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New pterosaur fossils from the Early Cretaceous (Albian) of Queensland, Australia

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ARTICLE

NEW PTEROSAUR FOSSILS FROM THE EARLY CRETACEOUS (ALBIAN) OF QUEENSLAND, AUSTRALIA

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ABSTRACT—Pterosaur fossils from Australia are rare. All the specimens that have been described previously are Cretaceous in age, with the majority deriving from the Aptian–Albian shallow marine succession within the Eromanga Basin of western Queensland. The Queensland specimens have tentatively been referred to the pterodactyloid clades Pteranodontidae, Ornithocheiridae, and Archaeopterodactyloidea (cf. Ctenochasmatoidea), each in varying taxonomic guises. Due to their fragmentary nature, more specific referrals of these specimens have not been possible. As such, the overall composition and more precise relationships of Australia's Cretaceous pterosaur fauna have remained enigmatic. Since 1987, a number of new pterosaur specimens have been found in the shallow marine late Albian rocks of the Eromanga Basin of western Queensland. Four of these specimens are described herein: a partial mandible, a metacarpal IV, a wing phalanx, and a humerus. The mandible is assigned to Ornithocheiridae, gen. et sp. indet., whereas the metacarpal and wing phalanx are assigned Ornithocheiridae cf. *Anhanguera*. The morphology of the humerus suggests that it may belong to a ctenochasmatoid lophocratian. Based on these findings, we hypothesize that Australia's Early Cretaceous pterosaur fauna comprises a mix of taxa already known to occur in Europe and South America in addition to a slightly younger ctenochasmatoid. However, the older specimens may alternatively represent new taxa that combine cranial characteristics of an *Ornithocheirus*-like taxon or a closely related form, with an *Anhanguera*-like postcranium. A more precise characterization of Australia's Cretaceous pterosaur fauna cannot be resolved until more complete specimens are found.

INTRODUCTION

Pterosaur fossils have proven to be extremely rare in Australia. To date, only six specimens have been described. The continent's first pterosaur fossils were found in the late 1970s on the banks of the Hamilton River, approximately 70 km east of Boulia, western Queensland, in the shallow marine limestones of the Early Cretaceous (late Albian) Toolebuc Formation. This material comprised the rostral portion of a small mandible (QM F10613), an almost complete left scapulocoracoid (QM F10612), and a partial presacral vertebra (QM F10614). It was assigned to Ornithocheiridae (sensu Romer, 1956, 1966; broadly equivalent to Ornithocheiroidea sensu Unwin, 2003) aff. *Ornithocheirus* by Molnar and Thulborn (1980). Molnar (1987) described a partial pelvis (QM F12982) from the same locality as the material described by Molnar and Thulborn (1980). Molnar (1987) considered this pelvis to be very similar to that of *Pteranodon ingens*, particularly with regard to the morphology of the pubis as reconstructed by Eaton (1910). The unusual mix of characters displayed by the Hamilton River pterosaur material lead Molnar (1987) to suspect that more than one taxon might be present in this assemblage. Wellnhoffer (1991a) followed these assignments in part, suggesting that the scapulocorocoid and pelvis belonged to an indeterminate pteranodontid, but that the mandible was similar to English species of *Ornithocheirus*. Recently, Molnar and Thulborn (2007) reassigned the Hamilton River mandible to aff. *Lonchodectes* sp. (a euctenochasmatoid lophocratian sensu Unwin, 2003) and the postcranial remains to Ornithocheiroidea (sensu Kellner, 2003) aff. *Anhanguera*.

Other Queensland pterosaur fossils include a partial rostrum, also from the Toolebuc Formation, but collected near Hughenden, assigned to a new genus and species, *Mythunga camara* (Molnar and Thulborn, 2007). Molnar and Thulborn (2007) placed *Mythunga camara* in the Archaeopterodactyloidea of Kellner (2003)—a clade that is broadly equivalent to and synonymous with the Ctenochasmatoidea of Unwin (1995), except for the inclusion of *Germanodactylus* and the exclusion of *Lonchodectes* (Unwin, 2003). Molnar and Thulborn (2007) also figured but did not describe a partial pubis (QM F27104) from the Toolebuc Formation near Elizabeth Springs, southwest of Boulia, assigning it to Ornithocheiroidea (sensu Kellner, 2003) aff. *Anhanguera*, noting its close agreement to the Hamilton River pubis described by Molnar (1987). An undescribed flight metacarpal (NMV P197962) is also known from either the Toolebuc or the Allaru Formation east of Boulia (Molnar and Thulborn, 2007).

Australia's first and to date only Late Cretaceous pterosaur fossil is the shaft and proximal extremity of a right ulna (WAM 60.57) from the Maastrichtian Mira Formation at Toothawarra Creek, Western Australia (Long, 1990). Bennett and Long (1991) tentatively interpreted this specimen as an azhdarchid, similar in size and morphology to *Arambourgiania* from Jordan (BMNH 9228).

Fragmentary and largely indeterminate pterosaur fossils are also known from the Early Cretaceous of Victoria and New South Wales. In southern Victoria, Rich and Rich (1989), Rich (1996), and Rich and Vickers-Rich (2000) note the occurrence of pterosaurs in the late Aptian–early Albian Otway Group (NMV P185861, a crushed metatarsal; figured in Rich and Vickers-Rich, 2000), and in the middle Valanginian–Aptian Upper *Strezelecki* Group (NMV P197962, a partial sacrum; figured in Rich and

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Vickers-Rich, 2000). Smith (1999) published photographs of pterosaur fossils from the opal-bearing Albian Griman Creek Formation at Lightning Ridge, northern New South Wales. All these specimens are yet to be described.

The only pterosaur fossils described from New Zealand are the distal extremity of a left ulna and a partial tooth, collected from the Late Cretaceous (Campanian–Maastrichtian) Mata series at Mangahouanga Stream on the North Island (Wiffen and Molnar, 1988; Molnar and Wiffen, 1994). The identity of this specimen is also uncertain, although Wiffen and Molnar (1988) reported that the ulna was most similar to *Anhanguera araripensis* (sensu Kellner and Tomida, 2000) and *Dsungaripterus weii* (sensu Young, 1964).

Herein we report on the discovery of four new Australian pterosaur specimens, collected from various localities throughout Queensland's Eromanga Basin since 1987 (Fig. 1): a partial mandible from a Toolebuc age-equivalent formation east of Hughenden; a metacarpal IV from near Boulia, and a wing phalanx from Dunluce Station, between Hughenden and Richmond (both from the late Albian Toolebuc Formation); and a humerus from the late Albian Mackunda Formation at Vellum Downs, approximately 100 km southwest of Hughenden. All these specimens are held in the Geoscience Collections of the Queensland Museum, Brisbane. As with previously described Australian pterosaur fossils, being isolated and fragmentary these specimens are difficult to identify with certainty. However, detailed comparisons with more complete taxa from other continents reveal a number of features that help to further elucidate the composition of northern Australia's Early Cretaceous pterosaur fauna.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, U.S.A.; **BMNH**, Natural History Museum, London (formerly the British Museum of Natural History); **BSP**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **CAMSM**, Sedgwick Museum, Cambridge, U.K.; **MZ**, Institut und Museum für Paläontologie der Universität Zürich, Switzerland; **NMV**, Museum Victoria, Melbourne, Australia; **NSM-PV**, Division of Vertebrate Paleontology, National Science Museum, Tokyo, Japan; **QM**, Queensland Museum, Brisbane, Australia; **RGM**, National Natuurhistorisch Museum, Leiden, The Netherlands; **SMNK**, Staatliches Museum für Naturkunde Karlsruhe, Germany; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany.

MATERIALS AND METHODS

Taxonomic Nomenclature

This study utilized the taxonomic phylogenetic scheme for pterodactyloid pterosaurs outlined in Unwin (2003). Following Unwin (2001, 2003), Steel et al. (2005), and Unwin and Martill (2007), Ornithocheiridae is here taken to include *Ornithocheirus*, *Anhanguera*, *Coloborhynchus*, *Brasileodactylus*, *Arthurdactylus*, *Haopterus*, *Ludodactylus*, *Caulkicephalus*, and *Boreopterus*. *Liaoningopterus* (Wang and Lü, 2003) is also provisionally considered an ornithocheirid. We follow Unwin (2001) and consider *Ornithocheirus simus* (CAMSM B54.428) to be the type species of *Ornithocheirus* and the type for Ornithocheiridae after Seeley (1869).

