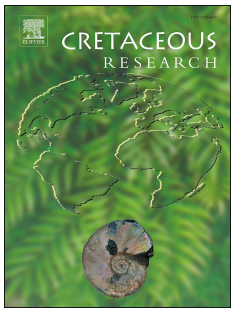
Accepted Manuscript



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

Megan L. Jacobs, David M. Martill, Nizar Ibrahim, Nick Longrich

PII: S0195-6671(18)30354-9

DOI: https://doi.org/10.1016/j.cretres.2018.10.018

Reference: YCRES 3995

To appear in: *Cretaceous Research*

Received Date: 28 August 2018

Revised Date: 18 October 2018

Accepted Date: 21 October 2018

Please cite this article as: Jacobs, M.L., Martill, D.M., Ibrahim, N., Longrich, N., A new species of *Coloborhynchus* (Pterosauria, Ornithocheiridae) from the mid-Cretaceous of North Africa, *Cretaceous Research* (2018), doi: https://doi.org/10.1016/j.cretres.2018.10.018.

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

Megan L. Jacobs[a*], David M. Martill[a], Nizar Ibrahim[a**], Nick Longrich[b]

[a] *School of Earth and Environmental Sciences, University of Portsmouth, Portsmouth PO1 3QL, UK*

[b] *Department of Biology and Biochemistry and Milner Centre for Evolution, University of Bath, Bath BA2 7AY, UK*

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

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

Keywords:

Pterosauria;

Ornithocheiridae;

Coloborhynchus;

Cretaceous;

Kem Kem beds;

Morocco

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 wingspans 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; Veldmeijer, 2003a, 2006; Wang et al., 2002, 2012; Wang and Zhou, 2003, 2004; Wellnhofer, 1985, 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 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 Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; **CAMSM**, Sedgwick Museum of Earth Sciences, Cambridge, UK, **FSAC**, Facultié des Sciences Aïn 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

ORNITHOCHEIROIDEA Seeley, 1891

ORNITHOCHEIRIDAE Seeley, 1870

Genus *Coloborhynchus* Owen, 1874

Type species: *Coloborhychus 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 Aïn 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

facies (*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 anteriorly positioned 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.

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

A partial rostrum with dentition from the Kem Kem beds near Begaa 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. fluviferox* 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

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*. *fluviferox* 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 *Siroccopteryx* (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

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.

Acknowledgements

We are very grateful to the following for their support and commentary: Samir Zouhri (Casablanca, Morocco), David Unwin (Leicester, UK). Andy Gale (University of Portsmouth) kindly assisted with photography. We would like to thank Dino Frey (Karlsruhe, Germany) and an anonymous reviewer whose comments have greatly improved the manuscript.

363 **References**

364 Alloul, T., Rage, J.C., Hamdidouche, R., Jalil, N.E. 2018. First report on Cretaceous vertebrates from
365 the Algerian Kem Kem beds. A new procoelous salamander from the Cenomanian, with remarks on
366 African Caudata. Cretaceous Research 84, 384-388.

367 Averianov, A.O., Arkhangelsky, M.S. and Pervushov, E.M. 2008. A new late Cretaceous azhdarchid
368 (Pterosauria, Azhdarchidae) from the Volga Region. Paleontological Journal, 42, 634.

369 Bantim, R.A., Saraiva, A.A., Oliveira, G.R., Sayao, J.M. 2014. A new toothed pterosaur
370 (Pterodactyloidea: Anhangueridae) from the Early Cretaceous Romualdo Formation, NE
371 Brazil. Zootaxa 3869, 201-223. http://dx.doi.org/10.11646/zootaxa.3869.3.1

372 Barrett, P. M., Butler, R. J., Edwards, N. P., Milner, A. R. 2008. Pterosaur distribution in time and
373 space: an atlas. Zitteliana 61-107.

374 Bowerbank, J.S., 1851. On the Pterodactyles of the Chalk formation. In Proceedings of the zoological
375 Society of London Oxford, UK: Blackwell Publishing Ltd. 19, 1, 14-20.

376 Campos, D. A., Kellner, A. W. A. 1985. Panorama of the Flying Reptiles Study in Brazil and South
377 America (Pterosauria/ Pterodactyloidea/ Anhangueridae). Anais da Academia Brasileira de
378 Ciências 57, 453-466.

379 Cau, A., Vecchia, F.M.D., Fabbri, M. 2012. Evidence of a new carcharodontosaurid from the Upper
380 Cretaceous of Morocco. Acta Palaeontologica Polonica 57, 661-665.

381 Cavin, L., Brito, P.M. 2001. A new Lepisosteidae (Actinopterygii, Ginglymodi) from the Cretaceous of
382 the Kem Kem beds, Southern Morocco. Bulletin de la Société géologique de France 172), 61-670.

383 Cavin, L., Tong, H., Boudad, L., Meister, C., Piuz, A., Tabouelle, J., Aarab, M., Amiot, R., Buffetaut, E.,
384 Dyke, G., Hua, S. 2010. Vertebrate assemblages from the early Late Cretaceous of southeastern

385 Morocco: an overview. Journal of African Earth Sciences 57, 391-412.
386 DOI: 10.1016/j.jafrearsci.2009.12.007

387 Cavin, L., Boudad, L., Tong, H., Läng, E., Tabouelle, J., Vullo, R. 2015. Taxonomic composition and
388 trophic structure of the continental bony fish assemblage from the early Late Cretaceous of
389 southeastern Morocco. PloS ONE 10, p.e0125786. https://doi.org/10.1371/journal.pone.0125786

390 De Broin, F.D.L. 2002. *Elosuchus*, a new genus of crocodile from the Cretaceous of the North of
391 Africa. Comptes Rendus Palevol. 1, 275. https://doi.org/10.1016/S1631-0683(02)00049-0

392 Dutheil, D.B., Brito, P.M. 2009. Articulated cranium of *Onchopristis numidus* (Sclerorhynchidae,
393 Elasmobranchii) from the Kem Kem beds, Morocco. In: Jalil, N-E. (Ed.): 1st International Congress on
394 North African Vertebrate Palaeontology, Program & Abstracts, Marrakech, 25-27.

