

RESEARCH ARTICLE

A test of the validity of range of motion studies of fossil archosaur elbow mobility using repeated-measures analysis and the extant phylogenetic bracket

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SUMMARY

Recent studies have presented range of motion (ROM) data in degrees for dinosaur forelimb joints, usually *via* physical manipulation of one individual. Using these data, researchers have inferred limb orientations, postures, gaits, ecological functions and even phylogenetic trends within clades. However, important areas of concern remain unaddressed; for example, how does ROM at a forelimb joint change after soft tissues are lost in archosaurs? And are fossil ROM methodologies amenable to reproducibility and statistical analysis? Here, we investigated these questions using the extant phylogenetic bracket of dinosaurs. Repeated measures of elbow joint ROM from *Struthio camelus* and *Alligator mississippiensis* forelimbs were statistically analyzed as they were sequentially dissected through five levels of tissue removal treatment. Our data indicate that there are no statistically significant differences in repeated measures of ROM between observers who use the same techniques. Extrinsic soft tissues, such as integument, muscles and ligaments were found to impede ROM at the elbow joint. Intrinsic soft tissues, such as articular cartilage, may increase ROM. The hypothesis that the articular surfaces of the bones within the elbow joints of archosaurs provide a general approximation of mobility is supported. Final ROMs were less than the initial ROMs in both taxa, which suggests that prior reports of elbow joint ROMs in degrees for nonavian dinosaurs may represent conservative estimates. We conclude that if observer bias and other variables are controlled for, ROM studies of fossil archosaur limbs can obtain useful degree data for inferring joint mobility *in vivo*.

Key words: range of motion, functional morphology, dinosaur, archosaur, forelimb, biomechanics, pronation, repeated measures, Crocodylia, Struthioniformes.

Received 25 January 2012; Accepted 7 March 2012

INTRODUCTION

Study of the fossilized bones of extinct archosaurs, such as dinosaurs, has generated a great deal of interest into their probable appearance and habits *in vivo*. One way to infer what these were is to articulate separate bony elements together to reconstruct different aspects of the specimen. An understanding of comparative anatomy and physiology in extant archosaurs can then be used to recreate posture, locomotion, etc. (Abel, 1925; Nicholls and Russell, 1985). A general knowledge of the effect that soft tissue has on individual joint thickness and range of motion (ROM) in archosaurs would be helpful in determining these attributes (Holliday et al., 2001), but this is rarely quantified (Bonnar et al., 2010; Dzemski and Christian, 2007). Thus, as it is difficult or impossible to gauge the effects of degraded soft tissue in fossilized taxa, it is often debated whether soft tissue restricts or increases a ROM at any particular joint in fossil archosaurs (Bennett, 1997). Likewise, it has been questioned whether the articular surfaces of fossilized archosaur bones faithfully represent the morphology of articular cartilage *in vivo* (Holliday et al., 2001). Unfortunately, various ROM investigators may also acknowledge that they are using methodologies that are not conducive to repeatability (Hultkrantz, 1897; Yalden, 1966), and rarely mention the necessity of statistically analyzing degree data, which raises questions about the empirical validity of such studies. Despite these concerns, the practice of physically manipulating fossil archosaur (particularly dinosaur) forelimbs to obtain ROMs in

degrees is currently a growing area of interest. For example, direct and indirect elbow joint ROM studies of fossil archosaur forelimbs are important sources of phylogenetic and paleoecological data (Hankin and Watson, 1914; Bramwell and Whitfield, 1974; Bennett, 1991; Sereno, 1993; Tereshchenko, 1994; Tereshchenko, 1996; Carpenter and Smith, 2001; Gishlick, 2001; Carpenter, 2002; Bonnar, 2003; Wilhite, 2003; Senter, 2005; Senter, 2006a; Senter, 2006b; Senter and Parrish, 2006; Senter and Robins, 2005; Bonnar and Senter, 2007; Langer et al., 2007; Thompson and Holmes, 2007; Senter, 2007; Carpenter and Wilson, 2008). To the best of our knowledge, previous authors have not recognized that studies of fossilized limb joint ROMs meet the requirements for a repeated-measures analysis, in which repeated measures between multiple observers are statistically analyzed for significant differences. This methodological approach offers a way of simultaneously addressing several of the concerns raised above.

Here, the response of elbow joint ROM to a soft tissue removal treatment was examined using the extant phylogenetic bracket (EPB) of dinosaurs (Witmer, 1995), specifically the ostrich *Struthio camelus* Linnaeus 1758 and the American alligator *Alligator mississippiensis* (Daudin 1802). The dependent variable of interest was elbow joint ROM in degrees. ROM data from shoulder, wrist and finger joints were collected at the same time, but the results of those experiments will be published separately. The elbow joint data

are presented first here. These data were analyzed with the primary goals of testing whether there is a significant difference in repeated measures between observers using the same techniques, and whether there is a significant increase or decrease in the degrees of flexion/extension from a fully fleshed to a skeletonized elbow (Figs 1, 2). Secondary questions important to this study involved quantitatively assessing the effect of soft tissue upon elbow ROM, assessing whether there are statistically significant differences in elbow joint ROM between *A. mississippiensis* and *S. camelus*, evaluating the effect of soft tissue on pronation/supination (long-axis rotation) of the radius, and outlining the variables that can affect the validity of reported ROMs in fossil archosaurs if they are not controlled for.

MATERIALS AND METHODS

Experimental animals

Three frozen specimens of wild *A. mississippiensis* and three fresh *S. camelus* wings from butchered farm animals were acquired for the EPB study. This sample provided six available elbow joints in the *A. mississippiensis* specimens, and three in the *S. camelus* specimens. The *A. mississippiensis* specimens were juvenile females with lengths of 137, 127 and 102 cm. The left forelimb of the 137 cm *A. mississippiensis* specimen was observed to be damaged upon delivery, which did not appear to affect ROM. The *S. camelus* specimens were from domesticated male and female yearlings of adult size (Cooper, 2005). The male provided right and left wings, and the female a right wing. *Alligator mississippiensis* specimens were examined immediately after being thawed, and all specimens were kept refrigerated for the duration of the study once measurements started. Measurements were taken in 2007 at Northern Illinois University. The skeletonized limbs were donated to the Biology Department Museum of Northern Illinois University.

