Annotated catalogue of marine squamates (Reptilia) from the Upper Cretaceous of northeastern Mexico

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Abstract

Recent work in the Upper Cretaceous of northeastern Mexico has produced a diversity of vertebrate remains. For specimens referable to Squamata, both old and new, an annotated catalogue is here provided, wherein are summarised the geological context and morphological features of each specimen. All specimens appear to represent marine squamates, including an aigialosaur-like reptile preserving integumentary structures, several vertebrae possibly representing mosasauroids, the first Mexican mosasaur known from significant cranial material, an isolated mosasaur mandibular fragment, and the holotype of *Amphekepubis johnsoni* (considered to belong to *Mosasaurus*). These discoveries are auspicious and should deepen our understanding of palaeobiogeographic and evolutionary patterns.

Keywords: Mosasauridae, Aigialosauridae, Upper Cretaceous, Mexico, catalogue

Introduction

Vertebrates from the marine Upper Cretaceous of northeastern Mexico are poorly known in comparison with those from North America and Europe. Recent and ongoing work on marine assemblages in South America (e.g., Páramo-Fonseca, 1997a, b) as well as North Africa (e.g., Cavin, 1995, 2001; Bardet et al., 2003a, b) and the Middle East (Bardet & Tunoğlu, 2002), however, renders their Mexican counterparts crucial for understanding the palaeobiology and palaeobiogeography of vertebrates as diverse as actinopterygians and mosasaurs, given that the Late Cretaceous Mexican Gulf was located at the junction of the Pacific Ocean, the Western Interior Seaway and the Atlantic Ocean.

Recent field work in the Cretaceous of northeastern Mexico (Fig. 1) has demonstrated that, although often conceived of as poor, these strata can be locally rich in vertebrate remains. These discoveries are not only important for addressing biogeographic questions about the relationships between South and North American and Tethyan marine assemblages. They also provide significant morphological, phylogenetic and palaeoecological information on certain groups. Of particular interest here are the squamates. In this catalogue we summarise the regional and local geology and the depositional
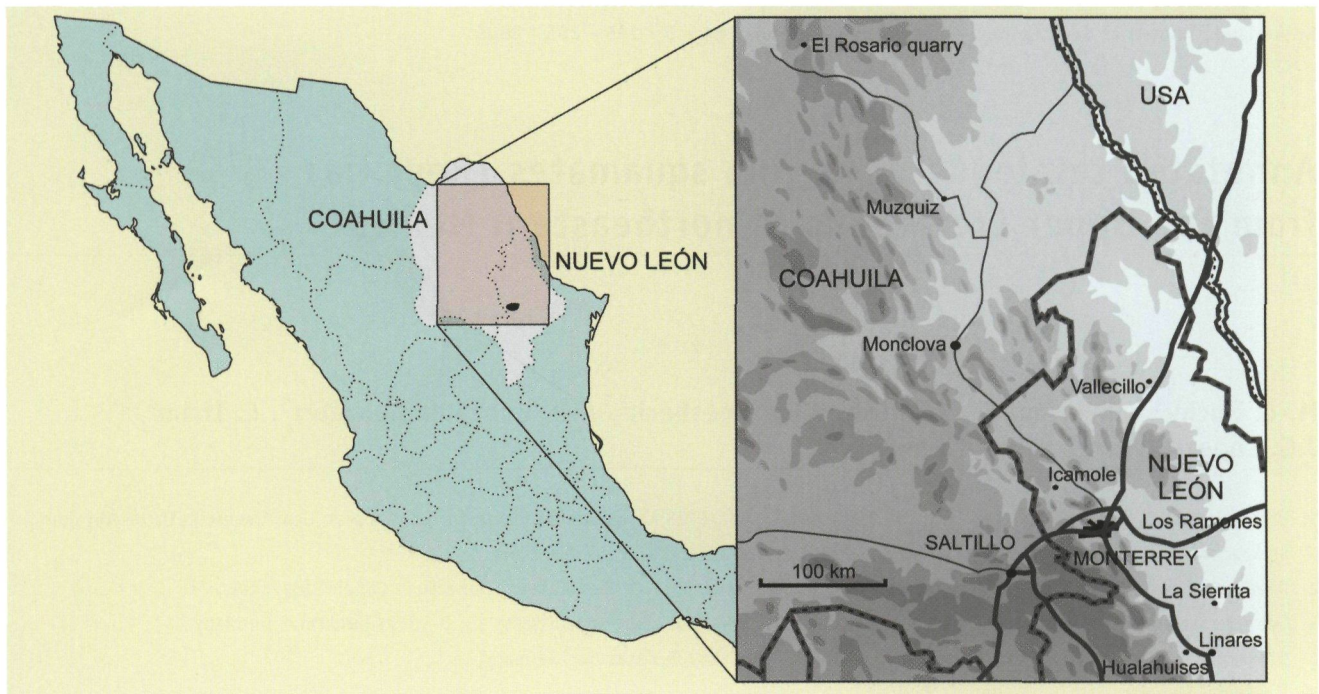
Fig. 1. Map of northeastern Mexico showing locations of the vertebrate fossil-bearing sites discussed in the text.

environment of specimens old and new and provide brief morphological descriptions for the most recent specimens. It is hoped that this catalogue will encourage workers to explore further the Upper Cretaceous of northeastern Mexico.

Abbreviations – MUDE - Museo Del Desierto, Saltillo (Coahuila, Mexico); MHM - Museo Historico de Múzquiz, Múzquiz (Coahuila, Mexico); SMNK - Staatliches Museum für Naturkunde (Karlsruhe, Germany); UANL-FCT - Universidad Autónoma de Nuevo León, Facultad de Ciencias de la Tierra, Linares (Nuevo León, Mexico); UPI - Evolutionsmuseet (Paleontologiska Museet), Uppsala, Sweden.

