A new ?chaoyangopterid (Pterosauria: Pterodactyloidea) from the Cretaceous Kem Kem beds of Southern Morocco

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ABSTRACT

A new genus and species of edentulous pterodactyloid pterosaur with a distinctive partial rostrum from the mid-Cretaceous (?Albian/Cenomanian) Kem Kem beds of southeast Morocco is described. The taxon is tentatively assigned to Chaoyangopteridae based upon its edentulous jaws, elongate rostrum and slightly concave dorsal outline. The rostral cross-section is rounded dorsally and concave on the occlusal surface. The lateral margins are gently convex dorsally becoming slightly wider toward the occlusal border, and a row of small lateral foramina parallel to the dorsal margin determines it as a taxon distinct from other chaoyangopterids. *Aptorhamphus gyrostege* is a pterosaur of medium to large size (wingspan likely somewhere between ~ 3 m and ~ 7 m). This new species brings the number

of named Kem Kem azhdarchoids to three, and the number of named Kem Kem pterosaurs to five, indicating a high pterosaur diversity for the Kem Kem beds.

Keywords: Pterosauria; Azhdarchoidea; Chaoyangopteridae; Morocco; Cretaceous; Kem Kem beds

1. Introduction

The fossil record of African pterosaurs, volant Mesozoic archosauromorph reptiles, is relatively poor (Ibrahim et al., 2010; Rodrigues et al., 2011). With the exception of the Late Jurassic Tendaguru Beds in Tanzania (Reck, 1931; Unwin and Heinrich, 1999; Costa et al., 2015), the majority of African pterosaur material consists of isolated teeth, vertebral fragments and partial limb bones (Swinton, 1948; Dal Sasso and Pasini, 2003), with some associated material reported from the Late Cretaceous (Maastrichtian) of central Morocco (Pereda-Suberbiola et al., 2003; Longrich et al., 2018). Within the last twenty years numerous pterosaur remains have been recovered from the Cretaceous Kem Kem beds of southeast Morocco (Wellnhofer and Buffetaut, 1999; Ibrahim et al., 2010; Rodrigues et al., 2011; Martill and Ibrahim, 2015; Martill et al., 2018; Jacobs et al., 2019), and it is fast becoming one of the most important regions for understanding the diversity and evolution of pterosaurs in Africa (Fig. 1).

Most pterosaur remains from the Kem Kem beds occur as isolated three-dimensionally preserved elements, that are often broken and are mainly collected by local commercial fossil hunters (Martill et al., 2017). There are at present, four named species of pterosaur

from the Kem Kem beds, including the ornithocheirids *Siroccopteryx moroccensis* (Mader and Kellner, 1999) and *Coloborhynchus fluvifer* (Jacobs et al., 2018), and the azhdarchoids *Alanka saharica* (Ibrahim et al., 2010) and *Xericeps curvirostris* (Martill et al., 2018). Here, we describe a new genus and species of azhdarchoid pterosaur from the Kem Kem beds.

FIG. 1 HERE

2. Geographical and geological context

2.1. Locality

The specimens described here were discovered at Aferdou N'Chaft, near Hassi el Begaa, Er Rachidia Province, southeast Morocco (Fig. 1). They were purchased by one of the authors (DMM), while visiting the Tafilalt region for fieldwork at the mine site in 2016. The colour and other aspects of the specimen's preservation are consistent with other material from Aferdou N'Chaft. The Aferdou N'Chaft mesa is a small outlier of the main Kem Kem Hamada that gives its name to the Cretaceous non-marine strata in the Tafilalt region. Fossils are abundant in just a few thin (~20 cm to ~1 m thick) mudflake conglomerate horizons that occur widely across the region from Goulmima in the north to Zguilma in the south. Fossils at Aferdou N'Chaft are particularly well preserved, even when fragmentary, with bone showing excellent preservation of micro-histology.

2.2 Geology and stratigraphy

The Aferdou N'Chaft mesa and the adjacent Hamada du Kem Kem plateau consist of a ~50 m to ~90 m thick sequence of mainly Cretaceous (?Albian/Cenomanian) age strata, represented by a series of fluvial, cross-bedded sandstones with thin mudstones and

intraformational conglomerates of mudstone rip up clasts (Fig. 2). These strata are informally called the Kem Kem beds, and are overlain by shallow marine carbonates of the Cenomanian-Turonian Akrabou Formation (Ettachfini and Andreu, 2004; Martill et al., 2018). These Cretaceous strata rest with angular unconformity on indurated marine Palaeozoic rocks of mainly Siluro-Devonian age (Martill et al., 2018) (Fig. 2). Vertebrate fossils are common in the mud-flake conglomerates of the Kem Kem beds, and although usually fragmentary, they are often well-preserved. Details of the Kem Kem beds' stratigraphy, localities and fossil content can be found in Lavocat (1954a, b); Sereno et al., (1996); Sereno and Larsson (2009); Cavin et al., (2010) and Ibrahim et al., (2014a, b) and references therein. The Kem Kem beds mostly represent fluvial sedimentation dominated in its lower part by fine sands, sometimes referred to as the Ifezouane Formation, which fine upwards into interdigitating deltaic, estuarine and perhaps playa-lake deposits identified as the Aoufous Formation (Martill et al., 2018). Vertebrate remains occur in both formations, but are more abundant in the intraformational conglomerates of the upper part of the Ifezouane Formation (Martill et al., 2018).

FIG 2 HERE

The Kem Kem beds are notable for yielding a diverse range of fossil vertebrates (Cavin et al., 2010; Ibrahim et al., 2014a, b). In particular, this unit contains a remarkably high number of large predators including the giant theropod dinosaurs *Spinosaurus* (Stromer, 1915; Ibrahim et al., 2014a) and *Carcharodontosaurus* (Stromer, 1931; Sereno et al., 1996), the large noasaur *Deltadromeus* (Sereno et al., 1996), the carcharodontosaur *Sauroniops* (Cau et al., 2013) and several unnamed abelisaurids (Russell, 1996; Mahler, 2005; D'Orazi Porchetti et

al., 2011; Richter et al., 2013; Chiarenza and Cau, 2016). Herbivores are rare, with only occasional remains of sauropod dinosaurs reported (Lamanna and Hasegawa, 2014; Ibrahim et al., 2016), of which *Rebbachisaurus* is the only named taxon (Lavocat, 1954a). A diverse assemblage of crocodylomorphs is present (Sereni and Larsson, 2009), in addition to turtles (Gaffney et al. 2002, Gaffney et al. 2006), snakes (Rage and Dutheil, 2008; Klein et al., 2017) amphibians (Rage and Dutheil, 2008) and possibly birds (Riff et al., 2004).

