A new tapejarid (Pterosauria, Azhdarchoidea) from the mid-Cretaceous Kem Kem beds of Takmout, southern Morocco

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ABSTRACT

A new pterosaur, *Afrotapejara zoughri* gen. et sp. is described on the basis of a partial rostral fragment from the Cretaceous Kem Kem beds of Takmout, near Erfoud in southern Morocco. The taxon is distinguished from all other Tapejaridae on the possession of a dorsal expansion of the rostral margin a short distance from the rostral tip. Tapejaroid features include edentulity, expansion of the rostral median crest and the presence of small foramina on the lateral margins and occlusal surface. The new specimen is the third edentulous pterosaur taxon from the Kem Kem beds and is the first unambiguous occurrence of Tapejaridae in Africa.

1. Introduction.

Pterosaur remains are rare in Africa (Kellner et al., 2007), with most records reporting disarticulated or isolated and fragmentary remains ranging from the Late Jurassic (Reck, 1931; Unwin and Heinrich, 1999; Costa et al., 2015) to the Late Cretaceous (Wellnhofer and Buffetaut, 1999; Pereda Suberbiola et al., 2003; Ibrahim et al., 2010; Rodrigues et al., 2011; Martill and Ibrahim, 2015). Despite this generally patchy and fragmentary nature of the African pterosaur record, considerable diversity has been revealed, especially for the mid to Late Cretaceous of North Africa, and particularly for the Kem Kem beds (Wellnhofer and Buffetaut, 1999; Ibrahim et al., 2010; Rodrigues et al., 2011; Martill and Ibrahim, 2015) and phosphate formations (Pereda Suberbiola et al., 2003; Longrich et al., 2018) of Morocco.

In the Kem Kem beds of southern Morocco pterosaurs are represented by at least three genera of tooth-bearing ornithocheiroids (*Siroccopteryx*, *Coloborhynchus*, *Ornithocheirus*) and two named edentulous azhdarchids (*Alanqa saharica*, *Xericeps curvirostris*). Fragmentary, but undiagnostic material has tentatively been referred to Tapejaridae (Wellnhofer and Buffetaut, 1999) and we here provide evidence that Tapajaridae are indeed present in the North African Cretaceous.

2. Locality and geological context

2.1. Locality

The specimen described here (FSAC-KK 5004) was acquired by a commercial fossil trader based in the town of Erfoud who sources fossils from several localities in the Tafilalt region of southern Morocco. The specimen was reportedly collected from a series of small excavations in the Kem Kem beds near a small plateau called Ikhf N' Taqmout (Takmout). At this locality the Kem Kem beds are

exposed in scrubby desert on the southern flanks of the larger Jebel Ougnane plateau (Fig. 1). Three main areas of fossil mining occur here, but it is not known from which of these areas the specimen came (Fig. 2). This northern region of the Tafilalt Basin is a well-known source of fossils from the Kem Kem beds. Two of the digging area lie on an open plain on the west side of the Oued Ziz valley. One important fossil locality lies close to the prominent tajine-shaped hill of Al Gualb (1,100 m) and is close to the *Spinosaurus aegyptiacus* excavation site described by Ibrahim et al. (2014). This extensive area of fossil digging is centred around 31°36'55.87"N – 4°15'42.67" W. A second important area of fossil digging, and lying slightly closer to the Taqrout plateau is within and adjacent to a sandstone quarry at Lamaaka at 31°38'51.13" N – 4°13'41.47" W. This latter area is the most likely source of the fossil described here. The matrix of the specimen is comparable with that of both these localities. A third area of fossil digging lies close to the village of Douira on the eastern flank of the valley of the Oued Ziz at 31°51'16.07" N – 4°11'01.45" W. Although the matrix of the fossils here is comparable with that of the specimen, this locality is usually not referred to as Taqrout. At all of these localities fossils are excavated from thin (5 cm to [rarely] 80 cm) event horizons notable for argillaceous rip up clasts, small silicate pebbles and isolated bones and teeth (Fig. 3). Significantly, the matrix of FSAC-KK 5004 does not match that of the well-known site of Hassi Begaa in the southern Tafilalt (see Martill et al. 2018).