Early Turonian Agua Nueva Formation at Vallecillo, Nuevo León

Geological setting

The laminated limestones of the Agua Nueva Formation are mined in commercial quarries around the village of Vallecillo, 100 km north of Monterrey (Fig. 1). The Agua Nueva Formation usually consists of layers of dark-grey limestone and shale, rich in microfossils and trace fossils, whereas macrofossils (other than inoceramids) are rare. In the area of Vallecillo, however, the Agua Nueva Formation includes a member of finely laminated marlstone rich in vertebrates, mainly fishes (Blanco et al., 2001; Blanco-Piñón et al., 2002). The marlstones of this member include the early Turonian *Watinoceras coloradoense* to *Pseudaspidoceras flexuosum* ammonite zones (Bengtson, 1996; Kennedy et al., 2000; Fig. 2). During the Turonian, the Vallecillo area was located on the outer shelf,

approximately 150 km east of the shallow-water Aurora carbonate platform (Goldhammer & Johnson, 2001).

Ammonites were frequently embedded vertically in the sediment, indicating a non-solidified, muddy to soupy substrate. At present, the only benthic faunal elements known from the Vallecillo assemblage are species of *Inoceramus* and *Mytiloides*. Other benthic organisms appear to be absent, as are trace fossils of ecto- and endobenthic organisms. This faunal picture is corroborated by the millimetre-scale lamination of the sediment. These characteristics indicate at least episodic anoxia at the sea floor. A global Oceanic Anoxic Event (OAEII) is known from the late Cenomanian that regionally persisted into the early Turonian (de Graciansky et al., 1986), which could explain the apparent anoxia in the Vallecillo Basin.

More than 400 actinopterygians and elasmobranchs, three turtles, a single pliosaur tooth and an aigialosaur-like reptile (UANL-FCT-R27) have been collected thus far as the result of an on-going collaboration between the University of Karlsruhe, the SMNK, the MUDE and the UANL-FCT (Blanco et al., 2001; Blanco-Piñón et al., 2002). These Vallecillo vertebrates, which are reposited at UANL-FCT, SMNK and MUDE, are generally compressed to a thickness of a few millimetres. Most specimens are partially or completely articulated. Soft-part preservation is rare, but impressions of fins and contents of the digestive tract are frequently found. Bones are generally completely replaced by calcite. Aragonitic shells of invertebrates are always dissolved.

The good preservation of vertebrate fossils is explained by the absence of water currents and turbulence, at least on the sea floor, combined with anoxic bottom conditions and the fine grain size of the sediment (a micritic lime mud).
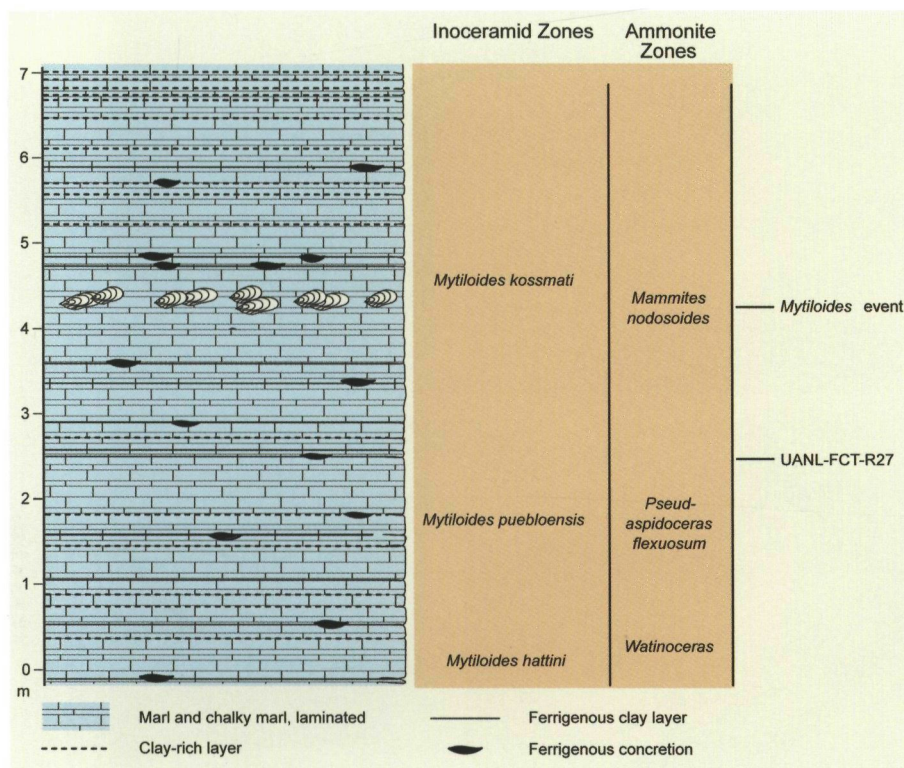
Fig. 2. Section of lower Turonian marls at Vallecillo, N.L., with stratigraphic zonation after Kennedy et al. (2000) and origin of UANL-FCT-R27 from the upper P. flexuosum Zone. Precise limits of stratigraphic zones are still uncertain.

Specimen UANL-FCT-R27 (Fig. 3)

Preservation – This specimen comprises a partial, articulated postcranial skeleton with integumentary structures (abdomen, hind limb, tail), a long segment of tail, complete left pelvic girdle and hind limb, and part of the left lumbar region including parts of distal ribs from more cranial, non-preserved vertebrae (Fig. 3a, b). Pebble-like structures in the abdomen presumably represent contents of the viscera. Three smaller slabs represent the counterparts of the caudal-most dorsal vertebrae and a partial manus or (Fig. 3c). The specimen is preserved in dorsal view on the largest slab (Fig. 3a). The slabs were collected by the quarry owner for the UANL-FCT.

