

# The manus of archaeopterygians: implications for avian ancestry

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**ABSTRACT** – Recent, apparent confirmation that the digits of the avian manus are II, III, and IV, and not I, II, and III as in theropods, brings into question the purported homologies thought by many to have existed between the wrist and manus of early birds and those of maniraptoran theropods. A close examination of the wrist and manus of five archaeopterygians confirms the presence of numerous previously recognized, as well as unrecognized, derived avian characters. These include, but are not limited to, Metacarpal II very short, slightly wrapping around and probably fused to Metacarpal III for much of its length; Metacarpal II with small Processus extensorius for attachment of M. extensor carpi radialis; Metacarpal IV with proximal end lying well distal to proximal ends of metacarpals II and III, wrapping under and fused to ventral surface of Metacarpal III; joint between Metacarpal II and Phalanx 1 of Digit II ginglymoid near plane of wing, allowing Digit II to function as a primitive alula; joints between metacarpals III and IV and their respective phalanges relatively immobile; and “palmar” surfaces of distal phalanges facing anteroventrad or anteriad when wing is extended. The above features are not found in theropods, but their more highly derived counterparts are found in all modern birds with wings, whether volant or not. The avian, rather than theropodian, structure of the wrist and manus of archaeopterygians indicates significant functional differences between the forelimbs of archaeopterygians and theropods, which is not surprising if different digits are involved. Some prominent “feathered dinosaurs” are recognized as having a more advanced avian manus than that found in archaeopterygians, indicating their avian, rather than dinosaurian, ancestry.

**Key Words:** *archaeopterygians, avian, forelimbs, manus, theropods, wrist morphology.*

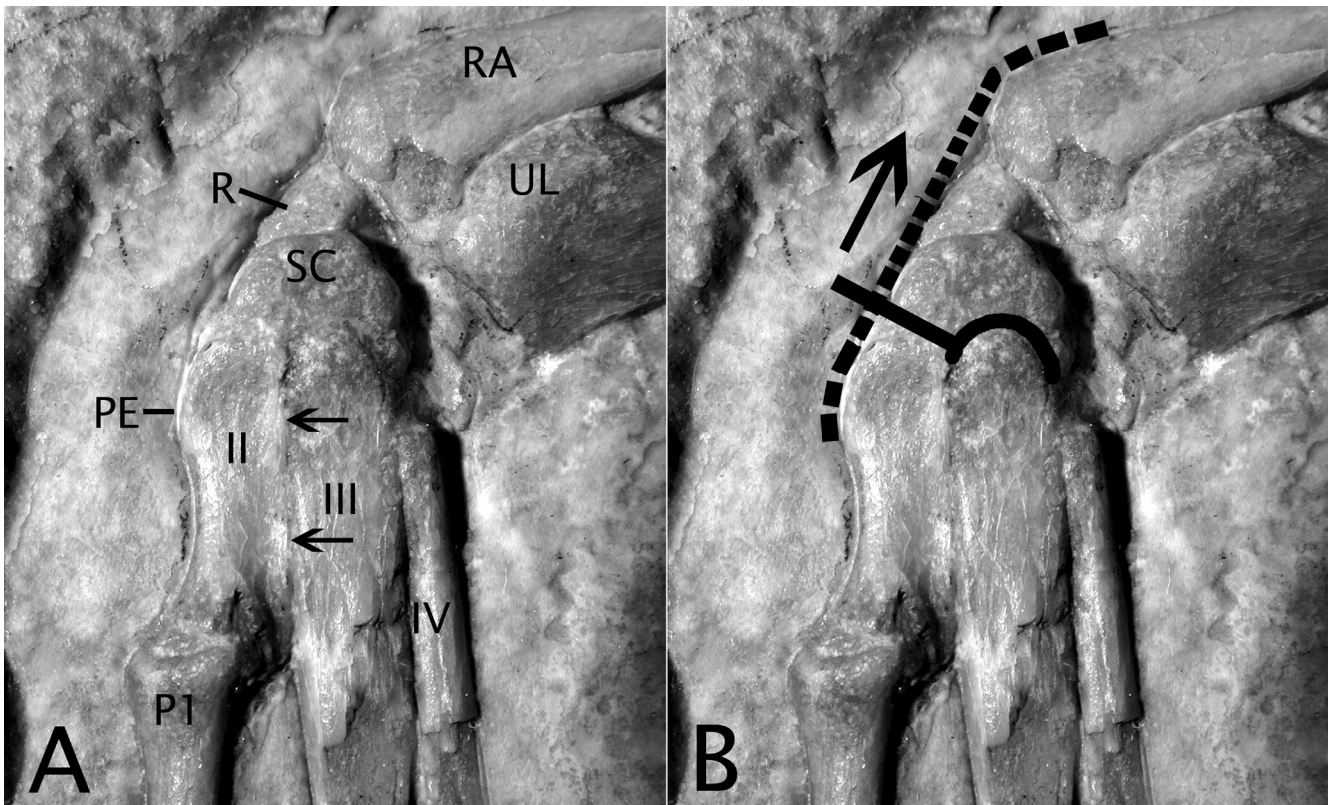
**La main des archéoptérygiens: implications pour l'origine des oiseaux** - Des études récentes paraissent confirmer que les doigts de la main des oiseaux sont II, III et IV, et non I, II et III comme chez les théropodes, ce qui remet en question les homologies supposées entre le carpe et la main des oiseaux primitifs et des théropodes maniraptorien. Un examen détaillé du carpe et de la main de cinq archéoptérygiens confirme la présence de nombreux caractères dérivés aviens, déjà observés ou non. On peut citer entre autres le métacarpien II très court, recouvrant en partie le métacarpien III et probablement fusionné à celui-ci sur une grande partie de sa longueur ; le métacarpien II portant un petit Processus extensorius pour l'insertion du M. extensor carpi radialis ; le métacarpien IV avec son extrémité proximale placée très distalement par rapport aux extrémités proximales des métacarpiens II et III, fusionnée à la surface ventrale du métacarpien III ; une articulation ginglymoïde entre le métacarpien II et la première phalange du doigt II, permettant au doigt II de fonctionner comme une alula primitive ; les articulations entre les métacarpiens III et IV et leurs phalanges respectives relativement immobiles ; et les surfaces « palmaires » des phalanges distales dirigées antéroventralement quand l'aile est en extension. Ces caractères ne sont présents chez les théropodes, mais leurs équivalents plus dérivés sont connus chez tous les oiseaux modernes pourvus d'ailes, volants ou pas. La structure avienne, plutôt que théropode, du poignet et de la main des archéoptérygiens indique des différences fonctionnelles significatives entre les membres antérieurs des archéoptérygiens et des théropodes, ce qui n'est pas surprenant si des doigts différents sont impliqués. Certains « dinosaures à plumes » sont considérés comme ayant une main avienne plus avancée que celle trouvée chez les archéoptérygiens, ce qui indique des ancêtres aviens plutôt que dinosauriens.

**Mots clés:** *archéoptérygiens, oiseaux, membre antérieur, main, théropodes, morphologie du poignet.*

## INTRODUCTION

As the earliest known birds, and with their complex mosaic of avian and reptilian characters, archaeopterygians

have sparked keen interest since the first specimens were discovered in the 1860's. As a consequence, there have been numerous publications that have touched on many aspects of archaeopterygians, and there have been three major efforts to



**Figure 1** - Left wrist of Berlin specimen of *Archaeopteryx*. **A.** Note lines of articulation between semilunate carpal and metacarpals II and III; distal position of proximal end of Metacarpal IV; overlap of Metacarpal III by posterodorsal corner of Metacarpal II (arrows); and alignment of posterior edge of semilunate carpal with posterior side of Metacarpal III. **B.** Lines delineating articulation between semilunate carpal and metacarpals II and III and force vector showing direction of pull of *M. extensor carpi radialis* added. II, Metacarpal II; III, Metacarpal III; IV, Metacarpal IV; P1, Phalanx 1, Digit II; PE, Processus extensorius; R, radiale; RA, radius; SC, semilunate carpal; UL, ulna.

synthesize all of our knowledge about these early birds. The first of these was the classic work by Heilmann (1926), and the second was the book presenting papers from the Eichstätt Conference (Hecht et al., 1985). The most recent effort was the extensive review by Elzanowski (2002). Although some might imagine that by now we have learned as much as we possibly can about the evolution of early birds from archaeopterygians, this probably reflects a rather pessimistic, and undeserved, view. There is still much we can learn about early birds from archaeopterygians, as was shown by the latest specimen of *Archaeopteryx* to be described (Mayr et al., 2005) and as will be shown herein.

