On the nature of the pteroid in pterosaurs

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SUMMARY

The nature of the pteroid, a rod-like bone projecting from the carpus in pterosaurs, has long been disputed. Three lines of evidence, morphological, developmental and histological, indicate that the pteroid is a true bone, rather than ossified cartilage. The origin of the pteroid is unclear: it may be a modified carpal, the first metacarpal, or a neomorph.

1. INTRODUCTION

Pterosaurs are an extinct group of diapsid reptiles that evolved powered flapping flight, a complex mode of locomotion which had profound effects on their morphology, neurology and physiology. The pterosaur wing consisted of a composite, multi-layered membrane supported and controlled by the fore and hind limbs (Wellnhofer 1987; Marill & Unwin 1989; Unwin & Bakhurina 1994). The forelimb was modified, by elongation of the axial elements, to form the principal wing spar (figure 1a). The manus consisted of four digits, typically with a phalangeal formula of 2,3,4,4. The first three digits were relatively small and bore claws, whereas the fourth was hypertrophied and formed the distal 60%, or more, of the wing spar.

In adult pterosaurs the wrist consists of four elements (figure 1b). During ontogeny two bones in the proximal row, probably the radiale and ulnare (Wellnhofer 1970), fused to form a proximal syncarpal (Bennett 1993), whereas three bones in the distal row fused to form a distal syncarpal (Wellnhofer 1985). Anterior to this element lies a medial carpal. This bone bears a deep, ventral facing cotylar facet that articulated with the pteroid, a rod-shaped structure unique to pterosaurs. Occasionally, the pteroid has been described as consisting of two bones: an elongate element and a basal element (see, for example, Wellnhofer 1975a), but in all the examples we have examined the latter proved to be the medial carpal. Virtually all aspects of the pteroid, the type of bone tissue from which it is constructed, its homology and its function have given rise to controversies. None has yet been resolved.

The first descriptions of pterosaurs (see, for example, Cuvier 1809) ignored the pteroid and supposed the pterosaur hand to contain digits one to four. The interpretation by Goldfuss (1831) of the pteroid as the first digit, or thumb, and thus the wing-finger as the fifth digit, sparked off a protracted debate concerning the identity of these structures. Throughout the nineteenth century Goldfuss’ interpretation was widely assumed to be correct. However, some, such as Owen (1870), preferred the Cuverian notion and this idea received firm support from Williston (1904, 1911) who argued that the pteroid was not a digit. Williston emphasised the correspondence between the phalangeal counts of the clawed digits and wing-finger of pterosaurs (2,3,4,4) and digits one to four of other reptiles (2,3,4,5), an idea that is now universally accepted (for examples, see Wild 1978; Padian 1984; Wellnhofer 1991a).

Some workers (see, for example, Goldfuss 1831; Zittel 1882; Wellnhofer 1968; Bramwell & Whitfield 1974; Wellnhofer 1975a) have argued that the pteroid was formed from true bone. Others (Quenstedt 1855; Winkler 1870; Williston 1904, 1911; Hooley 1913; Hankin & Watson 1914; Wilman 1925) suggested that it may have arised by secondary calcification of a tendinous structure, an idea that has more recently been supported by Wild (1978), Padian (1984) and Padian & Rayner (1993). Calcification of tendon leads to the formation of metaplastic bone (Haines & Mohuiddin 1968), a mineralized tissue quite distinct from true bone. The superficial appearance of metaplastic bone, its pattern of mineralization and, most importantly, its microstructure all differ from true bone and thus provide a practical and reliable means of identifying the nature of the pteroid. Until now, however, material suitable for histological comparisons was not available.

The Lower Cretaceous Santana Formation of the Chapada do Araripe, north-east Brazil, has yielded a wealth of pterosaur remains, including many superbly preserved, uncrusched specimens (Wellnhofer 1985; Kellner 1991; Wellnhofer 1991a, 1991b; Martill 1993). New pterosaur material from Araripe, housed in the Staatliches Museum für Naturkunde Karlsruhe, provided materials for histological studies of the pteroid and other wing bones. Results of this work, combined
with examination of the pteroid in other pterosaurs, has enabled us to resolve some of the problems concerning this enigmatic structure. Here we present evidence to show that the pteroid is a true bone, and we briefly outline three possible hypotheses as to its origin.

