

1 A new edentulous pterosaur from the Cretaceous Kem Kem  
2 beds of south eastern Morocco

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11 ABSTRACT

12 A new genus and species is erected for a highly distinctive pterosaur mandible from the

13 Cretaceous Kem Kem beds 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, presence on the posterior section of the mandibular symphysis of short

16 paired ridges bounding a central groove, and the presence of elongate foramina on its

17 occlusal and lateral surfaces. A slight dorsal curvature determines it as a distinct genus of

18 azhdarchoid, as does an autapomorphy: the presence of a continuous longitudinal groove on

19 the ventral midline of the mandibular symphysis. The new species brings to three the number

20 of named pterosaurs from the Kem Kem beds and together with an unnamed tapejarid, points

21 to a relatively diverse pterosaur assemblage in these deposits.

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

23

24

25 1. **Introduction.**

26

27 Pterosaurs, Mesozoic flying reptiles, have a fossil record that is profoundly biased in several  
28 ways (Dean *et al.*, 2016). The vast majority of finds have been made in Europe, North  
29 America and Asia (essentially Laurasia throughout much of the Mesozoic) and South  
30 America, while the record from the remaining continents (Africa, Australia, Antarctica) is  
31 very poor, but slightly better in Africa than elsewhere (e.g. Barrett *et al.*, 2008). Until  
32 recently, the African record consisted almost entirely of isolated finds of teeth or fragments  
33 of vertebrae and limb bones, the one exception being the Upper Jurassic Tendaguru  
34 assemblage from Tanzania, consisting of >100 finds, although these too are isolated and  
35 fragmentary (Reck, 1931; Unwin and Heinrich, 1999; Costa *et al.*, 2015). During the last two  
36 decades a substantial, and growing, number of pterosaurs remains have been collected from  
37 the Cretaceous Kem Kem beds of south-eastern Morocco (Wellnhofer and Buffetaut, 1999;  
38 Ibrahim *et al.*, 2010; Rodrigues *et al.*; 2011 Martill and Ibrahim 2015) and this assemblage is  
39 rapidly becoming the single most informative source as regards the diversity and evolution of  
40 African pterosaurs.

41 Most remains from the Kem Kem beds occur as isolated, and usually broken skeletal  
42 elements often extracted as a by-product of commercial excavations for dinosaur teeth.

43 Presently, two pterosaur taxa have been named, the ornithocheirid *Coloborhynchus* (=   
44 *Siroccopteryx*) *moroccensis* (Mader and Kellner, 1999) and the azhdarchid *Alanqa saharica*  
45 Ibrahim *et al.*, 2010. Both are based on portions of jaws, which seem to be taphonomically  
46 selected for in the Kem Kem beds. Other pterosaur remains are documented from the Kem  
47 Kem sequence, but are rarely diagnostic. Nevertheless, an isolated occurrence of an unnamed  
48 tapejarid (Wellnhofer and Buffetaut, 1999) suggests a more diverse assemblage. A claim for  
49 pteranodontians (Wellnhofer and Buffetaut, 1999) was based on an isolated jaw that is more

50 likely an azhdarchoid rostral tip (Ibrahim et al. 2010). Here we describe a new genus and  
51 species of pterosaur that further emphasises the taxonomic, morphological and presumably  
52 ecological diversity of the Kem Kem beds assemblage.

53

#### 54 *1.1 Abbreviations used*

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

66

## 67 **2. Context**

68

69 The specimen described here, FSAC-KK 10700 was discovered by local workers in mines at  
70 the small mesa of Aferdou N'Chaft, near the oasis village of Hassi el Begaa, Er Rachidia  
71 Province, south eastern Morocco (Fig. 1). It was purchased by one of the authors (DMM,  
72 January 2017) at the mine site, and thus its precise stratigraphic horizon and locality can be  
73 confidently established. At this locality a ~50 m to ~90 m thick sequence of mid-Cretaceous  
74 age is represented by a series of fluvial, cross-bedded sandstones with thin mudstones and

75 intraformational conglomerates of mudstone rip-up clasts (Fig. 2). These strata rest with  
76 angular unconformity on marine Palaeozoic sediments and are overlain with a disconformity  
77 by Cenomanian marine limestones of the basal Akrabou Formation. Vertebrate remains occur  
78 frequently in the conglomerates and in general are well preserved, but fragmentary. Details of  
79 the stratigraphy, localities and fossil content of the Kem Kem beds sequence can be found in  
80 Lavocat (1954b); Sereno et al. (1996); Sereno and Larsson (2009), Cavin et al., (2010) and  
81 Ibrahim et al. (2014a,b) and references therein. The Kem Kem beds represent mostly fluvial  
82 ecosystems dominated by fine sands in its lower sections, fining upwards into interdigitating  
83 deltaic, estuarine and playa lake deposits in its upper sections.

