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An Early Cretaceous pterosaur with an unusual mandibular crest from China and a potential novel feeding strategy

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The Aptian Jiufotang Formation of northeast China is a Konservat Lagerstätte particularly rich in pterosaurs, notably azhdarchoids. Here we describe a new genus and species of toothed pteranodontoid pterosaur, *Ikrandraco avatar* gen. et sp. nov., based on two laterally flattened specimens. *Ikrandraco avatar* is diagnosed by a suite of features, including a very low and elongate skull, strongly inclined quadrate, and a deep, blade-like bony mandibular crest with a hook-like process on its posterior edge, an unusual structure so far unique to this taxon. The particular skull shape hints at a distinct feeding habit for pterosaurs that potentially includes temporary skimming and an extensible skin acting as a throat pouch that was more developed than in any other pterosaur known so far. The presence of two other taxa of purported piscivorous pterosaurs in the Jiufotang Formation suggests distinct resource exploitation in this part of China during the Early Cretaceous.

Pterosaurs represent an important group of Mesozoic reptiles, being the first vertebrates to occupy the aerial niche[1]. Despite being represented in all continents, their fossil record is very uneven[2]. Only a few deposits bear complete and well-preserved specimens, thus contributing to the current knowledge on pterosaur anatomy, diversity and evolution[3,4]. Among those is the Jehol Group of northeastern China, with pterosaurs found in the Jiufotang and Yixian formations playing a crucial role in providing novel information about the evolutionary history of those flying reptiles. In the last decade, more specimens have been recovered from these lacustrine deposits than from any other region in the world, revealing a large diversity of species. Regarding pterodactyloids, the most productive deposit of those two has been the Lower Cretaceous Jiufotang Formation[5], with some specimens showing quite distinct morphologies. So far, only dsungaripteroid pterodactyloids[6] have been recovered, some closely related to the taxa known from the renowned Early Cretaceous (Aptian-Albian) Romualdo and Crato formations of northeastern Brazil[7]. Among those are tapejarines[8,9] and anhanguerians[10,11], thus suggesting a very interesting biogeographical tie between those pterosaur faunas[11,12]. The Jiufotang Formation, however, has a higher diversity of more inclusive clades, as exemplified by the presence of istiodactylids, chaoyangopterines, and one basal dsungaripteroid[3,13–15], representing therefore a unique pterosaur fauna composition.

Here, we describe a new pterosaur species from this unit with very distinct cranial and mandibular morphology, uniting a low and elongate crestless skull with a lower jaw that has a developed dentary crest with a hook-shaped posterior process. Such combination of morphological features has no parallel among the known pterosaur species and suggests a specialized foraging habit of this new flying reptile.

Results

Systematic paleontology. Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Dsungaripteroidea Young, 1964
Pteranodontoidea Marsh, 1876
Ikrandraco gen. nov.

Type species. *Ikrandraco avatar*, type by monotypy.

Etymology. *Ikran*, from the fictional flying creature portrayed in the movie Avatar that shows a well developed dentary crest, and *draco*, from the Latin meaning dragon.

Diagnosis. The same for the type species.

Ikrandraco avatar sp. nov.

Etymology. Avatar, in allusion to the homonymous science fiction movie.

Holotype. A partial skeleton including complete skull and mandible, atlas, axis, three mid-cervical vertebrae, part of the sternal plate, some ribs, partial right and left wings and part of the foot (IVPP V18199), deposited at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences in Beijing, China.

Referred specimen. A complete skull, mandible, atlas, axis, and third cervical vertebra (IVPP V18406), deposited at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences in Beijing, China.

Horizon and locality. Jiufotang Formation, Early Cretaceous (Aptian) 120 Ma[5]. IVPP V18199 was collected in Lamadong, Jianchang, and IVPP V18406 comes from Sihedang, Lingyuan, western Liaoning, China.

Diagnosis. *Ikrandraco avatar* can be distinguished from all other pteranodontoid pterodactyloids by the following autapomorphies: slightly arched dorsal margin of the skull above the nasoantorbital fenestrae; lateral depression on the nasal; median hook-like process on the posterior edge of the dentary crest; two well-developed pneumatic foramina piercing the lateral surface of the axis. It can further be separated from other pteranodontoids by the following combination of characters: very low skull (height over quadrates about 18.7% of skull length); strongly inclined quadrate (150°); lack of a premaxillary crest; presence of a deep, blade-like bony mandibular crest with deepest point at mid-length; and a ventral pneumatic foramen on the proximal portion of the second phalanx and third phalanges of the wing finger.

Description. Both pterosaur specimens are laterally compressed, a common condition among vertebrates from the Jiufotang Formation. The holotype (Figs. 1, 2a,b, 3) shows that the tip of the cranium and the first and second right wing finger phalanges slightly displaced from the rest of the skeleton by a fracture. A piece of fossil wood is associated with the skeleton. Based on the fusion of the extensor tendon process this specimen can be considered an adult individual. In the referred specimen (Figs. 2c,d) some of the cortical bone, particularly of the vertebrae, is missing and the bones are not as well preserved as in the holotype.