2. MATERIALS AND METHODS

(a) Materials

The principal focus of this study was an adult individual of *Tropeognathus robustus* (SMNK 1133PAL). This specimen, a large (6 m wingspan) pterosaur from the Lower Cretaceous Santana Formation of Brazil, consists of a fragmentary skull with mandible and parts of the postcranial skeleton. The right wing is almost entire and was originally preserved in natural articulation. The right wrist is complete and includes a large and well developed pteroid lacking only a small portion of the articular condyle and the distal tip. Histological preparations were made from the left pteroid, of which only the articular condyle and proximal portion of the shaft are preserved. Remains of other Santana Formation pterosaurs including Anhanguera (NSM-PV19892), ?Anhanguera (SMNK 1136PAL), Santanadactylus (BSP 1982 I 89; 1987 I 1) and Tupuxuara (IM 1052) provided further morphological details.

Additional comparative data were obtained from the following pterosaurs: Dimorphodon (BMNH, GSM), Campylognathoides (SMNS), Dorygnathus (SMNS, BSP), Rhamphorhynchus (AMNH, BMNH, BSP, JM), Sordes (PIN), Anurognathus (BSP), Pterodactylus (BMNH, BSP), Dsungaripterus (IVPP), a dsungaripterid from Tatal, in western Mongolia (PIN), Nyctosaurus (FMNH), Pteranodon (AMNH, BMNH, FMNH), Zhejiangopterus (ZMNH), Quetzalcoatlus (TMM) and a pterosaur formerly named Ornithodexmus (BMNH).

Repository abbreviations: AMNH, American Museum of Natural History, New York, U.S.A.; BMNH, Natural History Museum, London, U.K.; BSP, Bayerische Staatsammlung für Paläontologie, München, Germany; FMNH, Field Museum of Natural History, Chicago, U.S.A.; GSM, Museum of the Geological Survey, Keyworth, United Kingdom; IMCF, Iwaki Coal and Fossil Museum, Iwaki, Japan; IVPP, Institute for Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; JM, Jura Museum, Eichstätt, Germany; NSM, National Science Museum, Tokyo, Japan; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; TMM, Texas Memorial Museum, Austin, Texas; ZMNH, Zhejiang Museum of Natural History, Hangzhou, China.

(b) Methods

Bone material was examined by direct observation, low-power binocular microscopy and petrological microscopy. Histological work was done as follows: after encasement in Araldite 105, thin sections were prepared from a pteroid (SMNK 1133PAL), a radius (SMNK 1135PAL) and a sesamoid (SMNK 1133PAL). Each thin section was ground manually using 260 and 400 mesh carborundum grit until the required level of histological detail was visible. Sections were sprayed with clear varnish and examined under...
plane polarized light and crossed polars using a Leitz Orthomat microscope.

3. RESULTS

(a) General appearance and morphology of the bone

The pteroid of Tropeognathus robustus (SMNK 1133PAL) is rod-like, with an expanded articular condyle at the proximal end and a long, slender shaft (figure 2a-f). The condylar end of the bone is curved ventromedially (twisted) subtending an angle of about 25° in the vertical plane and about 30° in the horizontal plane with respect to the shaft axis.

The articular condyle is asymmetrical (figure 2f). The medial half of the condyle is larger, with a rounded, subtriangular outline bearing a well-developed convex articular facet that fits snugly into the relatively open medial margins of the medial carpal glenoid. The lateral part of the condyle, separated from the medial surface by a shallow intercondylar fossa, bears a thinner, roller-shaped articular facet (figure 2d) that fits into the narrower, lateral margins of the medial carpal glenoid. The dorsal portion of the pteroid condyle bears a wide, shallow, tongue-shaped, semicircular facet (figure 2e) that extends on to the colllum and fits tightly against the roof of the joint on the medial carpal.

The colllum of the articular condyle is stout and has a rounded trapezoidal cross-section, the long axis running obliquely from dorsolateral to ventromedial. The cross-section becomes oval as the colllum develops into the shaft, its long axis gradually becoming horizontal, emphasizing the medial twist of the condylar region. The colllum has an elongate, ventral concavity containing a deep, sediment filled oval pit (figure 2a, c), the remains of a large pneumatic foramen that opened into the hollow interior of the colllum.

