PALÆO VERTEBRATA

Pterosaurs (Pterosauria) from the Cerro del Pueblo Formation (Late Campanian) of Coahuila, Mexico

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Abstract: The Late Campanian Cerro del Pueblo Formation, located in southeastern Coahuila, Mexico, has produced a diverse array of vertebrate fossils. However, pterosaur remains from this unit are notably scarce. In this study, we describe new pterosaur material from the formation. The specimens include a fragmentary vertebra identified as belonging to an indeterminate, but derived pterodactyloid, along with the distal condyle of a left metacarpal, referable to an azhdarchoid pterosaur, and a left manus print. While these specimens provide additional evidence of pterosaur presence in the region during the Late Cretaceous, their fragmentary nature limits precise taxonomic and ichnotaxonomic identification. Nevertheless, they highlight the potential for future discoveries that could refine our understanding of the diversity and distribution of pterosaurs in Mexico.

Keywords: Pterosauria, Pterodactyloidea, Azhdarchoidea, Coahuila, Mexico.

Submitted 24 February 2025, Accepted 23 October 2025
Published Online 21 November 2025, doi: 10.18563/pv.48.2.e1

INTRODUCTION

Pterosaurs were among the most successful groups of Mesozoic tetrapods (Nunes and Costa, 2021), with a global distribution (e.g. Barrett *et al*., 2008). Pterosaurs appeared during the Late Triassic 228 million years ago and disappeared 66 million years ago at the end of the Cretaceous. They were the first tetrapods to evolve powered flight with a unique membraneous anatomy of the flight apparatus (Witton, 2013). In the context of high-performance powered flight, the bones of pterosaurs were pneumatic and exceedingly thin-walled, reinforced by thin and hollow trabecular struts.

Some of the most diverse pterosaur faunas are documented from the Late Jurassic of Germany, the Early Cretaceous of Brazil and China, and the Late Cretaceous of North America (Wang *et al*., 2014). In addition to their fossil remains, pterosaur tracks have been found in many parts of the world, including Australia, China, France, and the United States (Lockley *et al*., 2008).

Environmental factors may have influenced the distribution of pterosaurs in North America during the Late Cretaceous, with many taxa appearing to be associated with coastal or nearshore environments (Witton, 2010). Despite the overall rarity of their fossil record, pterosaur remains from this interval include *Pteranodon* from the Pierre Shale Formation (Bennett, 1994), *Cryodrakon* from the Dinosaur Park Formation of Canada (Hone *et al*., 2019) and *Navajodactylus* from the Kirtland Formation (Padian *et al*., 1993; Sullivan and Fowler, 2011), as well as fragmentary material from the: Lance, Navesink, Peedee formations and others (Thomas *et al*., 2025). These occurrences indicate that pterosaurs persisted throughout the Campanian, although their diversity and abundance may have been lower compared to earlier periods.

Pterosaur fossils are extremely rare in Mexico and reported from only four localities. To date, only two species of Mexican pterosaurs have been described: the dimorphodontid *Dimorphodon weintraubi* from La Boca Formation (Early-Middle Jurassic) of Tamaulipas (Clark *et al*., 1998 – though some analyses have placed this taxon separate from *Dimorphodon*); and the nyctosaurid *Muzquizopteryx coahuilensis* from the Austin Group Formation (Late Cretaceous: Cenomanian-Coniacian) of Coahuila (Frey *et al*., 2006), from which an ornithocheirid has also been reported (Frey *et al*., 2020). In addition, pterodactyloid material has been described from the Tlayua Quarry (Early Cretaceous: Albian), near Tepexi de Rodriguez, Puebla (Frey and Stinnesbeck, 2014). Some indeterminate long bone fragments from pterosaurs have been reported from the Cerro del Pueblo Formation (Late Cretaceous: Upper Campanian) (Rodriguez-de la Rosa, 1996; Frey and Stinnesbeck, 2014; Rivera-Sylva *et al*., 2019). The most recent evidence of pterosaurs from Mexico are tracks from Las Encinas Formation (Late Cretaceous: Maastrichtian) of Coahuila (Stinnesbeck *et al*., 2016). The tracks report by Rodriguez-de la Rosa (2003) for the Cerro del Pueblo Formation were wrongly dated and they belong to the Maastricthian Cañón del Tule Formation (Aguillon-Martínes, 2010), making the track from this paper the first report of a pterosaur track for the Cerro del Pueblo Formation.

