Muzquizopteryx coahuilensis n.g., n. sp., a nyctosaurid pterosaur with soft tissue preservation from the Coniacian (Late Cretaceous) of northeast Mexico (Coahuila).

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ABSTRACT – Here we describe the first near complete and articulated pterosaur from Mexico. It comes from Late Cretaceous (Early Coniacian) laminated limestones of the Austin Group in the vicinity of Muzquiz, Coahuila (NE Mexico). The specimen is named a new genus and species, *Muzquizopteryx coahuilensis* gen. et sp. nov. is referred to Nyctosauridae and represents the earliest known member of this taxon. With a wingspan of about two metres it represents the smallest known adult nyctosaurid pterosaur. The preservation of mineralised tendons and the *in situ* preservation of the carpus allow the reconstruction of some distal arm muscles and the discussion of the orientation of the pteroid bone.

Key words: *Northeast Mexico, Cretaceous, Coniacian, Pterosauria, Nyctosauridae, taxonomy, constructional morphology.*

Muzquizopteryx coahuilensis n.g, n.sp., première occurrence d'un ptérosaure nyctosauride avec des partes molles préservés dans le Coniacien (Crétacé supérieur) du nord-est du Mexique (Coahuila) – Nous décrivons ici le premier ptérosaure subcomplet et articulé du Mexique. Le spécimen provient des calcaires laminés du Crétacé supérieur (Coniacien inférieur) de la région de la ville de Muzquiz, Coahuila (NE du Mexique). Il représente le plus ancien ptérosaure nyctosauride connu, et est attribué à un nouveau genre et une nouvelle espèce, *Muzquizopteryx coahuilensis*. Avec une envergure d'environ deux mètres, c'est le plus petit ptérosaure nyctosauride adulte. La préservation de tendons minéralisés, ainsi que du carpe *in situ*, permet de reconstituer certains muscles distaux du bras et de discuter l'orientation de l'os ptéroïde.

Mots clés: *nord-est du Mexique, Crétacé, Coniacien, Pterosauria, Nyctosauridae, taxonomie, morphologie constructionnelle*

INTRODUCTION

Until now only one single pterosaur species has been described from Mexico. *Dimorphodon weintraubi* from the Early Jurassic La Boca Formation of Tamaulipas (Clark et al., 1998), is based on the fragmentary skeleton of a large rhamphorhynchoid that includes a remarkably preserved pes. Otherwise only undetermined bone fragments from a medium-sized (wingspan about five metres) ornithocheiriod pterosaur are reported from a dinosaur-yielding site at Rincon Colorado some 40 km west of Saltillo in the state of Coahuila (Rodriguez de la Rosa pers. comm., Rodriguez de la Rosa et. al. 1998; EF & MCB pers. obs.). Recently the fragmentary articulated wing of a pterodactyloid pterosaur, also with an estimated wing span of five metres, was found in the plattenkalk of the Tlayúa Quarry in the state of Puebla (EF pers. obs.). Strata at this locality are referred to the Aptian-Albian Tepexi Formation (Martill 1989, Pantoja Alor, 1992, Espinosa-Arrubarrena & Applegate, 1996, Rodriguez de la Rosa & Cevallos-Ferriz, 1998, Kashiyama et al., 2003). Fragmentary pterosaur material has also been reported from the El Gallo Formation (Maastrichtian, Late Cretaceous) in the vicinity of Tijuana (Aranda-Manteca, pers. comm., 2003 to WS). Further remains of pterosaurs comprise beautifully preserved footprints of different types of pterosaurs from the El Pelillal tracksite, Cerro del Pueblo Formation (latest Campanian) of southeast Coahuila (Rodriguez de la Rosa, 2003).

Here we report on the most complete pterosaur specimen found to date in Mexico. It was discovered in the El Rosario Quarry about 170 km WNW of Melchor Muzquiz in northern Coahuila (fig. 1A). The quarry owner sold the specimen to a stoneyard manager, who, in turn, transferred it to a mining manager. Slab and counterslab found a decent
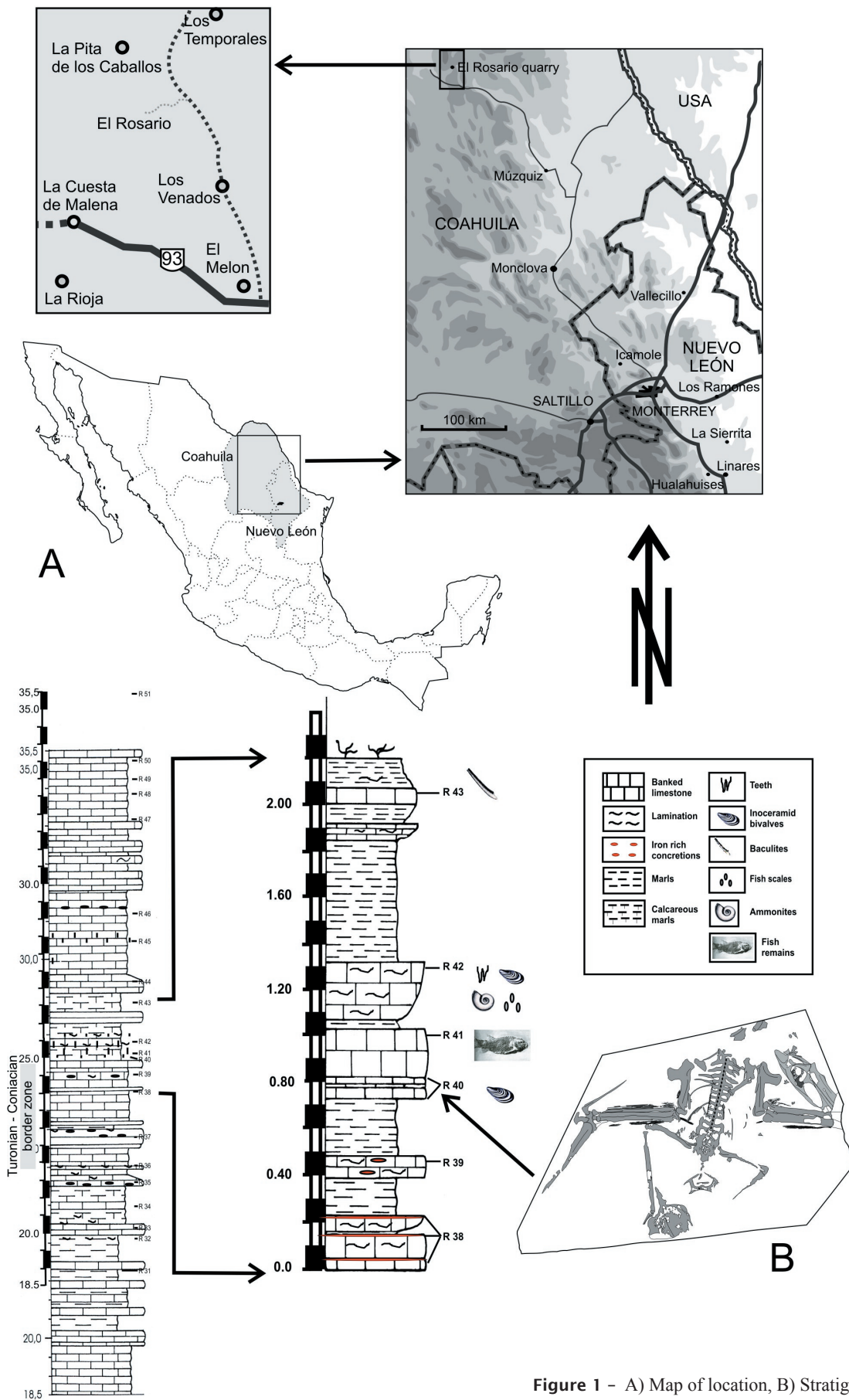
Figure 1 - A) Map of location, B) Stratigraphy.

preliminary resting place in the manager´s office, where they were securely embedded into a wall as ornamental stones between other fossils from the region. After the rumour of the discovery of the pterosaur, which was nicknamed "chango" (Spanish for "monkey") because of its long arms, reached AGG and AdS at the Museo del Desierto in Saltillo (Coahuila) efforts were undertaken to secure the specimen for scientific investigation. After successful negotiations, permission to remove the slabs from the office wall was granted and the slabs were collected with hammer and chisel.

The pterosaur represents the first highlight from the Muzquiz limestone deposit El Rosario (Buchy et al. 2004; Stinnesbeck et al., in press). The specimen is referred to Nyctosauridae, a group of late Cretaceous pterosaurs better known from the Niobrara Formation (late Coniacian – early Campanian) of Kansas (Marsh, 1876, Williston, 1902, 1903, Bennett, 1989, 1994, 1996, 2003a) and probably occurring in the Maastrichtian of northeast Brazil (Price, 1953, Wellnhofer 1991). The new specimen is now housed in the Colección Nacional de Paleontología, Universidad Nacional Autónoma de México (UNAM), Mexico City, under the accession number IGM 8621.

MATERIAL AND METHODS

The description is based on direct observation of slab and counterslab and in an overlay of the traced outlines of the specimen from slab and counterslab (figs. 2, 3). The line drawings were taken from Canon Powershot G3 digital photographs. For low-level taxonomy we follow largely the suggestions of Bennett (1989, 2003a). The higher lever taxonomy is so confused (Kellner 2003 *contra* Unwin 2003) that we do not feel confident enough to contribute to the discussion here on the level of a cluster analysis based on characters, especially because Bennett (pers. comm. 2003) is preparing a paper on this topic. We will instead demonstrate that an analysis of the nyctosaur construction may help to resolve contradictory arguments of the existing cladistic analyses.

GEOLOGY AND LITHOLOGY

The village of Muzquiz is located in the northeast Mexican state of Coahuila, approximately 300 km north of Saltillo and 100 km north of Sabinas (fig. 1A). The region north of Muzquiz is a barren semi-desert and a few scattered houses and farms can only be reached on dirt tracks that branch off the N-S main road (A2). A series of small quarries are located in this remote region, where thin-bedded laminated limestone is extracted and the products sold as floor flags, wall tiles and ornamental stone. The laminated limestone likely belongs to the Upper Cretaceous Austin Group, a lithology unit of marls and limestone, which is widely distributed in northeast Mexico and southern Texas but is generally poorly fossiliferous (Sohl et al., 1991). The

Austin Group was deposited under open marine middle to outer neritic conditions, and its age is considered to be Coniacian-Campanian by Sohl *et al*. (1991), or late Turonian-Santonian by Goldhammer & Johnson (2001).

In order to reach the now abandoned El Rosario Quarry, one has to follow the A2 road from Muzquiz in the direction Piedras Negras for about 140 km. There, a dirt road branches off eastbound, which leads straight into the Sierra Madre Oriental to the mining area. The El Rosario Quarry is on the left side of this dirt road, and the track leading to it branches off after about 30 km (GPS: N: 28° 52' 00" / W: 102° 24' 00"; NAD27 Mexico).