Despite the extensive research on archaeopterygians, many aspects of their life and physical structure remain controversial and subject to debate. There is one point, however, upon which all students of archaeopterygians seem to be in agreement: archaeopterygians could fly. The presence of well developed, aerodynamically advanced flight feathers (Heilmann, 1926, Feduccia and Tordoff, 1979; Griffiths, 1996) provided an initial basis for this interpretation, and recently the fact that archaeopterygians possessed the derived neurological adaptations required for flight was doc-

umented in detail by Alonso et al. (2004). Still, how well archaeopterygians flew, how they became airborne, what archaeopterygians can tell us about the evolution of flight, and many other aspects of their flight remain controversial and the subject of ongoing study and debate (see, e.g., Elzanowski, 2001a; 2002). Nonetheless, it would appear logical that if archaeopterygians were flying birds, albeit, very primitive flying birds, and if they possessed the neurological adaptations of flying birds, they would also possess certain osteological characteristics of the avian flight apparatus. At the very least, one would expect to find plesiomorphic states of some avian flight adaptations in the wrist and manus of archaeopterygians, that is, in those parts of the skeleton that would have been most impacted by the demands of feathered flight. These characters certainly would be more highly derived in modern birds, but their presence in a volant ancestor should be noticeable. The objective of this paper is to identify, describe, and discuss the implications of three of these features based on personal studies of the original Berlin, Eichstätt, London, Munich, and Solnhofen specimens. Although the latest specimens to be described (Wellnhofer and Röper, 2005; Mayr et al., 2005) were not seen, published



**Figure 2** - The small Processus extensorius of Metacarpal II of the Common Murre, *Uria aalge*, contrasts with the much larger extensor process seen in the equal-sized Crested Bustard, *Eupodotis ruficrista*, both flying birds, in ventral view. Scale bar = 10 mm

photographs suggest that the wrist and manus in these specimens share the same basic structural configuration found in all other specimens.

Although the question of the identity of the digits in birds, that is, whether they are II, III, and IV, as opposed to I, II, and III as found in theropod dinosaurs, appears to have been settled in favor of the II, III, and IV enumeration (Hinchliffe, 1985; Kundrát and Seichert, 2001; Feduccia and Nowicki, 2002; Larsson and Wagner, 2002; Galis et al., 2003; Feduccia et al., 2005), this remains a contentious issue of debate. Although I follow the II, III, IV enumeration in this paper, in the event that this should prove to be incorrect it does not really matter in so far as the functional aspects of the features discussed herein are concerned.

Martin (1991) discussed avian characteristics of the wrist and manus of archaeopterygians, and Zhou and Martin (1999) pursued the question of the avian identity of characters of the wrist and manus of archaeopterygians in greater detail. The latter described what they considered to be eight uniquely derived avian characters, or character complexes, found in these early birds. I am in agreement with most of their observations, and some of what I discuss here is an extension of their work. Surprisingly, Elzanowski (2002:142) stated “The modern avian features of the hand of *Archaeopteryx* as listed by Zhou and Martin (1999) could not be confirmed,” although he then goes on to discuss some of the

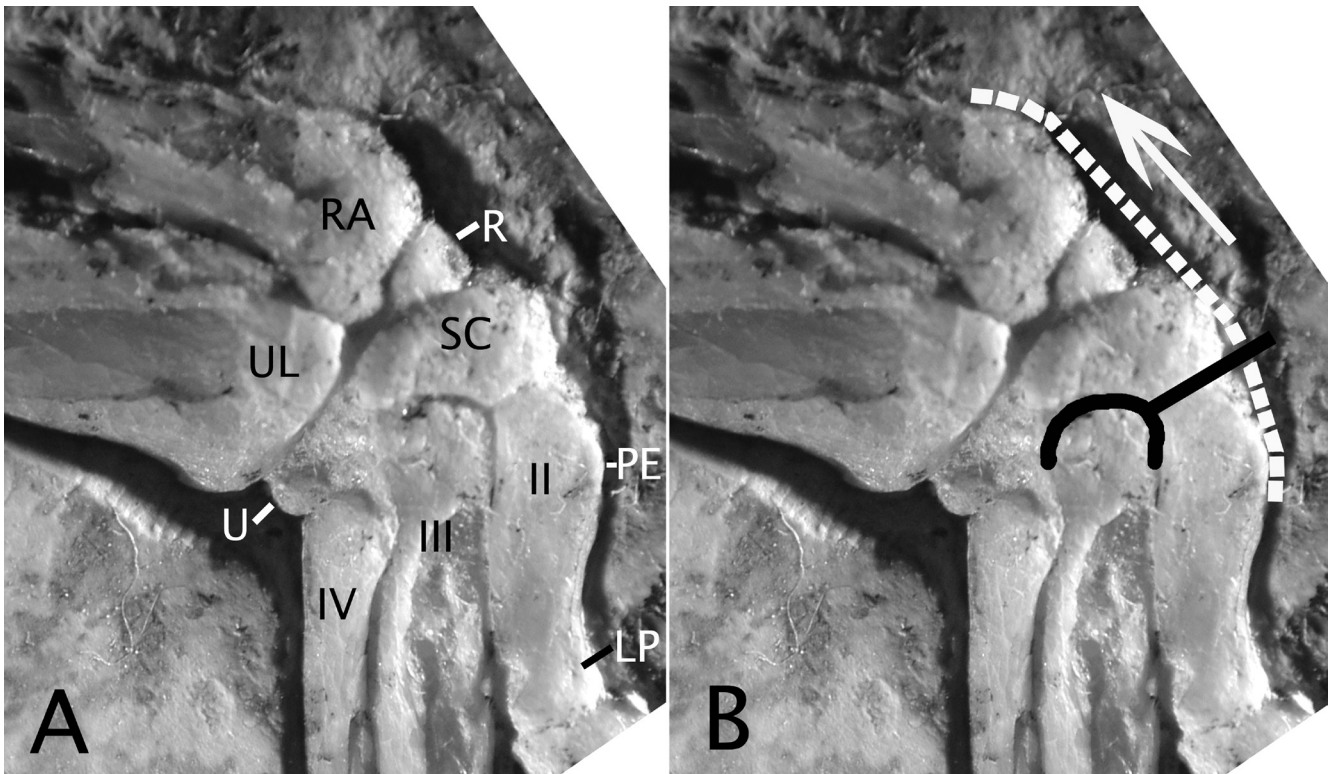
very same features (e.g., that the proximal end of Metacarpal IV lies distal to that of the other metacarpals and is compressed anteroposteriorly).

## DESCRIPTION AND ANALYSIS

*Wing Extension:* The extension of the wing in modern birds is a complex, semi-automated action based on muscle power and the tightly interlocked bones of the wing (Vasquez, 1992, 1994). One critical phase of this action is the contraction of the M. extensor carpi [metacarpi] radialis, the origin of which is on the Epicondylus dorsalis [lateral epicondyle] of the humerus and the insertion of which is on the Processus extensorius [extensor process] of Os metacarpale alulare [Metacarpal II]. Contraction of this muscle helps extend the wrist joint by pulling the carpometacarpus through its articulation with the carpals, an action that is facilitated by the advantages of the lever arm provided by the extensor process of Metacarpal II.

