PALÆO VERTEBRATA

One of the geologically youngest remains of an ornithocheirid pterosaur from the late Cenomanian (Upper Cretaceous) of northeastern Mexico: implications for ornithocheirid paleogeography and extinction

EBERHARD 'DINO' FREY[a]*, WOLFGANG STINNESBECK[b], DAVID M. MARTILL[c], HÉCTOR E. RIVERA SYLVA[d] & HÉCTOR PORRAS MÚZQUIZ[e]

[a] *State Museum of Natural History Karlsruhe, Department of Geosciences, Germany*
[b] *Institute of Earth Sciences, Heidelberg University, Germany*
[c] *School of theEnvironment, Geography and Geological Science, University of Portsmouth, PO1 3QL, United Kingdom*
[d] *Museo del Desierto, Saltillo,Mexico*
[e] *Museo de Paleontología de Múzquiz, Múzquiz, Mexico*
**Corresponding author: dinofrey@aol.com*

Abstract: Ornithocheirid pterosaurs were the largest of the toothed pterodactyloids and had a worldwide distribution, although their fossil record is fragmentary. They were also the only toothed pterosaurs that survived into the Late Cretaceous, becoming extinct by the end of th Cenomanian. Here we report on an ornithocheirid metacarpus from a late Cenomanian laminated limestone of north-eastern Mexico. The specimen comprises a fragmentary distal syncarpal, a crushed but complete metacarpal IV, two fragmentary preaxial metacarpals, and a possible fragmentary terminal left wing finger phalanx. It represents the geologically youngest known ornithocheirid worldwide, except for two recent discoveries reported from Australia. We suggest that ornithocheirid pterosaurs may have become extinct because of massive ecological disturbances (e.g. sea-level, climatic oscillations) across the Cenomanian/Turonian boundary, that may have obliterated their breeding and feeding sites, especially low lying offshore islands.

Keywords: *Pterosauria, Ornithocheiridae, late Cenomanian, Late Cretaceous, Coahuila, north-eastern Mexico*

Submitted 2 February 2019, Accepted 8 June 2020

Dedication: This paper is dedicated to the memory of emeritus research director of the Centre de Recherche sur la Paléobiodiversité et les Paléoenvironments at the Muséum National d'Histoire Naturelle, Paris, Jean-Claude Rage, who died unexpectedly on the 30th of March 2018. Jean-Claude was an outstanding vertebrate palaeontologist.

INTRODUCTION

Pterosaurs were the first tetrapods to achieve powered flight. Earliest fossils of this enigmatic group of archosauromorph reptiles are very rare specimens from the Upper Triassic of the Alpine region (Austria, Switzerland, Italy; e.g. Wild, 1984, Dalla Vecchia *et al.*, 1988, Dalla Vecchia, 2003), Greenland and Utah, USA (Britt *et al.*, 2018). They dominated the skies throughout the Mesozoic until the latest Cretaceous, when they became extinct together with the non-avian dinosaurs and many other taxa (Wellnhofer, 1991a; Unwin, 2006; Witton, 2013; Longrich *et al.*, 2018). While toothed pterosaurs characterize the Triassic and Jurassic and are also present during Cretaceous times, edentulous forms radiate during the Cretaceous surviving to the end of the period (e.g. Wellnhofer, 1991a, Unwin, 2006). Toothed forms apparently disappeared during the Cenomanian/Turonian boundary, with the Ornithocheiridae after Seeley (1870, *sensu* Unwin, 2003) and Andres & Myers (2014) being the last survivors (Pentland *et al.,* 2019).

The flight apparatus of pterosaurs is a double spar construction that supports a wing membrane of complex histology that is suggestive for a physiology aligned with thermoregulation (Martill & Unwin, 1989; Tischlinger & Frey, 2002; Frey *et al.*, 2003). In ornithocheirid pterosaurs, a Late Cretaceous clade of toothed pterosaurs, the main wing spar is formed by the humerus, radius/ulna, carpus consisting of a proximal and distal syncarpal, a metacarpus that is about half the length of radius/ulna, and a hypertrophied digit four consisting of four phalanges of decreasing size distally (e.g. Wellnhofer, 1985, 1991a,b; Campos & Kellner, 1985; Unwin, 2006; Rodrigues & Kellner, 2008; Witton, 2013). The wing finger exceeds the combined length of all proximal wing elements by at least one third, but in most taxa, it is twice as long. In contrast, the hind limbs are a little shorter than the combined humerus and radius/ulna, thus resulting in an aspect ratio of around 20, similar to albatrosses (Wellnhofer, 1985, 1991a; Frey & Martill, 1994; Lü & Ji, 2005; Elgin & Frey, 2011; Witton, 1013). Some ornithocheirid pterosaurs reached wingspans of five to six meters, or more (Martill & Unwin, 2012). They occurred nearly globally during the late Early Cretaceous (Barremian–Albian) and early Late Cretaceous (Cenomanian) and are reported from Eurasia, North Africa, Australia, North and South America, with the exception of Antarctica and Central America (Averianov, 2004, 2007; Steel *et al.* 2005, Unwin & Martill, 2007; Barrett *et al.*, 2008 and references therein, Fletcher & Salisbury 2010, Kellner et al. 2019).

The record of ornithocheirid pterosaurs is considerable, especially from South America (Wellnhofer, 1985, 1991b; Campos & Kellner, 1985; Martill & Frey, 1998; Kellner & Tomida, 2000; Martill *et al.*, 2007) and from Eurasia (Owen, 1851a, b, 1859a, b, c, 1861; Bowerbank, 1851, 1852 a, b; Bakhurina & Unwin, 1995; Unwin & Bakhurina, 2000; Unwin *et al.*, 2000; Unwin, 2001; Lü & Ji, 2005; Wang *et al.*, 2005; Averianov, 2007). Conversely, approved remains of Ornithocheiridae in North America are restricted to *Uktenadactylus wadleighi* (Lee, 1994) from the Paw Paw Formation, Texas, which is dated to about the Albian-Cenomanian boundary. To date, the youngest reports of Ornithocheiridae come from Australia: *Ferrodraco lentoni* Pentland et al., 2019, comes from the Cenomanian-Turonian Winton Formation, Queensland, Australia, and the jaw fragment of a possible ornithocheirid (WAM 68.5.11) has been documented from the Cenomanian-Coniacian Molecap Greensand (Kear *et al.*, 2010).

Fragments of pterosaur bones from Mexico, which have been assigned to Ornithocheiridae by Rodriguez-De la Rosa & Cevallos-Ferriz (1998), come from the late Campanian of Coahuila, north-eastern Mexico, but this material is taxonomically unsecure, and should be best interpreted as indeterminate. Furthermore, the specimen is no longer available (EF, WS 2002, pers. obs.). The fragments were collected from the Las Águilas area near the hamlet of Porvenir de Jalpa, municipality of General Cépéda. Today, pterosaur bone fragments are rarely found in the area, but none of the specimens can be assigned to any higher pterosaur taxon (Rivera *et al.*, 2019).

Here we describe the remains of the left wing of an ornithocheirid pterosaur comprising a complete left metacarpal that has been found in a laminated limestone quarry at Cidudad Acuña, Northeast Mexico. The specimen is of late Campanian age and thus represents one of the geologically youngest ornithocheirid remains worldwide; it allows to discuss the extinction of the toothed pterosaurs during the Late Cretaceous.

GEOLOGICAL SETTING AND AGE

The active Crema Bonfil quarry from where the material described here was discovered is located about 120 km northwest of Ciudad Acuña in northern Coahuila, Mexico, at only a few hundreds of meters distance from the south banks of Río Bravo and thus the border with Texas, USA (Figures 1 A, B). It is not recommended to visit the quarry area to date because of heavy smuggling activity and illegal migration in this sparsely populated region. We therefore abstained from visiting the quarry and thus cannot present a section. Nevertheless, lithological characteristics of the fossil-bearing slab, e.g. the platy aspect of the limestone, micrite texture, horizontal lamination at a millimetrical scale, and the mode of fossil preservation, corresponds to that of other vertebrate-bearing fossil-*Lagerstätten* of Late Cretaceous (Cenomanian to Santonian) ages in north-eastern Mexico, among them Vallecillo, and the quarry fields at Múzquiz & Jiménez (e.g. Stinnesbeck *et al.*, 2005, 2016; Ifrim & Stinnesbeck 2007; Ifrim *et al.*, 2008, 2011, 2014; Alvarado Ortega *et al.*, 2012; Giersch, 2014, Nyborg *et al.*, 2014). At these fossil sites, lithologies are dominated by laminated platy limestone and intercalated marl best characterized as *plattenkalk*. These sediments crop out in an area of about 15,000 square km and were deposited under oxygen-deficient conditions on an open shelf along the passive continental margin of the Palaeogulf of Mexico (e.g. Ifrim *et al.*, 2007, 2008, 2011; Nyborg *et al.*, 2014).