A variety of fishes are also known from this assemblage, perhaps the most notable being the giant sawfish *Onchopristis* (Dutheil and Brito, 2009; Cavin et al., 2010), in addition to several other elasmobranchs (Sereni et al., 1996; Dutheil, 1999). Among osteichthyans, lungfish (Tabaste, 1963), coelacanths, including the giant *Mawsonia* (Tabaste, 1963; Wenz, 1980, 1981), polypterids (Dutheil, 1999), ichthyodectids (Forey and Cavin, 2007), lepidotids (Cavin et al., 2010), notopterids (Brito et al., 2009) and several other groups (Forey and Grande, 1998; Cavin et al., 2010) are present.

3. Materials and methods

Fieldwork was conducted in the Taffilalt in the autumn of 2016 and 2017. Specimens from Morocco are accessioned to the Faculté des Sciences Aïn Chock, Université Hassan II, Casablanca, Morocco numbers prefixed **FSAC**. Other material examined is deposited in the Bayerische Staatssammlung für Paläontologie und Geologie, Germany, **BSP**; Canadian Museum of Nature, Ottawa, Canada, **CMN**; Henan Geological Museum, Zhengzhou, China, **HGM**; Musée du Moulin Seignorial, Velaux–La Bastide Neuve, France, **MMS**; Museu Nacional (Universidade Federal do Rio de Janeiro), Rio de Janeiro, Brazil, **MN**; Vertebrate

paleontology Collection, Museo Patagónico de Ciencias Naturales, General Roca, Río Negro, Argentina, **MPCN**; Magyar Természettudományi Múzeum, Budapest, Hungary, **MTM**; Naturmuseum St. Gallen, St. Gallen, St. Gallen Canton, Switzerland, **NMSG**; Research Center of Palaeontology and Stratigraphy, Jilin University, Changchun, China, **RCPS**; Saratov State University, Saratov, Russia, **SGU**; University of Portsmouth, School of Earth and Environmental Sciences collection, **UOP**; Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia, **ZIN**; Zhejiang Museum of Natural History, China, **ZMNH**.

Well preserved specimens (FSAC-KK 11 and 12) were scanned using X-ray computed tomography (XCT) to reveal internal architecture. 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 was positioned directly after the x-ray source to filter the x-ray spectrum. 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.

Specimens were photographed digitally using an Olympus E-420 camera and images processed using Corel Draw Graphic Suite X8.

140 4. Description

141

142 4.1. Systematic Palaeontology

143 PTEROSAURIA Kaup, 1834

144 MONOFENESTRATA Lü et al., 2009

145 PTERODACTYLOIDEA Plieninger, 1901

146 AZHDARCHOIDEA Unwin, 1992

147 ?CHAOYANGOPTERIDAE Lü et al., 2008

148 *APATORHAMPHUS* gen. nov.

149 *Derivation of generic name:* A combination of *apato* Gr. = deceptive, alluding to the
150 difficulty of identifying edentulous beaks, and *rámfos* Gr. = beak.

151 *Type species:* *Apatorhamphus gyrostega* gen et sp. nov. See below.

152 *Diagnosis:* As for the type and only species, below.

153

154 *Apatorhamphus gyrostega* gen et sp. nov.

155 *Derivation of specific name:* *gyrostega*. A combination of *gyro* Gr. = rounded, and *stega* Gr. =
156 roof. In reference to the rounded dorsal surface of the rostrum.

157 *Holotype:* Specimen FSAC-KK 5010. Partial probable premaxilla missing the anterior tip and
158 not extending posteriorly as far as the anterior border of the nasoantorbital fenestra. The
159 specimen is highly fractured. A 3D print of the specimen is accessioned as UOP-PAL-KK0001.

160 *Type locality:* Begaa, Province d'Errachidia, Morocco. The main area of fossil collection at

161 Begaa is centred on Aferdou N'Chaft, global coordinates 30°53'55.73" N 3°50'46.26" W.

Type horizon and stage: Kem Kem beds, ?Albian to lower Cenomanian, mid-Cretaceous.

Referred specimens: Five additional specimens are referred to this taxon: FSAC-KK 5011, FSAC-KK 5012, FSAC-KK 5013, collected from Begaa; and FSAC-KK 5014, from an unknown locality (3D replicas of these specimens are housed in UOP collection, numbers UOP-PAL-KK0002 to KK0005); BSP 1993 IX 338 (Wellnhofer and Buffetaut, 1999, fig. 2), a large incomplete rostrum identified as a pteranodontian, subsequently assigned to *Alanqa* (Ibrahim et al., 2010) and reassigned here to *A. gyrostega*. Specimen CMN 50859, identified by Rodrigues et al., (2011, fig. 1) as an indeterminate dsungaripteroid ? mandible is tentatively reinterpreted here as a mandible of *Apatorhamphus*.

Diagnosis: *Apatorhamphus gyrostega* can be diagnosed by a unique combination of characters including: cross-sectional profile has an inverted U-shape anteriorly, before developing a more teardrop-like outline as the lateral margins become slightly convex posteriorly (possibly autapomorphic); rostrum long and edentulous, with a straight occlusal border and slightly concave anterior dorsal border in lateral view (a common feature of chaoyangopterids). The bone wall is massively thickened at the rostrum tip (autapomorphy). The occlusal surface is moderately concave with slightly off-set paired foramina; foramina of the occlusal surface are slit-like anteriorly becoming circular posteriorly (possibly autapomorphic); a single row of slit-like neurovascular foramina on the lateral margins are aligned parallel to the dorsal margin (also present in *Jidapterus*). This combination of features is not found in any other pterosaur.

