Proceedings of the Geologists' Association 135 (2024) 660–675

Contents lists available at ScienceDirect

Proceedings of the Geologists' Association

journal homepage: www.elsevier.com/locate/pgeola

A large pterosaur from the Middle Jurassic (lower Bajocian) of Rutland, United Kingdom

Darren Withers [a], David M. Martill [b,*], Roy E. Smith [b], Michael Ashton [c], Anusuya Chinsamy [d], Charles Wood [e], Richard Forrest [f]

[a] 43 Godsey Lane, Market Deeping, Peterborough, Cambridgeshire PE6 8HY, UK
[b] School of the Environment and Life Sciences, University of Portsmouth, PO1 2DY, UK
[c] Ashton Geology Ltd, Oakhurst, Stanhope Avenue, Woodhall Spa LN10 6SP, UK
[d] Biological Sciences Department, University of Cape Town, Private Bag X3, Rhodes Gift 7701, South Africa
[e] Future Technology Centre, School of Mechanical Design and Engineering, University of Portsmouth, PO1 3HE, UK
[f] 20 Fernwood Drive, Radcliffe on Trent, Nottinghamshire NG12 1AA, UK

ARTICLE INFO

Article history:
Received 24 August 2024
Received in revised form 13 September 2024
Accepted 14 September 2024
Available online 5 October 2024

Keywords:
Pterosauria
Middle Jurassic
Bajocian
Lincolnshire Limestone, Rutland
United Kingdom

ABSTRACT

An incomplete, but large hollow bone is identified as pterosaurian on account of its pneumatic nature, thin bone wall, palaeohistology and the characteristic surface texture of the peridermal bone. Despite being incomplete it is tentatively identified as a ?left ulna, and is remarkable for its size. Coming from the lower Middle Jurassic Lincolnshire Limestone Formation of Rutland, eastern England, this is the first record anywhere in the World of a Bajocian pterosaur, and probably the first pterosaur recorded from Rutland. It is most likely from Discites to Laeviuscula zones part of the lower Bajocian succession, and represents one of the largest Jurassic pterosaurs yet recorded, with a wingspan tentatively estimated at between 3.5 and 4.0 m. The taxonomic identity of the new specimen is uncertain, but it is likely allied to the Pterodactyloidea on account of its size, although presently it remains Pterosauria fam. et gen., et sp. indet.

1. Introduction

Pterosaurs, the volant reptiles of the Mesozoic, occur only rarely in strata of Early and Middle Jurassic age, with most discoveries being in the UK, Germany (Barrett et al., 2008) and China (Lü, 2006; Table 1). In the United Kingdom, knowledge of Middle Jurassic pterosaurs is based largely on isolated and usually incomplete bones from the Bathonian Great Oolite Group of central England (O'Sullivan and Martill, 2018). Recently more complete pterosaur remains from the Isle of Skye including the angustinaripterine *Dearc sgiathanach* Jagielska et al., 2022 and darwinopteran *Ceoptera evansae* Martin-Silverstone et al., 2023 have added to our understanding of Middle Jurassic pterosaurs and their diversity (Jagielska et al., 2022, 2023; Martin-Silverstone et al., 2022, 2023). Descriptions of their morphology and estimates of their wingspan are based on extrapolations from better preserved, often complete skeletons in the Lower Jurassic (Toarcian) of Germany (Padian, 2008a,b), the Middle to Upper Jurassic of China (Lü, 2006) and the Upper Jurassic (Kimmeridgian to Tithonian) also of Germany (Arratia et al., 2015; Martill et al., 2023). Examples of pterosaurs from the Bajocian are, until now unknown, and their presence during this stage is based on ghost lineages determined for Rhamphorhynchidae and possibly Campylognathoididae known from the Toarcian and Kimmeridgian/Tithonian of England and Germany (*e.g.,* Padian, 2008a,b). Here we describe a long bone from the lower Middle Jurassic strata of Ketton, Rutland that is identified as pterosaurian on account of its thin bone wall along the diaphysis and aspects of its palaeohistology.

2. Material and methods

The specimen described here, OAKRM 2023.66 is accessioned to the Rutland County Museum, Oakham, Rutland, UK. It comprises two portions of a long bone that fit perfectly together to form an incomplete single element with only one articulatory end preserved, most likely the proximal. It is largely devoid of matrix externally, but an enlarged lumen of the diaphysis is filled with a buff-coloured oolitic limestone typical of the Lincolnshire Limestone Formation (see below). The specimen was obtained from the Heidelberg Materials Cement works, Ketton, Rutland in eastern England. The diaphyseal portion has lost much of the periosteal bone revealing a cast of the internal surface composed of oolitic limestone. The proximal fragment retains its cortical bone but is somewhat worn and thus the specimen is far from perfect.

---

* Corresponding author.
E-mail address: david.martill@port.ac.uk (D.M. Martill).

https://doi.org/10.1016/j.pgeola.2024.09.003
0016-7878/

Table 1
Lower and Middle Jurassic named pterosaur taxa known from diagnostic partial or near complete skeletons. The Tiaojishan Formation of China spans the boundary of the Middle–Late Jurassic with a range likely of Callovian–Kimmeridgian (Zhang et al., 2008) thus the precise date of the pterosaur assemblage remains uncertain.

Taxon	Stage	Formation/locality	Wingspan (m)	References
Changchengopterus pani	Callovian–Kimmeridgian	Tiaojishan Fm.; Mutoudeng Town, Qinglong County, Hebei Province, China	~0.35	Lü, 2009
Darwinopterus modularis, *D. linglongtaensis*, *D. robustodens*	Callovian–Kimmeridgian	Tiaojishan Fm.; Linglongta, Jianchang County, Liaoning Province	~0.8	Lü et al., 2009 Wang et al., 2010 Lü et al., 2011
Dendrorhynchoides curvidentatus, *D. mutoudengensis*	Callovian–Kimmeridgian	Tiaojishan Fm.; Mutoudeng, Qinglong County, Hebei Province, China	0.4–0.5	Ji and Ji, 1998 Lü and Hone, 2012
Douzhanopterus zhengi	Callovian–Kimmeridgian	Tiaojishan Fm.; Linglongta, Jianchang, Liaoning, China	0.74	Wang et al., 2017
Fenghuangopterus lii	Callovian–Kimmeridgian	Tiaojishan Fm.; Linglongta, Jianchang County, Liaoning Province	~0.9	Lü et al., 2010
Jeholopterus ningchengensis	Callovian–Kimmeridgian	Tiaojishan Fm.; Nei Mongol Zizhiqu, China	0.9	Wang et al., 2002
Jianchangnathus robustus	Callovian–Kimmeridgian	Tiaojishan Fm.; Jianchang County, China	1.17	Cheng et al., 2011
Jianchangopterus zhaoianus	Callovian–Kimmeridgian	Tiaojishan Fm.; Linglongta, Jianchang County, Liaoning Province, China	0.32	Lü and Bo, 2011
Kunpengopterus sinensis, *K. antipollicatus*	Callovian–Kimmeridgian	Tiaojishan Fm.; Linglongta, Jianchang County, western Liaoning, China.	~0.85	Wang et al., 2010 Zhou et al., 2021
Pterorhynchus wellnhoferi	Callovian–Kimmeridgian	Tiaojishan Fm.; Nei Mongol Zizhiqu, China	0.85	Czerkas and Ji, 2002
Qinglongopterus guoi	Callovian–Kimmeridgian	Tiaojishan Fm.; Mutoudeng, Qinglong County, Hebei Province, China	0.34	Lü et al., 2012
Sinomacrops bondei	Callovian–Kimmeridgian	Tiaojishan Fm.; Mutoudeng, Qinglong County of Hebei Province, China	~0.33	Wei et al., 2021
Wukongopterus lii	Callovian–Kimmeridgian	Tiaojishan Fm.; Linglongta, Jianchang, western Liaoning, China	0.73	Wang et al., 2009
Kryptodrakon progenitor	Callovian/Oxfordian	Shishugou Fm.; Wucaiwan, Junggar Basin, Xinjiang, China	1.47	Andres et al., 2014
Angustinaripterus longicephalus	Bajocian or Bathonian/Callovian	Lower Shaximiao Fm.; Sichuan, China	1.6	He et al., 1983 Barrett et al., 2008
Dearc sgiathanach	Bathonian	Lonfearn Mbr., Lealt Shale Fm.; Trotternish, Isle of Skye, Scotland	2.04	Jagielska et al., 2022 Etienne et al., 2024
Ceoptera evansae	Bathonian	Kilmaluag Fm.; Elgol, Isle of Skye, Scotland	1.6	Martin-Silverstone et al., 2022, 2023
Dolicorhamphus (=*Rhamphocephalus*) *bucklandii*, *D. depressirostris*	Bathonian	Taynton Limestone Fm.; Stonesfield, Oxfordshire, UK	~1.5	O'Sullivan and Martill, 2018; Andres, 2021
Klobiodon rochei	Bathonian	Taynton Limestone Fm.; Stonesfield, Oxfordshire, UK	~2.0	O'Sullivan and Martill, 2018
Allkaruen koi	Toarcian–Bathonian	Cañadón Asfalto Formation; Patagonia, Argentina	?	Codorniú et al., 2016
Dorygnathus banthensis	Toarcian	Posidonia Shale; Holzmaden, BW, Germany	1.5	Padian, 2008a
Campylognathoides liasicus, *C. zitteli*	Toarcian	Posidonia Shale; Holzmaden, BW, Germany	1.75 (for *C. zitteli* SMNS 9787)	Padian, 2008b
Parapsicephalus purdoni	Toarcian	Whitby Mudstone Formation; Whitby, UK	~1.0	Newton, 1888; O'Sullivan and Martill, 2017
Rhamphinion jenkinsi	?Pliensbachian–Toarcian	Kayenta Formation; Arizona, USA	~1.5	Padian, 1984
Dimorphodon macronyx	Hettangian	Blue Lias Formation; Lyme Regis, Dorset, UK	1.45	Sangster, 2021

Examination of the specimen involved a visual inspection under a binocular microscope. A thin-section was cut to examine the palaeohistology and measure the bone wall thickness with a petrological microscope using PPL, XPL and XPL with tint wedge. The specimen was photographed using a Nikon D5600 DSLR camera and topographically scanned using an Einscan Pro +. The 3D model was manipulated using Geomagic Design X and images were processed using CorelDRAW® Graphic Suite X8. The specimen underwent X-ray computed tomography (XCT) using an X-ray microscope (Xradia 520 Versa, Carl Zeiss X-ray Microscopy) with automatic filter wheel and flat panel extension. A voltage of 160 kV and power of 10 W (63 μA) were used in conjunction with the standard Zeiss HE6 filter to precondition the X-ray spectrum. The tomographic scan collected 1601 projections using Zeiss' proprietary software Scout & Scan, with a detector exposure of 3.46 s, frame average of 20, and binning of 1. A geometric magnification of 1.34 enabled a pixel size of 55.7 μm to be achieved. Since the sample was too large for auto referencing, the sample was removed to collect the required reference and placed back inside the instrument. The reconstruction used a smoothing correction of 0.7 (as per Zeiss' recommendation for bin = 1 datasets) and an automatic centre shift correction through Zeiss' Reconstructor software. A standard beam hardening constant of 0.05 was used. The total scan time was 32 h 30 min.

Forelimb lengths for a range of Jurassic pterosaurs were compiled from the literature (n = 65) representing 19 nominate genera (Table S1). Linear regression performed on a bivariate plot of wingspan *versus* ulna length for the entire dataset was used to predict the wingspan of OAKRM 2023.66 using the predicted minimum length when complete of ~300 mm and wingspan calculated at 2.1 times the forelimb length. This method follows that of Etienne et al. (2024).