A thin section of the fossil-bearing limestone slab displays a micritic microfacies (biomicrite, wackestone). The microfaunal content consists of inoceramid bivalve prisms and abundant planktonic foraminifers tentatively identified as planomalinids, heterohelicids and early globotruncanids (e.g. hedbergellids, whiteinellids, rotaloporids), but with a notable absence of foraminiferal morphotypes with a double-keeled shell ornament. This combination implies a late Cenomanian age for this horizon rather than an early Turonian age (Bolli *et al.*, 1989).

MATERIAL AND METHODS

The specimen (MUZ-910) was obtained by one of us (HPM) from a quarry worker. It has been professionally prepared with mechanical tools. The specimen was scanned with an Epson Paragon 2800 scanner at a resolution of 2800 dpi. The image was handled and traced with CorelDraw X6 (64 bit). Photos were taken with an Olympus E 620 SLR camera with an Olympus Zuiko standard lens (14-42 mm, f/3.5-5.6), and Olympus Zuiko macro lens (35 mm, f/3.5). A thin section of the fossil-bearing limestone slab was produced at the Institute of Earth Sciences at Heidelberg University, Germany, and analysed using a petrological microscope.

Taxonomy: In the past two decades, the taxomic definition of Ornithocheiroidea and Ornithocheiridae, respectively, underwent various changes. In Unwin (2003), Pterodactyloidea branch in two groups, the first group, Lophocratia, includes the Azhdarchoidea, Dsungaripteroidea, and Ctenochasamtoidea, while the second, the Ornithocheiroidea contains, Ornithocheiridae and its sister groups the Pteranodontinae and Nyctosaurinae. In contrast, Kellner (2003) postulated Ornithocheiroidea as a sub-group of Dsungaripteroidea. Ornithocheiroidea are split into Tapejaroidea and Pteranodontoidea. In the latter taxon, pteranodons form the sister taxon of all toothed Cretaceous pterosaurs without further ranking. However, in Rodrigues & Kellner (2013), the taxon Ornithocheridae *sensu* Seeley 1870 is re-introduced. In the phylogenetic analysis of Andres & Myers (2013) Ornithocheiridae fall within Pteranodontoidea as a sister group of Anhangueridae, with five unranked taxa. Pteranodontoidea comprise *Pteranodon* and Istiodactylidae. The root of all other Cretaceous toothed pterosaurs remains unranked. In Myers *et al.* 2014, the taxon Ornithocheiroidea re-appears and includes pteranodontids, istiodactylids, anhanguerids, and many others. Consequently, most taxa of Cretaceous toothed pterosaurs have changed the genus or higher taxonomic rank within phylogenetic trees, such as *Coloborhynchus*, *Arthurdactylus*, *Ludodactylus* (Rodrigues & Kellner 2008, 2013 and literature therein). The paper of Rodrigues & Kellner (2013) nicely demonstrates the dependence of the phylogenetic trees from (a) the number, selection and definition of taxa, and (b) the selection of the character set and (c) adding new character sets and (d) merging characters form the phylogenetic analyses of Wang *et al.* (2008) and Lü *et al.* (2010) into a new tree. *Aetodactylus halli* Myers, 2010 from the middle Cenomanian Tarrant Formation of the Eagle Ford Group, North Texas, has been described as the geologically youngest American ornithocheirid (Myers, 2010). However, according to a new phylogenetic analysis, *Aetodactylus halli* has been referred to a newly erected cosmopolitan taxon, the Lanceodontia, which is, for the moment, still within Ornithocheiroidea (Pêgas *et al.* 2019). *Arthurdactylus conandoylei* has been moved into this group. However, Lanceodontia is not widely accepted. With respect to this taxonomic confusion, we follow the most transparent taxonomic definition of Ornithocheiroidea and

Ornithocheiridae by Unwin 2003. Based on this taxonomy, the specimen from Ciudad Acuña is unequivocally referable to Ornithocheiridae, otherwise the specimen could not be discussed adequately at all, because most of the taxonomical approached described above do no refer to the morphology of metacarpals at all.

Figure 1. A: Map of Mexico; the state of Coahuila is marked in dark green; the red rectangle frames the area, where laminated limestone is quarried. **B**: Geographical map of the area northwest of Ciudad Acuña; the area the Crema Bonfi quarry is situated is framed in red; note that no precise location data are available.

SYSTEMATIC PALEONTOLOGY

Pterosauria Kaup, 1834
Monofenestrata Lü *et al.*, 2010
Pterodactyloidea Plieninger, 1901
Ornithocheiroidea Young, 1964
Family Ornithocheiridae Seeley, 1870, *sensu* Unwin, 2003
Gen. et spec. indet.

Locality: The Crema Bonfil quarry, located about 120 km north-west of Ciudad Acuña, near the south banks of Rio Bravo in northern Coahuila (Figure 1B).

Geological age: Cretaceous, late Cenomanian.

Collection number: MUZ-910. The specimen is housed in the Museo de Paleontología de Múzquiz, Coahuila, México.

The metacarpal IV (Figure 2) is identified as coming from the wing skeleton of an ornithocheirid pterosaur by its relative shortness, with a ratio of the maximum width at the proximal articular face to maximum length of about 1:6. All other Late Cretaceous pterosaurs, except for two istiodactylids (see below), have ratios of 1:10, or more (Wellnhofer, 1991a, b; Unwin, 2004).

PRESERVATION

The wing bones are preserved on a sub-rectangular limestone slab measuring approximately 200 x 180 mm. The slab is about 30 mm thick and consists of a millimetrically laminated light buff to pale yellow micrite. The upper surface displays a poorly preserved inoceramid bivalve, which has been partially removed during preparation of the pterosaur bones. Only the highest elevations of the metacarpal reached the top surface of the slab. All bones have been compacted during burial. They were impacted and crushed flat, and thus they do not preserve their original diameters. Some mid-shaft bone splinters have been pressed out of the contour by two or three millimeters, implying that the sediment was not fully lithified when destructive compaction occurred. In all preserved bones the compacta is smooth and white to light grey coloured. The bones display numerous compaction cracks, but minor plastic deformation is also present. The proximal and distal articular areas as well as the proximal crests of mc IV are less compacted, because of the thicker compacta in these parts of the element (Figure 2).

The left mc IV is seen in cranial aspect, because the proximal tuberculum is exposed, as are the proximoventral and dorsal crests and the proximal sulci. The cranial-most surface of the condyle is abraded. The compacta of mc IV is only missing on the proximal-most elevation of the proximal cranioventral crest and the proximal quarter of the cranial face of the bone, mostly close to the proximal sulci where compacta flakes are < 0.5 mm thick. The sediment infilling the bone is stained yellow. The remains of the left distal syncarpal lie adjacent to the ventral third of the proximal articular face of mc IV and likely expose parts of the distal articular face. No compaction has occurred on these robust elements. The compacta of the syncarpal is light buff colored. Yellow stained sediment is exposed on the wing finger phalanx in one small area in the middle of the preserved bone fragment, in which the compacta is missing. Elsewhere, the compacta of this bone is complete but crushed. Some marginal fragments have flaked off, probably during collection and/or preparation. The tip and a proximal section of unknown dimensions of wing finger phalanx IV are missing.

Size: The metacarpal of the MUZ-910 ornithocheirid has almost the same length as that of an unnamed ornithocheirid from the Crato Formation (Elgin and Frey 2012). Applying the same proportions of the metacarpal to other wing bones, the wingspan of the specimen from northern Coahuila is calculated to between 3 and 3.5 meters.

Ontogenetic stage: Based on a metacarpal alone, the individual age of the specimen is difficult to assess because the symphyses in pterosaurian wing bones close early during ontogeny (Elgin and Frey 2008). The symphyses of the metacarpal from Múzquiz are completely closed. This, together with the smooth and dense compacta as well as the wingspan, suggest a subadult to adult individual.

