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A new toothed pteranodontoid (Pterosauria, Pterodactyloidea) from the Jiufotang Formation (Lower Cretaceous, Aptian) of China and comments on Liaoningopterus gui Wang and Zhou, 2003

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A new toothed pteranodontoid (Pterosauria, Pterodactyloidea) from the Jiufotang Formation (Lower Cretaceous, Aptian) of China and comments on *Liaoningopterus gui* Wang and Zhou, 2003

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Pteranodontoids consist of a diverse and cosmopolitan clade of Cretaceous pterodactyloid pterosaurs. In the Jiufotang Formation (Lower Cretaceous, Aptian) of northeastern China, pterodactyloids are represented by azhdarchoids and pteranodontoids, including istiodactylids and anhanguerians. Here, we describe a new pterosaur from this unit that represents a new species of toothed pteranodontoid. Its overall morphology is consistent with other toothed pteranodontoids but shows some interesting features such as the orbit being more ventrally positioned than in all other species from this clade. It differs markedly from all other pterosaurs from this unit, including *Liaoningopterus*, *Guidraco* and *Ikrandraco*, with which the new taxon is possibly related. In addition to the description of the new taxon, we also describe the anhanguerid *Liaoningopterus gui* in more detail. The new species, *Liaoningopterus gui*, *Guidraco venator* and *Ikrandraco avatar*, are large pterosaurs with very distinct tooth morphologies, suggesting that they had different prey preferences, partially explaining how the Jiufotang Formation could bear such a high diversity of pterosaur species.

Keywords: Lower Cretaceous; Jiufotang Formation; China; Pterosauria; *Linlongopterus*; *Liaoningopterus*

1. Introduction

Pteranodontoids are derived pterosaurs that lived during the Cretaceous period, being found on all continents (Kellner 2003). The clade was defined as 'the most recent common ancestor of *Anhanguera* and *Pteranodon* and all their descendants' (Kellner 2003) and has been recovered by posterior, independent phylogenetic studies (e.g. Andres and Ji 2008; Andres and Myers 2013; Andres et al. 2014). Pteranodontoids are diagnosed by some postcranial features (both axial and appendicular), such as tall and spike-shaped neural spines of the midcervical vertebrae; scapula shorter than the coracoid and with a suboval proximal surface; and humerus with a warped deltopectoral crest, posteriorly directed medial crest and subtriangular distal end (Kellner 2003).

Among pteranodontoids, the recently erected clade Anhangueria has been defined as 'all pteranodontoids more closely related to *Anhanguera blittersdorffi* than to *Istiodactylus latidens* and *Cimoliopterus cuvieri*' (Rodrigues and Kellner 2013). These pterosaurs are cosmopolitan, being known from Cretaceous strata of all continents (except Antarctica), and are outstandingly rich in the Romualdo Formation of Brazil (Kellner et al. 2013) and the Cambridge Greensand of England (Rodrigues and Kellner 2013).

The Jiufotang Formation (Aptian; He et al. 2004) of northeastern China presents a rich and diverse pterosaur assemblage, which to current knowledge is represented only by dsungaripteroids. From these, there is one basal species (Wang, Kellner, et al. 2008), exceptionally well-represented azhdarchoids – chaoyangopterids and tapejarines (Dong et al. 2003; Wang and Zhou 2002, 2003; Kellner and Campos 2007; Lü, Unwin, et al. 2008) and, among pteranodontoids, some species of istiodactylids (Wang, Campos, et al. 2008; Lü, Xu, et al. 2008), the recently described *Ikrandraco avatar* (Wang et al. 2014), and two anhanguerians: *Liaoningopterus gui* and *Guidraco venator* (Wang and Zhou 2003; Wang et al. 2012).

In this paper, we describe a new toothed pteranodontoid pterosaur from the Jiufotang Formation, possibly related to anhanguerians, and provide new osteological information of *Liaoningopterus gui*.

1.1 Institutional abbreviations

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; SNSB-BSPG, Staatliche Naturwissenschaftliche Sammlungen Bayerns/Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.

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2. Material and methods

Specimens IVPP V15549 and IVPP V13291 are deposited at the IVPP in Beijing, China, where they were first-hand analysed. In order to assess the phylogenetic position of the species herein described, an analysis was performed based on a modified version of a previously published matrix (Wang et al. 2014), which was selected among other pterosaur phylogenies for the focus on toothed pteranodontoids instead of the interrelationships of more inclusive groups. Analysis was performed on Tree Analysis Using New Technology (TNT), version 1.1 for Windows with a menu interface (Goloboff et al. 2008). 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 tree bisection-reconnection (TBR) algorithm (although the software uses both TBR and subtree pruning-regrafting [SPR]), with 5000 random addition sequence replicates. Branches were collapsed when their minimum length was equal to zero.

3. Systematic palaeontology

Pterosauria Kaup, 1834

Pterodactyloidea Plieninger, 1901

Pteranodontoidea Marsh, 1876, *sensu* Kellner, 2003

3.1 ***Linlongopterus jennyae*** **gen. et sp. nov.**

3.1.1 Linlongopterus gen. nov.

Type species. *Linlongopterus jennyae*, type by monotypy.
Etymology. From the Chinese words lin, meaning forest, and long, dragon; and pteros, from the Greek meaning wing.
Diagnosis. The same as for the type species.

3.1.2 Linlongopterus jennyae sp. nov.

Etymology. Species name in honour of the late Elfriede Kellner, also known as Jenny, a great supporter of palaeontological studies.
Holotype. IVPP V15549, partial associated skull and mandible, deposited at the IVPP in Beijing, China.
Locality and horizon. Jianchang, Jianchang County, western Liaoning Province, China. Jiufotang Formation, Aptian (120 Ma) (He et al. 2004).
Diagnosis. Pteranodontoid pterosaur with the orbit ventrally positioned, with the ventral margin almost level with the nasoantorbital fenestra. The following combination of characters also distinguishes it from other members of this clade: lacrimal process of the jugal thin; lacrimal process of the jugal oriented vertically; lower temporal fenestra with a broad ventral margin; slight lateral bend on the anterior end of the rostral process of the pterygoid.

Description and comparison

Generalities: Specimen IVPP V15549 (Figures 1 and 2) is preserved on a slab that was broken into two pieces. These slabs were brought to the preparation laboratory of the IVPP in Beijing and were glued together and then prepared. On the smaller slab there are the tips of the rostrum and mandible, and the larger slab includes most of the preserved skull and the mandibular rami. Because some little fragments are missing in the processing of the collection, it makes the two pieces seem not contiguous. Actually, the boundaries of them match very well, and there is no missing part between the two pieces, and they belong to the same individual. The external surface of the cortical bone in some portions of the skull is also missing.

Ontogeny: Although representing a large individual, the holotype of *Linlongopterus jennyae* shows several bones displaced from their original anatomical position, clearly showing that they were not fused, such as the jugal, quadrate and pterygoid. The holotype of *Anhanguera santanae* (Wellnhofer 1985) shows the same displacement of cranial and lower jaw elements, and also includes unfused carpals, indicating osteological immaturity. Furthermore, the bone surface in this new pterosaur is rough and consistent with Bennett's (1993) immature grains, suggesting that it is a sub adult.

Skull: As mentioned above, the skull is partially preserved and exposed mostly in right lateral view. Due to compression, part of the palate is displaced ventrally to the skull. Some bones are dislocated from their original anatomical position, such as the left jugal, quadratojugal and quadrate and the right pterygoid. Similar to other toothed pteranodontoids, the nasoantorbital fenestra is large and elongate, with ventral and dorsal margins that gradually diverge posteriorly.

Premaxilla: The right premaxilla comprises the tip of the rostrum and extends posteriorly, forming the dorsal part of the skull, including the dorsal margin of the nasoantorbital fenestra (Figure 1). The preserved portions do not possess a median crest, and if one was present, it would be uncommonly short and restricted to the middle part of the rostrum. Based on the premaxillary crest morphology and modest length of the rostrum of known anhanguerians (about 50% of the skull length; e.g. Kellner and Tomida 2000; Wang and Zhou 2003), we find this unlikely.