A Processus extensorius is present on Metacarpal II of archaeopterygians (Fig. 1). Although it is not as well developed as in most modern birds, examples from living species illustrate that a prominent extensor process is not required for flight (Fig. 2). Martin (1991) referred to the extensor process in archaeopterygians as a “rounded bulge,” but Zhou and Martin (1999) and Elzanowski (2002) did not



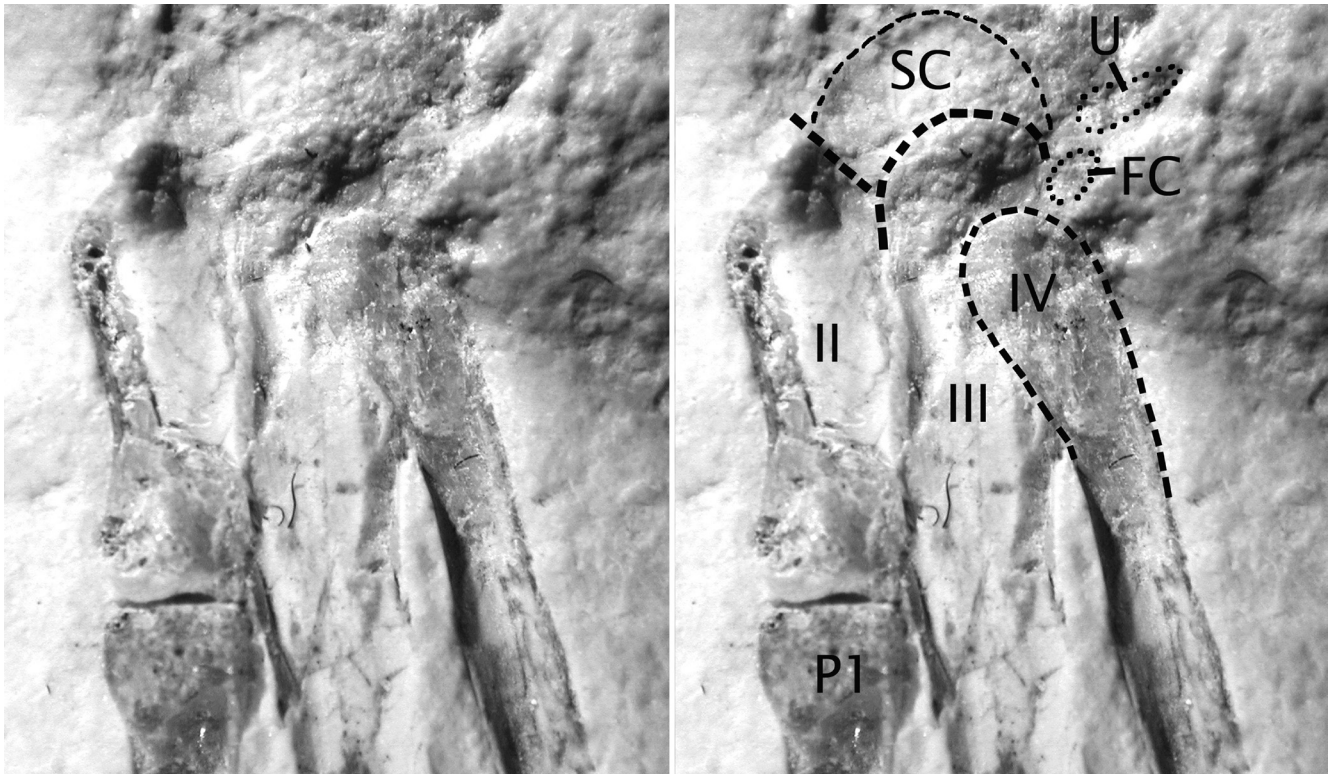


**Figure 3** - A. Right wrist of Eichstätt specimen of *Archaeopteryx*. LP, ligamental pit; U, ulnare; other abbreviations as in Figure 1. B. Lines delineate articulation between semilunate carpal and metacarpals II and III, and force vector shows direction of pull of *M. extensor carpi radialis*.

mention it. It can be inferred that the extensor process in archaeopterygians served a purpose similar to that in modern birds by the following observation.

As noted by Zhou and Martin (1999; Character 1), the semilunate carpal of archaeopterygians articulates unequally with Metacarpal II and Metacarpal III [Os metacarpale majus] (Figs. 1, 3). In fact, the semilunate carpal is nearly centered over Metacarpal III, and the articulation between these two bones is a fairly symmetrical curve, with the concave distal end of the semilunate carpal receiving the broad, convex proximal end of Metacarpal III (in dorsal view). The curved articulation, by providing a greater surface area of attachment than a straight line articulation, increases the degree of interlocking between the two bones. In contrast, the articulation of the semilunate carpal with Metacarpal II is along a fairly straight line that intersects Metacarpal III at its anteroproximal corner at an angle of approximately 60 degrees to its long axis (Figs. 1, 3). This description contrasts with the suggestion by Zhou and Martin (1999; Character 6) that the proximal end of Metacarpal II is simple and round. Also, if one accepts the interpretation that the proximal end of Metacarpal II is that part of the bone at its line of articulation with the semilunate carpal (Figs. 1, 3), then the suggestion by Zhou and Martin (1999) that the distal end of Metacarpal II is markedly narrower than the proximal end cannot be supported.

The explanation for the differences observed between the articulation of the semilunate carpal with Metacarpal II and Metacarpal III rests with the interpretation that the insertion of *M. extensor carpi radialis* was already in an avian position, attaching to the extensor process of Metacarpal II and functioning to extend the wrist joint on contraction. Contraction of the *M. extensor carpi radialis* placed a force on Metacarpal II that was at approximately 90 degrees to the plane of articulation of Metacarpal II with the semilunate carpal (Figs. 1B, 3B), thus maximizing the transfer of force to the semilunate carpal in precisely the direction needed to initiate rotation of the semilunate carpal on the proximal carpals, or to hold the manus in an extended position during flight. The angled articulation, in dorsal view, between the semilunate carpal and Metacarpal II is more advantageous than having the articular surface at 90 degrees to the long axis of the metacarpal, as seen in theropods, for two additional reasons. First, in the latter case, a pull on the extensor process would place greater force on the anterior portion of the articular surface than the posterior portion, which would impart a rotational vector to the metacarpal, causing the distal end of Metacarpal II to pull away from Metacarpal III. Second, the extensor process would be displaced farther distad, forcing the *M. extensor carpi radialis* to wrap around the anterior end of the semilunate carpal, thereby reducing its effectiveness because its force on contraction would be



**Figure 4** - Left wrist of Munich specimen of *Archaeopteryx*, *A. bavarica* Wellnhofer, 1993, on counterslab. The broad proximal end of Metacarpal IV is seen wrapping under Metacarpal III well short of the semilunate carpal. Metacarpal III is represented by impression only, whereas metacarpals II and IV are split between the slabs. See Figure 5A for ventral view of left wrist on main slab. Approximate lines of contact between the bones indicated by dashed lines on right. Positions of ulnare and fourth carpal approximate, after Wellnhofer (1993). FC, fourth carpal; other abbreviations as in Figure 1.

