



PALEONTOLOGY

The first ornithocheiromorph humerus from Wuerho (Urho), China, with a new isotopic age of the Tugulu Group

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Abstract: Pterosaur remains are rare from the lowermost Cretaceous, hampering our understanding of the taxonomic and morphological diversities of pterosaurs during this period. The Lower Cretaceous Tugulu Group in Wuerho, China is renowned for hosting the Wuerho Pterosaurian Fauna (WPF), which has so far yielded numerous fossil remains of two dsungaripterid pterosaurs, *Dsungaripterus weii* and *Noriopterus complicidens*. Here we report a partial ornithocheiromorph humerus from the WPF, representing a deeply divergent clade from Dsungaripteridae. The scarcity of ornithocheiromorphs from the WPF might be interpreted by niche partitioning with dsungaripterids. Meanwhile, we also report a U-Pb zircon age of 134.27 ± 0.36 Ma dated by LA-ICP-MS for the tuffaceous layer at the uppermost part of the Shengjinkou Formation, confirming the Valanginian age of the WPF presented by a previous study. The Wuerho region is one of the few localities producing abundant pterosaur fossils and the only one with an earliest Cretaceous age. The new finding here also suggests that Ornithocheiromorpha had rapidly diversified and achieved a global distribution during the earliest Cretaceous, presumably through a series of modifications on the locomotor apparatus including the warped deltopectoral crest of the humerus, which might substantially improve their flight efficiency.

Key words: ornithocheiromorpha, Tugulu Group, Valanginian, Wuerho (Urho), China.

INTRODUCTION

Pterosauria is known to have scattered fossil records controlled by sampling biases (Butler et al. 2013). In contrast to the abundant pterosaurian fossil records of the Late Jurassic and middle-late Early Cretaceous, which fortunately benefit from the presence of several Lagerstätten such as the Solnhofen Limestone (Tithonian) from Germany, Tiaojishan (Oxfordian), Yixian and Jiufotang Formations (Barremian–Aptian) from northeastern China, and Crato and Romuldo Formations (Aptian–Albian) from Brazil (Barrett et al. 2008), the records of the lowermost Cretaceous (Berriasian–Valanginian) largely comprise of isolated and fragmentary materials, such as ornithocheiromorphs from the Hastings

Group, England (Rigal et al. 2018), and jaws and postcranial remains of highly controversial taxonomic status from the Cornet bauxite of Romania (Dyke et al. 2011, Averianov et al. 2014). Such sampling hiatus was in accordance with the lack of Lagerstätten during this period, resulting in a dramatic drop in character completeness and taxonomic diversity of pterosaurs (Butler et al. 2013, Dean et al. 2016), which severely hampers our understanding of the faunal turnover between pterosaur assemblages of the Upper Jurassic, which are dominated by rhamphorhynchids, wukongopterids and basal pterodactyloids, and those of middle to upper Lower Cretaceous, which are otherwise dominated by ornithocheiroids (sensu Kellner 2003). The extent to which pterosaur evolution

was affected by the Jurassic–Cretaceous transition is thus obscured (Tennant et al. 2017).

More than 60 pterosaur species have been described from China (Wu et al. 2017), preponderantly from the Middle–Late Jurassic Yanliao Biota (e.g., Wang et al. 2002, Lü et al. 2010) and the Early Cretaceous Jehol Biota (e.g., Wang et al. 2005, Jiang et al. 2023), both flourishing in northeastern China. The Lower Cretaceous Tugulu Group in Wuerho has yielded the first two named pterosaurs from China, *Dsungaripterus weii* (Young 1964) and *Noriopterus complicitens* (Young 1973), which are important components of the Wuerho Pterosaurian Fauna (WPF) and both pertain to *Dsungaripteridae*. However, since the first descriptions of these two species, reports of new pterosaur specimens from Wuerho were limited (Chen et al. 2020, Song et al. 2024), without the introduction of pterosaurs other than *dsungaripterids*. This rendered WPF extremely low in pterosaur diversity. Except for body fossils, numerous pterosaur tracks were also recovered from this area, with *N. complicitens* being hypothesized to be possible trackmakers of some (Li et al. 2021).

During the last decade, we have spent several field seasons collecting fossils from the Tugulu Group in Wuerho. *D. weii* is the most abundant vertebrate taxon from the WPF, whereas *N. complicitens* is much less common (Young 1973, pers. obs.). New materials of fishes, turtles, crocodiliforms, saurischians, and stegosaurs were also recovered, with most of them still under study. Among these discoveries, we noticed a partial pterosaur humerus with a distinct morphology from those of *dsungaripterids*, demonstrating that it could be assigned to Ornithocheiromorpha (sensu Andres et al. 2014, following phylogeny of Andres 2021). This new finding increases the phylogenetic diversity of the pterosaur assemblage from Wuerho. We also report another U–Pb zircon age for the tuffaceous

layer of the uppermost Shengjinkou Formation, and the result is indistinguishable from Zheng et al. (2024), providing additional support for the Valanginian age of the WPF. This renders Wuerho among the few earliest Cretaceous pterosaur-bearing sites, and probably the most productive one.

Institutional Abbreviations—AMNH,

American Museum of Natural History New York, USA; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MGUH**, Geological Museum, Copenhagen, Denmark; **NHMUK**, Natural History Museum, London, UK; **USNM**, United States National Museum of Natural History, Washington, D.C., USA.