Five alveoli are preserved on the anterior part of the right side of the rostrum, the first and the last showing the tooth preserved *in situ*, although broken (Figure 3). It cannot be confidently determined if alveoli are present on the very tip of the skull, as seen in anhanguerids and related taxa (e.g. Rodrigues and Kellner 2013). On the dorsal margin of the premaxillary tip, the cortex of the right side is broken and some of the teeth from the left side can be observed.

Maxilla: The maxilla occupies great part of the lateral surface of the skull and forms the ventral margin of the nasoantorbital fenestra. From the breakage until the level of the anterior margin of the nasoantorbital fenestra, two teeth can be seen, still in their sockets (Figure 1), but due to

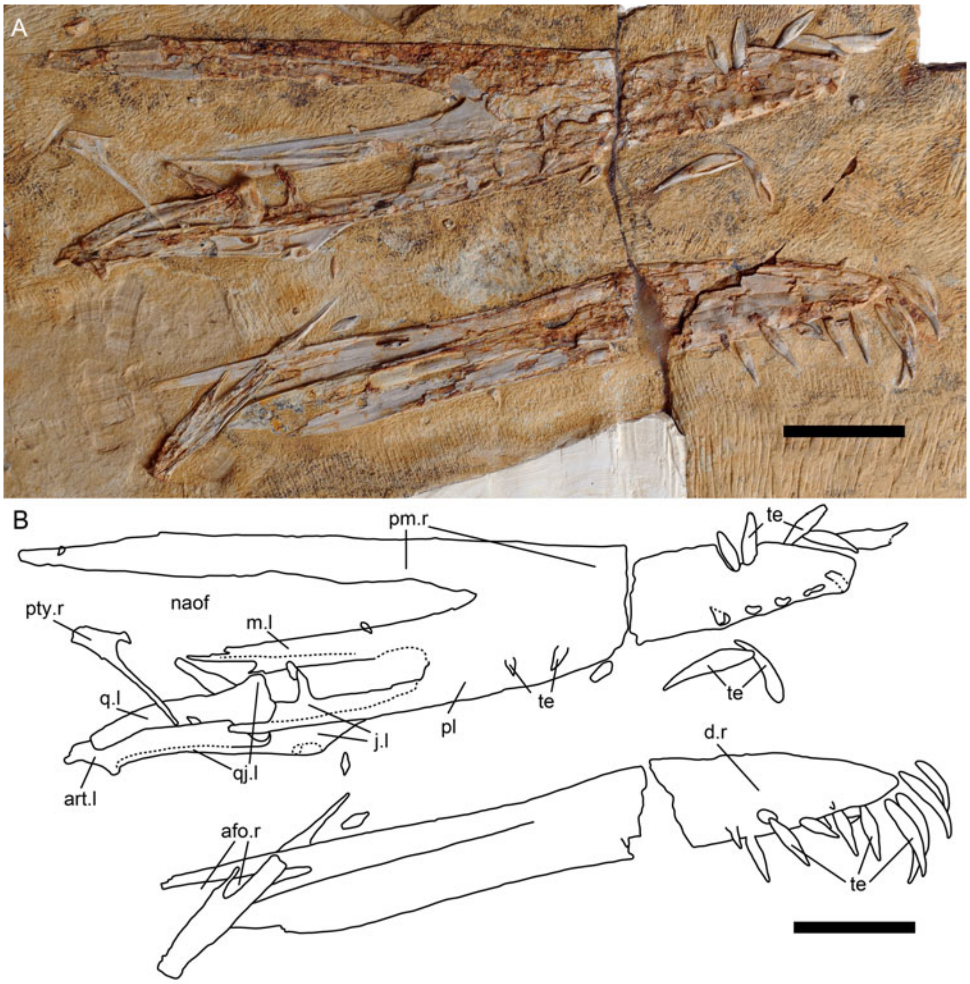

Figure 1. (Colour online) General view of specimen IVPP V15549, holotype of *Linlongopterus jennyae* **gen.** et **sp. nov.** (A) Photograph; (B) respective line drawing. afo, adductor fossa; art, articular; d, dentary; j, jugal; l, left; m, maxilla; naof, nasoantorbital fenestra; pl, palatine; pm, premaxilla; pty, pterygoid; q, quadrate; qj, quadratojugal; r, right; te, teeth. Scale bar: 50 mm.

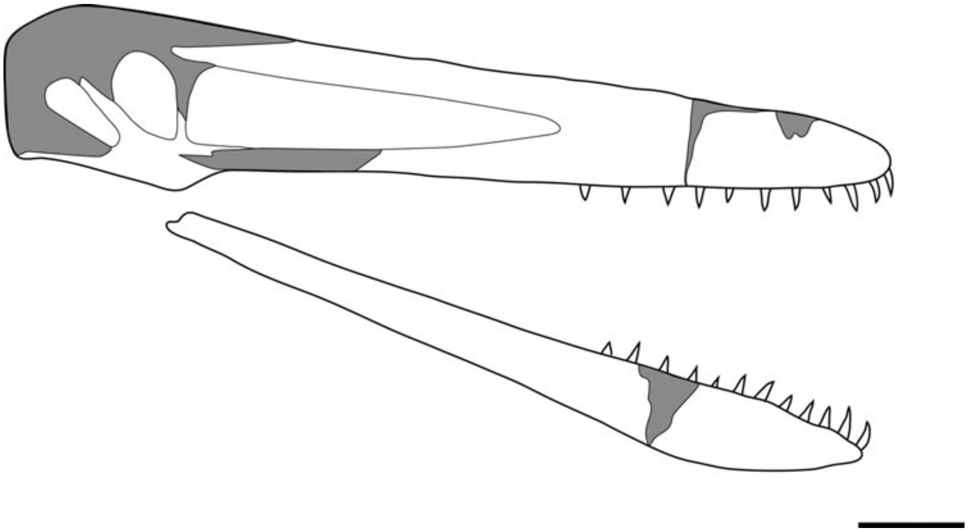

Figure 2. Line drawing reconstruction of the skull and mandible of *Linlongopterus jennyae* based on holotype IVPP V15549. Preserved bones in white. Scale bar: 50 mm.

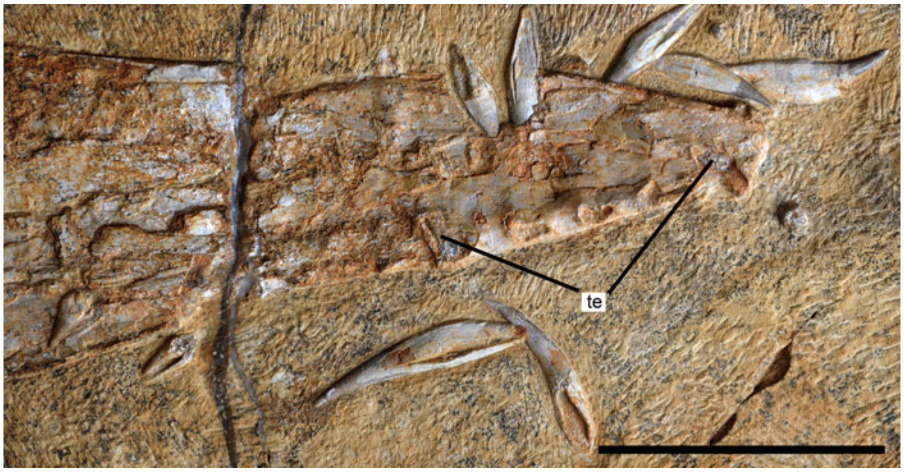

Figure 3. (Colour online) Tip of the skull of specimen IVPP V15549, holotype of *Linlongopterus jennyae* **gen.** et **sp. nov.**, in right lateral view. Teeth and alveoli in the lower half are from the right side; teeth in the upper half are from the left side. te, teeth. Scale bar: 50 mm.

poor preservation of the rest of the alveolar margin, it is not possible to determine the total number of alveoli in this bone, nor determine its distribution. Immediately anteriorly and ventrally to the nasoantorbital fenestra, the bone is lower than in the adjacent portion and it is likely that the right bone was lost and that the medial part of the left maxilla is observable. Ventrally to the nasoantorbital fenestra, the ventral-most margin of the maxilla was lost.