84

85 The Kem Kem sequence is noted for its highly diverse vertebrate assemblage (Ibrahim et al.,  
86 2014, Cavin et al. 2016) which contains a surprisingly high number of large-bodied predators,  
87 including the giant theropods *Spinosaurus* Stromer, 1915 (Ibrahim et al. 2014) and  
88 *Carcharodontosaurus* Stromer, 1931 (Sereno et al. 1996) and the large *Deltadromeus* Sereno  
89 et al., 1996, the possibly distinct carcharodontosaur *Sauroniops* (Cau et al. 2013), a large  
90 abelisaurid (Russell 1996; Mahler 2005; Chiarenza and Cau 2016) and possibly two small  
91 abelisaurids (D’Orazi Porchetti et al. 2011; Richter et al., 2013). The only herbivorous  
92 dinosaurs so far reported are rare remains of sauropods (Lamanna et al. 2014; Ibrahim et al.  
93 2016), with *Rebbachisaurus garasbae* being the only named taxon (Lavocat, 1954a). In  
94 addition there are multiple crocodylomorph genera, including a diverse fauna of terrestrial  
95 notosochians (Sereno and Larsson 2009) and at least one giant, the pholidosaur *Elosuchus* de  
96 Broin, 2002, estimated to have reached a length of around 10 m (NI pers. obs.). Other  
97 tetrapods include amphibians (Rage and Dutheil, 2008), diverse turtles (Gaffney et al., 2002,  
98 Gaffney et al., 2006), snakes (Rage and Dutheil, 2008; Klein et al., 2017) and, possibly, rare  
99 birds (Riff et al. 2004).

100

101 **3. Description**

102

103 *3.1 Systematic palaeontology*

104

105 PTEROSAURIA Kaup, 1834

106 MONOFENESTRATA Lü et al., 2009

107 PTERODACTYLOIDEA Pleininger, 1901

108 AZHDARCHOIDEA Nessoov, 1984

109 NEOAZHDARCHIA Unwin, 2003

110 *XERICEPS* gen. nov.

111

112 *Derivation of generic name:* A combination of *Xero* Gr. = dry, pertaining to the Sahara113 Desert where the specimen was found, and *cep* from *Capere* L., to catch, alluding to the

114 forceps-like beak.

115

116 *Diagnosis:* As for type and only species below.

117

118 *Xericeps curvirostris* gen et sp. nov.

119

120 *Derivation of specific name:* *Curvi*, L., pertaining to the curvature of the mandible, *rostris*,

121 L., supposing the entire rostrum is curved.

122

123 *Holotype:* FSAC-KK 10700, University of Casablanca, Ain Chock, Casablanca, Morocco.

124

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

127

128 *Type Horizon and age:* Kem Kem beds, ?Albian to Lower Cenomanian, mid Cretaceous (Fig.  
129 2).

130

131 *Diagnosis:* Pterodactyloid pterosaur of medium to large size (that is with a wingspan  
132 somewhere between ~ 3 m to ~ 8 m: it is likely nearer the lower end of this range). Lower  
133 jaw is upcurved, with occluding surface curved in lateral view. Ventral margin lacking keel,  
134 but with continuous longitudinal midline sulcus (autapomorphy) a pair of ridges, probably  
135 formed by the lateral margins of the dentary and confined to the posterior portion of the  
136 mandibular symphysis, that project slightly dorsal to the dentary margin, thereby defining a  
137 broad midline groove. Deep sulcus of occluding surface anterior of mandibular symphysis  
138 shallowing anteriorly into jaw tip. Thickening of lateral cortical margins of dentary  
139 anteriorly. Lateral surface of lower jaw tip distinctly convex (Figs 3,4,5).

