

A new specimen of nyctosaurid pterosaur, cf. *Muzquizopteryx* sp. from the Late Cretaceous of northeast Mexico

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ABSTRACT

Here we describe a second nyctosaurid pterosaur from the Late Cretaceous laminated limestone deposits of northeast Mexico. The specimen was discovered in the Múzquiz quarry area in northern Coahuila and comprises an isolated right wing skeleton including the humerus, radius/ulna, carpus, wing finger metacarpus and the proximal segment of wing finger phalanx I. The specimen is likely to be a primarily isolated wing, at least the basal wing finger phalanx of which was complete prior to collection. The specimen is referred to cf. *Muzquizopteryx* sp. on account of its humerus morphology, which is coincident with that of *Muzquizopteryx coahuilensis*, although a lack of diagnostic characters at the species level prevents any further identification. Its discovery from the Late Turonian deposits of northern Coahuila near Múzquiz, confirms it as the oldest nyctosaurid discovered to date.

Keywords: *Muzquizopteryx*, Nyctosauridae, Pterosauria, Late Cretaceous, northeast Mexico.

RESUMEN

Se describe un segundo pterosaurio nyctosaurido de los depósitos laminares del Cretácico tardío del Noreste de México. El espécimen fue descubierto en calizas laminares del área de Múzquiz, al norte de Coahuila, México, y consiste de un ala incompleta derecha que incluye: el húmero, radio/ulna, carpo, pteroiide, metacarpo del dedo del ala y la porción proximal de la primera falange del dedo del ala o dedo IV. El espécimen es una parte del esqueleto postcraneano, preservado en dos láminas, y al menos la primera falange del dedo del ala estaba completa antes de la colecta. El espécimen es referido a cf.

Muzquizopteryx sp. con base en la morfología del húmero, el cual concuerda con la de *Muzquizopteryx coahuilensis*, conocido del Turoniano Tardío del norte de Coahuila cerca de Muzquiz. Sin embargo, debido a la falta de caracteres diagnósticos a nivel de especie, no es posible llegar a una determinación más exacta. Este hallazgo del Turoniano Tardío proveniente de los depósitos del noreste, cerca de Muzquiz, correspondería al registro más antiguo de *Nyctosauridae* descubierto hasta la fecha.

Palabras clave: *Muzquizopteryx*, *Nyctosauridae*, *Pterosauria*, Cretácico tardío, noreste de México.

INTRODUCTION

Nyctosauridae comprises two genera, *Nyctosaurus* (Marsh, 1876) and *Muzquizopteryx* (Frey et al., 2006). They were edentulous pterodactyloid pterosaurs identified by the hatchet-shaped deltoid crest of the humerus, a straight pteroid with an articular head almost perpendicular to the shaft, a wing finger composed of three instead of four phalanges, the completely reduced three preaxial digits in the wing, and a scapula that does not contact the supraneural plate (Williston, 1903; Bennett, 2003). Further characters have been proposed by Unwin (2003), who placed the nyctosaurs within Pteranodontidae, and Kellner (2003, 2004), who retains Nyctosauridae as a clade of its own, following Bennett (1994). Because the controversy on the phylogenetic position of nyctosaurid pterosaurs is unresolved to date, the character states presented in the cladistic analysis of Unwin (2003) and Kellner (2003, 2004) cannot be regarded as diagnostic to date.

Nyctosauridae appear to have been endemic to the North American Western Interior Seaway (WIS) south into the Palaeogulf of Mexico. While one single species, *Nyctosaurus lamegoi* (Price, 1953) has been reported from the Gramame Formation (Late Cretaceous, Early Maastrichtian) of the Paraíba Basin, northeast Brazil, its identification as *Nyctosaurus* has not been universally accepted (Kellner, 2003). *N. lamegoi* would be the largest nyctosaur with a wingspan estimated four metres (Price, 1953).

The majority of nyctosaur specimens come from the Santonian (Late Cretaceous) Niobrara Formation, Kansas, U.S.A., and are all referred to the genus *Nyctosaurus* (Marsh, 1876). Three different species have been described: *N. gracilis* (Marsh, 1876), *N. bonneri* (Miller, 1972a, 1972b), and *N. nanus* (Marsh, 1881). Bennett (1994) suggests *N. bonneri* is a junior subjective synonym of *N. gracilis*, both of which are from the Upper Chalk of the Smoky Hills. *N. nanus* comes from the Lower Chalk of the same region and was identified as *Nyctosaurus* by Schoch (1984). Bennett (2003) described two nyctosaurid specimens from the Lower Chalk of Trego County, which both have a huge branching crest on top of the skull. These specimens were referred to *N. gracilis* and the crest was supposed to grow during late ontogeny. However, the specimens have a wingspan of only two metres and could therefore also represent adult *N. nanus* (Everhart, 2009). Before the discovery of the crested specimens, nyctosaurids were thought to have

occipital crests similar to that of a *Pteranodon longiceps* or *P. ingens* (e.g., Wellnhofer, 1991).

