

# Zitteliana

An International Journal  
of Palaeontology and Geobiology

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für Paläontologie und Geologie

28



DAVID W. E. HONE & ERIC BUFFETAUT (Guest Editors)

**Flugsaurier: pterosaur papers in honour of  
Peter Wellnhofer**

München 2008

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## B28

DAVID W. E. HONE & ERIC BUFFETAUT (Eds)

### Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

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**Cover Illustration:** Modell eines *Rhamphorhynchus* aus dem Oberjura von Eichstätt. Entwurf: P. Wellnhofer, Modell: R. Liebreich,  
Foto und Collage: M. Schellenberger, L. Geißler, BSPG München.

**Umschlagbild:** Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer;  
design: R. Liebreich; photograph and collage: M. Schellenberger, L. Geißler, BSPG Munich.

# Morphological evolution of the wing of pterosaurs: myology and function

By  
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## Abstract

The musculature of the forelimb of a representative large pterodactyloid pterosaur (*Anhanguera*) is reconstructed in order to examine the function of those muscles that might shed light on the evolution of the pterosaur wing. The reconstruction suggests that during the evolution of the pterosaur wing, digit IV did not rotate about its long axis such that extensor muscles spread the wing and flexor muscles folded it, but rather the range of motion of the metacarpophalangeal joint of digit IV migrated posteriorly so that flexor muscles spread the wing and extensor muscles folded it. Thus the function of the flexors and extensors of digit IV may be thought of as having been reversed. A morphological scenario for the evolution of the pterosaur wing is proposed, according to which the evolving pre-pterosaur would not have passed through non-adaptive stages, whereas any scenario involving a rotation of digit IV about its long axis would have required that the evolving pre-pterosaur pass through non-adaptive stages. The proposed scenario also explains the anteriorly directed orientation of digits I–III and the loss of the fifth phalanx of digit IV in pterosaurs.

**Key words:** Pterosauria; *Anhanguera*; myology; wing; evolution.

## Kurzfassung

Die Muskulatur des Vordergliedmaßen eines typischen Vertreters der Groß-Pterodactyloidea (*Anhanguera*) wird rekonstruiert, um die Funktion jener Muskeln zu untersuchen, die Aussagen zur Evolution des Flugsaurier-Flügels ermöglichen könnten. Die Rekonstruktion lässt darauf schließen, dass während der Evolution der Flugsaurier-Vorderextremität sich der Flugfingers nicht um seine Längsachse drehte, so dass die Extensormuskeln den Flügel aufspannten und die Flexormuskeln ihn falteten. Statt dessen war der Bewegungsbereich des Metacarpophalangeal-Gelenks des Flugfingers nach rückwärts verlagert, so dass die Flexormuskeln den Flügel ausbreiteten und die Extensormuskeln ihn falteten. Die Funktion der Flug-

finger-Flexormuskeln und der Flugfinger-Extensormuskeln muss also umgekehrt gesehen werden. Ein morphologisches Szenario für die Evolution des Flugsaurier-Flügels wird vorgeschlagen: Demnach ist eine Evolution der Pro-Flugsaurier über nicht-adaptive Stadien, die bei Annahme einer Rotation des Flugfingers um seine Längsachse erforderlich wären, auszuschließen. Das vorgeschlagene Szenario erklärt auch die nach vorne gerichtete Orientierung der Finger I–III und den Verlust der fünften Phalanx des Flugfingers.

**Schlüsselwörter:** Pterosauria; *Anhanguera*; Myologie; Flügel; Evolution.

## 1. Introduction

The forelimb of pterosaurs was highly modified for flight and consisted of: a robust humerus with a large deltopectoral crest; elongate radius and ulna; most carpals fused into two large complex syncarpals; a strut-like preaxial carpal supporting a medially directed pteroid bone (BENNETT 2001, 2007a); and a manus with digits I–III moderately sized and consisting of 2, 3, and 4 phalanges, respectively, with strongly curved unguals, and digit IV much larger with four hyperelongate phalanges, lacking an ungual, and folding posteriorly. The moderate size, presence of unguals, and arrangement such that they flexed anteriorly in flight position permitted digits I–III to be used for quadrupedal locomotion (BENNETT 1997a; UNWIN 1997) and presumably for climbing, whereas the large size, great length, and unconventional arrangement such that it swung backward in flight position enabled digit IV to spread and support the wing yet fold it out of the way when the animal was not flying. Such an arrangement of fingers with one swinging away from the others is unique among vertebrates.

Little or no work has been done toward understanding how the pterosaur manus and its backward folding wingfinger evolved. The most common interpretation seems to be that digit IV rotated about its long axis so that the homological flexor side of digit IV faced posteriorly while the flexor side of digits I–III faced anteriorly, which would have enabled digit

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IV to flex backward for convenient wing folding; however, that interpretation has rarely been stated in print. BENNETT (1991, 2001) suggested that the orientation resulted from a  $\sim 180^\circ$  rotation of digit IV about its long axis, but did not discuss how that might have evolved. PETERS (2002) proposed that a  $90^\circ$  rotation of the wing metacarpal evolved in the nonvolant ancestors of pterosaurs in order to permit finger wagging as an intraspecific display. However, although rotation of the wing metacarpal may seem acceptable when considering only the skeletal elements of the forelimb, advocates of rotation have not considered how rotation would have affected the soft tissues of the antebrachium and manus.

Because reconstructions of the pectoral musculature of representative pterosaurs provided important insights into the evolution of the advanced pectoral girdle of the Dsungaripteroidea (BENNETT 2003), it seemed likely that reconstruction of pterosaurian forelimb musculature would provide important insights into the evolution of the pterosaur forelimb. Unfortunately, little work has been done on reconstructing pterosaur wings muscles. SHORT (1914) reconstructed two muscles: a ‘pteroid muscle’ originating from the side of the humerus from deltopectoral crest to lateral epicondyle, passing over the pteroid, inserting on the wing metacarpal, and acting as the primary extensor of the wrist; and a ‘knuckle extensor’ originating from much the same part of the humerus and inserting on the extensor tendon process of the first wing phalanx. BRAMWELL & WHITFIELD (1974) reconstructed *m. triceps*, *m. biceps*, and *m. brachialis*, modified SHORT’s pteroid muscle as originating from the body wall and inserting on the pteroid without passing on to the wing metacarpal and so acting to spread the propatagium, and repeated SHORT’s digit extensor with a reduced area of origin on the humerus. WELLNHOFER (1991a) reconstructed the pteroid muscle as originating from the scapulocoracoid and spreading the propatagium, and repeated BRAMWELL & WHITFIELD’s digit extensor from the distal humerus to the extensor tendon process of the first wing phalanx. FREY et al. (2006) reconstructed *m. triceps*, *m. biceps*, a *m. tensor propatagialis* spreading the propatagium, and five flexors and extensors of the wrist and wingfinger in *Muzquizopteryx* based on preserved tendons and traces of soft tissues. Given those few incomplete reconstructions of forelimb musculature, it was decided to reconstruct all forelimb musculature of *Anhanguera* based on comparisons of the forelimb bones and their muscle attachment scars, as well as those of the closely related *Pteranodon*, with the known osteology, myology, and osteological correlates of soft tissues in the closest living relatives of pterosaurs (i.e., the Extant Phylogenetic Bracket method; WITMER 1995). This reconstruction is an extension of the previous reconstruction of the pectoral musculature of *Anhanguera* (BENNETT 2003).

The use of the Extant Phylogenetic Bracket method is complicated in this case by two things. Firstly, the relationship of the Pterosauria to other diapsids is not clear. It is generally accepted that the Pterosauria were the major sister-group of the Dinosauria (PADIAN 1984; SERENO 1991; BENTON 1999; HONE & BENTON 2007); in which case their closest extant relatives would be crocodylians and birds. However, I presented a phylogenetic analysis that suggested that the Pterosauria were basal archosauromorphs (BENNETT 1996), in which case their closest extant relatives would be lepidosaurs and crocodylians,

and others have also placed the Pterosauria far from the Dinosauria (PETERS 2000; UNWIN 2000; RENESTO & BINELLI 2006). My phylogenetic analysis has been criticized and dismissed as relying in *a posteriori* recoding of characters (BENTON 1999; BROCHU 2001; HONE & BENTON 2007), and this has allowed authors to ignore my argumentation about the suite of hind-limb characters that alone support the placement of pterosaurs as the sister-group of dinosaurs. No one has noted that had I simply argued on the morphological grounds discussed in my paper that the characters were not homologous in pterosaurs and dinosaurs, coded them as such, and presented my analysis, then there would have been no *a posteriori* recoding and no excuse to ignore my argumentation. Based on my analysis, I still prefer the interpretation of the Pterosauria as basal archosauromorphs to that of the Pterosauria as the sister-group of the Dinosauria. The second complication is that the avian manus has been profoundly modified and reduced from a pentadactyl pattern in order to adapt it to flight, which in many cases prevents unequivocal inference of character states at the outgroup node if pterosaurs are the sister-group of dinosaurs. Given my preference for the alternative interpretation and the problems that would result from using avian character states to infer pterosaurian character states, the following muscle reconstruction is based on the interpretation of the Pterosauria as basal archosauromorphs. However, I will note where the different interpretations of relationship would affect the reconstruction, and will refer to “basal archosauromorph pterosaurs” and “dinosaur sister-group pterosaurs” in order to differentiate between the two different interpretations of pterosaur relationship.

**Institutional Abbreviations:** AMNH – American Museum of Natural History, New York; BSP – Bayerische Staatssammlung für Paläontologie und Geologie, Munich; KUVV – Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence; LACM – Natural History Museum of Los Angeles County, Los Angeles; NSM – National Science Museum, Tokyo; and YPM – Peabody Museum of Natural History, Yale University, New Haven.

## 2. Methodology

The Extant Phylogenetic Bracket method (WITMER 1995) relies on the association between soft tissues (e.g., muscles) and their osteological correlates (e.g., processes and muscle scars) in the extant relatives of the fossil taxon of interest to permit one to infer the presence of soft tissues in the fossil taxon from the presence of the osteological correlates. The character states of the closest extant relatives of the fossil taxon of interest are used to infer the character state of the most recent common ancestor of the extant taxa (at the bracket node), which is also an ancestor of the fossil taxon of interest. The character state at the bracket node is then used to infer the likely character state in the most recent common ancestor of the fossil taxon of interest and its closest extant relative (at the outgroup node), and that character state is applied to the fossil taxon of interest. Note that, depending on the character states in the extant taxa, the inference may be decisive or equivocal as to the character state at the outgroup node.

