

NEW PTEROSAUR SPECIMENS FROM THE KEM KEM BEDS (UPPER CRETACEOUS, CENOMANIAN) OF MOROCCO

TAISSA RODRIGUES¹, ALEXANDER W. A. KELLNER¹, BRYN J. MADER² & DALE A. RUSSELL³

Received: October 11, 2010; accepted: February 1st, 2011

Key words: Pterosauria, Azhdarchidae, Morocco, Cretaceous, Cenomanian, Kem Kem beds.

Abstract. Although pterosaurs from Africa are still rare, in recent years several specimens have been described from the Kem Kem beds (Upper Cretaceous, Cenomanian) of Morocco. Here we describe four additional specimens from this informal lithostratigraphic unit: a jaw fragment, two mid-cervical vertebrae, and a humerus. All these specimens show three-dimensional preservation, differing much from the flat condition found in most pterosaur material. The vertebrae are particularly well preserved, and allow accurate observations on the pneumatization of the neural arch. Based on comparable material, we show that at least two edentulous pterosaur species were present in this informal lithostratigraphic unit, thus adding to the growing evidence of considerable pterosaur diversity in northwestern Africa during the “middle” Cretaceous. So far, the Kem Kem beds have the most diverse pterosaur fauna in this continent, with the presence of anhanguerids, azhdarchids, pteranodontids, and tapejarids.

Riassunto. Sebbene gli pterosauri rinvenuti in Africa siano ancora rari, negli ultimi anni diversi esemplari sono stati descritti dai cosiddetti Kem Kem beds del Marocco (Cretacico Superiore, Cenomaniano). Nell' articolo descriviamo quattro nuovi reperti provenienti da questa unità litostrotigrafica informale: un frammento di mandibola, due vertebre medio-cervicali e un omero. Tutti questi esemplari offrono una conservazione tridimensionale, differendo in questo dalle condizioni di appiattimento proprie di molti reperti di pterosauri. Le vertebre sono particolarmente ben conservate e consentono una accurata osservazione della pneumatizzazione dell' arco neurale. Sulla base di materiale di confronto noi mostriamo che almeno due specie edentule di pterosauri sono presenti in questa unità litostrotigrafica informale. Ciò incrementa l' evidenza di una considerevole diversità tra gli pterosauri che popolarono l' Africa nordoccidentale durante il “Cretacico medio”. I Kem Kem beds contengono la fauna a pterosauri più diversificata in questo continente, con la presenza di anhangueridi, azhdarchidi, pteranodontidi e tapejaridi.

Introduction

African pterosaurs are still poorly known, limited to relatively few incomplete skeletons and isolated remains (Swinton 1948; Montillet et al. 1982; Unwin & Heinrich 1999; Benton et al. 2000; Dalla Vecchia et al. 2001; Blackburn 2002; Dal Sasso & Pasini 2003; Ntamak-Nida et al. 2006; Blackbeard & Yates 2007; Kellner et al. 2007; Costa & Kellner 2009; Ibrahim et al. 2010). Morocco represents several of the recent finds of pterosaur fossils.

Sigogneau-Russell et al. (1998) first reported on some pterosaur material from a Lower Cretaceous calcareous lens in the locality of Anoual. These specimens, nearly 300 isolated teeth, were described by Knoll (2000), who identified them as belonging to ornithocheirids and gnathosaurines, the latter questioned by Rodrigues & Kellner (2010) who pointed out that at least some of the gnathosaurin teeth could actually belong to the Anhangueridae or closely related taxa.

Another Moroccan pterosaur occurrence is the sequence of cervical vertebrae from the Maastrichtian of the Oulad Abdoun Phosphatic Basin that represents the azhdarchid *Phosphatodraco mauritanicus* Pereda-Suberbiola, Bardet, Jouve, Iarochène, Bouya & Amaghazaz, 2003 (see Pereda-Suberbiola et al. 2003; Kellner 2010).

Notwithstanding these occurrences, most pterosaur material comes from the Cenomanian Ifezouane and Aoufous formations (informally known as the Kem Kem beds) (Serenio et al. 1996; Cavin et al. 2010).

-
- 1 Setor de Paleovertebrados, Dept. Geologia e Paleontologia, Museu Nacional/UFRJ. Quinta da Boa Vista s/n, São Cristóvão, 20940-040, Rio de Janeiro, Brazil. E-mail: taissa.rodrigues@gmail.com, kellner@mn.ufrj.br
 - 2 Queensborough Community College, 222-05 56th Avenue Bayside, NY 11364, USA. E-mail: bjmader@email.msn.com
 - 3 North Carolina State University, Dept. of Marine, Earth and Atmospheric Sciences, Jordan Hall 5145, Box 8208, Raleigh, NC 27695, USA. E-mail: dale_russell@ncsu.edu

So far, these deposits have yielded isolated anhanguerid teeth (Kellner & Mader 1997; Wellnhofer & Buffetaut 1999), isolated azhdarchid vertebrae (Kellner & Mader 1996; Rodrigues et al. 2006; Ibrahim et al. 2010) and fragmentary jaws referred to the Anhangueridae, Azhdarchidae, Pteranodontidae, and Tapejaridae (Mader & Kellner 1999; Wellnhofer & Buffetaut 1999; Kellner et al. 2007; Ibrahim et al. 2010), including two described species: the anhanguerid *Siroccopteryx moroccensis* Mader & Kellner, 1999 (see Mader & Kellner 1999; Rodrigues & Kellner 2008; but see Ibrahim et al. 2010 for a different classification of this species) and the azhdarchid *Alanqa saharica* Ibrahim, Unwin, Martill, Baidder & Zouhri, 2010 (see Ibrahim et al. 2010). The pterosaur specimens, although relatively common, tend to be fragmentary due to the high energy depositional environment of both these units (Cavin et al. 2010). Here we describe four specimens that have been only briefly mentioned in the literature (Kellner & Mader 1996; Rodrigues et al. 2006), adding to the better understanding of the Moroccan pterosaur fauna.

Institutional abbreviations: BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CCMGE, Museum of Central Scientific Research Institute for Geological Exploration, University of St. Petersburg, Saint Petersburg, Russia; CMN, Canadian Museum of Nature, Ottawa, Canada; FSAC, Faculté des Sciences Ain Chock, Université Hassan II, Casablanca, Morocco; LINHM, Long Island Natural History Museum, New York City, USA; MDM, Mifune Dinosaur Museum, Mifune, Japan; MGVU, Museo del Departamento de Geología / Universidad de Valencia, Valencia, Spain; MN, Museu Nacional / Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MTM, Magyar Természettudományi Múzeum, Budapest, Hungary; NHMUK, Natural History Museum, London, England; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; and TMM, Texas Memorial Museum, Austin, USA.

Anatomical abbreviations: cap, capitulum or radial condyle of the humerus; co, cotyle; con, condyle; dpc, deltopectoral crest of the humerus; ect, ectepicondyle of the humerus; ent, entepicondyle of the humerus; fo, foramen; fopn, foramen pneumaticum; hyp, hypapophysis; mus, muscle scar; nc, neural canal; ns, neural spine; poex, postexapophysis; poz, postzygapophysis; prz, prezygapophysis; ?ri, possible vestigial cervical rib; rid, ridge; sul, sulcus; tro, trochlea or ulnar condyle of the humerus; tub, tubercle; and ulc, ulnar crest of the humerus.

Geological Settings

The so-called ‘Continental Intercalaire’ comprises extensive deltaic and brackish deposits in the Lower Cretaceous of North Africa (Kilian 1931; Lapparent 1960; Cavin et al. 2010). In Morocco, it is known informally as the Kem Kem beds (Serenio et al. 1996), whose fauna, paleoenvironment and paleogeography were recently reviewed by Cavin et al. (2010). The age of the Kem Kem beds is not easy to be established due to the lack of marine intercalations, but by the constraint of

the overlying Akrabou Formation, whose lower part contains ammonoids characteristic of the lower part of the upper Cenomanian, and by comparison to other North African faunas of the ‘Continental Intercalaire’, it has been concluded that they were deposited during the Cenomanian (Serenio et al. 1996; Cavin et al. 2010).