GEOLOGICAL SETTING

In the Wuerho region, the Lower Cretaceous Tugulu Group is divided into the Hutubihe, Shengjinkou, and Lianmuqin formations in ascending order (Figure 1, Zhao 1980; but see the different division scheme in Jiang et al. 2008), dipping southeastward and unconformably overlain by the Upper Cretaceous Ailikehu Formation. The lithology of the Tugulu Group has been described by Zhao (1980) and Li et al. (2021). The age of the strata was poorly resolved, generally attributed to the Early Cretaceous (Zhao 1980). Based on the occurrence of *Psittacosaurus xinjiangensis*, Lucas (2006) suggested a Barremian–Aptian age for the Tugulu Group. Wang et al. (2020) inferred that the age of the pterosaur-bearing layers, mainly parts of Shengjinkou and Lianmuqin formations, was 130–120 Ma, based on the vertebrate fossil comparisons. In the review of the lithostratigraphy of Cretaceous strata in China, the Shengjinkou and Lianmuqin Formations were dated as Hauterivian–Barremian and Aptian–Albian, respectively (Xi et al. 2021). Recently, Zheng et al. (2024) obtained a U–Pb zircon age of 135.2 ± 0.9

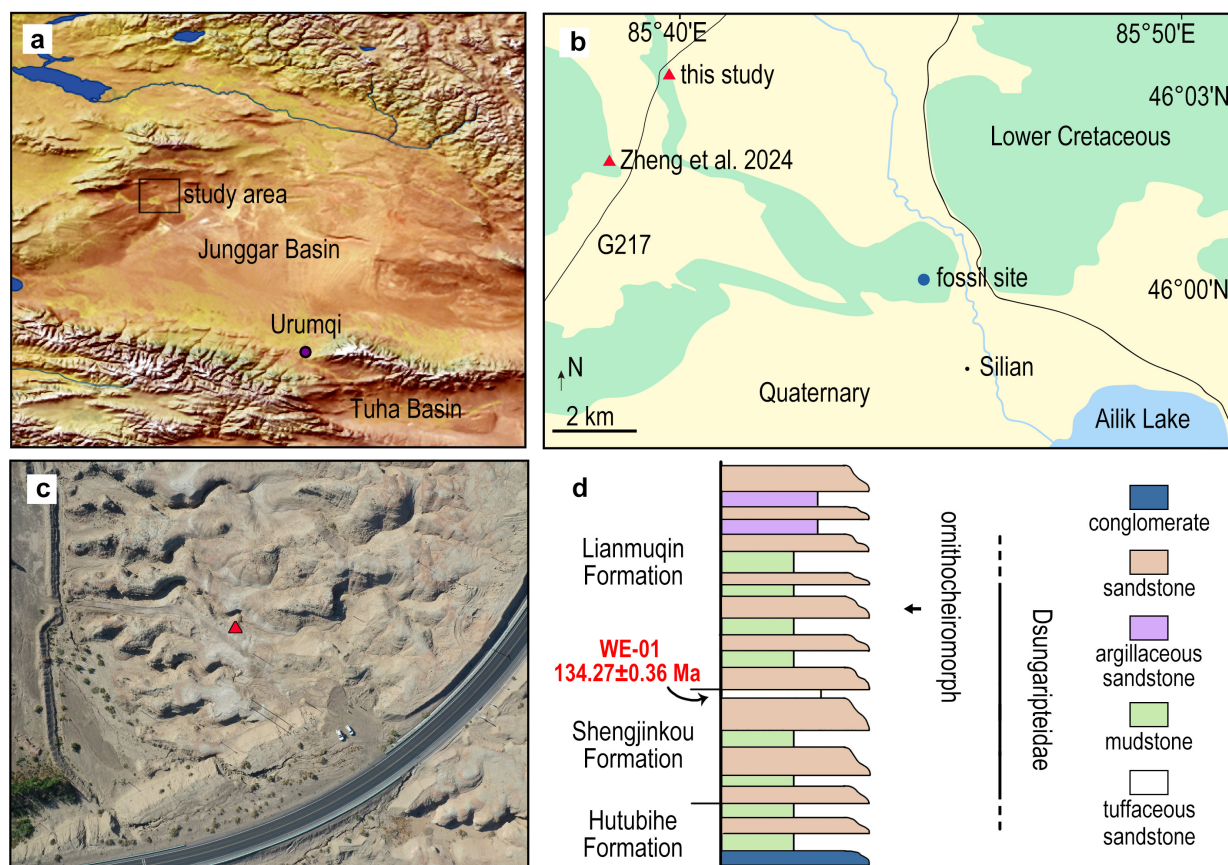


Figure 1. Sketch map of the fossil site and the tuffaceous sample sites. a) the study area; and b) its sketch geological map; c) sample area of the tuffaceous sandstones; d) simplified stratigraphic column of the study area according to Zhao (1980). The red triangles in b and c indicate the tuffaceous sites.

Ma for the whitish tuffaceous sandstones on the top of the Shengjinkou Formation, suggesting a Valanginian age of the WPF.

The new humerus (IVPP V 33251, Figures 2 and 3) was collected at the site about 6 km northwest of Ailik Lake in Wuerho District, Kalamay City, Xinjiang Uygur Autonomous Region, China. This site is roughly equal to locality 64043 of Young, 1973 (Dong 1973, Figure 1). The humerus-bearing horizon belongs to the Lianmuqin Formation, Tugulu Group.

MATERIALS AND METHODS

Isotopic analytical material

The only sample WE-01 was collected from the two-meter-thick whitish tuffaceous sandstone

layer at the uppermost of the Shengjinkou Formation. This layer is widely distributed in northwestern Wuerho, and the sample site is about 9 km to the northwest of the IVPP V 33251 site, near road G217 (Figure 1).

Isotopic analytical methods

Zircons extracted from sample WE-01 for U-Pb isotopic analyses were processed by conventional heavy liquid and magnetic separation techniques. Zircon grains were set in epoxy mounts, which were then polished to expose the interior of the grains. Zircons were documented with transmitted and reflected light micrographs as well as cathodoluminescence (CL) images to reveal their external and internal structures prior to U-Pb isotopic analyses to



Figure 2. The left ornithocheiromorph humerus (IVPP V 33251) from Lianmuqin Formation, Tugulu Group, Wuerho, in ventral view. Scale bar, 50 mm.

observe the erosion degree and choose potential target sites for U-Pb dating.

Zircon U-Pb dating were conducted by laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) at the Wuhan SampleSolution Analytical Technology Co., Ltd., Wuhan, China. The spot size and frequency of the laser were set to 32 μm and 10 Hz, respectively, in this study. Detailed operating conditions for the laser ablation system, the ICP-MS instrument, and data reduction are the same as described by Zong et al. (2017). Concordia diagrams and weighted mean calculations were made using Isoplot/Ex_ver3.75 (Ludwig 2012). Seven measurements of Plešovice zircon during the course of this study yielded a Concordia Age of 337.5 ± 2.3 Ma (2σ , MSWD = 0.54), which is consistent within errors with the reported value of 337.13 ± 0.37 Ma (Sláma et al. 2008).