The reconstruction of the forelimb skeleton upon which muscles are reconstructed and illustrated will be described and discussed first, the processes and muscle scars on the bones of the forelimb of *Anhanguera* and *Pteranodon* will be described next, then the character states of the muscles that can be inferred from the character states found in the extant relatives of pterosaurs will be discussed, and lastly the inferred characters states of the muscles will be matched up with the processes and muscle scars. In my reconstruction of pectoral musculature (BENNETT 2003), I relied heavily on DILKES' (2000) reconstruction of *Maiasaura* musculature and his review of character states in *Maiasaura*'s extant relatives for information as to the character states in pterosaur relatives; however, DILKES reconstructed only a few forelimb muscles and omitted all intrinsic muscles of the manus, so information on characters states in extant reptiles and birds has been drawn from other sources (ABDALA & MORO 2006; BOJANUS 1819; BYERLY 1929; GEORGE & BERGER 1966; HOWELL 1936; MEERS 2003; RABL 1916; WALKER 1973; ZAAF et al. 1999). Note that the terms flex and extend are used only in their homological senses in this paper, except as specifically noted.

### 3. Reconstruction of the forelimb skeleton

The reconstruction of the forelimb skeleton of *Anhanguera* upon which muscles will be reconstructed and illustrated is based in large part on WELLNHOFER'S (1991b: Abb. 24) reconstruction of AMNH 22555, with additional information from *Santanadactylus araripensis* (BSP 1982 I 89, WELLNHOFER 1985), *S. pricei* (BSP 1987 I 1, AMNH 22552, WELLNHOFER 1985, 1991b), and various specimens of *Pteranodon* (BENNETT 2001). The reconstruction was updated to reflect the fact that the preaxial carpal articulated with a "sesamoid" anteriorly and with the pteroid bone medially (BENNETT 2006, 2007a). Two of the small metacarpals are short and do not reach the carpus, whereas a third is longer and articulates with the carpus. The latter metacarpal is generally interpreted as Mc III, but there is some uncertainty. WELLNHOFER (1985: Abb. 15) interpreted it as Mc I, but later (WELLNHOFER 1991b: Abb. 18, 31 and 38) as Mc III. In addition, in his Abb. 31 the longest metacarpal is dorsal to the other two, whereas in his Abb. 38 it is ventral to Mc I and II, and in his Abb. 35a he reconstructs digit I ventral to digit III. Unfortunately, the preserved positions of the metacarpals and digits in the concretions were neither described or illustrated, so there is no evidence which digit articulated with the longest metacarpal. Here it is assumed that the longest metacarpal was Mc III and that it was ventral to Mc I and II. Metacarpals I–III are usually found closely appressed to the anterior surface of Mc IV in articulated specimens of large pterodactyls (BENNETT 2001; WELLNHOFER 1991b: Abb. 38), and in those specimens in which Mc I–III are not closely appressed, their positions can be interpreted as resulting from gravity pulling the upper metacarpals away from Mc IV. The position of Mc I–III lying along the anterior surface of Mc IV is consistent with the interpretation that Mc IV supported the small metacarpals. Note that if Mc III was longer than Mc I and II, the length differences could be explained as a graded reduction in length from Mc I to Mc IV, or viewed

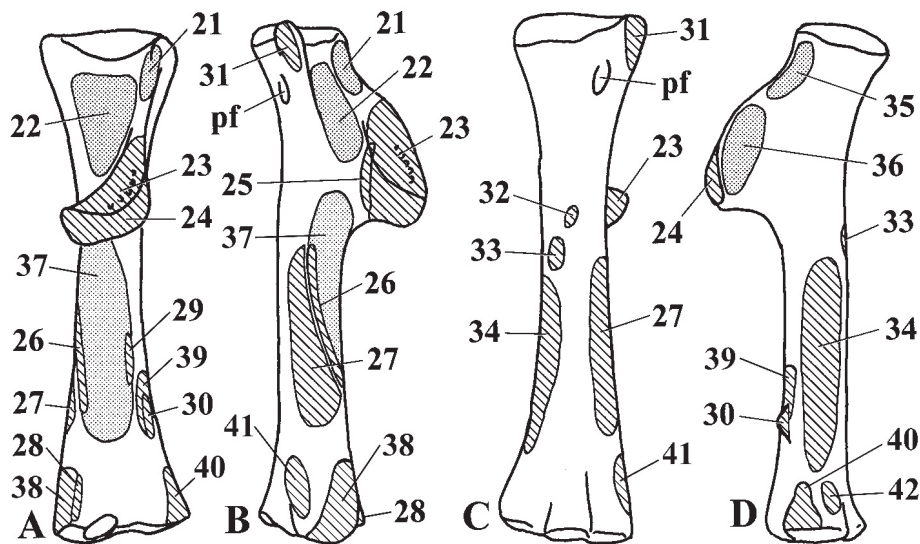
another way as a result of the hypertrophy of Mc IV tending to prevent reduction of Mc III. The further reduction of Mc III in *Pteranodon* presumably was because it too was bound to and supported by Mc IV.

### 4. Osteological correlates of muscles

Below, those bony processes and muscle scars that may have provided origins and insertions for forelimb muscles are reviewed. The morphology of a bone often changes markedly during ontogeny as it is remodeled due to the external forces applied to it and as processes and tubercles ossify (BRINKMAN 1988). Likewise, the appearance of muscle scars changes through ontogeny. On the immature bones of most specimens of *Anhanguera* a muscle scar may be a groove or a low ovoid elevation, whereas the scar in the same location on an adult specimen of *Pteranodon* will be a rugose ridge. In addition, in my earlier study of a large sample of *Pteranodon* (BENNETT 1993, 2001) it was noted that some muscle scars were present on almost all adult specimens, whereas other scars were present only on a small subset of adult specimens. I interpreted that subset as consisting of unusually old specimens, and interpreted the muscle scars, which consist of large areas of light scarring on the shafts of the humerus, radius, and ulna in areas where one would expect there to be fleshy origins of muscles, as the scars of fleshy muscle attachments. Thus, the presence of these scars suggests that there may be other fleshy muscle attachments that have left no scars at all on the available specimens, and dissections of extant vertebrates support this (HUTCHINSON 2001).

Information on muscle scars was drawn almost entirely from specimens of *Pteranodon* (BENNETT 2001) because *Anhanguera* specimens from the Santana Fm. all seem to be subadults or young adults, and so do not exhibit the profusion of muscle attachment scars on the bones of the antebrachium and manus that old specimens of *Pteranodon* do. Thus, the specimens described below are all *Pteranodon*, except as noted. BENNETT (2003) identified processes, muscles scars, and inferred areas of muscle attachment on the pectoral girdle and humerus of *Anhanguera* and numbered them 1–36. The previously assigned numbers will be retained, and additional features on the humerus and other wing bones will be numbered 37–67 in Figures 1 and 2 so as to avoid confusion.

**Humerus.** BENNETT (2003) described those osteological features associated with muscles of the pectoral region; therefore, only those features of the humerus associated with muscles of the wing are described below (Fig. 1). *Anhanguera* (AMNH 22552, NSM-PV 19892; KELLNER & TOMIDA 2000; WELLNHOFER 1991b) has a long shallow rugose groove (#26) running down the medial side of the shaft of the humerus. AMNH 22552 also has a small narrow rugose process (#28) on the ventral surface just proximal to the distal end of the humerus. Various specimens of *Pteranodon* (YPM 1175, 2606) have a larger area of scarring (#38) that extends posterodistally from #28 and covers the medial epicondyle. YPM 1175 also has an oval area of light scarring (#41) somewhat proximal and posterior to the epicondyle. *Anhanguera* (AMNH 22552) has two scars on the lateral side of the ventral surface of the shaft. One (#29) is a low oval rugose flange. The other (#30)



**Figure 1:** Left humerus of *Anhanguera* based on AMNH 22555 and BSP 1982 I 89 (WELLNHOFER 1985, 1991a) in ventral (A), posterior (B), dorsal (C), and anterior (D) views, showing muscle scars and other features (hatched) and inferred areas of muscle attachment (stippled). Identifications and/or inferred muscle attachments are as follows: 21 – *m. supracoracoideus* [I]; 22 – *m. coracobrachialis* [I] and possibly *m. humeroradialis* [O]; 23–25 – *m. pectoralis* [I]; 26, 29, & 37 – *m. brachialis* [O]; 27 – medial head of *m. triceps* [O]; 28 – *m. pronator teres* [O]; 30 & 39 – *m. supinator* [O]; 31 – *m. subscapularis* and *m. scapulohumeralis posterior* [I]; 32 – *m. teres major* [I]; 33 – *m. latissimus dorsi* [I]; 34 – lateral head of *m. triceps* [O]; 35 – *m. scapulohumeralis anterior* [I]; 36 – *m. deltoideus scapularis* [I]; 38 – *m. flexor carpi ulnaris* and *m. flexor carpi radialis* [O]; 40 – *m. extensor carpi ulnaris* and *m. extensor carpi radialis* [O]; 41 – *m. flexor digitorum longus* [O]; and 42 – *m. extensor digitorum longus* [O]. See text for description of the numbered features and inferred muscle attachments of wing musculature, and see BENNETT (2003) for discussion of pectoral musculature. Abbreviation: pf – pneumatic foramen.

is a more prominent flange, the supracondylar process, which is also present in other specimens of *Anhanguera* (NSM-PV 19892, BSP 1980 I 43, BSP 1980 I 122; KELLNER & TOMIDA 2000; WELLNHOFER 1985) and in specimens of *Pteranodon*. YPM 1181 has a small area of light scarring (#39) that extends proximodorsally from the supracondylar process (#30). YPM 1164 and 2302 have a large area of rugose scarring covering the lateral epicondyle (#40), and YPM 1181 has a small additional area of light scarring (#42) somewhat proximal and posterior to the epicondyle.