395 Fastnacht, M. 2001. First record of Coloborhynchus (Pterosauria) from the Santana Formation
396 (Lower Cretaceous) of the Chapada do Araripe, Brazil. Pal. Z. 75, p.23.
397 https://doi.org/10.1007/BF03022595

398 Frey, E., Martill, D. M., Buchy, M.C. 2003. A new crested ornithocheirid from the Lower Cretaceous
399 of northeastern Brazil and the unusual death of an unusual pterosaur. In: Buffetaut, E and Mazin, J.-
400 M. (eds). Evolution and palaeobiology of pterosaurs. The Geological Society, London, Special
401 Publications 217, 55–63. https://doi.org/10.1144/GSL.SP.2003.217.01.05

402 Forey, P.L., López-Arbarello, A., MacLeod, N. 2011. A new species of *Lepidotes* (Actinopterygii:
403 Semiontiformes) from the Cenomanian (Upper Cretaceous) of Morocco. Palaeontologia
404 Electronica, 14, 1-12. https://palaeo-electronica.org/2011_1/239/index.html

405 Gaffney, E.S., Tong, H., Meylan, P.A. 2002. *Galianemys*, a new side-necked turtle (Pelomedusoides:
406 Bothremydidae) from the Late Cretaceous of Morocco. American Museum Novitates 3379, 1-20.
407 https://doi.org/10.1206/0003-0082(2002)379<0001:GANSNT>2.0.CO;2

408 Gaffney, E.S., Tong, H., Meylan, P.A. 2006. Evolution of the side-necked turtles: the families
409 Bothremydidae, Euraxemydidae, and Araripemydidae; Bulletin of the American Museum of Natural
410 History 300, 1-698. https://doi.org/10.1206/0003-0090(2006)300[1:EOTSTT]2.0.CO;2

411 Ibrahim, N., Unwin, D.M., Martill, D.M., Baidder, L., Zouhri, S. 2010. A new pterosaur
412 (Pterodactyloidea: Azhdarchidae) from the Upper Cretaceous of Morocco. PLoS ONE, 5.
413 https://doi.org/10.1371/journal.pone.0010875

414 Ibrahim, N., Sereno, P.C., Dal Sasso, C., Maganuco, S., Fabbri, M., Martill, D.M., Zouhri, S., Myhrvold,
415 N. and Iurino, D.A. 2014. Semiaquatic adaptations in a giant predatory dinosaur. Science, 345(6204),
416 1613-1616. DOI: 10.1126/science.1258750

417 Ibrahim, N., Dal Sasso, C., Maganuco, S., Fabbri, M., Martill, D.M., Gorscak, E., Lamanna, M.C. 2016.
418 Evidence of a derived titanosaurian (Dinosauria, Sauropoda) in the “Kem Kem beds” of Morocco,
419 with comments on sauropod paleoecology in the Cretaceous of Africa. Cretaceous Period: Biotic
420 Diversity and Biogeography. New Mexico Museum of Natural History and Science Bulletin 71, 149-
421 159.

422 Kaup, J. 1834. Versuch einer Eintheilung der Saugethiere in 6 Stämme und der Amphibien in 6
423 Ordnungen. Isis 3, 311-315.

424 Kellner, A.W. and Mader, B.J., 1997. Archosaur teeth from the Cretaceous of Morocco. Journal of
425 Paleontology, 71, 525-527.

426 Kellner, A.W., Campos, D.A., Sayao, J.M., Saraiva, A.A., Rodrigues, T., Oliveira, G., Cruz, L.A., Costa,
427 F.R., Silva, H.P., Ferreira, J.S. 2013. The largest flying reptile from Gondwana: a new specimen of
428 *Tropeognathus* cf. *T. mesembrinus* Wellnhofer, 1987 (Pterodactyloidea, Anhangueridae) and other
429 large pterosaurs from the Romualdo Formation, Lower Cretaceous, Brazil. Anais da Academia
430 Brasileira de Ciências 85, 113-135.

Klein, C.G., Longrich, N.R., Ibrahim, N., Zouhri, S., Martill, D.M. 2017. A new basal snake from the mid-Cretaceous of Morocco. Cretaceous Research 72, 134-141. https://doi.org/10.1016/j.cretres.2016.12.001

Larsson, H.C., Sues, H.D. 2007. Cranial osteology and phylogenetic relationships of *Hamadasuchus rebouli* (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Morocco. Zoological Journal of the Linnean Society, 149, 533-567. https://doi.org/10.1111/j.1096-3642.2007.00271.x

Lavocat, R. 1954. Sur les dinosaures du Continental intercalaire des Kem-Kem de la Daoura. In: 19ème Congrès Géologique International, Alger, 1952, Comptes Rendus. Session XII-3 15, 65-68.

Lee, Y.-N. 1994. The Early Cretaceous pterodactyloid pterosaur *Coloborhynchus* from North America. Palaeontology 37, 755-763.

Longrich, N.R., Martill, D.M. and Andres, B. 2018. Late Maastrichtian pterosaurs from North Africa and mass extinction of Pterosauria at the Cretaceous-Paleogene boundary. PLoS biology, 16. https://doi.org/10.1016/j.cretres.2017.09.006

Mader, B.J., Kellner, A.W.A. 1999. A new anhanguerid pterosaur from the Cretaceous of Morocco. Museo Nacional. Nova Série, Geologia 45, 1–11.

Mannion, P.D., Barrett, P.M. 2013. Additions to the sauropod dinosaur fauna of the Cenomanian (early Late Cretaceous) Kem Kem beds of Morocco: palaeobiogeographical implications of the mid-Cretaceous African sauropod fossil record. Cretaceous Research 45, 49-59.

Martill, D.M. 2015. First occurrence of the pterosaur *Coloborhynchus* (Pterosauria, Ornithocheiridae) from the Wessex Formation (Lower Cretaceous) of the Isle of Wight, England. Proceedings of the Geologists' Association 126, 377-380.

452 Martill, D.M., Frey, E. 1998. A new pterosaur lagerstatte in NE Brazil (Crato Formation; Aptian, Lower
453 Cretaceous): preliminary observations. Oryctos 1, 79-85.