Jugal: The left jugal is seen in medial view and is closely associated but disarticulated with the quadrate. It lies still in articulation with most of the quadratojugal (Figure 4). The articular surface for the condyloid process is comparatively large and has an oval shape, similar to *Pteranodon* (Bennett 2001).

Only the base of the maxillary process of the jugal is preserved, but it can be observed that it forms a straight angle with the lacrimal process, which is similar to *Liaoningopterus gui* and other anhanguerids. However, the lacrimal process is vertically oriented and thin, thus differing from the broad condition seen in *Liaoningopterus gui* and *Guidraco venator* (Wang and Zhou 2003; Wang et al. 2012).

The base of the postorbital process of the jugal is inclined posteriorly and overlain by the quadrate. Based on this configuration, it is clear that the orbit is more ventrally positioned than in other pteranodontoids, with the ventral margin almost level with the ventral margin of the nasoantorbital fenestra.

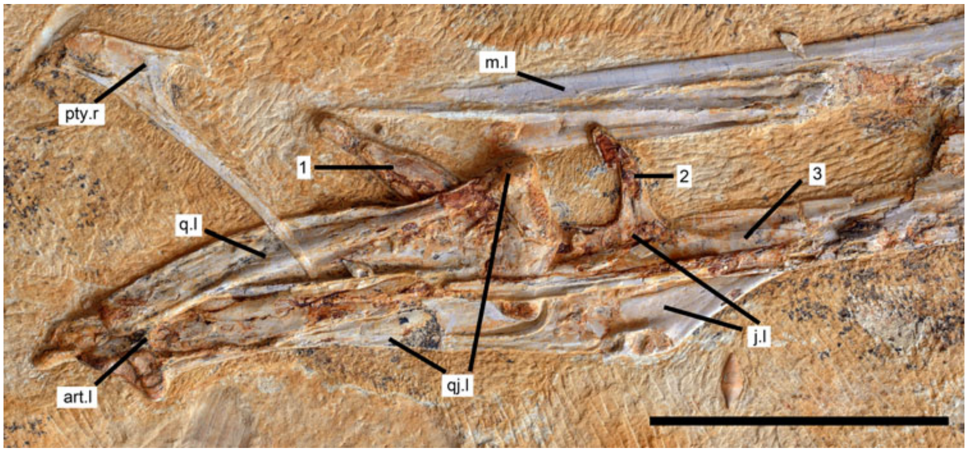

Figure 4. (Colour online) Posterior part of the skull of specimen IVPP V15549, holotype of *Linlongopterus jennyae* **gen.** et **sp. nov.**, showing some dislocated bones. art, articular; j, jugal; l, left; m, maxilla; pty, pterygoid; q, quadrate; qj, quadratojugal; r, right. 1, postorbital process of the jugal; 2, lacrimal process of the jugal; 3, maxillary process of the jugal. Scale bar: 50 mm.

Quadratojugal: Due to the dislocation of the quadrate, the left quadratojugal is clearly visible in medial view (Figure 4). Its articular head is detached from the rest of the bone and is still attached to the quadrate, participating in the condyloid process of the jaw articulation. The main part of the bone lays in anatomical position, just posterior to the jugal, and consists of an elongated bar. The anterodorsal margin of the quadratojugal and the postorbital process of the jugal are divergent, and form a wide angle, thus resulting in a comparatively large lower temporal fenestra with a broad ventral margin, differing in this respect from anhanguerids, *Guidraco venator* and *Ikrandraco avatar* (Campos and Kellner 1985; Wellnhofer 1985, 1991; Kellner and Tomida 2000; Veldmeijer 2003; Wang and Zhou 2003; Wang et al. 2012, 2014).

Quadrate: The left quadrate is seen in anterior view (Figure 4). The medial (pterygoid) process of the articular head is tongue shaped, long but not as seen in the istiodactylid *Hongshanopterus lacustris* (Wang, Campos, et al. 2008) or *Anhanguera santanae* (Wellnhofer 1985). On the opposite side, the quadratojugal is still connected with the quadrate, with both forming the condyloid process. There is a helical jaw joint, a common feature among dsungaripteroids (Kellner 2003). The quadrate shaft is rod-like and curved medially. The quadrate flange (termed medial lamella by Wellnhofer [1985]) shows a rugose surface with several small openings and depressions, but no pneumatic foramen could be visually assessed.

Palatine: The compression of the skull resulted in some distortion, and part of the palatal region, most probably the palatine (*sensu* Wellnhofer 1978; Bennett 2001; Kellner 2013; but see Ősi et al. 2010; Pinheiro et al. 2012 for different interpretation) is exposed ventrally to the maxillary teeth row (Figure 1), as well as sending a process posteriorly, partially overlying the jugal and quadrate. The bone is crushed and no detailed anatomical features can be observed. The main exposed part is located anteriorly to the nasoantorbital fenestra and the palatal fenestrae cannot be observed.

Pterygoid: One pterygoid, probably the right, can be observed isolated from other palatal elements (Figure 4). The marginal borders are elevated in relation to the centre of the bone, suggesting that it is exposed in dorsal view. A small process is located anteriorly in the medial margin and, when in articulation, contacted the vomer. The rostral process is an elongate lateral ramus that extends anteriorly, forming a concavity that comprises the posterior margin of the right choana. This process is slightly curved anteriorly and a little divergent in relation to the rostromedial process. There is no lateral process into the subtemporal fenestra, as present in *Anhanguera araripensis* (Wellnhofer 1985; Kellner and Tomida 2000). If a pterygoid fenestra is present, it is not visible in dorsal view.

Mandible: The mandible is seen mostly in left lateral view and lacks part of the middle portion (Figure 1). The anterior part of the symphysis and both mandibular rami can be observed. The left ramus is seen in left lateral view and some patches of bone along its length were lost, allowing the visualisation of the right ramus in medial view underneath it. The posterior part of the left ramus is preserved near some of the skull elements (jugal, quadrate) and seen in lateral view. The posterior part of the right ramus is displaced and shows a low and elongated adductor fossa, which is located farther from the articular than in anhanguerids and *Pteranodon* (Wellnhofer 1985, 1987, 1991; Bennett 2001; Veldmeijer 2003).

Dentary: The dentaries constitute most of the lateral surface of the mandible. The mandibular symphysis has a straight dorsal margin and bears no crest, at least not on the tip (Figure 5), as seen in crested pteranodontoids (e.g. Wellnhofer 1987; Kellner and Tomida 2000; Veldmeijer

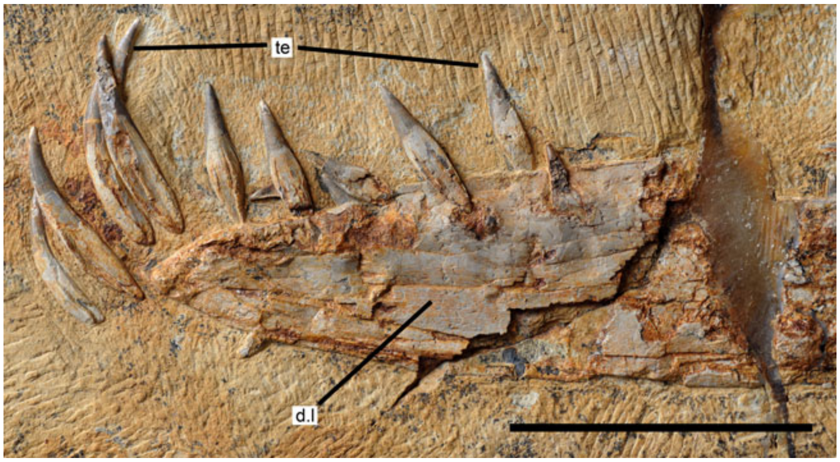

Figure 5. (Colour online) Tip of the mandible of specimen IVPP V15549, holotype of *Linlongopterus jennyae* **gen.** et **sp. nov.**, in left lateral view, showing both right and left side teeth. d, dentary; l, left; te, teeth. Scale bar: 50 mm.

