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RESEARCH

Recovering lost time in Syria: a gigantic latest Cretaceous azhdarchid pterosaur from the Palmyrides mountain chain

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Abstract
Azhdarchidae was a diverse group of toothless pterosaurs and one of the few lineages of flying reptiles to survive to the end of the Cretaceous. Despite including medium-sized forms, the group is notable for their gigantic representatives, which correspond to the largest known flying animals. Azhdarchids had a nearly global distribution during the Late Cretaceous, including the Arabian Plate, with records in Lebanon and Jordan, such as the iconic *Arambourgiana philadelphiae*. Here, we report the first azhdarchid, and indeed the first pterosaur, from Syria, recovered from early Maastrichtian phosphate deposits of the Palmyrides mountain chain, near Palmyra (Tadmur). It corresponds to a fragmentary left humerus, missing both its proximal and distal ends, with a preserved length of 289 mm. The Syrian pterosaur was exceptionally large, with extrapolations suggesting that, if complete, its humerus would be only about 10% smaller than the holotype humerus of *Quetzalcoatlus northropi*, the largest known pterosaur. The new pterosaur fossil also represents the uncommon record of a giant azhdarchid in marine deposits, confirming that these gigantic animals, though classically considered continental, could also inhabit nearshore environments. The find also underscores the widespread occurrence of gigantic azhdarchids until the latest Cretaceous, just prior to their Cretaceous/Paleogene extinction, and highlights the potential for fossil discoveries in understudied regions such as the Middle East.

Keywords Azhdarchidae · Pterosaurs · Azhdarchids

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Abbreviations

LU-GD	Latakia University–Geology Department, Syria
RTMP	Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada
TMM	Texas Memorial Museum, University of Texas, Austin, TX, USA
YUPC	Yarmouk University Paleontological Collection, Department of Earth and Environmental Sciences, Irbid, Jordan
ZIN PH	Paleoherpetological Collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia

Introduction

Pterosaur remains have been rarely reported from the Arabian Plate, with records in Lebanon and Jordan (Fig. 1; Supplementary data). Non-azhdarchoids were found in the former country, from Cenomanian marine deposits, including the almost complete skeleton of the pteranodontoid

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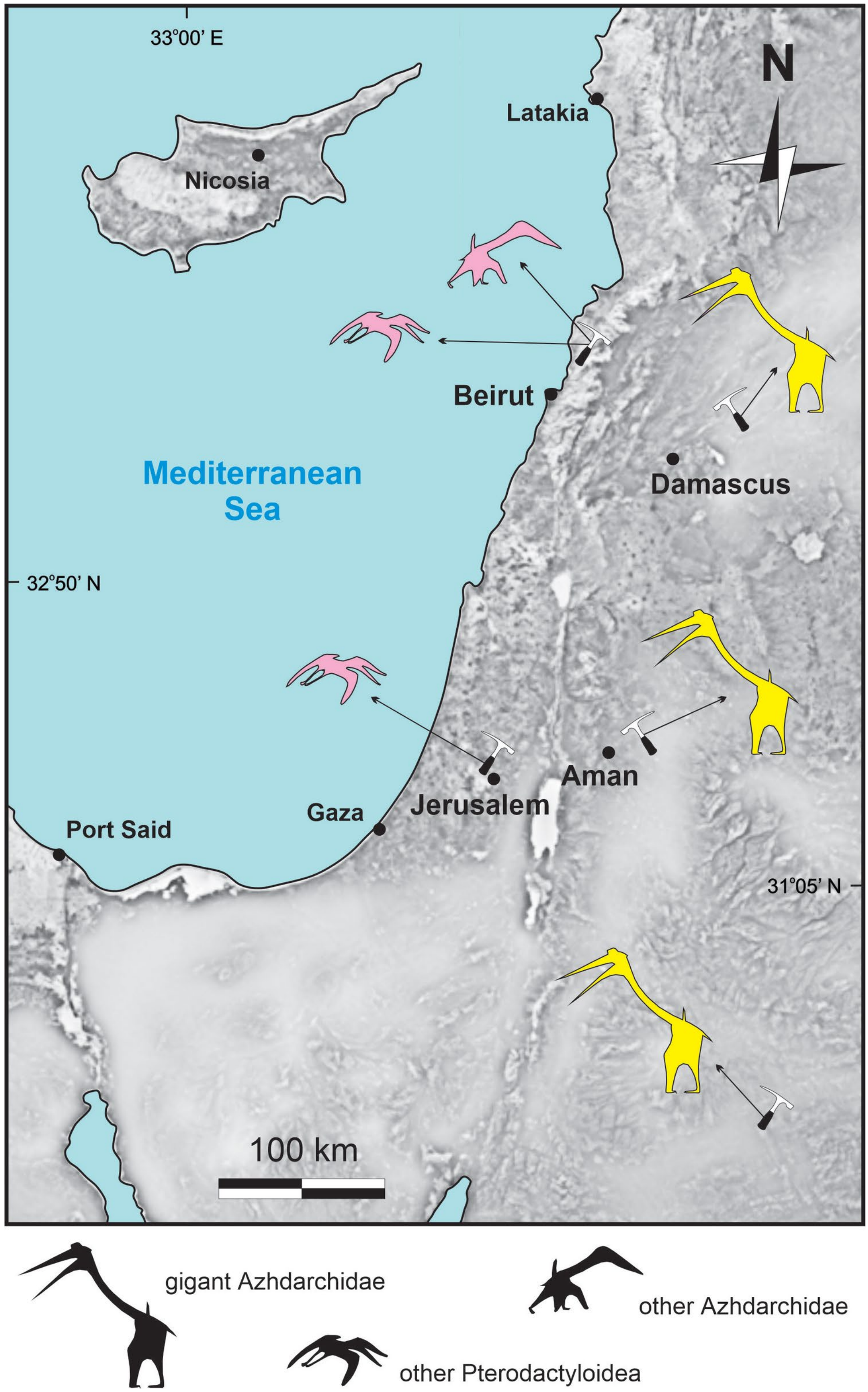

