A long-billed, probe-feeding pterosaur (Pterodactyloidea: †Azhdarchoidea) from the Cretaceous of Morocco, North Africa

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A B S T R A C T

The pterosaurs were the first vertebrates to evolve powered flight and staged a major radiation in
the Cretaceous. Cretaceous pterosaurs occupied many of the niches occupied today by birds,
including aerial insect hawkers, piscivores, and filter feeders. The diversity of this radiation remains

19 poorly known due to the uneven stratigraphic and geographic distribution of pterosaur fossils. Much
20 of what is known about pterosaur diversity comes from a handful of Lagerstätten, representing
21 primarily lacustrine, lagoonal, and marine palaeoenvironments, primarily in Laurasia. These sites
22 may fail to capture pterosaur diversity in other habitats and regions, such as Gondwana. Here, we
23 describe a unique small, long-beaked pterosaur from fluvial mid-Cretaceous (?Albian-Cenomanian)
24 strata of Morocco, North Africa, with adaptations for sediment probing. The upper and lower jaws
25 form a hyperelongate dorsoventrally flattened beak, with thickened bony walls. The morphology
26 most closely resembles that of probing birds such as kiwis, ibises, and curlews that probe in mud or
27 earth for invertebrates. The affinities of the new pterosaur are unclear. It likely represents an
28 azhdarchoid, but does not clearly fit within any known azhdarchoid clade. The new pterosaur adds
29 to the remarkable diversity of pterosaurs known from the mid-Cretaceous, and suggests that
30 pterosaur diversity remained undersampled.

31
32 *Keywords:* Pterosauria, Azhdarchoidea, Probe-feeding, Cretaceous, Kem Kem Group,
33 Morocco, Africa

1. Introduction

Pterosaurs, volant archosaurs of the Mesozoic, achieved their peak in diversity in the Early Cretaceous (Unwin, 2006; Witton, 2013). Pterosaurs inhabited numerous palaeoenvironments including coastal and shallow marine (Kellner, et al., 2003), lagoonal (Unwin and Martill, 2007; Martill et al., 2013) , lacustrine (Pan, et al., 2013), fluvial (Ibrahim et al., 2010; McPhee et al., 2020; Martill et al., 2020) and terrestrial (Vullo, et al., 2012) habitats. Pterosaurs evolved a diversity of feeding strategies, reflected in skull and jaw morphology. These included many niches that are today occupied by birds, such as aerial insect hawkers, piscivores, and filter feeders (Wellnhofer, 1996; Unwin, 2006; Witton, 2013). One feeding strategy widely adopted by birds, but until now not certainly known for pterosaurs, is probe feeding. Here we describe two partial jaw specimens from the Kem Kem Group of south eastern Morocco representing a new genus and species of probe-feeding, azhdarchoid pterosaur.

2. Geographical and geological context

2.1. Locality.

The specimens described here come from Aferdou N' Chaft, a small collection of outliers of the Kem Kem Plateau some four kilometres south of the oasis of Hassi El Begaa in the southern Tafilalt of south east Morocco (Fig. 1). This locality is known for abundant but isolated pterosaur remains (McPhee et al., 2020).

2.2. Geology and stratigraphy

The Kem Kem Group of south eastern Morocco is important as a window into the diversity of African Cretaceous pterosaurs (Ibrahim et al., 2010; Martill and Ibrahim 2015; Jacobs et

al., 2019, 2020; McPhee et al., 2020; Martill et al., 2020). The specimens described here come from intraformational, mud-flake conglomerates in the upper Ifezouane Formation, following the nomenclature of Ettachfini and Andreu (2004). This formation crops out widely at the base of an escarpment that borders the Tafilalt plain centred on the town of Erfoud, Errachidia province, and at the southern front of the Atlas Mountains near Tadighoust where the succession is intensely folded. Fossil vertebrate remains are mined over much of the outcrop, but preservation is particularly good at Hassi El Begaa. Bones are almost always isolated and often broken, but delicate structures and microscopic structures of the histology are frequently preserved. The age of these strata is problematic, due to rarity of biostratigraphically useful fossils. Correlations with the Baharia Formation of Egypt have been used to infer a Cenomanian age, in part due to the shared presence of the dinosaur *Spinosaurus* and the saw shark *Onchopristis* (Serenio et al., 1996). Limestones of the Akrabou Formation overlying the Kem Kem Group contain the ammonite *Neolobites vibrayeanus* (d'Orbigny, 1841), of late Cenomanian age; thus the Kem Kem Group is older. Likely the Kem Kem Group is ?Aptian/Albian to lower Cenomanian (Ibrahim et al., 2020).

3. Materials and methods

X-ray computed tomography (XCT) was conducted using an X-ray microscope (Xradia 520 Versa, Carl Zeiss X-ray Microscopy) at a voltage of 80 kVp with a power of 6 W and a tube current of 75 mA. 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° with an interval of 0.22°. The detector was exposed for 0.5 s (5 frames, 0.1 s exposure/frame) per projection. The pixel size varied for each sample. Projections were reconstructed using microscope software incorporating a filtered back

projection algorithm (Scout and Scan Reconstructor, Carl Zeiss Microscopy). For each dataset the centre shift was manually found, no beam hardening correction was utilised and smoothing correction of 0.5 was applied.

MeVisLab software was used to digitally remove matrix from the XCT scans and combine all XCT slices into a 3 dimensional digital model. The model was digitally manipulated in Geomagic Design X and images captured.

Specimens described here are accessioned in the collection of the Département de Géologie (Paléontologie), Faculté des Sciences Aïn Chock (FSAC), Université Hassan II - Casablanca, Km 8, Route de l'université 20100, Casablanca, Morocco, and are prefixed FSAC-KK.

4. Results

4.1. *Systematic palaeontology*

PTEROSAURIA Kaup, 1834

MONOFENESTRATA Lü et al., 2009

PTERODACTYLOIDEA Plieninger, 1901

LOPHOCRATIA Unwin, 2003

AZHDARCHOIDEA Unwin, 1992

?Family unknown

Leptostomia gen. nov.

Etymology: Lepto Gr. slender; *stoma* Gr. mouth.

101 *Type species: Leptostomia begaaensis* gen. et sp. nov. See below.

102 *Diagnosis:* As for species.

103 ***Leptostomia begaaensis*** gen. et sp. nov.

104 *Etymology:* After the oasis village of Hassi El Begaa near the type locality of Aferdou N'

105 Chaft.

106 *Holotype.* FSAC-KK 5075. Partial anterior rostrum, anterior to nasoantorbital fenestra and
107 missing tip (Figs 2-6).

108 *Paratype.* FSAC-KK 5076. Partial mandibular symphysis from anterior of union of mandibular
109 rami (Figs 7-8).

110 *Type locality.* Aferdou N'Chaft, Hassi El Begaa, Province d'Errachidia, Morocco.

111 *Type horizon and stage.* Upper Ifezouane Formation, Kem Kem Group, ?Albian — lower
112 Cenomanian.