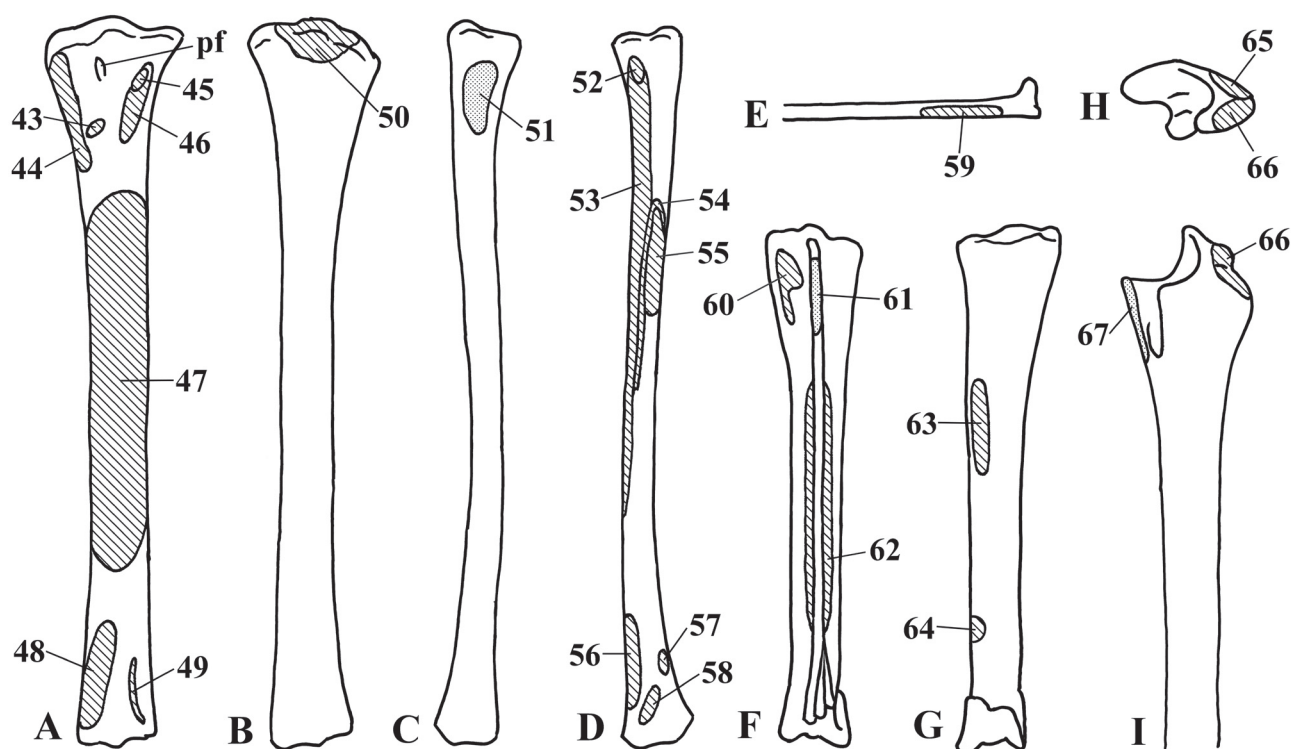
**Ulna.** There is a prominent biceps tubercle (#43) on the anterior face of the ulna, a short distance distal to the proximal articulation in *Anhanguera* (AMNH 22522, BSP 1980 I 122; WELLNHOFER 1985, 1991b) (Fig. 2). The tubercle is also present in *Pteranodon*, where it is divided into two parts by a transverse groove. Some specimens have additional light muscle scarring around the biceps tubercle, and YPM 2380 and 2684 have light scarring extending proximally along the anterodorsal margin (#44). In YPM 2348, 2499, and 2684 there is a small rugosity (#45) near the anteroventral margin of the ulna, and in YPM 1181 there is a larger area of light scarred bone (#46) adjacent to it. YPM 1181 and 2380 have a large area of light scarring suggestive of fleshy muscle attachment along the anterior midshaft (#47). In YPM 1175 and 1181 there is a suboval area of scarred bone (#48) near the distal end of the ulna on the anterodorsal surface, and in YPM 1181, 2348, and 2767 there is a curving markedly rugose crest (#49) on the anteroventral surface. In addition, though not indicated in Figure 2, there is a curving groove a short distance ventral to the rugose crest, that probably formed a pulley for a tendon. Many specimens of *Pteranodon* have a rugose crest (#50) on the posterior side

of the proximal end of the ulna. The crest is also present in AMNH 22552 and other specimens from the Santana Formation, but in those specimens it is not noticeably rugose.

**Radius.** Available specimens do not provide any clear information about muscle attachments to the anterior radius, but YPM 2452 has a small oval rugosity (#52) on the posterior surface near the proximal end (Fig. 2). YPM 1181 has a large area of light scarring (#53), which begins near #52 and extends distally along roughly two-thirds of the posterodorsal surface of the shaft of the radius. YPM 1181 and 2452 also show a strongly marked somewhat U-shaped scar (#54) along the proximal midshaft, and YPM 1181 has an area of light scarring within the legs of the U (#55). At the distal end, there are three areas of scarring: YPM 2348 has a rugose crest and area of weakly scarred bone (#56) that corresponds to the similar feature on the distal ulna (#49); and YPM 42819 has two small oval rugosities (#57 and 58).

**Carpus.** Various carpals have a few areas of rugose bone, but most probably are ligament attachments rather than muscle attachments. However, in many specimens of *Pteranodon* the non-articular surface of “Sesamoid A” (BENNETT 2001, 2007a) exhibits linear striations indicative of a large tendon attaching to the bone. In addition, in LACM 50926, and YPM 2688 and 2525 the pteroid has a marked rugosity (#59) along the anteroventral margin of the bend in the shaft a short distance from the articular end (Fig. 2).

**Metacarpus.** Metacarpals I–III do not preserve any direct evidence of muscle attachments, but Mc IV of YPM 42819 has a large rugose scar (#60) on the anteroventral surface near the proximal articulation (Fig. 2). Some specimens of *Pteranodon* (e.g., YPM 2452) have variable irregular scarring on the distal



**Figure 2:** Left ulna (A, B), radius (C, D), pteroid (E), metacarpal IV with adherent Mc I–III (F, G), and first wing phalanx (H, I) of *Anhanguera* based on AMNH 22555 (WELLNHOFER 1991a) anterior (A, C, E, F), posterior (B, D, G), proximal (H), and ventral (I) views, showing muscle scars and other features (hatched) and inferred areas of muscle attachment (stippled). Identifications and/or inferred muscle attachments are as follows: 43 – *m. biceps* and *m. brachialis*? [I]; 44 – *m. biceps*? and *m. brachialis* [I]; 45 & 46(?) – radio-ulnar ligament; 47 – *m. flexor digitorum longus* [O]; 48 – ventral ulno-carpal ligaments?; 49 – *m. pronator quadratus* [O]; 50 – *m. triceps* [I]; 51 – *m. biceps*, *m. brachialis*, and *m. humeroradialis* [I]; 52 – radio-ulnar ligament; 53 – *m. supinator* [I]; 54 and 55 – *m. pronator teres* [I]; 56 – *m. pronator quadratus* [I]; 57 and 58 – *m. flexor carpi radialis*? [I]; 59 – *M. extensor pteroidens* [I]; 60 – ventral carpo-metacarpal ligaments? or *m. flexor carpi ulnaris*? [I]; 61 – *m. abductor pollicis*? and 3rd *m. interosseus dorsalis*? [O]; 62 – intermetacarpal ligaments and *mm. interossei* [I]; 63 – *m. extensor carpi ulnaris* [I]; 64 – ligamentous pulley? in *Pteranodon*; 65 – *m. flexor digiti quarti* and/or *m. flexor digiti quarti brevis* [I]; 66 – *m. flexor digiti quarti* [I]; and 67 – *m. extensor digiti quarti longus* [I]. See text for description of the numbered features and inferred muscle attachments. Abbreviation: pf – pneumatic foramen.

third to half of the anterior surface of the shaft of Mc IV (#62) that may reflect intermetacarpal ligaments that anchored the proximally reduced Mc I–III to Mc IV. YPM 1175 and 2414 have an elongate oval rugosity on the posterodorsal surface of Mc IV some distance from the proximal end (#63). Many specimens of *Pteranodon* have a small well marked rugosity (#64) on the dorsal margin of the shaft a short distance proximal to the distal articulation where the shaft is necked down somewhat as it approaches the distal articulation, but still too far proximal to articulation to be the scar of a collateral ligament. Specimens of *Anhanguera* do not have such a neck and do not exhibit the rugosity.

**Phalanges of Digit I–III.** Digits I–III are generally too small to exhibit muscle attachment scars. However, the first phalanx of digit III has a large lateral flange toward the proximal end that represents a muscle attachment (BENNETT 2001). In addition, the unguals of digits I–III have marked flexor tubercles that represent muscle insertions.

**Phalanges of Digit IV.** In addition to scarring from collateral ligaments, the proximal end of the first wing phalanx

exhibits some muscle scarring (Fig. 2). The extensor tendon process is generally interpreted as a process for the insertion of muscles, and YPM 2660 has a area of marked scarring on the dorsal surface of the extensor tendon process (#66) and lighter scarring around it, as well as on the dorsal surface of the proximal end of the phalanx proper (#65). Many specimens of *Pteranodon* exhibit marked collateral ligament attachment scars on those dorsal and ventral ends of phalanges that participate in interphalangeal joints. However, YPM 2689 preserves a moderate-sized rugose area on the anterior surface of the proximal end of a wing phalanx that probably represents a muscle attachment (BENNETT 2001).

## 5. Inferred myology

Below, for each forelimb muscle the condition of the muscle in the extant relatives of pterosaurs is briefly reviewed and its probable character state in pterosaurs is inferred from the cha-



character state distribution in the extant relatives. Then the inferred character state of the muscle is matched with the processes and muscle scars described above. Some muscles are reconstructed without there being any muscle scars in the fossils that can be matched to them; however, in extant reptiles those muscles typically have fleshy attachments and are not associated with prominent muscle scars, so it is reasonable to suppose that the muscle in the fossil organisms also had a fleshy attachment that did not leave visible muscle scars.

