

New toothed flying reptile from Asia: close similarities between early Cretaceous pterosaur faunas from China and Brazil

Xiaolin Wang · Alexander W. A. Kellner ·
Shunxing Jiang · Xin Cheng

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Abstract Despite the great increase in pterosaur diversity in the last decades, particularly due to discoveries made in western Liaoning (China), very little is known regarding pterosaur biogeography. Here, we present the description of a new pterosaur from the Jiufotang Formation that adds significantly to our knowledge of pterosaur distribution and enhances the diversity of cranial anatomy found in those volant creatures. *Guidraco venator* gen. et sp. nov. has an unusual upward-directed frontal crest and large rostral teeth, some of which surpass the margins of the skull and lower jaw when occluded. The new species is closely related to a rare taxon from the Brazilian Crato Formation, posing an interesting paleobiogeographic problem and supporting the hypothesis that at least some early Cretaceous pterosaur clades, such as the Tapejaridae and the Anhangueridae,

might have originated in Asia. The association of the new specimen with coprolites and the cranial morphology suggest that *G. venator* preyed on fish.

Keywords Pterosauria · *Guidraco* · Jiufotang Formation · Early Cretaceous · China

Introduction

Research on pterosaurs is invigorated in the last years thanks to the intensive collecting activity in Jurassic and Cretaceous strata of western Liaoning. Known since the description of *Eosipterus yangi*, some 39 species have been described from this area so and the number continues to mount (Ji and Ji 1997; Wang et al. 2007; Cheng et al. 2011; Jiang and Wang 2011).

Three stratigraphic units have provided most of the pterosaur fossils from western Liaoning. The oldest is the Daohugou Formation (Bed) that has been regarded as part of the Tiaojishan Formation. Its age is disputed, ranging from Middle Jurassic (Chen et al. 2004; Ji et al. 2005; Liu et al. 2006) to Late Jurassic (Zhang 2002; He et al. 2004b; Zhang et al. 2008; Zhou et al. 2010) or even Late Jurassic–Early Cretaceous (Wang et al. 2005). The main pterosaur clade represented in those deposits is Wukongopteridae (Wang et al. 2009) known by four distinct species (Wang et al. 2009, 2010; Lü et al. 2010b, 2011). These deposits produced also some anurognathids (Wang et al. 2002) and scaphognathid or apparently closely related taxa (Lü et al. 2010a; Cheng et al. 2011), the first ones from Asia.

The two remaining units yield the Jehol Biota (Chang et al. 2003; Zhou et al. 2003). The lower one is the Yixian Formation, regarded as Barremian (Swisher et al. 1999, 2002; Wang et al. 2001) that furnished 14 distinct species representing anurognathids (Ji et al. 1999), archaeopterodactylids (e.g.,

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X. Wang · S. Jiang · X. Cheng
Key Laboratory of Evolutionary Systematics of Vertebrates,
Institute of Vertebrate Paleontology and Paleoanthropology,
Chinese Academy of Sciences,
PO Box 643, Beijing 100044, China
e-mail: wangxiaolin@ivpp.ac.cn

A. W. A. Kellner (✉)
Laboratory of Systematics and Taphonomy of Fossil Vertebrates,
Department of Geology and Paleontology, Museu Nacional
Universidade Federal do Rio de Janeiro (UFRJ),
Quinta da Boa Vista s/n, São Cristóvão,
20940-040, Rio de Janeiro, RJ, Brazil
e-mail: alexander.kellner@gmail.com

S. Jiang · X. Cheng
Graduate University of Chinese Academy of Sciences,
Beijing 100049, China

Lü 2003; Wang et al. 2005, 2007; Anders and Ji 2008), tapejarids (Wang et al. 2005), and boreopterids (Lü and Ji 2005; Lü 2010). The overlying Jiufotang Formation is regarded as Aptian (He et al. 2004a) and has the most diversity of Liaoning pterosaurs with 15 described species, representing stem dsungaripteroids (Wang et al. 2008a), anhanguerids (Wang and Zhou 2003b), istiodactylids (Wang et al. 2005, 2006, 2008b; Anders and Ji 2006), chaoyangopterids (Wang and Zhou 2003b; Lü et al. 2008), tapejarids (Wang and Zhou 2003a; Lü et al. 2007), and other taxa whose phylogenetic placement remains to be established (e.g., Dong et al. 2003; Lü and Ji 2005).