140

### 141 3.2 *Anatomy*

142 Specimen FSAC-KK 10700 is a partial dentary symphysis that lacks its anteriormost tip and  
143 extends posteriorly to a point that probably lies just slightly anterior of where the mandibular  
144 rami would have diverged (we suggest this as the lateral margins of the ventral groove very  
145 slightly begin to diverge posteriorly. Presumably the mandible broke at a weak point). The  
146 break for the missing anterior end is clean and sharp, suggesting that it was present when first  
147 discovered (see Table 1 for measurements). Posteriorly the break is less clean. The specimen  
148 is largely uncrushed, but there are some slight fractures with minimal displacement laterally,  
149 but not dorsoventrally. A lightly cemented medium to coarse sandstone matrix has been

150 removed from the specimen such that it is now completely free of matrix. The bone is a light  
151 reddish brown, which is typical for vertebrate fossils from Aferdou N'Chaft. The bone  
152 surface is smooth to the naked eye suggesting that the individual was osteologically mature  
153 (or nearly so) at time of death, but is slightly fibrous under the hand lens.

154 The specimen has a total length of 173 mm and (based on extension of the jaw margins as  
155 currently preserved and assuming the symphysis culminated in a point) an estimated length to  
156 the missing tip (assuming a point) of ~200 mm (Table 1). In lateral view the occlusal profile  
157 is slightly concave while the ventral profile is slightly convex giving the lower jaw a gentle  
158 upwardly curving sweep. The curvature of the ventral profile is slightly more pronounced.  
159 The dorsal and ventral margins diverge at approximately 8 degrees from the tip, this angle  
160 declining slightly posteriorly. In occlusal view the lateral margins diverge posteriorly at 5  
161 degrees and this angle remains constant for the length of the fragment. There are five small,  
162 elongate foramina in the ventral-most third of the right lateral surface, and five on the left  
163 lateral surface. These foramina are almost paired between the sides, but there are slight  
164 offsets. The lateral margins achieve their maximum transverse breadth at a point  
165 approximately two fifths below the dorsal surface, consequently each margin tapers very  
166 slightly to the dorsal margin and rather more to the ventral margin. The ventral margin is  
167 slightly flattened and has a continuous longitudinal midline groove extending from the  
168 anterior break to the posterior break. The margins of the groove are rounded and confluent  
169 with the lateral margins of the mandible. This groove shallows toward the tip, but is still  
170 detectable at the point of breakage.

171 Anteriorly the occlusal surface is gently concave, but this deepens to a steep sided U-shape  
172 posteriorly at a point where two parallel ridges rise from the occlusal surface and project  
173 above the dorsal margin of the dentary. Possibly these are the splenials, but they are fused  
174 with the mandible and no suture is seen, so perhaps they are outgrowths of the mandible.

175 These ridges, which define a broad midline groove, continue posteriorly as far as the broken  
176 posterior margin. There are several paired, elongate oval foramina, identical to those on the  
177 lateral margins on the occlusal surface.

178 The cross sectional outline of the symphysis posteriorly is a high oval that tapers slightly  
179 ventrally, with a slightly flattened ventral margin gently excavated by the ventral sulcus, and  
180 a larger depression dorsally formed by the deep sulcate occlusal surface. The lateral margins  
181 are moderately inflated (Fig.5).

182 The bone walls of the dentary, exposed in the posterior break are thin (~0.75 mm – 1.00  
183 mm) in the occluding surface, but thicker on the lateral margins (1.2 mm – 1.5 mm). At the  
184 anterior break, estimated at 27 mm posterior to the anterior tip of the mandible, the bone  
185 margins are thicker, reaching ~2 mm on the more dorsal part of the lateral margin and about 1  
186 mm thick on the occluding surface. The posterior break reveals the internal structure of the  
187 dentary, which appears to comprise a series of well-spaced trabeculae orientated sub-parallel  
188 to the occlusal surface and supported by small cross-struts.

189

#### 190 **4. Comparisons**

191 Three key aspects of edentulous pterosaur mandible tips are critical for establishing the  
192 distinctness of the new taxon and its systematic affinities: 1) the degree of curvature of the  
193 mandible seen in lateral aspect; 2) the rate of divergence of the lateral margins posteriorly as  
194 seen in dorsoventral view; and 3) the rate of divergence of the dorsal and ventral margins  
195 seen in lateral view (Fig. 4). The presence or absence of foramina, sulci and ridges on the  
196 mandibular shelf and details of their anatomy provide important additional insights into the  
197 systematics of *Xericeps*. Comparisons are made with a representative range of edentulous  
198 pterodactyloids including the pteranodontid *Pteranodon* Marsh, 1876, the nyctosaurs  
199 *Nyctosaurus*, Marsh, 1876, and *Muzquizopteryx* Frey et al. 2006; the azhdarchids *Alanqa*

