

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

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11 ABSTRACT

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

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

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22

23 1. **Introduction.**

24

25 Pterosaurs are a relatively rare component of the vertebrate assemblage of the Cretaceous
26 Kem Kem beds of south-eastern Morocco with most remains occurring as isolated, and
27 usually broken skeletal elements often extracted as a by-product of commercial excavations
28 for dinosaur teeth. Presently two pterosaur taxa have been named, the ornithocheirid
29 *Coloborhynchus* (= *Siroccoptyx*) *moroccensis* (Mader and Kellner, 1999) and the
30 azhdarchid *Alanqa saharica* Ibrahim et al., 2010. Both are based on portions of jaws, which
31 seem to be taphonomically selected for in the Kem Kem beds. Other pterosaur remains are
32 documented from the Kem Kem sequence, but are rarely diagnostic. Nevertheless, an isolated

33 occurrence of an unnamed tapejarid (Wellnhofer and Buffetaut, 1999) suggests a more
34 diverse assemblage. A claim for pteranodontians (Wellnhofer and Buffetaut, 1999) was based
35 on an isolated jaw that has all the characteristics of an azhdarchid rostral tip (Ibrahim et al.
36 2010). Reviews of the Kem Kem pterosaur assemblage can be found in Wellnhofer and
37 Buffetaut 1999; Ibrahim et al., 2010; Rodrigues et al.; 2011 Martill and Ibrahim 2015).
38 The Kem Kem sequence is noted for its highly diverse vertebrate assemblage (Ibrahim et al.,
39 2014, Cavin et al. 2016) which contains a surprisingly high number of apex predators,
40 including the giant theropods *Spinosaurus* Stromer, 1915 and *Carcharadontosaurus* Stromer,
41 1931 and the large *Deltadromeus* Sereno et al., 1996, the carcharodontosaur *Sauroniops* (Cau
42 et al. 2013), a large abelisaurid (Chiarenza and Cau, 2016) and at least two small abelisaurids
43 (D’Orazi Porchetti et al., 2011; Richter et al., 2013). The only herbivorous dinosaurs so far
44 reported are rare remains of sauropods (Lamanna et al., 2014; Ibrahim et al. 2016). In
45 addition there are multiple crocodylomorph genera including a diverse fauna of terrestrial
46 notosochians (Sereno and Larsson 2009) and with at least one giant, the pholidosaur
47 *Elosuchus* de Broin, 2002, estimated to have reached a length of around 10 m (NI pers. obs.).
48 Other tetrapods include amphibians (Rage and Dutheil, 2008), diverse turtles (Gaffney et al.,
49 2002, Gaffney et al., 2006), snakes (Rage and Dutheil, 2008; Klein et al., 2017) and rare birds
50 (Riff et al. 2004).

51

52 *1.1 Abbreviations used*

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

63

64 **2. Context**

65

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

77

78 **3. Description**

79

80 *3.1 Systematic palaeontology*

81

82 PTEROSAURIA Kaup, 1834

83 MONOFENESTRATA Lü et al., 2009

84 PTERODACTYLOIDEA Pleininger, 1901

85 AZHDARCHOIDEA Nesso, 1984

86 NEOAZHDARCHIA Unwin, 2003

87 *XERICEPS* gen. nov.

88

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

92

93 *Diagnosis:* See for type and only species below.

94

95 *Xericeps curvirostris* gen et sp. nov.

96

97 *Derivation of specific name:* *Curvi*, L., pertaining to the curvature of the mandible, *rostris*,
 98 L., supposing the entire rostrum is curved.

99

100 *Holotype*: FSAC-KK 17000, University of Casablanca, Ain Chock, Casablanca, Morocco.

101

102 Type locality. Aferdou N'Ch 'aft, near Hassi el Begaa, Er Rachidia Province, south-east
103 Morocco, coordinates: 30° 53' 56.63" N 3° 50' 45.80" W (Fig. 1).

