ARTICULATION AND FUNCTION OF THE PTEROID BONE OF PTEROSAURS

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ABSTRACT—For more than 100 years, most pterosaur workers have accepted the traditional reconstruction of the pteroid, articulated in the fovea of the preaxial carpal and directed medially along the anterior margin of a small propatagium in order to control it. A few workers have rejected the traditional reconstruction and advocated an alternative reconstruction with the pteroid directed anteriorly and controlling a large propatagium extending laterally past the wrist. Articulated specimens of a wide range of pterosaurs preserve a sesamoid associated with the tendon of *M. flexor carpi ulnaris* in the fovea of the preaxial carpal. No specimen preserves the pteroid articulated in the fovea, and because the sesamoid articulated there, the pteroid could not. Therefore, both the traditional and alternative reconstructions, which are based on the assumption that the pteroid articulated in the fovea, are falsified. The preaxial carpal acted as a strut to increase the leverage of *M. flexor carpi ulnaris* for wrist extension. The pteroid articulated with the side of the carpal, was directed medially toward the shoulder, and could be extended and depressed to control the propatagium.

INTRODUCTION

A recent article by Wilkinson and colleagues (2006) on the function of the pteroid bone of pterosaurs started with a statement that the pteroid has long been controversial. Perhaps, but there have been two separate controversies widely separated in time. The first controversy was but a part of the larger controversy about the homology of pterosaurian fingers. Cuvier (1821–1824) interpreted the manus as consisting of the small Digits I–III plus the hyperelongate Digit IV that supported the wing, whereas Goldfuss (1831) suggested that the pteroid represented a vestigial Digit I, the small fingers Digits II–V, and the wing-finger Digit V. Although Owen (1869) sided with Cuvier, most authors (Wagner, 1837; Fraas, 1878; Marsh, 1882; Zittel, 1882; Williston, 1903) sided with Goldfuss, until Williston (1904, 1911) and Plieninger (1906) presented convincing arguments that the phalangeal formula of pterosaurs, 2-3-4-4-x, is essentially unchanged from their non-volant ancestors except for the possible loss of an ungual on the wingfinger. That view has been accepted by almost all authors ever since (e.g., Romer, 1956; Kuhn, 1967; Wellnhofer, 1978, 1991a), although Unwin and colleagues (1996) resurrected the Goldfussian view as a viable alternative to the Cuvierian without actually supporting it.

The second controversy surrounds the orientation and function of the pteroid. Articulated skeletons of pterosaurs preserve the pteroid with its articular end adjacent to the preaxial carpal (the "lateral" carpal of some authors and the "medial" carpal of others) and the shaft either subparallel to the radius or directed medially toward the shoulder. Cuvier took no notice of the pteroid, and Wagner (1858) was the first to suggest that the pteroid lay along and controlled the anterior margin of a propatagium anterior to the arm and forearm and extending from the wrist to the shoulder. Marsh (1882:255) was the first to state that the pteroid articulated directly with the preaxial carpal: "the 'lateral carpal' unites both with the distal carpal and with the 'pteroid' by very free, well defined articulations"; and although not stated explicitly, based on the *Pteranodon* material available to Marsh, he must have meant that the convex articular end of the pteroid articulated in the concave fovea at the distal end of the preaxial carpal. This arrangement of bones was first illustrated by Hankin and Watson (1914; Fig. 1), and together the medially directed pteroid of Wagner and the fovea-pteroid articulation of Marsh constitute what is here termed the traditional interpretation of the pteroid, accepted by almost all pterosaur workers for over 100 years (but see Wild, 1978).

Two alternative interpretations have challenged one or the other of the two parts of the traditional interpretation. Bennett (1991, 2001) presented one alternative, challenging the fovea-pteroid articulation of Marsh by arguing that a sesamoid rather than the pteroid articulated in the fovea and that the pteroid articulated with the medial side of the preaxial carpal. Frey and Riess (1981) presented the other alternative, rejecting the medially directed pteroid of Wagner and arguing for an anteriorly directed pteroid controlling an extensive propatagium encompassing Digits I-III and extending laterally past the second interphalangeal joint of the wingfinger. The idea of an anteriorly directed pteroid had been anticipated by Hankin (1912), who presented it and a medially directed pteroid as alternative reconstructions without advocating either; however, Hankin and Watson (1914) rejected the idea in a footnote and carried on confidently with a medially directed pteroid. Frey and various co-authors (Frey and Riess, 1982; Frey and Martill, 1994; Unwin et al., 1996; Frey, Buchy, and Martill, 2003; but not Frey et al., 2006) continued to advocate an anteriorly-directed pteroid, and Pennycuick (1986, 1988) presented variant interpretations in which the pteroid held an extensor tendon away from the wrist to increase its leverage or could be flipped from a medially directed position to an anteriorly directed one to spread an extensive propatagium and then be flipped back to furl it. Meanwhile, Padian (1984), Wellnhofer (1985, 1987, 1991a), Padian and Rayner (1993), and Bennett (1991, 2000, 2001) presented various arguments against reconstructions with an anteriorly directed pteroid.

This brings us back to Wilkinson and colleagues (2006:119), who suggested that "at present, it is not possible to resolve the debate about pteroid function using fossil evidence alone" and argued for an anteriorly directed pteroid on the grounds of: 1)
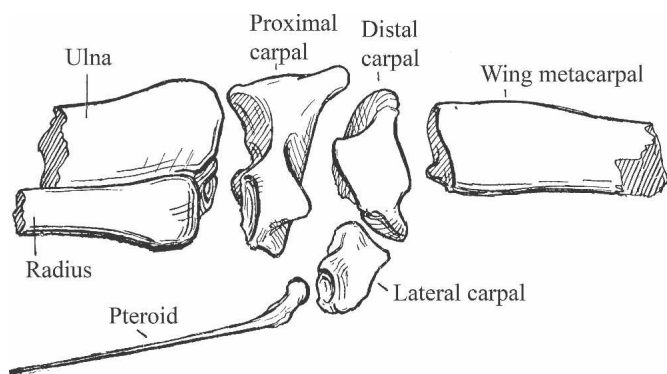
FIGURE 1.   Exploded reconstruction of the left carpus of *Istiodactylus latidens* in dorsal view from Hankin and Watson (1914), showing the pteroid articulating with an upward directed fovea of the preaxial (= lateral) carpal.

their interpretation of the motion of the pteroid on the preaxial carpal in *Anhanguera santanae*, and 2) wind-tunnel tests of model wing reconstructions in which an anteriorly directed pteroid controlling an extensive propatagium (Fig. 2) produced more lift than a reconstruction with a medially directed pteroid and a traditional-sized propatagium. Wilkinson and colleagues'

(2006) interpretation of the pterosaurian carpus had the preaxial carpal oriented with the fovea directed anteroventrally, the articular end of the pteroid articulating in the fovea, and the pteroid directed anteriorly and slightly downward at maximal extension and capable of combined flexion and rotation to a ventromedially directed orientation for wing folding. Regarding my arguments against a fovea-pteroid articulation, they wrote:

> "Bennett (2001) noted a small oval sesamoid bone is sometimes found preserved within the fovea of the medial carpal, and argued that the pteroid did not articulate here, but on a shallow articular facet on the ventral side of the medial carpal near its base. We found no such articular facet in any of the medial carpals we examined, and therefore reject this idea." (Wilkinson et al., 2006:121)

They went on to suggest that:

> "... the sesamoid in question was originally embedded in the tendon of a pteroid extensor or flexor muscle where it passed over the medial carpal, and ... was pulled into the fovea after death in some specimens as a result of disarticulation of the carpal-pteroid joint." (Wilkinson et al., 2006:121)

