

A large pterodactyloid pterosaur from the Late Cretaceous (Late Maastrichtian) of Western Australia

S. Christopher Bennett*, John A. Long†

Abstract

An incomplete right ulna of a large pterodactyloid pterosaur is described from the Late Cretaceous Miria Formation (Late Maastrichtian), Giralda Range, Western Australia. The bone represents the first pterosaur known from Western Australia, and the largest and geologically youngest pterosaur from Australia, and the youngest Mesozoic terrestrial tetrapod yet found in Australia. Comparisons with other pterosaurs give estimates of wingspan for the Western Australian pterosaur at between 3.6 (cf. *Santanadactylus*) to 4.9 metres (cf. *Pteranodon*). The presence of a ridge dividing the medial condyle on the proximal face of the ulna suggests that the bone belongs to an azhdarchid; if so this is the first record of the family Azhdarchidae in Australia.

Introduction

The fossil record of pterosaurs in Australia is rather poor, and has been limited to Early Cretaceous occurrences. A number of specimens, referred tentatively to *?Ornithocheirus* sp. from the Albian Toolebuc Formation of Queensland, were described by Molnar and Thulborn (1980) and Molnar (1987). Rich and Rich (1989) described a small crushed pterosaur bone from the Aptian-Albian of south-Western Australia. The specimen was tentatively identified as a tibiotarsus of what would be a rather small pterosaur, but is similar to the crushed metatarsals of *Pteranodon* from North America and is a metatarsal of a large pterosaur. This paper describes the proximal end of the ulna of a pterosaur from the Miria Formation (Late Maastrichtian) of Western Australia. The specimen, which has been previously discussed and figured in Long (1990, p. 78), is the first pterosaur from Western Australia, Australia's largest pterosaur, and the only Late Cretaceous pterosaur from Australia. It may also be the youngest known pteranodontid. Finally the specimen is also of interest in being Australia's only Late Maastrichtian terrestrial tetrapod as the otherwise youngest Mesozoic vertebrates are sauropod dinosaur bones from the base of the late Cretaceous (Winton Formation, central north Queensland, Coombs and Molnar 1981).

Discovery of the specimen

The specimen (WAM 60.57) was found in 1960 by E. Car of the Western Australian Museum as three bone fragments washed out of the Miria Formation in its type section at Toothawarra Creek (Figure 1). As this is the only Cretaceous unit exposed in the area and the rock still attached to the bone matches that of the Miria Formation, there is no

*Department of Systematics and Ecology, Museum of Natural History, University of Kansas, Lawrence, Kansas 66045, U.S.A.

†Western Australian Museum, Francis Street, Perth, Western Australia 6000.

doubt as to the exact age and stratigraphic source of the bone. In early 1990 one of us (JAL) recognised the bone fragments in the collection as belonging to one specimen and restored the bone. It was recognised as being unusual in its slender shaft proportions but an identification could not be assigned, so a cast of the bone was sent to Dr. Ralph Molnar of the Queensland Museum. Molnar suggested it might be a pterosaur bone, so further casts were sent to Dr. Peter Wellnhofer of Munich and one of us (SCB), and shortly afterwards the bone was confirmed to be a pterosaur ulna.

Geological setting

The Miria Formation (Miria Marl, Condon *et. al.*, 1956; Hocking *et. al* 1987) has been recently studied in detail by honours students in the Geology Department of the University of Western Australia. The unpublished dissertations which describe foraminifers from the Miria Formation confirm its Late Maastrichtian age, earlier suggested by microfossil studies by several workers (Edgell 1957; Belford 1958, McGowan 1968, Apthorpe 1979) and from diverse ammonite faunas described by Henderson & McNamara (1985a). Other fossils from the Miria Formation includes the nautiloid *Cimomia tenuicostata* (Glenister *et. al.* 1956), as well as undescribed brachiopods, echinoids, sponges, corals, bryozoans and sharks teeth. Other vertebrate remains which have come from the Miria Formation include one bone (WAM 90.10.2)