RESULTS

Description of the new humerus (IVPP V 33251)

IVPP V 33251 is a partial left humerus broken into two pieces missing the distal extremity (Figures 2 and 3, Table I). The proximal and distal fragments have preserved lengths of 98.5 mm and 46 mm, respectively. The total length of the humerus is estimated to be around 158 mm. The proximal end suffers from distortion and crushing, evidenced by the fact that the anterior half of the humeral head is set at an unnatural angle with the posterior half in proximal view (Figure 3e). The deltopectoral crest is also slightly dislocated distally suggested by the unmatched bone patches with the shaft near its distal end (Figure 3b and d). Fortunately, this does not affect the general morphology of the proximal end.

The humeral head is crescent-shaped with a concave ventral margin and a convex dorsal margin (Figure 3e) and is only moderately

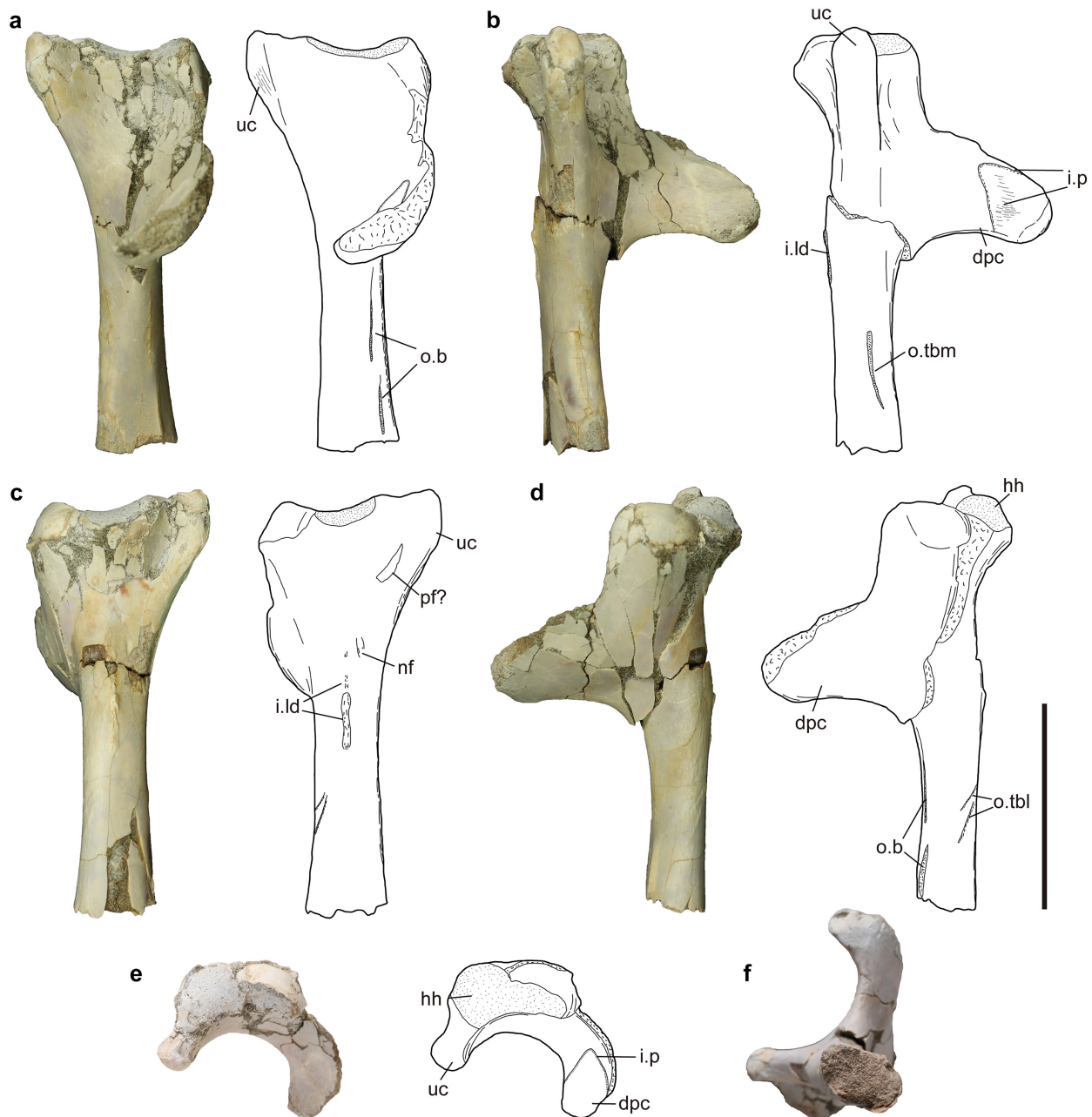


Figure 3. Proximal fragment of the left ornithocheiromorph humerus (IVPP V 33251) in ventral (a), posterior (b), dorsal (c), anterior (d), proximal (e), and distal (f) views. Abbreviations: dpc, deltopectoral crest; hh, humerus head; i.ld, insertion for *M. latissimus dorsi*; i.p, insertion for *M. pectoralis*; nf, nutrient foramen; o.b, origin for *M. brachialis*; o.tbm, origin for *M. triceps brachii caput medialis*; o.tbl, origin for *M. triceps brachii caput lateralis*; pf, pneumatic foramen; uc, ulnar crest. Scale bar, 50 mm.

deflected dorsally (Figure 3b). It is weakly saddle-shaped, i.e., anteroposteriorly concave and dorsoventrally convex. The deltopectoral crest is warped and thickened towards its anterior margin (Figure 3a and f) as in pteranodontoids

(Bennett 1989). Its proximal margin has been eroded, yet the preserved portion suggests that the former slopes distally and is confluent with the anterior margin. The deltopectoral crest is anteroposteriorly longer than wide with a slightly

Table 1. Measurements of the ornithocheiromorph humerus (IVPP V 33251) in mm.