OSTEOLOGICAL DESCRIPTION

Distal syncarpal (Figure 2)

A bone fragment located adjacent to the ventral third of the proximal articular facet of mc IV is referred to a left distal syncarpal because of its topographical position, the relief of its exposed parts, and its general robustness. The preservation of the element is too poor to describe details.

Left metacarpal (mc) IV (Figures 2, 3)

This bone is seen in cranial aspect on the slab. It is elongate, nearly rectangular in outline. The dorsal and ventral margins converge distally from a diameter of 41 mm to a diameter of 23 mm. While the ventral margin of the shaft is straight, the dorsal margin is slightly concave, with the deepest part of the concavity in its proximal half. Therefore, the dorsal and ventral margins are almost parallel to each other in the distal half of the shaft.

The proximal tuberculum occupies one fourth of the exposed part of the proximal articular face. The blunt tuberculum protrudes proximally from the middle of the proximal articular surface with an elevation of 3 mm. Towards the dorsal proximal crest, the proximal tuberculum is off-set by a shallow concavity, whereas the transition to the ventral proximal crest is straight. The dorsal and ventral areas of the proximal articular face adjacent to the proximal tuberculum are inclined distally, with an angle of about 5° against the vertical plane. Distally, the proximal tuberculum continues into a very low and short proximal crest that is barely visible. With a length of 16 mm it reaches only one tenth of the maximum length of the bone. Therefore, the dorsal and ventral parts of the proximal sulcus are separated in their proximal extremities only, and distally become confluent.

The dorsal half of the dorsal part of the proximal sulcus is overlapped by the proximal half of the dorsal proximal crest, which emerges from the dorsocranial quarter of the proximal articular facet. The margin of the dorsal proximal crest bulges dorsocranially for about 16 mm. Further distally, it becomes slightly concave and after 20 mm merges with the dorsal margin of mc IV.

The ventral proximal crest arises from the dorsocranial third of the proximal articular facet. It forms a dorsally directed flange commencing distal to the ventral part of the proximal sulcus. Level with the sulcus the crest is dorsally concave and nearly parallels the dorsocranial margin of the dorsal proximal crest. The concavity extends distally for about 20 mm and then bulges dorsocranially for another 20 mm. Distal to this bulge, the dorsocranial margin straightens and merges with the ventral margin of mc IV at about mid-shaft. Distally, the dorsal and ventral margins of the shaft are parallel and merge with the lateral faces of the distal condyles. The ventral condyle is one fifth shorter than the dorsal condyle. Each condyle forms one quarter of the entire distal cranial articular face as exposed. Both condyles are separated by a shallow intercondylar sulcus which forms half of the craniodistal articular face. While the distal half of the intercondylar sulcus is slightly convex proximodistally, its proximal half forms a shallow depression. Proximally adjacent to middle of the proximal margin of the intercondylar sulcus there is a long oval pneumatic foramen with the long axis paralleling the long axis of mc IV. It measures 8 x 4 mm.

The cranial face of mc IV lacks any structures. It may originally have been slightly vaulted, but due to diagenetic compaction the degree of this vaulting cannot be determined.

Preaxial metacarpals (Figure 2)

Two bone fragments located adjacent to wing finger phalanx IV parallel each other. Their preserved parts are straight. According to their position, they are here interpreted to most likely represent remnants of the preaxial metacarpals, but it is impossible to determine which ones and which part of them they represent.

Wing finger phalanx IV (Figure 2)

Although it is sometimes difficult to tell the tip of wing finger phalanx IV from a pteroid, the case is clear in the present specimen, because this spine-like element is straight and

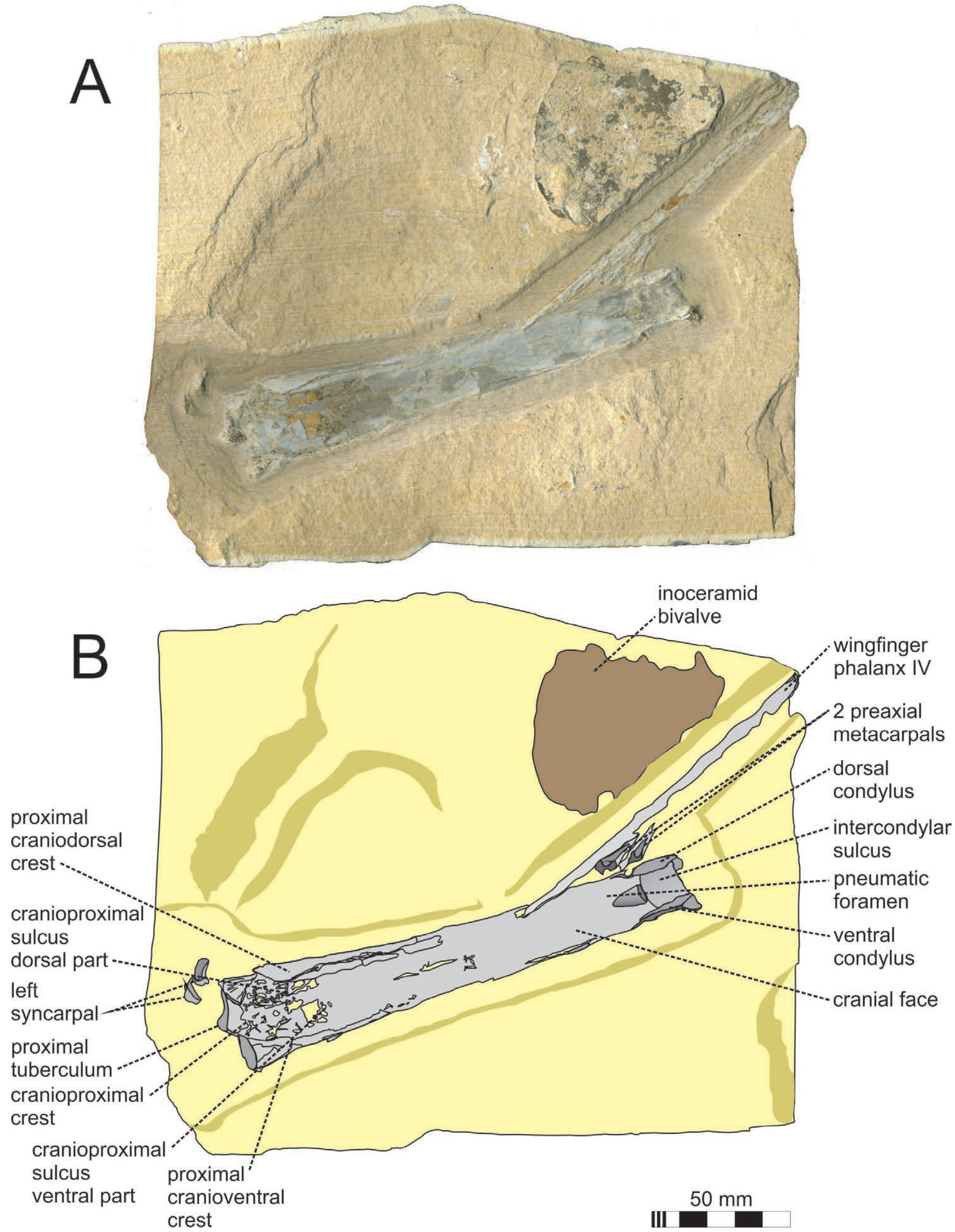

Figure 2. MUZ-910, Ornithocheiridae indet. **A**: Slab preserving a left mc IV associated with fragmentary carpals, preaxial metacarpals and a wing finger phalanx IV; **B**: Line drawing of the slab.

appears too long to represent a pteroid. From the distal tip of the bone, its margins diverge at an angle of about 5° proximally. There are insufficient features to determine whether it is from the left or right wing.