4.2. Preservation

The holotype specimen, FSAC-KK 5010, is a partial rostrum (see below) lacking the anterior-most tip and extending posteriorly to a point that is seemingly slightly anterior to the nasoantorbital fenestrae (Fig. 3-4). The anterior break is sharp and clean, suggesting loss during collection. Conversely, the posterior break appears to be ‘weathered’ and may represent pre-burial breakage (as the specimen was dug from a mine many metres deep, the weathering is unlikely to be Recent). The broken surfaces reveal the internal structure to be camerate. The occlusal surface is missing posteriorly and a fragment of the lateral and dorsal margins is missing from the right posterolateral margin (Fig. 3-4). The lateral and occlusal surfaces are fractured, with thin breaks extending anteroposteriorly along these surfaces. A thin veneer of fine sandstone partially covers the left lateral margin of the rostrum and in patches on the right lateral margin. The bone is a pale brown, with a smooth surface (Fig. 3), suggesting the animal was osteologically mature at the time of death (*sensu* Bennett, 1993; Prondvai et al., 2012).

4.2.1 Identification of FSAC-KK 5010 as part of a rostrum

Distinguishing between fragmentary rostra and mandibulae in edentulous pterosaurs is fraught with difficulties, especially when the specimens lack significant landmarks, such as the margin of the nasoantorbital fenestra or the diverging rami of the mandibular symphysis, as is commonly the case with pterosaur jaws from the Kem Kem beds. Here, we argue that the holotype specimen represents an anterior rostrum. The rationale for this determination is based on the relatively high lateral angle (14° See Table 1) of the rostrum compared to that of other edentulous Kem Kem pterosaurs. In those pterosaurs with straight dorsal and ventral surfaces to the anterior rostrum, only in pteranodontians (8.5° vs

5° for *P. longiceps* KUV 976, 2212 and YPM 1177) and *Bakonydraco* (15° vs 9°) is the lateral angle of the mandibular symphysis higher than that of the premaxillae (Bennett, 2001; Ósi et al., 2005, 2011) (see Table 1). In all other pterosaurs the lower jaw is either comparable (e.g. *Nyctosaurus* Bennett, 2003) or more slender than the premaxilla/maxilla. Although in some tapejarids the lower jaw lateral angle begins as a larger angle than the premaxilla, the ventral margin is a strongly curved surface. *Apatorhamphus gyrostega* is excluded from Pterandontia as it possesses numerous lateral foramina, and has thickened bony walls on the rostral tip. Although there are some similarities between *A. gyrostega* and the anterior mandible of *Bakonydraco galaczi*, including the rounded non-occluding surface and the presence of small foramina on the lateral margins and occlusal surface, the mandible of *Bakonydraco* expands rapidly posteriorly and dorsally. It also possesses a median ridge on the occlusal surface and a ventral sulcus on part of the ventral margin. Neither of these features are seen in the holotype or referred material of *A. gyrostega*. We thus consider FSAC KK 5010 to represent a fragmentary premaxilla/maxilla.

TABLE 1 HERE

4.2.2 Anatomical description

The holotype rostral fragment is 211 mm in length with an estimated length up to the missing tip of ~312 mm (based on the preserved extensions of the jaw margin and the length of FSAC-KK 5012). In lateral view the dorsal profile is very slightly concave while the ventral profile (occlusal margin) is straight. The dorsal and ventral margins diverge at ~12° from the tip, this angle slightly increasing posteriorly to 14°. In occlusal view the lateral margins diverge posteriorly at 4.8°, and this angle remains constant along the preserved rostrum. The occlusal surface is moderately concave anteriorly, deepening very slightly posteriorly (Fig. 3B, 4B). The occlusal margins curve very slightly inwards posteriorly (Fig. 3B,

4B) allowing the slightly inflated lateral margins to be seen in occlusal view. Several large, elongate foramina similar to those on the lateral surfaces are present on the occlusal surface in off-set pairs (Fig. 3, 4).

There is a single row of foramina on each lateral margin, with each row located closer to the dorsal margin than the occlusal. Three large, elongate foramina are present (single row on each side) along the left lateral margin (a fourth may be present beneath matrix), and five on the right side (Fig. 4A, 4C). The foramina decrease in size posteriorly and are positioned between the sides in alternating pairs, although the beginnings of an additional foramen is seen just behind the anterior fracture on both sides, suggesting that the offsetting breaks down posteriorly (Fig. 4A, 4C).

The lateral margins are slightly convex, reaching their maximum breadth approximately three quarters below the dorsal surface at the distal point of the specimen, and increasing to approximately one third below the dorsal surface at the proximal end. The dorsal margin is very rounded anteriorly, becoming a little more acute posteriorly.

Anteriorly the cross-section of the rostrum is a deep oval-shape that tapers slightly dorsally, with a large ventral depression formed by the deep concave occlusal surface and a rounded dorsal margin (Fig. 3E, 3F, 4E, 4F). Posteriorly the cross-section develops into a large 'teardrop' shape with visibly convex lateral margins, a deeper occlusal groove, and a slightly keeled dorsal margin (Fig. 3F, 4F).

The bone walls of the rostrum are thin at the posterior break of the occlusal surface (0.80 mm - 0.92 mm), but thicker on the lateral margins (1.5 mm - 1.6 mm) (Figs. 3E, 3F, 4E, 4F).

At the anterior break, estimated at 101 mm posterior to the rostral tip, the bone walls are much thicker, measuring 3.08 – 3.5 mm at the thickest point of the lateral margins, and 3.08

– 3.7 mm on the occlusal surface (Fig. 3E, 4E). The posterior break reveals the internal structure of the rostral bone (Fig. 3F, 4F), which appears to consist of a series of well-spaced, vertical to sub-vertical planar trabeculae orientated orthogonal to the long axis. These sheet-like trabeculae have an hour-glass outline viewed anteriorly. There are also a series of trabeculae that cross-cut these, thus dividing the internal cavity of the rostrum into a series of irregular camerae (Fig. 3F, 4F, and see 4.3 below).

FIGS. 3 and 4 HERE

4.2.3. Internal morphology

Specimens FSAC-KK 5011 and FSAC-KK 5012 were subject to XCT scanning to reveal the internal architecture of the partially exposed trabecular system (Fig. 5). A series of trabeculae occur along the length of the rostrum, and some form large horizontal partitions, extending from the left to the right lateral margins. These partitions occur continuously throughout the length of the preserved rostrum. Other trabeculae evidently radiate from the lateral, dorsal and occlusal margins, but appear to be irregularly arranged (Fig. 5). Several internal camerae of varying sizes are formed by the trabeculae, notably, in FSAC-KK 5011, where a pair of camerae are evident in the ventrolateral corners between the occlusal and lateral surfaces (Fig. 5). These camerae occur continuously throughout the rostrum. Several camerae are connected to the exterior by the foramina (Fig. 5). The posterior break of FSAC-KK 5012 also reveals a bony plate radiating from the dorsal and dorsolateral margins (Fig. 5). In specimen FSAC-KK 5011 an ossified mass on the right lateral margin is developed in the midsection, possibly due to an injury sustained during life (Fig. 5).

