laterally in more of a horizontal plane, which was a direct impediment to humeral flexion, and the flexor surface of the humeral head did not possess an elongated edge (Fig. 2C). This relationship indicates that the osteology of the complementary articular surfaces of the shoulder joint provides valid indicators of the ROM of humeral flexion/extension, a relationship that soft tissues serve to reinforce.

The drop in ROM between ROM3 and ROM4 is similar to that found for elbow joint ROM in these specimens (Hutson and Hutson, 2012). In ROM4, after we had removed the ligaments and joint capsule, we positioned the humerus into the center of the glenoid cavity and flexed and extended it until impaction occurred. Because of the lower repeated-measures mean for ROM4 in comparison to ROM3, as with elbow joint ROM (Hutson and Hutson, 2012), we can deduce that partial separation of complementary articular surfaces occurred during ROM1–ROM3 data collection. The combined elbow and shoulder joint data suggest that voluntary *in vivo* ROM in the EPB of dinosaurs, and by extension fossil archosaurs, lies between ROM1 and ROM5. Again, our methodology assumes that passively forcing ROM in fleshed dead specimens until firm resistance is met represents a proxy for the upper limit of voluntary *in vivo* ROM. As discussed previously (Hutson and Hutson, 2012), this assumption could be tested by measuring ROM in specimens that are not dead, *via* training, or from an accumulation of ROM values over a period of time of normal activity with the limb. This approach might reveal whether extant archosaurs separate complementary joint surfaces voluntarily in their elbow and shoulder joints, and therefore provide supportive or falsifying evidence for our proposal that *in vivo* ROM at these joints lies between ROM1 and ROM5.

In contrast to the findings for ROM1–ROM3, the difference in repeated-measures means between ROM4 and ROM5 reveals the effects of articular cartilage on the extent of humeral flexion/extension. For *A. mississippiensis*, our previous data (Hutson and Hutson, 2012) showed a decrease in elbow joint ROM from ROM4 to ROM5. As it has been demonstrated that the articular cartilaginous caps of extant archosaurs may undergo statistically significant changes in length and morphological fidelity compared with the bony articular surface beneath them (Bonnar et al., 2010; Holliday et al., 2010), this ROM loss might support the pre-existing hypothesis (Lipkin and Carpenter, 2008) that the removed articular cartilage acted to increase ROM (which indicates that the humeral *versus* glenoid ratios of area lost did not stay the same) (Meers, 1999), but the data were inconclusive for this transition in *S. camelus*. Here, for humeral flexion/extension, both observers recorded decreases in ROM after articular cartilage was removed (Fig. 6). While consistent with *A. mississippiensis* elbow joint ROM results (Hutson and Hutson, 2012), this result was unexpected because the articular cartilage of the glenoid lips was extensive and caused the lips to extend outward nearly parallel to one another. We predicted that this condition would cause a marked increase in the ROM of

flexion and extension after this seemingly constricting cartilage was removed. In hindsight, a possible explanation for the decrease in ROM from ROM4 to ROM5 may be that the protruding cartilaginous articular surfaces of the dorsal and ventral lips of the glenoid cavity served to delay impaction, by allowing the humerus to flex and extend through a greater arc than was produced by removing articular cartilage.

Interpreting the effects of osteology and soft tissues on humeral abduction/adduction ROM

The articular surface of the humeral head of *A. mississippiensis* projects further than the level of the tuberosities that bracket it, and its articular surface extends onto the outer tuberosity (Meers, 1999), as it does in various lacertilians (Lécuru, 1968; Peterson, 1973; Jenkins, 1993) and dinosaurs (Nicholls and Russell, 1985). This condition, plus the saddle-like morphology of the glenoid cavity, with recesses situated both forwards and backwards, allows the humerus to abduct and adduct using the humeral head as a pivot point (see Jenkins, 1993) (Fig. 1). We made the decision before data collection of humeral abduction/adduction that we would attempt in ROM1–ROM3 to position the humerus so that we solely measured abduction/adduction within the flattened plane of the proximal humeral epiphysis (Fig. 2A,C). It should be noted that if we had chosen to glide the articular surface of the outer tuberosity into the center of the glenoid cavity during ROM4 and ROM5 as per Meers (Meers, 1999), we might have obtained greater values of extreme abduction. However, our decision to treat the humeral head as being restricted to a center position, as per studies of lacertilian humeral ROM (Peterson, 1973; Jenkins, 1993), rather than gliding forwards and backwards as described by Meers (Meers, 1999), resulted in ROM4 and ROM5 means that were less than the ROM1 mean (Fig. 7).