Collection of repeated-measures data

Observers one and two (J.D.H. and K.N.H.) each repeatedly measured the elbow flexion/extension ROMs three times over five levels of sequential soft tissue dissection treatments: (1) ROM1 – all soft tissues, including full integument (i.e. skin, scales and feathers) remain attached; (2) ROM2 – integument is removed; (3) ROM3 – muscle bellies and their associated tendons are removed; (4) ROM4 – synovial joint capsules and ligaments are removed; and (5) ROM5 – articular cartilage is removed until no soft tissue remains on the bones (i.e. skeletonized to emulate fossilized archosaur bones).

Each treatment level and accompanying repeated measures were separated by 1 day of refrigeration while soft tissue was removed. Soft tissue was removed in ROM2–ROM4 with a scalpel and forceps. In ROM5, the articular cartilage was removed by soaking in a potassium hydroxide (KOH) solution at 60–70°C, with mild scraping as needed. The tissue was dissected away faster than it could decay, and all forelimbs were kept moist throughout the dissections and repeated measures.

Before collecting ROM data, we examined and practiced with two juvenile *A. mississippiensis* specimens and three adult *S. camelus* wings that had been obtained earlier from the same sources. One forelimb of each species was skeletonized so that we could conduct blind (i.e. without having any experience of the effect of soft tissues) ROM5 trials in imitation of researchers who are forced by necessity to do the same with fossilized archosaur limb elements. We then dissected the other specimens that we had obtained earlier, and trained together to collect data in as similar a manner as possible during each treatment level using an inclinometer

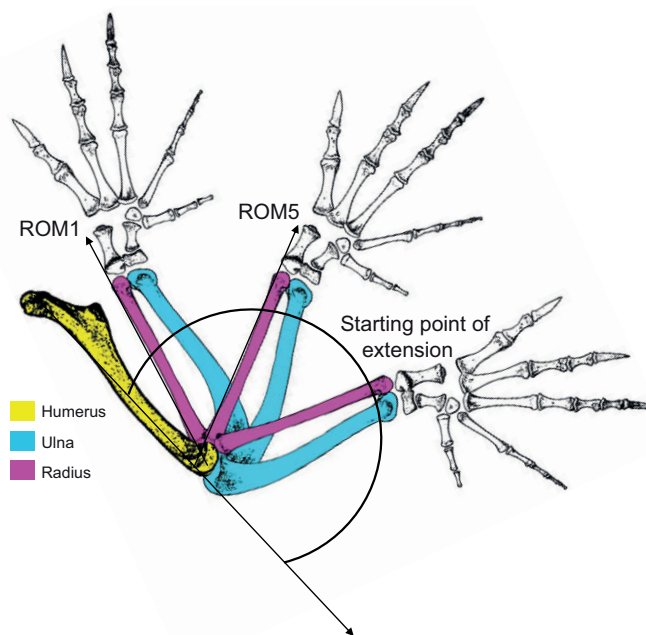


Fig. 1. A skeletonized left forelimb of *Alligator mississippiensis* in postaxial (medial) view, showing a stylized comparison between total ROM1 (94.5 deg) and total ROM5 (46.4 deg) means of elbow joint flexion and extension. This figure and the next have arbitrary starting points of extension, and are depicted primarily to illustrate the comparative difference in degrees between fully fleshed and bone-on-bone ROMs, which has important implications for fossil archosaur range of motion (ROM) studies. The radial piston mechanism and wrist folding are not depicted here.

(Model AF-P34214, Pinball Magic, Green Bay, WI, USA) accurate to 0.5 deg.

Repeated measures in degrees of elbow joint ROM were taken in a standardized fashion for each specimen. The inclinometer was pressed or positioned parallel to the long axis of a long limb bone for each degree measurement. All ROM measurements were obtained by moving the limb elements in as close to a vertical plane as possible, because the inclinometer required gravity to operate. It must be noted that tetrapod elbow joints are never perfectly planar hinges (Cuénod, 1888; Yalden, 1966), and so positioning the forearm to flex and extend vertically did not remove the effects of a slight long axis rotation of the forearm into pronation (inwards and forwards). However, this method was required for the inclinometer to operate effectively.

For the first three treatment levels, which still had attached soft tissue that was extrinsic to the elbow joint, the *S. camelus* humeri (upper arm bones) were physically held immobile with one hand. The humeri were held at an obtuse angle that allowed gravity to flex and extend the forearm. The *A. mississippiensis* humeri were immobilized in the same manner, but their smaller forearms were physically flexed and extended until firm resistance was met. For ROM4 and ROM5, all humeri were immobilized in blocks of modeling clay and held in place by one observer to allow the observer manipulating the specimen to articulate and move the radius and ulna (forearm bones; Figs 1, 2) with both hands. The radii and ulnae were then flexed and extended until their proximal articular surfaces disarticulated from each other or the humerus, or when the bones collided. The observer who was not physically manipulating the forelimbs recorded the degree measurements, but did not allow the first observer to see them until all measurements were finished,

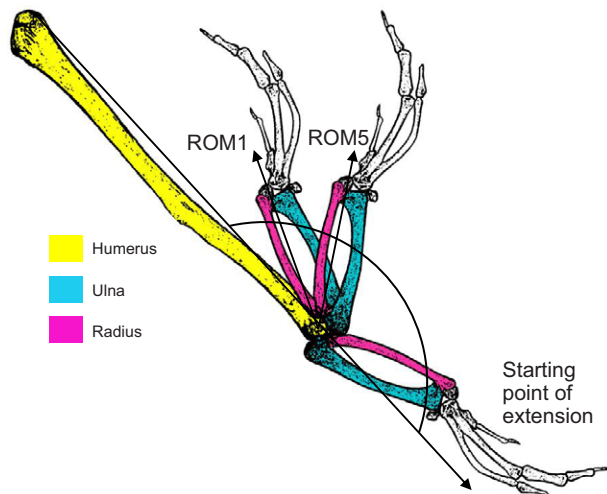


Fig. 2. A skeletonized left forelimb of *Struthio camelus* in postaxial (medial) view, showing a stylized comparison between total ROM1 (129.7 deg) and total ROM5 (103.3 deg) means of elbow joint flexion and extension. The radial piston mechanism and wrist folding are not depicted here.

and the order of data gathering was alternated with each set of measurements to control for observer bias.