Recently, an unusual skull representing a new genus and species closely related to a rare taxon (*Ludodactylus*) from the Early Cretaceous Crato Formation from Brazil (Frey et al. 2003) was found in the Jiufotang Formation near Lingyuan City. We further discuss the implication of this find.

Systematic palaeontology

Pterosauria Kaup 1834

Pterodactyloidea Plieninger 1901

Pteranodontoidea Marsh 1876, *sensu* Kellner 1996, 2003
Guidraco venator gen. et sp. nov.

Etymology Gui, malevolent ghost in Chinese culture combined with *draco*, from Latin meaning dragon; *venator*, the Latin word for hunter.

Holotype Skull and the anterior portion of a neck housed at the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences, Beijing, China (IVPP V17083) (Figs. 1 and 2).

Locality and horizon Jiufotang Formation, Early Cretaceous (Aptian), Sihedang, Lingyuan City, western Liaoning, China.

Diagnosis Pteranodontoid pterosaur with the following autapomorphies: nasoantorbital fenestra length about one fourth total skull length; high, casque-shaped frontal crest with subperpendicular anterior margin, and rounded dorsal margin; rostral teeth robust, large and inclined anteriorly, with crowns (2nd–4th upper; 1st–3rd lower) surpassing the margins of the skull during occlusion. The new species can be further distinguished from other pteranodontoids by the following combination of characters: ventral portion of lower temporal fenestra more constricted than in *Ludodactylus* and anhanguerids; maxillary process of the jugal not extending beyond anterior margin of the nasoantorbital fenestra; 6th tooth much smaller than 5th and 7th.

Description and comparisons

The holotype (IVPP V17083) of *Guidraco venator* gen. et sp. nov. is a skull with articulated cervical vertebrae that are

flattened, a common condition within pterosaurs. The bone surface, however, is very well preserved. The skull is exposed in right lateral view with most elements articulated or in close association. Several cranial elements such as the frontal and the premaxillae are unfused suggesting that this was a subadult animal at time of death (Kellner and Tomida 2000). The skull is 380 mm long (measured between the tip of the premaxillae and the posterior margin of the squamosal), with the rostrum (length: 205 mm) occupying 54% of the cranial length.

The orbit is oval, dorsoventrally elongated and differs from other pteranodontoids (except for *Ludodactylus sibiricki*), such as *Anhanguera*, *Dawndraco*, and *Pteranodon* (Campos and Kellner 1985; Bennett 2001; Kellner 2010), in having the ventral margin more rounded, which is a reflection of a more anteriorly inclined lacrimal process of the jugal.

The largest cranial opening is the pear-shaped nasoantorbital fenestra (95 mm long and 30 mm high) that reaches only about one fourth of the total skull length, being therefore smaller than in anhanguerids (Campos and Kellner 1985), istiodactylids (Wang et al. 2005), and boreopterids (Lü 2010), but larger than in the toothless Pteranodontidae (Bennett 2001; Kellner 2010). It is longer than three times its height (length/height = 3.17) and therefore proportionally slightly lower than in *L. sibiricki* (length/height = 2.86). The posterior margin is concave, contrasting to the straight condition observed in anhanguerids, pteranodontids, and *Ludodactylus*.

The lower temporal fenestra is pear-shaped, with the dorsal margin wider than the lower as in other pteranodontoids. However, in *G. venator*, the ventral portion is more constricted than in anhanguerids and *Ludodactylus*, but does not approach the comparatively more elongated and narrower condition observed in the Pteranodontidae (*Pteranodon*, *Dawndraco*).