Wilkinson and colleagues (2006) failed to realize the significance of the sesamoid, and failing to recognize the traces of the articu-
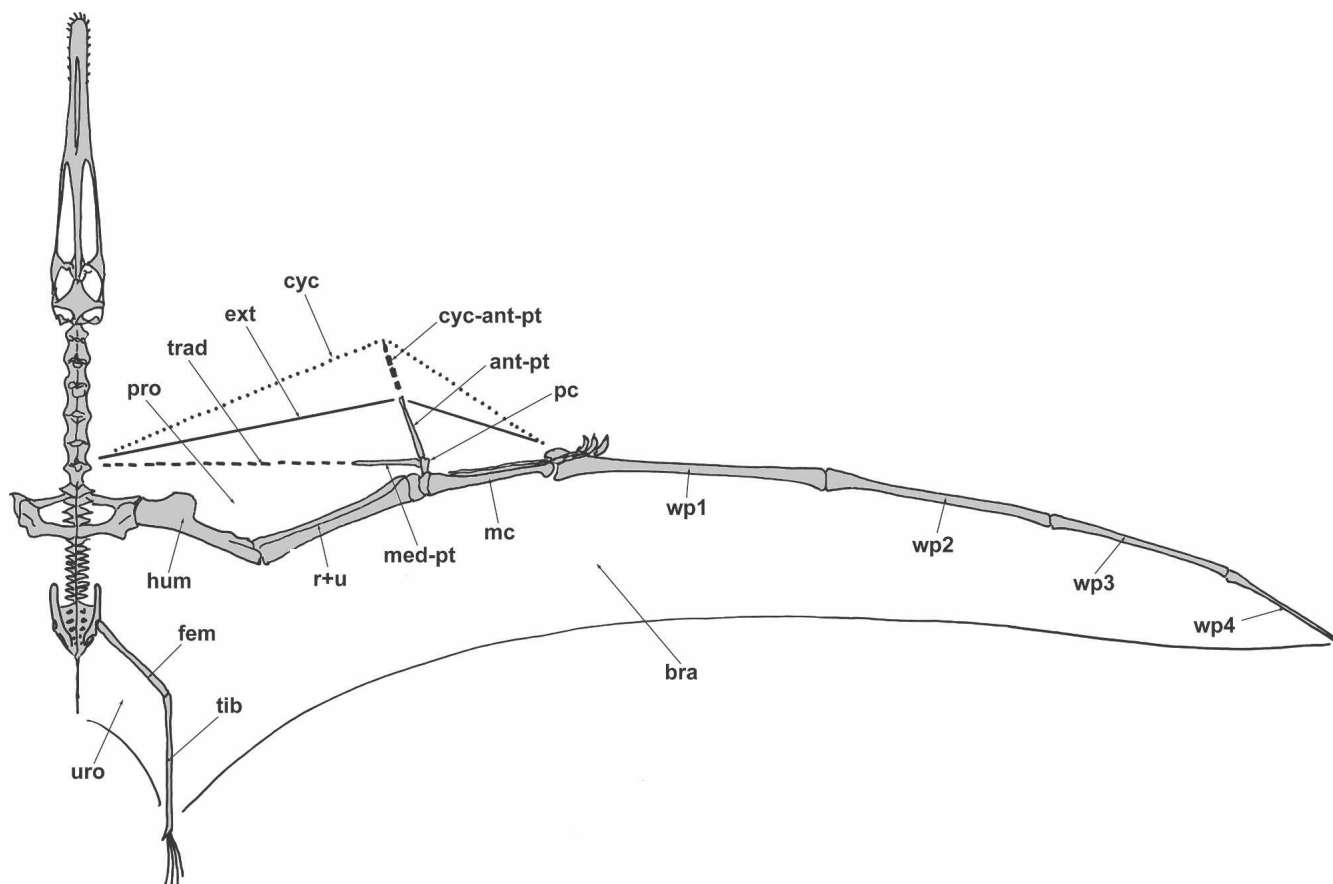

FIGURE 2.   Skeletal reconstruction of *Anhanguera* (modified from Wilkinson et al., 2006) showing a medially directed pteroid and traditional propatagium (dashed line), the anteriorly directed pteroid and extensive propatagium advocated by Wilkinson and colleagues (2006; dashed line), and a longer anteriorly directed pteroid 76% ulnar length as in *Cycnorhamphus* and resulting larger propatagium (dotted line). See text for explanation. **Abbreviations**: **ant-pt**, anteriorly directed pteroid; **bra**, brachiopatagium; **cyc**, leading edge of larger propatagium; **cyc-ant-pt**, *Cycnorhamphus*-length anteriorly directed pteroid; **ext**, leading edge of extensive propatagium; **fem**, femur; **hum**, humerus; **mc**, metacarpus; **med-pt**, medially directed pteroid; **pc**, preaxial carpal; **pro**, propatagium; **r+u**, radius and ulna; **tib**, tibia; **trad**, leading edge of traditional propatagium; **uro**, uropatagium; and **wp1-4**, wing phalanges 1-4.

lation for the pteroid in the small sample of preaxial carpals they examined, they chose to ignore and dismiss evidence that falsifies their hypothesis of an anteriorly directed pteroid. I reject their thesis that the available fossil evidence is insufficient to resolve the controversy about pteroid function, and in this article will review the fossil evidence and its implications for the traditional interpretation of pteroid orientation and function as well as alternative interpretations.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; **BSP**, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; **FHSM**, Fort Hays State University Sternberg Museum; **FMNH**, Field Museum of Natural History, Chicago; **KUVP**, University of Kansas Natural History Museum, Lawrence; **MCSNB**, Museo Civico di Scienze Naturali, Bergamo, Italy; **PTH**, Philosophisch-Theologische Hochschule, Eichstätt; **SMNS**, Staatliches Museum für Naturkunde Stuttgart; **SoS**, JuraMuseum (Solnhofen Sammlung), Eichstätt; and **YPM**, Peabody Museum of Natural History, Yale University, New Haven.

THE PREAXIAL CARPAL AND THE SESAMOID

Marsh (1882) noted that three different sesamoids were sometimes found associated with the carpus of *Pteranodon*, and Bennett (1991, 2001) noted that one of them, termed Sesamoid A to distinguish it from Sesamoids B and C, was found articulated in the fovea of the preaxial carpal of various specimens of *Pteranodon* and other taxa. The holotype of *Eudimorphodon ranzii* (MCSNB 2888; Wild, 1978; Fig. 3A) has Sesamoid A articulated in the fovea of the left preaxial carpal while the left pteroid lies with its articular end some millimeters proximal to the preaxial carpal. A referred specimen of *Peteinosaurus zambellii* (MCSNB 3359; Wild, 1978, but see Dalla Vecchia, 2003; Fig. 3B) presents almost an identical picture with Sesamoid A articulated in the fovea of the left preaxial carpal and the left pteroid lying a short distance proximal to the preaxial carpal. In both cases, Wild (1978) identified Sesamoid A as a small carpal but did not otherwise comment on it. A specimen of *Dorygnathus banthensis* (SMNS 51827; Fig. 4A) preserves Sesamoid A articulated in the right preaxial carpal. Articulated specimens from the Solnhofen Limestones usually have their joints damaged and obscured by amorphous masses of calcite, but some specimens clearly preserve Sesamoid A in the fovea of the preaxial carpal despite the calcite. SoS 4009 (=PTH 49-4; Fig. 4B), a large specimen of *Rhamphorhynchus muensteri*, preserves Sesamoids A articulated in both preaxial carpals and in each carpus the articular end of

the pteroid lies a short distance proximal to the preaxial carpal. A specimen of *Pterodactylus antiquus* (SoS 4592 [=PTH 1962/148], Fig. 4C) preserves Sesamoid A articulated in the preaxial carpal of the right carpus, although on the left Sesamoid A is not articulated in the fovea. The specimen of *Anhanguera santanae* (AMNH 22555) used by Wilkinson and colleagues (2006) as the basis of their reconstruction was preserved with both Sesamoids A articulated in their respective preaxial carpals (Fig. 5A), although Wellnhofer (1991b) did not document them as being found in articulation. Various specimens of *Pteranodon* (Bennett, 1991, 2001; Fig. 5B) are also preserved with Sesamoid A in the fovea. In addition to the above examples, Sesamoids A have also been found, but not documented as being found articulated in the preaxial carpal, in the holotypes of *Araripesaurus castilhoi* (Price, 1971), *Santanadactylus araripensis* (BSP 1982.I.89; Wellnhofer, 1985), and *S. spixi* (BSP 1980.I.121; Wellnhofer, 1985), and in undescribed materials of *Quetzalcoatlus* presently under study by Wann Langston, Jr. Although only a modest number of specimens are preserved with Sesamoid A articulated in the fovea of the preaxial carpal, they span the temporal, phylogenetic, and size ranges of pterosaurs; from the small basal *Eudimorphodon* of the Upper Triassic, to the mid-sized advanced rhamphorhynchoid *Rhamphorhynchus* and the small basal pterodactyloid *Pterodactylus* of the Upper Jurassic, to the large advanced pterodactyloid *Pteranodon* from the Upper Cretaceous.