113 *Diagnosis.* Small and edentulous pterosaur, with a long and slender beak lacking dorsal or
114 ventral crests. The following features are autapomorphic. Lateral and dorsal rostral angles
115 (*sensu* McPhee et al., 2020, Tb. 1) less than or equal to 3 degrees. Cross sectional outline of
116 anterior rostrum and mandibular symphysis semi-circular. Cross-section of beak with thick
117 cortices and reduced central cavity.

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120 *4.1.1 Description*

We identify FSAC-KK 5075 as a rostrum based on the lateral rostral angle being larger than the presumed counter-part mandible FSAC-KK 5076, and also presence of a median ridge as seen in several other pterosaurs (e.g. *Anhanguera*, *Hamipterus*, *Coloborhynchus* and *Lonchodectes*) (Unwin, 2001), as part of a character complex in which a rostral palatal ridge is associated with a mandibular palatal groove.

We identify FSAC-KK 5076 as a mandible based on the extremely low rostral angle and median palatal groove. In almost all pterosaurs the lower jaw is shallower than the upper (see McPhee et al., 2020).

Referral of the two specimens to a single species is supported by their similar sizes, and shared features. These include similar long, low, parallel-sided shapes, similar semi-circular, thick-walled cross-sections, similar distribution of foramina, and the corresponding ridge-and-groove complex. Despite the small size of the fossils, the bone is remarkably smooth on both specimens suggesting osteological maturity (*sensu* Bennett, 1993; Prondvai et al., 2012).

The holotype (FSAC-KK 5075) is a section of anterior rostrum missing its tip. The fragment is broken ahead of the nasoantorbital fenestra and measures 48 mm in length. Anteriorly it is 2.2 mm high and 5.0 mm wide. Posteriorly it is 3.9 mm high by 7.2 mm wide. It has a lateral rostral angle of 2.5° and dorsal angle of 3° (Table 1). An estimated 70 mm is missing anteriorly, assuming the rostrum tapered evenly to a sharp point as in other azhdarchoids. Longitudinally the dorsal margin is slightly convex, but this convexity is not reflected in the occlusal surface, which is straight.

The rostrum bears a median ridge on the occlusal surface extending the length of the specimen. The ridge becomes more pronounced posteriorly. Two grooves lie parallel to the

median ridge on the occlusal surface, each with a central row of small, slit-like foramina, which are offset (Figs 2-4). There are 12 foramina on the occlusal surface, each measuring approximately 1 mm long, and spaced 5-10 mm apart. The lateral margins of the occlusal surface are flat and angle up and away from the median ridge.

The dorsal surface is gently rounded, with two rows of foramina on each side. These are longer than those on the occlusal surface, measuring up to 5 mm long and located 8-20 mm apart. There are four foramina on the right lateral margin and six on the left lateral margin. Similar, slit-like foramina are common in Azhdarchoidea, e.g. *Alanqa saharica*.

The broken ends show a semi-circular cross section. The round cross section differs from the more triangular or U-shaped section of most azhdarchoids (e.g. *Apatorhamphus*). Cortices are thickened around the entire circumference of the bone, with a single large opening posteriorly and 3 small, circular opening anteriorly. Thickened cortices are seen in the jaws of both *Alanqa* and *Xericeps*. In *Alanqa*, the cortex of the occlusal surface is thickened, in *Xericeps* it is thickened around the entire circumference of the mandible. In neither is it developed to the degree seen in *Leptostomia*.

The paratype (FSAC-KK 5076) is a section of anterior mandibular symphysis. It is missing the tip anteriorly, and does not extend posteriorly as far as the divergence of the mandibular rami. It measures 67 mm in length, has an anterior height of 0.6 mm and width of 2.7 mm and posterior height of 2.5 mm and width of 5.8 mm. It is estimated that 35 mm are missing from the anterior end. The mandible is gently curved longitudinally, but this is accentuated towards the tip due to a repair. It has a lateral rostral angle of just 2° making it look flattened, and a dorsal rostral angle of 3.2°.

The mandible has a flat occlusal surface anteriorly that develops into a shallow median groove posteriorly, beginning approximately 17 mm from the tip. This central groove widens and deepens posteriorly and has two rows of small, paired foramina which are slightly offset. Foramina measure approximately 1 mm in length and are spaced 8 - 10 mm apart. 12 foramina are preserved on the occlusal surface. The margins of the occlusal surface are flat and gently angle down from the median ridge.

The ventral surface is gently rounded. This contrasts with the sharp ventral margin seen in *Alanqa*, or the U-shaped ventral margin seen in *Xericeps*. Two rows of elongate slit-like foramina are positioned on each side. Foramina measure up to 5 mm in length and are spaced approximately 11 mm apart. There are six foramina on the each of the lateral surfaces. The mandible has a semi-circular cross section with broken ends revealing that it is solid anteriorly, with a small central void posteriorly. The cross-section resembles that of the upper jaw. The rounded, dorsoventrally flattened section differs from either the V-shaped section in *Alanqa* or the deep, U-shaped section in *Xericeps*.

4.1.2 Internal structure of the holotype

FSAC-KK 5075 was XCT scanned to reveal details of the internal architecture (Fig. 5). The rostrum is hollow, with a flat, lenticular-shaped internal void extending along the entire length. The void measures is approximately 1 mm tall by 4 mm wide posteriorly and ~0.5 mm tall by 3 mm wide anteriorly. In places thin trabeculae cross from the roof to the floor of the median void (Fig. 5A, B). Cortices are thickened compared with many pterosaur rostra being approximately 2 mm thick at the median ridge (Fig. 5A). Lateral to the central void are two canals that parallel the void for the length of the specimen, becoming more

conspicuous with circular outlines anteriorly (Fig. 5B-F). Besides the median void and lateral canals there are a number of circular to slightly oval canals that diverge from the central void and extend obliquely to the bone exterior where they open into elongate foramina (Fig. 5A-F).

4.2. Referral to Pterosauria

The specimens described here are both fragmentary, and unlike any previously described for a pterosaur. Never the less, they can be referred to as Pterosauria based on a suite of features. The texture of the bone surface is consistent with that described for other pterosaurs (e.g. Bennett, 1993 fig. 2; Bennett and Penkalski 2018 fig. 2), being dense and smooth, with a fine ripple-like fibrous texture (Fig. 6). Other pterosaur features include fusion of the premaxillae of the rostrum and fusion of the dentaries of the mandible. The formation of a palatal ridge of the rostrum and a corresponding groove of the mandible is also characteristic of many pterosaurs. Loss of teeth is a derived character found independently in two pterosaur clades, Azhdarchoidea and Pteranodontia, both of which are present in North Africa (Longrich et al, 2018) and are edentulous. In addition, the presence of elongate foramina on the occlusal and lateral/dorsal surfaces is a derived feature present in the pterodactyloid clades Azhdarchoidea (Solomon et al., 2020; Martill et al., 2020) and Dsungaripteroidea (Chen et al., 2020).