New material from the Cerro del Pueblo Formation is described in this paper and expands the record of pterosaurs in this region and contributes to a broader understanding of their distribution during the Late Cretaceous.

Abbreviations- CPC = Colección Paleontológica de Coahuila, Saltillo, Mexico; **MUDE** = Museo del Desierto, Saltillo, Mexico; **TMP** = Royal Tyrrell Museum of Palaeontology, Drumheller, Canada.

GEOLOGICAL SETTING AND PALEOENVIRONMENT

The Difunta Group is located in the northeastern Mexican states of Chihuahua, Coahuila, and northeastern Nuevo León. This sedimentary sequence, dating from the Late Campanian to the Eocene (Soegaard *et al*., 2003), was deposited under deltaic conditions, representing marsh, lagoonal, and eulittoral to shallow marine environments (Eberth *et al*., 2004). The delta system drained eastward into the ancient Gulf of Mexico.

The Cerro del Pueblo Formation constitutes the basal unit of this sequence. It has a thickness of 162 m, increasing westward to 445 m between Saltillo and Rincón Colorado (Eberth *et al*., 2004). Strontium isotope dating has established an absolute age of 73 ± 1 Ma, placing it in the latest Campanian (Vogt *et al*., 2016).

The depositional environment of the Cerro del Pueblo Formation was influenced by cyclic fluctuations in paleoenvironments, ranging from intermittent shallow marine and brackish to freshwater or even subaerial conditions. The widespread occurrence of oysters throughout the formation suggests continuous mixing of saltwater and freshwater, leading to recurrent brackish conditions with variable salinity levels (Vogt *et al*., 2016).

The stratigraphic sequence exposed at La Parrita (Fig.1) consists of alternating layers of sandstone, siltstone, and shale, reflecting a dynamic depositional history. The lower portion contains ochre-gray shales with marine fossils such as the ammonite *Sphenodiscus*, indicating a connection to the Parras Shale (Vivas-González, 2013). Overlying this, siltstone layers rich in oysters suggest brackish conditions, while massive sandstone beds with abundant gastropods indicate a transition to a coastal marine setting. Higher in the sequence, thick shale deposits with a diverse fossil assemblage, including gastropods (*Cerithium nodosa*, *Lissapiopsis* sp.), oysters (*Flemingostrea* sp.), wood fragments, and vertebrate remains, point to an estuarine environment (Vivas-González, 2013; Stinnesbeck and Frey, 2014; Vogt *et al*., 2016). The uppermost portion consists of alternating shale and sandstone beds, with some units containing bivalves (*Inoceramus vamuxemi*), while others are devoid of fossils.

The alternating sedimentary deposits at La Parrita indicate that the locality experienced multiple marine regression and transgression events within a low-gradient depositional setting on a homogeneous coastal plain. This interpretation aligns with observations from other localities associated with the Cerro del Pueblo Formation (Eberth *et al*., 2004).

Table 1. Measurements of CPC 3093 and CPC 3094 in mm.

	CPC 3093	CPC 3094
Maximum length	12.4	26.8
Maximum height	7.5	24.6
Maximum width	7.0	17.5
Transverse diameter of the shaft	--	11.1

MATERIAL AND METHODS

The material described here was discovered by surface collecting during the 2001 to 2005 field seasons. The specimens are housed in the Colección Paleontológica de Coahuila at the Museo del Desierto in Saltillo, Coahuila. They were measured using a digital caliper, and a cloth measuring tape for circumference.

Photographs were taken with a Canon EOS Rebel T2i with a Canon Zoom Lens EF 35-80mm 1:4-5.6 III with filters 1-3 for close-ups.

SYSTEMATIC PALEONTOLOGY

Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Pterodactyloidea indet.

Material. Three-dimensionally preserved, small and slightly rolled partial cervical vertebra (CPC 3093).

Horizon and Locality. Cerro del Pueblo Formation (Late Campanian), La Parrita locality, 54 km west of Saltillo; Municipality of General Cepeda, Coahuila, Mexico.

Description. The specimen is the posterior half of a procoelous cervical vertebra preserving both postzygapophyses. The right postzygapophysis is complete while the articular part of the left is broken off. There is no neural spine present (Fig. 2; Table 1).