454 Martill, D.M., Ibrahim, N., Brito, P.M., Baider, L., Zhouri, S., Loveridge, R., Naish, D., Hing, R. 2011. A
455 new Plattenkalk Konservat Lagerstätte in the Upper Cretaceous of Gara Sbaa, south-eastern
456 Morocco. Cretaceous Research 32, 433-446. https://doi.org/10.1016/j.cretres.2011.01.005

457 Martill, D.M., Ibrahim, N. 2012. Aberrant rostral teeth of the sawfish *Onchopristis numidus* from the
458 Kem Kem beds (? early Late Cretaceous) of Morocco and a reappraisal of *Onchopristis* in New
459 Zealand. Journal of African Earth Sciences 64, 71-76.
460 https://doi.org/10.1016/j.jafrearsci.2011.11.009

461 Martill, D.M., Unwin, D.M. 2012. The world's largest toothed pterosaur, NHMUK R481, an
462 incomplete rostrum of *Coloborhynchus capito* (Seeley, 1870) from the Cambridge Greensand of
463 England. Cretaceous Research 34 1-9. https://doi.org/10.1016/j.cretres.2011.09.003

464 Martill, D.M., Unwin, D.M., Ibrahim, N., Longrich, N. 2018. A new edentulous pterosaur from the
465 Cretaceous Kem Kem beds of south eastern Morocco. Cretaceous Research 84, 1-12.
466 https://doi.org/10.1016/j.cretres.2017.09.006

467 Molnar, R.E., Thulborn, R.A. 2007. An incomplete pterosaur skull from the Cretaceous of north-
468 central Queensland, Australia. Arquivos do Museu Nacional, Rio de Janeiro 65, 461-470.

469 Myers, T.S., 2015. First North American occurrence of the toothed pteranodontoid pterosaur
470 *Cimoliopterus*. Journal of Vertebrate Paleontology, 35.
471 https://doi.org/10.1080/02724634.2015.1014904

472 Owen, R., 1861. Supplement (No. III) to the Monograph on the fossil Reptilia of the Cretaceous
473 Formations. - Monographs of the Palaeontographical Society, 1-19.

474 Owen, R., 1874. The Fossil Reptilia of the Mesozoic Formations. Palaeontographical Society
475 Monographs 5, 1–118.

476 Plieninger, F. 1901. Beiträge zur Kenntnis der Flugsaurier. Palaeontographica, 48, 65-90.

477 Rage, J.C., Dutheil, D.B. 2008. Amphibians and squamates from the Cretaceous (Cenomanian) of
478 Morocco - A preliminary study, with description of a new genus of pipid frog. Palaeontographica
479 Abteilung A 285, 1–22. DOI: 10.1127/pala/285/2008/1

480 Rodrigues, T., Kellner, A.W. 2008. Review of the pterodactyloid pterosaur *Coloborhynchus*. Zitteliana,
481 117,219-228.

482 Rodrigues, T., Kellner, A.W.A. 2013. Taxonomic review of the *Ornithocheirus* complex (Pterosauria)
483 from the Cretaceous of England. ZooKeys (308), 1-112. doi: 10.3897/zookeys.308.5559

484 Rodrigues, T., Kellner, A.W., Mader, B.J., Russell, D.A. 2011. New pterosaur specimens from the Kem
485 Kem beds (Upper Cretaceous, Cenomanian) of Morocco. Rivista Italiana di Paleontologiae
486 Stratigrafia 117 (1), 149-160

487 Rodrigues, T., Jiang, S., Cheng, X., Wang, X., Kellner, A.W. 2015. A new toothed pteranodontoid
488 (Pterosauria, Pterodactyloidea) from the Jiufotang Formation (Lower Cretaceous, Aptian) of China
489 and comments on *Liaoningopterus gui* Wang and Zhou, 2003. Historical Biology 27, 782-795.
490 https://doi.org/10.1080/08912963.2015.1033417

491 Seeley, H.G. 1870. The Ornithosauria: an elementary study of the bones of pterodactyles, made from
492 fossil remains found in the Cambridge Upper Greensand, and arranged in the Woodwardian
493 Museum of the University of Cambridge. Deighton, Bell.

494 Seeley, H.G. 1891. **O**n the shoulder girdle in Cretaceous Ornithosauria, Annals and Magazine of
495 Natural History 6, 438-445

496 Sereno, P.C., Dutheil, D.B., Iarochene, M., Larsson, H.C., Lyon, G.H., Magwene, P.M., Sidor, C.A.,
497 Varricchio, D.J., Wilson, J.A. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal
498 differentiation. Science 272, 986-991. DOI: 10.1126/science.272.5264.986

499 Sereno, P.C., Larsson, H.C. 2009. Cretaceous crocodyliforms from the Sahara. ZooKeys 28, 1-143. doi:
500 10.3897/zookeys.28.325

501 Steel, L., Martill, D.M., Unwin, D.M., Winch, J.D. 2005. A new pterodactyloid pterosaur from the
502 Wessex Formation (Lower Cretaceous) of the Isle of Wight, England. Cretaceous Research 26 (4),
503 686-698. DOI:10.1016/j.cretres.2005.03.005

504 Unwin, D.M. 2001. An overview of the pterosaur assemblage from the Cambridge Greensand
505 (Cretaceous) of Eastern England. Mitteilungen aus dem Museum fur Naturkunde in Berlin,

506 Geowissenschaftliche Reihe 4: 189–221. **https://doi.org/10.1002/mmng.20010040112**

507 Unwin, D.M. 2003. On the phylogeny and evolutionary history of pterosaurs. In: Buffetaut, E and
508 Mazin, J.-M. (eds). Evolution and palaeobiology of pterosaurs. Geological Society, London, Special
509 Publications 217, 139-190. https://doi.org/10.1144/GSL.SP.2003.217.01.11

510 Unwin, D.M., 2006. Pterosaurs: from deep time. New York: Pi Press. 347 pp.

511 Unwin, D.M., Martill, D.M. 2007. Pterosaurs of the Crato Formation. In: Martill, D.M., Bechly, G.,
512 Loveridge, R.F. (eds), *The Crato fossil beds of Brazil: window into an ancient world.* Cambridge
513 University Press, Cambridge, 475-524.

514 Veldmeijer, A.J. 2003a. Preliminary description of a skull and wing of a Brazilian Cretaceous (Santana
515 Formation; Aptian–Albian) pterosaur (Pterodactyloidea) in the collection of the AMNH. PalArch's
516 Journal of Vertebrate Palaeontology 0, 1-14.

517 Veldmeijer, A.J. 2003b. Description of *Coloborhynchus spielbergi* sp. nov. (Pterodactyloidea) from
518 the Albian (Lower Cretaceous) of Brazil. Scripta Geologica 125, 35-139.

519 Veldmeijer, A.J. 2006. Toothed pterosaurs from the Santana Formation (Cretaceous; Aptian-Albian)
520 of northeastern Brazil. A reappraisal on the basis of newly described material (PhD Thesis, Utrecht
521 University, Netherlands).