The skull is exposed in left lateral view in both specimens. It is very elongate and low, with a long postorbital region compared to other pteranodontoids. The orbit is oval, more rounded dorsally than ventrally (Supplementary Fig S1). The nasoantorbital fenestra occupies about one third of the skull length, with an elongate triangular profile and the anterior margin slightly more pointed in the holotype, possibly due to taphonomic compression. The anterior-most point of the nasoantorbital fenestra lies closer to the dorsal margin of the skull than to its ventral margin, as seen in *Tropeognathus* cf. *T. mesembrinus*[7]. The lower temporal fenestra has a tear-drop shape, with the dorsal part broader than the ventral.

As usual in pterodactyloids, the premaxillae and maxillae are fused. The premaxilla occupies the anterodorsal part of the skull, forming the dorsal margin of the nasoantorbital fenestra and shows no premaxillary sagittal crest. In the holotype, there is a sign of pathology in the left maxilla, where the bone is more rugose (Fig. 3b). The maxillary ventral margin shows some rounded depressions between the alveoli, which might have accommodated the lower teeth during occlusion. Although such features have occasionally been observed in other pterosaurs, in *Ikrandraco avatar* they are more numerous.

The jugal process of the maxilla ends between the postpalatine and the subtemporal fenestrae (Fig. 2). A thin palatal ridge extends between the 5th and 11th tooth sockets with maximum depth between the 9th and 10th (in the holotype; Figs. 2a,b). The nasal is elongate, pierced by a foramen, and has a marked depression. The nasal process is very thin and long, located medially, inclined anteriorly and bears a small foramen on its dorsal portion, differing from the large foramina observed in some anhanguerids[16,17]. A well-defined suture separates the nasal and the nasal process in the holotype (Fig. 3c), suggesting that this process is a distinct ossification and potentially not homologous with the extension of the nasal that forms the maxillae-nasal bar separating the external naris and the antorbital fenestra of non-pterodactyloid pterosaurs. Both frontals and parietals bear no crests. The lacrimal has a small foramen that is positioned more dorsally than in anhanguerids[16–18], and is also potentially not homologous with the foramen described in other pterosaurs. The jugal has a broad and slightly anteriorly inclined lacrimal process and, differing from other pteranodontoids, shows no lateral ridge. The quadrate has a helical jaw joint and a reduced medial flange, smaller than in other Dsungaripteroidea. It is further inclined for about 150°, similar to archaeopterodactyloids but differing from other pteranodontoids[6].

Due to taphonomic crushing, part of the palatal region became visible on both specimens, but elements are better observed in the holotype. As usual in pterodactyloids, the palatines are firmly fused to the premaxillae and maxillae and form the anterior margin of the choanae. The choanae occupy approximately 29% of the skull length (82.3 mm) and are divided by a thin process of the vomers. Their anterior margin is coincident with that of the nasoantorbital fenestra. The interpterygoid fenestra is well-developed, unlike the reduced condition seen in *Pteranodon*[19]. The pterygoid fenestra shows an oval shape. The postpalatinal fenestra (7.5 mm) is smaller than the subtemporal fenestra (17.3 mm). The pterygoid is elongate and forms the posterior and most of the lateral margins of the choanae.

The occipital region is better observed in the holotype (Fig. 3f). The supraoccipital crest is well-developed, much larger than in the Anhangueridae[16–19]. The basioccipital has a small foramen on its lateral flange. The occipital condyle has one developed lateral depression on each side. The basisphenoid has broad and short processes, a well-developed tuber, and separates the large posterior cranial fenestrae. The opisthotic bears a small foramen. The pseudomesethmoid, seen in both specimens, is well-developed and has a thick lateral margin, similar to the condition reported in *Tapejara*[20].

The dentary is the largest element of the lower jaw and shows a large mandibular symphysis (Table 1), with a pointed process on the tip (Supplementary Figs S2,S3). It is probable that the distal end of the mandibular symphysis showed some expansion, but due to flattening this cannot be confirmed in either specimen. On the ventral margin the dentary bears a well-developed, deep, blade-shaped, and elongate bony sagittal crest that begins at the tip and extends to the end of the symphysis. It is larger than in any known pterosaur species (Figs. 2,4). This structure further differs from the crest observed in some tapejarids like *Sinopterus*, where it is less ventrally projected and less laterally compressed[8]. The crest is symmetrical, with the deepest point about half its length (between the 9th and 10th alveoli). The ventral edge is extraordinarily thin and might have been covered by a horny sheet. The crest also has a hook-like process on its posterior margin (Fig. 2). This quite unusual structure, unique to *Ikrandraco avatar*, can be observed in both specimens and is not an artifact.

There are at least 21 pairs of teeth on each side of the upper jaw and 19 in the lower. Alveoli are small and oval, without expressive size