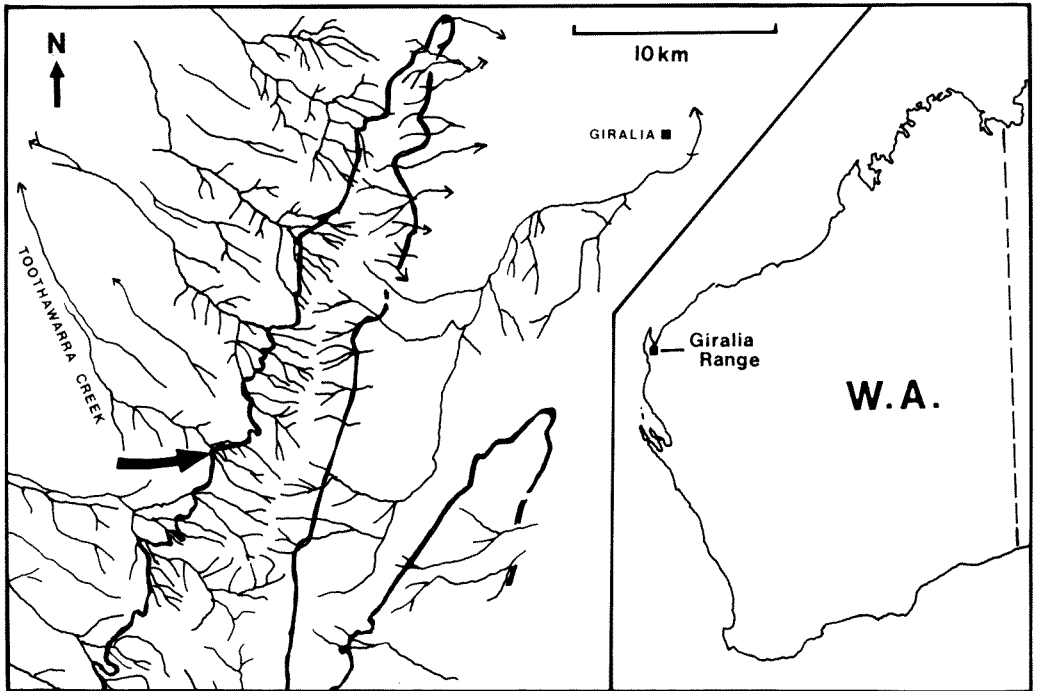


Figure 1. Locality map showing outcrop of the Miria Formation and where the pterosaur bone was found (arrow). After Henderson and McNamara (1985a).

tentatively assigned as a saurischian (possibly a theropod humerus) as well as several unidentifiable lumps of reptilian bone. The Late Maastrichtian age of the Miria Formation makes it the youngest Mesozoic terrestrial vertebrate site in Australia.

The deposition of the Miria Formation began in the wake of a Late Maastrichtian marine transgression (Apthorpe 1979), resulting in quiet shelf deposits in the northern Carnarvon Basin. Its lithology is a cream coloured calcarenite, 0.6-2 metres thickness, with abundant phosphatic grains and nodules. These suggest the unit has been condensed, with fragmentary fossil preservation indicating periods of higher water energy which winnowed the sequence (Henderson & McNamara 1985b).

Description of the pterosaur bone

The specimen (Figure 2) is an incomplete right ulna consisting of the proximal end and some shaft. Parts of the proximal end are broken and missing and as preserved it has a maximum width of 53.5 mm and a thickness of 31 mm. The shaft is broken at approximately the middle of the ulna where it is oval in cross-section and measures 22.5 mm by 17.8 mm. The length of the specimen is 134 mm. The anterior surface (Figure 2c) is pitted by weathering. The cortical bone has flaked off in many places, and where it is missing the internal cast shows impressions of small ridges and struts. The cortical bone is up to 1.0 mm thick along the shaft and is thinner toward the expanded proximal end.