FIG. 5 HERE

4.3. Referred specimens: rostra

Several specimens are referred to *Apatorhamphus gyrostega*. Specimen FSAC-KK 5011 compares closely to the holotype in its general morphology, exhibiting the same cross-sectional outline with a rounded dorsal margin and concave occlusal surface, slight inward curve of the occlusal margins, thickened bone walls and single row of prominent lateral foramina (Fig. 6A-C). The same morphology is observed in FSAC-KK 5012 and FSAC-KK 5014 (Fig. 6D-F and G-I respectively). Notably, specimen FSAC-KK 5012 demonstrates that the rostral tip (missing from the holotype specimen) is elongate and pointed (Fig. 6D-F). It is seemingly from a similar-sized individual, with the dorsal and ventral margins initially diverging from the tip at $\sim 8^\circ$ and the lateral margins diverging at $\sim 5^\circ$. The occlusal surface is gently concave (Fig. 6E).

A partial rostrum, specimen BSP 1993 IX 338, was previously assigned to *Alanqa saharica* (Ibrahim et al., 2010; Novas et al., 2012; Averianov, 2014). This referral was made on the basis that the occlusal surface closely reflects that of the holotype mandible of *Alanqa*, FSAC-KK 26, and the presence of paired foramina of the occlusal surface, identified by Ibrahim et al. (2010) as a characteristic of azhdarchids. At that time *Alanqa* was the only azhdarchid known from the Kem Kem beds, and consequently such referral was reasonable. However, a large azhdarchid jaw portion from the Kem Kem beds in a private collection (3D print replica specimen UOP-PAL-KK0006) matches more closely the morphology of the holotype of *Alanqa saharica*. Azhdarchids from which both jaws are known such as *Bakonydraco* (Ősi et al., 2005) exhibit a similar distribution pattern of the lateral foramina on both premaxilla and mandible. Additionally, excluding *Bakonydraco*, the condition of the occlusal surface of these taxa is shared between both jaws (Kellner and Campos, 1988;

Kellner, 1989; Kellner and Langston, 1996; Averianov, 2010). Furthermore, the morphology of BSP 1993 IX 338 is nearly identical to that of FSAC-KK 5010. The lateral margins of BSP 1993 IX 338 appear less convex, but as this specimen is evidently from a smaller individual, it is likely that the posterior outline of the cross-section is only visible in fully mature individuals. The pairing of the occlusal foramina also does not appear to alternate as frequently. Aside from these differences, the two specimens are closely comparable.

FIG. 6 HERE

4.4. Referred specimens: possible mandible

Specimen FSAC-KK 5013 matches the morphology of the holotype, but has a lower rostral angle in the range $\sim 6^\circ$ compared with $8\text{--}12^\circ$ for the holotype specimen. It has an oval cross-section, a gently concave occlusal surface and a single anteroposterior row of foramina on the lateral surface arranged parallel to the ventral margin. It also exhibits a straighter lateral margin and a straighter dorsal margin in lateral view, and may thus represent the mandible of *A. gyrostega* (Fig. 7).

The occlusal surface of FSAC-KK 5013, is almost perfectly complimentary to the holotype specimen FSAC-KK 5010 (Fig. 7A-B, Fig. 8). This mandibular fragment is distinguished from the rostrum by its straight ventral profile in lateral view, relatively straight lateral margins below the occlusal margin, shallower dorsoventral profile and its smaller lateral angle (Fig. 7A-F). In azhdarchids where material from both jaws are known (Cai and Wei, 1994; Kellner and Langston, 1996; Averianov, 2010), the rostral angle is greater than the lateral angle of the mandible, with the exception of *Bakonydraco* (Ősi et al., 2005).

FIG. 7 HERE

FIG. 8 HERE

5. Comparisons

5.1 Edentulous pterosaurs

The lack of dental alveoli excludes *A. gyrostega* from all pterosaur groups except the edentulous Pteranodontia (Pteranodontidae and Nyctosauridae) and Azhdarchoidea (Tapejaridae, Chaoyangopteridae, Thalassodromidae and Azhdarchidae). Dsungaripterids lack teeth anteriorly, however, the edentulous part of the jaw is rather short (Maisch et al., 2004; Witton, 2013).

5.1.1 Pterandontia

In *Pteranodon* the tips of the jaws are extremely finely pointed, with remarkably thin bone walls (Bennett, 2001), and the same seems to be true for *Nyctosaurus* (Bennett, 2003). The rostrum of *A. gyrostega* (Fig. 9A) deepens considerably dorsoventrally whereas the rostrum of *Pteranodon* is comparatively slender. Specimen BSP 1993 IX 338 shows that the rostrum of *A. gyrostega* is less pointed than that of *Pteranodon*. Pteranodontians also seem to lack the elongate foramina (Bennett, 2001) that are conspicuous on the jaws of many other, although not all, azhdarchoids (Ősi et al., 2001, Ibrahim et al., 2010; Martill et al., 2017). *A. gyrostega* does not appear to be a pteranodontian.

5.1.2 Azhdarchoidea

Apatorhamphus gyrostega displays several features found in Azhdarchoidea: the rostrum is deeper than the mandible in lateral view (Cai and Wei, 1994, Witton, 2009); and both the rostrum and mandible are relatively long and straight (Kellner and Langston, 1996; Witton,

2009), although there is a slight dorsal curvature of the holotype rostrum of *A. gyrostega* rostrum posteriorly.

Tapejaridae

Apatorhamphus gyrostega (Fig. 9A, D) is clearly distinguished from tapejarids by the absence of unique features such as the ventral deflection of the rostrum and mandible, and pronounced rostral and mandibular crests (Fig. 9K-L) (Frey, Martill and Buchy, 2003; Kellner, 2004; Lü et al., 2006, Kellner, 2013).

