Quadrupedal dinosaurs did not evolve fully pronated forearms: New evidence from the ulna

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Therians (marsupials and placentals), archosaurs, and chameleons are remarkable in that they evolved postures and gaits with inturned forelimbs. However, recent studies have indirectly recognized that, unlike fully pronated therian and chameleon forearms, dinosaur forearms were mechanically constrained by semi-pronated (misaligned) joints. This has led to the hypothesis that quadrupedal dinosaurs mitigated this constraint via proximal migration of the radius, indirectly forming a more pronated, tubular manus distally. To test this hypothesis, a standardized pose was used to examine the forearm pronation of ornithischian dinosaurs that were obligatory quadrupeds and facultative bipeds. Results show that only restructuring of the distal, not the proximal radius, causes additional pronation of the pre-axial edge of the carpus, but also unexpectedly reveal that the ulna may help form a tubular manus by supinating the post-axial edge. Thus, relative to the plane of the elbow joint the wrist and finger joints remain wholly semi-pronated. These findings do not support the hypothesis that a tubular cross-section evolved in dinosaurs to pronate the manus further to allow the finger joints to participate in locomotion. Instead these results indicate that quadrupedal dinosaurs tended to abandon propulsive use of their wrist and finger joints by converting their carpus + metacarpus into a vertical stilt-like extension of the forearm. Prior studies have overlooked that this divergent path to parasagittal forelimb kinematics had its phylogenetic basis in the retention of the semi-pronated forearm joint alignment that is plesiomorphic to tetrapods. Thus, this test provides the first functional explanation for the convergent responses of quadrupedal archosaurs to their misaligned forearm joints, and provides a foundation for elucidating why the quadrupedal evolution of archosaur forelimbs diverged from those of therians and chameleons.

Key words: Archosauria, Dinosauria, Theria, Chamaeleonidae, locomotion, posture, functional morphology, biomechanics.

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Introduction

The postural and locomotor evolution of amniote limbs is typically characterized by convergence on increasingly aligned joint planes of action as the limbs inturn to the body wall (Romer 1956). However, archosaurs seemingly did not evolve wrist and finger joints that were mechanically aligned with the elbow joint (Figs. 1, 2). In contrast to fully pronated therians (marsupials and placentals) and chameleons, the incompletely pronated wrist and finger joints of archosaurs with inturned elbows would have ineffectually pushed inwards instead of backwards (Gasc 1963).

Bonnan (2003) recently hypothesized that phylogenetic migration of the radius to a flexor position in front of the ulna at the elbow joint (hereafter termed the radial hypothesis) mitigated the mechanical constraint of misaligned elbow and finger joints. Specifically, Bonnan (2003) reasoned that proximal radial migration directly caused the observed additional pronation of the distal radial epiphysis at the wrist in quadrupedal sauropodomorphs. Bonnan (2003) then argued that this radial re-orientation pronated the metacarpus into a compact tubular structure (i.e., at least 180° of curvature of the metacarpal cross section, bringing digit I into opposition to digit V; Senter 2011), consequently aligning the finger joints with the elbow joint. This hypothesis suffers from several problems because Bonnan (2003) formulated the radial hypothesis within a restricted phylogenetic context. A broader context reveals that: (i) proximal radial migration is common amongst tetrapods, including other archosaurs such as ornithischians, birds, and pterosaurs (Fig. 3), but; (ii) research shows that in

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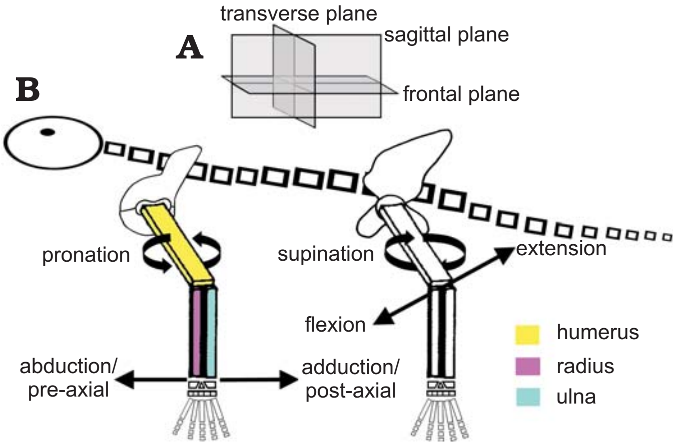

Fig. 1. An example of the stylized tetrapod skeleton and terminologies that are traditionally used to demonstrate the grades of forearm pronation. **A**. The three anatomical planes. **B**. Simplified tetrapod limbs with uniplanar joint alignments in the transverse plane, showing general limb terminology, including the directions required to pronate/supinate the limb segments, and thereby joint planes of action distal to these segments. Note that, like the hindlimb in this traditional characterization, the three major tetrapod forelimb bones are assumed to plesiomorphically lack any diaphyseal torsion or oblique planes of joint flexion/extension.

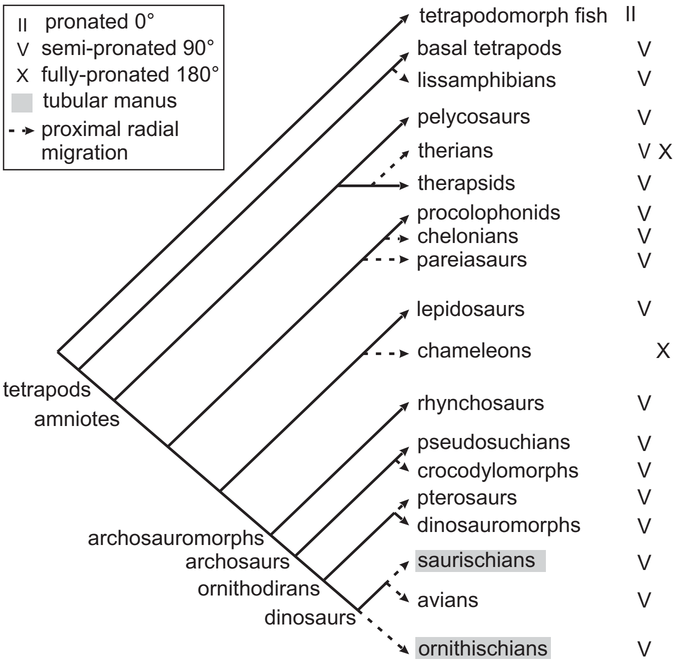

Fig. 3. The grades of forearm pronation, the incidence of tubular manual cross sections, and the prevalence of proximal radial migration overlaid onto a cladogram of major tetrapod clades. Note the isolated convergence upon tubular manual cross sections in non-avian saurischian and ornithischian dinosaurs. See Vialleton (1924) for reports of proximal radial migration in tetrapods. See text for a discussion of the reasoning that dinosaurs retained semi-pronation. Cladogram after Gauthier (1986).

other tetrapods, proximal radial migration is associated with the solidification of or even reversions to semi-pronation (90° of pronation of the wrist joint relative to the plane of the elbow joint; e.g., Fig. 4B), not increases in pronation (e.g., Zapfe 1979); (iii) Bonnan (2003) was not aware that the plesiomorphic grade of tetrapod forearm pronation is semi-pronation. Bonnan (2003) relied instead upon a suggestion that quadrupedal sauropodomorphs evolved an unspecified amount of additional pronation from an unpronated bipedal ancestor (Wilson and Sereno 1998). However, this assumption would have entailed a functionally improbable reversion to the unpronated forearm morphology of tetrapodomorph fish in the bipedal ancestors of quadrupedal dinosaurs (Fig. 3). Such a reversion would have revealed itself via dorsally facing palms in bipeds, and posteriorly directed manual digits (at least initially) in quadrupeds (compare to Fig. 5A). Neither of these conditions has ever been reported for an archosaur. Despite