522 Wang, X., Zhou, Z., Zhang, F., Xu, X. 2002. A nearly completely articulated rhamphorhynchoid
523 pterosaur with exceptionally well-preserved wing membranes and “hairs” from Inner Mongolia,
524 northeast China. Chinese Science Bulletin 47, 226-230. https://doi.org/10.1360/02tb9054

525 Wang, X., Zhou, Z. 2003. A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous
526 Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy. Chinese
527 Science Bulletin 48, 16-23. https://doi.org/10.1007/BF03183326

528 Wang, X., Zhou, Z., 2004. Palaeontology: pterosaur embryo from the Early Cretaceous. Nature 429
529 (6992), p.621. https://doi.org/10.1038/429621a

530 Wang, X., Kellner, A.W., Jiang, S., Cheng, X. 2012. New toothed flying reptile from Asia: close
531 similarities between early Cretaceous pterosaur faunas from China and
532 Brazil. Naturwissenschaften, 99, pp.249-257. DOI: 10.1007/s00114-012-0889-1

533 Wang, X., Kellner, A.W., Jiang, S., Wang, Q., Ma, Y., Paidoula, Y., Cheng, X., Rodrigues, T., Meng, X.,
534 Zhang, J. and Li, N., 2014. Sexually dimorphic tridimensionally preserved pterosaurs and their eggs
535 from China. Current Biology, 24,1323-1330. https:/doi.org/10.1016/j.cub.2014.04.054

536 Wellnhofer, P. 1985. Neue Pterosaurier aus der Santana-Formation (Apt) der Chapada do Araripe,
537 Brasilien. *Paläontographica* A 187, 105-182. [In German]

538 Wellnhofer, P. 1987. New crested pterosaurs from the Lower Cretaceous of Brazil. Mitteilungen der
539 Bayerischen Staatssammlung für Paläontologie und historische Geologie 27, 175-186.

540 Wellnhofer, P., Buffetaut, E. 1999. Pterosaur remains from the Cretaceous of
541 Morocco. Paläontologische Zeitschrift 73, p.133. https://doi.org/10.1007/BF02987987

542 Wilson, J.A., Allain, R. 2015. Osteology of *Rebbachisaurus garasbae* Lavocat, 1954, a diplodocoid
543 (Dinosauria, Sauropoda) from the early Late Cretaceous–aged Kem Kem beds of southeastern
544 Morocco. Journal of Vertebrate Paleontology 35. https://doi.org/10.1080/02724634.2014.1000701

545 Witton, M. P. 2013. Pterosaurs: natural history, evolution, anatomy. Princeton University Press.

546 Yabumoto, Y., Uycno, T., 2005. New materials of a Cretaceous coelacanth, *Mawsonia lavocati*
547 Tabaste from Morocco. Bulletin of the National Science Museum, Tokyo, 31, 39–49.

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.

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

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, *Coloborhynhcus clavirostris*, NHMUK 1822, Hastings Sand Formation (Valanginian), Sussex, England; H. *Coloborhynchus capito*, CAMSM B 54625, Cambridge Greensand (Albian), Cambridge, England; I, *Coloborhynchus fluvioferox* sp. nov. FSAC-KK 10701. Scale bars = 10 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.