As explained in the Materials and methods section, it was impossible in ROM1–ROM3 to measure the extremes of humeral adduction because of the impaction of the humerus against the body wall. However, as the humerus of each specimen could freely adduct against the side of the animal, it is possible that the humerus could have adducted farther than our measurements indicate, as discussed further below for ROM4 and ROM5. Thus, the repeated-measures means of ROM1–ROM3 represent measurements of the extreme end point of abduction. The ROM pattern throughout ROM1–ROM3 initially exhibited a positive slope similar to that found for humeral flexion/extension, and likewise the elbow joint ROM pattern previously reported for the EPB of dinosaurs (Hutson and Hutson, 2012). As with humeral flexion/extension, the greatest increase in the ROM of abduction/adduction was between the repeated-measures means of ROM2 and ROM3 (Fig. 7), which indicates that muscles and tendons constrain ROM and prevent dislocation more than integument. The high repeated-measures mean of ROM3 shows that we were able to abduct the humerus farther than we did in ROM2, before the joint capsule resisted. As we could not see how far the humerus was dislocating from the glenoid cavity in ROM3, it is possible that the humerus slid into adduction, using its articular extension onto the outer tuberosity (Fig. 2A,B).

The removal of the two shoulder ligaments and joint capsule after ROM3 (Fig. 1) required us to position the proximal humeral head into the center of the protruding cartilage-covered lips of the glenoid cavity. The extensive amount of articular cartilage on the glenoid lips appeared to heighten the depth of the recessed areas for abduction/adduction on either side of the lips. Because of this effect, we expected our ROM4 repeated-measures mean to be high in comparison to ROM1, but the mean was ~10deg lower than that

of ROM1 (Fig. 7; supplementary material TableS2). As with humeral flexion/extension, the drop in ROM from ROM3 to ROM4 indicates that separation of complementary articular surfaces progressively increased throughout ROM1–ROM3 as soft tissues extrinsic to the shoulder joint were removed. This result provides further support for our previous (Hutson and Hutson, 2012) conclusion that soft tissues extrinsic to limb joints serve to reinforce the ROM dictated by articular surfaces, but do not prevent forced joint separation; removing these soft tissues revealed the decreased ROM available before joint separation in ROM4.

The cause of the increase in ROM from ROM4 to ROM5 for humeral abduction/adduction was difficult to interpret from our data analysis. Notably, the rise in slope almost brought the repeated-measures mean of ROM5 up to the mean of ROM1 (Figs 4, 7; supplementary material TableS2). We initially believed that the increase in ROM from ROM4 to ROM5 may have been due to the removal of articular cartilage anterior and posterior to the glenoid cavity, which increased the saddle-shaped nature of the joint. However, a more likely explanation is that we did not include a skeletonized body wall to directly block extremes of adduction during our ROM4–ROM5 data collection. Thus, we believe that the lack of a ribcage could have increased the amount of space for adduction behind the scapulocoracoid, and produced higher repeated-measures means for ROM4 and ROM5. Notably, however, both the ROM4 and ROM5 means were still lower than that of ROM1, despite the possibility of increased adduction ROM. As with our humeral flexion/extension results, these results strongly suggest that the bony articular morphology of the shoulder joint in *A. mississippiensis* can provide a reliable estimate of fleshed ROM.

Interpreting the effects of osteology and soft tissues on humeral pronation/supination ROM

As with the other two humeral experiments, the humerus was rotated on its long axis until firm resistance was met in ROM1–ROM3, and until impaction and/or separation were observed in ROM4 and ROM5. The projecting articular surface of the humeral head, when combined with the saddle-like morphology of the glenoid cavity and loose soft tissues, allows the humerus of *A. mississippiensis* to rotate substantially about its long axis into pronation and supination. However, the humeral head cannot spin unimpeded, because of the presence of soft tissues in ROM1–ROM3 and the combined presence of adjacent tuberosities and projecting glenoid lips in all five levels of ROM. The extreme end point of pronation was impeded by the forwardly expanded edge of the ventral lip of the glenoid cavity, which was not possessed by the dorsal lip (Nicholls and Russell, 1985). Moreover, the ventral lip inclined upwards from back to front, which also restricted pronation. By contrast, the thinner, more vertically inclined dorsal lip of the glenoid cavity allowed more humeral supination.