4.3. Affinities within Pterosauria.

Due to the fragmentary nature of the animal, affinities within Pterosauria are unclear. Given the Cretaceous age of the specimen it likely represents a pterodactyloid. The lack of dental alveoli excludes *L. begaaensis* from all pterosaur groups except Pteranodontia (Pteranodontidae + Nyctosauridae) and Azhdarchoidea (Tapejaridae, Chaoyangopteridae, Thalassodromidae + Azhdarchidae). As the taxon is extremely autapomorphic within Pterosauria, in respect of its overall appearance, it is difficult to be confident where its affinities lie.

Many features present on *L. begaaensis* occur in a number of pterosaur families. Foramina on the jaws have been reported in several pterosaur groups including the non-pterodactyloid Raeticodactylidae (e.g. *Caviramus schesaplanensis*) (Fröbisch and Fröbisch, 2006), suggesting it is a plesiomorphic feature. Foramina on the jaws have also been reported in Ctenochasmatidae (e.g. *Plataleorhynchus streptophorodon*) (Howse and Milner, 1995), Lonchodectidae (e.g. *Lonchodraco giganteus*) (DMM pers. obs.), Ornithocheiridae (e.g. *Anhanguera fittoni* and *Coloborhynchus sedgwickii*) (Unwin, 2001, figs 9,10), Dsungaripteridae (e.g. *Dsungaripterus weii*) (Chen, et al., 2020), are widespread within Azhdarchoidea (Azhdarchidae, Chaoyangopteridae and Tapejaridae) and contrary to McPhee et al. (2020) are present in the thalassodromids *Thalassodromeus* (Pêgas, et al., 2018) and *Tupuxuara* (Kellner and Campos, 1994). The distribution of the foramina in *Coloborhynchus sedgwickii*, is very similar to that seen in the holotype specimen of *L. begaaensis*, with foramina arranged in rows parallel to the median occlusal ridge, and are also slightly offset. However, elongate, slit-like foramina like those seen in *L. begaaensis* are only reported in some dsungaripterids (Chen, et al., 2020, fig. 4A), and most, but not all azhdarchooids (see SI Table B).

The median palatal ridge seen on the rostrum is seen in several pterosaur clades. In Lonchodectidae a prominent, sharp median keel is present on the occlusal surface of the premaxilla/maxilla of *Lonchodectes* (Unwin, 2001, 2003) (Averianov, 2020). Similarly, a median palatal ridge is found in ornithocheirans including *Coloborhynchus* (Unwin, 2001, fig. 9) *Anhanguera* (Unwin, 2001, fig. 10), *Hamipterus* and *Iberodactylus* (Holgado et al., 2019). A posterior median boss is seen in many azhdarchoids (e.g. *Afrotapejara*, *Alanqa*, *Tupuxuara*). The structure does not extend the majority of the length of the occlusal surface, but may still be homologous with the occlusal ridge in *L. begaaensis* and other pterosaurs.

In the mandible, a median groove is found in several pterosaur groups including Lonchodectidae (e.g. *Lonchodectes* and *Lonchodraco*), where it is considered a possible synapomorphy of the family (Averianov, 2020), Ornithocheiridae (e.g. *Anhanguera*, *Hamipterus*, *Tropeognathus*) (Jacobs, et al., 2020) and Ctenochasmatidae (e.g. *Gnathosaurus*) (Howse and Milner, 1995).

The palatal keel and mandibular groove therefore appear to have either convergently evolved in different clades, or to represent a primitive feature diagnosing a larger group such as Ornithocheiroidea or Pterodactyloidea.

Both specimens are dorsoventrally compressed, a feature seen in the jaw tips of some lonchodectids, and considered a diagnostic character of the group by Unwin (2001) (Averianov, 2020). The presence of the elongate external foramina on the rostrum and mandibular symphysis has previously been considered a feature of Azhdarchoidea, with such foramina identified in Azhdarchidae (Averianov, 2010), Tapejaridae (Kellner, 2013;

Manzig et al., 2014) and Chaoyangopteridae (McPhee et al., 2020). However, similar foramina have now been reported for Dsungaripteridae (Chen et al., 2020).

Finally, the relatively thick cortices of the rostrum and mandible are also seen in several azhdarchoids, e.g. *Alanqa* in which the occlusal surface of the jaws is thickened, and *Xericeps* and *Aptorhamphus*, in which thick cortices are well-developed around the circumference of the jaws.

Taken together, the combination of characters seen here- elongate, slit-like foramina and the absence of dentition, and thick cortices- suggest that *L. begaaensis* more likely belongs to Azhdarchoidea.

4.3.1 Phylogenetic analysis

We undertook a phylogenetic analysis to explore the affinities of *Leptostomia*. We used a data set from Martill et al. (2020) with five additional characters, two from Andres, et al., ([2014], ch. 147-148), and three new characters (see SI character list and data matrix). A variety of methods were used to test the phylogenetic relationships of the new taxon. Due to limited codable characters and homoplasy, results are ambiguous and conflicting. A tree generated using unordered characters remained unresolved (SI Fig A, B), whereas the addition of ordered characters generated two trees, one with the new taxon nesting within Azhdarchoidea (SI Fig. B) and other with *Leptostomia* allied with ctenochasmatids and *Lonchodectes* (SI Fig. C). The phylogenetic placement of the new taxon therefore remains uncertain. The combination of edentulous jaws and elongate foramina suggests affinities likely lie with Azhdarchoidea. The presence of a median ridge in the rostrum and occlusal groove and dorso-ventrally compressed cross sectional outline of the mandible suggest that a possible relationship with Ctenochasmatids or Lonchodectids cannot be ruled out.

5. Discussion

Leptostomia differs from other edentulous pterosaurs in possessing a remarkably low rostral lateral angle (Fig. 9A), endowing it with a very long and slender beak. Its lateral angle is also very low when compared with toothed pterosaur with only some ctenochamatids having a similarly low lateral angle (Fig. 9B). Although the cranium and post cranial skeleton are unknown, using phylogenetic bracketing, and comparisons with birds, we have attempted tentative restoration of *Leptostomia* as an azhdarchoid (Fig. 10). While it has long been recognised that the pterosaur skull displays considerable morphological disparity (e.g. Navarro et al., 2018), *Leptostomia* reveals a greater range of variation for the pterosaur skull than hitherto realised (Fig. 11), showing the degree to which pterosaurs diversified by the mid-Cretaceous.

5.1 Paleobiology.

The extreme elongation and dorsoventral compression of the jaws suggest a feeding mode unlike any previously documented for Pterosauria. The morphology is instead approached by a number of long-billed bird species. Almost all of these birds are predators of small invertebrates such as worms, crustaceans, insects and molluscs, and specialise to various degrees on sediment probing.

One group of long-jawed birds, such as avocets (*Avoceta*), limpkin (*Aramus*), and stilts (*Himantopus* spp.) (See SI Table C for a more complete listing) primarily feed by using the jaws as forceps to grasp small invertebrates. However, most if not all of these also engage in shallow sediment probing. To detect prey, some of these species, such as stilts

and limpkins, tend to rely heavily on vision. Others, such as avocets, rely more on tactile cues (Pierce, 1996). Prey are often taken on low water, or by wading, typically along coastal mudflats, beaches, or estuaries, although limpkins feed in freshwater (Bryan; 1996).