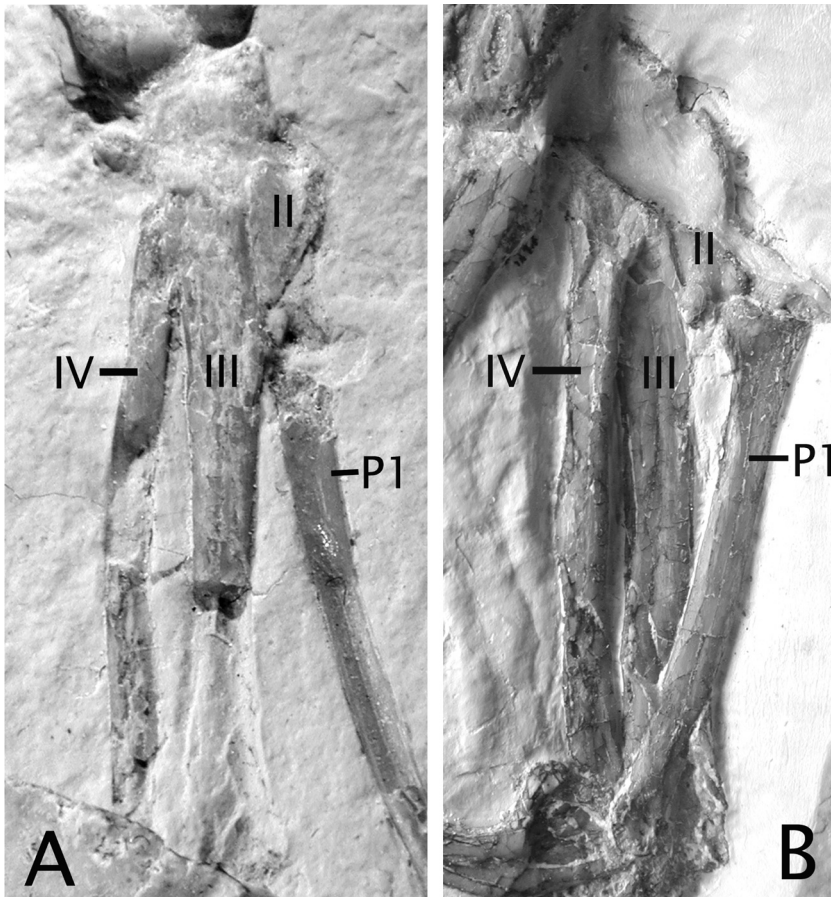
exerted at a greater angle.

It should also be noted that Metacarpal II does not just lie alongside of Metacarpal III. Rather, for much of its length, the posterior dorsal and ventral (when the wing is extended) edges of Metacarpal II slightly wrap around Metacarpal III, and it would appear that Metacarpal III is actually nestled within a slight depression on the posterior side of Metacarpal II. This wrapping effect can be seen in the dorsal views of the Berlin and Eichstätt specimens (Figs. 1, 3). In the Munich specimen, Metacarpal II is seen to rest against the ventral side of Metacarpal III (Fig. 4), but the position of the dorsal posteroproximal edge cannot be seen. This gives the appearance of an apparent shifting of Metacarpal II to a position slightly ventral to Metacarpal III, which was interpreted by Gishlick (2001) as implying that the proximal metacarpals formed an arch in archaeopterygians. Such a shift is not seen in other archaeopterygians specimens, however, so if shifting had occurred it would be unique to that specimen of *Archaeopteryx* and not a character applicable to all archaeopterygians, as implied by Gishlick (2001). Although Metacarpal III is thicker dorsoventrally and more robust at its proximal end than Metacarpal II (i.e., Metacarpal III has the structure more of a solid cylinder than the smaller, more complexly configured Metacarpal II; see, e.g., Fig. 1) (Zhou

and Martin, 1999, Character 5; *contra* Elzanowski, 2002), the longitudinal axes of both metacarpals of the Berlin and Eichstätt specimens appear to lie in approximately the same plane. The suggestion by Gishlick (2001) that there is an arched structure to the proximal metacarpals of archaeopterygians cannot be supported. Furthermore, the tight, interlocking relationship between Metacarpal II and Metacarpal III is indicative of a solid trend toward fusion of the metacarpals that appears to have been well underway (*contra* Elzanowski, 2002).

**Metacarpal IV:** The unique structure and positioning of Metacarpal IV has been noted before, but the significance of the avian nature of this bone perhaps has not been fully appreciated. Zhou and Martin (1999; fig. 2; Character 2) noted that Metacarpal IV slants ventrad distally, as in modern birds. However, as shown in their figure, although some of this slant is a result of the long axis of Metacarpal IV sloping ventrad distally relative to that of Metacarpal III, most of the slant is a result of a dorsoventrally narrowing of Metacarpal IV distad. In that the dorsal surface of the proximal end of Metacarpal IV in archaeopterygians is at approximately the same elevation as that of Metacarpal III, but the dorsal distal surface of the former is much lower





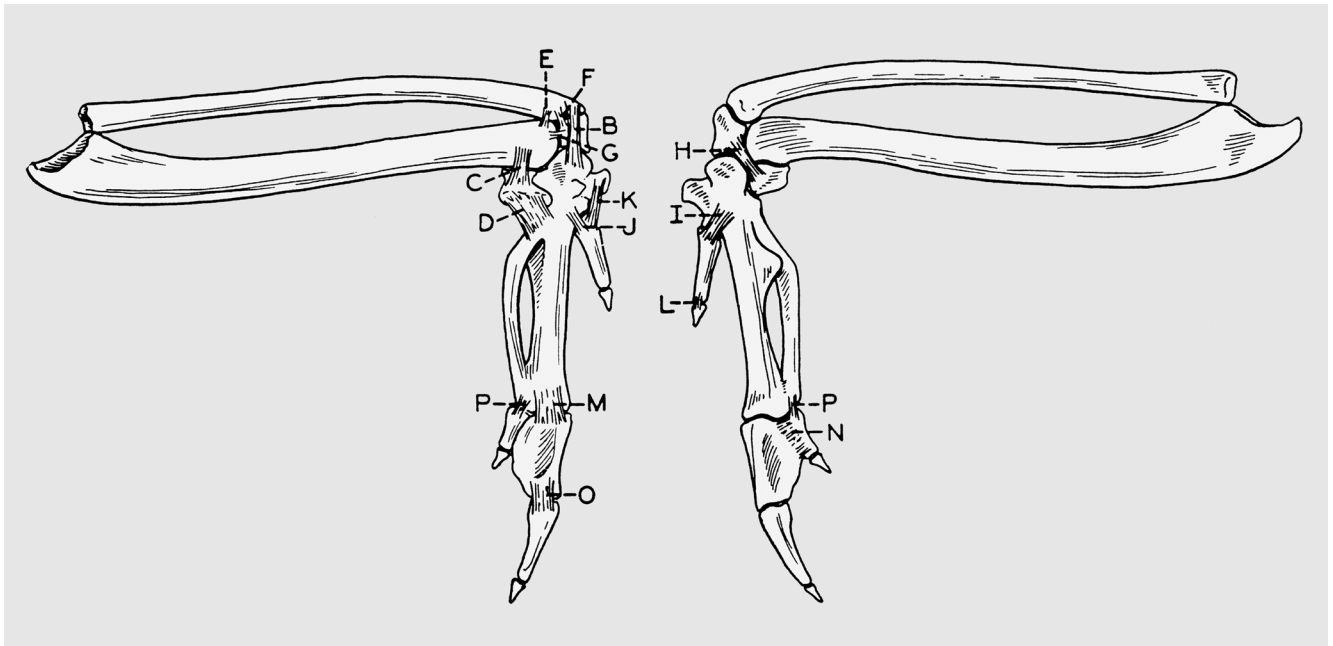
**Figure 5** - In archaeopterygians, Metacarpal IV bows away from Metacarpal III as in modern birds (see Fig. 2), as illustrated here in ventral views of the left metacarpals of the (A) Munich and (B) Solnhofen specimens. Note broadening of Metacarpal IV proximally and its fusion to the ventral side of Metacarpal III. Digit II in the Solnhofen specimen was rotated 180 degrees post-mortem. Abbreviations as in Figure 1. Not to scale.

than that of the latter, the dorsoventral narrowing of Metacarpal IV observed in modern birds was already present in archaeopterygians. How much of the ventral slanting distad might result from a more ventral position of the distal end of Metacarpal IV, relative to the distal end of Metacarpal III, remains unclear, but it does appear that some, but not all, of the observed slanting can be attributed to the more ventral position of the former. Zhou and Martin (1999; Character 2) also noted that the proximal portion of Metacarpal IV is markedly compressed anteroposteriorly and tightly attached to the posterior side of the Metacarpal III, as in modern birds, and Elzanowski (2002) noted that Metacarpal IV is deeper than wide throughout its length.