The bone shaft is long, straight and dorsoventrally compressed, with a relatively flat ventral surface and a more rounded dorsal surface. The shaft tapers distally to a slender tip with a blunt, rugose end, probably the result of fracture since in other pterosaurs the pteroid has a smooth and rounded distal termination. Toward the proximal end of the shaft the lateral margin swells outward forming a low and blunt protuberance with a rugose surface (figure 2a, c). A similar feature is seen in other Santana pterosaurs (e.g. ‘Santanadactylus’ spixi, Welinhofer 1985, figure 30) and probably represents the insertion site of a muscle or ligament. The ventral concavity of the colllum extends beyond the pneumatic foramen, on to the ventral surface of the shaft as a wide and shallow depression (figure 2a). Toward the lateral protuberance of the shaft this depression becomes a ventral groove, increasing in width and depth towards

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Figure 2. Tropeognathus robustus (SMNK 1133PAL), right pteroid in (a) ventral, (b) medial and (c) dorsal view, and left pteroid in (d) lateral view: scale bar = 30 mm. Details of articular region of left pteroid in (e) ventral and (f) proximal view: scale bar = 10 mm. Abbreviations: co, colllum; if, intercondylar fossa; lf, lateral facet; mf, medial facet; pf, pneumatic foramen; rp, rugose protuberance; sf, semicircular facet; vg, ventral groove.

Figure 3. Histological details of the pteroid (SMNK 1133PAL), radius (SMNK 1135PAL), wing-phalange three (SMNK 1133PAL) and sesamoid (SMNK 1133PAL) of *Tropognathus robustus*. (a) Transverse section of a trabecula within the pteroid exhibiting parallel fibred bone with numerous lacunae; (b) transverse section through cortical bone of the pteroid showing primary reticular fibro-lamellar bone; (c) longitudinal section of pteroid exhibiting osteocyte lacunae and vascular canals; (d) detail of longitudinal section of pteroid showing osteocyte lacunae with canaliculi; (e) longitudinal section of radius composed of primary reticular fibro-lamellar bone; (f) detail of (e), lacunae with canaliculi; (g) transverse section of wing-phalange three composed of reticular fibro-lamellar bone, cf. (a); (h) section
the distal end of the bone. A similar furrow has been reported on the pteroid of *Santanactylus pricai* and *Santanactylus spii* (Wellnhofer 1985).

The general features of the pteroid of *Tropeognathus* seem to apply to all known pterosaurs. The main differences are in the overall shape of the pteroid, which in ‘rhamphorhynchoids’ tends to be relatively short and stubby, and in the development of the articular region, which in ‘rhamphorhynchoids’ and early pterodactyloids tends to be less complex (see also Döderlein 1923). In large pterosaurs, such as *Anhanguera* and *Pteranodon*, the pteroid is usually pneumatized, but we were unable to discover evidence of this condition in small pterosaurs such as *Pterodactylus* and *Rhamphorhynchus*.

(b) Ossification of the pteroid

The ontogeny (young juveniles to large adults) of a few pterosaurs is represented by fossil evidence. These include: *Rhamphorhynchus* (Wellnhofer 1975b; Bennett 1995; Unwin 1995), *Pterodactylus* (Wellnhofer 1970; Unwin 1995), *Pteranodon* (Bennett 1993) and possibly *Ctenochasma* (Bennett 1995; Unwin 1995). Studies of these pterosaurs have revealed a number of general features with regard to patterns of bone ossification, fusion between individual bones and the relative timing of these events.

Significantly, in all pterosaurs examined the pteroid is ossified. This applies even to very young individuals of *Pterodactylus* (e.g. *P. kochi* BMNH 42736), possibly only a few weeks or months old, and in which some pedal bones are unossified (Wellnhofer 1970), epiphyses are not fused and there is no fusion of composite bones (e.g. scapulocoracoid, pelvis and synarcraids). The pteroid is also ossified in relatively young individuals of *Scaphognathus* (Wellnhofer 1975b), *Rhamphorhynchus* (Wellnhofer 1975a) and *Eudimorphodon* (Wild 1978).

