Pterorhynchus by Stephen A. Czerkas

A NEW RHAMPHORHYNCHOID WITH A HEADCREST AND COMPLEX INTEGUMENTARY STRUCTURES

STEPHEN A. CZERKAS and QIANG JI

The Dinosaur Museum, 754 South 200 West, Blanding, Utah 84511, USA;
Institute of Geology, Chinese Academy of Geological Sciences, Baiwanzhuang Road 26,
Beijing 100037, People's Republic of China.

Abstract

A new rhamphorhynchoid is described with a headcrest that is unprecedented among the long-tailed pterosaurs. The preservation of the headcrest presents significant implications regarding the physical appearance and aerodynamics of all pterosaurs. Also, "hair-like" integumentary structures of this pterosaur are shown to be complex multi-strand structures which presents evidence on the origin of feathers and the possibility of a remarkably early ancestral relationship between pterosaurs and birds.

INTRODUCTION

FLYING REPTILES known as pterosaurs are composed of two suborders including the long-tailed rhamphorhynchoids, and the short-tailed pterodactyls. There are other distinctive physical characteristics which also separate the two groups. The pterodactyls have comparatively more elongate metacarpals, and skulls which often, but not always, have bony crests. Rhamphorhynchoids typically do not have the bony headcrest as seen among the pterodactyls. Speculations as to the function of such headcrests have included sexual dimorphism, inter-species variation in ornamental display, and as an aerodynamic stabilizer. The discovery of the headcrest on the rhamphorhynchoid described below is the first example known to exist among the long-tailed pterosaurs and presents evidence that contributes greatly to a new understanding of the headcrests of all pterodactyls.

Fossils of both rhamphorhynchoids and pterodactyls have previously shown that pterosaurs in general had "hair-like" structures which covered much of their body. A detailed identification of what these structures actually are has remained somewhat ambiguous, although the correlation of such a hair-like body covering has been widely accepted as being demonstrative that pterosaurs had a warm-blooded physiology.

The preservation of the rhamphorhynchoid described herein is remarkable in revealing previously unknown details of both the headcrest and the "hair-like" body covering of pterosaurs. Directly correlating to the ossified crest is a far larger unossified crest. The "hair-like" structures are also unique in being preserved in fully three dimensionally forms as compared to two dimensional staining or impressions. The hairs are shown to be complex multi-strand structures instead of single strands or actual hairs. The complex nature of these filaments most closely resembles natal down feathers, but apparently without having barbules. As such, they may represent the earliest known form of feathers. This implies that such integumentary structures may have originated independently among pterosaurs from that of birds, or that birds and pterosaurs may share a common ancestor which had evolved this kind of insulation before fight had been achieved in either group.

SYSTEMATIC DESCRIPTION

Pterosauria Kaup 1834
Rhamphorhynchoidea Plieninger 1901
Rhamphorhynchidae Seeley 1870
Pterorhynchus wellnhoferi, gen. et sp. nov.

ETYMOLOGY

Pterorhynchus means "winged-head, or -snout", from *Ptero-*, (Greek) for "wing, flight"; *-rhynchus*, meaning "snout"; *wellnhoferi*, in honor of Peter Wellnhofer for his work on pterosaurs.

DIAGNOSIS

The sagittal headcrest distinguishes *Pterorhynchus wellnhoferi* from all other known rhamphorhynchoids. The crest is represented by both a small ossified part, and a soft tissue element that is much larger. The low ossified ridge has vertical striae and is located beneath the leading edge of the remaining crest which extends well above and across the posterior two-thirds of the skull. This much larger part appears to have been corneous in life presumably made of keratinous material. The length of the tail is about equal to the length of a wing. The tail membrane appears to be long and low extending along more than the distal two-thirds of the tail.