Institutional abbreviations: **OAKRM**, Rutland County Museum, Oakham, Rutland, UK; **SMNK**, Staatliches Museum für Naturkunde Karlsruhe, Germany; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **SNSB-BSPG**, Staatliche Naturwissenschaftliche Sammlungen Bayerns – Bayerische Staatssammlung für Paläontologie und Geologie, Munich.

3. Geographical and geological context

The specimen was collected by persons unknown from the quarry of the Heidelberg Materials UK cement works on the east side of Ketton village in Rutland (Fig. 1). This extensive quarry exploits the Lincolnshire Limestone Formation for cement production. The base of the quarry exposes the top of the Whitby Mudstone Formation (Toarcian) in drainage ditches, the Aalenian Northamptonshire Ironstone and Grantham formations, and the Lincolnshire Limestone Formation (Bajocian), and at the northern end of the quarry the Bathonian Rutland, Blisworth and lower Cornbrash formations,

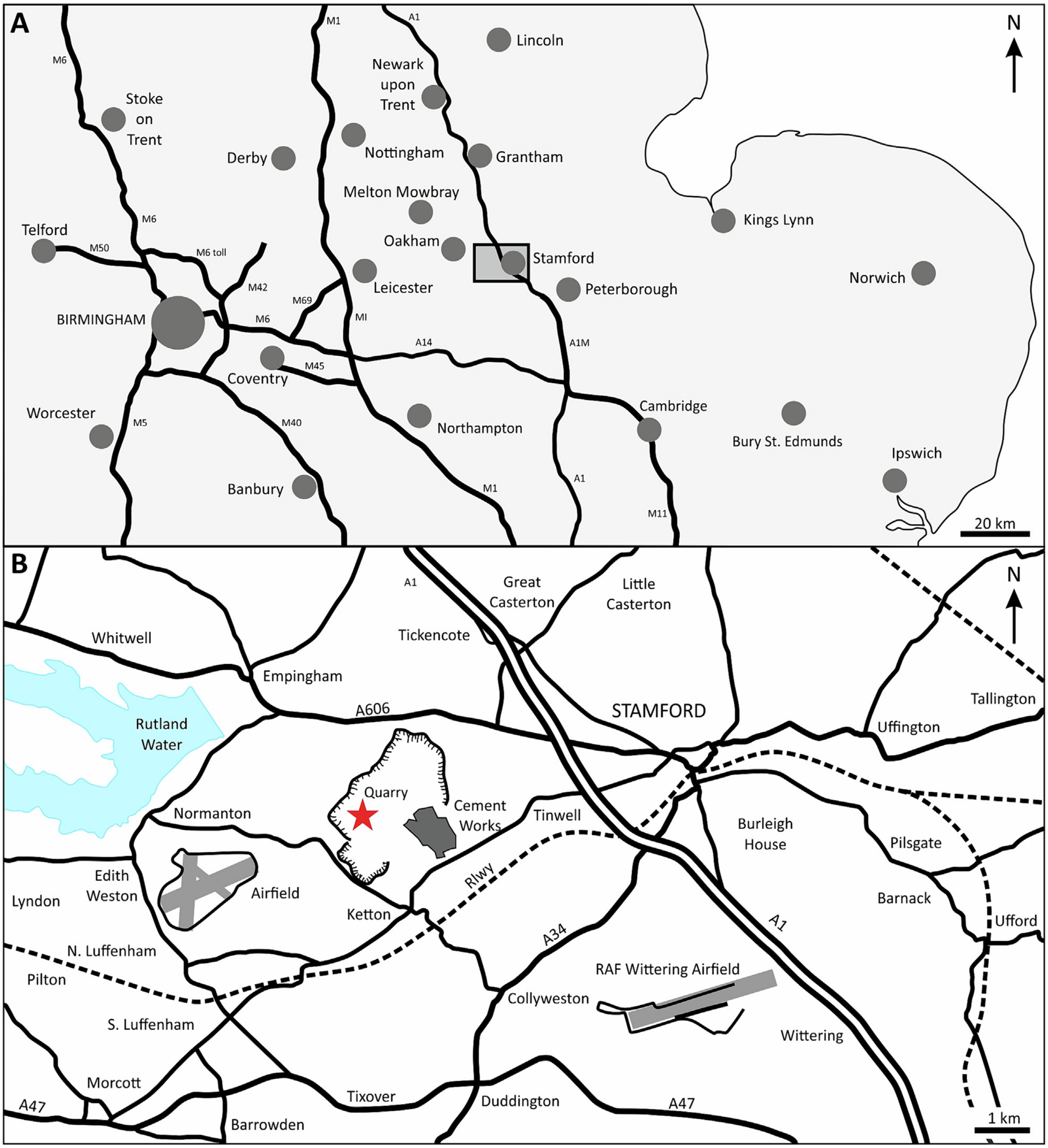


Fig. 1. A, route map showing the location of Ketton and the cement works in the vicinity of Stamford, Rutland. Note the location of nearby Oakham where the specimen now resides. B, detailed map showing the location of exposures of the Middle Jurassic strata in Ketton cement works.

Callovian upper Cornbrash Formation, and Kellaways Formation (Fig. 2). It thus displays one of the most complete sequences through the East Midlands Jurassic spanning the upper Toarcian to lower Callovian and perhaps base of the middle Callovian (Hudson and Clements, 2007).

Vertebrate remains are rare in the Jurassic of Rutland and, apart from some isolated teeth, are largely unknown for the Bajocian parts of the succession. Indeed, vertebrate remains occur only rarely in the Bajocian of the United Kingdom generally. The Bajocian part of the Rutland Middle Jurassic comprises two formations; the Lincolnshire Limestone Formation overlain by the Rutland Formation.

3.1. Biostratigraphy and age of the Lincolnshire Limestone Formation

Historically the biostratigraphical dating of the Lincolnshire Limestone Formation has been hampered by the dearth of ammonites, the tools of high-resolution biostratigraphy (Arkell, 1933; Kent, 1966; Ashton, 1980; Cox and Sumbler, 2002), the occurrence of single specimens (rather than in assemblages), and commonly the uncertain lithostratigraphical location of the fossils. Until the late 1970s the formation was considered to belong to the lower Bajocian Discites Zone, but current work updating and refining the pioneering studies of C. F. Parsons (Chandler and Ashton, *in prep*)

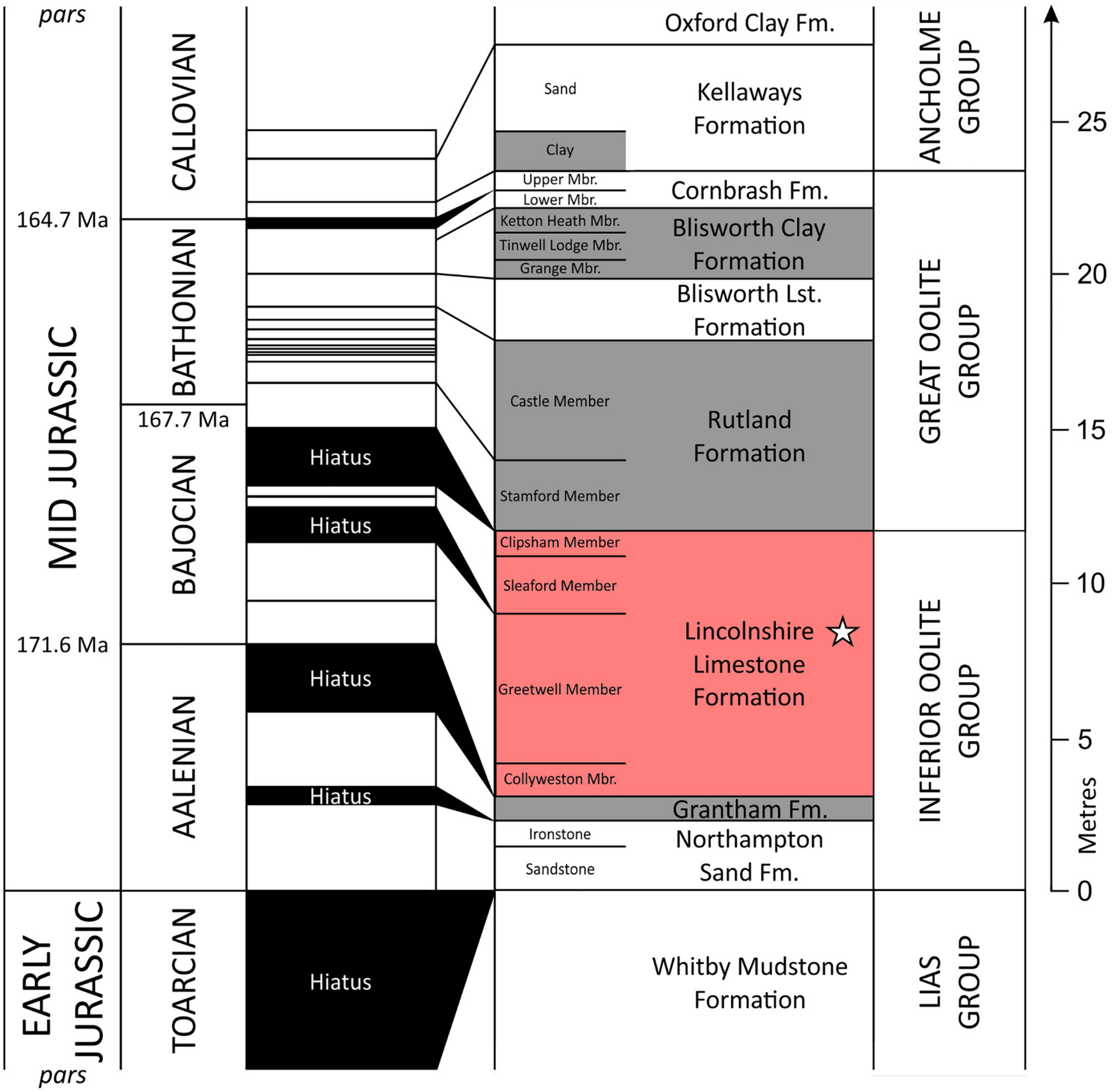


Fig. 2. Geological succession at Ketton. The quarry exposes Aalenian, and sometimes Toarcian strata in drainage pits in the base of the quarry. The main source for the cement is the Lincolnshire Limestone Formation of latest Aalenian and lower Bajocian age. Overburden in the northern sector includes strata as young as Callovian. The specimen described here comes from the Greetwell Member (star). Redrawn from Hudson and Clements (2007).

indicate a broader range to include the Ovale Zone at least and possibly younger levels (*cf.*, Ashton, 1976).

Following Hudson and Clements (2007) reporting the absence of ammonites from Ketton Quarry, three specimens have been found, all of which are members of the family Sonniniidae and are varieties of the morphogenus *Euhoploceras* (Chandler pers. comm.). None is ‘zone specific’ and all could range from the top Discites Zone up to the Trigonalis Subzone of the Laeviuscula Zone. Whilst none of the ammonite's locations are known in terms of the bed numbers illustrated in Hudson and Clements (2007, table 3) the matrices of all three are consistent with the lithologies of the Greetwell Member, as defined by Hudson and Clements (2007). Elsewhere this unit has yielded specimens attributed to the Discites Zone, most recently by Chandler et al. (2022). Regardless of the zonal details it seems highly probable that the new bone is of Bajocian age. The Bajocian is presently dated as 170.9 ± 0.8 Ma to around 168.2 ± 1.2 Ma (Gradstein et al., 2004).