Statistical analyses

Preliminary analyses based on a repeated-measures ANOVA revealed that handedness was not a significant factor affecting ROM within *A. mississippiensis* elbow joints. Three *A. mississippiensis* forelimbs were then chosen using a random number table (Zar, 1999) to test against the three *S. camelus* forelimbs. A univariate repeated-measures ANOVA was used to compare ROM of the two species: species was the between-subject factor (two levels), with treatment (five levels), observer (two levels) and repeated measures (i.e. time; three levels) as the three within-subject factors. The analysis was performed in STATISTICA® (StatSoft, Tulsa, OK, USA), which provided a conservative Greenhouse–Geisser and a more liberal Huynh–Feldt adjustment to the *P*-values to account for the correlation between repeated measures on the same subjects (von Ende, 2001).

RESULTS

Our data show that there were no statistically significant differences in the repeated measures taken by both observers using the same techniques. In contrast, the effect of the five levels of dissection treatment was statistically significant. Therefore, the effect of soft tissue on elbow joint ROM was successfully quantified. The ROMs of fully fleshed elbow joints in both species were found to be greater than that of the same joints when skeletonized to emulate the fossilized bones manipulated in ROM studies of dinosaur forelimbs. These data thus show that ROM studies of fossil archosaur elbow ROMs may underestimate *in vivo* ROM, provided that their techniques are similar to those used in this study. When differences in ROM are accounted for, the *S. camelus* specimens were found to have higher elbow joint ROMs than the *A. mississippiensis* specimens. The data also reveal that soft tissue affects elbow joint ROM in two ways. Soft tissue extrinsic to the joint inhibits ROM, whereas soft tissue intrinsic to the joint may have the opposite effect. Both types of soft tissue prohibit long-axis rotation of the forearm bones into pronation or supination at the elbow joint. Numerous

variables were encountered that can potentially introduce a large amount of variability when measuring elbow joint ROM.

DISCUSSION

Significant treatment, observer and species interactions

The ROMs in degrees of the *A. mississippiensis* and *S. camelus* elbows, as estimated by different observers across increased levels of tissue removal (Table 1), were analyzed as a repeated-measures design. The three-way interaction of species \times treatment \times observer was only marginally significant, given the disparity between the more liberal Huynh–Feldt adjustment ($P=0.026$) and the more conservative Greenhouse–Geisser adjustment for sphericity ($P=0.065$; Table 2). The basis for the interaction appears to be the increased ROM3 in *A. mississippiensis* as compared with *S. camelus* (Fig. 3), as well as the significantly lower ROM2 estimate by observer two for *A. mississippiensis* (Fig. 4). However, both the treatment \times species (Greenhouse–Geisser, $P=0.001$) and treatment \times observer (Greenhouse–Geisser, $P=0.005$) two-way interactions were significant. In the case of the former (Fig. 3), even when averaged across observers, the estimated ROM generally was greater for *S. camelus* than *A. mississippiensis*, with the exception of ROM3. For the treatment \times observer interaction, observer two estimates of ROM were significantly less for ROM2, which probably accounts for the major difference in the two response curves (Fig. 5).

The lack of a significant difference in overall ROMs for each species per observer is noteworthy (Table 2, Fig. 5). This shows that not only did each observer consistently obtain similar ROM measurements, but their overall ROMs were not significantly different for the two species. This indicates that the observer's combined measurements were not significantly different overall, and were particularly consistent with *S. camelus*. This may reflect the initial training and practicing on specimens beforehand, extensive efforts to make sure that the degree data for replicate measurements were obtained in the same manner, as well as the decision to use gravity as a uniform application of force for ROM1–ROM3 on *S. camelus* (discussed further below).

The larger variance, as shown by error bars, in replicate measurements for ROM1 is best explained by the observation that those measurements involved the greatest amount of impeding extrinsic soft tissue (Fig. 5). Despite training and practice, even tiny variations in angle (*S. camelus*) and force applied (*A. mississippiensis*) as a result of the presences of scales, skin folds and feathers, likely caused the largest range of reported ROMs. ROM2 exhibited the smallest variance in measurements (Fig. 3). The small variance in ROM2 is believed to have been caused by a tightly constrained motion brought about by the muscles and tendons, which surround and stabilize joints, and a lack of impeding integument that could produce large variations in how the forearm flexed or extended. By contrast, the removal of restrictive muscles and tendons in ROM3 considerably loosened all connections between bones.

Observers one and two did not exhibit similar slopes for replicate measurements made between ROM1 and ROM2 for *A. mississippiensis* (Fig. 4). The observers trained beforehand to apply a uniform force to the *A. mississippiensis* elbows throughout ROM1–ROM3, but the positive slope by observer one and the negative slope by observer two between ROM1 and ROM2 indicate that observer two exerted less force than in ROM1 (hence the decreased ROM plotted). Otherwise, if the same force had been applied, the loss of impeding musculature should have increased the ROM, as occurred with observer one. A return to similar replicate measurements in ROM3 by both observers likely reflects the

Table 1. Repeated measures of elbow joint flexion/extension across five dissection treatments (ROM1–ROM5) upon the experimental animals