In contrast to the standard situation in the Austin Group (Sohl et al., 1991) the laminated limestone at El Rosario is highly fossiliferous. Fossil fishes, like ptychodont sharks, tselfatiids, pycnodonts and other hitherto undetermined species are especially abundant in the El Rosario area and are characterised by an excellent state of preservation, including the distal parts of the fins and soft tissues.

Until now, in northeast Mexico, only Aqua Nueva Formation at Vallecillo has been known for abundant of well preserved Late Cretaceous fishes (Blanco-Piñón et al., 2002). However, some fossil fish specimens from Muzquiz are considerably better preserved than those from Vallecillo, because their bodies show partial three-dimensional preservation. Furthermore, preservation of skin, muscle tissue and fins is common. Local miners report that they extracted between seven and fifteen complete fossil fishes per day under standard working conditions, when the El Rosario quarry was operational. A similar story is told by the workers from the quarries in the vicinity of El Rosario, but scientific excavations are required to verify this. According to our initial investigation, the extraordinary preservation of soft-parts results from rapid phosphatisation, which seems to have occurred very soon after deposition (*cf*. Martill, 1988). In addition, other ecological-oceanographical parameters contributed to the excellent preservation, such as deposition of fine-grained lime mud, abundance of all kinds of organisms, the absence of currents and, in consequence, at least temporarily anoxic conditions on the sea floor that prevented access of scavengers to the carcasses. A soft and soupy substrate apparently occurred from time to time as is indicated by vertically embedded ammonites.

At El Rosario, approximately 50 m of alternating laminated limestone occurs in layers up to 0.30 m thick and up to 1.2 m thick intervals of millimetrically layered marly limestone and marls. The pterosaur specimen comes from a massive limestone bank, which is 45 mm thick (as thick as slab and counter-slab of the specimen together) and exposed 25 m above the base of the El Rosario profile (fig. 1B). The associated faunal assemblage includes both articulated and disarticulated fish skeletons, some with preserved softparts, and numerous invertebrates (e.g., ammonites, inoceramids, decapod crustaceans, planktonic foraminifers). The presence of *Cremnoceramus deformis erectus* indicates an early
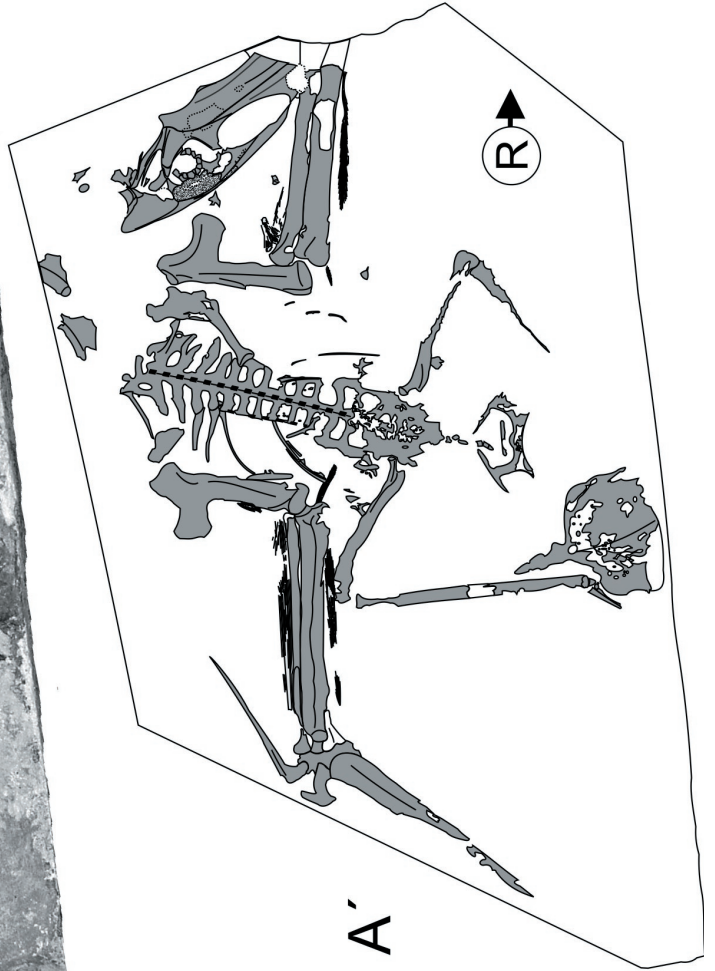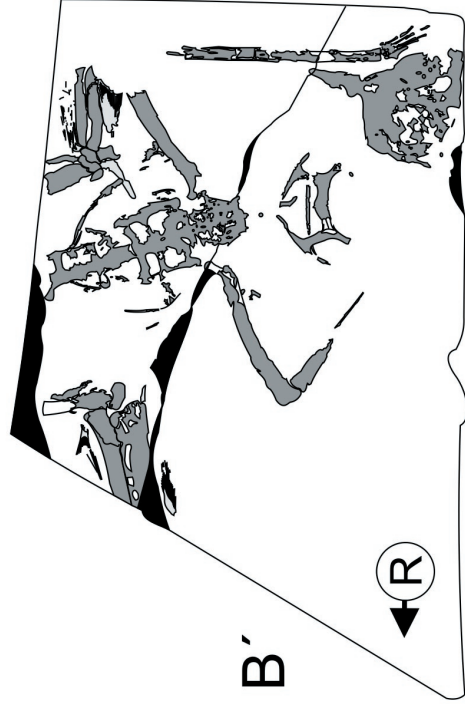
B

B'

A

A'

R = right side

scale bar = 100 mm

Coniacian age for the pterosaur-bearing layer. The pterosaur described here represents the first occurrence of flying reptiles in the Muzquiz assemblage from which also marine reptiles are also reported (Buchy *et al.*, 2004).

Systematic palaeontology
Pterosauria Kaup, 1834
Pterodactyloidea Plieninger, 1901
Nyctosauridae Marsh, 1876
Muzquizopteryx n.g.
Derivation of name – After Muzquiz, a town in Coahuila (northeast Mexico) 300 km north of Saltillo, in the vicinity of which the specimen was discovered and *pteryx* (Greek) for wing (Muzquiz wing).
M. coahuilensis n.sp.
Derivation of name – After the State of Coahuila (northeast Mexico); *Muzquizopteryx coahuilensis* = of Coahuila.

Holotype
Specimen UNAM IGM 8621.

Stratum typicum – Section within the Austin Group (Late Cretaceous: early Coniacian); buff to yellow laminated limestone from the El Rosario quarry, at 28°52,587'N, 102°24,216W. The nearest town is Muzquiz (Coahuila, NE Mexico), approximately 170 km ESE of El Rosario).

Taxonomy
Muzquizopteryx coahuilenis is referred to Nyctosauridae Marsh, 1876 based on the hatchet-shaped humerus with its subrectangular deltoid process, the shape of the pteroid bone, in which the articular head is bent 90° to the corpus and the rounded medial end of the scapula, which does not contact the epineural plate. Additionally the specimen shows mineralised tendons of the proximal wing muscles, which, until now, are only reported from adult specimens of *Nyctosaurus gracilis* (Bennett, 2003a).

The taxonomic position of the nyctosaurids within Pterodactyloidea has been debated since the first description of the species *Nyctosaurus gracilis* Marsh, 1876. Marsh (1876) placed *Nyctosaurus* in its own family Nyctosauridae, but later, it was referred to Ornithocheiridae Seeley, 1870 (Marsh, 1876, Lydekker, 1888, Hooley, 1913, Wellnhofer, 1991) or to Pteranodontidae (Bennett, 1989). Williston (1897, 1903) established the subfamily Nyctosaurinae to accommodate *Nyctosaurus* within Ornithocheiridae. Huene (1956) and Romer (1956) considered *Nyctosaurus* as a distinct genus within Ornithocheiridae. Another group of authors noted similarities between *Nyctosaurus* and *Pteranodon* Marsh, 1876. Miller´s (1972a, b) assumption that *Nyctosaurus* represents a subgenus of *Pteranodon*

is probably the most extreme view. Young (1964) and Wellnhofer (1978) placed *Nyctosaurus* within the familiy Pteranodontidae Marsh, 1876.

The controversy regarding the systematic position of *Nyctosaurus* is still unresolved. Kellner (2003), a monogeneric clade Nyctosauridae within Dsungaripteroidea Kellner, 2003. This is in marked contrast to Unwin (2003), who puts *Nyctosaurus* in Pteranodontia, a clade comprising Pteranodontidae plus *Nyctosaurus* as sister groups.

The new specimen described here (fig. 2) supports the separation of the family Nyctosauridae from the Pteranodontidae for reasons of constructional morphology (Williston, 1903, Kellner, 2003, Bennett pers. comm. to EF, 2003). As will be demonstrated later, the features listed below have a bearing on the flight mechanics of the wing construction of Nyctosauridae, which is unique among the Pterosauria.

We propose here an emended diagnosis for the Nyctosauridae (*cf.* Bennett, 1989, 2003a and pers. comm., 2003):

1)   The rounded medial end of the scapula does not contact the epineural plate to form a notarium. Whether or not there was a ligamentary or cartilaginous contact is hitherto unknown.

2)   The wing metacarpal is long in relation to the humerus length (ratio length of wing metacarpal to humerus length: 2.53 – 2.71; Unwin, 2003 after Williston, 1903 and Brown, 1986). *Muzquizopteryx* lays within this range.

3)   The wing finger consists of three phalanges. This feature is doubted by Miller (1972a), who describes four phalanges in *N. bonneri,* but new finds described by Bennett (2003a) confirm the lack of a fourth wing finger phalanx in the *Nyctosaurus bonneri* specimens described by Miller (1972a). The Chinese *Chaoyangopterus zhangi* Wang & Zhou, 2003, which was referred to Nyctosauridae, has four wing finger phalanges. This, the caudally rapidly diverging nasoantorbital fenestra and the femur, which is longer than the humerus suggests *Chaoyangopterus zhangi* is an azhdarchid pterosaur (Frey et al. 2003a). Unfortunately the shape of the scapulocoracoid is not clearly visible in fig. 1 of the description by Wang & Zhou (2003) such that conclusive proof for referral of the specimen to the azhdarchoids requires direct examination. According to Unwin (pers. comm. to EF, 2004) *Chaoyangopterus zhangi* doubtlessly is an azhdarchid.

4)   The hatchet-shaped deltoid process is separated from the head of the humerus. The proximal and distal margins of the deltoid process are concave (see also Williston, 1903). Azhdarchoid pterosaurs have a similar shaped deltoid process, but the proximal and distal margins are always parallel sided.