Discussion. The presence of zygapophyses on the specimen and its generally long and tubular centrum suggests that it was a cervical vertebra, as these processes are only present in the cervical region of the pterosaur vertebral column. However, given the limited material, it is difficult to determine the exact identity of the pterosaur to which this specimen belonged.

Pteranodontoids have cervical centra that are somewhat dorsoventrally compressed and are not close to circular in cross-section (e.g., *Pteranodon* - Bennett, 2001). In this aspect, they are broadly similar to the condition seen in most other derived pterosaur clades in the Cretaceous. For example, the cervical centra in the Dsungaripteridea (e.g., *Dsungaripterus* - Song *et al*., 2024) and Tapejaridae (e.g., *Tapejara* - Eck *et al*., 2011) are also somewhat compressed and are also saddle-shaped with there being no strong constriction here in the centrum. In contrast, the cervical centra of the Chaoyangopteridae tend to be longer and more circular in cross-section and lack postexapophyses (e.g., *Jidapterus* - Dong *et al*., 2003; *Meilifeilong* - Wang *et al*., 2023). The condition seen here is closest to that of the Azhdarchidae where the animals present long and cylindrical cervical centra that often have postexapophyses (e.g., see Thomas *et al*., 2025). Given the very fragmentary nature of the material we refrain from a more confident referral, but this specimen is a closer match for an azhdarchid cervical than other Late Cretaceous pterosaur clades.

Azhdarchoidea Nesov, 1984
Azhdarchoidea indet.

Material. Three-dimensionally preserved distal articular condyle of a left metacarpal IV (CPC 3094).

Horizon and Locality. Cerro del Pueblo Formation (Late

Campanian), La Parrita locality, 54 km west of Saltillo; Municipality of General Cepeda, Coahuila, Mexico.

Description. A pneumatic foramen lies just distal to, and slightly dorsal to, the preaxial root of the intercondylar groove. The intercondylar groove itself spirals slightly horizontally around the end of the condyle. Posteriorly, the dorsal and ventral halves of the condyle enclose the deep U-shaped intercondylar notch (Fig. 3; Table 1).