A second guild of birds forage mostly by probing to seize small, buried prey, inserting jaws deep into mud or earth. This group includes the more specialized scolopacids such as dunlin and related sandpipers (*Calidris* spp.), curlews (*Numenius* spp.), and woodcock (*Scolopax*) (Piersma, et al., 1996). It also includes ibises (Threskiornithidae) (Matheu, and del Hoyo, 1992), Hoopoes (*Upupa*) (Krištin, 2001) and kiwi (Apterygidae). Probing necessarily relies on tactile cues, and the eyes of probers are often smaller than in visual hunters. Prey include worms, crustaceans, and molluscs. They may be taken on mudflats of shorelines and estuaries, as in curlews, dunlins, and godwits. However, snipes and sometimes godwits feed in marshes. Others, such as kiwi, woodcock, hoopoe primarily feed on terrestrial invertebrates especially earthworms (Folch, 1992).

A third group of long-billed birds includes nectar feeders, such as sword-billed hummingbirds whose bill length may exceed that of the entire animal (Schuchmann, 1999).

A nectar-eating ecology can probably be ruled out given the rarity of flowers in the mid-Cretaceous and the relatively large size of the pterosaur.

5.2 Leptostomia as a probe feeder

A probe feeding strategy has been suggested for the Late Cretaceous azhdarchid *Quetzalcoatlus northropi* (Langston, 1981; Lehman and Langston, 1996), but its enormous size make it more likely to have been a terrestrial predator (Witton and Naish, 2008) or piscivore. The Jurassic pterodactyloid *Pterodactylus antiquus* was depicted as a probe-feeding shoreline animal by Bakker (1987), but no evidence for such a lifestyle was

presented (Hazlehurst and Rayner 1992). Possible prod mark trace fossils associated with the pterosaurian *Purbeckopus* traces from the Early Cretaceous of Dorset, England were described by Wright et al., (1997) as perhaps made by a probe feeding pterosaur. Similar peck marks associated with *Pteraichnus*-like tracks have also been interpreted as pterosaur feeding traces (Lockley et al., 1995), later interpreted as oval-shaped beak or prod marks (Lockley and Rainforth, 2002). Until now, however, no pterosaur has been reported with a beak morphology consistent with specialised probe feeding.

In birds the transition from pecking feeding behaviour to a probing behaviour involved several functional transformations (Zweers and Gerritsen, 1996). These include modifications to penetrate the substrate, 'remote touch' and to pursue, capture and retract prey from the substrate. These transformations manifest themselves as a series of adaptations including flattening of the bill either vertically or horizontally, lengthening and narrowing, often accompanied by strengthening of the bill.

Other transformations involve soft tissues such as the morphology of the tongue and behavioural traits that are unlikely to leave a fossil record (Zweers and Gerritsen, 1996). Although a curved beak is better adapted for probing, it requires a higher bone mass to maintain resistance from bending, a straight beak is also more versatile for a variety of feeding behaviours (Nebel, et al., 2005).

Two non-visual methods of prey detection are used by probe feeders: direct touch (chance encounter) and remote touch (Cunningham, et al., 2010b). Remote touch is the ability of an animal to detect prey hidden within the substrate, usually through vibration detection or changes in interstitial water pressure, detected by micro-organs known as mechanoreceptors mainly concentrated in the beak tip (Cunningham, 2010b; Piersma, et al.,

1998). These micro-organs can either be located in pits in the bone (foramina), within the rhamphotheca or in both (Cunningham, et al., 2013). They are present in many probing bird families including Apterygidae, Scolopacidae and Threskiornithidae (Cunningham, et al., 2010a, b, 2013).

Several potential adaptations to a probe-feeding lifestyle are seen in *Leptostomia begaaensis*. These include the long, narrow, dorso-ventrally compressed beak, which decreases the resistance caused by inserting the beak into the sediment. The cross-sectional outline of both the upper and lower jaw of *L. begaaensis* is remarkably similar to that of the Sanderling (*Calidris alba*), a remote sensing probing shore bird (Piersma, et al., 1996). The thickened bone walls, seen in many longirostrine pterosaurs and many birds including Charadriiformes *Calidris* spp.) and Pelecaniformes (*Ardea* spp.), strengthen the jaw against high compressional and bending stresses encountered during probing (Zweers and Gerritsen, 1996). Due to the lack of an anterior tip on both holotype and paratype specimens it is impossible to determine whether concentrations of foramina are present to allow for remote sensing but such an adaptation would be expected, and this prediction can be tested with discovery of additional specimens.

Finally, the environment is consistent with a probe-feeding ecology. The Kem Kem Group was a freshwater to brackish paleoenvironment, ranging from fluvial to paralic (Ibrahim et al., 2020). An exceptionally diverse freshwater fauna including fish, sharks, and the aquatic dinosaur *Spinosaurus* suggests high productivity (Ibrahim et al., 2020). In particular crab fossils in North African mangroves suggest a potential food source (Schweitzer et al., 2003).

Taken together the evidence suggests that *L. begaaensis* was a probe-feeding pterosaur. The degree of specialization of the jaws suggest it relied on probe-feeding more than birds such as solitary sandpipers, stilts, or limpkins, which engage in this behaviour intermittently. Instead it was probably more similar in behaviour to highly specialized probe-feeders such as curlews, woodcocks, and kiwis, which rely on probe-feeding for most of their diet. *Leptostomia begaaensis* probably hunted along the mud flats and sandbanks of the ancient Moroccan Kem Kem river system, its prey likely including worms, fiddler crabs and other crustaceans, and/or small molluscs such as *Unio* spp.

5.3 Evolutionary implications

By the middle of the Cretaceous pterosaurs had radiated to have a variety of diets including piscivory (*Alanqa*, *Ornithocheirus*) and insectivory (*Jeholopterus*), and use a variety of feeding mechanisms including durophagy (*Dsungaripterus*), filter feeding (*Pterodaustro*) and now a specialised probe feeder (*Leptostomia*). Pterosaurs used a variety of foraging strategies, feeding on the ground and on the wing (Witton and Naish, 2008). The presence of a specialized prober in the mid-Cretaceous documents the radiation of pterosaurs into a niche that previously appeared to have been unoccupied, and shows that the mid-Cretaceous radiation of pterodactyloids, and especially azhdarchoids, occupied more niches than has previously been appreciated. Given that we continue to discover new ecological niches occupied by the pterosaurs, and strong biases in both the habitats sampled and against the preservation of pterosaurs in general, it seems likely that we are greatly underestimating the range of ecological niches occupied by pterosaurs.

6. Conclusions

Leptostomia begaansis gen. et sp. nov. is interpreted as a probe feeding pterosaur whose affinities likely lie within Azhdachoidea. The specimen adds to the diversity of pterodactyl feeding strategies and to the overall diversity of pterosaurs in the Ifezouane Formation of Kem Kem Group of North Africa, bringing to nine the number of pterosaur taxa reported from these strata. The proposed probe-feeding strategy suggested by the rostrum morphology of *Leptostomia* has not previously been documented for the Pterosauria. It contributes to an emerging picture of a highly diverse mid-Cretaceous pterosaur fauna, and raises the possibility that this fauna remains undersampled.

