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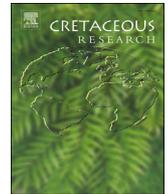
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## Cretaceous Research

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# Small, immature pterosaurs from the Cretaceous of Africa: implications for taphonomic bias and palaeocommunity structure in flying reptiles

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## ABSTRACT

Pterosaurs reached only modest sizes in the Triassic–Jurassic. By contrast, the Cretaceous saw a trend toward large to giant size (2 m to >6 m wingspans), and while small-medium (<1 m–2 m wingspans) sized forms are known from the Lower Cretaceous they are rare in the Upper Cretaceous. This pattern has been ascribed to the appearance of birds in the mid-Mesozoic, and their displacement of pterosaurs from niches previously occupied by small-medium sized forms. Here we show how new finds of small-very small pterosaurs (<1 m wingspans) from the mid-Cretaceous Kem Kem Group of Morocco point to several sampling biases of the data upon which these patterns are founded. Evidence for the size range of these pterosaurs strongly correlates with sample-size: as the sample increased (from <100 to >400 specimens) both very small and giant forms have been discovered. Histological analysis suggests that very small/small morphs are immature individuals rather than species in which adults were small-bodied. This new data shows that size distribution patterns based on all available specimens differ markedly from those based on a much more restricted sub-set of named taxa. Critically, this analysis reveals that pterosaur size ranges in the Cretaceous do not reflect a switch to large and giant size, but an extension of the size range from very small through to giant forms. Cretaceous niches previously occupied by small pterosaurs in the Triassic and Jurassic were increasingly occupied not by birds but by early ontogenetic stages of large and giant pterosaurs.

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## 1. Introduction

The fossil record of Triassic and Jurassic pterosaurs is composed almost entirely of individuals with wingspans in the 0.5–2.0 m range. A few reached slightly larger sizes, but rarely exceeded three metres (note Meyer and Hunt [1999] report a wing phalanx of a pterosaur with a wingspan estimated at 3.5–5.0 m). By contrast, most Cretaceous deposits yield individuals that are at least two to three metres in wingspan ranging up to 10 m in some Late Cretaceous forms. Except for pterosaurs from the Lower Cretaceous Jehol Biota of China, individuals with wingspans under two metres are

rare in Cretaceous deposits and seemingly absent from several important Lagerstätten such as the Crato and Santana formations of Brazil (Unwin and Martill, 2007) and the Javelina Formation of Texas, USA (Kellner and Langston, 1996). This pattern has been interpreted as evidence for an increase in the average size of pterosaurs, that began in the mid-Mesozoic and was driven, in part, by the concurrent radiation of birds which, it is argued, displaced pterosaurs from niches typically occupied by small forms (e.g. Romer 1966; Colbert 1980; Unwin 1988; Penny and Phillips 2004; Slack et al., 2006; Benson et al., 2014).

This hypothesis depends on the completeness of the pterosaur fossil record regarding small forms. Were they truly absent from most Cretaceous deposits, or is this merely a taphonomic artefact as hinted at by their relative abundance in the Lower Cretaceous Yixian and Jufotang formations and, though rare, their presence in other

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sequences such as the late Lower Cretaceous Cambridge Greensand of England and the early Upper Cretaceous Bissekty Formation of Uzbekistan? If small forms were originally present, but lost through taphonomic filters, or are as yet undiscovered, were they immature and mature individuals of small species, comparable in size to those typical of Triassic and Jurassic deposits? Or were they predominantly (as seems to be the case with the Jehol Biota) or exclusively, immature individuals of large and giant species? The latter, at least, must have existed suggesting that, logically, the absence of small forms in the fossil record is primarily a taphonomic artefact and not evidence of absence. This raises the question: what then was the ecological role of small forms, be they immature individuals or, if they existed, mature individuals of small species?

Testing these ideas is difficult: most Cretaceous pterosaur localities are no longer actively collected and, with a few exceptions, remains from most deposits are limited and fragmentary. Moreover, as noted, small forms are absent from most deposits that have yielded abundant remains.

Here, we report on an important new opportunity to test the hypotheses outlined above. This is provided by the collection, over the last two decades, of substantial numbers of specimens (400+) of pterosaurs from the Kem Kem Group of Morocco (Kellner and Mader, 1996; Mader and Kellner, 1999; Wellnhofer and Buffetaut, 1999; Rodrigues et al., 2006, 2011; Kellner et al., 2007; Ibrahim et al., 2010; Martill and Ibrahim, 2015; Martill et al., 2018, 2020; Jacobs et al., 2019, 2020; McPhee et al., 2020; Smith et al., 2020). Systematic studies of this assemblage have recognised nine named taxa (see Table S1) representing at least four distinct clades of pterodactyloid pterosaurs: Azhdarchidae, ?Chaoyangopteridae, Ornithocheiridae and Tapejaridae (Ibrahim et al., 2020).

Two features of this pterosaur assemblage are directly relevant to the hypotheses posed above. (1) The fossil remains span a large size range and include the remains of several small <2 m wingspan individuals described here for the first time, many examples of individuals 2–5 m in wingspan and a few specimens in which wingspans reached six metres, or more. Moreover, thanks to our rapidly improving knowledge of the anatomy of Cretaceous pterosaurs, based on complete, well-preserved remains from deposits such as the Yixian and Jiufotang formations of China and the Crato and Santana formations of Brazil the taxonomic identity of these remains, critically those consisting of rostra and mandibular symphyses, can be resolved to the species level. (2) The material, although isolated and fragmentary, is often three dimensionally preserved with good preservation of both macro- and microstructures (Williams et al., 2021). Set within the context of recent advances in our understanding of the ontogenetic development of the pterosaur skeleton and key features of different growth stages, the external textures of these bones combined with their histological characteristics can be used to distinguish between mature and immature individuals.

Analysis of the Kem Kem pterosaur assemblage focused on the size, ontogenetic status and taxonomic affinities of the new remains of small individuals allows us to tackle three key questions: (1) The extent to which the new finds resolve the question as to whether the absence of small individuals in the Kem Kem pterosaur assemblage reflects a taphonomic bias or ecological absence. (2) Whether, through determination of their ontogenetic status, the new finds of small individuals represent small-bodied species of pterosaur, or immature individuals of large or even giant species. (3) The extent to which there may have been ontogenetic niche partitioning in the Kem Kem pterosaur assemblage, as has been suggested for other pterosaurs such as *Pteranodon* (Bennett, 1993). Finally, we consider the extent to which answers to these questions might apply more broadly to other Cretaceous pterosaur assemblages.

## 1.1. Geological and palaeontological context

The material described here was collected by local fossil collectors near the oasis of Hassi el Begaa, Errachidia Province (Fig. 1), south-eastern Morocco, who excavate a series of vertebrate rich horizons in the upper part of the Ifezouane Formation of the Kem Kem Group (Martill et al., 2018). The age of the Kem Kem Group remains to be determined precisely but is usually regarded as 'mid' Cretaceous, with age estimates ranging from the Albian to the Cenomanian (Ibrahim et al., 2020). For details of the geological setting, stratigraphy, sedimentology, palaeoenvironments and fossil content of this deposit see Martill et al. (2018) and Ibrahim et al. (2020) and references therein.

## 2. Methods and materials

### 2.1. Material

This study focused on six specimens, five edentulous jaw fragments, from what appear to be small pterosaurs (Figs. 2–4) and a small mid-series cervical vertebra. All the jaw specimens demonstrate typical Kem Kem Group pterosaur preservation in lacking the anterior margin of the nasoantorbital fenestra for upper jaws, or the divergence of the mandibular rami for lower jaws (Ibrahim et al., 2010; Martill et al., 2018, 2020; McPhee et al., 2020; Smith et al., 2020). It is not always possible to distinguish an upper jaw from a lower jaw where the pair are nearly symmetrical.

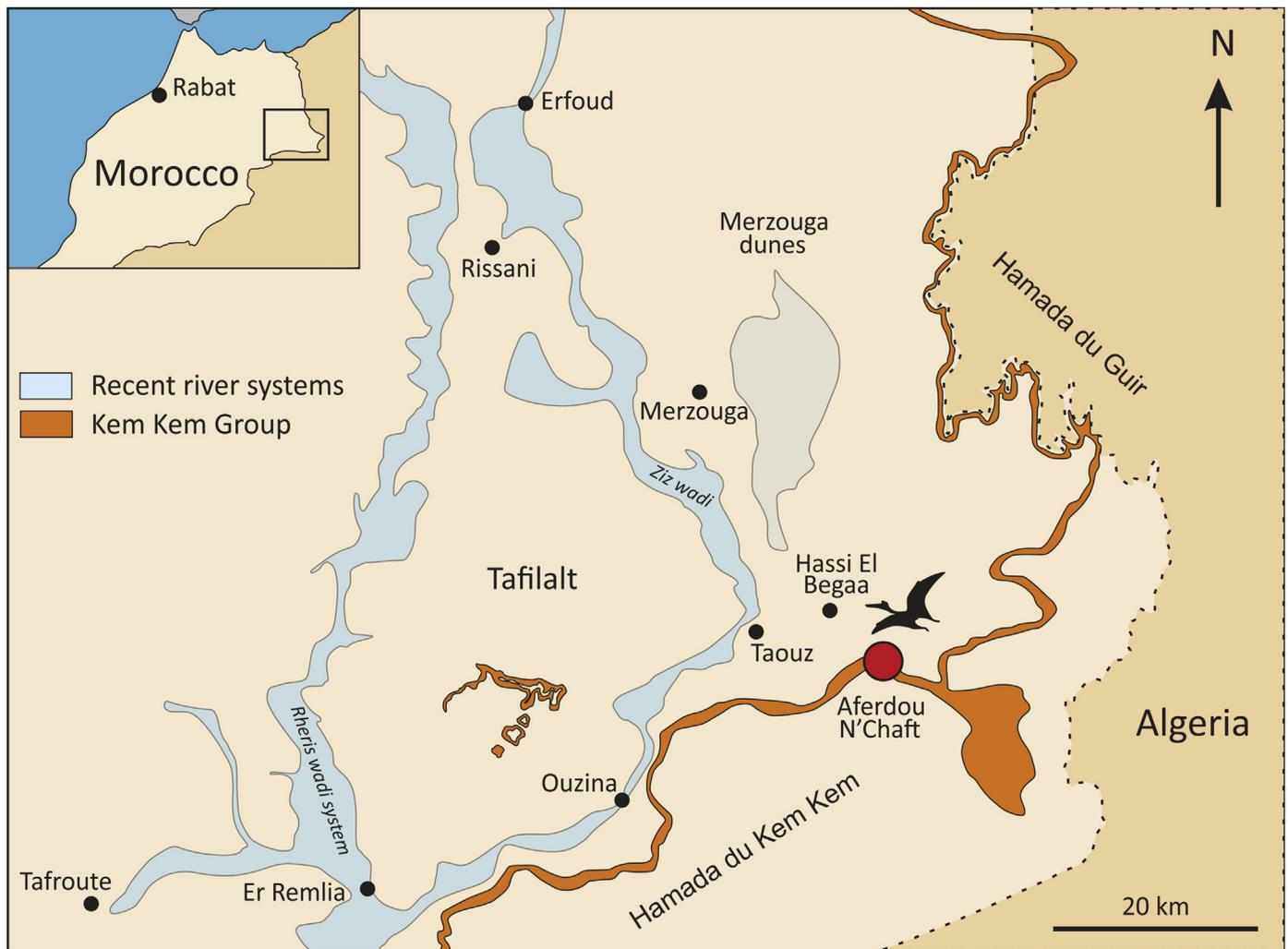
The specimens described here are accessioned in the Faculté des Sciences Ain Chock, Laboratoire de Géosciences, Université Hassan II, Casablanca, Morocco (FSAC), numbers FSAC-KK 5078 to FSAC-KK 5084 and FSAC-KK 5205. Comparisons were made with additional remains from the Kem Kem Group consisting of ~400 pterosaur skeletal elements, 79 of which comprise jaw fragments.