Fig. 1 Map of the Middle east area including all pterosaur records. Pre-Maastrichtian records in pink; Maastrichtian records in yellow

Mimodactylus libanensis from the Hjoûla lagerstätte (Kellner et al. 2019) and a partially preserved ornithocheiroid left forelimb from the Haqel lagerstätte (Dalla Vecchia et al. 2001). In addition, a pterodactyloid hindlimb was reported from the Cenomanian of'Ein Yabrud, north of Jerusalem (Tchernov et al. 1996).

As for azhdarchoids, the almost complete skeleton of *Microtuban altivolans* was described from the early Cenomanian Sannine Formation, Hjoûla lagerstätte, northern

Lebanon (Elgin and Frey 2011). In addition, from the Maastrichtian phosphates of the Ruseifa mine, north of Amman, Arambourg (1959) described the single holotypic cervical vertebra of *Titanopteryx philadelphiae*, later renamed *Arambourgiania philadelphiae* (Nessov et al. 1987; Nessov and Jarkov 1989; Frey and Martill 1996; Martill et al. 1998). Also, from the Ruseifa mine, additional material attributed to that taxon was described by Frey and Martill (1996), Martill and Moser (2018), and Rosenbach et al. (2024). The latter authors also described *Inabtanin alarabia*, a smaller azhdarchoid, based on the partial skeleton of an adult individual. Finally, two endocranial casts recovered from the latest Campanian phosphates of the Mishash Formation, at Oron, were referred to *Arambourgiania* sp. by Lewy et al. (1992), but subsequent analyses suggest that these may in fact represent avian remains (Averianov 2014).

Here, we report on specimen LU-GD 0001, the incomplete humerus of a giant azhdarchid pterosaur, discovered between 2003 and 2004 by local geologist Atieh Sokarieh, from the General Establishment for Geology and Mineral Resources in Damascus, and first examined by geologist Mohamad Jameel Ismail, co-author of this work. The specimen was discovered in the Sawaneh Formation, at the Al Sawaneh el Charquieh phosphate mine B, in the southwestern part of the Palmyrides mountain chain, and represents the first pterosaur record from Syria.