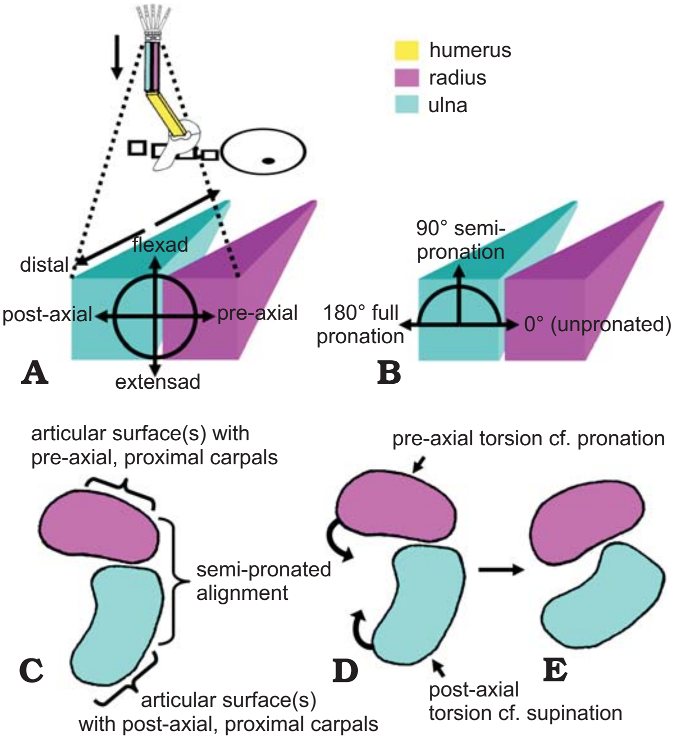

Fig. 2. Generalized shape and articular relations of left distal tetrapod radial and ulnar epiphyses in the position traditionally used in studies of dinosaurian pronation. **A**. Directional terminology; the skeleton is upside down to show the starting orientation most commonly used to assess grades of forearm pronation in distal view, the radius and ulna are depicted as bars in perspective here and in B to remove any association with a particular clade of tetrapods. **B**. The three phylogenetic grades of forearm pronation as conventionally viewed, i.e., due solely to reorientation of the distal radial epiphysis relative to an immobile, unchanging ulna. **C**. Stylized orientations of the distal radial and ulnar epiphyses of a semi-pronated archosaur with moderate elongation and torsion of the articular surfaces of the distal epiphyses with the carpus, illustrating the common elongation of their articular surfaces with the carpus into an arched cross section. **D**. Stylized demonstration of pre-axial torsion of the distal radial epiphysis in place coupled with post-axial torsion of the distal ulnar epiphysis in place. **E**. The end result of the coalescence of the extreme pre- and post-axial edges of the distal antebrachial epiphyses in D. The long axis of the humerus, which was used as a proxy for the plane of elbow joint flexion/extension, is vertical in all illustrations. Note that the articular contact between the radius and ulna, and therefore the middle of the plane of flexion/extension of the wrist joint, remain in a semi-pronated orientation, but the pre- and post-axial edges of the carpus and manus were dragged and collapsed into a tubular formation around that semi-pronated contact.

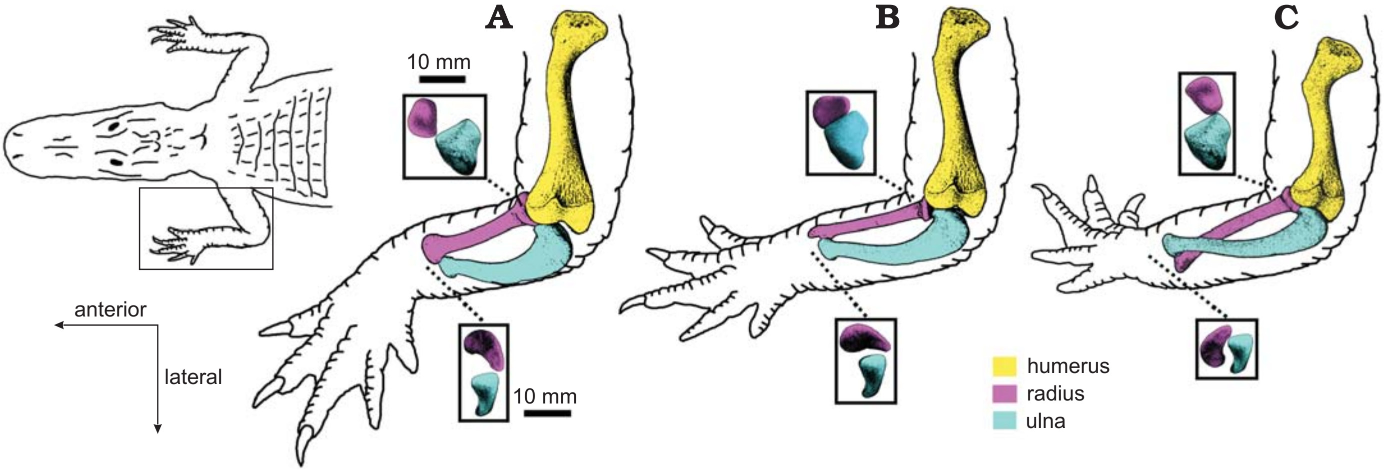

Fig. 4. A demonstration of the effects that changes in pronation of the distal radial epiphysis would have on manual orientation in a semi-pronated tetrapod (*Alligator mississippiensis* [Daudin, 1802]) that is using sprawling forelimb posture and kinematics. **A**. A forearm and manus forcibly unpronated (0°) to demonstrate the erroneous starting point of dinosaurian pronation according to Bonnan's (2003) radial hypothesis; this dislocation would orient the manual digits laterally in a sprawling forelimb. **B**. A naturally (for *A. mississippiensis*) semi-pronated (90°) forearm and manus, which orients the manual digits anteriorly in a sprawling forelimb. **C**. A forcibly fully pronated (180°) forearm and manus; this dislocation would orient the manual digits medially in a sprawling forelimb. In this and the following figure the upper row of boxes shows the radius and ulna in proximal view, while the lower row of boxes shows their positions in distal view. The orientations represented serve to demonstrate why stem tetrapods with laterally-directed forelimbs are assumed to have evolved semi-pronated forearm morphology from an unpronated morphology, in order to pre-axially rotate the wrist and finger joints 90° so that these joints could participate in locomotion via posteriorly directed flexion (Hutson 2010). Note also that, as a consequence of being a semi-pronated tetrapod, if an *A. mississippiensis* inturns its elbows to the body wall, then the manual digits will then point laterally (Vialleton 1924). Bonnan's (2003) radial hypothesis assumes that condition A was the starting point of quadrupedal dinosaur evolution instead of condition B; see text for further discussion. This and all subsequently figured *A. mississippiensis* forelimb elements are from the left forelimb of a juvenile specimen (FMNH 284695).