Preliminary description – The distal lumbar ribs are approximately the same length as the sacral ribs. More cranial vertebrae appear to have borne longer, more slender, more curved ribs than those vertebrae close to the sacrum, as is indicated by the preserved distal part of three ribs of the thorax (Fig. 3b). The (unfused) haemal arch of any given caudal vertebra is approximately the same length as the respective neural spine, and both structures are inclined caudally at an angle of about 45° (Fig. 3a).

Scales and scale impressions close to the base of the tail are large, rhomboidal and arrayed in oblique rows (Fig. 3a, b). These soft-tissue structures describe the outline of the tail and indicate that, proximally, more of the tail mass was present ventral to the vertebral column than dorsal to it.

The pubis extends craniomedially from the acetabulum and appears to taper medially but has only partially been exposed.

A pubic tubercle emerges from close to the acetabulum as a craniolaterally directed, rounded eminence. The ischium is as broad at its base as the base of the pubis. The ilium runs caudally from the acetabulum, its length equivalent to the length of about two presacral vertebrae. The first sacral rib is directed caudolaterally as preserved, the second close to laterally.

The femur is over 50% longer than the tibia and fibula. The space between the latter two bones is lenticular in outline. The tibia is bowed cranially and its shaft is about twice as thick as the shaft of the fibula. The distal end of the fibula is twice as wide as its shaft. The astragalus and calcaneum are fused, and the articular facets for the tibia and fibula are moderately separated on its concave proximal median margin. The fourth distal tarsal is subcircular in outline. The fifth metatarsal is strongly hooked, similar to what is seen in *Varanus*. The phalangeal formula is 2-3-4-5-4.

Comments – The anatomy and morphology of UANL-FCT-R27 will properly be described in a forthcoming work, and its affinities to other marine squamates discussed. For the moment we note that this specimen is similar in size and morphology to some described aigialosaurs, for instance in the length and orientation of the neural and haemal arches and the reduction of caudal postzygapophyses, and lacks many features diagnostic of Mosasauridae (see Carroll & DeBraga, 1992; DeBraga & Carroll, 1993). Few basal mosasauroids with such a well-preserved pes or integumentary structures have been described. Furthermore, UANL-FCT-R27 is the first such reptile known from Mexico and, provided the associated
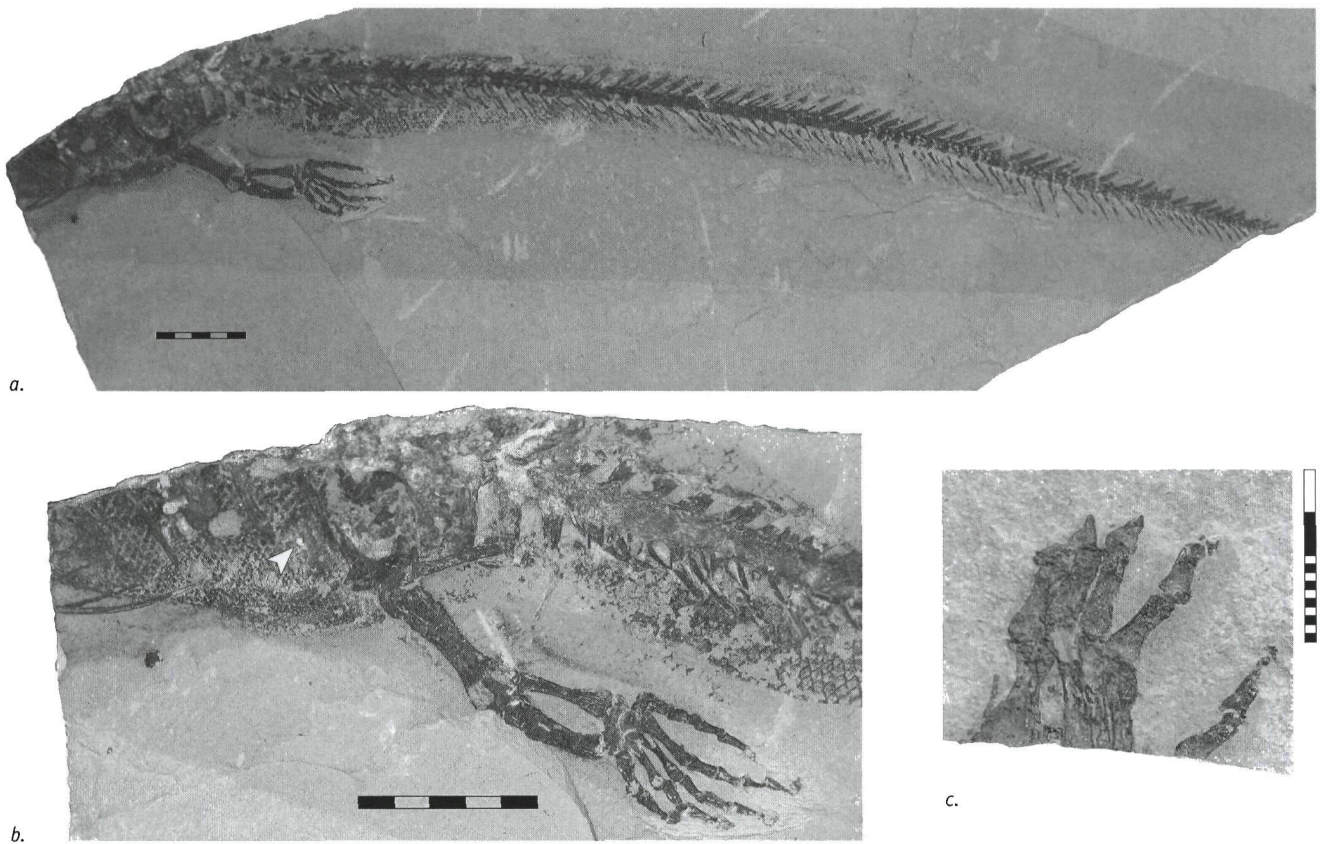
Fig. 3. Undescribed aigialosaur (UANL-FCT-R27) from near Vallecillo, N.L.; a. main slab, scale bar 50 mm. Note especially soft-tissue structures preserved on the tail; b. detail of pes and abdomen; the arrow indicates the pebble-like structure studied by EDS; scale bar 50 mm; c. partial manus or pes; scale bar 20 mm.

ammonites accurately reflect an early Turonian age, one of the oldest North American occurrences as well (see also Bell & VonLoh, 1998).

