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

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ABSTRACT

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

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

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

In recent years, finds from the mid-Cretaceous (?Albian to lower Cenomanian) Kem Kem
beds of south eastern Morocco have provided new insights into African pterosaur diversity, and
ornithocheirids in particular. Based on isolated elements, three pterosaur species have been named:
the ornithocheirid Siroccopteryx moroccensis (Mader and Kellner, 1999), the azhdarchoids Alanqa
saharica (Ibrahim et al., 2010) and Xericeps curvirostris (Martill et al., 2018). A probable tapejarid has
been described but not named (Wellnhofer and Buffetaut 1999), and a putative pteranodontid
described by the same authors lacks pteranodontoid autapomorphies and is most likely an
azhdarchid (Averionov et al., 2008, Ibrahim et al., 2010). All three named species are based on
anterior portions of upper or lower jaws, which appear to be taphonomically selected for in the Kem Kem beds. Less commonly found postcranial remains and abundant teeth have also been documented (Ibrahim et al., 2010; Kellner and Mader, 1997) but unfortunately are generally non-diagnostic. Here we describe a new specimen of *Coloborhynchus*, FSAC-KK 10701, which confirms the presence of this genus in North Africa and further increases pterosaur diversity within the Kem Kem vertebrate assemblage.

2. Geological setting and context

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

The Kem Kem beds encompass both the lower Ifezouane and upper Aoufous formations and can be traced from the Tindouf Basin in the south west to the Errachidia-Boudenib basins in the east (Cavin et al., 2010; Martill et al., 2011). The outcrop is extensive and continuous on the flanks of a narrow escarpment for more than 150 kilometres, but limestone scree from the overlying Akrabou Formation often obscures the red beds, in particular the upper portion of the escarpment. At
Aferdou N’Chaft the beds are exposed as an ~80 m thick sequence of fluvial, cross bedded sandstones with thin mudstones, and thin beds of intraformational conglomerates of rip-up clasts and quartzite pebbles (Fig. 2). These strata rest with angular unconformity on marine Palaeozoic strata, and are capped non-sequentially by the Cenomanian-aged marine limestones of the Akrabou Formation (Martill et al., 2018).

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

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

3. Methods

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

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

4.1 Systematics

PTEROSAURIA Kaup, 1834

PTERODACTYLOIDEA Plieninger, 1901

ORNITHOCHEREOIDEA Seeley, 1891

ORNITHOCHERIDAE Seeley, 1870

Genus Coloborhynchus Owen, 1874

Type species: Coloborhynchus clavirostris Owen, 1874

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

A revised diagnosis for Coloborhynchus.

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

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

Anterior margin of medial rostral crest convex in lateral view.

Symplesiomorphies

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

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

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

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

Anterior face of palate with triangular outline.

*Coloborhynchus fluviferox* sp. nov.

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

Holotype: FSAC-KK 10701 (Faculté des Sciences Ain Chock, Université Hassan II, Casablanca, MA). An anterior rostrum displaying the alveoli of the first, second and partial third tooth pairs.
Type locality: Southern Morocco, possibly Aferdou N’Chaft, Hassi El Begaa, Er Rachidia Province in south-eastern Morocco (see Ibrahim et al., 2010; Martill et al., 2018).

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

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

4.2. Description

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

In anterior view, the specimen is triangular in outline (Fig. 4) and is much taller than wide. The palatal surface extends onto the anterior surface (Fig. 5) where it bends dorsally level with tooth position 2 at an angle of ~90 degrees. A pair of shallow depressions is located on the anterior rostral
facades (fra of Fastnacht 2001, fig. 3) dorsal to the first tooth pair. The lateral margins converge
dorsally with a slight concavity to form a median crest on the anterior rostrum. The lateral margins
form low, rugose ridges that extend upward to the crest. The anterodorsal margin of the premaxilla
is slightly rugose and extends dorsally at an angle of approximately 60°, continuing to form an
antero- position premaxillary crest. The anterodorsal margin of the crest is covered by rugose
bone, similar to the anterior palatal surface.