FIG 1. HERE

2.2 Geological context

The strata exposed in the region of the western side of the Oued Ziz near Zrigate and Zaouia Jdida comprise the mid Cretaceous (?Albian–lower Cenomanian) Kem Kem beds of fluvial red-beds facies, overlain by limestones of the Upper Cretaceous (middle Cenomanian to Turonian) Akrabou Formation, this latter unit being rich in shallow water invertebrates, including bivalves (heterodonts and rudists), echinoids and corals (Fig. 3). The Kem Kem beds rest unconformably on Palaeozoic basement, but the contact is not exposed in this area, and the base of the Kem Kem beds is not seen.

In many places the Kem Kem beds are concealed by scree from the overlying Akrabou Formation, especially in the upper part, and exposures are patchily distributed. A simplified stratigraphic profile is given in Figure 3. A detailed stratigraphic log for this area is provided by Ibrahim et al. (2014) and was recorded from the eastern flank of Al Gualb mesa (also sometimes called Zrigate).

FIG. 2 and 3

3. Methods

The specimen has been analysed using light microscopy and comparative anatomy. Preparation includes use of air pen and air abrasives. Consolidation of the bone was by paraloid at 10%. Some repair of the specimen was undertaken by an unknown collector, and includes insertion of a scrap of bone from an unknown taxon. Presumably this was to make the specimen look more complete, and thus of higher commercial value. Geographical coordinates were obtained from Google Earth.

X-ray computed tomography (XCT) was conducted using an X-ray microscope (Xradia 520 Versa, Carl Zeiss X-ray Microscopy, USA) operating at a voltage of 80 kVp with a power of 6 W and a tube current of 75 μ A. A ZEISS LE1 filter positioned directly after the x-ray source to filter the x-ray spectrum.

A tomography was collected using a flat panel detector to acquire 1601 projection images over 360 degrees with an interval of 0.22 degrees. The detector was exposed for 0.5 seconds (5 frames, 0.1 s exposure/frame) for each projection. The pixel size varied for each sample.

The projections were reconstructed using the microscope software incorporating a filtered back projection algorithm (Scout and Scan Reconstructor, Carl Zeiss Microscopy, USA). For each dataset the centre shift was manually found, no beam hardening correction was utilised and a smoothing correction of 0.5 was applied.

3.1. Specimen repositories.

New specimens described here from the Kem Kem beds (Figs 4–9) have been deposited in the collection of the Département de Géologie (Paléontologie), Faculté des Sciences Aïn Chock (FSAC), Université Hassan II - Casablanca, Km 8, Route de l'université 20100, Casablanca, Morocco, and are prefixed FSAC-KK. Other repositories are: American Museum of Natural History, New York, USA (AMNH); Collection Desiree, the private collection of Rainer Alexander von Blittersdorf, Rio de Janeiro, Brazil (CD); Centro Paleontológico (CENPALEO) of the Universidade do Contestado, Mafra, Santa Catarina, Brazil Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil (CP.V); Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China (IVPP); Staatliches Museum für Naturkunde Karlsruhe, Germany (SMNK).

4. Results

4.1. Systematic palaeontology

PTEROSAURIA Kaup, 1834

MONOFENESTRATA Lü et al., 2009

PTERODACTYLOIDEA Pleininger, 1901

AZHDARCHOIDEA Nessel, 1984

TAPEJARIDAE Kellner, 1989

Genus *AFROTAPEJARA* gen. nov.

Derivation of generic name. A combination of *Afro* for Africa and *tapejara* from the Brazilian pterosaur *Tapejara*.

Diagnosis. As for type and only species below.

Species *Afrotapejara zouhri* gen. et sp. nov.

118 *Derivation of specific name.* After Dr Samir Zouhri, Moroccan palaeontologist based in Casablanca
 119 who has helped us so much in our work in Morocco.

120 *Holotype.* FSAC-KK 5004, University of Casablanca, Ain Chock, Casablanca, Morocco (Figs. 4, 5, 6, 7).