The premaxilla is long and contacts the frontal but does not reach the posterior end of the skull. There is no sagittal premaxillary crest, and it does not take part in the cranial crest. The suture with the maxilla is not clear, but a long groove subparallel to the dorsal margin of the skull indicates the limits between those bones, as has been observed in other pteranodontoids (e.g., Kellner and Tomida 2000). This groove originates slightly posterior to the anterior margin of the nasoantorbital fenestra, indicating that the premaxilla only takes part in the dorsal margin of this cranial opening, a common feature of derived pterosaurs (Pterodactyloidea).

The maxilla forms most of the lateral side of the skull and the anterior margin of the nasoantorbital fenestra. It extends posteriorly to at least half the length of the nasoantorbital fenestra.

The right nasal is displaced inside the nasoantorbital fenestra and overlaps another element, tentatively identified as the left nasal. It is a flat and thin bone that forms the

posterodorsal corner of the nasoantorbital fenestra. No nasal process could be observed in this specimen.

Displaced dorsally from its original anatomical position, the prefrontal has a triangular shape and contacts the lacrimal dorsally. The latter forms the dorsal part of the posterior margin of the nasoantorbital fenestra and shows a well-developed and rounded lacrimal foramen. It lacks the spike-like posteriorly oriented process diagnostic of *Ludodactylus* (Frey et al. 2003).

The frontal is the most conspicuous element of the posterior portion of the skull. It was rotated so that the anterior end, formed by two thin processes, is dislocated inside the nasoantorbital fenestra. Dorsally, this bone forms a comparatively broad frontal crest with a convex dorsal margin giving it a casqued-like appearance. No suture between parietal and frontal can be identified, but the former appears not to take part in the cranial crest. The anterior surface of this crest is subvertical and does not reach the same size and proportions recorded in thalassodromines (Kellner and Campos 2002), chaoyangopterids (Lü et al. 2008), and the pteranodontid *Geosternbergia* (Kellner 2010). The frontal crest of *G. venator* is also not posteriorly oriented as in the tapejarines (Wang and Zhou 2003a, b; Kellner 2004), the pteranodontids *Pteranodon* and *Dawndraco* (Bennett 2001; Kellner 2010), and *Ludodactylus* (Frey et al. 2003).

The jugal is triradiate, similar to *Ludodactylus*. The long maxillary process terminates before the anterior margin of the nasoantorbital fenestra, and the lacrimal process is strongly inclined anteriorly, making the ventral margin of the orbit rounder than in other pteranodontoids. The jugal shows a well-developed lateral ridge.

The quadratojugal can be easily separated from the surrounding elements, a feature uncommon in pterodactyloids. It is a small and thin bone that forms the ventral and lower anterior margin of the lower temporal fenestra and does not take part in the cranial articulation with the lower jaw.

As in most derived pterosaurs, the quadrate is elongated and shows a broad articulation surface with two developed condyles indicating the presence of a helical jaw joint.

The lower jaw is complete (length 330 mm). The dentary is long and forms an elongated symphysis (177 mm) over half the mandibular length that is slightly longer than in *Anhanguera piscator* and much longer than in *Tropeognathus mesembrinus* (symphysis/lower jaw length = 0.49 and ~0.30, respectively; no information for *Ludodactylus* is available). It does not approach the condition reported in *Pteranodon*, in which the symphysis reaches over 65% of the mandible length (Bennett 2001). *G. venator* also lacks the strongly convex dorsal margin of the mandibular symphysis present in the pteranodontoid *Aussiedraco molnari* from the Cretaceous Toolebuc Formation of Australia (Kellner et al. 2011).

The posterior portion of the left dentary is displaced ventrally, exposing the internal surface of the lower jaw. The subangular is broad posteriorly, forming the dorsal portion of the articulation surface for the quadrate. Anteriorly, it sends a long maxillary process that, in lateral view, covers the dorsal margin of the dentary. Medially, this bone occupies almost half the height of the posterior portion of the lower jaw, forming the dorsal margin and the internal bony wall of the elongated and slit-like adductor fossa. Ventral to this bone is the splenial, an elongate, plate-like, and thin element that comprises about one third of the medial wall of the lower jaw. The posterior limits between this bone and a prearticular cannot be determined.