Species	Joint	Observer	Flexion/extension (deg)														
			ROM1		ROM2		ROM3		ROM4		ROM5						
<i>Alligator mississippiensis</i>	Left elbow (137 cm)	1	79	88	80	136	120	122	175	170	174	63	65	67	39	43	38
		2	114	100	101	65	70	65	144	159	146	64	68	70	43	50	47
	Left elbow (102 cm)	1	83	90	97	108	117	122	159	160	153	74	70	65	40	41	45
		2	90	78	73	75	69	70	152	149	150	81	75	83	59	56	56
	Right elbow (137 cm)	1	106	109	103	105	135	136	155	154	152	59	54	56	50	47	53
		2	103	103	104	63	70	80	146	140	140	82	79	80	40	41	47
<i>Struthio camelus</i>	Right elbow (♂)	1	135	138	140	120	125	122	120	125	120	82	82	96	101	96	92
		2	132	135	146	122	121	119	105	111	105	101	102	103	98	100	96
	Left elbow (♂)	1	105	98	105	130	118	120	113	113	116	92	86	93	83	81	77
		2	109	116	119	106	112	111	117	117	118	87	89	88	126	136	128
	Right elbow (♀)	1	140	146	133	127	115	122	115	111	112	110	107	103	88	92	98
		2	144	145	149	112	107	110	74	72	74	86	91	86	123	128	116

looseness of the joint at this stage of dissection, and the lack of impeding integument and musculature. This lack of restrictive soft tissue likely caused more variance in replicate measurements, regardless of differences in applied force.

The overall increase in ROM between ROM1 and ROM3 in *A. mississippiensis* reflected our initial decision to physically move the *A. mississippiensis* forearms until firm resistance was met. This produced a ROM pattern whereby the steady removal of soft tissue from ROM1 to ROM3 produced looser articulations and less extrinsic soft tissue to physically impede flexion and extension (Fig. 3). This process culminated in ROM3, wherein both observers indirectly observed that the loose joint capsule around the *A. mississippiensis* elbow joint was allowing the forearm to dislocate. The tighter joint capsule of *S. camelus* resisted this dislocation, although this only partially explains why this species did not exhibit an increase in ROM from ROM1 to ROM3 (Fig. 3). We do not know whether the loose joint capsules of *A. mississippiensis* were the result of the specimens

being juveniles. The literature suggests that aerial and aquatic flapping amniotes (land-dwelling tetrapods) have tight joint capsules with ligaments to resist the bending and/or torsional stresses of leading edge streams and flapping (Norberg, 1970; Clark and Bemis, 1979; Vazquez, 1992; Vazquez, 1994; Prondvai and Hone, 2008). *Struthio camelus* is descended from aerial avians, and may have retained a tight elbow joint capsule. *Alligator mississippiensis*, though semi-aquatic, does not use its forelimbs to ‘fly’ underwater, or to paddle (Meers, 1999), which suggests that it does not need a comparably rigid elbow joint area. The observation that the radial and ulnar articulations with the humerus are not aligned in the plane of elbow joint flexion and extension, with one on top of the other, as in many other tetrapods with stiff elbow joints, supports this assumption (Martins, 1862; Alix, 1863; Alix, 1874; Hultkrantz, 1897; Parsons, 1899; Vialleton, 1924; Savage, 1957).

The negative slope of the *S. camelus* replicate measurements exhibited little change between ROM1 and ROM5 (Fig. 4). This

Table 2. Greenhouse–Geisser and Huynh–Feldt adjusted output from STATISTICA® of univariate repeated-measures ANOVA

	d.f.	F	P	Greenhouse–Geisser			Huynh–Feldt		
				Adj. d.f. 1	Adj. d.f. 2	Adj. P	Adj. d.f. 1	Adj. d.f. 2	Adj. P
Treatment	4	37.262	0.000000	1.604	6.41670	0.000380	3.183	12.731	0.000001
Treatment × Species	4	26.572	0.000001	1.604	6.41670	0.000999	3.183	12.731	0.000008
Error	16								
Observer	1	2.715	0.175	1.000	4.000	0.175	1.000	4.000	0.175
Observer × Species	1	4.353	0.105	1.000	4.000	0.105	1.000	4.000	0.105
Error	4								
RM	2	0.317	0.737	1.508	6.033	0.682	2.000	8.000	0.737
RM × Species	2	0.017	0.983	1.508	6.033	0.960	2.000	8.000	0.983
Error	8								
Treatment × Observer	4	9.843	0.000325	2.209	8.836	0.005	4.000	16.000	0.000325
Treatment × Observer × Species	4	3.689	0.026	2.209	8.836	0.065	4.000	16.000	0.026
Error	16								
Treatment × RM	8	0.410	0.907	1.935	7.740	0.671	4.654	18.615	0.825
Treatment × RM × Species	8	1.378	0.243	1.935	7.740	0.306	4.654	18.615	0.278
Error	32								
Observer × RM	2	0.117	0.891	1.167	4.668	0.784	1.766	7.063	0.869
Observer × RM × Species	2	2.146	0.179	1.167	4.668	0.210	1.766	7.063	0.188
Error	8								
Treatment × Observer × RM	8	0.552	0.808	2.971	11.885	0.655	8.000	32.000	0.808
Treatment × Observer × RM × Species	8	1.302	0.277	2.971	11.885	0.319	8.000	32.000	0.278
Error	32								

RM, repeated measures. Significant P-values are in bold.

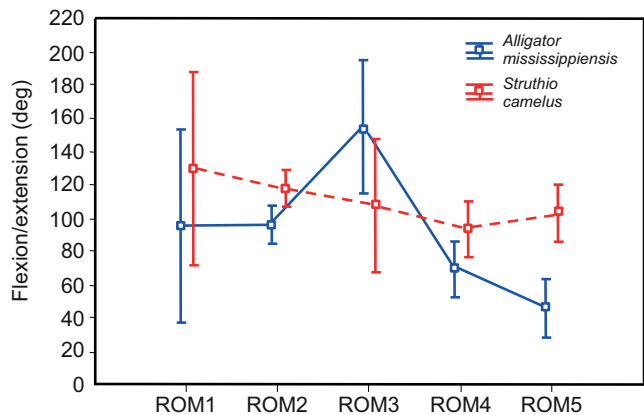


Fig. 3. Effect of five sequential levels of dissection treatment on the separate repeated measures of *A. mississippiensis* and *S. camelus* elbow joint ROMs. Error bars indicate the variance (95% confidence intervals) of degree measurements for this and following figures. Note that the ROM slopes of both species do not coincide, nor do they follow the same pattern throughout the five levels. The ROM slope of *A. mississippiensis* is not linear. The five treatment levels had less of an effect on the *S. camelus* ROMs than the *A. mississippiensis* ROMs, although the overall trend in ROM was downward from ROM1 to ROM5 in both species.