Figure 2 – *Muzquizopteryx coahuilensis* n. g. n. sp., holotype: A) slab, A´) interpretive line drawing of the slab, B) counterslab, B´) interpretive line drawing of the counterslab. The specimen is housed in the Colección Nacional de Paleontología, Universidad Nacional Autonoma de Mexico (UNAM). The collection number is IGM 8621.
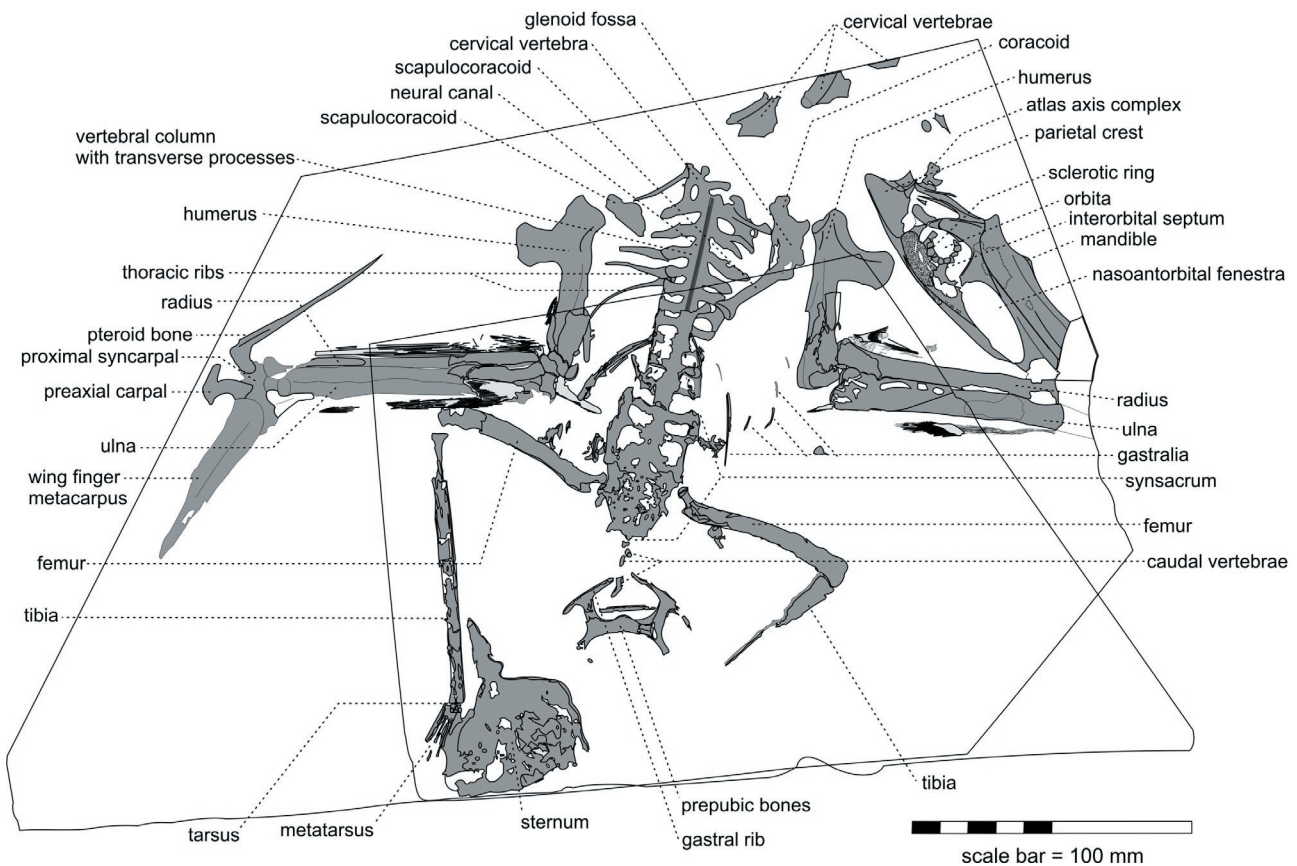
Figure 3 − *Muzquizopteryx coahuilensis* n. g. n. sp.; reconstruction of the skeleton by overlaying the line drawings of slab and counterslab as seen in fig. 1A´, B´.

5) The articular head of the pteroid is orientated at 90° to the shaft (see also Williston, 1903). These diagnostic characters are emended here by the following, which apparently also only occurs within Nyctosauridae:

6) Tendons of proximal wing muscles mineralised. Such mineralised tendons were also described for new finds of *Nyctosaurus* (Bennett, 2003a) and are not reported from any other pterosaur taxon until now.

DISCUSSION OF DIAGNOSIS

The rounded medial end of the scapula of *Muzquizopteyx coahuilensis* n.g. n.sp. is free (figs. 2A, A´, 3). Apparently the scapulocoracoid fell caudally prior to fossilisation, indicating that there was no syndesmal contact between the medial terminus of the scapula and the epineural plate (diagnostic feature 1), but might have been a ligament or a cartilage connection, which was no more viable at the time of embedding. The fused skull bones, the co-ossified prepubic bones, the large number of sacralia, which increases during ontogeny in pterosaurs (Bennett, 1993) and the mineralisation of the tendons of the proximal wing muscles (figs. 2, 3, 5) indicate that the specimen represents an adult. The diagnostic features (2) and (3) cannot be verified, because the entire wing skeleton distal to the proximal part of the wing finger metacarpal is missing (figs. 2, 3, 5). The diagnostic features (4) to (6) are preserved (figs. 2, 3, 5) and allow identification of the specimen as a nyctosaurid.

The skull is of the nyctosaurid type in showing edentulous jaws and a subtriangular nasoantorbital fenestra that is less high than the dorsal margin of the orbit (fig. 4). The retroarticular process is triangular in lateral view and directed straight caudally (Williston, 1902, Eaton, 1910) and the ventral margin of the mandible caudal to the the mandibular symphysis is strongly concave (Williston, 1902, Eaton 1910, Bennett, 2003a). Furthermore, the dorsal mandibular margin immediately rostral to the jaw articulation strongly curves dorsally so that the occlusal line of the jaw lies dorsal to the jaw joint (coronoid elevation; figs. 4, 5).

Muzquizopteryx n.g. differs from *Nyctosaurus* in the following features:

1) The maximum height of the orbit exceeds maximum height of the nasoantorbital fenestra. In *Nyctosaurus* the heights of both orbit and nasoantorbital fenestra are equal.

2) The orbit is subrectangular in outline. In
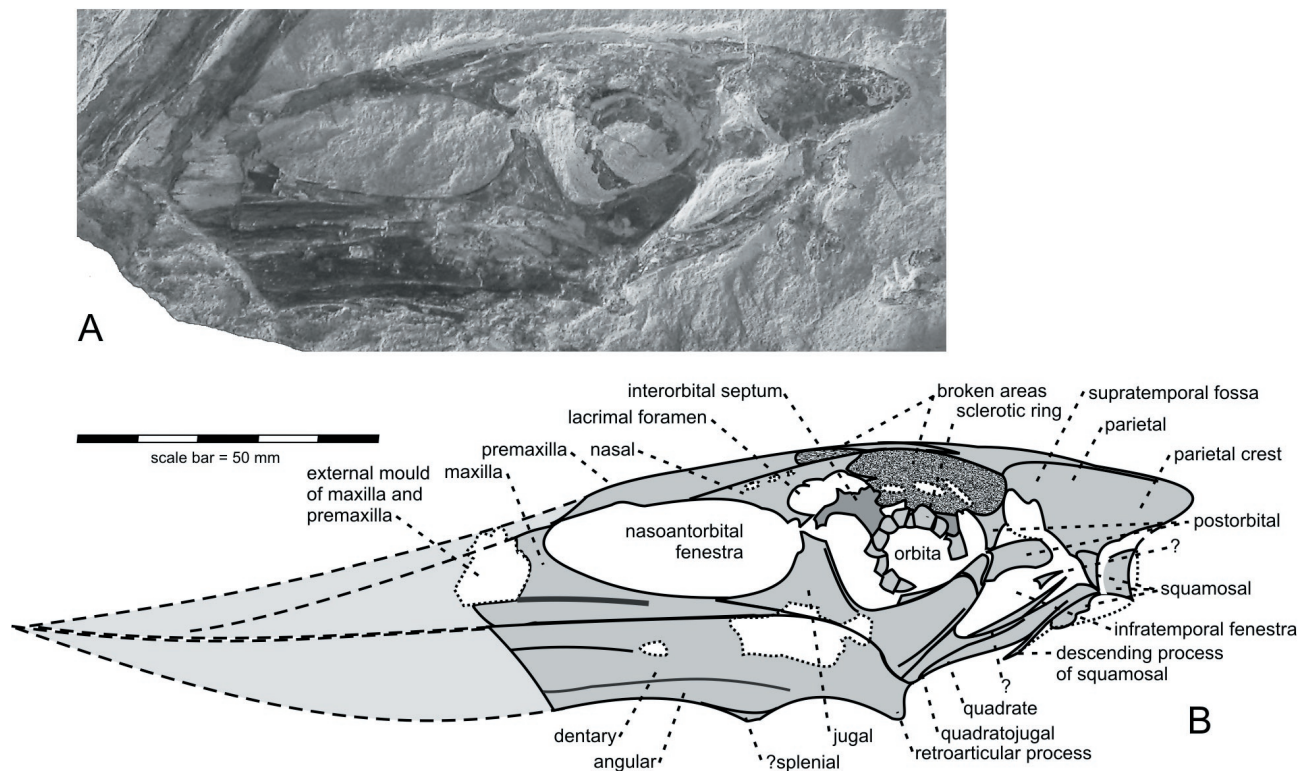
Figure 4 − *Muzquizopteryx coahuilensis* n. g. n. sp.; A) skull as preserved, B) reconstruction of the skull. Note the steep coronoid elevation and the deeply concave gular region of the mandible.

Nyctosaurus it is subtriangular.

3) The jaw articulation is situated ventral to the middle of the orbit. In *Nyctosaurus*, the jaw articulation lies level with the rostral margin of the orbit (Williston, 1902, Bennett 2003a).

4) The caudal terminus of the mandibular symphysis is level with the caudal margin of the nasoantorbital fenestra. In *Nyctosaurus* it lies level with its rostral margin.

BIOMETRY

Table 1 shows the biometrical data for *Muzquizopteryx coahuilensis* in comparison with equivalent data for related taxa taken from the literature. The ratios follow the suggestion of Unwin (2003) for "terminal pterosaur taxa", but the calculations presented here extend the range of ratios presented by Unwin (2003). All biometrical data of *Muzquizopteryx* are consistent with those given by other authors for *Nyctosaurus* (Williston, 1903, Miller, 1972a, Bennett, 2003a, Unwin, 2003). The wingspan of *Muzquizopteryx* is estimated by using the

forelimb to hind limb length ratio for *Nyctosaurus* given by Unwin (2003) of 4.84. The length of the hindlimb in *Muzquizopteryx coahuilensis* as preserved is 213 mm without the toes. With toes, its length would reach about 220 mm. One wing would then be a little more than one metre long (1064 mm). Provided the arm bones were held in maximum extension, the wingspan of *Muzquizopteryx* would have been approximately two metres.