The posteroventral margin of the lower jaw is formed by the angular that, in medial view, is an elongate, rod-like, thickened bone, extending anteriorly until being wrapped by the dentary. A similar long angular in medial view is found in anhanguerids (Wellnhofer 1985; Kellner and Tomida 2000). The articular, positioned medially between the surangular and the prearticular, is the smallest element of the lower jaw, forming the ventral part of the articulation with the quadrate and the ventral margin of the slit-like adductor fossa.

An almost complete sclerotic ring composed of several small plate-like bones is preserved almost inside the orbit. One incomplete hyoid bone is also present, displaced ventrally (Figs. 1 and 2).

Two main distinct tooth morphologies can be identified in *G. venator* that are somewhat similar to anhanguerids and *L. sibbicki* formed by the anterior and posterior teeth, respectively. The anterior teeth are elongate, thin but not needle-shaped differing from the Boreopteridae (Lü 2010) and the archaeopterodactyloid clade Ctenochasmatidae (e.g., Wellnhofer 1978; Wang et al. 2007). The enamel surface is smooth, but some show striations close to the root on the lingual surface differing from the strongly ornamented lingual surface reported in some anhanguerids (Kellner and Tomida 2000) and the well-ornamented condition observed in *L. sibbicki*. The first tooth in the upper jaw is long, thin, and directed anteriorly. The subsequent teeth (second to fourth and possibly also the fifth) of the upper jaw, and the first three teeth of the lower jaw are large, curved, and strong. During occlusion, they surpass the dorsal margin of the skull and the ventral margin of the lower jaw, respectively. The teeth decrease in size posteriorly from there with the exception of the 6th tooth that is smaller than the 7th.

The second tooth morphology starts with the tenth upper and ninth lower tooth. Teeth are much smaller, with a bulbous base, giving them a rather triangular appearance which is not the same as observed in the Istiodactylidae (see Howse et al. 2001; Wang et al. 2005). Their surface are also smoother and do not show the strong ornamentation observed in the anterior teeth as reported above.