The pteroid also exhibits the same pattern of ossification as other wing bones. For example, in very young individuals of *Pterodactylus kochi* (e.g. BMNH 42736), the superficial appearance of the pteroid is similar to that of other wing elements such as the humerus: translucent, rather grainy and with an ‘unfinished’ texture. In adult individuals of *P. kochi* (e.g. BSM 1937 I 18), the bone composing the pteroid is opaque and the external surface has a smooth, compact, dense appearance, again much like that of other wing bones. Similar observations have been made for *Pteranodon* and other pterosaurs (Bennett 1993).

There are further similarities to the external features of other appendicular elements. In one specimen of *Anhanguera* (NSM-PV19892), a sub-adult in which all composite elements are unfused (Kellner & Tomida 1993) and epiphyses are prominent in many wing bones, there appear to be traces of an epiphyseal boundary circumscribing the proximal end of the pteroid, just distal to the articular condyle. This apparently indicates the presence of an epiphysis, a typical developmental feature of true bone (Haines 1969), but not of metaplastic bone which forms in quite a different way (Haines & Mohiuddin 1968).

Finally, it is a frequently observed feature of the limb elements of many large and some medium-sized pterosaurs that the compact bone of the diaphysis is composed of a number of discrete, fine layers. The same construction, in this case consisting of three thin layers of cortical bone, is exhibited by the pteroid of a specimen of *Anhanguera santanae* (NSM-PV19892). However, this multi-layering does not occur in pterosaurian metaplastic bone, examples of which include the ossified tendons that surround the caudal vertebrae of most ‘rhamphorhynchoids’ (Ostrom 1969; Wellnhofer 1975a), and sesamoids, which occur in many large Santana pterosaurs including SMNK 1133PAL.

(c) Histology

Vertebrate hard tissues in the Santana Formation are little altered by diagenetic processes (Martill 1988). In the freshest concretions bone is dark brown, composed of apatite and shows fine detail under light and electron microscopy. The brown coloration is due to slight maturation of the original organic matrix of the bone. In weathered concretions bone appears whitish, due mostly to the oxidation of the original organic component, and a faint pink coloration indicates trace amounts of iron.

Transverse (figure 3a, b) and longitudinal (figure 3c) sections of the pteroid of *Tropeognathus robustus* exhibit primary reticular fibro-lamellar bone containing spindle-shaped osteocyte lacunae about 50 μm long and oriented parallel to the collagen fibres. Numerous fine canaliculi radiate outward from the lacunae toward the canaliculi of adjacent lacunae (figure 3d). Longitudinal sections of the radius (figure 3e, f) and transverse sections of the wing-phalange three (figure 3g) exhibit a similar appearance: primary reticular fibro-lamellar bone with a high density of spindle-shaped lacunae, each approximately 50 μm in length and with canaliculi radiating out from all sides (see figure 3f). Primary reticular fibro-lamellar bone has also been reported from the wing elements of other pterosaurs including: *Rhamphorhychus* (Bramwell 1972, appendix figure 1; Ricqlès 1976, figure 4c); and *Pteranodon* (Enlow & Brown 1957, plate 21, figure 9; Bennett 1993, figure 2). Thin sections through a sesamoid composed of metaplastic bone exhibit a quite different histology (see figure 3h,i). The trabeculae have an amorphous ground mass, indistinct collagen bundles and few lacunae. As is typical of metaplastic bone, the lacunae have short, blind canaliculi and are confined to the surface of the trabeculae.
4. DISCUSSION

(a) The nature of the pteroid

There is strong evidence to show that the pteroid is a true bone. Its external appearance is identical to that of other wing bones (even to the extent that Wellnhofer (1985, figure 14) misidentified a pteroid as the metacarpal three), but not to that of sesamoids, which often have an irregular, rough external appearance. The development of an articular condyle, an epiphysis and, in some pteroids, of multi-layered cortical bone is also a feature of true bones, but not of calcified tendons or sesamoids. Similarly, pterosaur bones of metaplastic origin, such as sesamoids, are not pneumatized, but pneumatic foramina are frequently encountered in vertebral and long bones. They also occur in the pteroid of Santana pterosaurs such as *Tropeognathus* (SMNK 1133PAL), *Anhanguera* (NSM-PV19892, AMNH 22552 and 22555) and *Tupuxuara* (IMCF 1052), and other pterosaurs including *Pteranodon* (BMNH R2959) and *Ornithodromeus* (BMNH R3877).