3.2. Sedimentology

The matrix within the bone cavity comprises a bimodal peloosparite/grainstone in which medium-grained ooids are interspersed with fine-grained peloids; there is no organisation to the ooid or peloid distributions (Fig. 3). Both allochems are micritised and original ooid fabrics are rare. Sparse medium-grained composite grains and coarse-grained, typically elongate, micritised bioclasts, some just micrite envelopes, supplement the dominant allochem types; the bioclasts are likely to be bivalves. The allochems are bound by poikilotopic, calcite spar and there is little sign of micrite matrix.

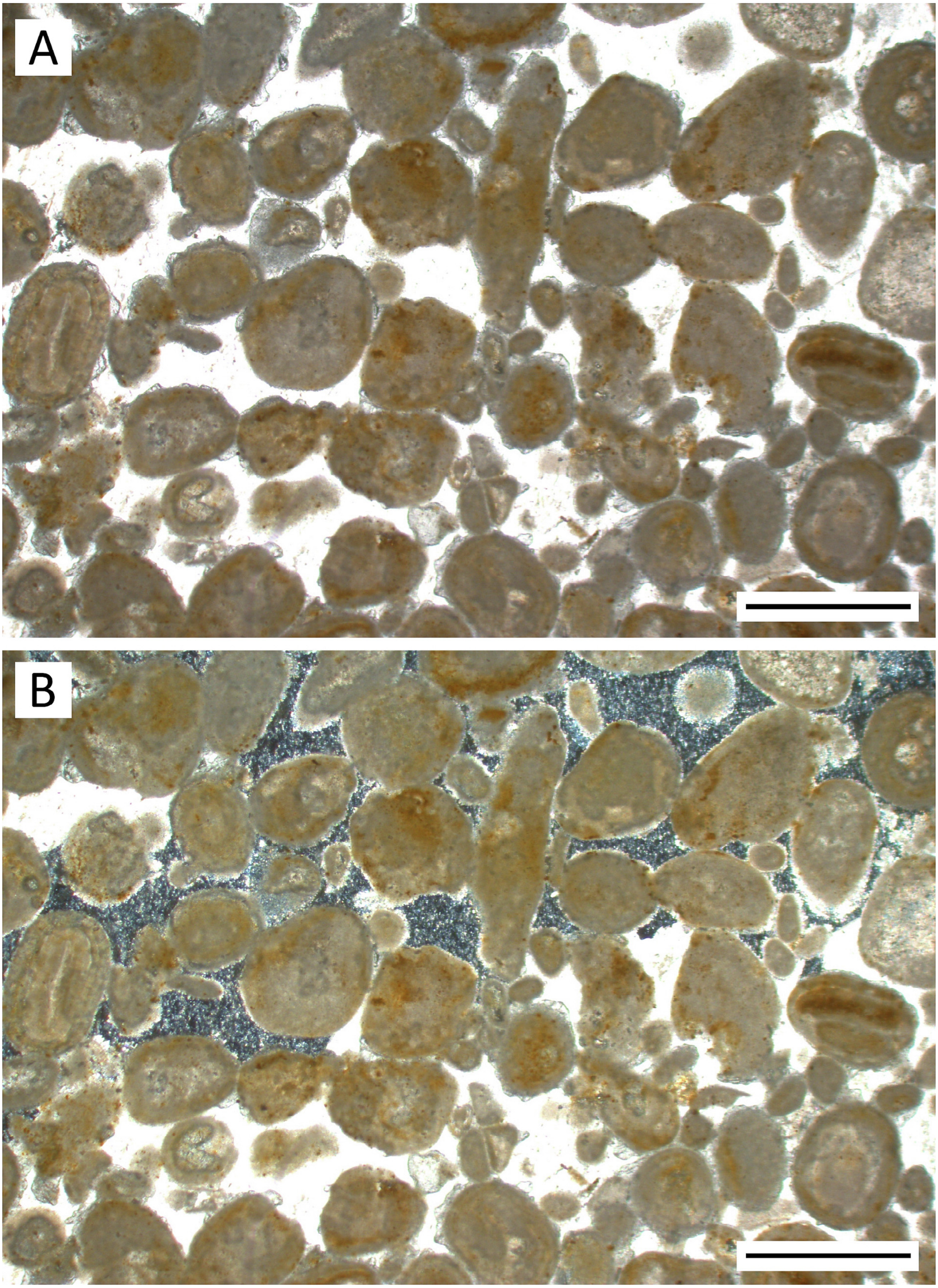


Fig. 3. Thin-section images of the sediment infill showing its oolitic nature and poikilotopic cement in PPL and XPL. See X in Figure 8 for site of the image. Scale bar represents 500 μm.

Collectively, these features suggest a depositional setting of moderate energy away from the main source of ooid generation. In the context of the Lincolnshire Limestone at Ketton Quarry a lower rather than upper part of the formation is suggested based on the descriptions in Hudson and Clements (2007, p. 249) where '*The Greetwell Member is composed mainly of peloidal and mixed peloidal-oolitic limestones; the* *latter are markedly bimodal in grain-size distribution*…'. Candidate beds are represented in LL9 and LL11 of Hudson and Clements (2007, table 3) but bed fabrics are commonly varied in such depositional settings and a precise bed allocation seems unlikely on the available evidence especially as the only record of poikilotopic spar in Hudson and Clements (2007) is from the Sleaford Member (p. 249), which constitutes part of the Upper Lincolnshire Limestone Formation. However, there is no mention of peloids at that level so, on balance a Lower Lincolnshire Limestone horizon seems most likely.

3.3. Depositional setting

In contrast to the stratigraphical investigations of the Lincolnshire Limestone Formation no detailed depositional environment interpretation of the formation has been published. However, the transgressive barrier/lagoon/tidal flat complex model, outlined by Ashton (1980), drawing on Ashton (1977), has been tested against subsurface data (Emery and Dickson, 1991) and cited in independent studies (Woodcock and Furness, 2021). Tucker (1985, fig. 16) used it as an example of an ancient [carbonate] ramp facies whilst Barron et al. (2012) placed the model in its palaeogeographical context. Parts of the model, most notably the evidence for tidal flat deposition in a humid tropical setting (Ashton, 1981) and the barrier complex make-up (Marshall and Ashton, 1980) have been reported more fully. Importantly the tidal channel elements of the barrier complex outlined by Ashton (1980) support the pioneering work of Taylor (1946).

4. Results

4.1. Systematic palaeontology

Pterosauria Kaup, 1834
Macronychoptera Unwin, 2003
Lonchognatha Unwin, 2003
Breviquartossa Unwin, 2003
?Monofenstrata Lü et al., 2010
?Pterodactyloidea Plieninger, 1901

Specimen: OAKRM 2023.66, Rutland County Museum, Oakham. Fragmentary diaphysis and proximal articulation of a ?left ulna (Figs. 4–6).

Horizon and age: Inferior Oolite Group, lower Lincolnshire Limestone Formation, Greetwell Member, likely Discites to Laeviuscula zones, Middle Jurassic, lower Bajocian.

Locality: Cement works quarry, Ketton, Rutland, eastern England. National grid reference SK 079 070 (Lat/Long Degrees 52° 39′ 06.9″N 00° 33′ 10.1″W).

Description: Specimen OAKRM 2023.66 is an elongate, gently curved bone with one extremity preserved and the other missing, with a clean break suggesting that it may have been lost during collection. Much of the diaphysis is preserved as an internal mould in cream coloured oolite (Fig. 4). The bone is in two pieces that fit together perfectly (Figs. 4–6). The cross-section where broken is a slightly depressed oval (Figs. 5F–G, 6B–C), and the present outline is in part a consequence of slight compression. Towards the articulation, where the bone is uncompacted at the site of the thin-section the cross-sectional outline is somewhat tear-drop shaped (Fig. 6B). The diaphysis is gently curved becoming straighter towards the articulatory surface and possesses a blunt, but obvious ridge extending along most of its length. A similar ridge is present on the ulnae of *Azhdarcho lancicollis* Nesov, 1984 (Averianov, 2010). The articulation has a terminal surface that subtends an angle of approximately 79° to the long axis of the shaft. It bears two prominent condyles, one of which has an approximately circular outline, the other an oval outline. No pneumatic foramen is present on the anterior side of the proximal end of the ulna as seen in many pterodactyloid pterosaurs (*e.g.*, Wellnhofer, 1991; Bennett, 2001; Averianov, 2010; Smith et al., 2023). The distribution of this feature within Pterosauria and its taxonomic significance remain understudied.

The surface of the internal mould displays some very faint grooves which would have been ridges of bone on its inner lining. They lie at an angle of approximately 45° to the bone's long axis. Results of the XCT scan reveal the bone to be hollow for much of its length (Fig. 7). Internally the bone is trabeculae-rich only at its proximal end where the lumen is subquadrangular in cross-section and the trabeculae are arranged in a grid-like pattern (Fig. 7B–D). Further along the diaphysis the lumen becomes sub-circular (Fig. 7E) to 'pear'-shaped in diameter and trabeculae are reduced (Fig. 7F–H).

4.2. Histology

The microanatomy of the thin-section taken from close to the articulation (see Fig. 6 for exact location) shows a large vacant medullary cavity surrounded by a narrow bone wall (Fig. 8). The thickest part of the bone wall is about 10 mm thick towards the articular end, but only 4.5 mm thick at the point of break. It is a little as ~1.00 mm thick on the wall of the diaphysis. The bone wall appears to have experienced intensive *localised* secondary reconstruction as indicated by the extensive development of erosion cavities that extend from the periosteal surface to near the endosteal margin of the bone wall. The thin-section reveals that the polarised light microscopy images were much more informative than the ordinary light microscopy images. Under polarised light it is evident that the growth mark evident in the compacta is a 'tide line' or reversal line, that marks the furthest extent of bone resorption (Fig. 9A′, B′, C′). Below the 'tide line' the bone tissue is composed of what superficially looks like dense Haversian bone, however, upon closer inspection, it is evident that this tissue is a type of compact coarse cancellous bone *i.e.,* former cancellous bone that becomes compacted by the deposition of bands of lamellar bone tissue with varying orientations. Overall, the bone wall comprises a large amount of endosteally formed bone tissue that surrounds the medullary cavity, and in some areas comprises the entire bone wall (Fig. 9). In other areas, the endosteal bone is overlain by a narrow band of periosteally formed primary bone tissue, and in some places, a thin narrow layer of lamellar bone lines the medullary cavity, which in some areas shows slight resorption (Fig. 9D, D′).

The narrow band of primary bone tissue can be divided into two layers: i) an inner, more earlier formed layer that is located directly above the endosteal bone, that is rather poorly vascularised by vascular canals with small lumens that mostly are simple blood vessels, although a few show osteonal development around their lumens and ii) the outermost layer of primary bone tissue *i.e.,* the subperiosteal bone tissue, is much more sparsely vascularised than the inner layer, and its overall organisation appears to be more lamellar textured (Fig. 9A, A′). This outermost layer of bone is not preserved entirely around the compacta, but in places where it is preserved, it shows some alternating layers of narrow bands of lamellar tissue (Fig. 9A′).

Although the endosteal bone superficially resembles dense Haversian bone, it is evident that it is a type of compacted coarse cancellous bone with a high concentration of what appears to be compacted "secondary osteons" with layers of lamellar bone with different orientations that compact the bone (Fig. 9A′, B′, C′).

In different parts of the cross-section, it is evident that the endosteally formed tissue undergoes extensive reconstruction as is evident by many large erosion cavities — some show narrow development of centripetally formed lamellar bone, although most seem to be in a state of erosion (Fig. 9B, B′). There are parts of the compacta (Fig. 9E) where extensive development of erosion cavities gives the tissue a rather cancellous appearance. It is worth noting that all the bone remodelling is restricted to the endosteally formed tissue.