Geological settings

LU-GD 0001 was found at the Al Sawaneh el Charquieh phosphate mine B, along with bony fish remains, shark teeth, and indeterminate vertebrae (pers. obs. by MJI, 2003). The mine is located in the central part of the southwestern Palmyrides mountain chain, approximately 200 km northeast of Damascus and 45 km southwest of Palmyra (Tadmur), Tadmur district, Homs Governorate (Al Maleh and Mouty 1994; Bardet et al. 2000; Alhalabi et al. 2024). The Palmyra fold belt forms a NE-SW chain of narrow ridges and folds extending for about 350 km (Brew et al. 2001; Alhalabi et al. 2024), the erosion of which exposed the Cretaceous age Soukhneh Group, including the deposits bearing the fossils described here, from the Sawaneh Formation (Al Maleh & Mouty 1994; Bardet et al. 2000; Alhalabi et al. 2024).

Al Sawaneh el Charquieh includes two phosphate mines, with approximately thirteen (mine A) and nine (mine B) meters of phosphatic layers within the Sawaneh Formation (Bardet et al. 2000). Mine A has three separate units, the middle of which consists of pinky to rusty phosphates with marine vertebrate remains, including selachians, osteichthyans, and reptiles (Bardet et al. 2000), being separated from the lower member by a distinctive chert. Mine B includes upper and lower phosphate members, separated by a distinctive chert, and is also rich in marine vertebrates (Bardet et al. 2000). The lower member is intercalated with chert beds, whereas the upper member grades into marls and includes a distinctive phosphate bed with calcareous nodules (Bardet et al. 2000; pers. obs. by MJI, 2003). LU-GD 0001 was most likely found during soft excavation of the upper member, in which pink stains (also described for the middle unit of mine A), seen as veins in LU-GD 0001, are common.

The Middle East phosphates, including those from Syria, have traditionally been considered late Campanian to early Maastrichtian in age (Henson 1939 in Dubertret 1963; Bolli 1951; Al Maleh and Mouty 1994). Yet, Bardet et al. (2000) reevaluated the Al Sawaneh el Charquieh deposits based on selachian biostratigraphy, restricting their age to the early Maastrichtian. As hinted by Sweida et al. (2010) and Ibrahim (2010), further studies are necessary to more securely determine the age of the Syrian phosphates within the latest Cretaceous.

Systematic paleontology

PTEROSAURIA Kaup 1834

PTERODACTYLOIDEA Plieninger 1901

ORNITHOCHEIROIDEA Seeley 1891 (*sensu* Kellner 2003)

AZHDARCHOIDEA Nessov 1984 (*sensu* Unwin 2003)

AZHDARCHIDAE Padian 1986

Azhdarchidae indet.

Material—LU-GD 0001, a large, incomplete left humerus, missing proximal and distal portions.

Locality and horizon—Al Sawaneh el Charquieh phosphate mine B (34° 12′ 8.63″ N, 38° 2′ 10.46″ E), near Palmyra, southwestern Palmyrides Mountain Chain, Syria; early Maastrichtian Sawaneh Formation, Soukhneh Group (Bardet et al. 2000).

Description

LU-GD 0001 corresponds to an incomplete left humerus (Fig. 2), remarkable for its exceptional size. Proximally, it is broken near the base of the deltopectoral crest, whereas the distal fracture seems placed shortly beyond midshaft. The preserved portion of the bone measures 288.7 mm. The maximal proximal width, measured from the preserved tip of the deltopectoral crest to the opposite margin of the dorsal surface, which would form the base of the humeral head, is 148.31 mm. At midshaft, the anteroposterior width of the bone is 80 mm. Although the element retains its overall morphology and three-dimensionality, erosion of the cortical bone that forms its exceptionally thin walls, particularly along the ventral and posterior surfaces of the shaft, exposed the internal sediment infill. These broken surfaces (especially the proximal one) also reveal that the inner bone