Cavin et al. (2010) emphasized that the Kem Kem beds actually include two formations: the Ifezouane Formation at the bottom and the Aoufous Formation at the top, as pointed out before (e.g., Ettachfini & Andreu 2004). The Ifezouane Formation is composed mostly of sandstone, while the Aoufous Formation presents marls with intercalations of sandstone and microconglomerates (Cavin et al. 2010). As most of the fossils from the Kem Kem beds were collected by commercial dealers, it is not possible to determine their provenience, both in terms of locality and lithostratigraphical unit (e.g., McGowan & Dyke 2009). Thus, the Kem Kem beds paleovertebrate fauna is, in fact, a compound assemblage, including terrestrial, freshwater and brackish vertebrates (Cavin et al. 2010).

Systematic Paleontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Dsungaripteroidea sensu Kellner 2003

Dsungaripteroidea indet.

Material: ?Lower jaw (CMN 50859)

The specimen CMN 50859 consists of the anterior fragment (preserved length is 43 mm) from an edentulous jaw, possibly a mandible (Fig. 1). It tapers anteriorly and shows the margin opposite to the occlusal surface rounded. In cross-section, the dorsal margin is concave and the lateral edges are elevated. The lateral sides are slightly convex, and a central oval lumen can also be observed. There is no median ridge or groove on the occlusal surface. Small slit-like foramina are also present on the occlusal and lateral surfaces, suggesting that this portion of the jaw was well vascularized or innervated. The ventral margin lacks any evidence of a sagittal crest or keel.

Proper identification of such a small fragment can only be made tentatively. The Dsungaripteridae, a clade which comprises pterosaurs that lack teeth on the tip of the jaws (Young 1964, 1973), can be ruled out since the cross-section is not circular in CMN 50859. Among tapejarids sensu Kellner (2003), all species of the Tapejarinae possess dentary crests (Wellnhofer & Kellner 1991; Li et al. 2003; Wang & Zhou 2003; Lü & Yuan 2005; Lü et al. 2006; Kellner & Campos 2007), a

feature absent in the preserved portion of CMN 50859. The new material also differs from the thalassodromin *Thalassodromeus sethi* Kellner & Campos, 2002 by the lack of the distinctive sharp dorsal edge (Kellner & Campos 2002).

The tips of the jaws in the tapejarid genus *Tupuxuara*, in the Pteranodontidae sensu Kellner (2003), Nyctosauridae, Chaoyangopteridae, and in most of the azhdarchids, are similar to CMN 50859 and we cannot properly assign the material to any of these. Compared with other Moroccan toothless jaws, the preserved portion of CMN 50859 shares the concave dorsal surface with BSP 1993 IX 338 (Wellnhofer & Buffetaut 1999), here regarded as a lower jaw (contra Ibrahim et al. 2010), and MN 7054-V (Kellner et al. 2007), tentatively referred to the Pteranontoidea (sensu Kellner 2003) (Wellnhofer & Buffetaut 1999; Kellner et al. 2007) or to the Azhdarchidae (BSP 1993 IX 338; Ibrahim et al. 2010). CMN 50859 lacks the low sagittal crest and has a quite distinct cross-section from the recently described azhdarchid *Alanqa saharica* (see Ibrahim et al. 2010), indicating that a second edentulous species was present in the Kem Kem beds compound assemblage. As comparisons are limited and CMN 50859 also can not be undoubtedly identified as a lower jaw, it is here referred in the Dsungaripteroidea, a clade which includes all toothless pterosaurs besides the Anhangueridae, the Istiodactylidae and the Dsungaripteridae (Kellner 2003, Wang et al. 2009; but see Unwin 2003 for a different hypothesis of pterosaur phylogeny).

Azhdarchidae Nessov, 1984

Azhdarchidae indet.

Material: Mid-cervical vertebrae (CMN 50801 and LINHM 014)

The two cervical vertebrae described here show similar basic morphology to one another. Both are elongated and clearly belong to the middle series (between cervical vertebrae 4 and 7).

CMN 50801 (Figs 2, 3) is well preserved, with no major signs of compression. The centrum is elongate (119 mm long, 18 mm minimum width) and somewhat flattened dorsoventrally. No lateral pneumatic foramina are present. Two well-defined longitudinal sulci are observed on the anterior part, at the ventrolateral surfaces. The anterior cotyle is saddle-shaped, bearing a short and blunt hypapophysis on the ventral surface. The posterior condyle is expanded, sub-oval in shape, somewhat flattened dorsoventrally, and has a shallow depression underneath. The neural spine is low and elongated anteroposteriorly, extending along the whole length of the neural arch. In anterior and pos-

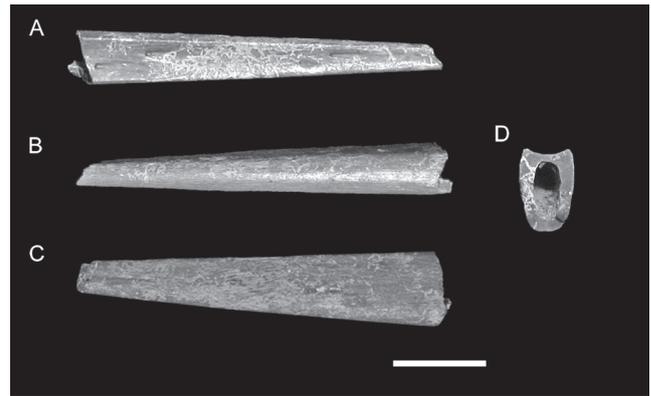


Fig. 1 - ?Mandible, CMN 50859. A) CMN 50859 in dorsal view; B) CMN 50859 in ventral view; C) CMN 50859 in left lateral view; D) CMN 50859 in proximal view. Scale bar = 10mm.

terior views, two proportionally large, oval pneumatic foramina are present lateral to the neural canal. A third pneumatic foramen is also present on the anterior side, located dorsally to the neural canal, but is absent posteriorly. The present specimen does not have the right prezygapophysis preserved. The articular facet of the left prezygapophysis is broad, dorsally flattened, and oriented anteroventrally. A small ossification is present ventral to the prezygapophysis and lateral to the centrum, which appears to be the vestige of the cervical rib (either a fused cervical rib or an apophysis for the articulation of an unfused one), including a foramen (foramen transversarium). A shallow sulcus starts at this foramen and ends at the middle part of the centrum. The postexapophyses are horn-like and slightly divergent from each other. Each bears small dorsolateral tubercles. The articular surfaces of the postzygapophyses are wide, flat and directed lateroposteriorly, somewhat inclined downwards.