In 2006 a small, nearly complete nyctosaurid pterosaur was described as *Muzquizopteryx coahuilensis* (UNAM IMG 8621; Frey et al., 2006). The adult individual had a wingspan of two metres and a bluntly rounded and straight caudally directed occipital crest. Coming from the Lower Coniacian (middle Late Cretaceous) of the El Rosario Quarry, approximately 170 km WNW of the town of Múzquiz (northern Coahuila, Figure 1) *Muzquizopteryx* represented the oldest known nyctosaur prior to the discovery of the new specimen (Figure 2).

Here we report on a second specimen of *Muzquizopteryx* comprising a partial wing skeleton. It is about 20 % smaller than the first specimen and was obtained by a private collector from a local quarry worker. *Muzquizopteryx coahuilensis* is the only valid pterosaur taxon from the Cretaceous of Mexico.

MATERIAL AND METHODS

The specimen is housed in the collection of the Museo del Desierto Saltillo (MUDE), Coahuila (collection number CPC-484). The original plate was split into two parts, but because the original orientation cannot be reconstructed, i.e., which of the two slabs was the bottom one, the plate with the better preservation is here defined as the main slab (Figure 3) and the other one as the counter slab (Figure 4). Besides the initial splitting of the slab, no preparation has been undertaken. Photographs were taken with a Canon D 400 SLR camera and traced with Corel Graphics Suite 12. The traced image of the counter slab was projected below that of the main slab in order to provide an image of the entire specimen (Figure 5).

GEOLOGY AND LITHOLOGY

The Múzquiz area in northern Coahuila, Mexico, is known for its evenly layered laminated limestone and fissile marly limestone that, owing to their platy fabric, are intensively quarried in the region for building faces, flagstones and wall tiles. These deposits are of Cenomanian to Early Coniacian age (Late Cretaceous) and contain vertebrate fossils with exceptionally well-preserved anatomical details of their soft tissues, as well as a diverse number of invertebrates