Under polarised light it is evident that the 'tide line' separates the periosteal and endosteal bone deposits (Fig. 9), and all the large erosion cavities visible are located within the endosteally formed compacted coarse cancellous bone. Narrow deposits of lamellar bone are visible along the margins of some of the erosion cavities,

Fig. 4. Pterosaur ?left ulna from the Lincolnshire Limestone Formation of Ketton, Rutland, specimen number OAKRM 2023.66. A–B, in anterior/posterior view; C/D in dorsal/ventral view. Scale bar represents 20 mm.

Fig. 5. Topographic scan images of OAKRM 2023.66 a pterosaur ?left ulna from Lincolnshire Limestone Formation of Ketton, Rutland showing the specimen in two pieces. A–B, in anterior/posterior view; C–D, in dorsal/ventral view; E, proximal view; F–G, cross-section at break between two pieces and H, cross-section at distal end. Scale bar represents 20 mm.

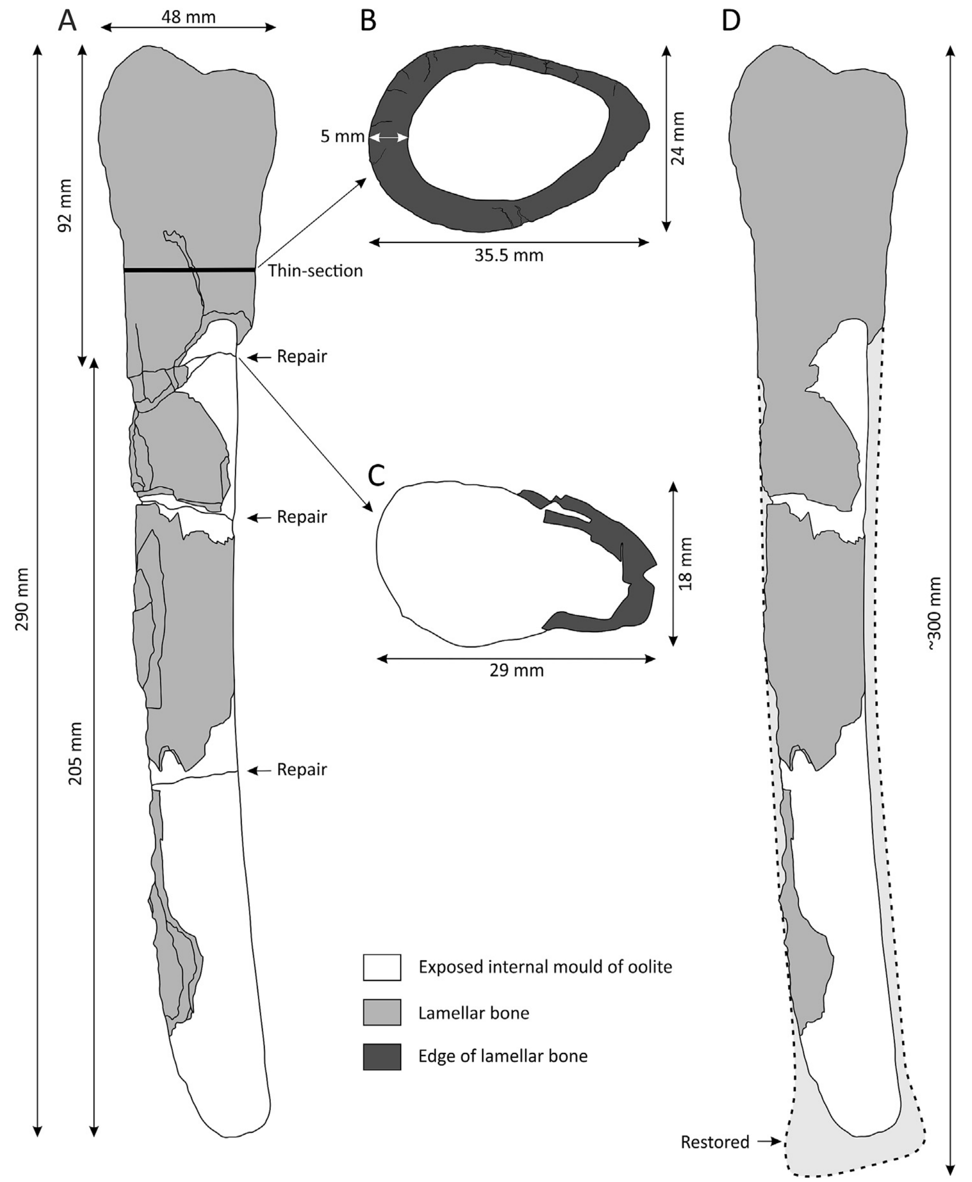


Fig. 6. Diagram illustrating features and dimensions of pterosaur ulna OAKRM 2023.66. A, specimen with diaphysis and proximal articulatory portion reunited; B, cross-section of proximal end taken from thin-section showing the thickness of the bone wall; C, cross-section at the break showing the missing bone; D, minimal restoration of OAKRM 2023.66 in order to obtain a realistic length measurement for estimating original wingspan.

whereas in others active resorption is underway, and can be seen to cut into the pre-existing secondary bone tissue (Fig. 9B, B′).

In parts of the compacta right up to the periosteal margin are small simple vascular canals with either longitudinal or shorter circumferentially organised vascular canals. The variable organisation of the vascular canals is visible under normal light, and under polarised light the actual organisation of the bone matrix is striking: just above the endosteally formed bone, there is a distinctive oblique arrangement of the bone fibrils, whereas in the subperiosteal bone, the angles of the fibres are predominantly organised in a different direction giving the bone matrix a superficial herring-bone organisation (Fig. 9C, C′). Note that the vascularisation and osteocyte lacunae all follow this oblique arrangement.

4.3. Morphometrics

Estimating the wingspan of pterosaurs on the basis of isolated and disarticulated material is fraught with difficulties and is rendered even more so when bones are incomplete (see for example Jagielska et al., 2023; Etienne et al., 2024 for recent Jurassic examples). The specimen is tentatively identified as the proximal portion of a pterosaurian ulna on account of a very gentle curve of the diaphysis, a slight angular off-set of the articular surface for the carpus to the long axis of the more distal part of the diaphysis, and the cross-sectional shape (Figs. 4–7). Consequently, calculations to estimate the original dimensions of OAKRM 2023.66 if it were complete are based on comparisons with the ulnae of a variety of pterosaur taxa where complete examples are known (Fig. 10). An estimated minimum length of 300 mm for OAKRM 2023.66 when complete was used to calculate wingspan (Fig. 6D) using a linear regression analysis (see methodology above; Fig. 11). This generated a wingspan estimate of 3.8 m. Due to the uncertainty in the original length of OAKRM 2023.66 as well as uncertainty of its taxonomic affinities within Pterosauria, we employed a minimalist approach to determining the original length. Consequently, we suggest a wingspan estimate of between 3.5 and 4.0 m.

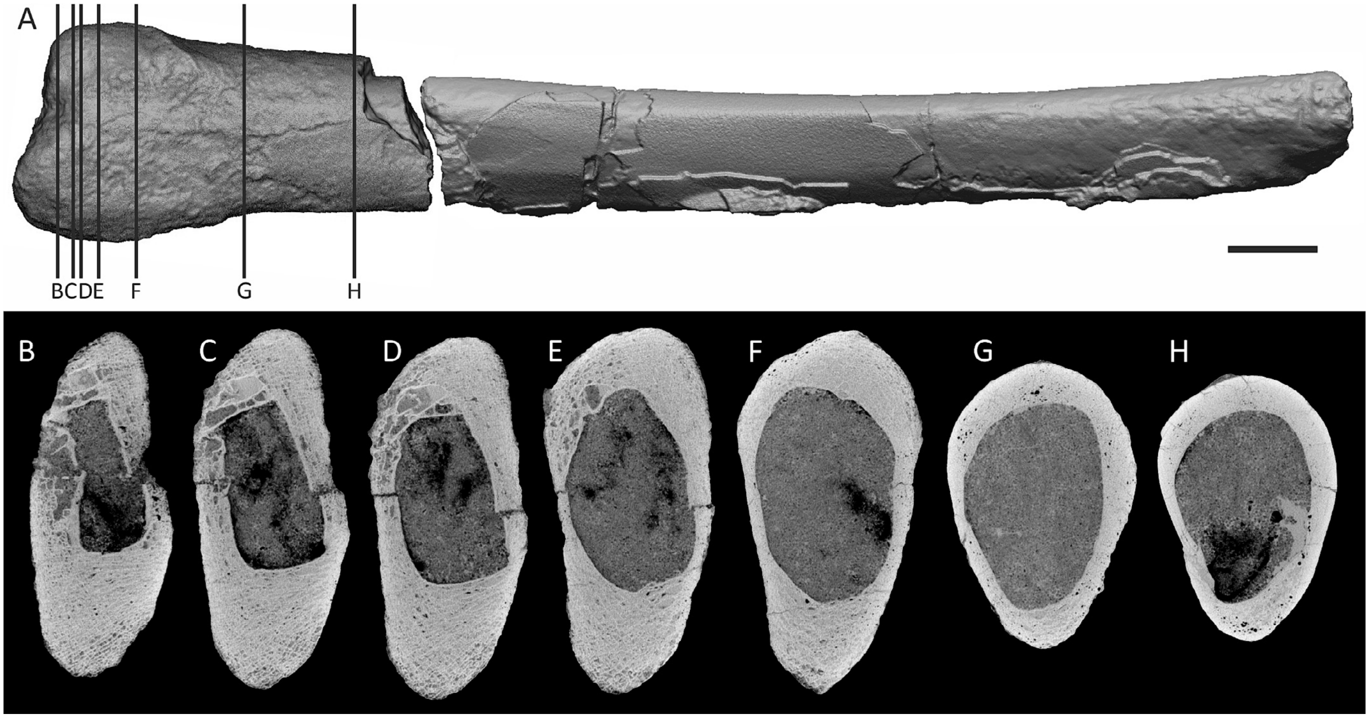


Fig. 7. XCT scan images of OAKRM 2023.66 revealing aspects of the internal architecture of the proximal end. A, specimen with lines of XCT section data indicated; B–D, XCT section revealing internal lumen with sub-quadrate cross-section and dense lattice of trabecular bone with grid-like pattern; E–F, XCT section revealing internal lumen with sub-circular cross-section; G–H, XCT section revealing internal lumen with pear-shaped cross-section.

5. Discussion

5.1. Affinities

Despite the extremely fragmentary nature of OAKRM 2023.66 it is readily identified as pterosaurian on account of its very thin bone wall and extensive internal lumen extending for much of the bone's length. Its aspect ratio and the morphology of its proximal end are comparable with those of several pterosaurian ulnae. The specimen is remarkably large considering that it is from early Middle Jurassic strata. Most pterosaurs from prior to the Upper Jurassic are typically in the wingspan range 1.0–3.0 m (Elgin and Hone, 2020; Jagielska et al., 2022, 2023; Etienne et al., 2024).

There have been claims for pterosaur remains previously from the Middle Jurassic of Rutland. Benton and Spencer (1995) record the rhamphorhynchine *Rhamphocephalus* from the Bathonian Great Oolite Group of Essendine railway cutting. According to Unwin (1996) no evidence was presented to support this referral. Unwin (1996) [incorrectly] recorded the site as the Essendine to Banthorpe railway cutting. In fact, this is the Essendine to Belmesthorpe railway (Banthorpe is the name given to a small forest some 2.4 km ESE of Essendine and is not near the railway), and the record dates back to Etheridge in Judd (1875) as a listing in appendix 1 of Judd's *Geology of Rutland*. Etheridge provides no repository for the specimen, nor does he state what the bone(s) might be. A detailed description of the stratigraphy and fossils of the Essendine to Stamford railway by Morris (1853) fails to list any pterosaur bones, although he does mention bones of the sauropod *Cetiosaurus*.

