

# Zitteliana

An International Journal  
of Palaeontology and Geobiology

Series B/Reihe B  
Abhandlungen der Bayerischen Staatssammlung  
für Paläontologie und Geologie

28



DAVID W. E. HONE & ERIC BUFFETAUT (Guest Editors)

**Flugsaurier: pterosaur papers in honour of  
Peter Wellnhofer**

München 2008

# Zitteliana

An International Journal of Palaeontology and Geobiology  
Series B/Reihe B

Abhandlungen der Bayerischen Staatssammlung für Paläontologie und Geologie

## B28

DAVID W. E. HONE & ERIC BUFFETAUT (Eds)

### Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

#### CONTENTS/INHALT

Dedication	3
PETER WELLNHOFER A short history of pterosaur research	7
KEVIN PADIAN Were pterosaur ancestors bipedal or quadrupedal?: Morphometric, functional, and phylogenetic considerations	21
DAVID W. E. HONE & MICHAEL J. BENTON Contrasting supertree and total-evidence methods: the origin of the pterosaurs	35
PAUL M. BARRETT, RICHARD J. BUTLER, NICHOLAS P. EDWARDS & ANDREW R. MILNER Pterosaur distribution in time and space: an atlas	61
LORNA STEEL The palaeohistology of pterosaur bone: an overview	109
S. CHRISTOPHER BENNETT Morphological evolution of the wing of pterosaurs: myology and function	127
MARK P. WITTON A new approach to determining pterosaur body mass and its implications for pterosaur flight	143
MICHAEL B. HABIB Comparative evidence for quadrupedal launch in pterosaurs	159
ROSS A. ELGIN, CARLOS A. GRAU, COLIN PALMER, DAVID W. E. HONE, DOUGLAS GREENWELL & MICHAEL J. BENTON Aerodynamic characters of the cranial crest in <i>Pteranodon</i>	167
DAVID M. MARTILL & MARK P. WITTON Catastrophic failure in a pterosaur skull from the Cretaceous Santana Formation of Brazil	175
MARTIN LOCKLEY, JERALD D. HARRIS & LAURA MITCHELL A global overview of pterosaur ichnology: tracksite distribution in space and time	185
DAVID M. UNWIN & D. CHARLES DEEMING Pterosaur eggshell structure and its implications for pterosaur reproductive biology	199
DAVID M. MARTILL, MARK P. WITTON & ANDREW GALE Possible azhdarchoid pterosaur remains from the Coniacian (Late Cretaceous) of England	209
TAISSA RODRIGUES & ALEXANDER W. A. KELLNER Review of the pterodactyloid pterosaur <i>Coloborhynchus</i>	219
JUNCHANG LÜ, LI XU & QIANG JI Restudy of <i>Liaoxipterus</i> (Istiodactylidae: Pterosauria), with comments on the Chinese istiodactylid pterosaurs	229
DAVID M. MARTILL First pterosaur remains from the Exu Formation (Cretaceous) of the Araripe Basin, Brazil	243
ERIC BUFFETAUT Late Cretaceous pterosaurs from France: a review	249

Editors-in-Chief/Herausgeber: Michael Krings, Gert Wörheide  
Production and Layout/Bildbearbeitung und Layout: Martine Focke  
Bayerische Staatssammlung für Paläontologie und Geologie

#### Editorial Board

A. Altenbach, München  
B.J. Axsmith, Mobile, AL  
F.T. Fürsich, Erlangen  
K. Heißig, München  
H. Kerp, Münster  
J. Kriwet, Stuttgart  
J.H. Lipps, Berkeley, CA  
T. Litt, Bonn  
A. Nützel, München  
O.W.M. Rauhut, München  
B. Reichenbacher, München  
J.W. Schopf, Los Angeles, CA  
G. Schweigert, Stuttgart  
F. Steininger, Eggenburg

Richard-Wagner-Str. 10, D-80333 München, Deutschland  
<http://www.palmuc.de/zitteliana>  
email: [zitteliana@lrz.uni-muenchen.de](mailto:zitteliana@lrz.uni-muenchen.de)

Für den Inhalt der Arbeiten sind die Autoren allein verantwortlich.  
Authors are solely responsible for the contents of their articles.