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416 **References**

417 Andres, B., Clark, J., Xu, X., 2014. The earliest pterodactyloid and the origin of the group.
 418 Current Biology 24, 1011-1016.

419 Averianov, A.O., 2010. The osteology of *Azhdarcho lancicollis* Nessel, 1984 (Pterosauria,
 420 Azhdarchidae) from the late Cretaceous of Uzbekistan. Proceedings of the Zoological
 421 Institute RAS 314, 264-317.

422 Averianov, A.O., 2020. Taxonomy of the Lonchodectidae (Pterosauria,
 423 Pterodactyloidea). Proceedings of the Zoological Institute RAS 324, 41-55.

424 Bakker, R., 1987. The dinosaur heresies: a revolutionary view of dinosaurs. Longman
 425 Scientific & Technical, 481 pp.

426 Bennett, S.C., 1992. Sexual dimorphism of *Pteranodon* and other pterosaurs, with
 427 comments on cranial crests. Journal of Vertebrate Paleontology 12, 422-434.

428 Bennett, S.C., 1993. The ontogeny of *Pteranodon* and other pterosaurs. Paleobiology
 429 19, 92-106.

430 Bennett, S.C., 1995. A statistical study of *Rhamphorhynchus* from the Solnhofen Limestone
 431 of Germany: year-classes of a single large species. Journal of Paleontology 69, 569-580.

- 432 Bennett, S.C., 2003. New crested specimens of the Late Cretaceous pterosaur
 433 *Nyctosaurus*. Paläontologische Zeitschrift 77, 61-75.
- 434 Bennett, S.C., Penkalski, P., 2018. Waves of bone deposition on the rostrum of the pterosaur
 435 *Pteranodon*. Geological Society, London, Special Publications 455, 69-81.
- 436 Bryan, D. C., 1996. Family Aramididae (Limpkin). In: del Hoyo, J., Elliott, A., Sargatal, J. (Eds.).
 437 Handbook of the birds of the World, volume 3, Hoatzin to Auks. Lynx Edicions, Barcelona,
 438 pp. 90-95.
- 439 Chen, H., Jiang, S., Kellner, A.W.A., Cheng, X., Zhang, X., Qiu, R., Li, Y., Wang, X., 2020. New
 440 anatomical information on *Dsungaripterus weii* Young, 1964 with focus on the palatal
 441 region. PeerJ 8, e8741. <https://doi.org/10.7717/peerj.8741>
- 442 Chiappe, L.M., Kellner, A.W.A., Rivaola, D., Davila, S., Fox, M., 2000. Cranial morphology of
 443 *Pterodaustro guinazui* (Pterosauria: Pterodactyloidea) from the Lower Cretaceous of
 444 Argentina. Contributions in Science 483, 1-19.
- 445 Cunningham, S.J., Alley, M.R., Castro, I., Potter, M.A., Cunningham, M., Pyne, M.J., 2010a.
 446 Bill morphology of ibises suggests a remote-tactile sensory system for prey detection. The
 447 Auk 127, 308-316.
- 448 Cunningham, S.J., Castro, I., Jensen, T., Potter, M.A., 2010b. Remote touch prey-detection by
 449 Madagascar crested ibises *Lophotibis cristata urschi*. Journal of avian biology 41, 350-353.
- 450 Cunningham, S.J., Corfield, J.R., Iwaniuk, A.N., Castro, I., Alley, M.R., Birkhead, T.R., Parsons,
 451 S., 2013. The anatomy of the bill tip of kiwi and associated somatosensory regions of the
 452 brain: comparisons with shorebirds. PLoS ONE 8, e80036.
 453 <https://doi.org/10.1371/journal.pone.0080036>

- 454 Ettachfini, E.M., Andreu, B., 2004. Le Cénomanién et le Turonien de la plate-forme
1
2
3 455 Préafricaine du Maroc. *Cretaceous Research* 25, 277-302.
4
5
6 456 Folch, A., 1992. Family Apterygidae (Kiwis). In: del Hoyo, J., Elliott, A., Sargatal, J. (Eds.).
7
8 457 Handbook of the birds of the World, volume 1, Ostrich to ducks. Lynx Edicions, Barcelona,
9
10
11 458 pp. 104-110.
12
13
14 459 Frey, E., Martill, D.M., Buchy, M.C., 2003. A new crested ornithocheirid from the Lower
15
16
17 460 Cretaceous of northeastern Brazil and the unusual death of an unusual
18
19 461 pterosaur. *Geological Society, London, Special Publications* 217, 55-63.
20
21
22 462 Fröbisch, N.B., Fröbisch, J., 2006. A new basal pterosaur genus from the Upper Triassic of
23
24
25 463 the Northern Calcareous Alps of Switzerland. *Palaeontology* 49, 1081-1090.
26
27
28 464 Hazlehurst, G.A., Rayner, J.M., 1992. Flight characteristics of Triassic and Jurassic
29
30
31 465 Pterosauria: an appraisal based on wing shape. *Paleobiology* 18, 447-463.
32
33
34 466 Holgado, B., Pêgas, R.V., Canudo, J.I., Fortuny, J., Rodrigues, T., Company, J., Kellner, A.W.A.,
35
36
37 467 2019. On a new crested pterodactyloid from the Early Cretaceous of the Iberian Peninsula
38
39 468 and the radiation of the clade Anhangueria. *Scientific Reports* 9, 1-10.
40
41
42 469 Howse, S.C.B., Milner, A.R., 1995. The pterodactyloids from the Purbeck Limestone
43
44
45 470 Formation of Dorset. *Bulletin of the Natural History Museum, London (Geology)* 51, 73-88.
46
47
48 471 Ibrahim, N., Sereno, P.C., Varricchio, D., Martill, D.M., Dutheil, D.B., Unwin, D.M., Baidder, L.,
49
50
51 472 Larsson, H.C.E., Zouhri, S., Kaoukaya, A., 2020. Geology and paleontology of the Upper
52
53
54 473 Cretaceous Kem Kem Group of eastern Morocco. *Zookeys* 928, 1-216.
55
56
57
58
59
60
61
62
63
64
65