Thalassodromidae

Apatorhamphus gyrostega exhibits features that exclude assignment to Thalassodromidae. In the thalassodromids *Tupuxuara* (Kellner and Campos, 1988) and *Thalassodromeus* (Kellner and Campos, 2002) (Fig. 9C, I, J), the dorsal surface of the rostrum forms a crest composed of the fused premaxillae (Martill and Naish, 2006). This is absent in *A. gyrostega*. Additionally, the foramina present on the rostral material of *A. gyrostega* are not seen in *Thalassodromeus* or *Tupuxuara*.

Azhdarchidae

Apatorhamphus gyrostega compares well, at least superficially, with members of Azhdarchidae, in that its jaw is edentulous and long with a straight occluding surface. Several azhdarchid pterosaurs are known from rostral material; *Quetzalcoatlus* sp. (Kellner and Langston 1996), *Zhejiangopterus linhaiensis* Cai and Wei, 1994, *Bakonydraco galaczi* Ősi et al., 2005, *Azhdarcho lancicollis* Nesov, 1984, *Volgadraco bogolubovi* Averianov et al., 2008, *Aerotitan sudamericanus* Novas et al., 2012, *Argentadraco barrealensis* Kellner and

375 Calvo, 2017 and *Mistralazhdarcho maggii* Vullo et al., 2018, in addition to the coeval Kem
 376 Kem genera *Alanqa saharica* Ibrahim et al. 2010 and *Xericeps curvirostris* Martill et al., 2018.
 377 Several of these taxa exhibit autapomorphies in their rostral anatomy that distinguish them
 378 from *A. gyrostega* and other azhdarchids.
 379 *Argentinadraco* is distinguished by one autapomorphy; a crest on the anterior portion of the
 380 ventral margin of the mandibular symphysis (Kellner and Calvo, 2017). *Bakonydraco*
 381 possesses a relatively short mandibular symphysis that is dorsoventrally deeper than the
 382 rostrum, and a transverse ridge that separates the dorsal surface of the mandibular
 383 symphysis into anterior and posterior portions (Ősi et al., 2005, fig. 2).
 384 There is a degree of similarity between FSAC KK 5010 and the anterior rostrum of
 385 *Bakonydraco galaczi* (Ősi et al., 2011 and pers. com. March 2019). In *Bakonydraco* and *A.*
 386 *gyrostega* the dorsal surface of both is rounded anteriorly, however, in *Bakonydraco*, this
 387 margin becomes acute posteriorly forming an almost sharp ridge (Ősi et al., 2011). The
 388 lateral angle of *Bakonydraco* is only 8.5° compared to 12° for *A. gyrostega*, (Table 1) and the
 389 lateral margins are less inflated in *Bakonydraco* (Ősi et al., 2011). However, in *Bakonydraco*
 390 the rostrum has a very slightly concave dorsal profiles in lateral view (Ősi et al., 2011, fig.
 391 2A,B; Fig. 10E), but the ventral profile is straight, comparable with these profiles in *A.*
 392 *gyrostega* (Fig. 10A).
 393 *Mistralazhdarcho* is easily distinguished from *A. gyrostega* by the presence of a ventral
 394 mandibular keel (Fig. 9G) and midline eminence on the mandible (Vullo et al., 2018), similar
 395 to those features in *Alanqa* (Ibrahim et al., 2010; Martill and Ibrahim, 2015). Both rostrum
 396 and presumed mandible of *A. gyrostega* differ from those of *Quetzalcoatlus* in that they
 397 have a much deeper dorsoventral profile, a “U”-shaped cross section and deeply concave

398 occlusal surface. The jaws of *Quetzalcoatlus* have a flat occlusal surface such that the
 399 rostrum has a “D”-shaped cross-section while the mandibular symphysis had a triangular
 400 cross-section (Kellner and Langston, 1996).

401 The jaws of several azhdarchid taxa resemble those of *A. gyrostega*. The rostrum of
 402 *Zhejiangopterus* exhibits a relatively deep dorsoventral profile (Unwin and Lü, 1994) (lateral
 403 angle 14° See Table 1) as also seen in *A. gyrostega* (lateral angle 12°). Further similarities in
 404 cross-section cannot be determined as *Zhejiangopterus* is only known from flattened
 405 specimens (Cai and Wei, 1994; Unwin and Lü, 1997). The presumed rostrum of *Aerotitan* is
 406 comparable with *A. gyrostega* by possessing an inverted U-shaped cross-section with a
 407 deeply concave occlusal surface (Fig. 9B), thick lateral margins, and a single anteroposterior
 408 row of relatively numerous lateral foramina (Novas et al., 2012) (Fig. 10B). However, it
 409 differs from *A. gyrostega* in that *Aerotitan* exhibits a relatively straight dorsal surface in
 410 lateral view (Fig. 10B), a shallower dorsoventral profile and by the position of the lateral
 411 foramina which are closer to the occlusal margin (Novas et al., 2012). The rostra of
 412 *Azhdarcho* (Fig. 10C) and *Volgadraco* (Fig. 10D) are also closely comparable to that of *A.*
 413 *gyrostega*. Both *Azhdarcho* and *Volgadraco* exhibit gently convex lateral margins (Averianov
 414 et al., 2008; Averianov, 2010), but not the same degree as in *A. gyrostega*.

415 Jaw fragments of the Kem Kem azhdarchids *Alanqa saharica* (Ibrahim et al., 2010) and
 416 *Xericeps curvirostris* (Martill et al., 2018) are comparable with those of *A. gyrostega*. Based
 417 upon UOP-PAL-KK0006, the jaw of *Alanqa* is distinct from *A. gyrostega*, being more elongate
 418 and significantly shallower dorsoventrally, with a planar occlusal surface on both jaws and
 419 shallower occlusal margins. *Alanqa* also exhibits a low ventral keel on the ventral surface of
 420 its mandible, resulting in a distinct sharp “Y”-shaped cross-section (Ibrahim et al., 2010) (Fig.

9E). *Xericeps* shows some similarities to *A. gyrostega*, including a deeply concave occlusal surface and an anterior inverted U-shaped cross section, alongside an anteroposterior row of lateral foramina, but is easily distinguished by its curved jawline.

The jaws of both *Alanqa* and *Xericeps* possess distinct bony processes toward the cranial end of their occlusal surfaces. In *Alanqa*, a single sagittal eminence extends above the dental margin profile of the mandible, while two complimentary protuberances are present on the occlusal margins of the premaxilla (Martill and Ibrahim, 2015). In *Xericeps*, a pair of thin bony ridges rise from the dorsal sulcus of the mandible and extend posteriorly parallel to the occlusal margin (Martill et al., 2018). Such processes are absent on *A. gyrostega*.