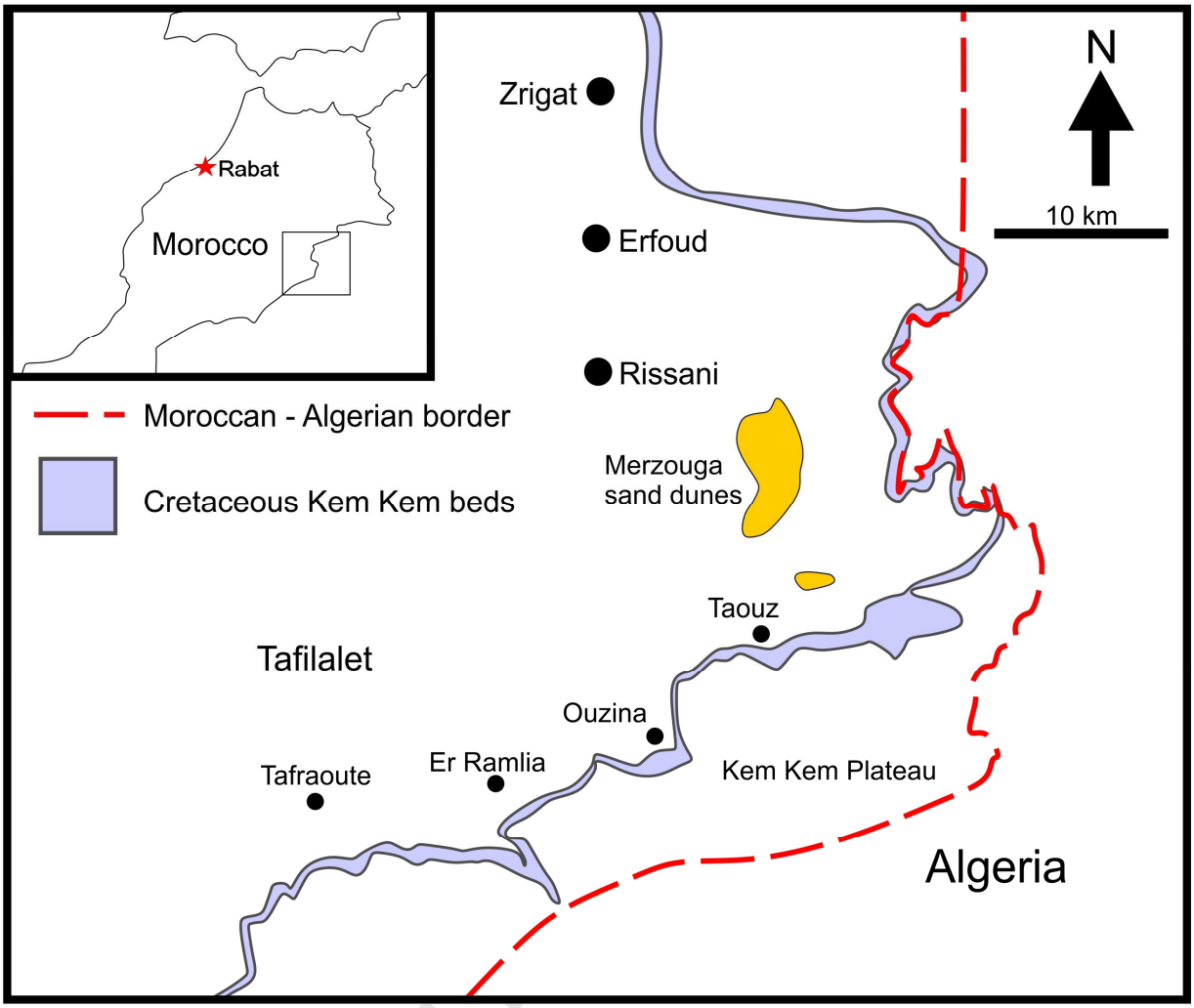
588

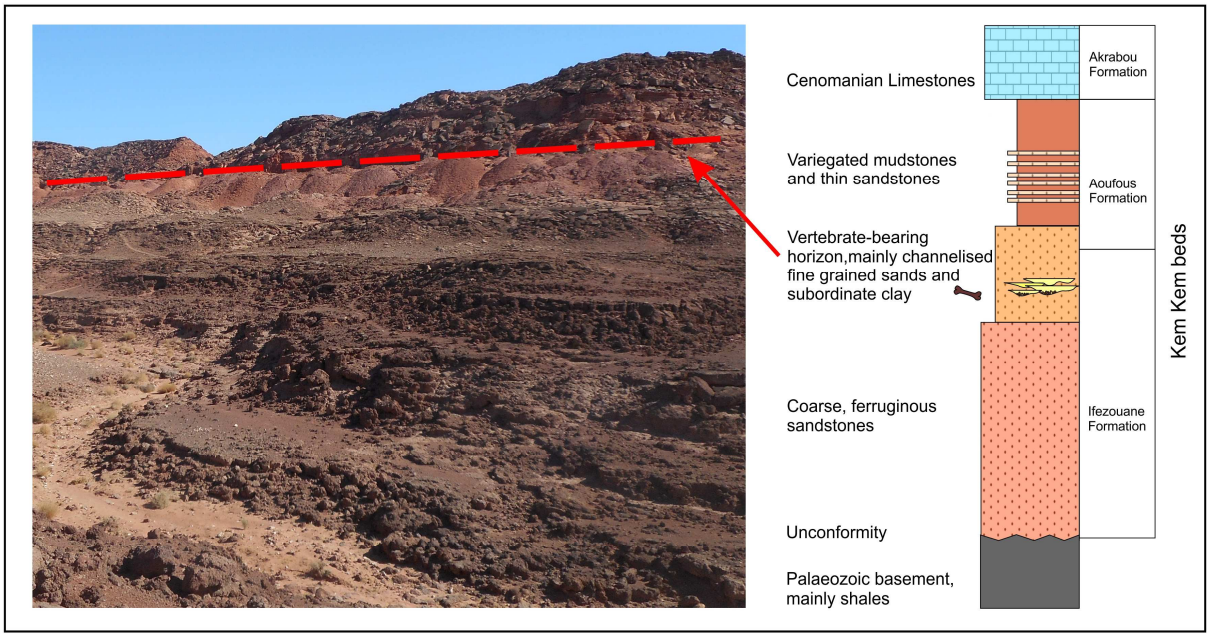
Measurement	(mm)
Height at Anterior extremity	61
Width at anterior face	31
Height at broken posterior border	54
Width at broken posterior border	39
Length of ventral surface along the median line	22.8
Space between first pair of alveoli	9.38
Space between second pair of alveoli	20
Space between third 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

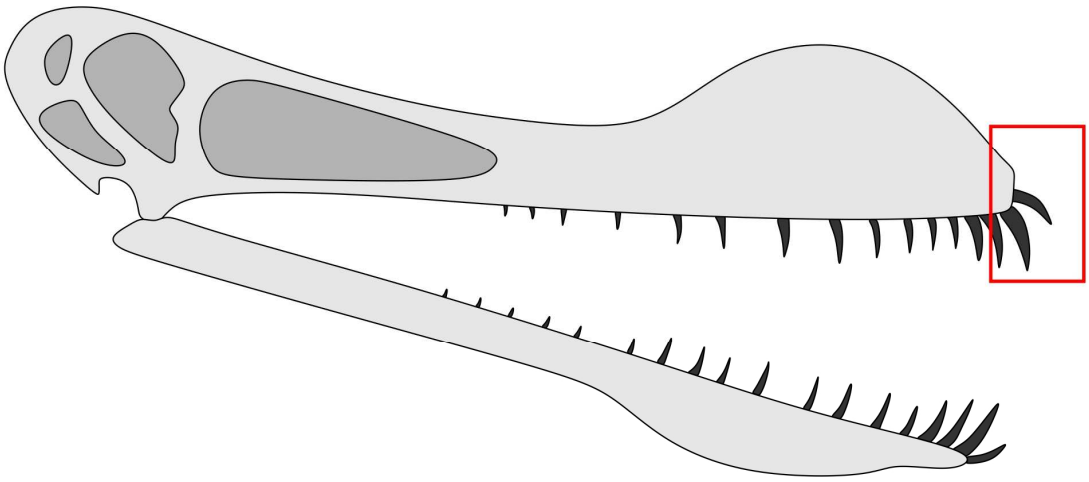
589 Table 1. Measurements of *Coloborhynchus fluviferox* sp. nov from the Kem Kem beds of Morocco.