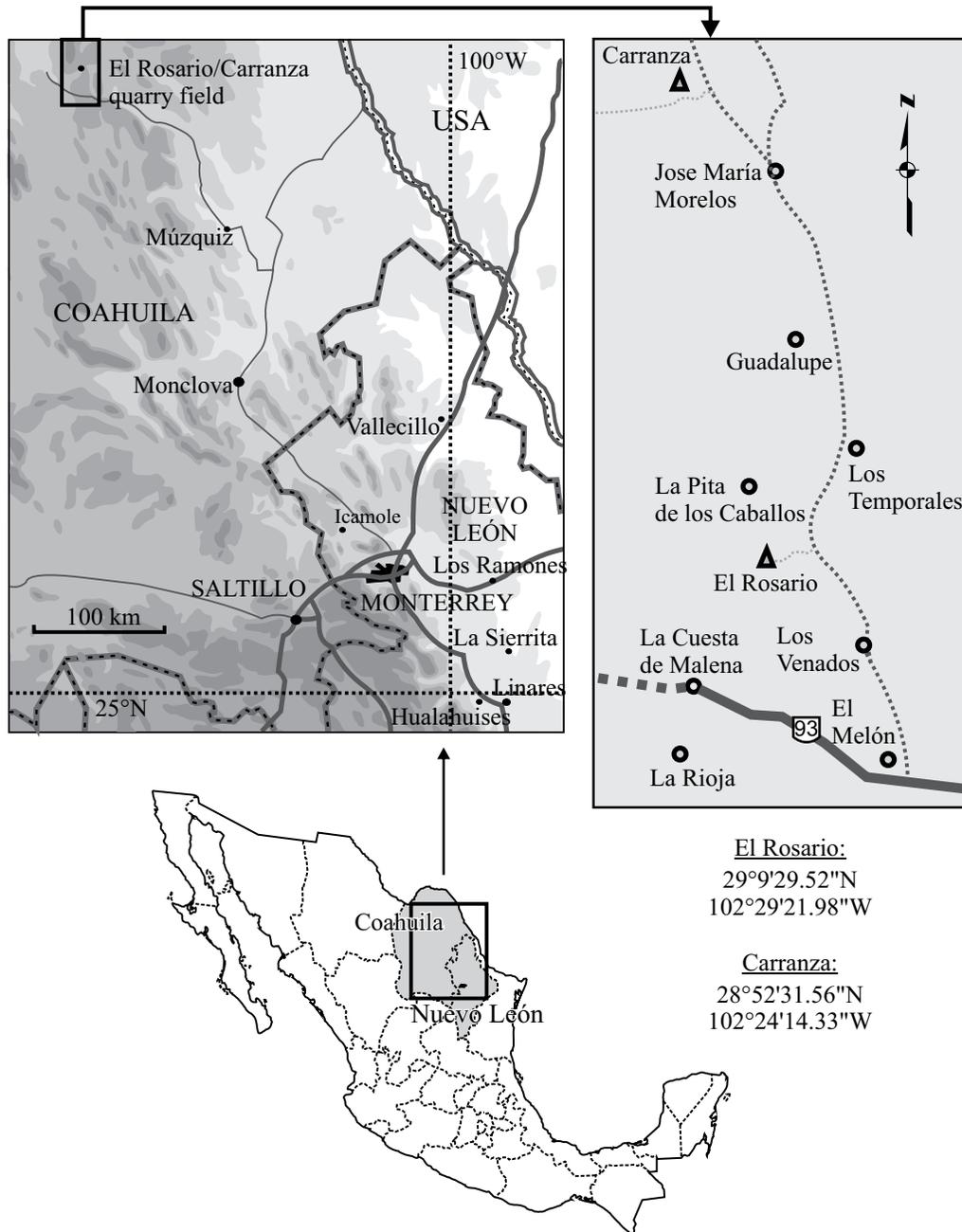


Figure 1. MUDE CPC-848: map of the finding area; asterisks mark the quarries of possible provenience of the new specimen.

(Stinnesbeck *et al.*, 2005). Sediment deposition was in an open marine shelf environment near the southern opening of the WIS, several hundreds of kilometres south of the North American coast line, at a depth of at least 50–100 m (Stinnesbeck *et al.*, 2005)

The new specimen is embedded within a yellow tan slab and counterslab, each about 20 mm thick, of micritic, evenly layered, laminated limestone with internal millimetric bedding which is best described by the German word *Plattenkalk*. According to the lithology and microfossil contents of the host matrix, the specimen most

likely comes from the El Rosario or La Carranza quarry field about 150 km north of Múzquiz, northern Coahuila (Figure 1). The matrix of the new specimen coincides with the lower part of the Yellow Member of the El Rosario section (Stinnesbeck *et al.*, 2005; Frey *et al.*, 2006; Figure 2). A micropaleontological analysis of the host matrix of cf. *Muzquizopteryx* revealed the following planktonic foraminifers: *Archaeoglobigerina cretacea*, *Dicarinella hagni*, *D. imbricata*, *D. primitiva*, *Heterohelix reussi*, *Marginotruncana schneegansi*, *M. sigali*, *Whiteinella cf. baltica*, and *W. brittonensis*. *D. primitiva* and *M. sigali* are