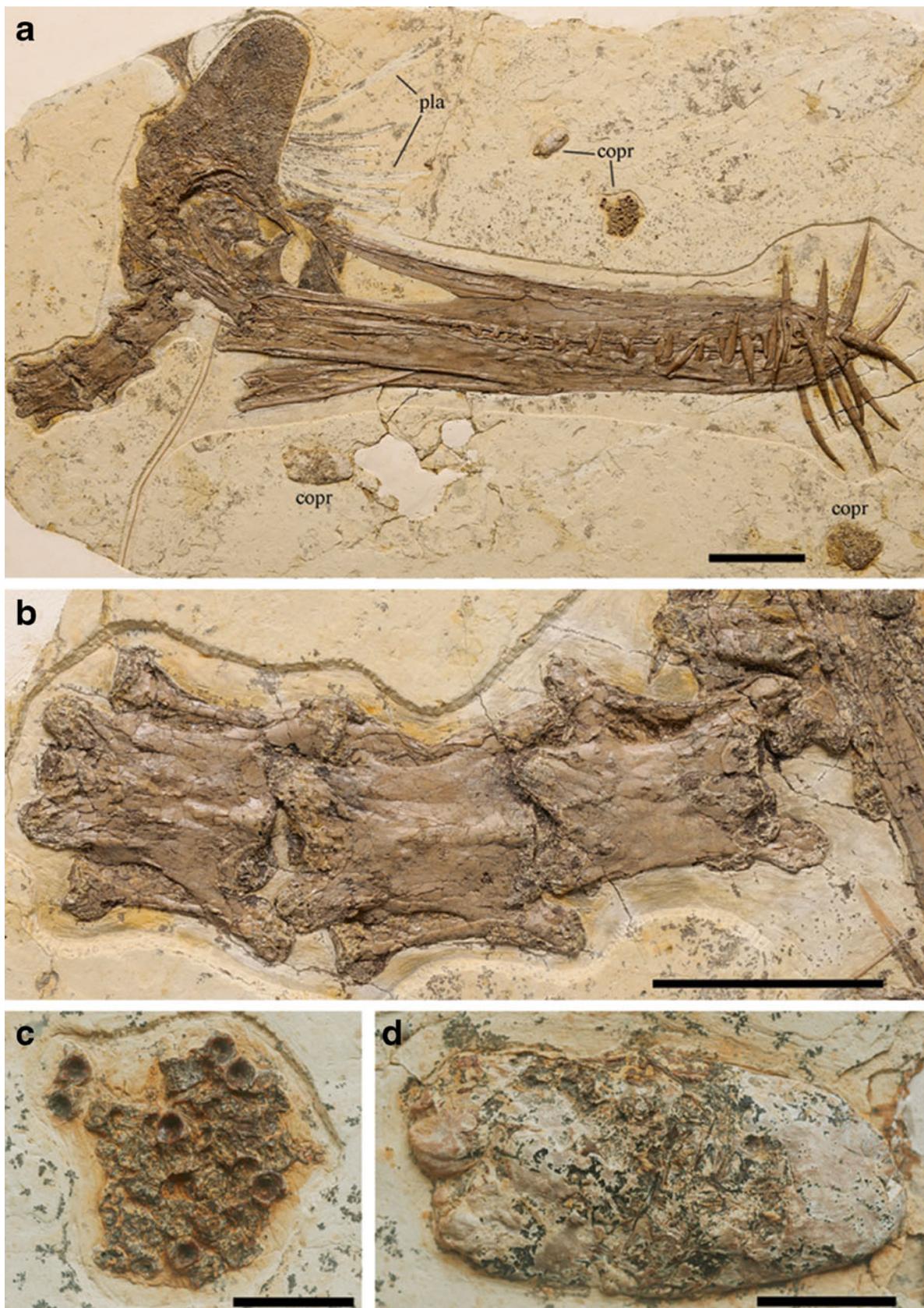


Fig. 1 *Guidraco venator* gen. et sp. nov., holotype (IVPP V17083), from the Jiufotang Formation (Early Cretaceous) of western Liaoning, China: **a** complete specimen, **b** cervical vertebrae, and **c** and **d** coprolites. *copr* Coprolite, *pla* plant. Scale bars 5,3,1,1 mm