Copyright © 2008 Bayerische Staatssammlung für Paläontologie und Geologie, München

Die in der Zitteliana veröffentlichten Arbeiten sind urheberrechtlich geschützt.  
Nachdruck, Vervielfältigungen auf photomechanischem, elektronischem oder anderem Wege  
sowie die Anfertigung von Übersetzungen oder die Nutzung in Vorträgen, für Funk und Fernsehen  
oder im Internet bleiben – auch auszugsweise – vorbehalten und bedürfen der schriftlichen Genehmigung  
durch die Bayerische Staatssammlung für Paläontologie und Geologie, München.

ISSN 1612-4138

Druck: Gebr. Geiselberger GmbH, Altötting

**Cover Illustration:** Modell eines *Rhamphorhynchus* aus dem Oberjura von Eichstätt. Entwurf: P. Wellnhofer, Modell: R. Liebreich,  
Foto und Collage: M. Schellenberger, L. Geißler, BSPG München.

**Umschlagbild:** Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer;  
design: R. Liebreich; photograph and collage: M. Schellenberger, L. Geißler, BSPG Munich.

Zitteliana	B28	243 - 248	4 Textfigs, 1Pl.	München, 31.12.2008	ISSN 1612 - 4138
------------	-----	-----------	------------------	---------------------	------------------

# First pterosaur remains from the Exu Formation (Cretaceous) of the Araripe Basin, Brazil

By  
David M. Martill\*

*Palaeobiology Research Group, School of Earth and Environmental Sciences,  
University of Portsmouth, Portsmouth, PO1 3QL, United Kingdom*

Manuscript received November 9, 2007; revised manuscript accepted February 28, 2008.

## Abstract

A fragmentary pterosaur proximal humerus from the basal member of the Exu Formation (Cretaceous) of Piauí, Brazil represents the first pterosaur element from this formation and may even be the first macrofossil from this dominantly arenaceous horizon. The fragment is tentatively assigned to *Lophocratia UNWIN*, 2003. The preservation is inconsistent with it having been reworked from the famously pterosaur-rich Santana Formation which underlies the Exu Formation in the region.

**Key words:** Cretaceous, Pterosauria, Exu Formation, Brazil

## Zusammenfassung

Der fragmentarische proximale Teil des Humerus eines Pterosauriers aus dem basalen Glied der Exuformation (Kreidezeit) von Piauí, Brasilien, repräsentiert das erste Pterosaurierelement aus dieser Formation. Es könnte sogar das erste Makrofossil aus diesem mächtigen Quarzsandsteinhorizont sein. Das Fragment wurde vorläufig *Lophocratia UNWIN*, 2003 zugeordnet. Die Erhaltung des Fossils ist schlecht, da es aus der für ihren Pterosaurierreichtum bekannte Santana Formation, dem Liegenden der Exu Formation in der Region, aufgearbeitet und umgelagert wurde.

**Schlüsselwörter:** Kreide, Pterosauria, Exu Formation, Brasilien

## 1. Introduction

The Araripe Basin of north east Brazil contains a largely Cretaceous sedimentary infill in which two fossil Konservat Lagerstätten occur, the Aptian Nova Olinda Member of the Crato Formation (MARTILL & FREY 1998; UNWIN & MARTILL 2007) and the ?Albian Romualdo Member of the Santana

Formation (MARTILL 1993). Both of these horizons are well known for the exceptional preservation of fossil vertebrates (MARTILL 1988, 1997; WENZ & BRITO 1990). The sequence is capped by the massively bedded Exu Formation sandstone with conglomerates that form an extensive plateau known as the Chapada do Araripe.