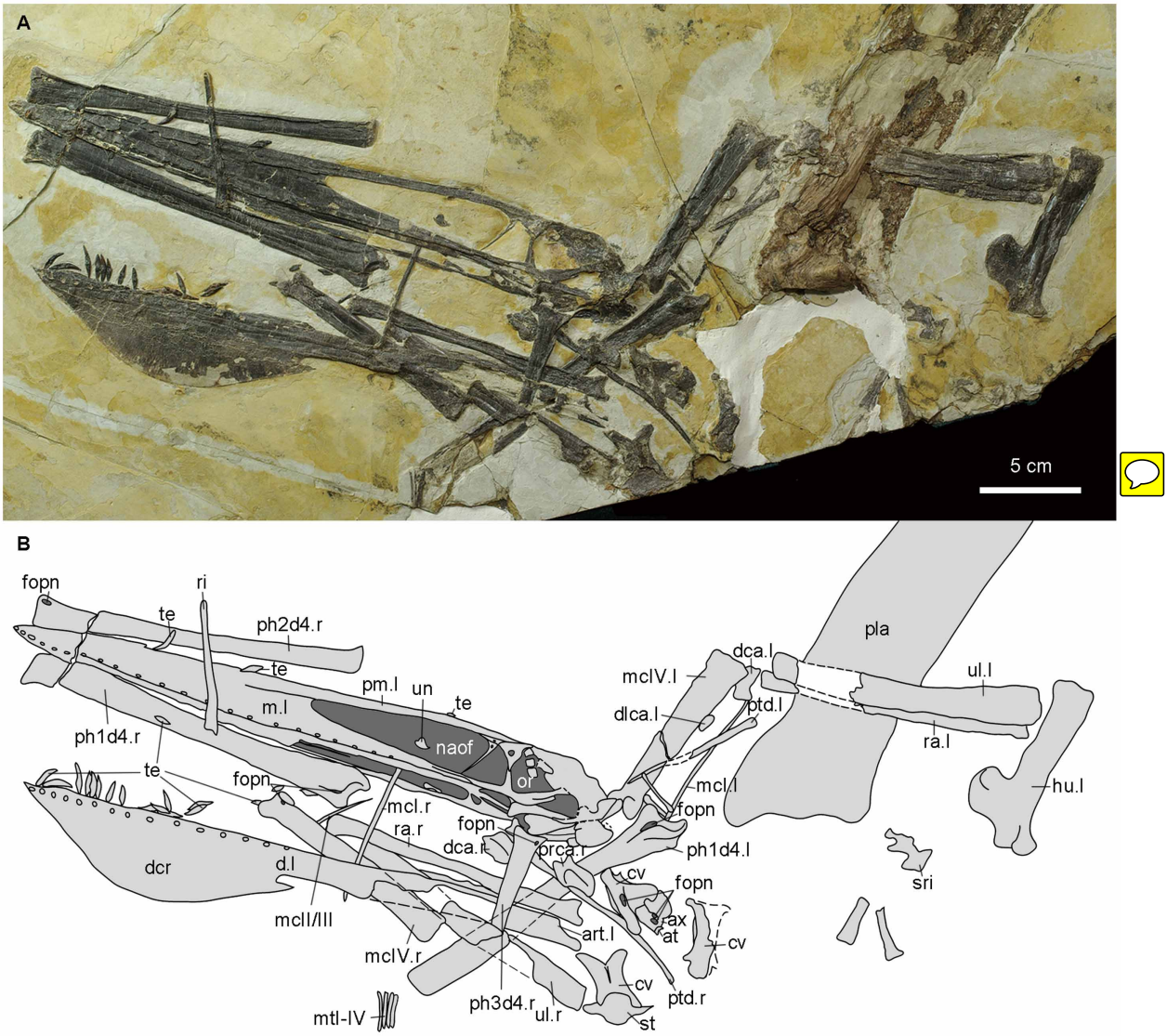


Figure 1 | ***Ikrandraco avatar*, holotype (IVPP V18199), nearly complete skeleton.** (a) Photograph; (b) respective line drawing. Abbreviations: art, articular; at, atlas; ax, axis; cv, cervical vertebra; d, dentary; dca, distal carpal; dcr, dentary crest; dlca, distal lateral carpal; fopn, pneumatic foramen; hu, humerus; naof, nasoantorbital fenestra; m, maxilla; mcI-IV, metacarpal I-IV; mt I-IV, metatarsal I-IV; or, orbit; ph1-3d4, first to third phalanx of manual digit IV; pla, plant; pm, premaxilla; prca, proximal carpal; ptd, pteroid; ra, radius; ri, rib; sri, sacral rib; st, sternum; te, teeth; ul, ulna; un, ungual; l, left; r, right. Scale bar: 5 cm. Line drawing by S.J.

variation, contrary to several other toothed pteranodontoids, including species from the Jiufotang Formation[10,11]. Upper teeth 1–3 and lower 1–2 are closer to each other with the alveolar distance increasing gradually towards the posterior end. The enamel is smooth and dark-brown. The crowns are small, differing in this respect from anhanguerians[21], with the anterior-most ones rounder and gently curved, and posterior ones smaller and more flattened laterally. Teeth are considerably smaller than those of *Guidraco* and *Liaoningopterus*[10,11] and those of any anhanguerid[17]. They are comparable in size with istiodactylids, but those pterosaurs have quite distinctive triangular and laterally compressed teeth[3,13] not present in the new taxon.

Only a small part of the neural spine of the atlas is preserved, closely attached to the axis, suggesting that they were fused. The axis presents a tall and blade-like neural spine and the centrum pierced by two lateral pneumatic foramina (Fig. 3d), thus differing from anhanguerids, which have a spike-like spine and one large lateral pneumatic foramen[16,17]. The third cervical vertebra shows a well-developed lateral pneumatic foramen, a high and spike-like neural spine, large postexapophyses, and no cervical ribs. Two remaining cervical elements, probably cervical vertebrae four and five, show no significant variation in centrum length compared to the third cervical.