	IVPP V 33251
Length	158*
Proximal articular facet, a-p length	31.08
Proximal articular facet, d-v depth	13.16
Deltopectoral crest, a-p length	33.02
Deltopectoral crest, p-d length	34.07
Distal end, a-p length	39*

*Estimated value

concave distal margin. A reversed '7'-shaped (left element in posteroventral view) scar on the ventral surface of the deltopectoral crest probably defines the insertion for *M. pectoralis* anteriorly (Bennett 2003). This scar extends posteroproximally from the anterior portion of the distal margin towards the proximal margin for most width of the deltopectoral crest, and then sharply turns anteriorly. Anteroposteriorly elongated striations with elongated pits surround the reversed '7'-shaped scar. These elongated pits are especially dense anterior to the scar, and fewer along the distal margin. The ventral surface of the deltopectoral crest closer to the shaft is instead rather smooth. The ulnar crest is moderately expanded in dorsoventral views (Figure 3a and c) and projects posteroventrally in proximal view (Figure 3e), similar to *Hamipterus* but in contrast to the condition in *Anhanguera piscator* and *Istiodactylus latidens* that it is much weaker and posteriorly directed (Kellner & Tomida 2000, Kellner 2003). A distinct constriction connects the humeral head and ulnar crest at their dorsal aspect (Figure 3e). A small dorsally opening nutrient foramen is present on the posterodorsal aspect of the shaft distal to the ulnar crest (Figure 3c), as in *Pteranodon* (Bennett 2001). There is no

pneumatic foramen between the humeral head and deltopectoral crest on the ventral surface. A possible pneumatic foramen is present between the humeral head and ulnar crest on the dorsal surface, but its fidelity cannot be ascertained as its preserved margin is wavy and unnatural (Figure 3c).

The shaft gradually expands anteroposteriorly towards the distal end, as commonly seen in pteranodontoids but unlike most other pterosaurs in which the mid-shaft has a nearly constant width. The cortical bone is extremely thin, with the R/t value measured at around 15 at the breakage close to the mid-shaft, typical for most ornithocheiroids but higher than those seen in dsungaripterids (Jiang et al. 2023). Several muscle scars on the shaft could be easily identified. The scar for *M. latissimus dorsi* is longitudinally oriented on the dorsal surface and roughly level with the distal end of the deltopectoral crest (Figure 3c), with no indication of subdivision for *M. teres major* as reported in *Anhanguera* (AMNH 22555, Bennett 2003). On the posterior surface, the origin for the medial head of *M. triceps brachii* is longitudinally oriented and positioned distal to the ulnar crest (Figure 3b), similar to *Anhanguera* and *Barbosania* (Bennett 2003, Elgin & Frey 2011). This scar curves ventrally near its preserved distal end. Another broader scar closely ventral to its distal end seen in *Hamipterus* (Wang et al. 2017) is not preserved in this specimen. On the ventral surface, a jagged intermuscular line runs distally from the distal end of the deltopectoral crest for around 25 mm (Figure 3a). Anterodistally not far from it occurs another longitudinal scar. These two possibly correlate to the origin of *M. brachialis* as reconstructed in *Anhanguera* (Bennett 2008). Another two much fainter and obliquely oriented scars lie anterodorsal to the purported origin of *M. brachialis*, with dense striations around them (Figure 3d). This area is

likely to be the origin of the lateral head of *M. triceps brachii* (Bennett 2003). These two scars are not seen in *Hamipterus* (IVPP V 18946.1), however, the significance of such differences is unclear.

Isotopic result of sample WE-01

Zircons from tuffaceous sample WE-01 were dated by LA-ICP-MS. The U-Pb isotopic ratios and calculated ages are listed in Table SI (Supplementary Material). Most zircon grains are colorless to light yellow, euhedral, and range from 60 to 180 μm in length with aspect ratios between 2:1 and 5:1. The analyzed zircon grains have high Th/U ratios (0.36-1.97) and mostly oscillatory zoning (Figure 4a), indicating a magmatic origin (Hoskin & Schaltegger 2003). As shown in Figure 4, $^{206}\text{Pb}/^{238}\text{U}$ ages of thirty-five spot analyses range from ~805 Ma to ~131 Ma, with a prominent peak at ~134 Ma. The twenty-four youngest grains give a Concordia age of 134.27 ± 0.36 Ma (MSWD = 2.9, $n=24$; 1σ) (Figure 4a), which is considered the best estimate for the maximum depositional age for sample WE-01.

DISCUSSION

The new humerus (IVPP V 33251) can be undoubtedly referred to Pteranodontoidea based on the warped deltopectoral crest, an unambiguous synapomorphy of the latter clade (Bennett 1989). Pteranodontoidea is composed of two main clades, i.e., Pteranodontia and Ornithocheiromorpha (sensu Andres et al. 2014). IVPP V 33251 could be excluded from Pteranodontia by the absence of the ventral pneumatic foramen immediately distal to the humeral head (Unwin 2003, Bennett 2001, Longrich et al. 2018). Although this foramen is absent in the nyctosaurid *Alcione*, this most probably represents a reversal (Longrich et al. 2018). Thus IVPP V 33251 most likely represents an ornithocheiromorph.

In Ornithocheiromorpha, the morphology of the deltopectoral crest is quite variable aside from its 'warped' nature and probably has taxonomic significance (Figure 5), although this received little interest in previous studies. In *Anhanguera piscator* (Kellner & Tomida 2000), *Barbosania* (Elgin & Frey 2011), USNM 13804 (Bennett 1989) and *Zhenyuanopterus* (Figure 5h), the deltopectoral crest is anteroposteriorly much shorter than proximodistally wide, with a