The vertebra LINHM 014 (Fig. 4) is also well-preserved, with a very elongate centrum (182 mm long, 32 mm minimum width) that lacks lateral pneumatic foramina. Longitudinal, ventrolateral sulci are also clearly visible in this specimen, as is the ossification regarded as the vestige of the cervical ribs. On the anterior side, a blunt hypapophysis is present. Ventrally, there are two large, round pneumatic openings, each one located laterally to the hypapophysis. Being paired structures, they can be considered original morphological features and not artifacts derived from preparation, pathological or taphonomic processes. The neural spine is low and the condyle laterally expanded. Two large pneumatic foramina are also observed lateral to the neural canal, in both anterior and posterior views. The articular region of the left prezygapophysis is missing. A prominent foramen is present beneath each prezygapophysis and continued as a ventrolateral sulcus, as seen in CMN 50801. The postexapophyses are

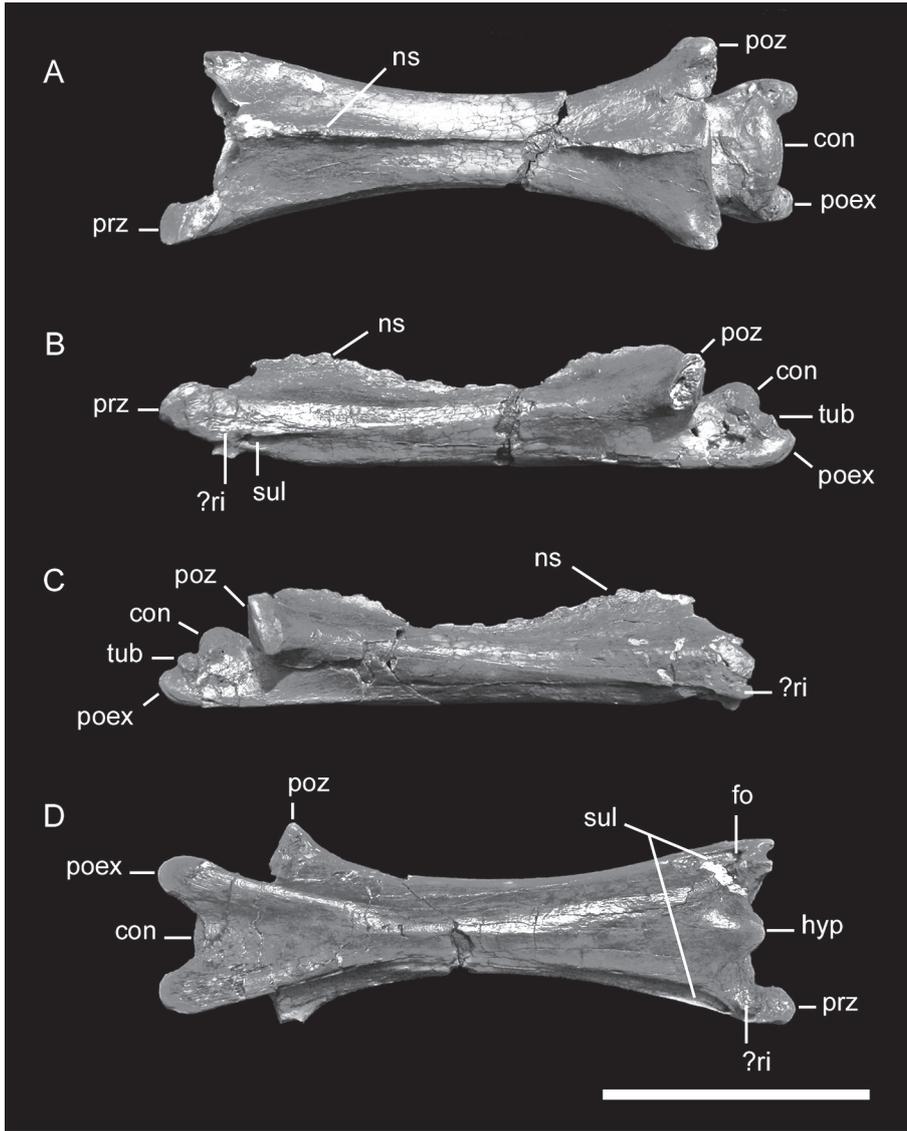


Fig. 2 - Mid-cervical vertebra, CMN 50801. A) CMN 50801 in dorsal view; B) CMN 50801 in left lateral view; C) CMN 50801 in right lateral view; D) CMN 50801 in ventral view. Abbreviations in the text. Scale bar = 50 mm.

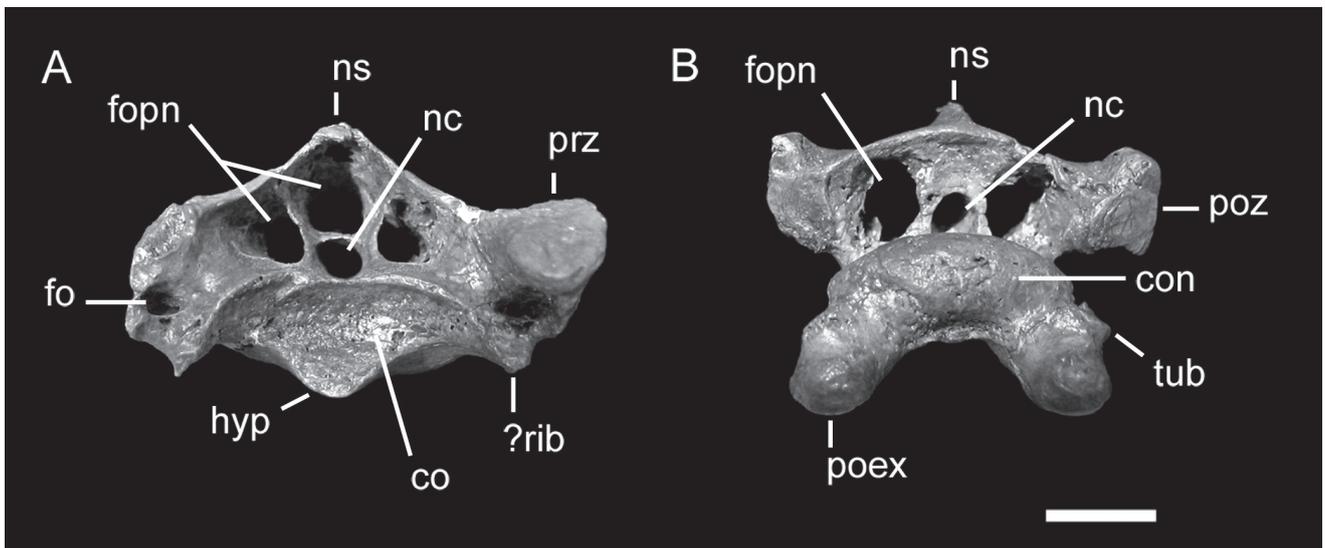
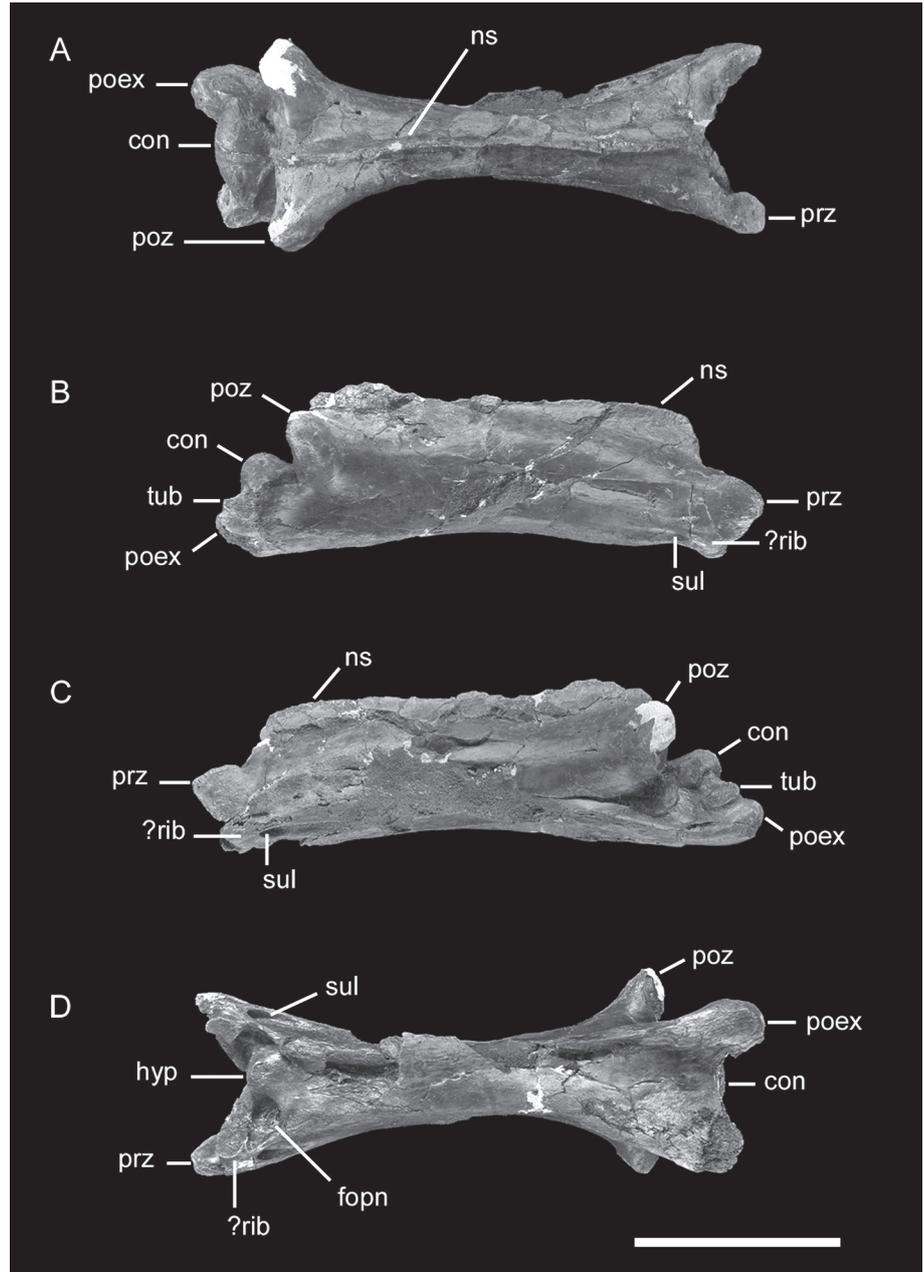


