A new and unusual edentulous pterosaur from the middle Cretaceous Kem Kem beds of North Africa

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ABSTRACT

A new genus and species is erected for a highly distinctive pterosaur mandible from the middle Cretaceous Kem Kem Formation of south-east Morocco. The new taxon is referred to Azhdarchoidea based on the absence of teeth, slenderness of its mandible with sulcate occlusal surface, and the presence of elongate foramina on lateral surfaces and the occlusal surface. A slight dorsal curvature determines it as a distinct genus of azhdarchoid, as does an autapomorphy: the presence of a continuous groove on the ventral margin of the mandibular symphysis. The new specimen brings to three the number of named pterosaurs from the Kem Kem beds and suggests high diversity of pterosaurs near the middle of the Cretaceous.

Key words: Pterosauria, Azhdarchoidea, Cretaceous, Kem Kem beds, Morocco.

1. Introduction.

Pterosaurs are a relatively rare component of the vertebrate assemblage of the Cretaceous Kem Kem beds of south-eastern Morocco with most remains occurring as isolated, and usually broken skeletal elements often extracted as a by-product of commercial excavations for dinosaur teeth. Presently two pterosaur taxa have been named, the ornithocheirid \textit{Coloborhynchus (= Sirocopteryx) moroccensis} (Mader and Kellner, 1999) and the azhdarchid \textit{Alanga saharica} Ibrahim et al., 2010. Both are based on portions of jaws, which seem to be taphonomically selected for in the Kem Kem beds. Other pterosaur remains are documented from the Kem Kem sequence, but are rarely diagnostic. Nevertheless, an isolated
occurrence of an unnamed tapejarid (Wellnhofer and Buffetaut, 1999) suggests a more
diverse assemblage. A claim for pteranodontians (Wellnhofer and Buffetaut, 1999) was based
on an isolated jaw that has all the characteristics of an azhdarchid rostral tip (Ibrahim et al.
2010). Reviews of the Kem Kem pterosaur assemblage can be found in Wellnhofer and
The Kem Kem sequence is noted for its highly diverse vertebrate assemblage (Ibrahim et al.,
2014, Cavin et al. 2016) which contains a surprisingly high number of apex predators,
including the giant theropods *Spinosaurus* Stromer, 1915 and *Carcharodontosaurus* Stromer,
1931 and the large *Deltadromeus* Sereno et al., 1996, the carcharodontosaur *Sauroniops* (Cau
et al. 2013), a large abelisaurid (Chiarenza and Cau, 2016) and at least two small abelisaurids
(D’Orazi Porchetti et al., 2011; Richter et al., 2013). The only herbivorous dinosaurs so far
reported are rare remains of sauropods (Lamanna et al., 2014; Ibrahim et al. 2016). In
addition there are multiple crocodylomorph genera including a diverse fauna of terrestrial
notosochians (Sereno and Larsson 2009) and with at least one giant, the pholidosaur
*Elosuchus* de Broin, 2002, estimated to have reached a length of around 10 m (NI pers. obs.).
Other tetrapods include amphibians (Rage and Dutheil, 2008), diverse turtles (Gaffney et al.,
2002, Gaffney et al., 2006), snakes (Rage and Dutheil, 2008; Klein et al., 2017) and rare birds
(Riff et al. 2004).

1.1 Abbreviations used

The specimen described here is accessioned to the collection of the Département de Géologie
(Paléontologie), Faculté des Sciences Aïn Chock (FSAC), Université Hassan II – Casablanca,
Km 8, route de l’université 20100, Casablanca, Morocco, prefixed FSAC-KK. Other
abbreviations used are: AMNH, American Museum of Natural History, New York; GIN,
Institute of Geology, Mongolian Academy of Sciences, Ulan Bataar, Mongolia; GMN,
Geological Museum, Nanjing, China; IMCF, Iwaki Museum of Coal Mining and Fossils,
Yumoto, Japan; RCPS, Research Center of Palaeontology and Stratigraphy of Jilin
University, Changchun, Jilin Province, China; SMNK; Staatliches Museum für Naturkunde
Karlsruhe, Germany; UALVP, University of Alberta Laboratory for Vertebrate
Palaeontology, University of Alberta, Edmonton, Alberta, Canada.