SYSTEMATIC PALEONTOLOGY

PTEROSAURIA Kaup, 1834
PTERODACTYLOIDEA Plieninger, 1901
ORNITHOCHEIROIDEA Seeley, 1870
ORNITHOCHEIRIDAE Seeley, 1870
Genus and Species Indeterminate

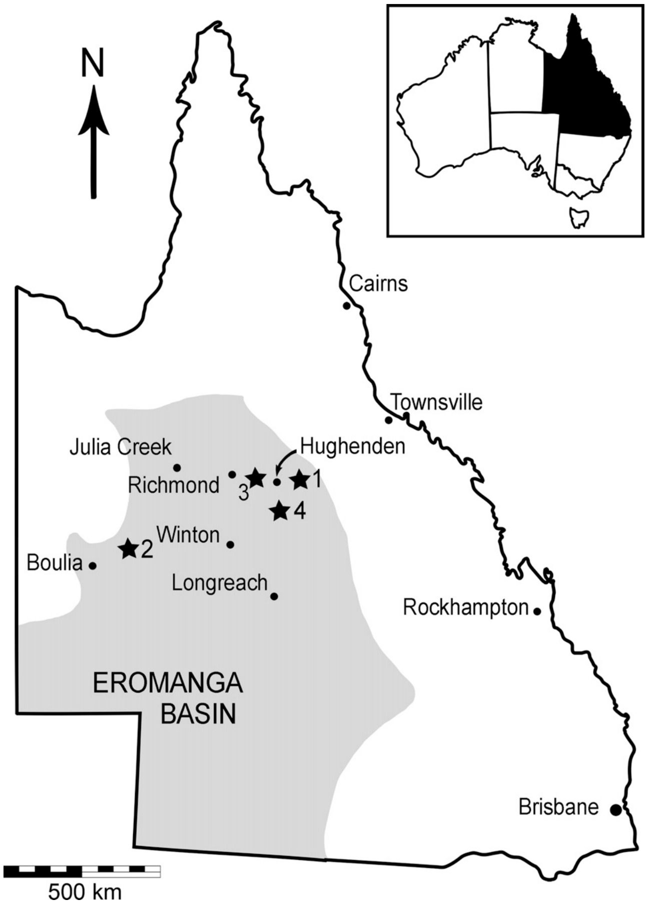

FIGURE 1. A map of Queensland showing the locations (stars) at which the new pterosaur specimens were found and the approximate extent of the Eromanga Basin, shown in grey. **1**, QM F44423; **2**, QM F44321; **3**, QM F44312; **4**, QM F42739.

Specimen—QM F44423, the partial mandibular rostrum of a presently indeterminate genus and species of ornithocheirid pterosaur.

Horizon and Locality—QM F44423 was found east of Hughenden in a Toolebuc age-equivalent formation (Figs. 1–2), considered to be of late Albian age (Boreham and Powell, 1987).

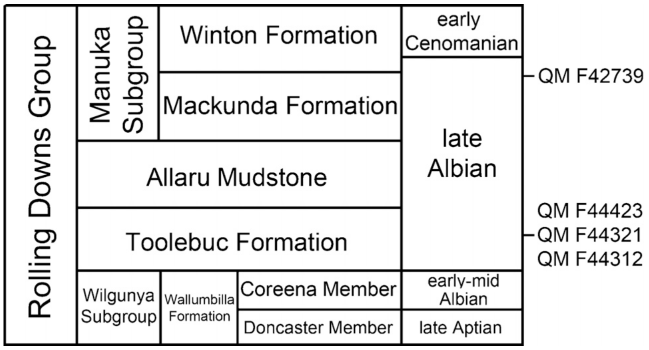

FIGURE 2. Stratigraphy of the Eromanga Basin, western Queensland, after Gray et al. (2002). The approximate stratigraphic position of the four new pterosaur specimens is shown on the right.

Description

Preservation—QM F44423 (Fig. 3) comprises the rostral portion of a small pterosaur mandible. Although no teeth were preserved in situ, a partial crown was found in close association with the specimen (Fig. 3I–J), and is assumed to belong to the mandible. The apex of this crown is absent, and only one side of the tooth has been prepared. The original position of the tooth cannot be determined.

The rostral end of the mandible is almost complete and includes the portion of the mandibular rostrum (and thus mandibular symphysis) from alveoli 1–7 on the right ramus and 1–8 on the left ramus. As there is matrix adhering to the rostral-most portion of the specimen, there is some uncertainty as to whether there may be a further pair of teeth rostral to those figured (Fig. 3). However, as the space remaining at the front of the mandibular rostrum would allow only for an unusually reduced and positioned tooth pair, we interpret the specimen as figured, with the first pair of alveoli being preserved. The ventral surface of the mandible has been damaged and the matrix in this area has not been completely removed.

Preserved within the matrix associated with QM F44423 are very fine bones, and other fragments that may belong to fish, as well as possible internal bone from the mandible.

Osteology—QM F44423 comprises a 134.5-mm section of the left ramus from close to the rostral-most tip to caudal to the eighth alveolus, and a 113-mm section of the right ramus that extends to caudal to the seventh alveolus (Table 1). Beyond the caudal extent of the right, the left ramus appears to have split along the symphysial surface.

The mandible is narrow and longirostrine in form, being only slightly deeper than it is wide for most of its length, though the total depth is unknown for much of the specimen. In lateral aspect, the dorsal surface of the mandible is straight, suggesting that the palatal surface as a whole was not flexed dorsally. The rostral-most portion of the mandible is not enlarged or expanded in any direction. The ventral surface is convex in both cranial and rostral aspect, and there is no indication of a sagittally aligned ventral crest. The width of the mandible increases gradually from 17.2 mm at the second pair of alveoli to 18.5 mm at the seventh.

Dorsally, the symphysis forms a median groove along the entire preserved portion of the mandible, increasing in depth caudally. Two pronounced medial ridges are positioned either side of the symphysial groove, becoming more pronounced caudally. The width of the symphysial groove and corresponding space between the ridges increases from 2 mm at the second alveolus to 6.5 mm at the seventh alveolus.

The preserved alveoli are directed slightly dorsolaterally. They are elliptical in shape with the long axis aligned mesiodistally. They show a gradual increase in size from rostral to caudal. The interalveolar distance also increases caudally.

Small foramina are apparent on the ventral and medial portions of the mandible, increasing in concentration towards the rostral tip.

The length of the preserved section of the associated tooth is 20 mm. This portion represents most of the crown, except for the apex. The tooth has a maximum base width of 5 mm and a minimal apical width 3 mm. Matrix obscures the cross-section of the tooth, but it appears to have been oval in shape, thereby matching the shape of the alveoli. The crown is slightly curved, but because the tooth is not in place in the mandible, the plane cannot be determined. There is no indication of carinae, serrations, or apicobasal striations.

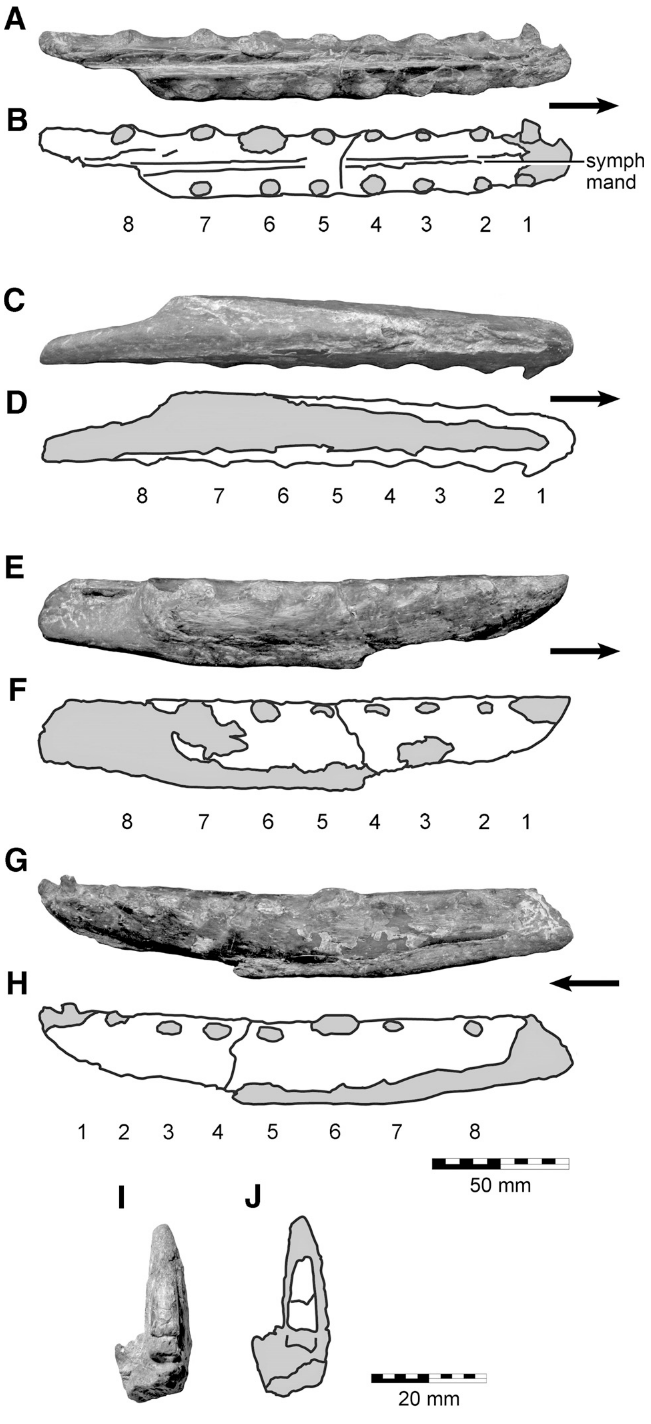

FIGURE 3. Ornithocheiridae, gen. et. sp. indet., QM F44423, the rostral portion of a mandible from a late Albian Toolebuc-age equivalent formation east of Hughenden, central-western Queensland, Australia. Photos and schematic interpretations in (**A**, **B**) dorsal, (**C**, **D**) ventral, (**E**, **F**) right lateral, and (**G**, **H**) lateral left aspects. (**I**, **J**) Associated partial tooth crown. Grey shading indicates remaining matrix and/or surface breaks. Cranial direction is indicated by an arrow in **A**–**G**, and numbers correspond to alveolar positions. **Abbreviation**: **symph mand**, mandibular symphysis.