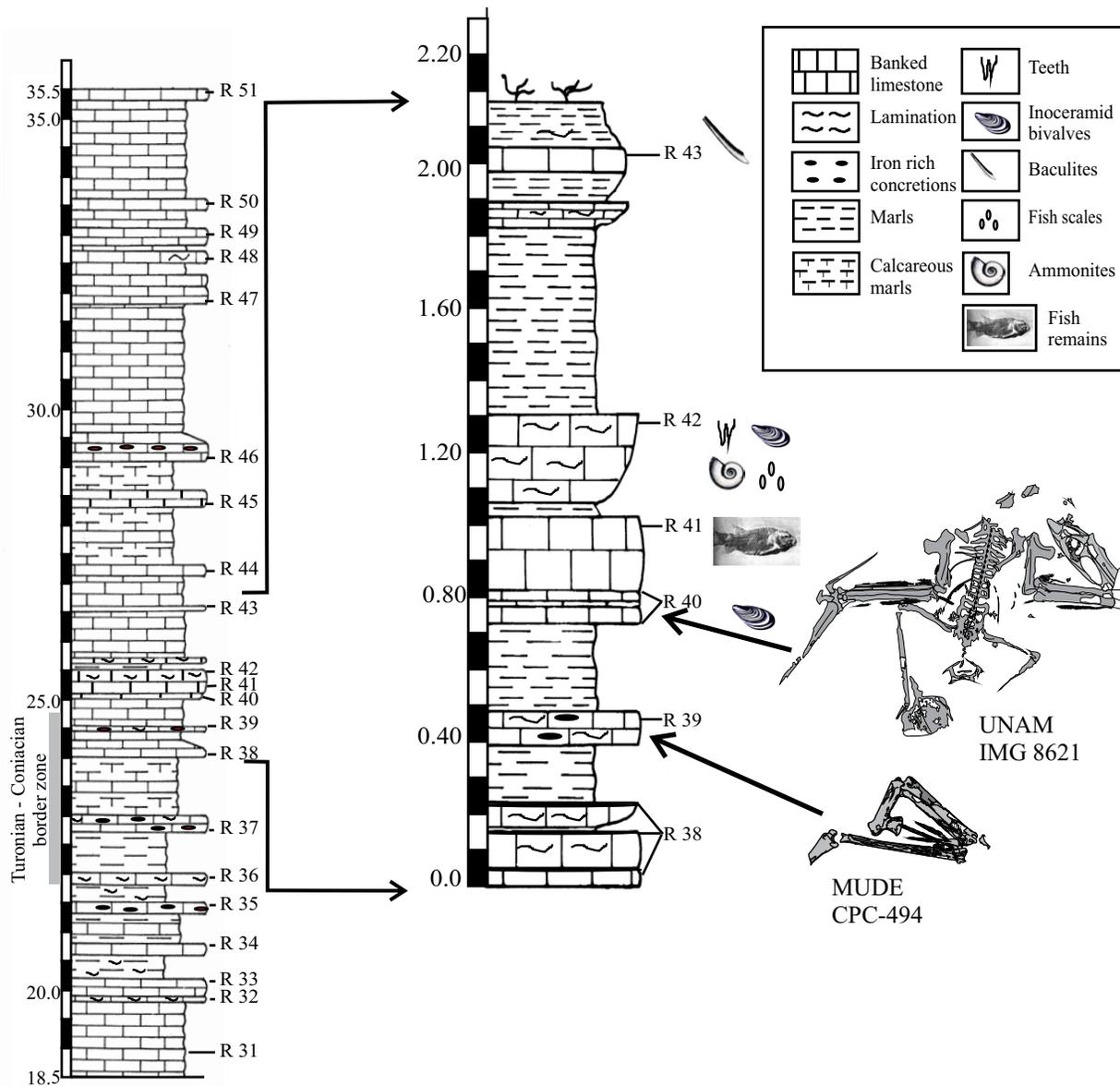


Figure 2. Geological section of the locality El Rosario with the finding horizons of both *Muzquizopteryx* marked, R = reference sample (modified from Stinnesbeck *et al.*, 2005).

diagnostic taxa of a Late Turonian age. This, combined with the absence of *H. helvetica* and *D. concavata* dates the new specimen of *cf. Muzquizopteryx* to a Late Turonian age (Premoli Silva and Sliter 1999) making it the oldest known nyctosaurid pterosaur (Figure 2).

Preservation (Figures 3-5)

Due to the manner in which the plate was split, the humerus, the proximal two thirds of radius and ulna, the distal two thirds of the wing finger metacarpal and the proximal fragment of the wing finger are distributed in the centre of the slab (Figures 3, 4). Most of the carpus and the adjacent thirds of the radius/ulna and wing finger metacarpal

are preserved exclusively on the main slab having left only external moulds on the counter slab (Figure 3). Pieces of compacta are only preserved on the counter slab (Figure 4). Overlapping projections of the main and counter slab indicates that a few chips of bone were lost in the distal third of the ulna and the proximal fifth of the wing finger metacarpal during splitting and possibly subsequent refitting attempts (Figure 5).

The slabs preserve the proximal portion of a right wing skeleton including the humerus, radius and ulna, carpus and the pteroid, wing finger metacarpal (mc IV) and the proximal fragment of the first wing finger phalanx which terminates at the border of the slab and was likely complete prior to collection (Figures 3, 4). All elements lie almost in natural articulation but are bent beyond bone lock. While the elbow