indicates that there was less treatment effect on the *S. camelus* elbow ROM than in *A. mississippiensis*. In hindsight, the steady decrease in *S. camelus* ROMs can be explained by our initial decision to use gravity as the constant source of force to extend the *S. camelus* forearms for ROM1–ROM3. Although this decision created a more uniform and therefore repeatable application of force, it created an unforeseen problem. In contrast to the *A. mississippiensis* specimens, the use of gravity to apply force caused *S. camelus* replicate measurements to decrease from ROM1 to ROM3. The *S. camelus* forearms steadily weighed less as tissue was dissected away, which progressively exerted less force upon the elbow joint, causing the forearm to extend less. However, weight loss does not completely explain why these replicate measurements did not increase. That discrepancy may be because the joint capsules around the elbow joints of *S. camelus* were observed to be much tighter than those in *A. mississippiensis*, particularly in the ulnar and radial collateral ligaments that bracket the elbow joint. This tightness may have caused a steadily increasing restriction in ROM in the first three treatment levels as soft tissue mass was taken away. Thus, the

techniques we initially decided upon did produce significantly different ROM patterns in both species for ROM1–ROM3.

The decrease in elbow ROMs for both species for ROM4 and ROM5 relative to ROM1 was partially the result of an initial observation that the forearms could not completely extend to the 180deg value in ROM1 (Fig. 3). We therefore made the decision to treat their elbows as joints that did not completely dislocate to produce natural movements (e.g. Yalden, 1966). This of course did not prevent the elbows from dislocating in ROM3 for *A. mississippiensis*, in which we could not see the articular cartilage because of the opaque joint capsule. However, we did apply this knowledge to ROM4 and ROM5. As detailed in the Materials and methods, we physically moved the forearm elements in the last two levels, but stopped flexion or extension immediately upon visual disarticulation of the elements, similar to reported methodologies in recent dinosaur forelimb ROM publications (e.g. Carpenter, 2002). For ROM4 in *S. camelus*, the endpoint of flexion was measured when the ulna completely disarticulated from the humerus, but with the radius in full articular contact with the humerus. Similarly, flexion during ROM5 in *A. mississippiensis* produced dislocation of the ulna from the humerus, but not the radius, which stayed in firm articulation with the humerus until it impacted in the radial fossa (humeral depression). Unlike the first three treatment levels, in which force was applied to the forearms perpendicular to the radial and ulnar diaphyses (shafts), in ROM4–ROM5 the observers pressed the forearms directly onto the humeral condyles. If the forearms had dislocated in ROM1–ROM3, one could not have observed this state visually because of the overlying soft tissue, but this state was inferred in ROM3. These observations combine to suggest that increased ROMs in levels prior to ROM4 and ROM5 in *A. mississippiensis* may have been partially due to decreased tension and obstruction from surrounding soft tissues, and perhaps associated dislocation within the elbow joint.

The effect of soft tissue on elbow ROM in *S. camelus* and *A. mississippiensis*

A major motive for undertaking this study was to quantitatively examine the question of whether soft tissue increased or decreased elbow joint ROM from ROM1 to ROM5 in *A. mississippiensis* and *S. camelus*. Similar research has been performed on domesticated animals to determine the effects of soft tissue on ROM. For example, Kolwe (Kolwe, 1920) and Roos et al. (Roos et al., 1992) have undertaken and summarized veterinary research measuring how the ROM of pronation and supination in cats and dogs may increase as

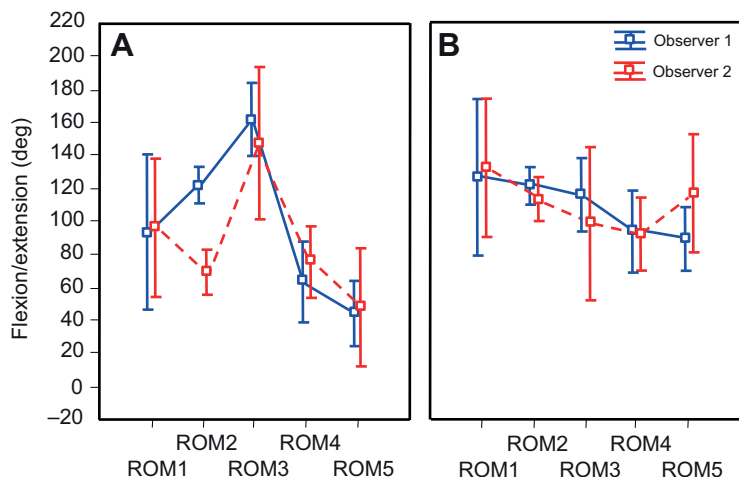


Fig. 4. Effect of the interaction between treatment (five sequential levels), species and observer on the separate repeated measures of (A) *A. mississippiensis* and (B) *S. camelus* elbow joint ROMs. Note that observer two's repeated measures were significantly lower for *A. mississippiensis* in ROM2, but were significantly higher for ROM5 in *S. camelus*. Both observers were responsible for the nonlinear trend in *A. mississippiensis* repeated measures.