2. Context
The specimen described here, FSAC-KK 17000 was discovered by local workers in mines at
the small mesa of Aferdou N’Chaft, near the oasis village of Hassi el Begaa, Er Rachidia
Province, eastern Morocco (Fig. 1). At this locality a ~50 m to ~ 90 m thick sequence of mid-
Cretaceous age is represented by a series of fluvial, cross bedded sandstones with thin
mudstones and intraformational conglomerates of mudstone rip-up clasts (Fig. 2). These
strata rest with angular unconformity on marine Palaeozoic sediments and are overlain with a
disconformity by Cenomanian marine limestones of the basal Akrabou Formation. Vertebrate
remains occur frequently in the conglomerates and in general are well preserved, but
fragmentary. Details of the stratigraphy, localities and fossil content of the Kem Kem
sequence can be found in Sereno et al. (1996); Sereno and Lasson (2009), Cavin et al., (2010)
and Ibrahim et al. (2014) and references therein.

3. Description

3.1 Systematic palaeontology

PTEROSAURIA Kaup, 1834
MONOFENESTRATA Lü et al., 2009
PTERODACTYLOIDEA Pleininger, 1901
AZHDARCHOIDEA Nessov, 1984
NEOAZHDARCHIA Unwin, 2003
XERICEPS gen. nov.

Derivation of generic name: A combination of Xero Gr. = dry, pertaining to the Sahara
Desert where the specimen was found, and cep from Capere L., to catch, alluding to the
forceps-like beak.

Diagnosis: See for type and only species below.

Xericeps curvirostris gen et sp. nov.

Derivation of specific name: Curvi, L., pertaining to the curvature of the mandible, rostris,
L., supposing the entire rostrum is curved.
Holotype: FSAC-KK 17000, University of Casablanca, Ain Chock, Casablanca, Morocco.

Type locality. Aferdou N’Ch ‘aft, near Hassi el Begaa, Er Rachidia Province, south-east Morocco, coordinates: 30˚ 53’ 56.63” N 3˚ 50’ 45.80” W (Fig. 1).

Type Horizon and age: Kem Kem beds, Albian to ?Cenomanian, mid Cretaceous (Fig. 2).

Diagnosis: Pterodactyloid pterosaur of medium to large size. Lower jaw is upcurved, with occluding surface curved in lateral view. Ventral margin lacking keel, with continuous sulcus (autapomorphy) and ridges (formed by the lateral margins of splenials?) projecting slightly above dentary margin, but not extending as far as jaw tip. Deep sulcus of occluding surface anterior of mandibular symphysis shallowing anteriorly into jaw tip. Thickening of lateral margins of dentary anteriorly. Lateral surface of lower jaw tip distinctly convex (Figs 3,4,5).

3.2 Anatomy

Specimen FSAC-KK 17000 is a partial dentary symphysis missing its anteriormost tip and extends posteriorly to a point that probably lies just slightly anterior of where the mandibular rami would have diverged (presumably broken at a weak point). The break for the missing anterior end is clean and sharp, suggesting that it was present (see Table 1 for measurements). Posteriorly the break is less clean, but some material may be missing due to the somewhat ‘rough and ready’ collecting techniques employed at Begaa. It is largely uncrushed, but there are some slight fractures with minimal displacement laterally, but not dorso-ventrally. A lightly cemented medium to coarse sandstone matrix has been removed from the specimen such that it is now completely free of matrix. The bone is a light reddish brown, which is typical for vertebrate fossils from Begaa. The bone surface is smooth to the naked eye, but is slightly fibrous under the hand lens.

The specimen has a total length of 173 mm, and an estimated length to the missing tip (assuming a point) of ~200 mm (Table 1). In lateral view both the occlusal and ventral surfaces are gently concave giving the lower jaw a gentle upwardly curving sweep. This is slightly more pronounced on the ventral margin. These margins diverge at approximately 8 degrees, reducing gently posteriorly. In occlusal view the margins diverge posteriorly at 5 degrees and this angle remains constant for the length of the fragment. There are five small, elongate foramina in the ventral-most third on the right lateral margin, and five on the left lateral margin. These foramina are almost paired between the sides, but there are slight
offsets. The lateral margins have their maximum cross section at a point approximately 2/5ths from the dorsal surface, thus each margin tapers very slightly to the dorsal margin and rather more to the ventral margin. The ventral margin is slightly flattened and has a continuous groove extending from the anterior break to the posterior break. The margins of the groove are rounded and confluent with the lateral margins of the mandible. This groove shallows toward the tip, but is still detectable at the point of breakage. Anteriorly the occlusal surface is gently-shaped, but this deepens to a steep sided U-shape posteriorly at a point where two parallel ridges rise from the occlusal surface and project above the dorsal margin of the dentary. Possibly these are the splenials, but no suture is seen. These ridges continue posteriorly as far as the broken posterior margin. There are several sub-paired elongate foramina, the same as those on the lateral margins on the occlusal surface. At the broken posterior end the walls of the dentary are thin (~0.75 mm – 1.00 mm) at the occluding surface, but thicker on the lateral margins (1.2 mm – 1.5 mm). At the anterior break, estimated at 27 mm posterior to the apex, the bone margins are thicker, reaching ~ 2 mm on the more dorsal part of the lateral margin and about 1 mm thick on the occluding surface. At the fractured posterior end the internal structure of the dentary appears to comprise a series of well-spaced trabeculae lying subparallel to the occlusal surface with small cross-bridges.