### 2.2. Imaging and thin sectioning

Specimens were imaged using a Nikon D3600 DSLR camera and Zeiss EVO series MA10 scanning electron microscope (SEM). Two jaw fragments (FSAC-KK 5082 and FSAC-KK 5084) representing mature and immature individuals were selected for histological analysis. A transverse thin section (see Fig. S1) was made of these specimens using standard protocols for geological thin section preparation (Reed and Mergner, 1953). Thin sections were imaged using a stereomicroscope in both PPL and XPL using a Leica camera attachment (Leica ICC50 W). Images were processed using Corel Draw Graphics Suite X8 and Combine ZP software. Histological terminology used is *sensu* Francillon-Viellet et al., 1990; Ponton et al., 2004; Chinsamy-Turan, 2005.

### 2.3. Morphometric analysis

Data for 79 azhdarchoid jaw fragments from the Kem Kem Group was collected using digital callipers and formed the basis for the morphometric analysis (see Table S2). All specimens lack the anterior margin of the nasoantorbital fenestra or divergence of the mandibular rami. The specimens were divided into four distinct morphological groups and were assigned, based on characters outlined in Table 1, to *Afrotapejara zouhrii* Martill et al., 2020, *Alanqa saharica* Ibrahim et al., 2010, *Apatorhamphus gyrostege* McPhee et al., 2020, and *Xericeps curvirostris* Martill et al., 2018. Of the examples assigned to *A. saharica* and *A. gyrostege*, 61 specimens had their dorsal/ventral and lateral angles (*sensu* Martill et al., 2020) measured, and 47 had their occlusal neural foramina frequency calculated. This was generated by dividing the preserved length of the occlusal surface by the number of foramina present (higher



**Fig. 1.** A map of southeast Morocco showing the outcrops of the Kem Kem Group, and the mine at Aferdou N'Chaft, near Hasbi El Begaa where the specimens described here were collected. Taken from Smith et al. (2020).

number = lower frequency). Bivariate plots of the lateral and dorsal angles and foramina frequency versus size (using maximum posterior occlusal width as a proxy for specimen size) were generated using Microsoft EXCEL version 2108.

#### 2.4. Determining ontogenetic status

Several size independent criteria have previously been used to determine osteological maturity of pterosaurs, including the degree of ossification of epiphyses, fusion of distinct ossifications, external texture of the cortex and internal bone structure (Bennett, 1993; Prondvai et al., 2012; Dalla Vecchia 2018; Griffin et al., 2020). Here we add a fifth criterion: frequency and distribution of neural foramina on the occlusal and lateral surfaces of the jaws.

The degree of ossification of epiphyses is not relevant to the material described here as they do not occur in association with the jaws or the vertebrae. Fusion of the left and right premaxillae to form the rostrum seems to begin very early in ontogeny, probably in the perinatal interval (Unwin and Deeming, 2019). The premaxillae are distinct in an osteologically highly immature specimen of the anurognathid *Sinomacrops bondei* (Wei et al., 2021) and, while seemingly co-ossified, retain a midline suture in *Batrachognathus volans* (Rjabinin, 1948) and possibly in a late-stage embryo of *Pterodaustro* (Codorniu et al., 2018). Among other pterosaurs, we

found no evidence among postnatal individuals of unfused premaxillae (resulting, for example, in their displacement with respect to each other) even in the smallest examples of *Pterodactylus kochi* (Wellnhofer, 1970), which are osteologically highly immature in almost all respects and are probably neonates. In basal pterosaurs including dimorphodontids (*Dimorphodon*), anurognathids (*Batrachognathus*) and campylognathoidids (*Eudimorphodon ranzi*, *E. cromptonellus*) the dentaries may remain separate even in growth stages that otherwise exhibit a relatively high degree of osteological maturity. By contrast, in rhamphorhynchids (e.g., *Qinglongopterus*) and pterodactyloids including *Pterodactylus* the dentaries are co-ossified, if not yet fully fused in highly immature individuals (Wellnhofer 1970; Lü et al., 2012). This even applies to prenatal individuals of *Hamipterus* from the Sheningkou Formation and an ornithocheirid from the Yixian Formation (Wang and Zhou, 2004; Wang et al., 2017; Unwin and Deeming 2019). In summary, other than in perinatal individuals, the rostra and mandibular symphyses of Kem Kem Group azhdarchoids are likely to exhibit complete fusion with little to no evidence of sutures.

The external texture of cortical bone can provide an approximation for osteological maturity. Textures range from 'fibrous', in osteologically highly immature (perinatal) individuals (e.g., *Pterodactylus kochi*; BMNH 42736) through porous ('immature grain' Bennett, 1993) in individuals that exhibit other features of



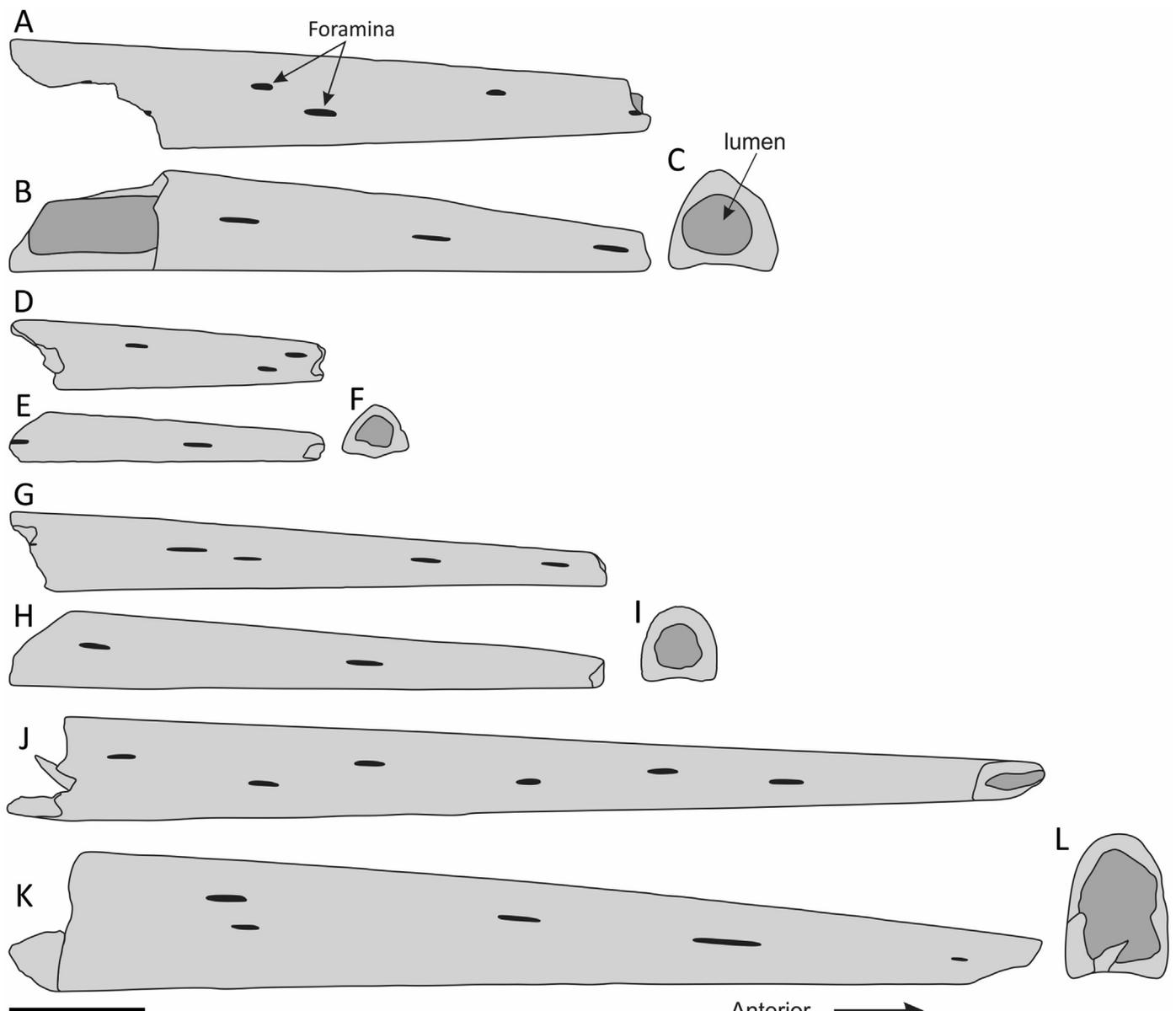
**Fig. 2.** Immature edentulous pterosaur jaw fragments from the Kem Kem Group. A-C, FSAC-KK 5079; D-F, FSAC-KK 5078; G-I, FSAC-KK 5081; J-L, FSAC-KK 5082. A, D, G, J in occlusal view; B, in left lateral view; E, H, K in right lateral view; C, I, L in posterior view. B has been mirrored for ease of comparison. Scale bar represents 5 mm.

osteological immaturity (Bennett 1993, fig. 2a), to dense and smooth (Bennett, 1993, fig. 2b), reflecting a well-developed external fundamental system (EFS) typical of individuals exhibiting a high degree of osteological maturity (Prondvai et al., 2012). This index is effective for identifying individuals that are highly immature, but resolution of later stages can be complicated where specimens are abraded (see also Griffin et al., 2020).