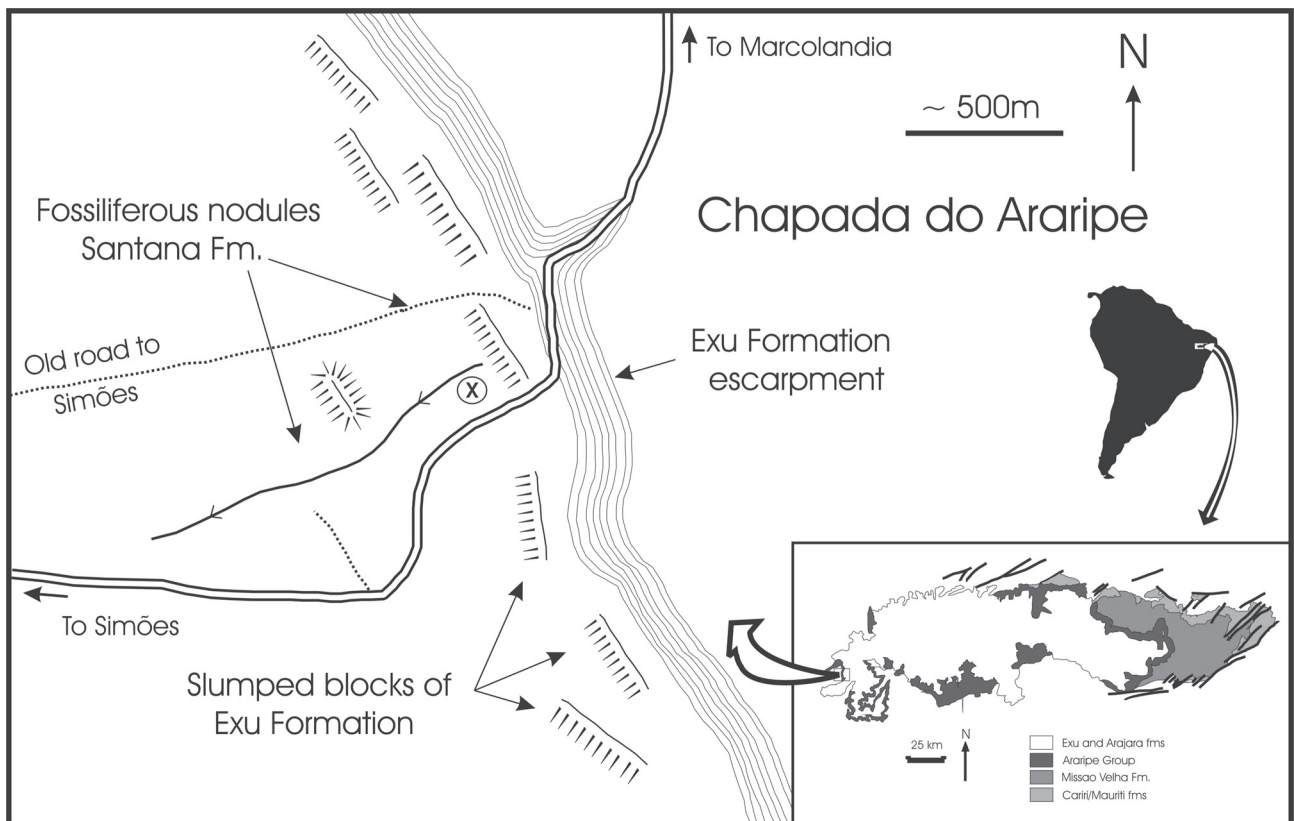
The precise age of the Exu Formation is unknown, but LIMA (1978) suggests a mid Albian age on the basis of palynomorphs. However, recent revisions of the age of the underlying Santana Formation based on palynomorphs suggests that the Exu Formation is probably somewhat younger (U. HEIMHOFER, pers. com. 2007). Although the formation is an important aquifer and supports a productive agriculture, its stratigraphy and sedimentology remain largely unstudied and the internal stratigraphy of the Exu Formation remains to be established. There appears to be a gradational coarsening upward from mudstones of the Santana Formation to the sandstones of the Exu Formation in the east of the region, but widespread slumping and jungle growth at the contact means that the basal boundary of the Exu Formation is rarely exposed. The situation is somewhat different in the west, where a basal unit of highly oxidised laminated mudstones, siltstones and fine sandstones termed the Simões Member by MARTILL & WILBY (1993) occurs widely, before passing up into massive sandstones with conglomerates.