4. Discussion

4.1 Comparisons.

Three main aspects of edentulous pterosaur mandible tips are here compared: the degree of curvature of the mandible seen in lateral aspect, the rate of divergence of the lateral margins posteriorly seen in dorsoventral view and the rate of divergence of the dorsal and ventral margins seen in lateral view (Fig. 3). In addition, observations are noted on the presence or absence of foramina, and sulci and ridges on the mandibular shelf. These comparisons are made with the pteranodontian *Pteranodon* Marsh, 1876, the nyctosaur *Nyctosaurus*, Marsh, 1876; the azdarchids *Alanqa* Ibrahim, Unwin, Martill, Zouhri and Baiddar, 2010, *Azhdarcho Nessov*, 1984, *Quetzalcoatlus* Lawson, 1975, *Zhejiangopterus* Cai and Feng, 1994 and *Bakonydraco* Ösi, Weishampel and Jianu, 2005; the tapejarids *Sinopterus* Wang and Zhou, 2003, *Tapejara* Kellner, 1989 and *Tupandactylus* Kellner and Campos, 2007; the thalassodromeids *Tupuxuara* Kellner and Campos, 1988, and *Thalassodromeus* Kellner and Campos, 2002; and the chaoyangopterids *Chaoyangopterus* Wang and Zhou, 2003, *Eoazhdarcho* Lü and Ji, 2005 *Jidapterus* Dong, Sun and Wu, 2003 and *Shenzhoupterus* Lü et al., 2008.
4.1.1 Pointed toothless jaws.

There are a number of similarities between the new specimen and the mandible of *Pteranodon*. Both are slender and taper to a sharp point (the sharp point is hypothesised for *Xericeps* on account of only a few mm appear missing and there is no suggestion of rounding toward the tip). Unfortunately few examples of *Pteranodon* are documented preserved in 3D, and so aspects of the width, depth ratio, or the morphology of the occluding surface cannot be determined. However, Bennett (2001, fig. 3) describes a fragmentary specimen that shows the occlusal surface preserved. It shows a symphysial shelf bordered by the mandibular lateral margins that is slightly squared off rather than the smooth U-shaped sulcus seen in FSAC-KK 17000. The cross-section shape of the *Pteranodon* mandible is an inverted triangle with slightly rounded ventral apex. *Pteranodon* does not appear to possess the narrow, elongate foramina seen on the surface of *Xericeps*.

In *Nyctosaurus* spp. the mandible is also gently tapered in both lateral and dorsoventral views, and the taper is extremely gentle resulting in a very sharp point. Bennett (2003, figs. 1, 2) figures a crested example from a private collection that appears to have a shallow depression in the dorsal surface of the mandible at the tip, giving it a somewhat spoon-like aspect. However, this is such a subtle shape change that it cannot be ruled out that it is an artefact of compression as, like *Pteranodon*, most examples have suffered from compression, resulting in significant damage. Nevertheless, there are examples that allow some attempt at restoration. Williston (1903) figures a partial mandible with some of the symphysis that shows the occlusal and ventral surfaces, although the tip is wanting. In this example the occlusal surface is seen to lie below the lateral margins of the mandible, while the ventral surface appears to be smoothly rounded, with no sulcus present.