The holotype of *Ikrandraco avatar* preserves partial wings. Although not articulated, they are closely associated. The left humerus is exposed ventroposteriorly (Fig. 3e). When compared to the length of the skull, it is smaller than in all other toothed pteranodontoids, but still larger than in the Nyctosauridae (Table 2). It shows a warped deltopectoral crest, with the proximal margin rounded, a typical pteranodontoid feature[6]. Both ulnae and the left radius are incomplete, but the right radius is well preserved and shows a diameter about half that of the ulna. The carpals are fused into proximal and distal syncarpals, the latter with a triangular outline (Supplementary Fig. S4). The pteroid is long and thin ~~and~~, with a preserved portion over half the length of the ulna. Both wing metacarpals are present. The left metacarpal I is an elongate element preserved in articulation with the distal syncarpal. A partially preserved thin bone could be right metacarpal II or III, indicating that

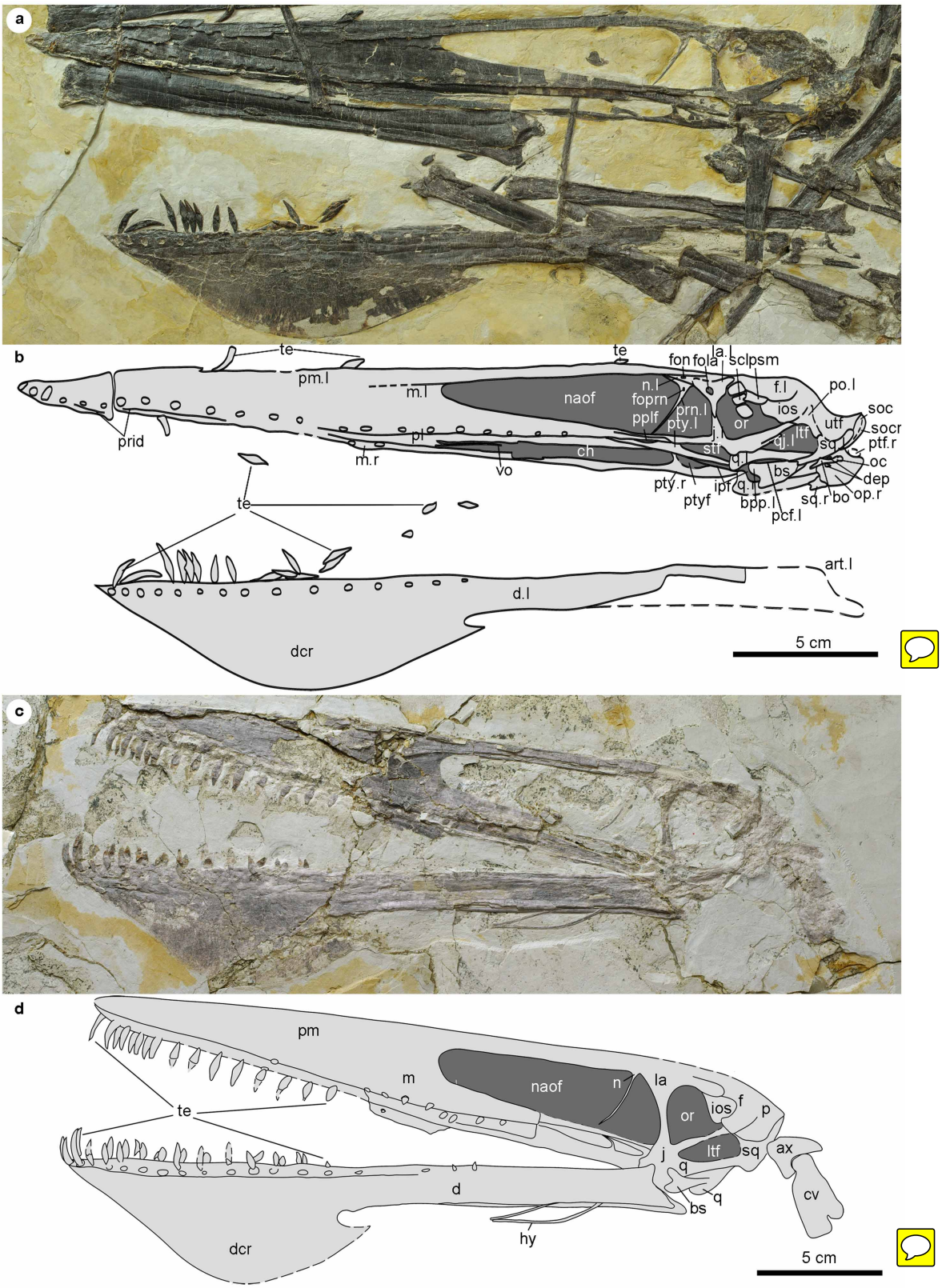


Figure 2 | ***Ikrandraco avatar*, skull and mandible.** (a–b) Photograph and line drawing of the holotype (IVPP V18199), (c–d) Photograph and line drawing of the referred specimen (IVPP V18046). Abbreviations: art, articular; ax, axis; bo, basioccipital; bpp, basisphenoid process; bs, basisphenoid; ch, choanae; cv, cervical vertebra; d, dentary; dcr, dentary crest; dep, depression; f, frontal; fon, foramen nasalis; fola, foramen lacrimale; foprn, foramen of nasal process; hy, hyoid; ios, interorbital septum; ipf, interpterygoid fenestra; j, jugal; la, lacrimal; ltf, lower temporal fenestra; n, nasal; naof, nasoantorbital fenestra; m, maxilla; oc, occipital condyle; op, opisthotic; or, orbit; p, parietal; pcf, posterior cranial fenestra; pl, palatine; pm, premaxilla; po, postorbital; pplf, postpalatinal fenestra; prid, palatal ridge; prn, processus nasalis; psm, pseudomesethmoid; ptf, posttemporal fenestra; pty, pterygoid; ptyf, pterygoid fenestra; q, quadrate; qj, quadratojugal; scl, sclerotic ring; soc, supraoccipital; socr, supraoccipital crest; sq, squamosal; stf, subtemporal fenestra; te, teeth; ul, ulna; utf, upper temporal fenestra; vo, vomer; l, left; r, right. Scale bar: 5 cm. Line d[illegible] by S.J.