This formation has largely been regarded as unfossiliferous but, during field work in 2005, a fragment of a pterosaurian humerus and plant remains were collected from exposures of the Exu Formation in the western Araripe Basin. The humerus, described here, apparently represents the first vertebrate fossil from this formation.

## 2. Locality

The pterosaur humerus was collected from slumped exposures of the Exu Formation on the western flanks of the Chapada do Araripe between Marcolândia in Pernambuco and Simões in Piauí. This is close to locality 23 of MARTILL (1993: 129). These exposures are slumped masses of light brown Exu Formation

\*E-mail: David.Martill@port.ac.uk



**Textfigure 1:** Sketch map of the new locality where slumped masses of the Exu Formation sandstones yield rare macrofossils. The cross in a circle marks the site where the partial pterosaur humerus was collected.

sandstones that have overridden the mudstones of the Santana Formation. The locality is easily accessed by scrambling down the bank at the side of the asphalted road (Textfig. 1). A small stream dissects the slumped masses of sandstones and a network of small paths provide access through the thorny scrub. Exposure is excellent, but determining the precise stratigraphic relationships of each slumped mass is difficult.

### 3. Stratigraphy

Due to the extensive landslide of the western flank of the Chapada do Araripe details of the stratigraphy are difficult to elucidate. Nevertheless, it is possible to identify the concretion-bearing Romualdo Member of the Santana Formation at the locality on account of its abundant laminated carbonate concretions with fossil fish and, as everywhere, the bright pink sandstones of the Exu Formation make up the escarpment face of the Chapada. Field brash of silicified laminated limestone may represent the Crato Formation, but no in situ material was found. A simplified stratigraphy for the Cretaceous part of the Araripe Basin in this region typically comprises black shales and laminated limestone that can be referred to the Crato Formation, which is overlain by bedded gypsum of the Ipubi Formation. A disconformity usually marks boundary between the Ipubi Formation and the overlying Santana Formation. There then follows a unit of finely laminated silts and fine sands, the Simões Member that near Araripina may reach 5 m in thickness. These laminated silts and sands can be identified

at the locality, but their relationship to the underlying Santana Formation cannot be observed. Above the Simões Member are 5 or more metres of well bedded buff coloured sandstones with small (2–10 cm in diameter) dark brown ironstone concretions. These are especially common on weathered ground where they accumulate as a lag (Plate 1) and it is in these concretions that fossils have now been located in the Exu Formation. The buff coloured sands are overlain by several metres of bright pink sandstones and conglomerates that comprise the remainder of the Exu Formation. Although a complete stratigraphic log cannot be constructed for the locality without considerable effort, a simplified stratigraphy is presented in Textfigure 2.