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

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

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

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

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

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

6. Discussion

6.1 Discussion of the *Coloborhynchus* concept.

The original description of the genus *Coloborhynchus* was provided by Owen (1874), who recognised a premaxillary morphology not previously seen in any other pterosaur at the time. Of particular note was the possession of a palatal surface upturned anteriorly through approximately 90 degrees, with the anterior-most tooth pair situated on the deltoid facet above the second tooth pair and projecting antero ventrally. In addition, Owen (1874) noted a concave depression on the part of the palate from which these anterior teeth projected. This palatal arrangement distinguished *Coloborhynchus* from the closely related Cretaceous pterosaurs *Ornithocheirus* and *Criorhynchus* the latter being shown to be a junior synonym of *Ornithocheirus* (see historical review by Unwin 2001).
Rodrigues and Kellner (2008) reviewed *Coloborhynchus*, providing a revised diagnosis for the genus that includes only *C. clavirostris*, and excludes all other specimen referrals. Notably, they erected a new genus for *Coloborhynchus wadleighi* (= *Uktenodactylus wadleighi*) and suggested that *Coloborhynchus capito* was probably generically distinct but they fell short of erecting a new genus for its reception. The phylogeny presented here suggests that *Coloborhynchus clavirostris*, *C. capito*, *U. wadleighi*, *C. cf. capito* NHMUK R481 and *C. fluviferox* form a monophyletic clade. This would justify their placement in a single genus but, given the range of morphologies seen in this grouping, and the fact that they are distributed widely in space and time, it may well be that more than one genus is present.

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


A partial rostrum with dentition from the Kem Kem beds near Bega was described by Mader and Kellner (1999) and designated the holotype of a new genus and species, which they named *Siroccopteryx moroccensis* Mader and Kellner, 1999. The holotype, LINHM 016, is the anterior part of a rostrum with partial dentition. The authors placed *Siroccopteryx* within Anhangueridae, at that time an ill-defined family level clade comprising several members of Ornithocheiridae *sensu* Unwin 2001 (see Unwin 2003).
Subsequent authors (Unwin 2001, Fastnacht 2001, Frey et al., 2003, Ibrahim et al., 2010, Martill and Unwin 2012) considered *Siroccopteryx moroccensis* to be a species of *Coloborhynchus*. These authors considered that the deltoid facet and anteriorly directed first pair of teeth was a character of the genus *Coloborhynchus*. However, there are a number of important differences (see below) between the holotype of *S. moroccensis* and the holotype of *C. clavirostris* (Owen, 1874) and other species referred to the genus (e.g. *C. wadlieghi* Lee, 1994; *C. capito* Seeley, 1870), as was previously suggested by Rodrigues and Kellner (2008). These authors noted a number of differences between the type species of *Coloborhynchus* (*C. clavirostris*) and *S. moroccensis*, and here we accept their retention of *Siroccopteryx* as a distinct genus.

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

Comparisons between *C. fluviiferox* with *Siroccopteryx moroccensis* and other Ornithocheirans show that it resembles *Ornithocheirus simus* and *Tropeognathus mesembrinus* in numerous features. The tall, narrow shape of the premaxilla in anterior aspect is shared by all three taxa. As in those taxa, the anterolateral margins of the premaxilla are convex in both anterior and lateral view, resulting in a bluntly rounded outline of the tip of the rostrum. The sagittal crest extends to the anterior end of the rostrum, as is the case in *O. simus* and *T. mesembrinus*. The rostrum lacks a constriction posterior to the anterior rosette, another feature shared by those
species. In *S. moroccensis*, the teeth are short, straight, and relatively uniform in size in contrast to *Coloborhynchus* and *Anhanguera*, where the three teeth immediately behind the anterior rosette are markedly reduced in size, and the first eight teeth behind the rosette lie parallel along the ventral margin of the jaw. Again, these features resemble *O. simus* and *T. mesembrinus*. The most striking similarity, however, is a broad, ventrally projecting palatal ridge starting immediately behind alveolus 7. This feature is unique to *S. moroccensis* and *T. mesembrinus* (not preserved in *O. simus*). Phylogenetic analysis supports the placement of *S. moroccensis* as sister to a clade comprised of *O. simus* and *T. mesembrinus*, supporting the separation of *C. fluviferox* and *S. moroccensis* as distinct taxa.

