

1 **A new species of *Coloborhynchus* (Pterosauria, Ornithocheiridae)**
2 **from the mid-Cretaceous of North Africa**

3 Megan L. Jacobs^{a*}, David M. Martill^a, Nizar Ibrahim^{a**}, Nick Longrich^b

4 ^a *School of Earth and Environmental Sciences, University of Portsmouth, Portsmouth PO1 3QL, UK*

5 ^b *Department of Biology and Biochemistry and Milner Centre for Evolution, University of Bath, Bath*
6 *BA2 7AY, UK*

7 **Corresponding author. Email address: megan.jacobs@port.ac.uk (M.L. Jacobs)*

8 ***Current address: Department of Biology, University of Detroit Mercy, Detroit MI 48221, USA*

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15 *Kem Kem beds;*

16 *Morocco*

17

18 ABSTRACT

19 Pterosaur faunas experienced dramatic turnover between the Early and Late Cretaceous, but fossils
20 documenting this transition are rare. The mid-Cretaceous Kem Kem beds of Morocco are one of a
21 handful of localities preserving pterosaurs from this important interval. Previously reported taxa
22 from the Kem Kem beds include the ornithocheirid *Siroccopteryx moroccensis*, the azhdarchoids
23 *Alanqa saharica* and *Xericeps curvirostris*, an unnamed tapejarid, and a putative pteranodontid.
24 Here, a new species of ornithocheirid, *Coloborhynchus fluviferox* sp. nov., is described on the basis of
25 a well-preserved anterior rostrum fragment. It is assigned to *Coloborhynchus* based on the presence
26 of an anteriorly directed first tooth pair protruding from a palatal surface, which is deflected dorsally
27 by 90 degrees. The new specimen differs from *Siroccopteryx moroccensis* and is distinguished from
28 other species of *Coloborhynchus* by numerous characters, including an anterior palatal surface that
29 defines a high isosceles triangle with two shallow, subcircular depressions located dorsal to
30 premaxillary tooth pair one. The central region of alveoli for the first tooth pair is level with the
31 dorsal borders of the second tooth pair and the mediodorsal crest rises steeply forming a blunt
32 termination of the rostrum. The new species brings the number of pterosaur species from the Kem
33 Kem beds to at least 5. The Kem Kem pterosaur assemblage resembles other Early Cretaceous
34 faunas in having a high diversity of toothed forms, but also resembles latest Cretaceous faunas in
35 having several edentulous azhdarchoids.

36 1. Introduction

37 Pterosaurs flourished from the Triassic until the end of the Cretaceous and had a near global
38 distribution (Unwin, 2003; Barrett et al., 2008; Witton, 2013; Longrich et al., 2018). Among the most
39 successful and widely distributed pterosaur clades are the Ornithocheiridae (Unwin, 2003),
40 characterised by long jaws with spike-like teeth. Many ornithocheirid species bore elaborate bony
41 sagittal crests at the tip of the jaws and on the cranium (Unwin, 2006; Witton, 2013).
42 Ornithocheiridae ranged from the Valanginian into the Cenomanian, with ~4m wing spans in smaller
43 species, and wingspans of up to 8 metres or more in giant morphs (Martill and Unwin, 2012; Kellner
44 et al., 2013).

45 However, as with all pterosaurs, the record of Ornithocheiridae is extremely patchy. The
46 group was originally based on fragmentary remains from the Early Cretaceous of southern and
47 eastern England (Seeley, 1870; Owen, 1874, Unwin, 2001), but discoveries in Lagerstätten such as
48 the Santana and Crato formations of Brazil and the Yixian Formation of China have increased our
49 knowledge of the Cretaceous members of that clade considerably in the last 30 years (Campos and
50 Kellner, 1985; Fastnacht, 2001; Frey et al., 2003; Martill and Frey, 1998; Unwin and Martill, 2007;
51 Veldmeijer, 2003a, 2006; Wang et al., 2002, 2012; Wang and Zhou, 2003, 2004; Wellnhofer, 1985,
52 1987).

53 In recent years, finds from the mid-Cretaceous (?Albian to lower Cenomanian) Kem Kem
54 beds of south eastern Morocco have provided new insights into African pterosaur diversity, and
55 ornithocheirids in particular. Based on isolated elements, three pterosaur species have been named:
56 the ornithocheirid *Siroccopteryx moroccensis* (Mader and Kellner, 1999), the azhdarchoids *Alanqa*
57 *saharica* (Ibrahim et al., 2010) and *Xericeps curvirostris* (Martill et al., 2018). A probable tapejarid has
58 been described but not named (Wellnhofer and Buffetaut 1999), and a putative pteranodontid
59 described by the same authors lacks pteranodontoid autapomorphies and is most likely an
60 azhdarchid (Averionov et al., 2008, Ibrahim et al., 2010). All three named species are based on

61 anterior portions of upper or lower jaws, which appear to be taphonomically selected for in the Kem
62 Kem beds. Less commonly found postcranial remains and abundant teeth have also been
63 documented (Ibrahim et al., 2010; Kellner and Mader, 1997) but unfortunately are generally non-
64 diagnostic. Here we describe a new specimen of *Coloborhynchus*, FSAC-KK 10701, which confirms
65 the presence of this genus in North Africa and further increases pterosaur diversity within the Kem
66 Kem vertebrate assemblage.