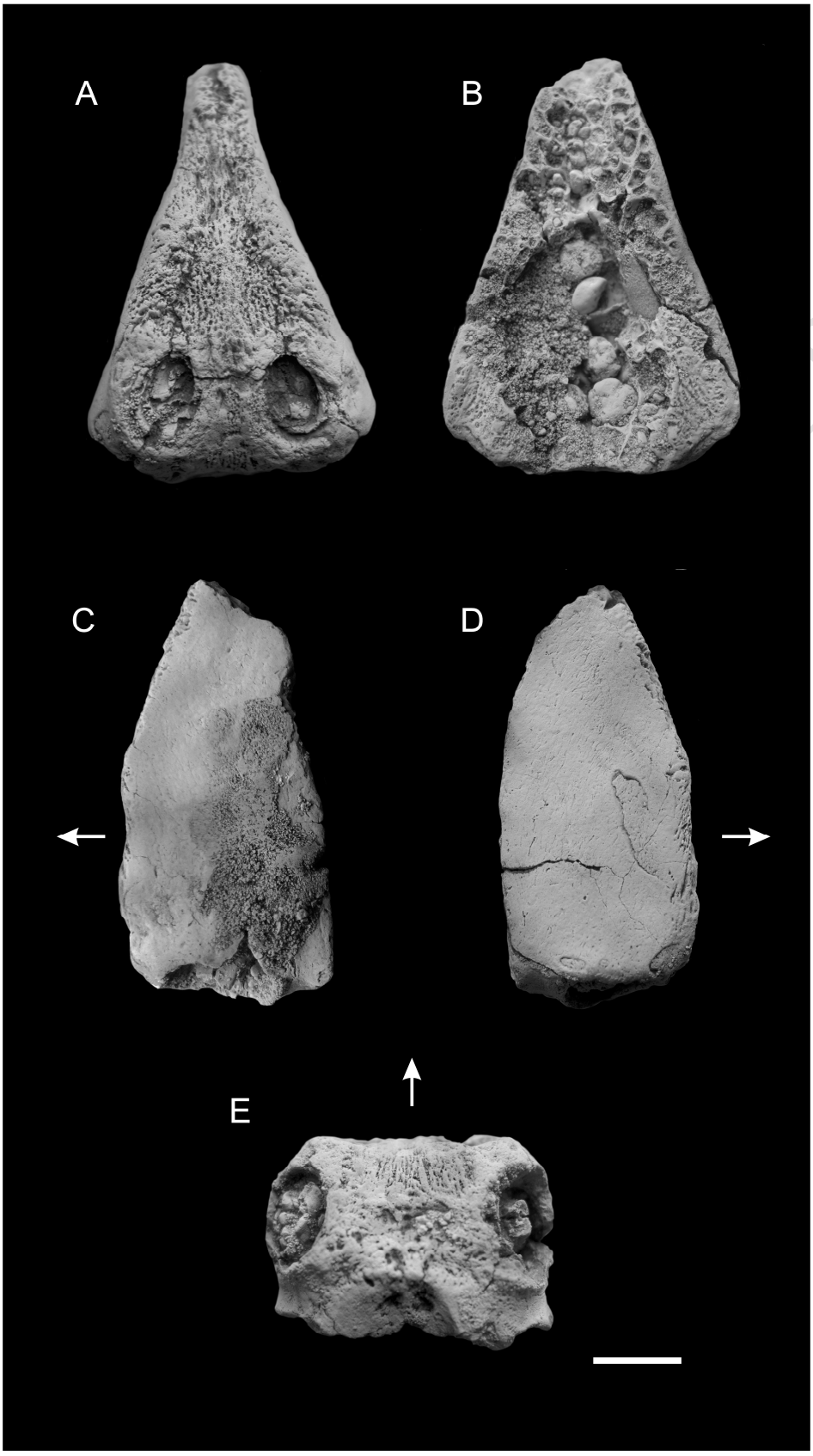
Specimen name	Number	Locality	Age	References
Anhanguera araripensis	BSP 1982 I 89; SAO 16494	Santana Formation, Brazil	Aptian-Albian	Wellnhofer, 1985
Anhanguera piscator	NSM-PV 19892	Santana Formation, Brazil	Aptian-Albian	Campos and Kellner, 1985
Anhanguera robustus	BSP 1987 I 47; SMNK 2302 PAL	Santana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

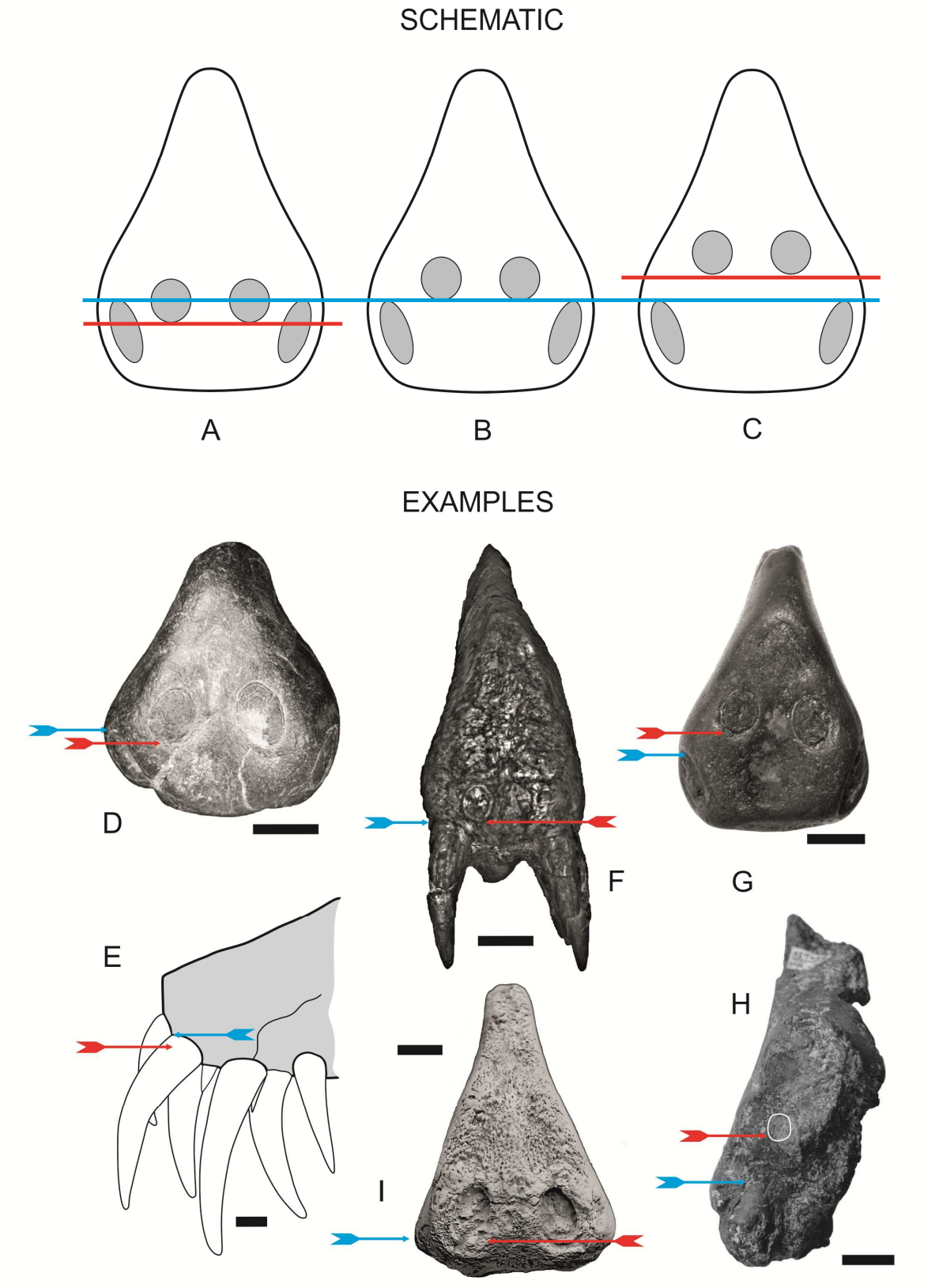
590 Table 2. List of comparative taxa used in character matrix