Sesamoids of all types usually ossify rather late in ontogeny, so the absence of Sesamoid A in a specimen may simply indicate that the sesamoid was not ossified, although it is also possible that in some specimens it may have been ossified but was lost before preservation. However, when Sesamoid A is present in articulated specimens, it is almost always found in the fovea of the preaxial carpal rather than anywhere else. In contrast, the pteroid has not been found preserved with its articular end in the fovea of the preaxial carpal in even one of all the available specimens of pterosaurs, more than 3000 specimens according to Unwin (2006).

In all the specimens listed above that preserve Sesamoid A in the fovea of the preaxial carpal, it is appropriately sized to fit in the fovea. In *Pteranodon*, Sesamoid A is suboval and has a convex articular surface covered with the same texture found on articular surfaces of typical synovial joints, and a flat nonarticular surface that is rugose with a distinctive linear pattern of striations that reflects the fact that it developed in intimate association with a tendon (Bennett, 1991, 2001; Fig. 5B,C). The width of the striated area of Sesamoid A perpendicular to the
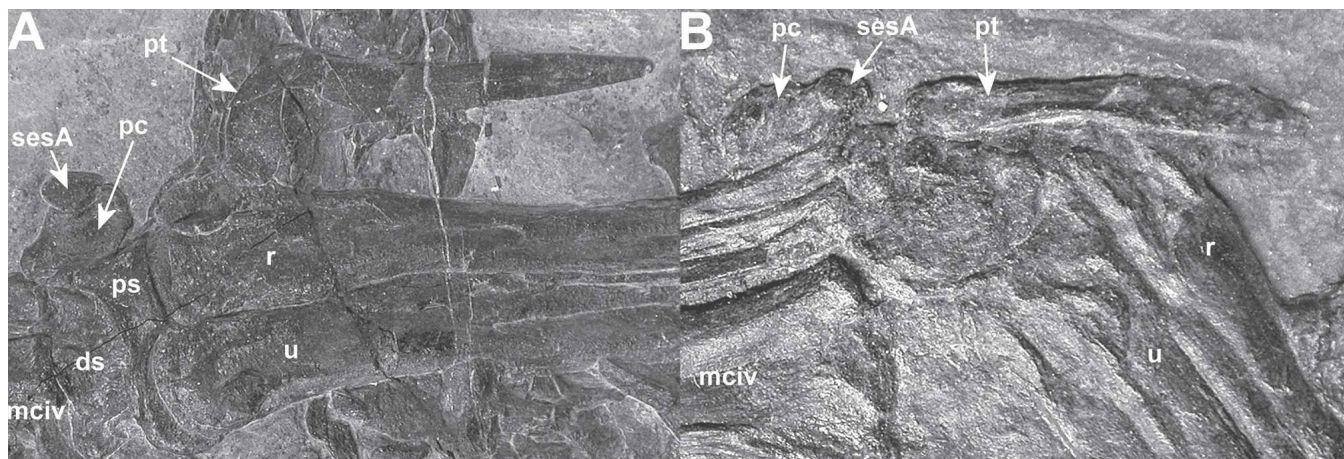

FIGURE 3. Photographs of **A**, the left carpus of *Eudimorphodon ranzii*, MCSNB 2888, in dorsal view; and **B**, the left carpus of referred specimen of *Peteinosaurus zambellii*, MCSNB 3359, in dorsal view. **Abbreviations**: **ds**, distal syncarpal; **mciv**, metacarpal IV; **pc**, preaxial carpal; **ps**, proximal syncarpal; **pt**, pteroid; **r**, radius; **u**, ulna; **sesA**, Sesamoid A; and **wp1**, wing phalanx 1. Photographs courtesy of the MCSNB.
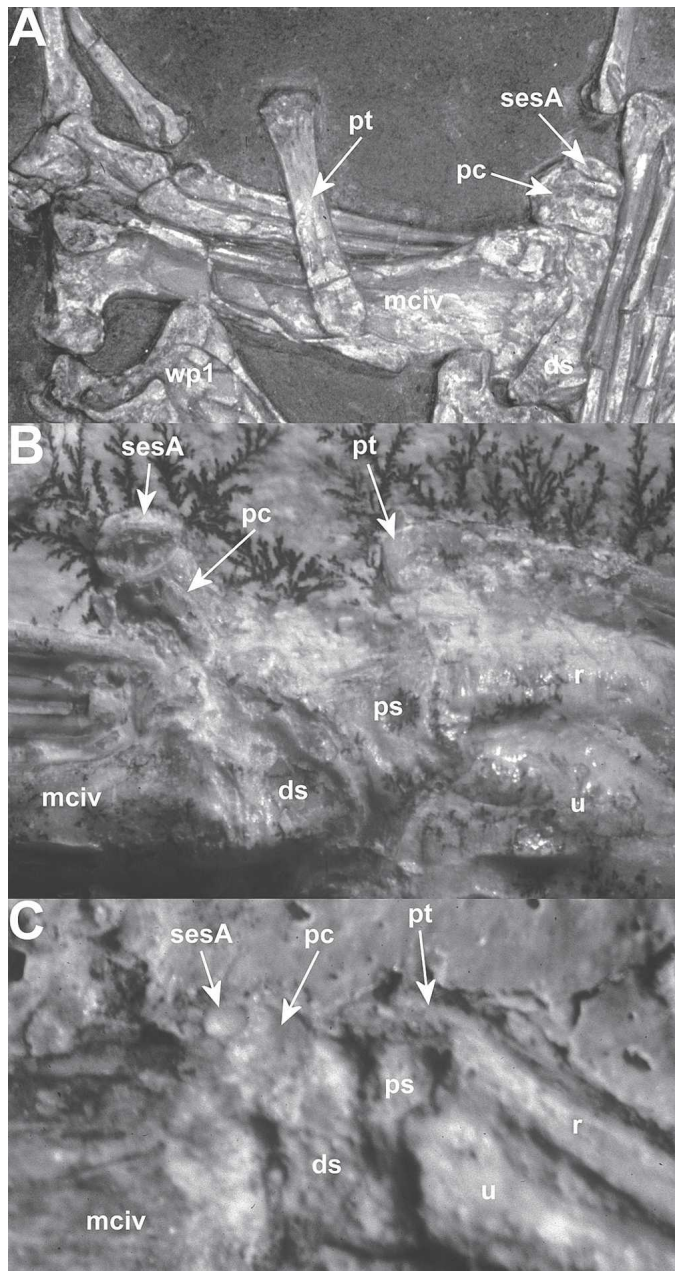
FIGURE 4. Photographs of **A**, the right carpus of *Dorygnathus banthensis*, SMNS 51827, in ventral view; **B**, the left carpus of *Rhamphorhynchus muensteri*, SoS 4009, in dorsal view; and **C**, the right carpus of *Pterodactylus antiquus*, SoS 4592, in dorsal view. Abbreviations as in Figure 3.

lineations is 14.5 mm in YPM 1175 (Fig. 5C), a specimen with an estimated wingspan in life of ~6.5 m. The associated tendon must have been at least that wide, which indicates that the tendon was quite large and that of a large and powerful muscle. The fact that a sesamoid developed in association with the tendon indicates that the tendon was subjected to much force as it passed over some part of the wrist, and the markedly convex articular surface with a surface texture indicative of a covering of articular cartilage indicates that Sesamoid A articulated with a complementary concavity. Specimens of *Pteranodon* are usually crushed and distorted to some extent, so one cannot compare the convexity with available concavities with confidence, but in the case of AMNH 22555, in which the bones were preserved uncrushed in a lime-

stone concretion and Sesamoid A was subsequently freed from the fovea, the convex curvature of Sesamoid A is complementary to the concavity of the fovea in which it was found, allowing for thin coverings of articular cartilage.

