

An examination of forearm bone mobility in *Alligator mississippiensis* (Daudin, 1802) and *Struthio camelus* Linnaeus, 1758 reveals that *Archaeopteryx* and dromaeosaurs shared an adaptation for gliding and/or flapping

Joel D. HUTSON

Department of Biological Sciences, Northern Illinois University,
1425 West Lincoln Highway, DeKalb, Illinois, 60115-2825 (USA)
jhutson@elgin.edu

Kelda N. HUTSON

Department of Earth Science, College of Lake County,
19351 West Washington Street, Grayslake, Illinois, 60030-1198 (USA)
khutson@clcollinois.edu

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ABSTRACT

In response to increased limb bone loads many tetrapod clades have converged upon similar adaptations to reinforce the elbow joint by reducing independent movements of the forearm bones. However prior studies have not examined how these changes occurred phylogenetically or functionally, such as during the transition from prehensile forelimbs in dinosaurs to gliding/flapping flight in bird wings. Here, a functional analysis of forearm bone mobility in extant archosaurs shows that crossing and uncrossing of the radius and ulna can be forced in alligators via a passive gliding mechanism recently described in lacertilians, while birds are adapted to inhibit this motion. A comparison of these findings with a sample of extinct quadrupedal archosaur forearms strongly suggests that, due to the highly conserved morphology of tetrapod forearms in general, the lacertilian mechanism broadly describes the plesiomorphic mechanism via which tetrapod forearm bones passively cross in response to locomotor-induced torsion. Bipedal dinosaurs retained adaptations for this passive mechanism, which indicates that they were unable to perform active long-axis rotations to align their semi-pronated, misaligned forearm joints. By contrast, analogous to birds and pterosaurs, quadrupedal dinosaurs evolved immobilizing adaptations to reduce or prohibit independent movements of the radius and ulna. Notably, the elbow joints of *Archaeopteryx* von Meyer, 1861 and dromaeosaurs are bird-like. This information, coupled with a lack of non-aerial adaptations for increased limb bone loads, strongly suggests that the forearms of deinonychosaurs were adapted to resist the bending and torsional stresses incurred by leading edge air streams during gliding and/or flapping.

KEY WORDS
range of motion,
extant phylogenetic
bracket,
radial morphology,
ulnar morphology,
independent flexion/
extension,
evolution of flight.

RÉSUMÉ

Un examen de la mobilité des os de l'avant-bras d'Alligator mississippiensis (Daudin, 1802) et Struthio camelus Linnaeus, 1758 révèle qu'Archaeopteryx et les dromaeosaures ont partagé une adaptation pour le vol plané et/ou pour le vol battu.

En réponse à l'accroissement du poids des os des membres, de nombreux clades de tétrapodes ont développé par convergence des adaptations visant à renforcer l'articulation du coude en réduisant le mouvement des os de l'avant-bras l'un par rapport à l'autre. Cependant, les études antérieures

MOTS CLÉS
Amplitude des
mouvements,
parenthèses
phylogénétique existante,
morphologie radiale,
morphologie ulnaire,
flexion et extension
indépendantes,
évolution du vol.

n'ont pas pris en compte la façon dont ces changements sont apparus phylogénétiquement ou fonctionnellement, comme par exemple lors de la transition de membres antérieurs préhensiles chez les dinosaures au vol plané/battu des ailes des oiseaux. Dans la présente étude, une analyse fonctionnelle de la mobilité des os du membre antérieur chez les archosaures actuels montre que le croisement et le décroisement du radius et de l'ulna peut être contraint chez les alligators par un mécanisme de glissement passif récemment décrit chez les lacertiliens, tandis que ce mouvement est empêché chez les oiseaux. La comparaison de ces découvertes avec un échantillon d'avant-bras d'archosaures quadrupèdes éteints suggère fortement que, en raison de la morphologie très conservatrice de l'avant-bras des tétrapodes en général, le mécanisme lacertilien décrit un mécanisme plésiomorphe par lequel les os des avant-bras des tétrapodes se croisent passivement sous l'effet de la torsion induite par la locomotion. Les dinosaures bipèdes possédaient ce mécanisme passif qui indique qu'ils étaient incapables de produire activement des rotations axiales leur permettant d'aligner les articulations de l'avant-bras en semi-pronation. En revanche, tout comme les oiseaux et les ptérosaures, les dinosaures quadrupèdes ont développé des adaptations permettant de réduire ou d'empêcher les mouvements indépendants du radius et de l'ulna. De façon notable, le coude de l'*Archaeopteryx* von Meyer 1861 et des dromaeosaures est construit comme celui d'un oiseau. Cette information, couplée à l'absence d'adaptations allégeant le poids des os des membres suggère fortement que l'avant-bras des deinonychosaures pouvait résister aux contraintes de courbure et de torsion occasionnées par la bordure antérieure des courants aériens durant le vol plané et/ou battu.

INTRODUCTION

In many terrestrial tetrapod clades passive displacements between the radius and ulna (Fig. 1) play an important role in quadrupedal locomotion (Haines 1946; Lécuru 1968; Renous & Gasc 1977). By contrast, various therians (marsupials and placentals) are capable of actively rotating their interconnected radius, carpus and manus about a common long axis with the ulna in order to change the grade of pronation of the wrist and finger joints (Fig. 2). This ability is amplified in bipedal therians, which greatly enhances their capacity for object manipulation (Haines 1946). Since various clades of Mesozoic archosaurs trended towards bipedalism (Romer 1956), the question of whether bipedal dinosaurs were capable of therian-grade long-axis rotations of the forearm bones is of great interest to functional morphologists, because if they weren't, their wrist and finger joints would have essentially been immobilized in the semi-pronated orientation (i.e. misaligned 90° relative to the plane of the elbow joint) plesiomorphic to tetrapods (e.g., Fig. 2B; Vialleton 1924; Gasc 1963; Hutson 2015).

Early studies of forelimb ranges of motion (ROM) occasionally reported that the forearm bones of bipedal dinosaurs were well-adapted for therian-grade long-axis rotations (von Huene 1926). Others have also assumed that dinosaurs and other extinct archosaurs could actively pronate their semi-pronated wrist joints into alignment with their elbow joints, which would have allowed therian- and chameleon-grade forelimb kinematics (Lull 1953; Krebs 1965; Lessertisseur & Sigogneau 1965). In recent decades ROM investigations have unanimously refuted these reports (see Hutson 2010 and references therein). The osteological

characters most commonly used in support of this consensus are a lack of proximal and distal synovial concavoconvex radioulnar joints (Fig. 2). Additional characters in the elbow joint which prohibit long-axis rotations include a radial capitular process that projects extensad analogous to a radial olecranon process, and/or a raised post-axial edge on the radius that contributes to the common intercondylar ridge formed by both the radius and ulna. This intercondylar ridge complements a recessed intercondylar groove on the humerus between the radial and ulnar condyles (Vialleton 1924; Lécuru 1969; Renous-Lécuru 1972). These features suggest that the manual dexterity of bipedal archosaurs was limited in comparison to bipedal therians. Moreover, this information could also help to constrain interpretations of forearm bone movements in quadrupedal archosaurs, as well as avian dinosaurs that were evolving stiffened radioulnar articulations for gliding and/or flapping flight.

Notably, the consensus outlined above matches the conclusions of skeletonized ROM studies of extant nontherian tetrapods (Vialleton 1924). In contrast, fleshed ROM studies report that what appear to be extensive long-axis rotations can be forced in the forearms of many extant nontherian tetrapods, including crocodilians (Table 1). These patent contradictions have not been recognized in studies of radioulnar mobility in dinosaurs (Bonnar & Senter 2007). Resolution of this discrepancy is critical to our understanding of the paleoecological roles of both bipedal and quadrupedal archosaurs.

In an effort to resolve the contradiction outlined above, an experimental approach was utilized that applied fleshed and skeletonized methodologies in sequence upon the extant phylogenetic bracket (EPB) of dinosaurs (Witmer 1995), *Alligator mississippiensis* (Daudin, 1802) and *Struthio came-*

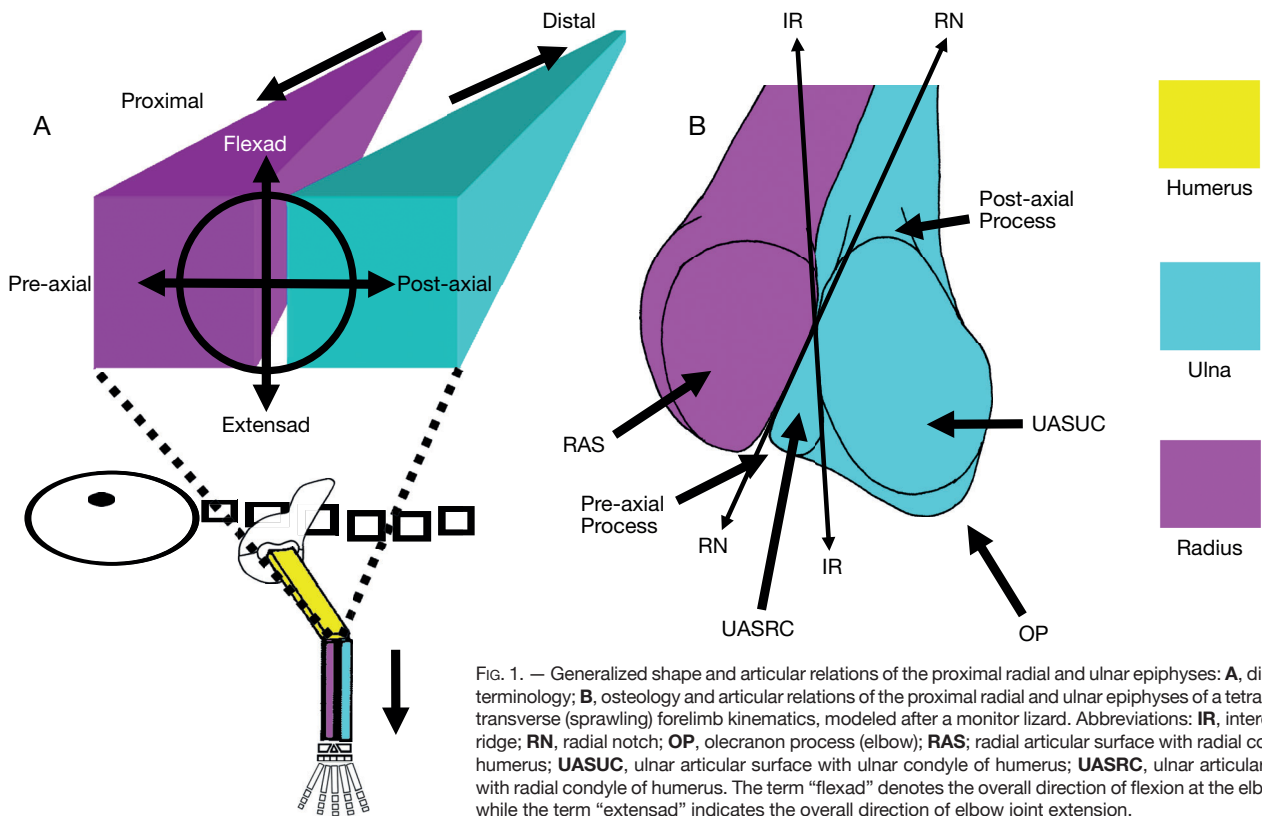


FIG. 1. — Generalized shape and articular relations of the proximal radial and ulnar epiphyses: **A**, directional terminology; **B**, osteology and articular relations of the proximal radial and ulnar epiphyses of a tetrapod with transverse (sprawling) forelimb kinematics, modeled after a monitor lizard. Abbreviations: **IR**, intercondylar ridge; **RN**, radial notch; **OP**, olecranon process (elbow); **RAS**, radial articular surface with radial condyle of humerus; **UASUC**, ulnar articular surface with ulnar condyle of humerus; **UASRC**, ulnar articular surface with radial condyle of humerus. The term “flexad” denotes the overall direction of flexion at the elbow joint, while the term “extensad” indicates the overall direction of elbow joint extension.