Xericeps is also distinguished by an autapomorphy: a sulcus extending anteroposteriorly along the ventral surface (Martill et al., 2017) (Fig. 9F) not seen in the possible mandible of *A. gyrostega*.

Rostral foramina. Elongate lateral foramina like those on *A. gyrostega* occur widely in azhdarchids, although seemingly absent in *Quetzalcoatlus* (Kellner and Langston, 1996) and *Zhejiangopterus* (Cai and Wei, 1994). Although foramina occur in other azhdarchoids, they are usually teardrop-shaped (*Caiuajara* Manzig et al., 2014; *Caupedactylus* Kellner, 2013), oval and generally less elongate. Lateral foramina appear to be generally organised in a single anteroposterior row along the rostrum in azhdarchids, whereas positioning of the foramina appears more random in other azhdarchoids (Kellner, 2013; Manzig et al., 2014), but we note, data is sparse. Exceptions include the azhdarchid *Volgadraco* (Fig. 10D), which appears to have relatively randomly distributed, fewer lateral foramina (Averianov et al., 2008). In *Azhdarcho* some specimens appear to possess foramina whereas others do not (DMU pers. obs.) and Averianov (2010) notes some variability in their distribution (we

suggest that perhaps these specimens are incorrectly referred to *Azhdarcho*). Considering that foramina are variable within azhdarchoid clades, and their variability within taxa, we consider them at present to be of limited taxonomic value until their distribution is better resolved. At present *A. gyrostega* appears to lack any unequivocal azhdarchid autapomorphies.

FIG. 9 HERE

FIG 10 HERE

Chaoyangopteridae

The lateral profile of the rostrum of *A. gyrostega* compares closely to that of chaoyangopterids such as *Jidapterus edentus* Dong, Sun and Wu, 2003 (see also Lü et al., 2008; Wu et al., 2017); *Chaoyangopterus zhang*i Wang and Zhou, 2003a, *Shenzhoupterus chaoyangensis* Lü et al., 2008 and possibly *Lacusovagus magnificens* Witton, 2008.

In *Chaoyangopterus* the occlusal margin of the jaw is straight and the dorsal margin is gently curved upward. This matches very closely to the holotype of *A. gyrostega*, except that the Kem Kem beds specimen is slightly more attenuate. Although *A. gyrostega* compares well with other chaoyangopterids (Fig. 8), it lacks the slight posteriorly upturned lateral profile of *Chaoyangopterus* (Wang and Zhou, 2003a), and is significantly longer and more slender than the rostrum of *Shenzhoupterus* (Lü et al., 2008). The supposed chaoyangopterid *Lacusovagus*, like *A. gyrostega*, possesses a rounded dorsal rostral margin (Witton, 2008), but *Lacusovagus* has proportionally much wider jaws than those of *A. gyrostega*. Additionally, the rostrum of *Lacusovagus* has a larger dorsal angle than *A. gyrostega* (Witton, 2008).

Jidapterus edentus was originally recovered as a chaoyangopterid by Lü et al., (2008), and this relationship was supported in an analysis by Wu et al., (2017). Based on their detailed description of *Jidapterus* the rostrum not only has the same shape as the holotype of *A. gyrostega* (Fig. 8), it also appears to have foramina in approximately the same locations, and a deep U-shaped palatal surface.

Consequently, we tentatively assign *A. gyrostega* to ?Chaoyangopteridae based on its similarity to *Jidapterus* and in other respects to *Chaoyangopterus*. Notably, the dorsal surface of the rostrum of chaoyangopterids becomes increasingly curved posteriorly in both *Jidapterus* and *Chaoyangopterus* and there is a hint of this curvature in the holotype of *A. gyrostega*, with the lateral angle changing from 11° to 14° posteriorly.

6. Discussion

6.1 Diversity of Kem Kem beds pterosaurs

With the description of *Apatorhamphus gyrostega*, a pterodactyloid pterosaur of medium to large size the number of named azhdarchoids from the Kem Kem beds has increased to three, and the total number of named Kem Kem beds pterosaurs to five. Pterosaur diversity in the Kem Kem deposits was higher than previously thought. As noted by Martill et al., (2018), the taxonomic profile of Kem Kem pterosaurs, consisting of several azhdarchoids and ornithocheirids, is comparable to that found in the Aptian-Albian Romualdo (=Santana) and Crato formations of Brazil (Unwin and Martill, 2007; Kellner et al., 2013; Pinheiro and Rodrigues, 2017) and the Yixian and Jiufotang formations of Lower Cretaceous China (Lü et al., 2013; Witton, 2013) (Table 2).

The Kem Kem beds of Morocco yield a diverse assemblage of vertebrates (Cavin et al., 2010; Läng et al., 2013), and the environments in which they were deposited likely offered a wide range of ecological niches for pterosaurs (river bank, river channel, marsh, pond/lake). It is not possible to establish autecology and diet based on the available material, but comparisons of the rostral anatomy of the Kem Kem azhdarchoids (Figs 8,9,10) demonstrates morphological differences between currently recognised species of azhdarchoid, hinting at adaptations to distinct trophic niches.

6.2. Comparisons with other Cretaceous pterosaur assemblages

The Kem Kem beds pterosaur assemblage presently comprises taxa from three, possibly four groups, ornithocheirids, azhdarchids, tapejarids and with the description of *A. gyrostega*, possibly chaoyangopterids (Table 2). Significant differences from later Cretaceous pterosaur sites, such as the Maastrichtian Javelina Formation of Texas and the Niobrara Chalk Formation of Kansas are likely a result of prolonged evolutionary change and significant differences in palaeoenvironmental setting in the case of the Kansas chalk assemblages (Everhart, 2005; Bennett, 2001, 2003). Comparisons with near coeval formations reveal numerous similarities (Jacobs et al., 2018). The Cambridge Greensand of eastern England, like the Kem Kem beds, contains at least three ornithocheirid taxa (*Coloborhynchus*, *Anhanguera* and *Ornithocheirus*; Jacobs et al., submitted). The genus *Coloborhynchus* is also known from slightly older (Barremian) deposits of the Isle of Wight in southern England (Martill et al., 2011; Martill, 2015). However, much of the material from these deposits is highly fragmentary and some authors have questioned earlier taxonomic assignments (e.g. Rodrigues and Kellner, 2008, 2013) referring some material to distinct genera. The possible presence of a chaoyangopterid in the Kem Kem beds is noteworthy as presently, this clade is

only known from the Early Cretaceous of China and possibly the Crato Formation of Brazil (Witton, 2008). If confirmed their occurrence in Morocco would indicate a much wider, near global distribution, for this clade. A Kem Kem beds record for Chaoyangopteridae would also significantly extend the known temporal range of the clade from around five million, to more than 20 million years, ranging from the Barremian to the Albian/Cenomanian.