The pterosaur bone(s) is listed as *Pterodactylus* sp. (Etheridge, in Judd, 1875). It was common practice in the 19th century to refer fragmentary pterosaur remains to the genus *Pterodactylus*, despite the genera *Rhamphorhynchus* and *Dimorphodon* had already been erected (*Rhamphorhynchus* von Meyer, 1846; *Dimorphodon* Owen, 1859), for example Marsh (1871) erected '*Pterodactylus*' *oweni* [non-*Pt. oweni* Seeley, 1864] and emended the preoccupation to *Pterodactylus occidentalis* without questioning the generic placement (Marsh, 1872, 1876). This practice continued well into the 20th century (*e.g., Pt. arningi* and *Pt. maximus* both Reck, 1931).

5.2. Histological discussion

The extremely thin-walled nature of the bone precludes it from being a non-avian theropod dinosaur (*e.g.,* Chinsamy-Turan, 2005), which typically has much thicker bone walls composed of zonal fibro-lamellar bone with abundant primary osteons (*e.g.,* Reid, 1990; Chinsamy-Turan, 2005; Varricchio, 1993). Thin-walled bones are generally typical of flying vertebrates such as pterosaurs and birds, although when comparing similar body sized birds and pterosaurs, pterosaurs have considerably thinner bone walls (Seitz, 1907; de Ricqlès et al., 2000; Steel, 2008; Chinsamy et al., 2009). However, based on its histological structure, OAKRM 2023.66 more closely resembles bones of pterosaurs rather than any known Mesozoic bird or non-avian dinosaur (*e.g.,* Padian et al., 1995; Chinsamy, 2002; Steel, 2008; Chinsamy et al., 2009, 2019; O'Connor et al., 2014).

Since the bone wall is thin, remodelling changes during growth have obliterated much of the bone formed during early stages of ontogeny. However, in some parts of the compacta, there is evidence that the bone formed early in ontogeny was fibro-lamellar which indicates that it was rapidly formed, although not as richly vascularised and not at high rates typical of early growth stages of birds (*e.g.,* Castanet et al., 2004; Starck and Chinsamy, 2002).

The extensive development of endosteally formed bone tissue in the Ketton compacta is also noteworthy. As early as 1907, Seitz described *Rhamphocephalus bucklandi* as having extremely thin-walled bone, with an extensive development of secondary endosteal bone tissues that were deposited under the narrow periosteal bone. These are also clearly features of the Ketton bone.

The poorly vascularised, lamellar textured subperiosteal bone of the Ketton bone represents an outer circumferential layer (OCL). This indicates that the individual from which the bone derived had passed its most rapid phase of development and had reached its adult body size (*e.g.,* Chinsamy-Turan, 2005; Chinsamy et al., 2009; de Ricqlès et al.,

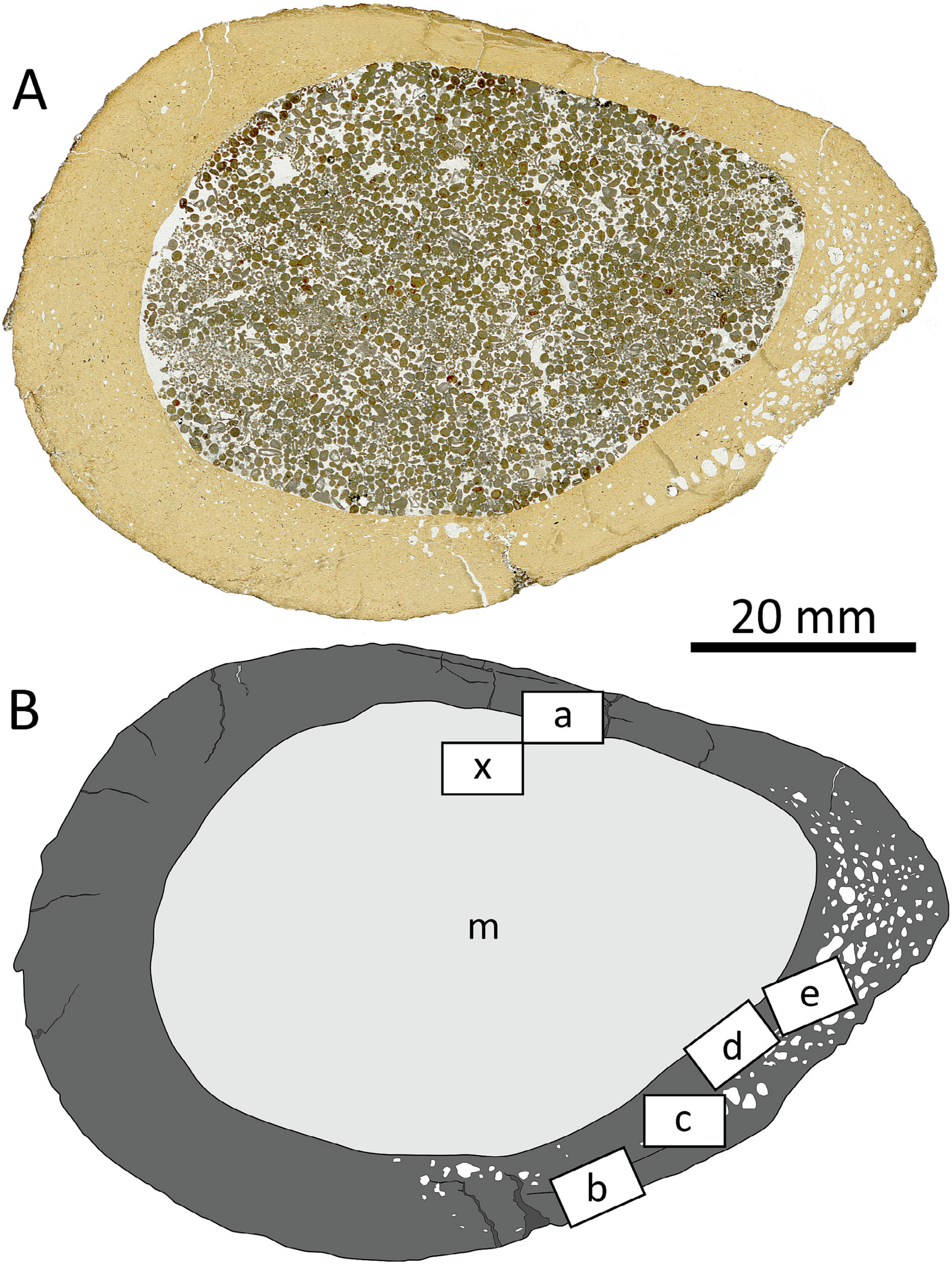
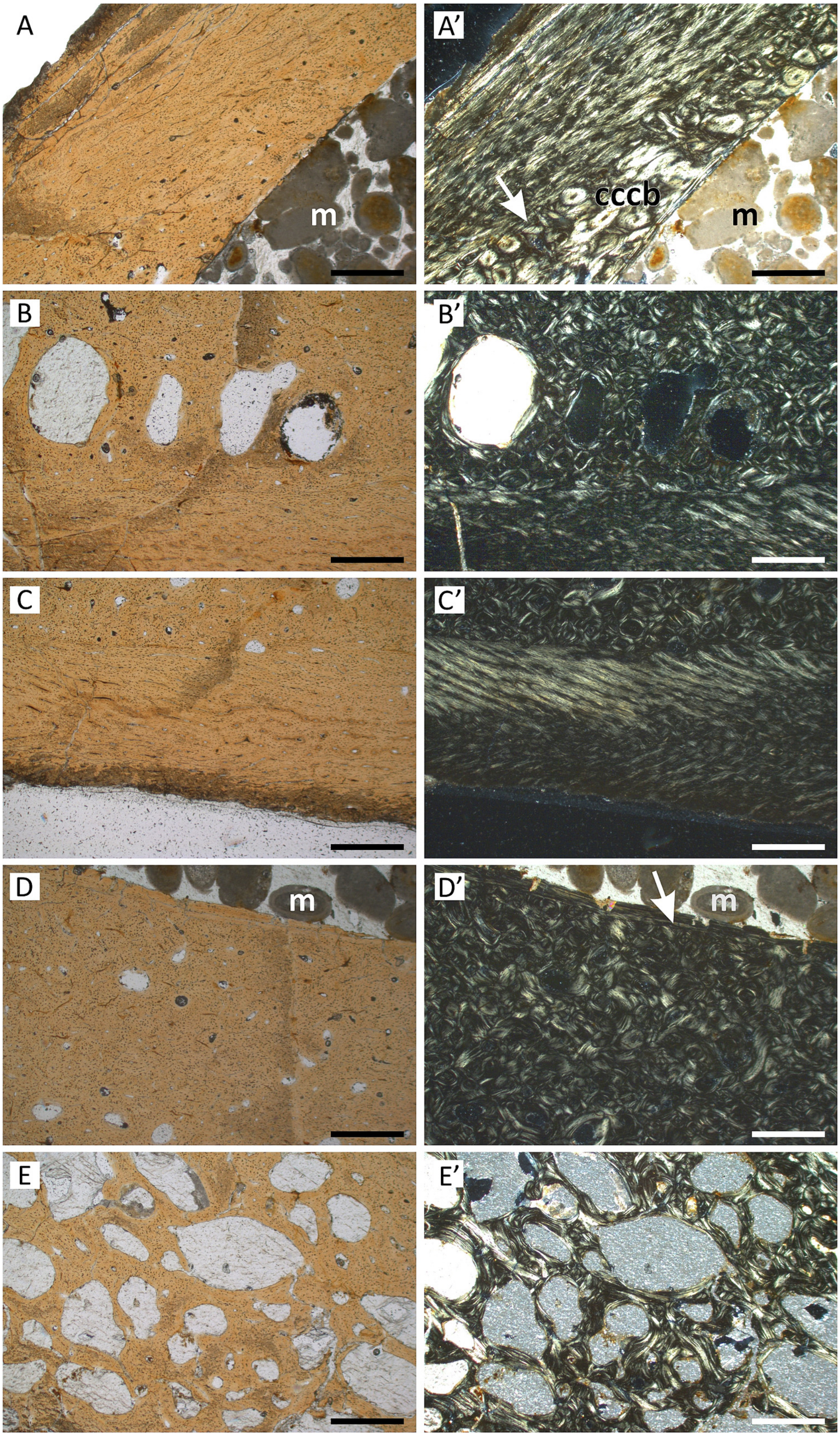


Fig. 8. A, cross-section of proximal end of diaphysis of pterosaur ulna OAKRM 2023.66 showing its overall microanatomy. Note the thin compact bone wall that surrounds the large open, centrally located medullary cavity (m). B, a diagram of the thin-section, showing the location of the higher magnification images in Figure 9, and X indicates the pelletal-ooid filled medullary cavity in Figure 3.