67

68 **2. Geological setting and context**

69 The newly discovered specimen described here comes from red beds of the poorly defined
70 “continental intercalaire” in eastern Morocco. These are commonly referred to as the ‘Kem Kem
71 beds’ (Serenio et al., 1996), cropping out on a long and steep escarpment along the Moroccan-
72 Algerian border region. Equivalent outcrops have also been identified along the southern margin of
73 the Atlas Mountain fold belt and on the Algerian side of the border (Alloul et al., 2018). The new
74 pterosaur specimen was obtained commercially in the Tafilalet town of Erfoud. Fossil collectors in
75 the region mine from Tilouine in the north to Ouzina in the south, and so the specimen’s provenance
76 cannot be established precisely. However, adhering matrix, the colour and the mode of preservation
77 of the specimen are typical of Aferdou N’Chaft, an outlier of Kem Kem beds southeast of Hassi El
78 Begaa, Er Rachidia Province in south-eastern Morocco (Fig. 1). Other sites preserve similar fossils,
79 but most of these are not as heavily mined for fossils and are thus less likely candidates.

80 The Kem Kem beds encompass both the lower Ifezouane and upper Aoufous formations and
81 can be traced from the Tindouf Basin in the south west to the Errachidia-Boudenib basins in the east
82 (Cavin et al., 2010; Martill et al., 2011). The outcrop is extensive and continuous on the flanks of a
83 narrow escarpment for more than 150 kilometres, but limestone scree from the overlying Akrabou
84 Formation often obscures the red beds, in particular the upper portion of the escarpment. At

85 Aferdou N'Chaft the beds are exposed as an ~80 m thick sequence of fluvial, cross bedded
86 sandstones with thin mudstones, and thin beds of intraformational conglomerates of rip-up clasts
87 and quartzite pebbles (Fig. 2). These strata rest with angular unconformity on marine Palaeozoic
88 strata, and are capped non-sequentially by the Cenomanian-aged marine limestones of the Akrabou
89 Formation (Martill et al., 2018).

90 The Kem Kem beds are mid-Cretaceous in age and are often assumed to be Cenomanian
91 (e.g., Rodrigues et al., 2011, Richter et al., 2013), but the age is poorly constrained. Sequence
92 stratigraphic methods have not been applied to the Kem Kem beds so far, and no radiometric dates
93 are available for the sequence (Cavin et al., 2010). The sequence is considered to be no younger than
94 Cenomanian (Martill & Ibrahim, 2012), based on the presence of the characteristic middle
95 Cenomanian ammonite *Neolobites* (Martill et al., 2018) within the overlying Akrabou Formation.

96 The Kem Kem sequence is famous for its abundance of well preserved, but fragmentary
97 remains of vertebrates, which occur primarily in thin conglomerate horizons. Pterosaur fossils are
98 largely uncrushed and preserve fine surface details (Ibrahim et al., 2010). Associated vertebrate
99 remains are exceedingly rare but have been reported for some groups. Partial skeletons include a
100 variety of fishes (Cavin et al., 2015), a sauropod dinosaur, *Rebbachisaurus garasbae* (Lavocat 1954),
101 and the predatory dinosaurs *Deltadromeus agilis* and *Spinosaurus aegyptiacus* (Serenio et al., 1996,
102 Ibrahim et al., 2014). A rich and highly diverse vertebrate assemblage is preserved, consisting of
103 freshwater osteichthyans (Cavin and Brito, 2001; Yiabumoto and Uycno, 2005; Forey et al., 2011;
104 Cavin et al., 2015), sharks (Dutheil and Brito, 2009; Martill and Ibrahim, 2012), amphibians (Rage and
105 Dutheil, 2008), turtles (De Broin, 2002; Gaffney et al., 2002, 2006), snakes (Klein et al., 2017),
106 crocodyliforms (Larsson and Sues, 2007; Sereno and Larsson, 2009), pterosaurs (Ibrahim et al., 2010;
107 Martill et al., 2018; Rodrigues et al., 2011) and dinosaurs (Serenio et al., 1996; Cau et al., 2012;
108 Ibrahim et al., 2014, 2016; Mannion and Barrett, 2013; Wilson and Allain, 2015). In addition, the Kem
109 Kem assemblage also preserves a diverse ichnofauna (Ibrahim et al., 2014), notably rare dinosaur

110 footprints. Details of the localities, geology and stratigraphy of the Kem Kem beds are found in
111 Lavocat, 1954, Sereno et al., 1996, and Ibrahim et al., 2014.