In proximal view the bone is roughly D-shaped (Figure 2a). The medial and lateral condyles extend across the entire anterior half of the proximal end. The posterior parts of both condyles are missing as is the tuberosity for the insertion of *M. triceps brachii*. The condyles face proximally and a little anteriorly but because they are incomplete, it is difficult to accurately describe their orientations. The medial condyle has a slight ridge running diagonally across it. The anteromedial margin of the medial condyle and approximately 15 mm of bone distal to it are broken away. Lateral to this is a depression for the proximal end of the radius. In the middle of the depression between the condyles are the pneumatic foramina. It is not possible to determine if there were foramina on the proximal surface. The biceps tubercle is 18 mm from the medial condyle. It is suboval 7 mm by 3 mm, rises about 1.5 mm above the shaft, and is angled slightly. It is not possible to identify any other features on the anterior surface because of weathering and loss of cortical bone. The posterior surface of the ulna is not badly damaged, but does not show many features. There is a muscle scar on the posterolateral surface that is directed proximally and is part of the insertion of the *M. triceps brachii*. There is a similar scar on the posteromedial surface that is angled toward the medial epicondyle of the humerus and probably is from the medial collateral ligament.

Comparisons

Hooley (1914) reviewed the pterosaur fauna of the Cambridge Greensand of England which includes at least four genera of pteranodontids and non-pteranodontids. He divided the proximal ulnae into three groups. Group A ulnae have a robust ridge on the anterior surface of the shaft which provides a platform to support the radius and *M. biceps brachii* inserts on the side of the ridge rather than on the biceps tubercle. Group B

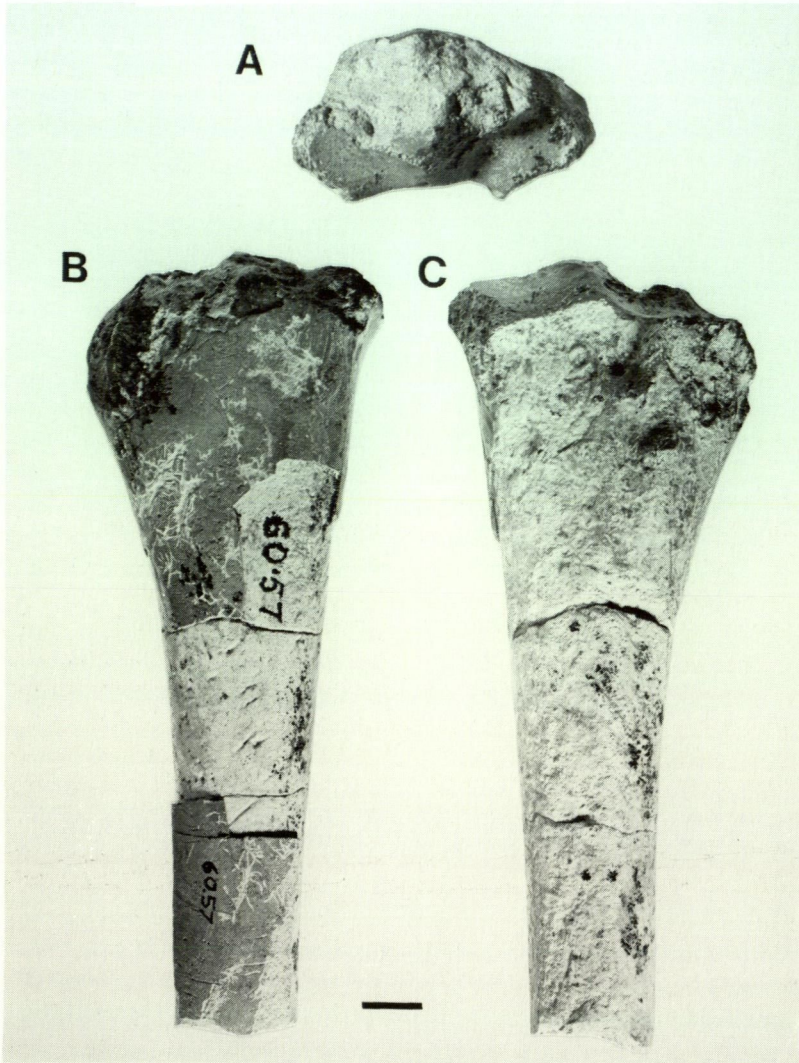


Figure 2. Right proximal ulna of ?azhdarchid pterosaur from Western Australia, WAM 60.57. A, in proximal view. B, in posterior view. C, in anterior view. Bar scale 1cm.

ulnae lack the ridge, have a biceps tubercle, and have a circular pit on the proximal surface posterior to the condyles. Group C ulnae, represented by a single specimen, are similar to Group B ulnae but lack the pit on the proximal end. All three types of ulnae have a pneumatic foramen on the anterior surface between the condyles. WAM 60.57 is similar to Group B ulnae but the damage to the proximal end makes it impossible to determine if a pit was present. Unfortunately, it is not clear if Hooley's groupings correspond to cladistic groups.