Compared to other methods for determining ontogenetic status, bone histology provides a relatively precise and well-recognised approach for determining osteological maturity in pterosaurs (de Ricqlès et al., 2000; Steel, 2008; Chinsamy et al., 2009; Prondvai et al., 2012; Griffin et al., 2020; Bantim et al., 2021). Peri-natal individuals and the earliest stages of postnatal growth are characterised by cancellous bone (Prondvai et al., 2012), although zonal fibro-lamellar bone was also reported in a neonate of *Pterodaustro* (Chinsamy et al., 2009). Well vascularised fibro-lamellar bone and uneven perimedullary and peripheral margins of cortical bone,

indicative of active resorption, are typical of the intermediate growth stages, as is the presence of large amounts of calcified cartilage in articular ends (Chinsamy et al., 2009; Prondvai et al., 2012). Individuals at, or approaching, osteological maturity typically exhibit secondary remodelling, parallel-fibred to lamellar bone, endosteal bone i.e. inner circumferential layer (ICL) of lamellar bone tissue (absent in immature individuals of *azhdarchids*, pteranodontids [de Ricqlès et al., 2000] and *Pterodaustro* [Chinsamy et al., 2008]), little to no calcified cartilage and an EFS (Prondvai et al., 2012; Griffin et al., 2020) resulting in the smooth finished external cortical surface texture noted above, reflecting slow accretion of bone or its cessation (Bantim et al., 2021). Lines of arrested growth (LAGs), absent in the earliest stages of growth, can provide an additional relative temporal framework (Chinsamy et al., 2009; Prondvai et al., 2012).

An additional index of relative ontogenetic stage relates to the number, size, and distribution of neural foramina on the occlusal



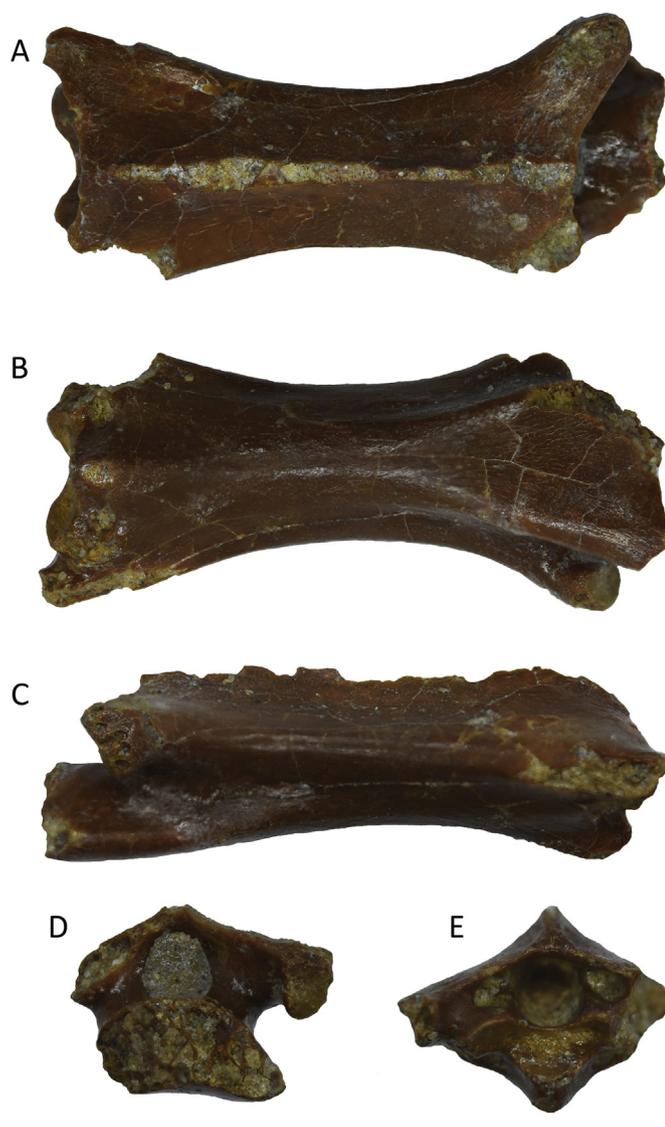
**Fig. 3.** Line drawings of immature edentulous pterosaur jaw fragments from the Kem Kem Group. A-C, FSAC-KK 5079; D-F, FSAC-KK 5078; G-I, FSAC-KK 5081; J-L, FSAC-KK 5082. A, D, G, J in occlusal view; B, in left lateral view; E, H, K in right lateral view; C, I, L in posterior view. B has been mirrored for ease of comparison. Scale bar represents 5 mm.

and lateral margins of the rostrum and mandibular symphysis. Small, relatively closely spaced foramina typify small/younger individuals while large and more widely spaced foramina occur on large/older individuals (Figs. 5-6). The foramina tend to be more elongate in larger/?older individuals. This idea is supported by the presence of comparable numbers of foramina occupying approximately the same positions in FSAC-KK 5205, a large, osteologically mature individual and FSAC KK 5080 a smaller, osteologically immature individual (Fig. 6). These specimens suggest that an individual retains the same number of foramina in the jaws throughout growth. Rather than add additional foramina as the jaws increase in size, existing foramina show a concomitant size increase and, perforce, the distance between them increases. Consequently, earlier ontogenetic stages can be identified based on the relatively higher numbers of foramina within a given space and their relatively small size compared to those of larger, older individuals (Fig. 6).

The indices described above can provide some indication of the osteological maturity of individuals such that three key stages of growth can be recognised: highly immature (perinatal); immature (main growth stage); mature (little or no growth). However, as previous studies have noted there can be considerable variability between different skeletal elements (Chinsamy et al., 2009; Prondvai et al., 2012; Dalla Vecchia 2018). The most effective approach is to combine evidence from as many indices as practical and to compare results with those for pterosaurs such as *Rhamphorhynchus* and *Pterodaustro* where osteological development has been well documented (e.g., Bennett, 1995; Chinsamy et al., 2008, 2009; Prondvai et al., 2012; Hone et al., 2020).

### 2.5. Terminology

In this paper we propose a series of size classes, partly as a terminological necessity and partly because exact sizes are difficult



**Fig. 4.** FSAC-KK 5083, a mid-series azhdarchoid cervical vertebrae from a small pterosaur. A, dorsal view; B, ventral view; C, right lateral view; D, posterior view; E, anterior view. Scale bar represents 10 mm.

to estimate even for relatively complete skeletal remains. While the classes, which relate to wingspan (wsp), are arbitrary, they generally conform to previous schemes.

Small: <1 m wsp. (this includes a nominal subclass very small: <0.5 m wsp).

Medium: 1–2 m wsp.

Large: 2–4 m wsp.

Very large: 4–6 m wsp.

Giant: >6 m wsp.

### 3. Results

#### 3.1. Morphometric analysis

##### 3.1.1. Morphotypes and size

The edentulous pterosaur jaw fragments from the Kem Kem Group exhibit a large size range in three of the four morphotypes present (morphotypes 1–3). Individuals of morphotypes 1 and 2 form near continuous size sequences. See Fig. 7 and Table 1.

##### 3.1.2. Dorsal/ventral and lateral angles

Of the 55 specimens measured of morphotypes 1 and 2, a large range of dorsal and lateral angles is seen (see Fig. 8, Table 1), but no correlation between dorsal angle and overall size was observed (see Fig. 8B). Similarly, no correlation between the lateral angle and overall size was observed for individuals of morphotype 1. By contrast there is a correlation between the lateral angle and size for individuals of morphotype 2 (see Fig. 8A), although this is likely a consequence of a slightly concave dorsal surface in *Aptorhamphus*.

There does not appear to be any correlation between size and dorsal/ventral angle for morphotypes 1 and 2, or for the lateral angle and size for morphotype 1. A correlation between lateral angle and size was observed for morphotype 2, but this too likely to be a consequence of *Aptorhamphus* having a slightly concave dorsal surface: the anterior tip of the jaw of a large individual will have a lower angle compared to a more posterior section of the jaw of a large individual, and thus does not reflect a true relationship between size and lateral angle. Consequently, dorsal/ventral and lateral angles are of limited value as a proxy for overall size/ontogenetic status of an individual. The small differences detected may be due to a combination of interspecific variation, sexual dimorphism and difference between the upper and lower jaws, all of which have proven difficult to determine.

##### 3.1.3. Foramina concentration

The occlusal foramina concentration was calculated and plotted against posterior occlusal width for 47 specimens of morphotype 1 ( $n = 20$ ) and morphotype 2 ( $n = 27$ ) (see Fig. 5). A correlation between size and foramina concentration was observed for both morphotypes, with a higher concentration of foramina observed in the very small specimens (see Fig. 5).

Two morphotype 1 specimens, FSAC-KK 5205 and FSAC-KK 5080, of notably different sizes, display a median boss on the occlusal surface. When the number and position of foramina are compared a similar number of foramina with a similar distribution is observed in both specimens (see Fig. 6). Specimen FSAC-KK 5205 is a large specimen interpreted as a mature individual, whilst FSAC-KK 5080 is a smaller specimen and is identified as a younger individual.

### 3.2. Systematic palaeontology

Pterosauria [Kaup, 1834](#)

Monofenestrata [Lü et al., 2009](#)

Pterodactyloidea [Plieninger, 1901](#)

Azhdarchoidea [Nesov, 1984](#) (*sensu* [Unwin 2003](#))

Azhdarchidae [Nesov, 1984](#)

Genus *Alanqa* [Ibrahim et al., 2010](#)

cf. *Alanqa saharica* [Ibrahim et al., 2010](#)

*Referred material.* Three jaw fragments, FSAC-KK 5078–5080 (Figs. 2A–F, 3A–F, 6A–D).