The mandible of the holotype of the chaoyangopterid *Eoazhdarcho liaoxiensis* Lü and Ji, 2005 (GMN-03-11-002) is displayed dorsoventrally on a slab of matrix and is crushed flat, exposing its occlusal surface. Thus, it cannot be determined if the jaw of *Eoazhdarcho* is straight in lateral aspect, or slightly curved as in *Xericeps*. However, the posterior divergence of the mandible’s lateral margins is considerably greater than that seen in *Xericeps*. In the holotype of *Jidapterus edentus* Lü and Ji, 2006 (RCPS CDA 01) the mandible is preserved in occlusal view, and thus the degree of curvature of its mandible also cannot be assessed. Other chaoyangopterids do display the mandible in lateral aspect. In *Chaoyangopterus zhangi* Wang and Zhou, 2003 the mandible appears to have a gently curved ventral margin to the lower jaw (Zhou, 2010), but an almost straight margin to the dorsal (occlusal) margin (a
7
gentle curvature that seems to produce a gape with the corresponding margin of the rostrum
might be an artefact of compaction), and the case is similar in Shenzhoupterus chaoyangensis
(Lü et al., 2008). Thus Xericeps differs from most chaoyangopterids in this respect.
In Thalassodromidae the mandibles are elongate, straight and gently tapered, usually with a
ventral keel of varying degrees of prominence, which does not extend far posteriorly, fading
out at around the start of the mandibular symphysis. This is the case for Tupuxuara. The tip
of the mandible also bears a keeled dorsal surface, which is not seen in the new Kem Kem
taxon.

In tapejarids the mandible is highly distinctive, being characterised by a downturned tip.
The downturn is particularly prominent in the South American forms Tapejara and
Tupandactylus, but is less well developed in the Chinese Sinopterus and Huaxiapterus Lü et
al., 2006 (Fig. 6). In some tapejarids there is a conspicuously developed rise in the mandible
margin on the dorsal surface seen in lateral view just posterior to the downturn (e.g. Tapejara
wellnhoferi Kellner 1989 [Eck et al. 2011]) (Fig. 6D), a feature not seen in any other
pterosaur clade. Tapejaridae also exhibit a distinct ventral keel, which is elaborated into a
ventral crest, a feature also not seen in the new taxon.

4.1.2. Upswept jaws.
Pterosaurs with upswept mandibles are encountered in several clades within the
Pterodactyloidea (Fig. 7, Table 2). In tooth-bearing forms such upwardly curving mandibles
are seen in the dsungaripterid Dsungaripterus Young, 1964 where even juveniles have an
upwardly curved mandible (Bakhurina and Unwin, 1995; Unwin and Bakhurina, 2000) and in
the ctenochasmatids Pterodaustro Bonaparte, 1970 and Ctenochasma Meyer, 1852, although
in the latter the jaws are only very gently upswept. In edentulous pterosaurs upwardly curved
mandibles are found in Pteranodon and Nyctosaurus (Bennett, 1994, 2003).

4.1.3. Other aspects of the pterosaurian mandible. A presumably significant difference
between the jaws tips of the new specimen and Pteranodon is in the thickness of the bone. In
Pteranodon the lateral margins of the jaw tip are extremely thin, (width of bone wall ~ 0.25
mm) compared with ~1.25 mm for Xericeps curvirostris.

4.1.4. Affinities. Although the fragmentary nature of the material complicates comparisons, a
number of characters are present that allow us to constrain its placement with respect to other
pterosaurs.
**Edentulous jaws.** The loss of teeth is a derived character that evolves two or three times in the Pterosauria: in the Azhdarchoidea, and either in a clade consisting of Pteranodontidae + Nyctosauridae, or independently in Pteranodontidae and Nyctosauridae, depending on which phylogeny one assumes. The absence of teeth implies affinities with one of these major lineages.

*Slit-like foramina in the symphyseal region of the lower jaw.* Slit-like foramina in the occlusal surface of the symphysis are a derived feature seen in azhdarchoids but not in pteranodontoids. However, they do not appear to be autapomorphic for the clade, unless they have been secondarily lost in some forms. They are present in some tapjearids having been reported for *Aymberedactylus* (probably = *Tupandactylus* Kellner and Campos 2007) where they are seen on the occlusal surface of the mandibular symphysis (Pegas et al. 2016) and in *Caiuajara* (Manzig et al. 2014) where they are densely distributed in two zones on the occlusal surface of the mandible.