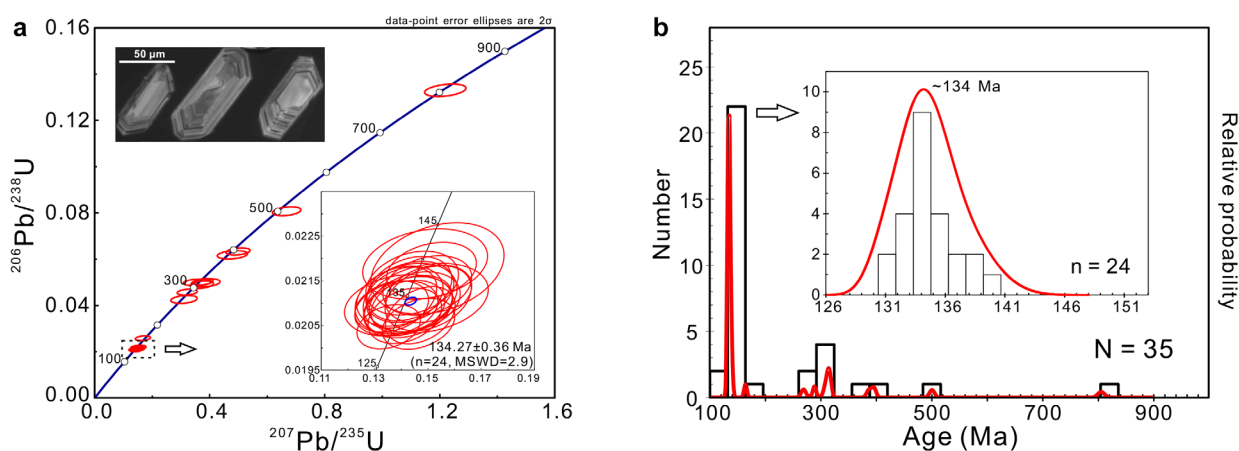


Figure 4. a) U-Pb Concordia diagram for sample WE-01; cathodoluminescence images of representative zircons are shown in the upper left corner; b) histogram of zircon LA-ICP-MS U-Pb ages from sample WE-01.

distally sloping proximal margin. Deltopectoral crests of *Mimodactylus* and *Haopterus* are also much shorter than wide but without a distally sloping proximal margin (Figure 5g). In contrast, deltopectoral crests of the Yixian pteranodontoid IVPP V 26166 (Jiang et al. 2021), IVPP V 33251, *Hamipterus*, *Ikrandraco*, and some istiodactylids like *Istiodactylus sinensis* and *Nurhachius* are instead as long as wide, or longer than wide (Figure 5b–e and g), similar to the condition in pteranodontids (Figure 5a). In addition, deltopectoral crests of *Anhangura piscator* and USNM 13804, as three-dimensionally preserved, possess a distinct anterior deflection near the anterodistal corner (Kellner & Tomida 2000, Bennett 1989) that gives their anterior margin a wavy profile. Such deflection is absent in *Hamipterus*, *Ikrandraco*, IVPP V 33251 and possibly also *Istiodactylus latidens* (Hooley 1913, Wang et al. 2014b, 2017). This feature, however, cannot be confirmed in many ornithocheiromorph taxa

as most specimens are preserved flattened. The pteranodontids *Pteranodon* (Bennett 2001) and *Tethydraco* (Longrich et al. 2018, but see Labita & Martill 2021), and nyctosaurids (Longrich et al. 2018) also do not have such an anterior deflection, suggesting that its absence might be primitive to pteranodontoids.

A posteriorly directed ulnar crest was considered common to pteranodontoids (Bennett 1989, Kellner 2003), as opposed to the ventrally or posteroventrally oriented ulnar crests of non-pteranodontoid pterosaurs. However, among pteranodontoids, a posteroventrally oriented ulnar crest is at least present in IVPP V 33251 and *Hamipterus*. Given that *Hamipterus* is deeply nested within Ornithocheiromorpha as recovered in recent phylogenetic analyses (Andres 2021, Kellner et al. 2019), the presence of a posteriorly directed ulnar crest should have a more complex distribution among pteranodontoids. However, we noted that

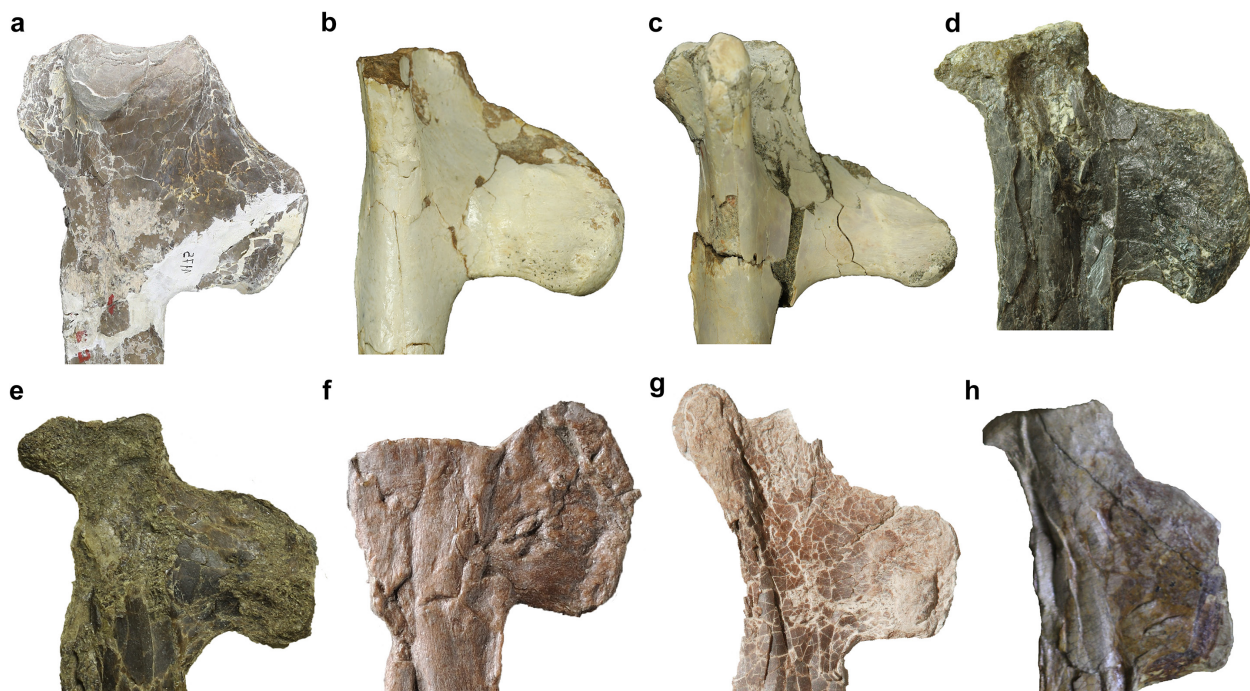


Figure 5. Proximal ends of pteranodontoid humeri. a) *Pteranodon* (YPM 1175, left reversed; available at YPM website); b) *Hamipterus* (IVPP V 18946.1, left); c) IVPP V 33251 (left); d) *Ikrandraco* (IVPP V 18199, left); e) IVPP V 26166 (right reversed); f) *Haopterus* (IVPP V 11726, right); g) *Nurhachius* (IVPP V 13288); and h) *Zhenyuanopterus* (GLGMV 0001, right). Not in Scale.