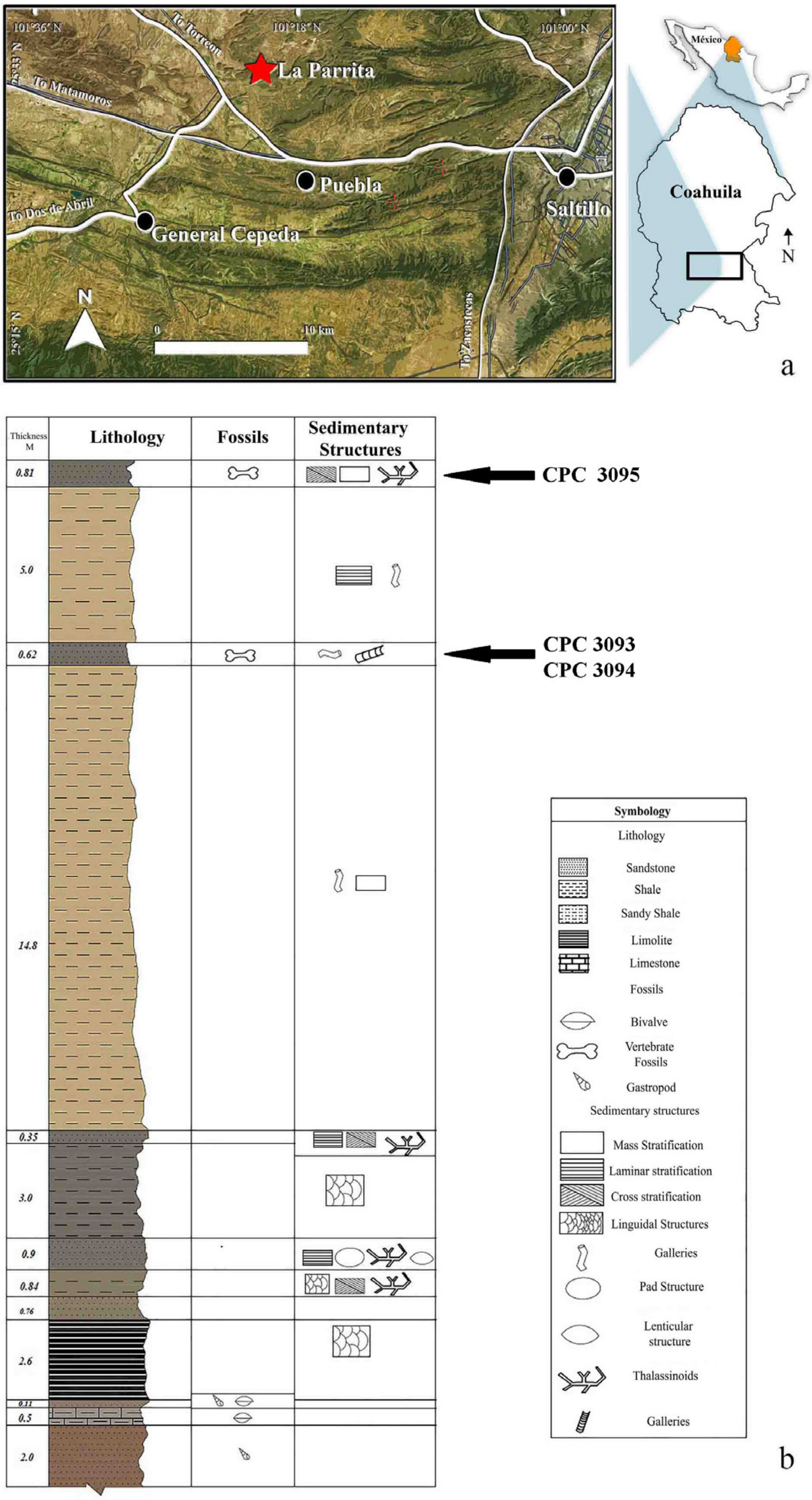

Figure 1. a) Map showing location of pterosaur locality; **b**) Stratigraphic column of La Parrita in southern Coahuila, Mexico.

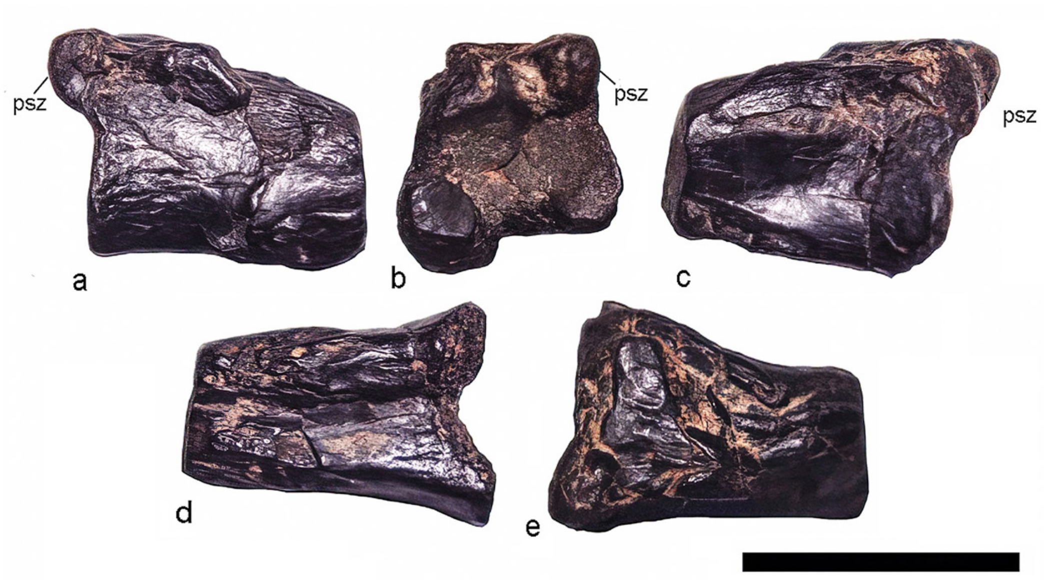

Figure 2. Cervical vertebrae (CPC 3093) in: **a**) right lateral; **b**) caudal; **c**) left lateral, d) dorsal, and e) ventral views. Scale = 1 cm. Abbreviation: psz = postzygapophysis.