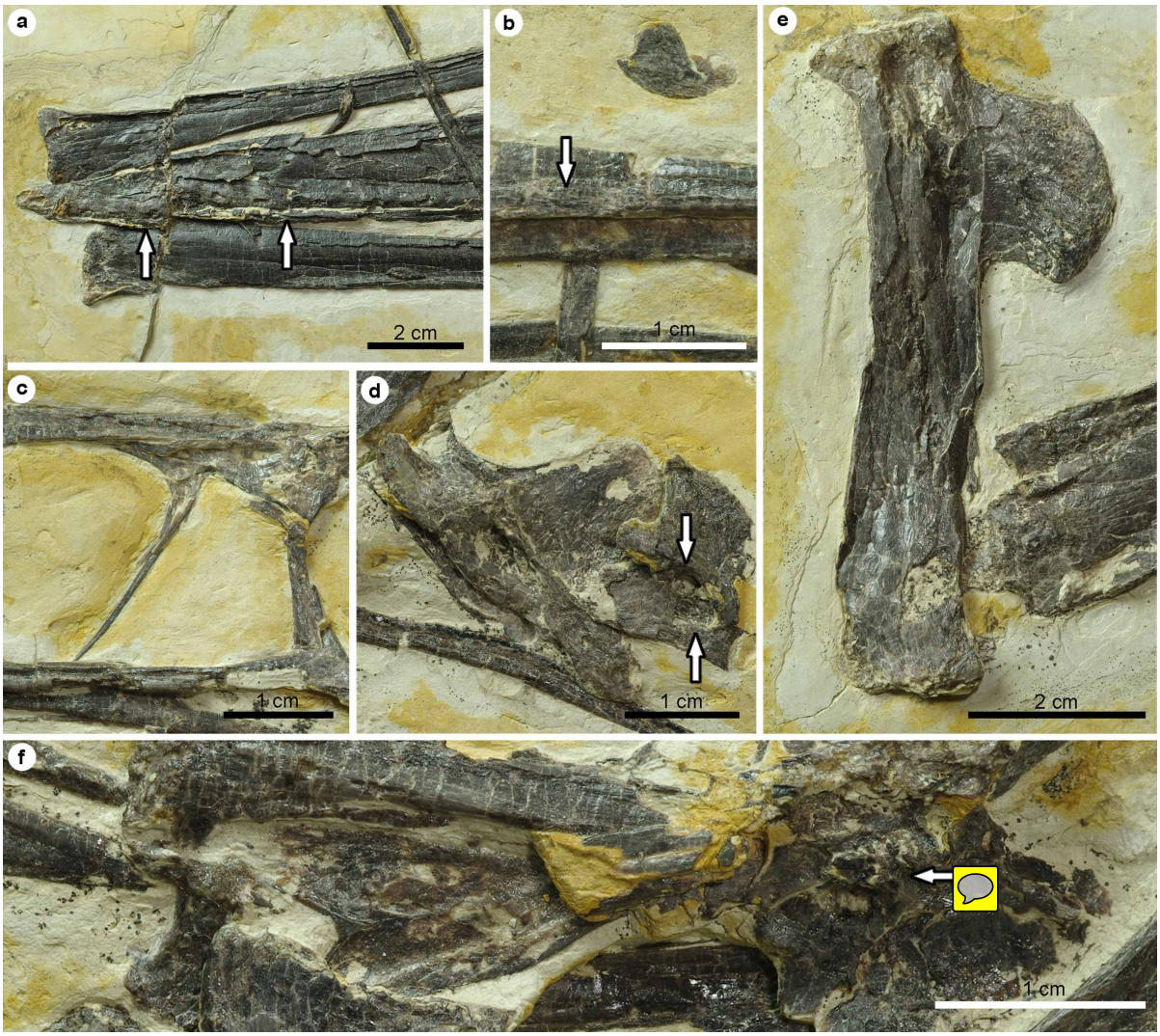


Figure 3 | ***Ikrandraco avatar*, holotype IVPP V18199.** (a) Anterior tip of the skull; arrows point the palatal ridge. (b) Left maxilla; arrows point a small pathology. (c) Nasal process and nasal. (d) Cervical vertebrae; arrows point the two foramina of axis. (e) Humerus. (f) Occipital region; the arrow points the basioccipital. ~~Line drawn by S.J.~~

metacarpals II and III were reduced, a common feature within derived pterodactyloids[6,19]. One manual ungual, preserved displaced inside the nasoantorbital fenestra, is comparatively high and short and is covered distally by a brown matter, likely the remains of a horny sheath. Both extensor tendon processes of the first wing phalanges are fused. A well-developed pneumatic foramen close to the anterior margin in both the second and third wing phalanges is observed as has been reported in *Pteranodon*[19], showing a high degree of pneumatization in the wing skeleton of the new species, possibly by subcutaneous diverticulae of an air sac system[22].