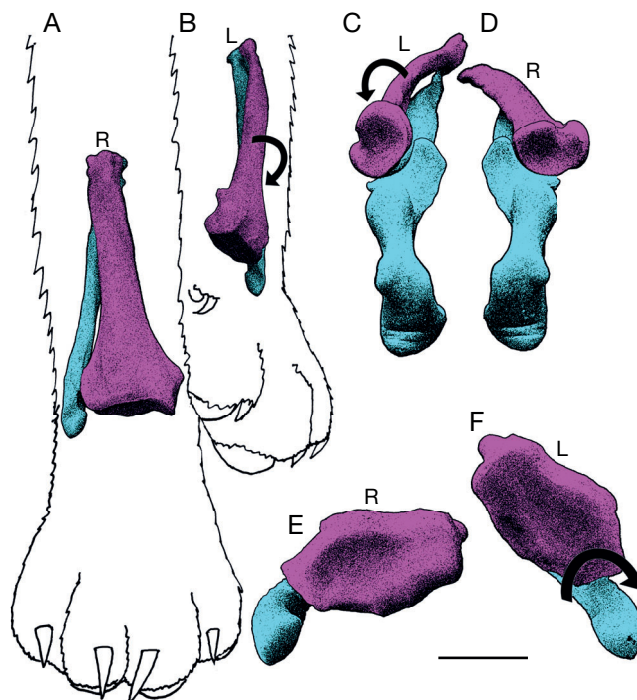


FIG. 2. — Traditional therian forearm long-axis rotation ranges of motion (ROM) test using a therian quadruped, the coyote *Canis latrans* Say, 1823 (FMNH 135222). Fully pronated radius in flexor (**A**), proximal (**D**), and distal (**E**) views. Semi-pronated radius in flexor (**B**), proximal (**C**), and distal (**F**) views. Note that a traditional skeletal ROM test of therian radial long-axis rotation is undertaken relative to a fixed ulna, with an oval proximal radial epiphysis rotating in place against the corresponding concavity of the radial notch (**C**), while the distal radial epiphysis rotates in an arc around the distal ulnar epiphysis (**F**). The firmly interconnected carpus and manus are aligned with, and rotate about a common long axis with the expanded articular surface of the radius. However, in a fleshed ROM test the unrestricted distal epiphyses of many therian radii and ulnae can exchange positions to varying degrees (Hultkrantz 1897), which is not shown here. ROM test is after Hildebrand (1954). Arrows indicate long-axis rotations of the radius relative to a fixed ulna. Radius was moved until it disarticulated. Abbreviations: **R**, right; **L**, left. Scale bar: **E**, **F**, 3 cm.

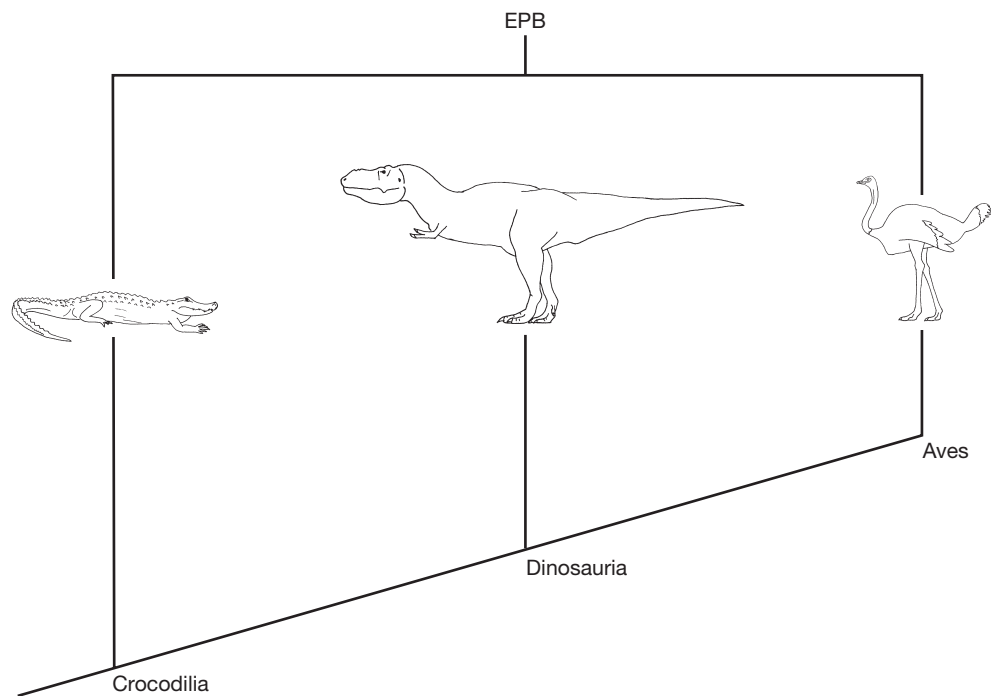


FIG. 3. — Basic representation of the extant phylogenetic bracket (EPB) of dinosaurs. If two extant clades both possess the same morphological and physiological characters, and they phylogenetically bracket (here crocodilians and avians) an extinct clade (here dinosaurs), then it can be inferred with varying degrees of confidence that the extinct clade also possessed those characters (Witmer 1995). For example, in this study highly conserved elbow joint morphologies are used to infer changes in forearm bone mobility from dinosaurs to avians.

TABLE 1. — Conflicting reports of the movements possible at the proximal radioulnar joint in fleshed versus skeletonized tetrapod forearms. Symbols: +, reported present in prior studies; –, reported absent in prior studies; N/A, not available.

	Lissamphibians (salamanders only)	Rhynchocephalians (tuatara)	Chelonians (turtles only)	Lacertilians (various)	Crocodylians	Dinosaurs and other extinct non-avian archosaurs	Avians (various)	Extinct non-mammalian Synapsids	Therian mammals (various)
Long-axis rotations in fleshed specimens	+	+	–/+	+	–/+	N/A	–/+	N/A	+
Long-axis rotations in skeletonized specimens	–	–	–	–/+	–	–	–	–/+	+

lus Linnaeus, 1758. The primary goal of this study was to identify the mechanism by which apparent long-axis rotations are proximally forced in the fleshed forearms of *Alligator mississippiensis*, and then use this knowledge to infer radioulnar mobility in extinct avian and nonavian dinosaurs. Therefore, morphological and degree data of proximal radial and ulnar articular surfaces from extinct

quadrupedal archosaurs and other tetrapods were compared to our results from the EPB. The EPB was employed because its use can constrain the likelihood that an extinct organism possessed a character lost after fossilization, such as soft tissues (Fig. 3). Using this approach, it was hoped that disputes concerning whether dinosaurs could achieve long-axis rotations within forearm space could be resolved (see Gasc 1963), as well as elucidating when the proximal radioulnar and elbow joint articulations of avian theropods began to evolve the reinforced morphologies necessary for gliding and/or flapping flight.

To help achieve the goal of ascertaining the mechanism of movement at the proximal radioulnar joints of archosaurs such as dinosaurs, quantitative EPB data on how forearm soft tissues and osteology affect repeated measures of forced long-axis rotations were obtained. The dependent variable of interest was the ROM of forearm long-axis rotation in degrees. ROM studies of bony articular surfaces have always played an important role in interpretations of the functional morphology of both extant and fossil vertebrates (see Hutson 2010 and references therein), but more recent work seeks to improve our understanding of joint ROM via studies of the effects of soft tissues (Chan 2007; Schwarz *et al.* 2007; Schaller *et al.* 2009; Bonnan *et al.* 2010; Holliday *et al.* 2010; see supplementary materials of Pierce *et al.* 2012; Pierce *et al.* 2013; Arnold *et al.* 2014), as well as introducing empirical approaches into what has predominantly been a qualitative field of interest (Dzinski & Christian 2007; Hutson & Hutson 2012; Cobley *et al.* 2013).

MATERIAL AND METHODS

EXPERIMENTAL ANIMALS AND FIGURE PREPARATION

Struthio camelus and *Alligator mississippiensis* specimens used in this study were previously described in Hutson & Hutson (2012). The figure preparation used here to enhance osteological surface detail was first presented in Hutson & Hutson (2013).

EPB REPEATED-MEASURES

The rationale behind the ROM data collection methodology used here was described in Hutson & Hutson (2012). Before ROM1 (fully fleshed) data were gathered, it was determined that when the radius and ulna were immobilized, forced long-axis rotations within the carpus itself were negligible (c. 1–5°). Therefore, when taking degree measurements, an inclinometer (Model # AF-P34214 from Pinball Magic, Green Bay, Wisconsin, USA) accurate to 0.5° was pressed against the flattened area over the extensor (dorsal) side of the carpus. This area provided a stiff, flat surface for keeping the inclinometer level and revealed the effect of forearm long-axis rotation upon the manus. To eliminate the effects of humeral long-axis rotation at the shoulder, the *Alligator mississippiensis* specimens were laid on their side with the humerus firmly held parallel to the horizontal, and the elbow joint flexed at 90°. The forearm was then grasped just proximal to the carpus and forced to rotate on its long axis into extremes of pre-axial rotation (cf. pronation) and post-axial rotation (cf. supination), which represented the endpoints used to calculate a total ROM degree measurement (Fig. 4). This process was repeated for treatment levels ROM2 (skinned) and ROM3 (muscles/tendons removed), in which soft tissues linked the forearm bones and their joints together. No repeated-measures data could be collected in ROM4 (articular cartilage only) and ROM5 (skeletonized) due to the removal of ligaments that guide independent movements in *Alligator mississippiensis*.

A methodology similar to that described for *Alligator mississippiensis* was attempted for repeated measures in *Struthio camelus* specimens (cf. Anderson 1892). Repeated-measures data could not be collected for ROM1–ROM5 in *Struthio camelus* because osteological and soft tissue adaptations (i.e. tight ligamentous connections) in this species prevented independent movements of the two forearm bones relative to one another. Details are given in the Discussion section.

EXTENT OF THE ULNAR ARTICULAR SURFACE WITH

THE RADIAL CONDYLE IN THE EPB AND OTHER TETRAPODS
Morphological data were taken from fossil archosaurs reposit in eleven North American museums. Particular attention was paid to well-preserved forelimbs of quadrupedal ornithischian dinosaurs. Quadrupedal saurischian sauropodomorph dinosaurs were not surveyed because their proximal forearm articulations were investigated previously by Bonnan (2003). Representative forelimbs of lacertilians, mammals, turtles and tortoises, lissamphibians, pareiasaurs, paraphyletic therapsids, and pelycosaurs from these museum collections