121 *Referred material.* Two specimens (FSAC-KK 5006 and FSAC-KK 5007) also from the Kem Kem beds of
 122 southern Morocco are referred to this taxon as they match closely the morphology of the anterior
 123 part of the holotype specimen (Fig. 8). A possible anterior mandibular symphysis BSP 1997 I 67
 124 illustrated by Wellnhofer and Buffetaut (1999) is tentatively regarded as the lower jaw of
 125 *Afrotapejara* (Fig. 9).

126 *Type locality.* Takrout, Oued Ziz valley, Errachida Province, southern Morocco (Figs 1-2).

127 *Type Horizon and age:* Kem Kem beds, mid Cretaceous? Albian to Lower Cenomanian (Fig. 3).

128 *Diagnosis.* Tapejarid pterosaur in which the anterior rostrum displays the down-turned tip typical of
 129 the family. Distinguished from other members of the clade by a combination of the following:
 130 presence of a row of small foramina on the lateral margins of the rostrum lying close to the lateral
 131 margin with the occlusal surface, and a small, boss-like protuberance on the occlusal surface, not
 132 reported for other Tapejaridae, but known in other members of Azhdarchoidea (e.g. *Alanqa*).

133 *Description:* Specimen FSAC-KK 5004 is a single portion of anterior rostrum preserved in three-
 134 dimensions. It lacks the anterior point of the rostrum, and does not extend as far posteriorly as the
 135 anterior border of the antorbital fenestra. In this regard it is similar to all other occurrences of
 136 pterosaur rostra and mandibles from the Kem Kem beds (Martill et al., 2018). It is free from matrix,
 137 but has an infill of buff coloured fine sandstone typical of the vertebrate bearing horizons in the
 138 northern Tafilalt. There are a number of cracks that have been repaired and an area of the dorsal
 139 margin has been repaired with a mix of sand, glue and an inserted piece of fibrous bone that is too
 140 thick to be pterosaurian. It is common practice for Moroccan fossil diggers in the Tafilalt to repair and
 141 enhance fossils in this way. The specimen measures 148 mm x 63 mm x 30 mm posteriorly and

tapering to 15 mm anteriorly (Table 1). It is estimated that 30 mm are missing anteriorly on the assumption that the rostrum tapered to a sharp point as in other tapejarids. The dorsal border is gently rounded and rises from the tip posteriorly at a constant rate until a point estimated at 20 mm from the tip, where the dorsal margin begins to rise more steeply to form a sagittal crest. This border is slightly broken anteriorly to reveal trabecular cross-struts orthogonal to the length of the rostrum. In anterior view the lateral margins appear planar, perhaps with a very slight inflation toward the occlusal margins. The occlusal surface is deeply sulcate with well-defined lateral borders that are almost acute. Posteriorly there is a median, linear eminence (boss) that appears to be rising posteriorly, but is terminated where the specimen is broken. The palatal surface is deflected ventrally (rostral deflection) by $\sim 7^\circ$. The lateral margins possess a number of small, elongate foramina typical of those seen on members of the Azhdarchoidea (e.g. Osi et al., 2005; Martill et al., 2018) including Tapejaridae (Wellnhofer and Buffetaut 1999; Kellner, 2013; Manzig et al., 2014). There is a single row of these foramina on both margins that lie close to and extend parallel with the occlusal border. Several foramina are also visible on the occlusal surface possibly arranged in off-set pairs.

TABLE 1

FIGS 4-9

4.2. *Internal histology*

The broken ends of the holotype and two referred specimens reveals details of the internal bone structure. In the holotype FSAC-KK 5004 the broken posterior margin of the specimen reveals an internal structure of trabeculae restricted to the lateral margins and dorsal border. There is a median cavity lacking trabeculae with an arcuate dorsal margin (Fig. 6). This thin layer of bone may represent a relic of the margin between the maxilla and premaxilla, but this suggestion is speculative. The broken dorsal margin of the crest reveals an internal framework of regularly spaced vertical cross-struts (Figs 4D, 5D).