Martin (1991), Zhou and Martin (1999; Character 3), and Elzanowski (2002) noted, correctly, that the proximal end of Metacarpal IV is widely separated from the semilunate carpal (Figs. 1, 3, 4). This feature can be seen in all specimens of archaeopterygians where the proximal end of Metacarpal IV can be observed, as well as in modern birds. The statement by Gishlick (2001) that Metacarpal IV would have contacted the semilunate carpal in the Munich specimen if the wrist had not been pulled apart is incorrect because the metacarpals of that specimen were not dislocated and Metacarpal IV is in its natural position. That Metacarpal IV did not contact the semilunate carpal is also demonstrated by the absence of any articular surface that might have con-

nected the two bones. Indeed, the semilunate carpal did not extend posteriad beyond the posterior border of Metacarpal III, so there was no part of it in a position to articulate with Metacarpal IV. Thus, just as in modern birds, Metacarpal IV did not participate in the wrist joint, although it might have served as a “stop” for the ulnare at maximum flexion of the wrist. And although there might have been a functional relationship between the proximal end of Metacarpal IV and the fourth carpal bone, the “x-bone” of Hinchliffe (1985), that lies between Metacarpal IV and the semilunate carpal (Fig. 4), there is no observable area of articulation on the proximal end of Metacarpal IV that would suggest a relationship.

An avian feature of the proximal end of Metacarpal IV not previously noted is the fact that it broadens ventrally and wraps under Metacarpal III (Figs. 4, 5). This character can be seen in all specimens of archaeopterygians where the ventral surface of the metacarpal can be observed, although it is not easily illustrated. In that Metacarpal IV is removed from the wrist joint, the expansion of Metacarpal IV under Metacarpal III proximally can be interpreted as providing a broader area of fusion between the proximal ends of the two metacarpals, thus preventing the dislocation of Metacarpal IV under stress. Indeed, once removed from the wrist joint, in the absence of fusion, there would be little to hold Metacarpal IV in position. This would be particularly disadvantageous if, as in modern birds, Metacarpal IV provided support



**Figure 6** - The collateral ligaments in the manus of birds lie on the dorsal (right) and ventral (left) surfaces of the bones, not on the lateral and medial sides as in other vertebrates. Adapted from Chamberlain (1943).

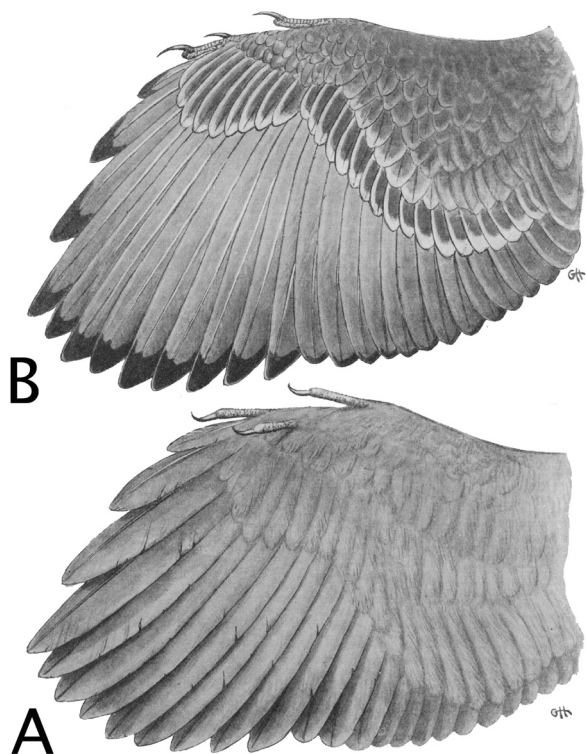
for primary feathers attaching to Metacarpal III. Thus, the fusion of Metacarpal III and Metacarpal IV proximally can be interpreted as a functional requirement to provide rigidity and strength to the precursor of the modern carpometacarpus once Metacarpal IV became disengaged from the wrist joint.

As seen in the Munich and Solnhofen specimens, the midshaft of Metacarpal IV bows away from that of Metacarpal III (Fig. 5), just as in most modern birds. This bowing is not as apparent in the Berlin and Eichstätt specimens, but some bowing, or at least separation, also can be seen in those specimens. The bowing is interpreted as providing support for the primary feathers that attach to Metacarpal III. Indeed, even in its broken and fragmentary state, the left manus of the Solnhofen specimen is immediately recognizable as having an avian-style carpometacarpus [compare Fig. 5B with Figs. 2 and 6(left)].

**Digit Rotation:** The third, and perhaps most significant, character to be discussed requires a brief explanation of the modern avian digit conformation. In plantigrade, quadrupedal animals, the palm of the manus is in contact with the substrate, or it faces posteroventrad as in digitigrade mammals. In bipedal animals, the palm is free to be placed into other positions. When we extend our arms and hold our hands in what we assume to be the position of that of modern birds in flight, that is, arms outstretched to the sides and the palms of our hands parallel to the substrate, our palms face ventrad and our wrist and fingers flex and extend dorsoventrad. In modern birds, however, there is minimal dorsoventral flexion/extension in the wrist and virtually none in

the digits because to meet the structural demands of flight the wing must be rigid in the horizontal plane along the longitudinal axis of the wing. Instead of flexion/extension in the dorsoventral, or vertical, plane, the manus of birds, as a single unit, is adapted for flexion/extension at the wrist joint in the *horizontal* plane (when the wing is extended). When the wing is folded against the body the ventral surface faces internally (mediad), and the extensor process of Metacarpal II points ventrad. It might be assumed, therefore, that *if* the digits *could* flex when the wing was extended, they would do so dorsoventrally, just as in other vertebrates, including theropods.

This interpretation would be incorrect, however, because the manual digits of birds have seemingly rotated 90 degrees relative to the position found in practically all other vertebrates. This is documented by the placement of the collateral ligaments of the metacarpals and phalanges (Fig. 6), which are found on the dorsal and ventral surfaces of these bones when the wing is extended, as opposed to their position on the lateral and medial sides of these bones as in other vertebrates (or, on the anterior and posterior sides of the finger phalanges in the human manus if arms are extended to the sides and palms placed in a plane parallel to the substrate). What this suggests is that the digits have rotated 90 degrees relative to the carpals and metacarpals, placing their palmar side facing anteriad. But, we must also ask if it was just the digits that have rotated, or did the metacarpals and wrist bones rotate as well? Or, alternatively, have the ligaments changed their position on the bones relative to the primitive condition by moving to a new position at 90 degrees to their original location? Archaeopterygians, as it



**Figure 7** - Heilmann (1926) illustrated the unguals pointing forward in ventral, or palmar, view (A) and posterior in dorsal, or anconal, view (B). Modified from Heilmann (1926).

turns out, are quite informative as to how the highly derived condition seen in birds came about.