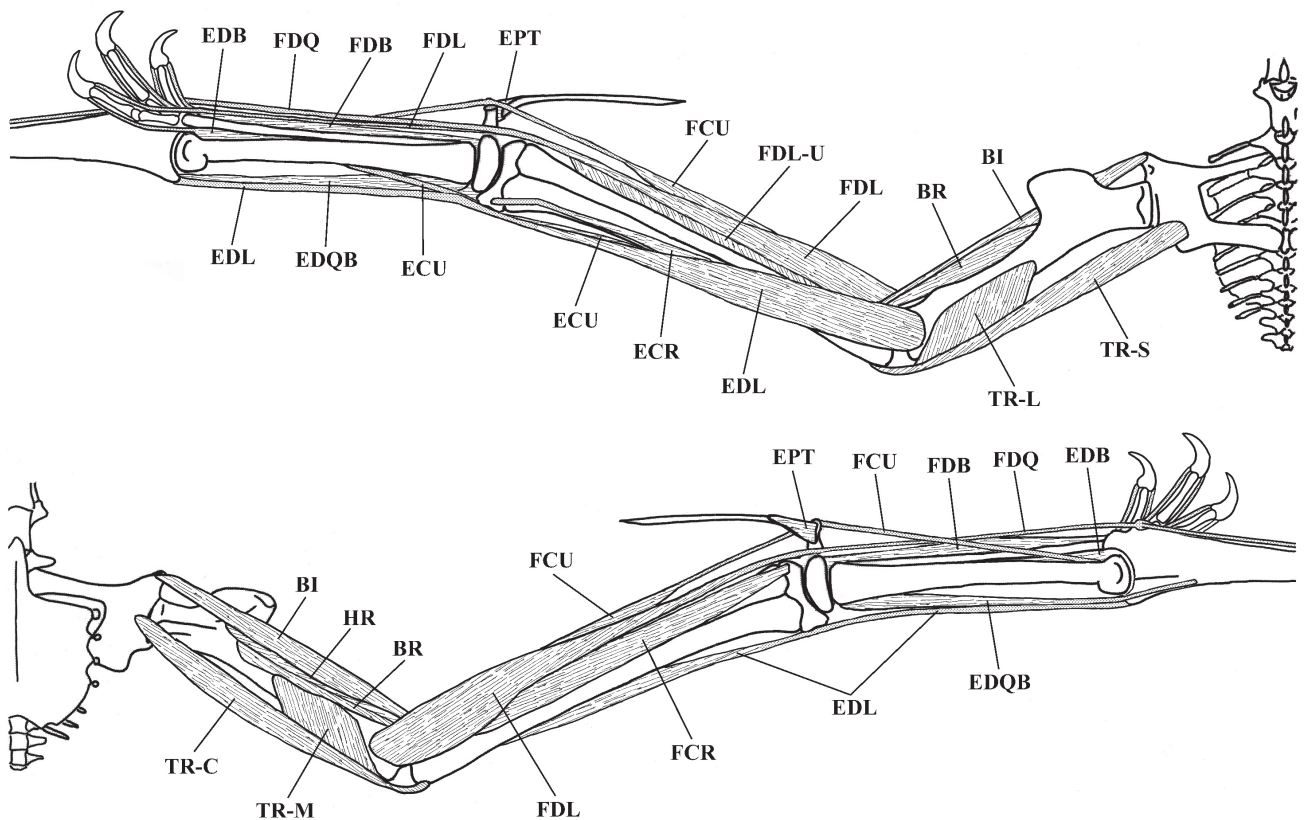
Reconstructions of the forelimb musculature of *Anhanguera*, based on the interpretation of pterosaurs as basal archosauromorphs, are shown in Figures 3–5. Where the inferred character states differ between the dinosaur sister-group and basal archosauromorph pterosaur outgroup nodes, those differences are noted (Tab. 1). Given the loss of digit V and the profound modification of the carpus and metacarpus in pterosaurs, *m. abductor digiti minimi*, *m. opponens digiti minimi*, *m. adductor digiti minimi*, *m. flexor digiti minimi*, and *m. transversus palmaris*, which are intrinsic muscles of the manus associated with digit V in turtles, lepidosaurs, and/or crocodylians, were presumably lost with digit V and are not reconstructed. Muscles are drawn with straight or slightly curving lines extending between the areas of origin and insertion, and the area of a muscle on a reconstruction should not be taken as necessarily

indicative of the size and power of the muscle.

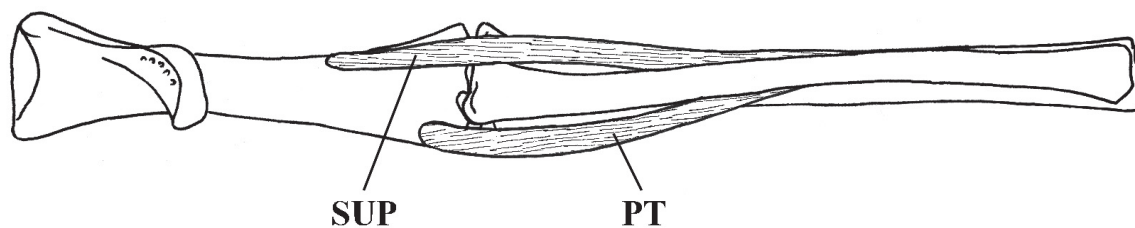
## 5.1 Brachial muscles

*M. biceps*. BENNETT (2003) reconstructed *m. biceps* of *Anhanguera* as originating from the prominent biceps tubercle of the coracoid and inserting on the biceps tubercle near the proximal end of the ulna (#43) and also on the proximal radius. It is possible that the adjacent lightly scarred area on the ulna (#44) also is part of the insertion of *m. biceps*. In *Pteranodon* the ulnar biceps tubercle is weakly divided in two by a groove running perpendicular to the long axis of the bone, and it is possible that the groove divides the insertion of *m. biceps* from that of *m. brachialis*, which probably would have inserted on the ulna near the insertion of *m. biceps*. No tubercle or scarred area that can be associated with *m. biceps* has been noted on the proximal radius, and it is likely that the insertion on the radius was fleshy (#51). The action on the elbow would have been flexion.

*M. brachialis*. Extant turtles, lepidosaurs, crocodylians, and birds have this muscle originating from much of the flexor side of the humerus. In turtles, lepidosaurs, and birds it inserts on the proximal radius and ulna, and in crocodylians on the proximal radius alone adjacent to the insertion of *m.*



**Figure 3:** Reconstruction of the left forelimb of *Anhanguera* with deep pectoral muscles in dorsal (A) and ventral (B) views. The small and/or deep muscles *m. abductor pollicis*, *mm. interossei*, *mm. lumbricales*, *m. pronator quadratus*, *m. pronator teres*, and *m. supinator* are not shown. Abbreviations: BI – *m. biceps*; BR – *m. brachialis*; EDB – *m. extensor digitorum brevis*; EDQL – *m. extensor digiti quarti longus*; EDQB – *m. extensor digiti quarti brevis*; EPT – *m. extensor pteroiideus*; FDB – *m. flexor digitorum brevis*; FDL – *m. flexor digitorum longus*; FDL-U – ulnar head of *m. flexor digitorum longus*; FDQ – *m. flexor digiti quarti*; FCR – *m. flexor carpi radialis*; FCU – *m. flexor carpi ulnaris*; HR – *m. humeroradialis*; TR-C – coracoid head of *m. triceps*; TR-M – medial head of *m. triceps*; TR-L – lateral head of *m. triceps*; and TR-S – scapular head of *m. triceps*.



**Figure 4:** Reconstruction of the left humerus and antebrachium of *Anhanguera* with deep muscles of the antebrachium in anterior view, drawn to the same scale as Figure 3. Abbreviations: PT – *m. pronator teres*; and SU – *m. supinator*.

*biceps*. In both basal archosauromorph and dinosaur sister-group pterosaurs the muscle probably originated from the anterior surface of the humerus and inserted on the proximal radius and ulna.

In *Anhanguera* the origin can be associated with the anterior surface of the shaft of the humerus (#37) and probably also with two rugose lines (#26 and 29) that may represent the lateral margins of the origin. Note that BENNETT (2003) considered #26 to be part of the origin of the medial head of *m. triceps*, but given the large area of fleshy origin for the medial head of *m. triceps* (#27) it may be that #26 was actually part of the origin of *m. brachialis*. The insertion can be associated with the proximal ulna and also the proximal radius. It is possible that it inserted on the biceps tubercle on the ulna (#43) with *m. biceps*, or alternatively it may have inserted on the lightly scarred area (#44) adjacent to the biceps tubercle. As noted above, in *Pteranodon* the biceps tubercle on the ulna is divided in two by a groove, and so may be the insertion of both *m. biceps* and *m. brachialis*. As with *m. biceps*, no tubercle or scarred area that can be associated with *m. brachialis* has been noted on the proximal radius, and it is likely that the insertion on the radius was fleshy (#51). The action on the elbow would have been flexion.

*M. humeroradialis*. The distribution of this muscle is problematic. BYERLY (1929) describes it in *Sphenodon*, it seems to be absent in lizards, and MEERS (2003) describes it in crocodylians, stating that it is unique to archosaurs and that *m. tensor propatagialis* in extant birds is its homologue. No supporting evidence was given for the suggestion that *m. tensor propatagialis* in birds is homologous to *m. humeroradialis*, other than the citation of an abstract (MEERS et al. 1993), which makes no mention of either muscle. Meanwhile, JASINOSKI et al. (2006) reject the homology, and suggest that *m. humeroradialis* is a derivative of the *m. deltoideus* complex and not present in birds as a separate muscle, in which case *m. humeroradialis* would be absent in extant birds. MEERS' (2003) statement that *m. humeroradialis* is unique to archosaurs seems to suggest that the muscles in *Sphenodon* and crocodylians are not homologous; however, in both *Sphenodon* and crocodylians the muscle originates from the proximal humerus and inserts on the proximal radius, ROMER (1944) accepted the homology, and so it is accepted here. The basal archosauromorph pterosaur outgroup node is decisively positive for presence and for an origin from the proximal humerus and an insertion on the proximal radius, whereas the dinosaur sister-group pterosaur outgroup node is equivocal for presence.

In *Anhanguera* the origin can perhaps be associated either with the distal part of #22 or the proximal part of #37 on the anterior surface of the shaft of the humerus, but there are no direct traces of its origin. The insertion would be on the proximal radius (#51), but again there are no traces of the insertion. The action on the elbow would have been flexion.

*M. triceps*. BENNETT (2003) reconstructed *m. triceps* of *Anhanguera* with scapular, coracoid, and medial and lateral humeral heads, the heads converging to insert by a tendon to the rugose crest of the posterior ulna (#50). The action on the elbow would have been extension.