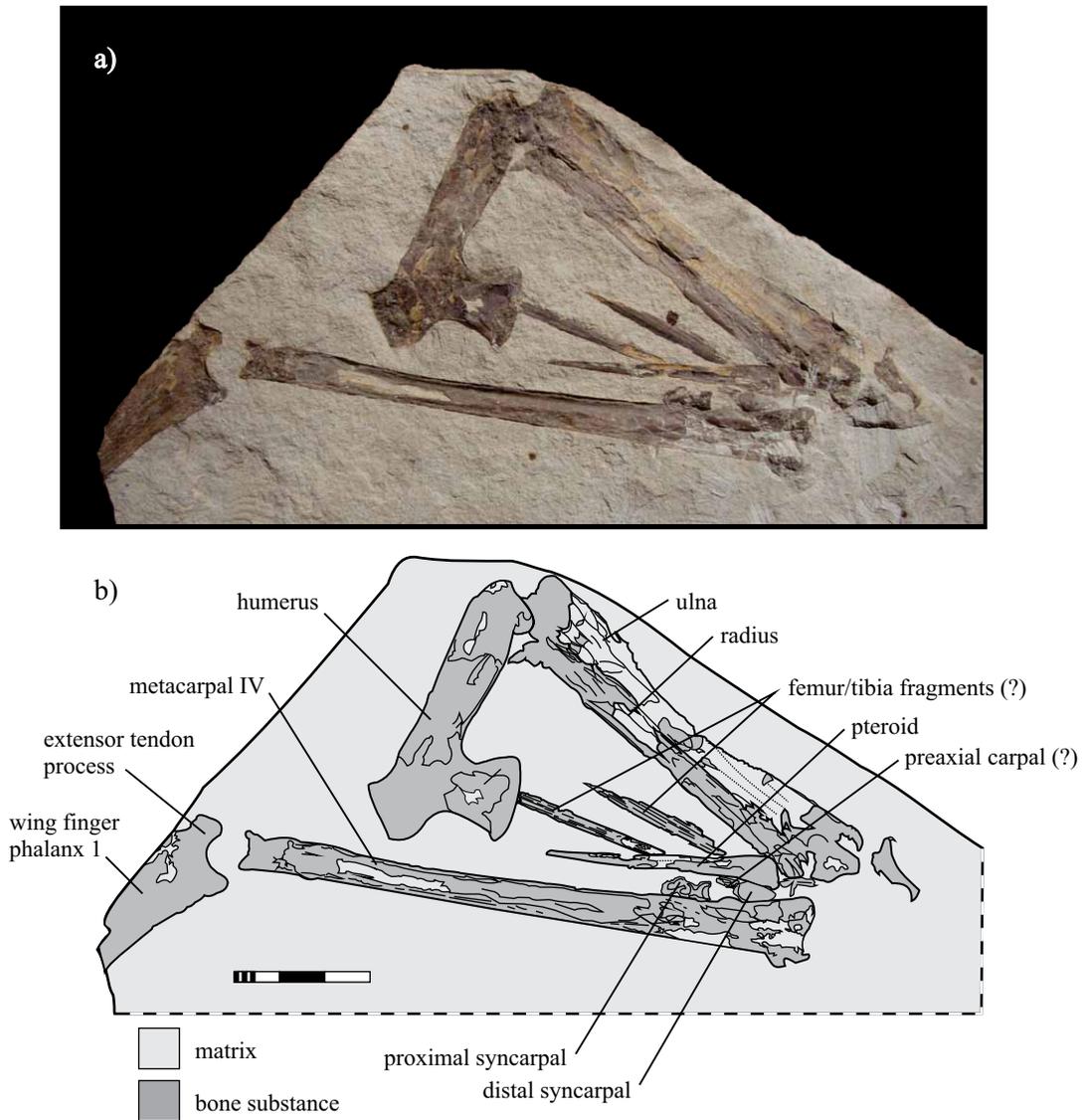


Figure 3. cf. *Muzquizopteryx* sp., main slab showing the right wing skeleton. The slab preserves the profound layer of the bones. a) photograph of the slab, b) line drawing, scale = 30 mm. Note that there is no suture between the extensor tendon process and the shaft of wing finger phalanx 1.

joint is in articulation, the carpus has disarticulated with the proximal and distal syncarpals lying along the ventral margin of the wing finger metacarpal. The proximal syncarpal therefore now lies distal to the other carpals (Figures 3, 5) while the distal syncarpal and the preaxial carpal are wedged between the articular end of the pteroid and the wing finger metacarpal (Figures 3, 5). The pteroid parallels the wing finger metacarpal and has rotated along its long axis so that its articular condyle is now facing cranially. The wing finger metacarpal has rotated 90° around its long axis and is now seen in cranial view lying slightly separated from the fragmented basal wing finger phalanx. Isolated fragments, likely the ipsilateral hind limb, lie parallel to each other between the pteroid bone and radius/ulna at an angle of about 10° to the latter elements (Figures 3-5). All bones show traces of impaction with typical longitudinal break lines. Due to

a late diagenetic compaction, the preserved diameter of the bones is regarded as representing their original dimensions. The humerus lies at an angle of about 75° to radius and ulna, which in turn lie parallel to each other. The metacarpal IV defines an angle of about 40° with radius and ulna and 135° with the first wing finger phalanx (Figure 5).

SYSTEMATIC PALAEONTOLOGY AND DESCRIPTION

Pterosauria Kaup, 1834
 Pterodactyloidea Plieninger, 1901
 Nyctosauridae Marsh, 1876
 cf. *Muzquizopteryx* Frey *et al.*, 2006
 cf. *Muzquizopteryx* sp.