Cretaceous pterodactyloids include four major clades, the Dsungaripteridae, Nyctosauridae, Pteranodontidae and Azhdarchidae (Bennett 1989). Comparisons of WAM 60.57 with representatives of those clades are more useful in determining the relationships of WAM 60.57 than considering other pterosaur ulnae, but difficulties arise due to the scarcity of casts or good figures of other specimens. The proximal ulna of dsungaripterids is known only from *Dsungaripterus weii*. The ulna has a straight shaft, thick walls, and does not have noticeable pneumatic foramina. The condyles are extended anteriorly above the shaft and are angled anteriorly. The margins of the condyles are massive and rounded. The condition of the biceps tubercle is not known because the anterior surface of the shaft is damaged. WAM 60.57 differs from the ulna of *Dsungaripterus weii* in having thin walls, the condyles do not extend as far above the shaft and are angled more proximally, and the margins of the condyles are sharp, not massive and rounded. Ulnae of two indeterminate large pterodactyloids share certain similarities and differ from all other ulnae discussed here in certain details. They are proximal ulnae referred to *Araripesaurus* sp. (Wellnhofer 1985, figure 44, 45; 1988) and a proximal ulna referred to *Ornithocheirus* sp. from the Early Cretaceous of France (Buffetaut & Wellnhofer 1983). In both specimens the shaft is posterodorsally curved, the condyles appear to be angled anteriorly, and the biceps tubercle is rather indistinct, although this may be due to immaturity or abrasion. The *Araripesaurus* sp. ulnae have small foramina on the proximal surface and a large pneumatic foramen on the anterior surface between the condyles, while the *Ornithocheirus* sp. ulna has a number of small pneumatic foramina on the proximal surface posterior to the condyles. The *Araripesaurus* sp. ulnae are associated with humeri that display the primitive morphology with a straight mid-section to the shaft. Therefore, the specimen cannot be pteranodontid or nyctosaurid (Bennett 1989), and it may well be dsungaripterid. Whatever taxa these ulnae represent they differ from WAM 60.57 in the posterodorsal curvature of the shaft, the anteriorly directed condyles, and the indistinct biceps tubercle.

The proximal ulna of pteranodontids is known from *Ornithodesmus latidens* (Hooley 1913), *Santanadactylus pricei* (Wellnhofer 1985) and *Pteranodon* (Eaton 1910). The shaft is relatively straight and the condyles are directed proximally. The ulnae of *Santanadactylus pricei* and *Pteranodon* have distinct biceps tubercles. That of *Pteranodon* has a longitudinal groove in the middle, while that of *Santanadactylus pricei* does not. The ulna of *Ornithodesmus* (Hooley 1913) has a robust ridge extending from the foramen distally along the shaft. The ridge forms a platform that supports the radius. The ridge presumably takes the place of the biceps tubercle, and like the Greensand ulnae mentioned above, the M. biceps brachii inserted on the side of the ridge. *Pteranodon* and *Ornithodesmus latidens* have a large pneumatic foramen just distal to and between the condyles, while *Santanadactylus pricei* lacks a pneumatic foramen on the anterior surface between the condyles, and instead has a large pneumatic foramen just proximal to the biceps tubercle. *Pteranodon* also has a nutrient foramen distal to the biceps tubercle.