## 4. Palaeontology

### 4.1 Systematic palaeontology

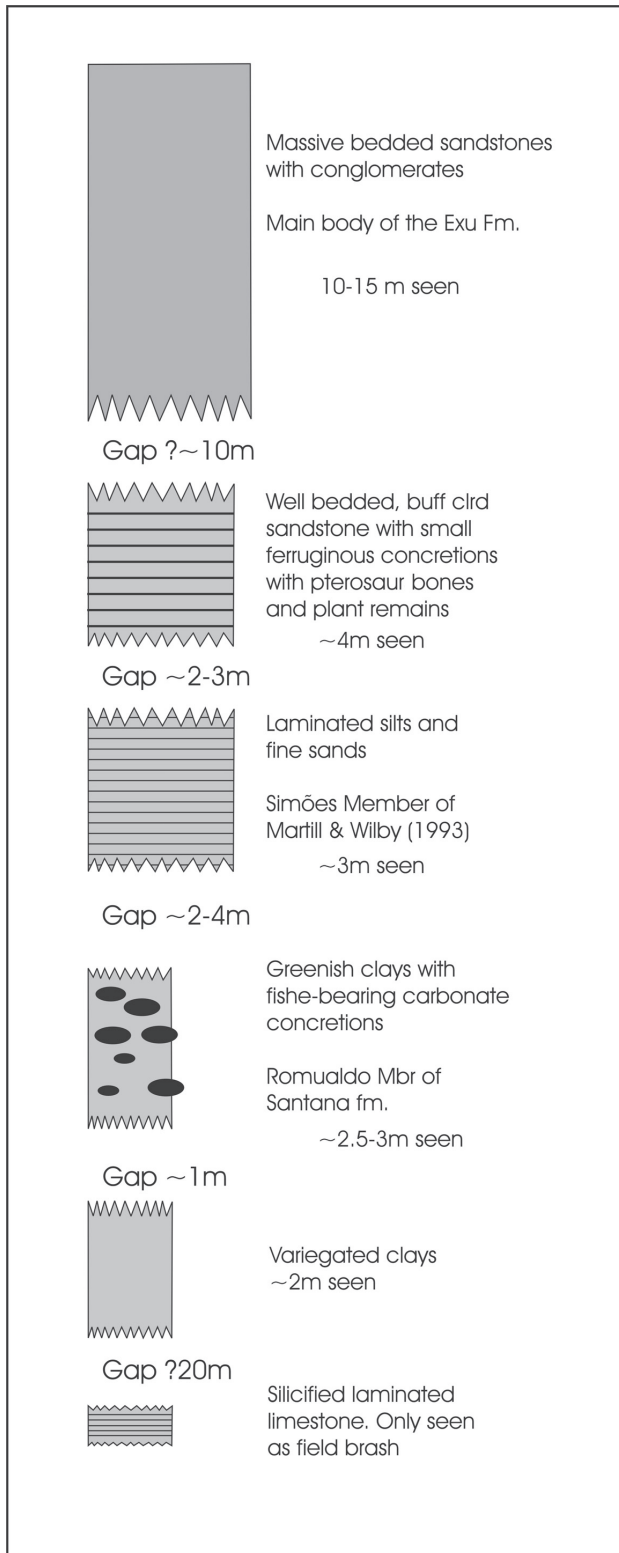
Pterosauria KAUP, 1834  
 Pterodactyloidea PLIENINGER, 1901  
 Lophocratia UNWIN, 2003  
 Lophocratia Indet.

Specimen: Fragment of proximal right humerus lacking the humeral head. Number SMNK PAL 6414 in the collection of the Staatliches Museum für Naturkunde Karlsruhe, Germany.

Locality: Natural exposure on road approximately 8km east of Simões, Piauí, north east Brazil. Map reference SB.24-



**Plate 1:** New fossil locality for the Exu Formation (Cretaceous) of the Araripe Basin, Brazil. (1) View of the western escarpment of the Chapada do Araripe (background) with landslipped mass of buff coloured sands (foreground) that yield the first Exu Formation vertebrate fossils; (2) Weathered face of the buff sandstones with ironstone concretions and harder cemented patches weathering out.

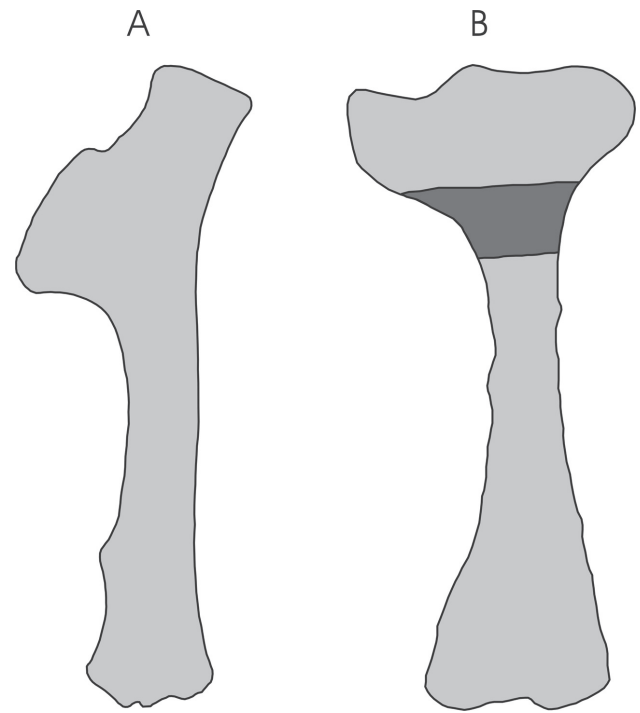


**Textfigure 2:** Simplified stratigraphic log for the slopes of the Chapada do Araripe between Marcolandia and Simões. Bed thicknesses are approximate as widespread slumping prevents accurate measurements.