*Description.* All three specimens have a similar morphology (Figs. 2A–F, 3A–F, 6A–D). They have an approximately equilateral triangular cross-sectional outline with a straight occlusal margin and rounded dorsal margin. Specimen FSAC-KK 5078 has an almost flat occlusal surface anteriorly, which becomes slightly convex posteriorly, while specimen FSAC-KK 5079 has a slightly sulcate occlusal surface. Specimen FSAC-KK 5080 has a flat occlusal surface anteriorly, becoming gently sulcate posteriorly, and has the anterior-most portion of a median boss on the occlusal surface, homologous with that on the holotype specimen (FSAC-KK 26) and FSAC-KK 5205. All three specimens have foramina in offset pairs on the occlusal surface, and a single row of medially located foramina

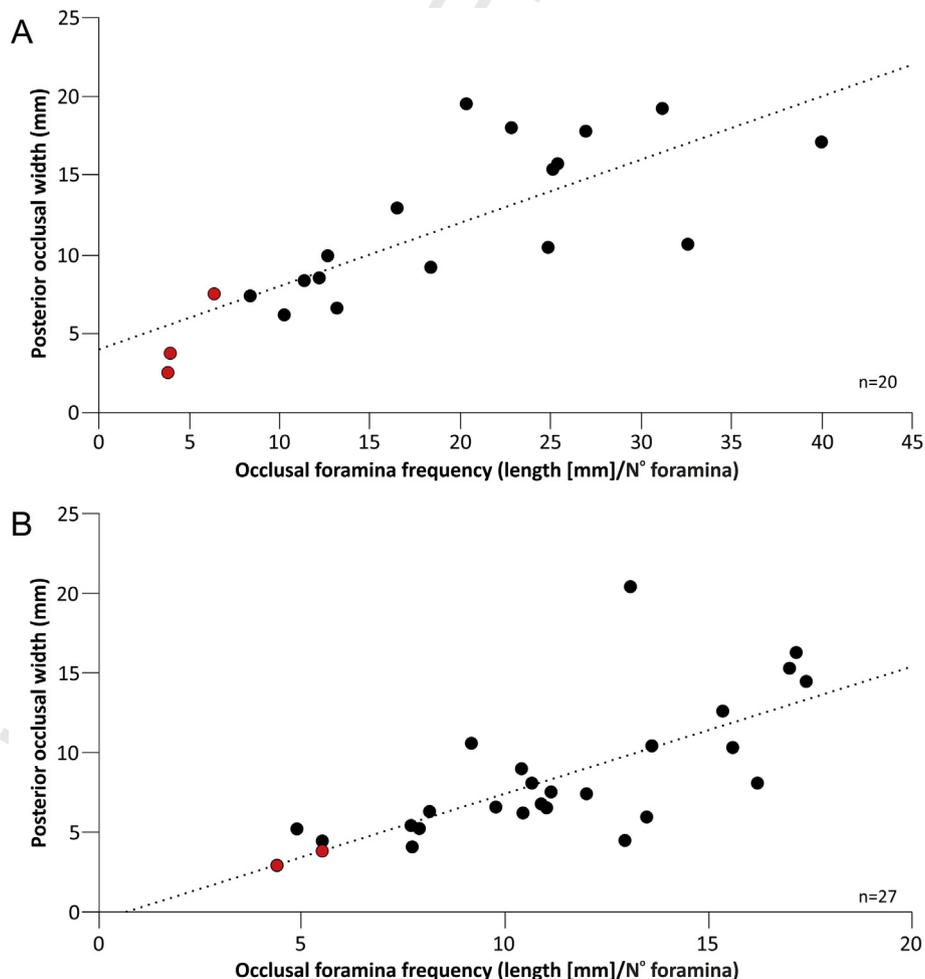
**Table 1**  
Morphotypes, size and angle ranges of the Kem Kem Group edentulous jaw fragments analysed.

Morphotype	Characteristics	Size range (mm)	Angles range (°)
1. <i>Alanqa</i> morphotype N = 25	Triangular cross-section, relatively low lateral rostral angle (<12°), single row of lateral foramina	Max posterior height: 2.0–39.6 Max posterior width: 2.5–19.2	Lateral: -4°–12° Dorsal: -3.5°–9°
2. <i>Aptorhamphus</i> morphotype N = 39	Inverted 'U' shaped cross section, straight beak	Max posterior height: 2.8–59.8 Max posterior width: 2.8–21.6	Lateral: -5°–13° Dorsal: -3°–6°
3. <i>Afrotapejara</i> morphotype N = 10	Triangular cross section, relatively high lateral rostral angle (>10°), two rows of lateral foramina	Max posterior height: 5.9–63.0 Max posterior width: 7.9–30.0	Lateral: -10°–20° Dorsal: -3°–9°
4. <i>Xericeps</i> morphotype N = 5	Inverted 'U' shaped cross section, dorsal curvature and a ventral sulcus	Max posterior height: 9.2–14.1 Max posterior width: 5.9–7.4	Lateral: -6°–7° Dorsal: -3°–4°

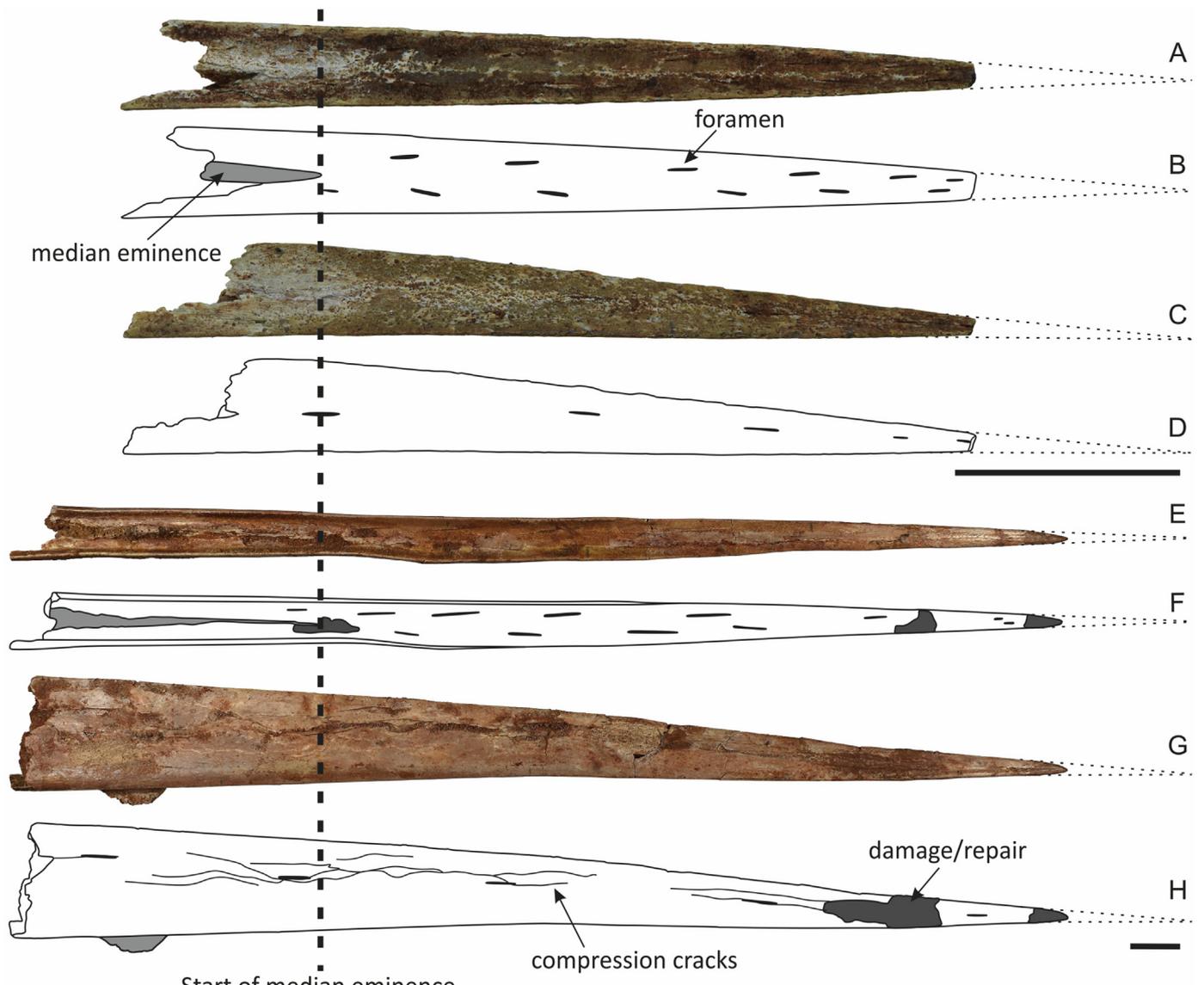
on the lateral surfaces. The anterior most tip of all specimens is missing (see Table 2 for measurements).

**Taxonomic assignment.** Specimens FSAC-KK 5078-5080 are assigned to cf. *Alanqa saharica* based upon their triangular cross-sectional outlines and rounded dorsal margin. A comparable cross-sectional

outline is only evident on two Kem Kem Group edentulous pterosaurs: *A. saharica* and *Afrotapejara zoughrii*. However, the cross-section of *A. zoughrii* more closely describes an isosceles triangle as opposed to an equilateral triangle seen in *A. saharica*. In addition, *A. zoughrii* also has two rows of foramina on the occlusal surfaces instead



**Fig. 5.** Graphs of Kem Kem Group edentulous jaw occlusal neural foramina concentration against jaw size for morphotype 1 (A) and morphotype 2 (B). Red points indicate specimens identified as immature individuals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 6.** Occlusal and lateral neural foramina concentration and distribution on two Kem Kem Group morphotype 1 pterosaur jaws. A-D immature individual (FSAC-KK 5080); E-H adult FSAC-KK 5205. A-B and E-F in occlusal view; C-D in left lateral view (mirrored for ease of comparison); G-H in right lateral view. Scale bar represents 20 mm.

of the single row present in *A. saharica*. For these reasons we assign specimens FSAC-KK 5078-5080 to cf. *Alanya saharica*.

#### ?Chaoyangopteridae Lü et al., 2008

Genus *Aptorhamphus* McPhee et al., 2020

cf. *Aptorhamphus gyrostega* McPhee et al., 2020.