WAM 60.57 is like the ulna of pteranodontids in the relatively straight shaft and proximally directed condyles. It is like *Pteranodon* and *Santanadactylus pricei* in

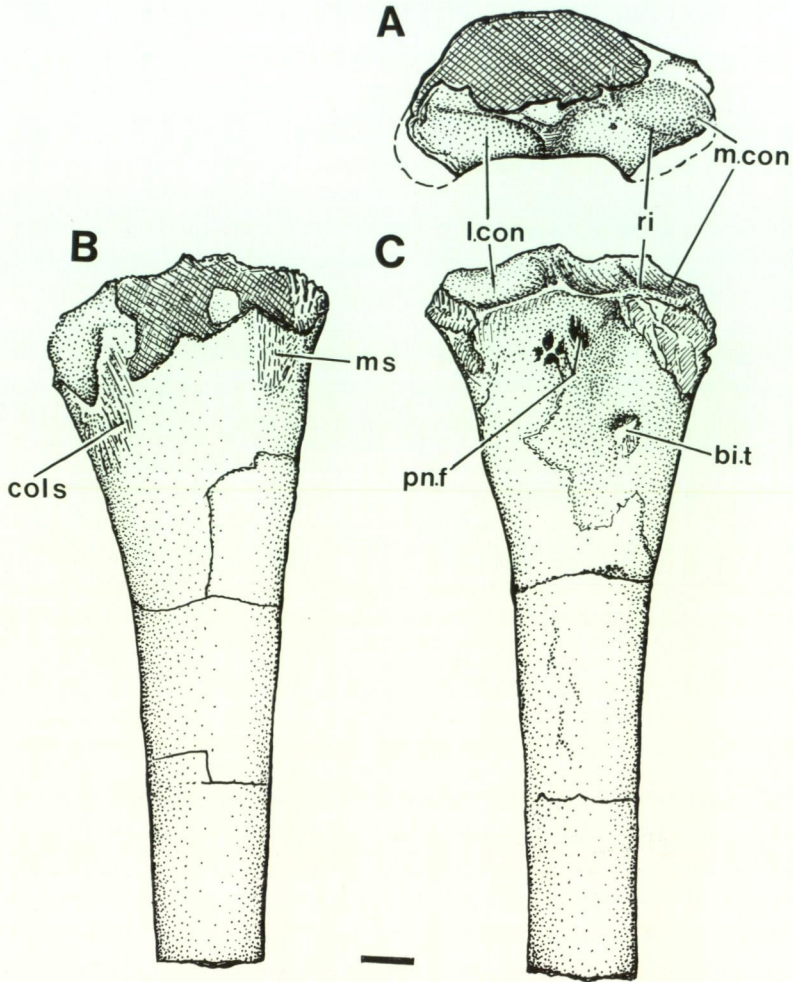


Figure 3. Right proximal ulna of ?azhdarchid pterosaur from Western Australia, WAM 60.57. A, in proximal view. B, in posterior view. C, in anterior view. Abbreviations: bi.t., biceps tubercle; col.s., collateral ligament scar; l.con, lateral condyle; m.con., medial condyle; m.s., muscle scar; pn.f. pneumatic foramina; ri, ridge. Bar scale 1cm.

possessing a distinct biceps tubercle and lacking a ridge to support the radius. It is like *Pteranodon* and *Ornithodesmus* in the position of the pneumatic foramina, although it has a number of small foramina instead of a single large foramen.

The ulna of nyctosaurids is not well known, and is represented only by badly crushed specimens of *Nyctosaurus gracilis*. The ulna has a straight shaft, proximally directed condyles, a distinct biceps tubercle, and a large single pneumatic foramen on the anterior surface between the condyles. The ulna is similar to that of *Pteranodon* except it lacks a

groove in the biceps tubercle. WAM 60.57 differs from the ulna of *Nyctosaurus* in that it has a number of pneumatic foramina on the anterior surface instead of single large foramen. In addition, WAM 60.57 is considerably larger than the largest known nyctosaur, *Nyctosaurus lamegoi*, from the Maastrichtian of Brazil (Price 1953).

The ulna of azhdarchids has not been described. However, specimens of *Arambourgiania* (Nessov and Jarkov 1989, = *Titanopteryx* Arambourg preoccupied) from Jordan and *Quetzalcoatlus* from Texas include proximal ulnae. The ulna of *Arambourgiania* (BMNH 9228) has a relatively straight shaft, proximally directed condyles, a distinct biceps tubercle, one or two rather small pneumatic foramina on the anterior surface between the condyles, and a weak ridge running along the medial condyle. The ulna of *Quetzalcoatlus* is similar to that of *Arambourgiania*, but lacks pneumatic foramina on the anterior surface, and it is not known if it had a ridge on the medial condyle. WAM 60.57 is very similar to the ulna of *Arambourgiania* and is virtually the same size. It differs from *Arambourgiania* in that it has a number of pneumatic foramina on the anterior surface just distal to the condyles, and its biceps tubercle is relatively smaller.