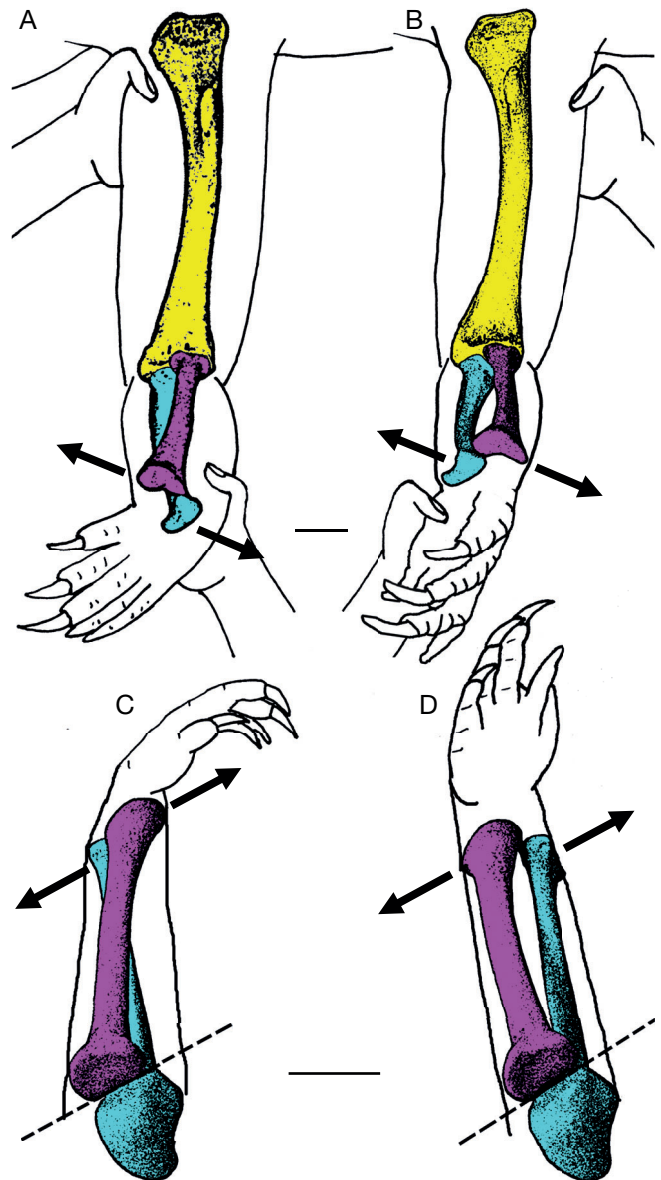


FIG. 4. — Stylized depiction of physically forced independent flexion/extension of fully fleshed *Alligator mississippiensis* (Daudin, 1802) radius and ulna. Flexor (A) and proximal (C) views of forced pre-axial long-axis rotation (cf. pronation). Flexor (B) and proximal (D) views of forced post-axial long-axis rotation (cf. supination). The humerus is immobilized while the manus and carpus are forced into long-axis rotations; the forearm bones displace due to their firm ligamentous connections to the carpus. The dashed lines in (C) and (D) represent the plane of the radial notch upon which the radius and ulna independently flex and extend against one another; compare directly to Figure 2. Note that in (A) and (C) forcing pre-axial long-axis rotation of the interconnected manus and carpus causes the radius to flex into adduction against the flattened radial notch of the ulna while the ulna simultaneously extends into abduction against the radius, which causes their diaphyses to cross. By contrast, in (B) and (D), forcing post-axial long-axis rotation causes the radius to extend into abduction and the ulna to flex into adduction, uncrossing their diaphyses. All figured *Alligator mississippiensis* forelimb elements are of the left forelimb of a 137 cm female specimen (FMNH 284695). Scale bars: 1 cm relative to distal (A, B) and proximal (C, D) forearm bone epiphyses.

were also used for comparison with these archosaurs and the EPB specimens (Appendix 1). Only undistorted specimens were used that could be demonstrated to have come from the same individual.

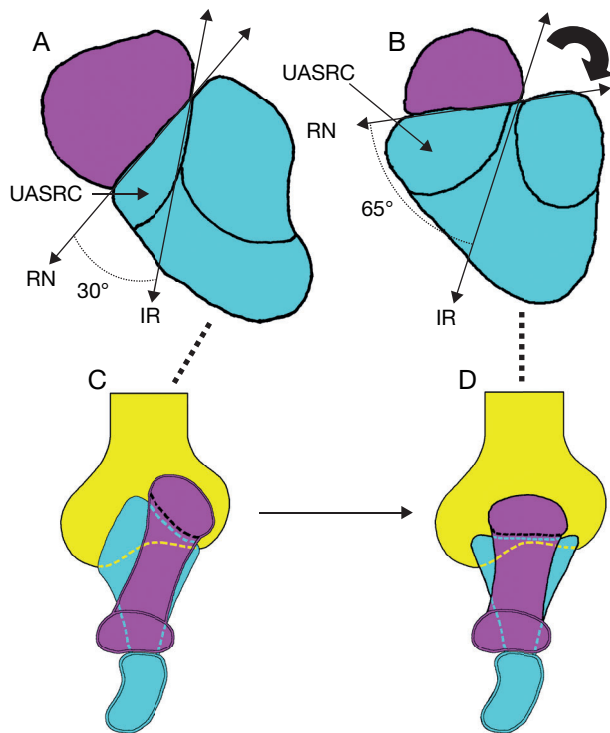


FIG. 5. — Demonstration of how a phyletic reduction in independent flexion/extension of the forearm bones can occur due to an increase in the degree of separation between the axes of the radial notch (RN) and intercondylar ridge (IR): **A**, outline of proximal radial and ulnar epiphyses of *Alligator mississippiensis* (Daudin, 1802) with a low angle separating the axes of the radial notch and intercondylar ridge; **B**, outline of proximal radial and ulnar epiphyses of *Struthio camelus* Linnaeus, 1758 (FMNH 489294), illustrating expansion of the pre-axial ulnar articular surface onto the radial condyle to form a more prominent pre-axial process and a larger angle between the axes of the radial notch and intercondylar ridge; **C**, distal/flexor view of a stylized outline of a semi-pronated tetrapod forearm comparable to (**A**); **D**, distal/flexor view of a stylized outline of a semi-pronated tetrapod forearm comparable to (**B**) that has decreased independent movements of the ulna and radius via expansion of the pre-axial ulnar process and migration of the proximal radial epiphysis to a flexor (median) position at the elbow joint. Together, these alterations make the axis of the radial notch functionally perpendicular to that of the intercondylar ridge. Note that although the humeral diaphyses are oriented vertically, axes of elbow joint flexion/extension are oblique in most tetrapods due to eversion of the elbow away from the body wall (Hopwood 1947; Manzi 1957; Yalden 1966).

Data collection was standardized by articulating the humeri, radii and ulnae of all specimens so that the long axis of the humerus was perpendicular to the horizontal plane. The elbow's plane of joint action (determined by the intercondylar ridge) was usually not perpendicular to the horizontal, since tetrapod forearms rarely, if ever, flex/extend as a unit against the humerus without some degree of long-axis rotation (Cuénod 1888). In tetrapods that have flattened radial notches (the common proximal articular facet between the radius and ulna), the degree of separation between the axes of the radial notch and intercondylar ridge (see Introduction) was used as quantitative representation of the difference in the plane of independent flexion/extension in each of these areas (Fig. 5). The term “independent flexion/extension” (*sensu* Landsmeer 1983, 1984) is used here in reference to the ability of many tetrapod radii and ulnae to passively flex and extend independently of one another at the elbow joint, providing that the morphology of the radial

notch and its surrounding soft tissues allows these opposing movements (Fig. 4). This definition of flexion/extension at the elbow joint is distinct from the definition for active flexion/extension of the entire forearm at the elbow joint in a bipedal stance. Specifically, independent flexion/extension describes the passive movements of the radius and ulna against each other and the humerus during the propulsive phase of a quadrupedal step cycle as they are being twisted in place between the retracting humerus and immobile carpus. As Landsmeer (1984) demonstrated, independent flexion/extension in lacertilians is the result of the external application of torsion (i.e. long-axis rotation) to the forearm and/or elbow joint (e.g., Fig. 4), and functions as the major means by which this torsion is passively alleviated. The torsion is alleviated partially due to the oblique orientation of the radial notch (Fig. 4), which causes the radius and ulna to flex and extend simultaneously at an angle to one another. These oblique angles of flexion and extension allow the radius and ulna to cross and uncross along their lengths (Fig. 4). For example, as the forearm is forced to twist post-axially between the humerus and wrist during sprawling forelimb retraction, the radius flexes into adduction while the ulna extends into abduction. These movements of crossing and uncrossing are not the same as isolated long-axis rotations of the radius in therians (Fig. 2), which do not necessarily require substantial flexion/extension of the forearm bones (Hultkrantz 1897).

In tetrapods that possess radial notches that are not planar, degree measurements were recorded of the plane of the intercondylar ridge versus the protrusion of the extreme tip of the pre-axial ulnar process away from the plane of the radial notch (measured from the tip of the post-axial, or coronoid process, of the ulna, to the tip of the pre-axial ulnar process). This approach was used in order to quantify an alternative adaptation for reduction in independent flexion/extension of the forearm bones (Fig. 6). If an intercondylar ridge or corresponding intercondylar groove was not apparent from visual inspection or by touch, then the common plane of elbow joint flexion and extension was determined by selecting a member of the clade, articulating its humerus and forearm, and then flexing the forearm against the humerus. The angle at which the forearm flexed relative to the long axis of the humerus was then delineated on the proximal articular surface of the ulna by modeling clay to provide a visual proxy for the intercondylar ridge. For large specimens, a sandbox or modeling clay was used to articulate forelimb elements. The proximal forearm views of specimens were photographed, and the degrees of separation between the radial notch/pre-axial process and intercondylar ridge were measured on a computer screen using a small goniometer (Model # ST-431B, from Sunmed, Guandong, China), accurate to 1°.

STATISTICAL ANALYSIS

The repeated-measures data from the EPB of dinosaurs were analyzed with a univariate repeated-measures analysis of variance according to the methods described in Hutson &

Hutson (2012). The null hypothesis of a repeated-measures design is that the means across all levels of treatment will be equal (Zar 1999). The goal of this analysis was to determine if ROM varied significantly as soft tissues were dissected away in stages from fully fleshed (ROM1) to skeletonized (ROM5) conditions. Only *Alligator mississippiensis* provided quantifiable ROM data, so data from all *Alligator mississippiensis* forearms (n=6) were analyzed alone. Additionally, the effect of handedness was analyzed as a within-subject factor (two levels; right or left forearm) ($\alpha=0.05$). Due to the low sample size (often n=1) of well-preserved, matching fossil archosaur radii and ulnae (Hutson 2015), and the limited availability of completely skeletonized museum radii and ulnae of extant tetrapods, it was not possible to statistically analyze the degrees of separation between the radial notches and tips of the ulnar processes versus the intercondylar ridges of ulnae (Figs 5; 6).

INSTITUTIONAL ABBREVIATIONS

AMNH	American Museum of Natural History, New York;
DMNH	Denver Museum of Nature and Science, Denver;
FMNH	Field Museum of Natural History, Chicago;
HDW-NIU	Harlan D. Walley-Northern Illinois University, DeKalb;
INHS	Illinois Natural History Survey, University of Illinois at Urbana-Champaign, Champaign;
MPM	Milwaukee Public Museum, Milwaukee;
NMMNH	New Mexico Museum of Natural History, Albuquerque;
TMM	Texas Memorial Museum, Austin;
TMP	Royal Tyrrell Museum, Drumheller;
TTU	Texas Tech University, Lubbock;
UCMP	University of California Museum of Paleontology, Berkeley;
UNC	University of North Carolina, Chapel Hill;
USNM	National Museum of Natural History, Washington, D.C.;
YPM	Yale Peabody Museum, New Haven, Connecticut.