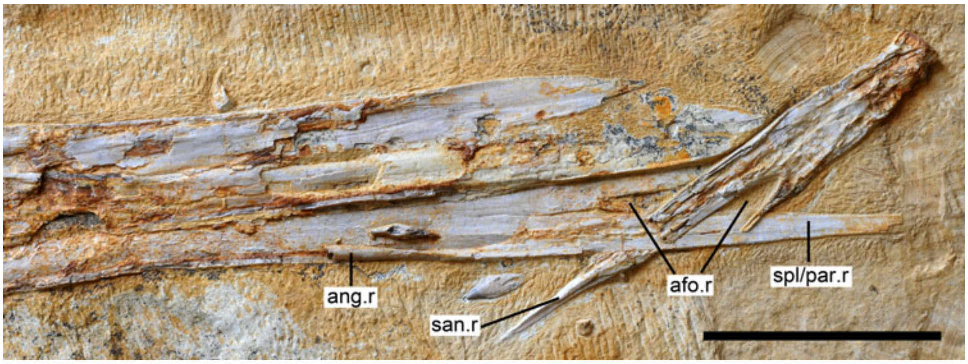

Figure 6. (Colour online) Posterior part of the mandible of specimen IVPP V15549, holotype of *Linlongopterus jennyae* **gen.** et **sp. nov.**, in left lateral view. afo, adductor fossa; ang, angular; par, prearticular; r, right; san, surangular; spl, splenial. Scale bar: 50 mm.

2003; Wang and Zhou 2003; Kellner et al. 2013; Wang et al. 2014). A portion of the dorsal part of the symphysis is visible but no sulcus can be identified because of the poor preservation.

Some teeth are preserved next to the mandibular symphysis, suggesting the presence of seven pairs in the preserved distal portion. Because of the absence of the cortical bone on the alveolar margin, only four alveoli can be seen on the left side, two of them with replacement teeth. There is one tooth preserved between the mandibular rami, but it is unclear if it was positioned inside its alveolus.

Surangular, angular and articular: Both surangulars are present, located anteriorly to the articular and comprising the dorsal margin of the adductor fossae, with a thin and elongate anterior process (Figure 6). The right angular is a thin and elongate bone and comprises the ventral margin of the mandibular ramus in medial view (Figure 6). Its sutures with the surrounding bones are unclear. Only the left articular is preserved and the articular surface has two paired depressions (Figure 4). The retroarticular process is elongate but it cannot be determined if it has a foramen, as seen in anhanguerids and in *Pteranodon* (Wellnhofer 1985, 1987, 1991; Bennett 2001; Veldmeijer 2003).

Splenial and prearticular: The right splenial and prearticular are present and comprise the ventral margin of the adductor fossae (Figure 6). Sutures between these bones cannot be discerned.

Dentition: The holotype of *Linlongopterus jennyae* has several preserved teeth, most of them isolated but close to their sockets. The first two pairs of lower teeth have gently curved crowns and roots, but posteriorly the crowns are slightly smaller and straighter (Figure 5). Crowns are either smaller or about the same size as the roots; some of the latter are a bit expanded. The enamel is dark-brown and presents faint longitudinal ridges. There is limited information on alveolar pattern, but the ones preserved (on the tips of the rostrum and mandible) are about the same size and equally spaced.

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Pteranodontoidea Marsh, 1876, *sensu* Kellner, 2003
Anhangueria Rodrigues and Kellner, 2013
Anhangueridae Campos and Kellner, 1985

3.2 Liaoningopterus gui Wang and Zhou, 2003

Holotype. IVPP V13291, partial skull and mandible preserved mostly in left lateral view, atlas and axis, and one midcervical vertebra, deposited at the IVPP in Beijing, China. The holotype is also the only known specimen.

Horizon and locality. Xiaoyugou, Lianhe, Chaoyang, western Liaoning Province, China (Wang and Zhou 2003). Jiufotang Formation, Aptian (He et al. 2004).

Revised comparative diagnosis. Anhanguerid pterosaur diagnosed by the following combination of characters: low and symmetric premaxillary crest, thus differing from *Anhanguera blittersdorffi*, *Anhanguera araripensis* and *Anhanguera spielbergi*; premaxillary crest begins near but not at the tip of the skull, thus differing from *Tropeognathus mesembrinus*; premaxillary crest ends far from the anterior margin of the nasoantorbital fenestra, differing from *Anhanguera blittersdorffi*, *Anhanguera araripensis*, *Anhanguera piscator* and *Anhanguera spielbergi*; dorsal margin of the rostrum posterior to the premaxillary crest and anterior to the nasoantorbital fenestra straight, differing from *Anhanguera blittersdorffi*, *Anhanguera araripensis*, *Anhanguera piscator*, *Anhanguera santanae* and *Anhanguera spielbergi*.

Expanded description and comparison

Generalities: The specimen is flattened and incomplete. From the skull, there is the rostrum seen in left lateral view, preserved until the first third or half of the nasoantorbital fenestra, and both left and right jugals, quadratojugals and quadrates are exposed in their lateral views. The mandible is partially preserved, showing a breakage that separates most of the symphysis from the mandibular rami. The first three cervical vertebrae are also

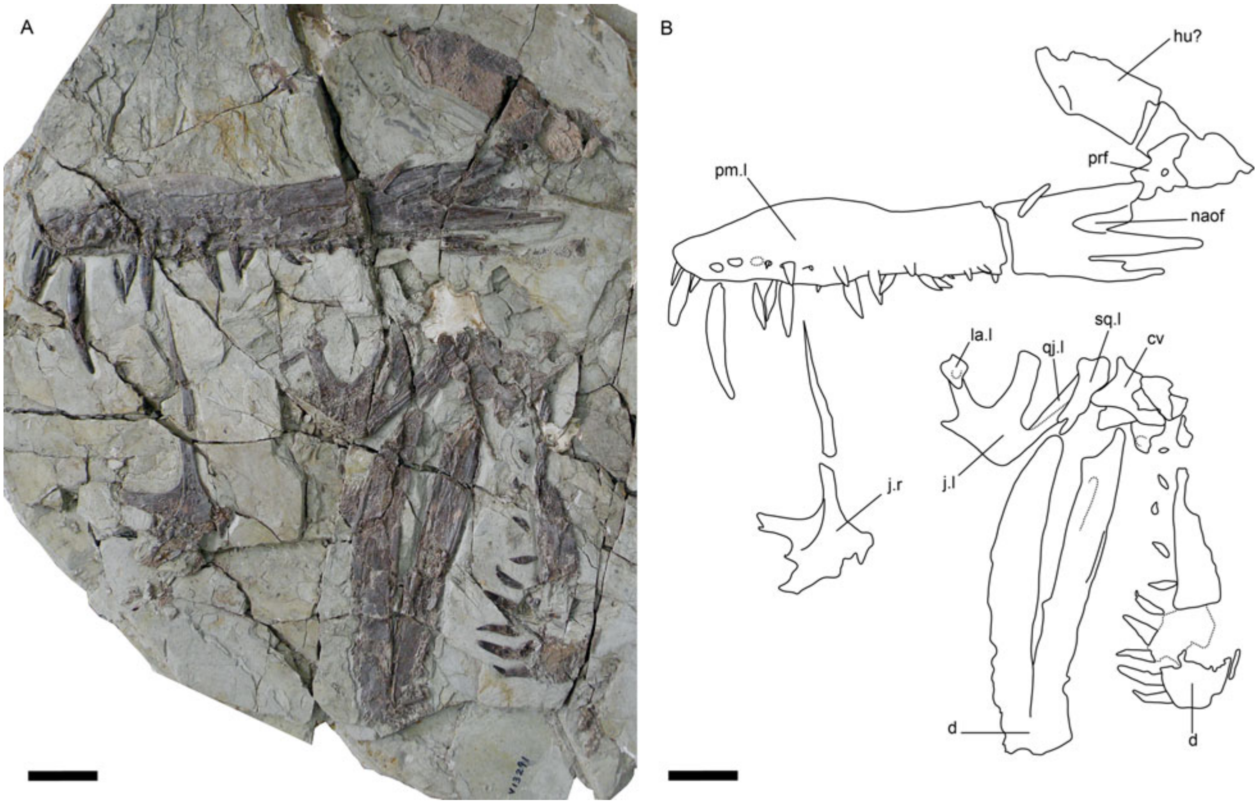

Figure 7. (Colour online) General view of specimen IVPP V13291, holotype of *Liaoningopterus gui*. (A) Photograph; (B) respective line drawing. cv, cervical vertebra; d, dentary; hu?, possible humerus; j, jugal; l, left; la, lacrimal; naof, nasoantorbital fenestra; pm, premaxilla; prf, prefrontal; qj, quadratojugal; r, right; sq, squamosal. Scale bar: 50 mm.

present, besides a very flattened and eroded long bone, which seems to be a humerus (Figure 7).