Fig. 3 - Mid-cervical vertebra, CMN 50801. A) CMN 50801 in anterior view; B) CMN 50801 in posterior view. Abbreviations in the text. Scale bar = 10 mm.

Fig. 4 - Mid-cervical vertebra, LINHM 014. A) LINHM 014 in dorsal view; B) LINHM 014 in right lateral view; C) LINHM 014 in left lateral view; D) LINHM 014 in ventral view. Abbreviations in the text. Scale bar = 50 mm.



horn-like and also bear dorsolateral tubercles.

The very elongate centrum, low neural spine, lack of lateral pneumatic foramina on the centrum, and a neural arch fully integrated into a tubular vertebral body allow the placement of both vertebrae in the Azhdarchidae (Kellner 2003, 2004; Unwin 2003; Andres & Ji 2008).

Among azhdarchids, ventrolateral sulci and canals are observed in *Azhdarcho lancicollis* Nessov, 1984 (see Nessov 1984; Averianov 2010), *Phosphatodraco mauritanicus* (see Pereda-Suberbiola et al. 2003), and some isolated specimens (Buffetaut 1999; Ósi et al. 2005; Henderson & Peterson 2006). The saddle-shaped anterior cotyle is similar to that of other azhdarchid vertebrae but differs from *Arambourgiania philadelphiae* (Arambourg, 1959), where the cotyle is as high

as, or higher than, wide (Martill et al. 1998).

A pneumatic foramen located dorsally by to the neural canal, as seen in CMN 50801, is also present in *Azhdarcho lancicollis* (including the same proportions seen in the holotype specimen, CCMGE 1/11915, Nessov 1984; Averianov 2010), but absent in *Arambourgiania philadelphiae* (see Martill et al. 1998) and other isolated azhdarchid cervical vertebrae (Company et al. 1999; Buffetaut 2001; Ósi et al. 2005; Henderson & Peterson 2006). The presence of this third pneumatic opening has been regarded as a possible generic character for *Azhdarcho* (Bennett 1989); however, it was later found to be also present in *Pteranodon* (Bennett 2001). It is also noteworthy that the pneumatic foramina present in the neural arch of *Azhdarcho lancicollis* vary in number, size and conspicuity, depending on the po-

sition of the vertebra in the neck (Nessov 1984; Averianov 2010). Detailed studies are still needed to evaluate how this feature evolved within the Pterodactyloidea and which are its systematic implications.

In anterior view, the anterior margin of the dorsal surface of CMN 50801 presents two concave areas separated by the median elevation of the neural canal, similar to the condition seen in *Azhdarcho lancicollis* (CCMGE 1/11915, Nessov 1984; Averianov 2010). At the posterior end, the dorsal surface forms a distinctive convex roof, thus differing from the Hungarian vertebra MTM Gyn/450 (Ósi et al. 2005), the Spanish vertebra MGUV 2271 (Company et al. 1999), and also from *Azhdarcho* (cast BSP 1992 I 19), all of which present two small concave areas, separated by the low neural spine. Furthermore, both Moroccan specimens do not show the ridge parallel to the neural spine observed on the right side of the neural arch of an azhdarchid vertebra from Japan (Ikegami et al. 2000).

The prezygapophyses in LINHM 014 are more divergent and shorter than in CMN 50801, the Hungarian azhdarchid vertebra MTM Gyn/448 (Ósi et al. 2005), *Arambourgiania philadelphiae*, *Quetzalcoatlus* sp. and *Azhdarcho lancicollis* (see Nessov 1984; Martill

et al. 1998, Ósi et al. 2005; Averianov 2010). In LINHM 014, the postzygapophyses are also shorter and less divergent than in the Hungarian vertebra MTM Gyn/450 (Ósi et al. 2005), and broader than in CMN 50801. However, LINHM 014 has a concave surface between the postexapophyses in ventral view, which is absent in FSAC-KK 34, another azhdarchid cervical vertebra from the Kem Kem beds of Morocco (Ibrahim et al. 2010). Furthermore, LINHM 014 has postexapophyses larger than the postzygapophyses, as also reported in other specimens (Buffetaut 1999; Company et al. 1999), and opposed to CMN 50801.

Azhdarchoidea (sensu Kellner 2003)

Azhdarchoidea indet.

Material: Humerus (CMN 50814)

CMN 50814 is a right humerus consisting of proximal and distal portions separated by a small gap. The preserved proximal part (Fig. 6) is 134 mm long and the widest preserved portion is 78 mm. The humeral head is wide (65 mm) and shows the saddle-shaped



Fig. 5 - Azhdarchidae cervical vertebrae in dorsal view. A) LINHM 014; B) CMN 50801, inverted; C) MTM Gyn/448; D) *Quetzalcoatlus* sp. (TMM 41544-16, cast NHMUK PV R 9323), inverted; E) *Azhdarcho lancicollis* (CCMGE 1/11915, cast BSP 1992 I 17), inverted; F) *Arambourgiania philadelphiae* (cast at the SMNK); G) MDM 349; H) MTM Gyn/450; I) FSAC-KK 34. Scale bars = 50 mm.

Fig. 6 - Proximal part of the right humerus, CMN 50814. A) CMN 50814 in ventral view; B) CMN 50814 in dorsal view. Abbreviations in the text. Scale bar = 50 mm.