Comparisons—The long, narrow mandibular rostrum and thinness of the cortex of the bone identify QM F44423 as a pterodactyloid pterosaur. This is in agreement with its Early Cretaceous age. In common with ornithocheirids among pterodactyloids, it comes from a medium-sized animal, possessing a jaw with widely spaced alveoli that are indicative of proportionately large, and presumably interlocking teeth. The specimen was therefore compared with a range of ornithocheirids and closely related ornithocheiroid taxa.

TABLE 1. Measurements taken of the mandible QM F44423.

Length as preserved—left ramus	134.5 mm
Length as preserved—right ramus	113 mm
Maximum preserved height (at fifth alveolus)	20 mm
Width at 1st pair of alveoli	14 mm
Width at 2nd pair of alveoli	17.2 mm
Width at 3rd pair of alveoli	17.2 mm
Width at 4th pair of alveoli	17.4 mm
Width at 5th pair of alveoli	18.1 mm
Width at 6th pair of alveoli	18.35 mm
Width at 7th pair of teeth	18.5 mm
Left alveoli (mesiodistal length × lingobuccal width)	
1	6 × 5.3 mm
2	6.2 × 4.5 mm
3	6 × 4.5 mm
4	6.5 × 5 mm
5	7.5 × 5.5 mm
6 (obscured by matrix)	
7	5.5 × 5 mm
8	6.5 × 5.5 mm
Right alveoli (mesiodistal length × lingobuccal width)	
1	5 × 4.5 mm
2	7 × 5.5 mm
3	5.5 × 4.5 mm
4	6.4 × 5 mm
5	6.5 × 5.5 mm
6	7 × 6 mm
7	7.5 × 6 mm
Width of mandibular symphysis (ridge to ridge) at	
Alveolus 7	6.5 mm
Alveolus 2	2 mm
Left mandibular ramus—interalveolar distance	
1–2	6 mm
2–3	8.2 mm
3–4	8.2 mm
4–5	7.2 mm
5–6	8.1 mm
6–7	~11 mm
7–8	13.5 mm
Right mandibular ramus—interalveolar distance	
1–2	7 mm
2–3	8.5 mm
3–4	7.3 mm
4–5	8.2 mm
5–6	8.4 mm
6–7	11.5 mm
Associated tooth preserved crown height	20 mm
Associated tooth width	
Thickest preserved (base)	5 mm
Thinnest preserved (near apex)	3 mm

Unwin (2001, 2003) and Bakhurina and Unwin (1995) diagnosed ornithocheirids primarily on the relative proportions of the rostral-most teeth (and hence alveoli). Ornithocheirids exhibit a characteristic ‘double peak’ dentition, with the largest mandibular teeth occurring around positions 2 and 6/7, and the smallest around position 4; a sequence that has been supported by other studies (Kellner et al., 2003; Lü and Ji, 2005; Steel et al., 2005). Associated with this increase in tooth size, the tip of the rostrum may also be transversely expanded, as is best exemplified in *Coloborhynchus* spp., *Anhanguera blittersdorffi*, *A. santanae* and *A. ‘piscator.’*

Tooth disparity in QM F44423 is minimal, and there is no evidence of transverse expansion of the rostral end of the dentary. *Ornithocheirus simus*, the type species for Ornithocheiridae (see Unwin and Martill, 2007; represented by five mandibular rostra from the Cambridge Greensand; Unwin, 2001), also has a mandible with near parallel-sided lateral margins rostrally, and with the first three to four pairs of teeth directed dorsally rather than laterodorsally. In common with other ornithocheirids, the rostral-most teeth in *O. simus* are still larger than those in the caudal part of the jaw, thus adhering to the typical ornithocheirid pattern of tooth disparity. *Anhanguera cuvieri*, another ornithocheirid from the Cambridge Greensand, in common with QM F44423, also lacks the marked expansion of the rostral end of the dentary seen in other species of *Anhanguera* (Unwin, 2001). However, as noted by Unwin (2001; pers. comm., 2008), the disparity in tooth size and a corresponding development in the terminal expansion of the jaws in ornithocheirids are very likely to be related both to size and to ontogenetic stage. Thus immature individuals of all species and mature individuals of small species may have jaws that are essentially straight with minimal tooth size disparity. By contrast, mature individuals of large species generally tend to have relatively larger rostral teeth and strongly expanded rostral jaw tips. In this light, the lack of a typically ornithocheirid sequence of tooth disparity in QM F44423 should be interpreted with caution.

Crests are present in most ornithocheirids, including *Ornithocheirus simus*, which has a sagittal crest at the rostral end of the mandible. Unlike *O. simus*, and many other ornithocheirids, the preserved extent of QM F44423 lacks any indication of a sagittal crest. However, the possible absence of a crest in QM F44423 may not be unusual for an ornithocheirid, because *Brasileodactylus*, sp. indet. (Sãyao and Kellner, 2000), *Boreopterus cuiae* (Lü and Ji, 2005), and *Ludodactylus sibbicki* (Frey et al., 2003) also lack a ventral keel on the dentary. In addition, as been noted previously by Bennett (1992, 2002), Campos and Kellner (1997), and Unwin (2005), the presence or absence of rostral crests in pterorsaurs is more likely to be an indication of sexual dimorphism rather than relatedness. We therefore remain ambivalent about the phylogenetic significance of the presence or the absence of a sagittal crest in QM F44423.

Excluding differences that may stem from early ontogenetic stage, relative size, or sexual dimorphism, QM F44423 fits the criteria for Ornithocheiridae as outlined in Unwin (2001, 2003). However, there are a number of other potential or unusual ornithocheiroids, ornithocheirids and other closely related taxa that need to be taken into account in determining the affinities of QM F44423. Likely ornithocheirids with which we compared QM F44423 include *‘Ornithocheirus’ wiedenrothi* (based on a cast of SMNS 56628, the holotype, and Wild, 1990), *Brasileodactylus*, sp. indet, and *Ludodactylus sibbicki*. *‘Ornithocheirus’ wiedenrothi* was not considered in the study of Unwin (2001). Although the species is valid, it most likely represents a type of ornithocheirid that is distinct from *Ornithocheirus*, and may warrant the future establishment of a new genus (D. Unwin, pers. comm., 2008). Pending a review of *‘Ornithocheirus’ wiedenrothi*, we will follow Unwin (2001) and do not consider it a member of *Ornithocheirus* senso stricto, but still a valid taxon of ornithocheirid.

Unwin (2001) considers the near perpendicular orientation of the first four pairs of teeth, relative to the long axis of the jaw, characteristic of *Ornithocheirus* (specifically *O. simus*). QM F44423 displays this character. *‘Ornithocheirus’ wiedenrothi* has a different state, with the first pair of teeth protruding rostrodorsally, and the remainder near perpendicular to the long axis of the jaw (Wild, 1990). The character state of the first tooth pair of QM F10613 (the mandible described by Molnar and Thulborn 1980), as determined by the internal angling of the alveoli, is similar to that seen in *‘Ornithocheirus’ wiedenrothi*. The rostral-most teeth of *Brasileodactylus*, sp. indet., and *Ludodactylus sibbicki* are different again, being proportionately enlarged and projecting dorsomedially, forming a weak rostral rosette.

Bennett (1994), in reference to Seeley (1870), uses the presence of a sagittal ridge on the palate, corresponding to a groove in the mandible, as a synapomorphy of Ornithocheiroidea, but also notes similar structures in Azhdarchidae. Additionally, Unwin (2003) notes that *Lonchodectes* has a deep ‘V’-shaped median sulcus on the surface of the mandibular symphysis. Sayão and Kellner (2000) consider “a well developed sulcus reaching the tip of the dentary” to be a defining feature of

Brasileodactylus araripensis. Similarly, Wild (1990), differentiated *'Ornithocheirus' wiedenrothi* from other *Ornithocheirus* species based on the presence of a median groove that extends to the rostral-most tip of the mandible. The groove in the mandible of QM F44423 and, to a lesser degree, QM F10613, is well developed. The preservation of the rostral tips of both mandibulae are poorly preserved and total extent of the groove is difficult to discern with certainty. However, the groove on QM F44423 extends at least as far as the first tooth pair, does not narrow or become shallower as it approaches this point, and may match the described character state of *'Ornithocheirus' wiedenrothi* and *Brasileodactylus araripensis*. The taxonomic importance of this character remains uncertain.

Recently, Molnar and Thulborn (2007) suggested that QM F10613 should be reassigned to aff. *Lonchodectes* spp. Molnar and Thulborn's (2007:469) decision is based on Unwin's (2001) referral of many Cambridge Greensand *Ornithocheirus* species to *Lonchodectes*. Molnar and Thulborn (1980, 2007) were never specific about which species of *Ornithocheirus* they were referring to with regard to QM F10613, only that it was "very similar to jaw fragments attributed to *Ornithocheirus* from the Cambridge Greensand" (Molnar and Thulborn, 1980:362). Molnar (pers comm., 2010) has since indicated that the Queensland specimens were compared mostly with material assigned to *Ornithocheirus* in the CAMSM and BMNH, in particular *'O.' sedgwickii*, *'O.' microdon*, *'O.' daviesi*, and *'O.' fittoni*, as well as some pieces only identified as *Ornithocheirus* sp. Unwin (2001) assigned *'Ornithocheirus' sedgwickii* to *Coloborhynchus*, *'Ornithocheirus' microdon* to *Lonchodectes*, and *'Ornithocheirus' fittoni* to *Anhanguera*. The type mandbile of *'Ornithocheirus daviesi'* (BMNH 43074) is from the Albian Gault Clay of Folkstone (Owen, 1874; Benton and Spencer, 1995). However, this taxon was considered a synonym of *Lonchodectes platysomus* by Unwin et al. (2000). The holotype mandible of *L. platysomus* (CAMSM BS4.SSS) is from the Cambridge Greensand (Unwin, 2001).