Premaxilla: Only the left premaxilla is visible, from the tip of the skull until the nasoantorbital fenestra. The preserved part shows that the dorsal margin of the rostral portion of the skull was straight (Figure 8). Due to compression, the palatal region is exposed, including part of the ventral portion of the premaxilla. This portion possesses a few small foramina (Figure 9(A)), which may indicate innervation or vascularisation.

The tip of the rostrum has its ventral margin gently curving upward. This feature is common among pteranodontoids such as anhanguerians and *Cimoliopterus cuvieri* (Bowerbank 1851), but is present in different degrees in different taxa. In *Liaoningopterus gui*, this gentle curvature is similar to that present in *Anhanguera*

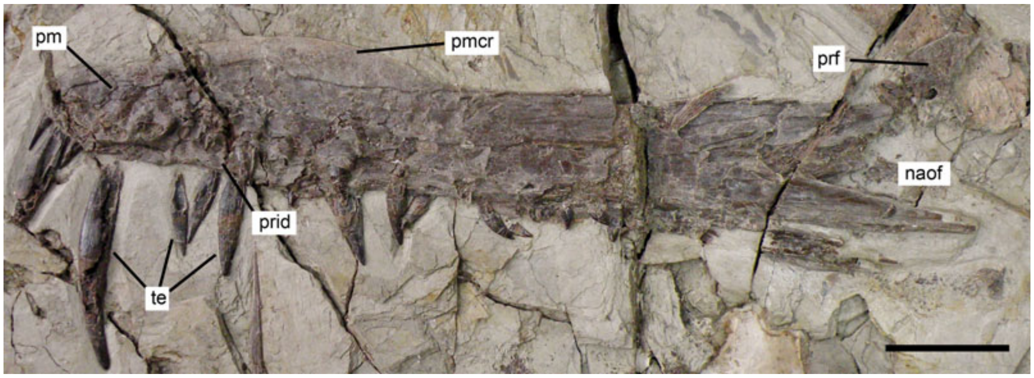

Figure 8. (Colour online) General view of the anterior portion of the skull of specimen IVPP V13291, holotype of *Liaoningopterus gui*, in left lateral view. naof, nasoantorbital fenestra; pm, premaxilla; pmcr, premaxillary crest; prf, prefrontal; prid, palatal ridge; te, teeth. Scale bar: 50 mm.

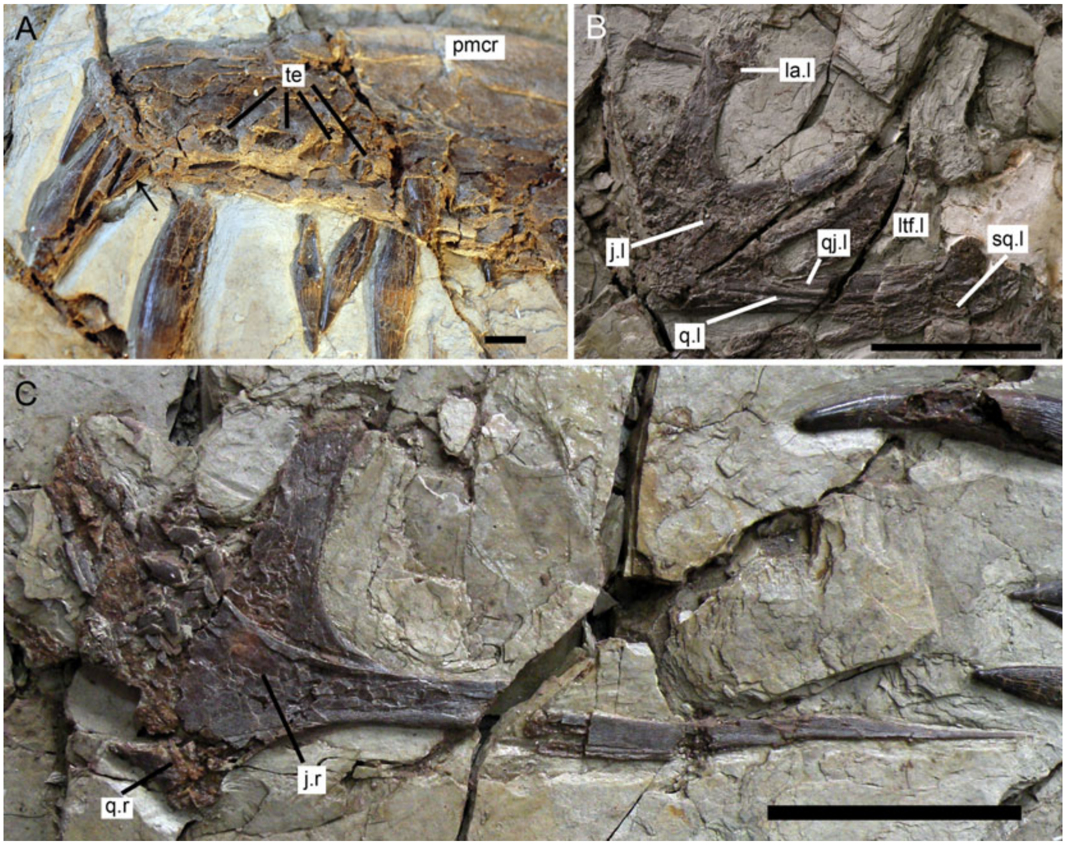

Figure 9. (Colour online) Detail of several bones of specimen IVPP V13291, holotype of *Liaoningopterus gui*. (A) tip of the skull in left lateral view. Scale bar: 10 mm; (B) left jugal and associated bones in left lateral view. Scale bar: 50 mm; (C) right jugal and associated bones in right lateral view. Scale bar: 50 mm. j, jugal; l, left; la, lacrimal; ltf, lower temporal fenestra; pmcr, premaxillary crest; q, quadrate; qj, quadratojugal; r, right; sq, squamosal; te, teeth. Arrow points to a large substitution tooth.

and *Caulkicephalus* (Campos and Kellner 1985; Wellnhofer 1991; Kellner and Tomida 2000; Steel et al. 2005), and is very distinct from the steeper inclination seen in *Coloborhynchus*, *Siroccopteryx* and *Uktenadactylus* (Rodrigues and Kellner 2008).

There is a very low and symmetric premaxillary crest (Figure 8), 120 mm long, and 17 mm maximum height (Wang and Zhou 2003). It begins near, but not at, the tip of the rostrum, at the level of the 5th tooth, and ends well before the nasoantorbital fenestra, at the 12th tooth (Wang and Zhou 2003). It contrasts with *Tropeognathus*, in which the crest is symmetric but higher and begins at the tip of the rostrum, and *Anhanguera blittersdorffi* and *Anhanguera spielbergi*, which have strongly asymmetric crests (Campos and Kellner 1985; Veldmeijer 2003). *Anhanguera piscator* also has a low and symmetric crest, but it ends nearer the nasoantorbital fenestra (Kellner and Tomida 2000). The crest ends well before the nasoantorbital fenestra in *Anhanguera santanae* (based on the holotype, SNSB-BSPG 1982 I 90; Wellnhofer 1985; Kellner and Tomida 2000), but in this species its shape cannot be assessed. In *Caulkicephalus trimicrodon* this structure also begins near but not at the tip of the rostrum and ends well before the nasoantorbital fenestra (Steel et al. 2005), but its shape cannot be determined. In any case, the premaxillae of *Caulkicephalus trimicrodon* show a marked dorsal concavity that is absent in *Liaoningopterus gui*.