The only preserved elements of the hind limbs are the metatarsals present in the holotype (IVPP V18199). Despite being incomplete, it is clear that the metatarsal IV is stouter than the others, with two very unusual depressions that might be puncture marks.

Phylogenetic position. A phylogenetic analysis was performed (see Methods and Supplementary Information) and recovered *Ikrandraco avatar* among the Pteranodontoidea, outside but closely related to the Anhangueria (Fig. 5). The new species belongs to the Pterodactyloidea based on the presence of a confluent naris and antorbital fenestra (also present in wukongopterids) and several postcranial characters including the lack of ribs on mid-cervical vertebrae[6]. Although the inclination of the quadrate is more similar to the Archaeopterodactyloidea[6], the new species possesses features typical of pteranodontoids such as a warped deltopectoral crest of the humerus and can be confidently assigned to that clade.

Discussion

Both specimens were found in two localities about 25–30 km apart and their exact stratigraphic level is not known. Therefore, there is a potential that the strata from which they belong were of distinct ages, which could suggest that they represent distinct species, what would have to be supported by anatomical differences[23]. The referred specimen (IVPP V18406) is about 6% smaller than the holotype, but both have similar proportions of the nasoantorbital fenestra and of the rostrum relative the skull length. The referred specimen has comparatively deeper dentary crest, but in both specimens, the deepest point of the crest lies between the 9th and 10th lower jaw alveoli. Other distinctions are the height of the skull and the height of the mandibular rami, which are lower in the holotype than in the referred specimen, and here mainly attributed as the result of taphonomic compression.

One of the most outstanding features of *Ikrandraco avatar* is the presence of a blade-like bony median crest at the anterior portion of the lower jaw. Several pterosaur species are known to bear crests, either bony or formed by a combination of bone and soft tissue.

Table 1 | Bone measurements of *Ikrandraco avatar*, in mm

	IVPP V18199 (holotype)	IVPP V18406 (referred specimen)
skull length (pm − sq)	286.5	>268.3
rostrum length (pm − naof)	144.3	>133.6
naof length	95.0	92.6
naof height	20.3	32.1
orbit length	32.5	31.5
orbit height	20.8	21.9
skull height (q − p)	32.8	50.1
upper tooth row length	168.8	168.7
mandible length	264.0	242.1
mandibular symphysis length	130.6	128.9
mandiblular rami height	11.1	14.5
lower tooth row length	>126.3	162.7
crest height	34.5	42.7
humerus length	78.7	-
deltopectoral crest length	16.3	-
radius length	122.5	-
radius mid-width	5.5	-
ulna length	>118.0	-
ulna mid-width	10.5	-
pteroid length (as preserved)	92.1	-
wing metacarpal length	99.5	-
ph1d4 length	162.1	-
ph2d4 length	154.6	-

However, *Ikrandraco avatar* is unique by possessing a crest only on the mandible, and none on the skull. Until now, blade-like crests were known exclusively in the Anhangueria and in *Cimoliopterus cuvieri*[21]. *Ludodactylus sibbicki* was reported to bear a dentary crest[24], however, upon personal examination of the holotype, no crest could be observed. *Cearadactylus atrox* possesses a crest only on the premaxilla[25], and the presence of a head crest, but none in the mandible, is more widely distributed within pterosaurs [e.g.[3,11,26,27],]).

With mounting evidence of the presence of crests in pterosaurs both basal and derived, their function is presently a contentious and hotly debated subject. Proposals range from sexual dimorphism (either presence × absence[28,29] and size differences between genders[23,30]), mutual sexual selection, thermoregulation, species recognition, aerodynamics and biomechanical functions [e.g.[30–34]].

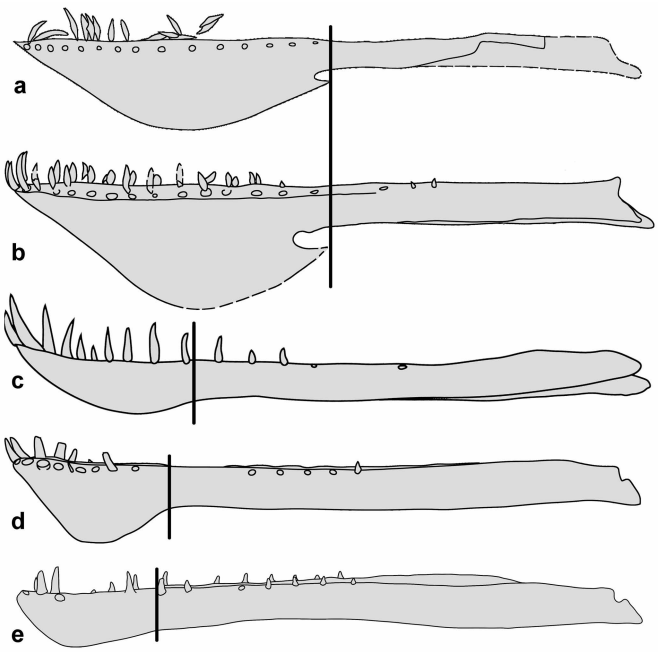


Figure 4 | Comparison between the dentary crest length in relation to the mandibular length in (a) *Ikrandraco avatar*, holotype IVPP V18199; (b) *Ikrandraco avatar*, referred specimen IVPP V18046; (c) *Anhanguera piscator* [after 17]; (d) *Anhanguera robustus* [after 17]; (e) *Anhanguera spielbergi* [after 18]. Not to scale. Line drawn by S.J.