PRESERVATION

The holotype is preserved on two slabs (fig. 2). All bones are crushed due to compaction during late diagenesis and most of them are split irregularly in a horizontal plane. Only the superposition of the medial terminus of the right scapula on the transverse processes of the vertebral column indicates that the specimen is exposed in dorsal view on the main slab (fig. 2A). Sedimentological evidence proves that the main slab is the bottom slab (Rindfleisch, 2004). Therefore the slab containing the less complete part of the skeleton is designated arbitrarily as the counter-slab, which

Species	Muzquizopteryx coahuilensis	Nyctosaurus cf. gracilis	Nyctosaurus gracilis	Nyctosaurus bonneri	Nyctosaurus bonneri	Nyctosaurus gracilis	Nyctosaurus gracilis
Collection number	IGM 8621	N. KJ2		SMM 11311	YPM 2395	SMM 7968	CMNH
Author	This paper	Bennet 2003	Williston 1903	Miller 1972	Miller 1972	Miller 1972	Miller 1972
orbita max.	24						
orbita min.	14						
nasoantorbital fenestra max.	43						
nasoantorbital fenestra min.	16						
cervical vertebra	24						
trunk	82						
synscarum	63						
right scapula	42	54,4	49*				
left humerus	81	72,3	87*	97*	132*	85*	87*
right humerus	80	72,3					
left radius/ ulna complex	112	142	144*		221*	136*	140*
left femur	78	70,9	81*	84*		78*	81*
right femur	78	71,9					
left tibia	109	70,9	132	120*			133*
left metatarsus	22						
max. length sternum	73		88				
cristosternum	35		ca. 30**				
max. width of sternum	65		80				
Ratios***							
humerus / femur	l:1,04, r:1,02	l:1,02, r: 1,00	1,07	1,15		1,01	1,07
ulna / tibia	1,03	2	1,09				1,05

Table 1 – *Muzquizopteryx coahuilensis* n. g. n. sp.; biometrical data in comparison with equivalent data and ratios from other nyctosaurs.
* Left and right body side not specified
** Williston 1903 gives the lengths of the presternal process cranial to the coracoids only
*** Morphometric data for terminal taxa according to Unwin 2003, which can be obtained from Muzquizopteron

is broken into two parts (fig. 2B). The break passes obliquely through the proximal third of the right radius ulna complex, cuts through the head of the right femur, and extends from the caudal margin of the acetabulum across the terminus of the left ilium. From there the fracture continues diagonally through the caudal fifth of the synsacrum, the rostral tip of the sternal crest and the distal third of the right tibia. The counter-slab contains the caudal half of the vertebral column, both hind limbs, the distal ends of both humeri and the proximal ends of both radii-ulnae, all of which are in articulation, the sternum and the prepubic bones with the co-ossified caudalmost pair of gastral ribs, which are disarticulated from the pelvis and now lie caudal to the trunk.

The main slab (fig. 2A, A´) is in one piece and contains most of the specimen. Three cervical vertebrae are preserved, including parts of the atlas axis system. The skull lacks an unknown portion of the rostral part of the rostrum and the lateral wall of the supraorbital part of the braincase. Of the left wing, the humerus, radius and ulna, and carpus are preserved. The pteroid bone is also preserved, as is the proximal part of the wing-finger metacarpal. A faint imprint of the wing finger metacarpal continues distally, but does not allow an exact reconstruction of the bone. The right wing is only represented by the humerus and most of the radius and ulna. The shoulder girdle comprises a fragment of the right scapulocoracoid with the scapular part and the glenoid fossa being completely preserved. The coracoidal part of the right scapulocoracoid is recognisable by its lateral process forming the ventral lip of the glenoid fossa, and a short fragment of the shaft. The left scapulocoracoid is preserved as an indistinctive fragment. The disarticulated sternum is preserved on the main slab as are the prepubic bones.

Due to the irregular splitting of the bones, the counter-slab (fig. 2B, B´) shows better preservation of the distal part of the right femur, the sacral vertebrae and the left pes, whereas on the slab the pelvic part of the sacrum, the tail and the proximal parts of the femora are in a better condition (fig. 2A, A´). The overlay of both slabs thus yields the maximum of information on the specimen (fig. 3). The subsequent anatomical description is based on this overlay.

The thorax is fragmentary on both slabs. Only fragments of ribs are preserved. Of those ribs that are still in articulation with the vertebral column the distal parts are missing. Soft-part preservation is seen adjacent to the cranial face of the left humerus and along the cranial and caudal faces of both radii-ulnae and comprises a series of mineralised tendons or ligaments.

OSTEOLOGY

Due to the compaction of the bones the osteological detail is camouflaged on the specimen. However, compaction did not affect the general outlines of the bones and their actual shape can be described.

Skull (fig. 4)

Cranium: The left side of the cranium is exposed and lacks the rostrum rostral to the nasoantorbital fenestra as well as the lateral parts of the supraorbital area of the braincase.

The premaxilla is a slender bone, which extends from the rostral break caudally, tapering to a sharp spine that terminates nearly level with the caudal margin of the orbit. It forms the rostral half of the dorsal margin of the nasoantorbital fenestra. The nasal is fused to the frontopostfrontal with a straight suture.

The maxilla forms the rostral margin of the nasoantorbital fenestra and the rostral two thirds of its ventral margin. Caudally, the maxilla ends at the broken area of the lateral wall of the braincase. The suture with the jugal is straight. Parallel to the ventral margin of the maxilla, a longitudinal compaction break is visible that extends from the rostral break caudally to half the longitudinal extension of the nasoantorbital fenestra.

The caudal half of the dorsal margin of the nasoantorbital fenestra is formed by the nasal which merges caudally with the frontopostfrontal. Rostrally the nasal lies ventrally adjacent to the premaxilla and ends in a sharp, rostrally pointing spine. Only the rostral margin of the lacrimal foramen is preserved as a rounded, caudally open notch, which indicates the former position of the now missing lacrimal in the rostrodorsal corner of the orbita. The external part of the lacrimal is missing. Caudal to the remnants of the lacrimal foramen, the nasal ends in the broken area of the braincase. The dorsolateral margin of the orbit is missing, as is the entire supraorbital part of the braincase.

The descending process of the postorbital exposes its original surface, and forms the postorbital bar. The caudal margin of this process forms the rostral margin of the supratemporal fossa. Because the caudal part of the surface of the postorbital body has broken away, the caudal process of the postorbital, forming the upper zygomatic arch, is now an isolated rounded trapezoid, slightly vaulted element. The caudal margin of the postorbital appears complete, which indicates the presence of a former suture with the squamosal. However, there is no contact preserved with the squamosal due to surface damage.

Due to the surface abrasion of the squamosal and the damage to its caudal margin, the outline of the back of the skull and the dorsal margin of the infratemporal fenestra are not preserved. Of the squamosal, only fragments along the caudal margin of the cranium are preserved including the descending process of the squamosal. This descending squamosal process extends along half the length of the quadrate in a rostroventral direction and is dorsally confluent with this bone. This indicates that the squamosal was fused with the dorsal margin of the quadrate.

The jugal forms the rostroventral and caudoventral margins of the orbit as well as the caudoventral margin of the nasoantorbital fenestra. The jugal has an elongate corpus with a trapezoidal outline. The ventral margin of

the rostral third of the corpus forms an even suture with the caudal process of the maxilla and terminates in a sharp, rostrally directed process. The caudoventral margin of the nasoantorbital fenestra is formed by the rostral margin of the antorbital ascending process and the dorsal margin of the rostrally directed process. Between the caudal terminus of the maxilla and the rostral end of the jaw articulation, the ventral margin of the jugal is concave, bringing the occlusion line of the jaws above the level of the jaw articulation.

The subtriangular antorbital and postorbital processes project from the corpus of the jugal in rostrodorsal and caudodorsal direction respectively. The antorbital process has concave rostral and caudal margins. The caudal margin of the antorbital process of the jugal ends in a sharp blade, which is increasingly prominent toward the ventral corner of the orbita. The caudal margin of the antorbital process forms at least the ventral half of the rostral margin of the orbita. The postorbital process is more slender at its base and one-sixth higher than the antorbital one. The rostral margin of the postorbital process is slightly concave and forms the ventral two thirds of the caudal margin of the orbit. The caudal margin of the process is marked by a rounded ridge, which begins at the suture with the postorbital and then increases in size ventrally toward the jaw articulation. The suture between the jugal and quadratojugal is slightly vaulted rostrally. The angle between the caudal margin of the antorbital process of the jugal and the rostral margin of its postorbital process is approximately 60°. This makes the outline of the orbit almost rectangular, but the shape of its dorsal margin cannot be reconstructed due to missing superficial skull elements from the dorsal orbital rim.

The quadratojugal is an elongate triangular bone, the most acute angle of which is oriented caudodorsally at about 20° degrees to the caudal margin of the jugal. From its suture with the jugal it tapers and ends in a needle fine process. The quadratojugal forms the ventral half of the caudal margin of the infratemporal fenestra.

The caudodorsal half of the infratemporal fenestra is bordered ventrally by the rod-like quadrate, which lies caudally adjacent to the quadratojugal, with which it has a slightly S-shaped suture, which fades away in its dorsalmost extermity.

Inside the orbit the interorbital septum is preserved, covering the dorsal third of the cavity. Rostrally the ventral margin of the septum is marked by a deep, semicircular notch. The caudal half is covered by the left sclerotic ring, of which 11 irregularly shaped polygonal elements are preserved *in situ*. The outline of the orbit appears to have been a rounded rectangle (fig. 4).

The nasoantorbital fenestra is ovoid with a ratio of maximum length to maximum height of approximately 2 : 4; it is about one third longer than is the orbit. The outlines of the temporal fenestrae cannot be reconstructed with confidence due to missing bones. The dorsal margin of the cranium caudally merges into a short head crest, which appears to be formed by the parietals and probably includes the dorsal part of the supraoccipital. The apex of the crest is rounded and points straight caudally. Its dorsal margin is reinforced by a low lateral ridge. Its length equals scarcely half the longitudinal diameter of the orbit.

Mandible: The mandible is preserved in tight occlusion with the cranium. From the rostral break to the level of the caudal end of the nasoantorbital fenestra, the dorsal margin of the mandible is straight. Level with the caudal margin of the nasoantorbital fenestra, it curves caudoventrally until the rostral margin of the caudodorsally orientated glenoid fossa for articulation with the quadrate. The inclination of the jaw joint is approximately 45° relative to the plane of occlusion of the rostral part of the jaws. The ventral margin of the mandible is concave ventral to the nasoantorbital fenestra. The mandible reaches its maximum depth level with the caudal third of the nasoantorbital fenestra,. There, a small elongate triangle of bone is exposed in lateral aspect, and is separated from the dentary by a slightly ventrally curved suture, and might represent the splenial. The dentary and the angular are the only other bones visible on the lateral face of the mandible. The suture between the two bones runs subparallel to the ventral margin of the mandible from its rostral break almost to its ventrocaudal margin level with the caudal end of the ?splenial, where it disappears. One longitudinal break is visible on the surface of the dentary, similar to the compression break affecting the maxillary (fig. 4B).

The suborbital part of the ventral margin of the mandible is deeply concave, and the bone tapers toward the retroarticular process, which shows a convex ventral margin and a concave dorsal one. The depth of the mandible at its rostral break equals the depth of the maxillopremaxillary part of the rostrum.