112

113 **3. Methods**

114 Phylogenetic analysis was conducted using a new character matrix composed of 22 taxa and
115 32 characters (SI). Four multistate characters are included for a total of 36 derived character states.
116 Because most ornithocheirid taxa are known primarily from isolated rostra, characters focus
117 primarily on the rostrum, crest and tooth arrangement. Two specimens referred to *Coloborhynchus*
118 *capito*, the holotype of *Coloborhynchus reedi* and NHM R481 were coded separately to test for the
119 possibility that they represent distinct taxa. The analysis was performed in PAUP 4.0 B10 using the
120 branch-and-bound search option and implied weighting with K=2.

121

122 Institutional abbreviations: **BSP**, Bayerische Staatssammlung für Paläontologie und historische
123 Geologie, Munich, Germany; **CAMSM**, Sedgwick Museum of Earth Sciences, Cambridge, UK, **FSAC**,
124 Faculté des Sciences Aïn Chock, Université Hassan II, Casablanca, Morocco; **IWCMS**, Isle of Wight;
125 County Museum Service; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese
126 Academy of Sciences, Beijing, China; **LINHM**, Long Island Natural History Museum, Levittown, New
127 York, USA; **MNHS**, Museum of Natural History Sintra, Sintra, Portugal; **MPSC**, Museu de
128 Paleontologia da URCA, Brazil; **NHMUK**, Natural History Museum, London, UK; **QM**, Queensland
129 Museum of Natural History, Australia; **RGM**, Nationaal Natuurhistorisch Museum (Naturalis), Leiden,
130 the Netherlands; **SAO**, Sammlung Oberli, St. Gallen, Switzerland; **SMNK**, Staatliches Museum für
131 Naturkunde, Karlsruhe, Germany; **SMU**, Shuler Museum of Paleontology, Southern Methodist
132 University, Dallas, USA.

133

134 **4. Systematics, palaeontology and description**135 *4.1 Systematics*

136 PTEROSAURIA Kaup, 1834

137 PTERODACTYLOIDEA Plieninger, 1901

138 ORNITHOCHEIROIDEA Seeley, 1891

139 ORNITHOCHEIRIDAE Seeley, 1870

140 Genus *Coloborhynchus* Owen, 1874141 *Type species: Coloborhynchus clavirostris* Owen, 1874

142 *Age and distribution:* Valanginian, Hastings Sands, St Leonard's-on-sea, UK; Upper Albian, Paw Paw
143 Formation, Fort Worth, Texas, USA; Middle to Upper Albian, Romualdo Member, Santana Formation,
144 Chapada do Ariripe, Brazil; Albian-Cenomanian, Cambridge Greensand Formation, Cambridgeshire,
145 UK.

146 *A revised diagnosis for Coloborhynchus.*

147 This diagnosis includes the characters recognised by Owen (1874) and incorporates some of those
148 described by Rodrigues and Kellner (2008), but we note that their diagnosis is at odds to that
149 provided by Owen (1874). It also includes an additional feature, the taper of the lateral margins of
150 the rostrum (see below). The genus is defined on a unique combination of autapomorphies and
151 symplesiomorphies and is thus a metataxon.

152

153 *Autapomorphies.*

154 Lateral margins of rostrum (seen in dorsal or occlusal view) taper caudally from tooth pair
155 three to at least tooth pair seven.

156 Anterior margin of medial rostral crest convex in lateral view.

157 *Symplesiomorphies*

158 A triangular, upturned anterior palatal surface, a structure here termed the deltoid facet.

159 Deltoid facet has a shallow, a circular or oval depression located between or slightly below
160 premaxillary tooth pair 1 depending on species. This feature is present in *Coloborhynchus*
161 and *Siroccoptyx*.

162 Palatal surface turned dorsally for approximately 90 degrees, bearing the premaxillary tooth
163 pair 1.

164 Premaxillary tooth pair 1 are fang-like, slenderly tapering and prominently curved antero-
165 ventrally.

166 Anterior face of palate with triangular outline.

167

168 *Coloborhynchus fluviferox* sp. nov.

169 *Etymology:* from the Latin *fluvi*, “a river”; and *ferox*, “fierce”. For a ferocious-looking pterosaur
170 inhabiting a vast, ferocious river system (the Kem Kem river system was home to several giant
171 predators like Spinosaurus and Carcharodontosaurus).

172 *Holotype:* FSAC-KK 10701 (Faculté des Sciences Ain Chock, Université Hassan II, Casablanca, MA). An
173 anterior rostrum displaying the alveoli of the first, second and partial third tooth pairs.

174 *Type locality:* Southern Morocco, possibly Aferdou N'Chaft, Hassi El Begaa, Er Rachidia Province in
175 south-eastern Morocco (see Ibrahim et al., 2010; Martill et al., 2018)

176 *Type Horizon and age:* ?Albian-Lower Cenomanian Kem Kem beds, Ifezouane Formation.