- 474 Ibrahim, N., Unwin, D.M., Martill, D.M., Baidder, L., Zouhri, S., 2010. A New Pterosaur
 475 (Pterodactyloidea: Azhdarchidae) from the Upper Cretaceous of Morocco. PloS ONE 5,
 476 e10875. <https://doi.org/10.1371/journal.pone.0010875>
- 477 Jacobs, M.L., Martill, D.M., Ibrahim, N., Longrich, N., 2019. A new species of *Coloborhynchus*
 478 (Pterosauria, Ornithocheiridae) from the mid-Cretaceous of North Africa. Cretaceous
 479 Research 95, 77-88.
- 480 Jacobs, M.L., Martill, D.M., Unwin, D.M., Ibrahim, N., Zouhri, S., Longrich, N.R., 2020. New
 481 toothed pterosaurs (Pterosauria: Ornithocheiridae) from the middle Cretaceous Kem Kem
 482 beds of Morocco and implications for pterosaur palaeobiogeography and
 483 diversity. Cretaceous Research 110, 104413.
- 484 Kaup, J.J., 1834. Versuch einer Eintheilung der Saugethiere in 6 Stämme und der Amphibien
 485 in 6 Ordnungen Isis 3, 311-315.
- 486 Kellner, A.W.A., 2004. New information on the Tapejaridae (Pterosauria, Pterodactyloidea)
 487 and discussion of the relationships of this clade. Ameghiniana 41, 521-534.
- 488 Kellner, A.W.A., 2013. A new unusual tapejarid (Pterosauria, Pterodactyloidea) from the
 489 Early Cretaceous Romualdo Formation, Araripe Basin, Brazil. Earth and Environmental
 490 Science Transactions of the Royal Society of Edinburgh 103, 409-421.
- 491 Kellner, A.W.A., Aguirre-Urreta, M.B., Ramos, V.A., 2003. On the pterosaur remains from the
 492 Río Belgrano formation (Barremian), Patagonian Andes of Argentina. Anais da Academia
 493 Brasileira de Ciências 75, 487-495.

- 494 Kellner, A.W.A., de Almeida Campos, D., 1994. A new species of *Tupuxuara* (Pterosauria,
495 Tapejaridae) from the Early Cretaceous of Brazil. Anais da Academia Brasileira de
496 Ciências 66, 467-474.
- 497 Kellner, A.W.A., de Almeida Campos, D., 2002. The function of the cranial crest and jaws of a
498 unique pterosaur from the Early Cretaceous of Brazil. Science 297, 389-392.
- 499 Krištin, A., 2001. Family Upupidae (Hoopoe). In: del Hoyo, J., Elliott, A., Sargatal, J. (Eds.).
500 Handbook of the birds of the World, volume 6, Mousebirds to Hornbills. Lynx Edicions,
501 Barcelona, pp. 396-411.
- 502 Langston, W., 1981. Pterosaurs. Scientific American 244, 122-137.
- 503 Lehman, T.M., Langston Jr, W., 1996. Habitat and behaviour of *Quetzalcoatlus*:
504 paleoenvironmental reconstruction of the Javelina Formation (Upper Cretaceous), Big Bend
505 National Park, Texas. Journal of Vertebrate Paleontology 16, 48A.
- 506 Lockley, M.G., Logue, T.J., Moratalla, J.J., Hunt, A.P., Schultz, R.J., Robinson, J.W., 1995. The
507 fossil trackway *Pteraichnus* is pterosaurian, not crocodilian: implications for the global
508 distribution of pterosaur tracks. Ichnos: An International Journal of Plant & Animal 4, 7-20.
- 509 Lockley, M.G., Rainforth E.C., 2002. The track record of Mesozoic birds and pterosaurs: am
510 ichnological and paleoecological perspective. In: Chiappe, L. M., Witmer, L. M. (Eds.)
511 Mesozoic birds: above the heads of dinosaurs. University of California Press, Berkeley,
512 California, pp. 405-418.
- 513 Longrich, N.R., Martill, D.M., Andres, B., 2018. Late Maastrichtian pterosaurs from North
514 Africa and mass extinction of Pterosauria at the Cretaceous-Paleogene boundary. PLoS
515 Biology 16, e2001663. <https://doi.org/10.1371/journal.pbio.2001663>

- 516 Lü, J., Unwin, D.M., Xu, L., Zhang, X., 2008. A new azhdarchoid pterosaur from the Lower
517 Cretaceous of China and its implications for pterosaur phylogeny and
518 evolution. *Naturwissenschaften* 95, 891-897.
- 519 Lü, J., Unwin, D.M., Jin, X., Liu, Y., Ji, Q., 2009. Evidence for modular evolution in a long-
520 tailed pterosaur with a pterodactyloid skull. *Proceedings of the Royal Society, B* 277, 383-
521 389.
- 522 Manzig, P.C., Kellner, A.W., Weinschütz, L.C., Fragoso, C.E., Vega, C.S., Guimarães, G.B.,
523 Godoy, L.C., Luccardo, A., Ricetti, J.H., de Moura, C.C., 2014. Discovery of a rare pterosaur
524 bone bed in a Cretaceous desert with insights on ontogeny and behavior of flying
525 reptiles. *PloS ONE* 9, e100005. <https://doi.org/10.1371/journal.pone.0100005>
- 526 Martill, D.M., Etches, S., 2013. A new monofenestratan pterosaur from the Kimmeridge Clay
527 Formation (Kimmeridgian, Upper Jurassic) of Dorset, England. *Acta Palaeontologica*
528 *Polonica* 58, 285-294.
- 529 Martill, D.M., Ibrahim, N., 2015. An unusual modification of the jaws in cf. *Alanqa*, a mid-
530 Cretaceous azhdarchid pterosaur from the Kem Kem beds of Morocco. *Cretaceous Research*
531 53, 59-67.
- 532 Martill, D.M., O'Sullivan, M., Newman, C., 2013. A possible azhdarchid pterosaur
533 (Pterosauria, Azhdarchidae) in the Durlston Formation (Early Cretaceous, Berriasian) of
534 southern England. *Cretaceous Research* 43, 26-39.
- 535 Martill, D.M., Smith, R., Unwin, D.M., Kao, A., McPhee, J., Ibrahim, N., 2020. A new tapejarid
536 (Pterosauria, Azhdarchoidea) from the mid-Cretaceous Kem Kem beds of Takmout, southern
537 Morocco. *Cretaceous Research* 112, 104424.

- 538 Matheu, E., del Hoyo, J., 1992. Family Threskiornitidae (Ibises and spoonbills). In: del Hoyo,
539 J., Elliott, A., Sargatal, J. (Eds.). Handbook of the birds of the World, volume 1, Ostrich to
540 ducks. Lynx Edicions, Barcelona, pp. 472-506.
- 541 McPhee, J., Ibrahim, N., Kao, A., Unwin, D.M., Smith, R., Martill, D.M., 2020. A new?
542 chaoyangopterid (Pterosauria: Pterodactyloidea) from the Cretaceous Kem Kem beds of
543 southern Morocco. Cretaceous Research 110, 104410.
- 544 Navarro, C.A., Martin-Silverstone, E., Stubbs, T.L., 2018. Morphometric assessment of
545 pterosaur jaw disparity. Royal Society open science 5, 172130.
- 546 Nebel, S., Jackson, D.L., Elnor, R.W., 2005. Functional association of bill morphology and
547 foraging behaviour in calidrid sandpipers. Animal Biology 55, 235-243.
- 548 d'Orbigny, A., 1840-1842. Paléontologie française: Terrains crétacés. 1. Cephalopodes.
549 Masson, Paris, pp. 1-120 (1840), 121-430 (1841), 431-662 (1842).
- 550 Padian, K., 2008. The Early Jurassic pterosaur *Dorygnathus banthensis* (Theodori, 1830) and
551 the Early Jurassic pterosaur *Campylognathoides* Strand, 1928. Special Papers in
552 Palaeontology 80, 1–107.
- 553 Pan, Y., Sha, J., Zhou, Z., Fürsich, F., 2013. The Jehol Biota: Definition and distribution of
554 exceptionally preserved relicts of a continental Early Cretaceous ecosystem. Cretaceous
555 Research 44, 30-38.
- 556 Pêgas, R.V., Costa, F.R. and Kellner, A.W., 2018. New information on the osteology and a
557 taxonomic revision of the genus *Thalassodromeus* (Pterodactyloidea, Tapejaridae,
558 Thalassodrominae). Journal of Vertebrate Paleontology 38, e1443273.