Unlike the ROM patterns generated for humeral flexion/extension (Fig. 6) and abduction/adduction (Fig. 7), the slope of the line for our pronation/supination means exhibited a negative slope from ROM1 to ROM3, plus ROM5 (Fig. 8). This pattern is similar to that reported for elbow joint ROM in *S. camelus*, which was inferred to be erroneous and caused by a problem with the amount of force applied to the elbow joint (Hutson and Hutson, 2012). Here, the negative slope of humeral pronation/supination was traced back to a problem in force application as well. The negative slope was judged to be due to an unplanned increase in the application of force between ROM2 and ROM4, in an attempt to keep the humerus pressed firmly into the center of the glenoid cavity as the soft tissue connections between them became looser. However, ROM5 was still

substantially lower than ROM1. We therefore predict that, if we had not increasingly applied force to this joint up to the point of near immobility in the deep, cartilaginous glenoid lips of ROM4 (which is why we did not report a repeated-measures mean for ROM4), the ROM pattern for pronation/supination would have exhibited a peaked pattern similar to that of flexion/extension and abduction/adduction. Regardless, when combined with a similar ROM pattern for elbow joint ROM (Hutson and Hutson, 2012), the low mean of ROM5 in all three humeral experiments, compared with that of ROM1–ROM3, provides additional support for our (Hutson and Hutson, 2012) conclusion that ROM1–ROM3 represent progressively increasing separation of complementary articular surfaces within the joint. Significantly, these results also indicate that hyperextending and hyperflexing skeletonized shoulder joint articular surfaces, so that the edges of articular surfaces pass over one another, do not generate skeletonized ROMs that are greater than those of fleshed ROMs (Bennett, 1991) (cf. Carpenter and Smith, 2001). These ROM data provide additional support for our proposal that the best approximation of *in vivo* ROM, using passively forced ROMs on dead specimens, lies between ROM1 and ROM5. Therefore, previous studies that do not allow the edges of complementary articular surfaces to pass into a joint may represent underestimates of *in vivo* ROM in elbow and shoulder joints (e.g. Senter, 2007; Lipkin and Carpenter, 2008).

Implications for forelimb joint ROM studies of dinosaurs and other fossil archosaurs

Our data, which indicate that *in vivo* ROM of the shoulder joint of *A. mississippiensis* lies between ROM1 and ROM5, can also be applied to the elbow joint ROMs of these specimens, and to *S. camelus* as well. While this pattern may not apply for other joints in the forelimbs or hindlimbs of the EPB of dinosaurs, these data combine to suggest that quantitative constraints on the boundaries of *in vivo* ROM can be estimated from measurements of ROM5 from fossilized limb bones, and also support the pre-existing hypothesis (Lipkin and Carpenter, 2008) that articular cartilage within these joints may increase ROM. The previously reported methodologies for many of the elbow and shoulder studies of dinosaur ROM have predominantly been somewhat cautious by stopping movements when the edges of articular surfaces met. As this methodology is more conservative than our method of moving forearm and upper arm bones until impaction or separation occurred, which produced ROM5 values lower than ROM1 values, we interpret our data as indicating that previous reports of elbow and shoulder joint ROM in dinosaurs likely underestimate *in vivo* ROM, which may also be tentatively applied to other extinct archosaurs (Bennett, 1997). This proposal can be tested further by analyzing our joint ROM data from the wrist and finger joints of the EPB of dinosaurs, as well as ROM investigations of differing types of joints. When combined with recent studies concerning the quantitative effects of articular cartilage on joint ROM (Bonnan et al., 2010; Holliday et al., 2010), we conclude that empirical studies of ROM can continue to provide an improved picture of *in vivo* ROM in fossil archosaur reconstructions.

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