COMPARISONS

Because most of the elements preserved on the slab are either undiagnostic, fragmentary, or are poorly preserved, the comparisons discussed here concentrate on mc IV. The majority of ornithocheirid pterosaurs are described from fragmentary cranial elements and are mostly diagnosed based on the position and orientation of the fangs in their jaws and the extent of their cranial crests, even when articulated material is available (e.g. Wellnhofer, 1985, 1991b; Campos & Kellner, 1985; Unwin *et al.*, 2000; Lü & Ji, 2005; Wang *et al.*, 2005; Lee, 1994; Lü & Ji, 2005; Averianov, 2007; Myers, 2010; Buffetaut *et al.*, 2010; Elgin & Frey, 2011; Martill, 2015; Martill *et al.*, 2015, 2018). Wing bones, especially the humerus, the carpals and the metacarpal IV, are considered to present marginal diagnostic features but are occasionally used (e.g. Unwin & Bakhurina, 2000; Averianov, 2007). Postcranial material that preserves metacarpal IV is sparse, and if preserved, reported bone biometrics almost exclusively refer to its length, but not to its width. Additionally, many mc IV are not preserved in anterior aspect and thus are osteologically not comparable with MUZ-910. The use of photographs from the literature yields imprecise measurement data, and finally, preserved mc IVs of ornithocheiroids and many other pterosaur groups are frequently insufficiently described. Therefore, MUZ-910 is only compared with the metacarpals of three ornithocheirid specimens in the collections of the State Museum of Natural History Karlsruhe, Southwest Germany (SMNK). The specimens expose their anterior faces and were directly measured: *Arthurdactylus conandoylei* from the Aptian Crato Formation of Brazil (SMNK PAL 1132; Frey and Martill, 1994), and the mc IVs of two undescribed near-complete ornithocheirids, (SMNK PAL 1134, SMNK PAL 1136, respectively), both coming from the ?Albian Santana Formation of Brazil (Figure 4 A-D).

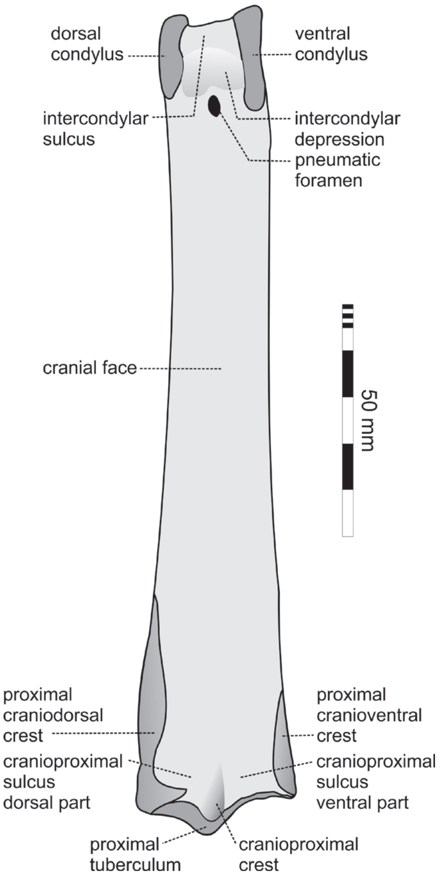

Figure 3. MUZ-910 Ornithocheiridae indet.: reconstruction of mc IV in cranial aspect.

Based on the ratio between maximum length and maximum proximal width (value 4.1), the Múzquiz orinithocheirid metacarpal IV largely resembles that of *Arthurdactylus conandoylei* (Frey & Martill, 1994). The same ratio is reasonably higher, reaching 4.9 in the mc IV of SMNK Pal 1134 and 5.0 in the undescribed ornithocheirid SMNK PAL 1136. In both SMNK specimens from the ?Albian Santana Formation the mc IVs are thus notably more slender.

The ratio of 1.8 between the maximum proximal and maximum distal width of mc IV in MUZ-910, is significantly higher than the same ratio in *Coloborhynchus* (1.48) and in *Arthurdactylus* (1.56), again with the latter being closest to MUZ-910 (Figure 4, Table 1). The shaft of MUZ-910 has a stronger taper distally than in these compared specimens. When comparing the length of the cranioproximal crest versus the maximum length of the bone, the differences are striking. In MUZ-910, this ratio is 10.0 and thus the crest is short as compared with the same ratio in *Coloborhynchus* (3.2) and the undescribed ornithocheirid (5.0 ; Figure 4, Table 1). In *Arthurdactylus* the crest is fully compacted and thus cannot be measured. The maximum length of mc IV compared with the maximum condylar length is 6.9 in MUZ-910 and 7.43 in *Arthurdactylus*, which is a reasonable match. However, the same ratio is 9.44 in *Coloborhynchus* and 9.41 in the undescribed ornithocheirid, showing that in the 3D preserved specimens the distal codyle is significantly shorter with respect to the bone length than in the compacted examples. Additionally, the condylar heads in the 3D specimens are separated by a narrow sulcus. In the compressed specimens, this sulcus is twice the size with respect to the width of the roller articulation (Table 1). It is thus likely that the compaction of the Múzquiz specimen created the similarities with *Arthurdactylus*. Assignment of the Múzquiz specimen to any particular genus and species is therefore inappropriate.

According to the most recent phylogenetic analyses (Kellner, 2003; Unwin, 2003; Andres in Longrich *et al.*, 2018; Zhou *et al.* 2019), Pteranodontidae and Istiodactylidae appear to be the closest relatives of Ornithocheiridae; they thus need to be considered. Pteranodontidae are ruled out here, because their mc IV is at least 10 times as long as it is wide at is proximal articular face (e.g. Eaton, 1910; Bennet, 2001; Witton & Habib 2010). Some Istiodactylidae, however, possess a mc IV with a robustness that ranges within that of Ornithocheiridae: *Nurhachius ignaciobritoi* Wang *et al.*, 2005, and *Istiodactylus sinensis* Andres & Qiang, 2006. The slenderness of mc IV in *Luchibang xinzhe* Hone *et al.*, 2020, ranges between that of ornithocheirids and pteranodontids. If the mc IV described herein was from an istiodactylid, it would represent a highly unlikely discovery, because (1) to present knowledge istiodactylids appear to be limited to the Early Cretaceous and (2) it would represent the first discovery of an istiodacylid pterosaur outside Eurasia. Therefore, the assumption that the bone comes from an ornithocheirid pterosaur appears to be the most plausible conclusion.

DISCUSSION

Although typical for the group, the general morphology of mc IV within ornithocheirids appears to be undiagnostic, not only as an isolated bone but also when examined in its skeletal context. Nevertheless, the comparison with three ornithocheirids housed in the SMNK, indicates that significant differences existed between the mc IVs of different ornithocheirids, even though some of these differences may be enhanced due to compaction during preservation. Even though, the extent of the proximal crests with respect to each other and to the maximum length of the bone, may have some potential to be diagnostic at genus level. Likely, more diagnostic features may be found on the mc IV with regard to the relief of the proximal articular face. Overall, the Múzquiz specimen compares well with the mc IVs of other ornithocheirids but can now only be referred to Ornithocheiridae indet. Nevertheless, its discovery in marine upper Cenomanian deposits of north-eastern Mexico makes it the geologically youngest specimen of this group in the western hemisphere, and quite likely worldwide.

Palaeobiogeographical and palaeoecological implications

The presence of an ornithocheirid pterosaur in Mexico partly fills a gap of distribution between North and South America, although not for the same time interval. South American ornithocheirids are most likely of Aptian to ?Albian age, while all North American specimens are Cenomanian in age and thus slightly younger. No ornithocheirid pterosaur is presently known from the Americas from deposits younger than Cenomanian. The Múzquiz specimen of late Cenomanian age thus provides evidence that ornithocheirids still roamed the skies of southern North America to at least this time, while they seem to have disappeared in South America by the end of the Albian, probably due to environmental changes (Longich *et al.*, 2018).

The abundance of pterosaurs, especially of ornithocheirids, in the northeast Brazilian Crato and Santana formations, could be due to potential breeding place availability in that region with optimum conditions for these pterosaurs. The predominantly piscivorous animals found an extremely rich food source (fish fossils are exceedingly abundant in both the Crato and Santana Formations (Maisey, 1991; Martill, 1996; Martill *et al.*, 2007; Longrich *et al.*, 2018) and save reproduction places, as the area was an archipelago of small islands secure from macro-predators. These presumed conditions were combined with a high fossilization potential in the depressions between the islands, a situation, which is exceedingly rare and may explain the abundance of pterosaur fossils in this area (Hasemann, 2002; Martins-Neto, 2006; Martill *et al.*, 2007). Ornithocheirids seem to have been dynamic offshore soarers, in contrast to the deep winged azhdarchoids (Witton & Naish, 2008; Vila Nova & Manso Sayão, 2012). This is suggested by the large aspect ratio (ratio of the square of the wingspan to the projected wing area), which is equal to the ratio of the wingspan to the standard mean chord of ornithocheirids. This ratio of about 20 is thus significantly larger than that of *Pteranodon* and even larger than that of an albatross with 15. Considering their poor terrestrial capabilities with extremely short legs with respect to the huge arms, ornithocheirids may have depended on offshore islands for reproduction. These habitats are also reflected by the record of Late Cretaceous pterosaurian ichnofossils. Narrow gauge footprints and trackways referable to azhdarchid type pterosaurs are frequently identified in coastal or shallow water environments (Ambroggi et al. 1954; Stokes, 1957; Lockley & Rainforth, 2002; Xing et al., 2013; Stinnesbeck *et al.*, 2017). With their long wings and short legs, ornithocheirids closely resemble non-pterodactyloids of the genus *Rhamphorhynchus*. Such a pterosaur construction would produce wide gauge tracks