An XCT scan of specimen FSAC-KK-5006 reveals a well-preserved internal structure, demonstrating the camellate nature of the jaw tip (Fig. 10). A series of trabeculae are revealed in which some form medially located parallel vertical septa (PVS) extending from the dorsal margin to the occlusal surface. These septae are present throughout the specimen, but are most prominent in the middle of the specimen and towards the posterior end. Other trabeculae radiate from these medial septae to the lateral margins of the specimen, but vary in number and position anteroposteriorly (Fig. 10, compare A-D). The septa define several large voids, the largest of which occurs centrally between the parallel vertical septae, and two voids laterally towards the occlusal surface (Fig. 10). Other, smaller camerae are present, but do not extend throughout the specimen. Foramina connect these voids with the bone exterior (Fig. 10 A-B). The XCT scan also reveals the triangular nature of the cross-section, and shows the bone to be thickened in the corners. The bone wall thickness is relatively consistent on the lateral margins being approx. 0.6 - 0.7 mm reaching a thickness of approximately 2 mm in the thickened corners (Fig. 10 A-B).

Fig 10

4.3. Affinities

Despite its fragmentary nature, specimen FSAC-KK 5004 is identified as a pterosaur on account of its exceptionally thin-walled bone, and remarkable similarities with more complete examples belonging to the Tapejaridae Kellner, 1989, especially with forms from the Santana Formation of north east Brazil, including the genera *Tapejara* and *Caupedactylus*. *Afrotapjara* is easily distinguished from other Kem Kem beds azhdarchids on account of its conspicuously downturned rostrum. In *Alanqa saharica* the occlusal margin in lateral view is a straight line, while in *Xericeps curvirostris* it is upwardly curved (Ibrahim et al., 2010; Martill et al., 2018).

In most Tapejaridae where 3-D preservation has occurred the palatal surface is sulcate (e.g. *Tapejara*, *Caupedactylus*, *Caiuajara* and the possible tapejarid *Bakonydraco*) as in *Afrotapejara*. The small foramina on the lateral border lying parallel and close to the occlusal border in *Afrotapejara* are also seen in *Caupedactylus* and *Caiuajara*.

4.4. Phylogenetic analysis

The data matrix used in the phylogenetic analysis (Table A Suppl.) is founded on a dataset of 117 characters constructed by DMU and published by Lü et al. (2010) to which we added a further 29 characters drawn from recent analyses by Andres et al. 2014 and Vidovic and Martill 2017 (Table B Suppl.).

The hypothetical ancestor used by Lü et al. (2010) was replaced by codings for *Euparkeria*. Other outgroups recently used in analyses of pterosaur phylogeny include *Scleromochlus* and *Herrerasaurus*. We rejected the former on the grounds that fine anatomical details of this taxon are open to a variety of interpretations leading to considerable ambiguity in the scoring of character states. *Herrerasaurus* is located within a clade, Dinosauria, that is widely considered to be the sister taxon to Pterosauria and is thus relatively derived within the context of Ornithodira (Dinosauria + Pterosauria). *Euparkeria* is represented by multiple individuals with a well described and relatively complete skeletal anatomy and is consistently recovered as basal to Ornithodira (Ewer 1965; Nesbitt 2011, Sookias and Butler 2013, Ezcurra 2016, Sookias 2016).

The analysis included 52 taxa comprising a number of representative basal forms (*Dimorphodon*, *Rhamphorhynchus*) and Monofenestrata, consisting of several basal monofenestratans such as *Darwinopterus* and *Cuspicephalus* (Witton et al. 2015), and a broad sampling of pterodactyls (Table A Suppl.). All taxa that have been assigned to Tapejaridae (sensu Unwin 2003) or its various

synonyms (Tapejarinae: Vullo et al. 2012; Manzig et al. 2014) were included in the analysis irrespective of their completeness.