**Referred material.** Two jaw fragments FSAC-KK 5081-5082 (Figs. 2G-L, 3G-L).

**Description.** Specimens FSAC-KK 5081 and 5082 (Fig. 2G-L) have a similar overall similar morphology, with an inverted 'U' shaped cross-sectional outline and a rounded dorsal margin. Both specimens have a flat occlusal margin and a gently sulcate occlusal surface. The occlusal surface of both specimens bears offset pairs of foramina, with a single row of medially located foramina on the lateral surfaces (see Table 2 for measurements). The anterior most tip of both specimens is missing.

**Taxonomic assignment.** Specimens FSAC-KK 5081-5082 are assigned to cf. *Aptorhamphus gyrostega* due to their closely comparable 'inverted U' shaped cross-sectional outlines. This cross-sectional outline is only exhibited by *A. gyrostega* and *Xericeps curvirostris*

among Kem Kem Group pterosaurs. However, *X. curvirostris* is curved dorsally and has a sulcate ventral margin. These features are not seen on specimens FSAC-KK 5080 or FSAC-KK 5082, therefore we assign them to cf. *Aptorhamphus gyrostega*.

#### Azhdarchidae indet.

**Description.** Specimen FSAC-KK 5083 (Fig. 4, Table 2) is a single partial mid-series elongate cervical vertebra. Both the left prezygapophysis and postzygapophysis are missing and the condyle is slightly damaged. It lacks an anterior dorsal foramen, which suggests it may represent a cervical IV using the criteria of Averianov (2010) (see Table 2 for measurements).

**Taxonomic assignment.** Specimen FSAC-KK 5083 is assigned to Azhdarchidae indet. due to it displaying several features typical of azhdarchid cervical vertebrae, including a neural tube subsumed into the centrum, a highly reduced neural spine, and the lack of lateral pleurocoels (e.g., Frey and Martill, 1996; Averianov, 2010). Assignment to a specific taxon is not possible because multiple azhdarchids are present within the Kem Kem Group, none of which have associated post-cranial material.

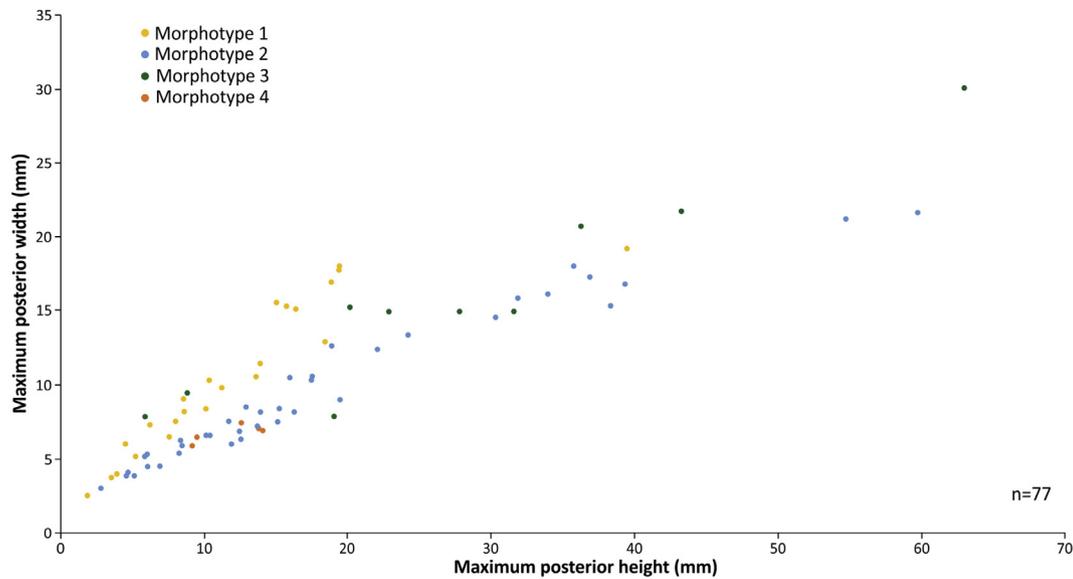


Fig. 7. Graph of Kem Kem Group edentulous jaw sizes for each morphotype.

### 3.3. Ontogenetic status

#### 3.3.1. Bone surface texture

The bone surface texture of the small jaw fragments (FSAC-KK 5078, 5079, 5081 and 5082) was examined by scanning electron microscopy. FSAC-KK 5079, FSAC-KK 5081 and FSAC-KK 5082 (Fig. 9C, A-B and D respectively) exhibited an open fibrous texture, with longitudinal grooves along the jaw. These are particularly well developed in FSAC-KK 5081 (Fig. 9A-B). By contrast, the bone surface of a more mature individual FSAC-KK 5011, is much smoother and the bone fibres are less pronounced (Fig. 9F). The smallest specimen, FSAC-KK 5078, has a polished surface (Fig. 9E), possibly an artifact of abrasion.

#### 3.3.2. Palaeohistology

**3.3.2.1. Jaw fragment FSAC-KK 5082.** The cross-section of the bone wall is approximately square, although the dorsal part of the compacta is more rounded. A narrow, compacted bone wall (maximum thickness of 0.5 mm) encloses a large predominantly vacant central cavity (referred to as a medullary cavity, Prondvai and Stein, 2014) (Fig. 10A). The periosteal margin is highly uneven and appears osteogenic (Fig. 10D). There are numerous places where vascular canals open directly onto the periosteal surface. The endosteal margin is likewise uneven, but here the reason is because it is a resorptive surface (Fig. 10D). This is seen in its encroachment onto the primary periosteal bone (Fig. 10C, D). Thus, the bone formed during even earlier stages of ontogeny has been resorbed through the expansion of the central cavity. Several Volkmann's canals penetrate the bone wall endosteally. No inner circumferential lamellar layer (ICL) is present, which suggests that endosteal remodeling has not yet been completed. The preservation of the bone is not ideal especially since the fibrillar organisation of the bone tissue is not well preserved. It is however apparent that the bone wall is reasonably well-vascularised by predominantly longitudinally oriented "vascular canals" that appear to be more or less evenly spaced throughout the compacta. Towards the periphery of the bone, many of these canals are relatively large without any osteonal development around them i.e., they are incompletely formed primary osteons. Osteocyte lacunae throughout the compacta are randomly organised and tend to be plump. In various

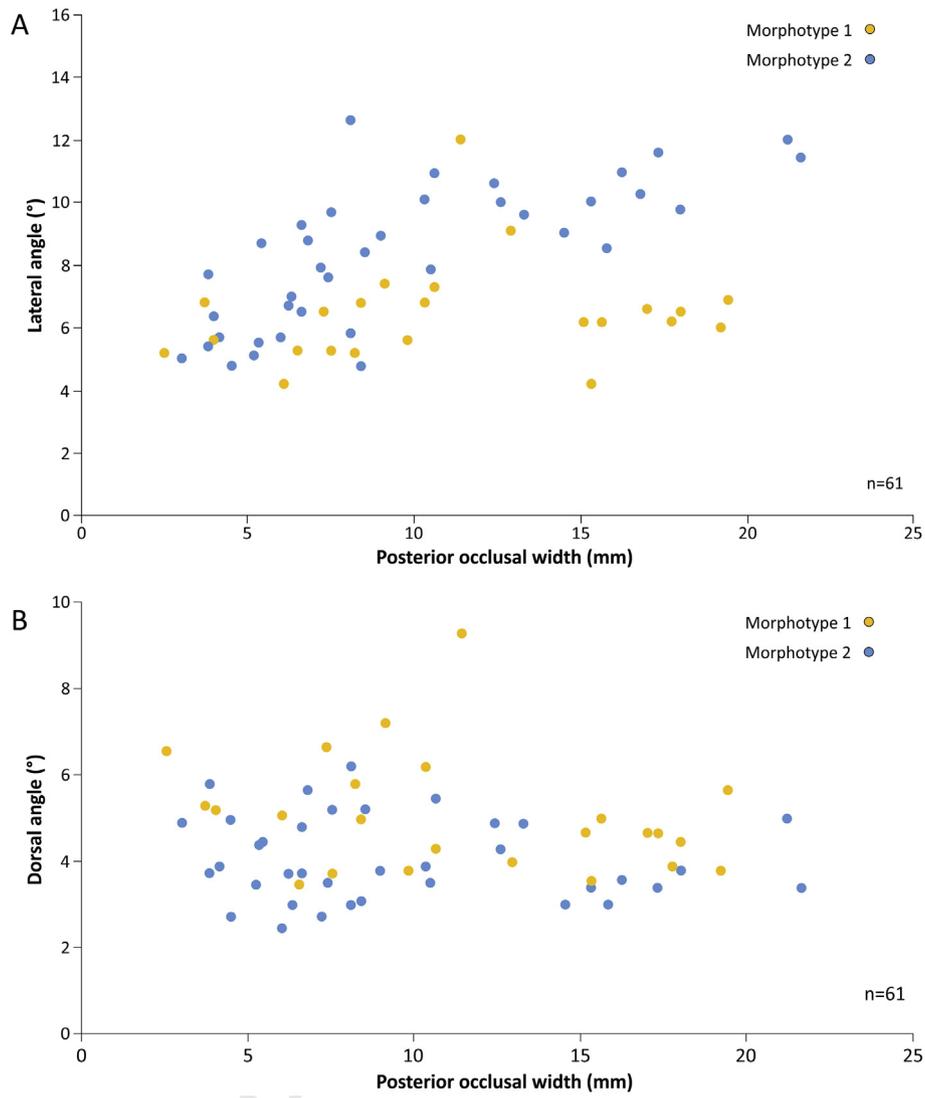
places, numerous canaliculi are seen radiating from the osteocyte lacunae (e.g., Fig. 10E). No LAGs or any other growth marks are observed anywhere in the compacta. Fig. 10B shows a large foramen that extends almost halfway into the compacta. The bone tissue around it is not well preserved, but this would most likely be endosteally formed lamellar bone tissue.

**3.3.2.2. Jaw fragment FSAC-KK 5084.** The cross section of this mandibular fragment is more "triangular" with the apex located dorsally while the occlusal region forms the base (Fig. 11A). The lateral/medial margins of the jaw fragment appear to be thickest. The microanatomy clearly shows a large mostly vacant central

Table 2

Specimen measurements. A, Kem Kem Group immature jaw fragments; B, small azhdarchid cervical vertebra from the Kem Kem Group and selected small cervical vertebrae from the Cambridge Greensand Member (CGM). \*Centrum length (CL) is measured from the anterior termination of the cotylar facet to the posterior termination of the condyle. Minimum centrum width (CW) refers to the narrowest point between the pre- and post-zygapophysial expansions. Relative elongation (RE) is determined by the ratio of centrum length to minimum width of a vertebra, rounded up to the nearest tenth of a unit. CGM measurements from Unwin, 1991.