EDS analysis of one of the pebble-like structures preserved within the rib-cage (Fig. 3b) indicates that it is composed mostly of Ca, C and O, presumably calcite.

Late Turonian to early Coniacian Austin Group at Múzquiz, Coahuila

Geological setting

Inhabited areas north and northwest of Múzquiz are isolated, the few lonely houses and farms accessible only via dirt tracks that branch off the main road (Fig. 1). Several limestone quarries are located in this remote region, where thinly bedded, laminated limestones are mined and sold as floor flags. The sediments likely belong to the Upper Cretaceous Austin Group, a sedimentary unit of marls and limestone that is widely distributed in northeastern Mexico and southern Texas and generally considered to be poorly fossiliferous (Sohl et al., 1991). The Austin Group was deposited under open marine (although not very deep) conditions, and its age is considered to be Coniacian-Campanian (Sohl et al., 1991).

At the El Rosario quarry (Fig. 1), approximately 180 km northwest of Múzquiz, 53 m of laminated limestone alternate with laminated marly limestone and marl. During past mining activities fossil fishes were frequently unearthed. A few of these are preserved three-dimensionally, and retention of skin, muscles and fins is common. According to our initial investigation, this extraordinary preservation of soft parts results from early, rapid, partial phosphatisation (Martill, 1988). Other ecological-oceanographical parameters, such as the fine grain-size of the lime mud, the abundance of organisms, the absence of strong currents and, consequently, at least temporarily anoxic conditions on the sea floor, also contributed to the excellent preservation (Rindfleisch, 2004; Stinnesbeck et al., in press; Frey et al., in press).

The assemblage includes fragments and complete specimens of fishes and numerous invertebrates (e.g., ammonites, inoceramids, crustaceans, planktonic foraminifera), a pterosaur (Frey et al., submitted), and the vertebrae described herein. The ammonite assemblage (*Peroniceras tridorsatum*, *Forresteria* (*F.*) *brancoi*, *F.* (*F.*) *alluaudi*, *Baculites yokoyamai*, *Scaphites* (*S.*) *frontierensis*, *S.* (*S.*) cf. *preventricosus*, *S.* (*S.*) *sagensis*, *S.* (*S.*) *uintensis* and *Neocrioceras* (*Schlueterella*) sp.) and the inoceramid assemblage which includes *Didymotis costatus*, *Mytiloides scupini*, *Cremnoceramus w. waltersdorfensis*, *C.*

deformis erectus and *C. crassus inconstans* indicate a late Turonian (0 - 25 m of section) to early Coniacian (above 25 m) age (Kennedy & Cobban, 1991; Walaszczyk & Cobban, 2000; Rindfleisch, 2004; Stinnesbeck et al., in press; Frey et al., in press). The precise occurrence in the section of the three specimens described here is unknown.

Specimen MHM PAS 337 (Fig. 4)

Description – This isolated fragmentary vertebra was obtained from a local collector. It is procoelous, and measures 59 mm in length. It exhibits only the very weakest of precondylar constrictions (Fig. 4a, b); as preserved the condyle itself is about 38 mm in width and 26 mm in height (Fig. 4d). The condyle is weakly inclined cranially at an angle of about 5° (Fig. 4c). Much of the cotyle has weathered away. The transverse processes are craniocaudally elongate at their base, the cranial margin being located near the lateral edge of the cotyle and the caudal margin approximately two-thirds down the length of the centrum, where they smoothly join the centrum in a gentle curve; the transverse processes are teardrop-shaped in cross-section, thicker cranially than caudally, and with the long axis of the cross-section in a horizontal plane (Fig. 4a - c). The dorsal portion of the neural arch is missing, and the neural canal is filled by a natural cast. The neural arch inserts about 3 mm caudal to the cotyle and extends caudally as far as the transverse processes do (Fig. 4a, c, d). The broken bases of the neural arch are thin (1 - 2 mm) cranially but thicken as they extend caudolaterally. The neural canal, its internal dimensions about 10 mm in width cranially, is narrow in comparison with the centrum (Fig. 4a). Ventrally the vertebra is gently convex along its entire length (Fig. 4b, c).

Comments – The inclination of the articular surfaces of the centrum suggest assignment to Platynota. Furthermore, the low angle of inclination of the condyle and cotyle, which are only little depressed compared to terrestrial platynotans, the near-absence of precondylar constriction and the insertion of the neural arch far cranially suggest an aquatic animal (Rage, 1989). Mosasaurs, aigialosaurs and dolichosaurs are currently the only aquatic platynotan taxa recognised from the Upper

Cretaceous (e.g. Calligaris, 1988; DeBraga & Carroll, 1993; Caldwell & Cooper, 1999; Lee & Caldwell, 2000; Pierce & Caldwell, 2004). However, knowledge of the vertebral anatomy of some of these groups is restricted. The large size and general morphology of the specimen strongly suggest mosasaur affinities.

Specimen MHM PAS 338A and B

Two articulated partial vertebrae were obtained from a local quarry worker. They are preserved in a slab split down the middle and are currently visible in coronal section. Preparation is necessary to allow identification. At present they appear to be procoelous and could represent a large platynotan. They appear more elongate than the isolated vertebra from the same location discussed above (MHM PAS 337).