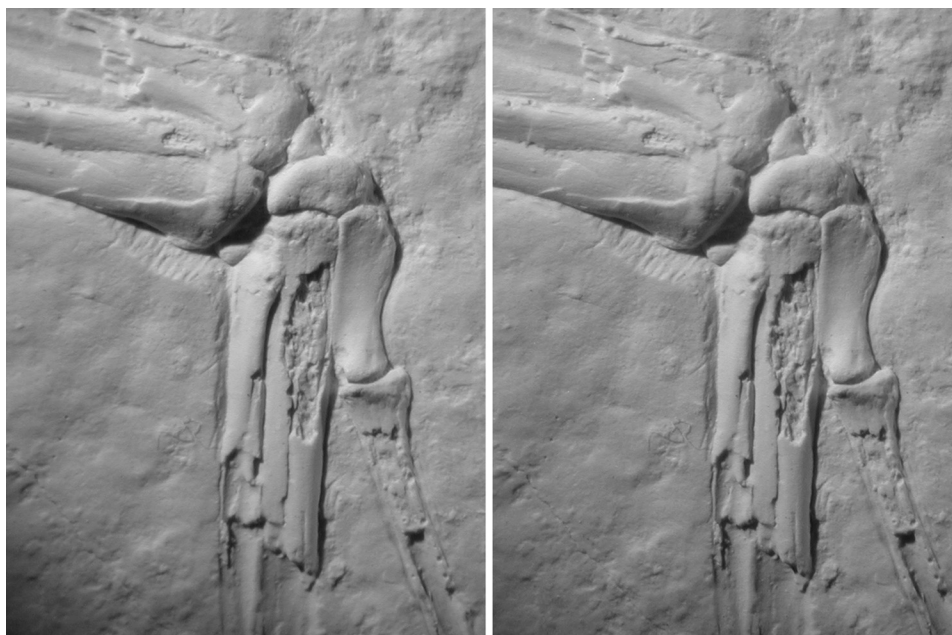
Interpreting digit orientation in archaeopterygians has been a problem for some time. Consider Heilmann's (1926) dilemma (Fig. 7). Clearly, as preserved, the unguals in the Berlin specimen point forward, as he illustrated them in his palmar, or ventral, view. But, in dorsal, or anconal, view, he apparently felt obliged to turn them backward. There might be a natural bias in our thinking that claws should point down, or back (posteriad), but yet the evidence seems clear. In most specimens of archaeopterygians the unguals point antieriad, or forward; where they do not, it is a result of post-mortem displacement. Numerous authors have looked at this question in an effort to determine if it is real or an artifact of preservation. Thulborn and Hamley (1982) attributed the facing upward position of ligamental pits in the distal manual phalanges and the forward facing unguals to post-mortem displacement, an interpretation that was followed by Yalden (1985) and Stephan (1994). Griffiths (1993), on the other hand, concluded that the natural position of the unguals was flat in the plane of the wing, facing antieriad, and that their observed position was not a post-mortem artifact. Elzanowski (2002:143) concluded that the "...claws were probably directed more or less ventrally, perpendicular to the wing surface...", but, nevertheless, "... [that the finger claws point forward] suggests an initial forward slant in vivo

or an intrinsic anatomical proclivity for the forward slant, ...". With respect to the ninth specimen, Wellnhofer and Röper (2005:13) noted that "In life the finger claws would have been oriented cranioventrally." I suggest that not only is the postulated forward slant a real character, it represents another major step toward the modern avian condition. Although rotation of the metacarpals and digits does not seem to have progressed to a full 90 degrees in archaeopterygians, as in modern birds, evidence for varying degrees of rotation of these bones is seen in the placement of the pits for attachment of the lateral collateral ligaments, the orientation of the articular facets between the metacarpals and the first phalanges of each digit, and the anterior concavity/posterior convexity (in dorsal view) of the phalanges.

In vertebrates, the origin, or proximal ends, of collateral ligaments binding metacarpals and metatarsals with manual and pedal phalanges, and the phalanges to each other, is usually marked by a deep, nearly circular pit, the exact placement of which on the side of the distal end of the proximal bone of the joint is variable. A focused attachment of the collateral ligaments proximally facilitates the rotation of phalanges and unguals around the ginglymoid joints, whereas the distal attachment of the ligaments is usually more broad based on the bone that is rotating around the joint.

Many pits for collateral ligaments can be observed in archaeopterygians. Ligamental pits can be identified on





**Figure 8** - Stereopair of right wrist of Eichstätt specimen. Note that the wrist is inclined into the slab anteroiad, giving a posterodorsal view of the metacarpals. The ginglymoid joint between Metacarpal II and Phalanx 1 of Digit II is nearly in the plane of the wing, allowing Digit II to function as a primitive alula. The concave nature of Metacarpal II is notable, with the dorsoventrally deep distal end functioning to prevent dorsoventral flexion/extension of Digit II. All of the features pointed out in the Berlin specimen (Fig. 1) are also visible in this specimen. The posterior edge of Metacarpal II can be seen wrapping over the dorsal edge of Metacarpal III. As in the Berlin specimen, the proximal end of Metacarpal IV appears as an anteroposteriorly compressed, rounded knob dorsally that narrows dorsoventrally rather rapidly distad. Note also how far the proximal end of Metacarpal IV is from the semilunate carpal. See Figure 3 for labeling of components. Photographs from a cast. An air bubble in the posterodistal corner of Metacarpal II gives a slightly artificial view of that area.

the distal end of Metacarpal II of the Berlin, Eichstätt, and Munich specimens, although these occur on the anterodorsal surfaces of the bone rather than on the anterior and posterior surfaces. Although the ligamental pits are not centrally located on the dorsal surfaces of the distal ends of these metacarpals as in modern birds, they approach that position. The ligamental pits on the distal end of Phalanx 1 of Digit II are more clearly rotated dorsad, but some of this rotation might be a result of post-mortem movement of the phalanx at the metacarpal/phalanx joint. However, the positions of the ligamental pits of Metacarpal II are not the result of post-mortem rotation because this metacarpal remains tightly bound to Metacarpal III.

Even more revealing is the fact that in the Eichstätt specimen it can be seen that the ginglymoid joint at the end of Metacarpal II is rotated almost 90 degrees, such that in dorsal view it is clear that flexion/extension of Phalanx 1 of Digit II was primarily in the anterior/posterior plane (Fig. 8). This would appear to suggest that it was a rotation of the metacarpal that brought about a change in position of the ligamental pits, rather than a migration of the collateral ligaments. Significantly, an anteroposterior flexion/extension of Digit II, even with a sizable ventral component, would have made it the first avian alula, albeit a very primitive one. In modern birds, by definition, the alula comprises a group of feathers that function to open and close an air slot along

the leading edge of the wing, which provides greater control during flight. Similarly, anteroposterior flexion/extension of Digit II in archaeopterygians would have created a wing slot for the same purpose, although it probably was not as effective as a modern alula composed of feathers. The development of an alula represents a very important advance in the development of flight, and it, together with the aerodynamically advanced flight feathers and derived neurological adaptations, suggests that archaeopterygians were quite adept at flight.

Elzanowski (2002) pointed out that Metacarpal II is concave dorsally, as seen in Figure 8. The proximal three-fourths of Metacarpal II slopes distad, as the bone narrows dorsoventrally distad from articulation with the semilunate carpal, but the appearance of this concavity is magnified by the extreme dorsoventral expansion of the distal end of the metacarpal (Figs. 1, 3, 8). This expansion can be interpreted as structural bracing against dorsoventral movement of Phalanx 1 of Digit II on the metacarpal. It might also reflect the normal widening of a metacarpal at its distal end, only now the bone is rotated and as a consequence the widening is in a dorsoventral, rather than anteroposterior, position.

Metacarpal III of the right manus of the Berlin specimen has a small ligamental pit on its distal end. It appears to be in a position that reflects a slight rotation of the metacarpal clockwise, but not to the extent seen in Metacarpal II.

Ligamental pits are indistinct in Metacarpal IV. As noted by Zhou and Martin (1999), the distal ends of metacarpals III and IV are simplified. That is, functional, moveable joints are absent. The typical ginglymoid articulation appears to be replaced by broadened, butt-like joints. The centers (in dorsal view) of both metacarpals are elevated at their distal ends, presumably to provide buttressing against flexion/extension at the joint, or because of rotation of the normally wider distal ends of the bones. Although a ligamental pit is still present on the anterodorsal side of Metacarpal III of the Berlin specimen, it is significantly smaller than that seen on the distal end of Metacarpal II of that specimen. The latter is a much smaller bone, but it still retains a functional ginglymoid joint. Strong connecting ligaments as found at normal phalangeal ginglymoid joints would not be expected at joints where movement is minimal or non-existent.