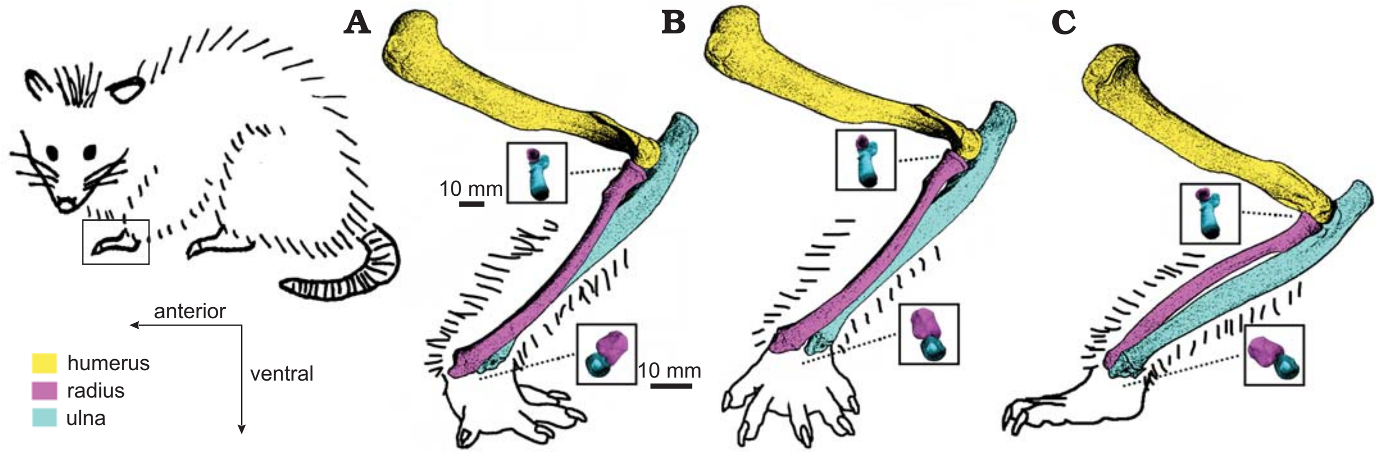

Fig. 5. A demonstration of the effects that changes in pronation of the distal radial epiphysis would have on manual orientation in a fully pronated tetrapod (the Virginia opossum *Didelphis virginiana* Kerr, 1792) that is using parasagittal forelimb kinematics with elbows inturned to the body wall. **A**. An unpronated forearm and manus, which if possible would point the manual digits posteriorly. **B**. A semi-pronated forearm and manus, which would point the manual digits laterally, analogous to many semi-pronated archosaurs, such as dinosaurs, that utilized quadrupedalism. **C**. A normal (for *D. virginiana*) fully pronated forearm and manus, which points the manual digits anteriorly. This demonstration illustrates why it was traditionally assumed that amniotes that evolve posteriorly directed elbows (i.e., archosaurs, therians and chameleons) would require an additional 90° of forearm pronation past the plesiomorphic 90°, because 180° of pronation is required to keep the wrist and finger joints aligned posteriorly during flexion, and therefore to continue operating in a parasagittal plane. Bonnan's (2003) radial hypothesis states that the radii of quadrupedal dinosaurs pronated to condition C, but the findings of this study show that the ulnae in these dinosaurs experienced an opposing supination that would have kept the planes of the wrist and finger joints wholly in condition in B, albeit with a tubular manus (e.g., Fig. 2E); see text for further discussion. The *D. virginiana* forelimb elements are from an adult specimen (FMNH 166984).

these and other problems (Bonnan and Yates 2007), the radial hypothesis has recently been extended to ornithischian dinosaurs that were obligatory quadrupeds, due to their convergence on proximal radial migration and a tubular manus with sauropodomorphs (Mallison 2010; Senter 2010, 2011).

The situation outlined above calls for a direct test of the grade of pronation of the distal radial epiphysis in ornithischians that evolved proximal radial migration (Fig. 3; Mallison 2010). Here, the osteological grades of forearm pronation in a representative sample of tetrapods were used to test whether ornithischian dinosaurs with obligatory quadrupedalism (stegosaurs, ankylosaurs, and ceratopsids) evolved additional pronation of the distal radial epiphysis past semi-pronation. This test was extended to facultatively bipedal ornithischian dinosaurs (basal iguanodontids and hadrosaurs) and compared to Bonnan's (2003) results for radial pronation in sauropodomorphs.

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

Material and methods

Specimens with well-preserved distal antebrachial epiphyses used in this study are listed in SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app60-Hutson_SOM.pdf. Humeral, radial, and ulnar elements were articulated in a standardized fashion to determine their degree of, and contribution to, osteological pronation of the forearm. To allow the grades of forearm and manual pronation in different tetrapod clades to be directly compared and contrasted, a model frequently used by human anatomists for illustrating the degree of pronation of the distal radial epiphysis was modified for use in other tetrapods (Morrey and Chao 1976). The articulated humeri, radii, and ulnae were positioned so that the long axis of the humerus was perpendicular to the horizontal (Fig. 2A), which represented a proxy for the plane of elbow joint flexion/extension. This procedure differed from that used in various prior studies, which utilized the more traditional approach of using the distal ulnar epiphysis as the sole frame of reference for radial orientation. However, it must be noted that the elbow's plane of joint action was not perpendicular to the horizontal, since tetrapod elbows are rarely, if ever, perfect uniplanar hinge joints (Hutson 2010). Because of the added difficulty in procuring, articulating, and positioning wrist elements in fossilized dinosaur specimens, the distal radial and ulnar epiphyses were used as a proxy for wrist and finger joint planes of action, which generally gives an accurate assessment of the grade of carpal/manual pronation due to the developmental alignment of the pre- and post-axial edges of the tetrapod forearm (Bonnan 2003). A sandbox or modeling clay was used to position one element in relation to another, depending on the size of the forelimb elements. The methodology for enhancing osteological detail in digital photographs of articulated forelimb elements was described previously (Hutson and Hutson 2013).

Comparisons of distal antebrachia in a standardized pose

Ankylosaur distal radial epiphyses.—Comparisons of articulated radii and ulnae in representative extant fully pronated (Fig. 6) and semi-pronated tetrapods (Fig. 7) were compared to those of ornithischian dinosaurs (Figs. 8, 9), archosauromorphs and basal archosaurs (Fig. 10), as well as pareiasaurs and various extinct synapsids (Fig. 11). Of the well-preserved ankylosaur forearm elements available (see SOM 1 for list of all non-illustrated specimens), only three forearms could be articulated (Figs. 8E, 9A, B), while another had matching contralateral distal epiphyses (Fig. 9D). Several of these elements had distorted diaphyses, but the outline of all distal radial epiphyses was generally uniform. Compared to other tetrapods, the distal radial epiphyses were most similar in morphology and orientation to certain pareiasaur distal radial epiphyses (e.g., Fig. 11A), which can also have a triangular outline with a flattened base extensad. Pareiasaurs did not evolve tubular manual cross sections or full pronation (Boonstra 1929, 1932). None of the distal radial epiphyses of these ankylosaurs exhibited pre-axial torsion similar to that of derived sauropodomorphs (Fig. 8A) that could explain the evolution of a tubular manus via the radial hypothesis (Senter 2011), although pre-axial elongation (expansion of the articular surfaces pre-axially) could not be ruled out. Otherwise, any pre-axial contribution to additional pronation, as exemplified by anurans (Ecker and Wiedersheim 1897; Schwarz 1935), or the formation of a tubular manus, could come from torsion of the carpus. Nonetheless, all radii retained a semi-pronated orientation that was flexad to their respective distal ulnar epiphyses. The other available ulnae also exhibited roughened, striated areas for interacting with radii in a semi-pronated orientation.

Ankylosaur distal ulnar epiphyses.—The distal ankylosaur ulnar epiphyses used in this study varied somewhat in outline in distal view (Figs. 8E, 9A, B, D, E), but all exhibited varying degrees of post-axial torsion into supination, as was reported previously by Moodie (1910). As in quadrupedal sauropodomorphs, the left distal ulnar epiphysis of the *Sauropelta edwardsorum* (AMNH 3032) specimen appeared to be melding post-axially and flexad with the radius (Fig. 8E; see also Currie et al. 2011: fig. $4C_4$). The recent finding that ankylo-