The dataset was analysed using PAUP* software (version 4.0a; build 166) (Swofford 2000) with the following settings: optimality criterion = parsimony; 'heuristic' search option; addition sequence 'simple'; optimisation = ACCTRAN. Characters that exhibited multiple states for a particular terminal taxon were treated as polymorphic. Multiple state characters were treated as unordered except for characters 7-9, 27, 45, 46, 78, 80, 93, 100, 114, 117, 124-126, 128, 136, 143 which were treated as ordered. Bootstrap values were generated from 600 replicates.

Two different phylogenetic analyses were conducted. First, all material assigned here to *Afrotapejara* was treated as a single taxon. The strict consensus tree, with node support values is shown in Figure 11 and the 50% majority rule tree in Figure 12. In the second analysis, the rostrum and mandible fragments were treated separately. A strict consensus tree is shown in Figure 13. Descriptive data for these trees is shown in Table 2.

Trees generated by both analyses are closely comparable, although with less resolution in the partitioned data set. The strict consensus tree (Fig. 11) shows good congruence with previous phylogenetic analyses (Unwin 2003; Lü et al 2010). As expected, *Dimorphodon* and *Rhamphorhynchus* form successive outgroups to Monofenestrata, the basal most taxa of which include *Darwinopterus* and *Rhamphodactylus*. Pterodactyloidea consists of Ctenochasmatoidea including ctenochasmatids and lonchodectids. Ornithocheiroidea is well defined and comprised of istiodactylids, ornithocheirids and pteranodontians. Taxa that in previous analyses resolved within Dsungaripteroidea form successive outgroups to Azhdarchoidea. The latter is very well supported (17 character state changes) and consists of two distinct clades: Tapejaridae and Neoazhdarchoidea (thallasodromeids + chaoyangopterids + azhdarhchids).

The clade Tapejaridae is well supported (seven character state changes) and distinguished by five unique features (characters 2, 11, 12, 49, 56) relating to the morphology of the jaws and the cranial

crests. *Afrotapejara* nests deep within Tapejaridae and exhibits all five of the diagnostic features for this clade (Fig. 11).

FIGS 11 – 13

TABLE 2

5. Discussion

5.1. Biogeography

Tapejarid pterosaurs were first reported from the Romualdo Member of the Santana Formation of north east Brazil's Araripe Basin (Kellner, 1989; Wellnhofer and Kellner 1999; Kellner 2013) and subsequently discovered in the slightly younger Crato Formation in the same basin (Kellner and Campos, 1999; Frey et al. 2003, Unwin and Martill, 2007). Wellnhofer and Buffetaut (1999) tentatively attributed a fragment of possible mandible from the Kem Kem beds of Morocco to Tapejaridae, but were unable to confirm the specimens identity, and Averianov (2014, fig. 1a) later suggested the fragment represented an early ontogenetic stage of the azhdarchid *Alanqa saharica*. This latter hypothesis can now be rejected on account of the size of the specimen being comparable with that of FSAC-KK 5004. During the beginning of this century several pterosaurs from the Early Cretaceous Jehol Group of China were referred to Tapejaridae, including *Sinopterus*, Wang and Zhou, 2003, *Eopteranodon* Lü and Zhang, 2005, *Huaxiapterus* Lü and Yuan, 2005 and *Nemicolopterus* Wang et al. 2008. While *Sinopterus* is clearly a valid taxon and has obvious tapejarid affinities (Wang and Zhou, 2003), *Huaxiapterus* and *Nemicolopterus* are probably junior synonyms of *Sinopterus*, and it is doubtful if *Eopteranodon* is tapejarid as it does not appear to possess the down turned jaw tips so characteristic of the clade.

A tapejarid, *Europejara olcadesorum* Vullo et al., 2012 was reported from the Early Cretaceous of Spain and was the first to be reported from Europe, despite more than 200 years of pterosaur

research. Tapejarids have yet to be reported from North America, South East Asia and Australasia. Although, a specimen (a partial jaw, TMM 42489-2) from the Javelina Formation of Texas, USA was referred to Tapejaridae by Kellner (2004) later analysis has demonstrated that its affinities lie closer to *Tupuxuara* and Thalassodromidae (Martill and Naish, 2006). The specimens from the Kem Kem beds described here are confirmation that tapejarids were indeed present in Africa, as first suggested by Wellnhofer and Buffetaut (1999).