### 4.2 Implications

The presence of a continuous groove on the ventral margin of the mandible of *Xericeps* appears to be a feature not seen elsewhere in the Pterosauria, and marks it as a distinct taxon. This autapomorphy, in combination with the distinctive curvature of the mandible, clearly shows that it should indeed be referred to a new genus. The presence of a smooth U-shaped occlusal surface and a series of sub-paired elongate foramina on the lateral and occlusal margins allies *Xericeps* with Azhdarchoidea. Elongate paired foramina in these locations are seen in the azhdarchids *Bakonydraco galaczi* Ösi, Weishampel and Jianu, 2005, *Alanqa saharica* and *Volgadraco bogulobovia* Averianov, Arkhangelsky and Pervushov, 2008, however, the curvature of the jaw is not seen in those Azhdarchidae for which the lower jaws are known: *Bakonydrako galaczi*, *Quetzalcoatlus* sp., *Alanqa saharica*, *Zhejiangopterus linhaiensis* Cai and Feng, 1994 and *Ahzdarcho lancicollis*. While the foramina are seen in some Azhdarchidae, they do not seem to be present in *Quetzalcoatlus* or *Zhejiangopterus* (DMU personal obs.) and are thus likely not diagnostic for the clade. We are satisfied that *Xericeps curvirostris* can be placed within Azhdarchoidea on account of the overall jaw shape and the presence of the lateral and occlusal foramina, but its incomplete nature prevents it from being placed with in a family.

### 5. Conclusions
Xericeps curvirsotris gen. et sp. nov. represents a new taxon of pterosaur that can be diagnosed and distinguished from the co-occurring Alanga saharica by the curved mandibular symphysis, distinct dorsal groove, convex lateral surface of the jaw, and ventral sulcus. The toothless jaws and slit-like foramina suggest affinities with Azhdarchoidea. The new pterosaur adds to the diversity of the Kem-Kem pterosaur assemblage, underscoring the high diversity of mid-Cretaceous pterosaurs, and the high diversity of the fauna of the Kem Kem beds.

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References


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Text figure captions

Fig. 1. Locality map showing the outcrop of the Kem Kem beds in the southern Tafilalt of south east Morocco and the locality of Aferdou N’Chaft, site of the new pterosaur.

Fig. 2. Simplified stratigraphic sequence for the Aferdou N’Chaft Kem Kem beds. Measurements are approximate, and vary over the region, sometimes considerably. At this locality the upper sequence of mudstones is particularly reduced due to an unconformable relationship between the Kem Kem beds and the limestones of the overlying Akrabou Formation.

Figure 3. Partial mandible of new azhdarchoid pterosaur *Xericeps curvirostris* gen. et sp. nov. FSAC-KK 17000, ammonium chloride coated. Mandible in A, left lateral, B, occlusal, C, right lateral and D, ventral views. Scale bar = 50 mm.

Figure 4. Measurements recorded from *Xericeps curvirostris* gen. et sp. nov.

Figure 5. Partial mandible of new azhdarchoid pterosaur *Xericeps curvirostris* gen. et sp. nov. FSAC-KK 17000, without coating. A, left lateral; B, occlusal; C, right lateral; D, ventral; E, proximal end, F, distal end views. Scale bars 10 mm.


Figure 7. Schematic diagrams of edentulous pterosaur mandible tip outlines in left lateral aspect. A, straight occlusal and ventral margins; B, straight occlusal and ventral margins, but with occlusal margin descending anteriorly; C, straight occlusal margin with convex ventral margin; D, concave occlusal margin with convex ventral margin; E, convex occlusal and
ventral margins; F, convex occlusal margin and concave ventral margin; G, concave occlusal
and ventral margin; H, straight occlusal margin and concave ventral margin. See also Table 2.

1. Detail of foramina

Table 1. Selected measurements for *Xericeps curvirostris* gen et sp. nov.

<table>
<thead>
<tr>
<th>Dimension</th>
<th>Value (mm)</th>
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<tbody>
<tr>
<td>Max. height posteriorly (A)</td>
<td>26</td>
</tr>
<tr>
<td>Height (B) at 4 × A</td>
<td>18</td>
</tr>
<tr>
<td>Max. height anteriorly</td>
<td>12</td>
</tr>
<tr>
<td>Rostral dorso-ventral taper B/A × 100</td>
<td>69.23%</td>
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<td>(Martin-Sylverston et al. 2017)</td>
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<tr>
<td>Max. width posteriorly (C)</td>
<td>16</td>
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<tr>
<td>Max. width anteriorly</td>
<td>8</td>
</tr>
<tr>
<td>Width (D) at 4 × C</td>
<td>12</td>
</tr>
<tr>
<td>Rostral lateral taper D/C × 100</td>
<td>75%</td>
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