

A new ornithocheirid pterosaur (Pterosauria: Ornithocheiridae) from the mid-Cretaceous Ifezouane Formation, Kem Kem Group of Morocco

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ABSTRACT

A new ornithocheirid pterosaur, *Akharhynchus martilli* gen. et. sp. nov. from the Ifezouane Formation, Kem Kem Group of Morocco is described, based on a well-preserved anterior rostrum fragment. It is assigned to a new genus based on one autapomorphy and a unique combination of synapomorphies, including the following: the medial rims of the first alveoli pair contact each other and the first alveoli pair are 50% smaller than the second alveoli pair. Comparative anatomy and a phylogenetic analysis demonstrate that *Akharhynchus* has affinities with *Tropeognathus* within Tropeognathinae.

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1. Introduction

Pterosaurs ranged from the Late Triassic to the end Cretaceous. They were incredibly morphologically diverse and had a global distribution, with a distinctive anatomy allowing powered flight (Wellnhofer, 1991; Unwin, 2005; Witton, 2013). Among them, the Ornithocheiridae (*sensu* Unwin, 2003) were a successful clade of piscivorous pterosaurs with long, slender, conical teeth in the anterior parts of the jaws, and shorter, laterally compressed triangular teeth in the posterior regions of the jaws. Some may have achieved a wingspan of up to 8 m (Martill and Unwin, 2012; Kellner et al., 2013). The clade ranged from the Valanginian to the end Cenomanian, and the cause of their extinction remains poorly understood (Martill and Smith, 2024). Averianov (2014) linked their extinction to the loss of prey items at the Cenomanian-Turonian extinction event which occurred during a peak global greenhouse interval and high sea levels. Ornithocheiridae, as with many pterosaur clades, has a somewhat patchy temporal and geographic distribution with the oldest remains being fragmentary material discovered in the Early Cretaceous strata of England during the 19th century (e.g., Owen, 1851, 1859, 1861; Seeley, 1869, 1870; Unwin, 2001). Subsequently, ornithocheirid remains have

been found on almost every continent (e.g., Barrett et al., 2008; Martill and Smith, 2024).

In recent years the mid-Cretaceous (?Albian-Cenomanian) Kem Kem Group of southeast Morocco has proved important for understanding Cretaceous pterosaur diversity in Africa. The assemblage has a remarkable diversity of pterosaurs with nine named taxa of both edentulous azhdarchoids and toothed ornithocheirids (Table 1) and at least three additional distinct azhdarchoid jaw morphologies (Smith et al., 2023a, b) hinting at even higher diversity. Four ornithocheirids have so far been described from the Kem Kem Group, all based on anterior fragments of the upper and lower jaws (Mader and Kellner, 1999; Jacobs et al., 2019, 2020; Smith et al., 2023a). Ornithocheirid remains (excluding teeth) in the Kem Kem Group are relatively rare compared to those of azhdarchoids, with very low abundances of identifiable post-cratal elements (Smith et al., 2023c). Here we describe a new specimen of anterior rostrum fragment from the Ifezouane Formation of the Kem Kem Group, representing a new genus and species of ornithocheirid.

2. Locality and geological setting

2.1. Locality

In Morocco the Kem Kem Group is exposed predominantly in the northwestern Sahara Desert and along the southern flank of the

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Table 1

Pterosaur taxa from the Kem Kem Group of Morocco.

Higher clade	Family	Taxon	Reference
Azhdarchoidea	Tapejaridae	<i>Afrotapejara zouhrii</i>	Martill et al. (2020)
	Azhdarchidae	<i>Alanka saharica</i>	Ibrahim et al. (2010)
	?Chaoyangopteridae	<i>Apatorhamphus gyrostega</i>	McPhee et al. (2020)
	Incertae sedis	<i>Leptostomia begaaensis</i> <i>Xericeps curvirostris</i> <i>Akharhynchus martilli</i> <i>Anhanguera cf. piscator</i> <i>Colororhynchus fluviiferox</i> <i>Ornithocheirus cf. simus</i> <i>Siroccoptyx moroccensis</i>	Smith et al. (2021) Martill et al. (2018) This paper Jacobs et al. (2020) Jacobs et al. (2019) Jacobs et al. (2020) Mader and Kellner (1999)
Ornithocheiroidea	Ornithocheiridae		

Atlas Mountains (Ibrahim et al., 2020, Fig. 1), with lateral equivalents in Algeria (Alloul et al., 2018; Ibrahim et al., 2020). The specimen described here (FSAC-KK 12500) was acquired by a commercial fossil trader based in the town of Erfoud, who sources fossils from a range of Kem Kem Group localities in the Tafilalt region. The specimen's preservation and adhered matrix is consistent with other Kem Kem Group fossils, but we are unable to be more precise as to which dig site the specimen came from.

2.2. Geological, stratigraphic and palaeoenvironmental context

The mid-Cretaceous Kem Kem Group is divided into two distinct units, a sandy lower unit, the Ifezouane Formation and a mudstone dominated upper unit, the Aoufous Formation, following the nomenclatural scheme of Ettachfini and Andrea (2004). The vast majority of vertebrate fossils (including all pterosaurs) come from intraformational, mud-flake conglomerates in the upper Ifezouane Formation (Martill et al., 2018). The Kem Kem Group is overlain by late Cenomanian to Turonian limestones of the Akrabou Formation and overlies a gentle topographic unconformity of Palaeozoic strata in the south or on gently folded Jurassic strata in the north and east (Fig. 1). Due to a lack of biostratigraphically useful fossils in the Kem Kem Group its precise age is unknown (Ibrahim et al., 2020). Currently the consensus is that the Kem Kem Group is ?Albian to lower Cenomanian in age and thus spans the Lower–Upper Cretaceous boundary. The Kem Kem Group represents a continental deposit dominated by a fluvial setting, with lacustrine and rare short-lived shallow marine environments (Adardor et al., 2021; Beevor et al., 2021). For more detailed geological, stratigraphic and palaeoenvironmental information see Ibrahim et al. (2020) and Smith et al. (2023c).

3. Material and methods

The specimen is accessioned to the collections of the Faculté des Sciences Aïn Chock, Université Hassan II, Casablanca, Morocco (FSAC-KK 12500). The specimen was imaged using a Nikon D3500 camera and images processed using CorelDRAW® Graphic Suite X8 software. It was topographically scanned using an Einscan Pro + and 3D model processed using Geomagic Design X.

3.1. Phylogenetic analysis

To assess the phylogenetic relationships of the new specimen within Ornithocheiroidea, a phylogenetic analysis was performed using the data matrix from Ozeki et al. (2023), consisting of 82 taxa and 180 characters. The matrix is unmodified except for the addition of FSAC-KK 12500, and was compiled in Mesquite 3.81. The phylogenetic analysis was performed using PAUP* version 4.0a169 using a heuristic search with the TBR algorithm, with Max trees = 100 and collapsing tree after the search. The search

recovered 100 trees. A strict consensus tree is published, with a consistency index = 0.58, retention index = 0.85 and a rescaled consistency index = 0.363. See supplementary information for character list and data matrix.

3.2. Nomenclatural acts

This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature. The LSIDs for the genus is: urn:lsid:zoobank.org:act:B97ECDC8-CA09-4567-BDB2-789EBB3CABF6 and species is: urn:lsid:zoobank.org:act:AB939E27-CA1F-492E-B7F3-1AC47044AFE2.