5.2. Comparisons with other Tapejaridae

The holotype specimen of *Afrotapejara zourhi* is very similar to the equivalent portion of the rostrum of most tapejarid genera in that it likely tapers anteriorly to a sharp point, has a concave lateral outline to the dorsal margin and has a rostral deflection. These features are used to diagnose Tapejaridae (Kellner, 2004). However, there is some variation in the degree of rostral deflection and dorsal curvature (and thus angle of sagittal crest) between genera and within taxa (Figs. 14, 15). Some of these features are known to vary with ontogeny, as in *Sinopterus* (Wang and Zhou, 2003) and *Caiuajara dobruskii* (Manzig et al., 2014) (Table 3), and may also be sexually dimorphic (*sensu* Bennett, 1992 for *Pteranodon* headcrests). Nevertheless, despite this variation, and the fragmentary nature of the *A. zourhi* holotype, we are able to make some comparisons with other Tapejaridae. The lateral angle of *A. zourhi* holotype is moderate (20°) and thus comparable with the lateral angle in *Caupedactylus ybaka* (specimen no. MN 4726-V = 19°) and some examples of *Sinopterus dongi* (e.g. IVPP V 13363 = 18°) (Table 3).

TABLE 3

The rostral deflection seems highly variable across Tapejaridae, ranging from as low as 7° in *A. zourhi* and as high as 41° in *Caiuajara dobruskii* (specimen CP.V-1001). Other tapejarids with a low rostral

deflection comparable with *A. zourhi* include *Caupedactylus* (*C. ybaka* MN 4726-V = 8°) and *Sinopterus* (*Sinopterus dongi* IVPP V 13363 = 10°). The dorsal angle does not seem to vary significantly between tapejarid genera, although the data available is limited to properly evaluate this parameter. The similarity between *A. zourhi* and *Sinopterus* and *Caupedactylus* might suggest a sub group within Tapejaridae of slender-beaked forms compared to those morphs with short, high skulls (Figs 14, 15, Table 3).

FIGS 14 - 15

5.3. Comparisons with extant animals

A number of recent tetrapods possess medially located (sagittal) bony head crests, including many members of Aves, Lacerta and Mammalia, some of which, at least superficially, resemble the sagittal crest of tapejarids. Among Mammalia sagittal crests are found in many taxa, including members of Carnivora and Primates, but are usually low, and surrounded by sufficient musculature (Ashton and Zuckerman, 2009) that they fail to make a feature on the skull roof visible during life.

Among Aves, Cassowaries *Struthio casuarius* (Ratites), and several species of hornbill (Bucerotiformes) possess elaborate bony crests (called a casque), and in all cases covered by an extension of the keratinous rhamphotheca which may exaggerate its size considerably. In the case of the Cassowary and the Helmeted Hornbill, *Rhinoplax vigil*, the lateral profile of the crest is similar to that of *Afrotapejara* for the preserved portion. However, the sagittal crest of the Helmeted Hornbill is a solid structure used in male to male combat (Kinnaird, et al. 2003; Chatterjee and Templin, 2012) whereas that of tapejarids is camellate. In general, the crest in Tapejaridae is a much more delicate structure constructed of very thin bony walls and delicate internal septae. However, it may have been strengthened by a rhamphotheca (See Frey et al., 2003, fig. 2a), as it is in the Cassowary.

An impressive sagittal crest occurs in the Veiled Chameleon, *Chamaeleo calyptrotatus*, from the Arabian Peninsula, where it appears to play a role in display, becoming increasingly larger and

developing elaborate stripes with age (Measey, et al., 2009). In the Cassowary, the casque is used for resonating sound, and perhaps for visual display (Naish and Perron, 2014). In all these cases, the sagittal crest becomes large and more ornate during ontogeny. We suppose that differences in the crest size in tapejarid species are also related to ontogeny, (see *Nemicolopterus* and *Sinopterus*) or sexual dimorphism (Bennett, 1992), but its true function remains a mystery.