Being an anhanguerid, *Lianingopterus gui* probably had a distal expansion of the skull, a structure that, as exemplified by *Anhanguera blittersdorffi* and all other species of the family, is located near the anterior end of the rostrum, although it is not terminal. As the specimen is laterally flat, an expansion is hard to be confirmed, but two features make a strong case for its presence. One is that the premaxillary alveolar margin is not straight, but rather makes a gentle upward curve from alveoli 2 to 4, and then descends until alveoli 5 and 6; the latter alveoli would thus be located in a constriction that follows the expansion (Figure 9(A)). Another feature is that, as typical of anhanguerids, the alveoli 2 to 4 are quite large, which is normally associated with the distal expansion, alveoli 3 being the largest and usually positioned in the broader part of the rostral tip. Alveoli 5 and 6 are smaller, and, as observed in non-flattened specimens, are associated with the constriction that follows the expansion, after which the rostrum usually broadens again (see Campos and Kellner 1985; Steel et al. 2005).

Maxilla: The suture between premaxilla and maxilla is largely obliterated, and therefore their limits are not visible. Some cracks on the surface of the bone also prevent the assessment if the putative suture line between the premaxilla and maxilla in front of the nasoantorbital fenestra is present, as observed in other anhanguerid skulls (Campos and Kellner 1985; Wellnhofer 1985, 1991).

Most the left maxilla can be seen, but parts of the right one are also visible below the ventral margin of the skull. The maxilla comprises most of the rostrum in lateral view and its jugal process extends until under the nasoantorbital fenestra, as showed by the presence of a toothed margin.

Lacrimal: Only part of the left lacrimal is visible, in articulation with the lacrimal process of the left jugal. The suture between those bones is clearly visible, and the lacrimal overlies the jugal. It presents a small posterior process directed into the orbit and shows the indication of a lacrimal foramen.

Jugal: As remarked above, both jugals are preserved but disarticulated from the skull (Figure 9(B),(C)). They conform to the general morphology present in other anhanguerids (Campos and Kellner 1985; Wellnhofer 1985, 1991; Kellner and Tomida 2000; Veldmeijer 2003), such as the presence of a well-marked ridge at the base of the lacrimal process, which is robust and vertically oriented (Wang and Zhou 2003).

The left jugal lacks the maxillary process, but shows both the lacrimal and postorbital processes (Figure 9(B)). The postorbital process is robust and, together with the lacrimal process, forms a rounded ventral margin of the orbit. Because both processes are divergent, the orbit had the dorsal part broader than the ventral, a common feature of anhanguerids.

The right jugal shows a very long and slender maxillary process that gets thinner gradually, ending in a sharp point (Figure 9(C)). The lacrimal process is broad, and its dorsal part is rugose, marking the area where it was overlain by the lacrimal. The external surface of the postorbital process is damaged and the interior part of the bone is exposed.

Quadratojugal: Only the left quadratojugal can be observed (Figure 9(B)). It is exposed in lateral view and fused to adjacent bones. It is elongate and participates in the ventral border of the lower temporal fenestra forming a slightly concave margin.

Quadrate: The right quadrate is very fragmented while the left quadrate is well preserved but lacks the articulation with the lower jaw (Figure 9(B),(C)). The ascending process is elongate and, with the quadratojugal and postorbital process of the jugal, forms the inferior margin of the lower temporal fenestra.

Squamosal: The left squamosal is partially preserved and is connected with the quadrate (Figure 9(B)). Its posterior margin marks the rear end of the skull in lateral view. The anterior process is partially preserved and forms part of the intertemporal bar, which is longer than the quadratojugal and postorbital process of the jugal, showing that the lower temporal fenestra was broader dorsally than ventrally. The ventrolateral process of the squamosal is also elongated and oriented ventrally.

Prefrontal: An isolated bone located at the dorsoposterior portion of the preserved skull (Figure 7) is consistent with the prefrontal, but the outer surface is not well preserved.

Mandible: The mandible is broken in two pieces (Figure 10). On the slab, the symphyseal portion is located ventrally to the rami, which is unusual. The symphysis and left ramus are exposed in left lateral view, while the right ramus is shown in medial view. The curvature of the left ramus, as seen in its dorsal and ventral margins, indicates that they were bowed, as seen in tridimensionally preserved anhanguerids (Wellnhofer 1985, 1987; Kellner and Tomida 2000; Veldmeijer 2003).

Dentary: The mandibular symphysis is not well preserved. The tip of the left dentary has lost the external surface exposing the internal part of the bone. Although some teeth are present, no alveoli can be seen.

The preservation of this specimen hinders direct observation of the tip of the dentaries, but it can be confidently assumed that only a minor portion was lost, as the preserved teeth are rather large, as typical from the anterior-most portion of anhanguerid mandibles (see Kellner and Tomida 2000).

The high tip of the mandible (45.4 mm at the highest point), in comparison to the height of the rami (36.3 mm at the highest point of the left ramus) and to the preserved caudal part of the symphysis, shows that a median dentary crest was present (Figure 10), although its exact shape cannot be determined. In all known anhanguerid mandibles, a dentary crest is present and is located at the anterior-most tip of the symphysis, with variable shapes and heights (Wellnhofer 1987; Kellner and Tomida 2000; Veldmeijer 2003)

Surangular, angular and articular: In both the left and right mandibular rami, the sutures between the surangular and adjacent bones are not recognisable, but this bone can be identified by its position, forming the dorsal margin of the adductor fossa (Bennett 2001) which, in *Liaoningopterus gui* as in other anhanguerids, is long and narrow (Wellnhofer 1985, 1987; Veldmeijer 2003). The angular can be observed in medial view, in the right ramus where it forms part of the ventral margin of the mandible. It is elongated and relatively thin. The suture with the splenial is well marked. The right articular shows the articulation surface with the upper jaw as paired fossae, which receive the two condyles of the helical jaw joint. The retroarticular process is fragmentary but was an elongated element.

Splenial and prearticular: The right splenial is a laminar bone, located in the medial portion of the ramus. It overlies dorsally the dentary and ventrally the angular,

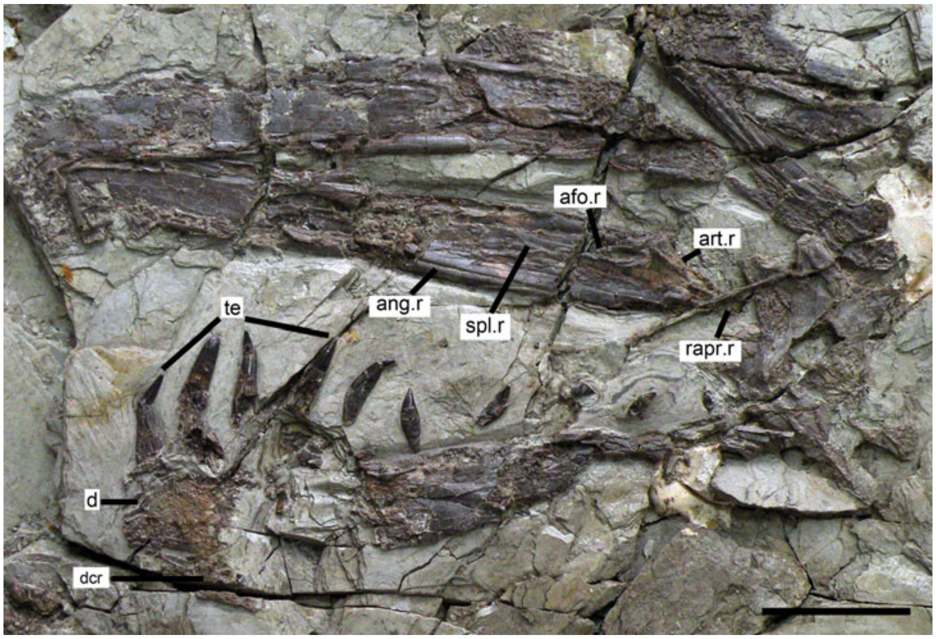

Figure 10. (Colour online) Mandible of specimen IVPP V13291, holotype of *Liaoningopterus gui*. The mandibular rami are preserved above the symphysis. afo, adductor fossa; ang, angular; art, articular; d, dentary; dcr, dentary crest; r, right; rapr, retroarticular process; spl, splenial; te, teeth. Scale bar: 50 mm.

forming the ventral margin of the adductor fossa in its entire length.