104

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

106

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

113

114 3.2 *Anatomy*

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

126 The specimen has a total length of 173 mm, and an estimated length to the missing tip
127 (assuming a point) of ~200 mm (Table 1). In lateral view both the occlusal and ventral
128 surfaces are gently concave giving the lower jaw a gentle upwardly curving sweep. This is
129 slightly more pronounced on the ventral margin. These margins diverge at approximately 8
130 degrees, reducing gently posteriorly. In occlusal view the margins diverge posteriorly at 5
131 degrees and this angle remains constant for the length of the fragment. There are five small,
132 elongate foramina in the ventral-most third on the right lateral margin, and five on the left
133 lateral margin. These foramina are almost paired between the sides, but there are slight

134 offsets. The lateral margins have their maximum cross section at a point approximately
 135 2/5ths from the dorsal surface, thus each margin tapers very slightly to the dorsal margin and
 136 rather more to the ventral margin. The ventral margin is slightly flattened and has a
 137 continuous groove extending from the anterior break to the posterior break. The margins of
 138 the groove are rounded and confluent with the lateral margins of the mandible. This groove
 139 shallows toward the tip, but is still detectable at the point of breakage. Anteriorly the occlusal
 140 surface is gently ~ shaped, but this deepens to a steep sided U-shape posteriorly at a point
 141 where two parallel ridges rise from the occlusal surface and project above the dorsal margin
 142 of the dentary. Possibly these are the splenials, but no suture is seen. These ridges continue
 143 posteriorly as far as the broken posterior margin. There are several sub-paired elongate
 144 foramina, the same as those on the lateral margins on the occlusal surface. At the broken
 145 posterior end the walls of the dentary are thin (~0.75 mm – 1.00 mm) at the occluding
 146 surface, but thicker on the lateral margins (1.2 mm – 1.5 mm). At the anterior break,
 147 estimated at 27 mm posterior to the apex, the bone margins are thicker, reaching ~ 2 mm on
 148 the more dorsal part of the lateral margin and about 1 mm thick on the occluding surface. At
 149 the fractured posterior end the internal structure of the dentary appears to comprise a series of
 150 well-spaced trabeculae lying sub parallel to the occlusal surface with small cross-bridges.

151

152 4. Discussion

153 4.1 Comparisons.

154 Three main aspects of edentulous pterosaur mandible tips are here compared: the degree of
 155 curvature of the mandible seen in lateral aspect, the rate of divergence of the lateral margins
 156 posteriorly seen in dorsoventral view and the rate of divergence of the dorsal and ventral
 157 margins seen in lateral view (Fig. 3). In addition, observations are noted on the presence or
 158 absence of foramina, and sulci and ridges on the mandibular shelf. These comparisons are
 159 made with the pteranodontian *Pteranodon* Marsh, 1876, the nyctosaur *Nyctosaurus*, Marsh,
 160 1876; the azdarchids *Alanqa* Ibrahim, Unwin, Martill, Zouhri and Baidder 2010, *Azhdarcho*
 161 Nessonov, 1984, *Quetzalcoatlus* Lawson, 1975, *Zhejiangopterus* Cai and Feng, 1994 and
 162 *Bakonydraco* Ósi, Weishampel and Jianu, 2005; the tapejarids *Sinopterus* Wang and Zhou,
 163 2003, *Tapejara* Kellner, 1989 and *Tupandactylus* Kellner and Campos, 2007; the
 164 thalassodromeids *Tupuxuara* Kellner and Campos, 1988, and *Thalassodromeus* Kellner and
 165 Campos, 2002; and the chaoyangopterids *Chaoyangopterus* Wang and Zhou, 2003,
 166 *Eoazhdarcho* Lü and Ji, 2005 *Jidapterus* Dong, Sun and Wu, 2003 and *Shenzhoupterus* Lü et
 167 al., 2008.

168

169 4.1.1 *Pointed toothless jaws.*

170 There are a number of similarities between the new specimen and the mandible of
171 *Pteranodon*. Both are slender and taper to a sharp point (the sharp point is hypothesised for
172 *Xericeps* on account of only a few mm appear missing and there is no suggestion of rounding
173 toward the tip). Unfortunately few examples of *Pteranodon* are documented preserved in 3D,
174 and so aspects of the width, depth ratio, or the morphology of the occluding surface cannot be
175 determined. However, Bennett (2001, fig. 3) describes a fragmentary specimen that shows the
176 occlusal surface preserved. It shows a symphyseal shelf bordered by the mandibular lateral
177 margins that is slightly squared off rather than the smooth U-shaped sulcus seen in FSAC-KK
178 17000. The cross-section shape of the *Pteranodon* mandible is an inverted triangle with
179 slightly rounded ventral apex. *Pteranodon* does not appear to possess the narrow, elongate
180 foramina seen on the surface of *Xericeps*.