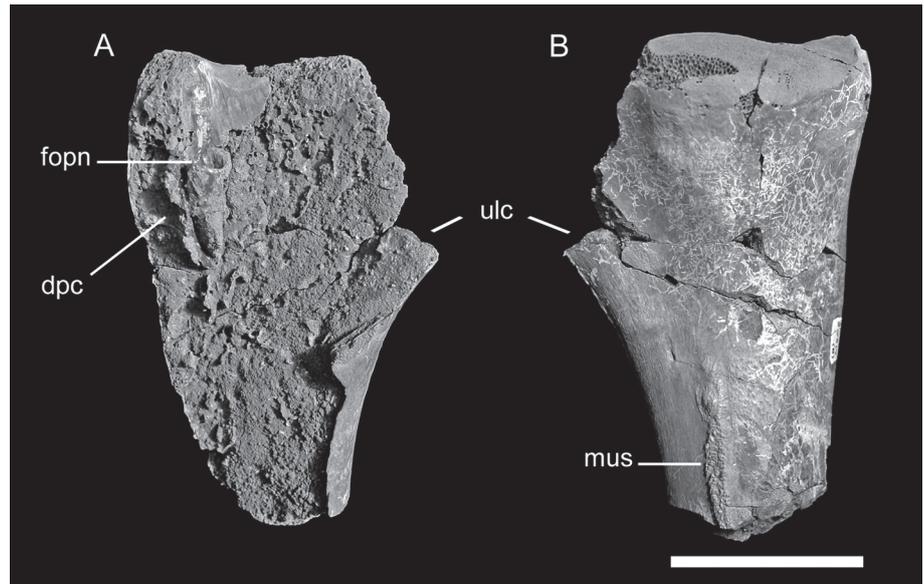
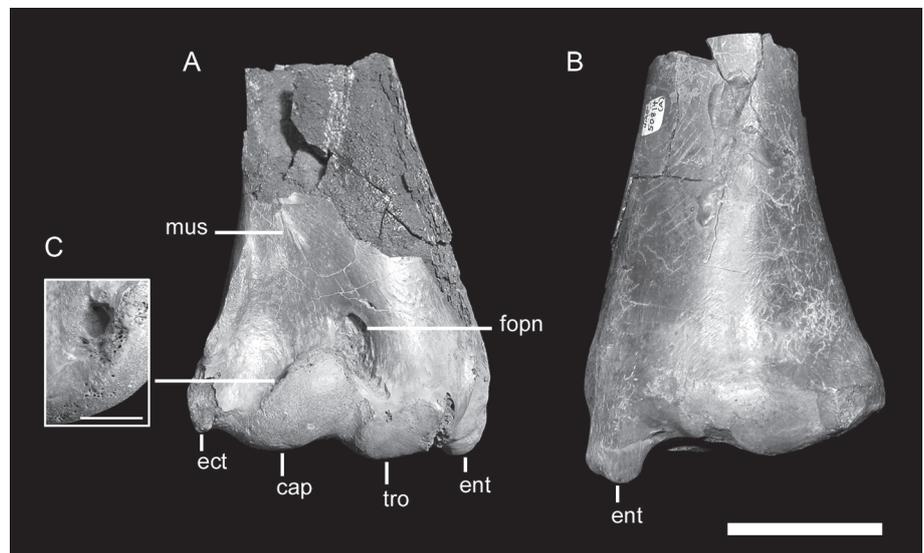


Fig. 7 - Distal part of the right humerus, CMN 50814. A) CMN 50814 in ventral view; B) CMN 50814 in dorsal view; C) inset showing the pneumatic foramen on the lateral side of the capitulum. Abbreviations in the text. Scale bar equals 50 mm in A and B, and 10 mm in C.



condition typical of pterosaurs. Breakages show a very thin cortical bone supported internally by a system of trabeculae. On the ventral surface there is a small pneumatic foramen (10.5 mm diameter) located medially at the base of the deltopectoral crest. An internal mould of this foramen is observed. Both the ulnar and deltopectoral crests are broken off. A well developed muscle scar (probably for *m. triceps*; see Bennett 2003), with a rugose surface, is observed on the dorsal surface of the shaft, close to the medial side. It starts about 80 mm from the humeral head, shortly below the level of the base of the ulnar crest, running for 44 mm until reaching the end of the preserved portion of the humerus, suggesting that it was longer.

The distal preserved portion of the humerus (Fig. 7) is 128 mm long. Ventrally, the capitulum (radial condyle) and the trochlea (ulnar condyle) are well delimited. The intertrochlear sulcus is deep and somewhat wide. There is a pneumatic opening of about 5 mm in

diameter on the lateral side of the capitulum, entering beneath it (fig. 7C). A second, larger pneumatic foramen (30 mm long and 11 mm wide; fig. 7A) and a strong muscle scar are present proximal to the capitulum. The ectepicondyle is well marked, and the entepicondyle is very robust and prominent. The distal end is complete and has a maximum width of 100 mm. In distal view, it is rectangular, with a depressed middle part.

A pneumatic foramen located on the ventral side of the proximal part of the humerus is present in *Nyctosaurus*, *Pteranodon* and the Azhdarchoidea, while a rectangular distal end in distal view is similar to the condition observed only in the Azhdarchoidea, differing from the sub-triangular shape present in the Pteranodontoidea (Bennett 2001; Kellner 2003). Thus, this specimen can be confidently referred as an azhdarchoid, although a more restricted identification to a particular taxon is not possible at the time.

Among azhdarchoids, there are some humeri ref-

erable to the Azhdarchidae preserved in three dimensions. CMN 50814 is somewhat similar in shape to *Montanazhdarcho minor* Padian, de Ricqlès & Horner, 1995 (McGowen et al. 2002), although substantially larger. The humeri of *Quetzalcoatlus* sp. (TMM 41544-9, cast MN 4715-V), *Quetzalcoatlus northropi* Lawson, 1975 (TMM 41450-3, cast MN 6952-V), *Montanazhdarcho minor* (McGowen et al. 2002), and a yet undescribed tapejarid specimen from Brazil (MN 6505-V) have a pneumatic opening beneath the capitulum. A pneumatic foramen proximal to the capitulum, as clearly observed in CMN 50814, also occurs in *Pteranodon* (Bennett 2001) and MN 6505-V. *Quetzalcoatlus* sp. has a shallow depression located on the same place, but its association with a pneumatic diverticulum is unclear, and *Quetzalcoatlus northropi* seems to lack this character. Furthermore, the distal articulation of CMN 50814 lacks the bony ridge present in *Quetzalcoatlus northropi* (Fig. 8C), *Quetzalcoatlus* sp. (Fig. 8D), and in *Azhdarcho lancicollis* (see Averianov 2010), and therefore the Moroccan specimen can not be referred to *Quetzalcoatlus* or *Azhdarcho*. The proximally located scar found in the Moroccan specimen is much stronger than in other pterodactyloid pterosaurs, including *Quetzalcoatlus northropi* and *Quetzalcoatlus* sp., where it is only slightly marked. In both *Quetzalcoatlus northropi* and *Quetzalcoatlus* sp. the entepicondyle is comparatively smaller than in CMN 50814 (Fig. 7, 8).

Discussion

Three edentulous pterosaur jaws from the Kem Kem beds were described by Wellnhofer & Buffetaut

(1999), who tentatively regarded them as one pteranodontid upper jaw (BSP 1993 IX 338), one azhdarchid upper jaw (BSP 1996 I 36) and one tapejarid lower jaw (BSP 1997 I 67). Recently, Averianov et al. (2008) considered all of them as belonging to the same azhdarchid taxon, from different parts of the jaw. As Ibrahim et al. (2010), we agree with the original description that BSP 1997 I 67 is a partial lower jaw and best referable to the Tapejaridae (Wellnhofer & Buffetaut 1999; Kellner 2004). As in all tapejarines, it has a concave dorsal surface and a deep crest (Wellnhofer & Kellner 1991; Kellner & Campos 2007). In fact, this fragment is very similar to the correspondent portion of the mandible of *Sinopterus dongi* Wang & Zhou, 2003 from the Aptian of China (Wang & Zhou 2003), although being larger.