It has been speculated that tapajarids may have been frugivores (Wellnhofer and Kellner, 1991; Pêgas, et al., 2016), although any direct evidence for this is lacking. Animals with skull morphologies resembling that of the tapejaridae have a wide range of diets that does include frugivory, however, they tend towards omnivory. The Helmeted Hornbill is a frugivore with some insectivory. Cassowaries are frugivorous, but also eat other plant material and small vertebrates. The veiled chameleon is mainly insectivorous, but does ingest plants as a source of water.

6. Conclusions

New material from the Kem Kem beds of south east Morocco confirms the presence of tapejarid pterosaurs in the fossil assemblage, alongside Azhdarchidae and Ornithocheiridae. Presently, only the remains of jaws can be satisfactorily assigned to the clade. One specimen displays sufficient morphology to distinguish the Moroccan material from other tapajarids and allows the erection of the new genus and species *Afrotapejara zoughri* gen. et sp. nov. This new taxon adds to the diversity of the Kem Kem beds pterosaurs and brings to 5 the number of named taxa from this stratum.

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458 Text figure captions

459

460 Fig. 1. A. Locality map showing the outcrop of the Kem Kem beds in the Tafilalt of south east

461 Morocco and the locality of Ikhf N' Taqmout, site of the new pterosaur.

Fig. 2. A detailed map showing areas of commercial fossil collecting from the Kem Kem beds in the southern entrance to the lower Oued Ziz gorge approximately 20 km north of Erfoud. The mesa of Ikhf N' Taqmout is indicated, as are dig sites near Zrigat and Douira.

- 467 Fig. 3. Simplified stratigraphic sequence for the Kem Kem beds in the region around Ikhf N' Taqmout.
- 468 Note that the vertical scale is approximate, with thicknesses varying significantly between localities.
- 469 It is rare to see the entire sequence of the Kem Kem beds due to debris sheets from the overlying
- 470 Akrabou Formation masking the outcrop.

472 Fig. 4. Holotype (specimen number FSAC-KK 5004) partial rostrum of *Afrotapejara zouhri* gen. et sp.
473 nov. from the Kem Kem beds of Ikhf N' Taqmout, Errachidia Province, southern Morocco. 4. A, right
474 lateral view; B, left lateral view; C, occlusal view; D, dorsal view; Scale bar = 50 mm.

476 Fig. 5. Line drawing highlighting key features of the holotype of *Afrotapejara zouhri* gen. et sp. nov.
 477 from the Kem Kem beds.

479 Fig. 6. Holotype (specimen number FSAC-KK 5004) partial rostrum of *Afrotapejara zoughri* gen. et sp.
 480 nov. from the Kem Kem beds of Ikhf N' Taqmout, Errachidia Province, southern Morocco, in cranial
 481 and caudal views. A, line drawing of cranial view; B, photograph of cranial view; C, line drawing of
 482 caudal view; D, photograph of caudal view. Note the large interanl cavity bordered by sub-vertical
 483 trabeculae in A. These continue anteriorly, converging to become subparallel and more medially
 484 located.

485
 486 Fig. 7. Line diagram illustrating the measurements taken from the holotype specimen FSAC-KK 5004
 487 used in Table 1.

489 Fig. 8. A specimen (BSP 1997 I 67) tentatively referred to Tapejaridae by Wellnhofer and Buffetaut,
 490 1999. These authors considered that it might represent a mandibular symphysis, an identification
 491 with which we agree and we refer this specimen to *Afrotapejara zouhri*.

492
 493 Fig. 9. Two referred specimens from the Kem Kem beds tentatively identified as premaxillae tips
 494 anterior of the ventrally flexed bend of the rostrum. Specimen FSAC-KK 5006 in A, right lateral, B,
 495 dorsal, C, occlusal, D, cranial and E, caudal views. Specimen FSAC-KK 5007 in F, left lateral, b, dorsal,
 496 c, occlusal, I cranial and J, caudal views. PVS = parallel vertical septa. Scale bars are 20 mm.