The presence of Sesamoid A in pterosaurs from their entire temporal and phylogenetic range plus the fact that when present it is almost always found articulated in the fovea of the preaxial carpal in articulated specimens indicates that all pterosaurs had a large tendon from a large and powerful muscle passing over the preaxial carpal. Bennett (1991, 2001) noted that the tendon must have been that of an extensor of the wrist because the preaxial carpal was capable of only a modest range of lateral and medial flexion, which was enough to accommodate movements of a tendon inserting on the metacarpal but would not be able to accommodate the greater range of movement that would be found in the tendon of an extensor of the wingfinger that crossed both the carpus and the metacarpophalangeal joint. The pattern of musculature in pterosaurs can be reconstructed based on comparisons of preserved osteological correlates of muscles with the pattern of muscles and their osteological correlates in the living relatives of pterosaurs (Witmer, 1995; Bennett, 2003a). Because the tendon was inserting on metacarpal IV, it must have been *M. flexor carpi ulnaris*. The *M. flexor carpi ulnaris* inserts on the ulna, pisiform, and ulnare in extant turtles, the pisiform in *Sphenodon* and extant lizards, and the ulnare in extant crocodilians and birds (Dilkes, 2000). In pterosaurs it would expected that the insertion of *M. flexor carpi ulnaris* would have moved distally as in birds to improve its leverage. The *M. flexor carpi radialis* inserts on the radius and/or the base of metacarpal I in extant turtles, the medial radius and radiale in *Sphenodon* and extant lizards, and the radiale in extant crocodilians (Dilkes, 2000). In pterosaurs the insertion of *M. flexor carpi radialis* probably moved distally at least onto the distal syncarpal, but there are no muscle scars or other evidence to suggest that it inserted further distally or that it was a particularly large muscle. Given the large size of the tendon of *M. flexor carpi ulnaris* and the absence of evidence of a large *M. flexor carpi radialis*, *M. flexor carpi ulnaris* must have been the primary extensor of the carpus. By passing over the preaxial carpal before inserting on the metacarpal IV, the tendon was held away from the axis of flexion and extension of the carpus and its leverage increased, but at the same time bending over the preaxial carpal imposed large forces on the tendon, which led to the development of Sesamoid A. Short (1914) reconstructed a similar tendon of an unidentified muscle originating on the humerus and inserting on the anterior surface of the wing metacarpal, but attaching to the non-articular end and shaft of the pteroid (the articular end of which was articulated in the fovea of the preaxial carpal) and then extending from the bend of the pteroid to insert on the anterior surface of metacarpal IV. Short's reconstruction is incorrect in that the pteroid did not articulate in the fovea and there is no evidence that a large tendon attached to it.

Frey and colleagues (2006) reconstructed an extensor muscle of the wingfinger associated with Sesamoid A and passing over the preaxial carpal based on the pattern of muscles in birds and the preserved position of an ossified tendon in a specimen of *Nyctosaurus* (Bennett, 2003b). However, the ossified tendon may have moved somewhat as the surrounding soft tissues decayed, so its position may not be indicative of its position relative to the preaxial carpal in life, and as noted above the limited lateral and medial flexion of the preaxial carpal prohibits it from being associated with an extensor of the wingfinger.

The available evidence supports the interpretation that Sesamoid A was not preserved in the fovea by chance in occasional specimens, but rather belonged there, which falsifies Marsh's (1882) half of the traditional interpretation of the pteroid as well as Wilkinson and colleagues' (2006) anteriorly directed pteroid interpretation. Wilkinson and colleagues (2006:121) would have
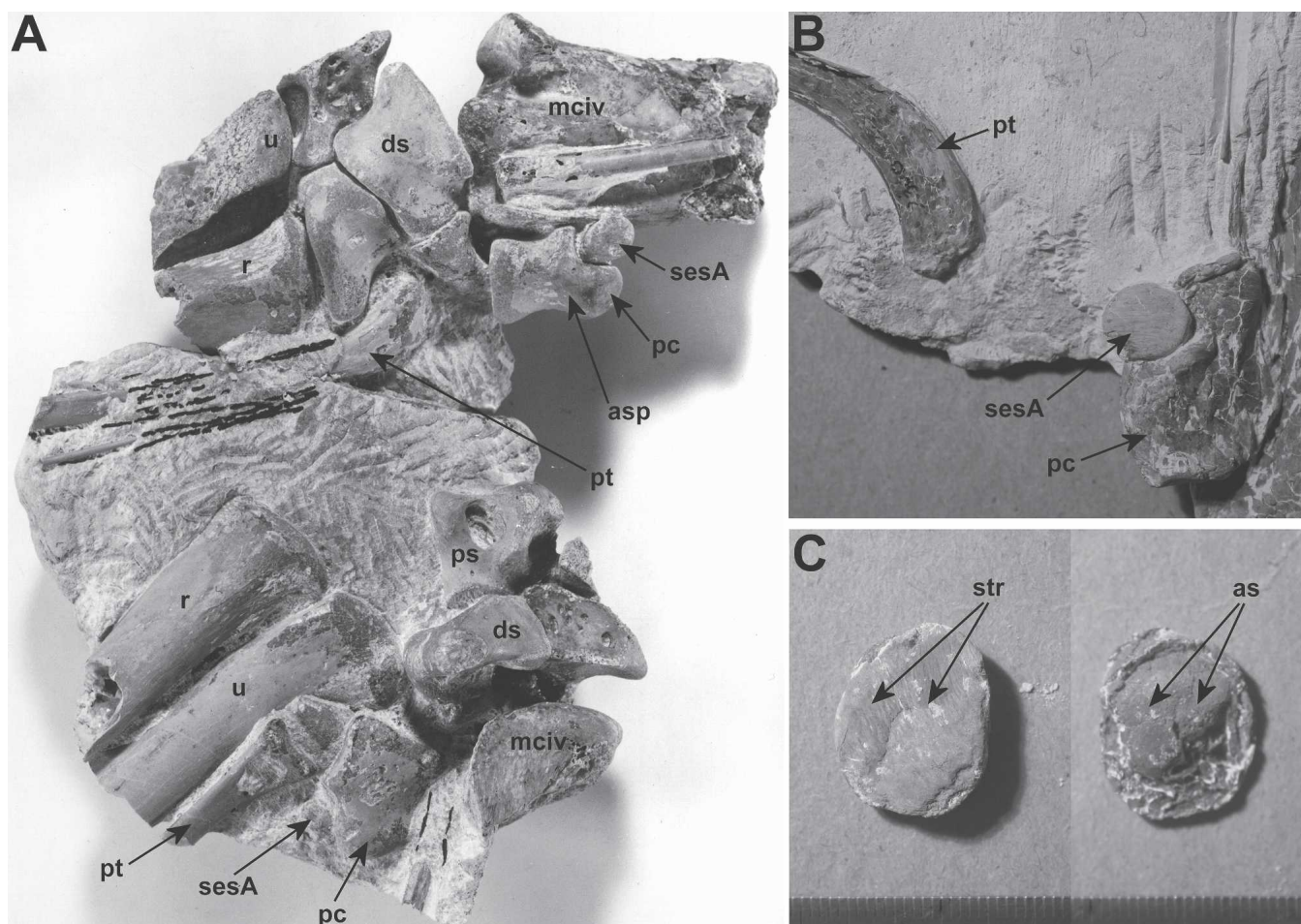
FIGURE 5. Photographs of **A**, the left (above) and right (below) carpal regions of *Anhanguera santanae*, AMNH 22555, in dorsal view, slightly disarticulated but *in situ* during preparation; **B**, the right preaxial carpal, Sesamoid A, and pteroid of *Pteranodon* sp. indet., YPM 2300, in dorsal or lateral view; and **C**, non-rticular (left) and articular (right) surfaces, respectively, of Sesamoid A of *Pteranodon longicep*s, YPM 1175. **Abbreviations**: **art**, articular surface for fovea; **asp**, articular surface for pteroid; **ds**, distal syncarpal; **mciv**, metacarpal IV; **pc**, preaxial carpal; **ps**, proximal syncarpal; **pt**, pteroid; **r**, radius; **str**, striations for attachment to its tendon; **u**, ulna; and **sesA**, Sesamoid A. Photograph of AMNH 22555 courtesy of P. Wellnhofer.