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

192 The mandible of the holotype of the chaoyangopterid *Eoazhdarcho liaoxiensis* Lü and Ji,
193 2005 (GMN-03-11-002) is displayed dorsoventrally on a slab of matrix and is crushed flat,
194 exposing its occlusal surface. Thus, it cannot be determined if the jaw of *Eoazhdarcho* is
195 straight in lateral aspect, or slightly curved as in *Xericeps*. However, the posterior divergence
196 of the mandible's lateral margins is considerably greater than that seen in *Xericeps*. In the
197 holotype of *Jidapterus edentus* Lü and Ji, 2006 (RCPS CDA 01) the mandible is preserved in
198 occlusal view, and thus the degree of curvature of its mandible also cannot be assessed. Other
199 chaoyangopterids do display the mandible in lateral aspect. In *Chaoyangopterus zhangii*
200 Wang and Zhou, 2003 the mandible appears to have a gently curved ventral margin to the
201 lower jaw (Zhou, 2010), but an almost straight margin to the dorsal (occlusal) margin (a

202 gentle curvature that seems to produce a gape with the corresponding margin of the rostrum
 203 might be an artefact of compaction), and the case is similar in *Shenzhoupterus chaoyangensis*
 204 (Lü et al., 2008). Thus *Xericeps* differs from most chaoyangopterids in this respect.

205 In Thalassodromidae the mandibles are elongate, straight and gently tapered, usually with a
 206 ventral keel of varying degrees of prominence, which does not extend far posteriorly, fading
 207 out at around the start of the mandibular symphysis. This is the case for *Tupuxuara*. The tip
 208 of the mandible also bears a keeled dorsal surface, which is not seen in the new Kem Kem
 209 taxon.

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

218

219 4.1.2. Upswept jaws.

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

227 4.1.3. Other aspects of the pterosaurian mandible. A presumably significant difference
 228 between the jaws tips of the new specimen and *Pteranodon* is in the thickness of the bone. In
 229 *Pteranodon* the lateral margins of the jaw tip are extremely thin, (width of bone wall ~ 0.25
 230 mm) compared with ~1.25 mm for *Xericeps curvirostris*.

231

232 4.1.4. Affinities. Although the fragmentary nature of the material complicates comparisons, a
 233 number of characters are present that allow us to constrain its placement with respect to other
 234 pterosaurs.

235

236 *Edentulous jaws*. The loss of teeth is a derived character that evolves two or three times in the
 237 Pterosauria: in the Azhdarchoidea, and either in a clade consisting of Pteranodontidae +
 238 Nyctosauridae, or independently in Pteranodontidae and Nyctosauridae, depending on which
 239 phylogeny one assumes. The absence of teeth implies affinities with one of these major
 240 lineages.

241

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

250

251 4.2 Implications

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

268

269 5. Conclusions

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

277

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286

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288

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438 **Text figure captions**

439

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

442

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

448

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

452

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

454

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

458

459 Figure 6. A selection of pterosaur mandibles showing a variety of morphologies when seen in
 460 lateral view. A, *Alanqa saharica*, Ibrahim et al., 2010, holotype specimen (FSAC-KK 26); B,
 461 *Noripterus complicidens* Young, 1973 (GIN 125/1010); C, *Xericeps curvirostris* gen. et sp.
 462 nov., (FSAC-KK 17000); D, *Tapejara wellnhoferi* Kellner, 1989 (SMNK PAL 1137); E,
 463 *Pteranodon* sp. (NHMUK R 4078); F, *Tupuxuara leonardi* (IMCF 1052); G,
 464 *Chaoyuopterus zhangii* Wang and Zhou, 2003 (IVPP V 13397). A, After Ibrahim et al.
 465 2010; D, after Eck et al. 2011.

466

467 Figure 7. Schematic diagrams of edentulous pterosaur mandible tip outlines in left lateral
 468 aspect. A, straight occlusal and ventral margins; B, straight occlusal and ventral margins, but
 469 with occlusal margin descending anteriorly; C, straight occlusal margin with convex ventral
 470 margin; D, concave occlusal margin with convex ventral margin; E, convex occlusal and

471 ventral margins; F, convex occlusal margin and concave ventral margin; G, concave occlusal
 472 and ventral margin; H, straight occlusal margin and concave ventral margin. See also Table 2.

473

474 1. Detail of foramina

475

476

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

478

Dimension	Value (mm)
Max. height posteriorly (A)	26
Height (B) at $4 \times A$	18
Max. height anteriorly	12
Rostral dorso-ventral taper $B/A \times 100$ (Martin-Silverston et al. 2017)	69.23%
Max. width posteriorly (C)	16
Max. width anteriorly	8
Width (D) at $4 \times C$	12
Rostral lateral taper $D/C \times 100$	75%

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480

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