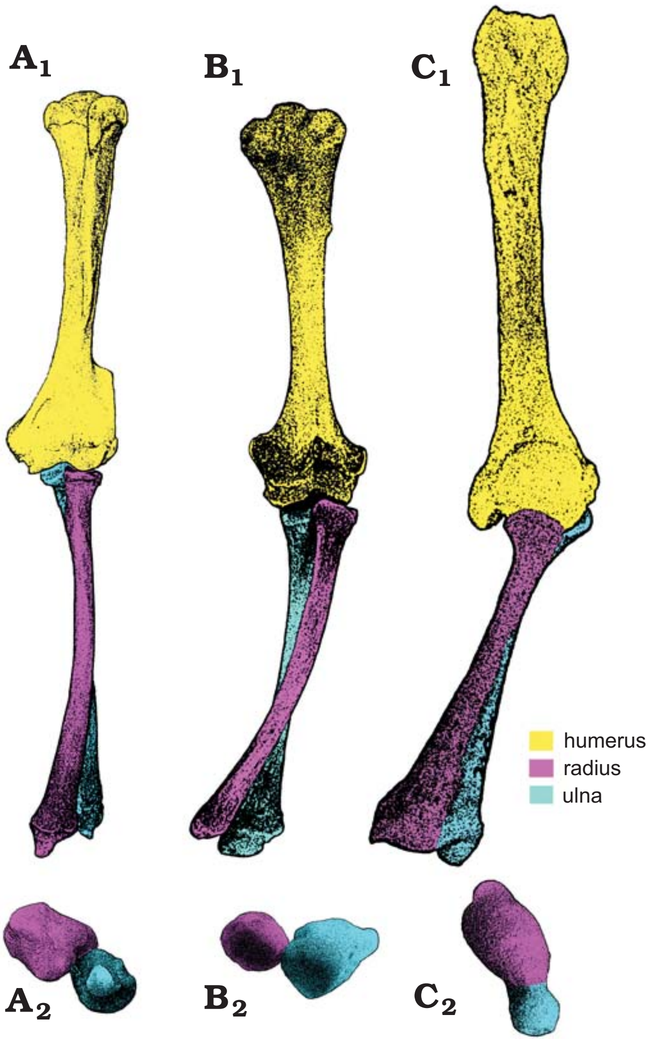

Fig. 6. Comparison of true standardized views of forearm pronation in tetrapods that have evolved a fully pronated manus, in flexor (A_1–C_1) and distal (A_2–C_2) views. **A**. A representative metatherian mammal (marsupial), Virginia opossum *Didelphis virginiana* Kerr, 1792 (FMNH 166984), oriented in a fully pronated orientation. **B**. A representative chameleon, *Furcifer pardalis* (Cuvier, 1829) (FMNH 250433). **C**. A representative anuran (toad), *Bufo blombergi* Myers and Funkhouser, 1951 (FMNH 210096). Flexor views are scaled to equal radial length; distal views are not to scale. The reader should note that the distal radial epiphyses of small therians and chameleons are often not located at exactly 180° of pronation relative to their ulnae, as it may not be necessary due to a crouching forelimb posture with moderately abducted elbows (Hutson 2010). Note also that, when present, the full pronation of an anuran manus is accomplished via carpal, not radial torsion (see Schwarz 1935: fig. 10), while the distal radial epiphysis remains in full contact with the plesiomorphically semi-pronated articulation (Ecker and Wiedersheim 1896).

saurs and sauropodomorphs converged upon the evolution of a tubular manus opens up the possibility that the convergence in ulnar torsion between these two clades may be correlated with the formation of a tubular manual cross section (Senter 2011).

Stegosaur distal radial epiphyses.—Only one stegosaur radius could be unequivocally paired with its matching ulna (Fig. 8C), but as demonstrated by the additional examples illustrated in Fig. 9N–Q, there is little morphological variation in the orientation of their distal radial epiphyses. Compared to derived sauropodomorphs, which often have distal radial epiphyses that extend pre-axially and extensad (Fig. 8A), the distal radial epiphyses of the stegosaurs examined all exhibit pre-axial elongation, i.e., swelling of their articular surfaces pre-axially. Although not as extensive as the distal radial re-orientations of neosauropods extensad (Fig. 8A), these characteristics might suggest that the evolution of a tubular manus in stegosaurs was caused solely by pre-axial elongation, rather than pre-axial torsion of the distal radial epiphysis. However, a stegosaur-like morphology of the distal radial epiphysis is also found in other tetrapods, including crocodilians (Fig. 7A), archosauromorphs (Fig. 10C), basal archosaurs (Fig. 10D, E), and all synapsid pelycosaurs examined (e.g., Fig. 11B). The latter tetrapods do not have tubular manual cross sections (Fig. 3), which indicates that a distal radial epiphysis that elongates and/or swells directly pre-axially does not necessitate the formation of a tubular manual cross section. Therefore, since the distal radial and ulnar epiphyses of all elements examined retain flattened, roughened articular contacts in a semi-pronated orientation, and the radius of the articulated specimen examined continues to contact the ulna in a semi-pronated orientation (Fig. 8C), stegosaurs appear to have retained a modified semi-pronated orientation of the distal radial epiphysis.

Stegosaur distal ulnar epiphyses.—When the distal antebrachial outline of an articulated stegosaur (Fig. 8C) is compared directly with those of neosauropods (e.g., Fig. 8A), the distal ulnar epiphyses of both clades are observed to have lost the pre-post-axially flattened morphology typical of other archosaurs (Figs. 7A, 10), in favour of a flattened flexoextensor morphology (Figs. 8C, 9R–U). Indeed, the distal ulnar epiphyses of stegosaurs and quadrupedal sauropodomorphs (Fig. 8A) seem to have converged upon additional post-axial torsion and/or elongation to meet the radius near the midline. Hennig (1925) recognized the peculiar morphology of the distal ulnar epiphyses in stegosaurs, and he hypothesized that it occurred to bring the ulna into firmer contact with the radius for support. Furthermore, Hennig (1925) stated that the flattened extensor surfaces of the distal radial epiphyses of stegosaurs (viz., *Kentrosaurus aethiopicus*) correspond to the distal ulnar surfaces, in essence causing them to coalesce. Notably, however, Hennig (1925) did not speculate on possible changes in digital ray alignment (i.e., supination of the post-axial digits) with this transformation in stegosaurs. Finally, Moodie (1910) stated that the distal ulnar epiphyses of *Stegosaurus* are straight, as compared to ankylosaurs. This statement was likely due to the reduction in the flattened, pre-post-axial cross section of stegosaurs (see Hennig 1925), as compared to ankylosaurs, which obscured the phyletic re-orientation of stegosaurian ulnae. These observations of the similarity between stegosaur and neosauropod ulnar cross sections suggest that the extreme amounts of re-orientation of the distal ulnar epiphysis in these clades may be correlated with the formation of a tubular manus.