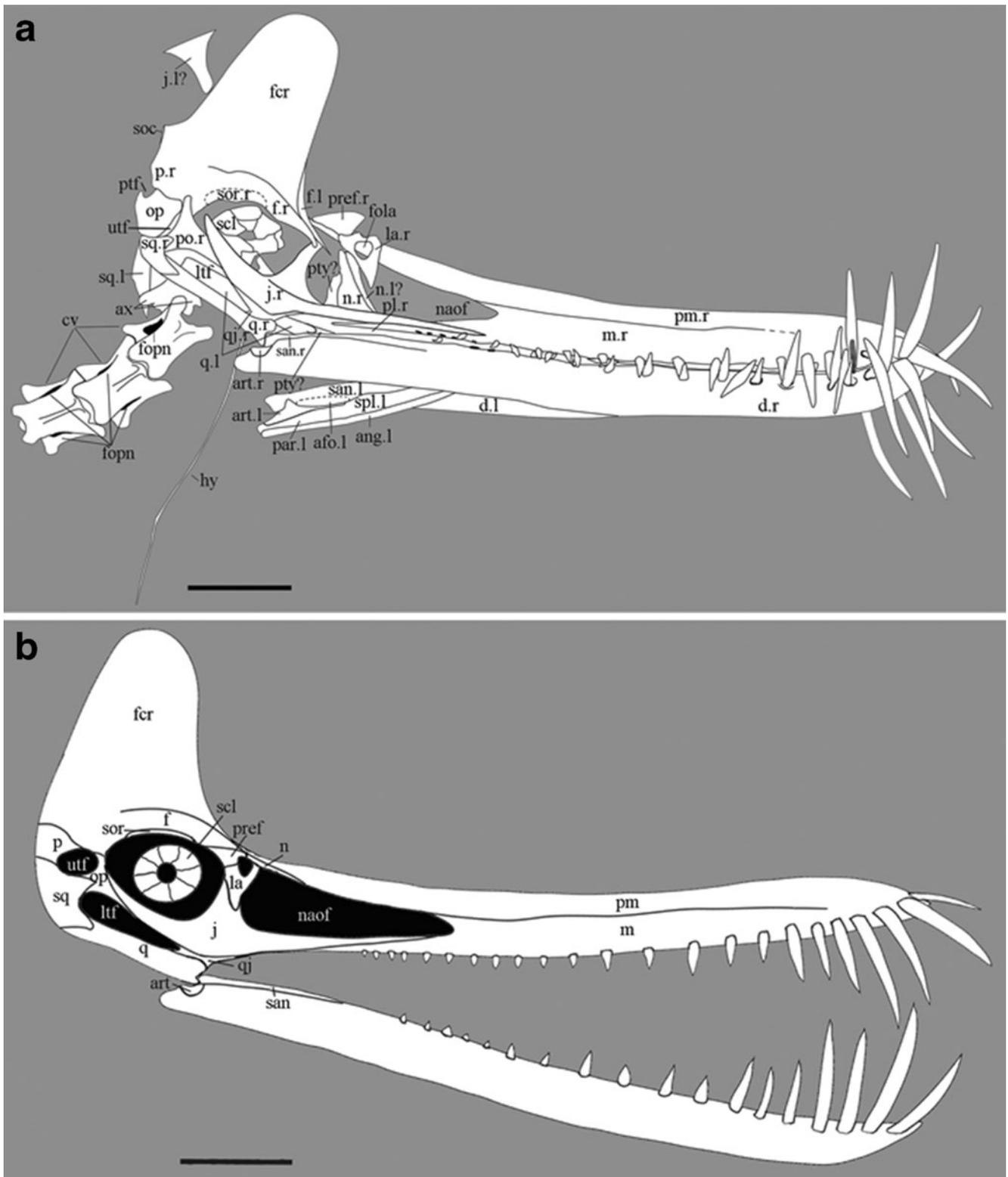
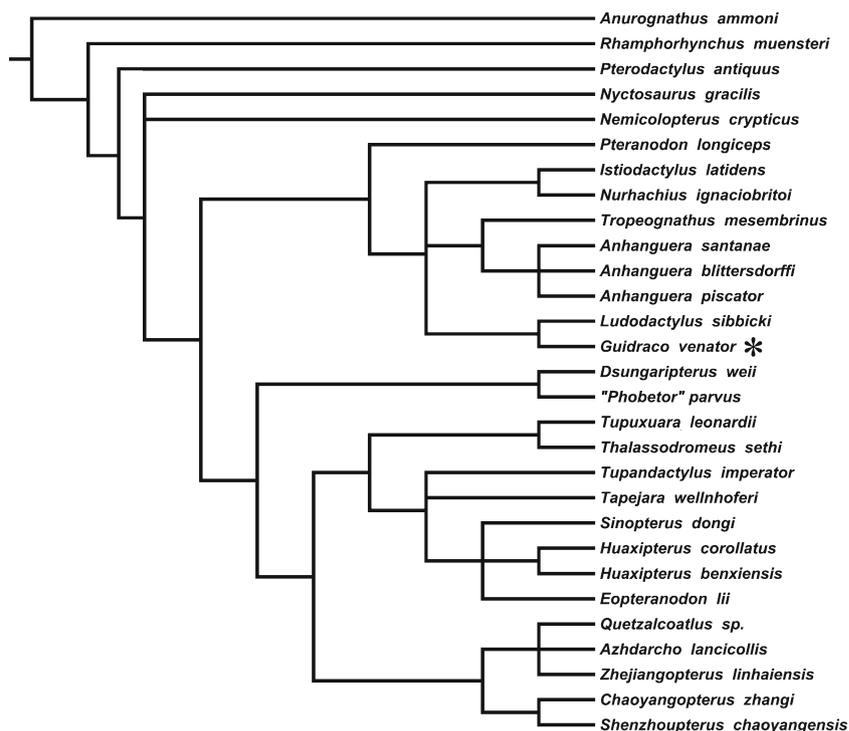