Figure 4. Comparison of mc IV of the Coahuila ornithocheirid MUZ-910 (A), with the right mc IV of *Arthurdactylus conandoylei* Frey et al., 1994 from the Aptian Crato Formation of Ceará, north-eastern Brazil (B, SMNK PAL 1132), and two three-dimensionally preserved mc IV from the ?Albian Santana Formation of Ceará, north-eastern Brazil (C, SMNK PAL 1136; D, D' SMNK PAL 1134). All mc IV are seen in anterior view, except for D which is seen in dorsal aspect. Note the similarity between the two compressed specimens; the scale bar is 30 mm.

with the manus prints significantly lateral to the pes prints with a short stride. This is partially confirmed by the description of the first non-pterodactyloid trackway (Mazin & Pouech, 2020). The lack of ornithocheirid trackways in the fossil record may be aligned with their assumed habitat preference as offshore soarers, resting on offshore islands. This basically coincides with the assumption of Mazin & Pouech (2020) that the rarity of non-pterodactyloid pterosaur trackways is due to a scansorial life style and not the inability to walk.

The end of toothed pterosaurs

The record of unequivocal ornithocheirid pterosaurs ends at the Cenomanian/Turonian boundary, and only edentulous pterosaurs survive to the end of the Maastrichtian. The wing skeleton of these latest Cretaceous pterosaurs has a mc IV that exceeds the length of the antebrachium (radius/ulna). This is never the case among Ornithocheiridae, where the mc IV is considerably shorter. To date, the latest occurrence of Ornithocheiridae is recorded from the Australian Winton and the Molecap Greensand formations, both reaching from the Cenomanian at least into the Turonian (Kear *et al.*, 2010, Pentland *et al.*, 2019). Pentland *et al.* (2019) state that these two remains of Ornithocheiridae may possibly be of early Turonian age, based on detrital zircon dating (Winton Formation; Tucker *et al.*, 2013) but also the pollen and dinocyst record (Molecap Greensand; Kear *et al.* 2010). Nevertheless, precise dating depends on the exact finding places and their precise stratigraphical position within the units. These date are not known to date, and the age of the Australian ornithocheirids, whether of Cenomanian or early Turonian age, remains questionable.

The discovery of a pterosaurian metacarpal with ornithocheirid characters in the Crema Bonfil quarry north of Melchor Múzquiz, northern Coahuila, Mexico, is unexpected. This specimen was discovered in upper Cenomanian deposits and thus post-dates all Ornithocheiridae worldwide with the potential exception of the Australian records. The new Mexican specimen not only provides a first evidence for the existence of ornithocheirid pterosaurs in southern-most North America, but it also demonstrates that in the western hemisphere Ornithocheiridae survived to the end of the Cenomanian.

The end of the Cenomanian is marked by a worldwide mass extinction in the oceans, caused by extreme atmospheric warming and CO_2 increase, leading to O_2 depletion and anoxic conditions in the oceans (OAE2) as well as sea-level oscillations (e.g., Schlanger & Jenkyns, 1976; Hancock & Kaufmann, 1979; Barron, 1983; Hallam, 1985, 1989; Kerr, 1998; Huber *et al.*, 2002; Leckie *et al.*, 2002; Amiot et al., 2010). The best preserved Ornithocheidae come from archipelagos and lagoons that are characterized by an abundance of fish as a food source. The environmental turnover across the Cenomanian/Turonian boundary impacted on the habitat structures of ornithocheirids, i.e. isolated islands for breeding and marine and freshwater regimes rich in fish. Therefore, it appears more than likely that the global habitat changes at the end of the Cenomanian ended the era of the last toothed pterosaurs, the Ornithocheiridae.

CONCLUSIONS

The discovery of an unequivocal ornithocheirid left mc IV aligned with a distal syncarpal, fragmentary preaxial metacarpals and a fragmentary wing finger phalanx IV, extends the occurrence of ornithocheirid pterosaurs in North America to the late Cenomanian. The specimen is likely the youngest known ornithocheirid in the world. It is also the southernmost Cenomanian ornithocheirid specimen in North America. The remains suggest a subadult to adult individual with a wingspan of 3 to 3.5 meters. In this area, ornithocherids apparently survived in a transitional zone between the Western Interior

Table 1. Measurements of the Coahuila ornithocheirid and the three specimens depicted in Figure 4 B-D.

Metacarpal IV	**new specimen MUZ-910**	***Arthurdactylus conandoylei* SMNK 1132, left**	***Coloborhynchus* sp. SMNK PAL XXXX, left**	**Ornithocheirid SMNK PAL 1134, left**
max. prox. width	41 mm	50 mm	52 mm	32 mm
max. length	167 mm	223 mm	255 mm	160 mm
max. dist width	23 mm	32 mm	35 mm	21 mm
length of cranioprox. crest	16 mm	?	65 mm	32 mm
length of prox. craniodors. crest	43 mm	?	70 mm	35 mm
length of prox. craniovent. crest	22 mm	?	44 mm	15 mm
width of intercondylar sulcus	10 mm	15 mm	9 mm	7mm
lenth of ventral condyle	24 mm	30 mm	27 mm	17 mm
length of dorsal condyle	18 mm	22 mm	24 mm	14 mm
ratios				
max. length/max. prox. width	4.1	4.46	4.9	5.0
max. prox./max. dist. width	1.8	1.56	1.48	1.52
max. length/length cranioprox. crest	10.4	?	3.92	5
max. length/max. condylar length	6.9	7.43	9.44	9.41

Wing finger phalanx IV	**new specimen MUZ-910**
preserved length	118 mm
proximal width	7 mm

Seaway and the Paleogulf of Mexico, an area populated by low offshore islands. These islands drowned with the rising sea-level across the Cenomanian/Turonian boundary and ornithocheirids may thus have lost their breeding and feeding territories. Considering their poor terrestrial capabilities with short hind limbs, as compared to their enormous wings, ornithocheirids were most likely island breeders, similar to extant albatrosses. This assumption is supported by the high abundance of ornithocheirid remains in the ?Albian Santana Formation, NE Brazil, which was also deposited in an archipelago within an epeiric seaway. The general absence of ornithocheirid trackways supports this scenario.

The morphology of the anterior face of the mc IV in ornithocheirids may well be diagnostic beyond family level. However, biometric data and accurate anatomical descriptions are presently unavailable for most specimens. It would certainly be worthwhile to examine and report this element in future osteological descriptions of ornithocheirids with respect to the relief of the anterior and proximal articular face as well as the topography of the distal roller joint, and also with regard to ontogenetic changes in morphology and proportions.

ACKNOWLEDGEMENTS

The Deutsche Forschungsgemeinschaft (DFG) covered travel and fieldwork expenses for EF (FR1314/19) and WS (STI128/24). We cordially wish to thank Feiko Miedema (State Museum of Natural History Stuttgart, Germany) and two anonymous reviewers for their constructive and competent comments that helped to enhance the manuscript to the present level.

BIBLIOGRAPHY

Alvarado Ortega, J., 2012. La Cantera Tlayúa – un sitio paleontológico extraordinario. Arqueología Mexicana 19, 80-87.

Amiot, R., Wang, X., Lécuyer, C., Buffetaut, E., Boudad, L., Cavin, L., Ding, Z., Fluteau, F., Kellner, A. W. A., Tong, H., Zhangm F., 2010. Oxygen and carbon isotope compositions of middle Cretaceous vertebrates from North Africa and Brazil: Ecological and environmental significance. Palaeogeography, Palaeoclimatology, Palaeoecology 297, 439-451. https://doi.org/10.1016/j.palaeo.2010.08.027

Ambroggi, R., De Lapparent, A. F., 1954. Les empreintes de pas fossiles du Maestrichtien d'Agadir: Notes du Service Geologique du Maroc 10, 43-66.