The ulna of *Pterodactylus* has not been described in sufficient detail for comparisons, but the ulna of *Rhamphorhynchus* presumably displays the primitive condition of the pterodactyloid ulna. The form is very similar to the general form seen in *Santanadactylus*, *Pteranodon*, *Nyctosaurus*, *Quetzalcoatlus* and WAM 60.57. The proximal end has condyles facing proximally, the shaft tapers to a relatively straight mid-section with a subcircular to suboval cross-section, and it does not have a ridge extending down the shaft supporting the radius. There are no visible pneumatic foramina and the shaft is relatively smaller in diameter and has relatively thicker walls than those of large pterodactyloids.

Size

It is difficult to estimate the size of a pterosaur from a single limb element, but it is routinely done. Comparisons of WAM 60.57 with complete ulnae of *Pteranodon* and *Santanadactylus pricei* suggest that the 134 mm long section is between one half to two-fifths of the total length. Therefore the complete ulna probably measured between 27 and 34 cm. The wing proportions of large pterodactylids are variable. Extrapolating from an estimated length of 30 cm the wingspan in life (flexed as in flight) would be: 3.6 m based on the proportions of *Santanadactylus araripensis* (Wellnhoffer 1985), 3.8 m based on the proportions of *Quetzalcoatlus* (Langston 1981) or 4.9 metres based on the proportions of *Pteranodon* (Bennett, unpublished data).

Discussion

On the basis of its large size and stratigraphic position it is clear that WAM 60.57 is a pterodactyloid. It is probably not a dsungaripterid because it is not thick-walled and the condyles do not face anteriorly. It is probably not a nyctosaurid because it is much larger than the largest known nyctosaurid, and the group is not known outside the Americas. WAM 60.57 is very similar to *Arambourgiania* from Jordan and both have a ridge dividing

the medial condyle that is not noted on the ulnae of dsungaripterids, pteranodontids or nyctosaurids. It is not certain that the ridge is a phylogenetically important character. If it is not there is nothing to suggest that the ulna is not a pteranodontid, however, on the basis of the ridge dividing the medial condyle the Australian ulna is tentatively referred to the Azhdarchidae.

This is the first record of a pterosaur from Western Australia, and the only late Cretaceous occurrence from Australia. If the specimen is an azhdarchid, it is the first record of an azhdarchid from Australia. Azhdarchids are known from Early Cretaceous of England, and the Late Cretaceous of Central Asia, Jordan, Senegal, New Jersey, Texas and Wyoming in North America (Bennett 1989). If the specimen were a pteranodontid it would be the only member of that clade post mid-Campanian.

The form of the pterodactyloid ulna changed little through the Cretaceous. As the size of the pterodactyloids increased, relatively large joints were needed and the shaft became pneumatic. Consequently the ulna became relatively stouter. The dsungaripterid ulna is derived in possessing a posterodorsal curvature of the shaft from the proximal end and the rather anteriorly directed condyles. The ulna of *Ornithodesmus* and Hooley's Group A ulnae are derived in the possession of a robust ridge supporting the radius and taking the place of a biceps tubercle. However, all other ulnae of larger pterodactyloids, including WAM 60.57, are similar and vary in what appear to be rather minor details. It is surprising that the ulnae of pteranodontids and azhdarchids would be similar because the humeri of the two clades are very different. Perhaps better knowledge of the two groups will reveal differences.

Phylogenetically important morphological variation of pterosaur postcranials is not yet well understood, although recent attempts to characterise such variation have made progress (Padian 1984; Howse 1986; Wiffen & Molnar 1988; Bennett 1989). The above review of variation in the proximal ulna indicates that there is considerable difference between taxa in the size and location of pneumatic foramina. It is not known whether this variation is of phylogenetic importance. In large samples of *Pteranodon* the size and position of the pneumatic foramina are relatively constant, however, further study of this and other aspects of postcranial variation in pterosaurs is needed.

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