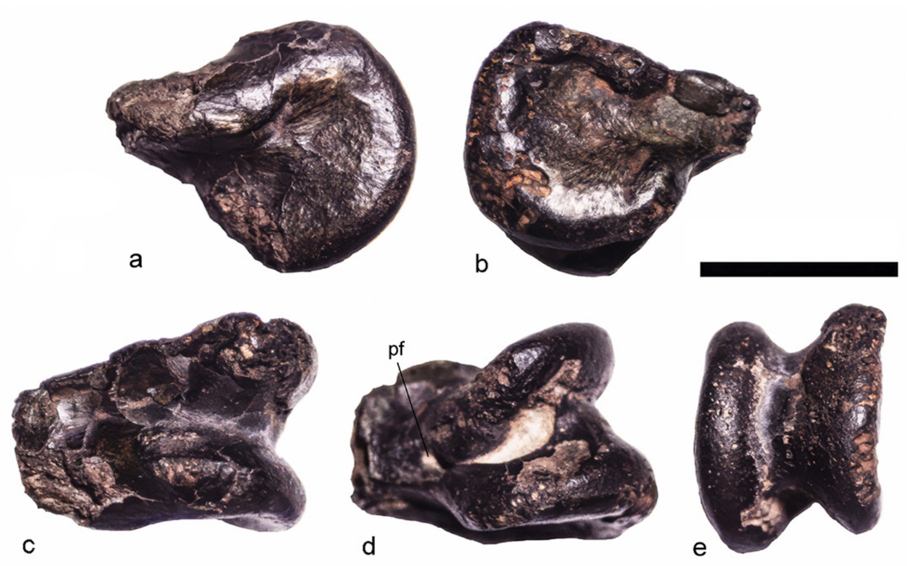

Figure 3. Left metacarpal IV (CPC 3094) in: **a**) right lateral; **b**) left lateral; **c**) dorsal, **d**) ventral, and **e**) cranial views. Scale = 2 cm. Abbreviation: pf = pneumatic foramen.

Discussion. The general morphology of the condyle aligns with that of azhdarchids, displaying the typical elongation and robust structure associated with azhdarchid pterosaurs. The spiralled intercondylar groove is seen in e.g. *Quetzalcoatlus* (Kellner and Langston, 1996; Andres and Myers, 2013), and *Cryodrakon* (Godfrey and Currie, 2005; Hone *et al*., 2019; Fig. 4), though in *Quetzalcoatlus* (Andres and Myers, 2013) and *Azhdarcho* (Averianov, 2010) it tends to be more transversely straight rather than helicoidal.

The pneumatic foramen observed in our specimen is noteworthy, as it has been inconsistently reported in azhdarchid metacarpals. Although pneumaticity is a hallmark of pterosaur postcranial anatomy (Claessens *et al*., 2009), its presence in the distal portion of metacarpal IV suggests potential variation in air sac distribution within Azhdarchidae (Witton and Naish, 2008), though it is present in at least one other azhdarchid *Azhdarcho*, in this position (Averianov, 2010).

Additionally, the U-shaped intercondylar notch is comparable in depth and width to *Quetzalcoatlus* sp., and notably differs to that seen in ornithocheirids this notch is reported to be slightly shallower and more rounded (Frey and Martill, 1996). A specimen described by Martill *et al*. (2013) from the Durlston Formation in the UK also possesses a pronounced intercondylar groove, but it appears less helicoidal than in our specimen, and no mention of pneumatic foramina was made for that material.

Cryodrakon boreas has a more robust condyle, than seen here, but overall the metacarpal of CPC 3094 is comparable in both size and overall morphology to this Campanian taxon. CPC 3094 is similar to the metacarpal seen in *Montanazhdarcho minor*, a species recovered from stratigraphic layers in Montana, which are considered time-equivalent to those from the locality where CPC 3094 was found. That of *Montanazhdarcho* shares similar dimensional properties, such as the length and the general proportions of the proximal and distal ends, and both specimens

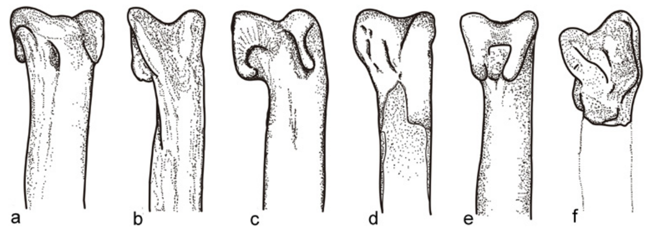

Figure 4. Metacarpal IV in: **a**) *Coloborynchus piscator* (after Kellner and Tomida, 2000); **b**) *Dsungaripterus wei* (holotype; after Young, 1964); **c**) *Pteranodon* (after Bennett, 2000); **d**) *Azhdarco lancicollis* (after Averianov, 2010); **e**) Azhdarchid TMP 87.36.16 (after Godfrey and Currie, 2005); **f**) CPC 3094; Not to scale.