The early ossification of the pteroid, preceding even the ossification of some of the phalanges of the pes in *Pterodactylus* (Wellnhofer 1970), is notable in that calcified tendons and sesamoids have only been recorded in sub-adults and adults. Finally, and most importantly, histological details of the pteroid, in particular the presence of primary reticular fibro-lamellar bone with numerous osteocyte lacunae and canaliculi, are typical of true bone, but not metaplastic bone which forms by mineralization of cartilage, usually at the approach of maturity and without the involvement of osteoblasts (Haines & Mohiuddin 1968). We conclude that the pteroid is part of the appendicular skeleton which, like other elements, was formed in cartilage with a perichondrium, from a mesenchymal condensation.

(b) The origin of the pteroid

Identification of the pteroid as a true bone is likely to revive the debate concerning its origin. Here we consider three possibilities: (a) that the pteroid is a modified carpal, or (b) derived from digit one of amniotes, or (c) a neomorph.

Carpals can be extensively modified and appear digit-like, as in the talpid moles (*Talpa*) and panda (*Ailurus*) (Gould 1980; Holder 1983a). If the pteroid is a modified carpal (Williston 1904; Wellnhofer 1968, 1975a) it is most likely to be a modified first distal carpal. If this is correct, then the medial carpal developed from distal carpal two and the distal syncarpal from distal carpal three to five. To derive a pterosaur carpus from the primitive condition the only other transformation required is lateral displacement of metacarpals one, two and three to contact the distal syncarpal. This hypothesis is attractive in that it requires relatively few modifications, but has gained little support from modern workers (see, for example, Wild 1978). Despite this, the idea merits further exploration, as does the possibility that the pteroid might, alternatively, have been derived from another carpal such as the medial centrale.

If the pteroid is a modified first digit, specifically the first metacarpal, the clawed digits must be the second, third and fourth digits, and the wing-finger the fifth digit, as Goldfuss (1831) first argued. The phalangeal formula for primitive diapsids such as *Younigina* and *Prolacerta* is 2,3,4,5,3. If this were the maximum phalangeal count in the immediate sister group of pterosaurs, then in addition to acquiring an additional phalange in the wing-finger, pterosaurs lost phalanges one and two in the first digit and one phalange from each of the second to fourth digits. If the starting point of the wing is a webbing of the fore limb it is likely that the whole hand was involved, as in the Chiroptera and Dermoptera. Difficulties arise, however, in explaining the subsequent modifications. Reduction of digit one is hard to account for since it would have been well suited for manipulating the propatagium, as in bats. Furthermore, it is not at all clear why the fifth digit gained an extra phalange because, as *Nydusaurus* shows, the wing-finger was quite capable of functioning with only three phalanges.

The pteroid may be a neomorph, i.e. an entirely new bone. In this case the only modifications necessary are the appearance of the pteroid, the loss of the ungual on digit four and the loss of the fifth digit, which is common in diapsids (Benton 1985). How the neomorph arose is unclear, but polydactyly offers one possibility. A sixth digit in the manus is not uncommon in amniotes (Prentis 1906; Holder 1983b) and almost always appears on the preaxial side (Johnson 1986). Furthermore, these structures are often accompanied by ligaments, tendons and muscles (Hall 1984). Perhaps the pteroid is a vestigial sixth digit composed of a metacarpal and associated musculature? Such a structure is likely to have been involved in webbing of the hand and would have served quite adequately as a support and manipulator for the nascent propatagium.

There do not yet appear to be sufficient grounds for preferring any of the hypotheses outlined above, or other less likely alternatives. Further study of pterosaur forelimb anatomy and ontogeny, more precise identification of the immediate sister group(s) of pterosaurs and the discovery of forms intermediate between pterosaurs and other diapsids may all help to throw light on this problem.

5. CONCLUSIONS

The pteroid is a true bone and not a secondarily calcified structure. The origin of the pteroid remains unclear; it may be a neomorph, a modified carpal, or the remains of digit one. Resolution of this question requires further investigation. The complex articulation with the medial carpal, development of muscle attachment sites and association with the propatagium show that the pteroid was an active component of the flight apparatus. Further studies should determine the functional role(s) of this most unusual bone.

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