Fig. 10. XCT images taken from 4 locations of referred specimen FSAC-KK 5006 showing cross section and internal structure. The XCT scan reveals partitioning of an internal chamber by bony trabeculae that tapers towards the anterior rostrum. A similar internal structure is envisaged for the holotype specimen. Images A-D show XCT slices, E-H are line drawings of the slices, while I shows the point at which the XCT slices are made.

503

504 Fig. 11. Strict consensus tree, with node support (Bootstrap values) resulting from a phylogenetic

505 analysis that includes *Afrotapejara* as a single composite taxon.

506

507 Fig. 12. 50% majority rule tree resulting from a phylogenetic analysis that includes *Afrotapejara* as a

508 single composite taxon.

509

510 Fig. 13. Strict consensus tree resulting from a phylogenetic analysis that treats *Afrotapejara* as two
 511 distinct taxonomic units based on the rostrum and mandibles.

512

513 Fig. 14. Outlines of skull or anterior rostrum of a selection of tapejarid pterosaurs. A, holotype of

514 *Tapejara navigans* Crato Formation, north east Brazil, SMNK 2344 PAL; B, holotype of *Tupandactylus*

515 *imperator*, Crato Formation, north east Brazil, MCT 1622-R; C, *Tapejara wellnhoferi*, Romualdo
 516 Member, Santana Formation, north east Brazil, referred juvenile specimen, SMNK PAL 1137; D,
 517 *Tapejara wellnhoferi*, Romualdo Member, Santana Formation, north east Brazil, referred specimen
 518 AMNH 24440; E, holotype *Caupedactylus ybaka*, Romualdo Member, Santana Formation, north east
 519 Brazil, MN 4726-V; F, *Caiuajara dobruskii*, Goio-Erê Formation, south east Brazil, CP.V 1449. G,
 520 holotype *Sinopterus dongi*, IVPP V 13363; H, holotype *Afrotapejara zoughri*, Kem Kem beds, south
 521 Morocco, FSAC-KK 5004. Specimens not drawn to scale. All skulls orientated such that the posterior
 522 processes of the maxilla and the anterior process of the jugal are approximately horizontal. A, after
 523 Frey et al., 2003, fig. 1a; B, after Kellner and Campos, 2007, fig. 1; C, after Eck, et al., 2011, fig. 2, 1a;
 524 D, after Wellnhofer and Kellner, 1981, fig. 1, reversed; E, after Kellner, 2013, fig. 1; F, after Manzig,
 525 et al., 2014, fig 3, reversed; G, after Wang and Zhou, 2003, fig. 1, reversed.

526
 527 Fig. 15. Simplified comparative diagram expressing the degree of ventral flexure of tapejarid jaw tips.
 528 The downturn angle is measured with respect to a best-fit horizontal line drawn through the maxilla-
 529 jugal bar beneath the nasoantorbital fenestra (see also Table 3).

530

531 Table captions

Table 1. A selection of measurements for FSAC-KK 5004 (see Fig. 7).

Parameter	Measurement
Average lateral angle	20°
Average dorsal angle	7°
Average angle of rostral deflection	7°
Average apical angle of cross section anteriorly	74°
Average apical angle of cross section posteriorly	78°
Average angle of crest	46°
Max length	148 mm
Anterior width (occlusal)	15 mm
Posterior width (occlusal)	30 mm
Anterior height	13 mm
Posterior height	63 mm
Est. post. height of rostrum inclusive of crest	80 mm
Estimated length from jaw deflection to tip	120 mm

Table 2. Statistical values for cladistics analysis.

Table 2

Criterion	<i>Afrotapejara</i> (combined)	<i>Afrotapejara</i> (partitioned)
Nb of MPT's	602100	1545405
Tree length	583	583

Consistency index	0.44	0.44
Rescaled consistency index	0.32	0.32
Homoplasy index	0.61	0.62
Retention index	0.72	0.73

542

543

544

545

546 Table 3. Rostral angles (see Fig. 7) measured for selected members of Tapejaridae. In those taxa

547 from the Jehol Group of China and the Crato Formation of Brazil the dorsal angle cannot be

548 determined due to severe compaction.

549