DISCUSSION

Until only recently, *Archaeopteryx* provided the earliest unambiguous example of feathers. This has led to the questions of the evolutionary origins of feathers as being specifically tied to the origin of birds. Consequently, the discovery of feather homologues in dinosaurs have led to the conclusion that feathers originated among theropods which were presumably ancestral to birds. Dissenters to this view have tried to account for the feathers as being artifacts of preservation (Gibbons, 1997; Feduccia, 1999), or have presented interpretations of other kinds of animals from earlier in time as having possible feather homologues (Jones, et al., 2000). Bakker (1975) conjectured that pterosaurs had "hairlike feathers". The comparison of the hair-like integumental structures on the theropod *Sinosauropteryx* and a recently discovered pterosaur have led to the speculation of both as possibly representing proto-feathers (Wang, et al., 2002). Proto-feathers were positively attributed to another similar pterosaur from China (Ji and Yuan, 2002). Along with the proto-feathers of *Pterorhynchus*, this suggests that the origin of feathers had a much earlier and broader distribution than just that of birds and their immediate ancestors.

Interpretations of pterosaurs having had a body covering of hair or even feathers date back to as far as the early 1800's (Goldfuss, 1831). This was based on a specimen of *Scaphognathus*. But the preservation of the integument on *Scaphognathus* was later determined as only being an artifact in the matrix and the observation by Goldfuss has since remained inconclusive (Wanderer, 1908; Wellnhofer, 1991). Other early speculations as to the possibility of hair-like body covering stemmed from the inferred high metabolism associated with flight (Newman, 1843; Seeley, 1864). These correlations were denied by Richard Owen, who firmly believed that pterosaurs must have been cold-blooded reptiles (Owen, 1870). It was not for almost a hundred years after Goldfuss had first speculated of an insulatory covering on pterosaurs before another specimen, that of *Rhamphorhynchus gemmingi*, was described as being preserved with physical evidence of a "hair-like" integument (Broili, 1927). Later, Broili described specimens of *Dorygnathus* (1938) and *Pterodactylus* (1939) as having a similar body covering. Since then, additional specimens of *Rhamphorhynchus* have also been described as having a hair-like integument (Wellnhofer, 1975).

Drawing significant attention to the issue was the discovery of several specimens attributed to *Sordes pilosus* which revealed that these pterosaurs had a dense body covering which resembled fur (Sharov, 1971). Despite this, the concept of pterosaurs having an insulatory body covering remained somewhat controversial due primarily to what it implied towards the metabolism of pterosaurs. Though largely accepted, the interpretation of pterosaurs having a "hair-like" body covering has been doubted (Unwin and Bakhurina, 1994). More obscure though is the precise nature of the "hair-like" structures and just exactly what they really are (Wellnhofer, 1991).

Much of the controversy and confusion concerning the integument of pterosaurs is due to regarding the body fibers as "hairs", "hair-like", or "tufts of hair". This description is an overly broad generality which has been very misleading towards the identification of what these fibers represent. Among vertebrates, only two kinds of integumentary fibers might resemble hair. One is hair itself which is exclusively a mammalian characteristic, and the other is feathers, notably that of natal down. Phylogenetically, pterosaurs are much more closely related to birds than to mammals, so it is more logical to speculate that their integument may be closer to that of birds than mammals. There are fundamental differences between the morphologies of mammalian hair and avian feathers. While both emanate from a follicle, a hair has a deep root that looks essentially like a continuation of the hair itself, whereas the base of the feather is formed by a calamus from which the barbs are attached. The term "tuft" may apply to either hair or feathers such as natal down, basically referring to the aspect of having several filaments collectively from a single follicle. Hair is highly variable in its structure and is capable of having one strand or several per follicle. But even where several hairs share a single follicle, their roots remain separate (FIGURE 14). Feathers differ significantly from hair in that their multiple strands, the barbs, emanate from a single hollow structure, called the calamus. The integumentary structures seen in *Pterorhynchus* bear a striking similarity to that of a natal down feather with only the notable absence of having the additional barbules branching from the barbs (FIGURES 15, 16). This absence is significant all the more because without the barbules, the barbs emanating from a calamus represents the hypothetical "Stage II" structure speculated as being an incipient step in the evolution of feathers (Prum, 1999).