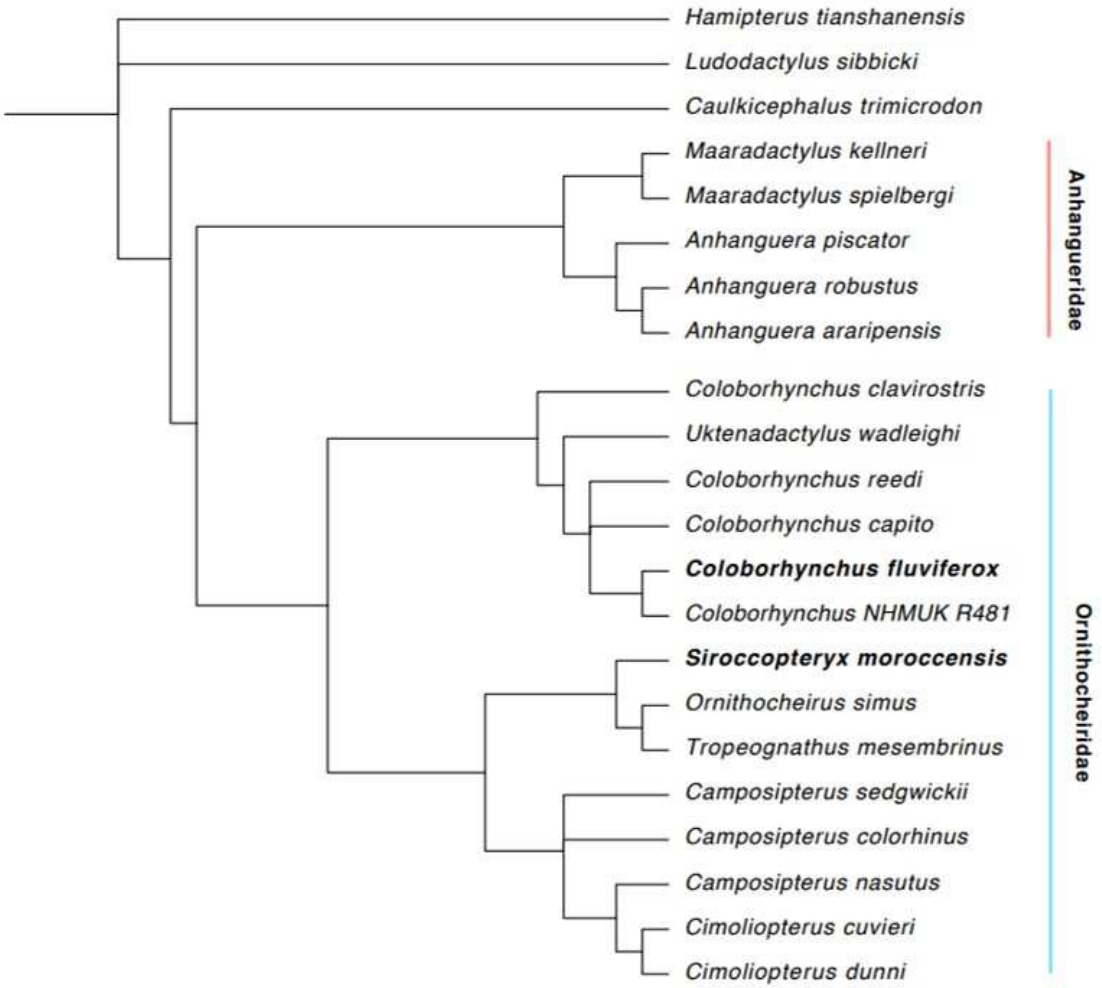

Rabat
Morocco
Zrigat
Erfoud
Rissani
N
10 km
Moroccan - Algerian border
Cretaceous Kem Kem beds
Merzouga
sand dunes
Taouz
Tafilalet
Ouzina
Er Ramlia
Tafraoute
Kem Kem Plateau
Algeria