RESULTS

The sequential removal of integument, muscles, and tendons had no significant effect on ROM in *Alligator mississippiensis* (see Appendices 2-4). The fleshed methodology forced crossing and uncrossing of the *Alligator mississippiensis* radius and ulna via coupled nonrotary independent flexion/extension at the flattened radial notch (Figs 4; 5A), as in lacertilians. In contrast to *Alligator mississippiensis*, *Struthio camelus* exhibited a modified radial notch that reduced or prohibited crossing or uncrossing of the forearm bones via the lacertilian mechanism (Fig. 5B). A comparison of the proximal ulnar epiphyses of representative tetrapod clades indicates that the vast majority of extinct and extant tetrapods possess passive independent flexion/extension comparable to *Alligator mississippiensis* and lacertilians (Figs 7-9). In these tetrapods the radius and ulna essentially retain their plesiomorphic pre-post-axial positions at the elbow joint (Fig. 1), which facilitates independent movements within forearm space. Bipedal dinosaurs retained this passive quadrupedal mechanism, providing further support for

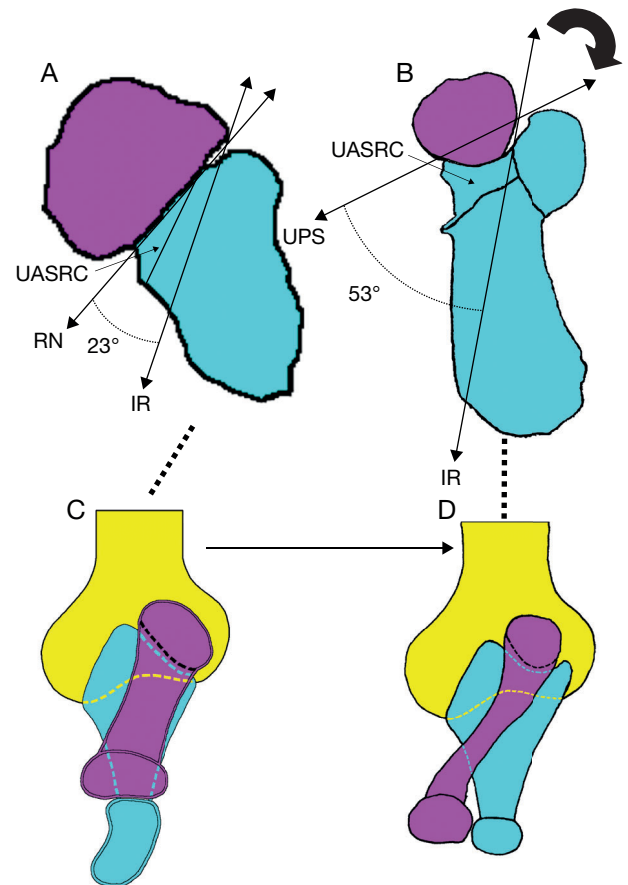


Fig. 6. — Demonstration of how a phyletic reduction in independent flexion/extension can occur due to a flexor protrusion of the tip of the pre-axial ulnar process away from the plane of the radial notch: **A**, outline of proximal radial and ulnar epiphyses of the synapsid pelycosaur *Dimetrodon loomisi* Romer, 1937 (AMNH 2093), with a low angle separating the axes formed by the shelf of the ulnar processes (UPS) and intercondylar ridge; **B**, outline of proximal radial and ulnar epiphyses of the opossum *Didelphis virginiana* Kerr, 1792 (FMNH 16698), illustrating expansion of the pre-axial ulnar articular surface around the radius to form a protruding pre-axial ulnar process that would reduce independent flexion/extension of either forearm bone; **C**, distal/flexor view of a stylized outline of a semi-pronated synapsid forearm comparable to **A**; **D**, distal/flexor view of a stylized outline of a fully pronated therian forearm comparable to **B**. Abbreviations: IR, intercondylar ridge; RN, radial notch; UASRC, ulnar articular surface with radial condyle of humerus; deg, degree.

the consensus that they were incapable of active therian-grade pronation/supination of the manus. Many tetrapod clades evolve adaptations to reduce radioulnar mobility by: 1) increasing the degree of radial notch/intercondylar ridge separation as in *Struthio camelus* (compare Figs 5, 7; Appendix 1), and/or; 2) evolving a protruding pre-axial ulnar process like those of quadrupedal dinosaurs (compare Figs 6, 7; Appendix 1). Both of these adaptations reduce or prevent passive independent flexion/extension of either forearm bone (Fig. 8). Amongst maniraptoran clades, the forearm bone articulations with the humerus in *Archaeopteryx* and dromaeosaurs are rigidly aligned perpendicular to the plane of elbow joint flexion and extension like those of birds. This information suggests that they either inherited forearms adapted for gliding and/or flapping flight, or used them for these activities themselves.

DISCUSSION

THE EFFECTS OF EXTRINSIC SOFT TISSUES ON THE ROM OF FOREARM LONG-AXIS ROTATION

The *Alligator mississippiensis* repeated-measures means for ROM1-ROM3 did not increase significantly between dissection treatments (see Appendices 2, 3). This result contrasts with previous findings from the larger joints of these animals (Hutson & Hutson 2012, 2013, 2014), changes in *Iguana iguana* Linnaeus, 1758 hip ROM (Arnold *et al.* 2014), as well as an analogous study done by Roos *et al.* (1992) of therian forearm pronation/supination, in which ROM typically increased as extrinsic soft tissues were removed. Additionally, the observers were unable to force long-axis rotations in ROM1-ROM3 for *Struthio camelus*, which agrees with most reports of similar immobility in the radioulnar joints of volant birds (Alix 1863, 1874; Vazquez 1994; cf. Anderson 1892). Because the *Struthio camelus* forearm bones did not loosen up enough to permit ROM1-ROM3 repeated measures as soft tissues were dissected away, and the repeated measures for ROM1-ROM3 did not vary significantly in *Alligator mississippiensis*, the authors tentatively conclude that these EPB taxa do not possess extrinsic ROM1 and ROM2 soft tissues (i.e. integument and muscles/tendons) that markedly affect the ROM of independent movements of either forearm bone. The lack of an increase in mobility in ROM3 after the *pronator* and *supinator* muscles in ROM2 had been dissected away may demonstrate that, rather than these muscles, the distal and proximal radioulnar ligaments function to passively limit (as in *Alligator mississippiensis*) and prevent (as in *Struthio camelus*) independent movements of the radius and ulna. This interpretation is analogous to previous interpretations of the ligaments encapsulating the intertarsal joint of *Struthio camelus*, i.e. that they function to passively limit ROM (Schaller *et al.* 2009). Alternatively, the authors may have applied too much force to observe an increase in ROM from ROM1 to ROM3.

IDENTIFICATION OF THE MECHANISM OF APPARENT FOREARM LONG-AXIS ROTATION IN *ALLIGATOR MISSISSIPPIENSIS*

The radioulnar ligaments of *Alligator mississippiensis* prevent isolated long-axis rotations of the radius relative to the ulna (Hutson & Hutson 2012). However, they still allow the radial and ulnar diaphyses to cross and uncross along a common long axis relative to an immobile humerus, particularly post-axially into supination. Before dissections reached ROM4, the crossing and uncrossing superficially appeared identical to long-axis rotations that can be forced relative to the ulna in many therian radii. However, unlike Hultkrantz (1897), Haines (1946), and Landsmeer (1983, 1984), the authors did not stop manipulations at ROM3, but transitioned immediately to ROM4. In ROM4 ligaments and capsules extrinsic to the wrist and elbow joints bracketing the forearm proximally and distally were removed, and then here and in ROM5 the authors attempted to replicate the apparent isolated long-axis rotations of the radius relative to the ulna that had been repeatedly measured in ROM1-ROM3. This sequential

coupling of the conflicting fleshed and skeletonized ROM methodologies (see Table 1) revealed that some mechanism other than therian-grade isolated long-axis rotations of the radius was responsible for the observed simulacra of long-axis rotations of the forearm in ROM1-ROM3 of *Alligator mississippiensis* (Fig. 4). The flattened complementary articular facets at the radial notches of many nontherian forearm bones do not allow long-axis rotations without dislocation (Hutson & Hutson 2012). Moreover, the tight articulation between the protruding intercondylar ridge (formed primarily by the ulna in most tetrapods) and the corresponding intercondylar groove of the distal humeral epiphysis, served to resist long-axis rotations of the entire forearm relative to the humerus (Vialleton 1924; Haines 1946). Additional dissection of the *Alligator mississippiensis* elbow joint revealed that the proximal radial and ulnar epiphyses pivoted against one another into abduction or adduction in forearm space as the carpus was pre- and post-axially rotated, via simultaneous independent flexion/extension against one another at the radial notch (Fig. 4). Landsmeer (1981, 1983, 1984, 1990) thoroughly described and illustrated the details of how this passive forearm mechanism occurs proximally at the elbow joint in a series of publications investigating rotary movements in lacertilian epipodia, but did not apply it to Haines' (1946) previous interpretations of radioulnar crossing/uncrossing in other extant and extinct nontherian tetrapods (see below for further discussion).

PROXIMAL ULNAR ADAPTATIONS THAT AFFECT INDEPENDENT FLEXION/EXTENSION OF THE FOREARM BONES *The EPB of dinosaurs*

A comparison of articulated proximal radial and ulnar epiphyses in the EPB of dinosaurs revealed that *Struthio camelus* possesses a larger ulnar articular surface with the radial condyle than *Alligator mississippiensis* (Fig. 5). The morphological landmarks for independent flexion/extension are homologous (see Fig. 5), which indicates that changes in mobility can be inferred. Early workers mistakenly believed that the stiffened morphology of a flexor radius and extensor ulna at the elbow was plesiomorphic to Tetrapodomorpha, due to the presence of these features in aquatic reptiles and monotreme mammals (see discussion in Hutson 2010). Romer (1956: 373) hypothesized that pre-axial ulnar expansion in basal archosaurs and dinosaurs was a derived structural adaptation for increased weight support (a summarization agreeing with previous viewpoints for both dinosaurs and therians [e.g., Osborn 1904]), but did not speculate on how this change might have affected radioulnar mobility. By contrast, Vialleton (1924) described how expansion of the ulnar articular surface onto the radial condyle effectively reduces independent movements of the radius. Specifically, pre-axial expansion of the ulnar articular surface extensad to the radius onto the radial condyle causes the the forearm bones to flex and extend at the elbow joint as one unit, reducing pre- and post-axial movements, and therefore increasing stability. This adaptation gives the impression that the proximal radial epiphysis has migrated to a more flexad position relative