Dentition: *Liaoningopterus gui* has a remarkable dentition, with extremely long and robust upper anterior teeth (Wang and Zhou 2003), much large in absolute size than in any other anhanguerid. The third upper tooth is the largest, just over 80 mm long (excluding the base, which was not preserved), but its size seems to be nearly followed by the second upper tooth, which was about to be shed (a large replacement tooth can be seen). These teeth are also quite thick in comparison to the others.

In the upper jaw, the anterior-most pairs of teeth are located at the tip of the rostrum, which, combined with its gently upward curvature, makes them procumbent. The first pair of upper teeth is located slightly dorsally to the second pair, with the space between them less than the size of the alveolus. Upper alveoli 1–4 are larger, 6 is smaller and 7–10 relatively large, but not as much as the anterior-most ones. Due to the poor preservation of the fifth alveolus, it is uncertain if it was smaller than alveoli 4 and 7, a feature normally considered distinctive of the genus *Anhanguera* (Kellner 2003). From the 10th onwards, the alveoli are smaller and extend until under the nasoantorbital fenestra. The anterior eight pairs of teeth are more densely placed, while the separation of the posterior teeth is larger than the size of their alveoli.

The crowns are long and gently curved in the first 10 pairs of teeth, while the posterior ones are shorter and somewhat conical. All teeth show enamel with longitudinal ridges, as observed before in other specimens referred to the Anhangueridae and related taxa (Rodrigues and Kellner 2010).

The lower jaw is not well preserved and the alveoli cannot be seen, so their location and separation cannot be measured. Apparently only the left teeth are preserved. Nonetheless, the overall pattern is also similar to the upper jaw, with larger anterior teeth and smaller posterior ones.

Atlas and axis: Just next to the preserved third cervical vertebra, a round articulation surface can be seen. This articulation is interpreted as the anterior cotyle of the intercentrum of the atlas (Figure 11). The atlas is fused to the centrum of the axis, which is partially visible, the main part crushed underneath the third cervical vertebra. A bone fragment preserved on the other side of the third cervical, opposed to the atlas, may be the neural spine of the axis.

Third cervical vertebra: One cervical vertebra from the mid series, possibly cervical 3, is exposed in ventral view (Figure 11). The centrum is short and a lateral pneumatic foramen on the left side can be observed. The prezygapophyses were not preserved, but the left postzygapophysis and both postexapophyses are present. The postzygapophysis is short and faces posteriorly. The postexapophyses are horn-like and very divergent, likely partially due to taphonomy.

Possible humerus: Lying dorsally to the main part of the skull is a flattened bone, in which most of the external surface was lost. It is elongate but broad. The margin preserved next to the skull is concave, but the other margin was broken.

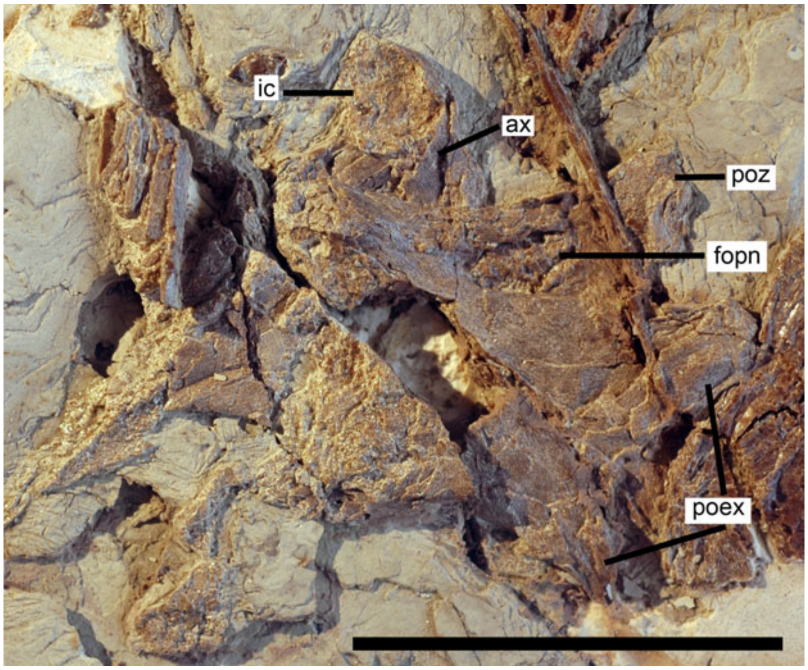

Figure 11. (Colour online) Cervical vertebral elements of specimen IVPP V13291, holotype of *Liaoningopterus gui*: ax, axis; fopn, foramen pneumaticum; ic, intercentrum; poex, postexapophysis; poz, postzygapophysis. Scale bar: 50 mm.

It also presents an articulation surface with apparently two condyles. It is tentatively identified a humerus.

4. Discussion and conclusions

In order to assess the phylogenetic relationships of *Linlongopterus jennyae*, a cladistic analysis was performed and resulted in 90 equally parsimonious trees with 213 steps each. From these, a strict consensus tree was obtained (Figure 12). The species was recovered within the Dsungaripteroidea (*sensu* Kellner 2003) based on an unambiguous synapomorphy: the presence of a helical jaw joint. However, the position within this group is less clear because the inclusion of this taxon collapsed several nodes, as the holotype and only known specimen of *Linlongopterus jennyae* is quite incomplete. It can be excluded from the Dsungaripteridae, which possesses a very particular dentition, and from the edentulous Azhdarchoidea, therefore, being referred to the Pteranodontoidea. The latter is further divided into three lineages. It can be confidently excluded from the edentulous Pteranodontidae and from the Istiodactylidae, which shows very characteristic laterally compressed and triangular tooth crowns (Kellner 2003). The remaining clade includes the Anhangueria and its sister groups (Rodrigues and Kellner 2013). The new specimen has features consistent with this clade, being excluded from the Anhangueridae due to the lack of median crests on the upper and lower jaws, and by the possession of anterior teeth that are similar in size, thus lacking the typical teeth size variation seen in *Anhanguera*, for instance.

Linlongopterus jennyae can be easily distinguished from the two known anhanguerians from the Jiufotang Formation, *Liaoningopterus gui* and *Guidraco venator*, and from the related form *Ikrandraco avatar*. To cite only the most outstanding features, *Liaoningopterus gui* has very enlarged upper anterior teeth, a premaxillary crest that begins near the tip of the rostrum, and a dentary crest (Wang and Zhou 2003), all features absent in *Linlongopterus*. *Guidraco venator* has very particular thin and elongate upper anterior teeth (Wang et al. 2012) which are also absent in the new species. *Ikrandraco avatar* has an elongate skull, a large, blade-like mandibular crest, and short teeth (Wang et al. 2014), features not seen in the new taxon.

Regarding morphologically similar pterosaurs from the older Yixian Formation, *Haopterus gracilis* has teeth that are overall similar (Wang and Lü 2001), but have a constriction between crown and root (Figure 13), thus differing from the present species. Comparisons with *Yixianopterus jingangshanensis*, regarded as a 'lonchodectid' (Lü et al. 2006), are complicated because the holotype and only known specimen of this taxon was heavily artificially modified, with several fake bones added (as shown in its description) and it cannot be determined if the few original teeth are from the upper or the lower jaw.