Vertebral column, synsacrum and ribs (figs. 2, 3)
Neck (figs. 2A, 3): On the main slab, there are two procoelous cervical vertebrae. They are positioned where the mid section of the neck would be and therefore are likely to represent two of the longest of the cervical vertebrae (*cf.* Bennett, 2001a).

The corpora of the vertebrae are approximately five times longer than they are high. The neural arch, which was about twice as high as the corpus, extends over its entire length. Further fragments of cervical vertebrae are visible in the vicinity of the occiput. These fragments lying adjacent to the occiput are likely to represent remnants of the atlas axis complex but preservation does not allow confident reconstruction. Remnants of the caudalmost cervical vertebrae lie adjacent to thoracic vertebrae one and two, and a tiny fragment of another cervical vertebra is visible on the border of the main slab (figs. 2A, 3) but the preservation is too poor to yield useful anatomical detail.

Thorax: The thoracic vertebral column consists of ten vertebrae, determined from a count of the pairs of

transverse processes. There are no intervertebral joints, but they might be obscured by a longitudinally continuous ridge of fibrous texture extending along the median line of all thoracic vertebrae and ending at the cranial terminus of the second synsacral vertebra. It is highly likely that the thoracic vertebrae broke horizontally at the base of the peduncles of the neural arches. Therefore this ridge probably represents the remnants of the fibrous envelopes of the spinal chord or an intervertebral ligament. The transverse processes are widest at the first thoracic vertebra, and they gradually decrease in width toward the tenth. The lateral extent of the transverse processes is one third larger than the estimated length of a vertebral segment and the length to width ratio is approximately 1:4. The relative size of each transverse process compared to the length of the vertebral segment bearing it remains nearly constant throughout the thorax. The decrease in length of the segments in caudal direction is linear. The cranial and caudal margins of the transverse processes are slightly concave and their lateral extremity is rounded. The paired transverse process of the cranialmost thoracic segment is inclined caudally against the long axis with an angle of 115°. This angle gradually declines toward thoracic segment five where it reaches 90°. This angle then remains constant until thoracic vertebra ten. The lateral extremity of the thoracic transverse processes five to ten are connected by a longitudinal rod-shaped mineralised structure with a fibrous texture. This feature, which is better preserved on the left side, connects the lateral extremities of the transverse processes of the sixth to eighth thoracic vertebrae on the left side and the fifth to seventh on the right. It probably represents a mineralised tendon, which co-ossified with all transverse processes of the fifth to tenth thoracic vertebrae. No such structure is seen on the cranialmost five segments.

Ribs and gastralia (figs. 2, 3): Only the proximal elements of a few ribs are preserved in articulation with the lateral extremity of the thoracic transverse processes one through five. The ribs on the left side are more complete than those on the right. The rib articulation of the cranialmost two thoracic vertebrae on the left and the cranialmost three on the right side appears to be co-ossified with the adjacent transverse processes. A rod-like bone, which lies cranially adjacent to the first thoracic vertebra might either represent a rib from the caudal half of the thorax or an element of the gastralia basket. The same holds true for all the rod-like bones that occur in the region of the thoracic vertebrae five to ten.

Synsacrum (figs. 2, 3): The synsacrum comprises at least eight vertebrae but only the cranialmost three can be identified by distinct transverse processes, of which the two cranialmost are inclined cranially at an angle of about 60° relative to the longitudinal axis. These two extend one third further laterally and are one third wider than the transverse processes of the tenth thoracic vertebra. The third pair of synsacral transverse processes appears to share

the proportions of the two cranial ones, but are inclined caudally at an angle of 110° against the longitudinal axis of the body. Caudal to the third synsacral vertebra the size of the vertebrae seems to decrease rapidly toward the caudal terminus of the synsacrum. These caudal segments formed a plate-like structure with very small apertures between the transverse processes. The poor preservation in this area does not allow the identification of more than five further segments with certainty.

Tail (figs. 2A, A′, 3): The cranialmost caudal vertebra is probably represented by a small hump at the median caudal terminus of the synsacrum, but no clear suture separates this element. Caudal to it, seven fragmentary and disarticulated caudal vertebrae are preserved. Their corpora appear to have been cylindrical but the length to width ratio cannot be determined. The terminal caudal vertebra is conical with a rounded terminal apex.

Appendicular Skeleton and girdles (figs. 2, 3, 6)
Shoulder girdle (figs. 2A, A′, 3): Of the left scapulocoracoid only an unidentifiable patch of bone is preserved. Of the right scapulocoracoid, the dorsolateral third of the coracoidal part, the glenoid fossa and the entire scapular part are preserved, and exposed in cranial view. The corpus of the scapula is almost parallel-sided with a rounded medial terminus, which is approximately twice as wide as the corpus. The width at the glenoidal portion is about three times that of the corpus. The ventral lip of the glenoid fossa is slightly curved ventrally with a concave ventral face. No trace of a suture is evident between the scapular and coracoidal portions of the scapulocoracoid. The corpus of the scapula is angled at about 55° relative to its vertical glenoid portion.

Sternum (figs. 2, 3): The caudal portion of the sternum forms a plate, which is about one fourth wider than it is long. It has a slightly convex caudal margin. The lateral margins are irregularly wavy and are almost parallel to each other. The cranial margin is V-shaped with the tip of the V pointing cranially. The shanks of the V define an angle of approximately 135°. Toward the base of the cristosternum the cranial margin of the sternal plate becomes increasingly more massive, which is indicated by the density of the bone. This thickening is best visible on the counterslab. The base of the cristosternum is marked by a long oval foramen with a maximum diameter of about 5 mm. The cristosternum is two thirds of the maximum length of the sternal plate. The width at its base is approximately one fifth of its length. Further cranially it widens into a pair of expansions to twice its basal width. The lateral constriction between base and expansions represents the articular facets for the furca of the coracoid. Cranial to the bulges the cristosternum gradually decreases in width toward its cranial, sharply rounded terminus.

Front limbs (figs. 2A, A´, 3, 5A): Both wing skeletons are preserved in a flexed condition. Based on Bennett (2001a) this might represent the strongest possible flexion of the preserved elements of the wing. In order to describe the orientation of the wing elements, it is assumed that the arm is in full extension (assumed flight position) with the deltoid process pointing cranially (fig. 6).

Humerus: The long axis of the shaft is almost straight and its cranial and caudal margins only slightly diverge toward the distal articular condyle. The head of the humerus, which is almost twice as wide as the narrowest point of the shaft, is angled at about 140° relative to the shaft in a caudal direction. The proximal articular facet is sigmoidal with the convex part situated medially.

The deltoid process emerges from the proximal third of the cranial face of the humerus at the transition between the head and the shaft. It is subrectangular in outline with a convex cranial and slightly concave distal and proximal margins. The concavity of the proximally facing margin continues into the cranial margin of the head of the humerus.

Radius and ulna: The radius and ulna complex is about one third longer than the humerus. The radius has approximately half the diameter of the ulna on the better preserved right wing. In both wings the two bones are preserved in articulation. Anatomical details are not preserved.

Carpus: The carpalia are in such a poor condition that little can be said about their individual shape. Nevertheless, they are preserved in articulation. The preaxial carpal is projecting cranially and shows a distinct suture with the distal syncarpal. Across the cranial terminus of the preaxial carpal is a transverse expansion, the longer part of which faces medially, almost in line with the distally orientated end of the corpus of the pteroid. The lateral expansion is only one fifth as long as the medially facing one. At the widest point the expansion is almost as broad as the corpus of the preaxial carpal. It appears likely that this transverse structure represents a sesamoidal element of an extensor tendon with attached mineralised fibres.

Pteroid: The left pteroid is complete and lies in articulation with the carpus. The rod-shaped corpus of the pteroid faces medially with a shallow groove along its long axis. The base of the articular head stands at 90° to the corpus and articulates with the proximal syncarpal.