3.3. Institutional abbreviations

AAOD (AODF), Australian Age of Dinosaurs Museum, Winton, Queensland, Australia; **BSPG** (formerly **BSP**), Bayerische Staats-sammlung für Paläontologie und Geologie, Munich, Germany; **CAMSM**, Sedgwick Museum of Earth Sciences, Cambridge, England, UK; **FSAC**, Faculté de Sciences Aïn Chock, Département de Géologie, Université Hassan II de Casablanca, Morocco; **IWCMS**, Dinosaur Isle Museum, Isle of Wight County Museum Service, Sandown, Isle of Wight, England (formerly **MIWG**); **KK**, Kronosaurus Korner Regional Museum, Richmond, Queensland, Australia; **LINHM**, Long Island Natural History Museum, Long Island, USA (there is no record of this institution); **NHMUK** (formerly **BMNH**), Natural History Museum, London, UK; **NSM-PV**, Division of Vertebrate Paleontology, National Science Museum, Tokyo, Japan; **QM**, Queensland Museum, Brisbane, Queensland, Australia; **SMNK**, Staatliches Museum für Naturkunde Karlsruhe, Germany; **SMU**, Shuler Museum of Paleontology, Southern Methodist University, Dallas, USA.

4. Results

4.1. Systematic palaeontology

PTEROSAURIA [Kaup, 1834](#)
PTEROACTYLOIDEA [Plieninger, 1901](#)
ORNITHOCHEIROIDEA [Seeley, 1891](#)
ORNITHOCHEIRIDAE *sensu* [Unwin, 2003](#)
TROPEOGNATHINAE [Holgado and Pegas, 2020](#)

Akharhynchus gen. nov.

Etymology. *Akhar* meaning “another” (Arabic); *ryncus* meaning “snout” (Greek).

Type species: *Akharhynchus martilli* gen. et sp. nov.

Diagnosis. As for the type and only species (see below)

Akharhynchus martilli gen. et sp. nov.

Etymology. Named in honour of Prof. David Martill, in recognition of his significant contributions to vertebrate palaeontology, and his generosity, kindness and friendship to the authors.

Holotype. FSAC-KK 12500. Anterior most fragment of premaxillae (Figs. 2–4)

Type locality. Tafilalt region of Morocco, exact locality unknown. Type horizon and age. Upper Ifezouane Formation, Kem Kem Group, ?Albian-Cenomanian, mid-Cretaceous.

Diagnosis. A unique combination of the following synapomorphies (autapomorphies are marked with an asterisk): first tooth-pair situated on the margin between the ventral border of the deltoid facet and anterior palate, medial rims of the first alveoli pair in contact, first alveolar pair are 50% smaller than the second alveolar pair, straight anterior margin of the palate in ventral view, palatal ridge commencing at the anterior margin of the third alveolar pair, rounded dorsal and lateral margins of the deltoid facet in anterior view*.

Description. Specimen FSAC-KK 12500 comprises of the most anterior portion of premaxillae, preserving three alveoli pairs and a partial fourth pair. Broken crowns are preserved in the first pair and left alveolus of the second pair. The specimen measures a maximum of 53 mm high, 62 mm long and has a maximum width of 37 mm (Table 2). The specimen is free of matrix, but with a small amount of quartz grit and sand infilling the broken posterior portion. The specimen was broken prior to burial as indicated by rounded bone surfaces on the bone margins.

In anterior view, the lateral margins of the deltoid facet (for definition see Jacobs et al., 2019) are slightly convex, with a curved dorsal margin. The deltoid facet bears a smooth rounded triangular ridge in the centre bordered laterally by two narrow, elongate depressions. The deltoid facet has a rugose texture with striations directed mediolateroventrally, with the ridges starting

at the central depressions. The ridged texture is restricted to the deltoid facet.

In lateral view, the dorsal margin extends at an angle of approximately 129° from the top of the deltoid facet into a posteriorly placed crest. The deltoid facet is posteriorly inclined at 78° to the ventral palate. Depressions are present on the lateral surfaces lateral to the second alveoli pair: on the left side there is a circular depression and on the right side there is an elongate depression (Figs. 2–4).

In ventral aspect, the lateral margins are straight, narrowing postero medially. The anterior margin is straight with a slight convexity at the first alveoli pair. There is an oval depression between the second alveoli pair. Posterior to the depression, a narrow ridge extends along the midline with a slight sulcus either side. The ventral surface is convex.

The first pair of alveoli are located on the ventral border of the deltoid facet with broken crowns preserved within the alveoli. The crowns are directed lateroventrally. The alveoli are almost circular with a maximum diameter of 8 mm and a minimum diameter of 6 mm. There is a prominent raised rim between the first and second pair of alveoli on the ventral surface, whereas on the anterior surface the alveoli rim is thin. The pair of alveoli are only 2 mm apart, with the medial alveoli rims touching.

The second pair of alveoli are circular and directed anteroventrally, with a maximum diameter of 10 mm and a minimum of 8 mm. The preserved broken crown in the right alveolus is directed ventrally. The third pair of alveoli are oval and directed ventrally, with a maximum diameter of 17 mm and a minimum diameter of 6 mm. Second and third pair are equally spaced, with a minimum of 5 mm and a maximum of 6 mm between them. The right fourth alveolus is not preserved. The left is preserved only as a portion of its anterior border. There are no raised rims for the second, third or fourth alveoli pairs.