177 *Diagnosis:* *Coloborhynchus* species with a deltoid facet: an anterior palatal surface upturned by 90
178 degrees. Deltoid facet defines a high isosceles triangle with concave dorsolateral margins in anterior
179 view. Deltoid facet with two shallow, sub-circular depressions located dorsal to anterior-most teeth
180 (tooth pair one), and dorsally this is a shallow groove defined by low ridges that transitions into a
181 broad rugose anterodorsal margin of the premaxilla. Central point of alveoli for first tooth pair level
182 with dorsal border of second tooth pair. Mediodorsal crest rises steeply from dorsally turned palatal
183 margin at an angle of 60°.

184

185 *4.2. Description*

186 Specimen FSAC-KK 10701 comprises of an anterior fragment of the premaxilla preserving
187 three pairs of alveoli with broken teeth remaining in the first two alveoli pairs (Fig. 3). The fragment
188 measures 61 mm high, 22.8 mm long and 39 mm in maximum width across the base of the anterior
189 facia (See table 2 for measurements). The specimen is free of matrix, but the spongiosa in the
190 internal trabecular bone are filled with fine quartz sand and grit, as is often seen in Kem Kem beds
191 fossils. The specimen was broken from the main rostrum prior to burial. The anterior surface has
192 exposed trabecular bone from pre-burial abrasion. There is a small crack on the left lateral facia that
193 has been repaired by the original collector.

194 In anterior view, the specimen is triangular in outline (Fig. 4) and is much taller than wide.
195 The palatal surface extends onto the anterior surface (Fig. 5) where it bends dorsally level with tooth
196 position 2 at an angle of ~90 degrees. A pair of shallow depressions is located on the anterior rostral

197 facies (*fra* of Fastnacht 2001, fig. 3) dorsal to the first tooth pair. The lateral margins converge
198 dorsally with a slight concavity to form a median crest on the anterior rostrum. The lateral margins
199 form low, rugose ridges that extend upward to the crest. The anterodorsal margin of the premaxilla
200 is slightly rugose and extends dorsally at an angle of approximately 60°, continuing to form an
201 anteriorly positioned premaxillary crest. The anterodorsal margin of the crest is covered by rugose
202 bone, similar to the anterior palatal surface.

203 The first pair of alveoli is located on the deltoid facet, with teeth that projected
204 anteroventrally. The alveoli are oval in outline with a maximum diameter of 11.7 mm and a
205 minimum of 7.2 mm, the long axis of which is directed dorsomedially towards the midline, with 9.4
206 mm separating the two alveoli. The ventral border of tooth pair one is level with the dorsal border of
207 tooth pair two (Fig. 6). The roots of broken teeth are retained within both alveoli. The alveolar
208 margins are raised. There is a marked oval depression ventral to the first pair of alveoli which
209 extends onto the ventral portion of the palatal surface. The second pair of alveoli are directed
210 lateroventrally. In lateral view, the anterior margin of the premaxilla is vertical, curving posteriorly
211 over the dorsal surface of the rostrum with a convex margin commencing dorsal to the paired
212 shallow depressions (Fig. 5). The anterior margins of a poorly preserved third pair of alveoli are
213 separated from the second by 21.3 mm. Broken teeth are preserved in the second pair of alveoli,
214 with the root of the left tooth exposed on the broken caudal surface of the specimen. The alveoli
215 have a more circular outline compared to the first pair, with a maximum diameter of 14.9 mm and a
216 minimum of 11.9 mm. The thickness of the bone cortex on the posterior edge is ~1 mm.

217 In ventral aspect, there is an oval shallow depression beneath the first pair of premaxillary
218 alveoli. A more pronounced depression starts at the posterior border of the second tooth pair with a
219 raised semi-circular anterior margin (Fig. 5).

220 *4.2.1. Comparisons*

221 The new specimen shares a number of features with several other ornithocheirids (See table
222 2 for list of comparative taxa and table 3 for character matrix.). Notably, the anteriorly directed first
223 tooth pair being situated on the deltoid facet and a palate upturned by approximately 90 degrees is
224 seen in *Coloborhynchus clavirostris*, *C. capito*, *Uktenadactylus wadleighi*, *Siroccopteryx moroccensis*,
225 and *Anhanguera* spp. However, in *C. fluviferox* these anteriormost teeth are placed more ventrally
226 compared to the condition in *C. capito* and *C. clavirostris* (Fig. 7). In *C. fluviferox* the first pair of
227 alveoli have an oval outline whereas in *S. moroccensis* the alveoli are circular (Fig. 6).