Anhanguera fittoni is distinguished from all other ornithocheirids by its broad and flattened jaw tips, and widely spaces tooth rows (Unwin, 2001). *Coloborhynchus sedgwikii* has the second and third pairs of teeth directed forwards and outwards forming a 'tooth-grab.' This is distinct from the condition in QM F44423, in which the front three pairs of teeth are directed near perpendicular to the long axis of the rostrum, and QM F10613, in which the first is directed forwards and outwards, but the second and third pairs of teeth are near perpendicular to the long axis of the rostrum. QM F10613 and QM F44423 also differ from *Lonchodectes microdon* and *L. platysomus* in that the rostral-most ends of the jaws are not dorsoventrally flattened, they have no parapet-like dental margins, and the alveoli are not small and round, but larger relative to the mandible and oval in shape.

Based on our own comparisons, we conclude that QM F10613 is more similar to *'Ornithocheirus' wiedenrothi* than any ornithocheirid taxa considered by Unwin (2001). As outlined above, Unwin (2001, 2003) did not consider *'Ornithocheirus' wiedenrothi* a valid species of *Ornithocheirus*. Nor does Unwin (2001, 2003) synonymize it with *Lonchodectes*. As with QM F44423, QM F10613 can be differentiated from *Lonchodectes* sensu Unwin (2001) by the absence of 'parapet-like dental margins' and other dental features. We therefore propose that QM F10613 is best placed in Ornithocheiridae, gen. et sp. indet., until further material suggests otherwise.

It is noteworthy that both QM F10613 and QM F44423 derive from late Albian strata in the northern part of the Eromanga Basin: QM F10613 from the Toolebuc Formation near Boulia, and QM F44423 from a stratigraphically equivalent formation near Hughenden. Many mandibular features seen in QM F44423 also occur in QM F10613. These include widely spaced alveoli, large alveolar size, width and depth of the mandible (not deep like *Lonchodectes*), lack of or an insubstantial keel, and no enlargement of the rostral end to form a rosette. However, they are dissimilar in that QM F10613 has unusually rostrodorsally angled front teeth similar to *'Ornithocheirus' weidenrothi*. Based on their close morphological similarity and equivalent age, it therefore seems likely that these specimens belong to two taxa that are closely related, if not ontogenetic or sexual variants of the same taxon.

Mythunga camara, recently described by Molnar and Thulborn (2007), is also known from part of the rostrum, specifically occluded maxillary and mandibular parts (QM F18896). Based on the identification of twelve cranial characters used in Kellner's (2003) phylogenetic analysis of Pterosauria, Molnar and Thulborn (2007) determined that *M. camara* could represent either a rhamphorhynchid, a plesiomorphic archaeopterodactyloid or an advanced pteranodontid other than *Anhanguera*. Molnar and Thulborn (2007) concluded that they could exclude *M. camara* from Rhamphorhynchidae based on its presumed confluent nares and preorbital fenestra, and from the remaining pteranodontids included in Kellner's (2003) analysis by individual comparison. As a consequence, they tentatively assigned *M. camara* to Archaeopterodactyloidea (sensu Kellner, 2003).

Contrary to Molnar and Thulborn (2007), we interpret the rostral end of QM F18896 to be incompletely preserved (as opposed to almost complete), such that the entire specimen most likely represents only one fifth of the total skull length. It is common for species within Ornithocheiridae to have a dental pattern characterized by enlarged teeth rostrally with a set of smaller teeth behind them, then another group of enlarged teeth and further reduced teeth caudally (Steel et al., 2005). The first upper tooth preserved on *M. camara* corresponds well in size and position with the 12th or 13th upper tooth of species of *Anhanguera* and *Coloborhynchus* to which we were able to compare it (e.g., *Coloborhynchus piscator*) when the rostral-most borders of the antorbital fenestrae are aligned and resized to account for scale. From the tooth directly following this caudally, the alignment of the alveoli and the relative size of teeth, where present, are within the range of variation seen within the clade. As such, we suspect that this specimen should be reassigned to Ornithocheiridae. A detailed study revising the phylogenetic relationships of this specimen is recommended, but beyond the scope of this paper. As the preserved portion of the *M. camara* holotype is not the same, nor does it overlap with the specimens described herein, direct comparisons with other Queensland specimens are not possible.

Taxonomic Conclusion—The combination of characters exhibited by QM F44423 indicate that it is referable to Ornithocheiridae using the criteria outlined in Unwin (2001, 2003). Among ornithocheirids there are many species with similar mandibular characters, but none that match the particular combination seen in QM F44423. We therefore refrain from referring QM F44423 to a specific ornithocheirid genus, and instead assign it to Ornithocheiridae, gen. et sp. indet., but note that it is most similar to *'Ornithocheirus' wiedenrothi* (Wild, 1990) and QM F10613.

ORNITHOCHEIROIDEA Seeley, 1870
ORNITHOCHEIRIDAE Seeley, 1870
cf. *ANHANGUERA* Campos and Kellner, 1985

Specimen—QM F44321, the proximal end of the left metacarpal IV of an *Anhanguera*-like pterosaur.

Horizon and Locality—QM F44321 was found in the late Albian Toolebuc Formation (Boreham and Powell, 1987) northeast of Boulia by Tom Hurley circa 2002. It derives from a horizon that is slightly higher stratigraphically than the 'fish hash' limestone east of Boulia in which previous Australian pterosaur specimens (QM F10613, QM F10614, QM F10612, Molnar and

Thulborn, 1980; QM F12982; Molnar, 1987) were discovered during the 1970s (Figs. 1–2).

Description

Preservation—QM F44321 (Fig. 4) comprises an 88.5-mm portion of the proximal end of a left metacarpal IV. The general shape and major features of the shaft and articular surface of the proximal extremity of the bone are apparent, but the fine details have been lost, most likely due to weathering.

Osteology—The diameter of the shaft is greatest proximally, decreasing distally towards the break. At the location of the transverse fracture, the shaft of the bone is oval in cross-section, with a dorsoventral diameter of 18 mm and a craniocaudal diameter of 12 mm (Table 2).

TABLE 2. Measurements taken of the metacarpal IV, QM F44321.

Specimen length	88.5 mm
Distal cross-section	
Dorsoventrally	18 mm
Craniocaudally	12 mm
Proximal cross-section	
Dorsoventrally	35.4 mm
Craniocaudally—center	21.5 mm
Craniocaudally—cranial	26 mm
Tuberculum cross-section	
Dorsoventrally	10 mm
Craniocaudally	8 mm
Length of proximodistally oriented sulci	25 mm

In proximal aspect (Fig. 4I–J), the ventral surface is flat. From the caudoventral to the craniodorsal edge, the outline of the bone curves to form an inverted 'J' shape. There are three proximodistally aligned ridges on proximal end of the cranial surface. The craniodorsal and the cranial proximal ridges are both low and broad, with the latter being continuous with a proximal tuberculum (see below). The third ridge—the cranioventral proximal ridge—is thinner and more pronounced, forming a sharp angle