Wing finger metacarpal: The proximal part of the left wing-finger metacarpal is the only preserved element of the metacarpus. Its diameter at its proximal articular surface and the tapering of the margins of the preserved part as well as the fragmentary external mould indicate that this bone was longer than the combined radius and ulna, but it is unclear by how much.
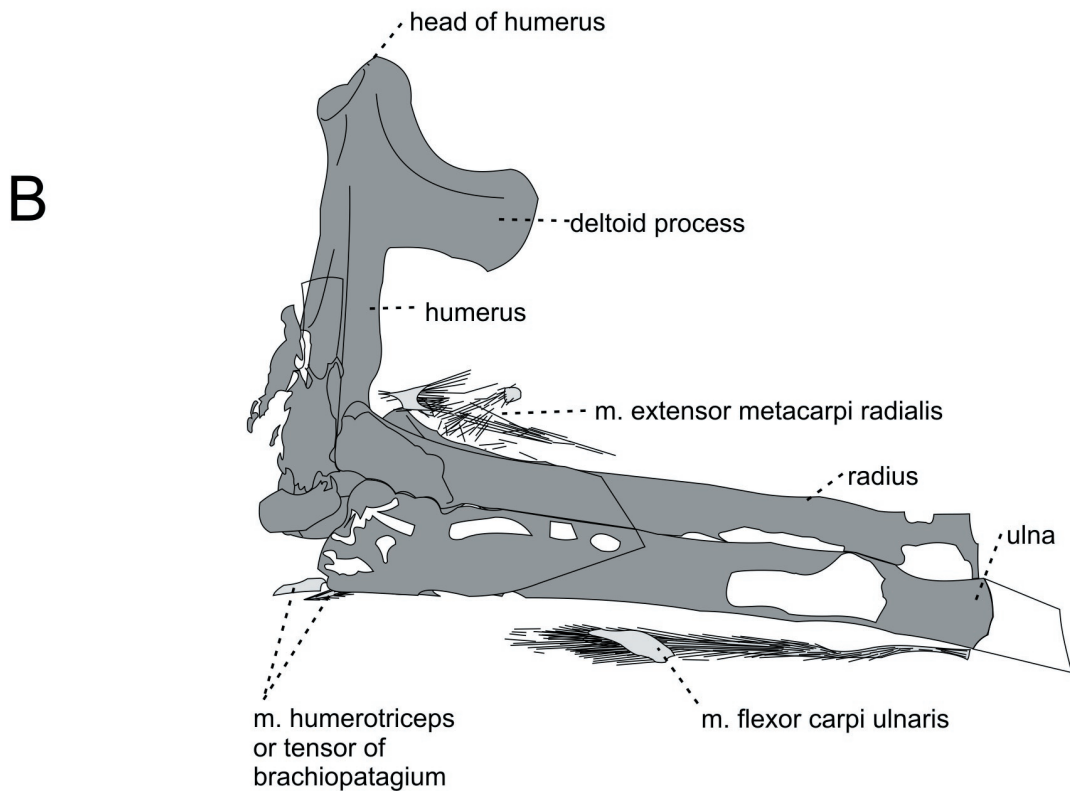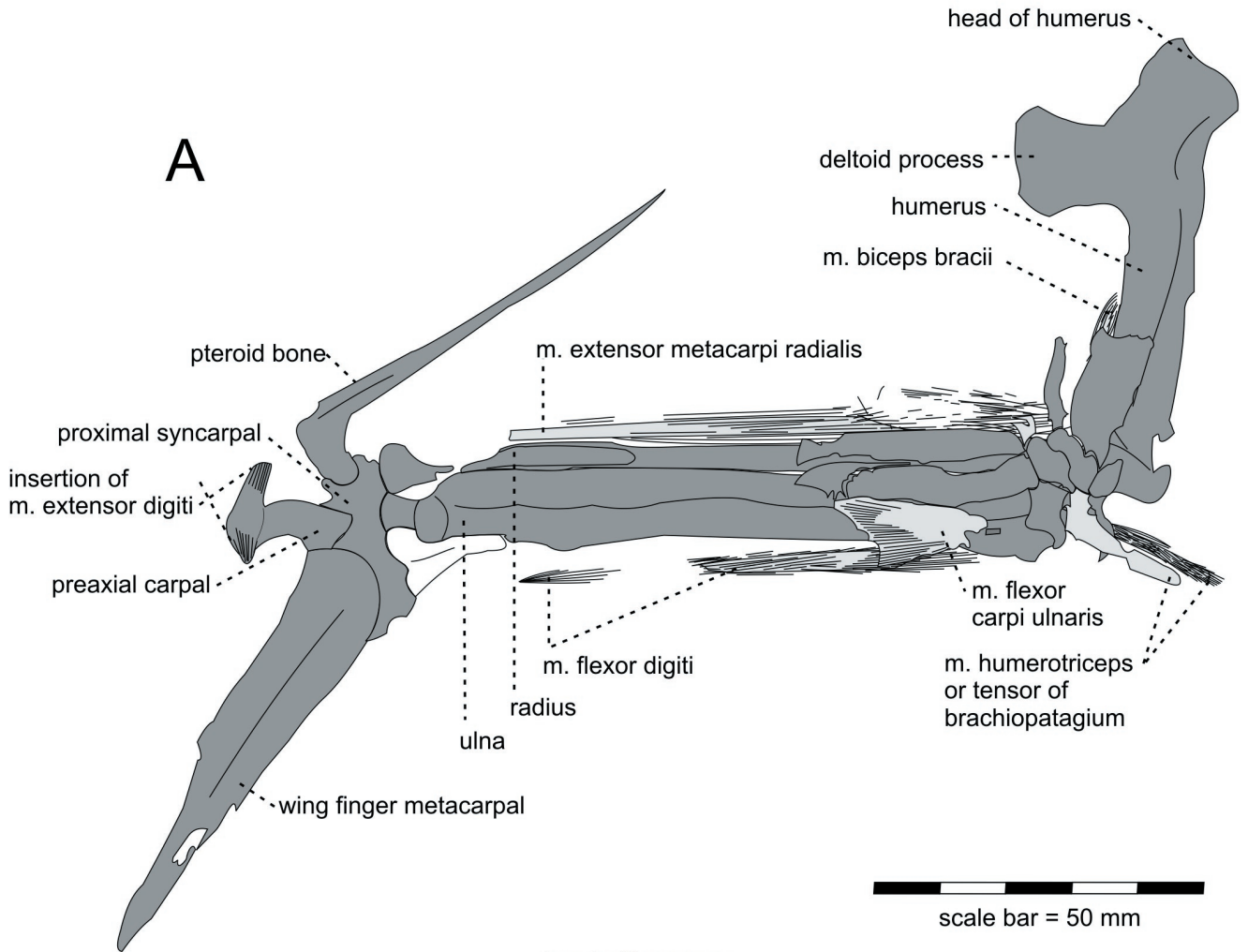
Mineralised tendons (fig. 5): Cranial to the left humerus, caudal to the elbow joint on both wings and cranial and caudal to the radius-ulna, elongate soft-part elements with a fibrous texture are preserved. Most likely they represent mineralised tendons of the proximal wing muscules. There is a patch of tendon cranial to the distal fifth of the left humerus. The fact that only a selection of tendons is mineralised, which is identical in both wings indicates that they must have been mineralised in the living animal already. The tendon cranial to the radius originates distally from a concentrated parallel-fibred string close to the carpus and diverges proximally, where it terminates in fibres fanning out to form an aponeurosis, which inserted at the distal articular condyle of the humerus, as is seen on the counterslab. This tendon is better preserved on the left side. A similar configuration is seen at the tendon caudal to the ulna, which is better preserved on the right side. A small tendon emerges from the olecranon of the ulna and extends from there proximally for about 10 mm.
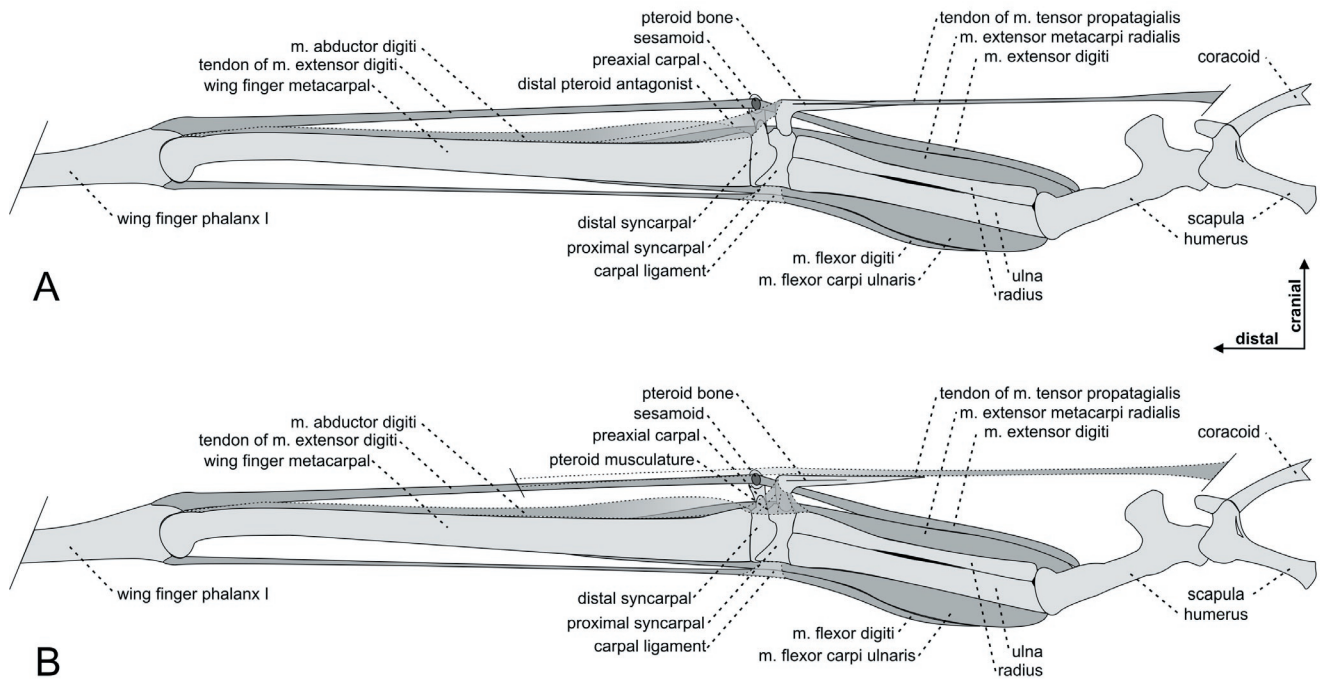
Pelvic girdle (figs. 2, 3): The cranial processes of both ilia are incompletely preserved adjacent to the transverse processes of the three cranial sacral vertebrae. The caudal parts of the ilia merge with the bony mass representing the caudal part of the synsacrum (see above). Despite the fact that the pelvic girdle being badly preserved, the position of the acetabula is marked by the articulated femoral heads, indicating that the acetabula were situated level with the fourth or fifth sacral vertebra. No trace of the ischium or pubis is evident.

Prepubic bones: Both prepubic bones consist of a caudal, craniomedially directed corpus, which bifurcates cranially in a cranially and a medially directed ramus. The medially directed ramus is the widest element of the prepubis and shows concave caudal and cranial margins. The cranial margin is more deeply concave than the caudal one and expands toward the midline, where its width is one third larger than its minimum width. Along the midline the medial rami of the contralateral prepubic bones are fused, and together with the caudalmost gastral rib form a laterally expanded pentagonal frame with one corner facing cranially. The caudal margin of the medial ramus merges into the caudolaterally directed parallel-sided corpus, which bears the articular surface for the pubis. This articular surface forms an obliquely extending straight margin. The cranially directed ramus of the prepubis has the same length as the corpus and is angled at about 100° to it. The medial and lateral margins of the cranial ramus are parallel. The cranial ends of the rami are fused with the caudalmost gastral rib, the two halves of which define an angle of 115°. Laterally the gastral rib extends beyond the lateral margins

Figure 5 (opposite page) − *Muzquizopteryx coahuilensis* n. g. n. sp., line drawings of the preserved softparts associated with the wing skeleton; A) left wing, B) right wing.

A

head of humerus

deltoid process

humerus

m. biceps bracii

pteroid bone

m. extensor metacarpi radialis

proximal syncarpal

insertion of
m. extensor digiti

preaxial carpal

m. flexor
carpi ulnaris

m. flexor digiti

radius

m. humerotriceps
or tensor of
brachiopatagium

ulna

wing finger metacarpal

scale bar = 50 mm

B

head of humerus

deltoid process

humerus

m. extensor metacarpi radialis

radius

ulna

m. humerotriceps
or tensor of
brachiopatagium

m. flexor carpi ulnaris

Figure 6 − Reconstruction of the distal arm musculature and tendons based on the wing skeletons of *Muzquizopteryx coahuilensis* n. g. n. sp. A) reconstruction with the pteroid bone as an attachment place for a tensor propatagialis tendon. The distal pteroid antagonist has been reconstructed to compensate the pull of the tensor propatagialis tendon. B) reconstruction with the pteroid as a free element for controlling shape and tension of the propatagium as suggested by Bennett (2000, 2001b).

of the cranial ramus of the prepubic bone, exceeding the lateral extension of the corpus. The rod-shaped bone, which lies almost parallel to the caudal part of the prepubic bones is either a thoracic rib or a gastral element.

Hindlimbs (fig. 2, 3): For the anatomical orientation, the hindlimb is supposed to be held in an assumed flight position with the femur directed laterally and the tibia/fibula and pes directed caudally.

Femur: The femur is about one fifth longer than the humerus. Its shaft is slightly sigmoidal in its longitudinal plane. Its minimum diameter is situated immediately distal to the fourth trochanter (fig. 3). The curvature is the most pronounced at the craniomedially orientated neck of the femur, which is about half the diameter of the shaft. The cranial margin of the femur becomes convex in its mid part with a gradually and slightly increasing curvature toward the knee joint. The caudal surface of the femur is marked by the hook-shaped fourth trochanter, which emerges from a crest that begins in the proximal fourth of the femur and extends proximally. The fourth trochanter is directed medially and is about half as long as the neck of the femur. On the exposed surface a shallow triangular sulcus separates the shaft from the trochanteric process.