Ibrahim et al. (2010) identified BSP 1996 I 36 as a lower jaw fragment, a view with which we agree, and referred it in a new species, *Alanqa saharica*. We agree that this mandible is diagnostic but we do not support the identification of the third jaw fragment BSP 1993 IX 338 as the upper jaw of the same taxon (Ibrahim et al. 2010), because it is based only on overall shape and size similarities. As it is shown above, the new lower jaw fragment described here (CMN 50859) has a much different cross-section with respect to the tip of the mandible of *Alanqa saharica*, suggesting the presence of another edentulous pterosaur from the Kem Kem beds compound assemblage. Therefore, we suggest that the material referred to *Alanqa saharica* should be constrained to the holotype and two other lower jaws (BSP 1996 I 36 and FSAC-KK 31), at least until more complete or associated material comes to light and confidently solves this ambiguity. Furthermore, BSP 1993 IX 338 is very low and therefore can be regarded as a

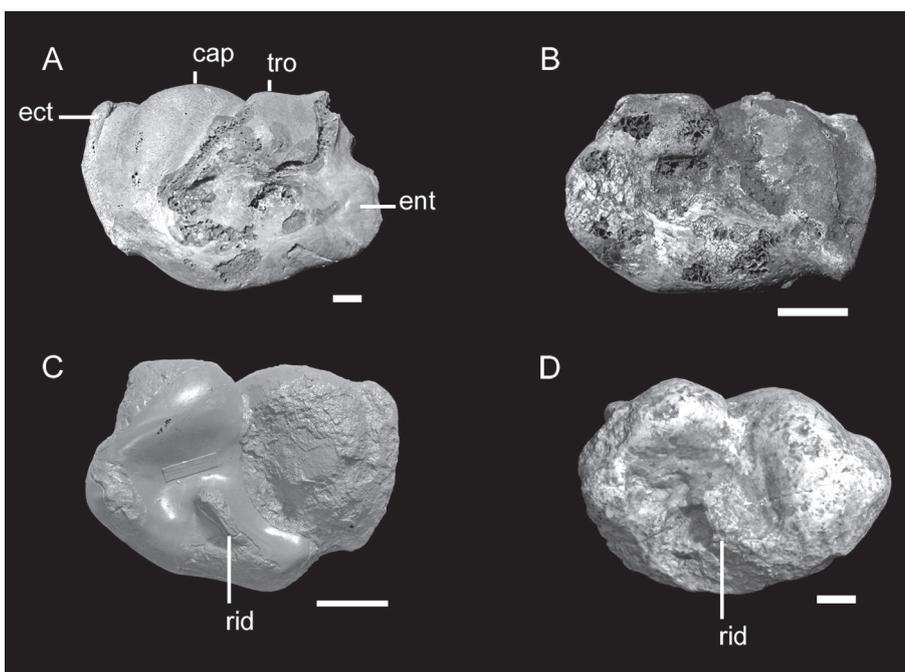


Fig. 8 - Azhdarchoidea humeri in distal view. A) CMN 50814; B) Tapejaridae (MN 6505-V); C) *Quetzalcoatlus northropi* (TMM 41450-3, cast MN 6952-V); D) *Quetzalcoatlus* sp. (TMM 41544-9, cast MN 4715-V). Abbreviations in the text. Scale bar equals 10 mm in A, B and D, 50 mm in C.

lower jaw, sharing the concave dorsal surface and lack of a sagittal crest with the lower jaw of *Pteranodon* and *Dawndraco* (e.g. Bennett 2001; Kellner 2010). For the time being, we agree with the original attribution by Wellnhofer & Buffetaut (1999) that BSP 1993 IX 338 is most probably a Pteranodontidae or closely related taxon (as also pointed out by Cavin et al. 2010).

Both vertebrae described here are referred to the Azhdarchidae. Apart from their overall resemblance, LINHM 014 is larger and comparatively less elongate than CMN 50801. Besides, the paired ventral pneumatic openings present only in LINHM 014 are unknown in any other pterosaur specimen. As both vertebrae were found in isolation, it is not possible to know if they pertained to different positions on the neck (such that the presence of these foramina would be typical of one of the cervical vertebrae but absent in others) or if these features suggest that two different azhdarchid species coexisted in this region. CMN 50801 shares an overall similar morphology with the specimen CCM-GE 1/11915, holotype of *Azhdarcho lancicollis*, which was referred as the ?fifth cervical (Bakhurina & Unwin 1995). Comparisons to the published proportions of *Phosphatodraco mauritanicus* (see Pereda-Suberbiola et al. 2003) indicate that both Moroccan vertebrae compare well with the putative sixth cervical; however, the described fifth cervical actually consists of two separate, closely articulated third and fourth cervical vertebrae (Kellner 2010). Therefore, both Moroccan vertebrae here described show proportions similar to what is actually the fifth cervical of *Phosphatodraco mauritanicus*. If these suppositions are correct, then both specimens are fifth cervicals and therefore representatives of two different azhdarchid taxa.

Both Moroccan vertebrae described here differ from the fifth cervical of *Quetzalcoatlus* sp. (TMM 41544-15, cast NHMUK PV R 9325), which is extremely elongate, demonstrating that they concern relatively small individuals when in comparison with derived azhdarchids.

The humerus CMN 50814 allows a better estimate of the wingspan of this individual. It can be estimated that at least between 35 mm and 50 mm of the shaft is missing, rendering a minimum total length of the humerus of about 300 mm. Comparisons with the estimated wingspans of *Quetzalcoatlus northropi* and *Montanazhdarcho minor* (whose holotypes possess complete humeri) rendered an estimate of ca. 5.5–6 m for this individual. Even if different growth rates in wing bones of the same individual are taken into consideration (as shown by Sayão 2003), such estimate indicates that CMN 50814 concerns a large but not gigantic pterosaur. As both distal epiphyses are well fused to the humeral shaft, CMN 50814 can be considered at least a sub-adult individual (Bennett 1993).

Conclusions

Despite the large number of pterosaurs known to date, the attribution of isolated edentulous jaws is still not well understood, as illustrated by the scarce number of characters in phylogenetic matrices that could be used in this regard (e.g., Kellner 2003; Unwin 2003; Andres & Ji 2008; Lü et al. 2009; Wang et al. 2009). Clades such as the Azhdarchoidea might comprise a relatively high morphological diversity, and more complete material is still needed to better understand this. Perhaps somewhat surprisingly, the identification of isolated postcranial material of edentulous taxa is less of a challenge. Certain features (e.g., the rectangular distal end of the humeri) provide clades good support and can be used in referrals to more inclusive clades with confidence.

Furthermore, the vertebrae here described provide a hint on azhdarchid evolution, showing a low but not vestigial neural spine, suggesting that the height of the neural spine reduced in at least some more derived and younger azhdarchid forms, such as the Maastrichtian species *Quetzalcoatlus northropi* and *Arambourgiania philadelphiae*, which also possess an extreme elongation of the cervical vertebrae (Kellner & Langston 1996; Martill et al. 1998; Henderson & Peterson 2006).

Pterosaur specimens from the Ifezouane and the Aoufous formations of Morocco, even though being incomplete and found isolated, can be extremely well preserved, as it is the case of the two cervical vertebrae here described. They comprise a rather wide range of dsungaripteroid clades, and represent so far the most diverse pterosaur fauna from Africa (Kellner et al. 2007; Ibrahim et al. 2010). Whether such a diverse fauna coexisted temporally or is an artifact of the lack of detailed stratigraphic information still remains to be accessed. In any case, the existence of such high diversity of clades shows the potential of new finds that these formations could yield.

Acknowledgments. The authors would like to thank Oliver Rauhut (Bayerische Staatssammlung für Paläontologie und Geologie), Lorna Steel (Natural History Museum) and Eberhard Frey (Staatliches Museum für Naturkunde Karlsruhe) for access to the pterosaur collections, Eric Buffetaut (CNRS, Laboratoire de Géologie de l'École Normale Supérieure) for providing information and bibliography on the Kem Kem beds, Julio Company (Universidad Politécnica de Valencia) for the articles, photos and replica sent, Attila Ósi (Hungarian Academy of Sciences) for photos of MTM Gyn/448 and MTM Gyn/450, and Naoki Ikegami (Mifune Dinosaur Museum) for the photo of MDM 349. The article was greatly improved by the many suggestions of the reviewers Fabio Dalla Vecchia (Institut Català de Paleontologia) and Kevin Padian (University of California). This study was partially funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq – grants 140407/2007-3 and 290019/2008-7 to T.R. and 307276/2009-0 to A.W.A.K.) and Fundação Carlos Chagas Filho de Amparo à Pesquisa do Rio de Janeiro (FAPERJ – grant E-26/102.779/2008 to A.W.A.K.), with support from the Deutscher Akademischer Austauschdienst (DAAD – to T.R.).