A.						
Specimen number	Taxonomic referral	Max length (mm)	Max posterior height (mm)	Max posterior occlusal width (mm)	Lateral angle (°)	Dorsal angle (°)
FSAC-KK 5080	cf. <i>A. saharica</i>	75.8	8.0	7.9	~5	~4
FSAC-KK 5078	cf. <i>A. saharica</i>	11.6	2.0	2.5	~5	~5
FSAC-KK 5079	cf. <i>A. saharica</i>	23.6	3.6	3.5	~7	~5
FSAC-KK 5081	cf. <i>A. gyrostega</i>	21.9	2.8	2.8	~5	~5
FSAC-KK 5082	cf. <i>A. gyrostega</i>	38.3	5.4	3.8	~6	~5
B.						
Specimen	CL (mm)	CW (mm)	RE (mm)			
FSAC-KK 5083	29.1	7.4	3.9			
CAMSM B 54398	19.8	4.9	4.0			
CAMSM B 54395	24.1	11.4	2.1			
CAMSM B 54688	24.2	9.7	2.5			
CAMSM B 54396	27.4	8.3	3.3			
CAMSM B 54387	28.7	11.0	2.6			
CAMSM B 54686	30.2	10.8	2.8			



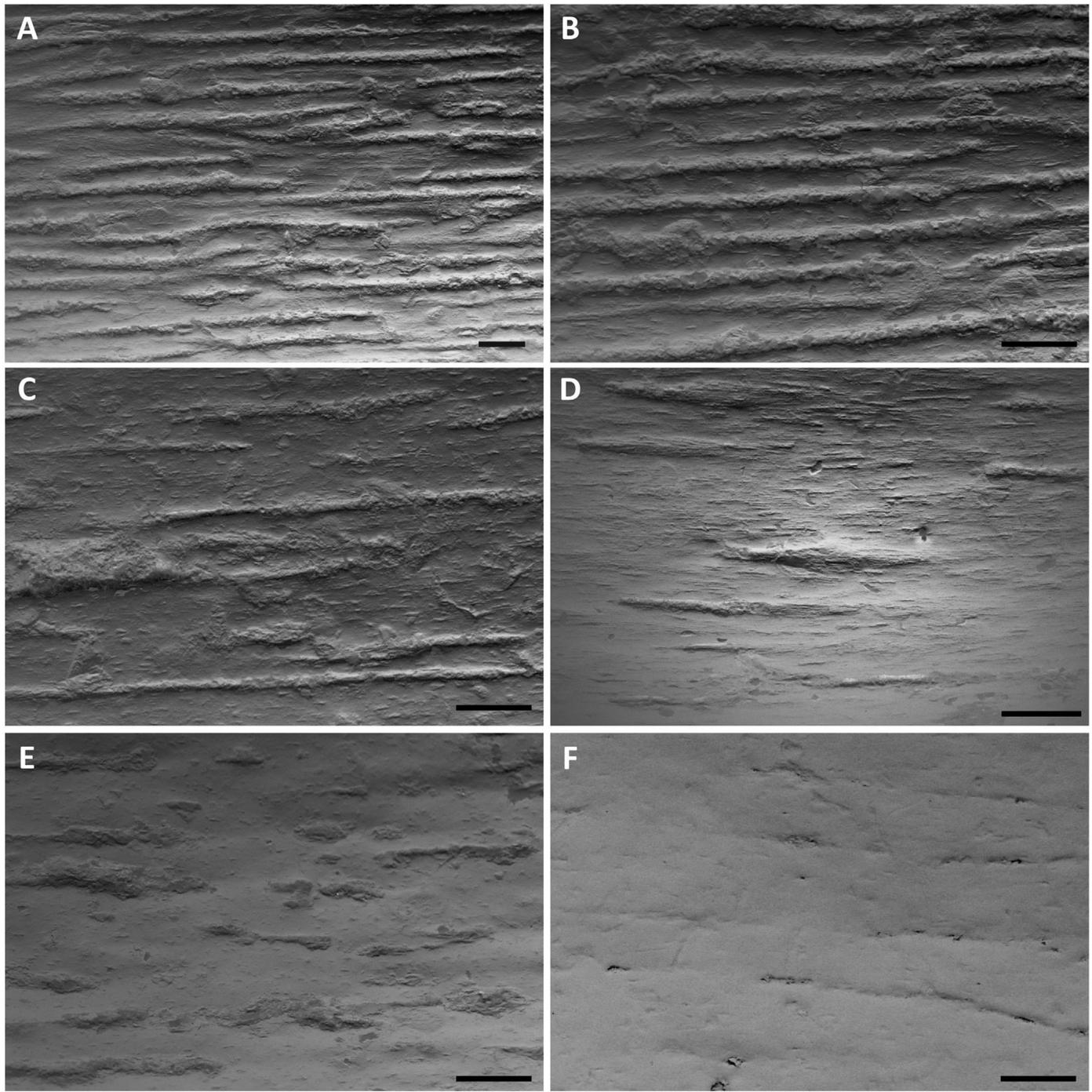
**Fig. 8.** Graphs of Kem Kem Group edentulous jaw angles against jaw size for morphotypes 1 and 2. A, lateral angles vs posterior occlusal width; B, dorsal angle vs posterior occlusal width.

medullary cavity, and several large erosion cavities are evident in the perimedullary region, with some very large cavities towards the occlusal side. The histology of this bone is better preserved than that of FSAC-KK 5082, although as an artefact of preservation the periosteal bone does not show birefringence as compared to the endosteal bone tissues. Overall, the bone wall is thick (approximately 6 mm) and essentially comprises of a well vascularised compacted bone tissue (e.g., Fig. S2B). The occlusal surface is highly remodeled, and only a narrow band of tissue forms the bone wall (Fig. S2C). In general, numerous longitudinal or radially organised vascular canals are distributed across the compacta, and in localised areas, the vascular organisation becomes more reticular (e.g., Fig. S2D). The outer 0.5 mm of the bone wall appears to have fewer vascular canals, but many of them open directly to the periosteal surface which appears quite uneven and osteogenic (e.g., Fig. S2J). The perimedullary region appears to be extensively remodeled/reconstructed. Several enlarged vascular canals occur, some of which are thinly lined with secondarily formed lamellar deposits (Fig. S2B). Many well-formed secondary osteons occur in the perimedullary region around the entire cross section. In certain parts of the compacta, there appears to be narrow annuli that interrupt

the normal bone deposition—vascular canals are fewer in this region, and when present they appear to cross over as radial canals (see e.g., Figs. S2E and H). In Fig. S2H no LAGs are visible, but in Fig. S2E, LAGs accompany the three bands of annuli. Although the actual fibrillar texture of the bone is not well preserved, the more organised osteocyte lacunae in these bands are discernable. Under polarised light, two (?three) annuli are evident in Fig. S2I, three annuli are visible in Fig. S2F. In Fig. 11C–D there are four annuli with the inner two accompanied by LAGs, and the periosteal surface is still clearly active (i.e., it is still depositing bone). The lateral sides of the jaw best preserve the growth record of the animal (Fig. 11C–D).

Image Fig. 11B shows a large foramen penetrating the bone. This is lined with a layer of lamellar bone tissue. All around the cross-section the medullary cavity is lined by an ICL composed of a lamellar tissue (Fig. 11E–F). The ICL has distinct osteocytes with a flattened aspect, compared to the plump randomly organised osteocyte lacunae in the rest of the compacta. Fig. 11E demonstrates shallow osteonal development around the vascular canals.

An unusual feature is seen in the endosteal region (Fig. 11G–H), where there is a distinct ICL, below which is a well vascularised woven bone tissue that is clearly endosteally formed. This tissue



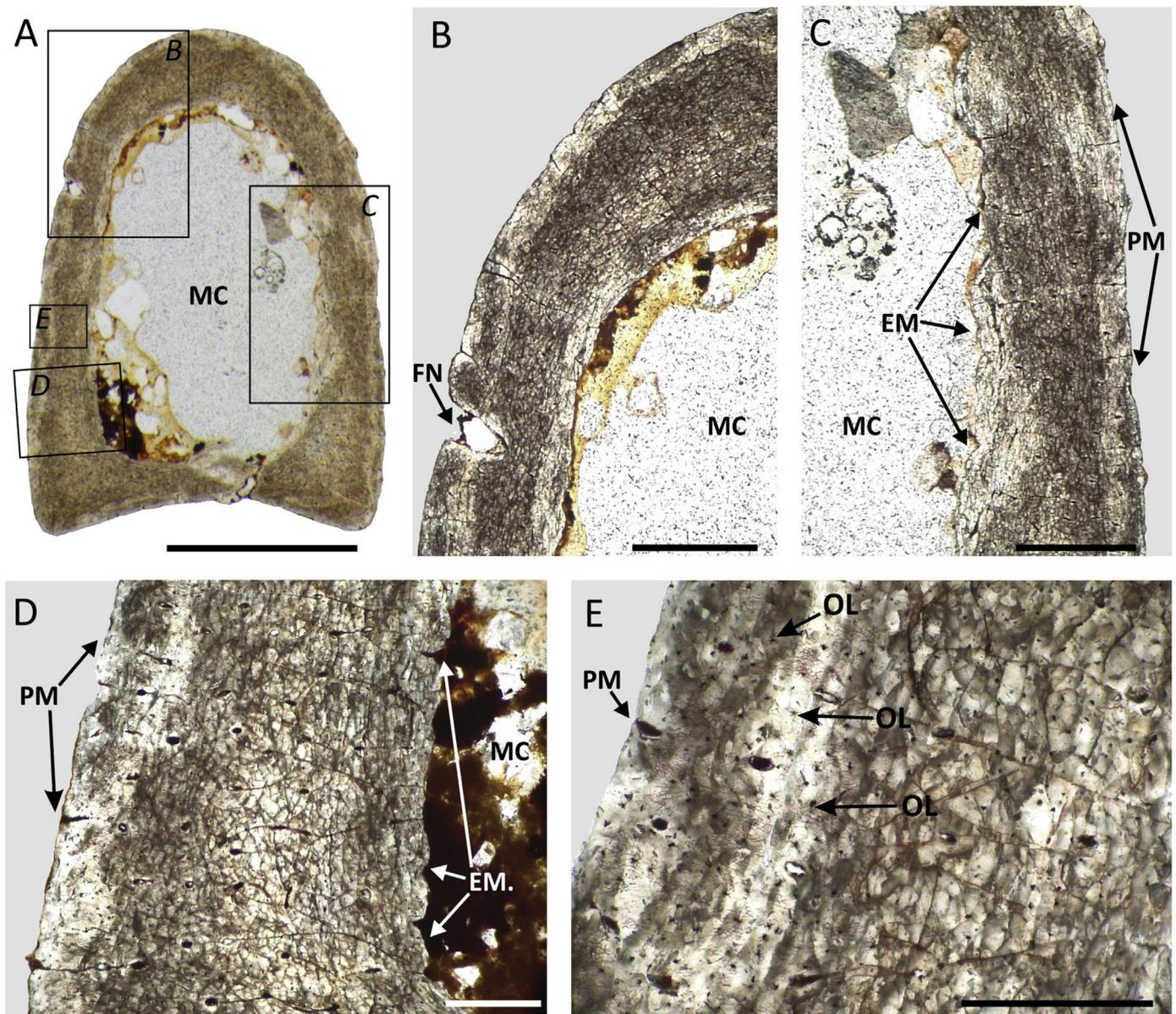
**Fig. 9.** SEM images of bone surface texture of Kem Kem Group pterosaurs pterosaur jaws. A-D immature individuals and E a more mature individual. A-B, FSAC-KK 5081; C, FSAC-KK 5079; D, FSAC-KK 5082; E, FSAC-KK 5078; F, FSAC-KK 5011. Scale bars represent 200  $\mu\text{m}$ .