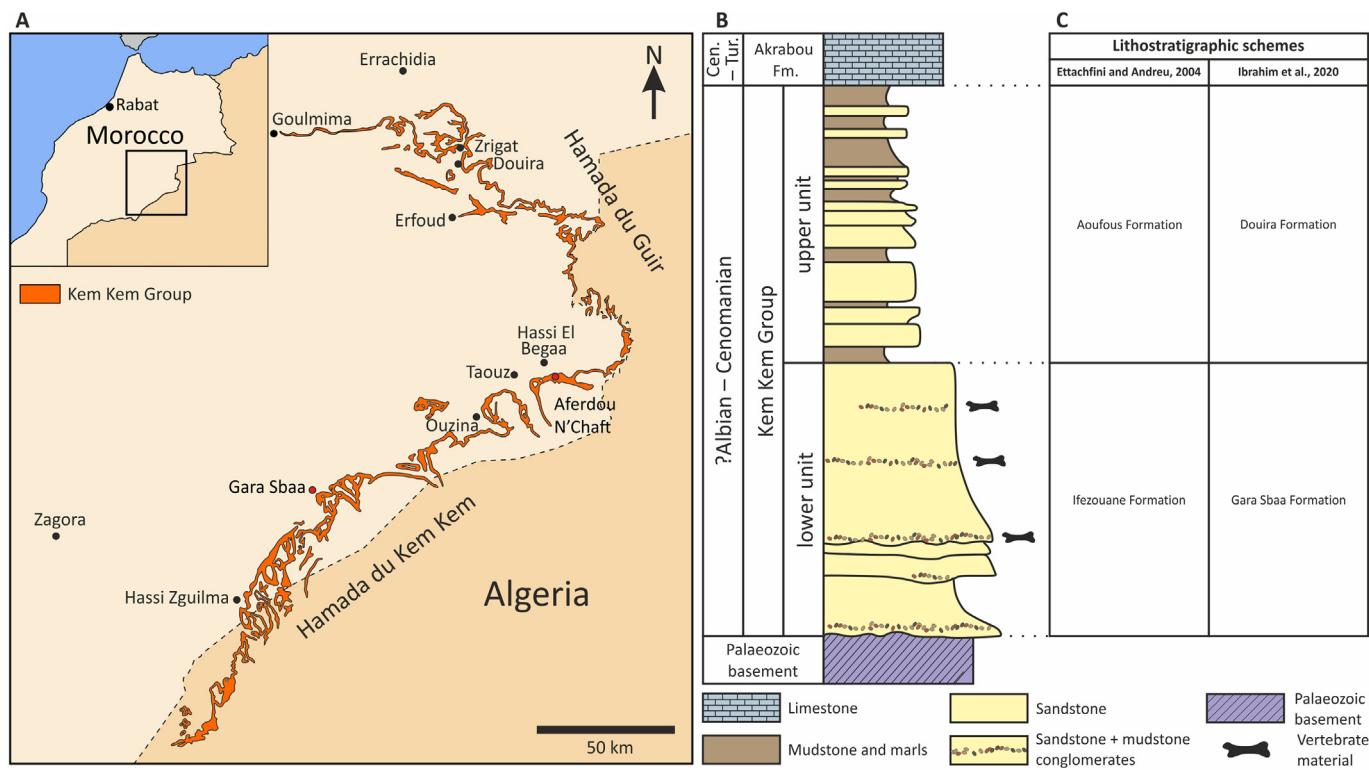


Fig. 1. A, map of south-east Morocco showing the Kem Kem Group exposures; B, generalised stratigraphic column of the Kem Kem Group; C, lithostratigraphic schemes proposed for the upper and lower units of the Kem Kem Group of Morocco. From Smith et al. (2023c).

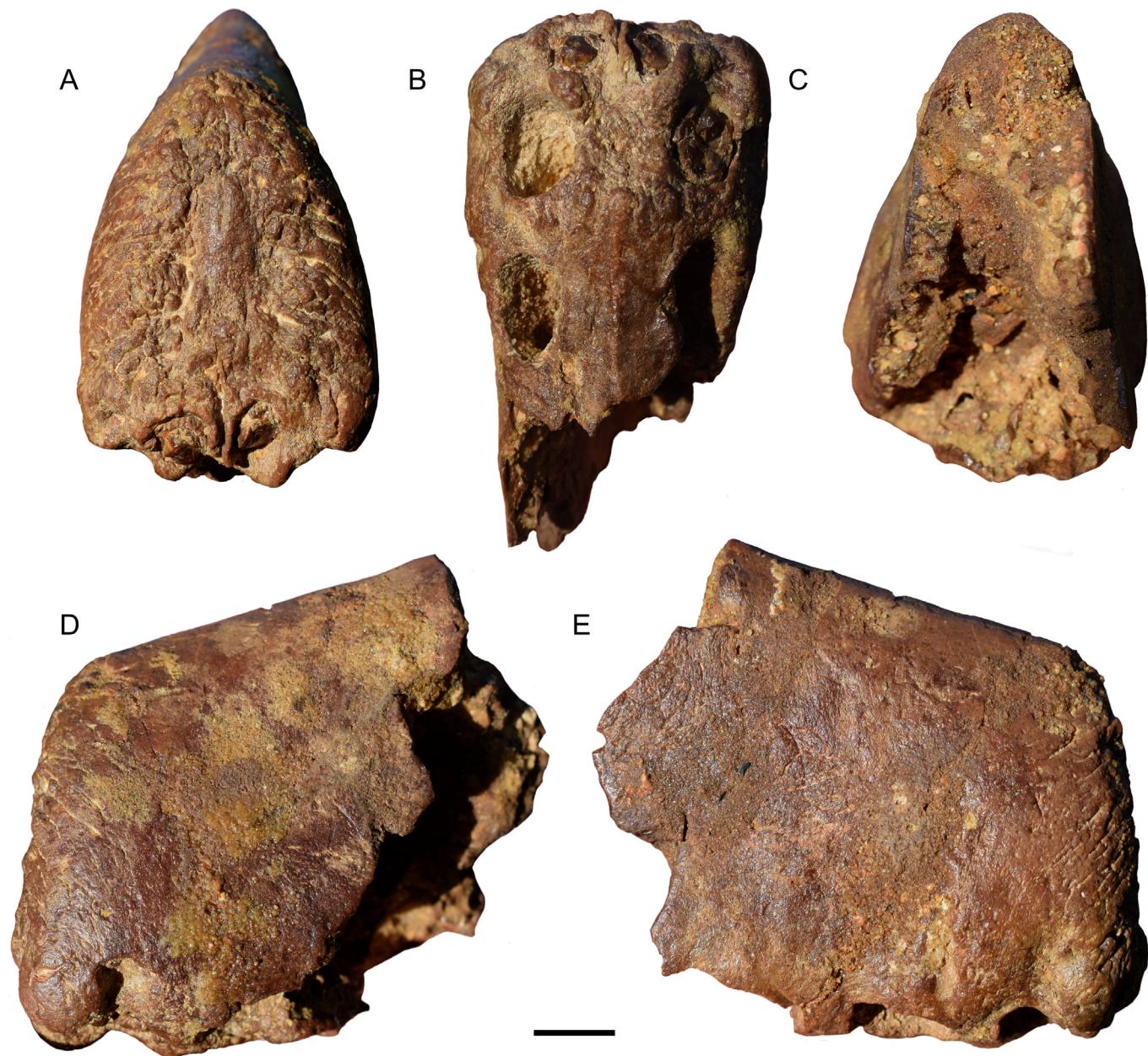


Fig. 2. Holotype rostrum of *Akharhynchus martilli* gen. et sp. nov. FSAC-KK 12500 from the Kem Kem Group of Morocco. A, anterior view; B, ventral view; C, posterior view; D, left lateral view; E, right lateral view. Scale bar = 10 mm.

5. Discussion

5.1. Comparisons with other ornithocheirids

Akharhynchus differs from all species of *Coloborhynchus* Owen, 1874, and most notably *C. capito* (Seeley, 1870), *C. clavirostris* Owen (1874), *C. fluviferox* Jacobs et al. (2019), and *Coloborhynchus* sp. (Jacobs et al., 2020), by several characters. Firstly, in *Coloborhynchus* the first alveoli pair are on the deltoid facet whereas in *Akharhynchus* the first pair are on the deltoid facet-palate boundary. The first alveoli pair are also notably smaller in *Akharhynchus* than in *Coloborhynchus*. The rest of the alveoli pairs in *Coloborhynchus* are directed lateroventrally, whereas in *Akharhynchus* the second pair of alveoli are directed ventrally. The lateral margins in anterior view are concave in *Coloborhynchus* whereas they are

convex in *Akharhynchus*. *Akharhynchus* does share straight and mediolaterally narrowing lateral margins and a broad anterior margin with *C. clavirostris*, and a straight anterior margin in ventral view with all species of *Coloborhynchus* (Figs. 5–7). However, the differences are such in number that *Akharhynchus* does not share any affinities with *Coloborhynchinae* sensu Holgado and Pégas, 2020.