Proto-feathers have been attributed to two pterosaurs which are of similar animals (Ji and Yuan, 2002; Wang, et al., 2002). Even more so, the morphology details seen in *Pterorhynchus* demonstrate that the integumentary structures of pterosaurs are not like hair, but are analogous to being proto-feathers. Specifically, they resemble natal down feathers where individual filaments are seen to spread from a single follicle. Instead of branching from a long rachis, the filaments stem from a short base like a calamus. There are no indications of the individual strands continuing within the skin as parallel roots as seen in some mammals where fluffy tufts composed of several hairs emanate from a single follicle. Therefore, the individual filaments are not representative of hair, but are analogous to being the barbs of a feather. Barbules, if present, cannot be discerned which suggests that they either did not exist, or that the limits of preservation have obscured them. Nonetheless, the morphology of having several barbs stemming from a short calamus indicates that the body covering of *Pterorhynchus* are feather homologues. Without barbules, these structures would represent the second stage of feather development as speculated by Prum (1999). The feather homologues of *Pterorhynchus* also demonstrate that a primary function achieved by these plumulaceous feathers was that of thermal insulation, and that feathers with a true rachis and barbs aligned into well developed vanes represent a derived condition.

The preserved impressions of pterosaur wing membranes have suggested that they were smooth, or naked, and not covered by external integumentary fibers as on the main body or neck of the animal (Padian and Rayner, 1993; Unwin and Bakhurnia, 1994; Frey and Martill, 1998). The wing membranes are thought to have been stiffened by internal fibers, called aktinofibrils (Martill and Unwin, 1989; Wellnhofer, 1987, 1991). The distal end of a wing membrane is preserved in

Pterorhychus which shows clear aktinofibrils that are aligned in parallel rows. However, at right angles to the aktinofibrils are minuscule pinnate fibers which though imperfectly preserved, resemble the larger integumentary structures from the body. These tiny tufts on the wings are set close together in rows and the diamond or V-shaped pattern caused from their general outlines are distinctly visible throughout. These tufts extend across the entire width of the membrane. They are also preserved more as three dimensional structures, whereas the aktinofibrils are preserved two dimensionally as stains within the matrix. Several of the tufts show distinct filaments that emanate from a round base, like a calamus. Therefore, the evidence suggests that the external surface of the pterosaur wing was not naked, but covered by tiny pinnate fibers which would have looked much like a fine layer of velvet. These fibers may have only been on the external, dorsal surface of the wing, whereas the ventral surface may have had naked skin. If so, this may account for some pterosaurs where a smooth outer surface of the wing membrane appears to have been preserved.

The discovery of feather homologues which are so primitive in their structure as to be regarded as “proto-feathers” suggests that either these structures evolved independently, or that both birds and pterosaurs share a distant common ancestor which could not fly. As such structures are not crucial towards aerodynamics, the hypothetical ancestor would have developed an insulative body covering and been arboreal before flight was achieved in either group. The arboreal characteristics and primitive morphology of the proto-maniraptoran, *Scansoriopteryx* (Czerkas and Yuan, this volume), is also consistent with this suggestion that the origin of feathers stems much further back in time even to where such an arboreal ancestry may have split into different lineages for both pterosaurs and birds.

The understanding of the physical appearance of pterosaurs is significantly altered by the discovery that the body covering was composed of feather homologues rather than a generic kind of hair. But the non-ossified head crest of *Pterorhynchus* goes on further to potentially change the life restorations of all pterosaurs and gives remarkable new insights into how these animals flew. *Pterorhynchus* is the only known rhamphorhynchoid which has an indication of a small bony ridge upon its snout. Just prior to the publication of this volume, a very primitive rhamphorhynchoid with a larger bony crest across much of its skull was described (Dalla Vecchia, et al., 2002). Even though similar ossified crests and even much larger ones have been known among various types of pterodactyls, their function has been, for the most part, attributed to simply that of ornamentation reflective of different species or perhaps sexual dimorphism. The remarkable preservation of the non-ossified headcrest on *Pterorhynchus* reveals that such bony ridges are directly indicative of a much larger cranial structure. This non-ossified portion of the head crest was a rigid structure presumably made of keratin. As can be seen in *Pterorhynchus*, the leading edge of the ossified ridge on the nasals directly correlates to the leading edge of the much larger unossified headcrest. This demonstrates that the ossified headcrests on pterodactyls must also be indications of far larger headcrests than previously supposed. The overall size of the entire headcrest is so disproportionately larger than the ossified basal part that this suggests a substantial development of an unossified crest may be present even before any physical indications appear in the actual bone. Therefore, even pterosaurs without ossified crests may have had a substantial crest of significant size.