could be medullary bone, or the medullary bone-like tissue described for *Bakonydraco* (Prondvai and Stein, 2014; Prondvai, 2017). This is not seen in any other area of the thin section. Some of the enlarged cavities appear to have been still actively resorbing primary bone tissues at the time of death (see the uneven margins of Fig. S2G).

### 3.3.3. Osteological maturity of the cervical vertebra

Specimen FSAC-KK 5083 (Fig. 4) is a mid-series azhdarchid cervical vertebra exhibiting several features that indicate an

osteologically mature individual, including fusion of the neural arch and centrum; well ossified articular surfaces and margins; well-developed pneumatic fossae and a smoother bone texture. However, the timing of the development of these features in the vertebral column of pterosaurs is complex and likely occurs at different stages of development (asynchronous fusion of Eck et al., [2011]). This is clearly demonstrated by an immature *Tapejara* specimen, where the atlas-axis complex and posterior cervicals were unfused, recalling an immature state, but with mid-series cervicals with fully fused neural arches and centra, suggesting



**Fig. 10.** Thin section PPL images of jaw fragment of cf. *Apatorhamphus gyrostega* FSAC-KK 5082, an immature individual. A, an overview image of the jaw cross-section, showing the positions of images B-E; B, image showing a large foramen; C-D, images showing uneven periosteal and endosteal margins; E, magnified image showing plump osteocyte lacunae with radiating canaliculi. Note that no LAGs growth marks are observed anywhere in the compacta. Scale bar A represents 2 mm, B-C represents 0.5 mm and D-E represents 0.2 mm. See Fig. S1 for location on jaw of transverse thin section. Abbreviations: EM: endosteal margin; FN: foramen; MC: medullary cavity; OL: osteocyte lacunae; PM: periosteal margin.

skeletal maturity as in FSAC KK 5083 (Eck et al., 2011). Thus, fusion of the neural arch and centrum occurs during early development in some azhdarchoid pterosaurs and therefore it is difficult to determine from an isolated mid-series cervical vertebra if it is from an immature or mature individual.

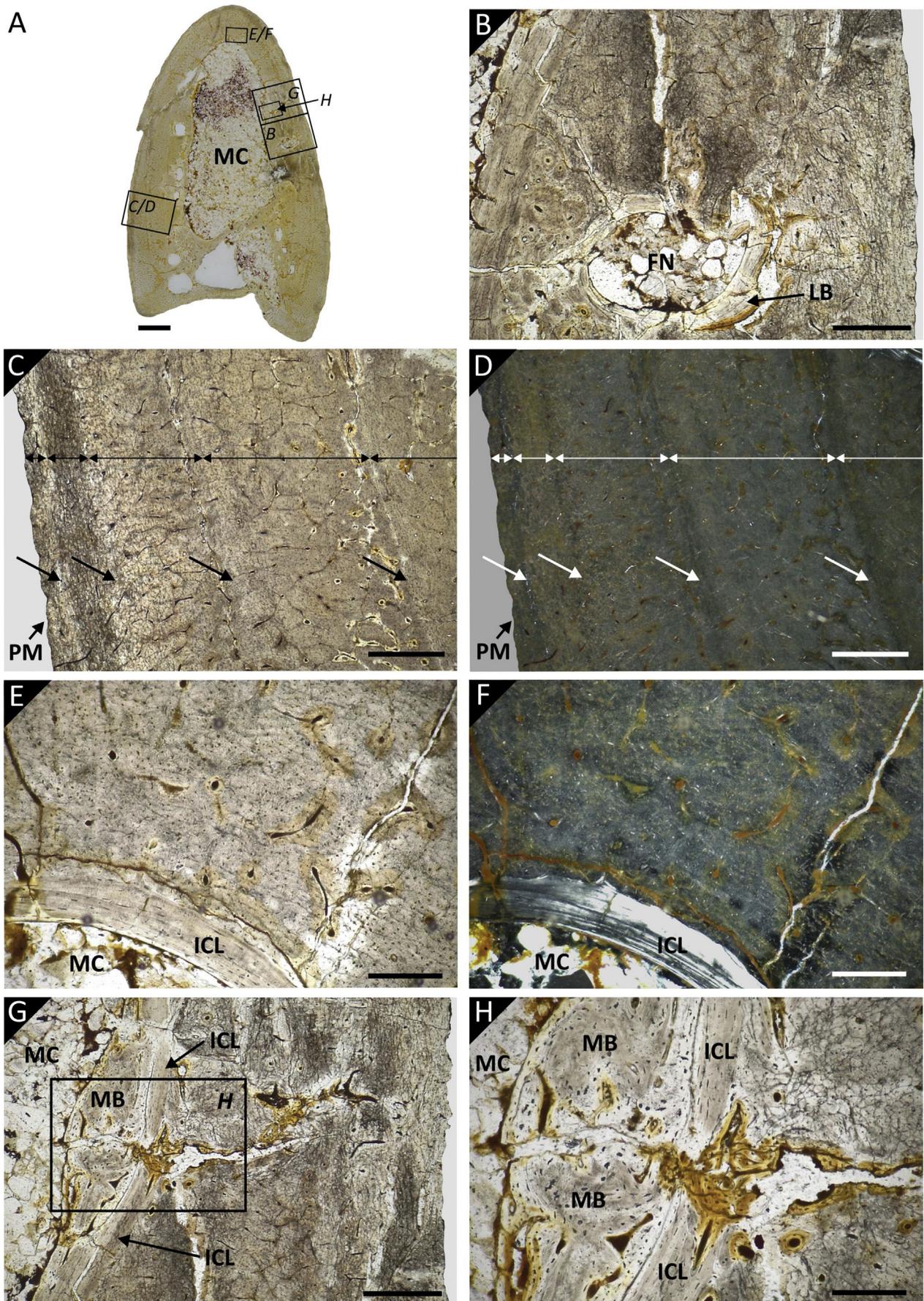
#### 4. Discussion

##### 4.1. Small pterosaurs in the Kem Kem Group

Small pterosaurs occur infrequently in the Kem Kem Group, with six specimens (FSAC-KK 5078-5083) that can be positively identified as representing small individuals. Estimating a wingspan for specimens represented by small fragments of the anterior jaws is challenging because they lack key markers for scaling (e.g., the

anterior margin of nasoantorbital fenestra or divergence of the mandibular rami). However, comparisons with the azhdarchid *Zhejiangopterus linhaiensis* Cai and Wei, 1994 (specimen ZMNH M1323) suggest a wingspan of between 0.7 m and 1.1 m for an individual represented by a small cervical vertebra (FSAC-KK 5083) (Fig. 4).

The surface texture of all the jaw specimens examined showed signs of varying degrees of osteological immaturity (see Fig. 9). In mature pterosaurs, the bone has a smooth texture, whereas in immature individuals it is 'rippled' with an open fibrous texture (Bennett, 1993). Specimens FSAC-KK 5079 and FSAC-KK 5081 are osteologically immature with an open fibrous texture (Fig. 9C and A-B respectively), while a similar, but somewhat less well-developed surface texture is seen in specimen FSAC-KK 5079, which likely represents a more mature individual. The bone surface



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texture of FSAC-KK 5081 is typical of the smallest/most immature individuals of *Pterodactylus* from the Jurassic Solnhofen Limestone Formation of Germany and that seen on some embryos (pers. obs. DMU). Although still immature, specimen FSAC-KK 5082 (Fig. 9D) represents a more mature individual than FSAC-KK 5079 or FSAC-KK 5081, because fibrous bone is still visible, although it is less pronounced. The bone texture of specimen FSAC-KK 5078 (Fig. 9E) is less informative as it appears to have been abraded.

The histology of specimen FSAC-KK 5082 compared to that of FSAC-KK 5084 suggests that FSAC-KK 5082 is a young individual. Overall, the bone wall thickness is relatively narrow, and there is no ICL present, which means that medullary expansion has not yet been completed (e.g., Enlow, 1963; Chinsamy-Turan, 2005). Peripherally the bone appears to still be forming and there is no sign of it slowing down. No annuli or LAGs were observed throughout the compacta. These findings suggest that this jaw fragment belongs to an individual that is less than 1 year old (assuming that an annulus does indeed form annually: Chinsamy-Turan 2005; Kohler et al., 2012; Chinsamy and Warburton 2021).