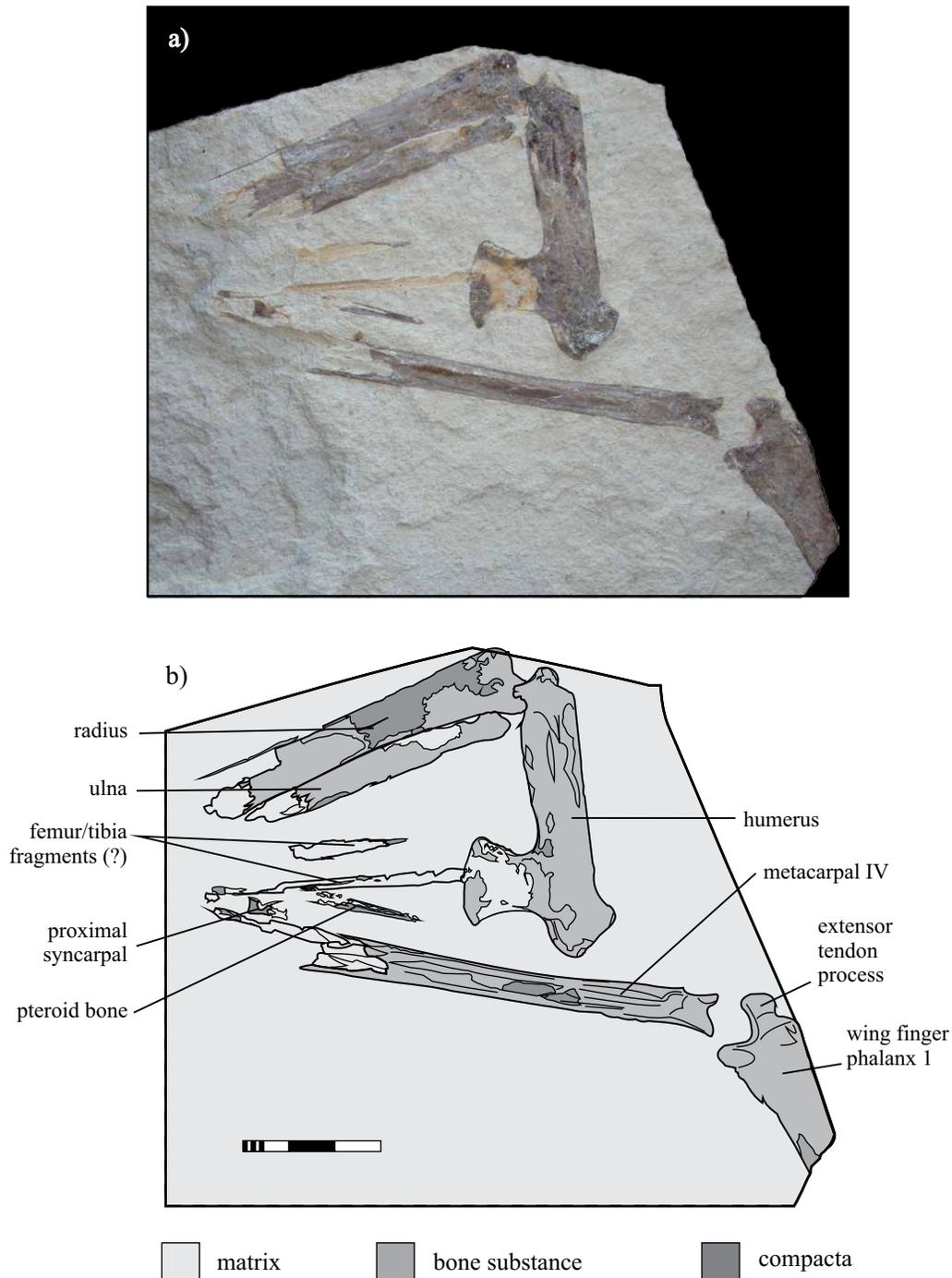


Figure 4. cf. *Muzquizopteryx* sp., counter slab. This is more fragmentary than the main slab but shows the surface layer of the bones. a) photograph of the counter slab, b) line drawing, scale = 30 mm. Note the suture between the extensor tendon process and the shaft of the humerus suggesting that the fusion was incomplete.

The specimen comes from a pterosaur that was 81 % the size of the holotype of *M. coahuilensis* (Figure 6). The humerus is hatchet-shaped with a deltopectoral crest displaying concave proximal and distal margins while the pteroid is straight with a semi-circular articular head, which is off set at almost 90° to the pteroid shaft. Both these features are diagnostic for Nyctosauridae Marsh, 1876 (Figures

3-5). The shape of the humerus coincides with that of *M. coahuilensis* to such detail (Figure 6) that both specimens are likely conspecific, however, the concavity of the caudomedial margin of the pteroid is slightly shallower than in that of *M. coahuilensis*. All other bones are too badly preserved for a direct comparison, but do not show any significant morphological differences when compared to