- Pierce, R. J., 1996. Family Recurvirostridae (Stilts and avocets). In: del Hoyo, J., Elliott, A., Sargatal, J. (Eds.). Handbook of the birds of the World, volume 3, Hoatzin to Auks. Lynx Edicions, Barcelona, pp. 332-347.
- Piersma, T., van Gils, J., Wiersma, P., 1996. Family Scolopacidae (sandpipers, snipes and phalaropes). In: del Hoyo, J., Elliott, A., Sargatal, J. (Eds.). Handbook of the birds of the world. Hoatzin to Auks, volume 3. Lynx, Barcelona, pp. 444–533.
- Piersma, T., Aelst, R.V., Kurk, K., Berkhoudt, H., Maas, L.R., 1998. A new pressure sensory mechanism for prey detection in birds: the use of principles of seabed dynamics? Proceedings of the Royal Society of London. Series B: Biological Sciences 265, 1377-1383.
- Plieninger, F., 1901. Beiträge zur Kenntnis der Flugsaurier. Palaeontographica 48, 65-90.
- Prondvai, E., Stein, K., Ósi, A., Sander, M.P., 2012. Life history of *Rhamphorhynchus* inferred from bone histology and the diversity of pterosaurian growth strategies. PLoS ONE 7, e31392. <https://doi.org/10.1371/journal.pone.0031392>
- Schuchmann, K.L., 1999. Family Trochilidae (Hummingbirds). In: del Hoyo, J., Elliott, A., Sargatal, J. (Eds.). Handbook of the birds of the world, volume 5, Barn-owls to Hummingbirds, pp. 468-680.
- Schweitzer, C.E., Lacovara, K.J., Smith, J.B., Lamanna, M.C., Lyon, M.A., Attia, Y., 2003. Mangrove-dwelling crabs (Decapoda: Brachyura: Necrocarcinidae) associated with dinosaurs from the Upper Cretaceous (Cenomanian) of Egypt. Journal of Paleontology 77, 888-894.

- 579 Sereno, P.C., Dutheil, D.B., Iarochene, M., Larsson, H.C., Lyon, G.H., Magwene, P.M., Sidor,
 580 C.A., Varricchio, D.J., Wilson, J.A., 1996. Predatory dinosaurs from the Sahara and Late
 581 Cretaceous faunal differentiation. *Science* 272, 986-991.
- 582 Solomon, A.A., Codrea, V.A., Venczel, M., Grellet-Tinner, G., 2020. A new species of large-
 583 sized pterosaur from the Maastrichtian of Transylvania (Romania). *Cretaceous*
 584 *Research* 110, 104316.
- 585 Unwin, D.M., 1992. The phylogeny of the Pterosauria. *Journal of Vertebrate Paleontology*
 586 12, 57A.
- 587 Unwin, D.M., 2001. An overview of the pterosaur assemblage from the Cambridge
 588 Greensand (Cretaceous) of Eastern England. *Mitteilungen aus dem Museum für Naturkunde*
 589 *in Berlin, Geowissenschaftliche Reihe* 4, 189-221.
- 590 Unwin, D. M., 2003. On the phylogeny and evolutionary history of pterosaurs. In: Buffetaut,
 591 E., Mazin, J.M., (Eds.). *Evolution and Palaeobiology of Pterosaurs*. Geological Society of
 592 London, Special Publications 217, London. pp. 139-190.
- 593 Unwin, D. M., 2006. The pterosaurs: from deep time. Pi Press, New York, 352 pp.
- 594 Unwin, D.M., Lü, J., 1997. On *Zhejiangopterus* and the relationships of pterodactyloid
 595 pterosaurs. *Historical Biology* 12, 199-210.
- 596 Unwin, D., Martill, D., 2007. Pterosaurs of the Crato Formation. In: Martill, D. M., Bechly, G.,
 597 Loveridge, R. F. (Eds). *The Crato fossil beds of Brazil: Window into an ancient world*.
 598 Cambridge University Press, pp. 475-524.

- 599 Vidovic, S.U., Martill, D.M., 2014. *Pterodactylus scolopaciceps* Meyer, 1860 (Pterosauria,
600 Pterodactyloidea) from the Upper Jurassic of Bavaria, Germany: the problem of cryptic
601 pterosaur taxa in early ontogeny. PLoS ONE 9, e110646. doi:10.1371/journal.pone.0110646
602 Vullo, R., Marugán-Lobón, J., Kellner, A.W., Buscalioni, A.D., Gomez, B., De la Fuente, M.,
603 Moratalla, J.J., 2012. A new crested pterosaur from the Early Cretaceous of Spain: the first
604 European tapejarid (Pterodactyloidea: Azhdarchoidea). PLoS ONE 7, e38900.
605 doi: 10.1371/journal.pone.0038900
606 Wang, X., Zhou, Z., 2003. A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early
607 Cretaceous Jiufotang Formation of western Liaoning, China and its implications for
608 biostratigraphy. Chinese Science Bulletin 48, 16-23.
609 Wellnhofer, P., 1978. Pterosauria. In: Wellnhofer, P. (ed.) Handbuch der Paläoherpetologie,
610 Gustav Fischer, Stuttgart, Teil 19, 82 pp.
611 Wellnhofer, P., 1996. The Illustrated Encyclopedia of Prehistoric Flying Reptiles: Pterosaurs.
612 Barnes & Noble Books, London, 192 pp.
613 Witton, M.P., 2013. Pterosaurs: natural history, evolution, anatomy. Princeton University
614 Press, Oxford, 304 pp.
615 Witton, M.P., Naish, D., 2008. A reappraisal of azhdarchid pterosaur functional morphology
616 and paleoecology. PLoS ONE 3, e2271. <https://doi.org/10.1371/journal.pone.0002271>
617 Wright, J.L., Unwin, D.M., Lockley, M.G., Rainforth, E.C., 1997. Pterosaur tracks from the
618 Purbeck limestone Formation of Dorset, England. Proceedings of the Geologists' Association
619 108, 39-48.

620 Young, C. C., 1964, On a new pterosaurian from Sinkiang, China, Vertebrate Palasiatica 8,
 621 221-225

622 Zweers, G.A., Gerritsen, A.F.C., 1996. Transitions from pecking to probing mechanisms in
 623 waders. Netherlands Journal of Zoology 47, 161-208.