FSAC-KK 5084 appears to be from a more mature individual, and although it experienced at least 4 growth cycles, it had still not reached skeletal maturity. We cannot be certain that earlier growth cycles may have been removed because of the extensive endosteal remodeling. There is a slight decrease in the amount of vascularisation towards the periphery but there is no OCL present. Furthermore, the periosteal surface appears to be osteogenic. Thus, even after 4 cycles of growth it has still not reached adult body size. Larger examples of *Aptorhamphus* jaws are known from the Kem Kem Group (McPhee et al., 2020) and may represent older individuals. Fig. 11C–D shows a substantial narrowing of the bone tissue after the 3rd annulus (i.e., 3rd from the endosteal side, 2nd from the periphery), this may be correlated with attainment of sexual maturity (as postulated for *Pterodaustro* Chinsamy et al., 2008). It is highly unlikely that this related to onset of flight as postulated for *Rhamphorhynchus* (Prondvai et al., 2012). The presence of the medullary bone or medullary bone-like tissue in FSAC-KK 5084 is noteworthy. If it is the former, it implies that this was a sexually mature female individual (e.g., Chinsamy et al., 2013), whereas if it were the latter, it could be a non-reproductive tissue perhaps related to the mobilisation of calcium (Prondvai and Stein, 2014).

Both the surface texture and histology of the small jaw fragments as seen in thin section suggests that they represent immature individuals of species represented by mature individuals with, in some cases, wingspans in excess of 6 m (Unwin et al., in prep.) rather than small species of pterosaur.

The large size range of jaw fragments (Fig. 7) and large range in foramina concentration on the occlusal surface (Fig. 5) suggests that the immature individuals represented by specimens FSAC-KK 5078–5082 are part of a size continuum of pterosaurs from very small immature individuals to large or even giant-sized adults, likely representing an age continuum from flaplings to mature adults.

#### 4.2. Palaeoecology of immature pterosaurs

Many studies discussing the ecology of Cretaceous pterosaurs assume that early growth stages of large to giant pterosaurs played

little or no role within these ancient ecosystems (Unwin, 1988; Slack et al., 2006; Benson et al., 2014), which is plausible if pterosaurs were altricial and cared for by adults for prolonged periods. Conversely, if pterosaurs were precocial or even super precocial with little to no parental care as evidence suggests (e.g., Manzig et al., 2014; Bennett, 2017; Unwin and Deeming, 2019; Hone et al., 2020; Naish et al., 2021), immature pterosaurs are likely to have occupied niches quite different from those inhabited by their large and giant adult counterparts primarily to avoid competition between different size classes. One consequence of ontogenetic niches is that the ecology of small, immature individuals may have overlapped with that of adults of small pterosaur species, resulting in competition for resources. This might help explain the rarity of small pterosaur species in the mid-Late Cretaceous (e.g., Benson et al., 2014) and a similar scenario has been suggested for theropod dinosaurs (Schroeder et al., 2021). We propose therefore that immature individuals from the Kem Kem Group likely occupied different ecological niches to those of their adult counterparts. An important consequence of this idea is that it facilitated an increase in the ecological diversity of the Kem Kem Group pterosaur assemblage without extending its taxonomic diversity. If this is more generally true for pterosaurs then it is possible that any pterosaur bearing deposit that, seemingly, has a low taxonomic diversity may nevertheless have had a high ecological diversity.

#### 4.3. Underrepresentation of small-bodied pterosaurs in the Kem Kem Group

A considerable quantity of pterosaur material has been collected from the Kem Kem Group in recent years (Ibrahim et al., 2010; Martill et al., 2018, 2020; Jacobs et al., 2019, 2020; MCPhee et al., 2020; Smith et al., 2020). This dataset has grown from a few tens of specimens to ~400 specimens and includes small and even very small individuals. Similarly, as the dataset has grown, specimens representing large and even giant individuals have also emerged (Unwin et al., in prep.). This suggests, unsurprisingly, that sample size is a key factor that constrains apparent size ranges of pterosaurs collected from a particular deposit. The apparent absence of small individuals in many Cretaceous pterosaur-bearing deposits may reflect a small sample size rather than genuine absence.

These observations further add to the complexity of Kem Kem Group pterosaur taphonomy which is highly unusual compared to other pterosaur-bearing deposits in that it is dominated by edentulous jaw tips (Martill et al., 2018), and totally lacks carpal elements (Smith et al., in prep.). There are as yet no detailed explanations for this bias towards the preservation of edentulous jaw fragments although there are several possible taphonomic factors that may have been in operation: transportation; palaeoecology and selective predation/scavenging behaviour, or any combination of these. Another potential factor is collecting bias. However, this is contradicted by our observations of fossil miners who collect every fragment of bone irrespective of its size or identity.

#### 4.4. Small pterosaurs in the mid to Late Cretaceous

Perinatal or immature individuals are absent from most mid to Late Cretaceous pterosaur-bearing deposits. This might, however,

**Fig. 11.** Thin section PPL (A–C, E, G–H) and XPL (D, F) images of jaw fragment of cf. *Aptorhamphus gyrostega* FSAC-KK 5082, a sub-mature individual. A, an overview image of the jaw cross-section, showing the positions of images B–H; B, image showing a large foramen penetrating the bone lined with lamellar bone tissue; C–D, images showing four annuli with the inner two accompanied by LAGs; E–F, images showing medullary cavity lined by an ICL comprising of a lamellar tissue; G, image of possible medullary bone and H, magnified image of possible medullary bone. Scale bar A represents 2 mm, B–D, G represents 0.5 mm and E–F,H represents 0.2 mm. See Figs. S1 and S2 for location on jaw of transverse thin section and additional images. Double headed arrows indicate the well vascularised zones that alternate with the narrow annuli/LAGs (indicated by single headed arrows). Abbreviations: **FN**: foramen; **ICL** inner circumferential layer of lamellar bone tissue; **LB**: lamellar bone; **MB**: medullary bone-like tissue; **MC**: medullary cavity; **PM**: periosteal margin.

reflect taphonomic or ecological biases rather than true absence. Firstly, most mid to Late Cretaceous pterosaur-bearing sites represent environments that small immature pterosaurs might not have inhabited. For example, the late Coniacian–early Campanian Niobrara Chalk Formation of the USA, it was deposited in an inland sea with most pterosaur finds reported approximately 200 km from the shore (Bennett, 1992; 1993). Small, immature individuals may have been excluded because these locations were too far from land or already occupied by large adults. Secondly, as demonstrated by Brown et al. (2013) for dinosaurs of the Dinosaur Park Formation of Alberta, Canada, there appears to have been a strong taphonomic bias against the preservation of small animals in Mesozoic alluvial environments. Primarily this relates to the ability of large carcasses/skeletons to better resist to biological destruction (e.g., predation and scavenging) and physical and chemical weathering (Brown et al., 2013).

That the seeming absence of small, immature individuals from Cretaceous pterosaur-bearing deposits largely reflects taphonomic bias is emphasised by their recovery from some exceptional conservation and concentration Lagerstätte where normal taphonomic biases operate less intensely or are absent. The late Barremian–Aptian Jehol Group of China (Chang et al., 2009) provides a good example. This sequence of deposits is dominated by very small to medium-sized pterosaurs: at least 14 genera have wingspans less than two metres, and in three of these the wingspan is less than one metre (see Table S3). The smallest pterosaur in the deposit, *Nemicolopterus crypticus* Wang et al. (2008) with a wingspan of just 0.25 m is most likely a juvenile of the tapejarid *Sinopterus* Wang and Zhou, 2003 (Naish et al., 2021) individuals of which have wingspans ranging from 1.2 to two metres or more (Wang and Zhou, 2003; Lü et al., 2006). Several other notable Cretaceous deposits also yield small pterosaurs including the Bissekty Formation of Uzbekistan (Averianov, 2010), the Cambridge Greensand Member of England (see Table 2B); the Goio Erê Formation of Brazil which has yielded a growth series of the tapejarid *Caiuajara dobruskii* including immature individuals with wingspans estimated to be as small as 0.65 m (Manzig et al., 2014) and the Lagarcito Formation of Argentina which has yielded a growth series of *Pterodaustro* in which individuals range from 0.3 m to 2.5 m in wingspan (Codorniu and Chiappe, 2004). A pterosaur trackway of *Pteraichnus koreanensis* from the Lower Cretaceous Hasandong Formation of South Korea provides additional evidence of small or immature pterosaurs, with average pes length and widths of 25.7 mm and 12.8 mm respectively (Lee et al., 2008).

Medium sized pterosaurs are found in several Late Cretaceous deposits including an azhdarchoid with a wingspan of 1.5 m from the Northumberland Formation of Hornby Island of British Columbia, Canada (Martin-Silverstone et al., 2016) and a specimen of *Pteranodon* with a wingspan of 1.76 m from the Niobrara Chalk Formation of Kansas, USA (Bennett, 2017).

## 5. Conclusion

Examples of small individuals from the Kem Kem Group provide the first evidence for small pterosaurs in the Cretaceous of Africa. Osteological considerations, including bone maturity, and the distribution of neural foramina indicate that these small examples are immature individuals of edentulous pterosaurs already reported from the Kem Kem Group, most probably *Alanqa* and *Apatorhamphus*. The continuum in size of individuals represented by jaws fragments suggests that immature and mature individuals of the same species likely lived alongside each other, but achieved this by occupying different ecological niches (Bennett, 2017). Immature individuals from the Kem Kem Group and other Cretaceous deposits are comparable in size to the many small species of pterosaur

reported from the Jurassic. It has been suggested that the lack of small species of pterosaur in the Cretaceous was due to displacement by birds (e.g., Romer 1966; Colbert 1980; Unwin 1988; Penny and Phillips 2004; Slack et al., 2006; Benson et al., 2014). We propose, however, that the niches previously occupied by small pterosaurs in the Jurassic were often occupied in the Cretaceous by immature individuals of large and giant species. Ontogenetic niche partitioning greatly expanded the ecological diversity of the Kem Kem Group pterosaur assemblage without extending its taxonomic diversity.

## CRedit authorship contribution statement

**Roy E. Smith:** Methodology, Investigation, Writing – original draft. **Anusuya Chinsamy:** Methodology, Investigation, Writing – original draft. **David M. Unwin:** Conceptualization, Investigation, Writing – original draft. **Nizar Ibrahim:** Writing – original draft. **Samir Zouhri:** Investigation, Project administration. **David M. Martill:** Conceptualization, Investigation, Writing – original draft, Supervision.

## 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.

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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.2021.105061>.