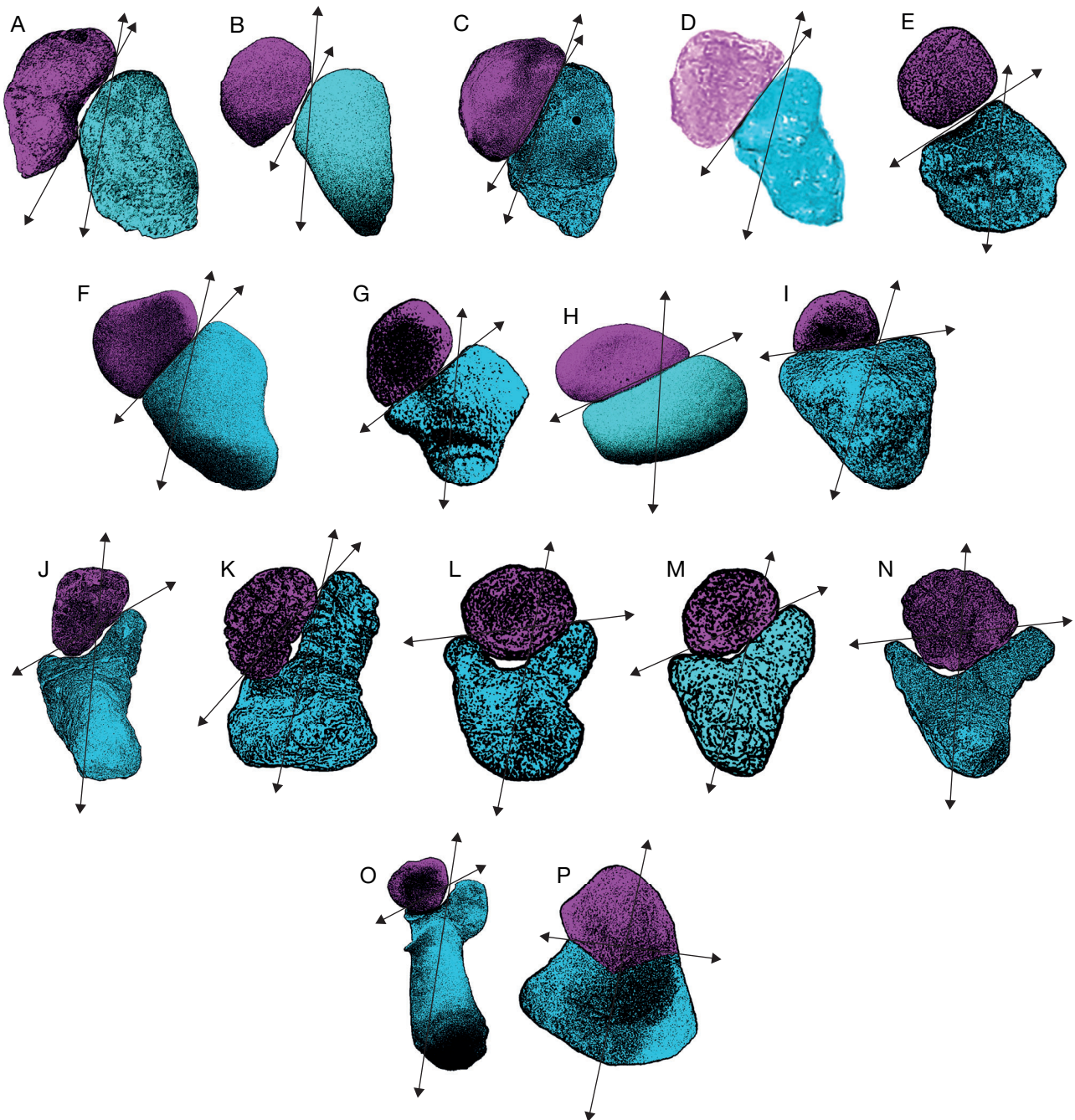


FIG. 7. — Comparison of proximal radioulnar articulations at the elbow joint that influence independent movements of the forearm bones in a representative sample of extinct and extant quadrupedal tetrapods: **A**, TMM 31025-140 reversed archosauromorph *Trilophosaurus buettneri* Case, 1928; **B**, INHS 23894 semi-aquatic turtle *Chrysemys picta* (Schneider, 1783); **C**, FMNH 22197 monitor lizard *Varanus komodoensis* Ouwens, 1912; **D**, AMNH 21293 reversed pelycosaur *Dimetrodon loomisi* Romer, 1937; **E**, FMNH 22010 salamander *Ambystoma tigrinum* (Green, 1825); **F**, FMNH 284695 alligatorid crocodilian *Alligator mississippiensis* (Daudin, 1802); **G**, FMNH 250433 chameleon *Furcifer pardalis* (Cuvier, 1829); **H**, HDW-NIU 1086 aquatic trionychid turtle *Apalone spinifera* (Lesueur, 1827); **I**, FMNH 489294 ratite *Struthio camelus* Linnaeus, 1758; **J**, USNM 11659 reversed *Stegosaurus* sp.; **K**, YPM 57489 high fidelity cast of MPM VP 6841 reversed ceratopsid *Torosaurus* cf. *latus* Marsh, 1891; **L**, AMNH 3032 ankylosaur *Sauropelta edwardsorum* Ostrom, 1970; **M**, YPM 5456 basal iguanodontid *Tenontosaurus tilletti* Ostrom, 1970; **N**, USNM 3814 hadrosaur *Edmontosaurus annectens* (Marsh, 1892); **O**, FMNH 166984 therian *Didelphis virginiana* Kerr, 1792; **P**, FMNH 210096 toad *Bufo blomeri* Myers & Funkhouser, 1951. Tetrapods with planar radial notches uninterrupted (**A-I**) and interrupted (**J-P**) by a protruding pre-axial ulnar process tip. The term “reversed” refers to elements from the right sides that have been digitally flipped. Note that higher degrees of separation between the arrows representing the planes of elbow joint flexion/extension (sub-vertical intercondylar ridge) and independent flexion/extension (sub-horizontal arrow connecting tips of ulnar processes) equate to reduced independent flexion/extension. Compare directly to Figures 5 and 6. The degrees of separation are reported in Appendix 1. Not to scale.

to that of the ulna, hence the origin of the term “proximal radial migration” (Vialleton 1924: 317, 318). Vialleton’s (1924) descriptions are similar to the conclusions of other authors (Cuénod 1888; Hultkrantz 1897; Savage 1957; see

Vazquez 1994 and references therein; cf. English 1977). However, what is missing from prior descriptions, which emphasized therians, was a functional consideration of the effect of ulnar expansion on independent flexion/extension

of the radius and ulna at the radial notch in nontherians. Vialleton's (1924) reasoning suggests that the more aligned the axes of the radial notch and intercondylar ridge, the higher the capacity for independent flexion/extension, if soft tissues allow such movements (see Fig. 5A). Savage (1957) hypothesized the same relationship for therian pronation/supination. Using previous descriptions, the authors infer that as pre-axial ulnar expansion causes a widening angle of separation between the radial notch and intercondylar ridge, up to the point of being perpendicular to one another, the amount of independent flexion/extension possible between the radius and ulna at the radial notch is correspondingly reduced (see Fig. 5B). Thus, the angle of separation between the radial notch and intercondylar ridge can be used to estimate the capacity for independent flexion/extension of the forearm bones. Unfortunately, this method cannot tell us to what degree soft tissues influence independent movements of the forearm bones relative to one another within the space of the forearm. However, osteological adaptations to reduce joint mobility are accompanied by increasingly restrictive soft tissue adaptations as well (Coombs 1978).

When the degrees of separation between the axes of the radial notches and intercondylar ridges of *Alligator mississippiensis* (Fig. 5A) and *Struthio camelus* (Fig. 5B) are compared, it becomes apparent that, as described by Alix (1863, 1874), avian radii and ulnae are adapted to flex and extend together in one plane at the elbow joint, as evidenced by the observation that the axes of avian radial notches are nearly perpendicular to their axes of elbow joint flexion/extension (Fig. 5D). By contrast, the axis of the radial notch in *Alligator mississippiensis* is more closely aligned with the axis of the intercondylar ridge, permitting the radius and ulna to flex and extend respectively independently of one another at the radial notch without difficulty (soft tissues allowing) when submitted to pre- and post-axial torsion (Figs 4; 5C).

The EPB of dinosaurs compared to other nontherian tetrapods.

Figure 7 compares EPB specimens to other articulated nontherian radii and ulnae in proximal view (Fig. 7F, I). The first two rows of specimens (Fig. 7A-I) represent nontherians with radial notches that are flattened, as in *Alligator mississippiensis* and *Struthio camelus*. The degrees of separation among the first nine taxa in Figure 7A-I range from a minimum of 12° in *Varanus komodoensis*, to a maximum of 65° in *Struthio camelus*. The data from other specimens with flattened, uninterrupted radial notches (not figured; Appendix 1) show a linear continuum of points from 9-90° when graphed on a scatter plot, rather than groupings of angular differences in separation, such the group of data points formed by the ornithischian dinosaurs in Figure 8. These data suggest that the capability for passive independent flexion/extension may also vary along a linear continuum. The degrees of separation in taxa with uninterrupted radial notches follow a linear trend with a positive slope, because the axis of the radial notch (X-axis) is the same as a line drawn between the tips of the pre- and post-axial processes (Y-axis). The taxa that make up this continuum

include *Alligator mississippiensis*, *Struthio camelus*, as well as an archosauromorph, basal archosaurs, a therapsid, lacertilians, chelonians, and a salamander (Fig. 9; Appendix 1). As was observed in manipulations of *Alligator mississippiensis* here, Haines (1946) easily forced what superficially appeared to be long-axis rotations within the forearms of a lacertilian, a terrestrial chelonian, and a rhynchocephalian; the lacertilian and chelonian both had low degrees of angular separation (here regarded as $\leq 45^\circ$ in Fig. 9), which are notably close to the angular differences of separation of *Alligator mississippiensis* specimens. Rhynchocephalians also possess an uninterrupted radial notch with a low degree of separation from the intercondylar ridge of the ulna (see Haines 1946: fig. 1), but skeletonized specimens were not available for this study.

Taxa with uninterrupted radial notches and high degrees of separation (here regarded as $\geq 45^\circ$ in Fig. 9) include *Struthio camelus*, chameleons, a salamander, and the chelonian *Apalone spinifera* (Lesueur, 1827). *Struthio camelus*, as stated above, has no independent mobility in its radioulnar joints and a radial notch axis that approaches perpendicularity to that of the intercondylar ridge (Fig. 5B). This morphology was likely inherited from volant birds with forearms adapted to resist the stresses of flight (Alix 1863, 1874; Vazquez 1994). Pterosaurs evolved an analogous morphology within their elbow joints (Wilkinson 2008: fig. 8), also likely due to the stresses of flight (see discussion in Vialleton 1924: 146-150). This convergence suggests that the appearance of radioulnar and elbow joint articulations adapted for aerial locomotion can be pinpointed in the fossil record of both pterosaurs and theropod dinosaurs (see further discussion below).

Long-axis rotations can be forced in salamander forearms (Haines 1946), despite a moderately high degree of separation (50°; Fig. 7E). Since salamanders are not saltatory, and therefore not subjected to extreme limb bone loads on their forearms like anurans (Fig. 7P), it is not clear why salamanders possess extensive ulnar articular surfaces with the radial condyle (see Haines 1946: fig. 4). Chameleons (Fig. 7G), in contrast to other lacertilians (Fig. 7C; Appendix 1), have evolved a more expanded ulnar articular surface with the radial condyle, and larger angles of separation between their radial notches and intercondylar ridges. Moreover, multiple specimens exhibited a slight enclosure of the radius by a concave radial notch of the ulna, an immobilizing adaptation that is discussed below in our comparison of EPB and extinct archosaur forearm elements. Distally, chameleons are adapted to alleviate long-axis torsion within their ball and socket intracarpal articulations (Gasc 1963), rather than at their stiffened antebrachicarpal articulations (Schwarz 1939). This transference of torsion alleviation from the forearm to the carpus may explain their reduction in radioulnar mobility (cf. Hultkrantz 1897), which converges upon antebrachicarpal adaptations observed in primates with a similar arboreal lifestyle (Gasc 1963).

Apalone spinifera (Fig. 7H) is an aquatic river turtle with a proximal epiphysis that contrasts with *Chrysemys picta* (Schneider, 1783) (Fig. 7B), a turtle that is better adapted

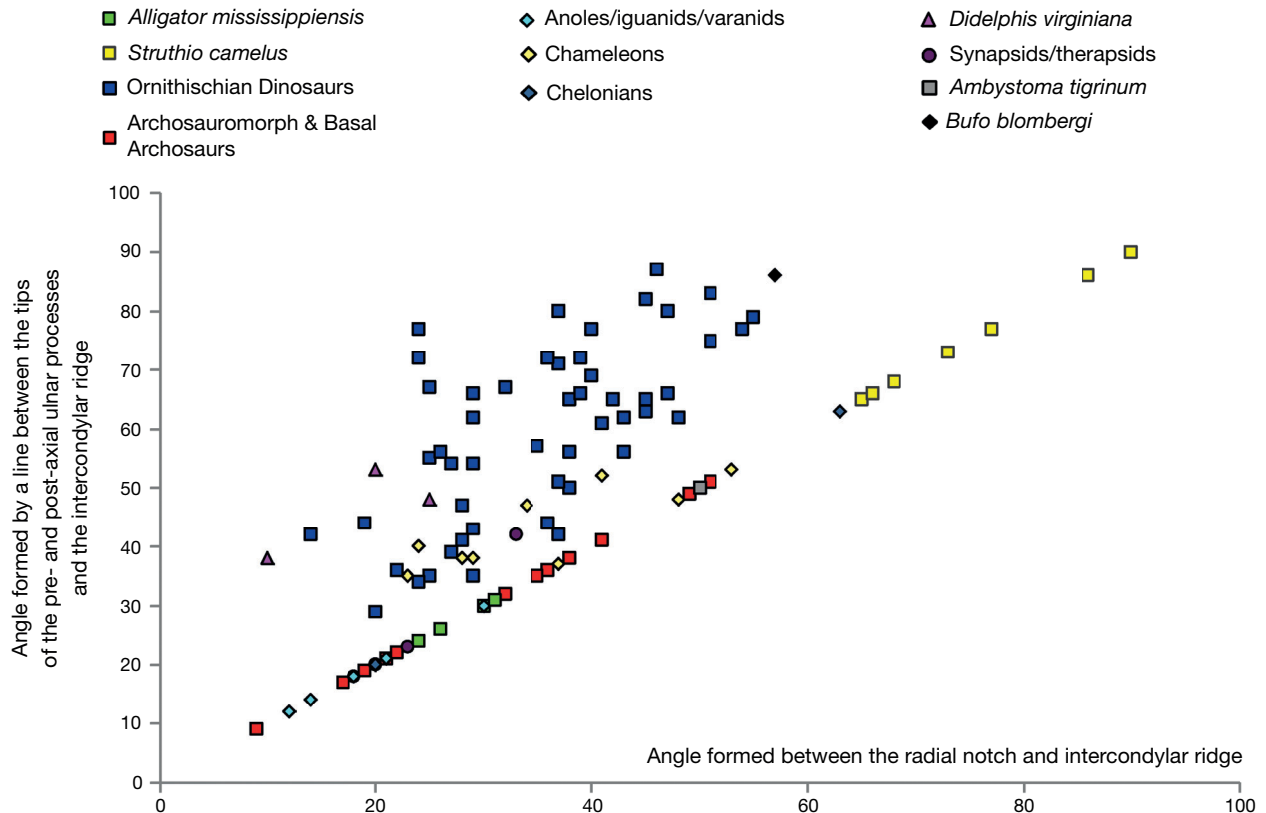


FIG. 8. — Differing strategies for inhibiting independent mobility of the forearm bones due to pre-axial expansion of the ulna onto the radial condyle. The linear trend with a positive slope indicates an increasing angle of separation between the axis of ulnar flexion/extension (intercondylar ridge) against the humerus and the axis of the radial notch, on which the ulna and radius flex/extend relative to one another (compare to Fig. 5). This widening angle is a result of pre-axial expansion of the ulnar articular surface extensad to the radius, causing them to flex and extend together at the elbow as one unit, decreasing independent mobility. Vertical departures from the linear trend reflect an alternative strategy for reducing independent flexion/extension at the elbow (by either the radius or the ulna) by having the tip of the pre-axial ulnar process protrude flexad from the plane of the radial notch to surround the radius extensad and pre-axially (compare to Fig. 6). Note that the evolution of pre-axial ulnar processes that cup the radius appear to be restricted to amniotes evolving parasagittal forelimb kinematics (dinosaurs, therians and chameleons). Units on the X- and Y-axes are in degrees.