The dorsoventral expansion of the distal end of the metacarpals in archaeopterygians is in contrast to the functional ginglymoid joints observed at these positions in theropods. This contrast in mobility should not be minimized as it is indicative of stark functional differences of the manus in these two vertebrate groups.

Zhou and Martin (1999) noted that the first and second phalanges of Digit III have a high, sharp ridge on their dorsal surfaces (Character 7), and that the posterior margin of the distal portion of Phalanx 1 of Digit III is slightly convex in shape (Character 8). They postulated that there was a link between these features and the development of attachment sites and support for primary feathers. I agree that these are two possible explanations, but I also suggest that both of these features are linked to the rotation of the digits. As with most non-ungual pedal and manual phalanges, in lateral view, the shafts of the phalanges of archaeopterygians are slightly arched, but the former ventral and dorsal surfaces of the manual phalanges are now partially rotated and in archaeopterygians face anteroventrad/anteriad and posterodorsad/posteriad, respectively. Thus, the high, sharp ridge is, in effect, the anterodorsal edge of the phalanx (when the wing is extended) that has assumed a more anconal, or dorsal, position, whereas the posterior convexity reflects the convexity of what was originally the dorsal surface of the phalanges (i.e., the top of the arch), now exposed in profile in dorsal view.

Finally, as noted by many observers, Digit IV crosses under Digit III just distal to the phalanx 1/phalanx 2 joint (see Ostrom, 1992; Griffiths, 1993; Elzanowski, 2002). Some have interpreted this to mean that Digit IV was providing support for the feathers of Digit III. Others have suggested that this was more than likely a taphonomic, or preservational, effect. It also might be that this cross-under provided structural support to Digit III to prevent bending along its long axis during flight. But there is one other aspect that needs to be considered. With the rotation of the digits and other modifications to the manus, the use of the unguals for grasping in the traditional sense was lost. That is, the use

of the unguals to grasp prey, or vegetation for climbing in the normal manner, does not work because the unguals now point antieriad, although in archaeopterygians they do not yet seem to point antieriad in a single plane. In this position, in order for Digit IV to serve any imaginable function, it had to extend forward under Digit III, as Heilmann (1926) depicted in his dorsal view (Fig. 7B). The presence of flight feathers would have prevented it from crossing forward over, or dorsal to, Digit III.

Wellnhofer (1992) and Elzanowski (2002) suggested that the joint between phalanges 1 and 2 of Digit IV was tightly linked or even might be fused in the Solnhofen specimen (*Wellnhoferia* Elzanowski, 2001b), but in the Berlin specimen of *Archaeopteryx* it appears that a functional ginglymoid joint might still have been in place. If this were the case, however, flexion/extension at this joint, and at the joint between phalanges 2 and 3, would almost have to have been in the dorsal-ventral plane (when the wing was extended). This would seem to preclude an angle of flexion/extension that would take the ungual of Digit IV under Digit III. Resolution of the question as to why and how Digit IV could have crossed under Digit II in life requires further detailed study of the joint structure in the original specimens. The suggestion by Gishlick (2001) that the axis of Phalanx 3 of Digit IV has a medial twist in the Munich specimen could not be substantiated, nor could any such twist be observed in any other specimen. Indeed, the presence in the Munich specimen of the typical phalangeal arching that is seen in all elongated manual phalanges of archaeopterygians argues against any such twisting having occurred.

## DISCUSSION

Key innovations, most of which appear to have arisen early in the Mesozoic, gave rise to the vertebrates we classify as birds. Among these innovations are feathers, rotation of metacarpals and manual digits to face antieriad in a single plane (when forearm extended), flexion/extension of the wrist and manus in the plane of the wing (when extended), and a trend toward fusion of carpal and metacarpal bones to form a carpometacarpus. To this list could be added a number of other derived avian characters, including many other osteological characters and even the neurological structures that enabled the coordination necessary to produce flight. It is unlikely that all of these innovations occurred at one time, but if they occurred sequentially there must have been one lineage that finally encompassed them all and ultimately gave rise to the neornithines. Prior to that point, as in the radiation of any vertebrate group with powerful new adaptations, there must have been many disparate, near parallel, dead-end lineages that had various combinations of characters that we currently regard as avian. And any one of these lineages might have had unique innovations of its own that set them apart from the main stem of avian evolution. The group of birds known as the Enantiornithes

is one good example of such a lineage.

*Avian Status of Archaeopterygians:* Despite the numerous avian features of archaeopterygians, and as noted by Zhou and Martin (1999), there seems to be a sense that this group was not on the main line of descent to modern birds. But we cannot yet be sure of this. For example, if the function of the unique structure of the articulation between Metacarpal II and the semilunate carpal is interpreted correctly (see above), how does one explain the fact that in later birds Metacarpal II becomes disengaged from the wrist joint and loses contact with the semilunate carpal? For this to have occurred, some mechanical advantage must have accrued to those ancestral birds with an extensor process farther removed from the wrist joint, as in modern birds, and even in the Cretaceous birds *Ichthyornis* Marsh, 1872 and *Confusiusornis* Hou et al., 1995. And this adaptation might well have been developing at the same time as that in archaeopterygians, just in a different lineage. On the other hand, the change in position of Metacarpal II might be explained by the complete fusion, or co-ossification, of Metacarpal II with Metacarpal III, which would have allowed Metacarpal II to migrate distad, away from the wrist joint. If, at the same time, the extensor process of Metacarpal II expanded anteriorly, a mechanical advantage facilitating extension of the wing could have accrued, leading to the condition seen in modern, and many Cretaceous, birds. In this latter scenario, it is possible to picture archaeopterygians as being on, or very near, the main line of descent to modern birds, but still at a primitive evolutionary level as far as the development of the carpometacarpus was concerned. Additional fossil specimens of very early birds, preferably non-archaeopterygians, are required before we will know how close archaeopterygians were to the base of the avian tree.

The rotation of the metacarpals and manual digits was a very important innovation in the evolution of birds, although it has not received the attention its significance warrants. Indeed, it has often been completely overlooked (see, e.g., the reconstruction of the Cretaceous bird *Confusiusornis* in Chiappe et al., 1999; figs. 69, 70). In archaeopterygians, Metacarpal II has rotated such that the ungual of Digit II faced more anteriorly than ventrally (with wing extended) and Metacarpal III had rotated such that the ungual of Digit III faced anteroventrally. With this conformation, the grasp of archaeopterygians was placed more in the near horizontal plane of the metacarpals/semilunate carpal, not as in any other vertebrate, and the unguals of each digit faced in a slightly different direction. As noted by several authors (see Griffiths, 1993, and references therein), the large flexor tubercles, sharp points, and types of claws of archaeopterygians suggest that the primary role of the manual unguals was for climbing. Given the oft-noted absence of trees at Solnhofen (e.g., Viohl, 1985), it would seem that archaeopterygian claws would have been most effective as climbing instruments when used in the manner of grappling hooks in the prevailing brush or shrub-like vegetation, rather than as

tongs grasping a tree trunk in front of the animal, in the manner of lizards or squirrels. And given their orientation, the claws of archaeopterygians would not have been effective at seizing prey.

It could be argued that rotation of the digits, by reducing the ability to grasp and hold prey, would put a predator at a disadvantage. However, this would not necessarily be true, particularly for a small predator that did not use its manus for capturing prey in the first place. The evolutionary success of crocodilians, lizards, and, for that matter, snakes, clearly demonstrates that a grasping manus is not required to excel at being a predator, and there is no evidence to suggest that the ancestors of archaeopterygians used their manus for capturing prey. Unfortunately, in spite of a complete lack of supporting data, the *assumption* that archaeopterygians used their manus for capturing prey is all too often regarded as fact.