2000). The narrow bands of alternating lamellar bone tissue that make up this outermost layer resemble the plywood like arrangement seen in several pterosaurs, including *Pteranodon* and azhdarchids (Padian et al., 1995; de Ricqlès et al., 2000; Steel, 2008). Interestingly this alternate layering bone of the periosteal bone tissue appears to be unique to some pterosaurs, but they are not found in all pterosaurs (*e.g.*, de Ricqlès et al., 2000; Chinsamy et al., 2009), and have not been reported in Mesozoic birds (*e.g.*, Chinsamy, 2002; O'Connor et al.,



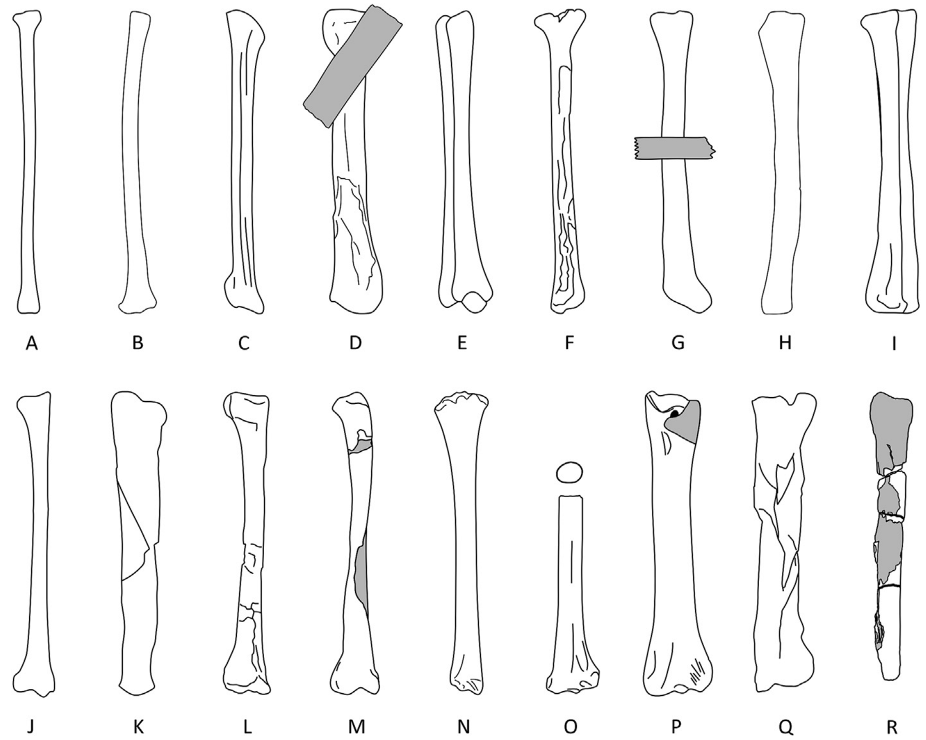


Fig. 10. Outlines of pterosaur ulnae ranging from the Late Triassic (A) to Late Cretaceous (Q) showing the conservative morphology of this element over time. Grey shading indicates missing or obscured areas, except in R, where it indicates preserved bone. A, *Raeticodactylus filisurensis* (Stecher, 2008, fig. 2); B, *Dorygnathus banthensis* (DMM photo of SMNK 50914); C, *Campylognathoides liasicus* (Wellnhofer, 1974, fig. 8b); D, *Campylognathoides zitteli* (DMM photo of SMNS 9787); E, *Pterodactylus antiquus* (holotype SNSB-BSPG AS I 739, drawn from DMM photo, but see also Tischlinger (2020) for quality photographs); F, large pterodactyloid wing from Solnhofen Limestone (Elgin and Hone, 2020, fig. 1[2]); G, *Balaenognathus maeuseri* (photo by H. Tischlinger, but see also Martill et al., 2023); H, *Darwinopterus modularis* (Lü et al., 2010, fig. 2f); I, juvenile *Pterodaustro guinazui* (Codorniú and Chiappe, 2004, fig. 2); J, *Tapejara wellnhoferi* (Eck et al., 2011, fig. 7[2]); K, *Muzquizopteryx coahuilensis* (Frey et al., 2006, fig. 5B); L, *Keresdrakon vilsoni* (Kellner et al., 2019, fig. 9c); M, *Caiuajara dobruskii* (Manzig et al., 2014, fig. 7); N, *Santanadactylus pricei* (Wellnhofer, 1991, fig. 27); O, *Santanadactylus araripensis* with cross-section (Wellnhofer, 1985, fig. 9c); P, *Pteranodon ingens* (Bennett, 2001, fig. 75A); Q, *Tethydraco regalis* (Longrich et al., 2018, fig. 4B); R, the Ketton specimen OAKRM 2023.66. Outlines redrawn from respective sources.

2014; Chinsamy et al., 2019), or modern birds (*e.g.,* Chinsamy-Turan, 2005; Chinsamy, 1995; Canoville et al., 2022), nor in any other vertebrate (de Ricqlès et al., 2000). In the Ketton bone, we also observed this unusual oblique arrangement of the bone matrix, which may also offer biomechanical strength to the thin bone wall (as Gross, 1934 reported in *Rhamphocephalus*).

The extensive development of compacted coarse cancellous bone noted in the Ketton bone has been previously observed in *Quetzalcoatlus* and *Dimorphodon* (de Ricqlès et al., 2000), and in the latter taxon, de Ricqlès et al. (2008) noted that the endosteal bone gives a "*false appearance of dense haversian bone tissues*". We also found this to be the case in the Ketton sample. Compacted coarse cancellous bone is formed during "metaphyseal relocation" in long bones, *i.e.,* when the metaphysis becomes incorporated into the diaphysis of the bone (Enlow, 1962). This directly suggests that the Ketton section was made from the proximal metaphysis. Dense Haversian bone is nonexistent in the Ketton bone, which agrees with previous pterosaur studies (*e.g.*, de Ricqlès et al., 2000; Steel, 2008; Chinsamy et al., 2009).

The innermost part of the bone wall consists of a narrow band of lamellar tissue that forms the inner circumferential layer (ICL) (*e.g.,* Chinsamy-Turan, 2005) that has been well described in the bones of various vertebrates. This tissue often forms once medullary expansion is complete, although it should be noted that there appears to be some resorption along the edges of the ICL in parts of the section.

5.3. Pterosaur ulnae

Identification of OAKRM 2023.66 is somewhat tentative, in part because of the fragmentary nature of the specimen, but also because pterosaur ulnae present few clear characteristics except when they are exceptionally well reserved in 3D. Thus, in many non-Cretaceous pterosaurs, even where skeletons are fully articulated, the ulna can be difficult to distinguish from the radius because the two bones are of very similar size and morphology, such that when adpressed by compaction and overlain by other bones, the ulnae are difficult to distinguish. This is problematic for ulnae from Cretaceous pterosaurs as the ulna is generally slightly longer than the radius, and also has a greater diameter of the diaphysis, besides the difference displayed at the articulatory surfaces. There are important morphological characters on the articulatory surfaces that make uncrushed examples relatively easy to identify, but in the case of OAKRM 2023.66, the articulatory surface is somewhat worn and conspicuous features of the condyles are absent. Excellent illustrations of the articulatory surface of Cretaceous pterosaur ulnae

Fig. 9. Thin-section photomicrographs of pterosaur ulna OAKRM 2023.66. Images on the left were taken under plane polarised light (ppl), and those on the right under cross polars (XPL). All images here are higher magnifications of the frames indicated in Figure 8. A and A′, the outer part of the bone wall appears to be periosteally formed, whereas the bone closest to the medullary cavity (m) although superficially resembling secondary osteons, under polarised light is compacted coarse cancellous bone (cccb) formed under a distinct resorption or tide line (arrow). B and B′, large resorption cavities are visible in the compacta. Under polarised light, it is evident that these occur in the cccb. Narrow deposits of lamellar bone are visible lining some of the erosion cavities, but in other areas resorption is active and cuts into the pre-existing secondary bone. Note that just bordering the tide line, the periosteal bone fibrils show an oblique organisation. C and C′, under polarised light the distinctive organisation of the bone fibrils is visible. Just above the tide line, the periosteal bone shows an oblique arrangement of the bone fibrils, whereas subperiosteally the bone fibrils are organised in a different direction giving the bone matrix a superficial herring-bone organisation. Note that the vascularisation and osteocyte lacunae all follow this oblique arrangement. D and D′, here, most of the bone wall comprises of the secondarily formed cccb, and the medullary cavity (m) is lined by a narrow band of lamellar bone (arrow). E and E′ show the cancellous texture of the bone wall where extensive erosion cavities occur. Scale bars represent 500 μm.

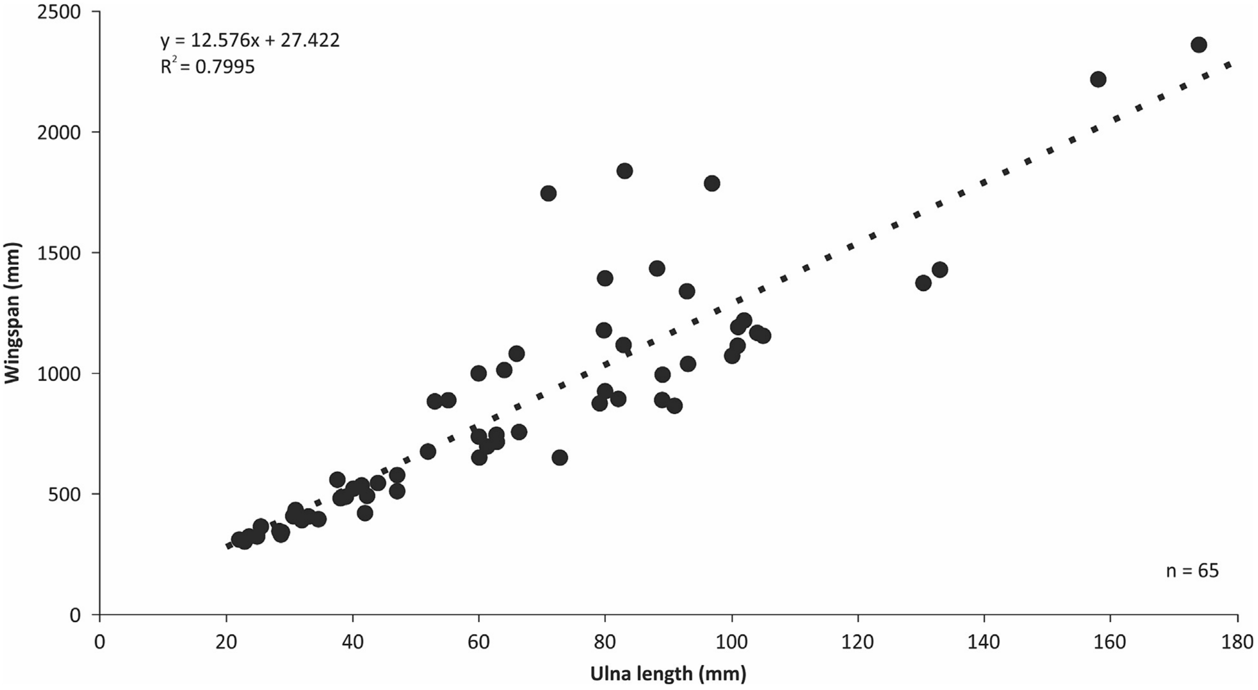


Fig. 11. Bivariate plot of ulna length *versus* wingspan for a range of Jurassic pterosaurs (Table S1).

are provided by Wellnhofer (1985, fig. 9, 1991, fig. 27), although their appropriateness for comparative purposes is noted given the age difference involved, but there are otherwise few detailed illustrations of Jurassic pterosaur ulnae.

6. Conclusions

The new specimen is identified as pterosaurian on account of the extreme thinness of its bone wall, the presence of an enlarged diaphyseal lumen and a laminated bone microstructure. Its identity as an ulna is based on comparisons with several pterosaur genera across a range of pterosaur families, but we note its unusually large size (wingspan conservatively estimated at 3.5–4.0 m) for a pterosaur from the Middle Jurassic. A lack of clear diagnosable feature in pterosaurian ulnae and the fragmentary/bioeroded nature of OAKRM 2023.66 prevent the bone from being identified more precisely and thus cannot be referred to any particular genus, or indeed family. The specimen is among the first pterosaur remains to be recorded from the Bajocian anywhere in the world, and it is also among the largest of any Jurassic pterosaur. It is also likely the first record of a pterosaur from Rutland, England's smallest county.