for terrestrial locomotion with a low (20°) angle of separation between its radial notch and intercondylar ridge. The radioulnar ROM observations by Haines (1946: fig. 3) of the terrestrial chelonian *Terrapene carolina* Linnaeus, 1758 agree with observations here that apparent long-axis rotation can be easily forced in *Chrysemys picta* forearms. The authors concur with Haines (1946) that this radioulnar mobility reflects the ability of some turtles to alleviate locomotor-induced torsion, whereas tortoises usually have fused forearm bones. In comparison, the forearm of *Apalone spinifera* is better adapted for the stresses of aquatic paddling. As a result, like most terrestrial tortoises, trionychid turtles like *Apalone spinifera* have a radius and ulna that are fused together with an expanded ulnar articular surface (Fig. 7H). The proximally expanded ulnar articular surface in *Apalone spinifera* results in a higher degree of separation between the radial notch and intercondylar ridge (63°). The authors interpret this chelonian comparison as another example (compare with Fig. 5) of a phyletic increase in the ulna's contribution to articulation with the radial condyle, extensad to the radius, causing a reduction of independent movements of the forearm bones relative to one another within forearm space (Vialleton 1924).

The EPB of dinosaurs compared to archosauromorphs and other archosaurs

Flexor migration of the plane of the radial notch was not the only adaptation observed that inhibits independent mobility of the forearm bones relative to one another. When comparing *Alligator mississippiensis* (Fig. 7F) and *Struthio camelus* (Fig. 7I) with other archosaurs, the authors note that ornithischian dinosaurs that utilized quadrupedalism (Fig. 7J-N) typically possess pre-axial ulnar processes that protrude flexad from the plane of the radial notch. Plesiomorphically, ornithischian dinosaurs were bipedal and possessed flattened radial notches (Santa Luca 1980; Maidment & Barrett 2014), which implies that a protruding pre-axial ulnar process is derived in quadrupedal taxa. This characteristic causes quadrupedal ornithischians to plot as outliers above the linear trend formed by tetrapods with uninterrupted radial notches in Figure 8.

Sauropodomorph dinosaurs were excluded from the survey of dinosaurian forearms because Bonnan (2003) thoroughly documented the evolution of interrupted radial notches in this clade, which are strikingly similar to the morphology of hadrosaur radial notches (Fig. 7N). Like bipedal ornithischians, Bonnan (2003) noted that dinosauromorphs and early facultatively bipedal sauropodomorphs possessed flattened

TABLE 2. — Proximal radioulnar mobility in representative tetrapods. Symbols: +, present; –, absent; *, mobility inferred by shared radioulnar morphology with other nontherians; †, like anurans, tortoises and highly aquatic turtles typically possess fused radii/ulnae; ‡, various clades (e.g., pterosaurs) have reduced mobility analogous to avians.

	Anurans (frogs and toads)	Urodeles (salamanders)	Rhynchocephalians (tuatara) *	Chelonians (various turtles) †	Lacertilians (various)	Crocodylians	Dinosaurs and other extinct non- avian archosaurs ‡	Avians (various)	Extinct non-mammalian Synapsids	Therian mammals (various)
Therian-grade long-axis rotations	–	–	–	–	–	–	–	–	–	+
Lacertilian- grade independent flexion/ extension	–	+	+	+	+	+	+	–	+	–

radial notches. The latter information suggests that, if the radius and ulna were unfused and not overly restricted by soft tissues, the capability for passive independent flexion/extension could have been present (cf. Bonnan & Senter 2007). As some sauropodomorphs evolved into large obligatory quadrupeds they evolved larger pre-axial ulnar processes with tips that protruded flexad, which effectively turned the radius and ulna into one stiffened unit during elbow joint flexion/extension by enclosing the proximal radial epiphysis between the pre- and post-axial ulnar processes in a vise-like grip (see pictorial evolution of this feature in Bonnan [2003: fig. 10]). Students of sauropodomorph limb morphology have long considered this feature, i.e. an ulna with a proximal epiphysis that grips the radius pre- and post-axially, to have been an adaptive response to increased limb bone loads caused by graviportalism (Osborn 1904; Romer 1956). Thus, these findings corroborate recent reports that the proximal radioulnar joint morphologies of quadrupedal ornithischian dinosaurs converged closely upon those of quadrupedal sauropodomorphs (Mallison 2010; Senter 2010; Maidment & Barrett 2014).

Unlike with quadrupedal ornithischians, examinations of archosauromorphs and basal archosaurs (Fig. 9) revealed no signs of extensively protruding pre-axial ulnar processes. For example, the proximal view of the forearm of the archosauromorph *Trilophosaurus buettneri* (Fig. 7A) is almost identical to those of proterosuchian archosauriformes (Young 1936: fig. 9). Here, the angles of intercondylar ridge/radial notch separation are comparable to those of *Alligator mississippiensis* (Appendix 1). Notably, quadrupedal archosauromorphs and basal archosaurs are not known to have reached the sizes

found in clades of large quadrupedal dinosaurs (Romer 1956), which may partially explain their lack of adaptations for immobilizing the proximal radioulnar articulations. Moreover, the evolution of cursorialism in archosaurs was coupled with a trend towards bipedalism (Romer 1956), which may have negated the need to strengthen the elbow joint for the stresses of running in most taxa. However, the only known cursorial quadrupedal archosaurs, sphenosuchian crocodylomorphs, may also have evolved proximal radial migration in response to increased limb bone loads (Whetstone & Whybrow 1983). Further studies could investigate this possibility.

The EPB of dinosaurs compared to therians

Although therians lie outside the EPB of dinosaurs (Witmer 1995), they provide many important convergence studies of transitions from mobile to immobile proximal radioulnar joints analogous to those of archosaurs (Table 2). For example, decreased ROM of pronation/supination and/or ulnar expansion at the elbow are observed to be adaptive responses to the increased limb bone loads associated with graviportal (Osborn 1904; Vialleton 1924), volant (Alix 1867; Simmons 1993), gliding (Shufeldt 1911; Simmons 1993), secondarily aquatic (Vialleton 1924; Savage 1957), raking/fossorial (Zapfe 1979; Barnosky 1981), and cursorial (Hildebrand 1954; Taylor 1974) lifestyles in therians. As pre-axial ulnar expansion at the elbow is minimal in pelycosaurs (Fig. 7D) and dicynodonts (Fig. 9K), this indicates that the ability to passively flex/extend the radius and ulna independently of one another during quadrupedal locomotion was plesiomorphic to quadrupedal synapsids, as it was with archosaurs.

THE FUNCTIONAL IMPLICATIONS OF HIGHLY CONSERVED PROXIMAL RADIOULNAR ARTICULATIONS IN THE CLADE TETRAPODOMORPHA

Radioulnar mobility in nontherian tetrapods

When compared to previous studies of nontherian forearm bone ROM (Haines 1946), the findings presented here provide compelling evidence that the proximal epiphyses of the radii and ulnae of many nontherian tetrapods are adapted for passive independent flexion/extension. The high degree of morphological conservativeness amongst the forearm articulations of tetrapods provides further support for this interpretation (Romer 1922; Table 2). Landsmeer (1983, 1984, 1990) progressively recognized that the mechanism that allows crossing/uncrossing within the forearm space of lacertilians was deceptively similar to therian pronation/supination, yet caused by passive nonrotary independent flexion/extension of the forearm bones relative to one another. Unfortunately, this similarity has caused many researchers to mistakenly believe that nontherian forearms are capable of therian-grade long-axis rotations *in vivo*, and by association, consequently capable of actively pronating into a fully pronated orientation. The agreement between Landsmeer's (1983, 1984) description of the functional morphology of independent flexion/extension in lacertilians and earlier studies of nontherian forearm rotary mobility (Cuénod 1888; Haines 1946), as well as observations here of the same phenomenon in *Alligator mississippiensis*, strongly suggest that this is the

plesiomorphic mechanism by which tetrapod forearms passively alleviate post-axial long-axis torsion at the radial notch during forelimb retraction. This mechanism allows the grade of forearm pronation to vary passively around the plesiomorphic grade of semi-pronation, but forcing full pronation results in dislocation (Hutson & Hutson 2012).

Radioulnar mobility and the grade of forearm pronation of bipedal archosaurs

This study's results indicate that archosaurs that evolved bipedalism retained the plesiomorphic adaptations for independent flexion/extension of the radius and ulna (Bonnar 2003; Maidment & Barrett 2014). The retention of an elbow joint adapted for passive and limited amounts of torsion alleviation, as well as a lack of distal and diaphyseal adaptations (e.g., strongly curved radial diaphyses; Vialleton 1924; Haines 1946) to increase the leverage of pronator/supinator musculature on the forearm bones, strongly suggests that isolated long-axis rotations were not possible between the forearm bones of bipedal archosaurs. Moreover, they would have retained semi-pronated forearms with medially facing palms (Vialleton 1924; Gasc 1963; Hutson 2015). Thus, when free of the ground, as with quadrupedal nontherians, it is unlikely that bipedal archosaurs were able to actively use independent flexion/extension of their forearm bones to manipulate prey or other objects in isolation from gross movements of elbow flexion/extension. However, this limitation would not have precluded grasping objects between their semi-pronated palms, or passive long-axis rotations in response to external torsion, such as during struggles with prey or conspecifics. Regardless, these results support the general consensus that the manual dexterity of obligatory bipedal dinosaurs and other bipedal archosaurs was limited in comparison to bipedal therians.

The transition from prehensile predatory forearms in theropods to forearms adapted for the stresses of flight

Therian forearms adapted for gliding and/or flapping exhibit adaptations similar to those found in other tetrapod clades with increased limb bone loads, namely forearm bones aligned in roughly the same plane as the axis of elbow flexion/extension. The ulna may also become reduced to a vestigial extensor remnant, such as in bats, colugos, and flying squirrels (Shufeldt 1911; Din 1959; Norberg 1970; Thorington 1984). In flying amniotes and amniotes with controlled gliding, stiffening adaptations within the wrist, radioulnar and elbow joints help resist the bending and torsional stresses of leading edge air streams and flapping (Norberg 1970). For example, it has long been observed that volant members of Aves (crown group birds) and Pterosauria both possess ulnar expansion/proximal radial migration (Vialleton 1924; Wilkinson 2008). However, recent observations that dromaeosaurs also possess these stiffening adaptations have been overlooked in discussions of their flight capabilities (Hutson & Hutson 2014), including those of *Archaeopteryx*.