Table 2

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FIGURES

Fig. 1. Map showing the Kem Kem beds outcrop in southeast Morocco, and the mine at Aferdou N'Chaft where most of the specimens described here were collected. Reproduced from Martill et al., (2018).

Fig. 2. View near Hassi el Begaa showing outcrop of the Kem Kem beds and one of the fossil mines dug into the strata, taken in 2017, and a simplified sedimentary log outlining the stratigraphy of the locality (grey area indicates strata found at the Aferdou N'Chaft site). Modified from Jacobs et al., (2018).

Fig. 3. Partial rostrum of *Apatorhamphus gyrostega* gen. et sp. nov. FSAC-KK 5010. A, left lateral; B, ventral; C, right lateral; D, dorsal; E, distal end F, proximal end. Scale bars = 20 mm.

Fig. 4. Outline drawing of partial rostrum of *Apatorhamphus gyrostega* gen. et sp. nov.

FSAC-KK 5010. A, left lateral; B, ventral; C, right lateral; D, dorsal; E, distal end; F, proximal

end. Scale bars = 20 mm.

Fig. 5. CT scan slices (top row) and line drawings (bottom row) illustrating internal structure of the rostrum of referred specimens of *Aptorhamphus gyrostega* gen. et sp. nov. A, FSAC-KK 5011; B, FSAC-KK 5012. Note the thickened bony wall and persistent horizontal cross member. Black = void space; dark grey = sediment filled voids; light grey or white = bone. Scale bar = 5 mm.

Fig. 6. Fragmentary rostra: A-C, FSAC-KK 5011; D-F, FSAC-KK 5012; G-I, FSAC-KK 5014, referred to *Aptorhamphus gyrostega* gen. et sp. nov. in left lateral (top), ventral (middle) and dorsal (bottom) views. Scale bars = 10 mm.

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931 **Fig 7.** Fragmentary mandibular symphysis, FSAC-KK 5013, tentatively referred to932 *Apatorhamphus gyrostega* gen. et sp. nov. A, left lateral; B, ventral; C, right lateral and D,

933 dorsal views. Scale bar = 10 mm.

Fig. 8. Reconstructed jaws of *Apatorhamphus gyrostega* gen. et sp. nov.. A, holotype of *A. gyrostega* gen. et sp. nov. (FSAC-KK 5010) aligned with fragments representing the anterior tip of the rostrum, FSAC-KK 5012, and possible mandible, FSAC-KK 5013. B, Tentative restoration of *A. gyrostega* as a ?chaoyangopterid, using the outline of *Shenzhoupterus chaoyangensis* (HGM 41HIII-305A) from Lü et al, 2008. C. The rostrum of *Jidapterus edentus* (RCPS-030366CY) from Wu, et al., 2017. Scale bars = 50 mm.

Fig 9. Reconstructed cross-sections of rostra of various azhdarchoid pterosaurs (Kem Kem taxa shaded grey). A-C = premaxillae; A, *Apatorhamphus gyrostega* gen. et sp. nov. (FSAC-KK 5010); B, *Aerotitan sudamericanus*, from Novas et al., 2012 (MPCN-PV 0054); C, *Tupuxuara* sp. (UOP-PAL-MS0001). D-L = mandibles; D, *Apatorhamphus gyrostega* gen. et sp. nov. (FSAC-KK 5013); E, *Alanqa saharica*, Ibrahim et al. 2010 (FSAC-KK 26); F, *Xericeps curvirostris*, Martill et al. 2018 (FSAC-KK 10700); G, *Mistralazhdarcho maggii*, Vullo et al., 2018 (MMS/VBN.09.C.001a); H, *Bakonydraco galaczi*, Prondvai et al., 2014 (MTM V 2007.111.1); I, *Tupuxuara* sp. (UOP-PAL-MS0001); J, *Thalassodromeus oberlii*, Headden and Campos, 2014 (NMSG SAO 251093); K, *Aymberedactylus cearensis*, Pêgas, de Castro, Leal and Kellner, 2016 (MN 7596-V); L, Tapejaridae indet., Wellnhofer and Buffetaut, 1999 (BSP 1997 167). Scale bars = 10 mm.

Fig 10. Comparison of fragments of the rostrum representing various azhdarchid pterosaurs. A, *Apatorhamphus gyrostega* gen. et sp. nov. (FSAC-KK 5010); B, *Aerotitan sudamericanus*, from Novas et al., 2012 (MPCN-PV 0054); C, *Azhdarcho lancicollis*, Averianov 2010 (ZIN PH 85/44); D, *Volgadraco bogolubovi*, Averianov et al., 2008 (SGU, no. 46/104a, mirrored for comparison); E, *Bakonydraco galaczi*, Ősi et al., 2011 (MTM V 2010.80.1), F, *Zhejiangopterus linhaiensis*, (ZMNH 1330). Scale bar = 20 mm.