## 5.2 Antebrachial muscles

Before considering the other muscles of the antebrachium, the long extensor and flexor of the digits will be considered in order to address the question of Mc IV rotation.

*M. flexor digitorum longus*. Extant turtles have this muscle originating from the flexor side of the ulna, in lepidosaurs and crocodylians the origin is on the medial epicondyle and the ulna, and in birds it is on the epicondyle alone. A common tendon divides into individual tendons that insert on the distal phalanges of digits I–V in turtles and lepidosaurs, on the distal phalanges of digits I–III in crocodylians, and on both phalanges of digit II in birds. In basal archosauromorph pterosaurs the origin would be on the medial epicondyle and ulna, and the insertion on the distal phalanges of at least digits I–III and probably digit IV as well. That would be much the case in dinosaur sister-group pterosaurs though the origin on the ulna and the insertion on more distal phalanges alone would be equivocal.

In *Anhanguera* the origin of the muscle can be associated with the scarring adjacent to the medial epicondyle of the humerus (#41) and the shaft of the ulna (#47), and the insertion can be associated with the distal phalanges of digits I–III and probably digit IV as well. It is likely that the muscle acted upon digit IV because the great size of the wingfinger and the large range of motion of its metacarpophalangeal joint would have required a large muscle originating proximally rather than a smaller intrinsic muscle of the manus. Given the different functions of digits I–III and digit IV in pterosaurs, it is probable that *m. flexor digitorum longus* split into two essentially independent (if not completely separate) divisions, one flexing digits I–III for terrestrial locomotion, and a second flexing digit IV for flight. The second division is here termed *m. flexor digiti quarti*, much as in humans *m. extensor hallucis brevis* is considered to be a part of *m. extensor digitorum brevis*. Note

**Table 1.** Differences between inferred muscle character states.

Muscle	Dinosaur sister-group pterosaurs	Basal archosauromorph pterosaurs
<i>M. humeroradialis</i>	Presence equivocal	Present
<i>M. triceps</i>	Presence of coracoid and 2 <sup>nd</sup> humeral heads equivocal	Coracoid and 2 <sup>nd</sup> humeral heads present heads present
<i>M. flexor digitorum longus</i>	Additional insertion on proximal phalanges equivocal	Insertion of distal phalanges only
<i>M. flexor carpi ulnaris</i>	Location of insertion equivocal	Insertion on the pisiform
<i>M. flexor carpi radialis</i>	Presence equivocal	Present
<i>M. extensor carpi radialis</i>	Location of insertion equivocal	Insertion on the radiale
<i>M. supinator</i>	Origin from lateral epicondyle of humerus	Origin equivocal
<i>M. abductor pollicis</i>	Location of origin equivocal	Origin from the palmar surface of the carpus
<i>M. extensor digitorum brevis</i>	Presence equivocal	Present
<i>Mm. lumbricales</i>	Presence equivocal	Present
<i>Mm. interossei</i>	Location of insertion equivocal	Insertion on the base of first phalanges

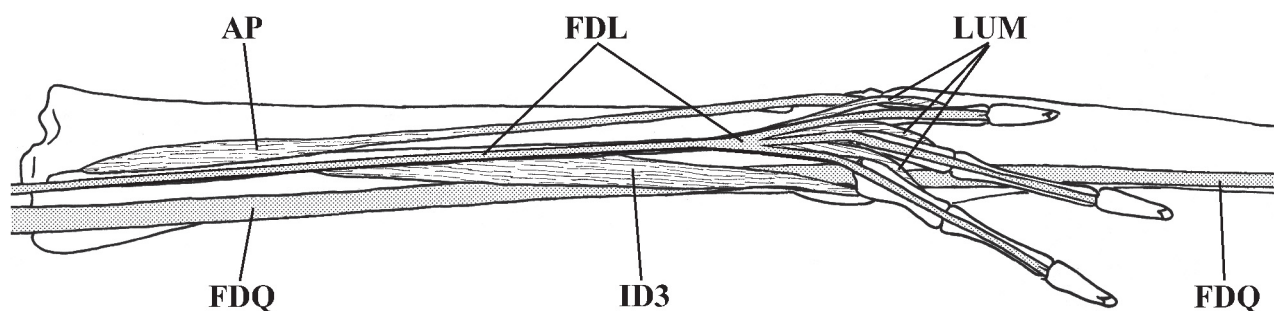
that although individual tendons of the two divisions of *m. flexor digitorum longus* are shown in Figure 3, individual bellies are not shown because they would be difficult to distinguish in dorsal and ventral views.

The division serving digits I–III probably crossed the carpus as a common tendon before splitting into individual tendons along the flexor side of Mc I–III, which then inserted on the flexor tubercles of the unguals of digits I–III. The action of the division serving digits I–III would have been flexion of the metacarpophalangeal and interphalangeal joints of digits I–III.

*M. flexor digiti quarti* would have had a separate tendon crossing the carpus, which inserted on the flexor side of the wingfinger. Because the interphalangeal joints of the wingfinger were essentially immobile in *Anhanguera* and most pterosaurs, almost all flexion and extension of the wingfinger took place at the metacarpophalangeal joint, and so the tendon must have inserted on the base of the first wing phalanx even if it extended along the finger to the fourth phalanx. If Mc IV had rotated about its long axis, then the insertion on the base of the first wing phalanx would be on its posterodorsally positioned posterior process (#67), and in order to get there the tendon would have had to pass posteriorly under the carpus and metacarpus following a spiral path for ~180°. Given the large size of the wingfinger, the tendon of *m. flexor digiti quarti* would also be large, and if it had spiraled around the carpus and metacarpus, it would have left traces of its passage. There are no such traces, and there is no evidence of rotation. If there was no rotation, then the tendon of *m. flexor digiti quarti* would have passed

along the anterior surface of the metacarpus ventral to the tendon of *m. flexor digitorum longus* serving digits I–III to insert on the dorsal surface of the anteroventrally positioned extensor tendon process of the wingfinger (#66), and would be positioned such that when the metacarpophalangeal joint was extended to fold the wing, the tendon would lie in the intercondylar sulcus of the distal end of Mc IV, which would have formed a pulley for the tendon (Fig. 5). That is the interpretation accepted here. The tendon probably passed along the wingfinger and inserted on each phalanx, in which case in addition to flexing the metacarpophalangeal joint it also could either have slightly flexed the interphalangeal joints anteriorly or applied tension to the anterior sides of the interphalangeal joints so as to resist the tension in the brachiopatagium that would tend to extend the interphalangeal joints posteriorly. The action of *m. flexor digiti quarti* would have been flexion of the wingfinger in a homological sense, but extension in a functional sense so as to spread the wing.

*M. extensor digitorum longus*. Extant turtles, lepidosaurs, and birds have this muscle originating from the lateral epicondyle of the humerus, whereas in crocodylians it originates as five separate shorter muscles from the distal ulna, ulnare, and radiale. In turtles it inserts on the distal ends of Mc I–V, in lizards on the bases of Mc II–IV and also the extensor side of digits II and III, in crocodylians on the unguals of digits I–V, and in birds on the base of the proximal phalanx of digit II. Both basal archosauromorph and dinosaur sister-group pterosaur outgroup nodes are decisively positive for presence, for an



**Figure 5:** Reconstruction of the left metacarpus and digits of *Anhanguera* with the intrinsic muscles of the manus in anterior view, drawn to twice the scale of Figures 3 and 4. Abbreviations: AP – *m. abductor pollicis*; FDL – tendon of *m. flexor digitorum longus* to digits I–III; FDQ – tendon of *m. flexor digiti quarti*; ID3 – *m. interosseus dorsalis* to digit III; and LUM – *mm. lumbricales*.

origin from the lateral epicondyle, and for insertions on digits I–IV, but the location of the insertions is equivocal.

It is possible that like *m. flexor digitorum longus*, this muscle split into two divisions because of the different functions of the digits, one serving digits I–III, and the other serving digit IV, which here is termed *m. extensor digiti quarti longus*. *M. extensor digiti quarti longus* would have passed from its origin on the lateral epicondyle of the humerus (#42) to insert on the extensor side of the wingfinger. As with *m. flexor digiti quarti*, because the interphalangeal joints of the wingfinger were essentially immobile in *Anhanguera* and most pterosaurs, almost all flexion and extension of the wingfinger took place at the metacarpophalangeal joint, and so the tendon must have inserted on the base of the first wing phalanx even if it extended along the finger to the fourth phalanx. If Mc IV had rotated about its long axis, then the insertion on the base of the first wing phalanx would be on its anteroventrally positioned extensor tendon process (#66), and in order to get there the tendon would have had to pass anteriorly over the carpus and metacarpus following a spiral path for ~180°. Given the large size of the wingfinger, the tendon would be large, and if it spiraled around the carpus and metacarpus, it would have left traces of its passage. There are no such traces, and as discussed below there is no evidence of rotation. If there was no rotation, then the tendon would have passed along the posterior surface of the metacarpus to insert on the posterodorsally positioned posterior process of the wingfinger (#67). That is the interpretation accepted here. Given that the tendon passed the posterior side of the posteriorly angled wrist, it must have been held in place under retinacula to prevent bowstringing. The tendon might have passed along the wingfinger and inserted on each phalanx, in which case in addition to extending the metacarpophalangeal joint it also could have extended the interphalangeal joints slightly; however, given that the brachiopatagium would also apply tension along the extensor side of the wingfinger, there would be little point to the such insertions, and so the tendon is not reconstructed distal to the base of wing phalanx 1. The action of *m. extensor digiti quarti longus* on digit IV would have been extension of the wingfinger in a homological sense, but flexion in a functional sense so as to fold the wing.

As for a division of *m. extensor digitorum longus* serving digits I–III, although it is inferred that it would originate from the lateral epicondyle and insert on digits I–III, the structure of

the pterosaur carpus and manus makes that unlikely. Regardless of whether or not there was rotation of Mc IV, the tendon of such a division of *m. extensor digitorum longus* would have had to spiral anteriorly over the carpus and Mc IV and then pass into the space between Mc I–III and Mc IV in order to reach the extensor sides of digits I–III. Rather, it is likely that the division serving digits I–III was either lost or originated from the carpus and the proximal ends of Mc I–III much as in crocodylians, and so would be similar to *m. extensor digitorum brevis* reconstructed below. If present, the action of the division serving digits I–III would have been extension of digits I–III, but given the uncertainty as to its presence and origin, it is not reconstructed.