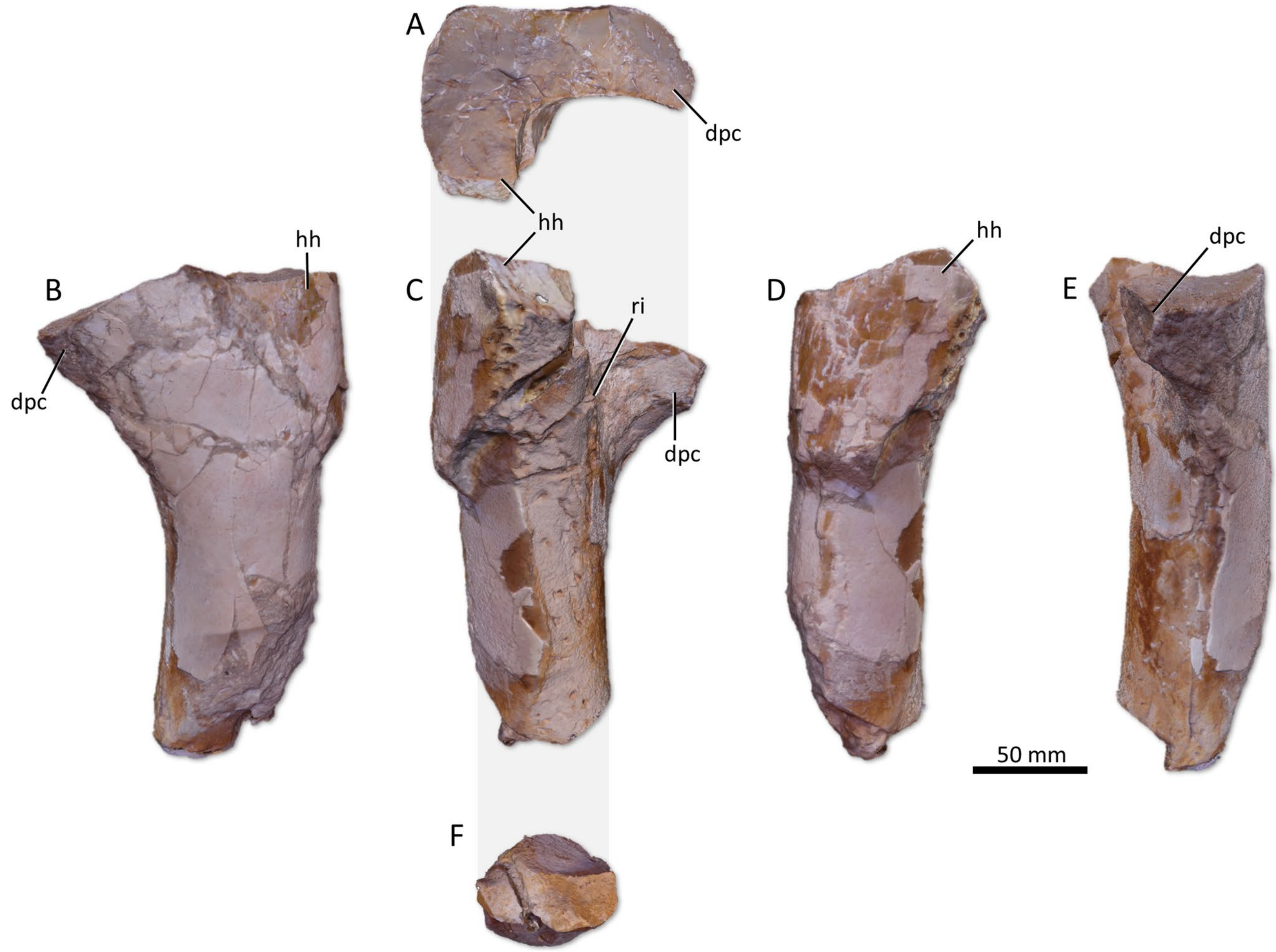

Fig. 2 Azhdarchidae indet., LU-GD 0001, Al Sawaneh el Charquieh phosphate Mine B, southwestern Palmyrides Mountain Chain, Syria; Early Maastrichtian Sawaneh Formation, Soukhneh Group (Bardet et al. 2000). Left humerus in A, proximal; B, anterior; C, posterior; D, dorsal; E, ventral; and F, distal views. Images generated via photogrammetric 3D rendering of the specimen. Abbreviations: dpc, deltopectoral crest; hh, base of humeral head; ri, ridge

is highly pneumatic and reinforced by an intricate web of trabeculae.

In anterior/posterior views, the humerus is slightly bowed ventrally. The deltopectoral crest, albeit with only its base preserved, corresponds to a prominent ventral ridge that projects from the shaft forming a gentle ventral curve. The base of the crest is comparatively thick, but its broken margin suggests that the ventral portion was likely more flattened. Its prominent torsion, as well as the unconstricted hatchet-shape of the crest, is evident in posteroventral view. The ventrally bowed deltopectoral crest, together with the dorsally thickened humeral head, delineates a marked concavity on the posteroventral surface of the bone. The combined deltopectoral crest and humeral head gives an L-shaped profile to the broken proximal surface.