Our conclusion that OAKRM 2023.66 is from a pterodactyloid pterosaur is also noteworthy and that if proven correct, this is among the earliest record of a pterodactyloid pterosaur. The oldest well-documented example of a pterodactyloid is *Kryptodrakon progenitor* from the Bathonian of China (Andres et al., 2014) and OAKRM 2023.66 extends the range for the group by approximately 2 ma.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pgeola.2024.09.003.

CRediT authorship contribution statement

Darren Withers: Writing – original draft, Investigation, Conceptualization, Writing – review & editing. **David M. Martill:** Writing – original draft, Methodology, Investigation, Formal analysis, Writing – review & editing. **Roy E. Smith:** Writing – original draft, Methodology, Investigation, Formal analysis, Writing – review & editing. **Michael Ashton:** Writing – original draft, Methodology, Investigation, Writing – review & editing. **Anusuya Chinsamy:** Writing – original draft, Methodology, Investigation, Formal analysis, Writing – review & editing. **Charles Wood:** Writing – original draft, Methodology, Investigation, Formal analysis, Writing – review & editing. **Richard Forrest:** Writing – original draft, Investigation, Writing – review & editing.

Declaration of competing interest

The authors report no declarations of competing interest.

Acknowledgements

We are especially grateful to the management team at Heidelberg Materials Cement works, Ketton, in particular 'Dick' Whittington, who has looked after us for field trips over the years, and Aurélien Colas, site manager, for kindly donating the specimen to Oakham Museum, thus keeping the specimen local. Special thanks to Robert Chandler for advice on the ammonite biostratigraphy of the UK Bajocian. Thanks to David Savory at Flag Fen Archaeology Park, Peterborough for making facilities available for specimen scanning. We thank Kenny Nye of the Peterborough Geological Palaeontological Group (PGPG) for organising the field trip on which the specimen was re-discovered, and Lorraine Cornwell for dealing with the specimen's accession to Rutland County Museum. DMM and RES are grateful to the University of Portsmouth for supporting our research, and especially to Geoff Long for producing the thin-section. Meg Jacobs is thanked for demonstrating that the two pieces did indeed fit together. DW thanks Dean Lomax for encouragement and support. We thank Dino Frey, Dave Unwin and Helmut Tischlinger for pterosaurian conversations. We thank our two referees and editor Malcolm Hart for comments that greatly improved the manuscript.

References

Andres, B., 2021. Phylogenetic systematics of *Quetzalcoatlus* Lawson 1975 (Pterodactyloidea: Azhdarchoidea). Journal of Vertebrate Paleontology 41, 203–217.

Andres, B., Clark, J., Xu, X., 2014. The earliest pterodactyloid and the origin of the group. Current Biology 24 (9), 1011–1016.

Arkell, W.J., 1933. The Jurassic System in Great Britain. Oxford University Press, Oxford (681 pp.).

Arratia, G., Schultze, H.-P., Tischlinger, H., Viohl, G., 2015. Solnhofen. Ein Fenster in die Jurazeit 1, 7–323 (2, 331–620).

Ashton, M., 1976. New evidence for the age of the Lincolnshire Limestone Formation (Bajocian) of Eastern England. Transactions Leicester Literary & Philosophical Society 70, 21–37.

Ashton, M., 1977. The Stratigraphy and Carbonate Environments of the Lincolnshire Limestone Formation (Bajocian) in Lincolnshire and Parts of Leicestershire. University of Hull (unpublished Ph.D. thesis).

Ashton, M., 1980. The stratigraphy of the Lincolnshire Limestone Formation (Bajocian) in Lincolnshire and Rutland (Leicestershire). Proceedings of the Geologists' Association 91, 203–223.

Ashton, M., 1981. Carbonate tidal rhythmites from the Middle Jurassic of Britain. Sedimentology 28, 689–698.

Averianov, A.O., 2010. The osteology of *Azhdarcho lancicollis* Nessov, 1984 (Pterosauria, Azhdarchidae) from the Late Cretaceous of Uzbekistan. Proceedings of the Zoological Institute of the Russian Academy of Sciences 314, 246–317.

Barrett, P.M., Butler, R.J., Edwards, N.P., Milner, A.R., 2008. Pterosaur distribution in time and space: an atlas. Zitteliana B 28, 61–107.

Barron, A.J.M., Lott, G.K., Riding, J.B., 2012. Stratigraphical Framework for the Middle Jurassic Strata of Great Britain and the Adjoining Continental Shelf. British Geological Survey.

Bennett, S.C., 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. Palaeontographica Abteilung A 260, 1–153.

Benton, M.J., Spencer, P.S., 1995. Fossil Reptiles of Great Britain. Chapman & Hall, London (386 pp.).

Canoville, A., Chinsamy, A., Angst, D., 2022. New comparative data on the long bone microstructure of large extant and extinct flightless birds. Diversity 14, 298.

Castanet, J., Croci, S., Aujard, F., Perret, M., Cubo, J., de Margerie, E., 2004. Lines of arrested growth in bone and age estimation in a small primate: *Microcebus murinus*. Journal of Zoology 263, 31–39.

Chandler, R.B., Ashton, M., 2024. The ammonite stratigraphy of the Lincolnshire Limestone Formation (lower Bajocian) of Eastern England. Advances and Challenges (in prep).

Chandler, R., Ashton, M., Gamble, H., 2022. A new ammonite discovery from the Lincolnshire Limestone Formation (lower Bajocian) of Eastern England. Proceedings of the Geologists' Association 133, 148–153.

Cheng, X., Wang, X., Jiang, S., Kellner, A.W.A., 2011. A new scaphognathid pterosaur from western Liaoning, China. Historical Biology 24, 101–111.

Chinsamy, A., 1995. Histological perspectives on growth in the birds *Struthio camelus* and *Sagittarius serpentarius*. In: Peters, S. (Ed.), 3rd Symposium of the Society of Avian Paleontology and Evolution, 1992: Courier Forschungsinstitut Senckenberg, pp. 317–323A.

Chinsamy, A., 2002. Bone microstructure of early birds. In: Chiappe, L.M., Witmer, L.M. (Eds.), Mesozoic Birds — Above the Heads of Dinosaurs, p. 520.

Chinsamy, A., Codorniu, L., Chiappe, L., 2009. Palaeobiological implications of the bone histology of *Pterodaustro guinazui*. The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology: Advances in Integrative Anatomy and Evolutionary Biology 292, 1462–1477.

Chinsamy, A., Marugán-Lobón, J., Serrano, F.J., Chiappe, L., 2019. Osteohistology and life history of the basal pygostylian, *Confuciusornis sanctus*. The Anatomical Record 303, 949–962.

Chinsamy-Turan, A., 2005. The Microstructure of Dinosaur Bone. Johns Hopkins University Press.

Codorniú, L., Chiappe, L.M., 2004. Early juvenile pterosaurs (Pterodactyloidea: *Pterodaustro guinazui*) from the Lower Cretaceous of central Argentina. Canadian Journal of Earth Sciences 41, 9–18.

Codorniú, L., Carabajal, A.P., Pol, D., Unwin, D., Rauhut, O.W., 2016. A Jurassic pterosaur from Patagonia and the origin of the pterodactyloid neurocranium. PeerJ 4, e2311.

Cox, B.M., Sumbler, M.G., 2002. British Middle Jurassic Stratigraphy (No. 26). Joint Nature Conservation Committee.

Czerkas, S.A., Ji, Q., 2002. A new rhamphorhynchoid with a headcrest and complex integumentary structures. Feathered Dinosaurs and the Origin of Flight, vol. 1, pp. 15–41.

de Ricqlès, A.J., Padian, K., Horner, J.R., Francillon-Vieillot, H., 2000. Palaeohistology of the bones of pterosaurs (Reptilia: Archosauria): anatomy, ontogeny, and biomechanical implications. Zoological Journal of the Linnean Society 129, 349–385.

de Ricqlès, A., Padian, K., Knoll, F., Horner, J.R., 2008. On the origin of high growth rates in archosaurs and their ancient relatives: complementary histological studies on Triassic archosauriforms and the problem of a "phylogenetic signal" in bone histology. Annales de Paleontologie 94, 57–76.

Eck, K., Elgin, R.A., Frey, E., 2011. On the osteology of *Tapejara wellnhoferi* Kellner 1989 and the first occurrence of a multiple specimen assemblage from the Santana Formation, Araripe Basin, NE-Brazil. Swiss Journal of Palaeontology 130, 277–296.

Elgin, R.A., Hone, D.W., 2020. A review of two large Jurassic pterodactyloid specimens from the Solnhofen of southern Germany. Palaeontologia Electronica 23, 2–11.

Emery, D., Dickson, J.A.D., 1991. The subsurface correlation of the Lincolnshire Limestone Formation in Lincolnshire. Proceedings of the Geologists' Association 102, 109–122.

Enlow, D.H., 1962. A study of the post-natal growth and remodelling of bone. American Journal of Anatomy 110, 79–102.

Etienne, J.L., Smith, R.E., Unwin, D.M., Smyth, R.S., Martill, D.M., 2024. A 'giant' pterodactyloid pterosaur from the British Jurassic. Proceedings of the Geologists' Association 135, 335–348.

Frey, E., Buchy, M.C., Stinnesbeck, W., Gonzalez, A.G., Di Stefano, A., 2006. *Muzquizopteryx coahuilensis* ng., n. sp., a nyctosaurid pterosaur with soft tissue preservation from the Coniacian (Late Cretaceous) of northeast Mexico (Coahuila). Oryctos 6, e40.

Gradstein, F.M., Ogg, J.G., Smith, A.G., 2004. A Geologic Time Scale 2004. Cambridge University Press.

Gross, W., 1934. Die Typen des Mikroskopischen Knochenbaues bei fossilen Stegocephalen und Reptilien. Zeitschrift fur Anatomie 103, 731–764.

He, X.L., Yan, D., Su, C., 1983. A new pterosaur from the Middle Jurassic of Dashanpu, Zigong, Sichuan. Journal of Chengdu College of Geology 1 (Supplement), 27–33.

Hudson, J.D., Clements, R.G., 2007. The Middle Jurassic succession at Ketton, Rutland. Proceedings of the Geologists' Association 118, 239–264.

Jagielska, N., O'Sullivan, M., Funston, G.F., Butler, I.B., Challands, T.J., Clark, N.D., Fraser, N.C., Penny, A., Ross, D.A., Wilkinson, M., Brusatte, S.L., 2022. A skeleton from the Middle Jurassic of Scotland illuminates an earlier origin of large pterosaurs. Current Biology 32, 1446–1453.

Jagielska, N., Challands, T.J., O'Sullivan, M., Ross, D.A., Fraser, N.C., Wilkinson, M., Brusatte, S.L., 2023. New postcranial remains from the Lealt Shale Formation of the Isle of Skye, Scotland, showcase hidden pterosaur diversity in the Middle Jurassic. Scottish Journal of Geology 59, sjg2023-001.

Ji, S.A., Ji, Q., 1998. A new fossil pterosaur (Rhamphorhynchoidea) from Liaoning. Jiangsu Geology 22, 199–206.

Judd, J.W., 1875. The Geology of Rutland and the Parts of Lincoln, Leicester, Northampton, Huntingdon, and Cambridge, Included in Sheet 64 of the One-inch Map of the Geological Survey: With an Introductory Essay on the Classification and Correlation of the Jurassic Rocks of the Midland District of England. vol. 64. HM Stationery Office.

Kaup, J.J., 1834. Versuch einer Eintheilung der Saugethiere in 6 Stämme und der Amphibien in 6 Ordnungen. Isis 3, 311–315.

Kellner, A.W.A., Weinschütz, L.C., Holgado, B., Bantim, R.A., Sayao, J.M., 2019. A new toothless pterosaur (Pterodactyloidea) from Southern Brazil with insights into the paleoecology of a Cretaceous desert. Anais da Academia Brasileira de Ciências 91, e20190768.