The potential functions of cranial crests that are limited to the rostral ends have been far less discussed than, for instance, the extremely enlarged cranial structures present in the Pteranodontidae and the Tapejaridae[19,30]. Admittedly, to infer functions on structures found in fossils that have not left recent descendants is a difficult task, particularly if modern analogs are also lacking. This is the case of the odd cranial structures of several pterosaurs, including the one observed in *Ikrandraco avatar*. Regardless of the primary force responsible for the evolution of head crests, it is likely that they played multiple roles[30]. Even if biomechanical purposes were not the driving force for the development of these structures, once present it is conceivable that they might have helped the animal in its daily activities.

The dentary crest in *Ikrandraco* is unusually long and deep. Although it cannot be ruled out that it might have been used as a display structure, involved in sexual display[32,33] or in species recognition[34], it seems odd for an animal to evolve such a bony projection in the lower jaw and not on the dorsal surface of the skull, where it would be far more visible. Perhaps if the animal would raise its head, this large dentary crest, covered with skin of bright colors might have had a display function, a difficult scenario to test when it comes to a fully extinct and distinctive group of flying animal such as pterosaurs. Furthermore, the dentary sagittal crest is very elongate, deep and laterally compressed. It also has a very sharp ventral margin, which is not a taphonomic artifact, and differs from the more blunt condition of some other crested pterosaurs, particularly the Anhangueridae (Fig. 4). It further presents a unique hook-shaped process at the posterior margin, a novel and unusual structure, to our knowledge never documented in any vertebrate before. The medial position of this structure is consistent with the notion that it could have served as an anchor for soft tissues. Being under the chin and just in front the hyoid bones, it could be possibly related to some sort of throat sac.

The presence of throat sacs in pterosaurs has been proposed several times before, based primarily on soft tissue impressions in specimens of *Rhamphorhynchus* and *Pterodactylus*[35,36]. In all described

Table 2 | Proportion between the humerus length to skull length in several pterosaur taxa

Species	Humerus/skull length (pm − sq)	Reference
Nyctosaurus KJ2	0.25	[43]
Ikrandraco avatar	0.27	present work
Darwinopterus robustodens	0.29	[44]
Pterodactylus antiquus (holotype)	0.29	[45]
Darwinopterus modularis (holotype)	0.32	[46]
Darwinopterus linglongtaensis (holotype)	0.34	[47]
Nurhachius ignaciobritoi	0.38	[3]
Zhenyuanopterus longirostris	0.39	[48]
Nemicolopterus crypticus	0.40	[15]
Anhanguera spielbergi	0.41	[18]
Anhanguera piscator	0.41	[17]
Germanodactylus cristatus	0.43	[45]

cases, the pouch starts at the posterior ventral part of the mandible and extends until the level of the third or fourth cervical vertebrae, but its exact properties and morphology is disputed. While some researchers have suggested a structure similar to that seen in pelicans[37], others have used the more neutral term "loose extensible skin", arguing that this gular structure might have helped them to swallow large prey items, as seen in the ostriches[38]. None of the pterosaurs where they are thought to be present show the hook-shaped dentary process present in *Ikrandraco avatar*. It is possible that a gular structure potentially made of extensible skin was more developed in the new species.

These anatomical features, allied with a low and elongate fusiform and streamline skull, suggests that *Ikrandraco avatar* could have foraged by flying low over the water and, upon visually locating a