Fig. 2 *Guidraco venator* gen. et sp. nov., holotype (IVPP V17083), **a** line drawing of the specimen and **b** reconstruction of the skull. *afo* Adductor fossa, *ang* angular, *art* articular, *ax* axis, *cv* cervical vertebra, *d* dentary, *f* frontal, *fcr* frontal crest, *fofa* foramen lacrimale, *fopn* foramen pneumaticum, *hy* hyoid bone, *j* jugal, *la* lacrimal, *ltf* lower temporal fenestra, *m* maxilla, *n* nasal, *naof* nasoantorbital fenestra, *op*

opisthotic, *p* parietal, *par* prearticular, *pl* palatine, *pm* premaxilla, *po* postorbital, *pref* prefrontal, *ptf* posttemporal fenestra, *pty* pterygoid, *q* quadrate, *qj* quadratojugal, *san* surangular, *scl* sclerotic ring, *soc* supra-occipital, *sor* supraorbital, *spl* splenial, *sq* squamosal, *utf* upper temporal fenestra, *l* left, *r* right, ? uncertain element. Scale bars 5 mm

Fig. 3 Phylogenetic relationships of *Guidraco venator* gen. et sp. nov. (see electronic supplementary information). The new species is indicated with an asterisk (*)



A partial neck consisting of the axis and three additional cervical vertebrae are the only postcranial elements known of *G. venator* (Figs. 1 and 2). The axis, exposed in right lateral view, has a long, spike-like neural spine, suggesting that the remaining cervical vertebrae of this taxon might have had a similar neural spine. The anterior part of the axis is overlain by the right quadrate, and it is unclear whether a lateral pneumatic foramen piercing the centrum of this bone as reported in some anhanguerids (Wellnhofer 1991; Kellner and Tomida 2000) and in *Pteranodon* (Bennett 2001) is also present.

Cervical vertebrae 3 to 5 are exposed in ventral view. They are strongly procoelous and of similar size with cervical vertebrae 3 slightly smaller. All three bear a well-developed pneumatic foramen piercing the lateral surface of the centrum whose size is similar to anhanguerids (Wellnhofer 1991; Kellner and Tomida 2000), larger than in *Dawndraco* and much larger than in *Pteranodon* (Bennett 2001). Ventrally, they show a blunt ridge. Although it is possible that this ridge might be an artifact due to compression and the expression of an ossified neural canal (see Fig. 58 of Kellner 2006), such a feature is not observed in other similarly flattened material (e.g., *Pteranodon*) and therefore might be considered as diagnostic for this taxon.

On the dorsal part of the slab, covered mainly by the frontal crest, some plant material is observed. Four additional structures, two dorsal and two ventral to the skull are present also. Two show an oval shape while the other two are rounded, apparently a result of compression. Basically, they comprise a whitish to beige matter (likely calcium

phosphate) containing dark brown tiny bone elements. The latter were identified as fish bones and scales that can be best observed in the more compressed structures. These are coprolites that were preserved with this pterosaur and the plant material (Fig 1).

Discussion

In order to access the phylogenetic position of *G. venator* gen. et sp. nov., we performed a phylogenetic analysis which is based on previous studies (e.g., Kellner 2003; Wang et al. 2005, 2009; Anders and Ji 2008). A strict consensus cladogram is shown in Fig. 3 (see electronic supplementary information for details).

G. venator has a nasoantorbital fenestra, a typical trait of the Pterodactyloidea. Although such a fenestra is also reported in the Wukongopteridae (Wang et al. 2009, 2010; Lü et al. 2010a), several features (e.g., overall size, shape of the cervical vertebrae, dentition) exclude *Guidraco* from the latter (and also from the Archaeopterodactyloidea), allowing its allocation to the Pteranodontoidae (sensu Kellner 2003).

The new Chinese taxon differs from the pteranodontoid Istiodactylidae (Howse et al. 2001) and the Pteranodontidae (Bennett 2001; Kellner 2010) by features such as the dentition and the shape of the nasoantorbital fenestra. A frontal crest is present in pteranodontids (Bennett 2001; Kellner 2010) but, in all cases, differs from that of *G. venator*.