624

Figure captions

626 **Fig. 1.** A map of southeast Morocco showing the outcrops of the Kem Kem Group, and the
 627 mine at Aferdou N'Chaft, where the specimens described here were collected. Adapted
 628 from McPhee, et al., (2020).

629 **Fig. 2.** Holotype partial rostrum of *Leptostomia begaaensis* gen. et sp. nov. FSAC-KK 5075. **A**,
 630 dorsal; **B**, ventral; **C**, right lateral; **D**, left lateral; **E**, anterior end; **F** posterior end. Scale bar A-
 631 D represents 5 mm; E-F represents 1 mm.

632 **Fig. 3.** Illustrations of the holotype partial rostrum of *Leptostomia begaaensis* gen. et sp.
 633 nov. FSAC-KK 5075. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, left lateral; **E**, anterior end; **F**
 634 posterior end. Scale bar A-D represents 5 mm and E-F represents 1 mm. Artwork courtesy of
 635 Mr Julian Kiely.

636 **Fig. 4.** Images of 3D models of the holotype partial rostrum of *Leptostomia begaaensis* gen.
 637 et sp. nov. FSAC-KK 5075, generated from an XCT scan. **A**, dorsal; **B**, ventral; **C**, right lateral;
 638 **D**, left lateral; **E**, anterior end; **F**, posterior end; **G**, oblique dorsal; **H**, oblique ventral. Scale
 639 bar A-D represents 5 mm and E-F represents 1 mm.

640 **Fig. 5.** XCT images taken from 6 locations of holotype rostrum of *Leptostomia begaaensis*
 641 FSAC-KK 5075, showing cross section and internal structure. Images **A-F** show XCT slices with

interpretative drawings below, **G** shows the point at which the XCT slices are made. Scale bar represents 2 mm.

Fig. 6. Images of the occlusal surface of the holotype rostrum of *Leptostomia begaaensis*

FSAC-KK 5075, showing a fine ripple-like fibrous texture exhibited by pterosaurs. **A**,

Specimen showing occlusal surface; **B**, surface texture on median ridge in anterior location;

C, surface texture on median ridge in more posterior location and at higher magnification.

Scale bars A-B represent 1 mm and C represents 5 mm.

Fig. 7. Paratype partial mandible of *Leptostomia begaaensis* gen. et sp. nov. FSAC-KK 5076.

A, ventral; **B**, dorsal; **C**, right lateral. Scale bars represent 5 mm.

Fig. 8. Illustrations of the paratype partial mandible of *Leptostomia begaaensis* gen. et sp.

nov. FSAC-KK 5076. **A**, ventral; **B**, dorsal; **C**, right lateral. Scale bars represents 5 mm.

Artwork courtesy of Mr Julian Kiely.

Fig. 9. A selection of pterosaur lateral rostral angles. **A**, edentulous taxa and **B**, toothed taxa,

highlighting the unusually low angle exhibited by *Leptostomia begaaensis* compared to

other taxa. Data and sources are in SI Table A.

Fig. 10. A hypothesised reconstruction of *Leptostomia begaaensis* as an azhdarchoid

pterosaur. Scale bar represent 50 mm. Artwork courtesy of Mr Julian Kiely.

Fig. 11. A selection of pterosaur skulls showing the diversity of morphologies. **A**,

Anurognathus ammoni (Unwin, 2003, fig. 8c); **B**, *Dorygnathus banthensis* (Padian, 2008, fig.

18); **C**, *Rhamphorhynchus muensteri* (Bennett, 1995, fig 5 [no 4]); **D**, *Dsungaripterus weii*

(Young, 1964, fig. 8); **E**, *Ludodactylus sibbicki* (Frey, et al., 2003, fig 1b); **F**, *Darwinopterus*

modularis (Lü, et al., 2009, fig 2c); **G**, *Cuspicephalus scarfi* (Martill and Etches, 2013, fig 2c);

H, *Pterodactylus antiquus* (Vidovic and Martill, 2014, fig 3c); **I**, *Ctenochasma* sp. (Wellnhofer, 1978, fig 5); **J**, *Gnathosaurus* sp. (Wellnhofer, 1978, fig 5); **K**, *Pterodaustro guinazui* (Chiappe, et al., 2000, fig. 7); **L**, *Sinopterus dongi* (Wang and Zhou, 2003, fig. 1); **M**, *Thalassodromeus sethi* (Kellner and Campos, 2002, fig. 1); **N**, *Tupuxuara leonardii* (Kellner, 2004, fig. 4); **O**, *Zhejiangopterus linhaiensis* (Unwin and Lu, 1997, fig. 1); **P**, *Shenzhoupterus chaoyangensis* (Lu, et al., 2008, fig 1c); **Q**, *Tapejara wellnhoferi* (Kellner, 2004, fig. 3); **R**, *Nyctosaurus* sp. (Bennett, 2003, fig. 6); **S**, *Pteranodon longiceps* (Bennett, 1992, fig. 3); **T**, *Pteranodon sternbergi* (Bennett, 1992, fig. 5a); **U**, *Leptostomia begaaensis*, gen. et sp. nov. (this paper). All skulls are modified from their respective references.

Table captions

Table 1. Measurements of holotype and paratype specimens of *Leptostomia begaaensis* gen. et sp. nov.

Supplementary information figure captions

Fig. A. Strict consensus tree, resulting from a phylogenetic analysis with unordered characters.

Fig. B. Strict consensus tree, resulting from a phylogenetic analysis with characters 1, 2, 7, 8, 9, 13, 27, 46, 78 and 150 ordered.

Fig. C. Strict consensus tree, resulting from a phylogenetic analysis with characters 7-9, 27, 45, 46, 78, 80, 93, 100, 114, 117, 124-126, 128, 136 and 143 ordered.

685

Supplementary information table captions

Table A. Rostra angles of a selection of edentulous and longirostrine pterosaurs, data is used in Fig. 10.

Table B. Examples of pterosaurs that exhibit similar anatomical features to those seen on *Leptostomia*.

Table C. Probe feeding birds, their probing habit and diet.

693

Declaration of interests

☒ 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.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

CRediT Author Statement

Roy Smith: Methodology, Investigation, Writing original draft. **David Martill:** Methodology, Investigation, Writing original draft, Supervision. **Alexander Kao:** Methodology, Software. **Samir Zouhri:** Investigation, Data Curation. **Nicholas Longrich:** Conceptualisation, Methodology, Investigation, Writing original draft.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

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Figure 8

Figure 9

Figure 10

Figure 11

Table 1

Parameter	Holotype	Paratype
Maximum length	48 mm	67 mm
Anterior height	2.2 mm	0.6 mm
Posterior height	3.9 mm	2.5 mm
Occlusal width anterior	5.0 mm	2.7 mm
Occlusal width posterior	7.2 mm	5.8 mm
Lateral angle	<2.5°	<2°
Dorsal angle	~3.0°	~3.2°

Table 1