exhibit similar, relatively straight shaft. Additionally, the distal articulation surfaces of CPC 3094 and *Montanazhdarcho minor* are similarly structured, which facilitates a robust articulation with the first phalanx of the wing.

These comparative features strongly suggest that CPC 3094 represents an azhdarchid pterosaur within the same size range as the holotypes of *Cryodrakon* and *Montanazhdarcho* (c. 5 m, based on comparisons to *Zhejiangopterus* – Cai and Wei, 1994), with evidence of their presence in regions of North America now forming part of the Western Interior Seaway.

Pteraichnidae Lockley *et al*., 1995

Pteraichnus sp.

Material. A natural mold of a left manus impression preserved on a sandstone slab. (CPC 3095).

Horizon and Locality. Cerro del Pueblo Formation (Late Campanian), La Parrita locality, 54 km west of Saltillo; Municipality of General Cepeda, Coahuila, Mexico.

Description. The print is much longer than wide (61.94 mm in length and 32.80 mm in width) and exhibits an asymmetrical, tridactyl morphology. The interdigital angles are 65° and 135° between digit I and II, and 135° between II and III. The digits are well-defined, with digit I slightly separated from the others and relatively short (11 mm), including a small claw impression of 3.52 mm, giving a total length of 18 mm. Digit II is slightly longer (22 mm) and lacks an evident claw impression, while digit III is the longest (36 mm) and the most distinctive in shape, being much more slender than the others. The palm impression is faint but discernible. (Fig. 5; Table 1).

Discussion. Manus and pes prints of pterosaurs are extremely rare in the Cerro del Pueblo Formation and are mostly represented by isolated prints. In La Parrita, a single sandstone slab was found containing a natural mold of a left manus print (CPC 3095; Fig. 5). The manus tracks of pterodactyloid pterosaurs are very distinctive consisting, as here, of the impressions of the three free manual digits spread out at wide angles and with digit 1 < 2 < 3 (Mazin *et al*., 2003). However, identifying pterodactyloid tracks to narrower taxonomic groups is difficult as the proportions of pterodactyloid manual digits are broadly similar to one another. The track here is typical of Late Cretaceous pterodactyloid tracks with a long and narrow digit III and shorter and more robust traces for digits I and II (e.g., Jung *et al*., 2022). Ornithocheiroids such as *Pteranodon*, do not have such a long digit III, which is only slightly longer than that of II (Hwang *et al*., 2002), and so suggests this trace

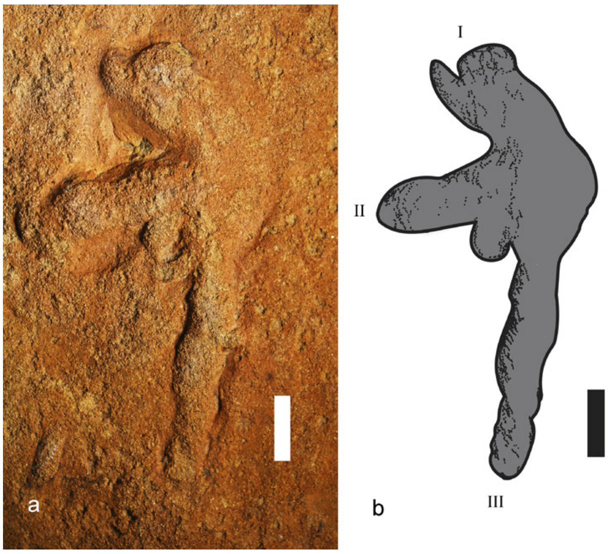

Figure 5. a) Left manus print of an azhdarchoid pterosaur (CPC 3095) from La Parrita site, and **b**) interpretative line drawing. Scale = 1 cm.

was not produced by a member of this group. The manual claw impression that is apparent here for digit I would be large compared to the size of the hand which is not seen in ornithocheiroid taxa and so suggests that this would be from an azhdarchoid clade. Members of other Late Cretaceous clades can show similar anatomy, with, for example the dsungaripterid *Noipterus* (Hone *et al*., 2017: fig 3) having manual digit lengths in the manus that are much closer to one another than seen here, and this is also the case in tapejarids (e.g., *Sinopterus*, Pegas *et al*. (2023), chaoyangopterids (e.g., *Meilifeilong* - Wang *et al*., 2023) and even early azhdarchids (*Zhejiangopterus* - Cai and Wei, 1994). As such, identifying the likely track maker here is very difficult from the available data.