The dentition of *G. venator* suggests a close relationship with the Anhangueridae but the lack of the typical

anhanguerid sagittal premaxillary and dentary crests, the shorter nasoantorbital fenestra, and the presence of a large frontal crest excludes the new species from that clade.

The cranial morphology clearly indicates that *Guidraco* is closely related to *Ludodactylus* with whom it shares the rounded ventral margin of the orbit and an extensive frontal crest. The main differences found in the Chinese taxon that justifies the separation at a generic level are the more inclined rostral teeth, the direction and position of the frontal crest, the absence of a spike-like lacrimal process, the comparatively smaller nasoantorbital fenestra, and the more constricted ventral portion of lower temporal fenestra. *Ludodactylus* was reported to bear a dentary crest (Frey et al. 2003), but none could be found when one of us (AWAK) examined the holotype.

The close relationship between *Guidraco* and *Ludodactylus* is rather surprising, given their occurrence in the Jiufotang and Crato Formations from China and Brazil, respectively. The Jiufotang deposits show the most diversified pterosaur fauna from China, with a total of 16 (including *G. venator*) species. The most abundant are the Tapejaridae, with tens of specimens representing four taxa (Wang and Zhou 2003a; Lü et al. 2007; Kellner 2010). Istiodactylids are known by fewer specimens, but five species were proposed (Anders and Ji 2006; Wang et al. 2008b). Four Chaoyangopteridae are reported (Wang and Zhou 2003b; Lü et al. 2008; Anders and Ji 2008), along with one Anhangueridae (Wang and Zhou 2003b), and one stem toothless dsungaripteroid (Wang et al. 2008a).

Two main units with pterosaurs are found in the Araripe Basin: the Crato and Romualdo Formations. The Crato Formation has yielded two Tapejaridae (Kellner 2004), one tentative chaoyangopterid (Witton 2008), and two pteranodontoids (Frey et al. 2003; Kellner and Tomida 2000), here including *Ludodactylus*. The Romualdo Formation is more diverse, with tapejarids and anhanguerids, the latter being predominant (Kellner and Tomida 2000; Kellner 2004). No istiodactylids were found in the Brazilian deposits so far.

Comparisons of the pterosaur faunas from Liaoning and the Araripe basin shows that the Jiufotang Formation shares more elements (i.e., tapejarids and anhanguerids) with the Brazilian deposits than even with the underlying Yixian Formation (Wang et al. 2005). However, anhanguerids are rather cosmopolitan (Kellner and Tomida 2000) and members of both clades have also been found in the Kem–Kem beds of Morocco (Wellnhofer and Buffetaut 1999) and might also be present in Europe. On the other hand, the close relationship of *Guidraco* and *Ludodactylus*, exclusively found in those deposits, indicates that the pterosaur fauna of Jiufotang shows a strong paleobiogeographic tie with the Crato Formation. The ages of the Brazilian deposit is poorly constrained and, based on the pterosaur fauna, might be closer to the

one of the Jiufotang Formation that was deposited around 120 million years.

Whenever biogeographic observations pterosaurs are made, it is important to emphasize that, unfortunately, our overall knowledge regarding the distribution of those volant vertebrates is still very limited compared to other Mesozoic reptiles such as nonavian dinosaurs (e.g., Jacobs et al. 2011; Bittencourt and Langer 2011). In particular, the paucity of the African record, where most specimens are rather incomplete (e.g., O’Conner et al. 2011; Rodrigues et al. 2011), hampers a more comprehensive knowledge of the pterosaur evolutionary history. Nonetheless, there have been suggestions that several of the main Early Cretaceous pterodactyloid clades may have originated in Asia such as the Anhangueridae and the Tapejaridae (Wang and Zhou 2006). The occurrence of *G. venator* is consistent with that notion.

As a last note, although the presence of coprolites containing fish bones with *G. venator* might be accidental, we believe it suggests that this pterosaur is fed on fish, not a spurious notion based on the cranial anatomy of this animal.

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