REFERENCES

- Andres B. & Ji Q. (2008) - A new pterosaur from the Liaoning province of China, the phylogeny of the Pterodactyloidea, and convergence in their cervical vertebrae. *Palaeontology*, 51: 453-469.
- Arambourg C. (1959) - *Titanopteryx philadelphiae* nov. gen., nov. sp. ptérosaurien géant. *Notes et Mém. Moyen Orient.*, 7: 229-234.
- Averianov A.O. (2010) - The osteology of *Azhdarcho lancicollis* Nessov, 1984 (Pterosauria, Azhdarchidae) from the Late Cretaceous of Uzbekistan. *Proceedings ZIN*, 314: 264-317.
- Averianov A.O., Arkhangelsky M.S. & Pervushov E.M. (2008) - A new Late Cretaceous azhdarchid (Pterosauria, Azhdarchidae) from the Volga Region. *Paleontol. J.*, 42: 634-642.
- Bakhurina N.N. & Unwin D.M. (1995) - A survey of pterosaurs from the Jurassic and Cretaceous of the Former Soviet Union and Mongolia. *Historical Biol.*, 10: 197-245.
- Bennett S.C. (1989) - A pteranodontid pterosaur from the Early Cretaceous of Peru, with comments on the relationships of Cretaceous pterosaurs. *J. Paleontol.*, 63: 669-677.
- Bennett S.C. (1993) - The ontogeny of *Pteranodon* and other pterosaurs. *Paleobiology*, 19: 92-106.
- Bennett S.C. (2001) - The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. Part I. General description and osteology. *Palaeontogr. Abt. A*, 260: 1-112.
- Bennett S.C. (2003) - Morphological evolution of the pectoral girdle of pterosaurs: myology and function. In: Buffetaut E. & Mazin J.M. (Eds) - Evolution and Palaeobiology of Pterosaurs, *Geol. Soc. London Spec. Publ.*, 217: 191-215.
- Benton M.J., Bouaziz S., Buffetaut E., Martill D.M., Ouaja M., Soussi M. & Trueman C.N. (2000) - Dinosaurs and other fossil vertebrates from fluvial deposits in the Lower Cretaceous of southern Tunisia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 157: 227-246.
- Blackbeard M. & Yates A.M. (2007) - The taphonomy of an Early Jurassic dinosaur bonebed in the northern Free State (South Africa). *J. Vert. Paleont.*, 27: 49A.
- Blackburn D. (2002) - Two Early Cretaceous pterosaurs from Africa. *J. Vert. Paleont.*, 22: 37A.
- Buffetaut E. (1999) - Pterosauria from the Upper Cretaceous of Laño (Iberian Peninsula): a preliminary comparative study. *Est. Mus. Cien. Nat. Alava*, 14: 289-294.
- Buffetaut E. (2001) - An azhdarchid pterosaur from the Upper Cretaceous of Cruzy (Hérault, France). *Cr. Acad. Sci. II A*, 333: 357-361.
- Cavin L., Tong H., Boudad L., Meister C., Piuz A., Tabouelle J., Aarab M., Amiot R., Buffetaut E., Dyke G., Hua S. & Le Loeuff J. (2010) - Vertebrate assemblages from the early Late Cretaceous of southeastern Morocco: An overview. *J. Afr. Earth Sci.*, 57: 391-412.
- Company J., Ruiz-Omeñaca J.I. & Pereda-Suberbiola X. (1999) - A long-necked pterosaur (Pterodactyloidea, Azhdarchidae) from the Upper Cretaceous of Valencia, Spain. *Geol. Mijnbouw*, 78: 319-333.
- Costa F.R. & Kellner A.W.A. (2009) - On two pterosaur humeri from the Tendaguru beds (Upper Jurassic, Tanzania). *An. Acad. Bras. Cienc.*, 81: 813-818.
- Dal Sasso C. & Pasini G. (2003) - First record of pterosaurs (Diapsida, Archosauromorpha, Pterosauria) in the Middle Jurassic of Madagascar. *Atti Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano*, 144: 281-296.
- Dalla Vecchia F.M., Arduini P. & Kellner A.W.A. (2001) - The first pterosaur from the Cenomanian (Late Cretaceous) Lagerstätten of Lebanon. *Cretaceous Res.*, 22: 219-225.
- Ettachfini E.M. & Andreu B. (2004) - Le Cénomaniien et le Turonien de la Plate-forme Préafricaine du Maroc. *Cretaceous Res.*, 25: 277-302.
- Henderson M.D. & Peterson J.E. (2006) - An azhdarchid pterosaur cervical vertebra from the Hell Creek Formation (Maastrichtian) of southeastern Montana. *J. Vert. Paleont.*, 26: 192-195.
- Ibrahim N., Unwin D.M., Martill D.M., Baidder L. & Zouhri S. (2010) - A new pterosaur (Pterodactyloidea: Azhdarchidae) from the Upper Cretaceous of Morocco. *PLoS ONE* 5(5): e10875. doi:10.1371/journal.pone.0010875.
- Ikegami N., Kellner A.W.A. & Tomida Y. (2000) - The presence of an azhdarchid pterosaur in the Cretaceous of Japan. *Paleontol. Res.*, 4: 165-170.
- Kaup J.J. (1834) - Versuch einer Eintheilung der Säugethiere in 6 Stämme und der Amphibien in 6 Ordnungen. *Isis*, 3: 311-315.
- Kellner A. W. A. (2003) - Pterosaur phylogeny and comments on the evolutionary history of the group. In: Buffetaut E. & Mazin J.M. (Eds) - Evolution and Palaeobiology of Pterosaurs, *Geol. Soc. London Spec. Publ.*, 217: 105-137.
- Kellner A.W.A. (2004) - New information on the Tapejaridae (Pterosauria, Pterodactyloidea) and discussion of the relationships of this clade. *Ameghiniana*, 41: 521-534.
- Kellner A.W.A. (2010) - Comments on the Pteranodontidae (Pterosauria, Pterodactyloidea) with the description of two new species. *An. Acad. Bras. Cienc.*, 82: 1063-1084.
- Kellner A.W.A. & Campos D.A. (2002) - The function of the cranial crest and jaws of a unique pterosaur from the Early Cretaceous of Brazil. *Science*, 297: 389-392.
- Kellner A.W.A. & Campos D.A. (2007) - Short note on the ingroup relationships of the Tapejaridae (Pterosauria, Pterodactyloidea). *Bol. Museu Nacional ser. Geologia*, 75: 1-14.
- Kellner A.W.A. & Langston Jr. W (1996) - Cranial remains of *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from Late Cretaceous sediments of Big Bend National Park, Texas. *J. Vert. Paleont.*, 16: 222-231.
- Kellner A.W.A. & Mader B.J. (1996) - First report of Ptero-