proximal views of the pteranodontoid humeri have been rarely documented or figured, mainly due to their poor preservations, thus a thorough examination of this feature proves hard at present.

Pneumatic features are also of great importance to pterosaur taxonomy. Among ornithocheiromorphs, *Hamipterus* differs from IVPP V 33251 in its autapomorphic presence of a ventral pneumatic foramen between the humeral head and deltopectoral crest (Wang et al. 2014a), representing a convergence with Pteranodontia and Azhdarchoidea (Unwin 2003, Kellner 2003, Longrich et al. 2018), although we note that this feature is possibly not universal to all the specimens of *Hamipterus*. This pneumatic foramen has otherwise not been reported in ornithocheiromorphs. A dorsal pneumatic foramen was seen in *I. latidens*, *A. piscator* and *Hamipterus* (Kellner & Tomida 2000, Unwin 2003, Wang et al. 2014a), but this feature cannot be assessed in IVPP V 33251. The distally displaced dorsal nutrient foramen seen in IVPP V 33251 is widely present in pterodactyloids like *Elanodactylus* (Andres & Ji 2008), *Pteranodon* (Bennett 2001), *Noriopterus complicidens* (Young 1973), *Tapejara* (Eck et al. 2011) and *Quetzalcoatlus northropi* (Andres & Langston 2021). It was sometimes misidentified as a pneumatic foramen (e.g., Andres & Ji 2008) but probably has little taxonomic value.

IVPP V 33251 represents the first ornithocheiromorph from the Tugulu Group of Wuerho. Comparison with other ornithocheiromorphs suggests that this individual achieved a wingspan of around 3 m at death. The rarity of ornithocheiromorphs in this region might be attributed to taphonomic biases, or represent true signals, which are not mutually exclusive. Taphonomic biases could result from different sizes, shapes or other properties of the bones. Size-dependent taphonomic biases

have been well documented in fossil records (Brown et al. 2021) and recent bone assemblages (Behrensmeyer et al. 1979). It could not explain the rarity of ornithocheiromorphs in the Tugulu Group, because the humerus reported here (IVPP V 33251) is similar in dimension to those of *D. weii*, whose remains are much more common in the same area. Another possibility remains that, ornithocheiromorph long bones are extremely thin-walled and probably more prone to damage pre-transport or during transportation than the thicker-walled long bones of dsungaripterids. However, although this might account for the scarcity of ornithocheiromorph long bones, the more robust-constructed bones of ornithocheiromorphs like syncarpals, articular ends of long bones and jaws should be similar in preservational potential to those of dsungaripterids. These elements are indeed very common in the Wuerho pterosaurian collection, yet they all pertain to dsungaripterids and none could be referred to Ornithocheiromorpha (Young 1964, Young 1973, pers. obs.). This indicates that taphonomic biases, if ever present, should not be the primary factor. If the relative abundance of ornithocheiromorphs and dsungaripterids in Wuerho represents a true signal, it could be explained by niche partitioning between these two clades. Dsungaripterids were hypothesized to forage along the shore, leaving abundant pterosaur footprints (Xing et al. 2011, Li et al. 2021). In contrast, ornithocheiromorphs, although representing a much more inclusive clade, were generally hypothesized to be piscivorous and commonly inhabit an environment away from the shoreline, with the possible exception of istiodactylids (Bestwick et al. 2018). The Tugulu Group in Wuerho represents a shallow-water deltaic depositional system (Jiang et al. 2008). This environment might favour the preservation of organisms that frequently inhabit the shoreline, such as dsungaripterids.

Although the tuffaceous sample was collected at a distinct site from the previous one (Zheng et al. 2024), they are only two kilometers away and from the same horizon. These two ages are indistinguishable considering the analytical uncertainties of the two dating methods. The new result confirms that the top of the Shengjinkou Formation is middle Valanginian in age and the WPF should be at least in part earlier than the early stage of Jehol Biota in northeast Asia (Yang et al. 2020, Yu et al. 2022). However, the lower and upper temporal constraints of the WPF are unclear, and thus the duration of the WPF is still an open question. Providing that fossil remains of *D. weii*, the most important component of the WPF, have been recorded in all three formations of the Tugulu Group (Young 1973, Zhao 1980, Song et al. 2024) cropped out in Wuerho, there should be no significant faunal turnover within the Tugulu Group in this region, and the WPF might not last for a long period. Zheng et al. (2024) argued that Jehol Biota did not expand as far west as the Junggar Basin, but it is also plausible that the deposition during the age of Jehol Biota, especially its second and third stages (Zhou et al. 2021), is entirely missing in Wuerho, which is marked by the unconformity between the Lower Cretaceous Lianmuqin Formation and the Upper Cretaceous Ailikehu Formation (Zhao 1980).