Specimen MHM PAS 336 (Fig. 5)

Preservation – The specimen comprises 16 articulated vertebrae preserved on the edge of a slab; they are visible in right lateral and partly ventral views (Fig. 5a). The centra underwent lateral compression during fossilisation, which may be responsible for the presence of a median ventral keel on all centra. The lateral surface of all centra is damaged. The cranial-most preserved centrum appears damaged in its cranial-most portion. The last preserved vertebra is crushed and its morphology indistinct. The neural arches are largely complete except the last two. The neural arches are fused to the centra (Fig. 5b). All haemal arches are missing, except on centra 6, 7 and 15, where the broken proximal-most portion of the arches are preserved. The haemal arches were not fused to the centra.

The terminal-most three vertebrae are slightly shifted laterally from their original position in the column. Due to this displacement, the condyle of centrum 15 is partly visible in caudolateral aspect. The cotyle of the first preserved centrum is partly exposed after partial preparation.

Description – The vertebrae are procoelous and the neural spines inclined terminally. They bore haemal arches and lack transverse processes and consequently belong to the middle region of the tail of an aquatic platynotan.
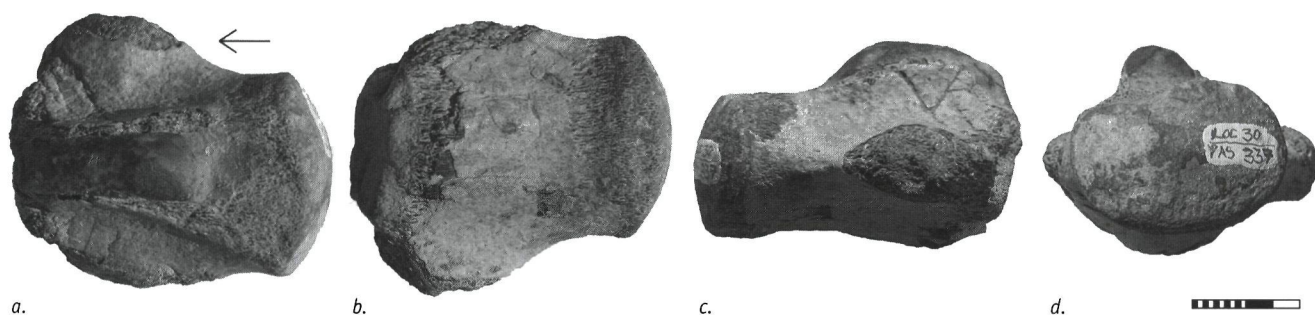

Fig. 4. Undetermined squamate, partial vertebra (MHM PAS 337) from the El Rosario quarry, north of Múzquiz, Coah., in a. dorsal, b. ventral (for both, arrow points cranially), c. right lateral and d. caudal views. Scale bar 20 mm.
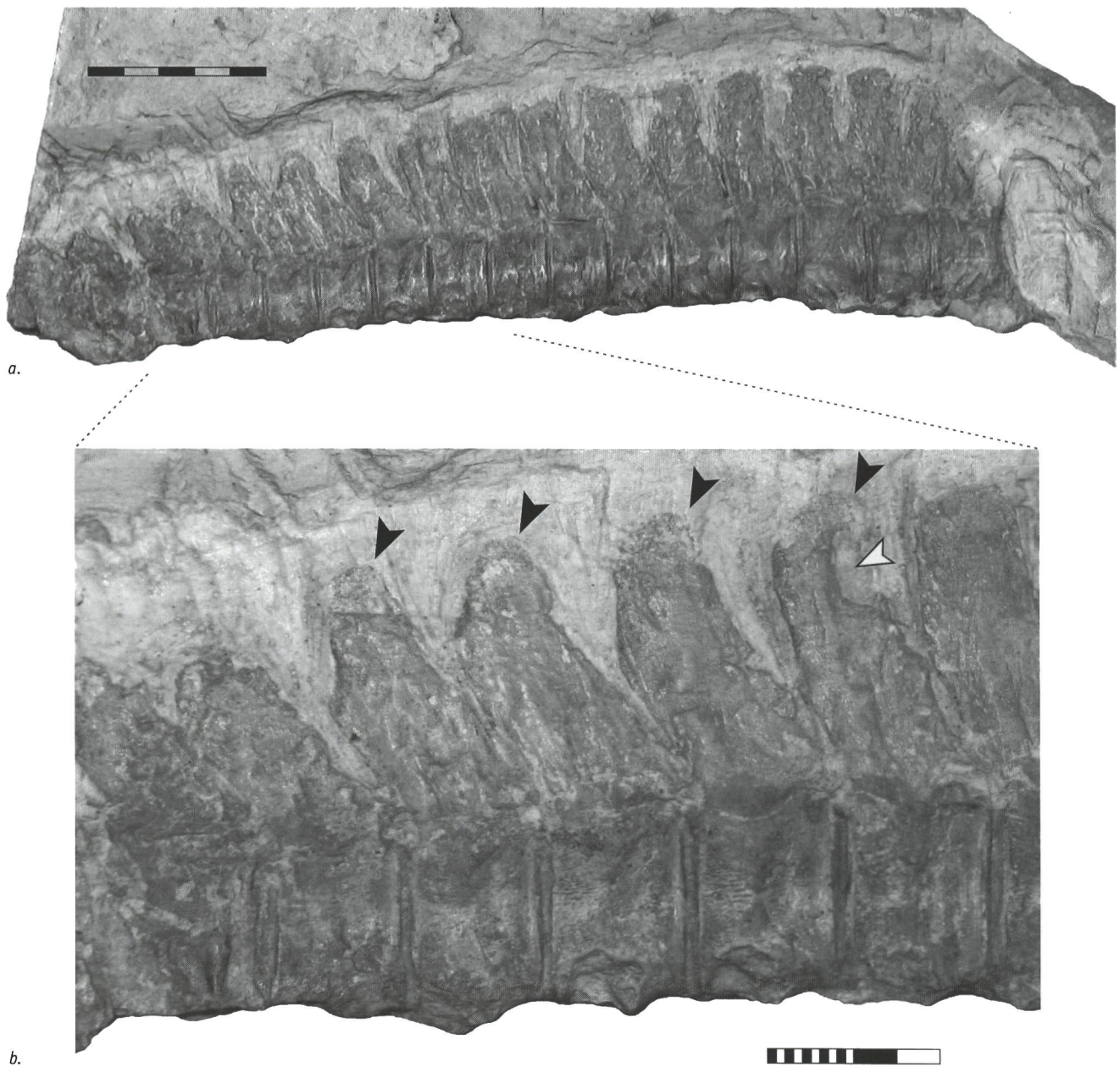
Fig. 5. *Undetermined mosasaur (MHM PAS 336) from the El Rosario quarry, north of Múzquiz, Coah.; a. whole specimen in right lateral view, scale bar 50 mm; b. detail of vertebrae 9 to 14; black arrows indicate the cartilaginous extremities of the neural spines; white arrow indicates a possible bite mark; scale bar 20 mm.*