Tibia: The tibia is about one third longer than the femur. Both tibiae are preserved facing caudomedially at an angle of 75° relative to the femora. The lateral and medial margins of the bone converge slightly from proximal to distal. Much of the compacta is missing so that the outline of the tibia cannot be described in detail. A fibula cannot be identified as a separate element. The proximal articular face of the tibia is concave, whereas the distal articular face forms a pair of rounded condyles, separated by a shallow sulcus.

Tarsals: Two tarsals are wedged between the distal roller joint of the tibia and the metatarsals. The proximalmost element is sub-circular; the distal tarsal is transversely elongate, showing three distinct humps, which are orientated in a transverse row. The bone lies mostly medial to the proximal element.

Metatarsals: The middle axis of the left pes extends at an angle of 145° relative to the tibia. The fifth metatarsal is elongately triangular with a concave medial and a slightly convex lateral margin. The proximal articular face is straight. The base of the fifth metatarsal overlaps that of the fourth. The base of it is half as long as the fourth metatarsal, which lies parallel and adjacent to it. Like the other metatarsals in the pes, the fourth is half the diameter of the fifth and with its base overlaps the base of the third metatarsal, which is 25% longer than the fourth and lies parallel to the latter. The second metatarsal forms an angle of 10° with the third. Its base overlaps that of the first, but its distal end is missing and thus its length remains uncertain. The first metatarsal is
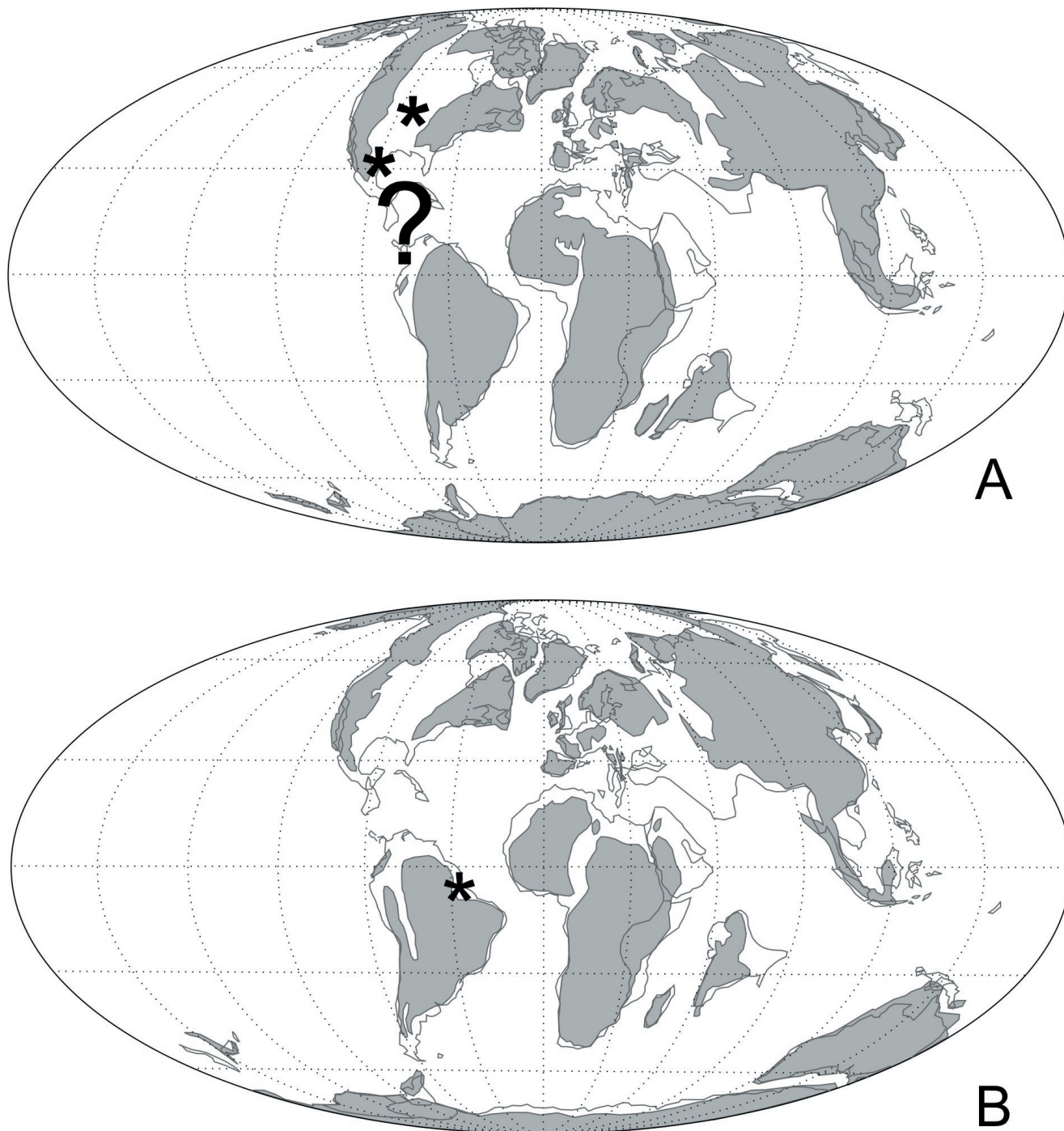
Figure 7 – Palaeogeographic situation of the western Tethys area during the late Cretaceous and the distribution of the nyctosaurid pterosaurs. A) Finds of nyctosaurids in the Coniacian/Santonian ; the area marked with "?" was probably rich in small islands; 1: *Muzquizopteryx*, 2: *Nyctosaurus* from the Niobrara Formation; B) The only find of a possible nyctosaurid in the Maastrichtian comes from Paraiba, northeastern Brazil. Maps redrawn after Smith et al., 1994.

slightly shorter than the fourth and with the second encloses an angle of 8°.

DISCUSSION

The specimen described here is not only the first diagnostic pterosaur from the Cretaceous of Mexico representing a new genus within Nyctosauridae, but

also represents the earliest known record of nyctosaurid pterosaurs. It throws new light upon the palaeobiogeography of nyctosaurs and reveals some anatomical detail of the wrist and the position of the pteroid previously unknown. Furthermore, it yields information on the growth stage of the individual and permits the reconstruction of some arm muscles based on the preservation of mineralised tendons (fig. 5A).

Palaeobiogeography

Until now nyctosaurid pterosaurs were known only from the Coniacian-Santonian marine deposits of the Western Interior Seaway and northeast Brazil. The specimen described as a nyctosaurid from the Jiufotang Formation of western Liaoling (Aptian, Early Cretaceous) by Wang & Zhou (2003) most likely represents an azhdarchoid pterosaur (see above; Unwin pers. comm.).

The majority of nyctosaur specimens come from the Upper Coniacian to Santonian sequence of the Niobrara Formation in western Kansas (USA; fig. 7). These remains have been referred to the two species *Nyctosaurus gracilis* and *Nyctosaurus bonneri* (Miller, 1972b). The Niobrara Formation was deposited in the Western Interior Seaway, which was up to 1000 km wide during the Late Cretaceous (Dercourt et al., 1993, Smith et al., 1994; fig. 7).

One possible nyctosaurid humerus identified by its hatchet-shaped deltoid process is reported from the Maastrichtian Gramame Formation in Paraíba (northeast Brazil), (Price, 1953, fig. 7; Wellnhofer 1991, p. 122 for colour photograph). The distribution of the Maastrichtian deposits in northeast Brazil suggests the presence of a large bay or a coastal basin during the Late Cretaceous (Price, 1953, Mabesoone, 1993).

Muzquizopteryx coahuilensis died in the Early Coniacian at the junction between the southern mouth of the Western Interior Seaway and the west end of the Tethys. During that period, this area was characterised by a number of islands and straits that were continuous towards the south to the northeast coast of the western part of Gondwana (northeast Brazil of today; fig. 7; Dercourt et al., 1993).

According to Bennett (2003a), *Nyctosaurus* was restricted to the east coast of the Western Interior Seaway. *Muzquizopteryx* proves that nyctosaurid pterosaurs already existed in the Early Coniacian south of the Western Interior Seaway. The possible nyctosaurid humerus from the Maastrichtian of northeast Brazil could indicate a dispersion of nyctosaurs from Mexican Gulf area to the South along the eastern shore of South America, but due to the restricted fossil record, this would be speculative. However it is matter of fact that, until now, nyctosaur remains are unknown from any other Upper Cretaceous pterosaur locality in the world. One might speculate that the nyctosaurs were endemics, which could only survive in certain environments, where the climatic conditions and food resources were favourable for this enigmatic type of pterosaur.

Age and size of the new individual

The co-ossification of the vertebrae (figs. 2, 3), the mineralization of the ligaments connecting the lateral extremities of the transverse processes (figs. 2, 3), the ossified tendons of some arm muscles (figs. 2, 5) and the synsacrum comprising at least eight vertebrae (figs. 2, 3) indicate that the pterosaur was adult when it died. Strong support for this interpretation is the fusion of the medial rami of the prepubic bones and the fusion of their cranial rami with the caudalmost gastral ribs (figs. 2, 3). Bennett (1993, 2001b) described the same type of prepubic fusion with the caudalmost arcade of gastralia for mature specimens of *Pteranodon*. According to Williston (1903) and Bennett (2003a) *Nyctosaurus gracilis* could reach a wingspan of four metres or more. The biometric data of *Nyctosaurus bonneri* given by Miller (1972a) show humerus sizes of more than 130 mm (see tab. 1). The maximum wingspan of *Nyctosaurus bonneri* is therefore estimated to be about four metres as well, but because there is no indication of its growth stage, it remains unclear whether or not *Nyctosaurus bonneri* could have grown even larger. The 110 mm long humerus of the dubious taxon *Nyctosaurus lamegoi* Price, 1953 indicates an animal with a wingspan of more than three metres, which would be within the size range of semi-adult *Nyctosaurus* specimens (Bennett, 2003a).

An estimate of the wingspan of *Muzquizopteryx coahuilensis* based on the data for *Nyctosaurus gracilis* and *N. bonneri* suggests an animal with an adult wingspan of no more than two metres. This makes *Muzquizopteryx coahuilensis* the smallest nyctosaurid if not the smallest known Late Cretaceous pterosaur, which doubtlessly was adult.

Anatomy of the wing

In contrast to the specimens of *Nyctosaurus gracilis* specimens described by Bennett (2003a) the mineralised tendons of *Muzquizopteryx coahuilensis* are preserved almost *in situ* (fig. 5). This allows the reconstruction of some of the principal muscle masses of the wing in previously unknown detail. The muscle systems discussed here are based on avian anatomy, because the parallelogram-shift movement of radius and ulna as well as the restricted mobility of the arm in basically one plane appear similar in both birds and pterosaurs (Salomon, 1993, Bennett, 2003b). The muscle designations used here do not necessarily imply homology, but refer to their topography.