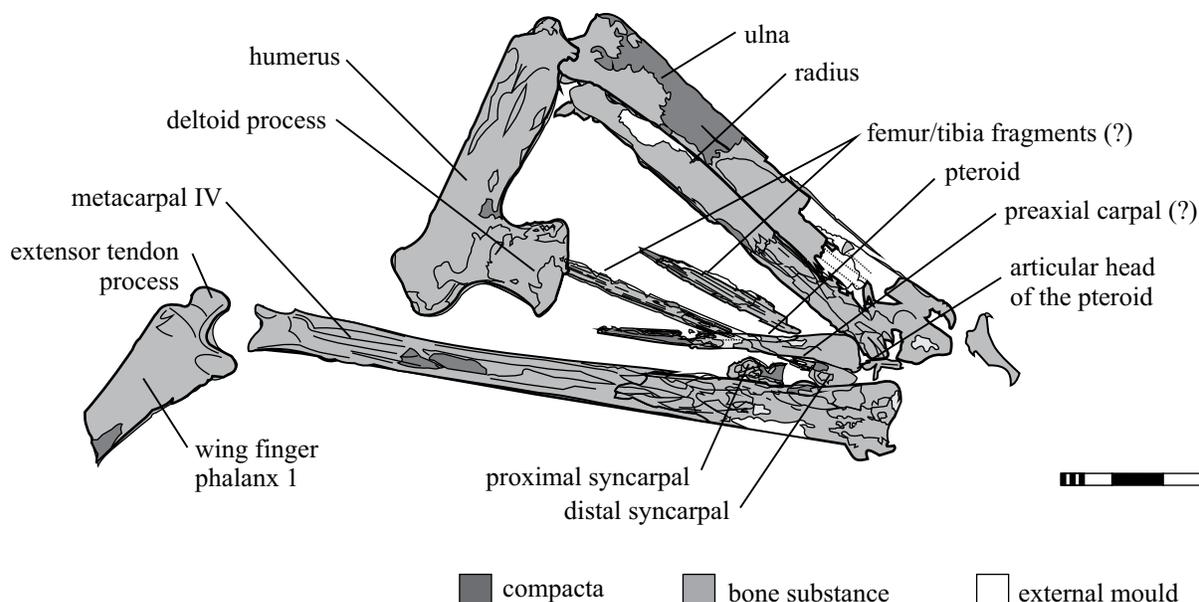


Figure 5. cf. *Muzquizopteryx* sp., projection of main slab and counter slab, scale = 30 mm.

their respective elements in *M. coahuilensis*. Furthermore, the ratios between the humerus and radius/ulna as well as the humerus and pteroid show only minor differences in the two specimens and these may be solely due to their preservation (Table 1). In contrast to the holotype of *M. coahuilensis* there are no mineralized tendons in the new specimen. As the described specimen does not preserve any diagnostic features to refer it to *M. coahuilensis*, but is otherwise morphologically coincident, we refer the new specimen to cf. *Muzquizopteryx* sp.

Description

The description of the material is based on the overlapping projection of the slab and the counter slab (Figure 5). The anatomical directions refer to the inferred flight position of the animal with the wing bones fully laterally extended. The caudal margin of the humeral shaft is straight while the cranial edge is slightly convex, with the deltopectoral crest emerging from the proximal third of this margin of the humeral shaft (Figures 3-6a). The distal margin of the deltopectoral crest is straight but offset from the cranial margin of the shaft by an angle of 55° (Figure 6). The proximal margin of the deltopectoral crest stands at a right angle to the cranial margin of the shaft but forms an angle of about 70° with the caudally inclined neck of the humerus. The cranial margin of the humeral neck is slightly convex. The humeral neck measures one fourth of the length of the shaft and is angled at about 130° against this (Figure 6a). The proximal articular face of the humerus is straight and orientated at 90° to the humeral neck. The distal articulation of the humerus is damaged but shows a fragmentary

distally facing articular condyles, which likely protruded cranially by a maximum of one fifth of the distal diameter of the shaft (Figures 3-6a).

The ulna overlies the cranial margin of the radius although both bones are damaged such that no anatomical features are visible. The absolute length of both bones can only be estimated due to their damaged distal articular ends (Figures 3-5). Due to the partial coverage of the distal syncarpal and the preaxial carpal by the pteroid and the wing finger metacarpal, nothing can be said about their features. The proximal syncarpal is visible in cranial view. The distal margin lies free and shows the convex articulation face for the cranioventral part of the proximal articulation facet of distal syncarpal and the dorsolateral process that articulates with the dorsal face of the distal syncarpal (Figures 3, 5).

Metacarpal IV is exposed in cranial view and shows an S-shaped articular facet for the distal syncarpal, whereby the ventral margin is medially convex and the dorsal margin is slightly concave. The dorsal margin of the shaft is straight while the ventral margin is slightly concave converging distally towards the distal articular end, which is half as wide as the proximal articular surface (Figures 3, 5).

The pteroid shows the typical elongate triangular shape diagnostic of nyctosaurids (Figures 3, 5). Its cranial margin is straight while the caudal one is slightly concave. The concavity of the caudal margin gradually increases proximally. The distal margin of the bone is straight, forming an angle of 104° with the cranial margin, and the transition between the two margins is evenly convex. The articular surface is a tiny semicircular protrusion at the caudodistal corner of the pteroid, which forms one sixth of the lateral margin of the bone.