200 Ibrahim, Unwin, Martill, Zouhri and Baidder 2010, *Azhdarcho* Nessov, 1984, *Quetzalcoatlus*  
201 Lawson, 1975, *Zhejiangopterus* Cai and Feng, 1994 and *Bakonydraco* Ösi, Weishampel and  
202 Jianu, 2005; the tapejarids *Sinopterus* Wang and Zhou, 2003, *Tapejara* Kellner, 1989 and  
203 *Tupandactylus* Kellner and Campos, 2007; the thalassodromeids *Tupuxuara* Kellner and  
204 Campos, 1988, and *Thalassodromeus* Kellner and Campos, 2002; and the chaoyangopterids  
205 *Chaoyangopterus* Wang and Zhou, 2003, *Eoazhdarcho* Lü and Ji, 2005, *Jidapterus* Dong,  
206 Sun and Wu, 2003 and *Shenzhoupterus* Lü et al., 2008.

207

#### 208 4.1.1. *Pointed toothless jaws*

209 There are a number of similarities between the new specimen and the mandible of  
210 *Pteranodon*. Both are slender and taper to a sharp point (the sharp point is hypothesised for  
211 *Xericeps* in that only a few mm appear to be missing and there is no suggestion of rounding  
212 toward the tip). Unfortunately, few examples of *Pteranodon* preserved in 3D have been  
213 documented, and so aspects of the width, depth ratio, or the morphology of the occluding  
214 surface cannot be determined with accuracy. However, Bennett (2001, fig. 3) describes a  
215 fragmentary specimen that exhibits the occlusal surface. This demonstrates a symphyseal  
216 shelf bordered by the mandibular lateral margins that is more rectangular rather than the  
217 smooth U-shaped sulcus seen in FSAC-KK 10700. The cross-sectional shape of the  
218 *Pteranodon* mandible is an inverted triangle with slightly rounded ventral apex, whereas the  
219 cross section of *Xericeps* is a moderately inflated oval. *Pteranodon* lacks the narrow, elongate  
220 oval foramina seen on the surface of the mandibular symphysis of *Xericeps*.

221 In *Nyctosaurus* spp. the mandible is also gently tapered in both lateral and dorsoventral  
222 views, and the taper is extremely gentle resulting in a highly attenuated jaw tip. Bennett  
223 (2003, figs. 1, 2) figures a crested example from a private collection that appears to have a  
224 shallow depression in the dorsal surface of the mandible at the tip, giving it a somewhat

225 spoon-like aspect. However, this is such a subtle shape change that it cannot be ruled out that  
226 it is an artefact of compression. As specimens of *Pteranodon* demonstrate, most examples of  
227 pterosaurs from the Niobrara Chalk have suffered from compression, resulting in significant  
228 distortion. Nevertheless, there are examples of *Nyctosaurus* that allow some attempt at  
229 restoration. Williston (1903) figured a partial mandible with some of the symphysis that  
230 shows the occlusal and ventral surfaces, although the tip is missing. In this example the  
231 occlusal surface is recessed below the lateral margins of the mandible, while the ventral  
232 surface appears to be smoothly rounded, with no sulcus present.

233 The mandible of the holotype of the chaoyangopterid *Eoazhdarcho liaoxiensis* Lü and Ji,  
234 2005 (GMN-03-11-002) is displayed dorsoventrally on a slab of matrix and is crushed flat,  
235 exposing its occlusal surface. Thus, it cannot be determined if the jaw of *Eoazhdarcho* is  
236 straight in lateral aspect, or slightly curved as in *Xericeps*. However, the posterior divergence  
237 of the mandible's lateral margins is considerably greater than that seen in *Xericeps*. In the  
238 holotype of *Jidapterus edentus* Lü and Ji, 2006 (RCPS CDA 01) the mandible is preserved in  
239 an oblique ventrolateral view. Consequently, the degree of curvature of the mandible is  
240 difficult to determine, but it appears to have been straight rather than curved. Moreover, the  
241 ventral margin of the symphysis seems to have borne a low keel rather than a sulcus as in  
242 *Xericeps*. Apart from these details it is notable, however, that in its general shape the  
243 mandibular symphysis of *Jidapterus* is closely comparable to that of *Xericeps*.