*M. flexor carpi ulnaris*. Extant turtles, lepidosaurs, crocodylians, and birds have this muscle originating from the medial epicondyle of the humerus, though in lizards it also originates from the shaft of the ulna. In turtles, lizards, and crocodylians the insertion is on the pisiform, whereas in birds it is on the ulnare. Both basal archosauromorph and dinosaur sister-group pterosaur outgroup nodes are decisively positive for presence and an origin from the medial epicondyle. The basal archosauromorph pterosaur outgroup node is decisively positive for an insertion on the pisiform, whereas the dinosaur sister-group pterosaur outgroup node is equivocal for the insertion.

BENNETT (2007a) reconstructed a large muscle originating from the medial epicondyle of the humerus, whose tendon attached to and passed over “Sesamoid A” (BENNETT 1991, 2001) that lies in the fovea of the preaxial carpal before inserting on the wing metacarpal, and argued that it was *m. flexor carpi ulnaris*, and indeed the relative positions of the humerus, “Sesamoid A”, and Mc IV indicate that the muscle must have been *m. flexor carpi ulnaris*. Further reflection has caused me to conclude that “Sesamoid A” is the pisiform. Although it is inferred that the muscle would insert on the pisiform, it is likely that the tendon or a ligament continued from the pisiform to the metacarpus so as to carry the tensile load to the metacarpus in much the same way that the plantar aponeurosis in humans carries tensile loads of *m. gastrocnemius* and *m. soleus* from the calcaneus to the metatarsophalangeal joint capsules. Such an arrangement would allow the anteriorly elongated preaxial carpal to hold the tendon out in front of the center of motion of the carpus and improve the muscle’s leverage for flexion of the carpus.

In *Anhanguera* the origin of the muscle can be associated



with the medial epicondyle of the humerus (#38). The tendon attached to the pisiform, the non-articular side of which has linear striations indicative of the firm attachment of the tendon, but the tendon probably did not terminate there and passed distally to ultimately insert on Mc IV ventral to Mc I–III. It is possible that the insertion was on the large scar near the proximal end of Mc IV (#60), but it seems more likely that the tendon inserted on the metacarpophalangeal joint capsule. Such an arrangement would streamline the leading edge of the metacarpus to some extent, and would be no heavier if the internal spaces behind the tendon were pneumatic. Note that I previously referred to this muscle as *m. extensor carpi ulnaris* (BENNETT 2006) because of its function in spreading the wing, but subsequently switched to refer to it as *m. flexor carpi ulnaris* (BENNETT 2007a) because I thought it would be less confusing if the name reflected its homology rather than its function. The action would have been flexion of the carpus in a homological sense, and extension in a functional sense.

**M. flexor carpi radialis.** Extant turtles, lepidosaurs, and crocodylians have this muscle originating from the medial epicondyle of the humerus. Dilkes (2000) stated that the *m. pronator superficialis* and *m. pronator profundus* in extant birds are homologous with *m. flexor carpi radialis* in turtles, lepidosaurs and crocodylians, but it is not clear why the avian pronators are not homologous to the *m. pronator teres* and *m. pronator quadratus* of turtles, lepidosaurs and crocodylians instead. In turtles *m. flexor carpi radialis* inserts on the radiale, centrale, and first distal carpal, in lizards on the distal radius, and in crocodylians on the distal radius and radiale. The basal archosauromorph pterosaur outgroup node is decisively positive for the presence of the muscle originating from the medial epicondyle of the humerus and for an insertion on the distal radius with an equivocal insertion on the radiale, whereas dinosaur sister-group pterosaurs may be equivocal as to presence.

In *Anhanguera* the origin of the muscle can be associated with the medial epicondyle of the humerus (#38), and the insertion probably was on the proximal syncarpal and perhaps also on the distal radius (#57 and/or 58). The action would have been flexion of the carpus, though it could also assist in flexion of the elbow.

**M. extensor carpi ulnaris.** Extant turtles, lepidosaurs, crocodylians, and birds have this muscle originating from the lateral epicondyle of the humerus. In turtles it inserts on the shaft of the ulna, ulnare, and pisiform, in lepidosaurs on the pisiform and base of Mc V, in crocodylians on the bases of Mc I–II, and in birds on the base of the metacarpus. Both basal archosauromorph and dinosaur sister-group pterosaurs are unequivocal for the presence and origin from the lateral epicondyle, but are equivocal for insertion other than that the insertion probably extended onto the base of the metacarpus.

In *Anhanguera* the origin of the muscle can be associated with the lateral epicondyle of the humerus (#40), and it seems most likely that the insertion was on the prominent attachment scar on the posterodorsal surface of Mc IV some distance from the proximal end (#63). The action would have been extension of the carpus.

**M. extensor carpi radialis.** Extant turtles, lepidosaurs, and crocodylians have this muscle originating from the lateral epicondyle of the humerus, though in crocodylians there are

two additional heads that originate from the radius and ulna. In turtles it inserts on the shaft of the radius and the radiale, and in lepidosaurs and crocodylians on the radiale. In birds the homologous *m. extensor metacarpi radialis* originates from the lateral epicondyle of the humerus and inserts on the extensor process of the carpometacarpus. Both basal archosauromorph and dinosaur sister-group pterosaur outgroup nodes are decisively positive for an origin from the lateral epicondyle. The basal archosauromorph pterosaur outgroup node is decisively positive for an insertion on the radiale, whereas the dinosaur sister-group pterosaur outgroup node is equivocal for insertion.

In *Anhanguera* the origin of the muscle can be associated with the lateral epicondyle of the humerus (#40), and the insertion on the proximal syncarpal. It is probable that the tendon passed over the pulley-shaped groove on the distal ulna posterior to the curving rugose crest (#49) before inserting on the syncarpal, in which case the pulley would have redirected the pull of the tendon to better function in wrist extension. The action would have been extension of the carpus.

**M. supinator.** Extant turtles and *Sphenodon* have this muscle originating from the ulna and inserting on the base of Mc I. In lizards, crocodylians, and birds it originates from the lateral epicondyle of the humerus and inserts along most of the length of the radius. Both basal archosauromorph and dinosaur sister-group pterosaur outgroup nodes are decisively positive for presence of the muscle. The dinosaur sister-group pterosaur outgroup node is decisively positive for an origin from the lateral epicondyle of the humerus, whereas the basal archosauromorph pterosaur outgroup node is equivocal for origin.

In *Anhanguera* the origin can be associated with the supracondylar process a short distance proximal to the lateral epicondyle of the humerus (#30) and the adjacent area of scarring (#39), and the insertion can be associated with the scarring along much of the shaft of the radius (#53). Crossing the elbow, this muscle could have assisted in flexion of the elbow in addition to supination of the forearm. Note that although it is reasonable to describe the action of this muscle as supination, the mechanics of the pterosaur elbow and wrist joints are not sufficiently well understood to determine what effect supination and pronation had on wing shape.

**M. pronator teres.** Extant turtles, lepidosaurs, and birds have this muscle originating from the medial epicondyle of the humerus, and in crocodylians it may originate from the proximal ulna in addition to the epicondyle. In lepidosaurs, crocodylians, and birds it inserts along the distal half to three-quarters of the radius. Both basal archosauromorph and dinosaur sister-group pterosaur outgroup nodes are decisively positive for an origin from the medial epicondyle and an insertion along the distal half to three-quarters of the radius.

In *Anhanguera* the origin of the muscle can be associated with the ridge on the medial epicondyle of the humerus (#28), and the insertion may be associated with the U-shaped scar (#54) on the shaft of the radius and the scarring it encloses (#55). The action would have been pronation in addition to assisting in flexion of the elbow, though as mentioned above, the mechanics of the pterosaur elbow and wrist joints are not sufficiently well understood to determine what effect pronation had on wing shape.

*M. pronator quadratus*. Extant turtles, lepidosaurs, crocodylians, and birds have this muscle originating from the side of the ulna. In lizards there is also an origin from the medial epicondyle of the humerus. In all but turtles it inserts on the side of the radius. Both basal archosauromorph and dinosaur sister-group pterosaur outgroup nodes are decisively positive for an origin from the side of the ulna and an insertion along the side of the radius.

In *Anhanguera* the origin of the muscle can be associated with the large area of scarring on the shaft of the ulna (#47), and the insertion can be associated with the complementary areas on the shaft of the radius (#54 and 55); however, it is possible that the muscle attachment extended further distally along the radius. The action would have been pronation, though as mentioned above, the mechanics of the pterosaur elbow and wrist joints are not sufficiently well understood to determine what effect pronation had on wing shape. Note that the muscle is not illustrated because it is so deep.

### 5.3 Intrinsic muscles of the carpus and manus

*M. extensor pteroides*. The pteroid is unique to pterosaurs, and the presence of the muscle scar on the anteroventral surface of the pteroid near its articular end (#59) indicates that there was a muscle inserting there that moved the pteroid. The origin probably was on the anterior and ventral surface of the preaxial carpal. Contraction of the muscle would extend and depress the pteroid, which in turn would extend and depress the leading edge of the propatagium (Bennett 2007a). The muscle is here termed *m. extensor pteroides*, and although it probably evolved from muscle tissue from some other muscle, it is not possible to determine which muscle that was.

*M. flexor digitorum brevis*. Extant turtles, lepidosaurs, crocodylians, and birds have this muscle, but it is quite variable. In turtles it originates from the superficial surface of the palmar aponeurosis of *m. flexor digitorum longus* and inserts on the sides of the proximal phalanges of digits I–V; in *Sphenodon* it originates from the ulna and the common tendon of *m. flexor digitorum longus* and inserts on the distal phalanges of digits I–V; in lizards it originates from the ulnare and inserts on the distal phalanges of digits I–IV; in crocodylians, it is subdivided into individual bellies that originate from the ulnare, distal carpals, and the tendon of *m. flexor digitorum longus*; and in birds a remnant of it originates from Mc III and inserts on digit III. Both basal archosauromorph and dinosaur sister-group pterosaurs are decisively positive for presence and for insertions on the distal phalanges of digits I–IV, and equivocal for the location of the origin.