us accept that Sesamoid A was associated with a hypothetical muscle that extended or flexed the pteroid, that in every articulated specimen the pteroid had been disarticulated from the fovea, and that Sesamoid A was then "pulled into the fovea . . . as a result of disarticulation" to usurp the pteroid's proper place. Given the area of the propatagium that it would be controlling, flexion or extension of an anteriorly directed pteroid would not require a large muscle, so the muscle would not have needed a large tendon. Without a large tendon, there would be no need for a large sesamoid. Parsimony leads us to reject their interpretation and accept that Sesamoid A belonged in the fovea. If Wilkinson and colleagues wish to explain away the presence of Sesamoid A in the fovea as an artifact of disarticulation, perhaps they can provide evidence to support their assertion that there was a large pteroid extensor or flexor that required a large sesamoid, and perhaps they can also explain why no pteroid has ever been found articulated in the fovea, and what the strongly convex articular surface of Sesamoid A articulated with if not the fovea of the preaxial carpal.

PREAXIAL CARPAL ORIENTATION

The morphology of the preaxial carpal of Triassic and Jurassic pterosaurs is not well understood because of its small size and because the individual bones usually are not freed from matrix.

The preaxial carpal is often short and small, and the distal fovea in which the sesamoid articulated may be only slightly offset and angled. In the large pterodactyloids of the Cretaceous the preaxial carpal is laterally compressed, and it articulated with the distal syncarpal through a biaxial joint, convex on the distal syncarpal and concave at the base of the preaxial carpal. Its fovea is markedly offset and angled from the long axis of the carpal. The articulation with the distal syncarpal is shaped such that it seems to permit the preaxial carpal to be reconstructed either with the fovea directed anterodorsally or rotated 180° so that the fovea is directed anteroventrally, and as a consequence there has been disagreement as to the correct orientation. Hankin and Watson (1914; Fig. 1) reconstructed the carpus of *Istiodactylus latidens* with the preaxial carpal oriented so that the fovea was anterodorsally directed, but the specimens of *Istiodactylus* did not preserve the carpal in articulation (Hooley, 1913), so Hankin and Watson's rationale for the anterodorsal orientation is unknown. Padian (1984) reconstructed the carpus of a disarticulated large pterodactyloid with the preaxial carpal oriented so that the fovea was anteroventrally directed, and noted that there was a slight medial component to the orientation of the fovea as well. It is likely that he reconstructed the carpal in that orientation because he thought the medial component would fit best with the traditional interpretation of pteroid articulation:

"The [fovea] . . . is open ventrally, anteriorly, and medially. The medial opening suggests an orientation for the pteroid consistent with the traditional reconstruction." (Padian, 1984:521)

Wellnhofer (1985) reconstructed the partially disarticulated carpus of *Santanadactylus spixi* and stated that the fovea was directed anterodorsally and slightly medially, and like Padian noted that the medial orientation was consistent with the traditional interpretation of pteroid articulation. However, in a later paper Wellnhofer (1991b) reconstructed the carpus of *Anhanguera santanae* and, citing Padian (1984), stated that the fovea was directed anteroventrally and slightly medially without referring to his own 1985 paper and again noted that the medial component was consistent with the traditional interpretation of pteroid articulation. Although it seems that Wellnhofer changed his mind about the orientation of the preaxial carpal, I cannot reconcile the fact that he described both the anterodorsally directed fovea of *S. spixi* and anteroventrally directed fovea of *Anhanguera* as being directed somewhat medially; perhaps the right and left preaxial carpals of *S. spixi* were misidentified after being freed from the concretion. Bennett (1991, 2001) reconstructed the preaxial carpal with the fovea facing anterodorsally based on the preserved orientation in *Pteranodon* specimens (e.g., YPM 2348, FSHM 2062), and noted that in this orientation Padian's (1984) "medial" component becomes a lateral component.

Articulated specimens show that the preaxial carpal was oriented with the fovea directed anterodorsally (Figs. 3, 4). The specimen of *Anhanguera santanae* (AMNH 22555, Fig. 5A) used by Wilkinson and colleagues (2006) as the basis of their reconstruction also supports this interpretation. The specimen was slightly disarticulated and preserved the preaxial carpals lying with the long axis of their oval cross-section oblique to the plane of the concretion and with the border bearing the fovea more dorsal. This could have resulted from a modest (~70°) rotation from an anterodorsal orientation caused by the tendon of *M. flexor carpi ulnaris* attached to the wing metacarpal pulling Sesamoid A and the dorsal side of the carpal laterally as the specimen was slightly disarticulated, whereas I cannot offer any explanation as to how the greater (~120°) rotation could have resulted if the carpal were normally oriented with the fovea anteroventral.

It is apparent that reconstructions of the preaxial carpal with the fovea directed anteroventrally have not been based on evidence from articulated specimens, but rather have been based on the incorrect notion that the pteroid articulated in the fovea. The available evidence supports the interpretation that the preaxial carpal was oriented such that the fovea was directed anterodorsally, which is inconsistent with, and so falsifies, Padian's (1984) and Wellnhofer's (1991b) reconstructions of a medially directed pteroid articulating in the fovea as well as Wilkinson and colleagues' (2006) anteriorly directed pteroid interpretation.

The anterodorsal orientation of the fovea is consistent with the tendon on *M. flexor carpi ulnaris* passing over the preaxial carpal because the muscle origin, Sesamoid A, and muscle insertion would then lie in a subhorizontal plane appropriate for wrist extension, whereas with an anteroventral orientation of the preaxial carpal the muscle origin, Sesamoid A, and muscle insertion would lie in an oblique plane inappropriate for wrist extension. Lastly, with the anterodorsal orientation of the preaxial carpal, the slight lateral component to the orientation of the fovea, although incompatible with the notion that the pteroid articulated in it, reflects the bend in the tendon of *M. flexor carpi ulnaris* as it passed posterolaterally to its insertion.

PTEROID MORPHOLOGY AND ARTICULATION

All pterosaurs possessed pteroid bones, and although there was a general trend of increasing relative size, there was much variation in shape (Fig. 6). In *Anurognathus* the pteroid is a
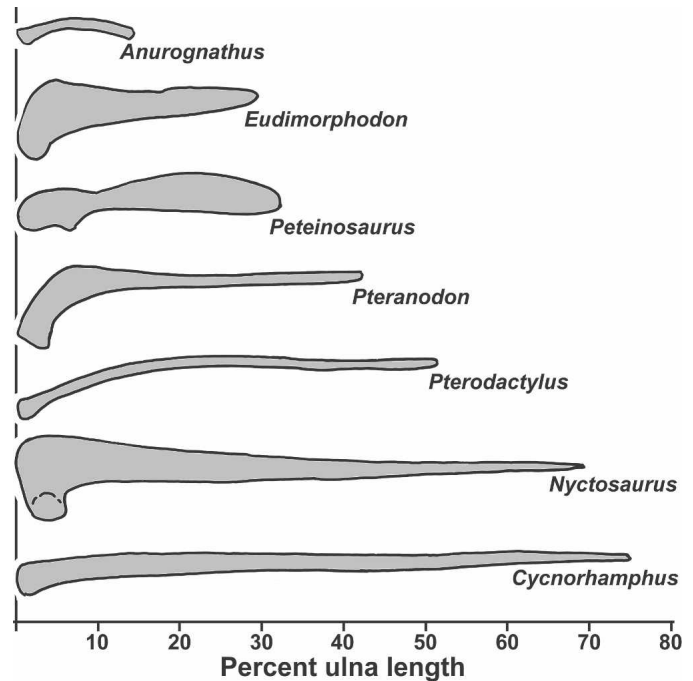