Andres, B., Myers, T. S., 2013. Lone star pterosaurs. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 103, 383-398. https://doi.org/10.1017/S1755691013000303

Averianov, A. O., 2004. New data on Cretaceous flying reptiles (Pterosauria) of Russia, Kazakhstan, and Kyrgyzstan. Paleontological Journal 38, 426-436.

Averianov A. O., 2007. Mid-Cretaceous ornithocheirids (Pterosauria, Ornithocheiridae) from Russia and Uzbekistan. Paleontological Journal 41, 79-86. https://doi.org/10.1134/S003103010701008X

Bakhurina N. N., Unwin D. M., 1995. A survey of pterosaurs from the Jurassic and Cretaceous of the former Soviet Union and Mongolia. Historical Biology 10, 197-245. https://doi.org/10.1080/10292389509380522

Barrett, P. M., Butler, R. J., Edwards, N. P., Milner, A. R. 2008. Pterosaur distribution in time and space. An atlas. Zitteliana B28, 61-107.

Barron, E. J. A., 1983. A warm, equable Cretaceous: the nature of the problem. Earth Science Reviews 19, 305-338. https://doi.org/10.1016/0012-8252(83)90001-6

Bennett, S.C., 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. General description of osteology. Palaeontographica, Abteilung A 260, 1-112.

Bolli, H. M., Saunders, J. B., Perch-Nielsen, K., Caron, M., Toumarkine, Luterbacher, H., M., Jenkins, D. G., Iaccarino, S, Rogl, F., Remane, J. (eds), 1989. Plankton Stratigraphy. Vol. 1: Planktic Foraminifera, calcareous nannofossils and calpionelids. 608 pp, Cambridge University Press.

Bowerbank, J. S. 1851. On the pterodactyls of the Chalk Formation. Proceedings of the Zoological Society, London, 1851, 14-20. https://doi.org/10.1111/j.1096-3642.1851.tb01125.x

Bowerbank, J. S. 1852a. On the pterodactyls of the Chalk Formation. In: Report of the British Association for the Advancement of Science for 1851, Ipswich. John Murray, London, 55.

Bowerbank, J. S. 1852b. On the pterodactyls of the Chalk Formation. Annals of the Magazine of Natural History, 10, 372-378.

Britt, B. B., Dalla Vecchia, F. M., Chure, D. J., Engelmann, G. F., Whiting, M. F., Scheetz, R. D., 2018. *Caelestiventus hanseni* gen. et sp. nov. extends the desert-dwelling pterosaur record back 65 million years. Nature Ecology and Evolution 2, 1386-1392. https://doi.org/10.1038/s41559-018-0627-y

Buffetaut, E., B. Gibout, B., Drouin, D., 2010. A pterosaur from the Toarcian (Early Jurassic) of the Ardennes (northeastern France). Carnets de Géologie, Letter 2010/01, 1-6. https://doi.org/10.4267/2042/32427

Campos, D. A., Kellner, A. W. A., 1985. Panorama of the flying reptiles study in Brazil and South America (Pterosauria/ Pterodactyloidea/ Anhangueridae). Anais da Academia Brasileira Ciencias 57, 141-142 and 453-466.

Dalla Vecchia, F. M., 2003. A review of the Triassic Pterosaur record. Rivista del Museo Civico di Scienze Naturali „Enrico Caffi“ Bergamo 22, 13-29.

Dalla Vecchia, F.M., Muscio, G., Wild, R., 1988. Pterosaur remains in a gastric pellet from the Upper Triassic (Norian) of Rio Seazza Valley (Udine, Italy). Gortiana - Atti Museo Friuliano di Storia Naturale 10, 121-132.

Eaton, G.F., 1910. Osteology of *Pteranodon*. Memoirs of the Connecticut Academy of Arts and Sciences 2, 1-38.

Elgin, R. A., Frey, E., 2008. You show me your sutures and I'll tell you your age. Age traces in a young *Anhanguera* skeleton. In Zuzana Krempaská (ed). 6th Meeting of the European Association of Vertebrate Palaeontologists, Abstract Volume, 33-45.

Elgin, R. A., Frey, E., 2011. A new ornithocheirid, *Barbosania gracilirostris* gen. et sp. nov. (Pterosauria, Pterodactyloidea) from the Santana Formation (Cretaceous) of NE Brazil". Swiss Journal of Palaeontology 130, 259-275. https://doi.org/10.1007/s13358-011-0017-4

Elgin, R. A., Frey, E., 2012. A nearly complete ornithocheirid pterosaur from the Aptian (Early Cretaceous) Crato Formation of NE Brazil. Acta Palaeontologica Polonica. 57, 101-110. https://doi.org/10.4202/app.2010.0079

Fletcher, T., Salisbury, S., 2010. New pterosaur fossils from the Early Cretaceous (Albian) of Queensland, Australia. Journal of Vertebrate Paleontology 30, 1747-1759. https://doi.org/10.1080/02724634.2010.521929

Frey, E., Martill, D. M., 1994. A new pterosaur from the Crato Formation (Lower Cretaceous, Aptian) of Brazil. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 194, 379-412.

Frey, E., Tischlinger, H., Buchy, M.-C., Martill, D. M., 2003. New specimens of Pterosauria (Reptilia) with soft parts with implications for pterosaurian anatomy and locomotion. Geological Society London, Special Publications 217, 233-266. https://doi.org/10.1144/GSL.SP.2003.217.01.14

Giersch, S., 2014. Die Knochenfische der Oberkreidezeit in Nordostmexiko: Beschreibung, Systematik, Vergesellschaftung, Paläobiogeographie und Paläoökologie. PhD, University of Heidelberg, 279.

Hallam, A., 1985. A review of Mesozoic climates. Journal of the Geological Society 142, 433-445. https://doi.org/10.1144/gsjgs.142.3.0433

Hallam, A., 1989. The case for sea-level change as a dominant causal factor in mass extinction of marine invertebrates. Philosophical Transactions of the Royal Society of London B 325, 437-455. https://doi.org/10.1098/rstb.1989.0098

Hancock, J. M., Kaufman, E. G., 1979. The great transgressions of the Late Cretaceous. Journal of the Geological Society 136, 175-186. https://doi.org/10.1144/gsjgs.136.2.0175

Hasemann, S., 2002. Santana Formation: geological setting and age. http://palaeo.gly.bris.ac.uk/Palaeofiles/Lagerstatten/santana/geology.html (page actualised 20th November 2002).

Huber, B. T., Norris, R. D., MacLeod, K. G., 2002. Deep-sea paleotemperature record of extreme warmth during the Cretaceous. Geology 30, 123-126.

Ifrim, C., Stinnesbeck, W., 2007. Early Turonian ammonites from Vallecillo, north-eastern Mexico: taxonomy, biostratigraphy and palaeobiogeographic significance. Cretaceous Research 28, 642-664. https://doi.org/10.1016/j.cretres.2006.10.004

Ifrim, C., Buchy, M.-C., Smith, K. T., Giersch, S., 2008. Palaeoenvironment and preliminary description of early Turonian (late Cretaceous) aquatic squamates from Vallecillo, north-eastern Mexico. In Everhart, M. J. (ed.). Proceedings of the Second Mosasaur Meeting. Fort Hays Studies, Special Issue 3, Fort Hays State University, Hays, Kansas, pp. 47-62.

Ifrim, C., Vega-Vera, F. J. Stinnesbeck, W., 2011. Epizoic stramentid cirripedes on ammonites from Late Cretaceous Platy Limestones in Mexico. Journal of Paleontology 85, 524-536. https://doi.org/10.1666/10-052.1

Ifrim, C., Wiese, F., Stinnesbeck, W., 2014. Inoceramids and biozonation across the Turonian-Coniacian boundary (Upper Cretaceous) at El Rosario, Coahuila, northeastern Mexico. Newsletters on Stratigraphy 47, 211-246.

Kear, B. P., De Acon, G. L., Siverson, M., 2010. Remains of a Late Cretaceous pterosaur from the Molecap Greensand of Western Australia. Alcheringa 34, 273-279. https://doi.org/10.1080/03115511003661651

Kellner, A. W. A., 2003. Pterosaur phylogeny and comments on the evolutionary history of the group. Geological Society, London, Special Publications 217, 105-137. https://doi.org/10.1144/GSL.SP.2003.217.01.10

Kellner, A. W. A., Caldwell, M. W., Holgado, B., Dalla Vecchia, F. M., Nohra, R., Sayão, J. M., Currie, P. J., 2019. First complete pterosaur from the Afro-Arabian continent: insight into pterodactyloid diversity. Scientific Reports 9, 1-9. https://doi.org/10.1038/s41598-019-54042-z

Kellner A. W. A., Tomida, Y. 2000. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian-Albian), Northeastern Brazil. Monograph of the Museum of Natural History, the University of Kansas 17, 1-135.