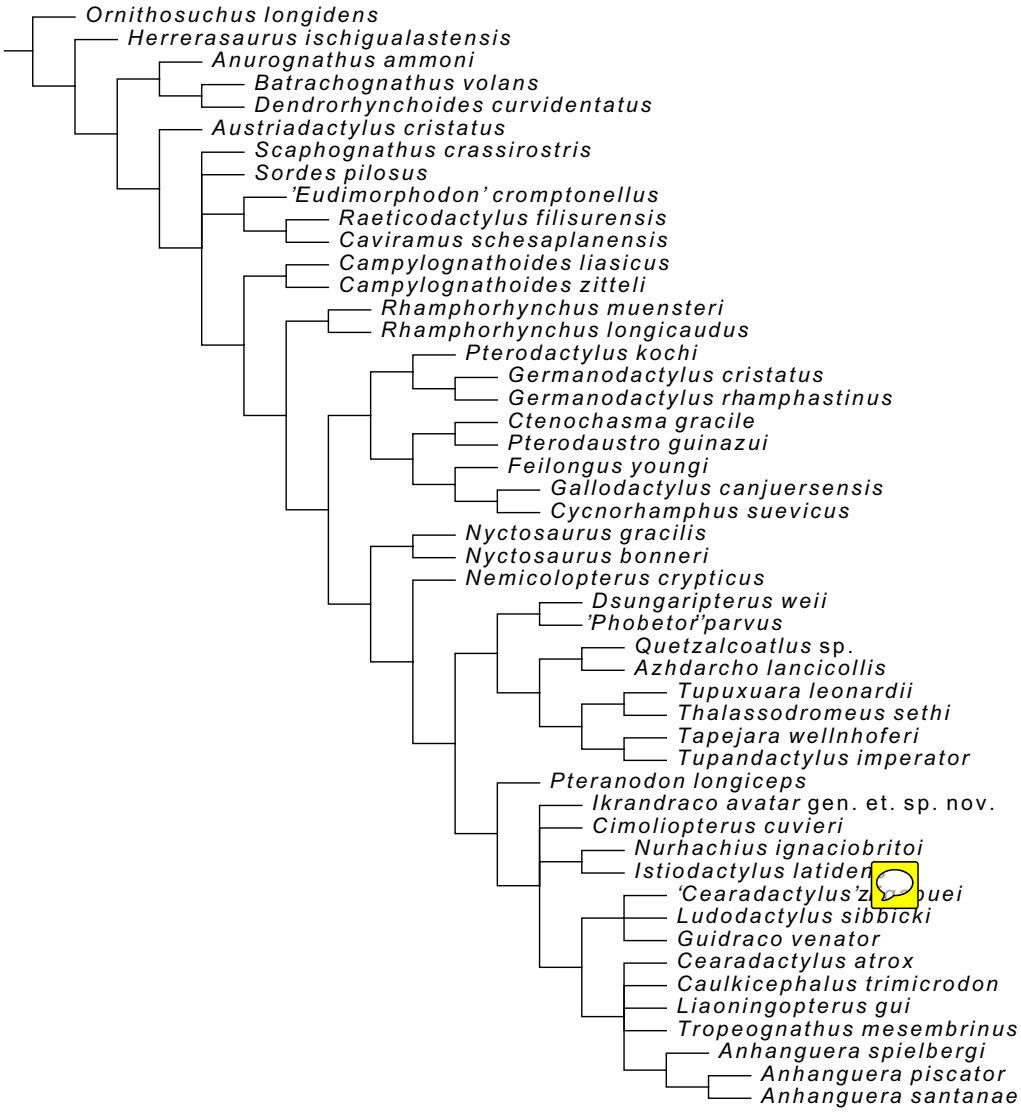


Figure 5 | The strict consensus tree of the 18 equally parsimonious trees with 211 steps each.

prey item near the surface, could have lowered the jaw partially immersing it. The deep and laterally compressed dentary crest with a sharp ventral margin would break the water resistance, allowing a temporary skimming activity. When the prey item was closer, the animal could open the jaws and capture the submersed prey, emerging the jaws from the water surface. It is conceivable that this crest might also have been covered by a smooth horny sheath, a structure already reported in other pterosaurs [e.g.[24]], which could potentially reduce drag. The presence of an analog to the avian throat pouch, anchored in the hook-shaped medial process of the dentary crest, could have acted as a storing device for the prey items, allowing the animal to perform subsequent captures before swallowing, and/or help to expel the water that might have gotten with the recently captured prey. It should be noted that the skimming-like behavior suggested here would not have been used extensively during foraging because *Ikrandraco avatar* lacks the extensive adaptations reported for recent skimmers[39] and also for the tapejarid *Thalassodromeus sethi*, that is also regarded to have been able to skim [[30], but see[40]]. *Ikrandraco* lived near large freshwater bodies represented by the Jiufotang Formation, where several small fishes have been found[41] and could potentially have been the prey item of this pterosaur.

Lastly, it is interesting to point out that *Ikrandraco avatar* comes from the same deposit as the anhanguerid *Liaoningopterus gui* and *Guidraco venator*, the latter from the same locality as the referred specimen IVPP V18406. Both are regarded as piscivorous but differ from the new species by the possession of much larger and more robust teeth[10,11]. Therefore, the distinct morphologies and potential different foraging habits of these species suggest different prey preferences and therefore distinct resource exploitation.

Ikrandraco avatar is a new genus and species of a pteranodontoid pterosaur from the Jiufotang Formation of China, and is one of the few pterosaur species known by more than one specimen. It is closely related to the Anhangueria, a clade formed by purported piscivorous pterosaurs. The new species is diagnosed by a suite of features, but most notably by a blade-like, deep, and elongate dentary crest, which possesses an unusual hook-shaped process at the posterior margin, and a low and elongate skull that lacks a premaxillary crest. We propose that this pterosaur fed on fishes from nearby freshwater lakes by flying low over the water, capturing its prey by lowering the mandible in the water, being capable of a reduced and temporary skimming. We also propose that it had a more developed throat pouch then in other pterosaur species. *Ikrandraco avatar* foraging habit increases the potential feeding modes of pterosaurs.

Methods

Specimens IVPP V18199 and IVPP V18406 are deposited at the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing, China, where they were first-hand analyzed. In order to assess the phylogenetic position of *Ikrandraco avatar*, an analysis was performed based on a modified version of a previously published matrix[21]. Analysis was performed on T.N.T. (Tree Analysis Using New Technology), version 1.1 for Windows with a menu interface – standard version[42]. All characters were unordered and given the same weight. *Ornithosuchus longidens* was considered the primary outgroup. Analysis was performed using the traditional search, with the TBR algorithm (although the software uses both TBR and SPR), with 5,000 random addition sequence replicates. Branches were collapsed when their minimum length was equal to zero. As some replications overflowed after a first round, traditional search was again employed, this time on trees from RAM. The analysis resulted in 18 equally parsimonious trees with 211 steps each. From these, a strict consensus tree was obtained and is here figured.

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Author contributions

X.W., T.R. and A.K. wrote the main manuscript; X.W. and S.J. found the specimens, S.J. prepared the figures; X.W., T.R., S.J., X.C. and A.K. contributed to the manuscript and research. All authors reviewed the manuscript.

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