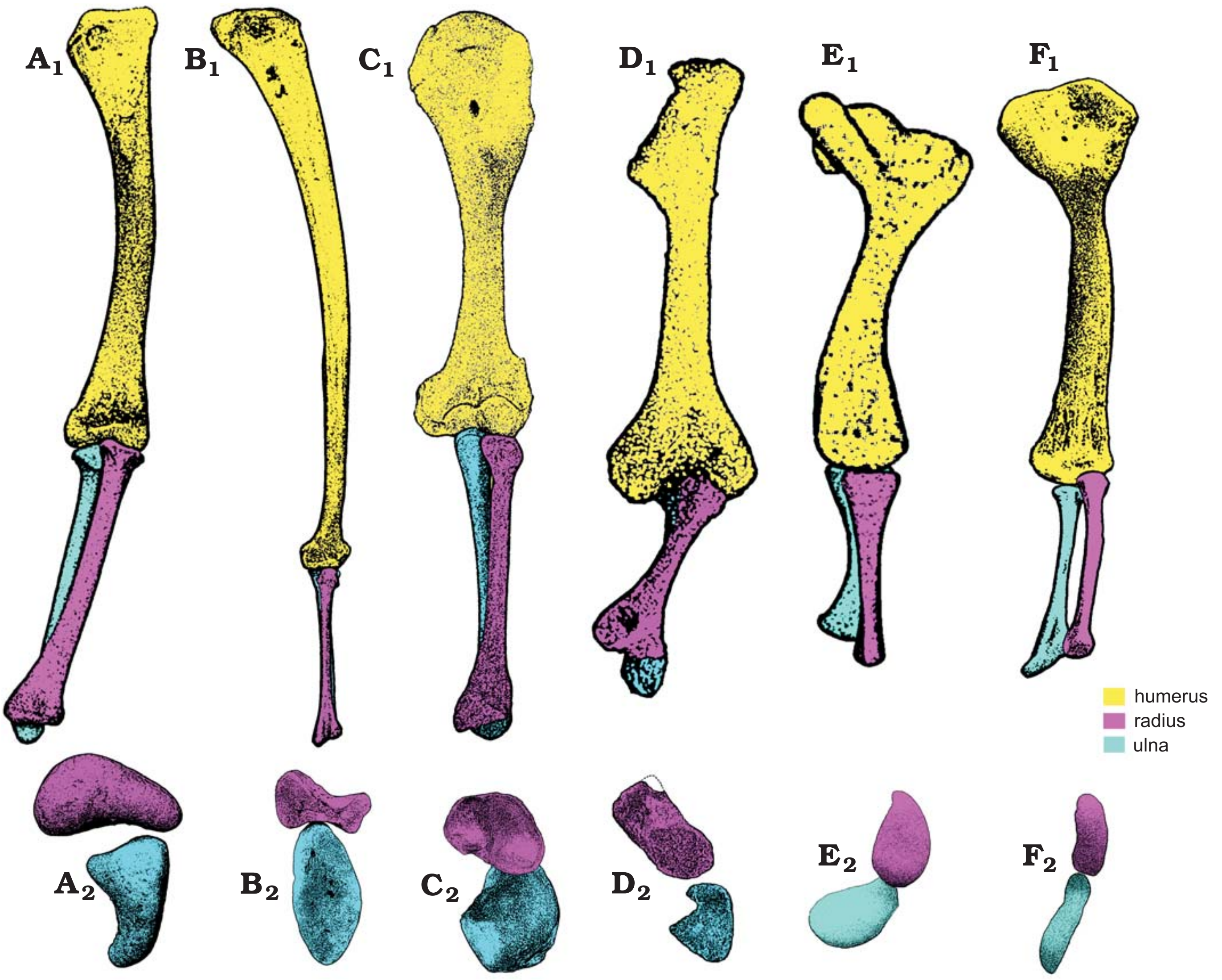

Fig. 7. Comparison of true standardized views of semi-pronated forearms in a representative sample of extant, nontherian tetrapods, in flexor (A_1–F_1) and distal (A_2–F_2) views. **A**. An allogatorid crocodilian, *Alligator mississippiensis* (Daudin, 1802) (FMNH 284695). **B**. A ratite bird, *Struthio camelus* Linnaeus, 1758 (FMNH 489294). **C**. A monitor lizard, *Varanus komodoensis* Ouwens, 1912 (FMNH 22197). **D**. A salamander, *Ambystoma tigrinum* (Green, 1825) (FMNH 22010). **E**. A semi-aquatic turtle *Apalone spinifera* (Lesueur, 1827) (HDW NIU 1086), reversed. **F**. A more terrestrial turtle, *Chrysemys picta* (Schneider, 1783) (INHS 23894). Reversed specimens in this and following figures refer to elements from the right sides that have been digitally flipped. Note that in E the radius and ulna are fused in the morphology shown, and that the humerus may not be rotated far enough to the left. Note also that, in vivo, articular cartilage and, in some cases wrist bones (e.g., intermedium), may separate the distal radial and ulnar epiphyses beyond what is pictured here for specimens C and F. Not to scale.

Ceratopsid distal radial epiphyses.—No matching fossil elements of ceratopsids were available for articulation and manipulation. However, the high-fidelity YPM 57489 casts made for Johnson and Ostrom’s (1995) study of forelimb posture in the MPM VP6841 *Torosaurus* cf. *latus* (Fig. 8D) were available for this study. The immobile DMNH WFQ: WRG94.014 cast made of the right forelimb of “Raymond”, the NSM PV-20379 *Triceratops horridus* found articulated in situ (Garstka and Burnham 1997; Fujiwara 2009) was also available for examination, as were the half-sized sculpted casts made of the CMN 41357 *Chasmosaurus irvinensis* (see Thompson and Holmes 2007). Despite modest pre-axial elongation, the distal radial epiphyses of ceratopsids clearly maintain semi-pronated articulations with their distal ulnar epiphyses, as shown in a distal view of the articulated YPM 57489 casts (Fig. 8D), and with isolated radial elements (Fig. 9F–I). Thus, the distal epiphyses of available ceratopsid radii were not found to extend pre-axially any further than are typically found in various tetrapods with semi-pronated distal radial epiphyses (e.g., Figs. 6C, 7D, 11C, D). This result indicates that large North American ceratopsids did not evolve additional amounts of holistic wrist or finger joint pronation from basal ceratopsians.

Ceratopsid distal ulnar epiphyses.—Notably, some basal ceratopsians, such as psittacosaurs, possess 25–45° of post-axial torsion of their distal ulnar epiphyses (Sereno 1987: 210–211), which indicates that this character may be plesio-

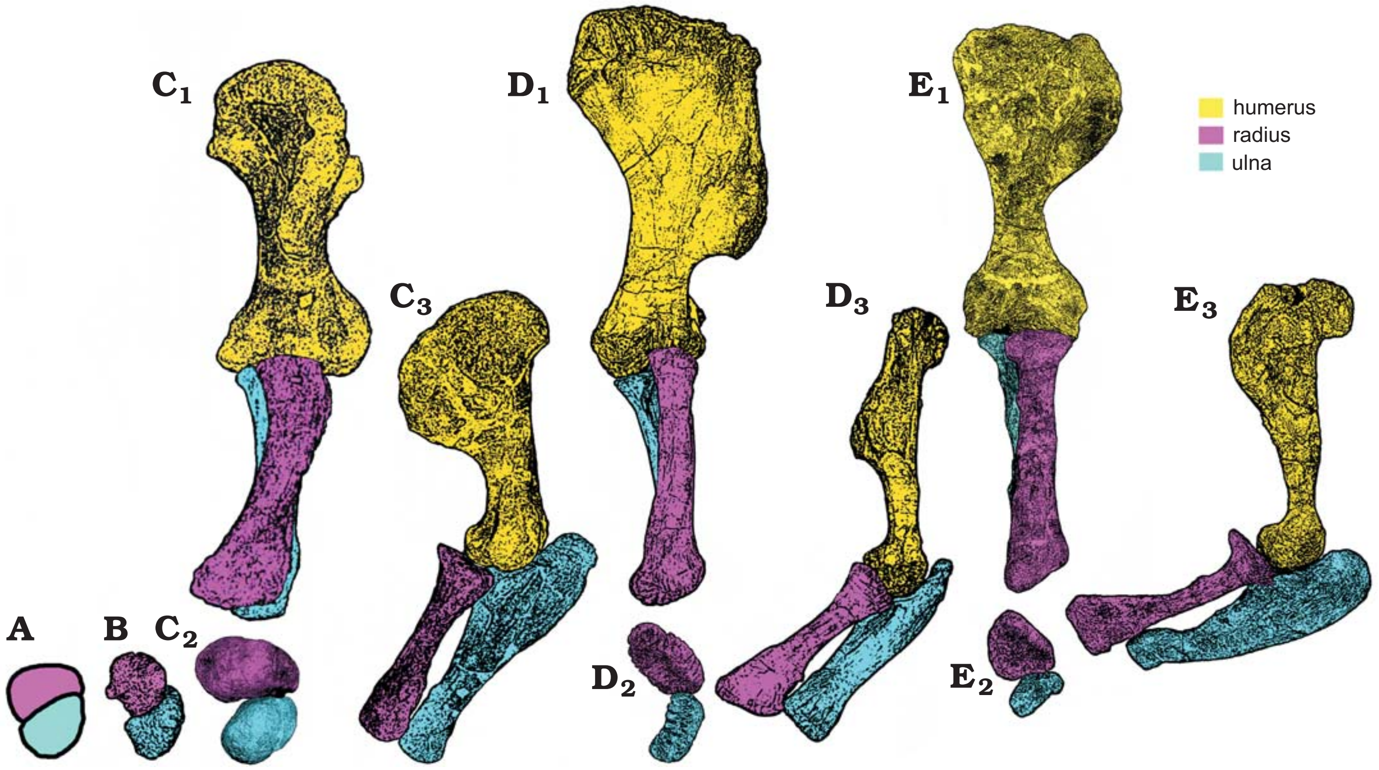

Fig. 8. Comparison of standardized views of semi-pronated forearms in ornithischian dinosaurs that utilized quadrupedalism. **A**. A tracing of a representative neosauropod sauropodomorph, *Apatosaurus excelsus* (Marsh, 1879) (YPM 1980), in distal view. **B**. A hadrosaur, *Edmontosaurus annectens* (Marsh, 1892) (USNM 3814), reversed, in distal view. **C**. A stegosaur, *Stegosaurus* sp. (USNM 11659), reversed, in flexor (C_1), distal (C_2), and pre-axial (C_3) views. **D**. A ceratopsid, *Torosaurus* cf. *latus* Marsh, 1891 (high fidelity YPM 57489 cast of MPM VP6841), reversed, in flexor (D_1), distal (D_2), and pre-axial (D_3) views. **E**. An ankylosaur, *Sauropelta edwardsorum* Ostrom, 1970 (AMNH 3032), in flexor (E_1), distal (E_2), and pre-axial (E_3) views. Pre-axial views are in full extension and scaled to equal radial length. Distal views not to scale.