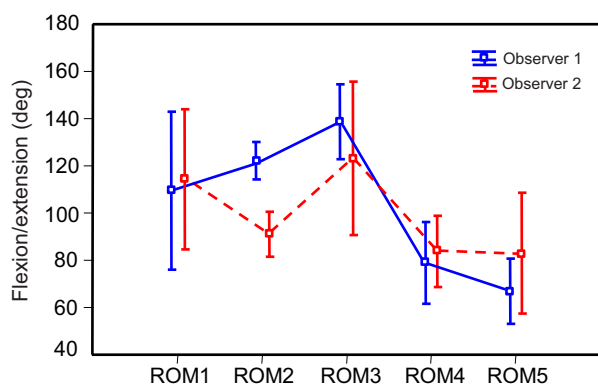


Fig. 5. Effect of the interaction between treatment (five sequential levels) and observer on the combined repeated measures of *A. mississippiensis* and *S. camelus* elbow joint ROMs. The slope of the lines indicates that the treatment factor had a significant effect on replicate measurements for both observers and that the observers differed significantly in their repeated measures for ROM2.

soft tissue (i.e. extrinsic tissue) is sequentially dissected away from the elbow to the wrist joint. Other researchers have noted that soft tissue impedes ROM in monitor lizards (Tereshchenko, 1994), and that muscle tonus serves to restrict limb joint ROM *in vivo* in comparison to dead specimens because of tension (Hultkrantz, 1897). The question of interest here relates to whether it is possible to use EPB results (Witmer, 1995) to extrapolate back to *in vivo* ROMs in fossil archosaurs. For example, Dzemski and Christian (Dzemski and Christian, 2007) sequentially dissected soft tissue away from *S. camelus* cervical vertebrae and measured ROMs in order to reanalyze how sauropodomorph dinosaur necks could have moved *in vivo*. That question was analogous to this study, but involved vertebral rather than limb joints, limiting its comparative value to our data, particularly as they did not find any significant values. However, Dzemski and Christian did state that soft tissue (we assume extrinsic) acted to restrict ROMs to a minor degree in *S. camelus*, and other bird cervical vertebrae. We observed that the scales and muscle bellies of *A. mississippiensis* restricted ROM by preventing the forearm from completely flexing.

Some qualitative reports in the literature claim that some types of soft tissue act to increase ROM at limb joints, supposedly because of enlarged articular cartilage in comparison to the corresponding bony surface beneath (Hay, 1911; Yalden, 1966; Shubin et al., 2006). Other authors have raised concerns that the articular cartilage of archosaurs does not faithfully represent the articular morphology of the bone underneath it (Holliday et al., 2001), as it does with therian mammals (marsupials and placentals) (Bonnar and Senter, 2007). Here, we confirmed that the forelimb bones of both *A. mississippiensis* and *S. camelus* do not articulate as precisely (in a resting position) as they do when covered with articular cartilage. This condition is most problematic in the wrist and elbow joints. In particular, the skeletonized ulnae of both species do not articulate precisely between the ulnar and radial condyles of the humerus. When articulated with the humerus in isolation, a skeletonized ulna has a different resting position than the resting position of the isolateral (from the same side of the body) radius would indicate. During ROM5 measurements, we usually moved the radius and ulna while they were articulating (touching), although this tended to disarticulate the radius from the radial condyle of the humerus. Moving the radius to the radial condyle of the humerus slightly

disarticulated the radius from the ulna, although they did not lose contact. Moreover, articulating the distal ends of the radius and ulna placed the proximal end of the radius where it would articulate with the radial condyle, but slightly disarticulated from the proximal end of the ulna. These problems illustrated the lost influence of a layer of articular cartilage both proximally and distally. Approximately 5 mm of articular cartilage was found to separate the proximal and distal ends of the forearm bones of *A. mississippiensis* (radial plus ulnar cartilage). The *S. camelus* specimens had less cartilage (1–2 mm), a difference that may have reflected the juvenile status of the *A. mississippiensis* specimens, or other factors. We considered, but rejected, applying modeling clay between the defleshed ROM5 bones to correct for the observed discordance in articulation (see Gishlick, 2001). We felt that attempting bone-on-bone ROMs more faithfully imitated the ROMs that fossil archosaur forelimb ROM studies attempt, which do not have a firm estimate of articular cartilage thickness. However, the bony articular surfaces of both *A. mississippiensis* and *S. camelus* retained enough morphological fidelity that we were able to articulate and move skeletonized limb elements.

Lastly, another problem in the elbow of *A. mississippiensis* was that the articular surfaces of the ulnar and radial condyles of the humerus extend just as far flexad (i.e. forwards) and extensad (i.e. behind) in ROM5, which would indicate visually that the forearm could hyperextend. We knew that they could not, however, because *A. mississippiensis* possesses a small cartilaginous olecranon process (elbow) that prevented hyperextension in ROM4. A ROM study with fossil archosaur forelimbs would not be able to determine this. These difficulties illustrated the lost effect of the articular cartilage that separated the proximal ends of the forearm bones *in vivo*, which our data suggest may cause fossil archosaur forelimb ROM studies to underestimate *in vivo* elbow joint ROM, provided that these studies follow our methods.

For the elbow, the general decrease in ROMs from ROM4 to ROM5 in *A. mississippiensis*, and for observer one in *S. camelus*, supports the assumption that articular cartilage may increase ROM (Fig. 4). Here, we did not observe any substantial effect on ROM or articular surface morphology during data collection between ROM4 and ROM5, except to note that the loss of articular cartilage made it much more difficult to articulate and move forelimb bones. However, the power of this study is low because of the limited sample size ($N=3$) for the *S. camelus* elbow replicates. Regardless, our data provide quantitative support (in a form other than that of geometric morphometric measurements) for previous claims that the articular surfaces of fossilized archosaur bones approximate the morphology of the articular cartilage *in vivo* (Carpenter, 2002; Bonnar and Senter, 2007; Bonnar et al., 2010). Regardless, further quantitative study is required to determine whether the ratio of area lost is equal in both articular surfaces (Tereshchenko, 1994).

Elbow joint dislocation: implications for locomotion, pronation/supination and the radial piston mechanism in extinct archosaurs

The topic of how far a joint can move, or dislocate without causing permanent damage, is important in several areas of research on fossil tetrapods. In this study we attempted to address whether dislocation of the forearm elements with each other, or with the elbow, could routinely contribute to locomotion, pronation/supination and the radial piston mechanism (proximodistal sliding of the radius during flexion and extension). In regard to the incidence of dislocation (i.e. that does not cause permanent damage), Yalden (Yalden, 1966) extensively described how many extant therians have carpal joints

that routinely dislocate past the limits of their articular surfaces. This type of innocuous dislocation during flexion and extension was not observed in *A. mississippiensis* and *S. camelus* elbows during ROM1, and X-rays taken of the joints in extremes of flexion and extension did not indicate that any dislocation was occurring. Moreover, prior experimentation had shown that the fully fleshed forearms of both species would not extend to 180deg, nor flex completely unless by dislocation. This dislocation could not have been forced without damaging the specimens. Researchers who study the elbow ROM of dinosaurs may not know this unless they also utilize the EPB (Carpenter, 2002; Bonnan and Senter, 2007). This information indicates that dislocation of the elbow joint does not normally contribute to locomotion in *A. mississippiensis* or idiomotion (limb movements other than for locomotion) in *S. camelus*.