FIGURE 6. Drawings of pteroids of various taxa arranged in order of increasing size relative to ulna length with the articular end to the left: *Anurognathus ammoni* (BSP 1922.1.42; Wellnhofer, 1975; 14%); *Eudimorphodon ranzi* (MCSNB 2888; Wild, 1975; 30%); *Peteinosaurus zambellii* (MCSNB 3359; Wild, 1975; 33%); *Pterodactylus kochi* (BSP AS.XIX.3; Wellnhofer, 1968; 53%) *Pteranodon* sp. indet. (KUVP 2062; 43%); *Nyctosaurus gracilis* (FMNH 25026; Williston, 1903; 70%); and *Cycnorhamphus suevicus* (Plieninger, 1907; 76%).

simple gently-curved rod of bone only 11% to 14% of ulnar length, which may nearly represent the plesiomorphic condition in pterosaurs because anurognathids are the sister group to all other pterosaurs (Kellner, 2003; Bennett, in press). The referred Milano specimen of *Eudimorphodon* has a simple rod-like pteroid much like that of *Anurognathus*, whereas in the holotype of *Eudimorphodon ranzii* the pteroid is 30% of ulnar length, robust, and hatchet-shaped with the articular end angled from the tapering shaft. In *Dorygnathus*, *Campylognathoides*, and *Rhamphorhynchus* the pteroid is simple and straight with a rather squared-off articular end and a blunt tip. Wellnhofer (1975, fig. 12a, b) suggested that the pteroid of *Rhamphorhynchus* consisted of two elements, a short basal element and a longer distal element; however, the two elements are the short preaxial carpal and the longer pteroid articulating with the side of the preaxial carpal. In basal pterodactyloids the pteroid is long and slender, gently curving and tapering. The articular end of the pteroid of *Pterodactylus antiquus* is suboval to subcircular and markedly convex. The pteroid of *Cycnorhamphus suevicus* is much like that of *Pterodactylus*, but reaches 76% of ulnar length, which is the relatively longest pteroid known. The pteroid of *Nyctosaurus* is 70% of ulnar length with a straight shaft tapering to a point, and differs from other pteroids in that the convex articular surface is at a 90° angle to the long axis of the bone. The pteroid of *Pteranodon* is ~43% of ulnar length and is reminiscent of the pteroid of *Eudimorphodon ranzii* with a short section adjacent to the articulation angled at 40° to 45° from the remainder of the tapering shaft. The articular end is suboval and moderately convex, the shaft ends in a blunt point. and the anterior margin of the bend has a rugose muscle attachment, but there is no evidence of muscle or tendon attachments on the distal end of the bone. No complete example of the pteroid of *Anhanguera* is

known so its relative length is unclear, but it is similar to that of *Pteranodon* except that the articular end is a saddle joint.

Because the sesamoid articulated in the fovea of the preaxial carpal, the pteroid could not, and therefore: 1) any complementarity between the shape of the articular end of the pteroid and the fovea is coincidental, and 2) the pteroid must have articulated elsewhere. Although there is some complementarity in taxa such as *Pteranodon* and *Santanadactylus spixi*, other taxa such as *Anhanguera* do not have any, and it is a testament to the ingenuity of Wilkinson and colleagues (2006) that they were able to conclude that the two bones fitted together—when I first encountered the articular end of the pteroid of *Anhanguera*, I viewed its lack of complementarity with the fovea as additional evidence that the pteroid did not articulate there.

Although I became convinced in 1987 that the pteroid did not articulate in the fovea, it was immediately apparent where it did articulate. Wild (1978) suggested that the pteroid of *Eudimorphodon ranzii* articulated with the distal end of the radius, but no articular surface was evident in the taxa I examined. Eventually I located the articular surface for the pteroid on the preaxial carpal, but it is not clearly differentiated from the remainder of the carpal and might have gone unnoticed had it not been for a specimen of *Pteranodon* (YPM 42819) that includes a preaxial carpal crushed dorsoventrally rather than laterally as is typical of *Pteranodon* material. The dorsoventral crushing made the articular surface prominent and drew attention to it. However, I erred in transferring the location of the articular surface onto the usual laterally crushed carpals, incorrectly illustrated it in my dissertation (Bennett, 1991), and did not notice the error until after the description was in press (Bennett, 2001, figs. 81, 82). Here I correct that error and also describe the articular surface for the pteroid on the preaxial carpals of *Anhanguera* and *Nyctosaurus*.

In *Pteranodon* the articular surface on the preaxial carpal is an indistinctly marked convex oval on the medial surface (Fig. 7), although in KUVP 2066 and YPM 2499, old individuals with prominent muscle attachment scars, the articular surface is surrounded by rugose bone that probably represents the margin of the joint capsule. The fact that the articular surface is indistinct indicates that the joint was not as well developed as other forelimb joints, probably because it was only lightly loaded in compression. When articulated with the preaxial carpal the pteroid is directed medially, and the combination of the convex oval articular surfaces on the pteroid and the preaxial carpal results in a freely mobile joint enabling the pteroid to be flexed and extended in the horizontal plane, depressed and elevated in a vertical plane, and rotated a little, but it could not be extended anteriorly.

The available specimens of *Anhanguera* are relatively immature, and their joint surfaces and muscle attachment scars are not as well marked as in fully mature specimens of *Pteranodon*. Given that the articular surface for the pteroid on the preaxial carpal is indistinct in mature specimens of *Pteranodon*, it should be virtually invisible in the immature specimens of *Anhanguera*, and so it is. There is almost no visible trace of an articular surface and the faint articular surface of the left preaxial carpal of AMNH 22555 shows up better in the photograph during preparation (Fig. 5A) than with the freed bone in hand. The articular surface lies in the same place as the convex oval articular surface in *Pteranodon* on the medial surface of the preaxial carpal and forms a saddle-shaped surface that is complementary to the saddle-shaped articular end of the pteroid. Together the two surfaces formed a saddle joint. The pteroid is directed medially when articulated with the preaxial carpal, and the saddle joint allows the pteroid to be flexed and extended in the horizontal plane, depressed and elevated in a vertical plane, and rotated a little, but it could not be extended anteriorly (Fig. 8).