morphic to ceratopsians. However, Paul (1987: fig. 3C) and Fujiwara (2009), when illustrating the level of pronation of the distal radial epiphyses of ceratopsids, made the distal ulnar epiphyses vertical in outline without any post-axial torsion into supination (contrast with Johnson and Ostrom 1995: fig. 12.6e). Here, by contrast, when articulated in a standardized pose all available ceratopsid ulnae in this study exhibited varying degrees of supination and/or modest post-axial elongation of their distal articular surfaces (Figs. 8D, 9J–M). The ceratopsid ulnae also exhibited a prominent rugose patch for articulation with the radius that may migrate slightly onto the post-axial edge (i.e., medially) of the distal ulnar epiphysis. The offset location of the articular surface in the high-fidelity YPM 57489 cast was corroborated by two distal ulnar epiphyses (USNM 6530) that were in perfect condition (Fig. 9J), which also drew attention to a second difference in interpretation with previous descriptions of the distal epiphyses of ceratopsid radii and ulnae.

The distal ulnar epiphysis illustrated by Fujiwara (2009) is flattened pre-post-axially. However, an examination of the DMNH WFQ: WRG94.014 cast of the NSM PV-20379 *Triceratops horridus* studied by Fujiwara (2009) indicated that the distal ulnar epiphysis of that specimen has been deformed pre-post-axially. This deformation only became apparent after the author had the opportunity to closely examine multiple distal ulnar epiphyses that are not deformed, such as the aforementioned USNM 6530 (Fig. 9J). This flattening not only hid the gentle post-axial torsion of the distal ulnar epiphysis of ceratopsids, but may also have hidden any signs of post-axial elongation of the extensor edge. Therefore, the L-shaped distal antebrachial cross section of Paul (1987) and Fujiwara (2009) need only be rotated as a unit post-axially until the distal ulnar epiphysis matches the morphology of the ulnae figured here in standardized poses. Thus, the distal antebrachial outline of large ceratopsids (which may have been evolving an incipient tubular manus; Fujiwara 2009) formed a gentle semi-pronated arch with contributions not only from pre-axial torsion/elongation of the distal radial epiphysis, but also a small amount of post-axial torsion/elongation from the distal ulnar epiphysis.

Basal iguanodontid distal radial epiphyses.—All observed distal radial epiphyses of tenontosaurs and camptosaurs appear to retain the plesiomorphic semi-pronated orientation and contact with their complementary ulnae, although some specimens of tenontosaurs exhibited marked post-axial inclinations into supination (Fig. 9AB), like those of various testudines (Fig. 7E, F).

Hadrosaur distal radial epiphyses.—Only three hadrosaur radii and ulnae could be assigned reliably to the same indi-

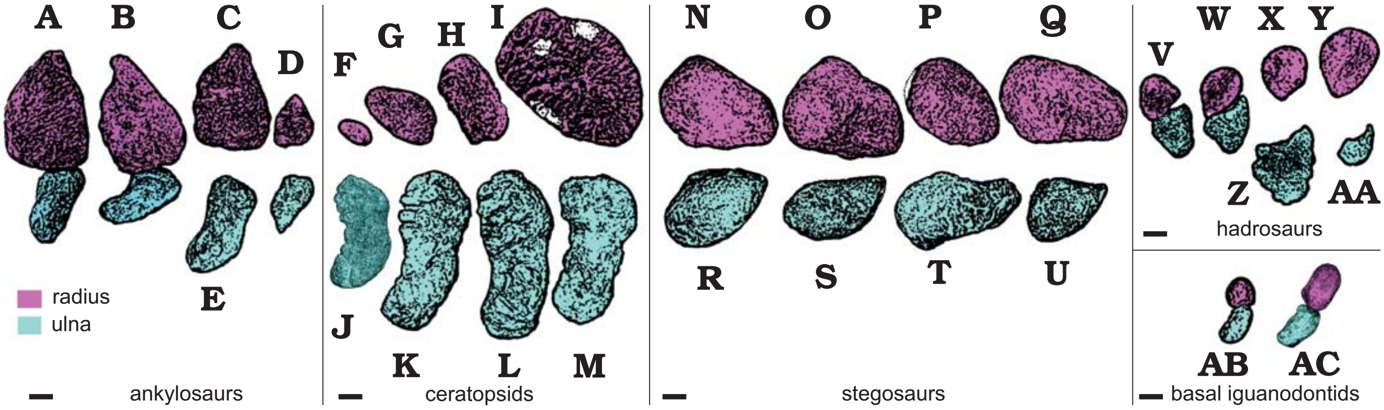

Fig. 9. Comparison of variation in the semi-pronated distal antebrachial epiphyses of select facultatively bipedal ornithischian dinosaurs and those with obligatory quadrupedalism. **A–C**. *Sauropelta edwardsorum* Ostrom, 1970. **A**. AMNH 3035. **B**. AMNH 3035, reversed. **C**. YPM 5338. **D**. *Texasetes pleurohalio* Coombs, 1995 (USNM 337987), radius reversed. **E**. *Panoplosaurus* sp. (YPM PU-21178 or 16970), reversed. **F**, **G**. *Centrosaurus* sp. **F**. Juvenile (TMP 94.12.798). **G**. TMP P81.19.292. **H–J**, **M**. *Triceratops* sp. **H**. Large ceratopsid (AMNH 5857), reversed. **I**. AMNH 5880. **J**. USNM 6530. **M**. FMNH 12003, reversed. **K**, **L**. *Triceratops horridus* Marsh, 1889. **K**. USNM 4842, reversed. **L**. USNM 4842. **N**, **P**, **Q**, **T**, **U**. *Stegosaurus* sp. **N**. USNM 4929. **P**. YPM 1854, reversed. **Q**. YPM 4835. **T**. YPM uncataloged, field number 9C-14-7J, reversed. **U**. USNM 7754. **O**, **R**, **S**. *Stegosaurus sulcatus* Marsh, 1887. **O**. YPM 4836, reversed. **R**. USNM 4937, reversed. **S**. YPM 4836, reversed. **V**. *Gilmoreosaurus mongoliensis* (Gilmore, 1933) (AMNH 6551). **W**. *Hypacrosaurus altispinus* Brown, 1913 (AMNH 5357), reversed. **X–AA**. Hadrosaurs. **X**. TMP 1981.29.2, reversed. **Y**. TMP 1981.41.13.7. **Z**. TMP 1980.29.101, reversed. **AA**. TMP 2005.09.84. **AB**. *Tenontosaurus* sp. (AMNH 3043). **AC**. *Camptosaurus* sp. (YPM 6794). In this and the following two figures radii and ulnae only touch if they are complementary; all others are oriented across from other elements in the standardized pose. Scale bars 30 mm.