228 The high triangular outline of the deltoid facet of *C. fluviferox* is more similar to that of
229 *Siroccopteryx moroccensis*, *C. capito*, and especially *Coloborhynchus* cf. *capito* NHMUK R481 (Martill
230 and Unwin, 2012). By contrast, in *C. clavirostris*, *U. wadleighi* and *Anhanguera* spp. it forms a near
231 equilateral triangle (Fig. 6). The anterodorsal margins of this triangle are distinctly concave in
232 anterior view, a condition most similar to NHMUK R481. In *C. fluviferox* the anterodorsal margin of
233 the premaxilla is convex in lateral view. A similar situation is also seen in *Coloborhynchus clavirostris*.
234 In *C. robustus*, *C. capito*, *U. wadleighi* and *S. moroccensis* this margin is straight to strongly concave
235 (Fig. 6). The anterodorsal margin of the crest is broad and rugose. In *U. wadleighi* there is a groove
236 on the anterodorsal margin, and in NHMUK R481 a rugosity similar to *C. fluviferox*. The deltoid facet
237 is also shared with other species of *Coloborhynchus*, *Siroccopteryx*, and *Anhanguera*. However,
238 whereas it faces anteriorly in those taxa, it actually faces slightly anterodorsally in *C. fluviferox*.

239 The semi-circular depression on the palate located just behind tooth pair two is absent in *C.*
240 *clavirostris* instead there is a low palatal ridge extending between the teeth. However, this
241 depression is seen in *U. wadleighi* and *C. capito*. Despite the fragmentary nature of the specimen,
242 the combination of features seen in *C. fluviferox* is unique and thus warrants the introduction of a
243 distinct species.

244

245 5. Phylogenetic Analysis

246 Phylogenetic analysis (Fig. 8) recovers a basal split within Ornithocheirae between taxa
247 related to *Anhanguera* (Anhangueridae) and *Ornithocheirus* (Ornithocheiridae). Within
248 Ornithocheiridae three clades emerge. The first comprises *Ornithocheirus simus*, *Tropeognathus*
249 *mesembrinus* and *Siroccoptyx moroccensis*. A second comprises *Coloborhynchus* spp. and
250 *Uktenadactylus wadleighi*. Within this clade, *C. fluviferox* is most closely related to *Coloborhynchus*
251 *cf. capito* NHMUK R481. *Coloborhynchus fluviferox* shares with *Uktenadactylus* a prominent
252 depression between the third pair of teeth, and with NHMUK R481 *Coloborhynchus* sp. a very tall,
253 triangular and anterior palatal surface of the rostrum, and an anterodorsal margin of the premaxilla
254 that rises up steeply. A third clade includes *Cimoliopterus* and *Camposipterus* spp. Support for some
255 of these arrangements is relatively weak given the limited number of characters that can be scored
256 and very high levels of homoplasy.

257

258 6. Discussion

259 6.1 Discussion of the *Coloborhynchus* concept.

260 The original description of the genus *Coloborhynchus* was provided by Owen (1874), who
261 recognised a premaxillary morphology not previously seen in any other pterosaur at the time. Of
262 particular note was the possession of a palatal surface upturned anteriorly through approximately
263 90 degrees, with the anterior-most tooth pair situated on the deltoid facet above the second tooth
264 pair and projecting antero ventrally. In addition, Owen (1874) noted a concave depression on the
265 part of the palate from which these anterior teeth projected. This palatal arrangement distinguished
266 *Coloborhynchus* from the closely related Cretaceous pterosaurs *Ornithocheirus* and *Criorhynchus* the
267 latter being shown to be a junior synonym of *Ornithocheirus* (see historical review by Unwin 2001).

268 Rodrigues and Kellner (2008) reviewed *Coloborhynchus*, providing a revised diagnosis for
269 the genus that includes only *C. clavirostris*, and excludes all other specimen referrals. Notably, they
270 erected a new genus for *Coloborhynchus wadleighi* (= *Uktenodactylus wadleighi*) and suggested that
271 *Coloborhynchus capito* was probably generically distinct but they fell short of erecting a new genus
272 for its reception. The phylogeny presented here suggests that *Coloborhynchus clavirostris*, *C. capito*,
273 *U. wadleighi*, *C. cf. capito* NHMUK R481 and *C. fluviferox* form a monophyletic clade. This would
274 justify their placement in a single genus but, given the range of morphologies seen in this grouping,
275 and the fact that they are distributed widely in space and time, it may well be that more than one
276 genus is present.

277 The close relationship between *C. fluviferox*, *C. capito* and *U. wadleighi* (see Fig. 8) appears
278 to be relatively well-supported, but the monophyly of *Coloborhynchus* (as defined here) is poorly
279 supported and an analysis using equally weighted parsimony did not consistently recover a
280 monophyletic clade of *Coloborhynchus*. Revision of the genus *Coloborhynchus* is beyond the scope of
281 this paper however, and more complete fossils will be needed to better understand the systematics
282 and taxonomy of the clade.

283

284 6.2 A note on the genus *Siroccoptyx* Mader and Kellner, 1999.

285 A partial rostrum with dentition from the Kem Kem beds near Begaa was described by
286 Mader and Kellner (1999) and designated the holotype of a new genus and species, which they
287 named *Siroccoptyx moroccensis* Mader and Kellner, 1999. The holotype, LINHM 016, is the anterior
288 part of a rostrum with partial dentition. The authors placed *Siroccoptyx* within Anhangueridae, at
289 that time an ill-defined family level clade comprising several members of Ornithocheiridae *sensu*
290 Unwin 2001 (see Unwin 2003).