Tropeognathus Wellnhofer, 1987 resembles *Akharhynchus* by having the first alveoli pair situated on the palatal-deltoid facet margin, with the rims of the first alveoli pair in contact. The deltoid facet is also posteriorly inclined. However, the palatal ridge in *Tropeognathus* starts at 5th tooth pair and the depression on the anterior portion of the palate is absent. The anterior margin of the palate is rounded in *Tropeognathus* and straight in *Akharhynchus*. The dorsal margin in *Tropeognathus* goes straight into a prominent

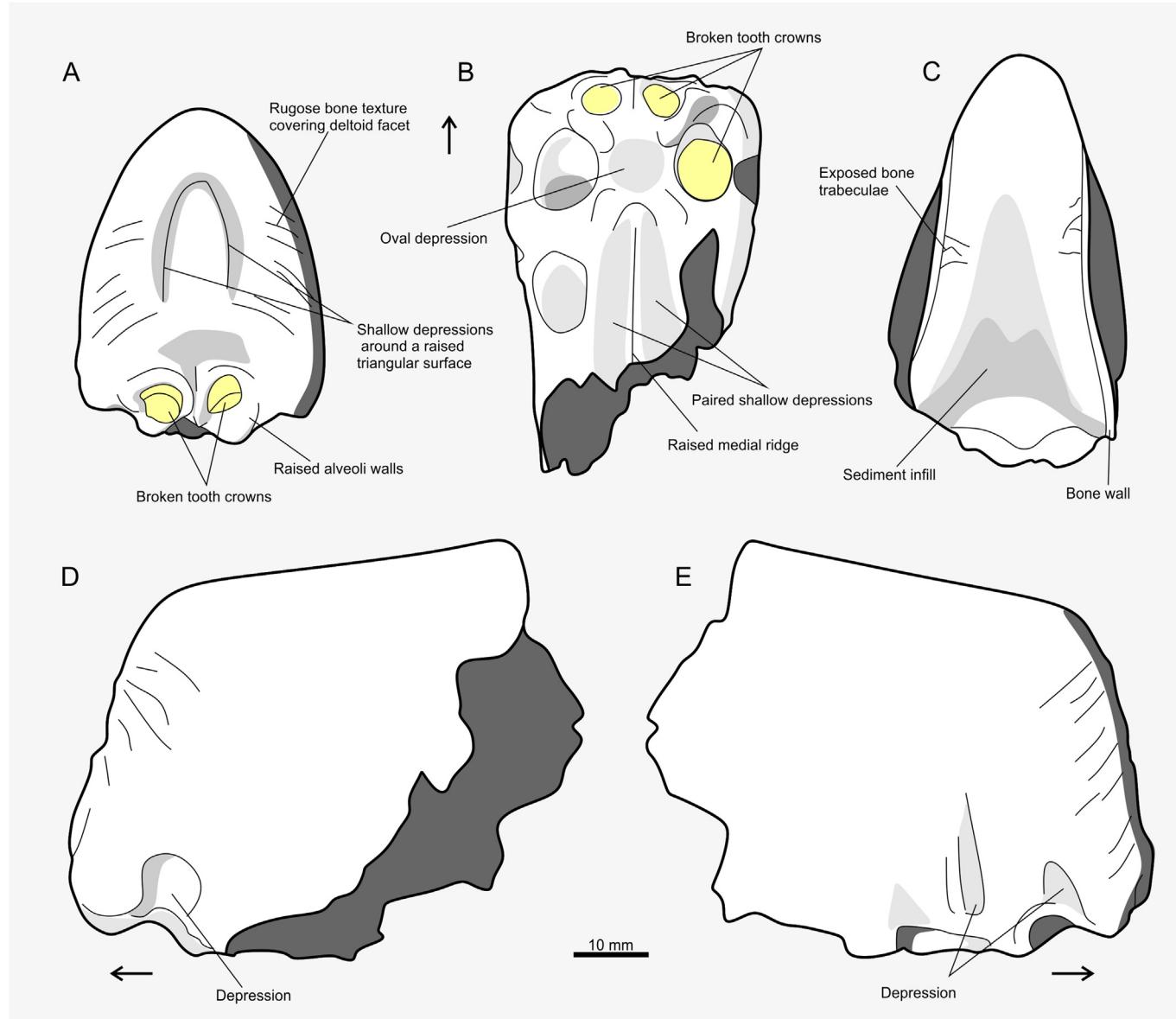


Fig. 3. Line drawings of the holotype rostrum of *Akharhynchus martilli* gen. et sp. nov. FSAC-KK 12500 from the Kem Kem Group of Morocco. A, anterior view; B, ventral view; C, posterior view; D, left lateral view; E, right lateral view. Scale bar = 10 mm.

anterior crest, whereas the incline is more gradual in *Akharhynchus*, and the deltoid facet in *Tropeognathus* has straight lateral margins compared to the convex margins in *Akharhynchus* (Fig. 6).

Akharhynchus is similar to *Ornithocheirus* Seeley, 1869, both the type species *Ornithocheirus simus* Owen (1861) (holotype: CAMSM B54428) and the referred Kem Kem Group specimen FSAC-KK 5025, with a small first alveoli pair relative to the second and third pairs and convex lateral margins. Both also possess a palatal ridge bordered by two long depressions commencing at the second alveoli pair, along with near circular first and second alveoli pairs and an oval third pair of alveoli. However, *Ornithocheirus* differs in having the first pair of alveoli situated on the ventral palate and are widely spaced apart. There is also no depression between the second alveoli pair (Figs. 5–6).

Siroccopteryx Mader and Kellner, 1999 shares with *Akharhynchus* straight lateral margins of the palatal surface, a straight anteroventral margin, in lateral view the deltoid palate is posteriorly inclined, and a straight dorsal margin inclined at 87.3° to the

deltoid facet. As well as convex lateral margins in anterior view. The notable differences are; *Siroccopteryx* has a narrower dorsal margin of the deltoid facet, whereas *Akharhynchus* is wide and rounded. In *Siroccopteryx* the first alveoli pair are situated on the deltoid facet, dorsal to the second pair, whereas in *Akharhynchus* the first pair are on the deltoid facet – palate boundary. The lateral margins in ventral view narrow in *Akharhynchus* but remain straight in *Siroccopteryx* and the palatal ridge starts at the 5th tooth pair in *Siroccopteryx*, whereas it starts at the 3rd tooth pair in *Akharhynchus* (Fig. 5).

There are no notable similarities between *Akharhynchus* and species of *Anhanguera* Campos and Kellner, 1985), *Caulkicephalus* Steel et al., 2005 and *Camposipterus* Rodrigues and Kellner, 2013. The major differences between these genera and *Akharhynchus* are the absence of a deltoid facet in *Caulkicephalus*, *Camposipterus* and juvenile specimens of *Anhanguera* and the first alveoli pair being directed anteroventrally, encompassing the entire anterior end of the rostrum (Fig. 7). In mature individuals of *Anhanguera*, there is a