The topic of harmless joint dislocation is also important in debates on whether the first aerial amniotes (pterosaurs) walked terrestrially using quadrupedalism or bipedalism. The relevant question is whether the articular surface of the proximal femoral (thigh bone) head could have moved past the extent of the articular surface in the hip joint (Unwin, 1988; Bennett, 1997). We will postpone a more detailed discussion of this topic until the results of our shoulder joint ROM study are published. However, this question was important to test here in the elbows of the EPB of dinosaurs. It is sometimes assumed that many tetrapod forearms can partially dislocate their proximal articulations from their respective humeral condyles during locomotion to physically pronate and supinate their forearm elements (Hultkrantz, 1897; Gasc, 1963). Moreover, until a recent series of refuting evidence from ROM studies performed with dinosaur forelimbs (Serenó, 1993; Carpenter and Smith, 2001; Carpenter, 2002; Bonnan and Senter, 2007), it had often been assumed that some dinosaurs could freely pronate and supinate their radii like therian mammals.

The radii and ulnae of the EPB specimens in this study were prevented from leaving the extensor articular surfaces of their humeral condyles because the joint capsule ended proximal to the limits of these articular surfaces, which firmly bound the entire area. The radii and ulnae were also observed to be tightly bound by radioulnar ligaments common to other tetrapods, albeit more loosely in *A. mississippiensis*, and this tension prevented long-axis rotation of either element in relation to the distal humerus, or to each other. One *A. mississippiensis* elbow joint was sacrificed prior to this study to observe forced axial rotation of the radius to a full 180deg of pronation. This experiment resulted in permanent dislocation of the radius from the radial notch and the elbow *via* torn radioulnar and collateral ligaments, particularly surrounding the elbow joint. Enlarged cartilaginous articular edges also expanded the sizes of the intercondylar ridges in each taxon, further restricting motion to conjoint flexion and extension. However, a small amount of proximodistal sliding of the radius (i.e. the radial piston mechanism) was possible relative to the ulnar shaft.

The radial piston mechanism reported among many tetrapods was observable in both *A. mississippiensis* and *S. camelus* (Gegenbaur, 1864; Fürbringer, 1886; Rabl, 1910) and had to be accounted for as the ROMs in degrees were measured. As the elbows were flexed, the change in depth of the radial condyle and the presence of an ulnar expansion extended to the radius partially caused the radius to slide distally and linearly along the ulna. Connective soft tissues served to amplify and guide this effect as well. The opposite effect was observed during extension. The distal radius pushed on the wrist and caused it to deviate in the ulnar direction upon elbow flexion and *vice versa* for elbow extension. The radial piston mechanism

did appear to increase the ROM of the elbow joints slightly by pushing the radius distally out of the way during flexion, which had the effect of delaying impaction of the radius between the ulna and humerus. However, dislocation of the radius from the ulna or radial condyle was not observed during ROM1 or ROM2, although in ROM3 for *A. mississippiensis* the loosened joint capsule allowed the forearm to dislocate slightly in every direction. Thus, our investigations of individual forearm element and elbow joint dislocation show that the extrinsic soft tissues in the experimental animal elbow joints combine to resist disarticulation.

ROM study methodologies and reproducibility

A carefully controlled analysis with repeated measures was chosen for this EPB experiment because the measuring of the ROMs of limb joints meets the criteria of introducing a potentially large amount of variability and observer bias (von Ende, 2001). Moreover, we were interested in how the elbow ROMs changed between successive levels of treatment. There were many variables that needed to be controlled for to obtain ROM data that could be statistically analyzed. For example, the methods of overlaying pictures of limb segments that had moved, or measuring ROM from a computer screen or overhead projector with a protractor or goniometer, were found to be inaccurate because the elbow is never a uniplanar hinge in tetrapods (Cuénod, 1888; Yalden, 1966). Thus, the forearm will slant either inwards or outwards during flexion, as well as rotate about its long axis. All of these attempts introduced an unacceptable amount of parallax. The method of finding the exact vertex of joint movement, and inserting a screw or pin to aid in the use of a protractor or goniometer (Yalden, 1966), was also found to be impractical because this point was often dissected away, and the small *A. mississippiensis* bones were susceptible to fracturing during pin insertion. Overall, the inclinometer was found to be the most accurate instrument and the easiest to use, if used correctly. If the element in motion was oriented to move vertically to reduce the effects of circumduction (i.e. a curving path of flexion and extension), the inclinometer could be placed upon any point without any further requirements. Thus, inclinometer measurements were found to change only with variations in how the observer manipulated the specimen.

Other variables that needed to be controlled were those associated with observer bias. The most important bias was experience, which we attempted to equalize by training together on the same specimens. Moreover, we initially found that once we knew what the ROM was in degrees for a joint, we would try to equal or exceed it the next time we measured it. It was assumed that hiding the measurements from the observer manipulating the specimen, by having a second observer gather degree data, would preclude this bias and result in a more consistent application of force and technique. In regard to our secondary questions concerning the methodology used in ROM on fossil archosaurs, the results above suggest that an inclusion of methodology into the discussions of fossil archosaur ROMs is essential. Even seemingly unimportant differences in methodology produce different ROMs.

Our results do not shed light on whether the direct method of obtaining joint ROMs is more accurate than indirect methods, such as those that mathematically estimate ROM from the articular surfaces of bones (Hultkrantz, 1897; Tereshchenko, 1994; Tereshchenko, 1996). A comparative test on this material would have to be undertaken to resolve this. Otherwise, we feel that our methodology compares favorably with other repeatable ROM techniques in use (Yalden, 1966), provided that more than one observer is on hand to repeat the measurements. The large amount of observer bias dictates

that a repeated-measures statistical analysis is the method of choice for researchers who plan on basing important physiological inferences on ROM data taken from fossil bones.