The pteroid of *Nyctosaurus* differs from that of other pterosaurs in that the articular surface is at 90° to the long axis, and as a consequence, the pteroid could not be directed medially toward the body if it articulated with the medial side of the preaxial carpal. Instead, the articulation is on the ventral surface of the preaxial carpal and angled somewhat anteriorly. When articulated with the preaxial carpal the pteroid is directed medially, and the combination of the flat to convex articular surface on the preaxial carpal and the convex articular surface on the pteroid the results in a freely mobile joint enabling the pteroid to be flexed and extended in the horizontal plane, depressed and el-
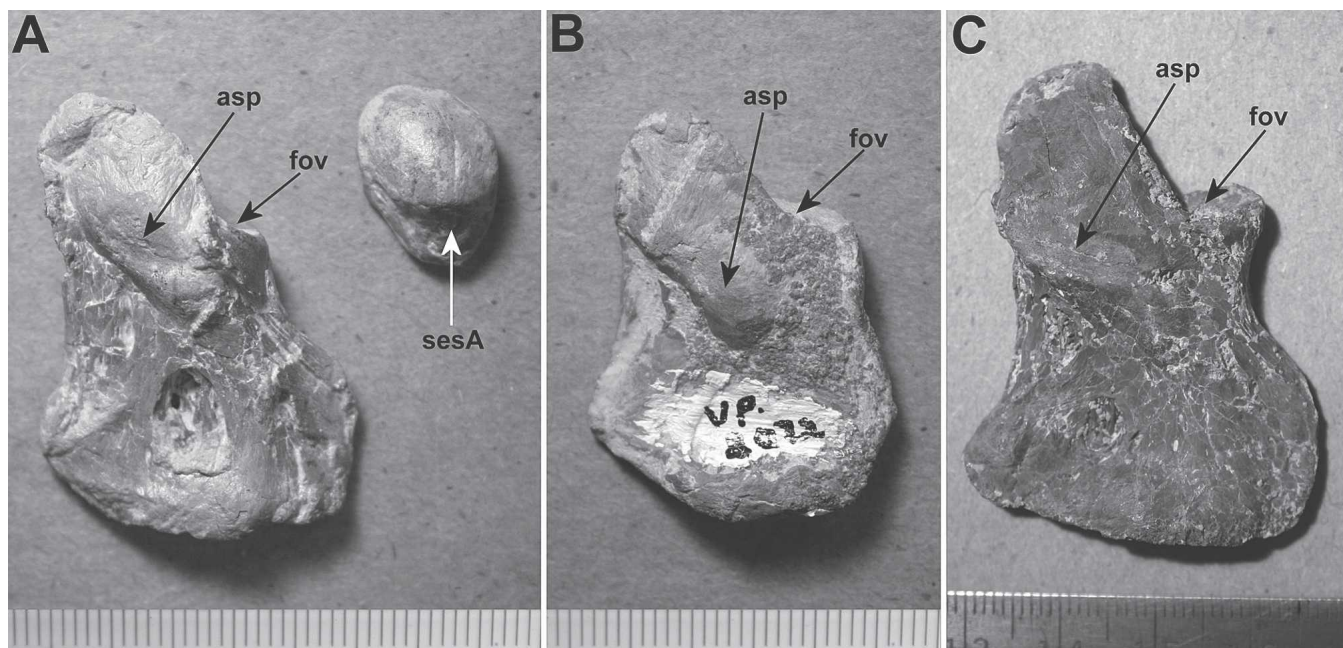

FIGURE 7. Photographs of the medial surface of right preaxial carpals of *Pteranodon* sp. indet. showing the articular surface for the pteroid: **A**, KUVP 2120; **B**, KUVP 2072; and **C**, YPM 2414. Small gradations in scales are mm.
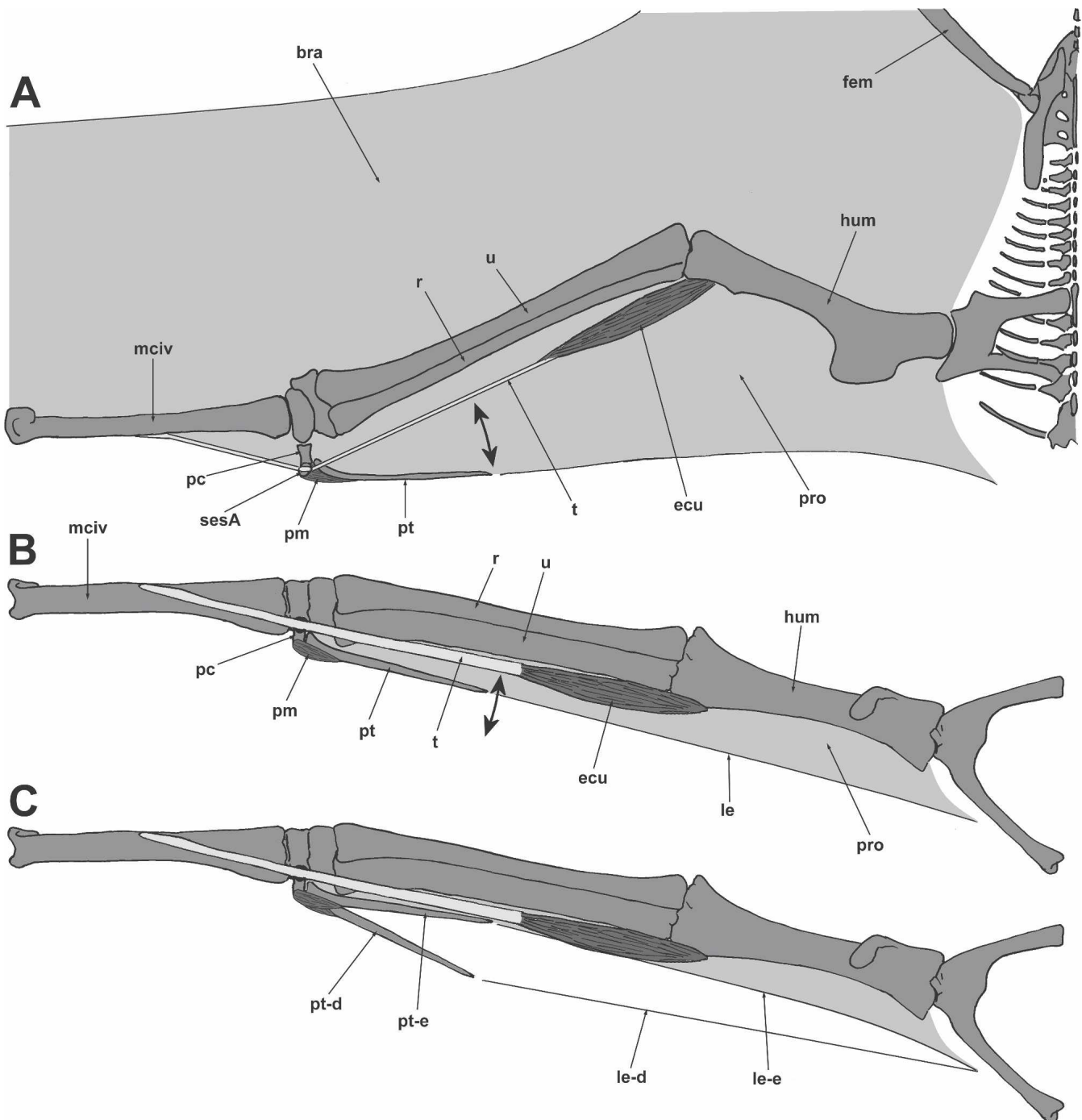
FIGURE 8. Reconstruction of the medial part of the right wing of *Anhanguera santanae*, based on AMNH 22555, extended as in flight in **A**, dorsal view with anterior toward the bottom of the page, and **B** and **C**, anterior views. A shows the pteroid extended anteriorly to spread the traditional-sized propatagium, and the double-headed arrow indicates flexion and extension of the pteroid in the horizontal plane. **B** shows the pteroid and leading edge of the propatagium in a neutral position and the double-headed arrow indicates elevation and depression of the pteroid in the vertical plane, whereas **C** shows changes in the position of the leading edge of the propatagium resulting from a 6° elevation and 12° depression of the pteroid from that neutral position. **Abbreviations**: **bra**, brachiopatagium; **ecu**, M. extensor carpi ulnaris; **fem**, femur; **hum**, humerus; **le**, leading edge of propatagium; **le-d**, leading edge of propatagium with depressed pteroid; **le-e**, leading edge of propatagium with elevated pteroid; **mciv**, metacarpal IV; **pc**, preaxial carpal; **pm**, pteroid muscle; **pro**, propatagium; **pt**, pteroid; **pt-d**, pteroid depressed 12°; **pt-e**, pteroid elevated 6°; **r**, radius; sesA, Sesamoid A; **t**, tendon of M.extensor carpi ulnaris; and **u**, ulna.

evated in a vertical plane, and rotated a little, but it could not be extended anteriorly.

As noted previously, the morphology of the preaxial carpal of Triassic and Jurassic pterosaurs is not well understood, and as a consequence it has not been possible to identify articular sur-faces for the pteroid on the preaxial carpals of those pterosaurs. However, articulated specimens of *Eudimorphodon*, *Peteinosaurus*, *Rhamphorhynchus*, and *Pterodactylus* preserve the pteroid with its articular end adjacent to the preaxial carpal and its shaft directed medially, and the pteroid must have articulated with the

side of the preaxial carpal as in large pterodactyloids. It also has not been possible to reconstruct joint motions of the pteroid on the preaxial carpal for those taxa, but the uniformity of allowed joint motions in *Pteranodon*, *Anhanguera*, and *Nyctosaurus*, combined with the similarity of preserved positions of the pteroid in articulated specimens, suggests that almost all pterosaurs had a pteroid extending medially from the wrist and capable of flexion, extension, depression, and elevation, but not capable of being directed anteriorly.