244 The mandible is preserved in lateral aspect in *Chaoyangopterus* and *Shenzhoupterus*. In  
245 *Chaoyangopterus zhangii* Wang and Zhou, 2003 the mandible appears to have a gently  
246 convex ventral profile (Zhou, 2010), and an almost straight profile for the dorsal (occlusal)  
247 margin. A gentle curvature of the occlusal margin that seems to result in a gape with the  
248 corresponding margin of the rostrum in *Chaoyangopterus* might be an artefact of compaction,

249 and the same seems to apply to *Shenzhoupterus chaoyangensis* (Lü et al., 2008). Thus the  
250 *Xericeps* mandible differs from most chaoyangopterids in respect of its lateral outline.

251 In Thalassodromidae the mandibles are elongate, straight and gently tapered, usually with  
252 a ventral keel of varying degrees of prominence, which does not extend far posteriorly, fading  
253 out at the posterior termination of the mandibular symphysis, as is the case for *Tupuxuara*  
254 (Witton, 2009). The tip of the mandible also bears a keeled dorsal surface, which is not seen  
255 in the new Kem Kem taxon.

256 In tapejarids the mandible is highly distinctive and characterised by a ventrally deflected  
257 tip. The deflection is particularly prominent in *Tapejara* and *Tupandactylus* from South  
258 America, but is less well developed in the *Sinopterus* and *Huaxiapterus* from China (Lü et al.,  
259 2006; Fig. 6). In some tapejarids there is a conspicuously developed elevation in the mandible  
260 margin on the dorsal surface evident in lateral view just posterior to the ventral deflection  
261 (e.g. *Tapejara wellnhoferi* Kellner, 1989 [Eck et al., 2011]) (Fig. 6D), a feature not seen in  
262 any other pterosaur clade. Tapejarids also exhibit a distinct ventral keel, which is elaborated  
263 into a ventral crest, a feature also not seen in the new taxon.

264

265 4.1.2 *Upswept jaws*. Pterosaurs with upswept mandibles are encountered in several clades  
266 within the Pterodactyloidea (Fig. 7, Table 2). In tooth-bearing forms upwardly curving  
267 mandibles are present in the dsungaripterid *Dsungaripterus* Young, 1964 where even small  
268 osteologically immature individuals have an upwardly curved mandible (Bakhurina and  
269 Unwin, 1995; Unwin and Bakhurina, 2000). An upwardly curved mandible is also present in  
270 the ctenochasmatids *Pterodaustro* Bonaparte, 1970 and *Ctenochasma* Meyer, 1852, although  
271 in the latter the jaws are only very gently upswept. In edentulous pterosaurs upwardly curved  
272 mandibles are found in *Pteranodon* and *Nyctosaurus* (Bennett, 1994, 2003).

273 Kellner et al. (2005) figure a Kem Kem beds specimen (MN 7054-V) identifying it as a  
274 pteranodontid mandible. However, it shares with azhdarchids the presence of small, elongate  
275 foramina on the lateral margins and occluding surface and, like *Xericeps* it appears to exhibit  
276 a gentle upward flexure. However, the rapid expansion of the ‘ventral’ margin of this bone  
277 relative to the occluding surface suggest that this specimen represents an anterior portion of a  
278 rostrum rather than a dentary. Were the rostrum MN 7054-V matched to the dentary of  
279 *Xericeps*, a gape would be present when the jaws were closed.

280

281 4.1.3. *Other aspects of the pterosaurian mandible.* A potentially significant difference  
282 between the mandible of the new specimen and that of *Pteranodon* is in the thickness of the  
283 bone. In *Pteranodon* the lateral margins of the mandible are extremely thin, (width of bone  
284 wall ~ 0.25 mm) compared with ~1.25 mm for *Xericeps curvirostris*.

285

286 4.2. *Affinities.* Although the fragmentary nature of the material complicates comparisons, a  
287 number of characters are present that allow us to constrain its placement with respect to other  
288 pterosaurs.

289

290 4.2.1. *Edentulous jaws.* The loss of teeth is a derived character that appears to have evolved  
291 on a minimum of at least two occasions within the Pterodactyloidea: in the Azhdarchoidea  
292 and in the Pteranodontia (Unwin 2003, Lü et al. 2009, Ibrahim et al. 2010). Alternative  
293 phylogenies (e.g. Bennett 1994) admit at least three (in Azhdarchoidea and separately in  
294 Pteranodontidae and Nyctosauridae) and potentially (e.g. Andres et al. 2014) up to five  
295 independent origins of this condition (separately in Pteranodontidae, Nyctosauridae,  
296 Tapejaridae, Thalassodromidae and Chaoyangopteridae+Azhdarchidae). The apparent

297 absence of teeth in *Xericeps* implies affinities with either pteranodontians, or one of the  
298 azhdarchoid clades.