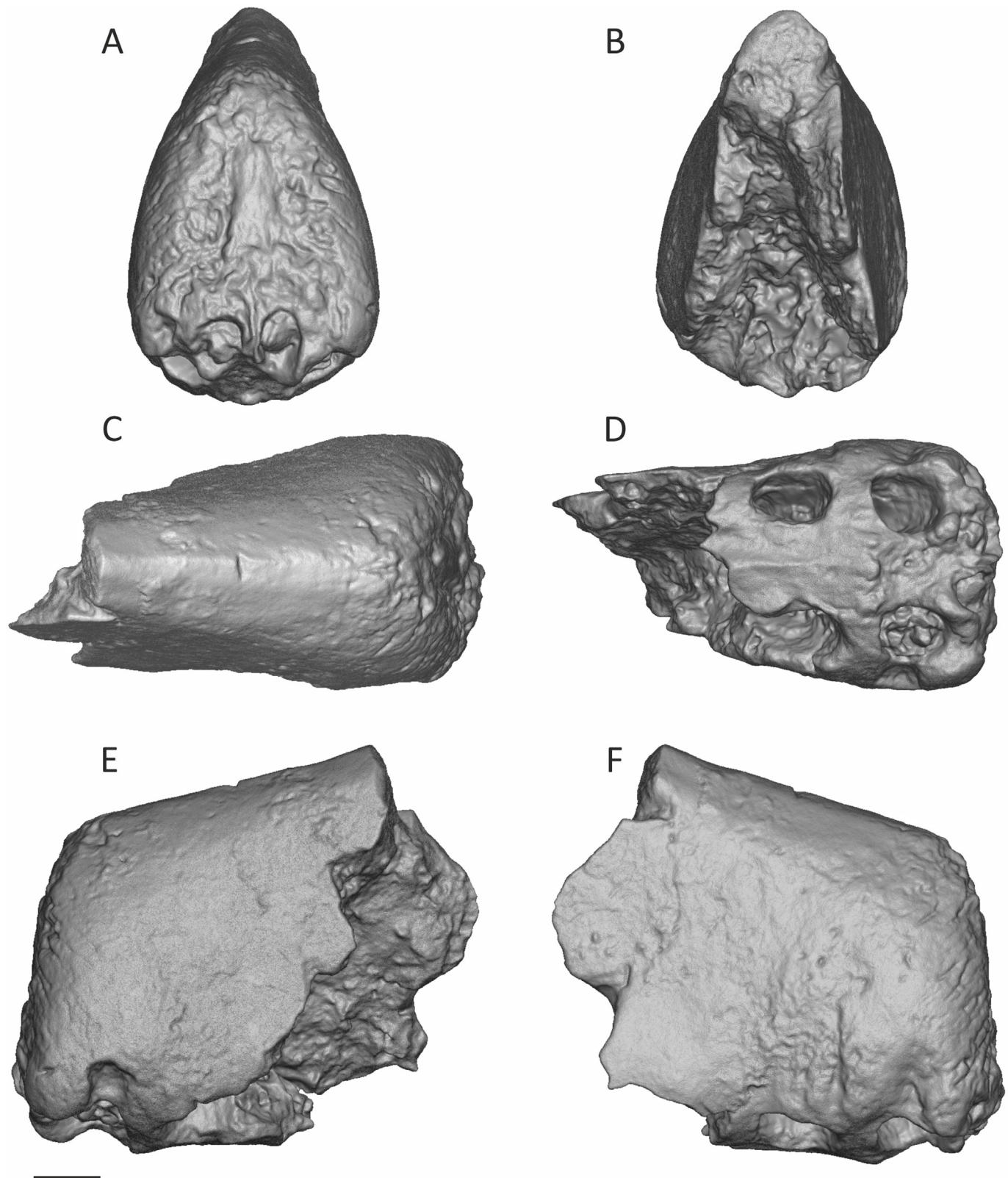


Fig. 4. Topographic scan images of the holotype rostrum of *Akharhynchus martilli* gen. et sp. nov. FSAC-KK 12500 from the Kem Kem Group of Morocco. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, left lateral view; F, right lateral view. Scale bar = 10 mm.

Table 2Measurements of holotype of *Akharhynchus martilli* gen. et sp. nov. FSAC-KK 12500.

Parameter	Measurement (mm)
Height at anterior extremity	51
Width at anterior face	38
Height at broken posterior border	60
Width at broken posterior border	29
Length of ventral surface along the median line	42
Space between first pair of alveoli	3
Space between second pair of alveoli	10
Space between third pair of alveoli	12
Maximum diameter of first pair of alveoli	7
Maximum diameter of second pair of alveoli	11
Maximum diameter of third pair of alveoli	12

subtle development of a deltoid facet, with the first alveoli pair located dorsal of the second pair (Duque et al., 2022).

Akharhynchus shares a palatal ridge and a straight anteroventral margin of the palate with *Aerodraco* Holgado and Pégas, 2020. However, it differs from *Aerodraco* in several characters, specifically, *Aerodraco sedgwickii* (Owen, 1859) bears a large pair of first alveoli which are situated on the deltoid facet, and an enlarged third alveoli pair (Fig. 6).

Uktenadactylus Rodrigues and Kellner, 2008 shares a few features with *Akharhynchus*, including a rounded dorsal margin with a gradual slope into an anterior crest, and a straight anteroventral margin. There is also a palatal ridge present in both, however in *U. wadleighi* (Lee, 1994) it is present between only the second and third alveoli pairs and is absent until the fifth alveoli pair (Fig. 6). In all other aspects, these two genera differ.

Ferrodraco Pentland et al., 2019 shares convex lateral margins of the deltoid facet and the first alveoli pair is small in respect to alveoli pairs two and three with *Akharhynchus*. In both taxa the first alveoli pair are on the palatal-deltoid facet margin and both have a palatal ridge which is more pronounced in *Akharhynchus*. There are several important differences that distinguish these genera, including the dorsal margin in lateral view is narrower and develops into a steep crest anteriorly in *Ferrodraco*. The first alveoli pair are laterally placed rather than medially as in *Akharhynchus*. The third tooth is laterally placed and circular, while in *Akharhynchus* it is more medially placed with an oval outline. There are also pronounced dorsoventral depressions between teeth on the lateral margin in *F. lentonii*, whereas *Akharhynchus* only has a depression adjacent to the second alveoli pair (Pentland et al., 2019, 2022) (Fig. 7).

Thapunngaka Richards et al., 2021 shares few features with *Akharhynchus*. With the first alveoli pair situated on the lateral margins, rather than placed anteriorly, in addition to a well-developed anteriorly developed crest (Richards et al., 2021, 2024), which is absent in *Akharhynchus* (Fig. 7).

A comparison with *Mythunga Molnar and Thulborn, 2007*, is not currently possible due to the type species *M. camara* Molnar and Thulborn (2007) (QM F 18896), missing the anterior most portion of the rostrum.

Akharhynchus also differs substantially from both *Hamipterus Wang et al., 2014* and *Iberodactylus Holgado et al., 2019*. The most notable difference is the lack of a developed deltoid facet and a curved dorsal margin in lateral view in both *Hamipterus* and *Iberodactylus*.

The newly described *Haliskia peterseni* Pentland et al., 2024, shares convex margins of the deltoid facet, with a central ridge with *Akharhynchus*, although this is reduced in *A. martilli*. Both have a palatal ridge, in *Haliskia* the ridge starts anterior to the second alveoli, rather than posterior as seen in *Akharhynchus*. Both taxa have the first alveoli pair situated on the ventral border of the

deltoid facet, which are directed ventrally in *Haliskia*, rather than lateroventrally in *Akharhynchus*. The first alveoli pair in *Haliskia* are broadly spaced with the central deltoid ridge extending ventrally between the alveoli, whereas the first alveoli pair in *Akharhynchus* are medially placed and almost contacting.

5.2. Phylogenetic affinities within Ornithocheiridae

The most parsimonious computed phylogenetic tree (Fig. 8) shows *Akharhynchus* falling within Tropeognathinae, as sister taxon to *Siroccoptyx* + *Tropeognathus* (Fig. 8), and closely related to *Thapunngaka*, *Ferrodraco* and *Mythunga*, which form a polytomy. Three other major groups of Ornithocheiridae are recovered, Anhanguerinae, Hamipteridae and Coloborhynchinae.

An interesting outlier is *Ornithocheirus simus*, which is the basal most taxon in Ornithocheiridae in our analysis, rather than further down the tree within Tropeognathinae, falling as a sister taxon to *Ferrodraco* and *Mythunga*, as in previous phylogenies (for example Pentland et al., 2019).