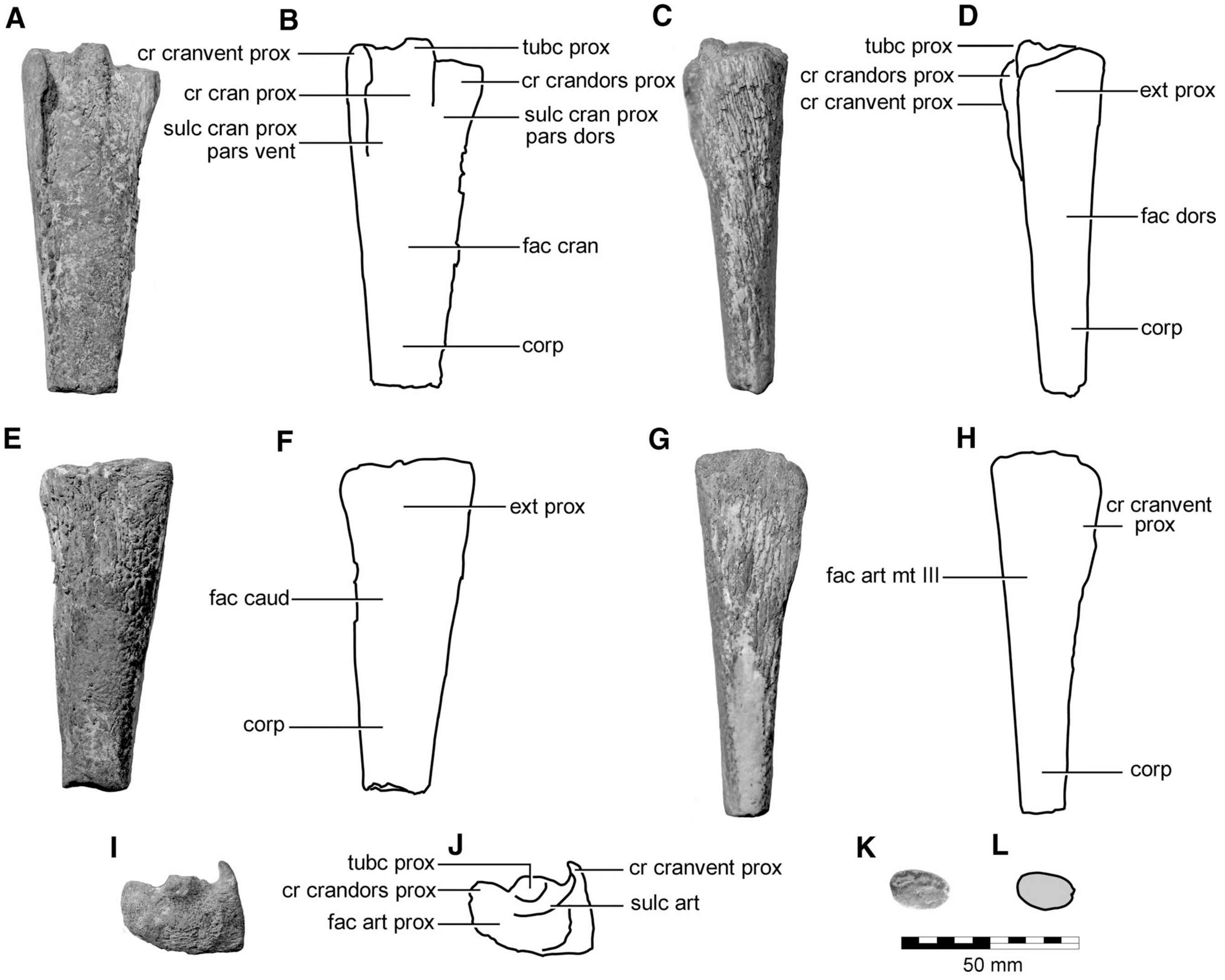

FIGURE 4. cf. *Anhanguera*, QM F44321, the proximal end of a left metacarpal IV from the late Albian Toolebuc Formation northeast of Boulia, central-western Queensland, Australia. Photos and schematic interpretations in (**A**, **B**) cranial, (**C**, **D**) dorsal, (**E**, **F**) caudal, (**G**, **H**) ventral, (**I**, **J**) proximal, and (**K**, **L**) distal aspects. Grey shading indicates position of remaining matrix and/or surface breaks. **Abbreviations**: **corp**, corpus (shaft); **cr cran prox**, proximal cranial ridge; **cr crandors prox**, proximal craniodorsal ridge; **cr cranvent prox**, proximal cranioventral ridge; **ext prox**, proximal extremity; **fac art mt III**, articular surface for metacarpal III; **fac art prox**, proximal articular surface; **fac caud**, caudal surface; **fac cran**, cranial surface; **fac dors**, dorsal surface; **sulc art**, articular sulcus; **sulc cran prox pars dors**, dorsal part of the proximal cranial sulcus; **sulc cran prox pars vent**, ventral part of the proximal cranial sulcus; **tubc prox**, proximal tuberculum.

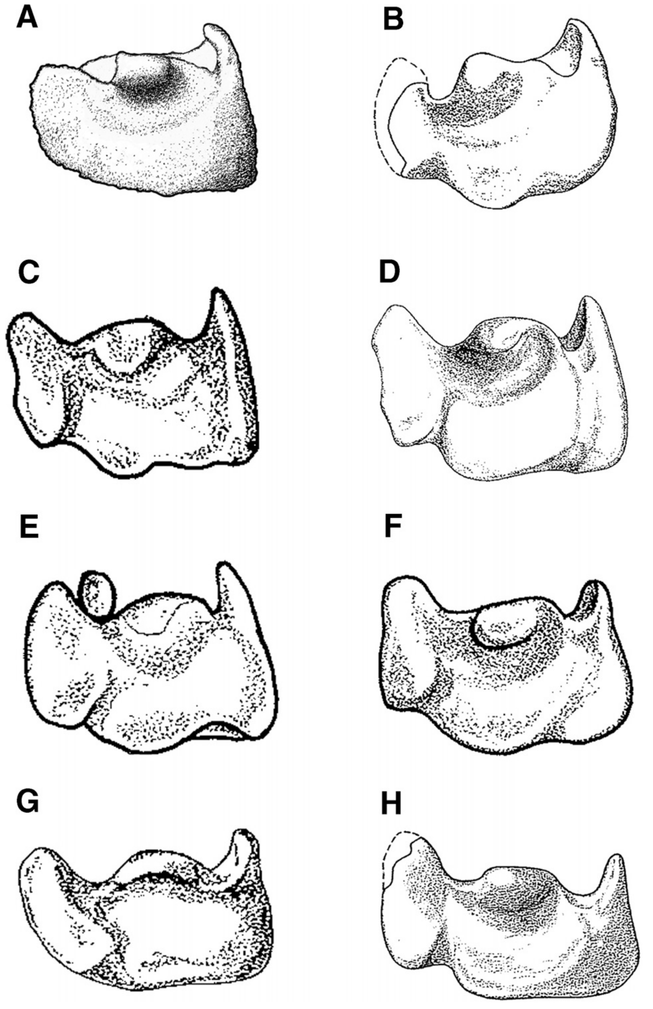

FIGURE 5. Schematic interpretations of the proximal extremity of metacarpal IV in proximal aspect for specimens referred to *Anhanguera* or cf. *Anhanguera*. **A**, QM F44321; **B**, BSP 1982 I 90 (Wellnhofer, 1985); **C**, AMNH 22552 (Wellnhofer, 1991b); **D**, BSP 1982 I 89 (Wellnhofer, 1985); **E**, BSP 1987 11 (Wellnhofer, 1991b); **F**, BSP 1987 66 (Wellnhofer, 1991b); **G**, BSP 1980 I 120 (Wellnhofer, 1985); **H**, AMNH 22555 (Wellnhofer, 1991b). Not to scale.

between the cranial and ventral surfaces in proximal aspect. Two shallow sulci, each approximately 25 mm in length, occur either side of the (central) proximal cranial ridge. At a point level with the proximal end of the proximal cranial ridge, the craniocaudal thickness of the shaft is 21.5 mm, whereas at the proximal end of the more ventral ridge it is 26 mm. The dorsoventral cross-sectional thickness of the bone is 35.4 mm.

The proximal cranial ridge protrudes from the surrounding proximal articular surface to form a low tuberculum. This tuberculum is 10 mm across dorsoventrally and 8 mm across craniocaudally. Surrounding the tuberculum is a shallow arc-shaped articular sulcus. Immediately around the depression is a large, mainly flattened articular surface. The dorsocaudal corner of the proximal surface is slightly raised.

Comparisons—QM F44321 shows similarities to derived pterodactyloids, which have much reduced metacarpals II and III, and a large articular surface on metacarpal IV (Fig. 5). *Dsungaripterus* differs from QM F44321 in having a larger proximal tuberculum compared to the size of the articular surface, much deeper delineations between the more convex sections of the articular surface and a more pronounced enlargement in diameter towards the distal articular extremity from the shaft (Bakhurina, 1982).

Tapejarids, as represented by *Huaxiapterus jii*, have a similar morphology to QM F44321 when viewed cranially, with the exception that the ventral articular surface rises to a dome-like shape to the same level as the proximal tuberculum (Lü and Yuan, 2005). The ventral articular surface QM F44321 is much flatter and lower.

In azhdarchids, as represented by *Montanazhdarcho*, the articular facets protrude laterally from the shaft (McGowen et al., 2002), unlike the smooth enlargement of QM F44321.

The arc-like articular sulcus in QM F44321 is incomplete in *Istiodactylus* (Hooley, 1913). Although other specimens from the Cambridge Greensand are also somewhat similar to QM F44321, they are not assigned beyond Ornithocheiridae.

Overall, we feel that QM F44321 shows the closest similarity to ornithocheirids, and in particular *Anhanguera* spp. Noticeable differences relate to the morphology of the proximal articular surface. Unfortunately, the wear on this part of QM F44321 makes it difficult to determine the presence or absence of a crest that disrupts the articular sulcus and the pattern of convex surface features; both of which seem to differ between specimens of *Anhanguera* with which QM F44321 was compared (Fig. 5).

In all the pterosaur metacarpal IVs that we examined, the morphology of the proximal end of the caudal surface closely reflects the morphology of the sulci and tuberculum on the articular surface. In BSP 1982 I 89 (Fig. 5D), AMNH 22555 (Fig. 5H: Wellnhofer, 1985), AMNH 22552 (Fig. 5C: Wellnhofer, 1991b), and BSP 1987 I 1 (Fig. 5E: Wellnhofer, 1991b), the proximal end of the caudal surface has two elongate sulci that coincide with the grooves in the articular face discussed above. BSP 1980 I 120 (Fig. 5G: Wellnhofer, 1985) does not have these grooves, as in QM F44321. Rather, the outline from the caudoventral edge to the craniodorsal edge is smooth and uninterrupted, forming a 'J' shape.