Extensor operation for wing finger metacarpal and wing finger (figs. 5, 6): The mineralised tendon along the cranial face of the radius lies adjacent to the bone and, in comparison with avian anatomy (Salomon, 1993) is referred to a remnant of m. extensor metacarpi radialis. This muscle, based on its preserved tendinal trace, was single-headed and most likely originated from the distal cranial face of the humerus (cf. Bennett, 2003b). The insertion tendon probably passed around the cranial face of the carpus ventral

to the pteroid and the preaxial carpal and inserted on the proximoventral part of the wing finger metacarpal (fig. 6). The presence of m. abductor digiti that originated on the cranial face of the wing finger metacarpal and inserted on the so-called olecranon process of the proximal base of the first wing finger phalanx by means of a long tendon is evidenced by the preservation of a mineralised tendon in *Nyctosaurus* cf. *gracilis* (Bennett, 2003a; fig. 6). Evidence for the existence of m. extensor digiti is indirect, but its presence is reconstructed here based on the remnants of a tendon, extending transversely across the cranial third of the preaxial carpal (fig. 5), precisely where the dorsally orientated pit would be, which is present on the dorsal face of the preaxial carpal in all pterosaurs. M. extensor digiti could have orginated from the craniodistal face of the humerus (Bennett, 2003b; fig. 6). Its tendon then passed cranially to the carpus through the pit in the dorsal face of the preaxial carpal to an insertion on the olecranon process of the first wing finger phalanx. The preaxial carpal served as a pivot, which kept the tendon of m. extensor digiti away from the arm (fig. 6) and allowed the m. extensor digiti tendon to slide in the pit during flexion and extension movements of the wing. Therefore, it was probably reinforced by a sesamoid, which is regularly found inside this pit (Bennett, 2001a: sesamoid A). Such a long m. extensor digiti would have had the right position to load the preaxial carpal exactly along its longitudinal axis, when the arm is pulled into and held in flight position. Additionally, the muscle would have had a better lever effect to hold the wing finger in flight position than the short m. abductor digiti, which was in a better position to move the wing finger into the flight position (fig. 6).

Flexor operations for wing finger metacarpal and wing finger (fig. 6): Two mineralised tendons are preserved along the caudal face of the ulna: one extending along the caudal edge of the ulna and one short and wide tendon covering the proximal sixth of the ulna dorsally. The latter element is likely to represent the originating tendon to m. flexor carpi ulnaris, which acted as the antagonist of the m. extensor metacarpi radialis. It is likely that m. flexor carpi ulnaris inserted on the proximocaudal face of the wing finger metacarpal with some fibres inserting at the carpus. The deeper mineralised tendon, extending subparallel to the caudal face of the ulna has half the diameter of the tendon of m. flexor carpi ulnaris but is more than five times longer. This tendon probably belongs to m. flexor digiti, which originated from the caudal face of the proximal part of the ulna at the elbow joint. Probably the insertion area also included the distal extremity of the caudal face of the humerus. The distal insertion tendon passed caudal to the carpus and inserted on the caudal articular process of wing finger phalanx I (fig. 6). Both flexor tendons had to be held in place by a carpal ligament system.

Unidentified muscle originating from the elbow (fig. 5): From the proximal extremity of the ulna arises a small mineralised tendon, which, on both wings, points medially at almost the same angle. There are two possible interpretations for this tendon: either it represents the distal insertion tendon of m. humerotriceps, which became dislocated postmortem, or it is the tendon of a muscle that controlled the tension of the plagiopatagium. Which of these two possibilities is the more plausible cannot be determined at present.

The position of the pteroid and some mechanical implications: The *in situ* preservation of the left wrist (fig. 5A) not only allows for the reconstruction of the position of the pteroid bone but also an interpretation of its mechanical role along with the preaxial carpal as a reinforced extensor system for the wing. The pteroid articulates with the proximal syncarpal proximal to the preaxial carpal and is separated from the base of the preaxial carpal by a gap. The preaxial carpal faces craniodistally. Across its cranial extremity, where the fovea should be, a tendon extends proximomedially but is truncated (fig. 5B; see also above). Distally, this massive tendon probably inserted on the so-called olecranon process – in fact a sesamoid of the tendon itself - of the first wing finger phalanx. The proximal part of the tendon could either represent the insertion tendon of a long m. extensor digiti of the wing winger as reconstructed in figure 8, or an unknown part of a tensor system for the propatagium.

The tip of the pteroid was orientated medially. It could have served as an insertion area of a propatagial tensor muscle (fig. 6A) functionally similar to m. tensor propatagialis in birds (Salomon, 1993) or m. occipitopollicalis in bats (Hill & Smith, 1984). It also could have served as a sliding structure for a propatagial tensor tendon, which inserted on the preaxial carpal, the metacarpus or the wing finger (fig. 6A), as was suggested by Bennett (2000, 2001b). Bennett (2000, 2001b) postulates short musculotendinal systems between the neck of the pteroid and the carpal bones that guaranteed the mobility of the pteroid to control shape and tension of the propatagium. Regardless of how the pteroid was put under tension, antagonists to the propatagial tensor systems must have compensated the load on the pteroid. Such antagonists would best act in line with the corpus of the pteroid (fig. 6A). Then, the neck and the articulation would have been loaded by compression, which would make sense in terms of the shape of the neck of the pteroid and its 90° angle to the corpus. A blunt ridge along the ventral side of the cranial margin close to the proximal end of the corpus of the pteroid and a low, blade-like extension of the laterally facing margin of the neck indicates the presence of such a structure (see Williston, 1903: plate XLII; fig. 4). The role of the groove on the corpus of the pteroid is unclear. Such a groove is visible on the pteroid of *Nyctosaurus gracilis* depicted by Williston (1903: plate XLII; fig. 5). A similar groove is present on the cranial and caudal faces of the pteroids of ornithocheirid pterosaurs from the Santana Formation (Early Cretaeous, NE Brazil; Unwin et al., 1996),

but is unknown in *Pteranodon* (Bennett, 2001a). The cranial groove in ornithocheirids terminates at a tuberosity, whereas the caudal groove expands into a shallow sulcus, which is confluent with a pneumatic foramen (EF, pers. obs. on the pteroid of *Coloborhynchus robustus* SMNK PAL 1314). Level with the cranial tuberosity, the groove diverges into a deep pit. These sulci may have housed fibrous, cartilaginous or muscular structures, which were likely to be part of the propatagial tensor system, which then could have acted as an additional extensor of the entire wing (fig. 6A). The angle between the shaft and neck of the ornithocheirid pteroid is much larger than in nyctosaurids (*cf.* Wellnhofer 1991), which requires further investigation on the three-dimensionally preserved material from Brazil. This should help to clarify the anatomical situation of the pterosaurian carpus.

The anatomy of the wrist of *Muzquizopteryx coahuilensis* provides additional evidence that the reconstruction of the pterosaurian carpus suggested by Hankin & Watson (1914), Frey & Riess (1981) and Pennicuick (1988), with a forwardly pointing pteroid, articulating with the pit of the preaxial carpal, is incorrect. The biomechanical argument for that reconstruction was the necessity to alter the wing camber for slow flight, take-off and landing. However, there is good evidence that alteration of the wing camber could have been achieved by the muscularised wing membrane itself (Frey et al., 2003b). Therefore, a less mobile and smaller forewing with a rounded leading edge shaped by the extensor tendons would be aerodynamically sufficient for the proximal part of the wing (fig. 6). In the distal part, the flat oval bones of the wing finger and the adjacent soft tissues formed the leading edge of the wing. The classical reconstruction of the carpus, where the pteroid also articulates with the pit of the preaxial carpal, but faces medially with a propatagial tendon pulling from its tip toward the shoulder (see Wellnhofer, 1991 for an overview), must also be rejected. Such an insertion would have loaded the pteroid unidirectionally, a load, which could not have been accommodated by the bone (Frey & Riess, 1981). The pteroid of *Muzquizopteryx coahuilensis* articulates with the carpus in the way described by Bennett (2001a, b) for *Pteranodon*, with the only difference being that a contact with the preaxial carpal is absent. However, the role of the pteroid as an attachment area for medially directed tendinomuscular systems remains a possibility (cf. Abel, 1907, 1919, Short, 1914, Bramwell & Whitfield, 1974, Padian, 1983, 1984).

Why should Nyctosauridae be separated from Pteranodontidae?

Despite the similarities in overall appearance between some nyctosaurids and pteranodontids in the morphology of the skull, the position of the head crests and the proportions of the appendicular skeleton, the two taxa show significant differences in the construction of their flight apparatuses, which have consequences for flight performance. The wing construction of the pteranodontids is very similar to that of ornithocheirids (Wellnhofer, 1991). The humerus of both pterosaur types shows a proximally situated triangular deltoid crest, which implies a short lever for the wing adductor musculature. The morphology of the carpus and the shape of the pteroid of pteranodontids are almost identical to those of ornithocheirids. Only the wing finger metacarpal is much longer relative to the radius-ulna in pteranodontids than in ornithocheirids. Mineralised tendons aligned with the wing skeleton have never been reported for pteranodontids, even though they occur in the same sediments, such as the Niobrara Formation (Bennett 2001a, 2003a), nor for any other pterosaur with detailed soft part preservation from other body areas (Frey et al., 2003b).

In contrast, the deltoid process of the nyctosaurid humerus is situated distal to the head of the humerus, which results in a long lever for the pectoral adductors. Those muscle fibres that insert along the distal margin of the deltoid process additionally act over a long lever with respect to the shaft of the humerus. Consequently pronation and supination of the entire wing in nyctosaurids must have had a larger range of angle of attack than in ornithocheirids and pteranodontids. The articulation of the pteroid in nyctosaurs indicates restricted movements in the horizontal plane, because the neck of the pteroid lies almost parallel to the preaxial carpal. The neck of the pteroid in ornithocheirids and pteranodontids curves away from the preaxial carpal at an angle of about 120°, which would allow a mobility of the bone of about 40° to 45°. Therefore, such a carpal construction would enable the animals to modify the area of the propatagium, which was impossible for the nyctosaurids, due to the 90° angle between shaft and articular head. Any ante-rotation would have been blocked by the preaxial carpal or the proximal syncarpal. Furthermore, the mineralised tendons in the wing of nyctosaurids indicate a wing with restricted mobility.

A precise reconstruction of the wing mobility of *Muzquizopteryx* is not possible due to the crushed joints, but the almost identical angulation of the bones in both arms indicates that the bone positions as preserved might represent the maximum possible abduction of the wing, at least post-mortem (fig. 5). The dimensions of the mineralised tendons would not have allowed much more abduction without being compressed.

In our opinion, the enigmatic nyctosaurid wing construction suggests that the nyctosaurs should not be included within the Pteranodontidae, but kept as a separate taxon. Further investigations are necessary to understand from which pterosaurian pre-construction the nyctosaurs could have evolved. The biomechanical consequence of the nyctosaurid wing construction for flight will be with investigated with life size radio controlled pterosaur models, in which the anatomy, mobility of the wing and material properties of the wing membranes of *Muzquizopteryx coahuilensis* are simulated to the maximum possible according to what is known of pterosaurian anatomy. The

mechanical constraints of the nyctosaurian wing construction may have been one reason why these enigmatic pterosaurs could not spread by flying across the Upper Cretaceous oceans.

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