6.3 Diversity of the Kem Kem pterosaur assemblage.

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

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

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

**Author Contributions**

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

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Figure captions

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

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

Figure 3. Outline of Coloborhynchus skull with red box showing location of specimen FSAC-KK 10701.
Figure 4. *Coloborhynchus fluviferox* sp. nov. FSAC-KK 10701, Ammonium chloride coated. Rostrum in A, anterior view; B, posterior view; C, left lateral view; D, right ventral view, and E, ventral view. Arrow indicates anterior. Scale bar = 10 mm.

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


Figure 7. Dental arrangement on the deltoid facet of *Coloborhynchus* spp. and related taxa. A, ventral border of tooth pair one lower than dorsal border of tooth pair two; B, ventral border of tooth pair one level with dorsal border of tooth pair two; C, ventral border of tooth pair one above dorsal border of tooth pair two. D, *Coloborhynchus* sp. IWCMS 2014.82, Wessex Formation (Barremian), Isle of Wight, England; E, *Coloborhynchus robustus*, Santana Formation (?Albian), Araripe Basin, Brazil; F, *Siroccopteryx moroccensis*, Kem Kem beds (?Albian/Cenomanian), Hassi El Begaa, Morocco; G, *Coloborhynchus clavirostris*, NHMUK 1822, Hastings Sand Formation (Valanginian), Sussex, England; H. *Coloborhynchus capito*, CAMSM B 54625, Cambridge Greensand (Albian), Cambridge, England; I, *Coloborhynchus fluviferox* sp. nov. FSAC-KK 10701. Scale bars = 10 mm.
Figure 8. Cladogram showing ornithocheirid relationships based on the data matrix shown in Table 3.