299

300 4.2.2. *Elongate foramina in the symphyseal portion of the lower jaw.* Slit-like foramina in the  
301 occlusal surface of the symphysis is a derived feature seen in azhdarchoids, but not in  
302 pteranodontoids. However, they do not appear to be synapomorphic for Azhdarchoidea,  
303 unless they have been secondarily lost in some forms. They are present in some tapjearids  
304 having been reported for *Aymberedactylus* (probably = *Tupandactylus* Kellner and Campos  
305 2007) where they are seen on the occlusal surface of the mandibular symphysis (Pegas et al.  
306 2016) and in *Caiuajara* (Manzig et al. 2014) where they are densely distributed in two zones  
307 on the occlusal surface of the mandible.

308

309 4.3 *Comparable jaw remains from the Kem Kem*

310 Two jaw fragments assigned to *Alanqa saharica* (Martill and Ibrahim 2015 figs 3-5),  
311 identified here as mandibular symphyses, are comparable to that of *Xericeps*, but their paired  
312 ridges are larger and more prominent. In *Xericeps* two bony ridges rise from the dorsal sulcus  
313 of the mandible extending posteriorly closely parallel to the occluding margins. These two  
314 ridges differ from those of *Alanqa* in that they are thinner, do not meet in the midline of the  
315 mandible, protrude only slightly above the jawline and do not extend beyond the lateral  
316 margins of the mandible.

317

318 4.4 *Implications*

319 The presence of a continuous groove on the ventral margin of the mandible of *Xericeps* has  
320 not been reported or figured elsewhere in the Pterosauria, and thus appears to distinguish this  
321 taxon. This autapomorphy, in combination with the distinctive curvature of the mandible, is

322 sufficient to justify the establishment of a new genus. The presence of a smooth U-shaped  
323 occlusal surface and a series of sub-paired elongate foramina on the lateral and occlusal  
324 surfaces of the mandible allies *Xericeps* with Azhdarchoidea. Elongate paired foramina in  
325 these locations are seen in the azhdarchids *Bakonydraco galaczi* Ősi, Weishampel and Jianu,  
326 2005, *Alanqa saharica* and *Volgadraco bogulobovi* Averianov, Arkhangelsky and Pervushov,  
327 2008, however, the curvature of the mandible is not seen in those azhdarchids for which the  
328 lower jaws are known: *Bakonydraco galaczi*, *Quetzalcoatlus* sp., *Alanqa saharica*,  
329 *Zhejiangopterus linhaiensis* Cai and Feng, 1994 and *Azhdarcho lancicollis*. While the  
330 elongate foramina are present in some azhdarchids, they do not seem to be present in  
331 *Quetzalcoatlus* (this may be due to the poor preservation of the jaws - Eberhard Frey,  
332 Karlsruhe, Pers. Comm.) or *Zhejiangopterus* (DMU personal obs.) and are thus likely not  
333 ubiquitous for the clade.

334 There is sufficient evidence (jaw shape, cortical bone thickness, dorsally projecting pair of  
335 ridges posteriorly and presence of foramina in the lateral and occlusal surfaces of the  
336 mandible) to support the assignment of *Xericeps curvirostris* to Azhdarchoidea. Determining  
337 the relationship of *Xericeps* to a clade within Azhdarchoidea (Tapejaridae,  
338 Chaoyangopteridae, Thalassodromidae, Azhdarchidae), assuming that it belongs within one  
339 of these rather than representing an entirely new clade, is more problematic.

340 The elongation of the mandibular symphysis and absence of a deep keel-like crest or any  
341 evidence for ventral flexure of the anterior portion of the symphysis, effectively precludes  
342 any likelihood of a close relationship between *Xericeps* and Tapejaridae.

343 By contrast, the mandibular symphysis of *Xericeps* does compare closely to that of  
344 chaoyangopterids and thalassodromeids. Most notably, there is an almost exact match in  
345 terms of shape between the mandibular symphysis of *Xericeps* and the holotype of  
346 *Chaoyangopterus*. A closely comparable elongate curved symphysis is also present in

347 *Jidapterus*, although that of *Shenzhoupterus* seems to have been somewhat less attenuate with  
348 a slightly more robust build. So far, paired ridges projecting above the dental margins of the  
349 mandible have not been reported in any chaoyangopterid although their absence in this clade  
350 cannot be entirely excluded as compression, breakage and, in some cases, poor bone  
351 preservation may have obscured them.