5.3. Ontogeny and sexual dimorphism within Ornithocheiridae

There are four prominent morphological forms within Ornithocheiridae with distinct rostrum morphologies; 1, a narrow and tall premaxillary crest (*Tropeognathus*, *Ferrodraco*), 2, a rounded dorsal surface, lacking the prominent crest (*Ornithocheirus*, *Akharhynchus*), 3, prominent deltoid facet with anteroventrally directed teeth with a prominent premaxillary crest (*Coloborhynchus*, *Uktenadactylus*) and 4, a low deltoid facet with anteroventrally directed teeth and a premaxillary crest (*Anhanguera*, *Maaradactylus*).

One possible explanation for these distinct jaw morphologies is sexual dimorphism. Many extant tetrapods show large differences between males and females in both morphology and size (Berry and Shine, 1980; Fairbairn et al., 2007; Mori et al., 2022). In extant Reptilia, the females tend to be on average larger, with some exceptions, such as some lizards (Cox et al., 2003) and turtles (Berry and Shine, 1980). Sexual size dimorphism is dictated by several factors including sexual selection, fecundity selection as well as natural selection for resource partitioning (Cox et al., 2007).

Sexual dimorphism has been demonstrated for several taxa within Pterosauria, including *Darwinopterus/Kunpengopterus* (Lü et al., 2011; Wang et al., 2015; Cheng et al., 2017); *Hamipterus* (Wang et al., 2014); *Pteranodon* (Bennett, 1992) and *Rhamphorhynchus* (Wellnhofer, 1975). In these taxa crestless/reduced crest individuals possessing a larger pelvic opening are regarded as females (e.g., Lü et al., 2011). This is corroborated by the association of eggs either in close proximity to a crestless individual (Lü et al., 2011) or within the body cavity (Wang et al., 2015). In *Pteranodon*, the males with much larger crests are on average 50% larger than females (Bennett, 1992).

Therefore, it is possible that the distinct ornithocheirid morphologies described above are the result of sexual dimorphism with one form possessing prominent crests or large anteroventrally directed teeth for display. As the male – female characterisation with Pterosauria has been proven within several genera in regard to crest size or presence/absence, so it is not unfeasible that the groups of morphologies we see within Ornithocheiridae are due to sexual dimorphism.

Arguments have also been made for ontogenetic variation to explain the crest differences between taxa. Both Bantim et al. (2015) and Pinheiro and Rodrigues (2017) demonstrated that crest and skull exhibit allometric growth, indicating that at least within anhanguerids the size of the crest is ontogenetic, or an artifact of increased crest size through evolution. A pterosaur bone bed in Brazil shows the development of a crest through ontogeny

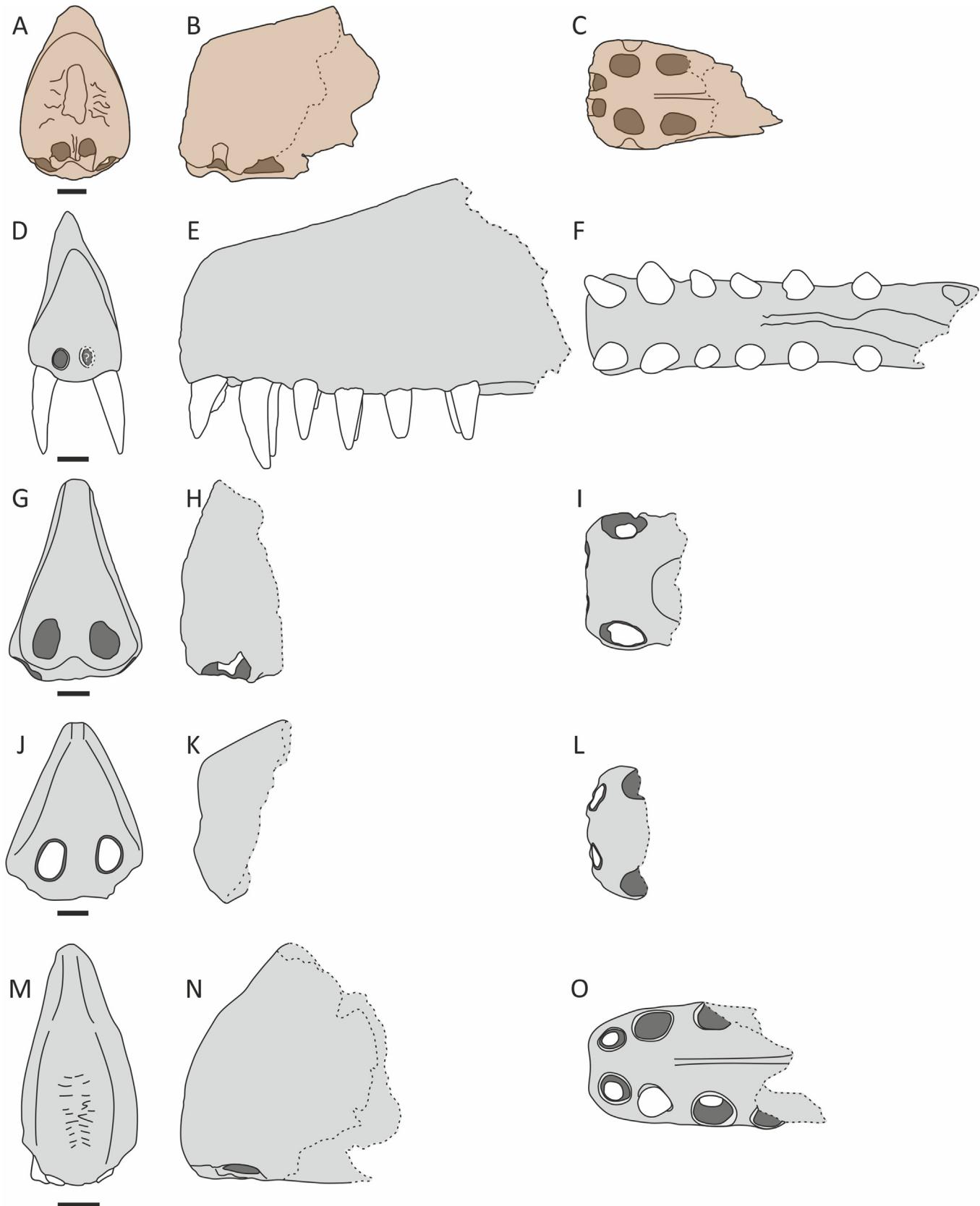


Fig. 5. Comparison line drawings of various Kem Kem Group ornithocheirid rostra. A-C, *Akharhynchus martelli* gen. et sp. nov. (FSAC-KK 12500); D-F, *Siroccoptyx moroccensis* (from Mader and Kellner (1999), fig. 2–3 and Smith et al. (2023a), fig. 26; LINHM 016); G-I, *Coloborhynchus fluviferox* (from Jacobs et al. (2019), fig. 4–5; FSAC-KK 10701); J-L, *Coloborhynchus* sp. (from Jacobs et al. (2020), fig. 9; FSAC-KK 5024/SMNK-PAL 45833); M–O, *Ornithocheirus* cf. *simus* (from Jacobs et al. (2020), fig. 7; FSAC-KK 5025/SMNK-PAL 45831). A, D, G, J, M in anterior view; B, E, H, K, N in left lateral view; C, F, I, L, O in ventral view. Scale bars represent 10 mm. Line drawings are based on figures in respective publications listed above.