	Taxon	Specimen number	Rostral lateral angle	Mand. Lateral angle	Dorsal angle	References	Notes
darchidae	Aerotitan sudamericanus	MPCN-PV 0054	10°	N/A	4°	Novas et al. (2012)	Presumed rost. 3D pres.
	Alanqa saharica	FSAC-KK 26	N/A	6°	5°	Ibrahim et al. (2010)	Presumed md. 3D pres
	Azhdarcho lancicollis	ZIN PH 85/44 ZIN PO 3471	8°	6°	7°	Averianov (2010)	Presumed md. and rost.
	Bakonydraco galaczi*	MTM V 2010.80.1., MTM Gyn/3	9°	15°	6°	Ősi et al., 2005, Ősi et al., 2011	3D pres.
	Mistralazhdarcho maggii	MMS/VBN.09.C.001a.	N/A	11°	6°	Vullo et al. (2018)	Presumed md. 3D pres.
	Quetzalcoatlus sp.	TMM 41954-62	8°	5°	?	Kellner and Langston (1996)	Partial crushing
	Volgadraco bogolubovi	SGU 46/104a	8°	N/A	6°	Averianov et al. (2008)	Presumed rost. 3D pres.
	Xericeps curvirostris	FSAC-KK 10700	N/A	4°	3°	Martill et al. (2018)	Presumed md. 3D pres.
	Zhejiangopterus linhaiensis	ZMNH 1330	14°	10°	N/A	Cai and Wei (1994)	Crushed
Chaoyangopteridae	Apatorhamphus gyrostega	FSAC-KK 5010, FSAC-KK 5013	12°	8°	5°	This paper	Presumed 3D pres.
	Chaoyangopterus zhangii	IVPP V 13397	5°	9°	N/A	Wang and Zhou, 2003a, Wang and Zhou, 2003b	Crushed
	Jidapterus edentus	RCPS-030366CY	10°	8°	N/A	Wu et al. (2017)	Crushed
	Shenzhoupterus chaoyangensis	HGM 41HIII-305A	13°	14°	N/A	Lü et al. (2008)	Crushed
Pteranodontia	Nyctosaurus gracilis	KJ1	5°	5°	N/A	Bennett (2003)	Crushed
	Pteranodon longiceps	KUVP 976, 2212, YPM 1177	5°	8.5°	N/A	Bennett (2001)	Crushed

Table 1. Lateral and dorsal angles for a selection of azhdarchoid pterosaurs.

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Formation	Age	Clade	Key references
		Anurognathidae Istiodactylidae Coloborhynchinae Ornithocheirinae Boreopterinae Pteranodontidae Nyctosauridae Ctenochasmidae Lonchodectidae Tapejaridae Thalassodromidae Chaoyangopteridae Azhdarchidae	
Javelina	Maas.	?	Lawson, 1975; Kellner and Langston, 1996
Niobrara Chalk	Sant.	Pt Ny	Marsh, 1876; Bennett 2001, 2003; Everhart, 2005
Bissekty	Turo.		Nesov, 1984; Averianov, 2010
Kem Kem beds	?Alb./Ceno.	Co Si	Mader and Kellner, 1999; Wellnhofer and Buffetaut, 1999; Ibrahim et al., 2010; Martill et al., 2018; Jacobs et al., 2019
Cambridge Greensand	Ceno.	Co Or An Lo Os	Unwin, 2001
Romualdo	Alb.	An Ar Ce Br Tr Sa Ta Th Tu	Kellner, 1984; Campos and Kellner, 1985; Wellnhofer, 1987; Kellner and Campos, 1988; Kellner, 1989; Kellner and Tomida, 2000; Kellner and Campos, 2002; Veldmeijer et al., 2005
Crato	Alb.	Lu As Ay Tp La	Frey and Martill, 1994; Campos and Kellner, 1997; Frey, Martill and Buchy, 2003; Frey et al., 2003; Unwin and Martill, 2007; Witton 2008; Pégas et al., 2016
Jiufotang	Apt.	Ve Li Gu Ik Nu Ls Ln Ss Ch Eo Ji Sh	Dong et al., 2003; Dong and Lü, 2005; Wang and Zhou, 2003a,b, 2006; Lü and Ji, 2005; Wang et al., 2005; Lü et al., 2008; Wang et al., 2012; Wang et al., 2014; Rodrigues et al., 2015; Lü et al., 2017
Yixian	Barr.	Ha Bo Be Ca El Es Fe Ge Gl Mo Ps En	Ji and Ji, 1997; Wang and Lü, 2001; Lü, 2003; Lü and Ji, 2005; Lü and Zhang, 2005; Wang et al., 2005; Wang and Zhou, 2006; Wang et al., 2007; Andres and Ji, 2008; Jiang and Wang, 2011; Lü et al., 2012a,b
Wealden Group	Hau.-Barr.	Is Cs	Howse et al., 2001; Steel et al., 2005; Martill et al., 2011; Sweetman and Martill, 2010

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Table 2. Important Cretaceous pterosaur-bearing formations, and their pterosaur assemblages.

Ages: Maas. = Maastrichtian, Sant. = Santonian, Turo. = Turonian, Alb. = Albian, Ceno. = Cenomanian, Apt. = Aptian, Barr. = Barremian, Hau. = Hauterivian. **Genera:** **Al** = *Alanqa*, **An** = *Anhanguera*, **Ap** = *Apatorhamphus*, **Ar** = *Arapesaurus*, **As** = *Arthurdactylus*, **Ay** = *Aymberedactylus*, **Az** = *Azhdarcho*, **Be** = *Beipiaopterus*, **Bo** = *Boreopterus*, **Br** = *Brasileodactylus*, **Ca** = *Cathayopterus*, **Ce** = *Cearadactylus*, **Ch** = *Chaoyangopterus*, **Co** = *Coloborhynchus*, **Cs** = *Caulkicephalus*, **El** = *Elanodactylus*, **En** = *Eopteranodon*, **Eo** = *Eoazhdarcho*, **Es** = *Eosipterus*, **Fe** = *Feilongus*, **Ge** = *Gegepterus*, **Gl** = *Gladocephaloideus*, **Gu** = *Guidraco*, **Ha** = *Haopterus*, **Ik** = *Ikrandraco*, **Is** = *Istiodactylus*, **Ji** = *Jidapterus*, **La** = *Lacusovagus*, **Li** = *Liaoxipterus*, **Ln** = *Linlongopterus*, **Ls** = *Liaoningopterus*, **Lu** = *Ludodactylus*, **Mo** = *Moganopterus*, **Nu** = *Nurhachius*, **Ny** = *Nyctosaurus*, **Ps** = *Pterofiltrus*, **Pt** = *Pteranodon*, **Qu** = *Quetzalcoatlus*, **Sa** = *Santanadactylus*, **Sh** = *Shenzhoupterus*, **Si** = *Siroccopteryx*, **Ss** = *Sinopterus*, **Ta** = *Tapejara*, **Th** = *Thalassodromeus*, **Tp** = *Tupandactylus*, **Tr** = *Tropeognathus*, **Tu** = *Tupuxuara*, **Ve** = *Vesperopterylus*, **Xe** = *Xericeps*, ? = Unnamed taxa. Circles represent genera.

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