The base of the humeral head would project proximally from the apex of a diagonal ridge that extends across the dorsoventral surface of the proximal portion of the bone. This ridge defines the dorsal margin of the V-shaped posteroventral concavity (see above) and, if complete, would develop distally into the ulnar crest. In anterior view, the base of the humeral head expands to form a dorsal, roughly cubic bulge. In dorsal view, a faint longitudinal ridge originates near the base of the humeral head and extends distally, almost reaching the distal fracture.

The humeral shaft is robust and subcircular in cross-section, its anteroposterior width slightly exceeding the dorsoventral depth. Although it widens proximally to form the deltopectoral crest and the humeral head, the bone does not exhibit a pronounced midshaft constriction.

Discussion

The pterosaur affinity of LU-GD 0001 is evident from the presence of an exceptionally thin cortical bone, coupled with an intricate internal trabecular structure. The extreme pneumaticity of the bone is clearly seen in proximal view, where the fractured surface exposes matrix-infilled pneumatic cavities and their supporting trabeculae. This degree of pneumatization is diagnostic of Pterosauria and exceeds that observed in any other coeval taxon (Martin and Palmer 2014).

LU-GD 0001 lacks both the proximal and distal ends, which are typically the most informative portions of the pterosaur humerus. Nevertheless, the specimen is relatively well preserved and retains its three-dimensional structure. Although precise comparisons are hindered by its missing portions, we consider it reasonable to assign LU-GD 0001 to Azhdarchidae. This is supported by the following combination of arguments: (i) azhdarchids were among the few pterosaurs that thrived during the Late Cretaceous (Longrich et al. 2018); (ii) the preserved portion of LU-GD 0001 is consistent with the morphology of large azhdarchid humeri (see below); and (iii) azhdarchids were the only pterosaurs known to include truly gigantic Late Cretaceous forms (Witton 2010; Witton and Habib 2010).

Apart from Azhdarchidae, only pteranodontid pterosaurs confidently attained large sizes during the Late Cretaceous, although not to the extreme seen in azhdarchids (Witton and Habib 2010). Yet, their humerus usually bears a deltopectoral crest that projects more prominently, its distal margin forming an angle close to 90° (or less) relative to the main axis of the shaft, as displayed, for instance by *Pteranodon longiceps* (Bennett 2001). This contrasts with the condition seen in most azhdarchids, in which the distal margin of the deltopectoral crest forms a gentler slope toward the shaft (e.g., *Quetzalcoatlus northropi*, TMM 41450–3.1; Lawson 1975; Andres and Langston 2021). The deltopectoral crest itself, however, is much more ventrally developed in azhdarchids than in pteranodontids.

Small to medium-sized azhdarchids, such as *Azhdarcho lancicollis* (ZIN PH 12/44) and *Cryodrakon boreas* (TMP 1992.83), typically bear gracile humeri, with anteroposteriorly compressed shafts (Averianov 2010; Hone et al. 2019). The bone becomes increasingly more robust as larger body sizes are attained within the group, so that gigantic azhdarchids possess massive humeri with thick shafts and expanded proximal and distal ends, culminating in the characteristic hourglass-shape of the bone seen in *Q. northropi* (TMM 41450–3.1; Andres and Langston 2021). LU-GD 0001 corresponds to a robust humerus with a comparatively thick shaft, but it appears to lack the pronounced midshaft constriction of *Q. northropi*, although its incompleteness precludes assessing the actual extent of the distal expansion. The humerus of the Moroccan pterosaur *Tethydraco regalis*, considered an azhdarchid by Labita and Martill (2021), is also considerably smaller and displays a slenderer shaft than that of LU-GD 0001. It is also worth noting that the characteristic "hatchet-shaped" deltopectoral crest of nyctosaurids—relatively abundant in Maastrichtian phosphates from Morocco (Longrich et al. 2018)—results in a more pronounced distal curvature of the deltopectoral crest compared to that of LU-GD 0001.