As preserved, the centra are pulley-shaped in lateral aspect, the lateral surfaces of the centra being impressed in the middle (Fig. 5). Terminally, the height of the centra decreases regularly (Table 1). Provided compression affected all centra in the same manner, they irregularly decrease in height relative to their length as well (Table 1).

All centra bear paired ventrolateral subcircular facets for the haemal arches, which are slightly elevated compared to the surface of the centra. The facet for each haemal arch extends over the terminal half of the centrum (Fig. 5b).

The base of each neural arch is as long as its respective centrum. The ventral half of the neural arches is inclined

terminally, the cranial and terminal margins being subparallel. The ventral half of each neural spine is separated from the preceding and succeeding spines by less than 2 mm. The dorsal half of all completely preserved neural spines rises nearly dorsally. The neural spines therefore exhibit an inflection around mid-height. In vertebrae 1 and 10 - 12, but not in 2 - 9, the dorsal half of the neural spine tapers dorsally, the cranial margin being inclined caudodorsally, the caudal margin subvertical (Fig. 5a). In vertebrae 13 and 14, the neural spines are notched craniodorsally (Fig. 5b). The dorsal terminus of the neural arches of vertebrae 1, 2, and 9 - 12 is formed by a semi-oval area of porous tissue, possibly cartilage, while the dorsal

limit of the bone is horizontal (Fig. 5b). Vertebrae 3 - 8 lack this extension, and the dorsal extremity of the neural spine is horizontal. The angulation of the ventral half of the neural spine is more pronounced in vertebrae 1 and 6 - 16, so that in these vertebrae the dorsal extremity of each neural arch extends from level with the centre of its respective centrum to level with the centre of the succeeding centrum (Fig. 5a). While the height of the centra decreases regularly terminally, the height of the neural spines increases slightly from vertebra 1 to 3, then decreases regularly terminally (Fig. 5a; Table 1).

Table 1. Biometry of the vertebrae MHM PAS 336, in mm.

Vertebra number	Height of the centrum	Length of the centrum	Ratio length to height of the centrum	Height of the neural spine
1	?25	?17	?0.68	37
2	25	17	0.68	42
3	24	18	0.75	43
4	23	18	0.78	41
5	22	16	0.72	40
6	21	17	0.81	38
7	21	16	0.76	37
8	20	15	0.75	35
9	19	15	0.79	34
10	19	15	0.79	32
11	18	14	0.77	31
12	17	13	0.76	30
13	17	15	0.88	23
14	16	15	0.93	20
15	14	14	1	/
16	/	14	/	/

Comments – The portion of tail was most likely isolated prior to embedding, for only matrix is present cranial to the first preserved vertebra (Fig. 5a). The terminal-most edge of the specimen is broken, and it is unknown whether more vertebrae were present terminally. An oval hole 7 mm in height, 5 mm in length, in the dorsal portion of neural arch 9 may be a bite mark (Fig. 5b). Smaller, subcircular depressions are visible in the neural arches of vertebrae 1, 3, 12 and 13, which may be of similar origin. The loss of this portion of tail could therefore reflect the actions of a large predator or scavenger.

Among aquatic platynotans, the specimen differs from aigialosaurs in the absolute size of the vertebrae, as well as the morphology of the neural spines, being as long as the centra and almost in contact in their ventral half (compare, for example, with Fig. 3a). Adequately preserved comparative material of early mosasaurs is rare, most specimens being disarticulated or lacking the tail, except the holotype of *Halisaurus sternbergii* (Wiman, 1920) (UPI specimen R163).

Campanian-Maastrichtian Méndez Formation

Geological setting

The Méndez Formation is a sedimentary unit of Campanian-Maastrichtian age widely distributed in the Gulf Coast plain of Mexico, east and southeast of the city of Monterrey (Keller et al., 1997; Stinnesbeck et al., 2001). The unit is up to 1,000 m thick and consists of rhythmically bedded marls, shales and minor sandstones. These were deposited in an open marine shelf environment in water depths of approximately 100 m near Los Ramones (40 km northeast of Monterrey) and more than 400 m in the La Sierrita region (40 km north of Linares) (Keller et al., 1997; Stinnesbeck et al., 2001; Fig. 1). Planktonic and benthic foraminifera are abundant and diverse throughout the Méndez Formation, whereas body fossils like inoceramids, ammonites and vertebrate remains are rare (Ifrim et al., 2004).