- sauria (Pterodactyloidea, Azhdarchidae) from Cretaceous rocks of Morocco. *J. Vert. Paleont.*, 16: 45A.
- Kellner A.W.A. & Mader B.J. (1997) - Archosaur teeth from the Cretaceous of Morocco. *J. Paleontol.*, 71: 525-527.
- Kellner A.W.A., Mello A.M.S. & Ford T. (2007) - A survey of pterosaurs from Africa with the description of a new specimen from Morocco. In: Carvalho I.S., Casab R.C.T., Schwanke C., Carvalho M.A., Fernandes A.C.S., Rodrigues M.A.C., Carvalho M.S.S., Arai M. & Oliveira M.E.Q. (Eds) - *Paleontologia: Cenários de Vida*. Vol. 1: 257-267, Rio de Janeiro.
- Kilian C. (1931) - Des principaux complexes continentaux du Sahara. *C. R. Soc. Géol. France*, 9: 109-111.
- Knoll F. (2000) - Pterosaurs from the Lower Cretaceous (?Berriasian) of Anoual, Morocco. *Ann. Paleontol.*, 86(3):157-164.
- Lapparent A.F. de (1960) - Les Dinosauriens du 'Continental Intercalaire' du Sahara central. *Mém. Soc. Géol. France*, n.ser. 88A: 1-57.
- Lawson D.A. (1975) - Response to Could pterosaurs fly? *Science*, 188: 676-677.
- Li J., Lü J. & Zhang B. (2003) - A new Lower Cretaceous sphenopterid pterosaur from the western Liaoning, China. *Acta Palaeontol. Sin.*, 42: 442-447.
- Lü J., Jin X., Unwin D.M., Zhao L., Azuma Y. & Ji Q. (2006) - A new species of *Huaxiapterus* (Pterosauria: Pterodactyloidea) from the Lower Cretaceous of western Liaoning, China with comments on the systematics of tapejarid pterosaurs. *Acta Geol. Sin.*, 80: 315-326.
- 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. *Proc. R. Soc. B*, doi: 10.1098/rspb.2009.1603.
- Lü J. & Yuan C. (2005) - New tapejarid pterosaur from western Liaoning, China. *Acta Geol. Sin.*, 79: 453-458.
- Mader B.J. & Kellner A.W.A. (1999) - A new anhanguerid pterosaur from the Cretaceous of Morocco. *Bol. Museu Nacional ser. Geologia*, 45: 1-11.
- Martill D.M., Frey E., Sadaqah R.M. & Khoury H.N. (1998) - Discovery of the holotype of the giant pterosaur *Titanopteryx philadelphiae* Arambourg, 1959 and the status of *Arambourgiania* and *Quetzalcoatlus*. *Neues Jahrb. Geol. Palaontol.-Abh.*, 207: 57-76.
- McGowan A.J. & Dyke G.J. (2009) - A surfeit of theropods in the Moroccan Late Cretaceous? Comparing diversity estimates from field data and fossil shops. *Geology*, 37: 843-846.
- McGowen M.R., Padian K., De Sosa M.A. & Harmon R.J. (2002) - Description of *Montanazhdarcho minor*, an azhdarchid pterosaur from the Two Medicine Formation (Campanian) of Montana. *Paleobios*, 22: 1-9.
- Monteillet J., Lappartient J.R. & Taquet P. (1982) - Un ptérosaure géant dans le Crétacé supérieur de Paki (Sénégal). *C. R. Acad. Sci. II*, 295: 409-414.
- Nesov L.A. (1984) - [Upper Cretaceous pterosaurs and birds from Central Asia] *Paleontol. Zh.*, 1: 47-57 [in Russian].
- Ntamak-Nida M.J., Ketchemen-Tandia B., Ewane R.V., Lissocck, J.P. & Courville P. (2006) - Nouvelles données sur les Mollusques et autres macro-organismes campaniens de Sikoum (Centre-Est du sous-bassin de Douala-Cameroun): intérêts bio-chronologiques et paléo-écologiques. *Afr. Geosc. Rev.*, 13: 385-394.
- Ósi A., Weishampel D.B. & Jianu C.M. (2005) - First evidence of azhdarchid pterosaurs from the Late Cretaceous of Hungary. *Acta Palaeontol. Pol.*, 50: 777-787.
- Padian K., de Ricqlès A.J. & Horner, J.R. (1995) - Bone histology determines identification of a new fossil taxon of pterosaur (Reptilia: Archosauria). *C. R. Acad. Sci. Paris*, 320: 77-84.
- Pereda-Suberbiola X., Bardet N., Jouve S., Iarochène M., Bouya B. & Amaghazaz M. (2003) - A new azhdarchid pterosaur from the Late Cretaceous phosphates of Morocco. In: Buffetaut E. & Mazin J.M. (Eds) - *Evolution and Palaeobiology of Pterosaurs*, *Geol. Soc. London Spec. Publ.*, 217: 79-90.
- Plieninger F. (1901) - Beiträge zur Kenntnis der Flugsaurier. *Paläontogr.*, 48: 65-90.
- Rodrigues T. & Kellner A.W.A. (2008) - Review of the pterodactyloid pterosaur *Coloborhynchus*. *Zitteliana B*, 28: 219-228.
- Rodrigues T. & Kellner A.W.A. (2010) - Note on the pterosaur material described by Woodward from the Recôncavo Basin, Lower Cretaceous, Brazil. *Rev. Bras. Paleontol.*, 13: 159-164.
- Rodrigues T., Kellner A.W.A., Mader B.J. & Russell D.A. (2006) - Brief report on new pterosaur (Pterosauria, Pterodactyloidea) specimens from the Cretaceous of Morocco. *J. Vert. Paleont.*, 26: 116A.
- Sayão J.M. (2003) - Histovariability in bones of two pterodactyloid pterosaurs from the Santana Formation, Araripe Basin, Brazil: preliminary results. In: Buffetaut E. & Mazin J.M. (Eds) - *Evolution and Palaeobiology of Pterosaurs*, *Geol. Soc. London Spec. Publ.*, 217: 335-342, London.
- Sereno P.C., Dutheil D.B., Iarochène M., Larsson H.C.E., Lyon G.H., Magwene P.M., Sidor C.A., Varricchio D.J. & Wilson J.A. (1996) - Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science*, 272: 986-991.
- Sigogneau-Russell D., Evans S. E., Levine J. F. & Russell D. A. (1998) - The Early Cretaceous microvertebrate locality of Anoual, Morocco: a glimpse at the small vertebrate assemblages of Africa. In: Lucas S.G., Kirkland J.I. & Estep J.W. (Eds) - *Lower and middle Cretaceous terrestrial ecosystems*, *New Mexico Mus. Nat. Hist. Sci. Bull.*, 14: 177-181.
- Swinton W.E. (1948) - A Cretaceous pterosaur from the Belgian Congo. *Bull. Soc. Belge Geol. Paléont. Hydr. Liège*, 77: 234-238.
- Unwin D. M. (2003) - On the phylogeny and evolutionary history of pterosaurs. In: Buffetaut E. & Mazin J.M. (Eds) - *Evolution and Palaeobiology of Pterosaurs*, *Geol. Soc. London Spec. Publ.*, 217: 139-190.
- Unwin D.M. & Heinrich W-D. (1999) - On a pterosaur jaw from the Upper Jurassic of Tendaguru (Tanzania). *Mitt. Mus. Nat. Berl., Geowiss. Reihe*, 2: 121-134.
- Wang X., Kellner A.W.A., Jiang S. & Meng X. (2009) - An

- unusual long-tailed pterosaur with elongated neck from western Liaoning. *An. Acad. Bras. Cienc.*, 81: 793-812.
- Wang X. & Zhou Z. (2003) - A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy. *Chin. Sci. Bull.*, 48: 16-23.
- Wellnhofer P. & Buffetaut E. (1999) - Pterosaur remains from the Cretaceous of Morocco. *Palaontol. Z.*, 73: 133-142.
- Wellnhofer P. & Kellner A.W.A. (1991) - The skull of *Tapejara wellnhoferi* Kellner (Reptilia, Pterosauria) from the Lower Cretaceous Santana Formation of the Araripe Basin, northeastern Brazil. *Mitt. Bayer. Staatss. Paläon. hist. Geol.*, 31: 89-106.
- Young C.C. (1964) - On a new pterosaurian from Sinkiang, China. *Vertebrata Palasiatica*, 8: 221-225.
- Young C.C. (1973) - [Pterosaurian fauna from Wuerho, Sinkiang II. In: Reports of Paleontological Expeditions to Sinkiang II.] *Inst. Vertebr. Paleontol. Paleoanthropol. Acad. Sin. Memoirs*, 11: 18-35. [in Chinese].