In general terms, LU-GD 0001 compares well with the humeri of giant azhdarchids in size, shaft robustness, and thickness/orientation of the deltopectoral crest. Nonetheless, it has certain peculiarities uncommon among other azhdarchids. Firstly, the base of its deltopectoral crest bends distally more gradually, tracing a smoother slope than in *Q. northropi* and *Hatzegopteryx thambema* (Buffetaut et al. 2002; Andres and Langston 2021). In this respect, it is more akin to *Cryodrakon boreas* (Hone et al. 2019) and *Mistralazhdarcho maggii*, a medium-sized azhdarchid with a particularly stout humerus (Vullo et al. 2018). Furthermore, LU-GD 0001 differs from all known azhdarchids with three-dimensionally preserved humeri by having a shaft that is slightly broader anteroposteriorly than dorsoventrally. Both *A. philadelphiae* (referred specimen YUPC-RUSEIFA-1) and *Q. northropi* possess humeri in which the dorsoventral diameter of the shaft is considerably greater than the anteroposterior diameter (Rosenbach et al. 2024).

We refrain from estimating wingspan based on such an incomplete specimen as LU-GD 0001. Even estimating the length of the humerus would be tentative, as the Syrian specimen appears to exhibit overall proportions that slightly differ from those of giant azhdarchids with more complete humeri, as highlighted above. Even so, certain morphometric proxies may be useful for comparing the size of LU-GD 0001 with that of more complete specimens, particularly the three-dimensionally preserved holotypic humerus of *Q. northropi* (TMM 41450–3.1). The minimum dorsoventral depth of the LU-GD 0001 shaft, measured near the distal breakage, is 76 mm. In comparison, the midshaft depth of TMM 41450–3.1 is ca. 88 mm (Andres and Langston 2021). At the same point where the dorsoventral depth was measured, the anteroposterior width of the LU-GD 0001 shaft is 80 mm, compared to a width of *ca*. 71 mm in TMM 41450–3.1. Yet, it should be noted that these measurements may not have been taken at equivalent points along the humerus, as the breakage in LU-GD 0001 is at an uncertain position. Although tentative and based on the assumption of isometry, we estimate that the complete humerus (Fig. 3) of the Syrian azhdarchid would be approximately 10% smaller than that of *Q. northropi* (TMM 41450–3.1), which had a wingspan estimated at between 10 and 11 m (Witton and Habib 2010; Andres and Langston 2021). Still, this would make LU-GD 0001 one of the largest pterosaurs known to date.

The trend toward gigantism in azhdarchids increases throughout the Cretaceous, with the largest forms known from the Maastrichtian, e.g., *A. philadelphiae* (Rosenbach