Kent, P.E., 1966. A review of the corelation of the Lincolnshire Limestone (Inferior Oolite). Transactions of the Leicester Literary and Philosophical Society (Section C Geology) 60, 57–69.

Longrich, N.R., Martill, D.M., Andres, B., 2018. Late Maastrichtian pterosaurs from North Africa and mass extinction of Pterosauria at the Cretaceous–Paleogene boundary. PLoS Biology 16, e2001663.

Lü, J., 2006. Pterosaurs From China (Chinese Edition). China Press (145 pp., in Chinese with Latin names).

Lü, J., 2009. A new non-pterodactyloid pterosaur from Qinglong County, Hebei Province of China. Acta Geologica Sinica 83, 189–199.

Lü, J., Bo, X., 2011. A new rhamphorhynchid pterosaur (Pterosauria) from the Middle Jurassic Tiaojishan Formation of western Liaoning, China. Acta Geologica Sinica 85, 977–983.

Lü, J., Hone, D.W., 2012. A new Chinese anurognathid pterosaur and the evolution of pterosaurian tail lengths. Acta Geologica Sinica 86, 1317–1325.

Lü, J., Unwin, D.M., Jin, X., Liu, Y., Ji, Q., 2009. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. Proceedings of the Royal Society B: Biological Sciences 277, 383–389.

Lü, J.C., Fucha, X.H., Chen, J.M., 2010. A new scaphognathine pterosaur from the Middle Jurassic of western Liaoning, China. Acta Geoscientica Sinica 31, 263–266.

Lü, J., Xu, L., Chang, H., Zhang, X., 2011. A new darwinopterid pterosaur from the Middle Jurassic of western Liaoning, northeastern China and its ecological implications. Acta Geologica Sinica 85, 507–514.

Lü, J., Unwin, D.M., Zhao, B., Gao, C., Shen, C., 2012. A new rhamphorhynchid (Pterosauria: Rhamphorhynchidae) from the Middle/Upper Jurassic of Qinglong, Hebei Province, China. Zootaxa 3158, 1–19.

Manzig, P.C., Kellner, A.W.A., Weinschütz, L.C., Fragoso, C.E., Vega, C.S., Guimarães, G.B., Godoy, L.C., Liccardo, A., Ricetti, J.H., de Moura, C.C., 2014. Discovery of a rare pterosaur bone bed in a Cretaceous desert with insights on ontogeny and behavior of flying reptiles. PLoS One 9, e100005.

Marsh, O.C., 1871. Notice of some new fossil reptiles from the Cretaceous and Tertiary formations. American Journal of Science 3, 447–459.

Marsh, O.C., 1872. Discovery of additional remains of Pterosauria with descriptions of two new species. American Journal of Science 3, 241–248.

Marsh, O.C., 1876. Notice of a new sub-order of Pterosauria. American Journal of Science 11, 507–509.

Marshall, J.D., Ashton, M., 1980. Isotopic and trace element evidence for submarine lithification of hardgrounds in the Jurassic of England. Sedimentology 27, 271–289.

Martill, D.M., Frey, E., Tischlinger, H., Mäuser, M., Rivera-Sylva, H.E., Vidovic, S.U., 2023. A new pterodactyloid pterosaur with a unique filter-feeding apparatus from the Late Jurassic of Germany. Paläontologische Zeitschrift 97, 383–424.

Martin-Silverstone, E., Unwin, D.M., Cuff, A.R., Brown, E.E., Allington-Jones, L., Barrett, P.M., 2022. A new pterosaur from Skye, Scotland and the early diversification of flying reptiles. bioRxiv, 480264.

Martin-Silverstone, E., Unwin, D.M., Cuff, A.R., Brown, E.E., Allington-Jones, L., Barrett, P.M., 2023. A new pterosaur from the Middle Jurassic of Skye, Scotland and the early diversification of flying reptiles. Journal of Vertebrate Paleontology 43, 2298741.

Morris, J., 1853. On some sections in the Oolitic District of Lincolnshire. Quarterly Journal of the Geological Society of London 9, 317–344.

Nesov, L.A., 1984. Upper Cretaceous pterosaurs and birds from Central Asia. Paleontologicheskii Zhurnal 1, 47–57.

Newton, E.T., 1888. On the skull, brain and auditory organ of a new species of pterosaurian (*Scaphognathus purdoni*), from the Upper Lias near Whitby, Yorkshire. Philosophical Transactions of the Royal Society of London 179, 503–537.

O'Connor, J.K., Min, W., Xiao-Ting, Z., Xiao-Li, W., Zhong-He, Z., 2014. The histology of two female Early Cretaceous birds. Vertebrata PalAsiatica 52, 112–128.

O'Sullivan, M., Martill, D.M., 2017. The taxonomy and systematics of *Parapsicephalus purdoni* (Reptilia: Pterosauria) from the Lower Jurassic Whitby Mudstone Formation, Whitby, UK. Historical Biology 29, 1009–1018.

O'Sullivan, M., Martill, D.M., 2018. Pterosauria of the Great Oolite Group (Bathonian, Middle Jurassic) of Oxfordshire and Gloucestershire, England. Acta Palaeontologica Polonica 63, 617–644.

Owen, R., 1859. The fossil Reptilia of the Cretaceous formation. Supplement No. 1, Pterosauria. Palaeontographical Society Monographs, pp. 1–19.

Padian, K., 1984. Pterosaur remains from the Kayenta Formation (?Early Jurassic) of Arizona. Palaeontology 27, 407–413.

Padian, K., 2008a. The Early Jurassic pterosaur *Dorygnathus banthensis* (Theodori, 1830). Special Papers in Palaeontology, vol. 80. The Palaeontological Association, London, pp. 1–64.

Padian, K., 2008b. The Early Jurassic pterosaur *Campylognathoides* (Strand, 1928). Special Papers in Palaeontology, vol. 80. The Palaeontological Association, London, pp. 68–107.

Padian, K., De Ricqlès, A.J., Horner, J.R., 1995. Bone histology determines identification of a new fossil taxon of pterosaur (Reptilia: Archosauria). Comptes Rendus-Academie des Sciences Paris Serie 2 Sciences de la Terre et des Planetes, fascicule A 320, 77–84.

Plieninger, F., 1901. Beiträge Zur Kenntnis der Flugsaurier. Paläontographica 48, 65–90.

Reck, H., 1931. Die deutschostafrikanischen Flugsaurier. Centralblatt für Mineralogie, Geologie und Paläontologie 1931, 321–336.

Reid, R.E.H., 1990. Zonal "growth rings" in dinosaurs. Modern Geology 15, 19–48.

Sangster, S., 2021. The osteology of *Dimorphodon macronyx*, a non-pterodactyloid pterosaur from the Lower Jurassic of Dorset, England. Monographs of the Palaeontographical Society 175 (661), 1–48.

Seeley, H.G., 1864. On the osteology and classification of Pterodactyles, part II, with descriptions of the new species, *P. hopkinsi* and *P. oweni*. Proceedings of the Cambridge Philosophy Society 1, 238.

Seitz, A.L., 1907. Verleichenden Studien über den mikroskopischen knochenbau fossiler und rezenter Reptilien. Nova Academiae Caesareae Leopoldino-Carolinae germinacae naturae curiosorum 37, 230–370.

Smith, R.E., Ibrahim, N., Longrich, N., Unwin, D.M., Jacobs, M.L., Williams, C.J., Zouhri, S., Martill, D.M., 2023. The pterosaurs of the Cretaceous Kem Kem Group of Morocco. Paläontologische Zeitschrift 97, 519–568.

Starck, J.M., Chinsamy, A., 2002. Bone microstructure and developmental plasticity in birds and other dinosaurs. Journal of Morphology 254, 232–246.

Stecher, R., 2008. A new Triassic pterosaur from Switzerland (Central Austroalpine, Grisons), *Raeticodactylus filisurensis* gen. et sp. nov. Swiss Journal of Geosciences 101, 185–201.

Steel, L., 2008. The palaeohistology of pterosaur bone: an overview. Zitteliana B28, 109–125.

Taylor, J.H., 1946. Evidence of submarine erosion in the Lincolnshire Limestones of Northamptonshire. Proceedings of the Geologists' Association 57, 246–262.

Tischlinger, H., 2020. Der "Collini-*Pterodactylus*"–eine Ikone der Flugsaurier-Forschung. Archaeopteryx 36, 16–31.

Tucker, M.E., 1985. Shallow-marine carbonate facies and facies models. Geological Society, London, Special Publications 18, 147–169.

Unwin, D.M., 1996. The fossil record of Middle Jurassic pterosaurs. Bulletin of the Museum of Northern Arizona 60, 291–304.

Unwin, D.M., 2003. On the phylogeny and evolutionary history of pterosaurs. Geological Society, London, Special Publications 217, 139–190.

Varricchio, D.J., 1993. Bone microstructure of the Upper Cretaceous theropod dinosaur *Troodon formosus*. Journal of Vertebrate Paleontology 13, 99–104.

von Meyer, H., 1846. *Pterodactylus* (*Rhamphorhynchus*) *gemmingi* aus dem Kalkschiefer von Solenhofen. Palaeontographica 1, 1–20.

Wang, X., Zhou, Z., Zhang, F., Xu, X., 2002. A nearly completely articulated rhamphorhynchoid pterosaur with exceptionally well-preserved wing membranes and "hairs" from Inner Mongolia, northeast China. Chinese Science Bulletin 47, 226–230.

Wang, X., Kellner, A.W.A., Jiang, S., Meng, X., 2009. An unusual long-tailed pterosaur with elongated neck from western Liaoning of China. Anais da Academia Brasileira de Ciências 81, 793–812.

Wang, X., Kellner, A.W.A., Jiang, S., Cheng, X., Meng, X., Rodrigues, T., 2010. New long-tailed pterosaurs (Wukongopteridae) from western Liaoning, China. Anais da Academia Brasileira de Ciências 82, 1045–1062.

Wang, X., Jiang, S., Zhang, J., Cheng, X., Yu, X., Li, Y., Wei, G., Wang, X., 2017. New evidence from China for the nature of the pterosaur evolutionary transition. Scientific Reports 7, 42763.

Wei, X., Pêgas, R.V., Shen, C., Guo, Y., Ma, W., Sun, D., Zhou, X., 2021. *Sinomacrops bondei*, a new anurognathid pterosaur from the Jurassic of China and comments on the group. PeerJ 9, e11161.

Wellnhofer, P., 1974. *Campylognathoides liasicus* (Quenstedt), an Upper Liassic pterosaur from Holzmaden. The Pittsburgh specimen. Annals of Carnegie Museum of Natural History 45, 5–34.

Wellnhofer, P., 1985. Neue Pterosaurier aus der Santana Formation (Apt) der Chapada do Araripe, Brasilien. Palaeontographica A 187, 105–182.

Wellnhofer, P., 1991. Additional pterosaur remains from the Santana Formation (Aptian) of the Chapada do Araripe, Brazil. Palaeontographica 215, 43–101.

Woodcock, N.H., Furness, E.N., 2021. Quantifying the history of building stone use in a heritage city: Cambridge, UK, 1040–2020. Geoheritage 13, 12.

Zhang, H., Wang, M., Liu, X., 2008. Constraints on the upper boundary age of the Tiaojishan Formation volcanic rocks in West Liaoning-North Hebei by LA-ICP-MS dating. Chinese Science Bulletin 53, 3574–3584.

Zhou, X., Pêgas, R.V., Ma, W., Han, G., Jin, X., Leal, M.E., Bonde, N., Kobayashi, Y., Lautenschlager, S., Wei, X., Shen, C., 2021. A new darwinopteran pterosaur reveals arborealism and an opposed thumb. Current Biology 31, 2429–2436.