Dsungaripterids were also reported from the Tugulu Group of other regions of the Junggar Basin. Li & Ji (2010) briefly reported one complete skull of *D. weii* from the Wucaiwan area, the northeastern margin of the basin. A partial skeleton of *Lonchognathosaurus acutirostris* (Maisch et al. 2004, Augustin et al. 2021c), and indetermined dsungaripterid postcranial remains (Augustin et al. 2021a, b) were recovered from the southern margin of the basin. Unfortunately, no radiometric age is available for these two sites. However, the persistence of dsungaripterids in all formations of the Tugulu

Group except for the basalmost Qingshuihe Formation in the southern Junggar basin (Augustin et al. 2021a, b, c), and the existence of *D. weii* in both northwestern and northeastern margins of the Junggar basin provide evidence for coeval deposition of Tugulu Group at these three sites. The Tsagan-Tsab Formation of Tatal, western Mongolia produced numerous remains of another dsungaripterid '*Phobetor*' *parvus* (Unwin & Bakhurina 2000). Shuvalov (2000) suggested a Berriasian–Valanginian age for the stratum based on biostratigraphic correlation, and K-Ar and Rb-Sr datings. Graham et al. (2001) reported two Ar-Ar ages, 131 ± 1 Ma and 126 ± 1 Ma, for the intercalated basalt of the Tsagan-Tsab Formation. More recently, Hasegawa et al. (2018) reported K-Ar ages of 131.1 ± 2.8 Ma and 129.0 ± 2.8 Ma for the basalt layer, which is consistent with the results of Graham et al. (2001). The radiometric ages from the latter two studies demonstrated that the Tsagan-Tsab Formation is Hauterivian, much younger than the Shengjinkou Formation in Wuerho, but presumably coeval with the Huajiying Formation that hosted the early stage of the Jehol Biota (Yang et al. 2020). In combination with the age data from the WPF, dsungaripterids might have thrived for more than 5 million years in East Asia and went extinct before the flourishing of the Jehol Biota. Recently, Averianov et al. (2022) reported a fragmentary wing metacarpal distal end from the Aptian Ilek Formation of western Siberia and referred it to *Lonchognathosaurus*. If true, this would significantly delay the last appearance of dsungaripterids. However, the main ground for this attribution, i.e., an anteroposteriorly oriented ridge on the dorsal condyle, is poorly sampled across pterosaur phylogeny and its taxonomic value needs to be attested.

Pterosaur records of the Berriasian–Valanginian are quite limited as universally

recognized (Barrett et al. 2008, Butler et al. 2013, Dean et al. 2016). Some occurrences, despite first thought to be the earliest Cretaceous, have highly ambiguous ages (e.g., Andres & Norell 2005, Haddoumi et al. 2016). Besides the Tugulu Group, pterosaur remains from this period were also reported from a handful of sites in East Asia, Europe and South America (Table II), dominated by poorly preserved specimens of which the phylogenetic positions were hardly tested by cladistic analyses. Nearly all main clades of Cretaceous pterosaurs except for Pteranodonta, including ctenochasmatoids, ornithocheiromorphs, dsungaripterids and azhdarchoids, have been documented from this

period. Among these, ctenochasmatoids have already diversified during the Late Jurassic and seem resilient to the Jurassic–Cretaceous transition (Tennant et al. 2017). Dsungaripterids are likely endemic to East Asia in the earliest Cretaceous (the age of *Domeykodactylus*-bearing stratum still needs further investigation), and the existence of azhdarchoids during this interval still needs further examination. Intriguingly, the patchy pterosaur fossil records of the lowermost Cretaceous notwithstanding, ornithocheiromorph occurrences have been recorded both in Laurasia and Gondwana, implying its global distribution. Moreover, Ornithocheiromorpha probably has already

Table II. Berriasian–Valanginian pterosaur occurrences beyond identification of Pterosauria or Pterodactyloidea. Taxonomy based on the phylogeny of Andres (2021) and clade definitions utilized therein.

Occurrence	Age	Taxonomy	Reference	Remarks
Matute Formation, Spain	Tithonian–Berriasian	Pteranodontoidea indet. Pterodactyloidea indet.	Puértolas-Pascual et al. (2023)	–
Purbeck Group, England	Berriasian	Ctenochasmatoidea <i>Gnathosaurus macrurus</i> <i>Plataleorhynchus streptorhodon</i> Ctenochasmatoidea indet. Ornithocheiromorpha Ornithocheiriformes indet. Azhdarchoidea ?Azhdarchidae indet. Pterosauria indet. (‘ <i>Doratorhynchus validus</i> ’)	Howse & Milner (1995), Martill et al. (2013)	“ <i>Ornithocheirus</i> species A” (NHMUK PV R 11958) was originally referred to Ornithocheiridae Seeley, 1870 by Howse & Milner (1995), the extent of which is subequal to Ornithocheiriformes Andres 2021.
Münder Formation, Germany	Berriasian	Ctenochasmatoidea <i>Ctenochasma roemeri</i>	Bennett (2007), Abel et al. (2021)	–
Cornet bauxite, Romania	Berriasian	?Dsungaripteridae indet. (or Azhdarchoidea indet.) ?Azhdarchidae indet. Pterodactyloidea indet.	Dyke et al. (2011), Averianov (2014)	The pterosaur remains from Cornet bauxite have highly controversial affinities. Dyke et al. (2011) assigned one rostrum to Dsungaripteridae based on its edentulous tip. Averianov (2014) interpreted the purported alveoli behind the edentulous tip as neurovascular foramina, and accordingly referred it to Azhdarchoidea. Besides, the midline groove in this specimen is not commonly seen on the occlusal surface of the rostrum but the mandibular symphysis. Thus the phylogenetic position of this specimen needs to be revised.

Table II. Continuation.