Kerr, A. C., 1998. Oceanic plateau formation: a cause of mass extinction and black shale deposition around the Cenomanian–Turonian boundary? Journal of the Geological Society 155, 619-626. https://doi.org/10.1144/gsjgs.155.4.0619

Leckie, R. M., Bralower, T. J., Cashman, R., 2002. Oceanic anoxic events and plankton evolution: Biotic response to tectonic forcing during the mid-Cretaceous. Paleoceanography 17, 13-1–13-29. https://doi.org/10.1029/2001PA000623

Lee, Y.-N., 1994. The Early Cretaceous pterodactyloid pterosaur *Coloborhynchus* from North America. Palaeontology 37, 755-763.

Lockley, M. G., Rainforth, E. C., 2002. The track record of Mesozoic birds and pterosaurs: an ichnological and paleoecological perspective. In: Chiappe, L. M. and Witmer, L. M. (eds.): Mesozoic birds: above the heads of dinosaurs: Berkeley and Los Angeles California; University of California Press, pp. 405-418.

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 Biol 16, e2001663. https://doi.org/10.1371/journal.pbio.2001663

Lü, J. C., Ji, Q., 2005. A new ornithocheirid from the Early Cretaceous of Liaoning Province, China. In: Acta Geologica Sinica, English Edition 79, 157-163. https://doi.org/10.1111/j.1755-6724.2005.tb00877.x

Lü, J. C., Unwin, D. M., Jin, X., Liu, Y., Ji, Q., 2010. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull. Proceedings of the Royal Society B 277: 383-389. https://doi.org/10.1098/rspb.2009.1603

Maisey, J. G. 1991. Santana fossils: an illustrated atlas. T. H. F. Publications, Pennsylvania State University, 459 pp.

Martill, D. M. 1996. Fieldguide to fossils no. 5: Fossils of the Santana and Crato Formations, Brazil. The Palaeontological Association, 160 pp.

Martill, D. M., 2015. First occurrence of the pterosaur *Coloborhynchus* (Pterosauria, Ornithocheiridae) from the Wessex Formation (Lower Cretaceous) of the Isle of Wight, England. Proceedings of the Geologists' Association. 126, 377-380. https://doi.org/10.1016/j.pgeola.2015.03.004

Martill, D. M., Bechly, G., Loveridge, R. F. (eds), 2007. The Crato fossil beds of Brazil. Window into an ancient World. Cambridge University Press, Cambridge, New York, Melbourne, 625 pp. https://doi.org/10.1017/CBO9780511535512

Martill, D. M., Frey, E., 1998. A new pterosaur Lagerstätte in NE Brazil (Crato Formation; Aptian, Lower Cretaceous): preliminary observations. Oryctos 1, 79-85.

Martill, D. M., Unwin, D. M. 1989. Exceptionally well preserved pterosaur wing membrane from the Cretaceous of Brazil. Nature 340, 1476-4687. https://doi.org/10.1038/340138a0

Martill, D.M., Unwin, D.M. 2012. The world's largest toothed pterosaur, NHMUK R481, an incomplete rostrum of *Coloborhynchus capito* (Seeley, 1870) from the Cambridge Greensand of England. Cretaceous Research 34, 1-9. https://doi.org/10.1016/j.cretres.2011.09.003

Martill, D. M., Unwin, D. M., Nizar, I. Longrich, N., 2018. A new edentulous pterosaur from the Cretaceous Kem Kem beds of south eastern Morocco. Cretaceous Research. 84, 1-12. https://doi.org/10.1016/j.cretres.2017.09.006

Martins-Neto, R. G. 2006. Insetos fósseis como bioindicadores em depósitos sedimentares: um estudo de caso para o cretáceo da Bacia do Araripe (Brasil). Revista Brasileira de Zoociências, 8, 159-180.

Mazin, J.-M., Pouech, J., 2020. The first non-pterodactyloid pterosaurian trackways and the terrestrial ability of non-pterodactyloid pterosaurs. Geobios 58, 39-53. https://doi.org/10.1016/j.geobios.2019.12.002

Myers, T. S., 2010. A new ornithocheirid pterosaur from the Upper Cretaceous (Cenomanian-Turonian) Eagle Ford Group of Texas. Journal of Vertebrate Paleontology 30, 280-287. https://doi.org/10.1080/02724630903413099

Myers. B., Clark, J. M., Xu, X., 2014. The earliest pterodactyloid and the origin of the group. Current Biology 24, 1011-1016. https://doi.org/10.1016/j.cub.2014.03.030

Nyborg, T., Ifrim, C., Moreno-Bedmar, J. A., Porras Múzquiz, H., Giersch, S., Vega, F. J., 2014. Late Cretaceous fish cans: Fish preserved in ammonite body chambers from the middle Santonian of Coahuila State, northeastern Mexico. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 273, 75-88. https://doi.org/10.1127/0077-7749/2014/0417

Owen, R., 1851a. On a new species of pterodactyl (*Pterodactylus compressirostris* Owen) from the Chalk; with some remarks on the nomenclature of the previously described species. Proceedings of the Zoological Society London, 21-34. https://doi.org/10.1111/j.1096-3642.1851.tb01126.x

Owen, R. 1851b. A monograph of the fossil Reptilia of the Cretaceous formations. Palaeontological Society, part 1, 1-110. https://doi.org/10.5962/bhl.title.61855

Owen, R., 1859a. On remains of new and gigantic species of pterodactyl (*Pter. filtoni* and *Pter. sedgwickii*) from the Upper

Greensand near Cambridge. Report of the British Association for the Advancement of Science 28, 98-103.

Owen, R., 1859b. On the vertebral column of the order Pterosauria (Ow.) as exemplified in the genera *Pterodactylus* (Cuv.) and *Dimorphodon* (Ow.). Proceedings of the Royal Society London 9, 703-704. https://doi.org/10.1098/rspl.1857.0143

Owen, R., 1859c. Supplement (No. I) to the Monograph on the Fossil Reptilia of the Cretaceous Formations: Order Pterosauria Owen*,* Genus *Pterodactylus* Cuvier. Monographs of the Palaeontological Society London, 1-19.

Owen, R., 1861. Supplement (No. III) to the Monograph on the Fossil Reptilia of the Cretaceous Formations: Order Pterosauria Owen, Genus *Pterodactylus* Cuvier. Monograph of the Palaeontological Society London, 1-19.

Pêgas, R. V., Holago, B., Leal, M. E. C., 2019. On *Targaryendraco weidenrothi* gen. nov., (Pterodactyloidea, Pteranodontoidea, Lanceodontia) and recognition of a new cosmopolitan lineage of Cretaceous toothed pterodactyloids. Historical Biology, 1-15. https://doi.org/10.1080/08912963.2019.1690482

Pentland, A. H., Poropat, S. F., Tischler, T. R., Sloan, T., Elliott, R. A., Elliott, H. A., Elliot, J. A., Elliott, D. A., 2019. *Ferrodraco lentoni* gen. et sp. nov., a new ornithocheirid pterosaur from the Winton Formation (Cenomanian–lower Turonian) of Queensland, Australia. Scientific Reports 9 (1), 1-13. https://doi.org/10.1038/s41598-019-49789-4

Rivera-Sylva, H. E., Frey, E., Stinnesbeck, W., Amezcua Torres, N., Flores Huerta, D., 2019. Terrestrial vertebrate paleocommunities from the Cerro del Pueblo Formation (Late Cretaceous; Late Campanian) at Las Águilas, Coahuila, Mexico. Palaeovertebrata 42-2e1, 1-12. https://doi.org/10.18563/pv.42.2.e1

Rodrigues, T., Kellner, A.W.A., 2008. Review of the pterodactyloid pterosaur *Coloborhynchus.* Zitteliana Reihe B: Abhandlungen der Bayerischen Staatssammlung für Palaontologie und Geologie B 28, 209-219.