In *Anhanguera* it is possible that the muscle originated from the distal ulna (#48); however, that seems unlikely because the muscle would have had to pass anteriorly for a short distance in order to bend over the anterior margin of the proximal syncarpal before passing distally toward digits I–III. It is more likely that it originated from the distal syncarpal, and that is what is reconstructed here. The insertion can be associated with the flexor tubercles on the unguis of digits I–III. It is possible that there was a belly of the muscle that inserted on digit IV, in which case it might have inserted on the dorsal surface of the proximal end of the first wing phalanx (#65) or directly into

the tendon of *m. flexor digiti quarti*; however, it is probable that the power of such a belly would have been insignificant in comparison to that of *m. flexor digiti quarti* and that the belly was lost, and so it is not reconstructed. The action of the muscle would have been flexion of the metacarpophalangeal and interphalangeal joints of the digits.

*M. extensor digitorum brevis*. Extant turtles, lepidosaurs, and crocodylians have this muscle consisting of individual bellies inserting on the distal phalanges of digits I–V, but it is absent in birds. In turtles it originates from the ulnare and adjacent carpals, in lizards from the ulnare, and in crocodylians from the ulnare, radiale, and bases of Mc I–III. Basal archosauromorph pterosaurs are unequivocal for an origin from the carpus and an insertion on the distal phalanges of digits I–IV, and dinosaur sister-group pterosaurs are equivocal for presence.

In *Anhanguera* the insertions of those bellies serving digits I–III can be associated with the extensor side of the distal phalanges of digits I–III, but because of the structure of the pterosaurian metacarpus with Mc I–III in front of Mc IV, it is likely that their origin had moved distally onto the metacarpus. That belly serving digit IV, which is here termed *m. extensor digiti quarti brevis*, could have originated from the carpus. It is probable that the insertion of *m. extensor digiti quarti brevis* was on the extensor side of the proximal end of the first wing phalanx, and as with *m. extensor digiti quarti longus* it is unlikely that there were more distal insertions on the wingfinger. The action on digits I–III would have been extension, and the action on digit IV would have been extension in a homological sense, but flexion in a functional sense so as to fold the wing.

The metacarpophalangeal joint of digit IV of *Pteranodon* allowed wing phalanx 1 to be extended to within ~5° of Mc IV (BENNETT 2001), and many articulated specimens of various pterosaurs exhibit similar extensions of the joint. This suggests that most pterosaurs were capable of active hyperextension of the metacarpophalangeal joint of digit IV to within 5–10° of Mc IV in order to fold the wing compactly when not in use. When the metacarpophalangeal joint of digit IV is extended that far the posterior process of the first wing phalanx is carried toward the anterior border of Mc IV such that a muscle inserting on the posterior process (#67) could not extend the metacarpophalangeal joint close to Mc IV. Full active hyperextension to within ~5° of Mc IV might have been possible if the insertion of the extensors of the metacarpophalangeal joint of digit IV wrapped around the proximal end of the first wing phalanx from distance; however, that seems unlikely. An alternative would be for *m. extensor digiti quarti brevis* to have inserted on the first wing phalanx some distance from the proximal end. Such an arrangement would not provide *m. extensor digiti quarti brevis* with much mechanical advantage to extend the metacarpophalangeal joint when it was fully flexed as in flight, but would provide tremendous mechanical advantage when the metacarpophalangeal joint was extended, bringing the insertion of the muscle proximal to the joint. If this were the case, it would allow a relatively small *m. extensor digiti quarti brevis* to keep the wing folded during terrestrial locomotion, and so would not require that *m. extensor digiti quarti longus* be activated during terrestrial locomotion. In support of the interpretation, it is possible that the small well-marked rugosity

(#64) near the distal end of Mc IV in *Pteranodon* represents the attachment of a ligamentous pulley that would redirect the pull of the tendon of *m. extensor digiti quarti brevis* so as to improve its action in extension of the metacarpophalangeal joint to fold the wing out of the way. It is possible that the lack of the rugosity in *Anhanguera* is correlated with the shorter metacarpus than in *Pteranodon*, which would not have required a ligamentous pulley to redirect the pull of *m. extensor digiti quarti brevis*.

***Mm. lumbricales.*** These muscles are absent in birds, but extant turtles, lepidosaurs, and crocodylians have them originating from the tendons of *m. flexor digitorum longus* and inserting on the extensor side of the proximal phalanges of digits I–IV or V. In both basal archosauromorph and dinosaur sister-group pterosaurs the muscles would have the same origins and insertions, though dinosaur sister-group pterosaurs are equivocal for presence.

In *Anhanguera* the first three *mm. lumbricales* probably originated from the sides of the tendon of *m. flexor digitorum longus* to digits I–III, passed dorsally over the digits, and inserted into the extensor tendons to the respective digits. The action would have been extension of the interphalangeal joints of digits I–III. It is probable that the fourth *m. lumbricalis* was lost because the essentially immobile interphalangeal joints of digit IV would have made it unnecessary.

***M. abductor pollicis.*** Extant turtles, lepidosaurs, and crocodylians have this muscle originating from the palmar surface of the carpus, and in birds it originates from the tendon of *m. extensor metacarpi radialis*. In all but crocodylians it inserts on the proximal phalanx of digit I, and in crocodylians it inserts on the base of Mc I. In basal archosauromorph pterosaurs the muscle would be expected to originate from the carpus and insert on the proximal phalanx of digit I, whereas in dinosaur sister-group pterosaurs the insertion is equivocal.

In *Anhanguera* the origin probably would be from the carpus, although it is also possible that it originated from the proximal shaft of Mc III (#61), and the insertion would be on the side of the first phalanx of digit I. Its action would have been to abduct digit I, presumably to spread the digits for terrestrial locomotion.

***Mm. interossei dorsales et palmares.*** Extant turtles, lepidosaurs, and crocodylians have these muscles originating from the bases of Mc I–V and inserting on the bases of the proximal phalanges of the digits I–V. Extant birds have a single pair of *mm. interossei*, which insert on the distal phalanx of digit II. In basal archosauromorph pterosaurs the muscles would have originated from the bases of Mc I–IV and inserted on the bases of the proximal phalanges of the digits I–IV, whereas dinosaur sister-group pterosaurs would have the same origins but are equivocal for insertions on the proximal or a more distal phalanx.

In *Anhanguera*, given that *mm. interossei* abduct and adduct digits, and that the metacarpophalangeal joint of digit IV did not allow any abduction and adduction, those *mm. interossei* that would have been associated with digit IV probably had been lost. In addition, because Mc I and II were reduced proximally and closely appressed to one another and to Mc I, there was relatively little space for *mm. interossei* between the metacarpals, and most of them must have been rather small if present. However, the 3rd *m. interosseus dorsalis* must have

been large because there is a large lateral flange on the first phalanx of digit III that must have been for its insertion. Note that BENNETT (2001) suggested that digits I–III might have been linked by intervening ligaments such that abduction of digit III would pull on digit II, which in turn would pull on digit I, and so spread the digits. If that were the case, the 3rd *m. interosseus dorsalis* and the *m. abductor pollicis* alone would have sufficed to spread digits. Most of the *mm. interossei* would have originated from the sides of Mc I–III, and an origin on the shaft of Mc III near the proximal end (#61) is reconstructed here for the 3rd *m. interosseus dorsalis*, although it is also possible that they originated from the anterior surface of the shaft of Mc IV (#62) or from the intermetacarpal ligaments that presumably attached there. The action of the *mm. interossei dorsales* would have been abduction from the midline of the manus, and the action of the *mm. interossei palmares* would have been adduction toward the midline of the manus.

## 6. Inferred ligaments

In addition to the typical collateral ligaments of the elbow, wrist, metacarpophalangeal, and interphalangeal joints that can be associated with epicondyles and the like (BENNETT 2001), a few osteological features do not seem to match up well with muscles and instead seem to be related to additional ligaments. The small oval rugosities on the proximal radius and ulna (#45 & 52) face one another across a small gap when the two bones are articulated, and so may represent the attachments of a short proximal radio-ulnar ligament. Similarly, the scarring (#48) on the distal ulna may be associated with ventral ulno-carpal ligaments, and the rugose scar on the anteroventral Mc IV (#60) may be associated with ventral carpo-metacarpal ligaments. The rugose ridges on the distal radius and ulna (#49 & 56) face one another, as can be clearly seen in YPM 2348 (BENNETT 2001), and probably represent the attachment of a short distal radio-ulnar ligament. The position of the rugose ridge on the ulna (#49) adjacent to the groove for the tendon of *m. extensor carpi radialis* suggests that it was also associated with a retinaculum holding the tendon in the groove. As discussed above, the small tuberosity proximal to the distal end of Mc IV in *Pteranodon* (#64) may represent the attachment of a ligamentous pulley that redirected the pull of *m. extensor digiti quarti brevis*.

## 7. Discussion

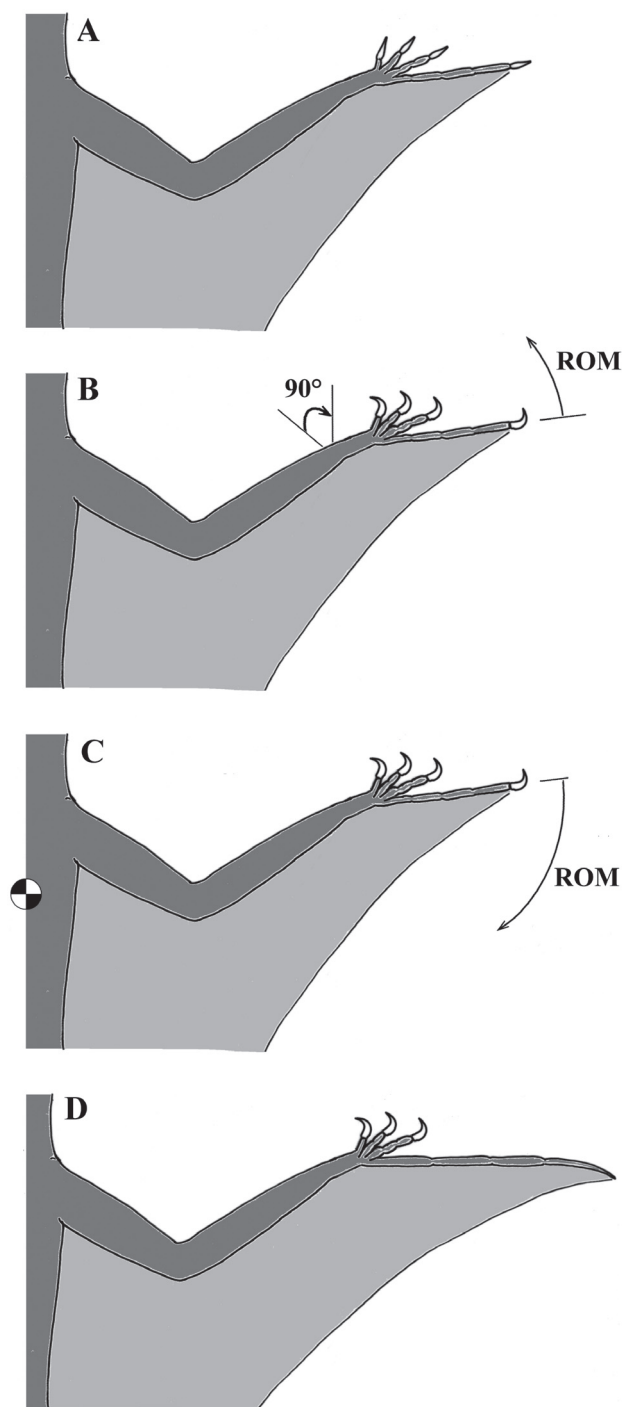
The reconstruction of the forelimb musculature of *Anhanguera* is based on the interpretation of pterosaurs as basal archosauromorphs. Although there would be some few differences if the reconstructions were based on the interpretation of pterosaurs as a dinosaur sister-group (Tab. 1), those differences are minor and would not affect the conclusions of the following discussion.