291 Subsequent authors (Unwin 2001, Fastnacht 2001, Frey et al., 2003, Ibrahim et al., 2010,
292 Martill and Unwin 2012) considered *Siroccoptyx moroccensis* to be a species of *Coloborhynchus*.
293 These authors considered that the deltoid facet and anteriorly directed first pair of teeth was a
294 character of the genus *Coloborhynchus*. However, there are a number of important differences (see
295 below) between the holotype of *S. moroccensis* and the holotype of *C. clavirostris* (Owen, 1874) and
296 other species referred to the genus (e.g. *C. wadlieghi* Lee, 1994; *C. capito* Seeley, 1870), as was
297 previously suggested by Rodrigues and Kellner (2008). These authors noted a number of differences
298 between the type species of *Coloborhynchus* (*C. clavirostris*) and *S. moroccensis*, and here we accept
299 their retention of *Siroccoptyx* as a distinct genus.

300 Notably, in *Coloborhynchus* the lateral margins of the rostrum taper caudally to give the
301 rostrum a spoon-like expansion at the rostrum. In *S. moroccensis* the lateral margins of the rostrum
302 are parallel sided. A further significant difference between *S. moroccensis* and species of
303 *Coloborhynchus* is in the size of the tooth pair 1. In species of *Coloborhynchus* the anterior most
304 teeth on the deltoid facet are large, followed caudally by increasingly larger teeth until tooth pair
305 three, whereas *S. moroccensis* has smaller teeth in the first alveolar pair, with teeth remaining a
306 similar size along the rostrum. Teeth in position four of *Coloborhynchus* have almost half the
307 diameter of the teeth in front. In *Siroccoptyx* all the teeth are short and very similar in alveolar
308 diameter from tooth pair 1 to 7.

309 Comparisons between *C. fluviferox* with *Siroccoptyx moroccensis* and other
310 Ornithocheirans show that it resembles *Ornithocheirus simus* and *Tropeognathus mesembrinus* in
311 numerous features. The tall, narrow shape of the premaxilla in anterior aspect is shared by all three
312 taxa. As in those taxa, the anterolateral margins of the premaxilla are convex in both anterior and
313 lateral view, resulting in a bluntly rounded outline of the tip of the rostrum. The sagittal crest
314 extends to the anterior end of the rostrum, as is the case in *O. simus* and *T. mesembrinus*. The
315 rostrum lacks a constriction posterior to the anterior rosette, another feature shared by those

316 species. In *S. moroccensis*, the teeth are short, straight, and relatively uniform in size in contrast to
317 *Coloborhynchus* and *Anhanguera*, where the three teeth immediately behind the anterior rosette
318 are markedly reduced in size, and the first eight teeth behind the rosette lie parallel along the
319 ventral margin of the jaw. Again, these features resemble *O. simus* and *T. mesembrinus*. The most
320 striking similarity, however, is a broad, ventrally projecting palatal ridge starting immediately behind
321 alveolus 7. This feature is unique to *S. moroccensis* and *T. mesembrinus* (not preserved in *O. simus*).
322 Phylogenetic analysis supports the placement of *S. moroccensis* as sister to a clade comprised of *O.*
323 *simus* and *T. mesembrinus*, supporting the separation of *C. fluviferus* and *S. moroccensis* as distinct
324 taxa.

325

326 6.3 Diversity of the Kem Kem pterosaur assemblage.

327 The discovery of a new species of *Coloborhynchus* in the Kem Kem beds increases the
328 number of pterosaur species in the assemblage to at least five, possibly six. Ornithocheirids include
329 *Coloborhynchus* (1 sp.) and *Siroccoptyx* (1 sp.), while azhdarchoids include *Alanqa* (1 sp.), *Xericeps*
330 (1 sp.), and an unnamed tapejarid. An unnamed taxon was first described as a possible
331 pteranodontid (Wellnhofer and Buffetaut, 1999), and then as an azhdarchid, *Alanqa* (Ibrahim et al.,
332 2010), based on the presence of slit-like neurovascular foramina, an azhdarchoid synapomorphy
333 (Martill et al., 2018). If this taxon represents a distinct azhdarchoid, it would increase the number of
334 Kem Kem pterosaurs to six. Considering that relatively few specimens have been described, and that
335 all Kem Kem pterosaurs are known from isolated and fragmentary skeletal elements, it is likely that
336 the assemblage will yield more taxa. The Kem Kem beds records high taxonomic diversity, as well as
337 a range of jaw morphologies in azhdarchoids and ornithocheirids, suggesting diverse feeding
338 strategies and diets. We note that this hypothesis will have to be tested more thoroughly.