The traditional interpretation has the pteroid lying along the leading edge of a propatagium that approximates a straight line between the shoulder and wrist. Although traces of soft tissues of the patagia are only rarely preserved, and traces of the propatagium are even rarer than those of the brachiopatagium presumably because the propatagium was thinner and less substantial than the brachiopatagium, those few articulated specimens that do preserve traces of the propatagium include articulated pteroids directed medially toward the shoulder and lying along the leading edge of the propatagium. For example, in one specimen of *Pterodactylus* (BSP 1937.I.18; Broili, 1938; Wellnhofer, 1970) the pteroids are flexed to lie subparallel to the antebrachium and the propatagia are contracted compactly adjacent to the brachia and antebrachia.

The presence of the muscle scar along the ventral surface of the bend of the pteroid in *Pteranodon* indicates that a muscle inserted there. The muscle presumably originated on the preaxial carpal, and such a short muscle would have no need of a tendon. Muscle fibers originating on the ventral surface of the preaxial carpal and inserting on the ventral surface of the pteroid would be ventral to the carpopteroid joint and so could depress the pteroid. Muscle fibers originating on the anterior extremity of the preaxial carpal, anteroventral to the fovea, and inserting on the pteroid would be anterior to the carpopteroid joint, and so could extend the pteroid in the horizontal plane. Although the carpopteroid joint is a saddle joint in *Anhanguera*, a pteroid muscle originating on the anterior and ventral parts of the preaxial carpal could act to extend and depress the pteroid just as in *Pteranodon*. Similarly, in *Nyctosaurus* the little bit of the pteroid that is lateral to the articular presumably provided area for the insertion of a muscle originating on the preaxial carpal, and such a muscle could extend and depress the pteroid.

Various authors (e.g., Short, 1914; Bramwell and Whitfield, 1974; Padian, 1984; Wellnhofer, 1985; Frey et al. 2006) suggested that there was a tendon extending from the shoulder, along the leading edge of the propatagium, and attaching to the non-articular end of the pteroid. However, there is no evidence of such a tendon, and there would be no need for a discrete tendon or ligament because the tensile loads necessary to spread and control the propatagium could be borne by the network of collagenous, elastic, and probably muscle fibers within the propatagium (Bennett, 2000; Frey, Tischlinger, et al., 2003). The pteroid was probably embedded in that network with collagenous fibers attaching to its periosteum along its entire length. Such an arrangement would allow the pteroid to control the movements of the propatagium, and post-mortem contraction of the elastic fibers within the propatagium coupled with the loose joint between the preaxial carpal and the pteroid probably account for the fact that the pteroid is often found with its articular end pulled medially a short distance from the preaxial carpal (Figs. 3, 4).

The only exception to the traditional reconstruction with the pteroid extended medially along the leading edge of the propatagium seems to be the anurognathids, in which the pteroid is so short that it probably had to be directed anteromedially in order to approach the leading edge of the propatagium. However, in no pterosaur is there any evidence that the pteroid was directed anteriorly in such a way as to extend the leading edge of the propatagium significantly beyond a straight line passing from the shoulder to the wrist as advocated by Frey and Riess (1981) and Wilkinson and colleagues (2006).

PTEROID FUNCTION

A pteroid embedded in the leading edge of the propatagium and capable of flexion and extension in the horizontal plane and depression and elevation in the vertical plane could control the propatagium, spreading it, folding it, and helping to camber the wing (Fig. 8). Extension of the pteroid would spread the propatagium, although it is unclear how important that would be because increased tension in the propatagium itself as it was stretched between the shoulder and wrist or as intrinsic muscle fibers contracted could also have spread it. Flexion of the pteroid could aid in folding the propatagium compactly when the pterosaur was not in flight, so as to keep the propatagium out of the way for terrestrial locomotion. Depression of the pteroid would depress the entire leading edge of the propatagium, increasing the slope of the propatagium and thereby increasing the camber of the inner part of the wing between the body and hindlimb medially and the wrist laterally. Camber of the inner wing could also be controlled by rotation of the humerus, elevation and depression of the hindlimb, and changes in the pattern of tension within the brachiopatagium; however, the ability to control the propatagium would increase the pterosaur's control of overall wing shape, and increase its ability to deal with varying flight conditions.

Depression of the pteroid bones of *Pteranodon* and *Anhanguera* would form the leading edge into a shallow V because depression of the pteroid would swing its medial end downward and the leading edge of the propatagium would assume a straight line between the medial end of the pteroid and the attachment to the shoulder. However, it is possible that the longer, more flexible pteroids of *Pterodactylus* and *Cycnorhamphus* bent under tension so that the leading edge assumed a curve when depressed.

The pteroid of *Anurognathus* was so short that it had to be directed anteromedially in order to contact the leading edge of the propatagium. As a consequence, it could not significantly affect spreading and folding of the propatagium; however, depression and elevation of the pteroid would depress and elevate the leading edge of the propatagium to some extent, thereby altering inner wing camber. If the short pteroid could aid in controlling the propatagium to some extent in order to control the camber of the inner wing, then selection for improved control of the propatagium and inner wing camber could have resulted in increased pteroid size such as seen in more advanced pterosaurs.

Wilkinson and colleagues. (2006) advocated an anteriorly directed pteroid in part because depression of a large propatagium would increase lift for take-off and low speed flight. They tested only three alternate reconstructions: one with no propatagium; one with an immobile traditional propatagium with its leading edge extending in a straight line from the wrist to the shoulder; and their preferred reconstruction with a mobile extensive propatagium elevated and depressed by the pteroid. Unfortunately, they did not consider the possibility that a medially directed pteroid could depress the leading edge of a traditional-sized propatagium to increase lift in the same way that their anteriorly directed pteroid and extensive propatagium could. Although wind tunnel testing is beyond the scope of this article, it is likely that a model with a mobile traditional propatagium could increase lift for take-off and low speed flight, although to a lesser extent than the extensive propatagium of Wilkinson and colleagues (2006).

CONCLUSION

This article has shown that the fossil record provides sufficient evidence to settle the question of pteroid orientation and func-

tion. The evidence shows that the traditional interpretation of the pteroid is incorrect in that the pteroid did not articulate in the fovea of the preaxial carpal as Marsh (1882) thought. It shows that the alternative interpretation of Frey and Riess (1981) is incorrect for the same reason and also because the pteroid was not anteriorly directed to control an extensive propatagium. It also shows that the further modification of the alternative interpretation by Wilkinson and colleagues (2006) is incorrect for those two reasons and also because the preaxial carpal was not oriented with the fovea directed anteroventrally. Wagner's (1858) interpretation of the function of the pteroid is correct in that the pteroid was directed medially along the anterior margin of a modest propatagium, which it controlled.

It is remarkable that the idea of an anteriorly directed pteroid controlling an extensive propatagium has been so tenacious of life. Opponents of the idea presented arguments and evidence against the idea, although they were not as vigorous as they might have been. However, proponents of the idea have been too ready to dismiss inconvenient evidence (e.g., Sesamoid A preserved in the fovea of preaxial carpal; no pteroid preserved in fovea in any specimen) and only reconstructed their anteriorly directed pteroid in a few large pterodactyloids, ignoring those taxa in which the reconstruction would be unworkable (i.e., *Cycnorhamphus* with its long pteroid that if anteriorly directed would result in a huge propatagium as in Fig. 2; *Nyctosaurus* in which the pteroid cannot be directed anteriorly if "articulated" in fovea). Despite that, in the end we can see what the articulated specimens were trying to tell us all along, that the pteroid was medially directed and did not articulate in the fovea of the preaxial carpal.

ACKNOWLEDGMENTS

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