The reconstruction of the long extensor and flexor of the wingfinger suggests that there was no rotation of Mc IV about its long axis. If there had been a rotation, the tendon of *m. flexor digiti quarti* would have had to spiral posteriorly under the metacarpus to insert on the posterior process of wing phalanx 1 and the tendon of *m. extensor digiti quarti longus* to digit

IV would have had to spiral anteriorly over the metacarpus to insert on the extensor tendon process of wing phalanx 1. The tendons would have followed spiral paths for  $\sim 180^\circ$  around the carpus and metacarpus, and would have left traces of spiraling tendons, and there is no evidence to suggest that Mc IV had been rotated about its long axis. In addition, rotation of Mc IV would have required that the pterosaur ancestor pass through intermediate stages in which digit IV would fold ventrally rather than posteriorly, stages which would not permit compact or convenient folding of the wing, and consequently that probably would not be arrived at by selection. So there was no rotation, but rather the range of motion of the metacarpophalangeal joint of digit IV must have been extended posteriorly, first allowing hyperextension, and then the entire range of motion migrated further posteriorly. The end result would be a wingfinger that was directed laterally spreading the wing when the metacarpophalangeal joint was fully flexed (in the homological sense) and lying close to the metacarpus folding the wing when the metacarpophalangeal joint was fully extended (in the homological sense). Thus spreading of the wing was accomplished by muscles that homologically were flexors of the metacarpophalangeal and interphalangeal joints, whereas folding of the wing was accomplished by muscles that homologically were extensors. The reconstruction of the metacarpus (Fig. 5) shows that the tendon on *m. flexor digiti quarti* serving digit IV lies inferior to the tendons of *m. flexor digitorum longus* serving digits I–III just as one would expect. Metacarpal IV has not changed its position relative to Mc I–III, but rather has simply grown large, and as it has done so it has grown upward behind Mc I–III, becoming so large that it could support Mc I–III on its anterior surface.

A morphological scenario by which the flight-adapted manus of pterosaurs could have evolved from the terrestrially adapted manus of a non-volant ancestor of pterosaurs is proposed here (Fig. 6). The hypothetical ancestor is an arboreal tetrapod (BENNETT 1997b) with a manus with a 2, 3, 4, 5, 2 phalangeal formula, though note that this scenario is independent of phylogeny and could be modified as needed to fit most different possible ancestors (basal archosauromorphs, ornithodirans, etc.). The manus is used in quadrupedal locomotion, and so is oriented with the palmar surface of manus facing ventrally. Falling or leaping from trees leads to selection to increase body surface area in order to slow the fall or prolong the leap, and a membrane of skin extending from the side of the body is evolved. Lacking internal supports, the membrane is spread between the fore and hind limbs. Further selection for increased body surface area to improve gliding or leaping leads to an expansion of the patagium onto digit IV of the manus, resulting in a small wing, and subsequent selection for increased wing area leads to elongation of digit IV (Fig. 6A). Note that digit V probably is lost either because it is not needed to spread the patagium or because it can no longer function in terrestrial locomotion once digit IV begins to elongate.

As digit IV elongates, it soon reaches a length at which it can no longer function in terrestrial locomotion, and has to be folded out of the way. Folding ventrally toward the palmar surface of the manus would not fold digit IV out of the way, whereas folding digit IV backward in the plane of the wing would. Given the orientation of the manus with its palmar



**Figure 6:** Stages on morphological scenario for the evolution of the pterosaur wing. **A.** Gliding or leaping ancestor evolves membrane spread by limbs and digit IV. **B.** Supination of antebrachium allows digits to flex and extend within the ancestral range of motion (ROM) in plane of the wing. **C.** Posterior migration of the ROM allows digit IV to fold toward antebrachium, but anteriorly directed unguis of digit IV has a large moment arm relative to the center of mass indicated by the circle with alternating black and white quadrants. **D.** Loss of the unguis from digit IV results in pterosaur wingfinger with only four phalanges.

surface facing ventrally for terrestrial locomotion, folding backward in the plane of the wing would require abduction



of digit IV; however, the osteology and reconstructed myology of *Anhanguera* indicate that wingfinger folding was not accomplished by abduction. Instead, the forearm and carpus supinate  $\sim 90^\circ$  such that the palmar surface of the manus faces anteriorly when the forelimb was in flight position, and the metacarpophalangeal joints flex and extend in the plane of the wing (Fig. 6B). The supination could be a direct consequence of an arboreal lifestyle if the animal is climbing on small supports rather than large trunks. Note that the pterosaur antebrachium does not allow much supination and pronation, and so what may have happened was a reduction in the amount of pronation and supination allowed by the antebrachium such that the antebrachium was left in a rather supinated orientation.

Once the antebrachium and carpus is supinated  $\sim 90^\circ$ , digit IV can fold backward in the plane of the wing by hyperextending the metacarpophalangeal joint. There are three reasons that the posterior shift of the range of motion of the metacarpophalangeal joint probably would have been selected for in a pterosaur ancestor with a patagium between the limbs and body once digit IV was enlarged to further expand the patagium laterally: 1) swinging digit IV posteriorly in flight would slacken the patagium, altering its shape, and so could provide aerodynamic control; 2) swinging digit IV posteriorly would permit it to be folded out of the way; and 3) permitting digit IV to swing posteriorly in flight would reduce the chance of damage to the wing skeleton and undesirable yaw when the wingtip struck an immovable object. Initially, there may have been only a modification of the metacarpophalangeal joint such that it allowed significant hyperextension. However, because the maximum range of motion of joints is typically less than  $180^\circ$ , as the posterior limit of hyperextension was moved backward, the anterior limit of flexion would soon also have to move backward, and the end result was a posterior migration of the range of motion of the metacarpophalangeal joint (Fig. 6C). After the posterior migration of the range of motion, the wingfinger is directed laterally spreading the patagium when fully flexed, and lies adjacent to the metacarpus and antebrachium folding the patagium when fully extended.

Although supination of the antebrachium allows digit IV to fold in the plane of the wing, it also results in the unguals of digits I–IV facing anteriorly. That would be disadvantageous when gliding in a cluttered forest environment because the ungual on digit IV would catch on leaves and other obstructions instead of sliding past them, and given the large moment arm of the ungual at the wingtip relative to the center of mass (indicated by the circle with alternating black and white quadrants in Figure 6C), catching on an object would send the animal spinning out of control, increasing the risk of injuries, and perhaps causing it to fall to the ground where it would be susceptible to predation. Any further selection for increased wing area that results in additional elongation of digit IV also increases the moment arm of the ungual at the wingtip relative to the center of mass and increases the likelihood of upset when the ungual catches on an object. Therefore, there is strong selection to lose the ungual. Once the ungual is lost, the distal phalanx can slide past objects rather than catching on them, and the animal arrives at the 2, 3, 4, 4, X phalangeal formula found in virtually all pterosaurs, and further elongation of the phalanges plus slight hyperextension of the interphalangeal joints results in the pterosaur wingfinger (Fig. 6D). The abo-

ve scenario results in the flight-adapted manus of pterosaurs without passing through any stages when the orientation of the plane of folding of the wingfinger would be non-adaptive, whereas if Mc IV had rotation about its long axis as suggested by BENNETT (1991, 2001) and PETERS (2002), there would have been stages when the plane of folding was non-adaptive.

The proposed scenario can also explain the unusual orientation of the manus seen in pterosaur trackways. BENNETT (2007a) showed that *Pteraichnus* manus prints consist of impressions of digits I–III, and in *P. stokesi* prints digits I and III are rotated outward  $\sim 110^\circ$  and  $\sim 150^\circ$  relative to the direction of travel, respectively, and so are directed posterolaterally. The  $\sim 90^\circ$  supination of the antebrachium and manus during the evolution of the pterosaur wing explains this posterolateral orientation of the digits that makes pterosaur trackways so readily identifiable.

BENNETT (2007b) noted that anurognathids retained mobile interphalangeal joints in digit IV, such that the wingfinger itself could be partially folded around the side of the body at rest and spread while in flight. In light of the present muscle reconstruction it would seem that the interphalangeal joints allowed hyperextension to fold the wing phalanges around the body and flexion to spread the wing. In order to do this, anurognathids must have retained the insertions of *m. flexor digiti quarti* (and *m. flexor digitorum brevis*?) on all wing phalanges to spread the wing, and may also have retained such insertions of *m. extensor digiti quarti longus* (and *m. extensor digiti quarti brevis*?) if hyperextension of the interphalangeal joints was active rather than passive (i.e., relying on the elasticity of the patagium). BENNETT (2007b) noted that the carpus of *Anurognathus* differed from that of typical pterosaurs in that it did not seem to have syncarpals, and it is possible that the different configuration of the carpus permitted the extensor tendons serving the wing phalanges to pass distally.

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