352 Elongate curved mandibular symphyses are present in some thalassodromeids such as  
353 *Tupuxuara* (Witton 2009, fig 3). Detailed descriptions of the mandible of *Tupuxuara* and  
354 *Thalassodromeus* have yet to be published, hence comparisons are limited. There are,  
355 however, three important details by which thalassodromeids appear to differ from *Xericeps*:  
356 first, the mandibular symphysis broadens relatively rapidly posteriorly becoming broader  
357 than it is deep at the posterior termination of the symphysis in *Thalassodromeus* (Veldmeijer  
358 et al 2005 fig 1E) and *Tupuxuara* (Unwin pers obs). By contrast in *Xericeps* the symphysis  
359 was likely somewhat deeper than wide at the same point (Figure 5e). Second, distinctive  
360 foramina piercing the occlusal and lateral surfaces of the mandibular symphysis appear to be  
361 lacking in *Thalassodromeus* (Kellner and Campos 2002; Veldmeijer et al. 2005) and  
362 *Tupuxuara* (Unwin pers obs) although this might be related in part to poor preservation of the  
363 external surfaces of cortical bones of the mandibular symphysis in the specimens examined.  
364 By contrast, a few small foramina appear to be present on the lateral surfaces of the  
365 symphysis of *Chaoyangopterus zhangi*, although compression and damage to external bone  
366 surfaces obscures fine detail. Third, thalassodromeids lack the distinctive paired ridges  
367 present on the posterior portion of the symphysis of *Xericeps*.

368 In azhdarchids such as *Quetzalcoatlus*, *Azhdarcho*, *Alanqa* and *Bakonydraco* the dorsal and  
369 ventral profile of the mandibular symphysis, seen in lateral aspect, are straight giving the  
370 symphyses a distinctive angular profile. One exception is *Zhejiangopterus* (Cai and Wei  
371 1994) although, in this case, it is only the posterior portion of the ventral profile of the

372 symphysis that is rounded, while the remainder is straight as in other azhdarchids. *Alanqa*  
373 *saharica* bears a structure on the posterior portion of the occlusal surface of the mandibular  
374 symphysis (Ibrahim et al. 2010; Martill and Ibrahim 2015) that is comparable in some  
375 respects to the paired ridges present in *Xericeps*. Details are obscured by encrusting sediment  
376 and damage to the bone, but sufficient to show a pair of ridges diverging posteriorly  
377 although, unlike *Xericeps*, these ridges converge closely and may even be confluent  
378 anteriorly. If these structures in *Xericeps* and *Alanqa* are homologous this would support the  
379 idea of a close relationship between these taxa as such structures have not been reported in  
380 other pterosaurs. A further possibility is that the holotype material of *A. saharica* pertains to a  
381 rostrum rather than a mandibular symphysis (Ibrahim et al. 2010) and that *A. saharica* and *X.*  
382 *curvirostris* represent the upper and lower jaws of a single, or two closely related, species.  
383 Only more complete material will allow this possibility to be resolved.

384 While we are confident that *Xericeps* is a non-tapejarid azhdarchoid it is too poorly known,  
385 at present, for its relationships within this group to be established with any certainty. We  
386 note, however, the possibility that *Xericeps* and *Alanqa* form a unique clade that likely  
387 belongs within Azhdarchidae, although this idea also needs testing.

388

## 389 **5. Discussion**

390 The description of *Xericeps* increases the number of named pterosaur taxa in the Kem Kem  
391 beds to three and the number of distinct clades to four, making this the most diverse  
392 Gondwanan pterosaur assemblage outside of South America. Additionally, as yet undescribed  
393 remains from the Kem Kem, currently under study by us, point to even higher pterosaur  
394 diversity.