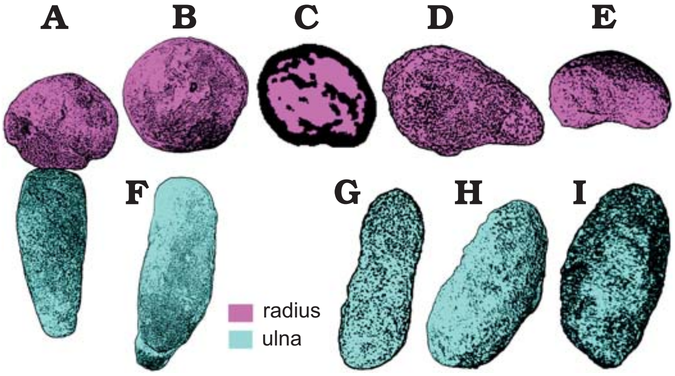

Fig. 10. A comparison of the semi-pronated distal antebrachial epiphyses of select archosauromorphs and basal archosaurs. **A**. Archosauromorph, *Trilophosaurus buettneri* Case, 1928 (TMM 31025-140), reversed. **B**, **F**. Phytosaur, *Machaeroprospus pristinus* (Mehl, 1928) (**B**, UCMP 121989; **F**, UCMP 121982). **C**. Phytosaur, *Heterodontosuchus ganei* Lucas, 1898 (USNM 2159). **D**. Aetosaur, *Typothorax coccinarum* Cope, 1875 (NMMNH L-5806). **E**. Rauisuchid, *Postosuchus alisonae* Peyer, Carter, Sues, Novak, and Olsen, 2008 (cast of UNC 15575). **G**. Aetosaur, *Typothorax antiquum* Lucas, Heckert, and Hunt, 2002 (NMMNH P-36075). **H**. Aetosaur, *Desmatosuchus haplocerus* Cope, 1892 (UCMP 25838). **I**. Rauisuchid, *Postosuchus kirkpatricki* Chatterjee, 1985 (TTU P9000). Phytosaur elements oriented after *M. pristinus* (UCMP 27235), aetosaur elements oriented after *T. coccinarum* (NMMNH L-5806). Note that nearly all specimens possess torsion of the distal ulnar diaphysis that effectively supinated the distal ulnar articular surface, and that most (except A, B) also exhibit pre-axial elongation of the distal radial epiphysis. Note also, however, that specimen A possesses distorted radial and ulnar diaphyses, so the orientation of the distal ulnar epiphysis may not be vertical as shown. Not to scale.

vidual: the USNM 3814 *Edmontosaurus annectens* (Fig. 8B), AMNH 5357 *Hypacrosaurus altispinus* (Fig. 9W), and AMNH 6551 *Gilmoreosaurus mongoliensis* (Fig. 9V). The right ulna of USNM 3814 was damaged proximal to its distal epiphysis, but this should not have affected the standardized pose. Both the right ulna and radius of AMNH 5357 have edges filled in with plaster in several locations, including the key area of the distal articular surface of the radius with the ulna, but as with USNM 3814, however, this did not obscure their overall articular relations in the standardized pose. As noted by Dilkes (1993), the distal radial epiphyses of hadrosaurs commonly bear a keel or flange where the interosseous ligament would have been located. Rasmussen (1998b) pointed out that some hadrosaurs lack this keel, and argued that the keel is an artifact of postmortem compression pre-post-axially. Inspection of a number of hadrosaur radii confirmed the presence of the keel, although it is much reduced in larger individuals (e.g., USNM 3814). The orientation of radii with elongated distal keels is with the keel extensad, which firmly places the radius within the pre-post-axial boundaries of the flexor concavity of the distal ulnar epiphysis. Moreover, various descriptions corroborate that the post-axial edge of this extensor keel has the majority of the striations and rugosities associated with close contact in the ulnar concavity for the radius (Lambe 1920). These features, plus the angle at which articulated hadrosaur radii leave the elbow joint when articulated with their complementary ulnae, result in an extensor keel directed slightly in the pre-axial direction. This orientation allows the roughened contact surface on the post-axial side of the keel to contact the raised post-axial rim of the ulnar concavity, which was higher than the pre-axial rim in all hadrosaur ulnae examined (Figs. 8B, 9V, W, Z, AA). Rasmussen (1997, 1998a, b, 1999) and Steeman (2001) investigated the question of whether iguanodontids and hadrosaurs evolved any additional pronation of the distal radial epiphysis, albeit without implicit recognition of the plesiomorphic nature of semi-pronation. Since the hadrosaur ulna evolved a raised rim directly post-axial

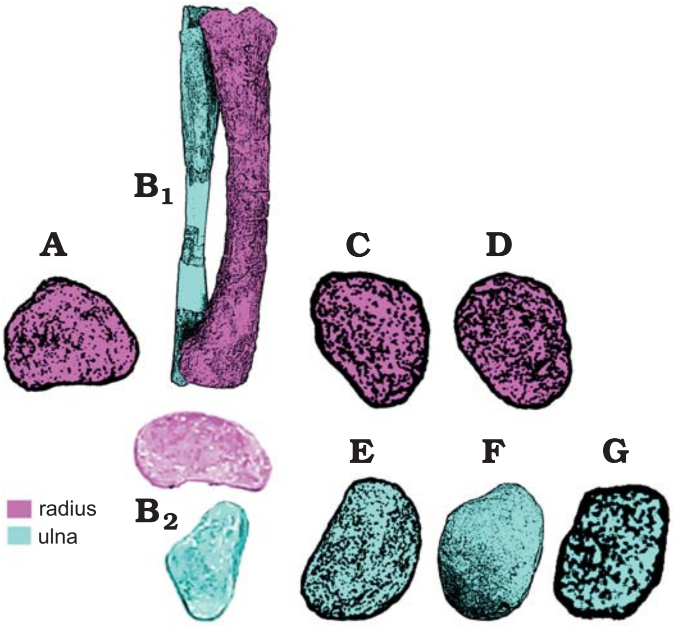

Fig. 11. A comparison of semi-pronated forearm views and distal antebrachial epiphyses of select pareiasaurs and synapsids. **A**. Pareiasaur, *Embrithosaurus schwarzi* Watson, 1914 (AMNH 2451), reversed. **B**. Pelycosaur, *Dimetrodon loomisi* Romer, 1937 (AMNH 21293), reversed, in flexor (B_1) and distal (B_2) views. **C**. Dinocephalian, *Moschops capensis* Broom, 1911 (AMNH 23930), reversed. **D**. Large dicynodont (AMNH 24096), reversed. **E**. Dinocephalian, *Jonkeria haughtoni* Broom, 1929 (AMNH 5577). **F**. Small dicynodont (uncataloged USNM), reversed. **G**. Dicynodont, *Kannemeyeria simocephalus* Weithofer, 1888 (AMNH 5591-93). Note that all specimens examined of the clades above possessed similar amounts of post-axial torsion of the distal ulnar diaphysis. Specimen in A oriented after *Bradysaurus baini* Seeley, 1892 ([FMNH] UC 1533 and UC 1525); specimens in C, F, and G after small dicynodonts *Diictodon* cf. *grimbeeki* (Broom, 1935) (USNM 412381 and USNM 452057). Not to scale.

to the radius, these findings corroborate Rasmussen's (1997) conclusion that the distal radial epiphysis in derived iguanodontids and hadrosaurs was shifted pre-axially into additional pronation relative to the distal ulnar epiphysis, analogous to neosauropods (Fig. 8A). Additionally, various articulated specimens and mummies (e.g., AMNH 5060) articulated in situ all display a distal radial epiphysis that has been shifted pre-axially into a slight amount of additional pronation. A detailed illustration in flexor view of this change in pronation at the wrist of of hadrosaurs was unrealizable with the specimens available, but an excellent photograph is shown in Parks (1920: pl. 8: 2).

Basal iguanodontid and hadrosaur distal ulnar epiphyses.—Basal iguanodontids (Fig. 9AB, AC) typically possess significant amounts of post-axial torsion into supination of their distal ulnar epiphyses, similar to that of testudines (Fig. 7E, F). Hadrosaurs, but also the derived iguanodontid *Ouranosaurus nigeriensis* (Rasmussen 1997), appear to have converged closely upon the distal antebrachial morphologies of quadrupedal sauropodomorphs. For the distal ulnar epiphysis, this means that the articular surface of the ulna in hadrosaurs exhibits extensive post-axial torsion and elongation (Fig. 8B), to the point that the ulna meets and cups the radius flexad, as in sauropodomorphs (Fig. 8A). Thus, as with thyreophorans and quadrupedal sauropodomorphs, in all specimens of hadrosaurs examined the post- and preaxial edges of the forearm look like two rays that have folded together, maintaining their semi-pronated origination as a vertex (compare with Fig. 2D, E).

Phylogenetic implications for studies of the forelimb in archosaurs

Radial versus vertical-support hypothesis for a tubular manus.—This study verifies prior reports that hadrosaurs evolved additional pronation of the distal radial epiphysis analogous to that of sauropodomorphs (Rasmussen 1997). However, the use of a standardized pose unexpectedly revealed that many tetrapods both extinct and extant (Fig. 10), possess distal ulnar epiphyses that are substantially torqued post-axially into supination. This supination markedly affects the cross section of the antebrachiocarpal region, and therefore may also affect the cross section of the carpus + metacarpus. Hitherto, this information has not been considered in relation to the grade of pronation of the entire wrist joint, nor all of the finger joints.