Rodrigues, T., Kellner, A.W.A. 2013. Taxonomic review of the Ornithocheirus complex (Pterosauria) from the Cretaceous of England. ZooKeys 308: 1-112. https://doi.org/10.3897/zookeys.308.5559

Rodríguez-De La Rosa, R. A., 2003. Pterosaur tracks from the latest Campanian Cerro del Pueblo Formation of southeastern Coahuila. In: Buffetaut E., and Mazin, J.M. (eds.): Evolution and paleobiology of pterosaurs. Geological Society of London, Special Publication 217, 275-282. https://doi.org/10.1144/GSL.SP.2003.217.01.16

Rodríguez de la Rosa, R. A., Cevallos-Ferriz, S. R. S., 1998. Vertebrates of the El Pelillal locality (Campanian, Cerro del Pueblo Formation), southeastern Coahulila. Journal of Vertebrate Paleontology 18, 4, 751-764. https://doi.org/10.1080/02724634.1998.10011104

Schlanger, S. O. and Jenkyns, H. C., 1976. Cretaceous oceanic anoxic events: causes and consequences. Geologie en Mijnbouw 55, 179-184.

Seeley, H. G. 1870. The Ornithosauria: an elementary study of the bones of pterodactyles, made from fossil remains found in the Cambridge Upper Greensand, and Arranged in the Woodwardian Museum of the University of Cambridge. Deighton, Bell and Co., Cambridge, U.K., 135 pp.

Steel, L., Martill, D. M., Unwin, D.M., Winch, J. D. 2005. A new pterodactyloid pterosaur from the Wessex Formation (Lower Cretaceous) of the Isle of Wight, England. Cretaceous Research 26 (4), 686-698. https://doi.org/10.1016/j.cretres.2005.03.005

Stinnesbeck, W., Ifrim, C., Schmidt, H., Rindfleisch, A., Buchy, M.-C., Frey, E., González González, A. H., Vega-Vera, F. J., Porras-Múzquiz, H., Cavin, L., Keller, G., Smith, K. T., 2005. A new lithographic limestone deposit in the Upper Cretaceous Austin Group at El Rosario, county of Múzquiz, Coahuila, northeastern Mexico. Revista Mexicana de Ciencias Geológicas, 22, 401-418.

Stinnesbeck, W., E. Frey, P. Zell, 2016. Evidence for semi-sessile early juvenile life history in Cretaceous ammonites. Palaeogeography, Palaeoclimatology, Palaeoecology 457, 186-194. https://doi.org/10.1016/j.palaeo.2016.06.019

Stinnesbeck, W., Frey, W., Espinoza-Chavez, B., Zell, P., Flores-Ventura, J., Rivera-Sylva, H., González-González, A.H., Padilla Gutierrez, J.M., and Vega, F.J., 2017. Theropod, avian, pterosaur and arthropod tracks from the uppermost Cretaceous Las Encinas Formation, Coahuila, northeastern Mexico, and their significance for the end-Cretaceous mass extinction. Geological Society of Ameria Bulletin 129, p. 331-348. https://doi.org/10.1130/B31554.1

Stokes, W. L., 1957. Pterodactyl tracks from the Morrison Formation. Journal of Paleontology 31, 952-954.

Tischlinger, H., Frey, E., 2002. Ein *Rhamphorhynchus* (Pterosauria, Reptilia) mit ungewöhnlicher Flughauterhaltung aus dem Solnhofener Plattenkalk. Archaeopteryx 20, 1-20.

Tucker, R. T., Roberts, E. M., Hu, Y., Kemp, A. I. S., Salisbury, S. W., 2013. Detrital zircon age constraints for the Winton Formation, Queensland: contextualizing Australia's Late Cretaceous dinosaur faunas. Gondwana Research 24, 767-779. https://doi.org/10.1016/j.gr.2012.12.009

Unwin, D. M. 2001. An overview of the pterosaur assemblage from the Cambridge Greensand (Cretaceous) of Eastern England. Mitteilungen des Museums für Naturkunde Berlin, geowissenschaftliche Reihe 4, 189-221. https://doi.org/10.1002/mmng.4860040112

Unwin, D. M. 2003. On the phylogeny and evolutionary history of pterosaurs. In: Buffetaut E. and Mazin, J.-M. (eds.): Evolution and Palaeobiology of Pterosaurs. Geological Society of London, Special Publications 217, 139-190. https://doi.org/10.1144/GSL.SP.2003.217.01.11

Unwin, D. M., 2004. *Eudimorphodon* and the early history of pterosaurs. In: Renesto, S. and Pagganoni, A. (eds): A symposium honouring the 30th anniversary of the discovery of *Eudimorphodon*, Bergamo 2003. Rivista del Museo Civico di Scienze Naturali „Enrico Caffi" Bergamo 22, 41-48.

Unwin, D. M., 2006. The pterosaurs: from deep time. PI Press, New York NY, 352 pp.

Unwin D. M., Bakhurina N. N., 2000. Pterosaurs from Russia, Middle Asia and Mongolia In: Benton, M. J., Shishkin, M. A., Unwin, D. M., Kurochkin E. N. (eds): The age of dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge, pp. 420-433.

Unwin, D. M., Lü, J., Bakhurina, N. N., 2000. On the systematic and stratigraphic significance of pterosaurs from the Lower Cretaceous Yixian Formation (Jehol Group) of Liaoning, China. Mitteilungen des Museums für Naturkunde Berlin, Geowissenschaftliche Reihe 3, 181-206. https://doi.org/10.1002/mmng.4860030109

Unwin, D. M., Martill, D. M., 2007. Pterosaurs of the Crato Formation, Research output. In: Martill, D. M., Bechly, G.; Loveridge, R. F. (eds): The Crato fossil beds of Brazil: window into an ancient world. Cambridge University Press, pp. 475-524. https://doi.org/10.1017/CBO9780511535512.018

Vila Nova, B. C., Manso Sayão, J., 2012. On wing disparity and morphological variation of the Santana Group pterosaurs. Historical Biology 24, 567-574. https://doi.org/10.1080/08912963.2012.658386

Wang, X.-L., Kellner, A. W. A., Zhou, Z., de Almeida Campos, D., 2005. Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. Nature 437, 875-879. https://doi.org/10.1038/nature03982

Wang, X., Kellner, A. W. A., Zhou, Z., Campos, D. A., 2008. Discovery of a rare arboreal forest–dwelling flying reptile (Pterosauria, Pterodactyloidea) from China. Proceedings of the National Academy of Sciences 105, 1983-1987. https://doi.org/10.1073/pnas.0707728105

Wellnhofer, P., 1985. Neue Pterosaurier aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. Palaeontographica, Abteilung A: Paläozoologie, Stratigraphie 187, 105-182.

Wellnhofer, P., 1991a. The illustrated encyclopedia of pterosaurs. Salamander Books, Ladysmith, British Colombia, 192 pp.

Wellnhofer, P., 1991b. Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Araripe. Palaeontographica, Abteilung A: Paläozoologie, Stratigraphie 215, 43-101.

Wild, R., 1984. A new pterosaur (Reptilia, Pterosauria) from the Upper Triassic (Norien) of Friuli, Italy. Gortiana - Atti Museo Friuliano di Storia Naturale 5, 45-62.

Witton, M. P., 2013. Pterosaurs: Natural History, Evolution, Anatomy. Princeton University Press, New Jersey, 291 pp. https://doi.org/10.1515/9781400847655

Witton, M.P., Habib, M.B., 2010. On the size and flight diversity of giant pterosaurs, the use of birds as pterosaur analogues and comments on pterosaur flightlessness. PLoS ONE 5: e13982. https://doi.org/10.1371/journal.pone.0013982

Witton, M. P., Naish, D., 2008. A reappraisal of azhdarchid pterosaur functional morphology and paleoecology. PLoS ONE 3, e2271. https://doi.org/10.1371/journal.pone.0002271

Xing, L. D., Lockley, M. G., Klein, H., Zhang J. P., He, Q , Divay, J. D., Qi, L .Q., Jia, C. K., 2013. Dinosaur, bird and pterosaur footprints from the Lower Cretaceous of Wuerhe asphaltite area, Xinjiang, China, with notes on overlapping track relationships. Palaeoworld 22, 42-51. https://doi.org/10.1016/j.palwor.2013.03.001

Zhou, X., Pêgas, R. V., Leal, M. E. C., Bonde, N., 2019. *Nurhachius luei*, a new istiodactylid pterosaur (Pterosauria, Pterodactyloidea) from the Early Cretaceous Jiufotang Formation of Chaoyang City, Liaoning Province (China) and comments on the Istiodactylidae. PeerJ 7, e7688. https://doi.org/10.7717/peerj.7688