The exact morphology of the tuberculum and surrounding arc-shaped sulcus on QM F44321 do not closely match that of any specimens. The tuberculum of QM F44321 is oval in cross-section and does not connect to a crest that disrupts the articular sulcus. Other specimens have varied morphologies, including crescent- (Fig. 5G), 'D'- (Fig. 5C), and 'tear-drop'-shaped (Fig. 5B, D, E), some of which connect to the crest that disrupts the articular sulcus (Fig. 5B, D, E, F, H).

Taxonomic Conclusion—QM F44321 is assigned to cf. *Anhanguera* because it is most similar to members of this genus, but appears to be distinct from any described species. We note that the morphology of metacarpal IV is not known for *Ornithocheirus*.

ORNITHOCHEIROIDEA Seeley, 1870
ORNITHOCHEIRIDAE Seeley, 1870
cf. *ANHANGUERA* Campos and Kellner, 1985

Specimen—QM F44312, the distal portion of an *Anhanguera*-like wing phalanx.

Horizon and Locality—QM F44312 was found on Dunluce Station, between Hughenden and Richmond (Figs. 1–2). It derives from the uppermost nodular limestone of the late Albian Toolebuc Formation (Boreham and Powell, 1987).

Description

Preservation—QM F44312 (Fig. 6) comprises a 111.5-mm portion of the distal extremity of a wing phalanx. The distal surface is eroded. The cranial half of the articular head is more eroded than the caudal half, forming a weakly concave surface between

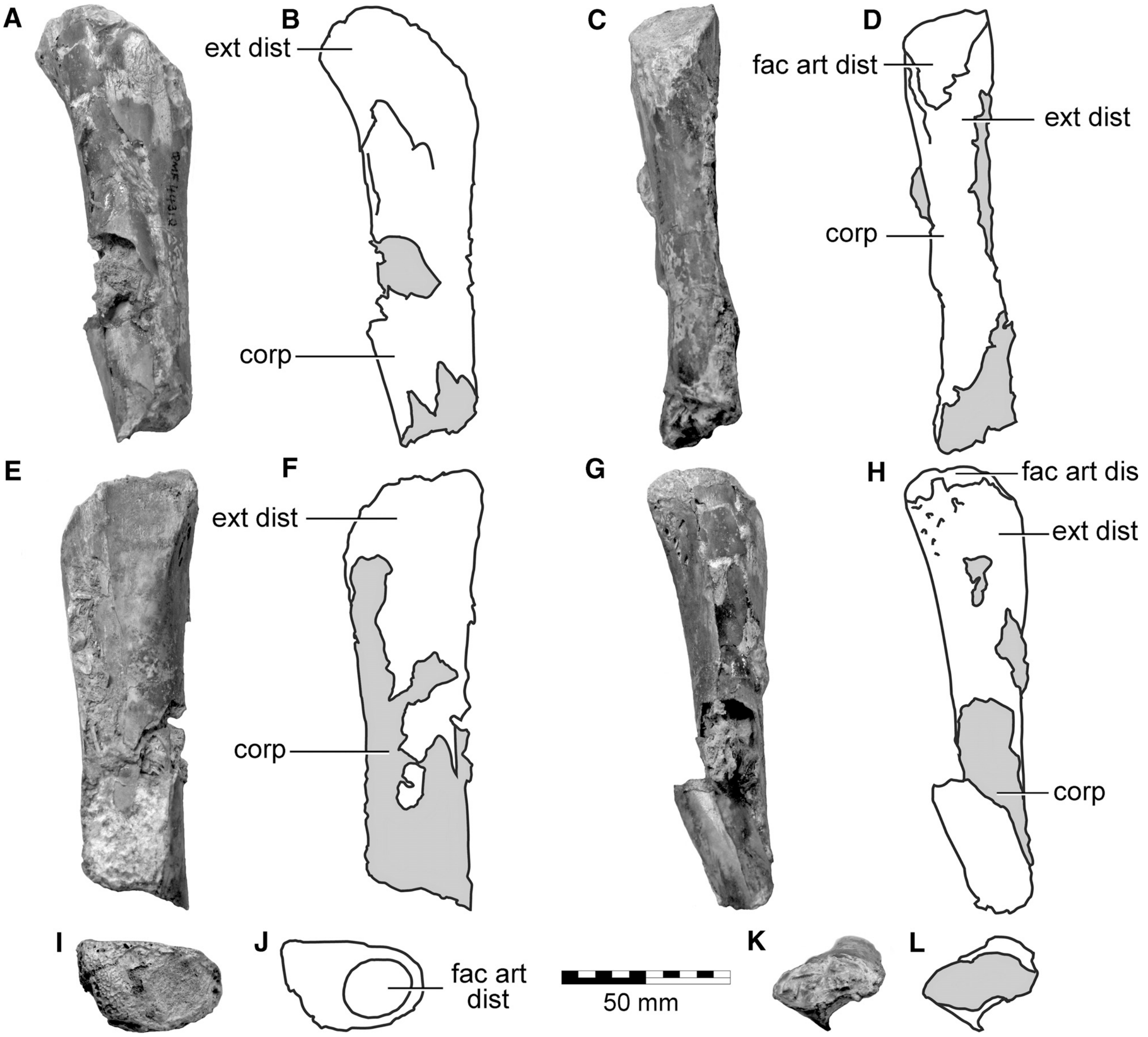

FIGURE 6. cf. ***Anhanguera***, QM F44312, the distal portion of a wing phalanx from late Albian Toolebuc Formation of Dunluce Station, between Hughenden and Richmond, central-western Queensland, Australia. Photos and schematic interpretations in (**A**, **B**) dorsal, (**C**, **D**) caudal, (**E**, **F**) ventral, (**G**, **H**) cranial, (**I**, **J**), distal, and (**K**, **L**) proximal aspects. Grey shading indicates remaining matrix and/or surface breaks. **Abbreviations**: **corp**, corpus (shaft); **ext dist**, distal extremity; **fac art** dist, distal articular surface.

the dorsal and ventral bone walls. The caudal half of the articular head retains its naturally convex shape. The surface of the shaft is less eroded than the distal extremity, but is fractured in places and distorted at these breaks.

A major fracture in the shaft occurs approximately 33 mm from the proximal end. This fracture exposes the internal spongiosa as well as small, thin, long bones of indeterminate affinity and at least two teleost centra that are 4 mm in diameter. The ventral surface has been flattened. A proximodistally aligned fracture runs down the length of the shaft, approximately 12 mm from the cranial edge. As a result of this fracture, the original cross-sectional outline of the shaft is difficult to ascertain.

Osteology—The distal extremity of the bone is enlarged compared with the shaft. At the broken end of the shaft the cross-section appears sub-oval (Fig. 6K–L), whereas from the proximal aspect the cross-section appears sub-triangular (Fig. 6I–J). It is 29 mm long craniocaudally and approximately 14 mm wide dorsoventrally (Table 3). At the proximal-most extent of the distal articular surface, approximately 30 mm from the tip of the bone, the shaft is approximately 35 mm wide in craniocaudal aspect and 23 mm dorsoventrally. The bone wall at the distal surface is 3 mm thick compared with the bone wall at the distal-most break, which is 1 mm thick.

Comparisons—Due to the size and bone wall thickness, QM F44312 was identified as a pterodactyloid pterosaur. Based on the shape of the articular end, and the degree of enlargement of the articular end compared to the shaft and distal end, QM F44312 appears to represent wing phalanx I or II.

TABLE 3. Measurements taken of the wing phalanx, QM F44312.

Total specimen length	111.5mm
Distal cross-section	
Dorsoventral	29mm
Craniocaudal	14mm
Proximal cross-section	
Dorsoventral	23mm
Craniocaudal	35mm
Bone wall thickness	
Shaft	1mm
Articular surface	3mm
Distance of proximodorsal crack from cranial edge	12mm
Distance of fracture from proximal end	33mm

The following features were used to distinguish the wing phalanges I and II of pterodactyloids: (1) The thickness of the phalangeal wall compared to the total cross-sectional area; (2) cross-sectional shape; (3) significant enlargement of shaft diameter towards the distal end; (4) the angle of the distal articular head to the shaft; and (5) absence of pneumatic foramina. The expression of these characteristics in QM F44312 is discussed below.

1. The cross-sectional area of the phalangeal wall is approximately 5% of the total cross-section of the shaft. A cross-sectional proportion of approximately 55% is diagnostic of dsungaripterids (Young, 1964; Unwin, 1995; Unwin et al., 1996). From this it can be concluded that QM F44312 does not share affinities with dsungaripterids.
2. QM F44312 has a sub-oval to sub-triangular cross-section of the shaft, similar to *Anhanguera*, specifically *Anhanguera pricei* (BSP 1980 122, MZ A/III 522, AMNH 22552; Wellnhofer, 1985, 1991b), pteranodontids (Bennett, 2001), and istiodactylids (Hooley, 1913). QM F44312 does not have the characteristic 'T-shaped' cross-section reported for wing phalanx II or III of azhdarchids (Martill and Frey, 1999). A wing phalanx I was not available for comparison, but it is unlikely that the cross-section, which is related to the function of the bone, would differ greatly between the first, second and third phalanges. Among ornithocheirids, coloborhynchid wing phalanges are rounded-square or circular in cross-section (Veldmeijer, 2003). We note that no wing elements are currently referred to *Ornithocheirus*.
3. QM F44312 does not have as extreme enlargement of the shaft, terminating in a large distal articular surface, as seen in pteranodontids (Bennett, 2001). This also excludes Hooley's (1913) istiodactylid, which appears to have a constricted shaft.
4. The distal articular head of QM F44312 is angled at approximately 45 degrees to the long axis of the shaft, whereas in *Istiodactylus sinensis* (Andres and Ji, 2006) it appears to be at approximately 90 degrees.
5. Prominent pneumatic foramina are absent on QM F44312. For this reason, it is again unlike members of the Pteranodontidae, which exhibit foramina on the distal extremity of the wing phalanx (Bennett, 2001).