Y-C-VI 308 9160.

Horizon: Unnamed member of the Exu Formation, above the Simões Member of MARTILL & WILBY (1993).

Age: Upper Cretaceous, most probably younger than Albian.



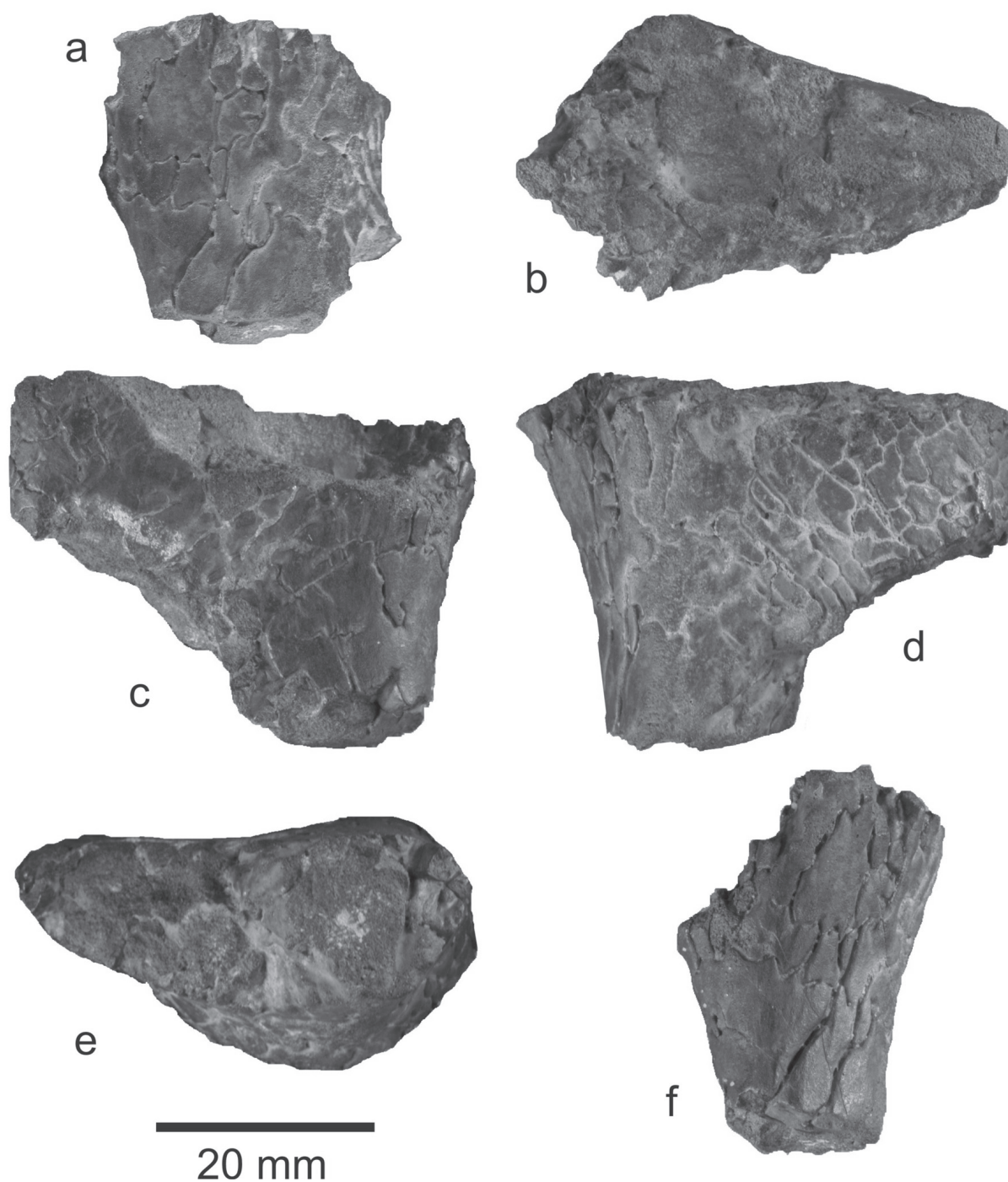
**Textfigure 3:** Pterosaur humeri. A, ornithocheirid type; B, lophocratan humerus, *Tapejara wellnhoferi* with the Exu Formation fragment shaded in dark grey. A, based on WELNHOFER (1991); B, based on FREY et al. (2003: fig. 4B' SMNK PAL 1137).