339

340 7. Conclusions

341 FSAC-KK 10701 is placed within the genus *Coloborhynchus* by phylogenetic analysis and
342 diagnostic features and appears to be most closely related to species of *Coloborhynchus* from the
343 Cambridge Greensand of England. The unique combination of features regarding the relative height
344 of the first tooth pair in relation to the ventral margin of the deltoid facet, the shape of the anterior
345 margin of the premaxillae in lateral view, and the location of anterior depressions in the horizontal
346 palate indicates that the new specimen is a distinct and diagnosable species despite its fragmentary
347 nature. It shows greatest similarity with *Coloborhynchus capito*, *C. reedi*, and *C. sp.* NHMUK R481
348 from the Cambridge Greensand. This is the first occurrence of the genus *Coloborhynchus* in the mid-
349 Cretaceous of Africa and extends the geographical range of the genus to the eastern margin of the
350 widening proto-Atlantic Ocean.

351 *Coloborhynchus fluviferox* adds to the diversity of pterosaurs in the Kem Kem vertebrate
352 assemblage, which includes the ornithocheirid *Siroccopteryx moroccensis* and the azhdarchoids
353 *Alanqa saharica* and *Xericeps curvirostris*. It is likely that the co-occurrence of such diverse groups
354 indicates trophic partitioning, a hypothesis that remains to be tested.

355 Author Contributions

356 NL, MJ, and DM designed the project, MJ, NL, DM, and NI, wrote the paper and prepared the figures,
357 NL, MJ and DM conducted the phylogenetic analysis.

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548

549 **Figure captions**

550 Figure 1. Locality map showing the outcrop of the Kem Kem beds in the Tafilalt region of south east
551 Morocco.

552 Figure 2. View near Hassi El Begaa, south east Morocco showing extensive outcrop of Kem Kem beds
553 on the escarpment of the Hamada du Kem Kem with a simplified sedimentary log. The limestones of
554 the Akrabou Formation form the top of the plateau. Folded Palaeozoic strata are present at the
555 base, but not seen in this photograph. The vertebrate yielding horizon is marked by a line of spoil
556 heaps which is a result from extensive mining for fossils.

557 Figure 3. Outline of *Coloborhynchus* skull with red box showing location of specimen FSAC-KK 10701.

558 Figure 4. *Coloborhynchus fluviferox* sp. nov. FSAC-KK 10701, Ammonium chloride coated. Rostrum in
 559 A, anterior view; B, posterior view; C, left lateral view; D, right ventral view, and E, ventral view.
 560 Arrow indicates anterior. Scale bar = 10 mm.

561 Figure 5. *Coloborhynchus fluviferox* sp. nov. FSAC-KK 10701 Line drawing highlighting features.
 562 Rostrum in A, anterior view; B, posterior view; C, left lateral view; D, right lateral view, and E, ventral
 563 view. Arrow indicates anterior. Scale bar = 10 mm.

564 Figure 6. Comparative line drawings of ornithocheirid pterosaur rostral tips. A-C, *Coloborhynchus*
 565 *clavirostris* Owen, 1874 (BMNH R 1822) in A, anterior; B, left lateral, and C, ventral views. D-F,
 566 *Coloborhynchus wadleighi* Lee, 1994 (SMU 73058) in D, anterior; E, left lateral, and F, ventral views.
 567 G-I, *Coloborhynchus robustus* Wellnhofer, 1987 (SMNK 2302 PAL) in G, anterior; H, left lateral, and I,
 568 ventral views. J-K, *Coloborhynchus piscator* Campos and Kellner, 1985 (NSM-PV 19892) in J, anterior,
 569 and K, left lateral views. L-M, *Siroccopteryx moroccensis* Mader and Kellner, 1999 (LINHM 016) in L,
 570 anterior; M, left lateral, and N, ventral views. O-Q *Coloborhynchus capito*, Seeley, 1870 (CAMSM B
 571 54625) in O, anterior; P, left lateral, and Q, ventral views. R-T, *Coloborhynchus fluviferox* sp. nov.
 572 (FSAC-KK 10701) in R, anterior; S, left lateral, and T, ventral views.

573 Figure 7. Dental arrangement on the deltoid facet of *Coloborhynchus* spp. and related taxa. A,
 574 ventral border of tooth pair one lower than dorsal border of tooth pair two; B, ventral border of
 575 tooth pair one level with dorsal border of tooth pair two; C, ventral border of tooth pair one above
 576 dorsal border of tooth pair two. D, *Coloborhynchus* sp. IWCMS 2014.82, Wessex Formation
 577 (Barremian), Isle of Wight, England; E, *Coloborhynchus robustus*, Santana Formation (?Albian),
 578 Araripe Basin, Brazil; F, *Siroccopteryx moroccensis*, Kem Kem beds (?Albian/Cenomanian), Hassi El
 579 Begaa, Morocco; G, *Coloborhynchus clavirostris*, NHMUK 1822, Hastings Sand Formation
 580 (Valanginian), Sussex, England; H. *Coloborhynchus capito*, CAMSM B 54625, Cambridge Greensand
 581 (Albian), Cambridge, England; I, *Coloborhynchus fluvioferox* sp. nov. FSAC-KK 10701. Scale bars = 10
 582 mm. D, G, after Martill (2015); E, after Fastnacht (2001); H, after Rodrigues and Kellner (2013).