Taxonomic Conclusion—QM F44312 is referred to the Ornithocheiridae cf. *Anhanguera* because it has a similar distal articular head morphology and cross-sectional shaft shape to *Anhanguera pricei*, thin bone walls, and no prominent pneumatic foramina.

LOPHOCRATIA sensu Unwin, 2003
CTENOCHASMATOIDEA Unwin, 1995
Genus and Species Indeterminate

Specimen—QM F42739, the proximal extremity of a left pterosaur humerus displaying characters associated with Ctenochasmatoidea.

Horizon and Locality—QM F42739 was found in the upper-half of the Mackunda Formation at Vellum Downs, approximately 100 km southwest of Hughenden (Figs. 1–2). The Mackunda Formation forms the lower part of the Manuka Subgroup of the Rolling Downs Group, and is considered latest Albian in age. It is a marginal marine, sandy siltstone (Moore, 1986) in which significantly fewer dinoflagellate fossils are preserved than in the other, earlier formations (Burger, 1986), reflecting the changing conditions of the regressing inland sea (Pole and Douglas, 1999).

Description

Preservation—QM F42739 (Fig. 7) comprises a 75-mm portion of a long bone including much of an articular end and an unknown portion of the shaft. It is interpreted as the proximal extremity of a left humerus. The surface bone of the proximal end is intact. The head has been damaged on both the cranial and caudal sides and an unknown portion is missing. The surface of the dorsal side of the caudal portion of the head is also damaged. The bone is undistorted. There are two complete transverse fractures through the shaft.

Osteology—The specimen is enlarged at the articular end but the shaft is otherwise straight, with a nearly constant diameter. At the distal end, the cross-section of the transverse fracture is approximately 10 mm dorsoventrally and 17 mm craniocaudally (Table 4). Approximately 69 mm proximally from the transverse fracture the craniocaudal width of the shaft is 21 mm. On the cranial side of the saddle-shaped articular surface the specimen is 9 mm thick dorsoventrally. The broken surface of the deltopectoral crest is 20 mm long proximodistally, averages 5 mm wide and is 'crescent-shaped.'

To the caudal side of the saddle-shaped articular surface, the specimen is 14 mm thick dorsoventrally. The cross-section of the sub-oval caudal broken surface is 22 mm proximodistally and 13 mm dorsoventrally. Damage to the dorsal surface is roughly circular in outline. It is approximately 10 mm in diameter and meets the surface break of the caudal side at the dorsocaudal edge.

Comparisons—QM F42739 was identified as pterosaurian based on its thin bone walls and overall morphology. It can be excluded from the expected assignation to Ornithocheiroidea because the deltopectoral crest is unwarped, and appears to be small in proportion to the preserved portion of the shaft; in ornithocheiroids the deltopectoral cress is distinctly warped, and at least 40% of the total length of the shaft (Bennett 1989, 1994, 2001; Unwin, 1995). A survey of known pterosaur humeri found no exact matches to the new specimen. Unwin (2003) used humeral characters, specifically an elongate, rectangular deltopectoral crest, as a synapomorphy of Lophocratia, a

TABLE 4. Measurements taken of the humerus, QM F42739.

Total specimen length	
Distal to articular facet	69 mm
Distal to caudal tip	75 mm
Distal cross-section	
Dorsoventral	10 mm
Craniocaudal	17 mm
Proximal cross-section	
Craniocaudal	21 mm
Dorsoventral—cranial side	9 mm
Dorsoventral—caudal side	14 mm
Craniomedially directed process—break	
Proximodistally	20 mm
Dorsoventrally	5 mm
Caudal break	
Proximodistally	22 mm
Dorsoventrally	13 mm
Dorsal break—diameter	10 mm

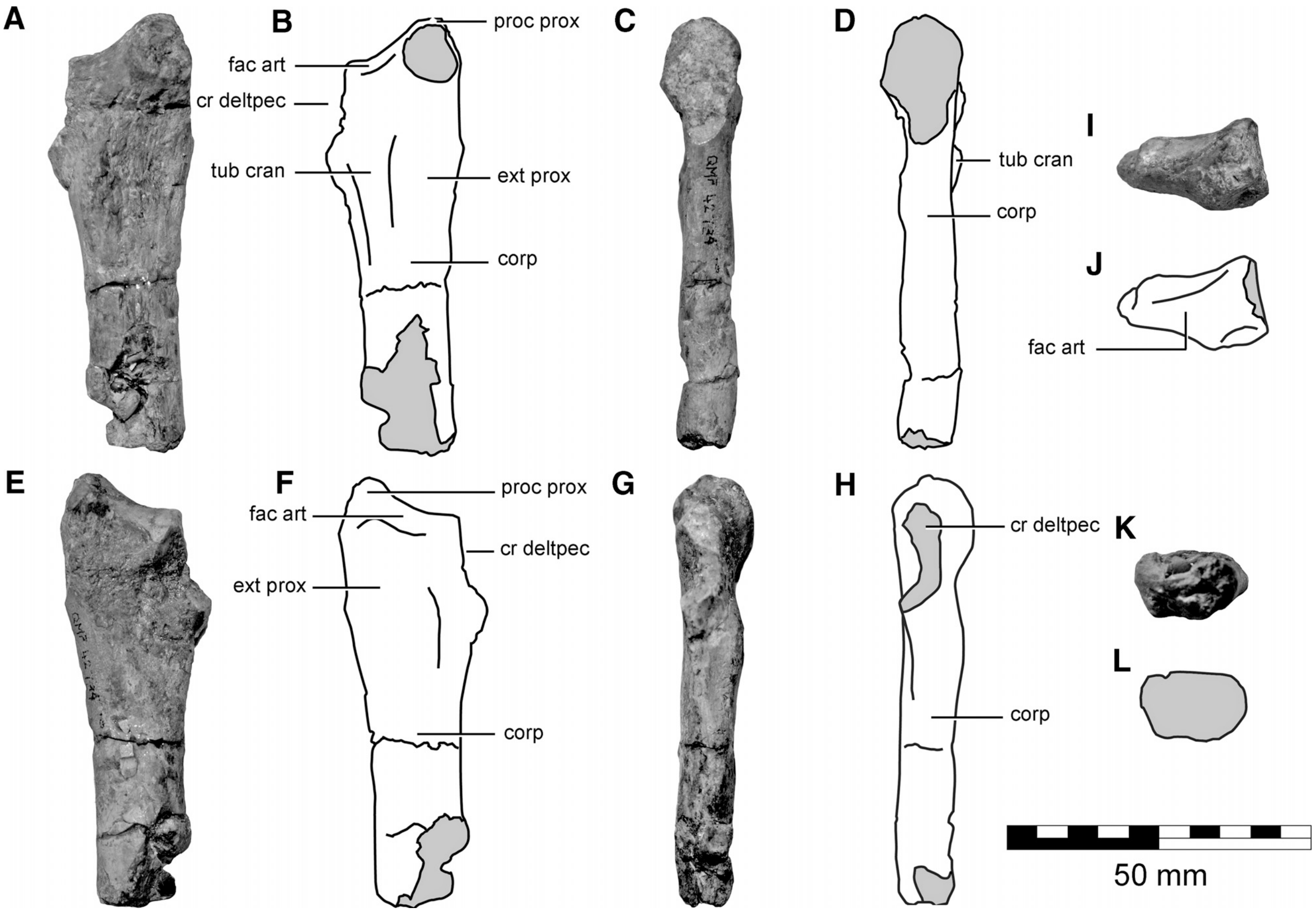

FIGURE 7. Ctenochasmatoidea, gen. et. sp. indet., QM F42739, proximal portion of left humerus from the late Mackunda Formation of Vellum Downs Station, approximately 100 km southwest of Hughenden, central-western Queensland. Photographs and schematic interpretations in (**A**, **B**) cranial, (**C**, **D**) dorsal, (**E**, **F**) caudal, (**G**, **H**) ventral, (**I**, **J**) proximal, and (**K**, **L**) distal aspect. Grey shading indicates remaining matrix and/or surface breaks. **Abbreviations**: **corp**, corpus (shaft); **cr deltpec**, deltopectoral crest; **ext prox**, proximal extremity; **fac art**, articular surface; **proc prox**, proximal process; **tub cran**, cranial tubercle.

clade that contains Dsungaripteroidea, Azhdarchoidea, and Ctenochasmatoidea.

The deltopectoral crest of QM F42739 is 30% of the preserved length of the shaft. It is therefore less than 30% of the total length of the shaft, as the shaft is incomplete and shows no changes distally, such as enlargement, which would indicate the proximal humeral extremity was immediately proximal to the break. Dsungaripterids have deltopectoral crests approximately 30% of the total length of the shaft (Codorniú and Chiappe, 2004), and thus are proportionally larger than in QM F42739. They also have relatively thick bone walls (Unwin, 1995; Unwin et al., 1996), unlike the new specimen. The morphology of the humerus in Azhdarchoidea seems highly variable, but is usually robust (Lawson, 1975; Buffetaut et al., 2002), with the articular head thickened (Buffetaut et al., 2002). There is no evidence of such thickening of the articular head in QM F42739. The preserved proportion of the shaft of QM F42739 is straight and constant in diameter, which is also a plesiomorphic rather than a derived character (Codorniú et al., 2006). For these reasons we believe we can eliminate Dsungaripteroidea and Azhdarchoidea, thus placing QM F42739 within Ctenochasmatoidea.