Among Late Cretaceous pterodactyloids, the most common tracks are those of azhdarchids, though these can be diagnosed by the long and narrow pes prints (e.g., see Witton and Naish, 2008) which are absent here (though a similar pes morphology is also present in some other azhdarchoids. However, in the absence of any complete manus for any late Cretaceous azhdarchid, and their extremely common tracks, as well as the preference for terrestrial environments (Witton and Naish, 2008) this is the most likely candidate tracemaker here. Overall, the size of the digits as preserved here in CPC 3095 are comparable to that of the small Chinese azhdarchid *Zhejiangopterus* (Cai and Wei, 1994), which has manual digits of lengths approximately 40 mm, 46 mm and 52 mm (digits I-III respectively) including the unguals. This would suggest that the animal that left the track was comparable in size and would therefore be around 2 m in wingspan.

DISCUSSION

During the Cretaceous, pterosaurs were widespread across North America, with the Western Interior Seaway serving as a major hotspot for pterosaur diversity (Bennett, 2018). Moving towards the end of the Cretaceous with the Late Campanian and into the Maastrichtian, pterosaurs are rather less well known in North America, except for the azhdarchids, though these are typically fragmentary (e.g. see Thomas *et al*., 2025).

While the study of pterosaurs in Mexico is still in its early stages, recent discoveries provide crucial evidence confirming the presence of azhdarchids in the region and extending their known range during the Campanian. These new finds, though fragmentary, suggest that additional material will likely be discovered, potentially offering more taxonomically informative specimens. Moreover, the presence of nyctosaurids and possibly ornithocheirids aligns with known assemblages from nearby regions such as southern Texas (Myers, 2010), reinforcing the idea that the southern part of North America played a key role in the biogeographic distribution of Late Cretaceous pterosaurs.

The discovery of these specimens is particularly significant because they originate from strata that have yielded a diverse assemblage of other vertebrates, including dinosaurs, crocodiles, and freshwater turtles (Rivera-Sylva *et al*., 2019). This assemblage underscores the ecological complexity of the Cerro del Pueblo Formation and highlights the potential for future discoveries to enhance our understanding of Late Campanian ecosystems in northern Mexico.

The scarce record of Mexican pterosaurs throughout the Late Cretaceous most likely reflects the general rarity and fragmentary nature of pterosaur fossils rather than ecological isolation. This pattern is consistent with other Late Cretaceous formations, such as the Hell Creek, where, despite extensive excavation, pterosaur remains are still relatively uncommon (Thomas *et al*., 2025).

CONCLUSIONS

The occurrence of azhdarchid remains from the Cerro del Pueblo Formation extends the distribution of those pterosaurs during the Cretaceous to the southernmost part of North America and supports the claim that Late Cretaceous inland pterosaur faunas were dominated by these highly specialized forms (Witton and Naish, 2008). The specimens here include both small animals, and larger individuals from perhaps 2 m to 5 m in wingspan, which would make them modest in size compared to many azhdarchids, though the ontogenetic stage of the animals described here is not known.

Recent discoveries of pterosaur fossils in Mexico have contributed significantly to our understanding of their diversity, distribution, and evolution in North America. The potential of new discoveries of pterosaurs from Coahuila is very high, and it seems likely that many specimens will become available as research focuses on the large number of localities already known.

ACKNOWLEDGMENTS

We would like to thank Lucía Alfaro-Ortíz (LLF) for providing the photographs and Jorge Ortíz-Mendieta (MHNA) for producing the map. We also appreciate Eberhard “Dino” Frey for his valuable comments on a previous draft of the manuscript. Special thanks are extended to Romain Vullo and an anonymous reviewer for their constructive suggestions, which greatly improved the quality of this work.

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