Previous work on facultatively bipedal ornithischians suggests that distal ulnar orientation may affect the grade of wrist and finger joint pronation. Rasmussen (1998b) agreed with Forster (1990) that the distal ulnar epiphyses of the basal iguanodontid *Tenontosaurus tilletti* (compare to Fig. 9AB) are supinated in place approximately 35°. Like other iguanodontids, *Tenontosaurus tilletti* has been shown to have evolved stiffening adaptations of the forelimb, presumably in response to facultative bipedalism (Forster 1990), as did *Camptosaurus* sp. (Carpenter and Wilson 2008), which have comparable values of torsion in their distal ulnar epiphyses (Fig. 9AC). Additionally, the phenomenon of marked supination of the distal ulnar epiphysis is found in other basal iguanodontids, such as in *Dryosaurus* sp. (Galton 1981: fig. 8S), basal bipedal ornithopods such as *Hypsilophodon foxii* (Galton 1974: fig. 40F), and even in early bipedal ornithischians such as *Heterodontosaurus tucki*, which is reported to possess 20–30° of torsion of the distal ulnar epiphysis (Santa Luca 1980: 177). Although Forster (1990) and Carpenter and Wilson (2008) reconstructed the carpi of tenontosaurs and camptosaurs, respectively, with arched cross sections, the relative contributions of radial and ulnar torsion to these arches and structural support were not addressed. Regardless, this correspondence in ulnar torsion indicates that supination of the distal ulnar epiphysis was widespread amongst ornithischians, and may even be plesiomorphic; various quadrupedal archosauromorphs and basal archosaurs also possessed this character (Fig. 10). Since Hennig (1925) suggested that coalescence of the distal antebrachial epiphyses was correlated with support, subsequent work has provided supportive evidence for this viewpoint.

When combined with available evidence on the biomechanics of the manus and antebrachiocarpal region of dinosaurs, the ulnar evidence presented here offers strong support for an alternative hypothesis that was also considered by Bonnan (2003), namely that a tubular manual cross section was a structural adaptation to support weight vertically. Notably, this vertical-support hypothesis has been paralleled by hadrosaur researchers as well, who, unlike Bonnan (2003), connected it indirectly with semi-pronation. Dilkes (1993, 2001) calculated that the cylindrical metacarpal cross sections of hadrosaurs (and therefore the cylindrical cross section of the distal antebrachial epiphyses) are biomechanically adapted to resist the torque engendered by increased bending stresses in a vertical, semi-pronated stance (see also Rasmussen 1998b; Steeman 2001).

Entaxony.—In relation to his radial hypothesis, Bonnan (2003) reasoned that the entaxonic (more robust pre-axial digits) manus of sauropodomorphs was related to propulsive use of their enlarged pre-axial digits, which he argued had been pronated by the distal radial epiphysis for this function. Thus, Bonnan's (2003) argument focused primarily on whether the planes of finger joint flexion/extension of the pre-axial edge of the manus were reoriented to flex posteriorly. However, Bonnan's (2003) radial hypothesis does not address the problem that, since dinosaurs did not reduce contact between the ulna and carpus (as therians did), the distal ulnar epiphysis and the post-axial edge of the carpus + manus would not have pronated along with the radius and pre-axial edge. Moreover, as noted previously by Dilkes (2001), collapse of the antebrachiocarpal region from a planar to a columnar cross section would have served to reduce the effectiveness of wrist joint flexion/extension for propulsion. Additionally, various quadrupedal dinosaurs trended towards hyperextension and reduction of the manual digits (Weems 2006), or even complete loss of the manual digits in some derived neosauropods (Fowler and Hall 2010), which would also have rendered them less effective for propulsion (Senter 2010, 2011). Finally, a tubular manus supinates the post-axial digits so far that they cannot possibly function in posteriorly directed propulsion. Again, the results of this study, which document an opposing torsion of the distal ulnar epiphysis, offer supportive evidence for an alternative hypothesis for the evolution of a tubular manus, namely that it evolved for vertical structural support (Bonnan 2003). In the latter hypothesis, all reorientations in the antebrachiocarpal area that collapse this region into a cylinder of bundled metacarpals and/or a tubular cross section can be viewed as distal adaptations for strength and reduction in mobility, as has been previously documented for the proximal radioulnar joints (Bonnan 2003; Mallison 2010).

Implications for a tubular manus in hadrosaurs.—The remarkable convergence of hadrosaurian and sauropodomorph distal antebrachial morphologies invites the question of whether hadrosaurs also evolved a tubular manual cross section. Rasmussen (1997, 1998b) and Steeman (2001) agreed with Dilkes (1993, 2001), who argued that the cylindrical metacarpal cross section of hadrosaurs was an adaptation to resist the stresses of standing and moving on a semi-pronated manus. These workers did not discuss the possible role of distal antebrachial torsion/elongation in connection with the formation of an arched manual cross section in hadrosaurs, likely because Bonnan (2003) had not yet published his radial hypothesis. However, it is important to note that the proximal view of the cylindrical cross section (i.e., solid cylinder) of the hadrosaurian metacarpus studied by Dilkes (2001) becomes a tubular cross section (i.e., hollow cylinder) if the outline of the missing fifth metacarpal is added (Gilmore 1924: 21). The fifth metacarpal of hadrosaurs is torqued into supination relative to the other metacarpals, so that it flexes in opposition to them (Rasmussen 1998a: 94–95). A hadrosaur wrist joint (TMP 1984.36.39) fully articulated in situ indicates that metacarpal V is directly distal to the most post-axially torqued section of the distal ulnar epiphysis, suggesting that the post-axial torsion of the distal ulnar epiphysis in hadrosaurs may be correlated with the evolution of a tubular manual cross section. The correspondence in the pre- and post-axial rays of the metacarpals of quadrupedal sauropodomorphs (Bonnan 2003), stegosaurs (Senter 2010), and ankylosaurs (Senter 2011) with coalescing distal antebrachial epiphyses lends credence to this hypothesis, because, unlike in therians, direct articulation between the ulna and carpus was not attenuated in dinosaurs (Carpenter et al. 1994).

Concluding remarks

The knowledge that dinosaurs retained wholly semi-pronated wrist and finger joints offers a revised evolutionary picture of their secondary reversions to quadrupedalism. Weems (2006) argued that a vertical metacarpus with hyperextended fingers was used during quadrupedalism by certain saurischians. The pronation information presented here indicates that his hypothesis should be modified and extended; dinosaurs that reverted to quadrupedalism tended to abandon propulsive use of their semi-pronated and therefore functionally ineffective wrist and finger joints, in favour of a stiffened antebrachiocarpal region and a vertical metacarpus. This postural option was also presumably adopted by crocodilians (see Hutson and Hutson 2014 and references therein), which implies that quadrupedal archosaurs responded to the semi-pronation constraint in similar ways. Therefore, these convergences may reveal a major difference between the quadrupedal evolutions of archosaurs and amniotes that did evolve full pronation, namely therians and chameleons.

To date, the vast majority of studies on archosaurian forelimb posture and gait have focused on limb bone scaling, trackways, and musculature, rather than on joint planarity. This is despite the fact that accurate osteological assessments of wrist and finger joint pronation are critical to studies of tetrapod forelimb posture and locomotion (Bonnan 2003). Further progress is contingent upon a deeper understanding of the evolutionary responses of amniote forelimbs during transitions to more derived postures and gaits. Unfortunately, pronation research has suffered from a lack of awareness that semi-pronated forearm anatomy is plesiomorphic to Archosauria, and indeed all tetrapods. Until now this lack of awareness has prevented anyone from asking why archosaurs, unlike therians and chameleons, did not evolve fully pronated forearms; a topic to be explored in future studies of how the seemingly detrimental retention of semi-pronation affected the evolution of terrestrial members of Archosauria.

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