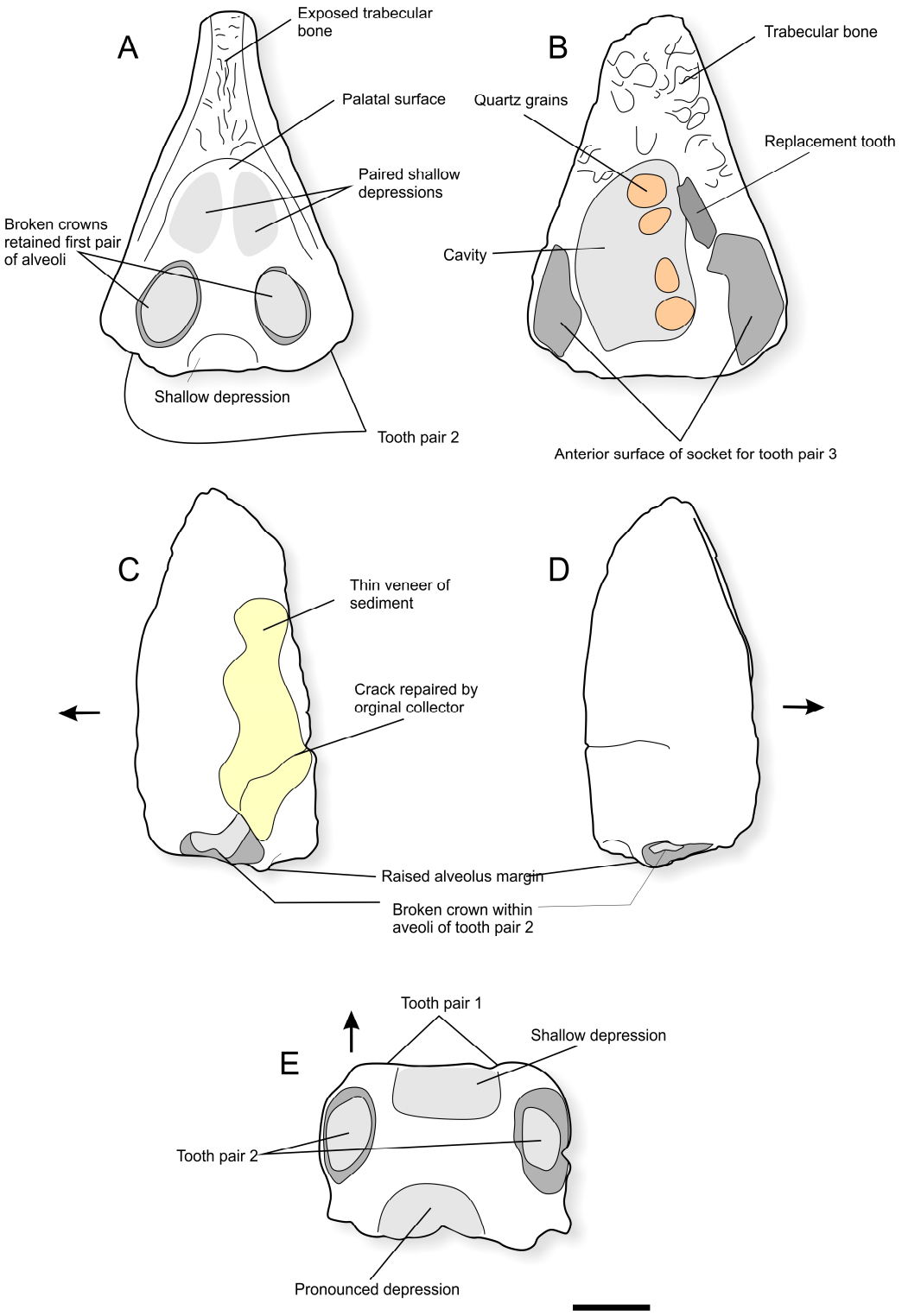


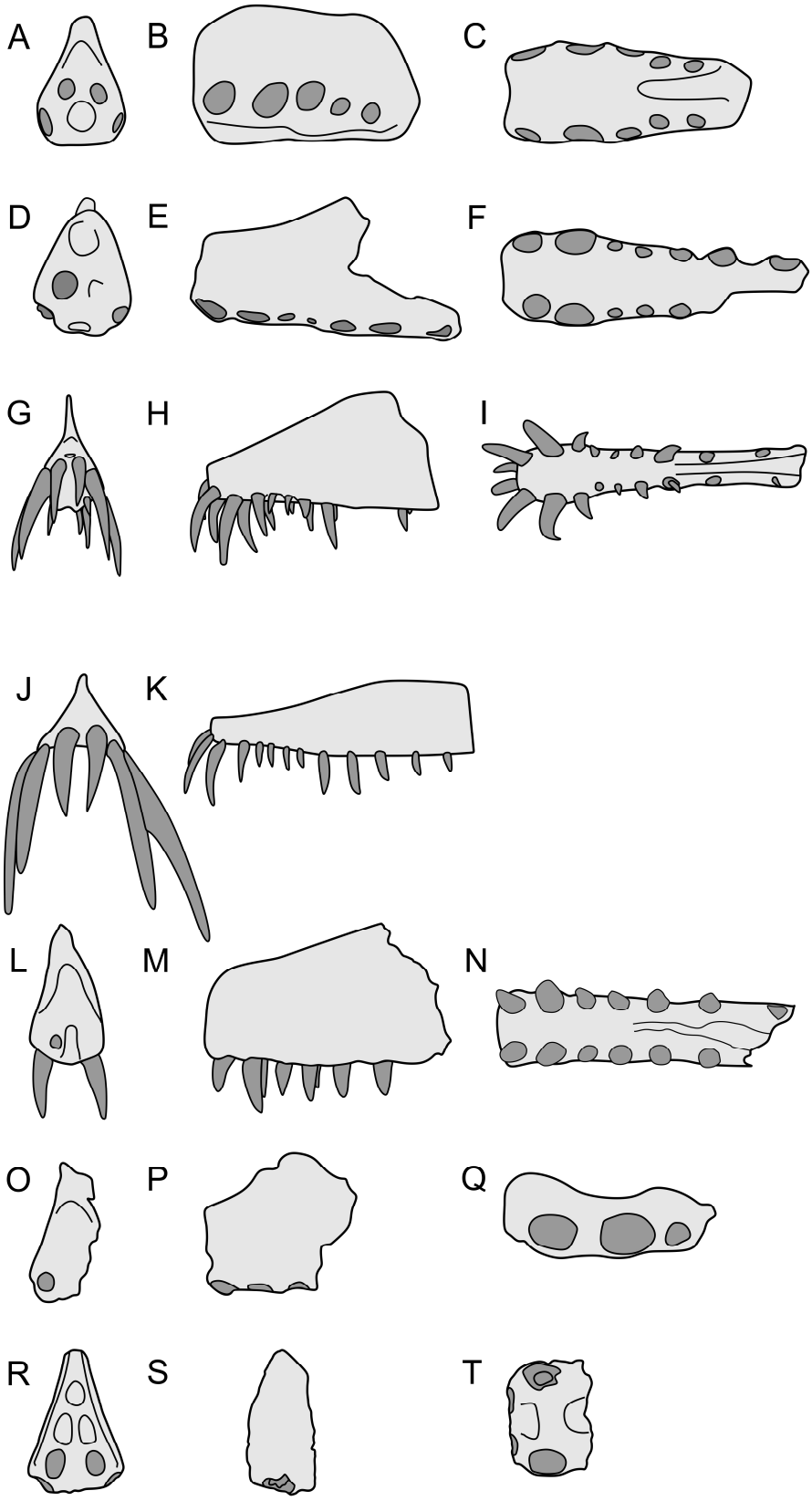



A
B
C
D
E


SCHEMATIC
A
B
C
EXAMPLES
D
F
G
E
H
I


Hamipterus tianshanensis
Ludodactylus sibbicki
Caulkicephalus trimicrodon
Maaradactylus kellneri
Maaradactylus spielbergi
Anhanguera piscator
Anhanguera robustus
Anhanguera araripensis
Anhanguerida
Coloborhynchus clavirostris
Uktenadactylus wadleighi
Coloborhynchus reedi
Coloborhynchus capito
Coloborhynchus fluviferox
Coloborhynchus NHMUK R481
Siroccopteryx moroccensis
Ornithocheirus simus
Tropeognathus mesembrinus
Camposipterus sedgwickii
Camposipterus colorhinus
Camposipterus nasutus
Cimoliopterus cuvieri
Cimoliopterus dunni
Ornithocheiridae


A
Exposed trabecular bone
Palatal surface
Paired shallow depressions
Broken crowns retained first pair of alveoli
Shallow depression
Tooth pair 2
B
Trabecular bone
Quartz grains
Replacement tooth
Cavity
Anterior surface of socket for tooth pair 3
C
Thin veneer of sediment
Crack repaired by orginal collector
D
Raised alveolus margin
Broken crown within aveoli of tooth pair 2
E
Tooth pair 1
Shallow depression
Tooth pair 2
Pronounced depression


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T