This analysis was carried out in PAUP 4.0 B10 using the branch-and-bound search option and implied weighting with $K=2$. A single best tree was found with consistency index = 0.4675, retention index = 0.7230 and rescaled consistency index = 0.3380.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>(mm)</th>
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<tbody>
<tr>
<td>Height at Anterior extremity</td>
<td>61</td>
</tr>
<tr>
<td>Width at anterior face</td>
<td>31</td>
</tr>
<tr>
<td>Height at broken posterior border</td>
<td>54</td>
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<tr>
<td>Width at broken posterior border</td>
<td>39</td>
</tr>
<tr>
<td>Length of ventral surface along the median line</td>
<td>22.8</td>
</tr>
<tr>
<td>Space between first pair of alveoli</td>
<td>9.38</td>
</tr>
<tr>
<td>Space between second pair of alveoli</td>
<td>20</td>
</tr>
<tr>
<td>Space between third pair of alveoli</td>
<td>26</td>
</tr>
<tr>
<td>Maximum diameter of first pair of alveoli</td>
<td>11.7</td>
</tr>
<tr>
<td>Minimum diameter of first pair of alveoli</td>
<td>7.2</td>
</tr>
<tr>
<td>Maximum diameter of second pair of alveoli</td>
<td>14.9</td>
</tr>
<tr>
<td>Minimum diameter of second pair of alveoli</td>
<td>11.9</td>
</tr>
<tr>
<td>Thickness of bone wall</td>
<td>~1</td>
</tr>
</tbody>
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Table 1. Measurements of *Coloborhynchus fluviferox* sp. nov from the Kem Kem beds of Morocco.
<table>
<thead>
<tr>
<th>Specimen name</th>
<th>Number</th>
<th>Locality</th>
<th>Age</th>
<th>References</th>
</tr>
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<tr>
<td><em>Anhanguera araripensis</em></td>
<td>BSP 1982 I 89; SAO 16494</td>
<td>Santana Formation, Brazil</td>
<td>Aptian-Albian</td>
<td>Wellnhofer, 1985</td>
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<td><em>Anhanguera piscator</em></td>
<td>NSM-PV 19892</td>
<td>Santana Formation, Brazil</td>
<td>Aptian-Albian</td>
<td>Campos and Kellner, 1985</td>
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<td><em>Anhanguera robustus</em></td>
<td>BSP 1987 I 47; SMNK 2302 PAL</td>
<td>Santana Formation, Brazil</td>
<td>Aptian-Albian</td>
<td>Wellnhofer, 1987</td>
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<td><em>Camposipterus colorhinus</em></td>
<td>CAMSM B54431</td>
<td>Cambridge Greensand, England</td>
<td>Cenomanian</td>
<td>Seeley, 1870</td>
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<td><em>Camposipterus nasutus</em></td>
<td>CAMSM B54556</td>
<td>Cambridge Greensand, England</td>
<td>Cenomanian</td>
<td>Seeley 1870</td>
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<td><em>Camposipterus sedgwickii</em></td>
<td>CAMSM B54422</td>
<td>Cambridge Greensand, England</td>
<td>Cenomanian</td>
<td>Owen, 1859</td>
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<td><em>Caulkicephalus trimicrodon</em></td>
<td>IWCMS 2002.189.1</td>
<td>Wessex Formation, Wealden, Isle of Wight</td>
<td>Cenomanian/Turonian</td>
<td>Bowerbank, 1851; Rodrigues and Kellner, 2013</td>
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<td><em>Cimoliosaurus cuvieri</em></td>
<td>NHMUK PV 39409</td>
<td>Chalk, Burham, Kent, England</td>
<td>Cenomanian/Turonian</td>
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<td><em>Cimoliosaurus dunnii</em></td>
<td>SMU Loc. 518</td>
<td>Britton Formation, Eagle Ford Group, Texas, USA</td>
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<td><em>Colorhynchus sp.</em></td>
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<td>Martill and Unwin, 2012</td>
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<td><em>Coloborhynchus capito</em></td>
<td>CAMSB 54625</td>
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<td>Seeley, 1870</td>
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<td>Hastings Beds, Wealden Group, East Sussex, England</td>
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<td>Owen, 1874</td>
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<td><em>Coloborhynchus fluviiformis</em></td>
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<td>?Albian-Cenomanian</td>
<td>This paper</td>
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<td><em>Coloborhynchus reedi</em></td>
<td>Referred specimen, whereabouts unknown.</td>
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<td><em>Hamipterus tianshanensis</em></td>
<td>IVPP V18931.1</td>
<td>Tugulu Group, Xinjiang, China</td>
<td>Early Cretaceous</td>
<td>Wang et al., 2014</td>
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<td><em>Linlongopterus jennyae</em></td>
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<td>Jiufotang Fm. Yixiang province, Peoples Republic of China</td>
<td>Barremian-Aptian</td>
<td>Rodrigues et al., 2015</td>
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<td><em>Maaradactylus kellneri</em></td>
<td>MPSC R 2357</td>
<td>Romualdo Member, Santana Formation, NE Brazil</td>
<td>Albian</td>
<td>Bantim et al., 2014</td>
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<tr>
<td><em>Maaradactylus spielbergi</em></td>
<td>RGM 401 880</td>
<td>Romualdo Member, Santana Formation, NE Brazil</td>
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<td>Veldmeijer, 2003</td>
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<td>Cambridge Greensand, Cambridge, England</td>
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<td>Owen, 1861; Unwin, 2001</td>
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<td><em>Sirocctopteryx moroccensis</em></td>
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<td><em>Tropeognathus mesembrinus</em></td>
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<td><em>Uktenadactylus wadleighi</em></td>
<td>SMU 73058</td>
<td>Paw Paw Formation, Texas, USA</td>
<td>Albian</td>
<td>Lee, 1994</td>
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Table 2. List of comparative taxa used in character matrix