Ctenochasmatoidea (sensu Unwin, 1995) comprises *Cycnorhamphus*, *Pterodactylus*, Lonchodectidae, and Ctenochasmatidae. This is a very similar content to that of Kellner's (2003) Archaeopterodactyloidea, though we note that Kellner includes *Germanodactylus* and not *Lonchodectes* in this grouping, whereas Unwin allies *Germanodactylus* with Dsungaripteridae, and places *Lonchodectes* within Ctenochasmatoidea.

The most similar specimen to which QM F42739 can be compared is a sub-adult, Late Jurassic pterodactyloid from Argentina, assigned to the Archaeopterodactyloidea (sensu Kellner, 2003) by Codorniú et al. (2006): MOZ 3625P. The assignment of this specimen was supported by the proximally placed and ventrally curved deltopectoral crest, the age of the material, and other plesiomorphic characters such as the straight shaft and relatively short deltopectoral crest. These characters are also seen in *Rhamphorhynchus*, *Pterodactylus*, *Gallodactylus*, and *Ctenochasma elegans*, but unlike the specimen described by Codorniú et al. (2006), the humeri of these taxa have a curved shaft. QM F42739 also displays these features, and, similar to MOZ 3625P, has a straight shaft. For these reasons QM F42739 and MOZ 3625P of Codorniú et al. (2006) have similar morphology and may be closely related. The actual assignment of these specimens to a more specific clade is impeded by the lack of any associated cranial material and other unrepresented key skeletal characters (Codorniú et al., 2006).

As mentioned above, *Mythunga camara* has also been tentatively referred to Archaeopterodactyloidea (sensu Kellner, 2003;

roughly equivalent to Ctenochasmatoidea sensu Unwin, 1995) by Molnar and Thulborn (2007). However, as discussed above, we believe that *M. camara* should be assigned to Ornithocheiroidea. Consequently QM F42739 is the only described specimen that supports the presence of non-ornithocheiroid pterosaurs in the Early Cretaceous of Australia.

Taxonomic Conclusion—Without further evidence, QM F42739 is tentatively identified as an indeterminate ctenochasmatoid lophocratian.

DISCUSSION

Compared with most other continents, the Australian pterosaur record remains very poor. According to Barrett et al. (2008), Australia, Antarctica, Africa, and South America account for only 12% of the world's pterosaur bearing localities, with Australia's paucity second only to Antarctica. With the inclusion of the new localities herein, Australia approaches Africa in terms of number of localities; however, the African localities listed in Barrett et al. (2008) exceed Australia's record in specimens found, and the diversity of pterosaurs represented. Australia has only a small number of specimens discovered thus far, and these specimens are incomplete, isolated elements. This study almost doubles the number of Australian pterosaur specimens described previously.

Based on the material described thus far, the Early Cretaceous pterosaur fauna of the Eromanga Basin appears to have comprised ornithocheirid pterodactyloids in the early part of the late Albian, and ctenochasmatoid lophocratians (sensu Unwin, 2003) in the latter part of the late Albian. Ornithocheirids are represented by seven or eight of the nine specimens thus far described. We consider non-ornithocheirids to be represented only by the Vellum Downs humerus (QM F42739), because we regard *Mythunga camara* (Molnar and Thulborn, 2007) as a likely ornithocheiroid.

It is notable that of the new ornithocheirid material from the Eromanga Basin described herein, the cranial remains compare most favourably to an *Ornithocheirus*-like taxon (most notably *'Ornithocheirus' wiedenrothi*), whereas the postcranial remains (excluding QM F42739) to *Anhanguera* or an *Anhanguera*-like taxon. Molnar and Thulborn (2007) reach a similar conclusion when reconsidering other Eromanga Basin pterosaur remains (but see previous comments regarding their referral of QM F10613 to aff. *Lonchodectes* spp.).

The most obvious explanation of the observations regarding the taxonomic composition of northern Australia's Early Cretaceous pterosaur fauna is that the Eromanga basin pterosaur fauna of the early Albian comprised both *Ornithocheirus* or *Ornithocheirus*-like taxon, and *Anhanguera* or *Anhanguera*-like taxon.

Ornithocheirid pterosaurs appear to have had a global distribution, with specimens recognized from China (Wang and Lü, 2001; Wang and Zhou, 2003), Morocco (Kellner and Mader, 1997), Mongolia (Bakhurina and Unwin, 1995), and North America (Lee, 1994), as well as the locations discussed earlier in this paper; namely, in South America, England, Germany, and Australia. Mixed assemblages containing combinations of *Ornithocheirus*, *Anhanguera*, and *Coloborhynchus* have been described from the Cambridge Greensand of England and the Santana Formation of Brazil, suggesting it is common for these pterosaurs to occur in the same area (Unwin, 2001). Therefore, the northern Australian pterosaur fauna may have comprised two or more ornithocheirid taxa (an *Ornithocheirus*-like taxon or closely related form, and an *Anhanguera*-like taxon), with the proposed assignments presented here reflecting this composition.

It is also possible that *Ornithocheirus* had an *Anhnaguera*-like postcranium. Among ornithocheirid pterosaurs, the postcranial anatomy is best known for *Anhanguera*, *Coloborhynchus*, and *Arthurdactylus conandoylei* (Frey and Martill, 1994). The postcranium of *Ornithocheirus* is poorly known, and the genus is diagnosed only on the basis of cranial characteristics. Similarly, *'Ornithocheirus' wiedenrothi*, a taxon that compares very favourably to some of the Queensland pterosaurs in terms of mandibular morphology, also has a poorly known postcranium (only a partial radius, a partial ulna and metacarpals II–III, a partial phalanx of digits II–III, and a partial thoracic rib are described; Wild, 1990). It is therefore difficult to establish whether there are significant differences between the postcranial anatomy of *Ornithocheirus*-like pterosaurs and other ornithocheirids. *Coloborhynchus* and *Anhanguera* are comparable postcranially (Veldmeijer, 2003), so it seems plausible that *Ornithocheirus* and other, possibly closely related forms such as *'Ornithocheirus' wiedenrothi*, would also conform to a similar postcranial morphology. Indeed, of the known material of *'Ornithocheirus' wiedenrothi*, Wild (1990:253–254) notes a close agreement between the distal ulna morphology of *Santanadactylus araripensis* (= *Anhanguera araripensis*; Kellner and Tomida, 2000) and *Araripesaurus santanae* (= *Anhanguera santanae*; Kellner, 1990; Wellnhofer, 1985; Kellner and Tomida, 2000). The possibility that *'Ornithocheirus' wiedenrothi* is more closely related to *Anhanguera* than to *Ornithocheirus* cannot be ruled out.

Until more postcranial material can be confidently assigned to *Ornithocheirus* and the precise taxonomic and phylogenetic affinities of *'Ornithocheirus' wiedenrothi* are properly established, the assumption of a mixed pterosaur fauna occurring in northern Australia during the Early Cretaceous cannot be confirmed.

Paleobiogeographic Implications

The Early Cretaceous pterosaur fauna of the Eromanga Basin appears to have comprised ornithocheirid pterodactyloids in the early late Albian when the Eromanga Sea was near its greatest extent, and at least one ctenochasmatoid lophocratian in the latest part of the late Albian, approaching the Cenomanian, when the sea was undergoing periods of regression leading up to its disappearance in the Late Cretaceous. However, we acknowledge that due to the small sample size this may not be a true signal; it may be the result of different habitat use, habit resulting in a preservational bias, or have another, unknown cause.

Australian ornithocheirids may have either included an *Ornithocheirus*-like taxon or closely related form, an *Anhanguera*-like taxon, or a taxon that combines *Ornithocheirus*-like cranial characteristics with an *Anhanguera*-like postcranium.

A mixed ornithocheirid pterosaur fauna throughout the early Albian would match, at least in part, the Early Cretaceous pterosaur fauna of South America, but with the notable absence of tapejarids. Interestingly, the Cambridge Greensand, another locality with ornithocheirid diversity, also lacks tapejarids (Unwin, 2001). Typical ornithocheirids are large-toothed and considered to be specialist piscivores, whereas tapejarids are edentulous (Unwin, 2005). This may indicate adaptation to specific environments and food sources. Feeding and habitat specialization may also explain the hypothesized faunal turnover, from ornithocheirid pterodactyloids to ctenochasmatoid lophocratians, as the environmental conditions of western Queensland underwent change associated with late Albian regression of the epicontinental Eromanga sea.

Shallow, epicontinental marine transgressions were common to both South America (Riccardi, 1987) and Australia (Campbell and Haig, 1999) during the Late Jurassic and Early Cretaceous. A preference for the habitats associated with these epicontinental seaways may have influenced pterosaur diversification and distribution, with some taxa occurring in restricted regions. Based on the material described to date, it may be that Australia's Early

Cretaceous ornithocheirid pterosaurs were endemic to the epicontinental seaways of the Eromanga Basin.

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