Of the first wing finger phalanx only the proximal

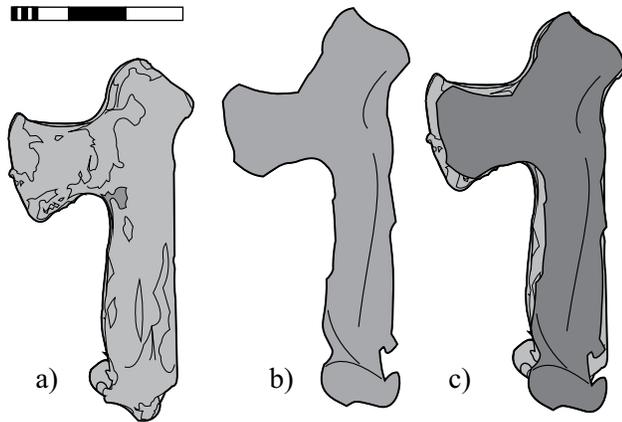


Figure 6. Humerus of cf. *Muzquizopteryx* sp. (a) compared with the right humerus of *M. coahuilensis* (b) drawn to the same scale (= 30 mm). (c) shows the structural coincidence of the two humeri, with the humerus of cf. *Muzquizopteryx* sp. drawn to equal length of that of *M. coahuilensis*.

segment is preserved. The extensor tendon process is internally fused with the shaft of the phalanx (Figure 3) but superficially shows a suture (Figure 4). Otherwise there are no remarkable features on the bone fragment (Figures 3-5).

Two unidentified bone fragments lying parallel to the radius are too thick to represent parts of the distal wing finger phalanges and thus likely come from the ipsilateral hind limb. However, the elements are fragmentary and preserve no osteological features (Figures 3-5).

Only one feature allows a statement on the age of the cf. *Muzquizopteryx* specimen: near complete fusion of the extensor tendon process with the shaft of the first wing finger phalanx (Figures 3, 4). Because the described specimen is only 81 % the size of the holotype of *M. coahuilensis*, a late fusion of the extensor tendon process with the basal wing finger phalanx occurred during the ontogeny *Muzquizopteryx* (Frey and Martill 1998; Bennett 1993; Elgin and Frey 2008). Therefore, the new specimen is osteologically immature and thus likely subadult individual at the time of death.

Taphonomy

The absence of any shoulder girdle remains, the grade of disarticulation and lack of mineralised tendons indicate that the specimen likely represents a primarily isolated fragment (Figures 3-5). The wing presumably separated from a pterosaur carcass in an advanced stage of decay where the main flight musculature was no longer viable. The cardinal ligaments of the wing were, however, still able to hold the bones in a near to natural position. From the status of decay and a comparison with the fully articulated holotype of *M. coahuilensis*, conclusions on the ligament stability are possible at least for this individual. Here the elbow joint is the most stable (Figure 3, 5). The

humerus and the radius/ulna remain in tight articulation with an angle of 75° between the bones. This is less than the articulation angle of the same bones in *M. coahuilensis* and may represent maximum humeroantebrachial flexion. The carpus has been completely disrupted (Figures 3, 5). The position of the syncarpals, the rotation of pteroid and wing finger metacarpal all indicate an advanced state of decay of the carpal ligaments. However, the separation of the carpals suggests that either at least some of the ligaments were isolated from each others and thus could react independently during advancing decay, or that the carpus was damaged by the bite of a predator or scavenger prior to deposition. The separation of the first wing finger phalanx from its articulation with metacarpal IV is explainable by muscular decay where only the massive extensor tendon was still viable. Following this, it is likely that the remains of the dermis and the wing membrane, connecting the fore arm to the body and hind limbs, would have prevented the complete decay of the wing finger. Examples of this style of preservation are common throughout the pterosaur fossil record (Frey et al., 2003; Martill and Frey, 1998; Unwin and Martill, 2007). If the wing membrane was still viable, the wing skeleton would occasionally detach from the body along with the ipsilateral hind limb. It is for this reason that the indeterminate long bone fragments are interpreted here as belonging to the left hind limb.

CONCLUSIONS

The new nyctosaurid specimen, comprised of an isolated fragmentary wing, likely originates from the Turonian limestone quarries of El Rosario or La Carranza 150 km north of Múzquiz, northern Coahuila (Figures 1, 2). While several bones are preserved close to their natural articulations, the carcass is interpreted as having floated on the surface waters for an extended period, allowing for a relatively advanced state of decay. Due to the presence of potential scavengers, however, the scenario of prolonged surface decay remains more unlikely than dismembering by either a scavenger or a predator. Due to the lack of diagnostic characters, the specimen can only be determined on a comparative level, using bone biometry and morphological coincidence. Despite this, it is sufficiently similar to the holotype of *M. coahuilensis* to warrant a referral to

Table 1. Table of measurements (in millimetres).

<i>Muzquizopteryx</i>	holotype	new wing
humerus	81	65.6
radius/ulna	112	98.4
pteroid bone	75.0	52.0
metacarpal IV	?	130.2
humerus : radius/ulna	0.72	0.6
humerus : pteroid	1.1	1.2

cf. *Muzquizopteryx* sp. making it the geologically oldest nyctosaurid discovered pterosaur to date. The specimen also provides evidence of the potential of the Múzquiz area to yield more nyctosaurid pterosaurs in the future.

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