A large body of evidence firmly supports a dinosaurian ancestry for birds from theropods (Forster *et al.* 1998). It has been stated that *Archaeopteryx* retained the unrestricted elbow

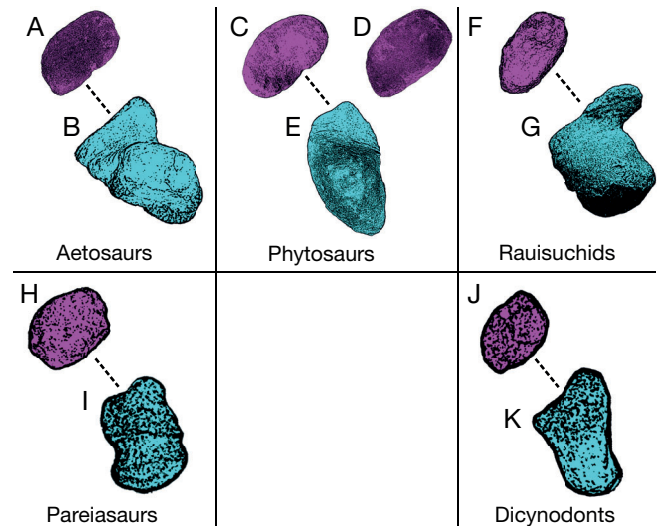


FIG. 9. — Comparison of isolated proximal radial and ulnar epiphyses of basal archosaurs, pareiasaurs, and therapsids: **A**, UCMP 28355 reversed aetosaur *Desmotosuchus haplocerus* Cope, 1892; **B**, NMMNH P 36075 aetosaur *Typothorax antiquum* Lucas, Heckert & Hunt, 2002; **C**, UCMP 121989 phytosaur *Machaeroprospus pristinus* (Mehl, 1928); **D**, UCMP 121992 *Machaeroprospus pristinus*; **E**, UCMP 121978 reversed *Machaeroprospus pristinus*; **F**, TTU P9002 reversed rousuchid *Postosuchus kirkpatricki* Chatterjee, 1985; **G**, cast of UNC 15575 *Postosuchus alisonae* Peyer, Carter, Sues, Novak & Olsen, 2008; **H**, AMNH 2451 reversed pareiasaur *Embrithosaurus schwarzi* Watson, 1914; **I**, AMNH 5604 reversed pareiasaur *Bradysaurus* sp. or *Proppapap* sp.; **J**, AMNH 24121 dicynodont *Placerias* sp.; **K**, AMNH 5591-93 dicynodont *Kannemeyeria simocephalus* Weithofer, 1888. Radial rows depict proximal radii oriented in relation to the plane of the radial notch in that clade. Ulnar rows depict proximal ulnae oriented so that the long-axis of the humerus is vertical. Dotted lines show where the radii and ulnae would articulate if they were from the same specimens. Note the flattened radial notches on the ulnae and complementary flattened radial articular surfaces of each clade (compare to Figure 7). These morphologies strongly suggest that these quadrupedal tetrapod clades retained the ability to passively and independently flex/extend their radii and ulnae during forelimb retraction. **H**, **I**, oriented after FMNH UC 1533 and FMNH UC 1525 *Bradysaurus baini* Seeley, 1892 specimens; **J**, **K**, oriented after small dicynodontid USNM 412381 and USNM 452057 *Diictodon* cf. *grimbeki* (Broom, 1935). Note that (**I**) may be damaged due to plaster on surface articulating with the ulnar condyle of the humerus. Not to scale.

joints of theropods (Lowe 1944; Ostrom 1974, 1976a, b), and therefore had forearm bone articulations that were too weak for the stresses of sustained powered flight (Heilmann 1926; Lowe 1935, 1944). However others have noted that *Archaeopteryx* specimens possess parallel forearm bones with ulnar expansion at the elbow, demonstrating that *Archaeopteryx* had an avian-like, strengthened elbow joint morphology (Owen 1863; Dames 1884; Wellnhofer 1974). Dromaeosaurs, which belong phylogenetically to a sister group of *Archaeopteryx* (Clark *et al.* 2002), also possess these features (see figures in Ostrom 1969; Gishlick 2001; Carpenter 2002; Burnham 2004; Senter 2006b), as may the closely related troodontids, some of which have been predicted to possess gliding/flapping wings (Zelenitsky *et al.* 2012). This information invites the question of whether avian-like forearms and elbow joints evolved within Maniraptora, or basal to this clade. Neither nonmaniraptoran ornithomimosaurs with “primordial” wings (Nicholls & Russell 1985; Zelenitsky *et al.* 2012), nor therizinosaurid maniraptorans evolved avian-like proximal radioulnar joints (Zanno 2006). Amongst other maniraptoran theropods, alvarezsaurs do possess these characters,

but the presence of hypertrophied muscle processes and other anteater-like features indicate that alvarezsaur forearms were adapted for tearing, raking, and pulling, not gliding/flapping flight (Senter 2005). Alvarezsaur forelimbs may be too heavily modified to ascertain if they exapted forearms reinforced for gliding/flapping, or whether they evolved these modifications separately. Regarding oviraptors, although it has been suggested that they were secondarily flightless maniraptorans, the authors are unaware of any descriptions that have shown that they possessed ulnar expansion (Lü *et al.* 2005). Therefore, most nonmaniraptoran and maniraptoran theropods basal to deinonychosaurs (dromaeosaurs + troodontids) plesiomorphically retained a pre-axial (lateral) position for the radius at the elbow (see figures in Carpenter 2002; Senter & Robins 2005; Senter 2006a), which indicates that the structural stresses incurred by bipedal prey capture and manipulation did not normally select for the immobility found in other archosaurs with forearms adapted for extreme limb bone loads. Finally, previous authors have not demonstrated that flying squirrel-like (i.e. semi-pronated) grappling and vertical climbing of tree trunks requires stiffening of the radioulnar joints (e.g., Walker 1972; Chatterjee & Templin 2004). Peters (2001) argued the opposite, specifically that semi-pronated pterosaur forearms stiffened for the stresses of flight were later exapted for trunk grappling and climbing. Functional analyses of trunk climbing, by flying squirrels that have reverted to semi-pronation due to the aerial stresses of gliding (Scholey 1986), may support Peters' (2001) suggestion.

In the absence of other forelimb characters correlated with lifestyles associated with increased limb bone loads, namely fossorialism, pulling and tearing, graviportalism, or aquatic flapping, the presence of an avian type of elbow joint and forearm bone alignment strongly suggests that the forearms of *Archaeopteryx* were adapted to resist the stresses of gliding and/or flapping, and/or implies that it was descended from gliding/flapping ancestors. The occurrence of these adaptations in dromaeosaurs, and possibly troodontids, has similar implications. Thus, although secondary flightlessness has been proposed for various nonmaniraptoran and maniraptoran theropods (see Paul 2002 and references therein), these features may only provide osteological support for pre-existing proposals that some deinonychosaurs were secondarily flightless. The authors note that, since pterosaurs also exhibited these adaptations (Wilkinson 2008), their presence could also help identify when the last common ancestor of pterosaurs began evolving gliding and/or flapping flight, if and when such fossils are found. Finally, while this information does not indicate unequivocally whether *Archaeopteryx* or other small dromaeosaurs possessed powered flapping flight, it also does not favor either side of the debate on whether dinosaurs evolved flight terrestrially or arboreally. Terrestrial proponents have argued that dinosaurs evolved the ability to flap while running, while arboreal proponents have argued that dinosaurs evolved the ability to glide first, and then flap (see Chatterjee & Templin 2004 and references therein). In either evolutionary scenario, reinforcement of the wrist, radioulnar and elbow joints would have been necessary.

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APPENDICES

APPENDIX 1. — Degrees of separation between the axes of the radial notch and the shelf formed by ulnar processes versus the axis of the intercondylar ridge of the ulna/radius.

	Species	Catalog number	Element(s)	Degrees of separation between Radial Notch and Intercondylar Ridge	Degrees of Separation between Shelf of Pre- postaxial Ulnar Processes and Intercondylar Ridge
Archosauromorphs (trilophosaurs)	<i>Trilophosaurus buettneri</i>	TMM 31025-140	R. antebrachium	19°	19°
	<i>Trilophosaurus jacobsi</i>	NMMNH P-43303	L. proximal ulnar epiphysis	26°	26°
	<i>T. jacobsi</i> (juvenile)	NMMNH P-43261	R. ulna	9°	9°
Basal Archosaurs (phytosaur)	<i>Rutiodon tenuis</i>	UCMP 121978	R. proximal ulnar epiphysis	24°	24°
	<i>Rutiodon tenuis</i>	UCMP 121968	L. ulna	21°	21°
	phytosaur	USNM 2686	R. proximal ulnar epiphysis	17°	17°
	phytosaur	USNM 2154	L. ulna	22°	22°
	<i>Pseudopalatus buceros</i>	NMMNH P-31294	L. ulna	32°	32°
	<i>Pseudopalatus buceros</i>	NMMNH P-35476	R. ulna	38°	38°
	<i>Pseudopalatus buceros</i>	NMMNH P-37890	L. ulna	32°	32°
Basal Archosaurs (aetosaurs)	<i>Typothorax coccinarum</i>	UCMP 34240	R. proximal ulnar epiphysis	49°	49°
	<i>Typothorax antiquum</i>	NMMNH P-36075	L. ulna	51°	51°
Basal Archosaurs (rauisuchids)	<i>Postosuchus kirkpatricki</i>	TTU P9000	R. ulna	36°	36°
	<i>Postosuchus kirkpatricki</i>	TTU P9000	L. ulna	35°	35°
	<i>Postosuchus alisonae</i>	Cast of UNC 15575	L. proximal ulnar epiphysis	50°	50°
Archosaurs (crocodilians)	<i>Alligator mississippiensis</i> (Daudin, 1802) (137 cm ♀)	FMNH 284695	L. antebrachium	30°	30°
	<i>Alligator mississippiensis</i> (same ♀ as above)	FMNH 284695	R. antebrachium	24°	24°
	<i>Alligator mississippiensis</i> (127 cm ♀)	FMNH 284694	L. antebrachium	30°	30°
	<i>Alligator mississippiensis</i> (same ♀ as above)	FMNH 284694	R. antebrachium	26°	26°
	<i>Alligator mississippiensis</i> (102 cm ♀)	FMNH 284693	L. antebrachium	31°	31°
	<i>Alligator mississippiensis</i> (same ♀ as above)	FMNH 284693	R. antebrachium	26°	26°
Archosaurs (ratites)	<i>Struthio camelus</i> Linnaeus, 1758 (♂)	FMNH 489293	R. antebrachium	65°	65°
	<i>Struthio camelus</i> (same ♂ as above)	FMNH 489294	L. antebrachium	73°	73°
	<i>Struthio camelus</i>	INHS 2043	L. antebrachium	77°	77°
	<i>Struthio camelus</i>	INHS 2048	R. antebrachium	73°	73°
	<i>Struthio camelus</i>	INHS 2044	L. antebrachium	77°	77°
	<i>Struthio camelus</i> (♀)	FMNH 489295	R. antebrachium	90°	90°
	<i>Struthio camelus</i>	INHS 2045	R. antebrachium	86°	86°
	<i>Struthio camelus</i>	INHS 2047	L. antebrachium	66°	66°
	<i>Struthio camelus</i>	INHS 2046	L. antebrachium	68°	68°
Archosaurs (ankylosaurs)	ankylosaur (hoplitosaur)	YPM 5189	R. ulna	46°	87°
	<i>Panoplosaurus</i> sp.	YPM PU-21178 (or 16970)	R. ulna	51°	83°
	<i>Texasetes pleurohalio</i> (or <i>Tomistoma</i>)	USNM 337987	L. proximal ulnar epiphysis	40°	69°
	ankylosaur	TMP 1982.16.264	R. antebrachium	41°	61°
	<i>Edmontonia rugosidens</i>	TMP 98.98.1	R. ulna	38°	65°
	<i>Sauropelta edwardsi</i>	AMNH 3032	L. antebrachium	39°	72°
	<i>Sauropelta edwardsi</i>	AMNH 3032	R. antebrachium	37°	80°
	<i>Sauropelta edwardsi</i>	AMNH 3035	L. antebrachium	25°	67°
	<i>Sauropelta edwardsi</i>	AMNH 3035	R. antebrachium	24°	77°
Archosaurs (basal ceratopsids)	<i>Leptoceratops gracilis</i>	AMNH 5205	L. ulna	19°	44°

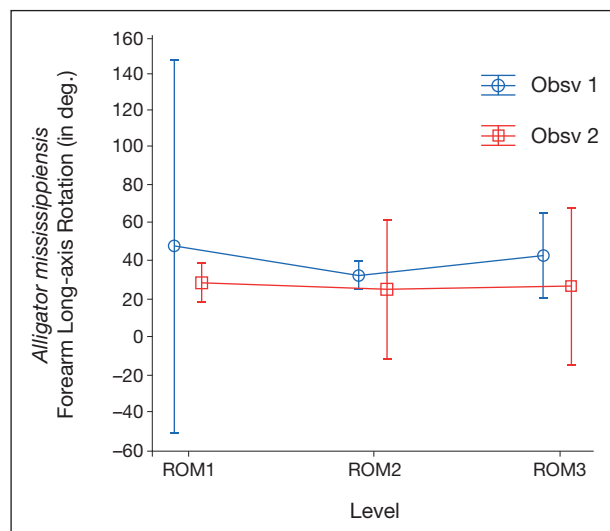
APPENDIX 1. — Continuation.