Evidence reaffirming these speculations that all pterosaurs may have been equipped with an unossified crest comes from additional specimens of pterodactyls recently described as having headcrests made of “soft tissue” (Frey and Tischlinger, 2000). The terminology “soft tissue” should not imply that the material was actually pliable or flesh-like as in the cockscomb of a rooster. One of these is a tapejarid in which the impression of the unossified crest extends from its prominent ossified nasal crest upwards and across the posterior length of the skull, essentially like that in *Pterorhynchus*. The main difference is that: 1. the ossified crest is much larger resulting in the leading edge being much more steeply inclined in the tapejarid, and 2. that the unossified crest is also taller, extending more prominently above the skull.

This demonstrates a direct relationship between the size of the ossified crest with the shape and potential extent of the unossified crest. A second specimen described by Frey and Tischlinger (2000) is that of a typical *Pterodactylus*, a pterosaur which has no bony development of a cranial crest, but in this case it does have indications of an unossified crest. The preservation appears to be incomplete but that it exists at all on a pterosaur without an ossified crest confirms the speculation that any pterosaur could have had a prominent cranial crest made up of keratinous material. Two other pterodactyls described recently by Bennett (2002) includes that of a *Germanodactylus* which has a very small ossified crest that was enhanced by a larger unossified crest, and that of a *Ctenochasma* in which the size of its crest was not determined. The overall size of the crest on the *Germanodactylus* is conspicuously small compared to that of *Pterorhynchus*, but still it is significantly larger than the bony ridge it stems from.

Long ago, another pterosaur, that of *Rhamphorhynchus gemmingi* was also reported as having a soft headcrest (Wanderer, 1908). Such a headcrest has been disputed, but in retrospect, with the additional evidence of non-bony headcrests in *Pterodactylus* and *Pterorhynchus*, it is notable that the skull of the *Rhamphorhynchus* described by Wanderer could really have had a headcrest after all. This speculation is further supported by the discovery of the very primitive rhamphorhynchoid, *Austriadactylus*, (Dalla Vecchia, et al., 2002) which suggests that headcrests probably existed even among the most primitive of pterosaurs.

The function of cranial crests on pterosaurs appears to go far beyond that of simply ornamentation of inter-species display. The curved vertical striping on the crest of *Pterorhynchus* may be more indicative of representing a camouflage pattern than that of a sexual display. Although the size, color patterns or the lack there of, probably did contribute to inter-species recognition to some extent. Nonetheless, the primary function of the headcrests appears to be mostly attributable to aerodynamics since such large structures would have had an inevitable influence on the animals ability to fly. In essence, the headcrests would have automatically acted somewhat like a sail, effectively becoming a rudder which contributed to the animals ability to maneuver during flight. The size of the headcrest may certainly have varied among different species, as well as, during the growth of the animal until its maturity, but this variation does not diminish the fact that a crest of any size would still contribute to the aerodynamics of the animal.

How pterosaurs could fly and controlled their ability to steer has long been a subject of some debate. Whether during active powered flight or gliding, the headcrest could not avoid contributing to the pterosaurs inherent ability to deflect itself through the air by simply turning its head. If these sail-like headcrests were only known among more advanced pterodactyls, it might suggest that this ability to steer from the front was a specialized adaptation which could be unique to only some species. But this adaptation for maneuvering during flight is so remarkable that it would be more problematic if it only applied to some pterosaurs, and not all, because this would not account for how other pterosaurs could fly without them. This is where the significance of the unossified headcrests of the *Pterodactylus* and *Pterorhynchus* repeatedly demonstrate that the function of these headcrests was an essential factor in the pterosaurs ability to fly.

The remarkable preservation of the feather homologues and keratinous headcrest in *Pterorhynchus* provide a significant new understanding of what pterosaurs were like. The feather-like body covering of pterosaurs demonstrates that the evolutionary origin of feathers is far broader than being just attributable to birds. The discovery of the pterosaur headcrests not only changes the physical appearance of what these animals looked in life, but it also reveals that they used their head as a rudder to maneuver during a form a flight that was unique to pterosaurs.