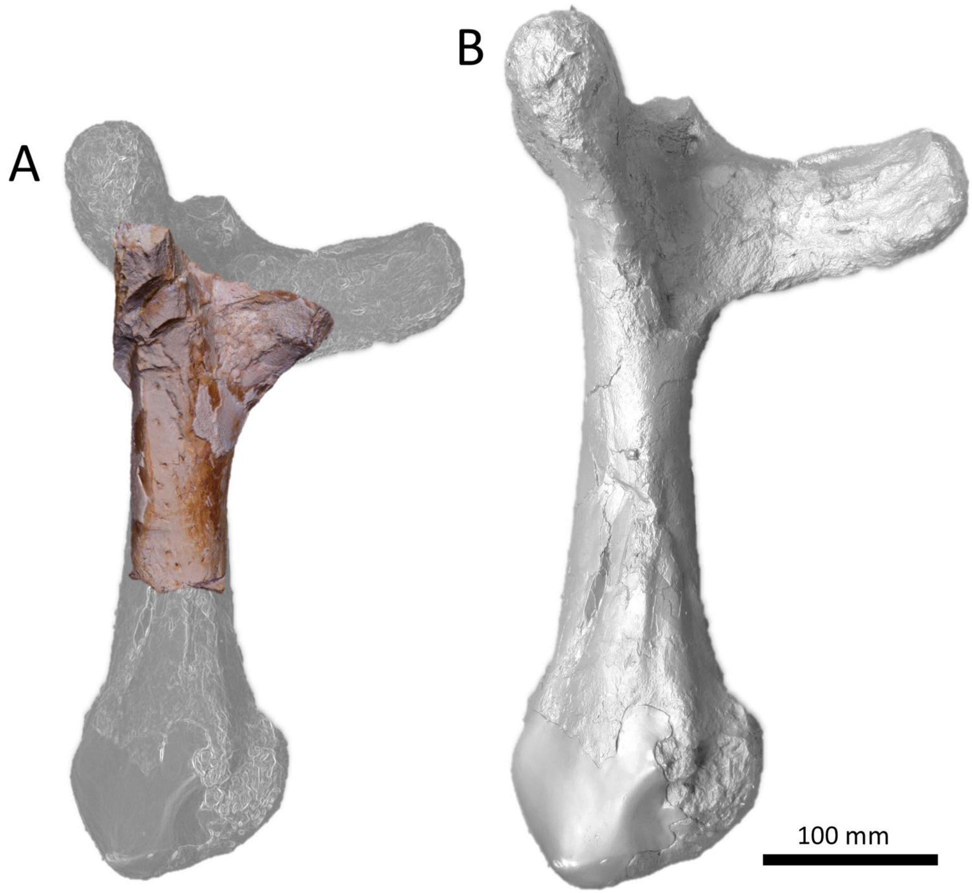

Fig. 3 Azhdarchidae humerus size. Comparison in the size of the Syrian azhdarchid LU-GD 0001 (**A**) (this work) and the holotypic humerus (TMM 41450–3.1) of *Quetzalcoatlus northropi* (**B**)

et al. 2024), *Q. northropi* (Lawson 1975; Andres and Langston 2021), and *H. thambema* (Buffetaut et al. 2002). Only two potentially gigantic taxa (i.e., wingspans exceeding 7 m; see Witton and Habib 2010; Kellner et al. 2013) have been reported from pre-Maastrichtian deposits: *Thanatosdrakon amaru* (Coniacian/Santonian of Argentina; David et al. 2022) and *C. boreas* (Campanian of Canada; Hone et al. 2019). Hence, the Syrian specimen fits to that pattern, providing additional evidence that giant azhdarchids were widespread on the Arabian Plate during the Maastrichtian. More broadly, it underscores the wide occurrence of gigantic azhdarchid pterosaurs just prior to their extinction during the Cretaceous/Paleogene biological crisis (Longrich et al. 2018).

It is noteworthy that the Syrian azhdarchid has been preserved in marine deposits, since the Syrian phosphates are part of the Late Cretaceous-Early Paleogene "Mediterranean (Tethyan) Phosphogenic Province," which nowadays crops out from the Middle East, across north Africa, up to nearshore basins in northeastern Brazil (e.g., Notholt 1985, Matsuda and Viviers 1989; Lucas and Prévôt 1996). With a plethora of marine vertebrates already described from Al Sawaneh el Charquieh phosphate mines (Bardet et al. 2000, Alhalabi et al. 2024), this new discovery mirrors the situation already seen in the phosphates of both Jordan, with *A. philadelphiae* (Frey and Martill 1996) and *I. alarabia* (Rosenbach et al. 2024), and Morocco, with *Phosphatodraco mauritanicus* (Pereda-Suberbiola et al. 2003) and *Tethydraco regalis* (Longrich et al. 2018). As already suggested by Labita and Martill (2021), these occurrences add to previous evidence that azhdarchid pterosaurs were not strictly continental animals, suggesting that these pterosaurs probably also lived near the coastlines of the Afro-Arabian Platform.

Conclusions

Despite the incompleteness of the Syrian azhdarchid (LU-GD 0001), it is significant given its size and geographic provenance. Firstly, it corresponds to one of the largest known pterosaurs and the first pterosaur found in Syria, adding to previously documented Middle East records from Jordan and Lebanon. It is also an additional record of an azhdarchid from marine strata, adding to the evidence that these gigantic animals were not strictly continental, but also able to live near the coastlines. The Syrian azhdarchid also reinforces the widespread distribution of those gigantic pterosaurs just prior to their extinction at the end of the Cretaceous. Finally, it is a witness that the Palmyrides phosphate mines of Syria are continuously yielding important fossil specimens, so that their exploration is likely to uncover further new finds, expanding our understanding of the Middle East ancient life.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00114-025-02032-9.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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