Specimen UANL-FCT-R6

This specimen (formerly catalogued as MZ0/0001) is a fragmentary jaw with three tooth bases, probably a portion of right mandible, and was described by Aranda-Manteca & Stinnesbeck (1993). It comes from the vicinity of Hualahuises, N.L. (Fig. 1), and no co-preserved fossils permit a stratigraphic assignment more precise than Méndez Formation. The tooth crowns were probably elliptical in cross-section, though only slightly compressed. The specimen was referred to Mosasauridae by its describers.

Specimen UANL-FCT-R4 (Figs 6, 7)

Preservation – The marl adhering to this specimen yielded the foraminifer *Gansserina gansseri*, whose FAD marks the base of zone CF 7 according to the zonal scheme of Li & Keller (1998). *Rugoglobigerina contusa*, whose FAD characterises the base zone CF 6, appears to be absent, excluding an age younger than CF 7. The microfossils thus date UANL-FCT-R4 as early Maastrichtian.

UANL-FCT-R4 comprises the skull roof (the frontal, most of the parietal, the medial portions of both prefrontals and both postorbitofrontals, as well as the caudal portion of the inter-narial bar) preserved in articulation, extending rostrally to the caudalmost extremities of the external nares (Fig. 6a). The dentigerous portions of both maxillae are almost completely preserved and articulate with the rostral extremity of the premaxilla (Fig. 6b). Portions of the jugal and pterygoid are also preserved, as are the ventral half of the right quadrate and the caudal two-thirds of both anterior lower jaws (Figs 6c, d, 7).

This specimen was discovered by private collectors east of Linares, N.L. (Fig. 1). A substantial portion of the post-cranial skeleton may have been present, according to collectors, but is has not yet been possible to verify this.

Comments – The specimen is currently under study. Here we illustrate it (Figs 6, 7) and seek only to demonstrate its distinctness.

Of the suprastapedial process of the quadrate of UANL-FCT-R4, only the ventral-most portion is preserved; it is almost in contact with the infrastapedial process (Fig. 7). These processes are in contact in the plioplatecarpine *Selmasaurus* Wright & Shannon, 1988. However, UANL-FCT-R4 differs from *Selmasaurus* in having a well-defined parietal table, a transversely elongate subrectangular parietal foramen in dorsal aspect, and rounded caudolateral frontal wings (Fig. 6a). As in *Clidastes propython* (Russell, 1967; Wright & Shannon, 1988), the suprastapedial process of UANL-FCT-R4 contacts the infrastapedial process and a crest emerging from the quadrate shaft (Fig. 7b, b', c, c'). Still, UANL-FCT-R4 is excluded from *Clidastes* in having a more massive and more brevirostrine skull, in the shape of the parietal table, 12 to 14 maxillary and 11 to 14 dentary teeth (Fig. 6b - d), a premaxillomaxillary suture sinusoidal in lateral view, the rostral extremity of the external naris situated between the third and fourth maxillary teeth, and a dorsally

Fig. 6. Undetermined mosasaur (UANL-FCT-R4) from near Linares, N.L.; a. skull roof in dorsal view; b. premaxillary-maxillary unit in ventral view; c. preserved portion of the right anterior lower jaw in lateral view; d. preserved portion of the left anterior lower jaw in lateral view. Scale bar 50 mm.
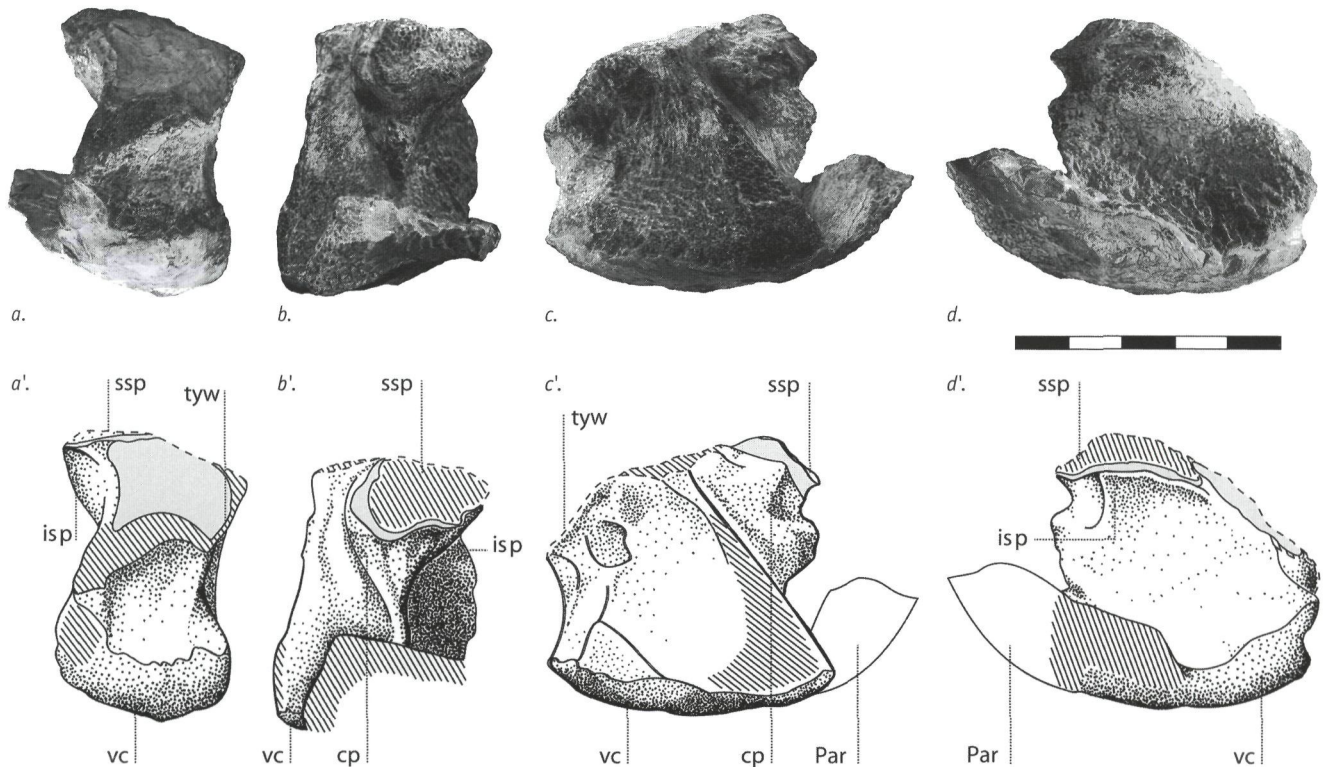
Fig. 7. Undetermined mosasaur (UANL-FCT-R4) from near Linares, N.L. Preserved portion of the right quadrate; a. lateral view, and a'. interpretative drawing; b. medial view, and b'. interpretative drawing; c. rostral view, and c'. interpretative drawing; d. caudal view, and d'. interpretative drawing. Abbreviations: cp – caudomedial process of the quadrate shaft; isp – infrastapedial process; Par – broken portion of the parietal preserved with the quadrate; ssp – suprastapedial process; tyw – tympanic wing; vc – ventral condyle. Weathered and/or broken areas are hatched. Dashed lines mark broken margins. Matrix shaded grey. Scale bar 50 mm.