583

584 Figure 8. Cladogram showing ornithocheirid relationships based on the data matrix shown in Table 3.

585 This analysis was carried out in PAUP 4.0 B10 using the branch-and-bound search option and implied

586 weighting with K=2. A single best tree was found with consistency index = 0.4675, retention index =

587 0.7230 and rescaled consistency index = 0.3380.

588

Measurement	(mm)
Height at Anterior extremity	61
Width at anterior face	31
Height at broken posterior border	54
Width at broken posterior border	39
Length of ventral surface along the median line	22.8
Space between first pair of alveoli	9.38
Space between second pair of alveoli	20
Space between third pair of alveoli	26
Maximum diameter of first pair of alveoli	11.7
Minimum diameter of first pair of alveoli	7.2
Maximum diameter of second pair of alveoli	14.9
Minimum diameter of second pair of alveoli	11.9
Thickness of bone wall	~1

589 Table 1. Measurements of *Coloborhynchus fluviferus* sp. nov from the Kem Kem beds of Morocco.

Specimen name	Number	Locality	Age	References
<i>Anhanguera araripensis</i>	BSP 1982 I 89; SAO 16494	Santana Formation, Brazil	Aptian-Albian	Wellnhofer, 1985
<i>Anhanguera piscator</i>	NSM-PV 19892	Santana Formation, Brazil	Aptian-Albian	Campos and Kellner, 1985
<i>Anhanguera robustus</i>	BSP 1987 I 47; SMNK 2302 PAL	Santana Formation, Brazil	Aptian-Albian	Wellnhofer, 1987
<i>Camposipterus colorhinus</i>	CAMSM B54431	Cambridge Greensand, Cambridge, England	Cenomanian	Seeley, 1870
<i>Camposipterus nasutus</i>	CAMSM B54556	Cambridge Greensand, Cambridge, England	Cenomanian	Seeley 1870
<i>Camposipterus sedgwickii</i>	CAMSM B54422	Cambridge Greensand, Cambridge, England	Cenomanian	Owen, 1859
<i>Caulkicephalus trimicrodon</i>	IWCMS 2002.189.1	Wessex Formation, Wealden, Isle of Wight	Barremian	Steel et al., 2005
<i>Cimoliopterus cuvieri</i>	NHMUK PV 39409	Chalk, Burham, Kent, England	Cenomanian/Turonian	Bowerbank, 1851; Rodrigues and Kellner, 2013
<i>Cimoliopterus dunni</i>	SMU Loc. 518	Britton Formation, Eagle Ford Group, Texas, USA	Cenomanian	Myers, 2015
<i>Coloorhynchus</i> sp.	NHMUK R481	Cambridge Greensand, Cambridge, England	Cenomanian	Martill and Unwin, 2012
<i>Coloborhynchus capito</i>	CAMSM B 54625	Cambridge Greensand, Cambridge, England	Cenomanian	Seeley, 1870
<i>Coloborhynchus clavirostris</i>	NHMUK 1822	Hastings Beds, Wealden Group, East Sussex, England	Cenomanian	Owen, 1874
<i>Coloborhynchus fluviferox</i>	FSAC-KK 10701	Kem Kem beds, Morocco	?Albian-Cenomanian	This paper
<i>Coloborhynchus reedi</i>	Referred specimen, whereabouts unknown.	Cambridge Greensand, Cambridge, England	Cenomanian	Seeley, 1870
<i>Hamipterus tianshanensis</i>	IVPP V18931.1	Tugulu Group, Xinjiang, China	Early Cretaceous	Wang et al., 2014
<i>Liaoningopterus gui</i>	IVPP V13291	Jiufotang Fm. Yixiang province, Peoples Republic of China	Barremian-Aptian	Wang and Zhou, 2003
<i>Linlongopterus jennyae</i>	IVPP V15549	Jiufotang Fm. Yixiang province, Peoples Republic of China	Barremian-Aptian	Rodrigues et al., 2015
<i>Maaradactylus kellneri</i>	MPSC R 2357	Romualdo Member, Santana Formation, NE Brazil	Albian	Bantim et al., 2014
<i>Maaradactylus spielbergi</i>	RGM 401 880	Romualdo Member, Santana Formation, NE Brazil	Albian	Veldmeijer, 2003
<i>Ornithocheirus simus</i>	CAMSM B54.428	Cambridge Greensand, Cambridge, England	Cenomanian	Owen, 1861; Unwin, 2001
<i>Siroccopteryx moroccensis</i>	LINHM 016	Kem Kem beds, Morocco	?Albian-Cenomanian	Mader and Kellner, 1999
<i>Tropeognathus mesembrinus</i>	BSP 1987 I 46	Santana Formation, Brazil	Aptian-Albian	Wellnhofer, 1987
<i>Uktenadactylus wadleighi</i>	SMU 73058	Paw Paw Formation, Texas, USA	Albian	Lee, 1994

590 Table 2. List of comparative taxa used in character matrix