Concerning *Liaoningopterus gui*, different phylogenies have indicated slightly different relationships with the Brazilian anhanguerids, e.g. *Anhanguera* and *Tropeognathus* (Lü and Ji 2006; Andres et al. 2014). In the case of the analysis by Lü and Ji (2006), *Liaoningopterus* was

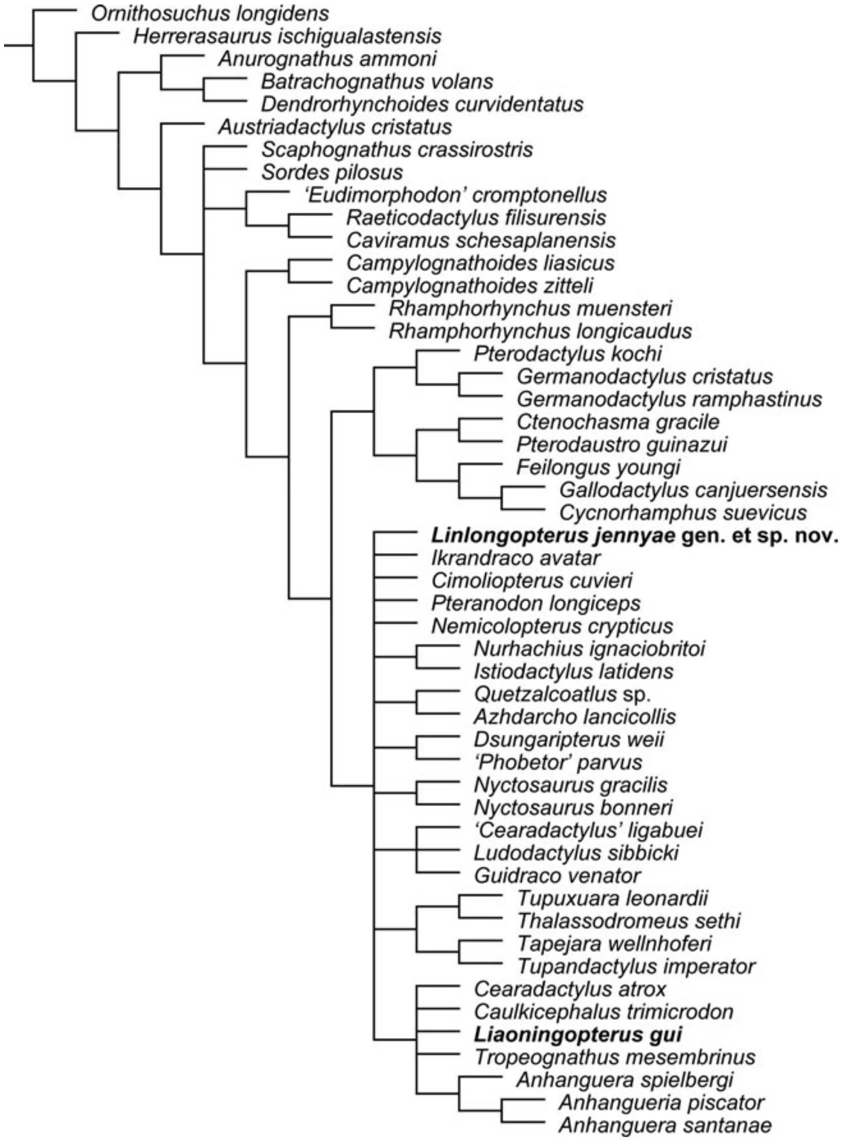

Figure 12. Phylogenetic relationships of *Linlongopterus jennyae* **gen.** et **sp. nov.** and *Liaoningopterus gui* (see Supplementary Material).

recovered as the sister-group of *Anhanguera* and *Tropeognathus*, and thus actually outside the Anhangueridae as defined by Kellner (2003). However, as noted before (Rodrigues and Kellner 2013), the coding responsible for this phylogenetic position is incorrect, and instead should be identical to the coding for the species of *Anhanguera*. A more recent phylogenetic proposal for pterosaurs (Andres et al. 2014) recovered *Liaoningopterus* as the sister-group of *Anhanguera*, with *Tropeognathus* being closer to other taxa such as *Ornithocheirus* and *Coloborhynchus*. Although a review of this phylogenetic analysis is beyond the scope of this paper, we note that there are problems in the coding too. For instance, the authors consider the absence or presence of a dentary crest (character 133) as a missing data, with which we disagree. Furthermore, they have coded one character (55; orbit, dorsal position) as multistate in *Liaoningopterus*, even though the taxon is only known by its holotype (a fact acknowledged in their list of species and specimens used in the phylogenetic analysis, provided as supplementary material). A recent phylogenetic proposal focusing on anhanguerians and related taxa (Rodrigues and Kellner 2013) recovered *Liaoningopterus* as one of the several wildcard taxa that brought instability to the analysis; this was mainly due to the amount of missing data in characters key to the group. In the present analysis, *Liaoningopterus gui* was recovered in a polytomy with *Cearadactylus atrox*, *Caulkicephalus trimicrodon*, *Tropeognathus mesembrinus* and *Anhanguera*.

Liaoningopterus gui is referred to the Anhangueridae by the possession of blade-like premaxillary and dentary crests which are confined to the anterior portions of the

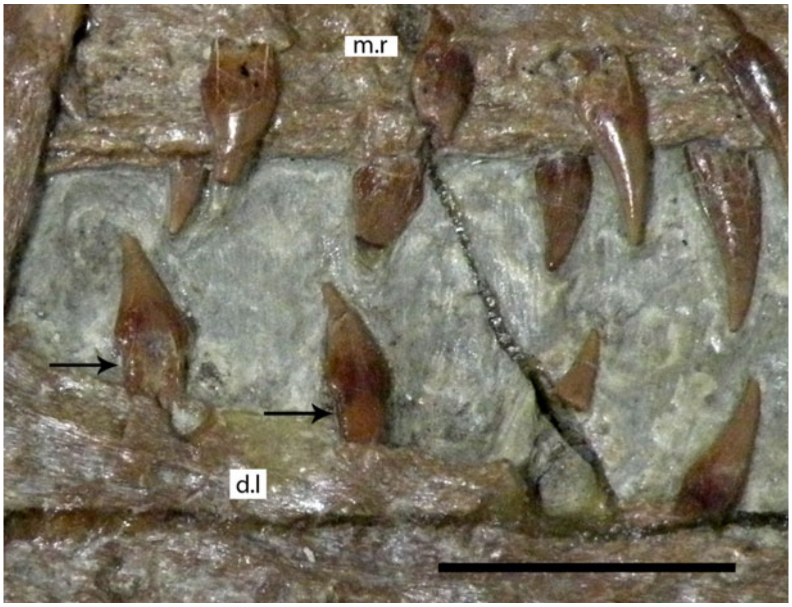

Figure 13. (Colour online) Teeth of specimen IVPP V11726, holotype of *Haopterus gracilis*: d, dentary; l, left; pm, premaxilla; r, right. Arrows point to the constriction between crown and root of the teeth. Scale bar: 10 mm.

skull and mandible (Wang and Zhou 2003). It is remarkably similar to the species of *Anhanguera* and to *Caulkicephalus trimicrodon*. Although it cannot be assessed if *Liaoningopterus gui* had an enlarged frontoparietal crest, it can be distinguished from *Caulkicephalus trimicrodon* because it lacks the characteristic small 5th, 6th and 7th alveoli of the latter (Steel et al. 2005). It also differs from most species of *Anhanguera* by the combination of a low and symmetric crest located comparatively far from the nasoantorbital fenestra (Kellner and Tomida 2000). It can be distinguished from *Anhanguera santanae* by having a straight dorsal margin of the skull, which in the latter is concave (Wellnhofer 1985). Besides the anatomical features, *Liaoningopterus* and *Anhanguera* come from different deposits, which were quite separated spatially in the Lower Cretaceous.

To date, the Jiufotang Formation has shown a variety of pterosaurs, with *Liaoningopterus gui*, *Linlongopterus jennyae* and *Guidraco venator* representing large species. They were collected in distinct geographic areas, but in the same stratigraphic unit. However, it is difficult to be sure if these taxa were indeed contemporaneous and sympatric species. If they were, those pterosaurs show very distinct tooth morphologies. Although only in *Guidraco*, there is some indirect evidence suggesting that it preyed on fish (Wang et al. 2012), all three are regarded to be piscivorous, likely a general condition among anhanguerians and closely related taxa. This variation in dentition points to possible different prey item preferences and/or perhaps also diverse feeding habits among pterosaurs from this deposit.

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Disclosure statement

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