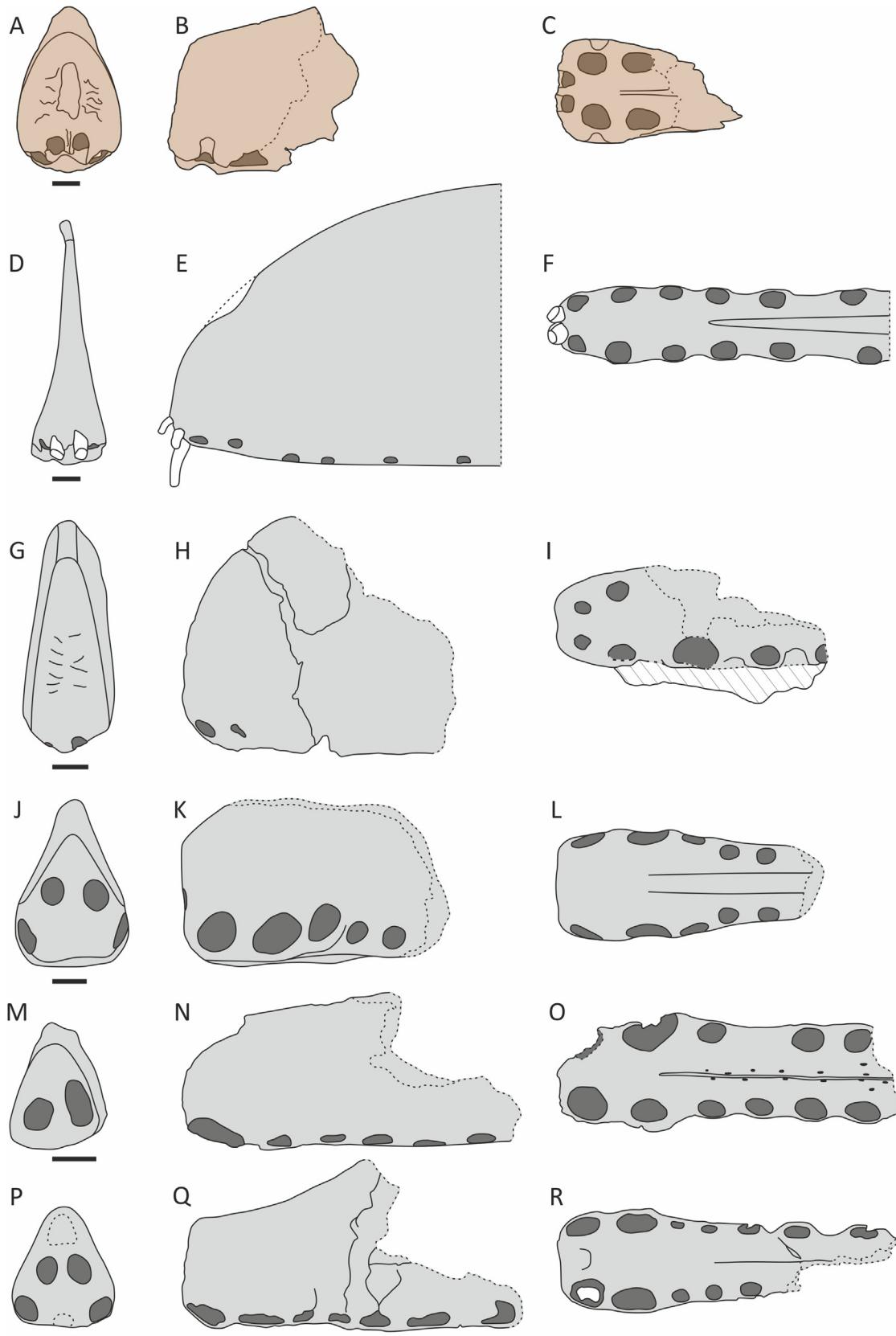


Fig. 6. Comparison line drawings of various ornithocheirid rostra. A–C, *Akharhynchus martilli* gen. et sp. nov. (FSAC-KK 12500); D–F, *Tropeognathus mesembrinus* (from Wellnhofer (1987), fig. 2 and Holgado and Pégas (2020), fig. 9; BSP 1987 I 46); G–I, *Ornithocheirus simus* (from Rodrigues and Kellner (2013), fig. 1; CAMSM B54428); J–L, *Coloborhynchus clavirostris* (from Holgado and Pégas (2020), fig. 1; NHMUK PV R1822); M–O, *Aerodraco sedgwickii* (from Holgado and Pégas (2020), fig. 6 and Rodrigues and Kellner (2013), fig. 10; CAMSM B54422); P–R, *Uktenadactylus wadleighi* (from Lee (1994), fig. 3 and Holgado and Pégas (2020), fig. 4; SMU 73058). A, D, G, J, M, P in anterior view; B, E, H, K, N, Q in lateral view; C, F, I, L, O, R in ventral view. Scale bars represent 10 mm. Line drawings are based on figures in respective publications listed above.