	Species	Catalog number	Element(s)	Degrees of separation between Radial Notch and Intercondylar Ridge	Degrees of Separation between Shelf of Pre- postaxial Ulnar Processes and Intercondylar Ridge
Archosaurs (ceratopsids)	<i>Triceratops</i> sp.	DMNH 996	L. ulna	22°	36°
	<i>Triceratops calicornis</i>	FMNH 12003	L. ulna	45°	63°
	<i>Torosaurus</i> cf. <i>latus</i>	YPM 57489 (high fidelity casts of mounted MPM VP6841 specimen)	L. antebrachium	20°	29°
	ceratopsid	TMP P67.20.29	R. ulna	36°	44°
	<i>Triceratops horridus</i>	USNM 4842	L. ulna	40°	77°
	<i>Triceratops horridus</i>	USNM 4842	R. ulna	37°	71°
	<i>Monoclonius flexus</i>	USNM 12745	L. ulna	27°	54°
	<i>Triceratops</i> sp.	YPM 57312	R. ulna	29°	62°
Archosaurs (stegosaurs)	<i>Stegosaurus</i> sp.	Uncataloged, YPM collections	L. ulna	29°	43°
	<i>Stegosaurus</i> sp.	YPM-1855, 1856	R. ulna	14°	42°
	<i>Stegosaurus</i> sp.	Uncataloged, YPM collections	R. ulna	25°	35°
	<i>Stegosaurus</i> sp.	YPM 1365A, 1855, 1856	L. ulna	24°	34°
	<i>Stegosaurus</i> sp.	YPM 1365A, 1855, 1856	R. ulna	27°	39°
	<i>Stegosaurus</i> sp.	USNM 11659	R. antebrachium	25°	55°
	<i>Stegosaurus</i> sp.	USNM 4929	R. antebrachium	29°	35°
	<i>Stegosaurus</i> sp.	USNM 4929	L. antebrachium	28°	41°
	<i>Stegosaurus sulcatus</i>	USNM 4937	L. ulna	26°	56°
	<i>Stegosaurus sulcatus</i>	USNM 4937	R. ulna	29°	54°
Archosaurs (ornithopods)	<i>Tenontosaurus tilletti</i>	YPM BB1	R. antebrachium	28°	47°
	<i>Tenontosaurus tilletti</i>	YPM 5456	L. antebrachium	35°	57°
	<i>Camptosaurus dispar</i>	YPM 1878	R. antebrachium	38°	50°
	<i>Camptosaurus</i> cf. <i>medius</i>	YPM 6794	R. antebrachium	43°	56°
	<i>Camptosaurus browni</i>	USNM 4282	R. antebrachium	37°	42°
	<i>Camptosaurus browni</i>	USNM 4282	L. antebrachium	37°	51°
	<i>Edmontosaurus annectens</i>	USNM 3814	L. antebrachium	47°	80°
	<i>Edmontosaurus</i> sp.	USNM 4278	L. ulna	55°	79°
	<i>Hypacrosaurus</i> sp.	USNM 7948	R. ulna	24°	72°
	<i>Hypacrosaurus</i> sp.	USNM 7948	L. ulna	32°	67°
	hadrosaur hatchling	TMP P81.16.373	R. ulna	47°	66°
	hadrosaur	TMP 2005.09.84	L. ulna	42°	65°
	hadrosaur	TMP 1980.29.101	L. ulna	43°	62°
	hadrosaur	TMP 1995.403.9	R. ulna	29°	66°
	hadrosaur	DMNH 20622	L. ulna	51°	75°
	hadrosaur	DMNH 42247	L. ulna	36°	72°
	gilmoresaur	AMNH 21591	R. ulna	48°	62°
	<i>Gilmoresaurus mongoliensis</i>	AMNH 6551	L. antebrachium	39°	66°
	<i>Saurolophus</i> sp.	AMNH 5271	L. antebrachium	54°	77°
	hadrosaur	AMNH 5899	R. ulna	45°	82°
	<i>Hypacrosaurus altispinus</i>	AMNH 5357	L. antebrachium	45°	65°
	tenontosaur	AMNH 3043	L. antebrachium	38°	56°
Synapsids (pelycosaurs)	<i>Dimetrodon loomisi</i>	AMNH 2093	R. antebrachium	23°	23°
	<i>Dimetrodon</i> sp.	USNM 407925	R. proximal ulnar epiphysis	20°	20°
	<i>Dimetrodon</i> sp.	USNM 407915	R. proximal ulnar epiphysis	18°	18°
Therapsids (dicynodont)	<i>Kannemeyeria simocephalus</i>	AMNH 5591-93	L. ulna	33°	42°
Mammals	<i>Didelphis virginiana</i>	FMNH 16698	L. antebrachium	20°	53°
	<i>Didelphis virginiana</i>	FMNH 16698	R. antebrachium	25°	48°
	<i>Didelphis virginiana</i>	INHS 821	L. antebrachium	10°	38°

APPENDIX 1. — Continuation.

	Species	Catalog number	Element(s)	Degrees of separation between Radial Notch and Intercondylar Ridge	Degrees of Separation between Shelf of Pre- postaxial Ulnar Processes and Intercondylar Ridge
Lacertilians	<i>Furcifer pardalis</i>	FMNH 250433	L. antebrachium	48°	48°
	<i>Furcifer pardalis</i>	FMNH 250433	R. antebrachium	53°	53°
	<i>Chamaeleo melleri</i>	FMNH 98770	L. antebrachium	23°	35°
	<i>Chamaeleo melleri</i>	FMNH 98770	R. antebrachium	28°	38°
	<i>Trioceros jacksonii</i>	FMNH 206753	R. antebrachium	29°	38°
	<i>Chamaeleo gracilis</i>	FMNH 22192	L. antebrachium	24°	40°
	<i>Chamaeleo gracilis</i>	FMNH 22192	R. antebrachium	41°	52°
	<i>Chamaeleo chamaeleon</i>	FMNH 31294	L. antebrachium	37°	37°
	<i>Chamaeleo chamaeleon</i>	FMNH 22385	R. antebrachium	34°	47°
	<i>Anolis equestris</i>	FMNH 31312	L. antebrachium	30°	30°
	<i>Anolis equestris</i>	FMNH 31312	R. antebrachium	14°	14°
	<i>Iguana iguana</i>	FMNH 22085	L. antebrachium	18°	18°
	<i>Iguana iguana</i>	FMNH 22085	R. antebrachium	21°	21°
	<i>Varanus komodoensis</i>	FMNH 22197	L. antebrachium	12°	12°
Testudines	<i>Chrysemys picta</i>	INHS 23894	L. antebrachium	20°	20°
	<i>Apalone spinifera</i>	HDW-NIU 1086	R. antebrachium	63°	63°
Lissamphibians (salamander)	<i>Ambystoma tigrinum</i>	FMNH 22010	L. antebrachium	50°	50°
Lissamphibians (toad)	<i>Bufo blombergi</i>	FMNH 210096	L. antebrachium	57°	86°

APPENDIX 2. — Graph of the effect of three sequential levels of dissection treatment on long-axis rotation ROMs by observers one and two in *Alligator mississippiensis* (Daudin, 1802) forearms, using the statistically insignificant treatment × observer interaction. Error bars are 95% confidence intervals (± 2 s.d.) for reported repeated-measures means. Note that the repeated-measures means exhibit a linear trend without an appreciable slope, particularly for observer two. This relationship illustrates the lack of an effect of dissection treatment on ROM.



APPENDIX 3. — Repeated measures in degrees of *Alligator mississippiensis* (Daudin, 1802) forearm independent flexion/extension ROMs across three levels of dissection treatment (ROM1-ROM3).

Subject	Joints	Observer	Independent flexion/extension (in deg.)								
			ROM1			ROM2			ROM3		
137 cm	L. Forearm	1	37	14	18	23	28	29	44	41	35
		2	33	25	26	24	24	32	33	38	34
137 cm	R. Forearm	1	40	32	36	42	43	35	43	44	43
		2	32	31	33	21	30	17	36	31	31
127 cm	L. Forearm	1	40	32	36	42	43	35	37	45	40
		2	32	31	33	21	30	17	26	25	30
127 cm	R. Forearm	1	60	65	50	36	34	44	62	55	44
		2	20	16	18	26	21	17	27	27	25
102 cm	L. Forearm	1	53	53	53	37	33	24	60	46	50
		2	33	32	32	24	34	32	10	17	10
102 cm	R. Forearm	1	66	61	75	31	34	28	28	28	29
		2	28	28	23	35	35	28	27	27	30

APPENDIX 4. — Greenhouse-Geisser and Huynh-Feldt adjusted output from STATISTICA® (StatSoft, Tulsa, OK, USA) of univariate repeated-measures ANOVA. Abbreviations: **Arm**, handedness; **RM**, repeated measures; **Treat**, treatment; **Obs**, observer.

	d.f.	F	P	Greenhouse-Geisser			Huynh-Feldt		
				Adj. d.f. 1 & 2	Adj. d.f. 2	Adj. P	Adj. d.f. 1 & 2	Adj. d.f. 2	Adj. P
Treat	2	1.867	0.267	1.334	2.667	0.292	2.000	4.000	0.267
Error	4								
Arm	1	4.743	0.161	1.000	2.000	0.161	1.000	2.000	0.161
Error	2								
Obs	1	9.608	0.0902	1.000	2.000	0.0902	1.000	2.000	0.0902
Error	2								
RM	2	6.732	0.0525	1.715	3.430	0.0662	2.000	4.000	0.0525
Error	4								
Treat × Arm	2	0.253	0.788	1.004	2.008	0.666	1.016	2.033	0.668
Error	4								
Treat × Obs	2	1.075	0.423	1.044	2.089	0.410	1.186	2.372	0.413
Error	4								
Arm × Obs	1	0.795	0.467	1.000	2.000	0.467	1.000	2.000	0.467
Error	2								
Treat × RM	4	0.318	0.858	1.701	3.402	0.717	4.000	8.000	0.858
Error	8								
Arm × RM	2	0.0329	0.968	1.652	3.305	0.949	2.000	4.000	0.968
Error	4								
Obs × RM	2	0.180	0.842	1.145	2.291	0.739	1.681	3.362	0.811
Error	4								
Treat × Arm × Obs	2	1.631	0.303	1.432	2.863	0.318	2.000	4.000	0.303
Error	4								
Treat × Arm × RM	4	0.350	0.837	1.410	2.820	0.667	3.779	7.559	0.828
Error	8								
Treat × Obs × RM	4	0.359	0.831	1.763	3.526	0.698	4.000	8.000	0.831
Error	8								
Arm × Obs × RM	2	0.223	0.810	1.011	2.023	0.686	1.046	2.093	0.692
Error	4								
Treat × Arm × Obs × RM	4	0.534	0.715	1.916	3.831	0.618	4.000	8.000	0.715
Error	8								