Extrinsic versus intrinsic joint soft tissues

Based on the nonlinear *A. mississippiensis* trend and the observation that ROM1 elbow flexion and extension did not rely on habitual separation of complementary articular surfaces in either species, the five treatment levels used in the present study need to be split into two segments. The nonlinear trend of the *A. mississippiensis* ROMs is due to the application of a uniform physical force in the first three levels. The data show an upward trend for the first three, but a downward trend for the last two levels (Fig. 3). These opposing slopes reflect the observation that data from ROM1–ROM3 came from an applied force as soft tissue extrinsic to the joint was removed, whereas data from ROM4 and ROM5 came from changes in area in articular surfaces after articular cartilage was removed, and hence had nothing to do with applied force. Therefore, ROM1–ROM3 measure a different change in ROM than ROM4 and ROM5 because the role of the soft tissues involved is different.

The first three treatment levels examine the effect of soft tissue extrinsic to the elbow joint. As this soft tissue was removed, the ROM increased for *A. mississippiensis* as long as the applied force stayed the same. This was because soft tissue that physically impeded ROM, such as the volume of muscle bellies, prevented the joints from fully flexing or extending. Unlike in *A. mississippiensis*, the initial decision to use the force of gravity for levels one to three in *S. camelus* resulted in an unforeseen decrease in force as mass (i.e. peripheral soft tissue) was removed. This steady decrease in force caused the ROM to decrease rather than increase because the opposing resistance of the tight joint capsule did not change. If a consistent physical force had been applied for *S. camelus* instead of gravity, as was done with *A. mississippiensis*, we predict that the trend would have exhibited a linear increase in ROM for ROM1–ROM3 as well. That would have provided a more accurate picture of the differences between ROM1–ROM3 and ROM4–ROM5.

The last two treatment levels solely examine the effect on ROM of articular cartilage within (intrinsic to) the elbow joint. For *A. mississippiensis*, a similar decrease in ROM was observed after articular cartilage was removed for both observers (Fig. 3). In other words, the available data show that ROM1–ROM3 exhibit a linear increase in ROM as the volume of impeding extrinsic soft tissue is dissected away, whereas ROM4 and ROM5 show a linear decrease in ROM as the volume and area of articular cartilage is removed. The increased area and/or depth of articular surfaces covered by cartilage provide a possible explanation for an increased ROM in ROM4 versus ROM5. For *S. camelus*, observer one measured an overall decrease in ROM, whereas observer two measured an overall increase. This divergence may be the result of individual differences in visual estimates of where the articular surfaces began and ended, despite earlier practice. Another possibility is that the discrepancy may represent real differences in the effect of articular cartilage on elbow ROM. In future experiments, using a larger sample size might resolve this dichotomy.

Ideally, the ROM of joints *in vivo* should have been used in this study in place of the ROM1 of dead specimens. This could have been attempted by immobilizing the upper arm of the juvenile *A. mississippiensis* specimens and taking repeated measures of their voluntary elbow joint ROMs. However, this methodology would have been impractical with the much larger, and therefore more dangerous, adult *S. camelus* specimens. Instead, we propose that *in vivo* ROMs could be achieved using digital inclinometers strapped directly to the

forearm of anesthetized or even freshly dead specimens. The desired ROM could then be isolated by electrically stimulating the relevant muscle or muscle groups (see Kolwe, 1920), or by simply recording a range of repeated measures of voluntary ROMs from the specimens over a period of time. Data from the digital inclinometer could be relayed directly to a computer for tabulation and statistical analysis. Then these data could be compared with a skeletonized ROM5 of the same limb segments.

Our dissection and joint movement results suggest that if applied force stays the same, a fully fleshed archosaur elbow joint will exhibit an increase in flexion and extension ROM as integument, muscles and tendons are removed. However, if only articular cartilage is considered, we predict that the elbow joint will exhibit a decrease in ROM if it is removed. The latter statement is the one more applicable to ROM studies of fossil archosaurs such as dinosaurs (Figs 1, 2). Even after the increase in ROM from ROM1 to ROM3 is taken into account, there is an overall decrease in the ROM of elbow flexion and extension from ROM1 (fully fleshed) through ROM5 (bone-on-bone) in both *A. mississippiensis* and *S. camelus* in this study. Our data suggest that reported fossil ROMs of dinosaur elbow joints likely underestimate the actual ROM *in vivo*, especially if, as in this study, the forearm elements were moved until disarticulation was observed. Future research is essential to test whether the effects of extrinsic versus intrinsic soft tissue also apply on limb joints with more ROM than the elbow joint, such as the shoulder and hip joints. Otherwise, this study affirmed the need for more ROM studies to help reconstruct the functional morphology of dinosaur forelimbs, as well as other fossil archosaur limbs.

ACKNOWLEDGEMENTS

This study was conducted during the graduate research of J.D.H. at Northern Illinois University. Practice *A. mississippiensis* specimens were loaned to us from Western Illinois University, thanks to Matthew F. Bonnan. All *A. mississippiensis* specimens were ultimately provided by Ruth Elsey of the Rockefeller Wildlife Refuge (Grand Chenier, LA, USA) and the *S. camelus* specimens were given freely by Mark Wiley of Freedom Sausage Inc. (Earlville, IL, USA). We are grateful to Carl von Ende for freely providing his invaluable expertise in repeated measures, and for the use of his statistical software. Chris Hubbard provided initial laboratory space and equipment, and kind suggestions from Phil Senter of Fayetteville State University and an anonymous reviewer helped improve this manuscript.

FUNDING

This work was supported by a Jurassic Foundation Research Grant; the Geological Society of America [grant numbers 8297-06, 8980-08]; a Northern Illinois University Dissertation Completion Fellowship; three Northern Illinois University Biology Departmental Graduate Research Grants (to J.D.H.), and Northern Illinois University Presidential Scholarship funds (to J. Michael Parrish). The authors declare no financial or competing interests.

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