## 4.2 Description

The humeral fragment measures 33 mm in length, with a maximum proximal diameter of 47 mm and 18 mm distally. The bone is preserved as an iron oxide (presumed to be goethite on account of its dark brown colour) cemented fine sandstone infill of the void space of the humerus. All cortical bone has flaked away to reveal an internal mould of the bone with trabeculae intact. There is no crushing and the missing termini have clean fractures suggesting that more of the bone was originally preserved. Although the cortical bone is missing, there is no evidence of wear due to abrasion, but the trabeculae are incised perhaps due to some slight chemical weathering. The exposed trabeculae are widely spaced, forming irregular polygonal cells that become denser proximally (Textfig. 4a,f) with individual trabeculae approximately 0.75 mm thick. The cross-sectional shape at the distal termination is a rounded asymmetrical triangle (Textfig. 4b), whereas the cross section is a flattened 'D' shape proximally (Textfig. 4e). The palmar surface expands proximally equating to the base of the deltopectoral crest (Textfig. 4c,d). Fossil plant material was also found at this locality and is enclosed within ironstone concretions, but the bone lacks any ironstone overgrowths.

## 5. Discussion

The internal structure of this bone fragment is typical of the proximal and distal parts of the larger long bones of pterodac-



**Textfigure 4:** Partial pterosaur proximal humerus from the lower units of the Exu Formation between Marcolandia and Simões, Piauí, Brazil. Specimen no. SMNK 6414. a: detail of trabeculae, b: proximal view, c: ventral fascia, d: dorsal fascia, e: distal view, f, cranial fascia.

tyloids (DE RICQLÈS 2000). The gentle proximal expansion of the diaphysis into the deltopectoral crest is reminiscent of the condition found in the humeri of the lophocratian pterosaurs *Tapejara* (Textfig. 4b) and *Lonchodectes* (UNWIN 2003: fig. 17)), rather than the near 90 degree deflection seen in ornithocheirids. Although referral here to Lophocratia UNWIN, 2003 is speculative given the highly fragmentary nature of the specimen, it is worth noting that the lophocratians *Tupuxuara*, *Tapejara*, *Tupandactylus* and possibly *Cearadactylus* occur in the underlying Santana and Crato Formations (UNWIN & MAR-

TILL 2007). Regardless, despite the lack of taxonomic precision, the discovery of this pterosaur fragment is significant in two respects. Firstly, it demonstrates that body fossils, although clearly rare, do occur in the Exu Formation. Perhaps this locality represents an unusual facies of this dominantly sandy unit, and further work should be undertaken to determine the geographical distribution of this fossiliferous horizon. Secondly, the preservation, although far from ideal, is of an uncrushed bone that is not enclosed within a calcareous concretion. Although the possibility exists that originally the



fragment was indeed enclosed in a concretion, and subsequent weathering released the fossil, perhaps with the bone compacta remaining on the concretion, it seems more parsimonious that the bone was preserved in three dimensions in uncompacted sandstone. If this latter scenario is correct, then it is most likely that the pterosaur bone is at least penecontemporaneous with the sediment and does not represent an element reworked from the underlying Santana Formation. If this is the case, then this specimen represents another occurrence of a pterosaur in a non-marine horizon.