exposed contact between the prefrontal and the postorbitofrontal lateral to the frontal (Russell, 1967; Fig. 6a).

The infra- and suprastapedial processes of the quadrate are fused in *Globidens*, *Prognathodon*, *Plesiotylosaurus* and *Ectenosaurus* (Russell, 1967; Wright & Shannon, 1988). The latter is a very longirostrine taxon, sharing with UANL-FCT-R4 only the thin tympanic wing of their quadrates, and the position of the rostral termination of the external naris level with the third maxillary tooth (Russell, 1967). No similarity can be observed between the quadrate of UANL-FCT-R4 and the same bone in *Plesiotylosaurus* (Camp, 1942; Fig. 7). *Globidens* has a very massive skull and characteristic low bulbous teeth (Russell, 1967, 1975), clearly distinct from the teeth of UANL-FCT-R4. However, in *Globidens* too, the prefrontal and postorbitofrontal exclude the frontal from the dorsolateral margin of the orbit. UANL-FCT-R4 differs from *Prognathodon* in the exposed contact of the prefrontal and postorbitofrontal lateral to the frontal, the rounded parietal table, and the thin tympanic wing of the quadrate (Figs 6a, 7a, a'). The premaxillo-maxillary suture, which is sinusoidal in lateral aspect, and the rounded caudolateral wings of the frontal are also unknown in *Prognathodon* (see Lingham-Soliar & Nolf, 1990).

UANL-FCT-R4 is different from hitherto described mosasaurs. It is the first mosasaur from Mexico known from significant cranial remains.

Specimen UANL-FCT-R24 (Fig. 8)

This specimen comprises 18 caudal vertebrae from the vicinity of Icamole, N.L. (Fig. 1). All were found in the same area, but excavation at the site did not yield more material. The sediment at the locality clearly belongs to the Méndez Formation, but a more precise stratigraphic determination has not yet been possible.
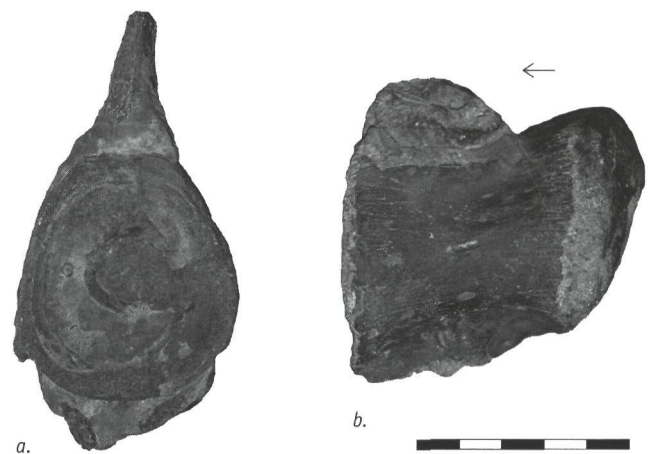

Fig. 8. Undetermined mosasaur (UANL-FCT-R24) from near Icamole, N.L.; a. one of the caudal vertebrae in terminal view; b. ventral view of a second caudal vertebra; arrow points cranially. Scale bar 50 mm.

The cranialmost caudal centra are subcircular in cross-section, with a diameter of approximately 70 mm, and longer than wide. They bear remnants of longitudinally elongate transverse processes (Fig. 7b). The more caudal centra are vertically oval in cross-section (Fig. 7a), approximately 50 mm in width and 55 to 60 mm in height, and bear poorly preserved chevrons whose bases are still embedded in matrix. These vertebrae possess few diagnostic features and can only be assigned to Mosasauridae indet.

Undetermined origin

University of Missouri specimen 509VP

This specimen is the holotype of *Amphekepubis johnsoni* Mehl, 1930. The taxon is based on a pelvic girdle, hind limb bones and nine caudal vertebrae. The exact stratigraphical origin of this material is uncertain, as is the precise geographical location of the find, 'about forty miles east and a little north of Monterrey, Nuevo León' (Mehl, 1930, p. 383). Based on the matrix, Mehl (1930) suggested that it comes from the San Felipe Formation (Coniacian-Santonian) but admits that it could be younger. The specimen has been referred to *Mosasaurus* (Camp, 1942; Lingham-Soliar, 1995).

Acknowledgements

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