Hastings Group, England	Berriasian– Valanginian	Ornithocheiromorpha ?Lonchodectidae <i>Serradraco sagittirostris</i> cf. <i>Lonchodraco</i> (or <i>S.</i> <i>sagittirostris</i>) ?Istiodactylidae indet. Anhangueridae <i>Coloborhynchus</i> <i>clavirostris</i> ?Azhdarchoidea indet. (‘ <i>Palaeornis cliftii</i> ’)	Witton et al. (2009), Rigal et al. (2018), Sweetman (2023)	Rigal et al. (2018) placed <i>Serradraco sagittirostris</i> in Lonchodectidae, but this was rebutted by Averianov (2020), who argued that <i>Serradraco</i> did not preserve diagnostic features of Lonchodectidae. The latter hypothesis was proved by the cladistic analysis of Andres (2021). ‘ <i>Palaeornis cliftii</i> ’ (NHMUK PV R 2253) was referred to Lonchodectidae by Witton et al. (2009) and considered to be distinct from Ornithocheiroidea sensu Unwin 2003 (which is roughly equal to Pteranodontoidea sensu Kellner 2003). Lonchodectidae has a controversial phylogenetic position but recently it was generally resolved as a subclade within Ornithocheiromorpha, which is in turn a deeply diverging lineage of Pteranodontoidea sensu Kellner 2003. Averianov (2012) instead considered NHMUK PV R 2253 to be an azhdarchoid. These authors reached the consensus that this specimen did not belong with Pteranodontoidea.
Mengyin Formation, China	Berriasian– Valanginian	Ornithocheiromorpha indet.	Young (1964), Xu & Li (2015)	Young (1964) indicated that a first wing phalanx from Mengyin Formation pertained to <i>Dsungaripterus</i> . However, the conspicuous proximal groove of the extensor tendon process, and the posteroventral pneumatic foramen, suggest its affinity with Ornithocheiromorpha instead of <i>Dsungaripteridae</i> .
Stadthagen Formation, Germany	Early Valanginian	Ornithocheiromorpha Anhangueria indet.	Abel et al. (2021)	–
Tugulu Group, Wuerho, China	Valanginian	<i>Dsungaripteridae</i> <i>Dsungaripterus weii</i> <i>Noriopterus complicidens</i> Ornithocheiromorpha indet.	Young (1964, 1973), this article	–
Rosablanca Formation, Columbia	Late Valanginian	Ornithocheiromorpha Ornithocheiriformes indet. Pterodactyloidea indet.	Cadena et al. (2020)	–
Sao Khua Formation, Thailand	Late Valanginian– early Hauterivian	Ornithocheiromorpha Ornithocheiriformes indet.	Buffetaut (2003), Tucker et al. (2022)	–

diversified during this period as implied by the establishment of several subclades like the Anhangueridae, Istiodactylidae and Lonchodectidae, although the presence of the latter two clades received some controversy (Table II). Nevertheless, this is quite in contrast to the condition in the Late Jurassic, when the fossil records of pterosaurs are much better but no unambiguous ornithocheiromorph has been documented (but see imprecise ages of some pterosaur-bearing strata in Table II).

The drivers for the rapid diversification and dispersal of Ornithocheiromorpha near the Jurassic/Cretaceous boundary remain unclear. Rhamphorhynchids are globally distributed during Late Jurassic (Alarcón et al. 2021) and have a similar piscivorous dietary to most ornithocheiromorphs (Bestwick et al. 2018, 2020). Rhamphorhynchids like *Rhamphorhynchus* and *Angustinaripterus* have elongated conical teeth at the mesial end of their dentition that are likely adapted for fish grasping, reminiscent of some ornithocheiromorphs like *Hamipterus*, *Anhanguera* and *Guidraco*. The morphological and functional convergences of rhamphorhynchids and ornithocheiromorphs imply that the demise of rhamphorhynchids at the Jurassic–Cretaceous transition might provide empty niches subsequently occupied by ornithocheiromorphs. However, that a much wider array of non-overlapping morphotypes, especially regarding the dentition, exist in the Ornithocheiromorpha than in Rhamphorhynchidae or other pterosaur

clades thrived in Late Jurassic (Bestwick et al. 2018), and their markedly distinct body sizes, indicate that the opportunistic replacement of the Late Jurassic pterosaur clades (Tennant et al. 2017) cannot exclusively account for the success of Ornithocheiromorpha during the Early Cretaceous. On the other hand, the uniquely constructed forelimb of ornithocheiromorphs, characterized by a series of modifications of muscle attachments and joint structures, like the dorsoventrally expanded notarial articulation of the scapula (Kellner 2003), warped deltopectoral crest (Bennett 1989) and the “ornithocheiroid carpus” (Unwin 2003, which itself comprises a set of modifications of the syncarpals, and accordingly the articular ends of the antebrachium and metacarpals), was established at deep nodes of Ornithocheiromorpha or Pteranodontoidea. These specializations in the locomotor apparatus are shared by all ornithocheiromorphs and potentially improve their flight efficiency, providing opportunities for them to explore new niches. For example, the warped deltopectoral crest as in IVPP V 33251, compared with the non-warped deltopectoral crest of non-pteranodontoid pterosaurs, alters the orientation of *M. pectoralis*, the principal depressor of the wing, hereby increasing its moment arm about the glenohumeral joint (Figure 6). The increased moment arm of *M. pectoralis* was presumably adapted to holding the wing in a static position more efficiently, which plays a vital role in soaring flight.

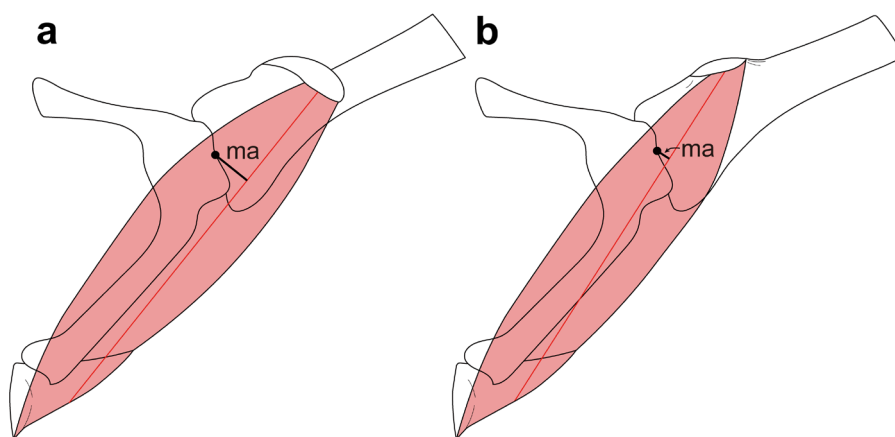


Figure 6. Pectoral regions of pterosaurs in anterior view, with a) a warped deltopectoral crest; and b) a non-warped deltopectoral crest. The black point indicates the glenohumeral joint. The red-shaded area indicates *M. pectoralis* and the red line approximates its average line of action; ma is the moment arm of *M. pectoralis*.

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SUPPLEMENTARY MATERIAL

Table S1.

How to cite

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