## Acknowledgements

I am indebted to Artur ANDRADE of the DNPM, Crato for assistance in Brazil and to Robert LOVERIDGE for photographing the specimen. Thanks to Mark WITTON for helpful discussion and Dan BONTER, Sam HEADS, Natalie MITCHELL and Judith WOHLRABE for help in the field. Thanks to Dave HONE for assisting with the refereeing and editorial process.

## 6 References

- FREY, E., BUCHY, M.-C. & MARTILL, D. M. (2003): Middle- and bottom-decker Cretaceous pterosaurs: unique designs in active flying vertebrates. – In: E. BUFFETAUT & J.-M. MAZIN (Eds), *Evolution and Palaeobiology of Pterosaurs*. – Geological Society of London Special Publication, **217**: 267–274.
- KAUP, J. J. (1834): Versuch einer Eintheilung der Säugethiere in 6 Stämme und der Amphibien in 6 Ordnungen. – *Isis* **3**: 311–315.
- LIMA, M. R. (1978): Microfósseis da Formação Exu. Cretáceo do Nordeste do Brasil. – *Anais XXX Congresso Brasileira Geologia*, **2**: 965–969.
- MARTILL, D. M. (1988): The preservation of fossil fishes in concretions from the Cretaceous of Brazil. – *Palaeontology*, **30**: 1–18.
- MARTILL, D. M. (1993): Fossils of the Santana and Crato Formations, Brazil. – *The Palaeontological Association Field Guides to Fossils*, **5**: 1–159.
- MARTILL, D. M. (1997): Fish oblique to bedding. – *Palaeontology* **40**: 1011–1026.
- MARTILL, D. M., BECHLY, G. & LOVERIDGE, R. F. [Eds] (2007): *The Crato Fossil Beds of Brazil: window into an ancient world*; Cambridge (Cambridge University Press), 624 pp.
- MARTILL, D. M. & FREY, E. (1998): A new pterosaur Lagerstätte in N. E. Brazil (Crato Formation: Aptian, Lower Cretaceous): preliminary observations. – *Oryctos* **1**: 79–85.
- MARTILL, D. M., & WILBY, P. R. (1993): Stratigraphy. – In: D. M. MARTILL (Ed.), *Fossils of the Santana and Crato Formations, Brazil*. – *The Palaeontological Association Field Guides to Fossils*, **5**: 1–159.
- PLIENINGER, F. (1901): Beiträge zur Kenntnis der Flugsaurier. – *Palaeontographica* **48**: 65–90.
- RICQLÈS, A. J. DE, PADIAN, K., HORNER, J. R. & FRANCILLON-VIELLOT, H. (2000): Paleohistology of the bones of pterosaurs (Reptilia: Archosauria): anatomy, ontogeny, and biomechanical implications. – *Zoological Journal of the Linnean Society*, **129**: 349–385.
- UNWIN, D. M. (2003): On the phylogeny and evolutionary history of pterosaurs. – In: E. BUFFETAUT & J.-M. MAZIN (Eds), *Evolution and Palaeobiology of Pterosaurs*. – Geological Society Special Publication, **217**: 139–190.
- UNWIN, D. M. & MARTILL, D. M. (2007): Pterosaurs from the Crato Formation. – In: D. M. MARTILL, G. BECHLY & R. F. LOVERIDGE (Eds), *The Crato Fossil Beds of Brazil: Window into an Ancient World*; Cambridge (Cambridge University Press), 475–524.
- WENZ, S. & BRITO, P. M. (1990): L'ichthyofaune des nodules fossilifères de la Chapada do Araripe. – In: D. DE A. CAMPOS, M. S. S. VIANA, P. M. BRITO & G. BEURLEN (Eds), *Atas do simpósio sobre a Bacia do Araripe e Bacias Interiores do Nordeste, Crato (14–16 de Junho de 1990)*, 337–349.
- WELLNHOFER, P. (1991): Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. – *Palaeontographica A*, **215**: 43–101.