Rotation of the manual digits was important for the evolution of birds because it changed the action of the digits from the vertical to the horizontal, thus setting the stage for the evolution of flight. Even with the incomplete rotation of Metacarpal II in archaeopterygians, there was a very significant advance toward avian flight capabilities because Digit II became the first rudimentary alula known for birds. This digit now began to experience flexion-extension within, or near, the plane of the wing. It can also be argued that digit rotation came well before flight evolved because if it were advantageous solely for flight, why did the manual digits of non-volant birds not revert to the primitive state once flight was lost? For example, in the presumed flightless *Caudipteryx* Ji et al., 1998 (see below) digit rotation is greater than in *Archaeopteryx*, and all lineages of flightless birds in the Cenozoic (e.g., phorusrhacoids, ostriches, some geese, many gruids, et al.) retained the typical avian fused carpometacarpus, unless it was lost entirely. Instead, the trend was to reduce the carpometacarpus when it lost its importance for flight, even in those instances in assumed predatory birds where one could imagine a grasping, theropod-like manus being very useful (e.g., in the large, predatory phorusrhacoids). Apparently, once achieved, digit rotation was too deeply ingrained to be reversed.

Thus, when all of the osteological features of the archaeopterygian manus are taken into consideration, it is clear that the manus of these vertebrates was well on the way toward achieving the avian condition and that it bore no relationship, structural or functional, to that of theropods.

*Implications for Avian Ancestry:* Naturally, the question arises, Did rotation of the digits begin when the manus had five digits, or fewer? If the former were true, would this have favored the loss of Digit I, or its retention? It would seem that Digit I, being shorter than the middle three digits, would not have been as effective as the longer digits when used as a climbing instrument in the manner of a grappling hook. Likewise, Digit 5, being the shortest digit and falling in position behind the middle three digits, would not



be particularly useful as a grappling hook either. Whether rotation of the digits drove the loss of Digit I and Digit V or came later, after their loss, we do not know; more fossils are required to answer this question. However, in support of the argument that rotation of the digits could have occurred after the loss of Digit I and Digit V, or that rotation and a change in function drove the ultimate loss of those digits, it should be noted that there were presumed primitive, pre-dinosaurian archosaurs in the Triassic in which there was “a clear shift of emphasis to manual digits II, III, and IV rather than I, II, and III.” (Olsen and Baird, 1986:75, in reference to the ichnogenus *Atreipus*, which also had a bird-like, tridactyl pes). This is not to suggest that *Atreipus* was related to the ancestry of birds, particularly in light of the lack of skeletal material referable to this ichnotaxon, but only to point out that there was precedence in some archosaurian lineages in the Triassic for retention of digits II, III, and IV over I, II, and III. Therefore, if the observation that the preserved digits in theropods and birds are different is accurate, then there is already supporting evidence in the fossil record for such an event occurring. The argument is inferential, but it cannot be dismissed.

Elzanowski (2002) pointed out that the manual digits in *Protarchaeopteryx* Ji et al., 1998 and *Caudipteryx* were rotated forward, but he concluded, as he did in the case of *Archaeopteryx*, that this was a result of post-mortem twisting of the digits. In fact, the rotation of the metacarpals and digits was nearly completed in *Caudipteryx*, and the rotation did not result from post-mortem twisting (personal observation). This taxon was initially described as a maniraptoran theropod dinosaur, but it is widely thought to be avian in origin and unrelated to theropods [see illustrations in Zhou and Wang (2000) and Zhou et al. (2000); arguments and references cited in Paul (2002) and Feduccia et al. (2005)].

Indeed, of the several “feathered dinosaurs” from the Cretaceous of China discussed by Norell and Xu (2005), the three genera with modern appearing feathers (i.e., *Protarchaeopteryx*, *Caudipteryx*, and *Microraptor* Xu, Zhou, Wang, 2000) have rotated digits. On the other hand, those genera possessing a filamentous covering, or what is commonly referred to as “dino-fuzz,” (i.e., *Sinosauropteryx* Ji and Ji, 1996; *Beipiaosaurus* Xu, Tang, and Wang, 1999; *Sinornithosaurus* Xu, Wang, and Wu, 1999; and *Dilong* Xu, Norell, Kuang, Wang, Zhao, and Jia, 2004) either have a typical theropod manus or a manus reconstructed as that of a theropod. The condition in *Yixianosaurus* Xu and Wang, 2003, as to the presence or absence of feathers and the structure of the manus, cannot be evaluated from published material. Given this dichotomy, should we assume that it is just coincidence that those specimens with feathers of a modern aspect have rotated manual digits whereas those with “dino-fuzz” have a theropod-like manus? Or, is it more parsimonious to assume that digit rotation was such an important adaptation that once derived in the ancestral Jurassic, or perhaps Triassic, lineages, one of which evolved feathers and led to birds, the manus never reverted to the primitive state? If the latter is the case, then theropods covered in “dino-fuzz”

were neither feathered nor related to birds [see Lingham-Soliar (2003a, 2003b) and Feduccia et al. (2005) for a more parsimonious explanation of the origin of “dino-fuzz” than as feathers].

Equally as important as digit rotation in the evolution of the avian manus was the disengagement of Metacarpal IV from the wrist joint and the expansion and gradual fusion, or co-ossification, of its proximal end to the ventral side of Metacarpal III. The complexity of this critical step in the formation of the avian carpometacarpus would suggest that it too was irreversible, especially given that a similar structural form and relationship to Metacarpal III is seen in Metacarpal IV of *Caudipteryx* (personal observation) and, as best as can be determined from published illustrations, *Protarchaeopteryx* and *Microraptor*. These three genera, often referred to as “feathered dinosaurs,” most probably represent ancient lineages of birds unrelated to dinosaurs.

Although it is not the objective of this paper to attempt to resolve the question of avian ancestry, it is important to point out the following. From their cladistic analysis, Maryańska et al. (2002:106) concluded that the maniraptoran theropod dinosaurs referred to as oviraptorosaurs were “secondarily flightless birds, more advanced than is *Archaeopteryx*.” However, Osmólska et al. (2004:165) stated that oviraptorosaurs had “grasping hands” and that their known postcranial skeletons “deviate only slightly from the structure of other theropods.” Their illustrations, except for that of *Caudipteryx*, clearly show the theropod form of the manus of oviraptorosaurs. Both of these studies included *Caudipteryx* as a basal oviraptorosaur; neither of them recognized the many avian characters of its manus. To posit *Caudipteryx* as a basal oviraptorosaur requires the loss in the more “advanced” oviraptorosaurs of the avian manus (and a reversion to a normal theropod manus) and a loss of feathers. Neither of these possibilities is considered likely.

Similarly, the so-called “four-winged dinosaur,” or *Microraptor*, was also referred to as a maniraptoran when first described, in this case as a dromaeosaurid. It, too, has a manus seemingly more advanced than *Archaeopteryx*, and it clearly possessed feathers. Was it a bird or a theropod dinosaur? Although there has been a recent tendency to consider the possibility that some dinosaurs are actually flightless birds [see Paul (2002) and discussion in Feduccia et al. (2005)], I think this is probably more a result of forms like *Caudipteryx* and *Microraptor* being confused with dinosaurs because of a lack of understanding as to what structures comprise synapomorphies for birds, and why, than because of any actual phylogenetic relationship between birds and theropod dinosaurs. I would suggest that all of the known “feathered dinosaurs” that bear true feathers and have rotated manual digits represent distinct, disparate lineages of early birds unrelated to theropod dinosaurs. Furthermore, I predict that as more specimens of early avian lineages appear, and as more synapomorphic characters of birds are recognized, the dinosaurian origin of birds will be seen to have been an interesting, indeed, perhaps even an exciting hypothesis that

was once important for spurring research in this arena, but ultimately a hypothesis that fell by the wayside under the weight of contravening facts.

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