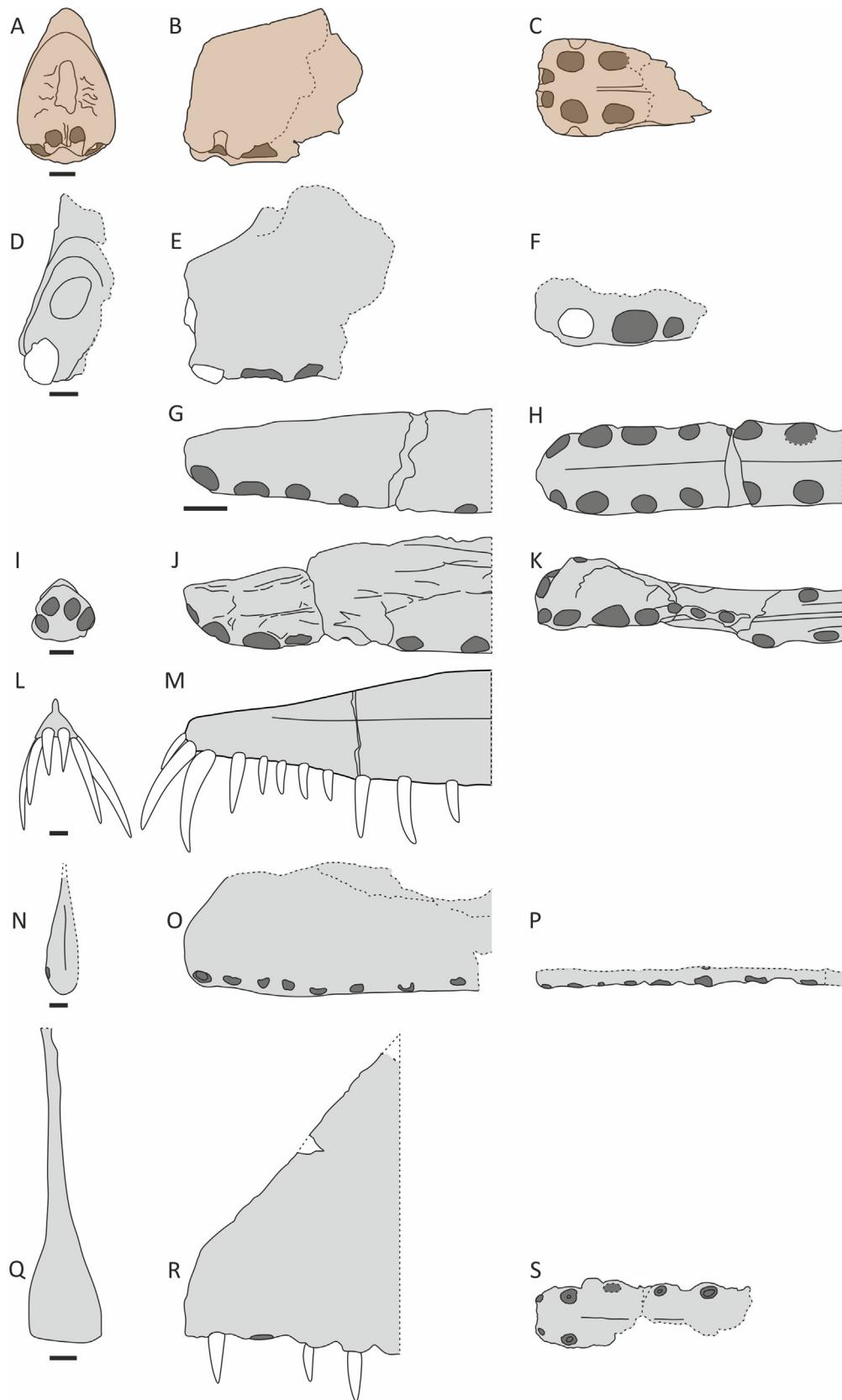


Fig. 7. Comparison line drawings of various ornithocheirid rostra. A–C, *Akharhynchus martilli* gen. et sp. nov. (FSAC-KK 12500); D–F, *Coloborhynchus capito* = *Nicorhynchus capito* (from Rodrigues and Kellner (2013), fig. 8; CAMSM B54625, with E mirrored for ease of comparison); G–H, *Camposipterus nasutus* (from Rodrigues and Kellner (2013), fig. 9; CAMSM B54556); I–K, *Caukicephalus trimicronodon* (from Steel et al. (2005), fig. 3; IWCMS 2002.189.1, with K mirrored for ease of comparison); L–M, *Anhanguera pectoralis* (from Kellner and Tomida (2000), fig. 5, 10; NSM-PV 19892); N–P, *Thapunngaka shawi* (from Richards et al. (2024), fig. 3; KKF0600, O mirrored for ease of comparison); Q–S, *Ferrodraco lentoni* (from Pentland et al. (2019), fig. 3–4 and Richards et al. (2024), fig. 8; AODF 876). A, D, I, L, N, Q in anterior view; B, E, G, J, M, O, R in lateral view; C, F, H, K, P, S in ventral view. Scale bars represent 10 mm. Line drawings are based on figures in respective publications listed above.

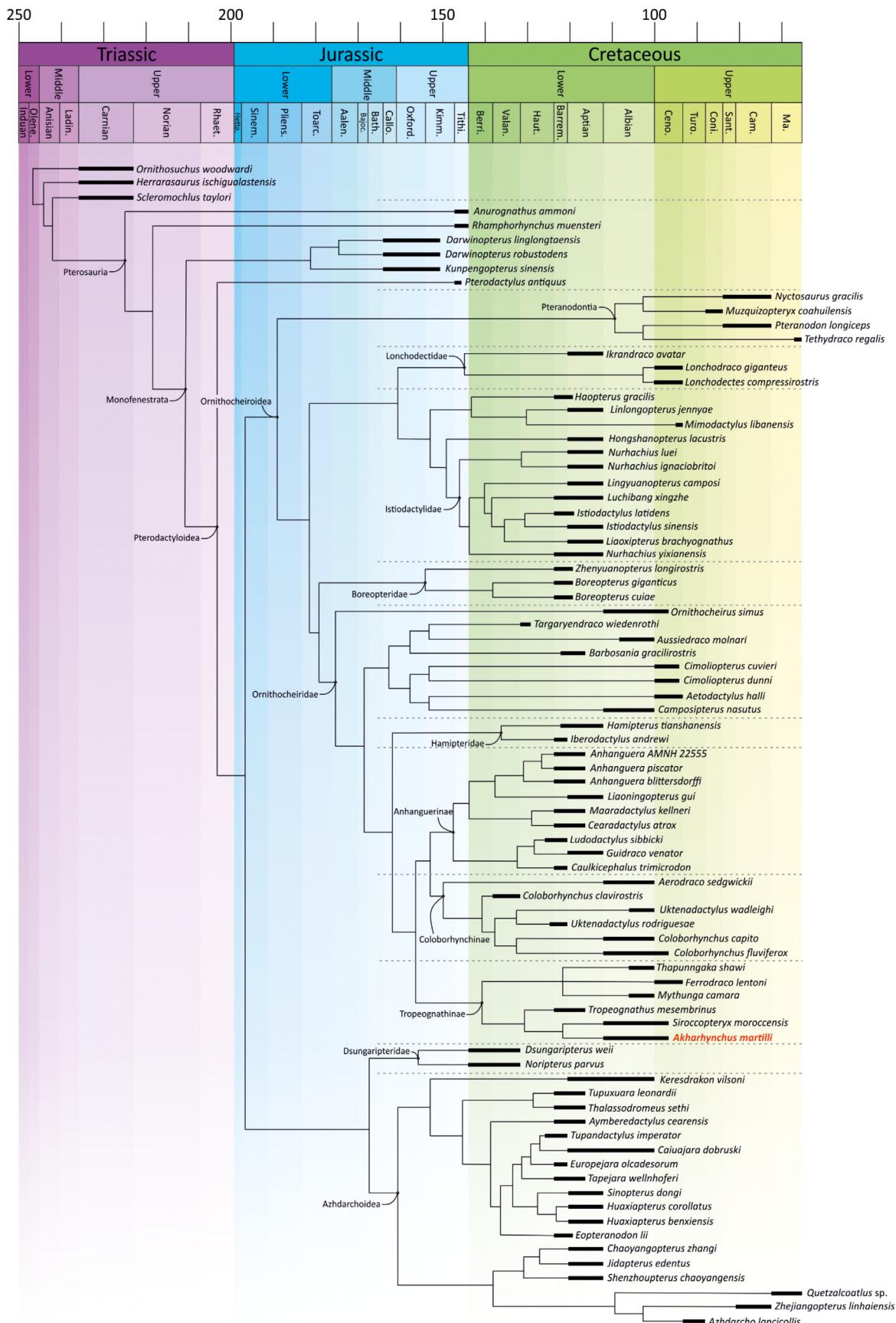


Fig. 8. Cladogram showing ornithocheirid relationships based on the modified data matrix of Ozeki et al. (2023).

for tapejarids (Manzig et al., 2014). It is highly likely that the forms we see are a combination of ontogenetic and sexual dimorphic stages, with the largest specimens representing fully mature adults. However, to resolve this more specimens, and a thorough comparative study are required.

6. Conclusion

A new specimen of pterosaur rostrum from the Kem Kem Group of southeast Morocco is distinct from all other ornithocheirids to warrant erecting a new taxon, *Akharhynchus martilli* gen. et sp. nov. The addition of the new taxon raises the pterosaur diversity of the Kem Kem Group to 10 named taxa, with five ornithocheirids, making it one of the most diverse pterosaur assemblages in the world, and the most diverse pterosaur assemblage from a fluvial setting. Morphological similarities between *Akharhynchus* and *Tropeognathus*, suggest a placement within Tropeognathinae, providing further evidence that the clade was widespread in the mid-Cretaceous.

CRediT authorship contribution statement

Megan L. Jacobs: Writing – original draft, Methodology, Formal analysis, Conceptualization. **Roy E. Smith:** Writing – original draft, Methodology, Conceptualization. **Samir Zouhri:** Writing – original draft, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2024.106015>.