395 The taxonomic composition of the Kem Kem assemblage, consisting of several  
396 azhdarchoids and an ornithocheirid, compares quite closely to that found in the Lower

397 Cretaceous of South America (Unwin and Martill, 2007; Kellner et al., 2013; Pinheiro and  
398 Rodrigues, 2017) and China (Lü et al., 2013; Witton, 2013). In both these regions  
399 assemblages consist predominantly of several azhdarchoids and one or more ornithocheirids.  
400 This contrasts quite sharply with assemblages from the Lower and early Upper Cretaceous of  
401 Europe, the Russian Platform and North America where ornithocheirids predominate and  
402 azhdarchoids are rare or absent (Witton, 2013). We suggest that this pattern has little, if  
403 anything, to do with palaeobiogeography, and is best explained in terms of ecology. The  
404 assemblages from South America, Africa and China all form part of, or appear to derive their  
405 biota from, essentially continental depositional environments. The ubiquitous presence of  
406 azhdarchoids is consistent with interpretations of these pterosaurs as ground-based feeders.  
407 By contrast, the North American, European and Russian Platform assemblages are located in  
408 marine environments, in which ornithocheirids, interpreted as aerial ‘grab’ feeders are  
409 generally to be found.

410 While it is difficult to establish the likely diet/feeding ecology of pterosaurs based on  
411 fragmentary jaw remains, the morphological distinctiveness of the jaws of the four reported  
412 taxa point to the occupation of distinct ecological niches. This is consistent with the idea that  
413 the Kem Kem beds biota was diverse and complex (Läng et al. 2013) and likely offered a  
414 wide variety of potential niches for aerial predators. Establishing the precise role of  
415 pterosaurs in this ecosystem will require much more complete remains.

416

## 417 **6. Conclusions**

418 *Xericeps curvirostris* gen. et sp. nov. represents a new taxon of pterosaur that can be  
419 diagnosed and distinguished from the co-occurring *Alanqa saharica* by the curved  
420 mandibular symphysis, distinct dorsal groove, convex lateral surface of the jaw, and ventral  
421 sulcus. The toothless jaws and elongate, slit-like foramina suggest affinities with

422 Azhdarchoidea. The new pterosaur adds to the diversity of the Kem-Kem pterosaur  
423 assemblage and emphasises the widespread temporal and geographic distribution of typical  
424 Early Cretaceous continental pterosaur assemblages previously reported from South America  
425 and China.

426

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444

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654

655 **Text figure captions**

656

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

659

660 Fig. 2. Simplified stratigraphic sequence for the Aferdou N'Chaft Kem Kem beds.

661 Measurements are approximate, and vary over the region, sometimes considerably. At this  
662 locality the upper sequence of mudstones is particularly reduced due to an unconformable  
663 relationship between the Kem Kem beds and the limestones of the overlying Akrabou  
664 Formation. The bone symbol indicates the horizon from which the new specimen was  
665 collected.

666

667 Figure 3. Partial mandible of new azhdarchoid pterosaur *Xericeps curvirostris* gen. et sp. nov.  
668 FSAC-KK 10700, ammonium chloride coated. Mandible in A, left lateral, B, occlusal, C,  
669 right lateral and D, ventral views. Scale bar = 50 mm.

670

671 Figure 4. Measurements recorded from the mandibular symphysis of *Xericeps curvirostris*  
672 gen. et sp. nov. In particular measurements of the angle of divergence posteriorly of the  
673 lateral and the dorsal and ventral margins proved useful for comparative purposes. The  
674 bottom illustration is based on *Pteranodon* and taken from Martin-Silverstone et al. (2017).

675

676 Figure 5. Partial mandible of new azhdarchoid pterosaur *Xericeps curvirostris* gen. et sp. nov.  
677 FSAC-KK 10700, without coating. A, left lateral; B, occlusal; C, right lateral; D, ventral; E,  
678 proximal end, F, distal end views. Scale bars 10 mm.

679

680 Figure 6. A selection of pterosaur mandibles showing a variety of morphologies when seen in  
681 lateral view. A, *Alanqa saharica*, Ibrahim et al., 2010, holotype specimen (FSAC-KK 26); B,  
682 *Noriopterus complicidens* Young, 1973 (GIN 125/1010); C, *Xericeps curvirostris* gen. et sp.  
683 nov., (FSAC-KK 10700); D, *Tapejara wellnhoferi* Kellner, 1989 (SMNK PAL 1137); E,  
684 *Pteranodon* sp. (NHMUK R 4078); F, *Tupuxuara leonardi* (IMCF 1052); G,  
685 *Chaoyangopterus zhangii* Wang and Zhou, 2003 (IVPP V 13397). A, After Ibrahim et al.  
686 2010; D, after Eck et al. 2011.

687

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

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